Viewing invasive species removal in a whole-ecosystem context

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Eradications of invasive species often have striking positive effects on native biota. However, recent research has shown that species removal in isolation can also result in unexpected changes to other ecosystem components. These secondary effects will become more likely as numbers of interacting invaders increase in ecosystems, and as exotics in late stages of invasion eliminate native species and replace their functional roles. Food web and functional role frameworks can be used to identify ecological conditions that forecast the potential for unwanted secondary impacts. Integration of eradication into a holistic process of assessment and restoration will help safeguard against accidental, adverse effects on native ecosystems.

Invasive alien species interact with other elements of global change to cause considerable damage to managed and natural systems and to incur huge costs to society[1]. In response, several measures have been developed and deployed to control, contain or eradicate a wide range of invasive species in affected areas. Where possible, ERADICATION (see Glossary) is the favored approach. Control, which reduces the presence of the invader, and containment, which limits further spread, both require indefinite investments of time, tools and money to keep an invader at bay. Although eradication can require large short-term investments, successful removal can be achieved within months or years and gives the best chance for native biodiversity to recover.

The results of eradication efforts so far are encouraging and have been detailed recently[2]. Many case studies demonstrate success for a range of taxa, particularly on small islands and at local scales. Additional examples include the removal of the exotic little red fire ant *Wasmannia auropunctata* from Santa Fe Island in the Galapagos[3] (which resulted in the increase in density of several native ant species), and the nearly complete removal from Laysan Island, Hawaii of the exotic annual grass *Cenchrus echinatus*, which once covered 30% of the vegetated area of the island (E.N. Flint, unpublished). Successful eradications often lead to dramatic recovery of native species and ecosystems. Removal of introduced rabbits from Pacific islands off Mexico (C.J. Donlan, unpublished) and the USA have allowed recovery of two rapidly declining endemic species of native succulents *Dudleya linearis* and *D. traskiae*[4]. Lowland vegetation on Santa Fe Island has recovered steadily following the removal of exotic goats *Capra hircus* nearly 30 years ago.

However, other cases suggest that more refined and integrated approaches to invasive removal could improve results. Successes are still largely confined to small islands. The ecological context of eradication is increasingly complex. Major damage caused by long-established invaders, systems that are affected by multiple invaders, and systems that are affected by both invaders and other global changes are now common. In these settings, straightforward deployment of standard eradication tools, such as poisons, trapping and mechanical harvesting, might not accomplish the desired level of recovery of native ecosystems[5].

We suggest that, although there is a crucial need for the continued development and application of effective eradication methodologies, a parallel need exists to place these methodologies in the context of the overall ecosystem that is being managed. Ideally, there should be both: (1) pre-eradication assessment, to tailor removal to avoid unwanted ecological effects; and (2) post-removal assessment of eradication effects, on both the target organism and the invaded ecosystem.

The requirements for successful removal of an invader have been discussed recently[2]. We focus on the possible impacts that result from the successful removal of invasive species, regardless of the methods employed to remove them. We reviewed recent literature for examples where the successful eradication of invasives had or was likely to have important secondary impacts, a task that was made difficult by the relatively few verified eradication successes that included the monitoring of post-removal system behavior.

Eradication: what can go wrong

Successful eradication efforts have generally benefited biological diversity. However, there is also evidence that, without sufficient planning, successful eradications can have unwanted and unexpected impacts on native species and ecosystems. These inadvertent impacts are of many types. Excessive poisoning of non-target organisms and transfer of poisons up food chains[6] are problems that can result from the removal method used[7,8]. Some eradication efforts fail because they do not eliminate the target organism, because they either miss individuals or do not include steps to reduce post-eradication susceptibility to reinvasion[3]. Eradication alone might not allow ecosystems to recover, because some invaders change the condition of the habitat so as to render it unsuitable for native species. For instance, in sites from the Middle East to the western USA, high soil salinity is caused by the invasive ice plant *Mesembryanthemum crystallinum*, and tamarisk *Tamarix* spp., which makes it difficult for salt-sensitive native species to re-establish[9]. In these cases, eradication must be followed by additional site restoration.

