Alien vs Predator

Do ecosystems need top predators?
A review of native predator-prey imbalances in south-east Australia

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Do ecosystems need top predators?
A review of native predator-prey imbalances in south-east Australia with reference to tree decline on the Mornington Peninsula

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Note: This is an extended version of 'Do ecosystems need top predators? A review of native predator-prey imbalances in south-east Australia'. *The Victorian Naturalist* 132: 4–11, 2015.

Summary

The role of native top predators in regulating terrestrial ecosystems in south-east Australia is briefly reviewed. Examples of ecological imbalance associated with a lack of native predators and overabundant native herbivores are identified. The cases of tree canopy loss due to excessive browsing by Koala, Common Ringtail Possum and Common Brushtail Possum, and orchid losses due to Swamp Rat, are discussed. The widespread loss of native top predators has left two introduced mesopredators, the Red Fox and Cat, to regulate both native and introduced herbivores in many areas, where a predator-prey balance now operates extensively in novel ecosystems. However, being ground-based predators they are not efficient at controlling ringtail possums in dense vegetation, and without the top predator Dingo they may be ecologically released, increasing their impact on sensitive fauna. Management approaches to keeping a balance between predators and herbivores are outlined.

Introduction

Many ecosystems are influenced or shaped by apex or top predators. Large carnivores can control populations of smaller mesopredators and herbivores, preventing them from monopolising or destroying resources needed for overall biodiversity (see Stolzenburg 2008).

This review explores whether top predators play or previously played a role in regulating terrestrial ecosystems in south-east Australia by controlling mesopredators and herbivores.

It is suggested that exotic mesopredators have partly replaced the original top predators and mesopredators, and despite their drawbacks they continue the necessary ecological function of herbivore control. Where herbivores, native or introduced, are not controlled top-down by predators, they may be bottom-up controlled by starvation and ecosystems can collapse.

Predator ecology

The founder of modern predator ecology is Robert Paine who discovered the role of 'keystone species' (Paine 1969). Paine's concept states that an ecosystem may experience a dramatic shift if a keystone species such as a top predator is removed, even though that species was a small part of the ecosystem in terms of biomass. Paine proposed that herbivore levels in stable and diverse ecosystems are top-down controlled by 'keystone' predators.

Earlier, for over 40 years animal ecology had been dominated by Charles Elton who proposed the 'food chain' concept (Elton 1927). Elton proposed that herbivores were bottom-up controlled by food supply. In Elton's ecosystem, top predators are unnecessary tack ons.

Much research from around the world indicates that top-down predator control is widespread in maintaining ecosystem stability and diversity (Ripple *et al*. 2014).

In simplistic models of ecosystems, predators and their prey undergo regular predator-prey cycles. The predator-prey cycle is governed by a pair of differential equations, the Lotka–Volterra equations:

$$\frac{dx}{dt} = \alpha x - \beta xy \qquad \frac{dy}{dt} = \delta xy - \gamma y$$

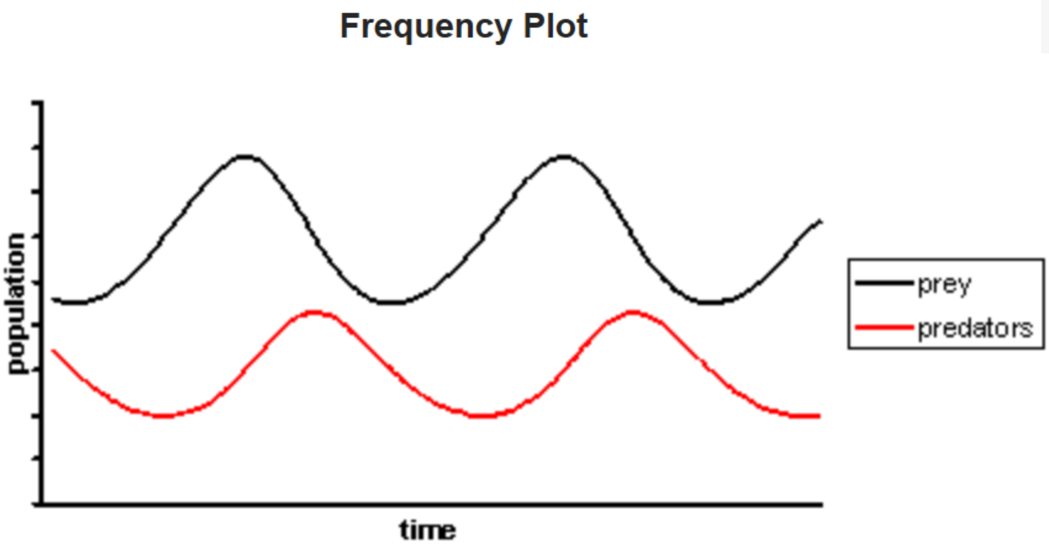

Figure 1. Predator-prey cycle

However the LV equations assume a one-predator-one-prey system, which is seldom the case, and also assume an unlimited food supply for the prey species. When the entire food supply is destroyed by the prey, such as when a tree canopy is eaten out, the cycle ceases and predator and prey populations both crash. This is highly relevant to ecological management.

Original top predators and mesopredators of south-east Australia

The original (pre-European) top terrestrial predators of south-east Australia include:

Table 1. Original major top predators of south-east Australia

Species	Status (Victoria, based on DSE 2013)
Thylacine *Thylacinus cynocephalus*	Extinct
Dingo *Canis lupus dingo* (?alien species) (Figure 2)	Fragmented, data deficient
Wedge-tailed Eagle *Aquila audax*	Widespread, secure
Peregrine Falcon *Falco peregrines*	Widespread, secure
Powerful Owl *Ninox strenua* (Figure 3)	Fragmented, vulnerable
Lace Monitor (Figure 4) *Varanus varius*	Fragmented, endangered

Figure 2. Dingo

Figure 3. Powerful Owl with a favourite prey item, Common Ringtail Possum

Figure 4. Lace Monitor

The original terrestrial mesopredators include:

Table 2. Original major mesopredators of south-east Australia

Species	Status (Victoria)
Spot-tailed Quoll *Dasyurus maculatus* (Figure 5)	Fragmented, endangered
Eastern Quoll *Dasyurus viverrinus* (Figure 6)	Regionally extinct (extant in Tasmania)
Western Quoll *Dasyurus geoffroii*	Regionally extinct (extant in WA where threatened)
Tasmanian Devil *Sarcophilus harrisii* (could now be considered a top predator)	Restricted to Tasmania where threatened
Laughing Kookaburra *Dacelo novaegineae* (Figure 7)	Widespread, secure

Figure 5. Spot-tailed Quoll, a predator of possums

Figure 6. Eastern Quoll, rat predator

Figure 7. Laughing Kookaburra

Original top predators and mesopredators of the Melbourne region

The fauna of the Melbourne region in the 1850s was documented by naturalist and hunter Horace William Wheelwright (1861). He spent most of his time on the northern Mornington Peninsula (Andrew et al. 1984) and described the larger carnivores as follows.

Dingo: ‘met with in all the thick forests, deeply-scrubbed gullies, in belts of timber bordering the large plains. . . throughout the whole country’. *Comment*: there are no truly wild dogs remaining in the Melbourne area, but domestic dogs now prey on wildlife.

Spot-tailed Quoll: ‘rather a rare animal. . . sparingly dispersed over the thick bush. . . They must be very destructive to the small game in the bush’. *Comment*: now extremely rare in most of its former Victorian range and extinct on the Mornington Peninsula, this quoll is fast and agile in trees, having feet adapted to climbing trees and raiding bird and possum nests.

Eastern Quoll: ‘one of the commonest of all the bush animals’. *Comment*: extinct on the Australian mainland, was presumably a major predator of native rats.

Powerful Owl: ‘by no means rare and seemed to remain in our forests throughout the year.’ *Comment*: feeds on arboreal marsupials, possums often are the staple diet especially Common Ringtail Possum, the owl population has been reduced and fragmented by loss of large hollow-bearing trees, now effectively absent in many areas but occurs in parts of the southern Mornington Peninsula.

Lace Monitor: ‘frequents gullies and ranges where the timber is high, and the localities wild and unfrequented.’ *Comment*: its varied diet includes Brushtail Possums and rats (Weavers 1989), extinct on the Mornington Peninsula.

