Perspective

Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances

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ABSTRACT

Invasive species have reshaped the composition of biomes across the globe, and considerable cost is now associated with minimising their ecological, social and economic impacts. Mammalian predators are among the most damaging invaders, having caused numerous species extinctions. Here, we review evidence of interactions between invasive predators and six key threats that together have strong potential to influence both the impacts of the predators, and their management. We show that impacts of invasive predators can be classified as either functional or numerical, and that they interact with other threats through both habitat- and community-mediated pathways. Ecosystem context and invasive predator identity are central in shaping variability in these relationships and their outcomes. Greater recognition of the ecological complexities between major processes that threaten biodiversity, including changing spatial and temporal relationships among species, is required to both advance ecological theory and improve conservation actions and outcomes. We discuss how novel approaches to conservation management can be used to address interactions between threatening processes and ameliorate invasive predator impacts.

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1. Introduction

Reducing the ecological impacts of invasive species is a central conservation goal globally (Glen et al., 2013). Invasive species have reshaped the function and composition of biomes across the globe (Loehle and Eschenbach, 2011), and considerable cost is associated with minimising their ecological, social and economic impacts (Scalera, 2009). One group of invasive species that has contributed disproportionately to the decline and extinction of biodiversity in the regions they invade is mammalian predators (Lowe et al., 2000). Through predation (Doherty et al., 2015), competition (Norbury, 2001), hybridisation (Daniels et al., 2001) and disease (Banks and Hughes, 2012), invasive mammalian predators are among the most damaging of all invasive species. The global cost of monitoring and controlling these predators is in the order of hundreds of millions, if not billions, of dollars annually (e.g. Clayton and Cowan, 2010; Gong et al., 2009).

Nine invasive predator species feature in the list of *100 of the World's Worst Invasive Alien Species* (Lowe et al., 2000), in addition to a further 21 introduced mammals that are known or potential predators of native fauna (IUCN, 2014). These mammals range from obligate carnivores (e.g. *Felis catus*) to opportunistic, generalist predators (e.g. *Rattus* spp.). Three of these taxa have had a disproportionate impact on global biodiversity: the domestic cat *Felis catus,* the red fox *Vulpes vulpes* and rats *Rattus* spp. On island ecosystems alone, the domestic cat has contributed to at least 14% of bird, mammal and reptile extinctions globally (Medina et al., 2011) and, along with the red fox, has also contributed to the extinction of more than 25 mammal species and subspecies in Australia (Woinarski et al., 2015). *Rattus rattus* is the most damaging species of rat and has contributed to the decline or extinction of 60 vertebrate species worldwide (Towns et al., 2006).

To date, management of the threats posed by invasive predators has focused largely on directly manipulating their populations using lethal control. The main methods include combining exclusion fencing and lethal control to create predator-free areas (Young et al., 2013); culling, often financed using bounty systems (Bonesi et al., 2007); and poisoning, using large-scale baiting programs (e.g. 1080 poison baiting) (Robley et al., 2014). A consistent feature of these methods is their sole focus on removing individuals to reduce or eliminate predation pressure on native prey. While these programs have at times been successful in limiting the effects of invasive predators on prey at local scales or on islands (Robley et al., 2014), they are extremely costly (Zuberogoitia et al., 2010), they have not arrested the ongoing declines of native fauna in most regions (e.g. Woinarski et al., 2015), and their applicability at larger spatial scales is questionable (Lieury et al., 2015). Further, such management programs often occur without consideration of the density-independent impacts of predators ('functional' impacts; outlined below), and with scant regard for how they might interact with other stressors that are impacting ecosystems at the same time (herein 'concomitant threats'). This has led to unpredictable outcomes of invasive predator control; sometimes it is ineffectual (Bodey et al., 2011), or worse, results in a net negative outcome for biodiversity (Marlow et al., 2015; Norbury et al., 2013). This suggests an urgent need to refine our understanding of invasive predator management, such as when and where to use lethal control, and to consider alternative means of reducing the impact of invasive predators on native biodiversity aside from lethal control.

