Opinion

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Novel trophic cascades: apex predators enable coexistence

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Novel assemblages of native and introduced species characterize a growing proportion of ecosystems worldwide. Some introduced species have contributed to extinctions, even extinction waves, spurring widespread efforts to eradicate or control them. We propose that trophic cascade theory offers insights into why introduced species sometimes become harmful, but in other cases stably coexist with natives and offer net benefits. Large predators commonly limit populations of potentially irruptive prey and mesopredators, both native and introduced. This top-down force influences a wide range of ecosystem processes that often enhance biodiversity. We argue that many species, regardless of their origin or priors, are allies for the retention and restoration of biodiversity in top-down regulated ecosystems.

Context determines ecological effect

Globalization has weakened barriers that previously bound species within distinct biogeographical regions, transforming historic communities into unprecedented novel ecosystems [1]. The spread of species into new areas has generated alarm amongst conservation managers and biologists, in particular when associated with the decline and extinction of native species. Major efforts have thus ensued to control or eradicate non-native species worldwide [2]. Nevertheless, most introduced species cannot realistically be eradicated [3] and many offer benefits [4]. We outline how the influence of non-native species can be context-specific, and modified by the presence of large (apex) predators. Trophic cascade theory highlights how apex predators shape ecosystems by limiting population densities of their prey and smaller predators. Many apex predators have been eliminated locally or globally [5]. Their repatriation can shift the ecological context that influences non-native ecologies, and enhance native–non-native coexistence (Box 1).

Resisting novel ecosystems

Killing non-native species constitutes a substantial component of conservation efforts worldwide, reflecting the view that introduced species threaten native species, and that lethal means can alleviate this threat. Eradication of non-native species has been achieved mainly in small and strongly delimited sites, including offshore islands and fenced reserves [6,7]. There have also been several accounts of population increases of threatened native species following eradication or control of non-native species [7–9]. These effects have prompted invasion biologists to advocate ongoing killing for conservation. However, for several reasons these outcomes can be inadequate measures of success.

Three overarching concerns are that most control efforts do not limit non-native species or restore native communities [10,11], control-dependent recovery programs typically require indefinite intervention [3], and many control efforts have had costly unintended consequences [4]. The eradication of non-native cats (*Felis catus*) from offshore islands of Australia and New Zealand led to irruptions of non-native rabbits (*Oryctolagus cuniculus*) and rats (*Rattus exulans*), harming native vegetation and bird populations [12,13]. Control of the non-native red fox (*Vulpes vulpes*) has likewise released rabbits and cats on mainland Australia, with negative impacts on vegetation and small vertebrates [14]. Lastly, short-term increases of threatened populations do not guarantee recovery. For example, lethal control of red foxes for the recovery of woylies (*Bettongia penicillata*) in southwestern Australia was initially a tremendous success, but the marsupial subsequently crashed, possibly due to disease and cat predation [15].

Biologists are increasingly questioning the merits of the native–non-native dichotomy, and there is growing recognition that eradication is often not viable or even desirable [2]. Many non-native species benefit biodiversity, sometimes substituting for the ecological roles of extinct taxa, and their eradication can harm the native species we wish to protect [4,16]. Bird species introduced to Hawaii are promoting the recovery of several native plants by dispersing their seeds [17], and North American crayfish are assisting the recovery of threatened predators in Spain [18]. Environmental change can also generate novel interactions among native species, akin to those normally associated with non-native species [19]. For example, climate warming has increased the impacts of native American bark beetles on their native conifer hosts, greatly increasing death rates across vast western regions of the continent [20].

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Box 1. Trophic cascades shines a new light on invasion biology

Ecologists have long debated the predominance of resource availability (bottom-up) versus predation (top-down) as drivers of populations. Over the past two decades the consequences of removing and repatriating apex predators have been studied across the globe, in a variety of habitats, and with a diversity of taxa [36]. Consistent patterns have emerged demonstrating that apex predators structure ecosystems by limiting population irruptions of both native and introduced species [37,52].

Apex predators are large-bodied predators that occupy the highest trophic level. These include, for example, large (>13–16 kg) members of the Carnivora [41], and large (>3 m) sharks [40]. Apex predators structure communities by limiting prey and mesopredator densities, which can otherwise increase to the point that they severely diminish their resources. Ecosystems devoid of apex predators tend to experience high grazing and predation pressure, a process that can cascade further to alter the ecological community and shift ecosystems to alternative states [5,36].

