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Ecosystem restoration with teeth: what role for predators?

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Recent advances highlight the potential for predators to restore ecosystems and confer resilience against globally threatening processes, including climate change and biological invasions. However, releasing the ecological benefits of predators entails significant challenges. Here, we discuss the economic, environmental and social considerations affecting predator-driven ecological restoration programmes, and suggest approaches for reducing the undesirable impacts of predators. Because the roles of predators are context dependent, we argue for increased emphasis on predator functionality in ecosystems and less on the identities and origins of species and genotypes. We emphasise that insufficient attention is currently given to the importance of variation in the social structures and behaviours of predators in influencing the dynamics of trophic interactions. Lastly, we outline experiments specifically designed to clarify the ecological roles of predators and their potential utility in ecosystem restoration.

Challenges for predator-driven ecosystem recovery

The world is losing species and habitats at an alarming rate [1,2]. Proactive and novel measures are needed to reverse this situation and promote ecosystem resilience. Top-order predators have been extirpated from much of the globe, but a growing literature demonstrates the diverse and underappreciated roles of predators in shaping ecosystems [3,4]. Where they have been retained or restored, apex predators can buffer against and/or ameliorate environmental challenges, including biological invasion [5], disease transmission [6] and climate change [7]. However, considerable obstacles prevent the use of predator management for ecosystem restoration and preservation. Here, we explore four key areas that demand consideration in ecological restoration programmes that make use of the interactions of top-predators: (i) the importance that ecosystem context has on trophic dynamics; (ii) focusing on the ecological functions of species rather than their identities and origins; (iii) improving understanding of how behaviour (not just abundance) affects species interactions; and (iv) what innovative experiments and management

techniques are required to clarify the functional roles and utility of predators as restoration agents?

Ecosystem context: an underappreciated dimension influencing trophic interactions

Although there is broad consensus that top predators can structure ecosystems and benefit biodiversity [4], current ability to forecast and harness the ecosystem services they provide is limited. This is because the effects of predators on ecosystems do not operate in isolation but are context dependent, being conditioned by other factors, such as the productivity of ecosystems, the diversity of species within them and human interference [4,8,9]. Another major obstacle is that the indirect effects of predators can be hard to foresee, owing to the sheer diversity of pathways and number of trophic levels they can potentially affect [4].

There is growing interest worldwide in the restoration of top predators as a means of manipulating ecological processes and species abundance for the benefit of biodiversity conservation [3]. However, the underpinning knowledge of the processes that govern the strength of the interactions of predators is poor. This knowledge gap hampers efforts to restore ecosystems by reintroducing top predators because it constrains the ability to predict the indirect impacts of predator removal or introduction. Below and in Box 1, we illustrate the importance of context in studies concerning the mesopredator release hypothesis (MRH; [10]). Mesopredator release is an irruption of subordinate predators following the decline or extinction of the dominant (apex) predator(s).

Examining the decline or extinction of apex predators from ecosystems and, importantly, their recovery and recolonisation (where this occurs), provides one of the best but rarest opportunities to assess how ecosystem context conditions the strength of the effects of predators on the structure and function of ecosystems. Such information can provide invaluable insights into the probable outcomes of attempts to restore ecosystems using predators. We illustrate these points further using studies from Fennoscandia.

