Ecological role of large mammalian predators in south-east Australia

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Abstract
Large mammalian predators (Dingo/Dog, Tasmanian Devil, Red Fox, Cat) play a major ecological role in south-east Australia as informed by experience with predator exclosures. Excluding Dogs, Red Foxes and Cats collectively causes increased mammalian herbivore pressure on vegetation with adverse effects on biodiversity. The exclosures indicate that large mammalian predators normally limit their prey, thereby protecting edible plants and their dependent species. Control of these predators should be generally avoided in native vegetation or undertaken to assist threatened fauna with caution due to potential habitat damage. (*The Victorian Naturalist*, **136** (1), 2019, 29–40)

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Introduction

Ecosystems are influenced or shaped by predators. Food webs (trophic structures) and predator-prey population dynamics are varied, complex and central to ecosystem function. Each animal species has an evolved trophic strategy consisting of many adaptations to its predators and food sources. Top predators can limit populations of smaller mesopredators, preventing them from overconsuming their small prey. Predators can also limit herbivores, preventing the overconsumption of plants and vegetation that support overall biodiversity (Hairston *et al.* 1960, Estes *et al.* 2011, Ripple *et al.* 2014).

Trophic imbalance occurs when one trophic level becomes disproportionately large or small, causing adverse trophic cascade effects in adjacent levels, including loss of species and disrupted ecosystem function (see Terborgh and Estes 2010). It may be temporary or chronic and starts when a key population experiences (a) significant change in bottom-up control—food supply, or (b) significant change in top-down control—predator pressure. Trophic imbalance can be catastrophic when herbivores without predators irrupt, destroying vegetation and depriving themselves and many other species of food and habitat.

In line with a global pattern, mammalian carnivores include major ground-dwelling predators in Australia (Glen and Dickman 2014). Their depletion or loss, which usually results from human activity, may cause an

- increase in number or change in behaviour of smaller predators—mesopredator release, with adverse impacts on small fauna, for example, Red Fox without Dingo (Letnic *et al.* 2009), Cat without Dingo (Johnson 2015), Cat without Red Fox (Risbey *et al.* 2000; Robley *et al.* 2004; Molsher *et al.* 2017);
- increase in number or change in behaviour of herbivores—herbivore release, with adverse impacts on flora and fauna (Cheal 1986; Coulson 1988, 2001, 2007; de Munk 1999; Coates 2008; Carr *et al.* 2010; Dexter *et al.* 2013; Yugovic 2015, 2016; Lindenmayer *et al.* 2018).

Many of the 18 native and eight human-introduced (alien/novel) mammalian herbivores in south-east Australia increase in number when mammalian predator pressure is relaxed (Yugovic 2015, 2016). Herbivore release becomes herbivore imbalance (overabundance) when site flora or fauna are lost to these herbivores, directly through consumption of plants or indirectly through habitat alteration. The role of large mammalian predators in limiting these herbivores is informed by evidence from predator exclosures.

Large mammalian predators are defined here as the Dingo/Dog, Tasmanian Devil, Red Fox and Cat in order of weight. Quolls, Short-beaked Echidnas and Platypus are medium-size, while Water Rats, rats, Brush-tailed Phascogales, microbats, dunnarts and antechinuses are small predators. Medium and small mammalian predators may also limit herbivores including invertebrates, but we have only exclosure evidence for large mammals. Scientific names of flora and fauna are in Appendix 1.

South-east Australia, as defined here, is the eastern Bassian biogeographic province (Ebach 2017), comprising areas receiving above about 500 mm rainfall including the temperate areas of south-east South Australia, much of Victoria, south-east New South Wales and Tasmania.

Predator exclosures

Predator exclosures are predator-proof fenced areas that exclude Dogs, Red Foxes and Cats in order to protect native fauna from these predators, sometimes with considerable success (Fig. 1). The protected fauna either pre-existed on the site or were deliberately reintroduced or introduced. The exclosures are run by government agencies, a university and one commercial business (Table 1). The first exclosure, Warrawong in the Mount Lofty Ranges, peaked at 34 ha and was finally 11 ha in area; it began operation in 1969 and closed in 2013. The first existing large exclosure, within Woodlands Historic Park, commenced in 1987.

The exclosures are of sufficient size (mean = 260 ha, range = 30–485 ha) to evaluate the effects of resident herbivores. Most (7/8) of the large (≥30 ha) existing predator exclosures in the region have experienced herbivore imbalance. The exception is Hamilton Community Parklands where herbivores have been controlled from the outset. A new exclosure at Tiverton near Mortlake is being prepared and it is too early to detect effects; in any case herbivores will be controlled or eliminated. The exclosures in relation to their surroundings provide an informal replicated experiment on the effects of herbivores under reduced predator pressure (n = 7).