Perhaps the ultimate predators were humans. Through hunting and also by imposing fire regimes (see Gammage 2011), Aborigines greatly influenced animal populations. In south-east Australia they traditionally hunted marsupial herbivores and wore brushtail possum skin cloaks (Figure 8). They may have preyed on dingoes as in Western Australia where the puppies were regarded as a delicacy although they were sometimes reared by the Aborigines for hunting (Meagher 1974). Early Europeans were also major predators of marsupials.

Figure 8. Victorian Aborigines, some still with brushtail possum skin cloaks (koogras), c. 1858

Long gone are the Pleistocene giant top carnivores *Thylacoleo*, *Megalania* and *Wonambi* and many of their large prey such as *Diprotodon*. After the extinction of much of the megafauna and later arrival of the Dingo, south-east Australia had a simplified food web which was then further modified by the arrival of Europeans with their introduced predators and herbivores.

Present day predators

Most of the native top terrestrial predators and mesopredators of south-east Australia are extinct or their populations are mostly fragmented and reduced.

The Dingo remains the top ground predator in remote eastern Victoria and adjacent New South Wales. However, due to persecution it is now absent from most of its former range which was throughout mainland Australia. Arriving several thousand years ago, the Dingo may have replaced the Thylacine on the Australian mainland. The Dog *Canis lupus familiaris* is widespread but there is no evidence of persistent feral populations (Menkhorst 1995) and they are subject to a government bounty which further decreases numbers.

Two introduced ground-based mesopredators are widespread and abundant in south-east Australia and in the effective absence of native top predators are surrogate top predators in many areas:

- Red Fox *Vulpes vulpes*
- Cat *Felis catus*

Neither predator is aerial or highly arboreal and so cannot replace local extinctions of these predator types, which changes the predator regime to being ground-based in affected areas.

Red Fox

Red Fox *Vulpes vulpes* is a widespread predator of native and introduced fauna that threatens many native vertebrate species in many situations, and it can carry a number of diseases and parasites including dog mange and hydatids. Control of foxes is widely undertaken to reduce their impact on native fauna and also on farms where they threaten livestock.

The fox is an opportunistic omnivorous predator and scavenger. In a study of foxes in the Dandenong Creek Valley in Melbourne over a two year period (White et al. 2006), 38% of 1317 collected fox scats contained mammal hair. Of these, 55% contained the hair of introduced mammals (Black Rat, House Mouse, European Rabbit), 45% contained hair of common native mammals (Common Ringtail Possum, Common Brushtail Possum), and 0.4% contained hair of a locally uncommon native mammal (Sugar Glider – two scats). Birds contributed to 5% of scats. Bone fragments were found to constitute 12% of scats and this did not differ significantly between seasons, suggesting reptiles were not major prey. Cold-blooded vertebrates are rarely taken by foxes in Victoria but tortoise eggs are frequently dug up and eaten (Menkhorst 1995). Reptiles are taken opportunistically.

The fox has partly replaced the original predators: Aboriginal people, the dingo and the two quolls. It takes a terrible toll on sensitive native fauna, but by eating native and introduced herbivores the fox imposes top-down regulation which is a basic ecological function. By preying on possums the fox contributes to tree canopy health, by preying on rabbits it assists native vegetation generally, and by preying on rats it assists orchids and other geophytes.

Cat

The Cat *Felis catus* preys on native and introduced fauna and there is a large feral population in Victoria. Cats prey on a wide range of species and also spread the parasitic disease toxoplasmosis to grazing animals, including many native species (Menkhorst 1995).

According to Menkhorst (1995): 'The widespread belief that feral Cats are a significant predator of birds appears to be misplaced. Although cat predation can be significant on small, isolated populations of birds, such as seabird colonies, and on species with low powers of dispersal, birds usually comprise less than 15% of the diet… In cleared or semi-cleared environments, young European Rabbits and House Mouse are the major prey items. In extensive tracts of bushland, where rabbits and mice are uncommon or absent, a wide range of native small mammals is eaten, including native rodents, Common Ringtail Possum, Feathertail Glider, Sugar Glider [and insectivorous bats] and species of antechinus. The relative frequencies of various species in stomach contents or scats suggest that Cats opportunistically prey upon the most abundant or readily captured species.'

In a study of the diet of domestic cats in homes bordering nature reserves in Canberra, 64% of prey items were introduced mammals, especially mice and rats. Native birds formed 14% of prey items and (native) reptiles 7% (Barratt 1997). Cats are likely to be major predators of reptiles in Victoria (Ian Smales, pers. comm.).

Introduced predator control

The negative effects of introduced predators have long been recognised in Victoria. Predation by cats and foxes are listed as potentially threatening processes under the Victorian *Flora and Fauna Guarantee Act 1988* (FFG Act). The Victorian *Catchment and Land Protection Act 1994* (CaLP Act) recognises foxes as established pest animals and requires private landowners and public land managers to prevent the spread of, and as far as possible, eradicate established pest animals. Because of the complexities associated with the status of domesticated cats as pets and farm animals, cats are not listed under the CaLP Act. However feral cats are recognised as pest animals by the Victorian state government (DPI 1994) and control is advocated in areas of high value such as national parks.

Effectiveness of control is an issue, for example most fox control effort does not have a significant effect on the fox population to alleviate impact (DPI 2007). Walsh et al. (2012) found that Malleefowl population growth did not benefit from fox baiting, suggesting that fox baiting is generally not a cost-effective management action for the conservation of this species. This study provides a 'powerful example of why management decisions should be based on evidence, rather than ecological intuition'.

Culling cats may do more harm than good. In an example of the 'hydra effect', Lazenby et al. in prep.) found that shooting or trapping feral cats may actually increase their numbers in southern Tasmania. When a dominant individual is removed from an open population subordinates come in to explore the territory that's freed up (ABC Science, 7 April 2015).

The Mornington Peninsula Shire has a strong commitment to biodiversity protection and enhancement. An important component of this approach is feral animal management (MPS 2012). A cat curfew which requires all cats to be contained within the owner's property at all times has been in place since 1997 and effectively means that cats are now kept indoors. Intensive fox and cat control programs have been undertaken within the higher quality bushland reserves since 2007. Control programs were extended to national parks on the

Peninsula in 2011. This level of introduced predator control is said to be 'head and shoulders' above control programs elsewhere (Malcolm Legg, pers. comm.). By comparison with other areas, the effects of these predator control programs and policies can be broadly assessed.

Native herbivores that may become overabundant without predators

Under low predator pressure, several native herbivorous mammals may increase and become overabundant in areas of south-east Australia, that is, they cause an ecological imbalance leading to loss of species diversity. They include:

Table 3. Native herbivores associated with ecological imbalance

Species	Original major predators	Examples of ecological imbalance
Common Ringtail Possum *Pseudocheirus peregrinus*	Powerful Owl, Spot-tailed Quoll, Lace Monitor, Dingo, Aborigines	Tree canopy loss in south-east Melbourne and on northern Mornington Peninsula
Common Brushtail Possum *Trichosurus vulpecula*	Thylacine, Dingo, Spot-tailed Quoll, Lace Monitor, Aborigines	Tree losses in River Red Gum woodland on fringes of Melbourne
Eastern Grey Kangaroo *Macropus giganteus*	Thylacine, Dingo, Aborigines	Overgrazing inside predator exclosures and by very high unrestrained populations in many locations in Victoria, especially on urban fringes
Western Grey Kangaroo *Macropus fuliginosus*	Dingo, Aborigines	Loss of plant diversity in Mallee national parks and reserves
Black Wallaby *Wallabia bicolor*	Dingo, Aborigines	Loss of plant diversity within predator exclosure, Royal Botanic Gardens Cranbourne
Koala *Phascolarctos cinereus*	Dingo, Aborigines	Tree canopy loss in several locations in Victoria
Swamp Rat *Rattus lutreolus*	Eastern Quoll, ?Aborigines	Widespread loss of orchid populations on Mornington Peninsula

Case studies

Koala

Overabundant Koala populations impact on their habitat by overbrowsing preferred food tree species in a few coastal areas and some islands of Victoria including Mount Eccles, Framlingham Forest, the Otway Ranges (Figure 9), French Island and Snake Island. Coast Manna Gum *Eucalyptus viminalis* subsp. *pryoriana* is particularly at risk, but Koalas can also impact on Swamp Gum *Eucalyptus ovata*, Southern Blue-gum *Eucalyptus globulus* and River Red Gum *Eucalyptus camaldulensis* (Menkhorst 2008, Gibson and Thomas 2012).

