

SOMETHING WENT MISSING: CESSATION OF TRADITIONAL OWNER LAND MANAGEMENT AND RAPID MAMMALIAN POPULATION COLLAPSES IN THE SEMI-ARID REGION OF THE MURRAY–DARLING BASIN, SOUTHEASTERN AUSTRALIA

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‘The question is not what you look at, but what you see.’ H.D. Thoreau

ABSTRACT: The nineteenth century mass mammal extinctions in the semi-arid zone of the Murray–Darling basin, southeastern Australia, are examined in the context of prior traditional land management. A model of grassland dynamics reveals a multi-trophic level productive pulse one to five years post-fire, followed by senescence and increasing flammability. Traditional Owner patch burning of grassland optimized human and mammalian food (including tubers, seeds and fungi) and decreased fire risk. Over at least 40 000 years, the persistence and abundance of fauna responded to this energetically closed self-reinforcing management. In 1830, depopulation (disease, massacres and displacement) effectively ended traditional management, an ecologically traumatic event that extinguished these productivity pulses. Associated mammal populations of c. 20 species collapsed, and all eco-engineering and mycophagous species, such as bilbies, bettongs and bandicoots, rapidly disappeared.

Traditional land management increased productivity, habitat heterogeneity and reduced wildfire risk, underpinning mammal abundance. This has remained unrecognized by most mammalogists and land managers. Blaming extinctions predominantly on the additions by Europeans (introduction of ungulates, feral grazers and predators etc.), disastrous as they were, fails to acknowledge the initial cause of rarity, i.e. loss of productivity, habitat and niches when traditional management was subtracted from country. As ecosystems continue to degrade, understanding the primary cause is fundamental to improved management. Although too late for extinct species, respect for, and inclusion of, traditional land management knowledge provides a direction for future land management.

Keywords: nineteenth century mammal extinctions, Traditional Owner land management, native grasslands, lower Murray–Darling, semi-arid, patch burning

INTRODUCTION

From a broad range of evidence (archaeological, anthropological, historical and ecological) this paper examines the collapse of the mammalian fauna of the mid Murray–Darling in the mid-nineteenth century (Figure 1).

1. Although well studied, the arguments for the rapid mass extinctions of mammals (1840–1890s) in the semi-arid mid Murray–Darling basin (and elsewhere) are essentially based on the additions by Europeans to land management (ungulates, rabbits, feral predators, land modification). Yet these do not adequately explain the rapidity or the timing of these declines across the entire landscape. Many species greatly reduced in abundance before the introduction of foxes, rabbits and hares and before the establishment of dense populations of feral cats.
2. Burbidge and Mackenzie (1989) found that semi-arid-zone mammals in a Critical Weight Range (35 g to 5.5 kg,

high metabolic rate cf. reptiles and less mobile than birds) had the worst extinction record (1840–1980s). They attributed the fundamental cause to the loss of biological productivity of the region (including the export of nutrients from European pastoralism). The size of these mammals strongly implicated the cat and fox as extinction vectors, while changed fire regimes were acknowledged as a possible contributing factor.

3. We present a model of grassland and fire that shows a productivity pulse of biota across trophic levels (fungi, tubers, invertebrates, mammals) that occurs one to five years post-fire (slightly extended in arid grasslands). Without fire, this productive pulse does not occur and senescence becomes evident within a decade. We contend that Traditional Owner land management (hereafter TO-LM) used fire to repeatedly create this pulse in grasslands and grassy field layer environments, thus providing predictable food resources. A suite of

- mammals adapted to this pulse providing increased food resources to the Traditional Owners.
4. Traditional Owner patch burning also created ecotones, lessened the extent of wildfires and increased the extent of mature vegetation and habitat heterogeneity, all of which benefited mammal populations and assisted persistence of Traditional Owner populations in this drought-prone region. The entire region was thus managed, more or less intensively, dependent on local ecological conditions.
 5. Many of the 24 mammal species that became extinct in the region (Menkhurst 2009; Dickman 1994) were directly associated with this productive pulse through their diet and habitat, e.g. mycophagous species and more specialist herbivores (four peramelids, four potoroids, a bilby and rodents). The more direct association the quicker their disappearance. The ‘eco-engineering’ of many mammals made the fire-induced pulse more stable and ecologically productive across trophic levels. This system was very productive yet highly vulnerable in the absence of burning.
 6. This region supported high densities of Traditional Owners economically reliant on riverine and grassland resources. Although continued in remote areas, burning of country effectively ceased at the landscape scale after 1830 due to depopulation (caused by disease, massacres, trauma and dispersal). This was also an ecologically traumatic event with immediate effects that cascaded through ecosystems. We argue that it was the subtraction of millennia-long TO-LM, particularly their use of patch burning, that caused the rapid decline in landscape productivity and mammal populations entering the extinction vortex.
 7. Our argument is both:
 - a) a variation on the fire-induced ‘mosaic hypothesis’ which has had an inconclusive literature and experimentation since first postulated by Bolton and Latz (1978) for the Mala (*Lagorchestes hirsutus*) in the Tanami Desert (Short & Turner 1994; Hiscock & Wallis 2005), and
 - b) supportive of Allen’s (1983) thesis that vegetation succession in the decades following cessation of TO-LM was the critical factor in the collapse of the mammal fauna in the region.

The post-fire, time-bound, productive, multi-trophic level pulse described here adds evidence to these postulates and explains the rapidity of decline.
 8. The ecological and historical processes we describe for the mid Murray–Darling basin in the mid-nineteenth century were a fundamental driver of mammalian extinction across the arid and semi-arid zones of the continent, and thus a major contributory

factor to Australia’s mammal extinction record, widely acknowledged as the worst globally (Woinarski et al. 2015).

Problems with ‘solely the additions’ arguments

While acknowledging the range of environmentally degrading processes accompanying European dispossession, we contend that these additions were subsequent to the initial subtraction—the ecological trauma following the cessation of TO-LM. Habitat destruction and fragmentation, grazing by introduced ungulates (sheep, goats and cattle), introductions of rabbits and predation by the Red Fox (*Vulpes vulpes*) and the feral Cat (*Felis catus*) have been highlighted by standard texts in mammalogy as the major causes of the initial and consequent extinctions of Australian mammal fauna (Gould 1863; Jones 1923; Troughton 1973; Ride 1970; Menkhurst 1995) including specific studies in the region (Menkhurst 2009; Bennett et al. 1989; Dickman 1994). TO-LM has been largely ignored, but perhaps sometimes hidden, under ‘changed fire regimes’.

In examining the mammalian declines in western NSW, Dickman (1994) found 50% of the species became extinct in the region and of the 27 species remaining 33% have declined. He identified feral cats as the major factor for the first extinction wave (from the 1840s). TO-LM was not mentioned. Our reading of the records of early explorers (Hovell & Hume 1831; Mitchell 1834; Sturt 1833; Eyre 1845) did not find any mention of cats in the arid and semi-arid zones. Interpretation of negative evidence is fraught, however, if either common or observed as an oddity, it is likely that cats would have been noted. The first records of cats in the region appear to be as adjuncts to squatter homesteads. Although feral cats can survive without drinking water, Jones (1923) concluded that their expansion into the arid and semi-arid regions was facilitated by the food and burrows provided by rabbits (i.e. not before the 1880s), when they were often released in the forlorn hope of controlling rabbits (Rolls 1969), thus suggesting their effective absence. Similarly, rabbits and foxes did not arrive in the region until after the 1880s (Burch 2017; Menkhurst 2009), when expansion of stock water points later in the nineteenth century probably assisted these species.

Early explorers (e.g. Sturt, Ayer and Mitchell) provided information on the early mammalian fauna of the semi-arid zone, but the presence of the Blandowski expedition (1856–57) within the region provided the first (and for over a century, the only) systematic collection of the regional fauna (Menkhurst 1995). Krefft (1865a,b) collated the records of that expedition and the observations on the Traditional Owners. He was reliant on the extant Nyeri Nyeri elders (and others) for specimen collection and

information, and these records were a vector for traditional knowledge (Krefft 1865a,b; Wakefield 1966; Allen 1972). Two of his observations are frequently referenced (e.g. Menkhorst 1995). The Pig-footed Bandicoot (*Chaeropus ecaudatus*), common when first recorded by Mitchell in 1836, had become ‘exceedingly rare, and disappearing as fast as the native population. The large flocks of sheep and cattle occupying the country will soon disperse those individuals which are still to be found in the so-called settled districts’ (Krefft 1865a). Subsequent mammalogists used this observation to blame the sheep and cattle. He also noted (p. 16) that the Greater Bilby (*Macrotis lagotis*) ... ‘like so many other species, has long ago retreated to north of the Murray’. We suggest that ‘long ago’ is more likely to be 20 than 10 years. The Traditional Owner population and economy had collapsed (around 1830) following smallpox and subsequent diseases (see below). Krefft (1865b), and many others, observed a remnant Indigenous population and had no interest in understanding (and probably little capacity to envisage) the prior economy and TO-LM. It would take over a century for western science to recognize the ecological agency of Traditional Owners (e.g. Tindale 1959; Rose 1987).

The early stage of the squatters’ invasion (observed by Krefft) began in the early 1840s to the 1860s, later in the northern Riverina (Kenyon 1914–15; Allen 1983; Boyce 2011; Ballinger 2011; Burch 2017). Past TO-LM managed grasslands were the major object of this imperial endeavour. However, in this semi-arid zone, water was also critical for cattle and sheep (within about 8 km) and farm dams (later mallee tanks and artesian wells) would only become established from the 1870s. The early effects of ‘undeveloped’ pastoralism left 75% of the Riverina and much of the Mallee habitat for 15 of the local mammal species, as it remained essentially unoccupied by squatters (Wakefield 1966; Allen 1983; Burch 2017). Until at least 1865, pastoralism remained focused around the limited water resources and shepherds continued to secure flocks (from Dingos) at night (Curr 1883; Allen 1983). Most native species can survive well without free water (Table 3) but had already massively declined in the absence of extensive pastoralism. In parts of Central Australia the mammal fauna survived pastoralism for over 70 years with the continuation of Traditional Owner burning (Latz & Griffin 1978). Despite its continuing reiteration, the additions postulate, and all its variants, appears unconvincing as a sole explanation and may be a function of a persistent European cultural perspective.

Here we show that the Traditional Owner patch burning created a self-reinforcing energetically closed productive pulse that provided them (and a suite of mammals) with predictable, elevated, varied, and sustainable food resources

across the landscape. When patch burning ceased, or was degraded, biological productivity was lost after about five years. Burbidge and McKenzie (1989) identified biological productivity loss as the primary cause of Critical Weight Range mammal extinctions in the arid and semi-arid zones.

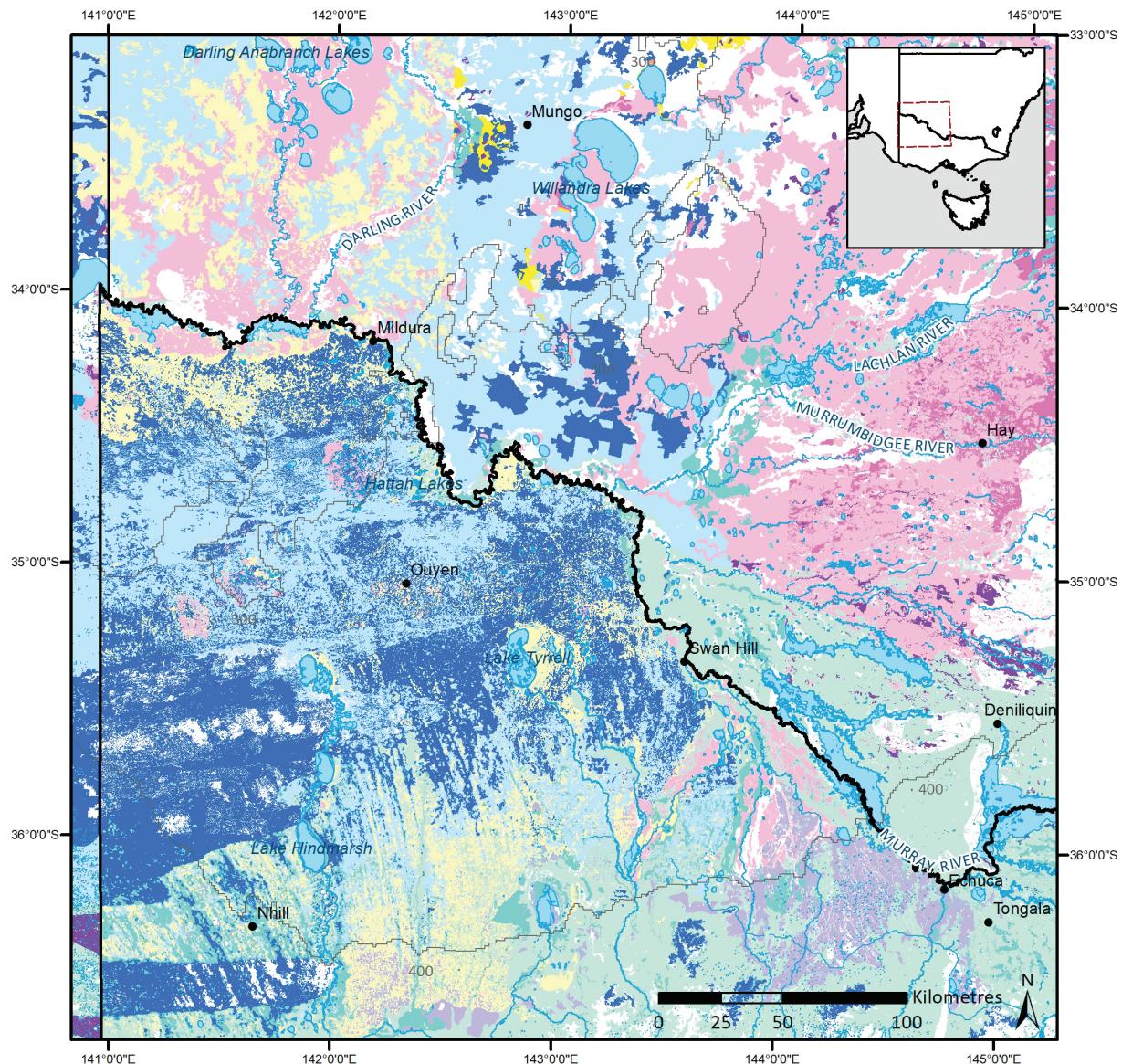
Menkhorst (2009) found loss of TO-LM plausible but rejected it because: a) ‘it struggles to account for the rapidity of the mammal declines’ as it would take some years to transform the fine-grain mosaic to coarse grain (awaiting senescence and bushfires); and b) there was scant evidence that Aboriginal people applied a patch-mosaic fire regime at a broad scale in this part of Australia. Neither of these reasons is sustainable on the evidence. Furthermore, our subtraction argument also fits the progressive loss of mammal species across the continent over the following century (e.g. Burbidge & McKenzie 1989; Latz & Griffin 1978). If, as we contend, the cessation of TO-LM is the initial causal factor driving mammal extinctions, then a suite of expanded actions (hitherto ignored) for redress of the acknowledged continental declines of ecosystems becomes available.