Direct observations at two sites (Cranbourne Gardens, The Briars) and/or discussions with site managers or experts (all sites), along with the known distribution of novel predators and inferences made by comparisons with surrounding areas at present and prior to the exclosure, confirmed that

- Aboriginal predation had ceased and the novel mammalian predator Dingo had been eradicated;
- novel mammalian predators (Dog, Red Fox, Cat in various densities) were the major ground predators;
- native and novel mammalian herbivores were the major plant consumers;
- vegetation and fauna habitats were relatively stable with generally healthy tree canopies.

Exclosures exclude or attempt to exclude ground predators only. In practice they are not always fully successful due to open gates and/or recurrent breaches in fences, sometimes resulting in low rather than zero predator density. Native diurnal and nocturnal aerial predators still have access.

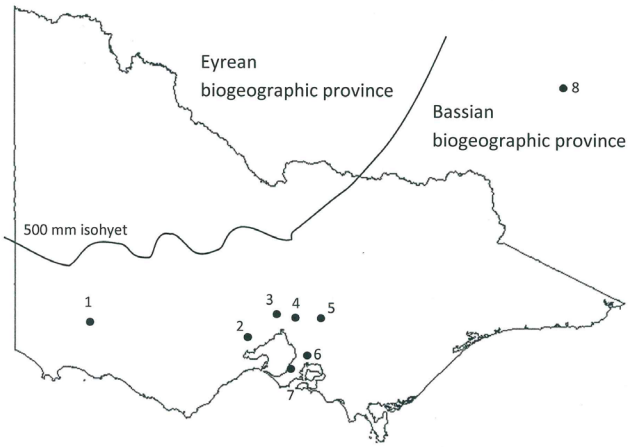

Fig. 1. Predator exclosures ≥30 ha: 1 Hamilton Community Parklands, 2 Mt Rothwell, 3 Woodlands Historic Park, 4 La Trobe Wildlife Sanctuary, 5 Coranderrk Bushland Reserve, 6 Cranbourne Gardens, 7 The Briars Wildlife Sanctuary, 8 Mulligans Flat Woodland Sanctuary.

Table 1. Predator exclosures and herbivore damage

Exclosure management ecological vegetation class	Herbivore[1,2]	Herbivore damage[3]
Mulligans Flat Woodland Sanctuary Gungahlin 485 ha ACT government *Grassy Woodland*	Eastern Grey Kangaroo Red-necked Wallaby Black Wallaby	Before exclosure, severely grazed ground layer existed due to large kangaroo numbers (McIntyre *et al.* 2010); after exclosure wallabies contributed significantly to grazing pressure (S McIntyre, pers. comm., 2018)
Mt Rothwell Little River 420 ha Mt Rothwell Biodiversity Interpretation Centre *Hills Herb-rich Woodland*	Eastern Grey Kangaroo Red-necked Wallaby Black Wallaby Brush-tailed Rock-wallaby Rufous-bellied Pademelon Common Brushtail Possum European Rabbit	Tree canopy damage (while Red Box is relatively possum-resistant); severely grazed ground layer, particularly by rabbits in 2014 (not currently due to control).
Woodlands Historic Park (Back Paddock) Greenvale 400 ha Parks Victoria *Hills Herb-rich Woodland*	Eastern Grey Kangaroo Black Wallaby Common Brushtail Possum European Rabbit	Tree canopy damage and loss (River Red Gum); severely grazed ground layer, site extinction of reintroduced Eastern Barred Bandicoot due to loss of cover (reason for exclosure, since reintroduced) (Coulson 2001, 2007; D Gilmore, pers. comm., 2016; D de Angelis, pers. comm., 2018; author, pers. obs. 2018), Fig. 2.
Cranbourne Gardens Cranbourne 250 ha Royal Botanic Gardens Victoria *Heathy Woodland* *Grassy Woodland*	Eastern Grey Kangaroo Black Wallaby Common Wombat Common Brushtail Possum Eastern Ringtail Possum Swamp Rat European Rabbit	Tree canopy damage (Narrow-leaf Peppermint, Silver-leaf Stringybark, one large tree saved by possum band); severely browsed shrub layer; heavily grazed ground layer. Wombat gates are kept open to release excess wallabies but this allows in more foxes, which has resulted in severe decline in Southern Brown Bandicoot (reason for exclosure) as wallabies have eaten their shelter (Yugovic 2016; author, pers. obs., 2018).
Coranderrk Bushland Reserve Badger Creek 142 ha Zoos Victoria *Grassy Forest* *Riparian Forest*	Eastern Grey Kangaroo Black Wallaby Common Wombat Common Brushtail Possum Eastern Ringtail Possum Swamp Rat European Rabbit	Tree canopy damage and loss (Narrow-leaf Peppermint); severely browsed shrub layer (except for relatively resistant Yarra Burgan which is overabundant due to reduced competition and now reducing diversity); heavily grazed ground layer (de Munk 1999, Carr *et al.* 2010; author, pers. obs., 2017).
The Briars Wildlife Sanctuary Mount Martha 95 ha Mornington Peninsula Shire *Grassy Woodland*	Eastern Grey Kangaroo Black Wallaby Common Brushtail Possum Eastern Ringtail Possum Swamp Rat European Rabbit	Tree canopy damage and loss (Narrow-leaf Peppermint, Swamp Gum, Snow Gum, while Manna Gum has possum sensitive and resistant forms as elsewhere, several large trees saved by possum bands); heavily grazed ground layer, orchid loss (author, pers. obs., 2018), Fig. 3.
La Trobe Wildlife Sanctuary Bundoora 30 ha La Trobe University *Plains Grassy Woodland*	Eastern Grey Kangaroo Common Brushtail Possum	Tree canopy damage (River Red Gum, both large trees saved by possum bands), severely grazed ground layer, endangered natural Matted Flax-lily suppressed and unable to flower (author, pers. obs., 2014).