Here, we review evidence of interactions between invasive predators and six widespread and important threats with strong potential to interact with invasive predators and their control: land clearing, altered fire regimes, large herbivore grazing, anthropogenic resource subsidies, altered prey populations, and the loss of top-predators (Fig. 1). These threats do not negate the importance of other potential threats, such as overexploitation or climate change, but have been identified as particularly likely to interact with threats from invasive predators (e.g. Newsome et al., 2015b; Ripple et al., 2014). We consider these six threats as belonging to one of two categories reflecting their underlying ecological cause: those that are mediated by alterations in vegetation structure ('habitat-mediated threats') and those that arise due to the composition of the ecological community ('community-mediated threats') (Fig. 1). We discuss the potential for synergies between invasive predators and the six threats by considering the impact of the threats on three mechanisms that can lead to exacerbated (or ameliorated) impacts of invasive predators: (1) changes to invasive predator abundance, (2) changes to the per capita impact of invasive predators, and (3) the impact of the concomitant threat itself on populations of native fauna. Based on this synthesis, we discuss novel approaches for improved invasive predator management.

1.1. Interactions between threats

Central to this synthesis is the notion of interactions between disturbances, both additive and synergistic (Brook et al., 2008; Didham et al., 2007). Additive effects of disturbances occur when two disturbances that overlap in space and time combine to impact an ecological response variable in a way that is equal to the summing of their independent effects. For example, if land clearing and invasive predators each reduce the population size of a native mammal by 20% in isolation, then populations subject to both land clearing and invasive predators will have a population reduction of 40%. By contrast, synergistic effects arise when two disturbances that overlap in space and time have an impact greater than the sum of their independent effects. Thus, considering the above example, if the combination of land clearing and invasive predators resulted in a 60% decline of the mammal population, the additional 20% above their respective effects represents a synergy. Today, most ecosystems are subject to multiple disturbances that operate at various spatial and temporal scales and interact to some degree, either additively or synergistically (Anson et al., 2014; Brook et al., 2008; Didham et al., 2007).

With regards to invasive predators, there are at least three situations where synergistic impacts are likely to occur. Two of these relate to the response of invasive predators themselves to an ecological disturbance (Didham et al., 2007). First, a disturbance may increase the abundance of an invasive predator by improving habitat amount and/or quality. For example, modified landscapes in Australia support higher abundances of introduced red foxes compared to intact areas (Graham et al., 2012; Towerton et al., 2011). An increase in the abundance of an invasive predator will in many cases lead to an increase in its impact on native fauna, and we refer to this is as a 'numerical' impact of invasive predators (Didham et al., 2007). Second, a disturbance may increase the per capita impact of invasive predators. That is, although the invasive predator's population density may remain stable, there is a shift in behaviour such that native fauna are more likely to be depredated when invasive
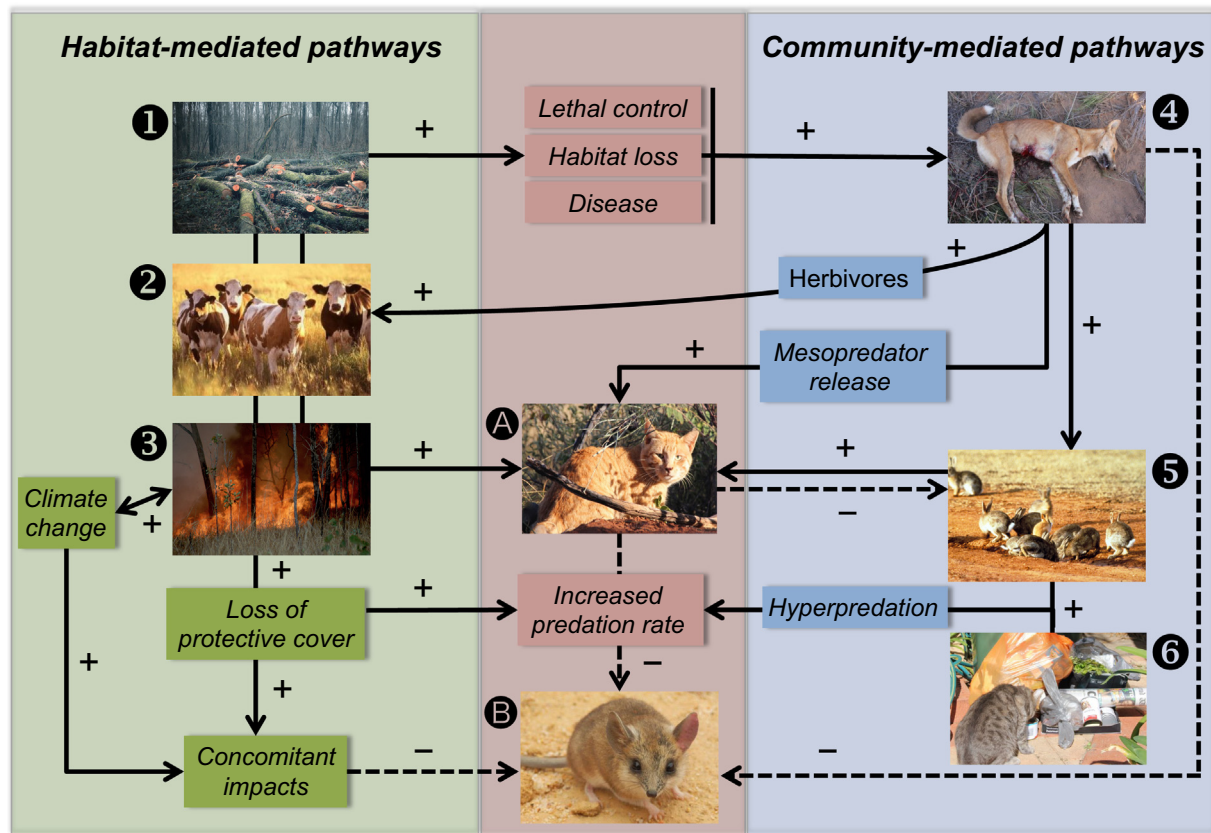
Fig. 1. Conceptual model of the relationship between community- and habitat-mediated interaction pathways and their effects on native fauna. Habitat-mediated pathways are processes that modify habitat structure or integrity and in turn exacerbate the impacts of invasive predators (A) on native fauna (B). Community-mediated interaction pathways are changes in the presence or abundance of a top-predator or its prey species that can lead to increased population densities or altered behaviour of invasive predators that in turn exacerbate their impacts on native fauna. The primary threats interacting with invasive predators are: (1) land clearing; (2) grazing; (3) fire; (4) top-predator decline; (5) altered prey populations; and (6) anthropogenic resource subsidies. Additional processes are indicated with italicised text. Solid lines represent positive effects (+) and dashed lines represent negative effects (−). Image credits: 1, endymion120 (Flickr, CC BY 2.0); 2, USDA (public domain); 3 & 5, CSIRO (CC BY 3.0); 4, 6, A & B, T. Doherty.