Our perspectives and presumptions

Our narrative has gaps, biases and incomplete knowledge. Most obviously, further direct traditional knowledge would be welcome. The current proposition relies upon evidence of science and humanities and knowledge of the prior economy of Traditional Owner society. Understanding of this last is fraught with difficulties and has evolved over time, at least in the western mind, usually within an implied social evolutionist context — hence ‘primitive hunter gatherers’, ‘nomads’, ‘intelligent parasitism’, ‘complex hunter-gatherers’ and ‘incipient agriculturalist’ to adopters of ‘agriculture’ (e.g. Elkin 1933; Meggitt 1965; Tindale 1959; Rose et al. 2003; Pascoe 2014; Sutton & Walshe 2021). Unfortunately, these definitions and related terminology have embedded cultural biases. We presume the following uncontroversial facts:

- The entire landscape was occupied by Traditional Owners in different language groups.
- Each group and individual maintained their country in a patchwork mosaic of different ecosystems related to their Dreamtime and to provide a diversity of predictable food resources across the seasons.
- This was done in highly variable and fire-prone environments. Fire and grasslands were important elements in this provision and persisted over the millennia and across massive environmental change, particularly in the Holocene (10 000 y BP) (e.g. Cupper 2005).
- TO-LM was based on a deep understanding of ecology and was incorporated into their cosmology and social

Pre-1750 Major Vegetation and Sub-Vegetation Coverage



Legend

Major Vegetation Groups

5 - Eucalyptus woodlands	8 - Casuarina woodlands	13, 16 - Acacia open woodlands & shrublands	14, 32 - Mallee woodlands, open woodlands & shrublands	19 - Tussock grasslands	22 - Chenopod shrublands
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Major Vegetation SubGroups

9, 10, 65	26, 71, 72, 73	20, 22, 23, 24, 45, 52	27, 61, 66, 67	36	31, 39
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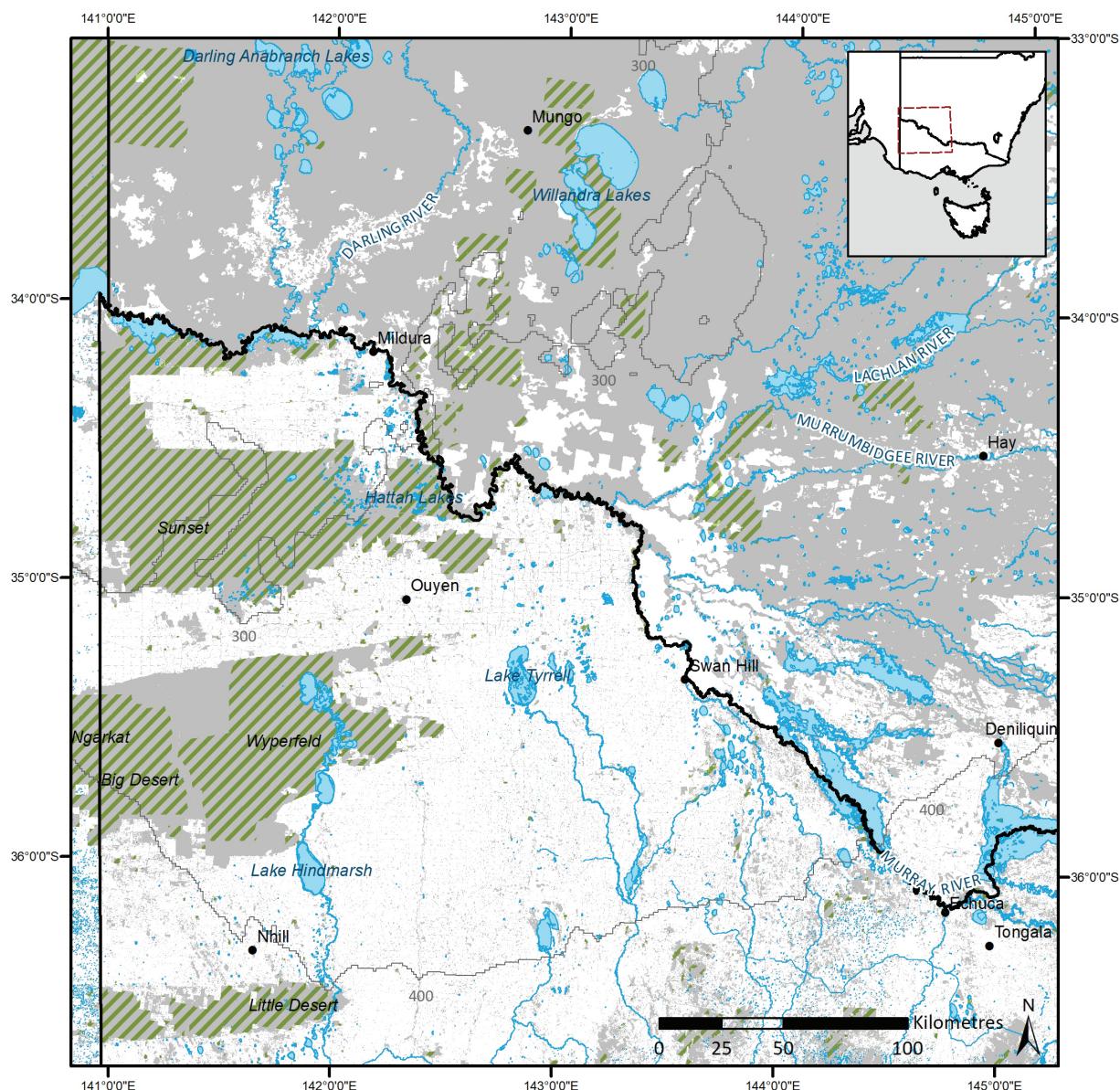
Other

300	Average annual rainfall 1961-1990 (mm)
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(Source: Pre-1750 Major Vegetation Groups - NVIS Version 6.0: Albers 100m analysis product CC by 4.0 State of the Environment, Pre-1750 Major Vegetation SubGroups - NVIS Version 6.0: Albers 100m analysis product CC by 4.0 State of the Environment, Australian Statistical Geography Standard: ASGS Edition 3 CC by 4.0 Australian Bureau of Statistics, 2016 SoE Inland Waters Average annual rainfall CC by 4.0 State of the Environment, Geography: Placenames Gazetteer CC by 4.0 Geoscience Australia, Directory of Important Wetlands CC by 4.0 Department of the Environment and Energy, Surface Hydrology Regional CC by 4.0 Geoscience Australia)

Figure 1 (a, top; b, right): Pre-1750 vegetation of the Mid Murray–Darling Basin as modelled by Geoscience Australia, showing major vegetation groups classified into those having major vegetation subgroups dominated by grass field layer (e.g. tussock, hummock — lighter shading) and non-grass field layer (e.g. shrubby — darker shading). Note the extent of grass field layers (lighter shadings) beneath the various canopies.

Current Major Vegetation and Cleared Vegetation Coverage



Legend

Major Vegetation Groups

- Rangelands - canopy of MVG identifiable but other layers highly degraded
- Cleared land - cropping and exotic pasture

Other

- Conservation reserve

- Average annual rainfall 1961-1990 (mm)

(Source: Present Major Vegetation Groups - NVIS Version 6.0 Albers 100m analysis product CC by 4.0 State of the Environment, Australian Statistical Geography Standard: ASGS Edition 3 CC by 4.0 Australian Bureau of Statistics, 2016 SoE Inland Waters Average annual rainfall CC by 4.0 State of the Environment, Geography: Placenames Gazetteer CC by 4.0 Geoscience Australia, Directory of Important Wetlands CC by 4.0 Department of the Environment and Energy, Surface Hydrology Regional CC by 4.0, Collaborative Australian Protected Areas Database CAPAD 2020 CC by 4.0 Commonwealth of Australia 2021)

organization (totemic or spirit system). We have interpreted but a small part of this deep knowledge, recognising that a more comprehensive understanding awaits interpretation.

STUDY AREA

The study area encompasses land of the following Traditional Owner language groups: Wergaia, Latje Latje, Dja Dja Wurrung, Yorta Yorta, Barba Barba, Wemba Wemba, Wadi Wadi, Dadi Dadi, Meru, Kureinji, Barkindji, Barindji, Yitha Yitha, Nari Nari, Madi Madi and, to the east, Wiradjuri (AIATSIS 2021). This is the region with the most rapid mass mammalian extinctions (>20) of the mid-late nineteenth century and is broadly defined as the parts of NSW, South Australia and Victoria south of latitude 32° S and within the mean 450 mm isohyet. It is centred on the confluence of the Murray and Darling rivers, which provide major riverine environments in this semi-arid zone. The boundaries of the region are somewhat arbitrary and should be viewed as porous; it is broadly encircled by the towns of Broken Hill, Wilcannia, Ivanhoe, Hay, Echuca, Bendigo, Nhill, Berri and Olary. Zoogeographically the region is within the Eyrean (arid) and Bassian (mesic) transition zones (semi-arid) (Blakers et al. 1984).

The modelled mapping of vegetation 1750, compiled by National Vegetation Information System (NVIS 2017) was used to extract the Major Vegetation Groups (MVG), and their Major Vegetation Subgroups (MVS #) dominated by a grassy or chenopod-grassy field layer were extracted to describe five broad structural vegetation types for the study area (Figure 1a). These were: Tussock Grasslands, Eucalypt Woodlands, Casuarina Woodlands, Acacia Open Woodlands and Shrublands, Mallee Woodlands and Shrublands and Mallee Open Woodlands and Sparse Shrublands, and Chenopod Shrublands. A variety of grassy field layers is ubiquitous across the landscape under all overstorey categories. The current extent of vegetation is shown in Figure 1b. The cleared land is essentially cropland and exotic pasture and the remaining, rangelands with a depleted MVG overstorey and a much-degraded field and shrub layer due to ungulate and European Rabbit grazing. The area of semi-arid national parks and reserve system in Victoria is about one million ha (Figure 1b). In Victoria, seven Ecological Vegetation Divisions occur in the region (Cheal 2010). All vegetation groups have been degraded, with most communities of grasslands and grassy woodlands having been cleared or otherwise grossly changed such that they are now considered threatened, e.g. Buloke Woodlands (Sluiter 1997); Box Mallee Woodlands (Sluiter & Schultz 2020); and Victorian Grassy Woodlands (Cresswell & Murphy 2016).

The plains of the Murray–Darling comprised warm-season (C4) grasslands that were a very productive,

high turnover ecosystem with their health and extent conditioned by regenerative fire regimes. In places, grasses dominate the field layer under open canopies (e.g. grassy woodlands) and can be an early seral stage in gaps in forests, restricted to riparian zones. The seral stages of grasslands are relatively rapid for terrestrial ecosystems and are measured in years rather than decades (Cheal 2010; McIvor 2005; Williams & Morgan 2015) (Table 1, Figure 3). However, when unburnt or overgrazed, short, either cool-season annuals (e.g. *Avena*, *Bromus*, *Hordeum* and *Lolium* spp.) or shrubs (e.g. *Atriplex*, *Maireana*, *Rhagodia*) become dominant (McIvor 2005).

Late Quaternary Vegetation of the study area

Basic vegetation types (and habitat) are expressions of soil, climate, available genetic plant and fungi material as well as fire and grazing regimes (fauna) that change over time. Whatever the combination of causes of the extinction of Australia's megafauna (climate, human, fire) around 46 000 y BP the continent's vegetation transitioned to become more flammable and fire-tolerant. Grasses (Poaceae) and tuber-forming taxa have been a feature of the southern Victorian plains for over 30 000 years (Canning 2009). In southeastern Australia there was lower biological activity under cooler conditions (3–5°C less than present), drier conditions and less surface water 33–12 K y BP with higher lake levels in early–mid Holocene (9–4 000 y BP) (Cupper 2005). The palaeobotanical record indicates that the vegetation in the region has undergone extensive change since the early Holocene (10–6.6 Ky BP) and around the 300 mm isohyet, mallee vegetation moved back and forth across the landscape (Bailey 1979; Cupper 2005). At that time *Casuarinaceae* woodland and chenopod shrublands (on dunes) dominated the landscape, but by the mid-Holocene (6.6–2.2 Ky BP) the woodland had been replaced by mallee and *Callitris* thickets, with mallee domination in the last 800 years (Luly 1990; Cupper 2005; Sluiter & Parsons 2012a,b; Sluiter 2008). Within these fluxes and variegated landscapes, grasslands and vegetation dominated by grassy field layers persisted at various scales (Figures 1a & 2). At various temporal and spatial scales, the abundance and distribution of fauna would have responded, sometimes in refugia and sometimes in radiation (Canning 2009). It was across these changing and variegated landscapes that TO societies and economies adapted. By 7000 y BP along the Darling River, the Barkindji diet consisted of 40% cereals. The lacustrine economy of Mungo man (c. 42 000 y BP) had changed to riverine grassland (Allen 1972). At the same time, Willandra Lakes archaeological sites (6 of 7) revealed that the vast majority of mammalian game was small to medium grassland species, not large macropods, which is a common ratio in archaeological sites across Australia (Allen 1972).