Trophic cascades theory is well suited to the study of invasion biology because both are concerned with the drivers and consequences of population irruptions, and both illustrate how species interactions can lead to shifts in ecological states [36,61]. State-shifts triggered by the loss of apex predators causing irruptions of non-native species have been documented on land (e.g., [37]) and at sea (e.g., [62]). In addition, the focal species in both disciplines (apex predators and non-native species) are subjected to lethal control that can lead to unintended deleterious outcomes [4,5].

In the following we draw on trophic cascade theory to offer an alternative view on the reasons why some introduced species, in some contexts, have net harmful effects. We focus on those introduced species considered to be particularly damaging, and argue that, depending on context, they too can provide net benefits. Apex predators limit population irruptions of both native and introduced species and can provide better outcomes than lethal control. In particular, we emphasize the need to study how apex predators, and other environmental drivers, modulate the functional roles of both native and non-native species in modern biological communities.

The 'world's worst invasive' species

Cases of introduced species driving extinctions and biodiversity loss have influenced the development of invasion biology. For example, introduced small and medium-sized mammalian predators are considered to be major drivers of decline and extinction of mammals across Australia [21,22] and of birds across New Zealand [3], many of which are endemic. Predation by the introduced brown tree snake (*Boiga irregularis*) in Guam has contributed to the extinction of several birds, reptiles, and a flying fox [23]. Nile perch (*Lates niloticus*) introduced to Lake Victoria, East Africa, are considered a major cause of extinctions, including much of the endemic haplochromine cichlid radiation [24]. Infectious diseases and their vectors are being transmitted worldwide, threatening both wild species and human health [25], and in some cases driving host extinction [26].

Inspired by these cases, the International Union for the Conservation of Nature (IUCN) compiled a list of species that are considered particularly harmful in their non-native ranges published as *100 of the World's Worst Invasive Alien Species* [27] ('World's Worst'). Their listed impacts can be grouped roughly into ten major categories: they compete with natives (63%), prey on natives (30%), cause agricultural losses (21%), are agents and transmitters of disease (16%), damage equipment and disrupt valued human activities (10%), graze natives (8%), alter fire regimes (7%), cause soil loss and alter soil properties (6%), and sting or poison humans and wildlife (5%) (Table 1).

The IUCN does note some positive aspects of 69 of the World's Worst, although these are primarily focused on human use and tend to be taxonomically biased (Table 1). The values of these species to their recipient ecosystems thus remain an important topic of research [16]. For instance, across its non-native range the lantana shrub (*Lantana camara*) provides a broad variety of benefits by promoting the regeneration of some native plant species, improving soil retention, and providing habitat for native animals, together with a range of medical uses and opportunities for local economies [11].

The ability to move as the environment changes can determine whether species persist or perish [28]. Several species that are declared pests in their introduced range are threatened or even extinct in their native range. The ecosystems into which the World's Worst have been introduced provide important habitat for those that are threatened in their native ranges. The conservation status of 33 of the World's Worst has been assessed for the IUCN's Red List of Threatened Species, of which four (12%) fall within the threatened categories (common carp *Cyprinus carpio*, rabbit, tilapia *Oreochromis mossambicus*, and wild goat *Capra aegagrus*). Other species, such as red deer (*Cervus elaphus*), although not threatened globally, are nonetheless threatened or extinct regionally. Retaining species in their introduced ranges, particularly in light of predicted environmental change, could help decrease their risk of global extinction.

Lack of co-evolution or ecological control?

When introduced species drive the decline of native species, it is often assumed that the absence of prior reciprocal evolution disadvantages the natives. Non-natives are frequently portrayed as predators of naïve prey, as species freed of specialized parasites and consumers, and as aggressive competitors that displace natives who have not evolved the mechanisms to fight back [3,29]. While evolutionary novelty can hamper coexistence in some cases, native species can also adapt through behavioral changes and trait evolution in response to novel organisms, within only a few generations [30]. The introduction of cane toads to Australia has triggered behavioral and morphological adaptations to the toad's toxin, enabling the recovery of native predator populations from initial declines [31]. The Australian soapberry bug (*Leptocoris tagalicus*) has undergone rapid evolution in response to the colonization of balloon vine (*Cardiospermum grandiflorum*), enabling it to better consume the seeds of the introduced plant with the lengthening of their mouthparts [30]. Similarly, naïve prey species such as marine iguanas (*Amblyrhynchus cristatus*) in the Galápagos archipelago [32] and macropods in Tasmania [33] show adaptive responses to novel predators. Host resistance to novel pathogens has also rapidly