1. Primarily herbivorous Common Brushtail Possum is included.
2. Herbivore has contributed to herbivore pressure, not necessarily currently due to control.
3. Damage has occurred, based on written accounts, discussions with managers or experts (all sites) and personal observations.

Fig. 2. River Red Gum defoliated by Common Brushtail Possums, Woodlands Historic Park, Greenvale, June 2018.

Fig. 3. Manna Gum woodland canopy killed by Eastern Ringtail Possums; possum-resistant form of Manna Gum in background, The Briars Wildlife Sanctuary, Mount Martha, May 2018.

The results of the exclosures (summarised in Table 1) are generally increased mammalian herbivory with a syndrome of negative trophic cascade effects which, depending on site characteristics and site herbivores and their level of control by management, may include:

- increase in native and novel grazers (e.g. kangaroos, wombats, rabbits);
- increase in native browsers (wallabies, possums);
- loss of herbivore condition and sometimes death by starvation;
- loss of trees depending on species;
- loss of shrubs;
- loss of ground layer vegetation, including orchids to digging rats;
- loss of ground cover habitat for fauna, including bandicoots;
- increase in establishment of introduced weeds (novel plants), leading to weed dominance of vegetation;
- increase in soil erosion on slopes.

These effects characterise a predator loss ecological dysfunction syndrome.

Such significant shifts have not been seen or reported from outside the exclosures. Mulligans Flat underwent little or no shift inside the fence as kangaroos were already abundant before the exclosure: 'Biomass estimates indicated extremely high grazing pressure, sufficient to negatively affect the habitat quality for ground-dependent fauna and some soil processes' (McIntyre *et al*. 2010: 329). Ongoing management of kangaroo populations enabled two levels of grazing pressure to be maintained experimentally after the removal of foxes (McIntyre *et al.* 2014). However, the increase in wallaby populations combined with the drought after 2011 has made grazing pressure difficult to control until impediments to wallaby management are overcome (S McIntyre, pers. comm., 2018).

The type of impact depends on the herbivore, with possums becoming markedly more ground-active and frequently damaging or killing trees, and all herbivores inhibiting canopy tree seedling recruitment. The severity of impact is determined by herbivore density in relation to edible vegetation, this density being influenced by factors such as physical shelter, available water, weather events and management control actions.

Discussion

Experience with predator exclosures

Predator exclosures may provide important backup populations of threatened fauna, opportunities to see rare species, and opportunities to research trophic cascades through manipulation experiments.

In order to prevent herbivore damage to the habitat of the protected mammal species and site ecosystem, corrective actions have been carried out, attempted or are proposed at all sites, including culling, sterilisation, reintroduction of native predators and possum (protective) banding of trees. Whether they work or not, these measures are not practicable outside exclosures in the broader landscape. Although these exclosure-specific issues are locally important, it is the knowledge that herbivore imbalance is a chronic problem in exclosures, and what this implies about the rest of the region, that is of interest here.