METHODS

Ecology of grassland biota, fire and ecotones

The abundance and vigour of the dominant grasses and associated tuber- and rhizome-forming species, their responses to fire and the tolerable fire intervals are reasonably well understood (e.g. Zimmer 1940; Parsons 1981; Morgan & Lunt 1999; McIvor 2005; Cheal 2010). An idealized model of the life history of the tall, warm season grasslands (*Themeda*, *Homopholis*, *Bothriochloa*, *Chloris*, *Enteropogon*, *Eragrostis*, *Panicum* spp. dominant), associated biota and fire was created from data in Morgan and Lunt (1999), from reviews and studies concerning the fire responses of fungi (McMullan-Fisher et al. 2011) and invertebrates (York 1999; York & Lewis 2017) and from the ecological strategies of the formerly super-abundant Bogong Moth (*Agrotis infusa*) (Warrant et al. 2016; Green et al. 2021). Data on major food sources utilized and cultivated by the Traditional Owners were examined, as were the diets of the extinct mammals (e.g. Latz 1995a; Strahan 1998a; Gott 2005). Literature of the humanities (anthropological, historical) and physical sciences (ecology, fire behaviour) were examined for evidence of the effects of patch burning on ecological processes at the landscape scale. Fire creates an area of ecotone on the burnt perimeter, often favoured by mammals, which we conservatively defined as 25 m either side of the fire boundary enabling us to calculate the ratio of burnt area to ecotone for fires over a square of between 1 and 1000 ha.

Traditional Owner use of fire and land-use history

Western science generally describes fire regimes in terms of frequency, seasonality, extent and intensity/severity. However, we recognize that this generalized instrument is inappropriate for describing the fine-grained mosaic burning of Traditional Owners, who maintained their ‘country’ for a variety of reasons within their dreaming, e.g. hunting and food gathering, specific habitat maintenance, woody weed encroachment, pest control and bushfire management (Gammage 2012; Skroblin et al. 2017, Cahir & McMaster 2018; Stefferson 2020; Sutton & Walshe 2021). Primary records of explorers (e.g. Hovell & Hume 1831; Sturt 1848; Mitchell 1838), squatters and other observers (e.g. Curr 1886; Clark 1998), early ethnographers (e.g. Dawson 2009; Howitt 1904) and land-use historians (Kenyon 1914–15; Randell 1982; Hateley 2010; Burch 2017) were examined for evidence of traditional land use and management, cultural practices and fauna noting that these are all ‘European’ sources.

These sources were complemented by archaeological, palaeobotanical and anthropological literature of the region and elsewhere (Meggett 1965; Bates 1985; Latz

1995b; Gott 2005; Bird et al. 2013; Cahir & McMaster 2018; Sutton & Walshe 2021). Most early ethnographers and later anthropologists were focused more upon social organization and rituals, rather than the Traditional Owner economy and ecology (see Rose et al. 2003; for exceptions see Bates 1985 and Rose 1987). Occasionally, more accurate assessments of the ecological agency of the Traditional Owners have been published (e.g. Tindale 1959; Sutton & Walshe 2021).

Grasslands and TO-LM in the Mallee and Wimmera

Between the period of light pastoral use (late 1840s) and the commencement of agricultural settlement from the late 1880s to the 1920s, large parts of the Victorian Mallee were extensively surveyed for land subdivision. One of us (JB) examined all this early cartographic material for any evidence of Traditional Owner land use that was present at that time and recorded by surveyors (Burch et al. 2020; Burch in prep.).

Early observations of fauna and current ecology

Early and recent scientific literature on the fauna of the region and Australia-wide was examined and habitat and range descriptions extracted (e.g. Gould 1863; Krefft 1865a,b; Troughton 1973; Ride 1970; Watts & Aslin 1981; Dickman 1994; Menkhorst 1995; Bennett et al. 1989 & 2006 and various authors in Strahan 1998a). In the region, Krefft (1865a) was the only early fauna survey (1856–7, based heavily on Traditional Owner knowledge, although Mitchell (1838), Sturt (1833) and others made many important observations.

Interpretation of data

Current remnant populations are very unlikely to reflect the optimal habitat for any species. Indeed, present occurrence may represent persistence in depauperate environments (see Tree 2019). We examined modern ecological research, accepting that it derived from degraded palettes for the regionally extinct species (but extant elsewhere) and their relatives. Of particular interest was the increasing understanding of the eco-engineering functions of mammals (Davies et al. 2019) and diets, particularly mycophagy (Vernes & Trappe 2007). Evidence (below) indicates that these spectra were more fully understood within Traditional Owner knowledge and management than present emerging science (e.g. Bird et al. 2013; Sutton & Walshe 2021).

Species with known records in the area but considered marginal have been excluded, e.g. the mesic Bindjulang (*Dasyurus maculatus*) and Yellow-footed Antechinus (*Antechinus flavipes*). It is likely that some additional arid-zone species may have occurred in the region but at the

limits of their ranges (see examples in text). Taxonomy follows Woinarski et al. (2015), sub-species nomenclature

is ignored and accepted Traditional Owner names used where possible (e.g. dasyurids, Abbott 2013).

Table 1: Tolerable fire intervals of Ecological Vegetation Divisions in the semi-arid zone and Riverina, Victoria (derived from Cheal 2010).

Ecological Vegetation Division (see Cheal 2010)	Tolerable fire interval (years) see below		
	Maximum ¹	Min. high severity (Canopy burnt) ²	Min. low severity (Ground cover only) ³
1. Alluvial Plains Grassland.	30	3	2
2. Inland Plains woodland.	1501	30	5
3 Riverine Woodland / Forest.	∞ 1	30	10
4. Chenopod Shrubland	∞ 1	30	30
5. Saltbush Mallee.	2001	40	40
6. Hummock Grass Mallee	901	20	20
7. Heathland Sands	45	15	8 y where <i>Xanthorrhoea</i> dominant; other – 15

Tolerable fire intervals are the time (years) between two successive fire events (of differing intensities) at a site in order that a vegetation community and its constituent species can persist (see Cheal 2010).

1. Maximum time interval — if exceeded, the vegetation community becomes senescent and changes to a different vegetation community. These figures are necessarily predictive and conceptual as there are no data beyond a handful of decades. They are based on individual plant longevities, their ability to regenerate in the absence of fire or other disturbance, and field observations.
2. Minimum high severity — minimum time (years) required between two successive high-severity fire events at a site in order that a vegetation community or its constituent species can persist and have every reasonable chance of reaching maturity and producing propagules before the following fire event. High-severity fires usually burn complete stands of larger trees and their crowns leaving few and scattered unburnt patches within the fire perimeter.
3. Minimum low severity — minimum time required between two successive fire events at a site, the first of which is a low-severity fire with a high proportion of unburnt landscape scattered within the fire perimeter, in order that a vegetation community or its constituent species can persist and have every reasonable chance of reaching maturity and setting seed. Low-severity fires usually burn shrubs and lower strata plants, and do not usually appreciably burn tree canopies. Low-severity fires are also significantly patchy, with many unburnt patches within the fire perimeter.

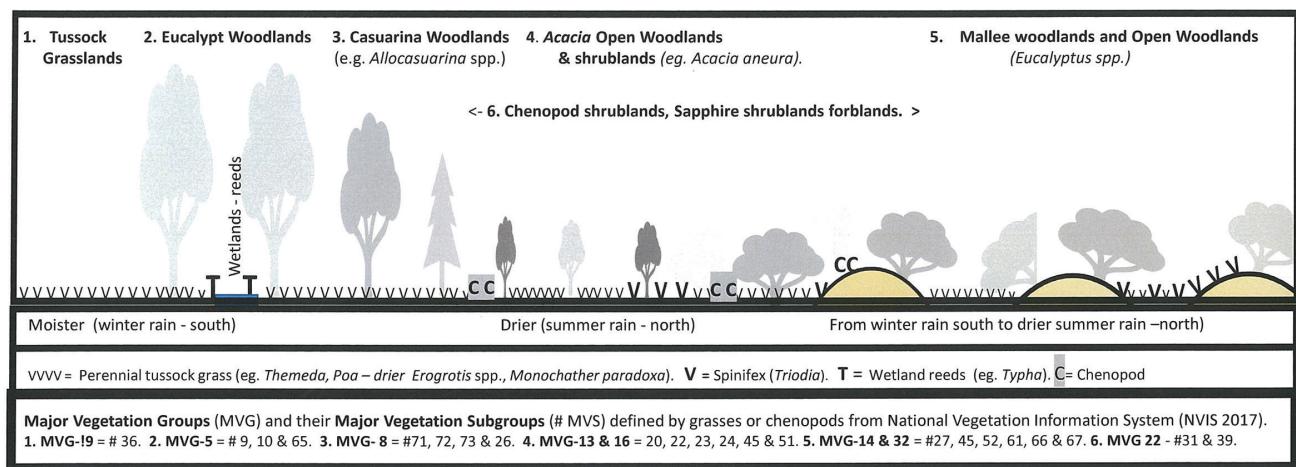


Figure 2: Idealised grassland and grassy field layers across major vegetation groups shown in Figure 1. Field layers dominated by grasses are ubiquitous across major vegetation groups with distributions adjusting to changing environmental and overstorey fluxes over the Holocene and shorter-term perturbations.

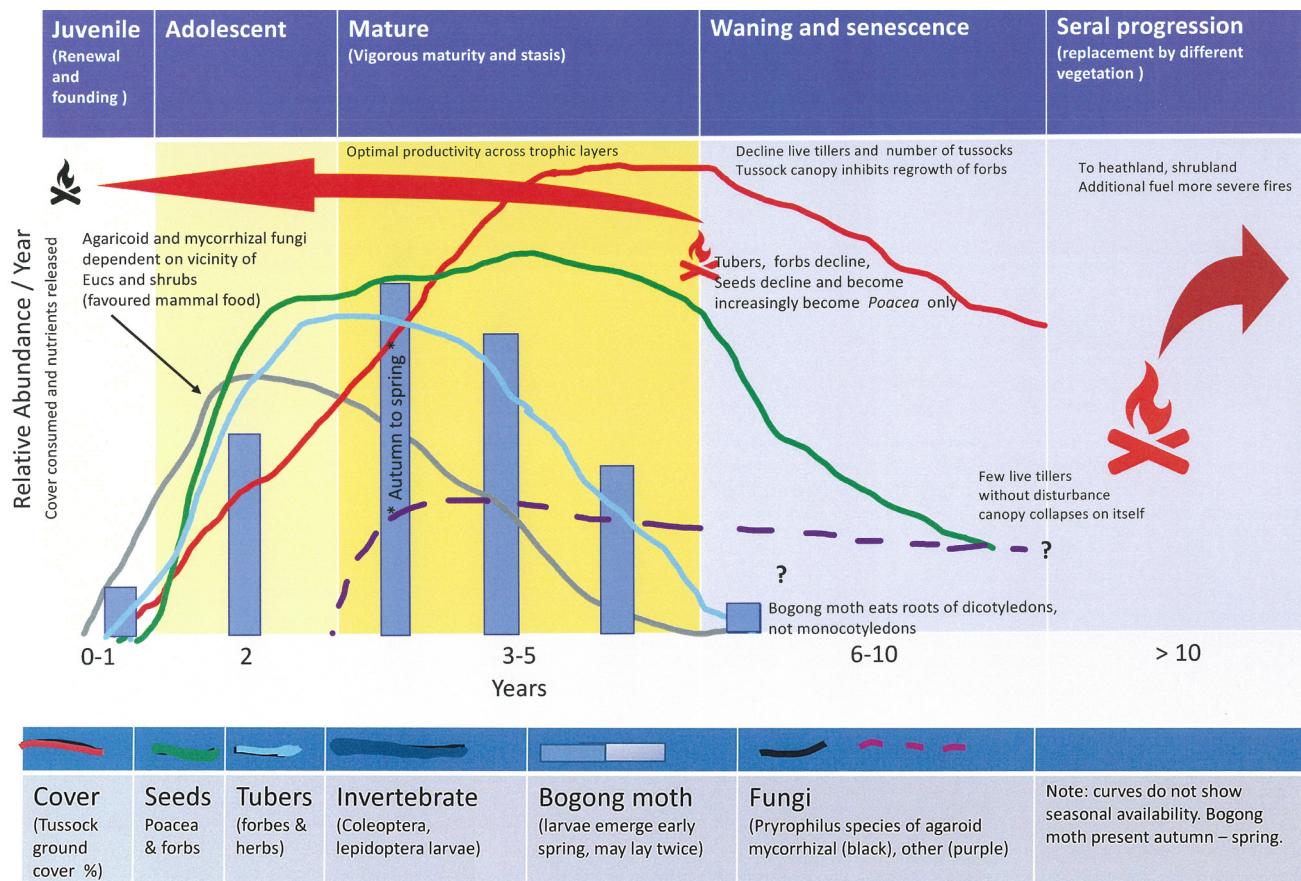


Figure 3: Idealized relative abundance of mammalian food resources across trophic levels in grassy field layer in response to fire. Note ectomycorrhizal fungi curve reliant on vicinity of trees and shrubs; e.g. grassy woodland (see Figure 4). Adapted from Morgan and Lunt (1999) and other biological data (see text).

RESULTS

Grasslands, fire, ecotones and landscape effects

Schematic models of the life history of grasslands, particularly in relation to the grassy field layer and fire, are provided in Figures 2 and 3. Mesic tussock grasslands in southeastern Australia are dominated by the tall *Poa* / *Rytidosperma* spp. or *Themeda* spp. and a multi-trophic level productivity pulse begins in the adolescent stage and peaks within the mature stage 3–5 years post fire (Figure 2). This post-fire pulse supports the most vigorous growth of tuberous and rhizomatous species and forbs as it also does in Mallee-*Triodia* vegetation (Zimmer 1940; Parsons 1981) (Figure 2, Table 2). The forbs (not grasses) in grassland of the self-mulching soils of the lower Murray–Darling basin are the major food source of the once super-abundant Bogong Moth (*Agrotis infusa*) (Green et al. 2021). Post-pulse, the grassland matures to senescence and the forbs are largely eliminated (Figure 2; Morgan & Lunt 1999). Some grain-producing annuals (e.g. *Panicum* spp.) and some wetland species also have a post-fire pulse. In Mallee-*Triodia*, visible plant species counts went from 18 to 63 following a 4 ha fire and produced a pulse of

grasses, perennial tuberous and rhizomatous species from seed (persistent in the soil seed bank) and tubers (Parsons 1981; Zimmer 1940). In the more arid zones, grasslands are often dominated by Spinifex (*Triodia* spp.) and here the productivity pulse occurs 1–8 years post-fire, dependent on rain (Zimmer 1940; Cheal 2010) (Table 1). Tuber-forming plants, occurring in the productive pulse of various grass field layers, are listed in Table 2.