predators co-occur with the threat. For example, predation rates of hispid cotton rats *Sigmodon hispidus* increased following prescribed fire in Georgia, USA (Conner et al., 2011). This is a 'functional' impact of invasive predators, as their impact on native prey populations is independent of their population density (Didham et al., 2007). Third, where the concomitant threat itself strongly affects a native species' population, invasive predators may exacerbate its effects such that the loss of individuals from the population due to predation has disproportionate impacts on the population and its rate of decline (e.g. Allee effects) (Soulé et al., 1988), and we refer to these as 'compounding' impacts of invasive predators.

2. Key threats that interact with invasive predators

2.1. Habitat-mediated threats

The alteration of vegetation through processes such as fire, grazing and land clearing can negatively impact fauna by removing food and shelter resources (Robinson et al., 2013), reducing habitat connectivity (Bar-Massada et al., 2014), increasing competition within and between species (Hagen et al., 2012), and lowering their population sizes (Soulé et al., 1988). Additionally, larger-bodied predators with greater energy needs, more specialised diets and larger home ranges are often less able to adapt to habitat fragmentation than smaller and more generalist mesopredators such as domestic cats (Crooks, 2002; Ordeñana et al., 2010), potentially resulting in habitat-mediated mesopredator release and associated negative impacts on prey species.

2.1.1. Land clearing

Land clearing removes natural habitat and typically replaces it with agricultural, urban or industrial development (Hagen et al., 2012). Remnant vegetation is therefore fragmented and isolated within a human-dominated matrix (Hagen et al., 2012), which may be less suitable for native than introduced predators (Crooks, 2002; Ordeñana et al., 2010). For example, in coastal California, habitat fragmentation had a detrimental impact on large-bodied native carnivores and those with specialist habitat requirements, such as mountain lions *Felis concolor*, bobcats *F. rufus* and coyotes *Canis latrans*, whereas generalist urban mesopredators like introduced opossums *Didelphis virginiana* and domestic cats were more abundant in small fragments and probably benefited from human resource subsidies obtained from the surrounding matrix (Crooks, 2002). In the same region, a numerical effect was observed where the loss of coyotes from urban habitat fragments resulted in greater numbers of domestic cats (mesopredator release) and an associated decline in native bird species diversity (Fig. 2) (Crooks and Soulé, 1999; Soulé et al., 1988).