Before they were established, the exclosure sites had lost their predator-naive fauna and their herbivore and vegetation levels were relatively stable under novel predator pressure. The systems appeared to be in dynamic equilibrium. Possum-sensitive eucalypt canopies were generally healthy as evidenced by the existence of many large trees that were later killed within the exclosures—they could not have survived and grown to those sizes with possum overbrowsing. Canopy trees were often regenerating after the withdrawal of livestock grazing. Kangaroos were in moderate densities except for peri-urban areas with local Dog regulations. The contributions from the Dog, Red Fox and Cat in providing that essential background predator pressure would have varied with site characteristics and herbivores present.

The evidence from the predator exclosures indicates that the loss of mammalian ground predators causes trophic imbalance—an ecological dysfunction caused by a drop in system predator pressure (Table 1). Herbivore populations without predators generally increase to unsustainable levels resulting in the loss of food and habitat for themselves and other species (Forsyth and Cayley 2006). These sometimes catastrophic disruptions suggest that ecosystems with mammalian herbivores need corresponding mammalian predators for

stability and diversity, in line with a global pattern (see Terborgh and Estes 2010). A stable trophic relationship between the ecosystem mammals regardless of species appears to be necessary to maintain flora and fauna diversity over large areas.

The difference predators make is amply demonstrated by Woodlands Historic Park, which has an internal exclosure, the Back Paddock. Mature River Red Gum woodland occurs inside and outside the exclosure, allowing comparison. Inside the exclosure, the ongoing loss of mature and immature red gums to brushtail possums, ringbarking by rabbits, severe grazing by rabbits, kangaroos and wallabies, and accelerated soil erosion combine to make an ecological disaster. It will take centuries to get living large trees back, assuming any regrowth can survive the herbivores. There has been little or no eucalypt recruitment of any species since the exclosure was established. Of the existing trees, stands of Grey Box and scattered Yellow Box are mostly only lightly browsed while the red gum woodland is overbrowsed in general, indicating a possum preference for, and susceptibility of, River Red Gum. The 'predator landscape' outside the fence is obvious from its generally healthy mature trees, continuous canopy tree recruitment and higher ground layer plant cover. Occasional trees are overbrowsed, suggesting that foxes only barely control brushtail possums.

The exclosure experience implies that if the novel mammalian predators Dog, Red Fox and Cat were to suddenly disappear, vast areas of the mainland would look like the exclosures. There might be a plague of rabbits to start with. Eucalypt tree canopies would decline over large areas due to overbrowsing. Many lowland species would be at risk, including River Red Gum, Silver-leaf Stringybark, Yellow Gum, Yellow Box, Messmate Stringybark, Swamp Gum, Snow Gum and Narrow-leaf Peppermint. Some eucalypts, such as Southern Blue Gum and Coast Manna Gum, are resistant to possums but relished by Koalas, while Red Box is relatively resistant to vertebrate herbivores. Flora and fauna would be depleted or lost, ground layers would be stripped and erosion would accelerate. Recruitment of canopy trees would be rare or non-existent.

Whether the herbivores would eventually reach equilibrium with their new, devastated and predator-free landscape is hypothetical as such habitats do not exist outside exclosures in Australia. The situation would be unprecedented as predators have controlled these herbivores and their ancestors over evolutionary time. In North America, New Zealand, and elsewhere, the consequence of human-induced mammalian herbivore imbalance is loss of biodiversity (see Stolzenburg 2008; Ripple *et al.* 2010).

Apart from some accounts (Table 1), the exclosure experience is not well documented, for several reasons:

- most exclosures have little or no baseline ecological data. Exceptions include Mulligans Flat (e.g. McIntyre *et al.* 2010). The relevant variables to measure were (a) mammalian predator and herbivore density and biomass by species, and (b) plant cover and biomass by species and vegetation layer;
- there was no awareness that the site ecosystem was predator dependent;
- managers are seldom funded to monitor, document and publish the results of their work and, in any case, they or their employers may not wish to publicise their ecological dysfunctions or the consequential culling of mammalian herbivores, especially native species;
- there is a tendency to view each exclosure's imbalance problems as being unique when they are not.

Herbivores

Herbivores impose a herbivore regime consisting of various forms of plant biomass reduction. In deciding where to feed, they weigh the pain of hunger against the fear of predators—the herbivore prey dilemma.

Mammalian herbivores are vital for ecosystem stability and diversity in south-east Australia by controlling vegetation cover. Kangaroos limit grass cover and wallabies limit shrub cover, thus facilitating ground layer plant diversity (J Kirkpatrick, pers. comm., 2018). Swamp Rats eat the rhizomes of sedges with the potential for overdominance such as Sandhill Swordsedge and Thatch Saw-sedge (author, pers. obs., 2018).