The seed-bed and plant response after a cool fire are qualitatively different from post-grazing. Soil moisture is increased (plant foliage mass is decreased), while the pH and many soil nutrients are elevated (e.g. Chungu et al. 2020). Hodges (2021) and Hodges et al. (2021) found that of 55 species of temperate grasslands, 45 (82%) had improved germination following smoke, heat or both treatments. Furthermore, in temperate grasslands, low intensity fires transfer relatively little heat energy to the substrate, which preserves the composition and resilience of the heat-sensitive, subterranean fungal community and floral diversity. Both of these change (decline) if fire frequency exceeds once every three years, perhaps as symbiotic relationships are severed, e.g. mycorrhizal fungi and tuberous forbs (Christensen 1998; Edgidi et al. 2016;

Table 2: Major tuber-forming genera occurring in the Murray–Darling and in diets of Traditional Owners showing species occurrences in various grasslands/heathlands/adjacent wetlands and response to fire in Ecological Vegetation Divisions (Table 1). All these species are known or probable mammal food. Data from Brandt and Cherikoff (1985) and Gott (2005 & 2008).

Column codes:

1. Most common or restricted to grassland and grassy field layers (+); broader distribution (-).
2. Fire response: most abundant after fire (+); no or unknown response (-).

	Grasslands/heathlands in Ecological Vegetation Divisions (typical dominant grass species)									
	1. Alluvial Plains Grassland <i>Panicum / Homopholis / Themeda</i>		2. Inland Plains woodland <i>Themeda</i>		3. Riverine Woodland / Forest <i>Poa spp.</i>		6. Hummock Grass Mallee <i>Triodia spp.</i>		7. Heathland Sands	
Genera / Species # also Fruit / Seeds	1	2	1	2	1	2	1	2	1	2
<i>Arthropodium</i> spp.	+	-	+	-						
<i>A. strictum</i>										
<i>A. minus</i> et al.										
<i>Bulbine</i> spp.	-	-	+	-			+	+		
<i>Bulbine bulbosa</i>										
<i>Microseris walteri</i>	+	+	+	+	+	+	+	-	-	+
<i>Burchardia umbellata</i>			-	-					+	+
<i>Wurmbea</i> spp.	+	-	+	-			-	+	+	+
<i>Pteridium esculentum</i>	-	+		+	+	+			+	+
<i>Geranium</i> spp.	-	+	+	+						
<i>Geranium</i> sp. (3)										
<i>Hypoxis</i> s.l. (including Pauridia) spp. <i>Hypoxis exilis</i> , <i>H. hygrometrica</i> (et al.)	+	+	+	+	+	+				
<i>Caesia calliantha</i>	-	-	-	-						
<i>Cynogoton</i> spp. Adj. wetlands					+	-				
<i>Typha</i> spp.					+	-				
Adj. wetlands										
<i>Dianella</i> spp.	+	-	+	-			-	+		
<i>Dianella tarda</i> (et al.)										

Fisher et al. 2016). Prescribed burning is not equivalent to TO burning and may have deleterious on biotic balance (e.g. fungi, Trappe et al. 2006). There is a direct link between frequent, low intensity burning in grasslands (=patch burning) and multi-trophic layer species diversity, resilience and productivity. We contend that the distribution and abundance of vertebrates, particularly mammals, positively responded to this suite of attributes and their determination by fire management.

In the presence of partner trees and shrubs (e.g. *Eucalyptus*, *Allocasuarina*, *Melaleuca*), a suite of pyrophilous (fire-loving) fungal species produce fruit-bodies on recently burnt sites, typically in the first and

second years after fire, often in large numbers (Warcup 1990; Robinson et al. 2008; Claridge et al. 2009; McMullan-Fisher et al. 2011; T. May pers. comm.) (Figure 3). The majority of pyrophilous macro-fungi produce fruit-bodies in the first autumn following a spring or summer fire including agaricoid fungi and mycorrhizal species (Warcup 1990; Robinson et al. 2008; McMullan-Fisher et al. 2011). Such fungi support a range of invertebrates and are favoured by mycophagous mammals (Claridge 2009; McMullan-Fisher et al. 2011) (Table 3, Figures 4 & 5). The importance of fungi in mammalian diets (e.g. volume, seasonality) is becoming increasingly recognized, as is the role of these mammals as dispersal agents and

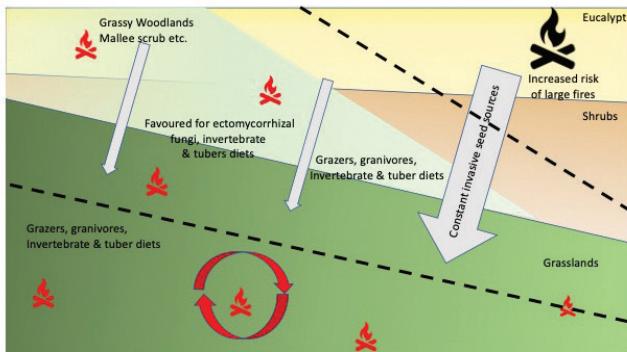


Figure 4: Idealized diagram showing fire regime, grasslands and vegetation having grassy field layer.

consequent vegetation health (Claridge 2002). Fourteen (60%) of the extinct species had fungi in their diets (Table 3). Vernes (2014) found 38 species of fungi in Long-nosed Bandicoot (*Pereameles nasuta*) scats, most common in autumn to winter, confirming the seasonality found in other mammalian studies (e.g. Cheal 1987). Mycophagous mammals preferentially graze on burnt ground with frequent movement between burnt and unburnt habitats (Vernes & Trappe 2007) and exclusion plots have shown lower seedling colonization and an altered community composition without these mammals (Gehring et al. 2002). Frequent fires (c. three- to five-year intervals) reduce the abundance of wood-consuming fungi (due to lack of food), suggesting that a lack of frequent fire would affect fungal grassland communities and probably invertebrates (e.g. York & Lewis 2017). This aspect of the productive pulse requires a grassy field layer and partner vegetation (e.g. grassy woodlands, mallee, open forest) and probably dissipates over large areas of pure grasslands (Figures 4 & 5). The effect of grazing, browsing and predation on burnt areas by the suite of mycophagous, insectivorous, herbivorous and omnivorous mammals (Table 3) was

likely significant on the subsequent floristic communities (e.g. Claridge 2002). Over the millennia, these complex, multi-trophic level interactions would have supported a more stable (and predictable) biota.

Post-fire vegetation and hypogaeal fungi define optimal habitat for the Smoky Mouse (*Pseudomys fumeus*), a species of mesic habitats, where females have heightened breeding success, site fidelity and population stability, in marked contrast with fluctuating, transient populations in sub-optimal habitat (Cockburn 1981; Ford et al. 2003). A similar fire–fungi–density relationship has been recorded for three species of bettong, including the Woylie (*Bettongia penicillata*) (Christensen 1998). A meta-analysis (148 studies) of small mammals found elevated food resources (supplemented) increased reproductive rates, significantly increased population densities by 150%, which became even greater when predation was reduced and populations were open to immigration (Prevedello et al. 2013). Thus, the predictable food resources of the grassland productive pulse would have produced elevated population levels that supported a meta-population in the broader landscape (Figures 5, 6, 7 & 8).

A regime of burning grassland every three to five years maintains the grassy field layer in a stage which optimizes the biological productivity pulse for both human food and a suite of mycophagous, insectivorous and herbivorous mammals (Gott 2005 & 2008) (Tables 2 & 3). This period may be extended in arid grasslands (Table 2). It also removes the fire risk of mature senescent swards. Significantly, this pulse provided vital autumn and winter food during this resource-limited season (see Table 3). Some of these species (e.g. bilby, potoroids, peramelids) are now recognized as ecosystem engineers, individuals moving tonnes of soil per annum (Davies et al. 2019). Elevated population levels of mycophagous and digging mammals would have initiated soil disturbance, spread fungal spores through adjacent environments, enhanced

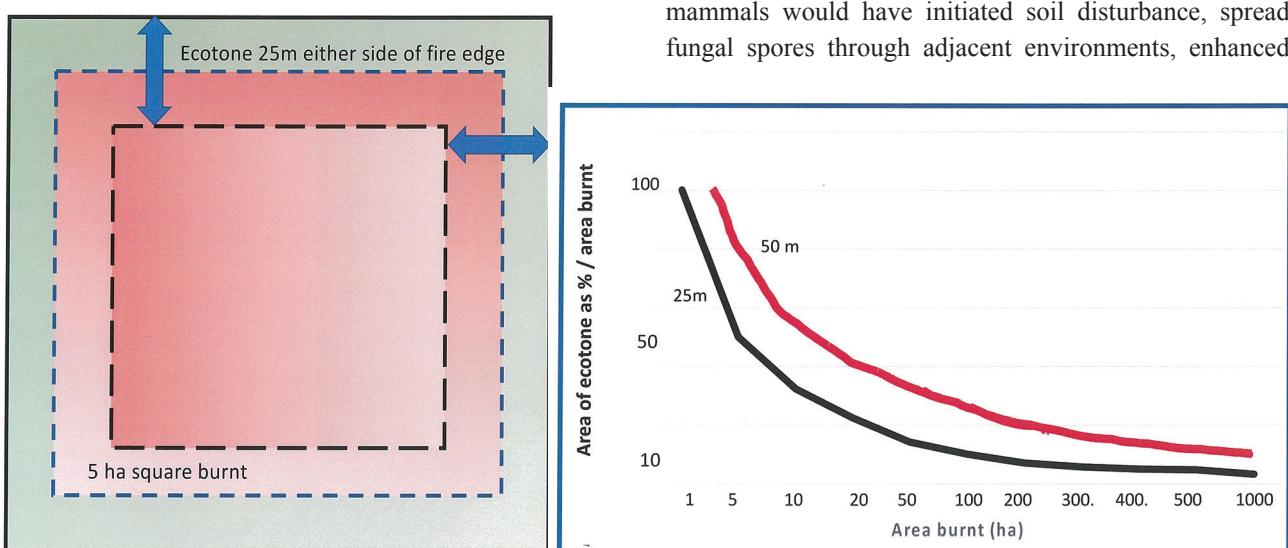


Figure 5: Diagram showing ecotone (25 m either side of the fire boundary edge). Left: 5 ha square. Right: the percentage area of ecotone relative to square area burnt.

Table 3: Extinct mammal species (n=20) of the semi-arid and surrounding landscapes in southeastern Australia, centred around the Murray–Darling confluence, showing habitat, diet, post-fire succession and approximate decade of extinction. Two species of Hairy-nosed Wombats (*Lasiorhinus* spp.) were also present and became extinct (see text).

Codes:

Range & Habitat: (Australian Vegetation communities) (S) = Spinifex; (M) = Semi-arid Mallee; (A) = Acacia Wooded landscapes; (G) = Temperate Lowland Grasslands; (W) = Grassy Temperate Woodlands. * = habitat component associated with post-fire; ** = associated with early post-fire.

Status: Commonwealth EPBC Act listing: extinct, critically endangered, endangered, vulnerable where none or different Mammal Action Plan status provided *in italics* from Woinarski et al. (2015).

Diet: * Major or significant dietary items increase in abundance post-fire.

TO names ^ = identified as Murray or not identified (presumed); # Darling (Barkindji) (Krefft 1866a).

