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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