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Box 1. When a harmful exotic harbors an endangered native species

Exotic saltcedar *Tamarix* spp. shrubs have replaced much of the native riparian vegetation of the arid western USA, where they consume large quantities of water, narrow river channels, salinize soil and degrade wildlife habitat[a].

Saltcedar removal has been repeatedly delayed in parts of its range because it provides significant nesting habitat for an endangered native songbird[b]. The southwestern willow flycatcher *Empidonax traillii extimus*, currently reduced to fewer than 500 breeding pairs, nested historically in riparian cottonwood (*Populus* spp.)–willow (*Salix* spp.) stands in the southwestern USA (Refs c,d). Urbanization, agriculture, fire, water diversion and livestock grazing all contributed to the decline of its native habitat[b]. The replacement of much of the habitat that remained by saltcedar required the flycatcher to make use of the invader, which it seems to prefer in some areas, despite its reduced breeding success[e,f]. Stepwise saltcedar removal could strongly benefit the flycatcher by giving native trees the opportunity to re-establish and provide replacement habitat[g]. However, some saltcedar-invaded areas might no longer be able to support native vegetation, because lowered water tables and saline soils, the results of saltcedar dominance, might complicate native re-establishment[h–j]. Region-wide flood suppression hinders re-establishment of flood-associated native species such as cottonwoods and increases the likelihood of saltcedar reinvasion[j,k].

Managers are confident that, if accompanied by planning and careful restoration, saltcedar removal can benefit the endangered flycatcher as well as other native species[g]. However, poorly planned removal without steps such as flooding and vegetation restoration, might fail, harming an endangered species in the process.

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Successful eradications can also have undesired effects that result from the successful removal of the invader. In several cases, removal of one exotic species has led to the establishment or increase of one or more other invasive species. For example, several eradications of exotic herbivores have been linked to increases in exotic plant populations. Removal of one invader can lead to increased impacts of another invader; for example, when removal of exotic prey leads to increased predation on native prey by exotic predators[10]. Finally, removal of invasive plant species can reduce habitat or resources available for native fauna if the removal is not accompanied by further restoration measures (Box 1). These unexpected outcomes will become more probable both as the variety of interacting invaders contained in an ecosystem increases, and as exotics in late stages of invasion largely or wholly eliminate native species and replace their functional roles. Although researchers have begun to explore the implications of multiple, interacting invaders, little attention has been paid to the implications of these interactions for eradication efforts.

Secondary effects: a conceptual framework

A useful basis from which to tackle when and why secondary effects of eradication occur is that systems containing invasives function according to the same basic principles as do other systems. Invaded systems can, therefore, be considered using the frameworks that are usually used to analyze community and ecosystem dynamics.

Trophic cascades in multiply invaded systems

A large literature has been devoted to how food-web interactions limit populations of producers, consumers and predators[11–13]. Much work has been done on the relative roles of top-down regulation of food-web components by higher-level consumers or predators, and of bottom-up regulation of populations by food availability or resource limitation. Evidence from several ecosystem types shows that both top-down and bottom-up population regulation of producers and consumers occur under some conditions[14–16]. The existence of these regulatory links can give rise to TROPHIC CASCADES[16,17] (but see Ref. 13).

When combined with the use of simple terrestrial food webs[6] (Fig. 1), this framework helps to explain how many animal eradications have allowed population recovery of native species. Removal of an exotic predator can release native prey from strong top-down regulation, increasing prey abundance with potential cascading impacts on other food-web components, including native predators (Fig. 1b). Similarly, exotic herbivores in the absence of predators can become sufficiently abundant to exert top-down pressure on native plants[14]. Removal of these herbivores can lead to rapid recovery of native plant populations[4].