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Table 1. Harmful and beneficial effects of the 'World's Worst'[a]

Group (number of species)	Native animals	Human utility	Native plants	Human health	Soil	Water	Fire
Plants and algae (37)	light-orange	light-orange	light-orange		light-orange	light-orange	light-orange
Insects (14)	red	red	red	red	green		
Mammals (14)	light-orange	light-orange	light-orange	red			
Fish (8)	red	light-orange	red			red	
Pathogens (7)	red	red	red	red			
Molluscs (6)	red	light-orange					
Amphibians (3)	light-orange	red	green		green		
Birds (3)	light-orange	light-orange					
Crustaceans (3)	light-orange	light-orange					
Reptiles (2)	red	green					
Seastar (1)	red						
Comb jelly (1)	red	red					
Flatworm (1)	red						

[a]The species listed in the World's Worst [27] have effects on ecosystem components that are considered both harmful and beneficial. Cell colors denote that the effects are listed as negative (red), positive (green), or both (light-orange). Based on a summary of Lowe *et al.* [27] and synthesized after the method of McLaughlan *et al.* [16]. The listed effects are detailed in Table S1 in the supplementary material online.

evolved, permitting increasing host–pathogen coexistence. Increasing resistance of Hawaiian birds to avian malaria is enabling the recolonization of low-elevation disease-prone regions [26,34].

The growing number of observations of rapid adaptation in novel ecosystems [29,30], together with the phenomenon of 'native invaders' [19], suggest that the harms associated with non-native species are not inevitable outcomes of their history or biology. Thus, the phenomenon we usually refer to as 'invasive species' can instead be considered a general process of species undergoing population irruptions. From this point of view we can simultaneously consider native and non-native irruptions from a community ecology, rather than an invasion biology, perspective [35]. Within community ecology, population irruptions and their consequences are well-known responses to the loss of top-down regulation (Boxes 2 and 3).

Top-down regulation of novel ecosystems

Apex predators have profound influences on the structure and function of ecosystems by limiting populations of their prey and of mesopredators, both native and introduced. This predation forces cascades throughout ecosystems that permeate a wide range of ecosystem processes from herbivory, predation, behavior, and reproduction to fire, disease, atmosphere, soil, and water. The understanding of the importance of predation has come to challenge the earlier bottom-up view of ecology that posited that animal population size is determined primarily by resource availability [36]. Apex predators are however also some of the most imperiled species worldwide, primarily due to conflicts with humans. This weakening of top-down forcing on a global scale has had conspicuous impacts on the structure of ecosystems, contributing to biodiversity loss, extinctions, and desertification [5].

Where apex predators decline, ecosystems become predominantly bottom-up driven [37]. This leads to a Malthusian population dynamic in which the limit to population growth is the elimination of resources. Under such conditions, some species are likely to attain high abundances at a cost to other species. This process occurs in both novel and historic communities. Where top-down regulation is weak, species can irrupt in both their native and introduced regions (Box 2), and co-occurring natives and non-natives that share similar trophic levels or functional roles can irrupt simultaneously (Box 3). The ensuing harmful effects of natives and non-natives alike are a result of high population densities relative to those of other species they interact with. Thus, under conditions of effective top-down control, introduced mesopredators are less likely to cause the extinction of their prey, introduced herbivores are less likely to degrade landscapes, plants are less likely to form monocultures, and a disease is less likely to become epidemic [37–39].

Top-down regulation is determined not only by the abundance of predators but also by their size, diet, hunting method, and social stability [5,37,38,40]. Apex predators play a unique ecological role because they hunt large prey, have slow life cycles, and maintain large territories and low densities [41–43]. Their loss can result in population irruptions of mesopredators [44], that can reach much higher densities than their larger cousins [41,43]. Bottom-up driven ecosystems can therefore experience higher predation rates [37,45]. In the absence of top-down regulation, predator–prey dynamics tend to oscillate in boom-and-bust cycles, a process that fails to suppress irruptions and can drive extinctions [38]. Apex predators decouple this resource-driven population dynamic and stabilize prey densities [46].