Cleared land and linear features associated with fragmented landscapes (e.g. roads) can act as movement pathways and hunting grounds for predators, allowing them improved access to structurally complex habitats and hence exacerbating their functional impact on prey species (Červinka et al., 2013; Latham et al., 2011). This can lead to increased abundance of invasive predators in modified landscapes (Graham et al., 2012; Towerton et al., 2011). For example, studies have found that the occurrence of introduced foxes and cats is positively associated with edge
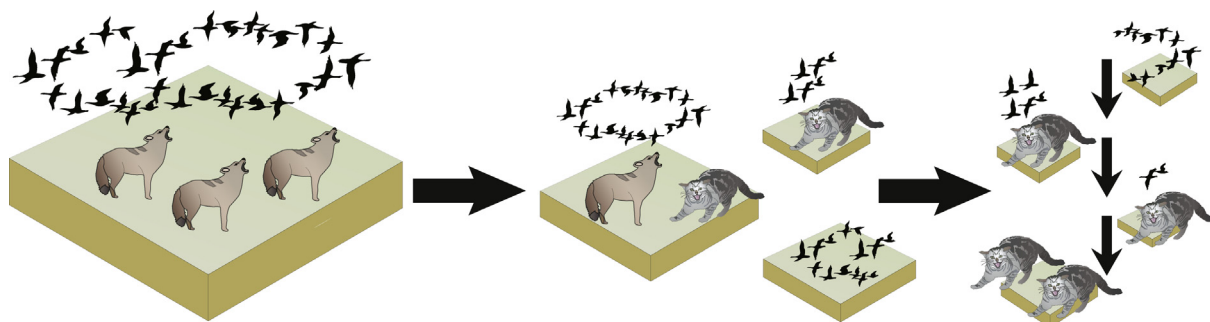
Fig. 2. Fragmentation of sage-scrub habitat in California causes decline of the top-predator (coyote *Canis latrans*) and release of mesopredators (introduced domestic cats *Felis catus*). Cats exert greater predation pressure on birds than do coyotes, leading to reduced bird diversity in smaller fragments (Crooks and Soulé, 1999).

habitats, roadside vegetation and the number of habitat patches in the landscape (Graham et al., 2012), and that foxes are more common in cleared areas than in continuous forest (Towerton et al., 2011). Consequently, synergies may occur between the compounding impacts of fragmentation (e.g. reduced resource availability and population declines of native species), numerical effects brought about by increased invasive predator abundance (and hence predation pressure), and functional impacts brought about by increased access to prey.

The intensity of land use within the matrix can further affect invasive predators and their impacts. Barreto et al. (1998) sought to determine the role of predation by invasive American mink *Neovison vison* in the decline of water vole *Arvicola amphibius* populations in Britain. The underlying cause of vole population declines was habitat loss due to agricultural intensification. However, a functional response also occurred whereby habitat degradation exacerbated the impact of mink predation by removing reed and sedge beds that provided voles with protective cover (Barreto et al., 1998; Carter and Bright, 2003). By comparison, a numerical predator response was illustrated in Israel where increased fox abundance and predation pressure caused by agricultural intensification resulted in the decline of two species of gerbil *Gerbillus* spp. (Shapira et al., 2008).

2.1.2. Altered fire regimes

Fire is one of the most widespread ecological disturbances globally (Bowman et al., 2009). Similar to land clearing, fire can allow predators improved access to structurally complex habitats (Birtsas et al., 2012; McGregor et al., 2014), thereby potentially facilitating functional impacts on prey. Birtsas et al. (2012) found that visitation rates of foxes and dogs *Canis familiaris* at sampling stations in an intensely burned area were greater than in both a moderately burned area and an unburned area. Pastro (2013) found that foxes and cats occurred more frequently on ecotones between burnt and unburnt grasslands when compared to continuous habitat. Fire can also lead to increases in local predator occurrence, thereby leading to potential numerical effects (Borchert, 2012; Schuette et al., 2014).