Species Common name (<i>Scientific name</i>) (TO name – Krefft 1866a^ #)	Status	Range and habitat * post-fire ** early post-fire	Diet * post-fire pulse	Regional extinction	Comments	Source
					Soil turnover	(Prendergast 2015)
Chuditch (<i>Dasyurus geoffroii</i>) Ketric ^	End.	Scrubby * (M, G, W)	* Carnivore – Insectivore, small mammals and birds	1860–70s?	Restricted to WA since 1900s (now only in SW); changed fire regimes, feral cats and clearing implicated in decline.	Menkhorst (1995), Serena & Soderquist (1998)
Luaner (<i>D. viverrinus</i>)	Vul. End.	Grasslands, open forest & woodlands ** (G, W)	* Carnivore, insectivore, larvae beetles, small animals	1890s	Depleted populations survived on mainland till 1950s.	Godsell (1982), Abbott (2020), Peacock & Abbott (2013)
Red-tailed Phascogale (<i>Phascogale calura</i>) Kultarr ^	Near threat.	Red Gum and Buloke woodlands * (W)	* Insects, small mammals, birds	mid-1800s?	Arboreal in mature forest but extensive ground feeder.	Bradley (1998), Menkhorst (1995)
Numbat (<i>Myrmecobius fasciatus</i>)	Vul.	Mature, open-forest and woodlands * (A, W)	* (?) Almost exclusively termites (ants incidental)	Probably very early – 1850s	Fire in habitat as preventative burn (see text, ABC 2021). Many termites consume grasses.	(Friend 1998)
*Pig-footed Bandicoot (<i>Chaeropus ecaudatus</i>) Landwang ^	Extinct	Grassy plains, Callitris sand hills, Open Geborro (Box) forest-grassy ground cover ** (G, W, M)	* Specialist herbivore, Eating only most nutritious parts, newgrowth & seeds	c. 1860s?	Type locality in Vic. (1836). Prevailed generally near Murray R., rapidly declining by late 1850s. Diet deduced from dentition. TO knowledge indicated a favoured food was <i>Panicum</i> sp.	Menkhorst (1995), Mitchell (1834), Krefft (1866a), Ashby et al. (1990), Friend (1990), ALA (2021)
Golden Bandicoot (<i>Isoodon auratus</i>)	Vul.	Spinifex (arid) low woodlands over tusock ** (?) (S, M, A, W)	* Insect larvae, termites, roots and tubers	1870s	Common In mid-Murray–Darling (1850s), very rapid decline. Arid zone common till 1930s (see text).	Mackenzie et al. (1998), Menkhorst (1995), Ellis et al. (1991)
Western Barred Bandicoot (<i>Perameles bougainville</i>) Thill ^, Moncat #(?)	End.	<i>Triodia</i> and <i>tussock</i> grasslands, mallee & Grassy Box on plains, Woodlands on sandridges, saltbush ** (S, M, W)	* Omnivorous digger: invertebrates, seeds, roots, herbs & forbs	1850–90s?	Common along Murray River (Krefft (1866a)), heavy soil plains favoured by pastoralist (Menkhorst 1995) and TO-LM. Extinct on mainland, extant on islands off WA. <i>P.gunni</i> : Soil - 2.2 (t/ha/ individual/yr).	Krefft (1866a), Friend (1990), Menkhorst (1995), Kemper (1990), Richards (2012)
Bilby (<i>Macrotis lagotis</i>) Wuirrapur ^ Jecko #	End.	* Variety of arid semi-arid canopy (e.g. <i>Acacia</i> shrubland) with ground cover sometimes sparse, elsewhere spinifex (<i>Triodia</i> , <i>Plectrachne</i> spp.) * (S, M, A)	* (?) Insects and larvae, seeds, bulbs, fruit and fungi	mid-1800s	Remained common in arid zone until rapid decline in early 1900s. Broader diet – benefits from, but less sensitive than other species to, productive pulse. Soil: 1.2–5.99 (t/ha/individual/ yr) - Max. 30 (t/ha/individual/yr).	Krefft (1866a), Johnson (1998), Hercus (1985), Menkhorst (1995)
Rufous Bettong (<i>Aepyprymnus rufescens</i>)	Least concern (Qld)	Open forest and woodland – grassy field ** (G W, R)	* Browse/graze flowers, seeds tubers, roots, (underground) fungi	1900s	A more mesic species, early extinction in riverine and plains, last specimen possibly around Bendigo 1900s.	Dennis & Johnson (1998), Menkhorst (1995)

Woylee or Brush-tailed Bettong (<i>Bettongia penicillata</i>) Pattuck ^	End.	Open forest and woodlands, understorey of tussock grasses/shrubs, Thickets of Tangled Lignum (Vic) ** (M, W, R)	* primarily fungivorous, also bulbs, tubers, insects and resin	1860s?	Common in 1850s, Murray River (Vic.), clumped understorey of tussock grass /low shrub (WA). Soil: 2.6–9.7 (t/ha/individual/yr).	Christensen (1998), Kreft (1866a), Menkhorst (1995)
Boodie or Burrowing Bettong (<i>B. lesueur</i>) Booming ^	Critically End.	Wide range, loamy soil deep enough (burrows), damper low lying in sand ridge country. ** (All)	* Omnivore – tubers, roots, bulbs, seeds, nuts and fungi	1860s	In various parts of Australia “common … many areas the most abundant mammal”. Disappeared from Victoria by 1863, persisted elsewhere till 1930-40s. Shared warrens with rabbits for several decades (WA). Soil: 1.3–6.0 (t/ha/individual/yr).	Burbidge (1998), Richards (2012)
*Eastern Hare-wallaby (<i>Lagorchestes leporides</i>) Turrat ^	Extinct	Tussock grassland ** (G, W)	* Browser-grazer * <i>L. hirsutus</i> eats spinifex but prefers more nutritious forbs and grasses	>1860s	Tolerably abundant 1840s in NSW, common on Murray plains in 1850s, last record 1890 (NSW).	Gould (1863), Krefft (1866a), Strahan (1998a)
Bridled-tailed Wallaby (<i>Onychogalea fraenata</i>) Merrin ^	End.	Grassy woodlands, grasslands ecotone with scrub ** (G, R, W)	* mixed forbs, grasses and browse, chenopods	Probably very early?	Abundant 1840s, most common small macropod along Murray. Elsewhere some pockets remained common (shot for pelts) until 1900s.	Gould (1863), Gordon & Lawrie (1980), DAWE (1997), Kearney et al. (2012)
Wurrung Crescent Nailtail Wallaby (<i>Onychogalea lunata</i>)	Extinct	Central desert (WA), most type of woodland country, favoured Mulga grasslands including Spinifex	*grasses	‘west of the Darling’ disappeared from Flinders Ranges c. 1890s	Single Blandowski specimen. Once common in WA. Disappeared in Finders Ranges c. 1890s, western Desert (c.1940s), last records (WA) 1950s.	Burbidge (1998), Wakefield (1966)
Greater Stick-nest Rat (<i>Leporillus conditor</i>) Koel / Kohl ^	End.	** Samphire shrublands of semi-arid zone, diet of succulents. ** (M, S)	* Herbivorous, succulents	1840–50s	Disappeared from Murray River by 1856. A favoured food source is fire dependent, absent 7 years post fire.	Krefft (1866), Robinson (1998), Ellis (1995), (Parsons 1997)
* Lesser Stick-nest Rat (<i>L. apicalis</i>) Tillikin ^	Extinct	* Samphire shrublands and salt bush. ** (M, S)	Herbivorous, succulents	1860s?	Very common along the Murray 1857. More arboreal than <i>L. apicalis</i> . Late 19 th C at Broken Hill, extinct 1901.	Robinson (1998), Ellis (1995)
* Long-tailed Hopping mouse (<i>Notomys longicaudatus</i>)	Extinct	? clayey soils, associated with Greater Bilby & Boodie in similar habitat * (S, A)	? * Other <i>Notomys</i> , seeds roots, insects	Coonbaralba Ranges (Sturt 1830), presumably very early	Favoured clay soils, c.f. <i>N. mitchelli</i> . Presumed food source (see text). Last specimen 1901–2 in NT.	Ellis (1995), Sturt (1847), Dixon (1998), Gould (1863), Woinarski et al. (2015)
* Gould's Mouse (<i>Psuedomys gouldii</i>)	Extinct	Grassy plains and sand hills ** (G, W)	? *seeds, grasses and other	>1850	Very common and widespread in 1840s, very rapid decline	Gould (1863), Woinarski et al. (2015)
Desert Mouse (<i>Pseudomys desertor</i>)	Least concern	Mature spinifex, Kangaroo Grass	*Predominantly granivore, vegetable matter, insects	?	Common in 1850s. Dry watercourses with dense grass cover (NT). During drought small populations survive in favoured habit (mature spinifex) (Kerle 1995).	Watts (1998), (Krefft 1866a), Watts & Aslin (1981)
Plains Mouse (Rat) (<i>P. australis</i>)	Vul.	Spinifex grassland, dunes and arid riparian woodland ** (S, M)	*Predominantly granivore, vegetable matter, insects	Very early	May exist in large colonies, subject to predation (Dingo, fox and owls) but this not assessed as single reason for decline (Watts 1995).	Watts (1998), Ellis (1995), Watts & Aslin (1981), Kerle (1998)



Figure 6: Woornoonoomal and other 'richly grassed' plains, 12 kilometres west of Ouyen (Bage 1865). Note TO track (lower left) and annotations: (lower) 'Mallee interspersed with ? small richly ? grassed plains'. Extract (8 km x 4 km) from PROV VPRS 8168/P0003, RUN160; NURNURNEMAL OUYEN PAIGNEE. MOURMPAL; BAGE. Map has no scale.

water retention and ecosystem health and also provided sites for plant species establishment (including by disrupting the cryptogamic soil crust). Individual potoroids may turn over more than 9 tonnes/ha/yr (Prendergast (2015)). Some fungi also reduce plant drought stress (Claridge 2002; Tommerup & Bouger 2000; McMullan-Fisher et al. 2011). Regular mosaic grassland burning regenerated nutrients back into sites and the associated eco-engineering mammals optimized *in situ* soil moisture, producing a highly productive self-reinforcing energetically-closed system. Multi-trophic level mammal food for Traditional

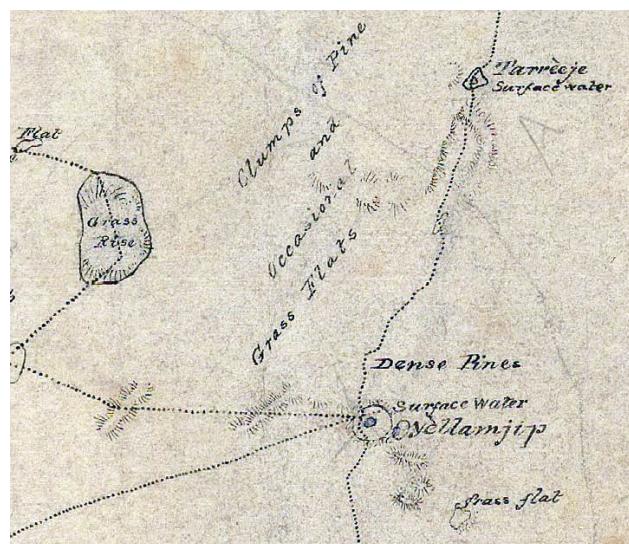


Figure 7: The Walpeup Plain, a large 'Grass Pine' plain 27 kilometres WSW from Ouyen, and 'Grass Flats' (White 1852). Note TO tracks and grassy plains. Extract (25 km x 25 km) from PROV VPRS 8168/P0005, WIMMERA23; SURVEY OF MALLEE SCRUB; WHITE. Original Scale 8 miles to 1 inch.

Owners was more abundant and predictable in time and space (Table 2). Conversely, disruption and elimination of such a management regime would see a rapid decline in habitat quality and consequent mammal populations. In the complete absence of such a fire regime, mammalian populations dependent on this productivity pulse would decline well within a decade (Table 1, Figures 2 & 3).

The area of an ecotone 25 m either side of the perimeter of the fire ground is 50% of a 5 ha fire, 8% of a 50 ha fire, and minimal at 1000 ha, the percentage doubling at 50 m. Smaller patch fires and elongated areas produce relatively large areas of ecotone. The vegetated area of the ecotone provides protective cover (from predation and heat stress; denning sites) for mammals directly adjacent to the productive pulse. Mala (*Lagorchestes hirsutus*) have been recorded travelling 150 m to feed on burnt areas (Bolton & Latz 1978; Vernes & Trappe 2007) and the Eastern Bettong (*Bettongia gaimardi*), may travel 1.5 km between nest and feeding area. Thus a feeding catchment, supporting elevated population levels around a grassland productive pulse, may extend for tens of km² (Figures 5, 6 & 7). Within the burnt grasslands, protective cover for small to medium-sized mammals is achieved around 2–6 years after fire and thereafter access and biological diversity and richness decline as vegetation thickens into senescence (Figure 2). Within a decade after fire, the abundance of palatable human and mammal food and surrounding ecotones disappears and becomes vulnerable to invasion by shrubs, e.g. *Acacia* spp. and/or trees, e.g. *Eucalyptus*, *Allocasuarina*, *Callitris* and *Myoporum* spp. (Figures 3 and 4).

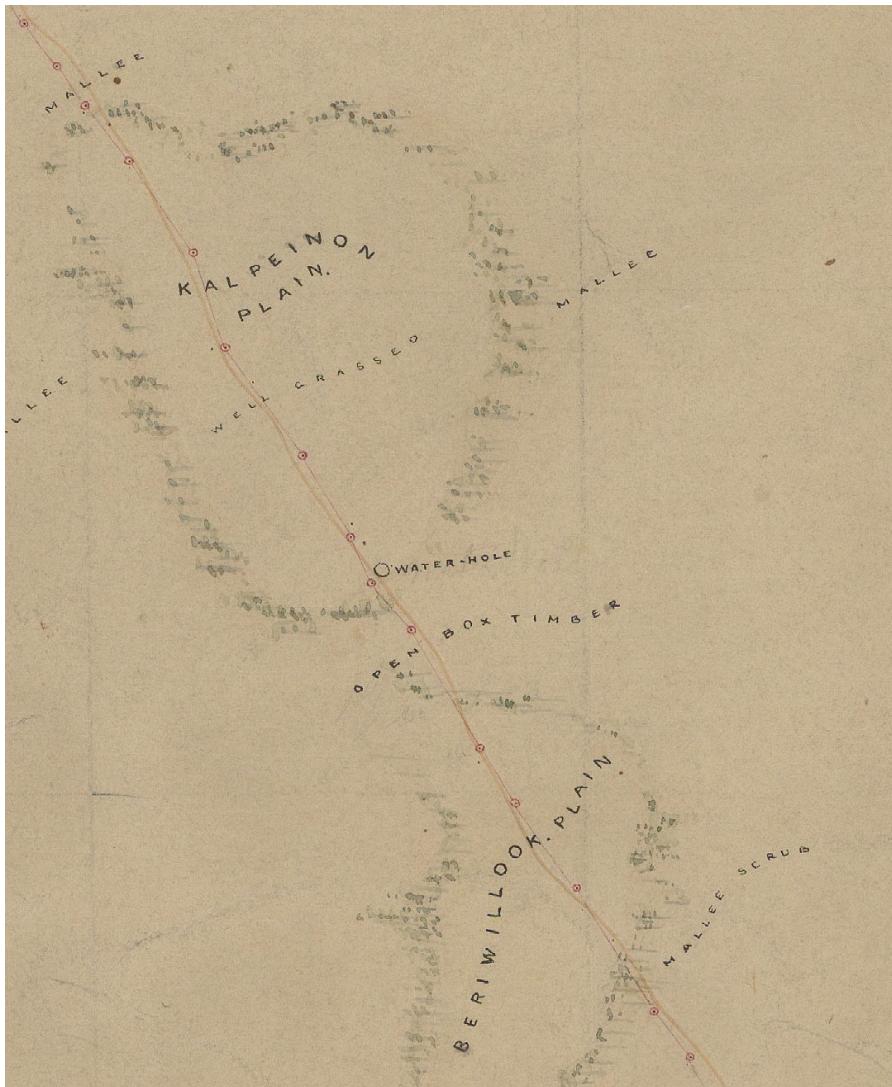


Figure 8: Kalpeinon and Beriwillook plains, about 42 kilometres SW of Swan Hill, on a TO pathway between Lake Tyrell and Lake Lalbert (Pritchard 1851). It shows a TO well and pathway moving through a patchwork of plains: label on Kalpeinon reads 'well grassed'. Extract (4 km x 4 km) from PROV VPRS 8168/P0005, WIMMERA1; ROAD FROM MOORTHOORRA TO LALBERT. Original Scale 2 inches to 1 mile.