Lethal control does not typically replace the ecological function of apex predators [5]. For example, most Australian conservation reserves are subjected to poison-baiting campaigns that aim to reduce the abundance and impacts of introduced mesopredators, particularly of red foxes. These campaigns also kill dingoes (*Canis dingo*), an apex predator. Across the continent, the distribution of healthy dingo populations is the main predictor of low fox densities [47] and of high marsupial persistence [48]. The attempt to promote biodiversity with lethal control in Australia has inadvertently driven losses of native species [37,49].

Top-down regulation is one of several major drivers of ecosystem processes that influence novel interactions. For example, reduced livestock grazing and fire intensity combine with stable dingo populations to provide superior outcomes for the prey of non-native cats in Australia

Box 2. Species irrupting in their native and introduced ranges

North American beavers (*Castor canadensis*) can irrupt in the absence of apex predators in their introduced habitat of Tierra del Fuego, South America [63], but also in their native range where wolves (*Canis lupus*) are culled [64]. Similarly, the native Eurasian beaver (*Castor fiber*) in Sweden can reach high densities and exhaust their resources where wolves are scarce [65]. Photo by Steve, licensed under CC BY-SA 2.0 via Wikimedia Commons.

Red deer[a] and mule deer (*Odocoileus hemionus*) suppress tree regeneration where introduced to predator-free islands such as New Zealand [66] and the Queen Charlotte Islands, Canada [67], but also in their native North American range where wolves and cougars (*Puma concolor*) have been removed [68]. In both native and introduced regions, high deer densities can diminish invertebrates, small mammals, and birds [5,39,69,70]. Photo by Mario Modesto Mata, licensed under CC BY-SA 3.0 via Wikimedia Commons.

Koalas (*Phascolarctos cinereus*) were introduced to a predator depauperate Kangaroo Island, South Australia, where they increased to high densities and began exerting extensive browsing pressure. On mainland Australia, where they are native, koalas can also reach high densities, possibly consequent upon predator control. In both locales koalas are subjected to management operations aimed at reducing their numbers [71]. Photo courtesy of Jens Westphalen and Thoralf Grospitz.

Boar[a] (*Sus scrofa*) can irrupt in their native and introduced ranges in the absence of predators. In their native range of Eurasia, wolves and tigers (*Panthera tigris*) are important predators. Across their introduced range wolves, cougars, black bears (*Ursus americanus*), coyotes (*C. latrans*), bobcats (*Lynx rufus*), and dingoes can influence their densities [21,72]. Photo by NASA, licensed under Public Domain via Wikimedia Commons.

The non-native red fox has contributed to the extinction of several Australian mammals as a result of widespread persecution of dingoes [37,73]. The native red fox similarly suppresses its prey and competitors in mainland Fennoscandia where wolves and lynx have been extirpated [52]. Photo courtesy of Les Peters.

[a]Included in the World's Worst

[50]. The outcomes of trophic cascades are therefore likely to be context dependent, and there will be situations in which they do not occur. For example, only seven large species within the Carnivora are currently known to exert trophic cascades [5]. In addition, some regions do not provide a suitable habitat for apex predators (e.g., fragmented habitat). In this case novel solutions, such as the use of guardian animals to protect threatened bird colonies, are being trialed [51].

Cascades extending through novel ecosystems

Apex predators suppress irruptions both directly and indirectly (Figure 1). Direct predation affects the species that the apex predator hunts. Indirect effects occur when the reduction in the hunted species increases the abundance – and associated interactive strength – of other species. Trophic cascades in novel ecosystems have been documented in a range of habitats influencing a wide range of taxa. Sea eagles recolonizing the Finnish archipelago suppress the introduced American mink (*Neovison vison*), for example, with cascading benefits to native birds, amphibians, small mammals, and plants [52]. In Australia, dingoes suppress introduced mesopredators, thereby promoting the survival of bilbies (*Macrotis lagotis*) [53], an important ecological engineer whose vigorous digging traps seeds and improves soil [54].