Increases in predation rates of small mammals following fire (Conner et al., 2011; Leahy, 2013) support the notion of both functional and numerical impacts. Christensen (1980) recorded high rates of fox predation on a threatened marsupial soon after fire in south-western Australia, and Wayne et al. (2006) hypothesised that a negative relationship between possum abundance and fire intensity arose because fire caused possums to spend more time on the ground and predators were attracted to areas of disturbance, hence making possums more vulnerable to predation. In support of this, McGregor et al. (2014) found that feral cats

preferred to hunt in recently burnt or grazed grasslands in northern Australia.

Fire can cause direct mortality of prey (Hailey, 2000; Smith et al., 2012), and may lead to population reductions due to changes in resource availability (Sutherland and Dickman, 1999). Fire therefore represents a compounding threat. A key mediating factor in the interaction between fire and predation is the availability of refuges for prey species (Robinson et al., 2013; Torre and Díaz, 2004). Native rodents in north-western Australia experienced greater predation by feral cats in a high intensity fire treatment, compared to a low intensity, patchy burn and an unburnt control (Leahy, 2013). In semi-arid mallee shrublands, the post-fire response of a range of small mammal and reptile species is dependent on the availability of structurally complex spinifex hummocks (Kelly et al., 2011; Nimmo et al., 2012), potentially because of their role in providing protection from predators (Cogger, 1974). These hypotheses suggest that fire-induced changes in vegetation structure change the availability of protective cover, and hence alter the vulnerability of prey to predation. If the provision of refuges is important to reducing predation pressure, lower intensity fires that retain patchiness should reduce the predation-related impacts of fire on native species. This area will benefit from further experimental work that assesses the relative importance of numerical and functional impacts in post-fire environments. Interactions between fire and predation are likely to be further exacerbated by future increases in fire frequency and intensity that are predicted in global climate models (Pechony and Shindell, 2010), or by increased rates of prescribed burning by land managers attempting to reduce the risk of large wildfires (Penman et al., 2011).

2.1.3. Grazing by large herbivores

Herbivores can influence functional impacts of predators by removing vegetation cover and exposing prey (Kuiper and Parker, 2013; Steen et al., 2005), potentially leading to increased predation rates. High densities of livestock (Jones, 2002) and native herbivores (Foster et al., 2014) can negatively impact other animal species, and many studies have documented recovery of native fauna populations following cessation of grazing (Legge et al., 2011) or greater faunal densities in ungrazed compared to grazed areas (Kuiper and Parker, 2013). Although McGregor et al. (2014) found that feral cats in northern Australia preferred to hunt in recently grazed or burnt sites, in New Zealand, introduced stoats *Mustela erminea,* feral cats, possums *Trichosurus vulpecula* and mice *Mus musculus* were all more abundant in ungrazed compared to grazed areas (Alterio et al., 1998; Whitehead et al., 2014). These contrasting responses illustrate that invasive predators often have divergent responses to processes such as fire and grazing, and the composition and interactions of predator–prey assemblages will shape the ecological outcomes (Doherty et al., 2014).

2.2. Community-mediated threats

2.2.1. Top-predator declines

Top-predators regulate trophic structures of ecosystems by limiting herbivores through predation and suppressing mesopredators via consumptive (direct predation) and non-consumptive (fear-mediated) effects (Estes et al., 2011; Ritchie and Johnson, 2009). Despite their ecological importance, most top-predators have suffered range and population declines across the globe over the past 200 years due to habitat loss, overexploitation and persecution by humans (Ripple et al., 2014). Such declines typically disrupt ecological communities, releasing herbivores and mesopredators from top-predator suppression, and often initiating trophic- and fear-mediated ecological cascades (Berger, 2010; Estes et al., 2011; Johnson et al., 2007).