In 19th-century Sweden, elimination of wolves (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) triggered an irruption of a native mesopredator, the red fox (*Vulpes vulpes*)
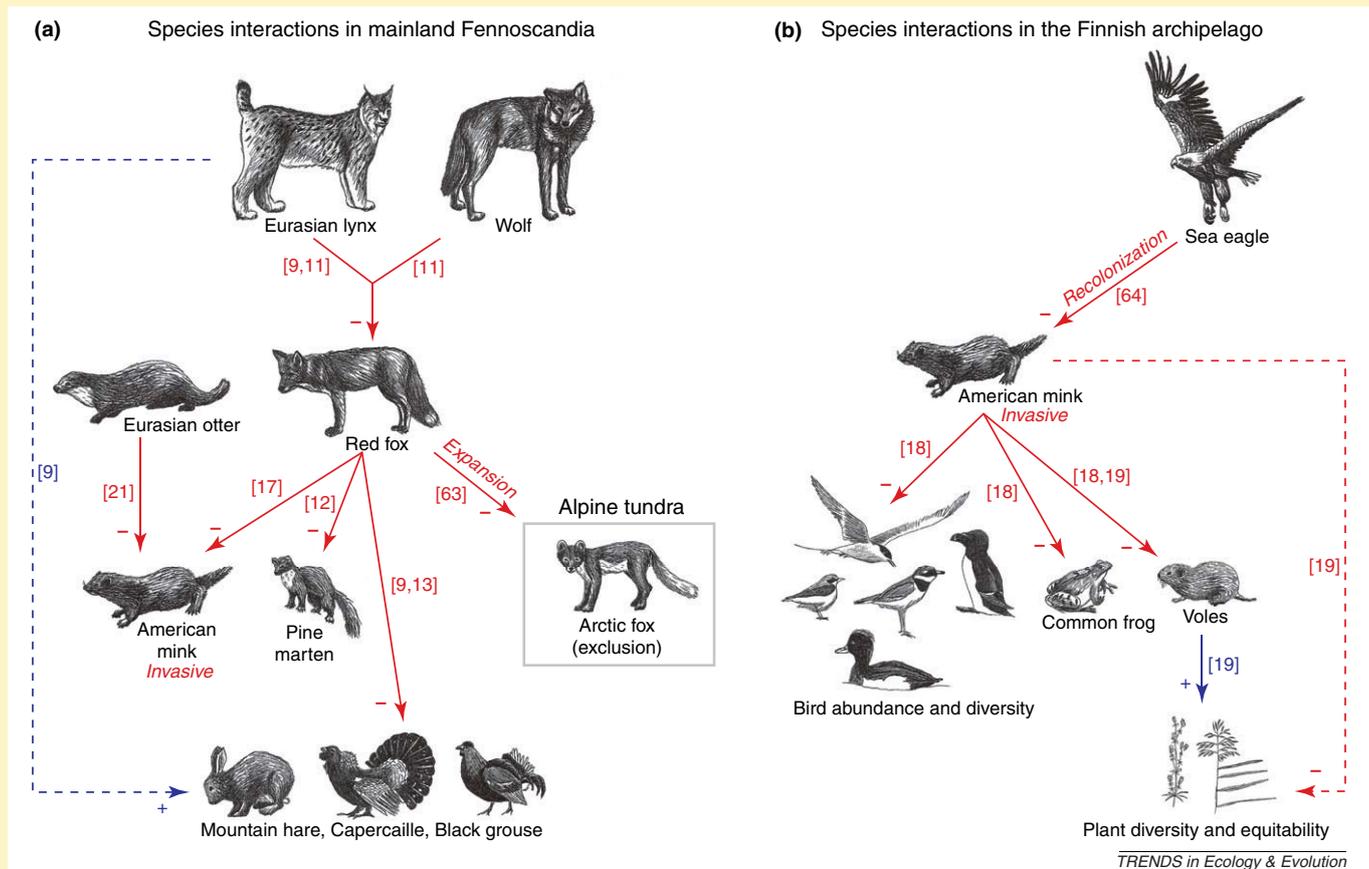
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Box 1. Complex predator communities can mitigate the effects of mesopredators and invasive predators

Historic extirpation of top predators in Fennoscandia caused meso-predator release of the native red fox, which in turn suppressed prey and competitors (Figure Ia). Lynx recolonisation now reverses the pattern by increased red fox control and indirect release of prey. However, the top-down impacts are mediated by ecosystem productivity, and depend on predator densities. The alpine tundra has a simple predator community, where large predators are rare and the red fox was at its northern distribution limit. Hence, recent red fox expansion has an invasive character and causes the native arctic fox to retreat. In the more complex mainland ecosystem, native predators (red fox and otter) can exert top-down control of invasive mink. The arctic–red fox interaction has an important non-lethal, behavioural

component. The arctic fox avoids breeding in red fox territories and this behavioural response implies that a very low red fox density is a sufficient explanation for arctic fox decline and exclusion [63].

Islands in the Finnish archipelago harbour simple communities and the invasive American mink has strong direct and indirect effects on abundance patterns and species diversity (Figure Ib). Recolonisation of sea eagles, following decline owing to pollution during the mid-20th century, might increase ecosystem complexity and mitigate mink impacts on native species. In this case, non-lethal effects might be strong as the behaviour of the mink is affected by eagle presence; the mink reduces swimming distances when it risks eagle predation because it is more exposed to eagles when swimming [64].