The Koala overpopulation problem has been much studied (for example Martin 1985a, 1985b, Menkhorst 2008, Todd et al. 2008, Wallis 2013). The Victorian government has moved away from translocation as a management technique and has used in situ chemical sterilisation to manage overabundant populations in several locations (Menkhorst 2004, 2008). Unfortunately the procedure is stressful and kills an unacceptable number of animals.

With koalas starving and Manna Gum woodland canopies decimated, koala culls have been conducted in the Otways (The Age, 4 March 2015):

> More than 600 starving koalas were killed in secret culls in the Cape Otway area of western Victoria, it has been revealed.
>
> Wildlife officials did three euthanasia sweeps to kill 686 koalas in 2013 and 2014, in a covert campaign that was designed to avoid any backlash from green groups and the community.
>
> The secret cull was conducted under the previous Liberal government near the Great Ocean Road to address overpopulation issues.
>
> The marsupials were starving due to overpopulation in the Cape region, which is said to have the greatest density of koalas in Australia.
>
> The koalas were captured and sedated before being put down.

Despite the culls, overpopulation remains a problem in the area (ABC News, 4 March 2015).

Several factors control Koala populations, notably predators, road kill, fire, disease and food supply. There is evidence that predation by Aborigines and Dingoes kept Koala numbers very low prior to European settlement (Strahan and Martin 1982, Menkhorst 1995).

Figure 9. Southern Blue-gum forest defoliated by Koala overbrowsing, Kennett River, Otway Ranges

Possums

Common Ringtail Possum and Common Brushtail Possum are widespread primarily folivorous mammals that feed on many eucalypt and other species. Tree canopy loss due to mammal overbrowsing was not described when the vegetation of Victoria was in its 'original and natural' condition (see Hateley 2010) and seems to have developed since European arrival. As early as the 1870s Aborigines at Framlingham in western Victoria were 'accusing' brushtail possums of killing trees: 'The possums were no longer hunted and their numbers had risen… Possums also benefited when dingoes were culled.' (Low 2002).

Possums have been involved in tree canopy loss in many areas of suburban and rural Victoria (e.g. Yugovic 1999b, Carr in Low 2002) (Figure 10). Loss of the tree canopy has cascade effects, particularly on birds, mammals and invertebrates. Curiously, *Eucalyptus viminalis* subsp. *pryoriana* (rough-barked form), a common tree in heathy woodland in southern Victoria, is relished by Koalas but avoided by possums (author, pers. obs.).

Figure 10. Possum-induced tree canopy loss, Kirtin Reserve, Mornington

In Mount Eliza on the Mornington Peninsula an overpopulation of Common Ringtail Possum is responsible for an ongoing and unprecedented epidemic of eucalypt tree death. All indigenous eucalypts are susceptible but Swamp Gum *Eucalyptus ovata* and Narrow-leaf Peppermint *E. radiata* are preferred by possums and are defoliated and killed first. Repeated defoliation is required to kill a healthy tree. With up to 16 ringtail possums per hectare, this is the highest density of ringtail possum recorded in natural eucalypt dominated vegetation in Australia. This is evidenced by detailed observations (Ecology Australia 2014) and the recovery of trees following installation of possum bands (Yugovic 2013b)(Figures 11, 12).

Figure 11. Possum band or guard on Swamp Gum *Eucalyptus ovata*, Mount Eliza, clear plastic band on trunk (lower centre) protects tree crown from possums while unprotected side limb (on right) has died, before installation of guard the entire tree was largely defoliated, recovery took approximately 12 months

Figure 12. Possum bands on Swamp Gum, Kunyung Road, Mount Eliza

Possum damage is readily diagnosed as hanging (pendant) branches have all their leaves since possums don't climb down branches, while ascending branches are variably defoliated (Figure 13). Insects, pathogens and disturbance in comparison affect all leaves on a limb or more usually throughout a tree, so possum-induced tree decline is easily distinguished from all other forms of tree decline. A possum-stressed tree may survive years of partial defoliation. Occasional trees with hanging leafy branches can survive with a defoliated crown. Typically a tree perseveres for a few years and, while still supporting a little eaten-back foliage, then dies. In comparison a drought stressed tree dies with more foliage. Trees in critical and in terminal condition are recognisable – the latter cannot be saved by definition.

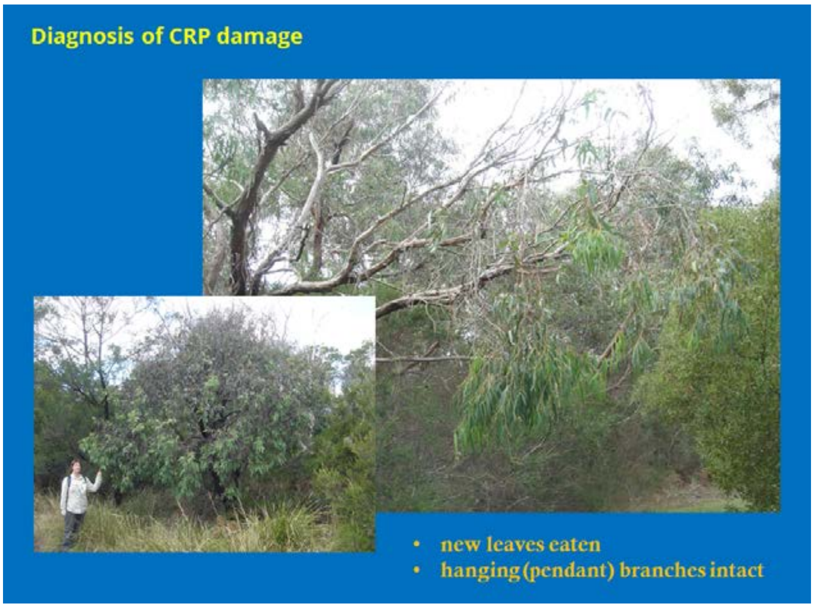

Figure 13. Diagnosis of ringtail possum damage

Ecology Australia (2014) found brushtail possums at 'low density in Mount Eliza for a peri-urban environment'. While this is so for the bushland reserves they sampled, brushtail possums do contribute significantly to browsing pressure on trees in gardens throughout Mount Eliza where they are near buildings with shelter. Brushtails eat adult leaves which thins the foliage evenly through trees, while ringtails are more damaging by being smaller and able to reach their preferred shoots and young leaves at the ends of branches, preventing leaves from attaining adult size. As a leaf normally lives for one year and is then shed, trees unable to replace their fallen leaves may be killed by repeated defoliation within a few years. The two possums thus have different browsing patterns which are readily seen in trees (Figure 14). Scats on the ground also reveal which species is accessing particular trees. Ringtail possum is a causal factor in tree loss in Mount Eliza, while brushtail possum is a contributing factor. In combination the two possum species are especially deadly to trees.

Figure 14. Possum browsing patterns, Mount Eliza

Many eucalypts native to southern Victoria are browsed by possums. Swamp Gum *Eucalyptus ovata* and Narrow-leaf Peppermint *E. radiata* are highly susceptible while Coast Manna Gum *E. viminalis* subsp. *pryoriana* (rough-barked heathy woodland form) is not eaten. Possums have preferred trees within Manna Gum *Eucalyptus viminalis* (half-barked grassy woodland form), with some trees, particularly narrow-leaved individuals resembling *pryoriana*, being lightly browsed or avoided. Possum stressed eucalypts also seem to have low capacity to recover from fire. Once the eucalypts are dead, starving ringtail possums switch to less preferred species such as Sweet Bursaria *Bursaria spinosa* and Silver Banksia *Banksia marginata*. This does not sustain them and only increases vegetation damage. Coast Tea-tree *Leptospermum laevigatum* may also be killed by ringtail possums in coastal scrub.

Several factors control populations of ringtail possum including availability of shelter, density of understorey vegetation, predation (originally mainly by humans, dingoes, spot-tailed quolls, large raptors and large owls, and now mainly by cats, foxes, large raptors and large owls where they occur), fire, and food quality and availability. Numbers can plummet during intense heat waves. However, ringtails have high fecundity (Kerle 2001) so populations can rapidly recover to reach habitat carrying capacity.

Both possums have higher densities in Melbourne urban bushland due to increased food resources in adjacent residential areas (Harper et al. 2008) which may contribute to high browsing pressure in Mount Eliza. However, possum-induced tree canopy loss occurs across the rural northern Mornington Peninsula from Mount Martha to Cranbourne (Figure 15) and was locally severe in the 1990s (e.g. Yugovic 1999a) before it became severe in urban areas in the 2010s. In Mount Eliza, entire canopies are now dead or declining, and the ‘prognosis for the eucalypts remaining in the landscape is extremely poor’ (Ecology Australia 2014).