Tolerable Fire Intervals (to maintain a vegetation community) and recovery times under different fire intensities and frequencies are short in grasslands (Cheal 2010) (Table 1). Grassy field layers (under several shrub and canopy types) can be maintained (or created) by a burning regime of a low intensity fire every three to five years, e.g. Grassy Woodland of north-western Victoria (Cheal 2010; Table 2). The relative lack of litter (burnable material) under shrubs and around tree-trunks means that a low intensity fire can maintain the grassy field layer (Cheal 2010) while only minimally impacting on the canopy trees. Fire kills young (emergent) shrubs and trees, conserving the advantage of grassland species and assisting *in situ* regeneration. The extensive, fire-sensitive chenopod shrublands (alluvial black soil plains / alkaline soils) can survive low intensity fires (at longer intervals) which would protect them from high intensity fires (Table 1). Fire resistant cryptogamic crusts in grasslands help conserve moisture, inhibit invasion of exotic plants and thus tend to conserve grassland *in situ* (Morgan 2006 & 2015). A slightly more intense fire kills the shrub layer and

extends the grassland (Cheal 2010; Stefferson 2020). Grass species are adapted to relatively frequent fire. Almost half the grasses of western NSW significantly increase their germination in presence of smoke (Native Millet *Panicum decompositum* from 7.7 to 63.1%, *P. effusum* from 0 to 16.7%) while germination of less-productive invasive natives, e.g. C3 *Austrostipa scabra* is reduced (30.2 to 19.9%) (Read & Bellairs 1999).

Edward Curr (1883) estimated that the whole country was burnt every five years and saw the results of TO-LM — tussocks on Victoria's northern plains grew 0.6–6m apart. The TO-LM fire regime supported the extent of the taller, perennial tussock grasses (C3 species *Austrostipa bigeniculata*, *A. aristiglumis*, *Poa labillardierei* and others; the C4 species — *Themeda triandra*, *T. avenacea*, *Homopholis proluta*, *Eragrostis* spp. and others) and annuals such as Native Millet (Cahir & McMaster 2018; McIvor 2005; Morgan & Lunt 1999). The tetraploid, semi-arid variant of *T. triandra*, now highly restricted, was probably more widespread, affecting the productivity and flammability of the semi-arid grassland (see Box 2, Morgan

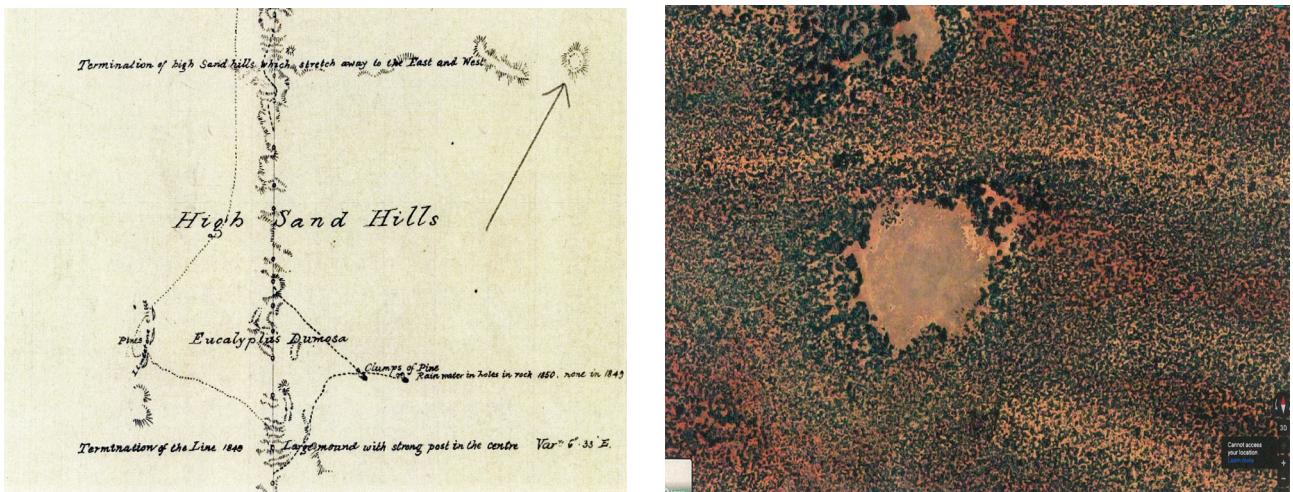


Figure 9: Mapped (White 1850) but not labelled (left), this plain (right) was viewed as an unexplained anomaly when vegetation was mapped for the Land Conservation Council in the late 1980s, but it persists to the present. Source: Google Earth imagery, TerraMetrics, 2021, Peter Woodgate, pers. comm. Aug. 2021.

pers. comm. June 2021). The absence of TO-LM would see the decline of the warm-season (C4) species (e.g. *T. triandra*) and, with grazing and associated changed fire regimes the invasion of these grasslands and shrublands by less productive winter-season species would be accelerated (e.g. *Austrostipa* spp.) (McIvor 2005; Allen 1983 and references therein).

At the meso- and macro-scale, patch burning across fire prone environments has other impacts in the reduction of large bushfires, enhancement of habitat heterogeneity and the extent of mature long-unburnt vegetation (Bird et al. 2013; Trauernicht et al. 2015). Over the millennia, all of these attributes enhanced mammal abundance, diversity and persistence. The absence of patch burning elicits changes well within decades. In 1953, when many Martu left their arid country in WA, the mean size of fires was 62 ha. Upon their return in 1981 the mean size of fires was 52 000 ha. The extent of all types of mature vegetation had dramatically declined and the Boodie (*Bettongia lesueur*) had become extinct over this 30-year period (Bird et al. 2013). Perhaps coincidentally, the first major bushfire in our region burnt through the Wimmera (and much of Victoria) on 6 February 1851 (Clarke et al. 2021). Traditional Owner fires are embedded in many Australian ecosystems but fire regimes have dramatically changed since European colonization (Tindale 1959; Latz 1995b; Gott 2005 & 2008; Cahir & McMaster 2018) (Figure 3).

Traditional Owner use of fire

Context

Tindale (1959) was one of the earlier anthropologists to see the scale of Traditional Owners as ecological agents using fire: ‘Thus man probably has had a significant hand in the moulding of the present configuration of parts of Australia.

Indeed, much of the grasslands of Australia could have been brought into being as a result of his exploitation.’ Since then, our understanding of the sophistication of Traditional Owner use of fire in land management has dramatically increased (Gott 2005 & 2008; Cahir & McMaster 2018; Cahir et al. 2016; Sutton & Walshe 2021). Traditional Owners used fire for a wide range of reasons, including hunting, food gathering, clearing travel ways, vermin control, signalling and cooking. Wik elders maintained that the main purpose for firing patches of country was to make the country ‘open and safe for travelling on foot … open enough to see long distances beyond camps. People also knew that firing incidentally led to green pick that drew marsupials to recently burned areas, but this was not its main purpose’ (Sutton & Walshe 2021). In the arid zone Latz and Griffin (1978) concluded: ‘Burning appears to have been almost habitual and the effect so self-evident that the two events, burning followed by food increase, were seen to be almost synonymous providing religious duties were maintained’ (see also Peasley 2009). TO-LM and fire were mediated through their dreaming (ceremonies, totems, rites etc.), embedded in which was a deep understanding of ecology that sought to sustain the status quo (Elkin 1933; Newsome 1980; Bates 1985; Davenport et al. 2005a,b; Bird et al. 2013; Sutton & Walshe 2021). Knowledge directly from elders showed that grassy field layers and their substrates were important determinants in traditional burning techniques that helped determine ‘fire country and non-fire country’ (Skroblin et al. 2017; Stefferson 2020). In the arid and semi-arid zone, the good rain-grass-fuel load would have determined the ‘when’ and ‘where’ of fires, so as to avoid risk of later larger conflagrations (e.g. Bradstock et al. 2002). TO-LM produced fine-grained mosaics and created locally predictable food resources i.e. preferred



Figure 10: Persisting grasslands within Victorian mallee country. The yellow-flowered daisy (*Podolepis aristata* subsp. *affinis*) is almost solely restricted to these grassland patches and the thickened root provided TO and mammal food (Gott 2008). Note: Sharp boundary between grassland and surrounding mallee with no topographic or obvious soil changes; and the absence of stumps and logs indicate it was not a prior Buloke or Belah woodland. Photograph: D. Cheal.

flora and fauna habitat (Burbidge 1985, Latz 1995a; Gott 2005 & 2008; Gammie 2012; Bliege Bird et al. 2008).

The mid Murray–Darling

Prior to European settlement, the riverine–grassland economy along the Murray River supported among the highest densities of Traditional Owner populations on the continent. These had increased, intensified resource use and become more complex over the previous 2000 years (Allen 1972; Williams et al. 2015; Burch 2017; Sutton & Walshe 2021). Most European explorers commented on the frequency of the Traditional Owners' use of fire (Cahir et al. 2016). Along the Darling River in 1835 Mitchell (1838) observed: 'the new grass springing up in places where it had been burnt presented a shining verdure' (11 April, 1835) and 'the thick scrub having been previously burnt' [June 5] and on 19 June observed Traditional Owner haystacks of *Panicum* (Native Millet) 'extended for miles' growing almost as a monoculture but interspersed with 'smaller heaps' of Yam-daisies (*Microseris*). Such environments require fire and are natal areas of Bogong Moths (Green et al. 2021; Box 2). In 1836, Mitchell observed of Dja Dja Wurrung country: 'On highest mountains and in places the most remote and desolate, I have always found every dead trunk on the ground and any living tree of any magnitude also, the marks of fire; and thus it appeared that these annual conflagrations extend to every place' (Mitchell 1838; Golding 2018). Hawdon (1952) noted on the riverine corridor of the Murray (20 February 1838): 'The stock had scarcely anything to eat,

the Natives having set fire to everything in the shape of food ...'. Whether this observation was TO-LM, or at that time, an intentional act of resistance to invasion we do not know; however, apart from Beilby (1849) this is among the last records of extensive burning that we found in the region (apart from recent times).

Cahir and McMaster (2018) examined the early Europeans' observations of Traditional Owner use of fire in Victoria, concluding that burning practices were managed, frequent and generally over small areas of grassland plain. Some of their observations are pertinent to our narrative, recognising, as they did, that these are a subset of a much depleted TO-LM system. The Traditional Owners in central Victoria were 'In the habit of burning off the old grass so as to have good fresh grass for their kangaroos, wallabies, emus, turkeys and other smaller granivores birds' (Lang 1847) and they were 'careful to see that no harm was done to the vegetables that yielded food' (Smyth 1878) and 'aboriginal fires were common and docile during the summer' (Murray 1843). Observers noted that fires were also commonly used around water courses (e.g. Curr 1883). John Webster (quoted in Cahir et al. 2018), an overlander, would observe near the border of Victoria and South Australia (Meru country) (Dec. 1840, p. 123) 'the firing of the grass had been quite recent' and, along the grassy river flats of the Murrumbidgee and the Murray (Dec. 1840, p. 123) 'all the trees here ... bear the evidence of frequent fires ... caused by many years of conflagrations of grass' and a fortnight later witnessed TO firing in which 'the dry portions of the grass only were consumed'. Also,

along the Murray River near Swan Hill, James Kirby, a drover, observed (1840) ‘in the distance where the blacks had not burnt reeds, it looked like large fields of ripe wheat; and near where they had burnt them, it had the appearance of a splendid crop just before it comes to ear’. Reed beds were patch burnt for food, habitat and spear shafts (Curr 1883). In July 1841, winter burning of Yam Daisies, which increased yields, (*Microseris*) was observed by Robinson (Gott 2005 & 2008; Cahir & McMaster 2018).

Traditional Owners of the region had substantial sedentary camps/congregation places; each group conducted seasonal movements (always carrying a fire stick) to ‘care for their country’ across the landscape (Dawson 2009; Gott 2005; Gammage 2012; Burch 2017 & 2018; Cahir et al. 2018; Stefferson 2020). Patch burning of grasslands (including wetland verges) kept them at their most productive for food resources (Gott 2005; Gott et al. 2015; Cahir & McMaster 2018) (Figure 3, Table 2). Furthermore, Bird et al. (2008) found that for foragers, particularly of small game, the fire-induced habitat heterogeneity was important as it directly affected catch per unit effort (see Figure 8) and prevented habitat loss. Seasonal movements would also allow management of special sites (refugia) required for persistence across drought, flood and climatic variations. Early Europeans frequently described the artefacts of Traditional Owner management, grasslands and grassy woodlands of park-like appearance despite being within a very fire-prone environment. Areas of extensive bushfires were not observed. It would be several decades after 1830 that large bushfires would become an environmental feature in the study area.

Grasslands and TO-LM in the Victorian Mallee

Brough Smyth (Smyth 1878) considered the Mallee an ‘impenetrable thicket’. However, it supported more grasslands than this assessment indicates. The extent of Traditional Owners’ occupation and use of the Victorian Mallee has been contentious. Recent research, some of which related to use of grasslands, is suggestive of TO-LM (White et al. 2003; Burch in prep., Beilby 1849). In early cartographic material, there are frequent references to grassy plains (Burch et al. 2020; Burch in prep.). The light pastoral use of parts of the Victorian Mallee between the late 1840s and the start of agricultural settlement from the late 1880s through to the 1920s has meant that evidence of earlier Traditional Owner land use has survived in maps and records made for land subdivision (Burch et al. 2020). Furthermore, Aboriginal grinding stones have been found across ‘the mallee’ (Ross 1984) suggesting long-term Traditional Owner presence. We contend that such management benefited the mammal fauna. Once ceased, mammals disappeared even with no or minimal grazing.