However, several native and novel mammalian herbivores have become overabundant in free-range populations under reduced predator pressure. These include Eastern Grey Kangaroo, Western Grey Kangaroo, Black Wallaby, Koala, Common Brushtail Possum, Eastern Ringtail Possum and Swamp Rat (Yugovic 2015). For example, Koalas reintroduced to Cape Otway in 1981 without their predators (Aboriginal people and Dingoes) have killed their Manna Gum woodland food tree canopies and starved in large numbers, prompting euthanasia programs (e.g. Smith 2015).

While predator exclosures provide ecological insights, so do herbivore exclosures. For example, recovery of native vegetation inside kangaroo exclosures in Hattah-Kulkyne National Park has shown that large uncontrolled populations of Western Grey Kangaroo reduce biodiversity (Cheal 1986).

Without predators and with enough physical shelter, mammalian herbivores generally increase, sometimes exponentially as with kangaroos in Woodlands Historic Park (Coulson 2001), until culling is undertaken or declining food supply slows down breeding. With poor nutritional conditions kangaroos may cease to breed (Poole 1983). Female brushtail possums may produce one litter per year instead of two (Menkhorst 1995), which may explain why mass deaths of possums are not seen. However, the larger population, compounded by the longer life expectancy of each animal, is by then already causing chronic damage. With preferred food plants in decline, the hungry herbivores may switch to less preferred species and maintain a population size that prevents recruitment of preferred food species, including canopy trees.

Livestock grazing is a managed herbivore imbalance in favour of the livestock. Many native flora and fauna species have been depleted or lost to sheep grazing in particular (e.g. Kirkpatrick and Bridle 2007). Most (6/8) of the exclosure sites were previously grazed by sheep and their sheep-sensitive flora are likely to have been depleted or lost before the exclosures were established. The herbivore impacts we see in the exclosures today reflect similarities and differences between the native and novel herbivores. For example, kangaroos severely graze the ground layer as did the sheep but, although sheep prevented tree seedling recruitment, they could not climb the trees and defoliate them like possums.

Some areas naturally lack native mammalian herbivores and corresponding mammalian predators. Subalpine Snow Gum woodland does not support Koalas or possums, partly due to a tendency for Snow Gum not to form tree hollows large enough for possums at such high elevations and for snow cover to inhibit animal movement (J Morgan, pers. comm., 2018; I Mansergh, pers. comm., 2018). Areas above the tree line—alpine areas—have no native mammalian herbivores, even Common Wombats, and so have an unusual ecology shared with lakes, swamps and coastal islands in the lowlands. However, damaging novel megaherbivores, Horse and Sambar Deer, are seasonally present in the high country.

Impacts of predators

It is widely accepted that the Red Fox and Cat have a major detrimental impact on the Australian fauna at the continental level (Dickman 1996; Woinarski *et al.* 2015). However this appears to be less so in the high rainfall southeast, possibly because the generally denser vegetation provides better protection from predators.

Most fauna of the eastern Bassian biogeographic province have survived the transition to novel predators (DELWP 2018), predator-adapted species that can coexist with the new predators without being dependent on conservation management. The replacement predators came with a cost. The Dingo probably wiped out the Thylacine and Tasmanian Devil and possibly the flightless Tasmanian Native Hen on the mainland (Johnson 2015). Similarly, the Red Fox may have eliminated the Rufous-bellied Pademelon, Southern Bettong and Eastern Barred Bandicoot, as evidenced by their presence in Tasmania, which has no foxes. The Cat is not known to have caused an extinction; however, it spreads disease toxoplasmosis to native mammals (Brunner *et al.* 1981). Some conservation dependent evolutionarily naive species also have populations that are significantly more suppressed now than they were by the native predators.

A global review of predator-prey manipulation experiments found alien predators to be more harmful to prey populations than native predators, and they 'can impose more intense suppression on remnant populations of native species and hold them further from their predator-free densities than do native predators preying upon coexisting prey' (Salo *et al.* 2007). This is presumably so in many cases, but the original full predator suite of south-east Australia is not there to compare, and the only cases included from south-east Australia are Bush Rat, which doesn't increase with fox control (Banks 1999), and Eastern Grey Kangaroo, which does (Banks *et al.* 2000). Neither prey species is threatened, and kangaroos actually require predator control as shown by their overabundance within predator exclosures.