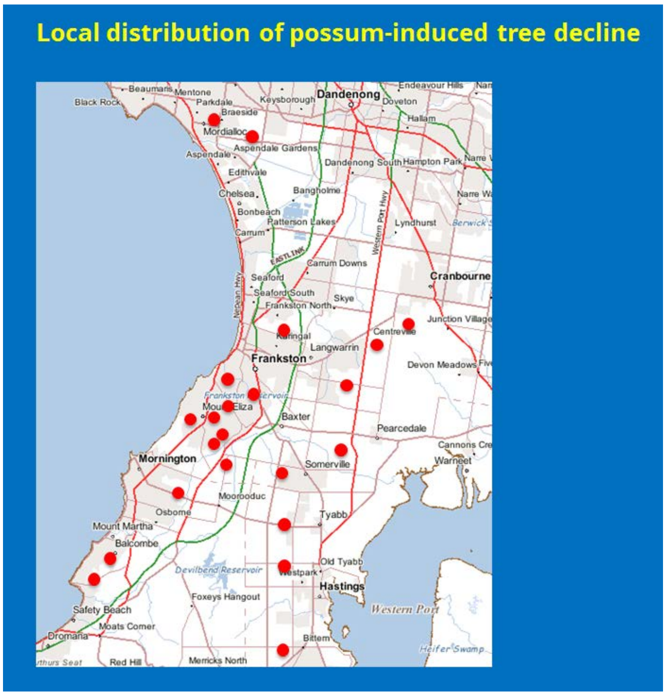

Figure 15. Local distribution of possum-induced tree canopy loss, south-east Melbourne and Mornington Peninsula, each affected site has 10 or more possum-affected dead or dying closely adjacent trees, canopy decline is not restricted to these sites as extensive areas are also affected between sites

Within the severely affected area shown above entire canopies are killed by ringtail possums, while outside this area scattered trees are killed. Possum induced tree decline is not confined to the Mornington Peninsula as it occurs elsewhere in southern Victoria for example at Braeside, Mordialloc, Wheelers Hill and Ocean Grove.

Described locally as an ‘ecological emergency’, possum overbrowsing and occasional tree losses were occurring in Mount Eliza as early as the 1980s (author, pers. obs.). This continued through the Millennium Drought (1996–2010) and first became severe (with complete canopy losses) during the 2010–2012 La Niña event suggesting that high rainfall may favour possums. However there were many previous La Niñas before the drought (Bureau of Meteorology, Mornington weather station) and none caused complete canopy loss.

Could a predator-prey imbalance between domestic cats and ringtail possums help explain the late onset of the decline in Mount Eliza? With the native predators long gone, domestic cats were at artificially high densities due to being fed and sheltered by their owners and were the last remaining major predators until 1997 when they largely disappeared from the landscape due to the local cat curfew. However, given the ringtail possum overpopulation developed some 15 years after the curfew was introduced, it seems that some factor(s) other than or in addition to lack of cats has caused the increase.

Biomass accumulation is a necessary condition for ringtail possum overpopulation. Biomass builds up in a more-or-less continuous mid-storey or sub-canopy layer in the vegetation composed of shrubs and small non-eucalypt trees which can be either indigenous or introduced. The possums construct their dreys in these dense understoreys and can avoid travel on the ground between food trees where they are vulnerable to ground predators. Dense, long unburnt understoreys are prevalent on the northern Mornington Peninsula. When a dense mid-storey develops, cats and foxes become largely irrelevant to ringtail possums.

In addition to bushland remnants, street and garden trees in Mount Eliza with dense understoreys are also severely affected by ringtail possum overbrowsing (Ecology Australia 2014). In the general absence of biomass reduction, there has been a general increase in understorey biomass on road reserves and in adjacent gardens over time, particularly with the 2010–2012 La Niña event stimulating growth of both eucalypts and understorey.

It took some 30 to 50 years in Mount Eliza for the dense mid-storeys to develop in reserves and gardens from the time of intensive residential development from the 1950s to the 1980s. Prior to then, as agricultural land, the understoreys were kept largely open by burning and grazing by domestic livestock (historical photography, e.g. DLS 1938). Thus there was a time lag of decades between the urbanisation of Mount Eliza and the possum overpopulation.

The grassy woodlands of the north-west Mornington Peninsula were once more open than the bushland remnants and gardens of today as shown by annotations on George Smythe's (1841) historical survey plan (Figure 16). This was likely due to Aboriginal burning and macropod browsing and grazing (Yugovic 2013a). In both forest or woodland, open mid-storeys are marginal habitat for ringtail possums due to (a) limited shelter and (b) their need to cross ground to reach eucalypt food trees which exposes them to ground predators. This creates a balance between browsing pressure and canopy health which is readily seen in healthy vegetation. The carrying capacity becomes temporarily higher with dense understoreys and no effective predators – until the tree canopy dies and the possum population crashes.

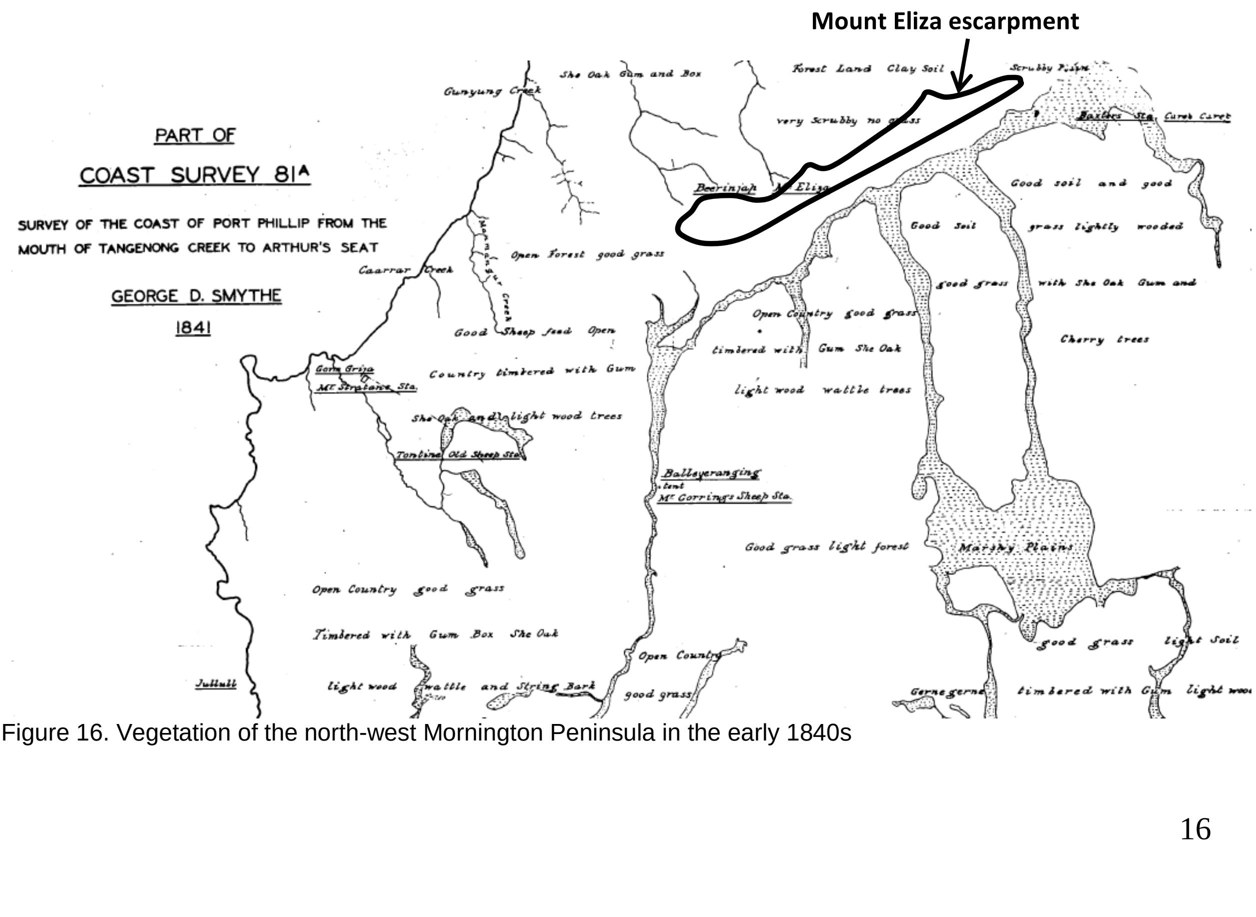

Figure 16. Vegetation of the north-west Mornington Peninsula in the early 1840s

The Mornington Peninsula tree decline phenomenon appears to be a syndrome of (1) susceptible eucalypts, (2) high biomass accumulation and (3) low predator pressure leading to (4) ringtail possum overpopulation (Figures 17, 18). Low predator pressure appears to be a necessary condition – if there was high predator pressure there would be no possum overpopulation. This assumes the original full suite of aerial, arboreal and ground predators could control ringtail possums in both open and dense vegetation, and is therefore speculative. The lack of early reports of possum-induced tree decline in Victoria and reports of dense understoreys in many areas at the time (Hateley 2010) suggest that they could.