(a) Species interactions in mainland Fennoscandia

(b) Species interactions in the Finnish archipelago

Eurasian lynx Wolf [9,11] [11] Eurasian otter Red fox [9] [21] [17] [12] [63] Expansion [9,13] American mink *Invasive* Pine marten Alpine tundra Arctic fox (exclusion) Mountain hare, Capercaille, Black grouse

Sea eagle Recolonization [64] American mink *Invasive* [18] [18] [18,19] [19] Common frog Voles Bird abundance and diversity [19] Plant diversity and equitability

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Figure I. **Complex predator communities can mitigate the effects of mesopredators and invasive predators**. Red arrow, negative impact; blue arrow, positive impact; hatched arrow, indirect impact. Numbers in square brackets correspond to references.

[11]. A century later, an epidemic of sarcoptic mange caused fox populations to crash, boosting several species vulnerable to fox predation [12,13]. In southern Finland, the recovery of lynx had a similar suppressive effect on foxes, with a concomitant increase in forest grouse (*Tetrao tetrix*) (G.X. Ludwig, PhD Thesis, University of Jyväskylä, 2007) and mountain hare (*Lepus timidus*) [9]. However, the degree to which larger predators suppressed foxes was dependent on ecosystem productivity. Suppression of foxes was strongest in the most productive areas, where apex predators reached their highest densities [11]. However, increased productivity can dampen the impacts of apex predators because complex systems have more interaction pathways [14]. Also, resource competition between predators, a major driver of intraguild killing, might be relaxed if there is a surfeit of prey [4,15]. Thus, depending on the

specific characteristics of a system, increased productivity can either increase or dampen the effects of apex predators.

High predator diversity can also provide a buffer against invasion, and native predators tend to have lesser impacts on native prey than do invasive predators [16]. Ecological release of mesopredators from apex predator suppression can devastate some ecosystems, but paradoxically in others, high mesopredator abundance might be beneficial. For example, red foxes have decimated biodiversity in Australia, but not in southern Fennoscandia despite meso-predator release. In fact, prior to a mange-induced fox decline, it appears foxes suppressed another smaller predator, the invasive American mink (*Neovison vison*) [17]. Mink invasion on islands lacking mammalian predators has reduced prey abundance and diversity, with cascading effects on vegetation [18,19]. These findings suggest that

foxes have been beneficial by suppressing mink in mainland Fennoscandia. As a further twist, the impacts of mink might increase as apex predators (lynx and wolves) recolonise and suppress foxes [9]. Similarly in the British Isles, invasive mink increasingly suffer from competition with recovering populations of the native Eurasian otter (*Lutra lutra*). High otter densities appeared to hamper mink establishment and spread until the 1960s, when otters declined owing to water pollution [20]. Recent otter recovery has reversed the ecological release of mink [21]**.**

Together, these studies highlight: (i) that the roles of predators are spatially and temporally context dependent; (ii) that predator diversity can promote resilience against introduced predators and ecosystem change; (iii) the importance of considering habitat quality and productivity in trophic interactions; and (iv) the dynamic temporal dimension in species interactions. These points demonstrate that the probable outcomes of predator-driven ecosystem restoration must be predicted and assessed according to the specific and local conditions in which they are planned to occur, and that extrapolation beyond regions or across time periods may not be justifiable.

What's in a name? Ecological function versus the identities and origins of predators

Although ecological context deserves greater consideration, we argue that other predator management issues are overemphasised, distracting one from the importance of ecological function. Two such issues are the identity (taxonomic) and origin (native versus introduced) of a predator. This is particularly clearly illustrated in the way that wolf-like canids (*C. lupus* spp.) are defined, perceived and managed [22,23]. For example, in Australia, 'pure-bred' dingoes (*C. l. dingo*) are considered rare in parts of the continent owing to hybridisation with domestic dogs (*C. l. familiaris*). Hence, dingoes, feral dogs and their hybrids are frequently referred to collectively as wild dogs [8,24], and treated equally as pests for which the management goal is extermination.

