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Ecologically functional landscapes and the role of dingoes as trophic regulators in south-eastern Australia and other habitats

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Summary Large carnivores can play a pivotal role in maintaining healthy, balanced ecosystems. By suppressing the abundances and hence impacts of herbivores and smaller predators, top predators can indirectly benefit the species consumed by herbivores and smaller predators. Restoring and maintaining the ecosystem services that large carnivores provide has been identified as a critical step required to sustain biodiversity and maintain functional, resilient ecosystems. Recent research has shown that Australia's largest terrestrial predator, the Dingo (*Canis lupus dingo*), has strong effects on ecosystems in arid Australia and that these effects are beneficial for the conservation of small mammals and vegetation. Similarly, there is evidence from south-eastern Australia that dingoes suppress the abundance of macropods and red Fox (*Vulpes vulpes*). It is likely that dingoes in south-eastern Australia also generate strong indirect effects on the prey of foxes and macropods, as has been observed in the more arid parts of the continent. These direct and indirect effects of dingoes have the potential to be harnessed as passive tools to assist biodiversity conservation through the maintenance of ecologically functional dingo populations. However, research is required to better understand dingoes' indirect effects on ecosystems and the development of dingo management strategies that allow for both the preservation of dingoes and protection of livestock.

Key words: *biodiversity conservation, dingo, kangaroo, mesopredator, red fox, trophic cascade.*

Introduction

A large body of recent research has shown that large carnivores play a pivotal role in maintaining healthy, balanced ecosystems (Estes *et al.* 2011). Large carnivores have conspicuous effects on herbivore populations when they kill animals for food and frequently kill smaller predators (mesopredators) and suppress their populations. Whilst the direct effects of large carnivores on their prey and competitors are relatively easily observed, they typically have strong indirect effects as well. Species that interact strongly with large herbivores and mesopredators are likely to benefit from the presence of large carnivores. Because the effects of large carnivores are not just limited to animal communities and can extend to vegetation communities and even influence the geomorphology of landscapes, they have been described as ecosystem architects.

The disruption to ecosystems caused by the removal of top predators, such as big cats (*Panthera* spp.), wolves (*Canis lupus*), the Dingo (*Canis lupus dingo*) and sharks (*Carcharhinus* spp.), has been identified as a major factor contributing to the loss of biodiversity in aquatic and terrestrial systems throughout the world (Myers *et al.* 2007; Letnic *et al.* 2009; Estes *et al.* 2011). Consequently, restoring and maintaining the ecosystem services that large carnivores provide has been identified as a critical global imperative if we are to sustain biodiversity and maintain functional ecosystems (Estes *et al.* 2011).

Maintaining ecologically functional densities of large carnivores are a challenging but essential component in creating resilient, ecologically functional landscapes (Ritchie *et al.* 2012). This is particularly relevant as ecological resilience thinking is increasingly being used to underscore the development of regional catchment planning throughout the terrestrial ecosystems of Australia (Marshall & Stafford Smith 2010; Natural Resources Commission 2011; Rickards & Howden 2012). In this study, we provide an overview on the role that the dingo plays in maintaining ecologically resilient ecosystems. In our overview, we place a strong focus on the forested ecosystems of south-eastern Australia because there is now an emerging body of research showing that dingoes structure these environments in a fashion similar to that which has been well described for arid environments (Letnic *et al.* 2012).

Australia's Top-order Predator

Australian large carnivores include avian, aquatic, reptilian and mammalian predators. For the purpose of this study, the discussion is confined to Australia's largest land predator, the dingo and its hybrids with the domestic Dog (*Canis lupus familiaris*). The status of the dingo is clouded by their adverse impacts on livestock producers, the issue of hybridization between dingoes and domestic dogs and the fact that 'pure-bred' dingoes are now rare in some regions of the continent (Elledge *et al.* 2006; Claridge & Hunt 2008). In evidence of this, wild canids in Australia are referred to euphemistically as 'wild dogs' rather than dingoes in most legislation and policy documents concerning management strategies that aim to reduce wild canid numbers (Letnic 2012). Hybridization between wild *Canis* and domestic dogs is not restricted to Australia and occurs commonly in other parts of the world, causing global concern for the conservation of wild *Canis* genotypes (Iacolina *et al.* 2010). Throughout this article, we use the term dingo to refer to *Canis lupus dingo*, *C. l. dingo* × *C. l. familiaris* hybrids and feral dogs. The reason for this is that hybrids between dingoes and dogs are difficult to distinguish and rare through most of the continent (Elledge *et al.* 2006; Radford *et al.* 2012), and this uniquely Australian word precedes the term wild dog (Letnic 2012).