The Eurasian otter *Lutra lutra* provides a good example of how larger native predators can have both temporally and spatially suppressive effects on the activity of introduced predators such as the American mink (Bonesi et al., 2006). Bonesi et al. (2006) found that increased otter populations, and hence intensified interspecific competition, were responsible for invasive mink population declines across the UK. This is supported by changes in mink abundance, diet and activity following local increases in otter abundance in Spain and the UK (Bonesi and Macdonald, 2004; García et al., 2009; Harrington et al., 2011). Australia's dingo *Canis dingo* provides further evidence of how top-predators can regulate invasive mesopredator populations. Dingoes can have spatially and temporally suppressive effects on invasive mesopredators (Brawata and Neeman, 2011; Wallach et al., 2010), with cat and fox activity being higher in areas where dingoes are poisoned (Brook et al., 2012; Colman et al., 2014). By limiting abundance or by changing the behaviour of invasive predators, larger predators can reduce both numerical and functional impacts of mesopredators on prey species.

2.2.2. Altered prey populations

Introduced prey species, such as rabbits *Oryctolagus cuniculus* and rats, can harm native fauna populations through grazing, habitat degradation, competition, predation and disease transmission (Banks and Hughes, 2012; Scott and Kirkpatrick, 2007). These species also provide invasive predators with a reliable food source, which in turn can amplify their impact on native fauna by supporting a larger predator population—a numerical impact termed 'hyperpredation' (Smith and Quin, 1996). The extinction of the Macquarie Island parakeet *Cyanoramphus erythrotis* was attributed to hyperpredation by cats following the introduction of rabbits (Taylor, 1979), and similar patterns have been described for the impact of cats on Australian conilurine rodents (Smith and Quin,

1996) and on endangered insular vertebrates worldwide (Medina et al., 2011). Further to this, declines in the abundance of a predator's primary prey can lead to increased rates of predation on more-vulnerable species. In New Zealand, invasive predators (cats, ferrets *Mustela fura* and stoats) increased their rates of predation on endangered birds and reptiles following sudden declines in numbers of rabbits—a primary prey species—caused by rabbit haemorrhagic disease (Fig. 3) (Murphy et al., 2004; Norbury, 2001). This is a functional process, termed 'prey-switching', which can potentially have severe population-level impacts on endangered prey, especially if prey-switching occurs during important stages of their reproductive cycle (Bodey et al., 2010).

2.2.3. Anthropogenic resource subsidies

Anthropogenic resource subsidies often support higher densities of generalist predators than occur in the species' natural habitats (Bateman and Fleming, 2012; Newsome et al., 2015b), potentially leading to numerical impacts on native prey. Introduced mongooses *Herpestes javanicus* in Puerto Rico (Quinn and Whisson, 2005) and feral cats in Australia (Denny, 2005) are among 36 species of predators known to benefit from anthropogenic resources (Newsome et al., 2015a). Resource subsidies can also facilitate higher growth rates and population densities of invasive rats (Ruffino et al., 2012), with subsequent negative impacts on native species (Pierce et al., 2003). As a numerical driver of predator populations, these subsidies may facilitate human-mediated hyperpredation. For example, stray and pet cats that are fed by humans hunt in nature reserves out of instinct, not hunger, so there is no limit on the number of cats that a reserve can 'support', potentially resulting in hyperpredation of prey species (Schneider, 2001).

3. Synthesis and applications

We have demonstrated how invasive predators can interact with other threatening processes, potentially exacerbating their impacts on endangered native species. Ameliorating such occurrences presents conservation practitioners with a considerable challenge, not least because of the wide range of ecosystems in which these interactions operate. Given that these processes are largely driven by human influences, implementation of appropriate land management practices should help reduce invasive predator impacts. Below, we discuss how novel approaches to conservation management that recognise the importance of primarily habitat- (3.1) or community-mediated interaction pathways (3.2–3.4) can be used to address interactions between threatening processes and ameliorate invasive predator impacts.
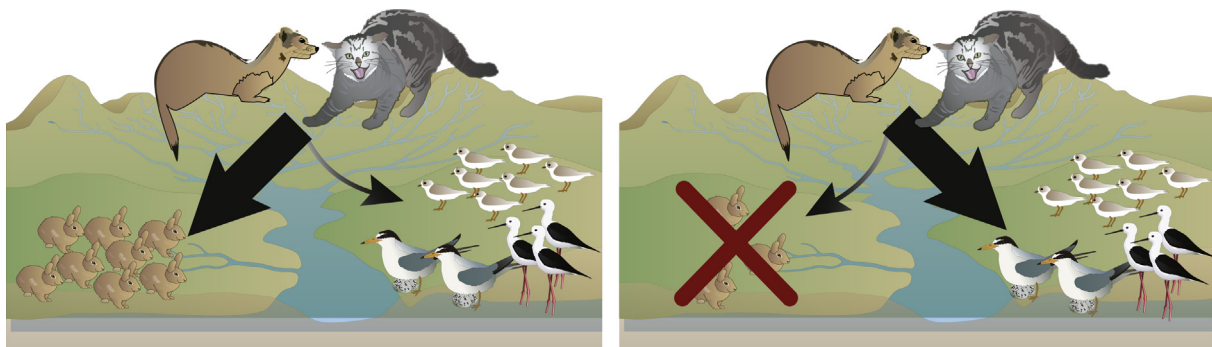