Box 3. Native and non-native species irrupting simultaneously

In the absence of apex predators such as wolves and cougars, both native (deer) and non-native (wild horses, *Equus ferus*; donkeys, *Equus africanus*) ungulates can reach high densities in North America. Ensuing over-grazing can lead to biodiversity loss and desertification [39,60]. Photo by the Bureau of Land Management, licensed under Public Domain via Wikimedia Commons.

In California, the absence of coyotes from fragmented coastal scrub simultaneously releases introduced mesopredators (cat[a] and opossum *Didelphis virginiana*) and native mesopredators (striped skunk *Mephitis mephitis*, raccoon *Procyon lotor*, and grey fox *Urocyon cinereoargenteus*), that cause a decline of scrub-breeding birds [74]. Photo by Luc Viatour, licensed under CC BY-SA 3.0 via Wikimedia Commons.

In North America native rodents (e.g., white-footed mice *Peromyscus leucopus* and deer mice *Peromyscus maniculatus*), and non-native rodents (e.g., house mouse[a], *Mus musculus*; Norway rat, *Rattus norvegicus*), can reach high densities in the absence of effective top-down control, increasing the risk of human exposure to zoonotic diseases [38]. Photo by George Shuklin, licensed under CC BY-SA 3.0, via Wikimedia Commons.

In Australia, culling dingoes causes population irruptions of introduced (rabbits[a], goats[a], and donkeys) and native (macropods) herbivores, which deplete vegetation [21,37]. Similarly, in the absence of predators, bettongs (*Bettongia lesueur*), and bilbies (*Macrotis lagotis*), endangered ecosystem engineers that share similar functional roles to rabbits [75], can attain high densities and diminish biodiversity [7]. Photo by Arian Wallach.

Overfishing of large predators in the Black Sea triggers a complex cascade: increases of small pelagic fish, declines in zooplankton, and increased phytoplankton and eutrophication. The subsequent shift of commercial fishing to smaller fish leads to an irruption of both native (*Aurelia aurita*) and non-native (comb jelly[a] *Mnemiopsis leidyi*) gelatinous carnivores [62]. Photo by Boston Aquarium, licensed under CC BY-SA 3.0 via Wikimedia Commons.

Overfishing of sharks and other large predators in the Atlantic and Caribbean releases native and non-native mesopredators. However, native mesopredators (small groupers) are also overfished, further driving irruptions of non-native lionfish[a] (*Pterois volitans*), a mesopredator that contributes to the decline of herbivorous fish, thereby releasing seaweed and suppressing coral [76]. Photo by Alexander Vasenin, licensed under CC BY-SA 3.0, via Wikimedia Commons.

[a]Included in the World's Worst.

Although competition by non-native plants is probably not a major driver of extinctions [55], it is considered a common threat posed by the World's Worst (Table 1), and in some circumstances can simplify plant communities [56]. The constraining influence of apex predators on native and non-native herbivores is well studied, and has implications for novel plant communities. High grazing pressure can facilitate communities dominated by less-palatable plants, including non-native species. Plant diversity forms a 'biotic resistance' that limits competitive