Predator–prey interactions

However, the presence of multiple invaders at different trophic levels complicates matters. Consider the case where an exotic predator and an exotic prey species co-occur (Fig. 1c). Removal of the invasive predator only could lead to MESOPREDATOR RELEASE (release of the invasive prey from top-down

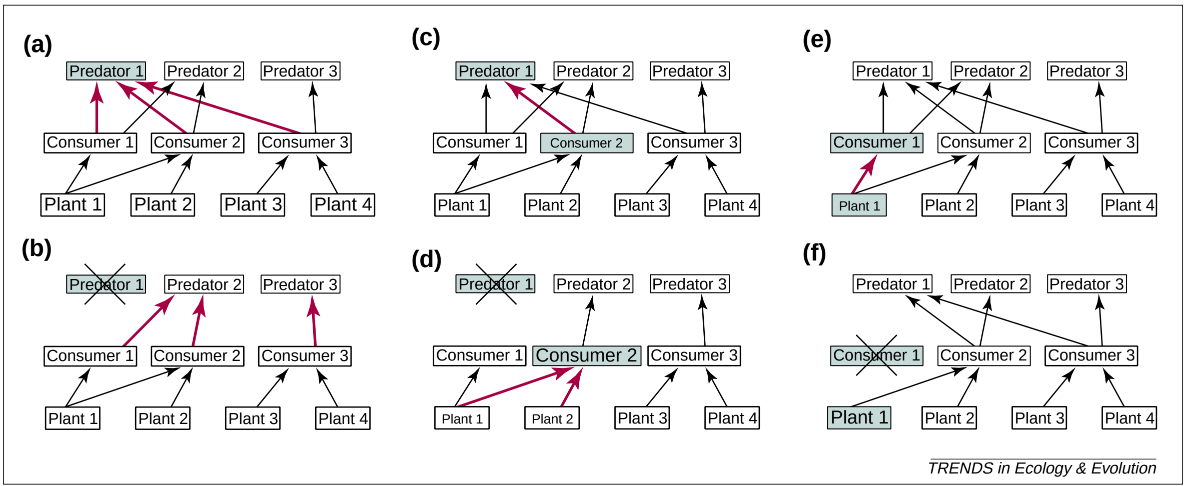

Fig. 1. Idealized food webs indicating trophic interactions between species. Closed boxes represent exotic species and open boxes represent native species. Arrow thickness indicates the strength of trophic interaction. Font size represents population size. (a) shows a community containing a single exotic predator. In (b), removal of this predator increases native prey populations. (c) shows a community containing both an exotic predator and an exotic herbivore. In (d), removal of only the exotic predator releases the exotic herbivore population, with cascading impacts on two plant species. (e) shows a community containing both an exotic herbivore and an exotic plant species. In (f), removal of the exotic herbivore only releases the exotic plant population.

regulation) (Fig. 1d). If the exotic prey consume native species, the removal of the exotic top predator could lead to net negative impacts on native populations of conservation value[18]. For example, exotic cats on Stewart Island, New Zealand, prey upon the kakapo *Strigops habroptilus*, an endangered flightless parrot. However, the diet of the cats consists overwhelmingly of the three species of exotic rats on the island[19]. Cat eradication would probably increase the impact of rats on the kakapo as well as on other native biota unless rats were simultaneously removed. The potential for mesopredator release following cat eradication is widespread. Introduced rats *Rattus* spp., house mice *Mus musculus*, and/or rabbits *Oryctolagus cuniculus* co-occur with exotic cats on 22 islands where the diets of cats have been studied. In nearly every case, cats exert important top-down controls on these other exotics by preying heavily on rabbits if they are present, and heavily on rats if rabbits are not present[20] (Table 1). Mice are also an important part of the diet of feral cat on islands at temperate, but not tropical, latitudes[20]. The potential for these trophic effects is probably strongest on islands lacking native predators; however, it applies, in principle, to any system in which exotic predator populations take advantage of abundant exotic prey.

The effects of mesopredator release can cascade to alter ecosystem-scale properties as well as altering native populations. Studies before cat eradication on subantarctic Marion Island showed that the cats ate many exotic house mice, which prey heavily upon a flightless endemic moth *Pringleophaga marioni*, which is important to nutrient cycling[21–23]. Removal of the cats only might have allowed increases in mouse populations, causing cascading declines in endemic moth abundance and, ultimately, changes in soil nutrient availability.

When exotic predators and prey co-occur, eradication of only the exotic prey can also cause problems by forcing the predator to switch to native prey. In New Zealand, introduced rats *R. rattus* and possums *Trichosurus vulpecular* are an important part of the diet of the stoat *Mustela ermina*, an exotic mustelid[10]. Efforts to remove all three species by poisoning the prey species had an unexpected result: the stoat populations were not eliminated by either the prey eradication or the poison application and, in the absence of abundant exotic prey, the stoats switched their diets to native birds and bird eggs.