Dingoes are listed as at risk from the key threatening process of hybridization with feral dogs under the NSW *Threatened Species Conservation Act* 1995. Dingoes are listed as threatened under the *Flora and Fauna Guarantee Act 1988* in Victoria, 'native wildlife' under the *Territory Parks and Wildlife Conservation Act 2006* in the Northern Territory and as vulnerable internationally on the IUCN Red List (Sillero-Zubiri *et al.* 2004).

The IUCN Red List, NSW, Victorian and N.T. governments all recognize the importance of dingoes in regulating trophic systems across a range of Australian habitats including forested eastern landscapes, arid rangelands and tropical savannahs (Sillero-Zubiri *et al.* 2004; Department of Sustainability & Environment 2011; Office of Environment & Heritage 2011; Department of Land Resource Management 2012). For example, the NSW Office of Environment and Heritage states that the dingo plays a vital role in maintaining the balance in ecosystems and that most of the remaining dingo populations are in the east of the State, in forests between the Great Dividing Range and the coast (http://www.environment.nsw.gov.au/animals/TheDingo.htm).

Dingoes eat a wide variety of animals. In eastern Australia, they primarily consume kangaroos (*Macropus* spp.) and Swamp Wallaby (*Wallabia bicolor*) (Newsome *et al.* 1983a,b; Triggs *et al.* 1984; Robertshaw & Harden 1986; Glen *et al.* 2011) as well as smaller species such as Ringtail Possum (*Pseudocheirus peregrinus*), Brushtail Possum (*Trichosurus vulpecula*) and the Rabbit (*Oryctolagus cuniculus*) (Newsome *et al.* 1983a,b; Triggs *et al.* 1984; Lunney *et al.* 1990). Dingoes also consume birds, reptiles, arthropods and vegetation (Triggs *et al.* 1984). In arid regions, reptiles and small mammals are important dietary items of dingoes (Letnic *et al.* 2012).

Livestock are not an important source of food for dingoes; it has been estimated that livestock only comprise between one and seven per cent of their diet, and it is unknown from dietary studies whether livestock are consumed as prey or carrion (Corbett 1995). Sheep (*Ovis aries*) or Cattle (*Bos taurus*) were rarely detected in analysis of dingo stomach contents in south-eastern Australia (Newsome *et al.* 1983b). However, dingoes do attack and kill sheep and can have adverse impacts on sheep producers (van Bommel & Johnson 2012).

Role of top-order Predators in Ecologically Functional and Resilient Landscapes

Large carnivores, particularly mammalian carnivores that have high metabolic rates and hence food requirements, are often described as keystone species or trophic regulators. This is because large mammalian carnivores, such as wolves, dingoes and big cats typically, suppress the populations of large mammalian herbivores such as Deer (*Cervus* spp.) and kangaroos and also the populations of smaller predators such as Red Fox (*Vulpes vulpes*) and Coyote (*Canis latrans*) (Estes *et al.* 2011; Ritchie *et al.* 2012). By suppressing the abundances and hence impacts of herbivores and smaller predators, top predators can indirectly benefit the species consumed by herbivores and smaller predators. Trophic cascades occur when top predators' direct and indirect interactions influence the abundance of species across more than one level in a food web (e.g. top predators suppress herbivores and indirectly enhance palatable vegetation biomass) (Estes *et al.* 2011).

A recent review published in the journal *Science* highlights the unanticipated impacts of top predator removal on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species and biogeochemical cycles (Estes *et al.* 2011). The authors conclude that breakdown of top-down regulation associated with the loss of apex consumers has been a major driver of biodiversity loss and is perhaps 'humankind's most pervasive influence on the natural world'. In their review, Estes *et al.* (2011) challenge ecologists and biodiversity managers to shift their thinking from the paradigm that bottom-up processes are the key driver of ecological systems. They contend that because top-predators' effects of ecosystems are so universal and far-reaching that the burden of proof of their roles in trophic regulation should be shifted to proving that they do (or did) not exert strong cascading effect rather than having to prove that they do.