References to ‘park-like landscapes,’ so frequent in the grasslands and grassy woodlands, were very infrequent in the Mallee. In 1865 a private surveyor, Edmund Bage, recorded the presence of a large waterless plain [Woornoonoomal], over 2000 acres (~800 ha), southwest of Ouyen (Bage 1865) (Figure 6). Furthermore, extensive areas around saline discharge boinkas were probably naturally grassy, but have converged towards chenopod shrublands due to past grazing pressures from stock (Sluiter pers. comm. 2021). The presence of this rich grassland (Woornoonoomal) was confirmed by Nathaniel McKay in 1891 with mapping suggesting the presence of smaller plains alongside (Burch 2018). We contend that such waterless plains are artefacts of TO-LM, but were probably not maintained for the free-water-dependent large macropods, rather the mammalian Traditional Owner food resources in Table 3. Woylies (*Bettongia penicillata*) were recorded from the southern Murray mallee (Menhorst & Beardsell 1982). Represented in Murray River archaeological sites, *Bettongia penicillata* were a consistent feature of Aboriginal hunting over the past 6000 years, but have not been recorded on the Murray Plains since shortly after European settlement (Fusco et al. 2015). These species can persist, without drinking free water and can occupy habitats such as at Woornoonoomal (Strahan 1998a) (Table 3). By 1891, after a good season and with abandoned pastoral wells providing new water sources, Woornoonoomal was hosting large numbers of the larger macropods. The most significant ‘park-like landscape’ is the Walpeup ‘parklands’ west of Ouyen, mapped by Edward Riggs White (White 1852). Walpeup appears to be a derivation from the Wergaia word ‘Walpa’ meaning fire (Ryan 2022: 297). In 1908 a party assessing the possibility of a railway west from Ouyen described the Walpeup Plain (remnant woodland): ‘Its richness and the beauty of the vegetation were a surprise. I have seen nothing in Northern Victoria to equal the latter. For miles in all directions belts and clumps of pine, myall, belar, bulloak and apple bush were growing in rich luxuriance. It was like a great park on which infinite skill had been expended to produce striking landscape effects’ (*The Argus* Tuesday 28 January 1908, p. 5). These are now very open Buloke Woodlands from Walpeup north to Pink Lakes, scattered grassland remnants of which persist throughout the Central Sunset country.

The first settlers of Ouyen found a similar, if smaller, ‘park’ just to the west of the Ouyen Plain, suggestive of mature trees over a grassy field layer long managed by fire: ‘there is a magnificent beauty spot, known locally as the “Fairy Dell”. It is a gorge situated between two pine ridges. Here there is a natural plantation of stately pines that give the “Dell” quite a parklike appearance’ (*Weekly Times* 21 November 1908 p. 44).

Large plains and parks are infrequent in the Mallee back country, but references to small grassy plains occur frequently in surveyors' reports in the Victorian Public Records Office. In the Wimmera 23 report and map, it is noted that east of Walpeup 'Clumps of pines and occasional grass flats' occurred, the latter mapped in the southeast corner of the map (White 1852) (Figure 7).

Examination of pre-agricultural maps reveals evidence of further small grassy plains suggestive of human involvement in their maintenance (Burch et al. 2020; Burch in prep.). Given the rapid and recent (perhaps c.1000 y BP) expansion of the mallee (Luly 1990) these grassy plains, often associated with Traditional Owner wells (Sandell 2011), are suggestive of TO-LM that sought to keep the landscape habitable through patch burning of grasslands. Burning the larger grassland plains and 'parks' in combination with smaller grassy areas would have provided networks of productive pulses of habitat heterogeneity and predictable food across the landscape. We suggest that such management would have promoted persistence of meta-populations of some of the extinct Mallee mammals in Table 3. The early cartographers were searching for pasture that perhaps had not burnt for over two decades, but remained significant enough in the landscape of the 1850–60s to be mapped. Many of those that did not go directly under the plough (1880s and onwards) appear to have been quickly subsumed by either encroaching mallee eucalypts or trashed, as they surrounded Traditional Owner wells that were converted to 'tanks' (White et al. 2003; Sandell 2011). Most were not identifiable in later vegetation surveys; however, a few survived to the present (Figure 9).

In remote areas of the Mallee, active, albeit probably much depleted, TO-LM continued or resumed, probably into the 1850s, and mammal populations survived. During a short but extensive trip through the Big Desert and Sunset Country, Beilby (1849) observed distant Traditional Owner burning and, on 6 and 8 October, grassy oases and grassy knolls with Traditional Owner wells: 'a sandy desert which had been covered with heath, but was lately burnt' and 'crossed a long grassy plain fringed with lofty pine and she-oak, with clumps of high mallay studding it here and there. This plain contained about 600 acres and was well grassed' and 'a tract of mallay which had been burnt two or three years ago' and 'the little vegetation they (sandhills) support having been recently burnt' and 'we struck upon a patch of very luxuriant grass and herbs, situate between two scrubby hills, and fenced in like a paddock by a fringe of dense high mallay'. He concluded that the Traditional Owners 'resort here in considerable numbers during the seasons ... There were many old miamias on the ridge around the well, and incredible quantities of the bones of small animals or birds,

and egg shells'. Travelling through same country, Morton (1861 in Bennett et al. 1989) observed many 'kangaroo rats' (likely Woylies), wallaby (?Bridled Nailtail) and pademelons (Eastern Hare-wallaby) — the last two being particularly abundant near grassy clearings or open mallee.

Early European contact and Traditional Owner depopulation

In 1829, Charles Sturt, the first European to explore the lower Murray–Darling region, entered a region of relatively high population density of Indigenous people and a managed productive grasslands environment (Williams et al. 2015; Burch 2017; Sutton & Walshe 2021). In early 1830, approaching the confluence with the Darling River, Sturt was confronted by 600 Aboriginal warriors arrayed for battle. Conflict was avoided and such mass Indigenous military strength was never recorded again; however, other forms of resistance continued (Christie 1979; Elder 1998; Burch 2017).

Sturt's parties in 1829 and 1830 were probably the only colonial settlers to have an opportunity to observe the Aboriginal communities of the Murray–Darling and their land management before they were devastated by the impacts of settlement. The first impact was the introduction of smallpox. Smallpox may have reached the region in the early 1800s, but an epidemic was observed by Sturt along the Darling River in 1829, killing Traditional Owners in 'great numbers'. The oral history of Aboriginal people remembered the progress of smallpox along the Murray River in 1830 and its devastation of the semi-sedentary communities of the riverine corridor. One report suggested that the community of Kulkyne was subsequently deserted for a period (Burch 2017). Such destruction is entirely consistent with the 80–90+% loss of life in native American communities devastated by smallpox (Cronon 1983).

Mitchell explored the much-depleted Murray–Darling in 1834 and 1836 but there was no rush to settle the area. For the next decade much of the Murray–Darling was simply traversed by 'overlanders' droving sheep and cattle from Melbourne and Sydney to Adelaide. Pastoral settlement did not commence in many areas until the late 1840s. The invasion of squatters is well documented for Victoria (e.g. Curr 1883; Kenyon 1914–15; Ballinger 2011; Burch 2017) and New South Wales (Jervis 1949 & 1956; Bean 1956). It began in 1840 and by 1847, where water was available, sheep (still enclosed at night) and cattle grazed areas of grassland. However, large areas of drier country remained ungrazed in remote parts — the Big Desert, Sunset Country and northern Riverine plains — and TO-LM persisted in these areas (Beilby 1849; Allen 1983). Pastoral occupation was not continuous. On the Darling, Traditional Owner resistance led to the abandonment of some stations. Nevertheless, all riverside stations were

retaken by 1860, with some subsequently abandoned in the drought of the 1890s (Allen 1972; Christie 1979). In the Victorian Mallee much of the back country was abandoned after drought, and the invasion of rabbits, in the mid to late 1870s, and remained unoccupied into the twentieth century (Burch 2017).

The devastation of Aboriginal communities continued during these ‘overlanding’ and pastoral periods. Sturt managed contact with Aboriginal communities well, but others did not, and massacres occurred. Mitchell’s party committed a massacre at Mt Dispersion in 1836 and another occurred at Rufus River in 1841. Lyndall Ryan (2022) has led a project mapping massacres across Australia and this documents other massacres along the Murray. Two massacres associated with the overlanding period occurred near the junction of the Murray and the Darling, and two others, one at the junction of the Murray and the Murrumbidgee and the other at Beveridge Island, arose out of conflict with pastoral settlers. Undoubtedly other, undocumented, massacres occurred.

Pastoral settlement continued, if not accelerated, the decline in Traditional Owner populations. New diseases were introduced, leading to already depleted populations declining by 50% in the first five years of colonial settlement (Burch 2017). Smallpox recurred with a further outbreak in 1850 killing an estimated 30% of the surviving population of the Darling River Barkindji (Allen 1972; Mitchell 1835; Dowling 2021). Syphilis became endemic with infection rates among the Dja Dja Wurrung along the Loddon River going from 3% to 90% (Curr 1883; Christie 1979; Cannon 1990; Elder 1998; Cahir & McMaster 2018; Dowling 2021). Upon arrival at Tongala near the Murray River in 1841, Curr (1883) observed a remnant Bangerang people, describing what we would now call population trauma, who suffered a further 60% loss of its tribe over the next decade.

Pastoral settlement targeted Traditional Owner-managed grasslands, destroying Aboriginal communities’ food and economy. In 1840, north-central Victoria supported ‘millions of murnong [Microseris] all over the plain and sheep grazing could make it disappear within 2 years’ (Curr 1883; G. Robinson in Clark 1998; Ballinger 2011 (large macropods were not common in these areas at the time)). Although large macropods selectively graze Murnong to the detriment of its local abundance (Sluiter pers. comm. 2021), introduced ungulates were the major cause of this mass decline. However, witnessing such degradation, Curr (1883), attributed the absence of Traditional Owner regenerative grassland fire to the productivity loss of the grasslands.

A much-depleted burning regime persisted (for food and caring for country, see observations above) but an

inability to maintain landscape scale TO-LM in the face of such depopulation and disruption was inevitable. We contend landscape scale TO-LM became functionally extinct across the southern half of the study area soon after 1830 (Burch 2017; Cahir & McMaster 2018) and the grasslands’ productive pulse disappeared. In the drier northern Riverina, the delayed presence of squatters allowed a depleted form of TO-LM to continue until the 1880s (Allen 1983).

Extinct and depleted species, their habitats and TO-LM

Over the Holocene, until the last few centuries, mammal species would have adjusted their distributions and abundances (periods of refugia and radiation) to adapt to changing availability of habitats across the region. Likewise, TO-LM would have adapted patch burning to ensure predictable food supply (including mammals) across the fluxes and variegated vegetation of their country. Empirical data indicate such landscape management can be accomplished even at very low densities of intact Traditional Owner populations (e.g. Bird et al. 2013). This meant more predictable habitat and food resources and a consequent reduction in extensive bushfires, all of which advantaged mammals and maintained population levels (Bird et al. 2013). Species would have responded to the post-fire productive pulse of grasslands, edaphic factors and inter-specific competition.

Over the generations, traditional owners would have acquired and utilized intimate knowledge of mammal populations and favoured habitats. This knowledge base would have evolved to include responses to climatic change, droughts, floods and fire (bush fires and patch burning). The productive pulse described here would have been easily observed for people travelling country and attending to a multi-trophic level diet. In an oral culture such knowledge would have been woven into their dreaming (rites, totemic system, ceremonies etc.) (Sutton & Walshe 2021). Newsome (1980) described the convergence of ecology and traditional beliefs of the Dreaming of the Arunta. Their sacred site for the totemic Red Kangaroo (*Macropus rufus*) was the drought refugium and its song-lines the dispersion paths post-drought. The Martu understood niche creation and predator-prey relationship (Bird et al. 2013). The Gunditjmara explained the demise of a favoured food (honey dew) was due to consumption by the over-abundance of the Common Brushtail Possum (*Trichosurus vulpecula*) caused by the eradication of the Dingo (*Canis dingo*) (Dawson 2009). Traditional Owner relocation of Brushtail Possums occurred in the Riverina, and although such observations are rare in the literature, they may well have been more common (Sutton & Walshe 2021). There are numerous contemporaneous extinctions

of semi-arid clans and their mammalian clan totems across the Nullarbor Plain (Boodie, Southern Hairy-nosed Wombat) suggestive of a profound interconnection (Bates 1985). Howitt (1904) recorded totems of peoples in the region that included many of the mammals listed in Table 3.

The Blandowski Expedition (1856–57) was the first (and only for more than 100 years) detailed fauna survey of the region. Its zoologist, G. Krefft, collected the last record of 13 of the 27 mammal taxa (c. 40% of the total mammalian fauna) that would become extinct in the region. This became the invaluable baseline for numerous assessments of the mammalian collapse (Krefft 1865a; Bennett et al. 1989; Dickman 1993; Menkhurst 2009; Allen 2009 & 2010; Table 3). Comprehensive assessments of the mammal fauna have recorded rapid extinctions of the larger rodents, bandicoots and small macropodids (size range 0.15–1.6 kg) (Bennett et al. 1989; Dickman 1993; Menkhurst 2009). Krefft (1865a) relied on Traditional Owner collectors who knew the when and where of the species' habitats. We take his (most likely those of the Nyeri Nyeri) assessments of relative abundance at the time (common to rare) as we now understand these terms.

Similar to archaeological records, Krefft observed that by 1857 small and medium-sized (Critical Weight Range) mammals remained important in the daily diet: 'Native cats (*Dasyurus geoffroii*), all species of rats and mice, and the smallest wallabies (*Halmaturus*) are also eaten, and some of them obtained almost every day' (Allen 1972; Krefft 1865a).