Regardless of the taxonomic status or origins of a predator, we believe a more critical consideration is to identify its functional role. This is particularly pertinent because, as we have established above, the functional roles of predators vary with ecosystem context. Taking these ideas further, we urge wildlife managers to consider the local context for managing predation regardless of the identity of the predators [25]. The dingo provides an interesting case. It is referred to as invasive by some and native by others, having arrived in Australia relatively recently (≤5000 years ago). It has also undergone hybridisation with domestic dogs [26]. Mainland Australia has lost all of its native, large-bodied (>5 kg) terrestrial predators, and represents one of the most depleted predator guilds in the world [27]. The ecosystems of Australia are, therefore, in many respects less complex than elsewhere and potentially more susceptible to impacts of environmental change [28], including biological invasion. This lack of resilience has been implicated in a large number of extinctions during the past 200 years [27]. The dingo and, in some parts of the continent, dingo–dog hybrids, by fulfilling the role of apex predator and suppressing the abundance of the invasive

red fox, have aided persistence of native species that have vanished from dingo-free areas [8,29,30].

Similarly, although they are generally and rightfully recognised as damaging predators supported by invasive prey [31], in some island ecosystems feral cats (*Felis catus*) function as apex predators that buffer the impacts of other invasive animals [32]. In some New Zealand islands, for example, cats suppress invasive rats, protecting native birds from rat predation. On Little Barrier Island, cats were removed without consideration of their ecological role. This resulted in catastrophic declines of birds owing to mesopredator release of rats [32].

These examples, in which established apex predators such as dingoes and cats can in some contexts provide benefits for biodiversity, highlight the importance of pragmatically considering the local and contemporary ecological functions of invasive predators for conservation [33].

Behaviour can be just as important as abundance

Much of the understanding regarding species interactions, including many of the examples already mentioned, comes from correlative studies of species abundance. Although this approach has advanced ecological theory, most studies have failed to consider how these patterns of species abundance are dictated ultimately by the behaviour and fates of individuals. In the case of predators, the behaviour of individuals and structure of social groups can have strong effects on the behaviour, health, survival and, ultimately, the populations of other species with which they interact. Just as one needs to be aware of how variation in broad-scale factors such as habitat productivity influence predator management and restoration attempts, one also needs to consider how variation at the scale of populations and individuals influences management outcomes.

In Australia, studies on dingoes demonstrate how lethal control can alter predator social structure, with unpredictable effects on ecosystems and production systems. Following control, dingo populations displayed reduced social and territorial behaviours [34], and the prevalence of invasive species was greater where the social integrity of dingo packs was fractured [5]. Dingo abundance responded unpredictably to control and was a weaker predictor of positive ecosystem states than was social integrity. The integrity of dingo packs might be the key to maintaining functional and diverse ecosystems because dingoes defend territories and hunt more effectively in packs than alone [35].

Behavioural changes in prey can also be ecologically important. Predators typically have a strong influence on prey behaviour (Box 1). By inducing fear and stress, predators can reduce the ability of other species to obtain resources, their assimilation efficiency and reproductive output [36,37]. For example, predator-induced stress can impair the reproduction of prey species, and has been identified as a key mechanism driving population cycles of snowshoe hares (*Lepus americanus*) in Canada [38]. Similarly, elk (*Cervus elaphus*) in wolf-prone areas consume poorer forage, have higher stress levels, lower reproductive rates and lower calf recruitment than in wolf-free areas [39–41]. If these non-lethal effects of predators are translated into prey demography, they could have

cascading effects on species at lower trophic levels analogous to the effects of direct killing by predators.

Greater emphasis is needed on the behaviour and social structure of predators as changes in these can be as influential as changes in abundance. The link between the social interactions of predators and ecosystem structure might help to explain why predator effects are frequently not well described by linear functions of predator abundance versus target organism abundance [5,42,43]. In short, because the effects of predators on ecosystems are a function of both their abundance and behaviour, abundance measurements alone can underestimate the effects of predators on ecosystems and ignore the mechanisms via which these are realised [36,43]. Therefore, when initiating predator-driven restoration attempts, it will be critical to have knowledge of how the social dynamics of predators and shifts in the behaviour of individuals can influence ecosystems. Without such information and appropriate consideration, restoration attempts are at risk of resulting in unpredictable and/or undesirable outcomes.

Desperate times need bold measures: reintroductions and innovative management

There is great variability and uncertainty surrounding the ecological functions of predators, including unpredictable or even counterintuitive outcomes from species interactions. What is certain is that loss of native species and their functions, as well as addition of invasive species with new functions, has altered ecosystem structure and impacted biodiversity at a global scale and, in many cases, resulted in the development of ecosystem states that are both novel and irreversible. Ecosystems with low diversity have low resilience and are particularly sensitive to disruption [44]. Ecosystems degraded by humans might be equally sensitive. Conservation management often fails to stem or reverse these negative trends. We believe that this is a strong argument for bold and unconventional approaches to restoration, particularly in degraded and already altered habitats, where there is little to lose but potentially much to gain [45,46]. In doing so, great opportunities exist to elucidate the ecological roles of predators.