The numbers of native wildlife taken by Red Foxes and/or Cats are large but difficult to estimate (RMIT ABC 2014). These numbers should be compared with estimated numbers of prey taken by native predators before the arrival of the Red Fox and Cat to make sense. Eastern Quolls were 'one of the commonest of all the bush animals' in the Melbourne area in the 1850s (Wheelwright 1861) and were presumably eating large numbers of prey such as native rats. Regardless of the actual number, most progeny of herbivores must succumb to some form of early mortality or there would be a vast overabundance of herbivores. Consider that an average female ringtail possum produces some 10 progeny during her lifetime based on average longevity, litter size and litter frequency (see Menkhorst 1995); in a stable population an average of only two offspring survive to maturity. Similarly, a Swamp Rat produces some 20 progeny of which 18 die young in a stable ecosystem.

Few herbivores survive their predators. Even if they make it to maturity, they may be picked off later when old and weak. As visibly starved individuals or carcasses of most prey species are seldom seen in free-range populations exposed to predators, it would appear that starvation is not usually a major cause of mortality. Predation is a natural process so the numbers of wildlife taken by predators are not necessarily alarming from an ecological perspective, since the removal of excess animals is essential in stable ecosystems. What matters more is the population size of any threatened native fauna.

Tasmania

If the Dingo were to establish in Tasmania it could eliminate the evolutionarily naive Tasmanian Devil as it evidently has on the mainland (Johnson 2015). Similarly, if the Red Fox were to establish it could eliminate the Rufous-bellied Pademelon, Southern Bettong and Eastern Barred Bandicoot, which would also be disastrous. In any case, devils appear able to eliminate foxes by entering fox dens and eating the cubs (DoEE 2017).

Herbivores are not often seen as a conservation problem in Tasmania, an exception being Maria Island (DPIPWE 2017a). This may be due to a level of control by marsupial predators and Cats experiencing mesopredator release without the Thylacine, supplemented by human culling of marsupial herbivores and rabbits. However, Common Brushtail Possums cause or worsen tree decline in eastern Tasmania (RPDC 2003) and grazing by cattle, sheep and sometimes macropods threatens many flora (DPIPWE 2017b, 2018a).

Mammalian herbivores were once primarily controlled by Aboriginal people, Thylacines, devils and quolls. Tasmania is now effectively a large predator exclosure in which predation by humans and Thylacines has ceased. Humans legally cull large numbers of herbivores in primary production areas (DPIPWE 2018b), which is a form of surrogate predator pressure. Devils and quolls are important predators but, even before the emergence of devil facial tumour disease, their predation was apparently insufficient as there was significant tree decline. As the staple diet of Cats is usually rabbit (DPIPWE 2013), Cats may assist in limiting the herbivore regime.

The herbivore regime in Tasmania compared to the mainland has not been studied, but high macropod levels and heavy herbivore pressure on vegetation have been noted by ecologists (e.g. D Gilmore, pers. comm., 2016; M Dell, pers. comm., 2018). This may be a Thylacine legacy effect. The trophic ecology model predicts that if a top predator is removed there are trophic cascade effects. The balance between the herbivores and vegetation may shift unless

mesopredators increase to maintain system predator pressure, which appears to have happened to some extent in Tasmania.

There are no predator exclosures in Tasmania that would elucidate the role of the existing predators. However, on Maria Island, intense grazing from macropods introduced in the 1960s has degraded habitats, despite the presence of Cats. Devils, first introduced in 2012, are likely to be impacting on the recruitment of all marsupial herbivore populations and the annual culling of macropods has been suspended (DPIPWE 2017a).

The Dingo appears to be a mainland ecological analogue of the Thylacine, and the Red Fox an analogue of the Tasmanian Devil. Just as the Tasmanian Devil could coexist with the Thylacine, the Red Fox can survive with the Dingo. Where Dingo/Dogs and Thylacines are missing kangaroos become overabundant. The fox and devil have limited effect on kangaroos, which justifies culling them where Dingo/Dogs and Thylacines are missing. The fox and devil are ecologically similar opportunistic predators and scavengers with key differences. The larger devil is more adapted to large prey/carcasses by having different jaw musculature, bone structure and teeth. The devil may eliminate the fox but may not survive the Dingo, which could rule out its reintroduction to most of the mainland. The fox has several sensitive prey species but may be better at controlling brushtail possums.

Role of predators

Predators impose a predator regime consisting of various forms of prey biomass reduction, lowering prey numbers and a 'landscape of fear' that affects prey behaviour (Laundré *et al.* 2010). The predator loss syndrome indicates that predation is a primary form of mammalian herbivore population control in south-east Australia, consistent with a global pattern (see Terborgh and Estes 2010).