There has been much debate over the roles that bottom-up (food limited) and top-down (predation limited) processes have in determining the structure of ecosystems (Hopcraft *et al.* 2010). Although many authors have treated these processes as being mutually exclusive, a growing body of research suggests that, within ecological communities, top-down and bottom-up effects often operate simultaneously. This can occur because predators tend to focus their predation on prey within an optimal size range. Thus, predators may suppress the populations of their preferred prey, whilst the populations of other species within the community that are subject to only occasional predation may be limited more by food availability than predation (Hopcraft *et al.* 2010). Hence, within any ecological community, some species will be more subject to top-down regulation than other species, although ultimately individuals of all species require energy to survive.

The mesopredator release hypothesis describes a trophic cascade that occurs when large predators indirectly benefit the prey of smaller predators by suppressing the abundance of the smaller predator (Crooks & Soulé 1999). The effects that top predators have on ecosystems are best understood by comparing areas where they are present with areas from which they have been removed. Numerous studies, in Australia and globally, have demonstrated that when top-order predators no longer exist in the environment, mesopredators can increase in numbers and negatively impact populations of their smaller prey species (Ritchie & Johnson 2009).

The Role of Dingoes in Australian ecosystems

In the last 5 years, there have been a number of studies published in reputable peer-reviewed journals which argue that dingoes fulfil an important functional role in Australian ecosystems by killing and thereby reducing the abundances and impacts of mesopredators such as foxes and the feral Cat (*Felis catus*) and feral and native herbivores such as kangaroos; these include Johnson and Van Der Wal (2009), Wallach *et al.* (2010), Glen and Dickman (2011), Letnic *et al.* (2009), Letnic and Dworjanyn (2011), Moseby *et al.* (2012), Kennedy *et al.* (2012) and Brook *et al.* (2012). There is also evidence that dingoes have suppressive effects on feral herbivores with adult body sizes <150 kg such as the feral Goat (*Capra hircus*), deer and Pig (*Sus scrofa*) (Newsome 1990; Letnic *et al.* 2012).

In a review of studies conducted to date on the ecological impacts of dingoes, Letnic *et al.* (2012) found the effects of dingoes on other species scale with their body size. Large species (>5 kg) subject to direct predation by dingoes tend to be suppressed by dingoes, whilst small species (<5 kg) tend to benefit from the presence of dingoes, owing to their suppressive effects on foxes. Across Australia, the loss of dingoes has been linked to the irruption of foxes, widespread losses of small and medium-sized native mammals, the depletion of plant biomass due to the effects of irrupting herbivore populations and increased predation rates by foxes (Johnson *et al.* 2007; Letnic *et al.* 2012).

Whilst the larger portion of the research on the ecological function of dingoes has focused on arid regions of Australia, there is evidence relating to their effects on the abundances of macropods and foxes in eastern Australia. For example, Robertshaw and Harden (1986) working in the forests of north-eastern NSW showed that numbers of Swamp Wallaby and red-necked wallaby were greater in areas subject to dingo control than in areas where dingoes were not controlled. Similarly, Newsome *et al.* (1983a) working in the forests and heaths of south-eastern NSW found that Eastern Grey Kangaroo (*Macropus giganteus*) numbers declined with increasing dingo activity. Johnson and Van Der Wal (2009) and Letnic *et al.* (2011) reported negative relationships between indices of dingoes and fox abundance in eastern NSW and at a continental scale, respectively. In forested environments of eastern Australia, there is evidence also that dingoes exclude foxes and cats at a microhabitat scale (Mitchell & Banks 2005; Wang & Fisher 2012).

Although most research from south-eastern Australia on the effects of dingoes has examined their direct suppressive effects on foxes and macropods, it is likely that they also generate strong indirect effects, as has been observed in the more arid parts of the continent. Glen *et al.* (2011), working in the Barrington Tops, found that high numbers of the Tiger Quoll (*Dasyurus maculatus*) were associated with low fox numbers and suggested that dingoes may benefit quolls by suppressing fox numbers.