Without prey eradication, the co-occurrence of exotic predators and exotic prey can impact heavily on native prey populations by HYPERPREDATION. The availability of abundant exotic prey can inflate exotic predator populations, which then increase their consumption of indigenous species[24]. This phenomenon was first elaborated to explain why native Australian mammals suffered population declines in areas invaded by cats only if exotic rabbit and mouse densities were also high[25]. The removal of exotic prey to curb hyperpredation of native species by exotic predators has been suggested[26]. However, managers must consider carefully whether native populations can withstand further, temporary increases in predation when the inflated predator population no longer has exotic prey to sustain it.

Herbivore–plant interactions

When exotic herbivores and plants co-occur (Fig. 1d), control or eradication of only the exotic plants could, in theory, lead to increased exotic herbivory on native plants. However, we do not know of a case in which this has occurred. This might reflect the paucity of successful plant eradications, the prioritization of

Table 1. Importance of exotic rats in the diet of introduced cats on islands[a]

Islands without introduced rabbits	Occurrence of rats in diet (%)	Islands with introduced rabbits[b]	Occurrence of rats in diet (%)
Galapagos: Isabela	73	Gran Canaria	4
Santa Cruz	88	Te Wharau, NZ	3
Lord Howe	87	Kourarau, NZ	Trace
Raoul	86	Orongorongo, NZ	50
Little Barrier	39	Mackenzie, NZ	2
Stewart	93	Kerguelen	0
Campbell	95	Macquarie	3

[a]Data from Ref. 20.
[b]Abbreviation: NZ, New Zealand.

animal removals from multiply invaded ecosystems, or an absence of strict bottom-up regulation of exotic herbivores by plant biomass availability.

When exotic herbivores and plants co-occur, eradication of the herbivores only can lead to release of exotic plants from top-down control (Fig. 1f). In nearly all documented cases where exotic plants co-occur with exotic herbivores on islands, herbivore removal has had mixed results for native vegetation (but see Refs 27,28). Feral herbivore removal from Santa Catalina Island, Channel Island National Park, led to an increase in native species richness, but also to large absolute and relative increases in cover by exotic annuals[29]. Rabbit eradication on Round Island, Mauritius, led to strong recovery of three endemic or locally restricted tree species (*Latania loddigesii*, *Pandanus vandermeerschii* and *Hyophorbe lagenicaulis*) and six reptile species [two skinks (*Leiolopisma telfaririi* and *Scelotes bojerii*), three geckos (*Phelsuma guentheri*, *P. ornata* and *Nactus serpensinsula*) and a snake (*Casarea dussumerii*)], including five endemics[30]. However, rabbit removal also caused the spectacular release of a previously sparse exotic grass *Chloris barbata*, rendering it a significant component of the vegetation on the island[30] (Box 2). Asiatic water buffalo *Bubalus bubalis* eradication from Kakadu National Park, Australia spurred large-scale regeneration of the wetlands of the park[31]. However, alien plant species also proliferated, in particular, introduced para grass *Brachiaria mutica*, which now covers approximately 10% of the major floodplain habitats in the park.

Although the removal of feral pigs *Sus scrofa*, sheep *Ovis aries* and goats has allowed some native plant species to recover slightly in Hawai'i[32], many Hawai'ian lowland grasslands have responded to ungulate removal with increases in the cover of flammable exotic grasses[33]. Accompanying increases in fire frequency accelerate a positive feedback loop among invasive grass establishment, fire, and loss of native woodlands and forest[34].

The effects of exotic herbivore removal on native vegetation, under certain circumstances, might also have indirect negative effects, because of the presence of other exotic animals. Rabbit removal on Macquarie Island in the Southern Ocean led to major increases in cover by a native tussock grass *Poa foliosa*, which is the preferred habitat of the introduced ship rat. Tussock expansion could bring the rats into contact with burrow-nesting bird colonies on the island, which have escaped rat predation so far[35].