Figure 17. Change in predator regime, northern Mornington Peninsula

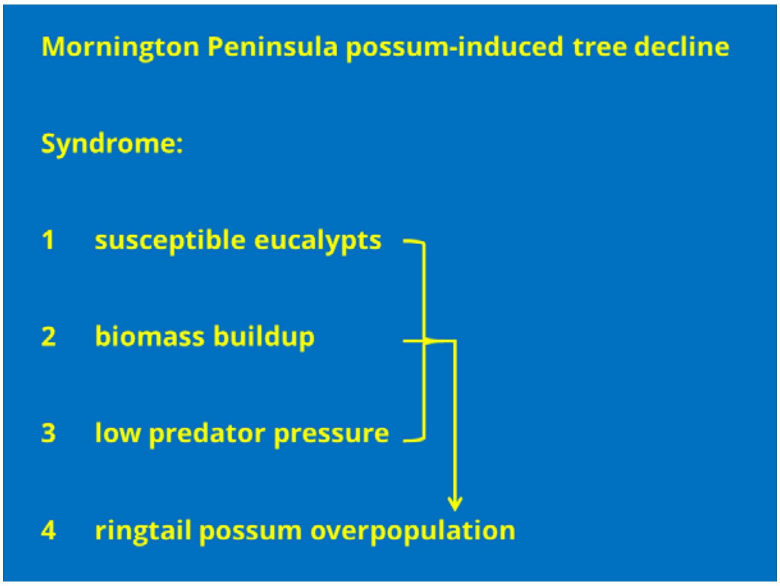

Figure 18. Mornington Peninsula tree decline syndrome

All the native predators of ringtail possum are locally extinct in Mount Eliza. Powerful Owls took possums from tree canopies while Spot-tailed Quolls took possums from within trees. The latter have great speed and agility in trees due to feet adapted for climbing: presence of a first toe, and serrated pads on the palm and sole (Troughton 1957). Lace Monitors may have been important arboreal predators. Also extinct is the semi-arboreal Tiger Snake which bites and envenomates possums in their dreys and catches them soon after on the ground. Aerial and arboreal predators, native or introduced, are missing from the current predator regime.

While the original grassy woodlands of the north-western Mornington Peninsula had open understoreys, the isolated forest on the steep Mount Eliza escarpment may have had a dense understorey. The annotation ‘forest land clay soil very scrubby no grass’ on Smythe's plan (Figure 16) applies mostly to the plateau to the north but could also refer to the escarpment seen from below. The ‘clay soil’ was clearly the skeletal soil of the restricted Ordovician sediments (sandstone, slate and chert) which include most of the escarpment (see GSV 1967).

Historical aerial photography (DLS 1938) indicates that, in 1937, logging and clearing of the escarpment had recently commenced, but there were many large old trees remaining and the canopy was healthy throughout the escarpment and plateau area. The many large old trees indicate that possum-induced tree decline had not occurred in the area, suggesting that ringtails had been in balance even in Smythe's scrubby vegetation.

The Mount Eliza escarpment supports a mixed eucalypt forest and woodland of Manna Gum, Narrow-leaf Peppermint and Swamp Gum with locally abundant Blackwood and an isolated occurrence of Messmate Stringybark. Depending on geology, fire regime and wallaby browsing pressure it may have supported dense understorey vegetation consistent with Smyth.

Spot-tailed Quoll is strongly associated with dense vegetation (DSE 2003), being ‘dispersed over the thick bush’ in the Melbourne area (Wheelwright 1861). Indeed quolls (unknown species) occurred on the escarpment. They were reportedly eliminated during sweeps by chicken farmers from the Moorooduc Plain below in the 1930s (M. Legg, pers. comm.).

Indirect evidence that it was Spot-tailed Quoll on the Mount Eliza escarpment is the 1930s report date since from about 1910 only three isolated populations of Eastern Quoll were known in Victoria (none on the Mornington Peninsula) following the mysterious epidemic of 1901–03 which annihilated many marsupials in Victoria (Troughton 1957, Menkhorst 1995).

It appears that under the original predator regime ringtail possums were controlled in both open and dense understorey vegetation, but with the now altered and simplified predator regime (introduced ground predators only), ringtails possums are uncontrolled in dense understorey vegetation. This leads to overpopulation, tree canopy loss, starvation and ecological collapse with the local extinction of species that depend on canopy trees.

In Mount Eliza, the locally extinct aerial predators (such as Powerful Owl and Grey Goshawk) and arboreal predators (Spot-tailed Quoll, Lace Monitor, Tiger Snake) appear to be missing pieces in a jigsaw puzzle explaining the tree decline.

Many areas elsewhere in south-east Australia including sites supporting Swamp Gum currently have dense understoreys with native and introduced predators (Victorian Biodiversity Atlas, data) with ringtail possums and tree canopies apparently in balance.

From extensive observations, susceptible eucalypts, dense unburnt understoreys and low predator pressure coincide on the northern Mornington Peninsula to produce the tree decline. Unaffected adjacent areas lack at least one of these necessary conditions. Heathy woodland is not affected by possums since Coast Manna Gum *Eucalyptus viminalis* subsp. *pryoriana* (rough-barked form) is not eaten by possums. This form appears to have a leaf chemical defence adaptation to heathy woodland, a habitat in which shrubs are abundant and there is no avoiding possums otherwise. However, the widespread grassy woodland form of *E. viminalis* (half-barked form, subspecies indeterminate) is generally susceptible to possums.

Certainly the best management response in the affected areas now is to reopen the understoreys as culling of possums and reintroducing predators are impractical. This also has major benefits for ground layer flora diversity, which slowly declines under shady scrub. Weed control in the first year following biomass reduction may be necessary to ensure that indigenous plants establish in any gaps created rather than weeds.

While stands of canopy trees in woodlands with dense mid-storeys are susceptible to ringtail possums in affected areas, isolated trees in paddocks, gardens and on roadsides are unaffected as ringtails generally avoid crossing more than 10 metres of ground. Being scansorial, brushtail possums more readily travel on the ground between food trees but they become wary and spend less time on the ground when they smell fox scent (Kerle 2001). It is possible that if ground predators were absent ringtails would also change their behavior and eventually cross more ground to reach the isolated trees. Early accounts of ringtail behaviour prior to the arrival of the fox suggest that it was often active on the ground (Anson et al. 2013). According to the top-down herbivore control model, the background level of predator pressure is keeping the isolated tree subpopulation healthy, and also makes the biomass reduction of mid-storeys a practical management option to save trees in woodland formations.

On the Mornington Peninsula, possums generally feed on indigenous trees where they are available, avoiding many (but not all) commonly planted trees. This tends to concentrate browsing pressure. Feeding of possums by people can be a factor in some areas, allowing populations to build and further increasing pressure on trees. Human-fed possums still browse on trees – they have to do something with their time – but they leave the least palatable trees till last. Site inspection of trees suggests that simple isolation by minor pruning of the damaged tree or its connecting vegetation would in most cases provide immediate respite from possums. However a possum guard is usually also necessary.

With thousands of affected trees only a limited number of large trees in prominent locations can realistically be saved by possum guards though this is a worthwhile action.

There is a common perception that a dense layer of invasive Sweet Pittosporum under canopy eucalypts affects them adversely through competition or even chemical interaction. However, eucalypts seem to get on with Pittosporum as well as with any other competing tree, as can be seen where they occur together naturally in Gippsland. Close observation indicates that the usually sick canopy above dense Pittosporum is due to high ringtail possum densities. No allelopathic interaction is known between these genera and treatment with Pittosporum leaf-extract actually increases germination in *Eucalyptus viminalis* (Tunbridge et al. 2000).