Humans are, or once were, the ultimate mammalian predator. Aboriginal people preyed on Dingoes (Johnson 2015), rendering them mesopredators. Aboriginal hunting, supported by the Dingo and a range of native predators, is likely to have once controlled many herbivore populations in Australia. We have no reports by early Europeans of mammalian overpopulation or mammal-induced vegetation loss such as stripped ground layers or dead tree canopies. There may have been a predator-prey balance between the Humans, Dingoes and native predators and the herbivores which, along with Aboriginal mosaic burning, could account for the large trees and rich biodiversity described by early Europeans (see Hateley 2010). Predation by Humans (for food) has all but ceased, but culling of certain herbivores, mainly rabbits and kangaroos, occurs in some areas.

Part of a global pattern of large mammalian predator loss in regions occupied by people (Wolf and Ripple 2017), the large native mammalian predators of south-east Australia are extinct or their ranges have contracted. The Marsupial Lion is long gone. Europeans sent the largest remaining carnivore, the Thylacine, extinct through the bounty system and habitat loss (Paddle 2000) and are responsible for several smaller predator declines. Reasons vary with species and include hunting, burning, poisoning, habitat loss and alteration, disease (Eastern Quoll), roadkill, and competition with and predation by novel predators. Much of the mammalian predator pressure is now exerted by novel predators, robust species that can survive or even thrive with or near humans.

The negative effects of predator exclusion indicate a widespread positive influence of novel predators in many contemporary bushland ecosystems. Rather than being pest animals with no redeeming features, they appear to provide an ecosystem service by limiting herbivores in these novel ecosystems. The canids (Dingo, Dingo-Dog, Dog, Red Fox) are important in regulating ecosystems throughout the mainland, particularly by controlling the numbers and behaviour of macropods and brushtail possums, and possibly by preventing mesopredator release of the Cat. The only felid (Cat) may be the least important predator as it doesn't effectively control herbivores larger than rabbits. Continual canid and felid predator pressure on herbivores is pervasive but not always obvious except when it is removed and systems are damaged by excess herbivory.

A general lack of awareness of the secondary ecosystem effects of predator exclusion may have extended the life of an antipredator management paradigm. It is evidently not a good

idea to remove all mammalian ground predators, particularly foxes, where predator pressure from Humans, Dingoes, quolls and goannas is missing. Furthermore, there is evidence that foxes suppress Cats, which benefits small native fauna (e.g. Risbey *et al.* 2000). Fox control is either non-existent or is generally temporary, localised or ineffective in areas where Dingoes and native predators are locally extinct, otherwise the result could be catastrophic.

The exclosures, for example, demonstrate that foxes often protect tree canopies from possums. A long-term study of the Red Fox diet in southeast Australia found that it consists largely of insects, rats, rabbits, possums and plant material (Davis *et al.* 2015). Overall frequencies of native fauna of listed conservation significance in fox scats were generally <0.2% except for Broad-toothed Rat which was 1.5%, with higher frequencies in some regions. Brushtail and ringtail possums had a combined frequency of 13% with up to 35% in West and South Gippsland. These observations and data suggest that mature eucalypt woodlands, having hollows for brushtail possums (and many other fauna), depend on foxes to prevent canopy destruction by excessive resident possums. The Red Fox is a surrogate top predator performing a keystone predator role similar to that of the previous Dingo, and before then the Thylacine and Tasmanian Devil, and now it protects the trees from possums. There is no redundancy in these fox-dependent ecosystems as there are no practicable alternatives to the Red Fox.

The positive role of foxes in ecosystems has been seldom researched but is sometimes accidentally discovered. At Jervis Bay, for example, intensive fox control allowed a tenfold increase in Black Wallabies, which are eating out the understorey except for unpalatable Austral Bracken. The forest habitat may be transformed into 'a low diversity bracken fern parkland… through a trophic cascade, similar to that caused by overabundant deer in the northern hemisphere' (Dexter *et al.* 2013: 1). This fox control program also caused a collapse in mammal fauna that apparently included the Greater Glider (Lindenmayer *et al.* 2018).

The predator loss syndrome indicates that control of large mammalian predators, particularly the Red Fox where it is surrogate top predator in lieu of the Human and Dingo, should be generally avoided in native vegetation where possible, or undertaken to assist threatened fauna with caution due to the potential for trophic imbalance leading to habitat damage and depletion or loss of flora and fauna. Control should be accompanied by monitoring of mammalian herbivore pressure, vegetation structure, sensitive species and habitat conditions.