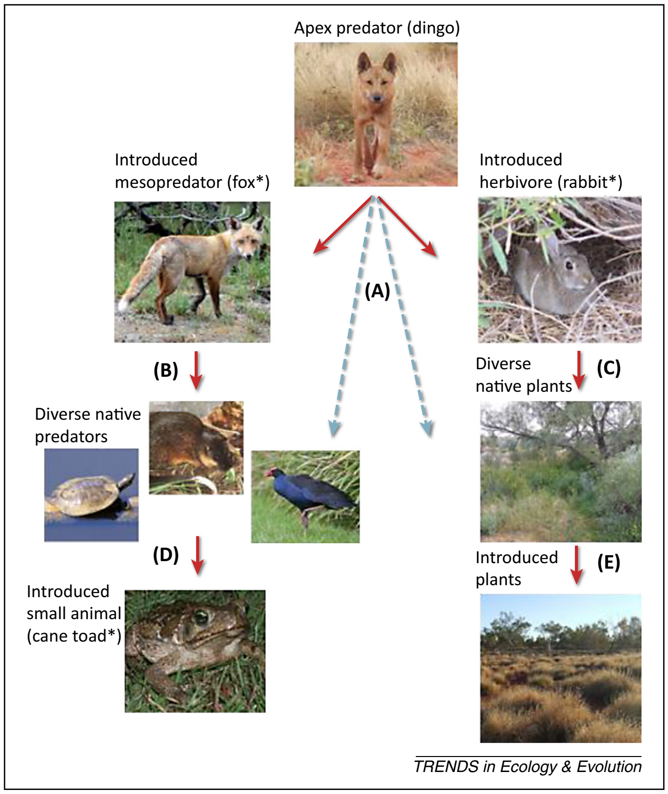

Figure 1. Apex predators can alleviate the harmful effects of non-native species both directly, by hunting them, and indirectly, by promoting the diversity of their predators and competitors. Red arrows denote a negative effect, broken blue arrows a positive effect (trophic cascades), and letters highlight interactions with examples from Australia. **(A)** Apex predators suppress population irruptions of introduced mesopredators and herbivores, benefiting plant and animal diversity [21,37]. **(B)** An increase in mesopredators suppresses, and in some cases even eliminates, their prey [14]. **(C)** High densities of introduced herbivores suppress plant biomass and diversity [37,60]. **(D)** Higher abundance and diversity of animals might include species that have strong trophic effects on small introduced animals [31]. **(E)** High plant diversity limits introduced plants from taking over [57]. Photo credits: Arian Wallach (dingo, rabbit, vegetation); Les Peters (fox); Peripitus (turtle), Toby Hudson (rail), ZooPro (rodent), and United States Geological Survey (cane toad) licensed under CC BY-SA 3.0 via Wikimedia Commons. *Included in the World's Worst.

dominance by any one species [57]. Even in systems in which non-native plants are competitively superior, ecosystem structure can enable coexistence [58,59]. Apex predators can therefore help to restore a more-diverse plant community in which non-native monocultures are less likely to form [39,60].

Reestablishing top-down regulation of novel ecosystems

Much of the globe has undergone significant 'trophic downgrading' [36]. It is from within this context that our views of introduced species have been shaped. Examining the ecologies of these same species where apex predators are flourishing may yield a different view of the ability of ecosystems to absorb new species (Box 4). The recovery of apex predators offers an alternative response to introduced species that can simultaneously reduce the harm they cause, reduce the harm society feels compelled to cause them, and capitalize on their values. This approach is not without its challenges: society remains apprehensive towards both large predators and non-native organisms, and both are subjected to eradication efforts. Nevertheless, considering rapid environmental change, some species will need to move to survive, and resident ecosystems will need large predators in order to adapt. Overall, to achieve better outcomes for biodiversity we will have to transition our efforts away from killing introduced species and towards promoting ecological mechanisms that enable coexistence.

Box 4. Outstanding question

Can apex predators help to recover threatened species in novel ecosystems?

Lethal control of non-native species is the standard approach for the recovery of many native species. This approach bears high costs and risks. We propose to test an alternative method in which the primary recovery action is the conservation of apex predators. To clarify mechanisms, the apex predator must be large [40,41] and directly interact with the threatening non-native species.

The experiment would provide an opportunity to answer two important questions: can threatened species recover by reestablishing trophic cascades? Can apex predators modify the ecological functions of 'invasive' non-native species, to the extent that they provide a net benefit to local biodiversity?

To test this, we propose long-term trials that compare sites within novel ecosystems undergoing different treatments: (i) standard lethal control of non-native species in the absence of apex predators, (ii) no intervention in the absence of apex predators, and (iii) apex predator recovery is the sole treatment.

The trials can be established as new experiments, by initiating apex predator recovery, or as 'natural experiments', by utilizing existing differences in management practices. The relative abundances and interactions of the apex predators, the offending non-native species, and the threatened native species would be closely monitored.

In a second stage, locally extinct species could be reintroduced. The reintroduction would follow standard protocols, but would differ in that the conservation of apex predators fully replaces lethal control of non-native species.

Three conditions would have to be met for a reintroduction to proceed:

(i) The apex predator population is both protected and stable.
(ii) Species known to suppress the reintroduced species are at sufficiently low densities.
(iii) Key biodiversity indices are improving.

As with many large-scale ecological experiments, it will be difficult to achieve the full set of requirements for standard experimental design where the replication of treatments is not feasible. This limitation can be mitigated with replicated sites inside each treatment and by the use of inferential statistics to assess the relative drivers of observed patterns [21,77].

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tree.2015.01.003.

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