In the Melbourne region, large River Red Gums *Eucalyptus camaldulensis* with open grassy understoreys have been killed by brushtail possums that den in natural hollows (D. Gilmore, pers. comm.). Dense understoreys are not needed by the less arboreal (scansorial) brushtails.

The largest red gums are highly susceptible as they shelter the brushtail possums in hollows that only develop in large trees. Possums can feed in their home tree before venturing down onto the ground where they face ground predators (foxes) in order to reach other food trees.

Brushtail possums are a major cause of tree decline along the Murray River.

The following account is from Michael O'Brien (2006):

> I own a property on the Murray River floodplains, downstream of Echuca. My property has river red gum wetlands that have quite naturally not received any flooding since 1995.
>
> For the last 15 years my red gum wetland and many other red gum wetlands in the region have suffered massive decline in tree health and in some instances all of the trees have been killed. It is changing the look of the landscape and is quite obviously a regional catastrophe.
>
> But what is the cause? Ask any of the experts and they insist it is 'drought', but in my district the average rain for the past 15 years has only been slightly below the long term average and in reality the red gums have probably had as much flooding as they ever did in dry periods.
>
> The actual cause of the tree death is something much more cute and cuddly, common brushtail possum's. Brushtail possums are abundant in these hollow red gums. At times I have spotted up to 15 mature possums in one tree. Each summer the trees grow a few leaves and then for the remainder of the year the possums strip them clean. The trees can only take about three years of this kind of constant bombardment before they die. From the 200 large trees within my wetland at least 75% have died in the last 10 years, and the remainder are in poor health.
>
> Prior to European settlement in the area, the local Aboriginals heavily utilised brushtail possums for food, clothing etcetera. So much so that one of the early pastoralists in the area referred to them as the 'possum-eaters'.
>
> As an experiment I possum guarded a number of random trees last November.
>
> The following photograph I took this morning of one of the possum-guarded trees. The trees in the photograph were all in similar health at the time of guarding last November.
>
> Possum attack is a widespread problem in the Murray floodplains now that possums are unable to be utilised and managed, and probably explains a lot of the premature death of red gums that people are witnessing in this natural dry period.

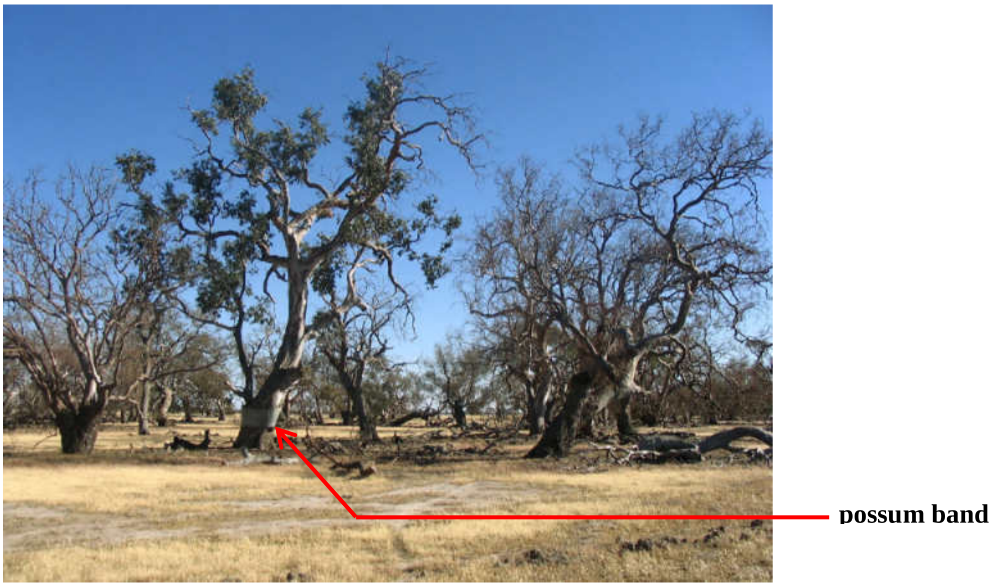

Figure 19. Possum band on River Red Gum *Eucalyptus camaldulensis*, downstream of Echuca

Possums are protected under the Victorian *Wildlife Act 1975*. Since 2003 the state government has permitted the trapping of Common Brushtail Possums in buildings for the purpose of release on the same property up to a maximum of 50 metres from the capture site after sunset on the day of capture or, if that is not reasonably possible, taking them to a registered vet for euthanasia within 24 hours of capture. Relocation of possums is prohibited. Common Ringtail Possums remain fully protected and may not be trapped (DELWP website).

The questions that land managers throughout the wide geographic range of these possums need to answer is 'what steps will most efficiently and effectively maintain tree canopy health' and 'what is controlling tree canopy folivore numbers'? Basic ecology suggests that if it is not predators then it will be other biotic factors such as competition with other species or starvation, or physical factors such as drought, heat, fire and availability of shelter. If it is to be starvation there are dire consequences for trees and the species that depend on them.

Mornington Shire response

Mornington Peninsula Shire is responding to the possum problem by protecting key trees and through public information, in cooperation with the local conservation association.
The following is from the media release of May 2014 (MPS 2014):

Protecting possum-damaged trees
Recent investigation of trees in Mount Eliza has identified cases of tree foliage damage caused by possum feeding. . . Mornington Peninsula Shire in partnership with Mount Eliza Association for Environmental Care is taking steps to protect key trees in the Mount Eliza area from over-feeding by possums, as well as offering specially grown seedlings to residents who have lost trees due to possum damage. . .

Tips for installing possum bands

The following guidelines are based on extensive experience with possum bands:

1 Protect trees in poor or critical condition, terminal condition is too late.
2 Protect dominant canopy trees, not subdominant trees that will die anyway.
3 Remove connections, possums can jump 1 metre.
4 Use clear plastic sheeting, self tapper screws.
5 Use an arborist if climbing is required.
6 Damaged trees can be regenerated by cutting to ground level for coppice regrowth
7 State or local government agency to protect trees on public land.

Figure 20. Arborist installing possum band on Manna Gum, adjacent planted Spotted Gum *Corymbia maculosa* and many exotic eucalypts and other trees are not eaten by possums

Rats

Swamp Rat *Rattus lutreolus* is a native specialist herbivorous rat of eastern Australia. It feeds on the basal shoots and stems, rhizomes and other below ground storage organs of monocotyledonous plants including geophytes. This rat is by no means restricted to swamps. Major factors controlling population sizes are, or were, predation (by dingoes, snakes, quolls and owls), food supply, fire and availability of shelter. Swamp Rats are cover dependent, preferring dense grassy vegetation in which to make their nests and runways and find food.

By digging up and eating tubers, rats can rapidly deplete or eliminate orchid colonies such as Dainty Wasp-orchid *Chiloglottis trapeziformis* (Figure 21), Common Bird-orchid *Chiloglottis valida*, Purple Diuris *Diuris punctata* and Nodding Greenhood *Pterostylis nutans* (pers. obs.).

In recent years on the Mornington Peninsula, numerous orchid colonies in several locations that were carefully tended for many years by land managers and volunteers have been devastated by what is thought by locals to be increased Swamp Rat numbers/activity although the introduced Black Rat may be the culprit in some cases. Build-up of grassy biomass favouring Swamp Rat is also a factor for Purple Diuris but not for the other affected species – their vegetation habitat has not changed appreciably in recent years. Orchids are too rare to be staple diet items so the rats rely on more common food sources such as introduced Onion-grass *Romulea rosea*. But once an orchid colony is discovered it is dug up and eaten.

This decline in orchids is alarming in isolated nature reserves where there is little or no potential for them to recolonise. It has necessitated wire mesh guards at several locations to protect the remaining tubers. But wire guards have their own problems: they attract attention from people, impede access for biomass reduction and weed control, and prevent access by Blue-tongue Lizards which control invertebrate predators of orchids.

Figure 21. Wire mesh guard over last Dainty Wasp-orchid colony in Mount Eliza protecting it from digging rats which had reduced the colony from several hundred to less than 10 plants, full recovery occurred after guarding

Swamp Rat numbers may increase with high rainfall due to increased food supply (Braithwaite and Lee 1979) and since the drought ended in 2010 this could be related to increased Swamp Rat numbers/activity. However the known orchid colonies were healthy and unaffected by rats for decades before the drought started in 1995 including during years of high rainfall (1991–93). There being no other discernable change in the environment, this leaves the predator control program commencing in 2007 as the only available explanation.