Where there are no mammalian herbivores, fox control may have no negative impacts and can be beneficial. For example on Middle Island, close to the mainland at Warrnambool, fox deterrence using Maremma dogs is assisting nesting Little Penguins (Wallis *et al.* 2017). The penguin colony appears to have established after potential predation by Aboriginal people and Dingoes had ended in the area.

There are strong ethical, scientific and cultural reasons for enhancing the currently persisting intact Dingo populations in Victoria where contiguous national parks are over one million hectares in area, notably in semiarid and mountainous areas. While legally protected in remote eastern Victoria, the current widespread persecution should be replaced by better protection (I Mansergh, pers. comm., 2018).

Where there is no mammalian herbivore imbalance, which applies to much of the Bassian region, it is likely due to herbivore-resistant vegetation, the absence of particular herbivores, or a trophic status quo operating effectively with the existing mammalian predators and prey (until an exclosure is created). Novel megaherbivores Horse and Sambar Deer, without megapredators, are overabundant and causing enormous damage. In more remote areas, the novel predators may compete with the remaining native predators, but they all operate in the essential regulation of their mammalian herbivore prey.

For more information:
When predators go missing—rise of the herbivores: native mammalian herbivore imbalance and the predator-prey ecology of southeast Australia (February 2019). <www.spiffa.org/do-ecosystems-need-top-predators>

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Appendix 1. Scientific names of flora and fauna

Flora	
Austral Bracken	*Pteridium esculentum*
Coast Manna Gum	*Eucalyptus viminalis* subsp. *pryoriana*
Grey Box	*E. microcarpa*
Manna Gum	*E. viminalis*
Matted Flax-lily	*Dianella amoena*
Messmate Stringybark	*E. obliqua*
Narrow-leaf Peppermint	*E. radiata*
Red Box	*E. polyanthemos*
River Red Gum	*E. camaldulensis*
Sandhill Sword-sedge	*Lepidosperma concavum*
Silver-leaf Stringybark	*E. cephalocarpa*
Snow Gum	*E. pauciflora*
Southern Blue Gum	*E. globulus* subsp. *globulus*
Swamp Gum	*E. ovata*
Thatch Saw-sedge	*Gahnia radula*
Yarra Burgan	*Kunzea leptospermoides*
Yellow Box	*E. melliodora*
Fauna	
antechinuses	*Antechinus agilis*, *A. flavipes, A. minimus*, *A. stuartii*, *A. swainsonii*
bandicoots	*Isoodon obesulus*, *Perameles gunnii*
Black Wallaby	*Wallabia bicolor*
Brush-tailed Phascogale	*Phascogale tapoatafa*
Brush-tailed Rock-wallaby	*Petrogale penicillata*
Bush Rat	*Rattus fuscipes*
Cat	*Felis catus*
Common Brushtail Possum	*Trichosurus vulpecula*
Common Wombat	*Vombatus ursinus*

Fauna cont.	
Dingo	*Canis lupus dingo*
Dog	*Canis lupus familiaris*
dunnarts	*Sminthopsis crassicaudata* *S. leucopus*, *S. murina*
Eastern Barred Bandicoot	*Perameles gunnii*
Eastern Grey Kangaroo	*Macropus giganteus*
Eastern Quoll	*Dasyurus viverrinus*
Eastern Ringtail Possum	*Pseudocheirus peregrinus*
European Hare	*Lepus europaeaus*
European Rabbit	*Oryctolagus cuniculus*
goannas	*Varanus gouldii*, *V. rosenbergi*, *V. varius*
Greater Glider	*Petauroides volans*
Horse	*Equus caballus*
Koala	*Phascolarctos cinereus*
Little Penguin	*Eudyptula minor*
Marsupial Lion	*Thylacoleo carnifex*
microbats	various small insectivorous bats
Platypus	*Ornithorhynchus anatinus*
rats	*Rattus fuscipes*, *R. norvegicus*, *R. rattus*
Red Fox	*Vulpes vulpes*
Red-necked Wallaby	*Macropus rufogriseus*
Rufous-bellied Pademelon	*Thylogale billardierii*
Sambar Deer	*Cervus unicolor*
Short-beaked Echidna	*Tachyglossus aculeatus*
Southern Bettong	*Bettongia gaimardi*
Spot-tailed Quoll	*Dasyurus maculatus*
Swamp Rat	*Rattus lutreolus*
Tasmanian Native Hen	*Tribonyx mortierii*
Thylacine	*Thylacinus cynocephalus*
Water Rat	*Hydromys chrysogaster*