Fig. 3. Prey-switching by invasive predators in New Zealand. Introduced rabbits *Oryctolagus cuniculus* are a primary prey species for invasive predators (feral cats *Felis catus* and mustelids *Mustela* spp.). The predators also prey on endangered native birds and reptiles, but increase their rates of predation (larger arrow) on these groups following declines in rabbit numbers caused by rabbit haemorrhagic disease (Murphy et al., 2004; Norbury, 2001).

3.1. Maintaining habitat complexity

Land clearing, fire and grazing—processes that reduce habitat complexity—appear to be the strongest facilitators of invasive predator impacts, as they have the capacity to lead to numerical, functional and compounding impacts. As threatening processes in their own right, they can also exacerbate impacts on native species by improving habitat suitability for invasive predators and increasing hunting efficiency. Maintenance of habitat complexity can help reduce invasive predator impacts, and in some situations, this is likely to be more effective than lethal control. For example, in northern Australia, where feral cats are a major driver of mammal declines, no effective broad scale control method for feral cats currently exists. Research has shown that feral cats selectively hunt in grasslands that have been recently burnt or grazed (McGregor et al., 2014), and that small mammals experience higher predation rates in these habitats (Leahy, 2013). Landscape-scale fire and grazing experiments indicate that appropriate management of these two processes can conserve habitat refuges and boost native mammal populations, even in the absence of direct control of feral cats (Kutt and Woinarski, 2007; Legge et al., 2011).

Given the important role of habitat complexity in mediating the impacts of invasive predators, conservation practitioners should consider fire management, habitat protection, and revegetation projects as crucial components of their predator abatement plans. Currently, such factors are generally considered as separate projects to predator management, which often focus largely on lethal control, but this need not be the case. Practitioners should seriously consider, and where possible scientifically examine, whether conservation funds are better spent by implementing lethal control programs that require continuous interventions (particularly on non-island ecosystems, see below), or whether such funds would be better committed to long-term projects aimed at improving the capacity of native fauna to persist alongside invasive predators. In some cases, the use of artificial refuges may provide a stopgap to temporally diminish predation pressure (Arthur et al., 2005), although their effectiveness should be assessed experimentally (Lettink et al., 2010).

3.2. Re- not de-wilding

Native top-predators that regulate the impacts of invasive predators are an invaluable tool for conservation managers, and their decline can allow invasive mesopredators to persist and inflict their impacts on biodiversity unchecked. Improved management of invasive predators can be achieved through positive management of existing top-predator populations or reintroductions into areas of their former range ('rewilding') (Bonesi and Macdonald, 2004; Ritchie et al., 2012; Soulé and Noss, 1998; Wallach et al., 2015). Restoration of top-predator populations can also have reciprocal benefits for ecosystems through regulation of over-abundant herbivores and subsequent recovery of vegetation (Newsome et al., 2015a; Ripple et al., 2014; Ritchie et al., 2012). In some cases, native top-predators may also depredate vulnerable species (e.g. Oakwood, 1997) and this should be considered in any rewilding plans.

Large carnivores are experiencing global declines, due largely to human-wildlife conflicts and the separation of predators and people as a management tool, as well as habitat loss and fragmentation (Ripple et al., 2014). However, data from Europe show that a coexistence model between humans and carnivores, supported by legislation and context-specific management, can be successful in conserving top-predators (Chapron et al., 2014). This approach is likely to be most effective in places where catastrophic invasive predator impacts have been exacerbated by persecution of native top-predators, such as dingoes in Australia (Johnson et al., 2007). Co-existence strategies that are receiving greater attention include the use of guardian animals to reduce conflict between predators and livestock owners (Gehring et al., 2010), including the successful use of guardian dogs to reduce cheetah *Acinonyx jubatus* predation of livestock in Namibia (Potgieter et al., 2013). Surprisingly few studies have examined the cost-effectiveness of guardian animals (but see van Bommel and Johnson, 2012). Further research in this area, across a range of livestock species and herd sizes, is urgently required. Alternative approaches (such as those outlined above and below) will be needed for ecosystems that lack native mammalian predators, which is the case for most islands around the world (Courchamp et al., 2003).