We need to know more about relationships with the introduced rat species (Brown Rat, Black Rat) and the native Bush Rat *Rattus fuscipes* in all this. Black Rats are aggressive towards Swamp Rats so they are trapped in some areas by land managers, which assists Swamp Rats. They are generalist omnivores and scavengers rather than specialist herbivores, but Black Rat can dig extensively and it is not clear how much damage it causes. It is a thought to be a problem for the endangered Frankston Spider-orchid *Caladenia robinsonii* in Rosebud. Curiously, Bush Rat has been considered absent from the Mornington Peninsula (Seebeck 1995), but there are recent records in the Victorian Biodiversity Atlas.

The local absence of snakes in many urban bushland reserves means even less predator pressure on native and introduced rats. With the lack of predators now almost complete the rats undergo an 'ecological release'. Population sizes are thereafter controlled more by food supply than by predation. Ironically, the local extinction of snakes in much urban bushland may be largely due to lack of recruitment caused by predation on juvenile snakes by cats, so it is a complex situation. As an area becomes urbanised, the adult snakes may live on for many years but eventually die or are killed or captured without being replaced.

The questions that land managers throughout the wide range of these digging rats need to answer is 'what is the most effective and efficient method to maintain geophyte diversity' and 'what is controlling digging rat numbers'? Basic ecology suggests that if it is not predation then it will be other biotic factors such as competition or starvation, or physical factors such as drought, fire and availability of shelter. Starvation has dire consequences for geophytes, particularly where habitats are fragmented and potential for recolonisation is limited.

Predator exclusion at Cranbourne

The Royal Botanic Gardens Cranbourne provides an experiment in predator control in which cats and foxes have been largely excluded from 250 ha of bushland by a predator exclusion fence and ongoing control within and surrounding the Gardens since 2003 (Terry Coates, pers. comm.). The purpose of predator exclusion is protection of Southern Brown Bandicoot.

Figure 22. Predator fence along perimeter of RBG Cranbourne

In the heathy woodland section, tree canopy health has not been significantly affected by possums even though shrub shelter is ample for possums. This may partly result from top-down control of possums by rare visiting or transient Powerful Owls and low numbers of feral Cat, but bottom-up control is probably more important: Coast Manna Gum *Eucalyptus viminalis* subsp. *pryoriana* appears to be resistant to possums.

In the grassy woodland small areas of dead Narrow-leaf Peppermint *Eucalyptus radiata* with stunted possum-damaged peppermints on the edge and dense adjacent Swamp Paperbark *Melaleuca* understorey vegetation suggest possums were causal (drought is not known to kill an entire stand of trees). This is likely to be an instance of the high biomass, lack of native predator syndrome that doesn't relate to the predator fence and possibly predates it.

In most of the grassy woodland some peppermint trees are possum damaged but the peppermint woodland canopy is generally coping. This can be explained by low suitable shrub cover leading to low ringtail density and limited tree hollows resulting in low brushtail density. Management burns further reduce the shrub cover, giving trees additional respite.

The possum population is therefore mostly bottom-up controlled: food quality controls numbers in heathy woodland while limited shelter controls numbers in grassy woodland. The grassy woodland canopy would be at risk if shrubs suitable for ringtails were to increase. Ironically, the large increase in shrub-browsing Black Wallaby inhibits shrub recruitment.

There are probably more Swamp Rats and Black Rats due to reduced fox and cat density (Terry Coates, pers. comm.). It is not clear what effects rats are having on orchids but no extinctions are known to have occurred (Bronwyn Merritt, pers. comm.). Swamp Rat numbers are likely to be controlled by predators (snakes and nocturnal birds of prey) and by the quality of the staple diet of rhizomes of Sandhill Sword-sedge *Lepidosperma concavum* which remains abundant. It has been deemed necessary to physically cage out herbivores including rats from plantings of Frankston Spider-orchid *Caladenia robinsonii*.

Without predators, Black Wallabies increased exponentially for several years and then largely stabilised (Terry Coates, pers. comm.). There has been a corresponding major loss of plant diversity and vegetation cover due to wallaby browsing, undermining the very purpose of the ‘botanic gardens’. The native vegetation now looks drab and species-poor even in spring where it used to have impressive wildflower displays. Managers have responded by opening the wombat gates at night in the hope that excess wallabies will leave and not return. While there is a net movement of wallabies out of the exclosure into surrounding areas (where habitat is limited) many individuals return through the gates. This means that foxes are able to enter the site and they are now being controlled, making the fence somewhat redundant.

There has been talk of removing the fence to allow the wallabies out and, by implication, allow limited predator control of wallabies to regulate numbers and browsing pressure on the vegetation. Trapping of foxes could be graduated to achieve a balance with both bandicoots and wallabies at sustainable levels. It is noted that bandicoots were there before the fence due to extensive dense vegetation providing protection from foxes (and previously quolls etc.).

Benefits of introduced predator control

Predator control is sometimes undertaken where significant native vertebrates are at risk such as Southern Brown Bandicoot, Superb Lyrebird, Malleefowl and Swamp Skink. These species require fox and/or cat control or dense vegetation shelter from these predators. However they no longer occur in many areas and it is usually not feasible to reintroduce them.

Foxes disperse weed seeds although they probably also disperse native plant seeds. Examples include Blackberry *Rubus fruticosus* spp. agg. spread by internal transport (foxes eat the fruit) (Brunner et al. 1976) and Cleavers *Galium aparine* spread by external transport (on fur). Fox control should reduce the spread of Blackberry but birds are also important dispersal vectors.

Blue-tongue Lizards and other large reptiles are preyed upon especially by cats, so control efforts should assist survival. It is possible that in many areas the habitat carrying capacity for large reptiles, in terms of food supply, is not being reached due to heavy mesopredator predation, endangering local populations. By eating large invertebrate herbivores such as Garden Snail *Helix aspersa*, blue-tongues indirectly benefit sensitive plants including many orchids and other species such as Button Everlasting *Coronidium scorpoides*.

When introduced predator control may cause or amplify an ecological imbalance

Predator pressure is a major factor regulating populations of several introduced mammals including House Mouse, Brown Rat, Black Rat and European Rabbit. Under reduced predator pressure these pest animals have larger populations with generally adverse ecological effects, especially the rabbit. These effects are offset by increased food supply for native predators where they occur, particularly raptors, but native predator pressure is generally reduced and often unable to keep up with the feral species which may become overabundant.

Lack of predator pressure on possums and rodents may lead to long-term change in native vegetation. Because many of the possum affected trees are within suburban gardens, they are generally not replaced. In reserves, replacing canopy trees via natural regeneration is technically feasible but is challenging and may require biomass reduction such as fire as well as the presence of adjacent surviving canopy trees to provide seed sources. Where there are no surviving canopy trees, site reintroduction of canopy trees via planting or direct seeding may have to be considered. Similarly, once an orchid becomes locally extinct there may be no way it can recolonise naturally, due to isolation of the habitat. And there is little or no point in reintroducing sensitive species, even eucalypts, under sustained herbivore pressure.

Discussion

Apex predators are regarded as important for biodiversity in many ecosystems around the world (Ripple et al. 2014). The loss of a top predator sets up a trophic cascade, with ecosystems disrupted and forest canopies sometimes lost under herbivore pressure (e.g. Terborgh et al. 2001). This seems to also apply in south-east Australia.

There are, however, systems that do not need natural vertebrate apex predators although they are present in low numbers: saltmarsh and bird breeding colony ecosystems for example as these systems lack natural vertebrate herbivory (see Yugovic 1998).

It is widely accepted that introduced predators threaten many native species in south-east Australia, particularly mammals (e.g. Dickman 1996), but how does predator pressure differ now from originally? Often a predisposing problem underlying local extinction is isolation of habitat which is either natural or more usually is caused by land clearing and disturbance. Would the original suite of predators cause the same local extinctions if they were still present? These and similar questions of predator ecology need further research.

Figures on the numbers of native wildlife taken by cats and other introduced predators are often stated but are difficult to verify. Regardless of the actual numbers, it should be noted that the progeny of herbivores must succumb to some form of mortality or there would be a vast overabundance of herbivores. For example, a ringtail possum typically produces some 10 progeny over her lifetime, based on average litter size and frequency and longevity (see Henry 1995). For a stable population a female only has to produce 2 mature offspring in her lifetime. The other 8 animals she produces will die. Similarly, a female Swamp Rat will typically produce some 20 progeny (see Seebeck 1995), of which 18 will die by some means. Is it not better that they die quickly in the jaws of a predator rather than slowly through starvation which would also damage the ecosystem and the species it contains?