The notion that dingoes provide prey species in eastern Australia with refuge from predation by suppressing fox numbers is supported by continental scale analyses of rodent and marsupial distributions by Smith and Quin (1996) and Johnson *et al.* (2007), respectively. These studies showed that the persistence of extant indigenous rodents and marsupials is associated with the presence of dingoes and the absence or low abundance of foxes (Smith & Quin 1996; Johnson *et al.* 2007). In NSW, Victoria and southern Queensland, hot spots for native rodents and medium-sized marsupials occur in the Great Dividing Range and coastal regions where dingoes remain common (Smith & Quin 1996; Johnson *et al.* 2007).

Questions are frequently raised regarding the impacts that dingoes have on native species of conservation concern (Fleming *et al.* 2012). Dingoes certainly prey on native species weighing <5 kg, including some threatened species (Claridge *et al.* 2010) and thus like other native predators may well have a direct effect on their populations. However, the fact that dingoes have coexisted with other extant Australian animals for at least 3500 years suggests that dingo predation alone is unlikely to pose a major threat to any extant species, with the possible exception of already critically endangered prey species within the optimal size range for dingoes such as the northern Hairy-nosed Wombat (*Lasiorhinus krefftii*) (Letnic *et al.* 2012). Indeed, recent experimental evidence suggests that prey species weighing <5 kg can benefit from the presence of dingoes. This can occur when the prey species' rate of population increase exceeds the sum of the rate of predation by both the large predator and mesopredator. This criterion is likely to be met if the prey species is more vulnerable to predation by the mesopredator, and the top predator limits the rate of killing by the mesopredator (Ritchie & Johnson 2009). In Australian ecosystems, this occurs because foxes tend to occur at higher densities than dingoes and also because foxes are more efficient predators of small and medium-sized prey than dingoes (Claridge *et al.* 2010; Johnson & Ritchie 2012).

It is likely that the interactions of top-order predators only become ecologically effective above a certain threshold population density (Letnic *et al.* 2011). This may occur because the effects of predators on their prey/competitors will to a degree be determined by the frequency of their encounters with a predator. For example, in the case of dingo interactions with foxes, presumably, there is a threshold population density of dingoes above which dingoes exert strong impacts on fox populations with positive flow-on effects for fox prey (Letnic *et al.* 2011). Determining these thresholds will be a critical issue for conservation managers aiming to maintain or restore ecosystems with effective densities of top-order predators.

With increasing realization that dingoes can function as a keystone species, ecologists have expressed growing interest in utilizing their effects on other species as a means of managing ecological processes (Johnson *et al.* 2007; Dickman *et al.* 2009; Dexter *et al.* 2012; Choquenot & Forsyth 2013). For example, using dingoes to suppress fox numbers is likely to be a more effective strategy for managing fox impacts across large, remote areas than distributing poison baits (Letnic *et al.* 2011). This is because poison baiting programmes require ongoing funding and must be conducted intensively to achieve effective fox suppression. However, because dingoes can have adverse impact on livestock producers, such programmes clearly would have to be balanced with the needs of agriculture and would require the implementation of diverse strategies to minimize the impacts of dingoes on livestock such as barrier fencing, the creation of dingo-free buffer zones and the use of livestock-guardian animals (van Bommel & Johnson 2012; Letnic *et al.* 2012). The development of dingo management strategies that allow for both harnessing of their ecological effects and protection of livestock is a major challenge facing biodiversity managers in Australia today (Ritchie *et al.* 2012).

Conclusion

There is a large body of peer-reviewed literature both within Australia and internationally that demonstrates the importance of top-down trophic regulation and the keystone role that large carnivores, such as the dingo, can play in sustaining functional ecosystems. Dingoes tend to have a net positive effect on biodiversity through their suppressive effects on foxes and introduced and native herbivores. These effects of dingoes have the potential to be harnessed as passive tools to assist biodiversity conservation through the maintenance of ecologically functional dingo populations. However, research is required to facilitate the development of dingo management strategies that allow for both the preservation of dingoes and protection of livestock.

There are some who argue that there has been insufficient research in the forests and coastal landscapes of Australia to definitively prove the ecological functional role of dingoes (Fleming *et al.* 2012). Taking into consideration the scientific literature and the call by Estes *et al.* (2011) to presume that apex predators exert strong trophic cascades unless proven otherwise, we argue that the onus of proof should be to prove that dingoes do not fulfil an ecological functional role rather than having to prove that they do.

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