Herbivore removal from islands has strong negative effects on vegetation in some cases. The removal of sheep and cattle *Bos taurus* from Santa Cruz Island led to an explosive expansion of exotic fennel *Foeniculum vulgare*, starthistle *Centaurea solstitialis*, and other introduced herbs, increases in relative cover of exotics, but the observable recovery of only one native species, Bishop pine *Pinus muricata*, after nine years of monitoring[36–38]. Moreover, the sudden expansion of exotic forbs provided abundant food for feral European bee *Apis mellifera*, colonies, and complicated eventual bee eradication from the island[39]. The greatest potential for negative impacts on native vegetation perhaps exists when herbivore eradication removes the disturbance that is necessary to suppress establishment of late successional (tree or shrub) exotics[40]. The removal of feral cattle from degraded grasslands on San Cristobal Island in the Galapagos allowed previously suppressed exotic guava *Psidium guajava* to grow rapidly into dense, extensive thickets[41].

Box 2. Replacing extinct herbivores in the Mascarene Islands

Before their extinction, two species of giant tortoise (*Geocholone triserrata* and *G. inepta*), endemic to the Mascarene Islands, browsed the native vegetation and dispersed fruits of endemic trees such as the Ile aux Aigrettes ebony *Diospyros egrettarum*. Trade in tortoise meat, together with the introduction of rats and pigs in the 16th–18th centuries, extirpated the native browsers from the archipelago.

Introduced goats *Capra hircus* and rabbits *Oryctolagus cuniculus* replaced the tortoises as herbivores, suppressing numerous introduced grazing-intolerant plant species until the late 20th century. However, the eradication of exotic herbivores from Round Island and Ile aux Aigrettes in the 1970s and 1980s released populations of exotic weeds such as *Chloris barbata* on Round Island and false acacia *Leucaena leucocephala* on Ile aux Aigrettes. Native tussock-forming grasses declined on Round Island, and increasingly tall exotic vegetation threatened low-growing endemics such as *Aerva congesta*, now found only on Round Island.

To restore and maintain native vegetation, scientists at the Mauritian Wildlife Foundation are exploring the introduction of a taxonomic and functional

substitute for the extinct tortoises, the Aldabran tortoise *G. gigantia* (Fig. I). Four adult Aldabran tortoises were released into a fenced enclosure on Ile aux Aigrettes in November 2000, and the first post-introduction vegetation survey took place in May 2001. Viable fruits of the endemic ebony have already been found dispersed in tortoise feces away from parent trees. It is hoped that the introduced tortoises will not only shift the competitive balance in favor of native plants, but also restore the broader functional roles of their extinct congeners in the ecosystems of the Mascarene archipelago.

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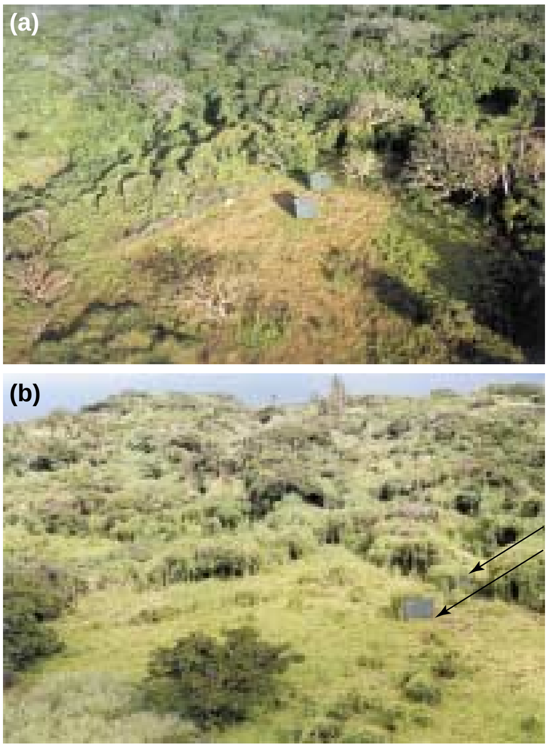

Fig. 2. An adverse effect of eradication. The photographs show a camp site on Sarigan Island, Commonwealth of the Northern Mariana Islands, before (a) and after (b) successful eradication of feral goats *Capra hircus* and pigs *Sus scrofa* in 1998 explosively released a previously undetected exotic vine *Operculina ventricosa*. Arrows in (b) indicate the locations of the two buildings visible in (a). Reproduced, with permission, from Curt Kessler, Zoology Unlimited.