3.3. Management of resource subsidies

Anthropogenic resource subsidies can facilitate invasive predator impacts by supporting larger predator populations. This phenomenon is most common in peri-urban areas (Bateman and Fleming, 2012; Newsome et al., 2015b; Ritchie et al., 2014) where native prey experience concomitant threats such as habitat fragmentation (Bar-Massada et al., 2014) and road mortality (Ramp et al., 2006). Removing resource subsidies such as food (Bino et al., 2010) or shelter (Denny, 2005) can reduce population densities of overabundant predators, and this should benefit native prey through decreased hyperpredation. In non-urban areas, carcass dumps left by farmers or hunters (including culls by land management agencies) are often-overlooked predator subsidies (Newsome et al., 2015b). These resource hotspots are exploited by a range of scavengers, such as red foxes in Europe (Cortés-Avizanda et al., 2009) and Australia (Forsyth et al., 2014), and may sustain fox populations during periods of low prey availability (Read and Wilson, 2004). Excluding invasive predators from these sites would likely aid population management, although this may be difficult in remote areas. As an alternative, management could capitalise on the natural attraction of predators to these areas by conducting targeted lethal control in the vicinity.

3.4. Integrated multi-species pest management

Invaded ecosystems often host multiple invasive mammal species, and facilitation between these species can result in 'invasional meltdown' and greater impacts on native species (Courchamp et al., 2003). Selectively removing predators from invaded ecosystems can have undesirable consequences through the release of their introduced prey (Bergstrom et al., 2009) or other introduced predators (Marlow et al., 2015; Norbury et al., 2013; Rayner et al., 2007). Management of a single species, without regard for its flow-on effects on other species, may result in ecological surprises and unintended consequences. A critical aspect of multi-species management is therefore our ability to predict a priori the likely impacts (or range of possible impacts) of manipulating a species' abundance. Models that can make such predictions are very promising (Bode et al., 2015; Dexter et al., 2012; Raymond et al., 2010), although few have been validated.

Optimal approaches for managing multiple invasive mammals will vary between mainland and island ecosystems. On islands, where eradication is often possible, modelling suggests that multi-species eradication schedules should initially focus all resources on removing the predator, then gradually shift resources to removing the introduced prey (Bode et al., 2015). Multi-species eradications are more likely to be successful in a shorter period of time and with lower effort and cost than single-species eradications (Griffiths, 2011), and such programs are also likely to benefit from applying principles of ecological restoration, rather than focussing solely on pest control (Courchamp et al., 2003; Zavaleta

et al., 2001). On the mainland, effective control is more difficult because invasive predators typically have a high reproductive output and can often reinvade rapidly, hence making eradication impossible in most contexts, unless it is within a fenced reserve. Native top-predators that have a suppressive effect on introduced species may be a useful alternative to lethal control in some areas (Wallach et al., 2015). Predation of livestock by native top-predators is an additional issue, which in some cases can be managed using livestock guardian animals (e.g. Potgieter et al., 2013). If lethal control is used, it should be applied using whole-of-ecosystem approaches to prevent unexpected and undesirable outcomes (Colman et al., 2014; Marlow et al., 2015; Norbury et al., 2013; Ruscoe et al., 2011).

3.5. Conclusions

Interactions between multiple threatening processes are being recognised increasingly as a catalyst for species extinctions. We have demonstrated how habitat modification and alteration of predator–prey assemblages can exacerbate the impacts of invasive predators. Conservation practitioners must identify and address habitat- and community-mediated interaction pathways if these impacts are to be reduced. Rather than focussing on single processes, this will require explicit acknowledgement of the multiple threats operating in stressed ecosystems and use of management actions that address these threats in unison. Such integrated approaches are essential if further extinctions and their cascading effects are to be avoided.

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