The profound influence of predators in south-east Australia is so pervasive that it is easily overlooked. For example, without predators, it is likely that rabbits would be in abundance almost everywhere. This is clearly evidenced within the predator exclosure at Mount Rothwell, Little River, where overabundant rabbits had grazed out the understorey in 2014, leaving large bare areas. The absence of rabbits in Mount Eliza is due to predators (dogs, cats and foxes). The area is better off without this pest although exotic grass cover is also higher. Without predators, rabbits would recolonise Mount Eliza and the Shire and residents would have to build rabbit-proof fences around many sites including every vegetation garden.

Wherever in south-east Australia there is *no* herbivore overpopulation causing vegetation loss such as tree canopy loss, which is almost the entire region, this is likely due to a predator-prey *balance* in operation coupled with physical factors. In the more developed areas these are mainly the familiar introduced predators that are now integrated into novel ecosystems. They have several negative effects but the restricted systems without them are far worse off.

However, it appears that in some cases the introduced predators are not, or are not capable of, keeping up with key native and introduced herbivores (such as rabbits) which are overabundant and causing ecological damage. Depending on the situation, low predation rates are partly due to predator inefficiency (for example the fox and cat have low efficiency with ringtail possum in dense mid-storey vegetation), and partly due to predator control which may in some cases leave some areas effectively without predators.

For example, Mount Eliza has bushland reserves where there are no threatened species and possums and swamp rats are the only native mammals apart from bats and occasional sugar gliders, and where cats are largely absent due to the local cat curfew. Foxes and cats are also actively controlled. These effectively predator free areas are undergoing eucalypt canopy loss caused by possums and orchid colony losses caused by swamp rats (Yugovic 2013b). In these novel ecosystems it is questionable to remove all predators when possums are killing canopy trees and dependent species including sugar glider and orchids are going locally extinct.

Systems without top predators are likely to undergo trophic imbalance with adverse ecological cascade effects on flora and fauna (see Stolzenburg 2008). Whether the predators or prey are native or introduced during trophic imbalance seems to make little difference to overall biodiversity – overabundant herbivores, native or introduced, inevitably degrade ecosystems. Current land management is pushing systems towards domination by browsing and grazing mammals, with other influences such as predation and regular fire being reduced.

A feature of the introduced mesopredators is their apparently higher predation rates on certain native species compared to the original suite of predators, for example the fox appears to have eliminated the pademelon on mainland Australia. This increased predation may be related to particular efficiencies in new predator-prey relationships, but may also be related to 'mesopredator release' (Crooks and Soulé 1999). Mesopredator release is thought to operate extensively in Australia in areas where the top predator Dingo is rare or absent, resulting in higher mesopredator populations and predation rates (Johnson et al. 2007).

Outside the 5,600 km arid zone dingo fence, for example, dingoes appear to suppress fox populations and thereby assist small to medium native mammals (Letnic et al. 2009). Similarly, there is evidence from south-east Australia that dingoes suppress macropods and foxes and thus generate strong indirect and beneficial effects on the prey of foxes (Letnic et al. 2009). This suggests that mesopredator release of the fox operates extensively in south-east Australia where dingoes are absent, to the detriment of small and medium mammals.

An interesting predator manipulation experiment in semi-arid Western Australia found that when dingoes and foxes were both removed cats increased and predation on small mammals increased further (Risbey *et al*. 2000), suggesting a hierarchy of predators (dingo, fox, cat) and ecological release processes. As the authors acknowledge, this needs replication. The evidence for an increase in cat abundance following fox control is inconsistent between studies, and there is also limited knowledge on the impacts of feral cats and foxes on native predators (Robley *et al*. 2004). Interactions between predators such as aggression, competition for prey and predation on juveniles need further research.

Besides predation, fire is important factor regulating herbivore pressure on ecosystems. But could fire alone maintain diversity by controlling herbivore numbers? The relative contribution of predators and fire in maintaining ecosystems is likely to depend on herbivore and fire regime. Kangaroos have always been able to escape fire. Extensive fire may eliminate or reduce ringtail possums until a mid-storey re-establishes, or cover-dependent swamp rats until ground cover is restored, but these are temporary effects. Furthermore, herbivores can move in and eat the regeneration anyway if the fire is small in area, and fine scale mosaic burns were probably implemented by the Aborigines (Gammage 2011). Fire may therefore need to be extensive and/or frequent to have a significant effect on herbivore levels. This may not be practicable or sustainable in terms of fuel levels let alone effects on biodiversity, leaving continual predator pressure as an efficient and targeted control factor.

According to proponents, ‘rewilding’ with apex predators has benefits for ecosystem stability and diversity (e.g. Soulé and Nos 1998, Monbiot 2013). The predators are either regionally extinct or are related to extinct Pleistocene predators. For example Komodo dragon could replace *Megalania* in order to control feral water buffalo in northern Australia (Flannery 1994, Bowman 2012). However, many people would find it unacceptable to replace extinct marsupial predators with placental predators such as large cats in south-east Australia, although they could provide a means of controlling populations of feral pigs, horses and deer.

Flannery (1994) also proposes reintroducing the long extinct Tasmanian Devil to mainland Australia where it could play a role in checking foxes and cats. Devils are thought to enter fox dens and eat the cubs (DSEWPaC 2012), which may explain why fox introductions to Tasmania have not been successful. Devils also prey on possums. There have been moves to reintroduce devils to Wilsons Promontory but no program has been formalised.

Given the major change in predator regimes since the arrival of Europeans, there may be other cases of predator-prey imbalances in south-east Australia beside mammals. Reduced predation could help explain another major ecological imbalance: the Noisy Miner problem. The usual explanation for the overabundance of this aggressive bird is fragmentation of woodlands which increases the edge habitat favoured by the species (e.g. Chubb 2011). However, the predator regime of this species needs research.

Similarly, the decline of Coast Banksia *Banksia integrifolia* due to longicorn beetle larvae (borers) on Seaford Foreshore and the decline of Black Sheoak *Allocasuarina littoralis* due to borers in Mount Eliza may be related to the loss of predatory cockatoos or parasitoid wasps.

Conclusion

Many ecosystems in south-east Australia appear to benefit from or require top predators in maintaining stability and complexity as do ecosystems elsewhere. Whether the introduced mesopredators have net benefits is site dependent and debatable given their toll on sensitive fauna but they do carry on the necessary function of herbivore control.

Unlike North America and Europe where top predators such as wolves, lynx, cougars, jaguars and bears are being returned to ecosystems with beneficial effects, the return of the dingo is impractical in much of Victoria as it can prey on livestock and may interbreed with domestic dogs to produce packs of wild dogs. The dingo survives in remote eastern Victoria however.

Due to the widespread loss of native top predators and mesopredators, in many areas we are left with two introduced mesopredators (the fox and cat) to control herbivores. However, being ground-based predators they are not efficient at controlling ringtail possums in dense understorey vegetation, and furthermore without the top predator dingo they appear to be ecologically released, increasing their impact on sensitive fauna.

We should adopt an ecological logic or paradigm in which predators, native or introduced, are required to control herbivores, native or introduced, in order to maintain overall biodiversity. Our challenge from here is to protect the biodiversity of south-east Australia by regulating predator pressure within the context of novel ecosystems.

Possible management approaches to maintaining a balance between predators and herbivores in south-east Australia include:

- Land managers should be aware of the complexities of predator ecology and feral animal control, and should anticipate and look for ecosystem responses including changes in herbivore pressure on vegetation.

- Predator control should be undertaken strategically where identified significant fauna are under identified predator threat, in combination with monitoring of canopy health, sensitive plant populations and other ecological indicators.

- Where necessary, large trees should be protected from mammal folivores, especially in prominent locations. This is happening in Mount Eliza with the Mornington Peninsula Shire installing possum bands on trees on roadsides and in reserves, with good results.

- Due to their potential detrimental effect on canopy trees, constructed nest boxes for brushtail and ringtail possums are often not appropriate. Release of rescued or trapped possums into bushland should not be undertaken where habitats are already at carrying capacity for possums. The protected status of these species in designated areas with possum-induced tree decline should be reviewed in order to protect trees and biodiversity.

- Managing woodlands back towards their original open structure through biomass reduction counters the impact of ringtail possums by reducing habitat carrying capacity and increasing their exposure to ground predators.

- Well planned reintroductions of native predators should be supported.

- We should redouble our efforts to protect all native apex predators in order to allow these keystone species to perform their important ecological role of controlling herbivore pressure within natural areas.

Good luck and good management!

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