In most settings, removing introduced herbivores is an important and reasonable first step in ecosystem restoration. However, in some cases (particularly on islands without native herbivores), herbivore removal might actually cause harm if there are no concurrent efforts to control exotic vegetation (Fig. 2). The clearest benefits from exotic herbivore removal are likely to occur in settings that are still dominated by native vegetation. In other settings, close monitoring after herbivore removal, as well as pre-eradication assessment, can help reduce unexpected negative consequences of the removal of invasives[42].

Native species dependence in exotic-dominated habitats

Increasingly, exotic species have been present in ecosystems for long enough to dominate or replace native species and habitats. In these cases, an ecosystem or functional framework might be useful in which one asks whether removal of the invader will largely or entirely remove from the system a function necessary to other biota in it. For example, an invasive plant species might provide usable habitat for native fauna in the absence of original vegetation. Rapid removal of the invader without restoring native vegetation might not only increase the chances of a new invasion, but also leave native fauna without cover or food. Several examples of the potential for this type of problem have been described[43]. However, examples of successful eradications that actually led to such habitat loss have not been identified. This most probably reflects the lack of successful eradications of plants, which usually provide habitat for other biota. The case of *Tamarix* (Box 1) illustrates how, under certain conditions, consideration of this kind of undesirable impact can be important.

Conclusion

The type of species being removed, the degree to which it has replaced native taxa, and the presence of other non-native species can affect the eventual impacts of removal of an invasive species. Managers can take some simple steps to reduce surprise outcomes. Pre-assessment, including qualitative evaluation of: (1) trophic interactions among exotics and between natives and exotics; and (2) potential functional roles of exotics, is necessary for managers to anticipate the need for special planning. Post-eradication monitoring is also extremely valuable, not least because it allows managers to document the positive outcomes of eradication successes. It also provides the opportunity to learn from mistakes and gives managers the chance to curtail negative effects before they become severe. More frequent ecological studies that take advantage of eradication programss as being large-scale ecosystem experiments will speed the accumulation of knowledge about system responses to exotic species removals.

Specific guidance for tailoring eradication efforts to complex situations is emerging. In the case of stoat–rat–opossum eradication in New Zealand[10], follow-up study showed that the timing and method of poisoning used were important in determining stoat population declines (as a result of secondary poisoning) as well as determining effects on native birds[44]. A model of interactions between exotic cats and rabbits found that simultaneous removal of both species maximized the chances of success, but suggested that the next best alternative was to remove rabbits first and cats later[26]. Data from several cases show that attempts to restore a native species without removing all invaders that consume it are likely to fail[45]. Many attempts to reintroduce native marsupials to areas from which they have been extirpated have failed because of the presence of uncontrolled exotic terrestrial predators such as cats and foxes *Vulpes fulva*. Success rates of reintroductions are an order of magnitude greater (82% versus 8%) on islands without exotic predators[46]. As they accumulate, these kinds of analyses – whether based on post-eradication data or modeled on ecological principles – will enable the design of better eradication and restoration strategies.

Invasive species eradication is an increasingly important component of the conservation and management of natural ecosystems. However, in natural systems, a shift in emphasis from strict invasives management towards broader ecosystem restoration goals is required. This will place more emphasis on the full diagnosis of causal factors and the desired ecological outcomes of eradications[47]. As knowledge about effective eradication methods accumulates, attention should turn to combining such methods with broader ecological principles to form cost-effective removal strategies that accomplish overall restoration goals.

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Glossary

Eradication: removal of every individual and propagule of an invasive species so that only reintroduction could allow its return.
Hyperpredation: abnormally high predation of indigenous prey species by a predator population that is inflated by the availability of highly abundant exotic prey.
Mesopredator release: rise in a population of one species caused by the removal of a species that preys upon it. It can lead to a net increase in predation on native populations of conservation concern[a].
Trophic cascade: when changes in one species affect the abundances of other species across more than one link in the food web[b].

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