Australia provides an excellent opportunity for restoration experiments, as much of its biodiversity is under threat. In the Australian tropics alone, more than 20 endemic species of mammal might face extinction over the next few decades owing to inappropriate fire regimes, intensified livestock grazing and predation by feral cats [47]. In Tasmania, recent introduction of the red fox and concurrent decline of the native apex predator, the Tasmanian devil (*Sarcophilus harrisii*), is predicted to cause extinction of many species formerly abundant on both mainland Australia and Tasmania [48]. We contend that this grave situation justifies serious consideration of management programmes in which apex predators are reintroduced or allowed to recolonise habitats where they once occurred. Importantly, owing to the large size of Australia and its diversity of habitats ranging from alpine to arid, there is considerable scope to examine how broad environmental gradients affect the outcomes of predator reintroductions. Recent empirical data suggest that dingoes induce a community-wide trophic cascade by limiting

native and introduced herbivores, and exotic mesopredators, with profound flow-on effects for smaller animals and vegetation [5,30]. Landscape-scale reintroduction experiments, including reintroducing dingoes to areas where they have been extirpated and returning devils to mainland Australia, could examine whether dingoes and devils can help restore ecosystems via their competitive and predatory intraguild interactions with the similarly sized red fox. However, in the case of reintroducing devils, owing to a lack of detailed information regarding their functional role relative and/or additional to foxes, the potential outcomes would be more difficult to predict and reintroductions would need to be carefully controlled. In a further complication that demonstrates the difficulty of predator reintroductions, we caution that devils should not be reintroduced to areas with dingoes, as owing to significant potential dietary overlap and their smaller body size (5–14 kg), theory [49] predicts that devils would be vulnerable to attack by the considerably larger (11–22 kg) and often social dingo. Indeed, the introduction of dingoes has been implicated as a factor contributing to devil extinction from mainland Australia approximately 3000 years ago [35].

Although we and others [3] have drawn attention to the urgent need to restore predators and their functional roles, such initiatives present significant challenges and potential negative effects. First, a major obstacle is the impact of apex predators on livestock and fisheries production, which often leads to lethal control, legal or otherwise [50,51]. Second, the introduction of apex predators could increase the risk to threatened or endangered prey species, particularly in areas already altered by humans [52]. Such a situation is highlighted by the recent recolonisation and expansion of wolves in Finland, which has caused rapid declines of endangered forest reindeer (*Rangifer tarandus fennicus*) [53]. Third, in many parts of the world, maintaining and restoring predators (e.g. big cats and crocodiles) poses significant threats to human life.

What solutions are available? In terrestrial ecosystems, we believe that livestock guardian animals present a viable option for maintaining predator functions while also minimising stock loss [54]. Although lethal predator control can be effective in reducing predator numbers, it must occur regularly and at sufficient (often large) scales, and is therefore costly and labour intensive. Lethal control can also produce a cascade of unintended, negative effects, including the irruption of herbivore populations and depletion of forage [3,5,55], mesopredator release resulting in the concomitant suppression of small prey [4] and, ironically, increased attacks on other valued species [56]. By contrast, guardian animals offer continuous protection of livestock against predation, but might also deter large herbivores from grazing areas, thereby reducing competition and increasing the food available for livestock [57]. Although it remains to be tested, livestock protection dogs, which often establish large territories, could also deter and/or exclude smaller predators, such as cats and foxes, thereby delivering further benefits to native biodiversity. In cases where the reintroduction of apex predators might pose too great a risk (e.g. to endangered prey and/or human life), management that simulates apex predators and their ecological effects might present a feasible alternative. Such

approaches, although largely untested, could include a combination of culling target species (mesopredators and herbivores), and using trained dogs to invoke fear in these same species (both directly through chasing and indirectly through species' responses to dog scent). This could alter habitat use and activity of the target species, affecting vital rates and hence further suppressing their populations.

Concluding remarks

The ecological effects of apex predators pervade ecosystems globally, but harnessing these effects for positive economic, social and environmental outcomes will require social, economic and biological hurdles to be overcome. We suggest the following four areas require urgent research:

Ecosystem productivity and complexity

The effects of predators on ecosystems do not operate in isolation but interact in complex ways with other factors, such as the productivity of ecosystems and the diversity of species within them. To enable managers to best harness the ecosystem services that predators provide, there is a need for better knowledge of the processes that govern the strength of their interactions with other species and the complexity of their effects.

Behaviour and its importance in trophic interactions

Currently, a disproportionate emphasis is placed on abundance when examining the effect(s) of one species on another. Abundance measurements alone can underestimate the effects of predators on ecosystems and the mechanisms via which these are realised [36,43]. Non-consumptive effects of predators, the psychological and physiological manifestation of fear and stress [39,40], can also shape ecosystems [58]. Also, because the effects of predators tend to be non-linear [43], it is critical that researchers determine what species population characteristics are needed for the species to be ecologically effective [59]. Identifying such thresholds will be difficult, but an adaptive management approach, monitoring the spatial and temporal response of one species to manipulation of another, could provide such information. This would allow management to define more appropriate and dynamic targets, and could also help to set upper bounds on 'problem' predators that pose a direct threat to human lives or pose unacceptable economic costs.

Holistic views ('balance sheets') of the effects of predators

Future research must incorporate biodiversity, economic and social aspects when assessing the net gain or cost of maintaining and restoring predators. This is crucial as predators affect these dimensions, which are valued by society. Conservation social science [60] has much to offer as it explicitly examines how and why humans relate to their environment. Without such knowledge, traditional ecological and conservation-based research of predators and their importance will probably often fail [61,62].

Experiments to increase understanding

With some notable exceptions [9,55], there is a lack of studies that have monitored and investigated predator

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Box 2. Testing predator interactions with short-term experiments

Ideally, the MRH would be tested by replicated Before-After, Control-Impact (BACI) experiments involving the removal or introduction of apex predators. This requires a very large spatial scale, extensive replication and a duration of many years [65], making such proposals ambitious and expensive. An alternative approach focusing on individual behavioural responses could provide answers much more quickly. If there is strong interference competition, as is often the case among carnivores, removal of apex predators should cause subordinate competitors to alter their behaviour within days, whereas demographic responses can take months or years [66]. Behavioural shifts can be expected to lead to a demographic response in the longer term [67].

Key questions include whether mesopredators alter their home ranges, habitat use, diets or temporal activity patterns following removal of a dominant competitor. The approach uses a two-site, treatment-reversal design. At each site, apex- and mesopredators are fitted with GPS collars. Initial monitoring (perhaps 2–3 months) collects detailed information on home ranges, habitat use and temporal activity patterns. GPS collars allow location data for each animal to be collected simultaneously, so that both static (spatial) and dynamic (temporal) interactions can be investigated (competitors might avoid each other in space or time).

Next, apex predators are removed from Site 1, while movements and behaviour of mesopredators continue to be monitored. After several weeks, the treatments at Sites 1 and 2 are reversed. Apex predators are removed from Site 2 and allowed to reinvade Site 1. For many species, reinvasion is rapid (e.g. foxes reinvade poisoned areas within days; [68]). If competition is important, a corresponding change in behaviour of the mesopredator is expected within a similar time frame. This experimental design overcomes the limitations of low spatial replication by allowing each site to act consecutively as a treatment and then as an experimental control, or vice versa.

The diets of apex and mesopredators are monitored at both sites throughout the experiment to detect any shifts caused by the manipulation. Because mesopredators tend to consume smaller prey, it is likely that their effects are not equivalent to those of apex predators. Monitoring mortality rates of prey populations can detect any differences in the relative impacts of the predators.

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communities over long time periods to separate out short-term versus more long-term 'equilibrium' community states caused by predators. Long-term studies could be conducted as part of existing predator management. Experiments testing the short-term responses of predators to the removal or addition of putative competitors (Box 2) could also provide useful insights.

In closing, we emphasise that predators can play a vital role in ecosystem restoration as ecological engineers. However, restoring the functional roles of predators is hindered by significant challenges. Management must recognise that predators can have both desirable and undesirable impacts depending on ecosystem contexts, and also that the ecological effectiveness of predator populations might be dictated as much by their social structure and behaviour as by population density. Research addressing these challenges is urgently required.

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