These extinct mammal species are discussed in relation to their dependency on the post-fire productivity pulse of grasslands (Figures 2 & 3) and to TO-LM. The declining conservation status of these species (and relatives) across the continent over the next century is examined to test the veracity of this eco-historical postulation. The fate of large, more generalist grazers (*Macropus* spp.) provides the contrast. The initial critical factor that pushed the suite of mammals into the extinction vortex was not their CWR (size) per se but the disappearance of the productivity pulse that supported their niches and food availability. Depleted food, habitat fragmentation and decreased populations were then increasingly vulnerable to the spread and population increases of Red Foxes and feral cats.

Physiological aspects may have helped determine population collapse or survival and expansion. The Field Metabolic Rate (FMR) and water influx of arid-zone marsupials are 35% less than similar sized mesic species (eutherian mammal equivalent is 30% less), with smaller species having higher metabolic rates than larger macropod species (Withers 1992; Nagy & Bradshaw 1991 and 2000; Pavey et al. 2009; Riek & Bruggeman 2013). Higher

metabolic rates and ability to extract water from food meant that the abundance and persistence of small to medium-sized species (Table 3) benefited from the productive pulse at the landscape scale of TO-LM. Furthermore, while some small to medium-sized heterothermic species (e.g. dasyurids, myrmecobiids) can utilize energy-saving torpor, this is not available to homeothermic species such as bandicoots, small macropods and, we predict, bettongs, which would increase their vulnerability to food depletion (Geiser & Kortner 2010; Geiser pers. comm. 2021). In addition, the soon extinct rodents were genetically robust at the time of European settlement, so genetic impoverishment is not an argument for their decline (Roycroft et al. 2021).

The species

Twenty-four species were recorded, four of which became extinct very quickly; the others have extant (mostly remnant and small) populations elsewhere in Australia (see below and Table 3). Whatever the macro-habitat, most species, through their diets (or nesting requirements), have a meso- or micro-habitat component that consists of, or is enhanced by, or otherwise includes, some form of fire-managed grassland or grassy field layer, from *Triodia* to other grasses (Table 3) or other habitat consequent of TO-LM. All species described below were Traditional Owner food sources.

Potoroids, Peramelids and Bilby

The potoroids, three species of bettongs, are larger than the bandicoots, more fungivorous and associated with grasslands and grassy field layers and fire (e.g. Johnson 1997). They all declined rapidly (Strahan 1998a; Menkhurst 2009). The *Bettongia penicillata* favours clumped low field layers of tussock grass, in places under a eucalypt canopy, and has a diet largely of hypogea fungi supplemented by bulbs and tubers. Fire does not seem to induce stress in Woylies (Hing et al. 2017). In 1857, it remained common in thickets of lignum (*Duma florulenta* and *D. horrida*) along the Murray River, riverine Black Box and channel country in the southern Mallee and northern Wimmera (Kreft 1865a; Menkhurst 1995; Sluiter pers. comm. 2021). Many early observers noted the Boodie (*B. lesueur*) as the most abundant native animal across the semi-arid/arid zone but it had disappeared from Victoria by 1863 (Burbidge 1998). Fungi are an important part of its diet, as are bulbs and tubers, and communal warrens are dug in the moister parts of the environment (Burbidge 1998; see also Winter & Johnson 1998). Clans across the Nullarbor took their names from food sources most important in their country; hence one clan was the Boodie people = Boodie country (Bates 1985).

The Rufous Bettong (*Aepyprymnus rufescens*) is a more mesic species and a southern, disjunct population was centred around the Murray River (Menkhurst 1995), where its habitat of mesic tussock grasslands *Poa* spp. was actively managed by Traditional Owner fires (see Webster's observations *op. cit.*). The tubers (*Eleocharis*, *Cynogeton*, *Typha* spp.) in reed beds (actively managed by Traditional Owners) may also have been an important part of its habitat (Curr 1883). It eats roots, tubers and fungi (where abundant), particularly in dry times when browse is sparse (Dennis & Johnson 1998). Once common east of Euston (Krefft 1865a), it rapidly disappeared from the plains. The last Victorian specimen was obtained from near Bendigo at the end of the nineteenth century (Table 3).

Peramelid populations typically move to exploit post-fire habitats and are predominantly insectivorous, with bilbies more carnivorous. These species also exploit tubers, fruit and small animals and dig for dietary items, with the importance of their mycophagy increasingly recognized (Strahan 1998a; Seebeck et al. 1990; Tommerup & Bouger 2000; Claridge 2002). This region was the first to experience the collapse of the peramelid fauna that continued across the arid–semi-arid zone over the next century. Krefft (1865a) observed that the Western Barred Bandicoot (subspecies of *Perameles bougainville*) remained 'common on all parts the Murray River in 1857' but along with the Pig-footed Bandicoot (*Chaeropus ecaudatus*) rapidly entered a trajectory of continental decline (Krefft 1865a; Kemper 1990; Friend 1990; Johnson & Burbidge 1998). We interpret Krefft's term 'common' to mean specimens being readily available to his Traditional Owner collectors. That said, grassy habitats over the fertile heavy clay soils in northwestern Victoria and the extensive Mallee–Box community that had been maintained by TO burning were preferentially selected by early pastoralists. The Golden Bandicoot (*Isoodon auratus*) had a wide range across arid Australia in habitats associated with spinifex (arid) and other tussock woodland–grasslands, which had field layers burnt by Traditional Owners (Davenport et al. 2005a; Bird et al. 2013; Sutton & Walshe 2021). The peramelid species rapidly declined in this region and a century later (1930–50s) in the arid zone, broadly coinciding with decline in TO-LM (Ashby et al. 1990; Burbidge et al. 1988; Friend 1990; Menkhurst & Seebeck 1990; Ellis et al. 1991; McKenzie et al. 1998). The decline of what was recorded as *Isoodon obesulus* in the semi-arid zone has been attributed to the cessation of Traditional Owner patch burning (Braithwaite 1998). The biology and life history strategies of this species are relatively well studied within current mesic environments — a diet of fungi, invertebrates, seeds and subterranean vegetable matter and a habitat of post-fire dry heathland (Seebeck et

al. 1990; Opie et al. 1990; Braithwaite 1998). This species is not included in Table 3.

In contrast with other bandicoots, the Pig-footed Bandicoot (*Chaeropus ecaudatus*) was the most herbivorous of the bandicoots feeding on coarse native millet (?*Panicum decompositum*) (Nyeri Nyeri knowledge to Krefft 1865a) but Central Australian Traditional Owners observed that it ate ants, termites and roots. Mitchell obtained the first specimen in 1834 from the grassy plains near the Murray–Murrumbidgee confluence. But by 1857 it had declined to be 'exceeding rare'. The last record in NSW to the north of our study area was in 1845 (Atlas of Living Australia 2021). The lack of grassland burning and resultant productivity loss rapidly pushed this specialist herbivore into the extinction vortex. Pig-footed Bandicoots survived longer in the arid zone and in Traditional Owner memory with the progressive decline to extinction broadly coinciding with curtailment of TO-LM between 1920 and 1950 (Friend 1990; Kemper 1990).

The potoroids, peramelids and bilbies are now recognized as soil engineers, each individual moving tonnes of soil/ha/year (Claridge 2002; Davies et al. 2019; Prendergast 2015). The food available in the grassland productivity pulse increased populations of these species and reinforced their productivity and resilience. An early observer noted that Long-tailed Hopping-mice (*Notomys longicaudatus*) were 'very partial to the mounds thrown up' by the Boodie and Greater Bilby (Gould 1863; Dixon 1998) (Table 3). Once patch burning ceased, adverse change (increased desiccation, lack of regeneration, collapse of predator–prey mosaic relationships) would have very rapidly cascaded through and across ecosystems.

Outside the region, TO-LM continued for decades and many mammals persisted in such regions (Table 3). In 1899–1900, when the Wangkangurru people walked off their country in the eastern Simpson Desert (SA), the Greater Bilby and Eastern Hare-wallaby (Table 3) were still common food resources (Hercus 1985). These then disappeared in less than two decades (Jones 1923). The Martu people of the WA desert had burnt mature *Triodia* grass hummocks in the cool-dry season to capture the Greater Bilby (*Macrotis lagotis*), Boodie and the Rufous Hare-wallaby. The latter two disappeared after many Traditional Owners walked off country in 1953 and were cleared out in 1964 (Davenport et al. 2005; Bird et al. 2013). The Greater Bilby's broader diet allowed persistence through a 17-year gap in TO burning, and tight mosaic burning, based around vegetation and substrate, was used to avoid large fires and recover habitat (Skroblin et al. 2017) (Table 3).

Dasyurids

The post-fire productivity pulse of grasslands was likely to have provided increased food availability for the predominantly insectivorous dasyurids. The population of the arboreal Red-tailed Phascogale (*Phascogale calura*) in the region was disjunct from three populations further west in South Australia and Western Australia (Bradley 1998). Krefft (1865a) found it was already rare near the Murray–Darling junction and this past habitat has been attributed to mature Red Gum and Belah woodlands and largely restricted to woody vegetation with a mature canopy (Bradley 1998; Menkhorst 1995; Sluiter pers. comm. 2021). Its diet includes insects, small birds and mammals and it feeds extensively on the ground. Along the Murray River, mature River Red Gum forest is now largely devoid of shrubs and the lower vegetation strata support a richness of invertebrates (e.g. 450 species in two trees, Yen et al. 2002). Two once-widespread vegetation communities (both now threatened) are recognized in Victoria: Northwest Plains Buloke Grassy Woodland (relatively fertile soils seasonally waterlogged) and Shrubby Pine–Buloke Woodland (sandy loams over finer-grained substrates). Persistence of both types requires the absence of high severity/intensity fires for many decades (Table 2). Such habitats (and phascogale food) can be maintained by low intensity, Traditional Owner patch burning, and the floristic diversity and productivity of remnant woodlands (as recorded in the 1980s) would likely be enhanced by patch burning where there is a grassy field layer.

The larger meso-predator dasyurids, *Dasyurus viverrinus* and *D. geoffroii* occurred a broad range of habitats feeding on larger invertebrates (and their larvae), reptiles, small birds and mammals (to rabbit-size). In free-ranging, arid zone carnivorous marsupials, high energy diets rich in vertebrate species (e.g. mammals) reduces the use of torpor (Pavey et al. 2009). Flexible use of torpor permits them to survive even on a diet of invertebrates, although this poorer quality food may adversely affect distribution and abundance of dasyurid meso-predators (Geiser pers. comm. 2022).

We contend that both these species benefited from the grasslands productivity pulse in the region: *D. viverrinus* in the mesic south and *D. geoffroii* in the north. *D. viverrinus* is most associated with grasslands, grassy field layers and their ecotones (Godsell 1982) and populations occurred in the southern areas where it was a totem for multiple Traditional Owners (e.g. Yung Bulug – Dja Dja, Wurrung; Howitt 1904) but it disappeared from the region late in nineteenth century. Elsewhere, it was able to prey switch (to invertebrates in pastures, rabbits, poultry) becoming common in places before its collapse, presumably from an epidemic, in the early twentieth century, and ultimate

extinction on the mainland in the mid-twentieth century (Peacock & Abbott 2013; Abbott 2013). Further north ‘Native cats (*Dasyurus geoffroyii*), all species of rats and mice, and smaller wallabies (*Halmaturus*) are also eaten, some of them obtained almost every day’ suggesting it remained common in Nyeri Nyeri country (Krefft 1865b). *D. geoffroii* populations once covered three-quarters of the continent, but rapidly collapsed. The last specimen from NSW in 1841, SA in 1888 (?), Northern Territory in 1896, Queensland in 1907, and Victoria in 1857 (Krefft 1865a; Jones 1923; Serena & Soderquist 1998). The timing of the continental collapse precedes fox, rabbit, ungulate invasions or epidemics, but is consistent with the loss of the TO-LM maintained grassland productivity pulse. Extant *D. geoffroii* populations occur in low densities in southwestern WA (Serena & Soderquist 1998). Decades after continental collapse, small populations of both species survived in metropolitan areas with the presence of cats and foxes (*D. geoffroii* in Perth in the 1930s, *D. viverrinus* in Melbourne and Sydney in the 1950s) (Serena & Soderquist 1998; Menkhorst 1995).

Three, possibly four, species of small dasyurids declined but were able to adapt to changes in the region. The ecologies of the Kultarr (*Antechinomys laniger*) and the Southern Ningaui (*Ningaui yvonneae*), endangered and vulnerable in NSW respectively, are not well known and they may always have been rare in the region (Krefft 1865a; Valente 1998; McKenzie & Dickman 1998). The Mulgara (*Dasyurus cristicauda*) is known from bone remains at a single site (Ellis 1992). However, their past and current habitats and declines suggest some association with TO-LM. Their smaller energetic requirements and broader amplitude of prey may have assisted their survival. The rare Common Dunnart (*Sminthopsis murina*) reaches highest densities in grassy habitats burnt 2–4 years previously and feeds on *Mus musculus* (House Mouse) on disturbed sites (Fox 1998; Morton 1998; Sluiter pers. comm. 2021).

Smaller macropods

In May 1857, Blandowski procured a specimen of the Wurrung or Crescent Nailtail-wallaby (*Onychogalea lunata*) west of the Darling River. The limited available data fit our pattern. The Wurrung ate grasses, was hunted by Traditional Owners and occupied grasslands often with open eucalypt canopies (Burbidge 1998). Its decline to extinction appears to follow the curtailment of TO-LM (L. Hercus pers. comm. 1988; Burbidge 1998). The Bridled Nailtail-wallaby (*O. fraenata*) was the most common small wallaby around the Murray–Darling and was common elsewhere at the time of European settlement (Gould 1863; Krefft 1865a). Until the twentieth century, it remained common enough in some areas for it to be hunted for its

pelt, but rapidly declined thereafter (Gordon & Lawrie 1980). Remnant populations occupy a fairly narrow niche characterized by a field layer of forbs and native grasses (Gould 1863; Ellis et al. 1992) highly suggestive of a grassland fire pulse and TO-LM burning (Figure 2). The only extant population occurs near Dingo (Qld), with invasive Buffel Grass (*Cenchrus ciliaris*) as a key threat (DAWE 1997). Despite substantial effort, resources and investigation of options, the restitution of TO-LM does not seem to have been considered to date (Kearney et al. 2012).

Gould (1863) reported the Eastern Hare-wallaby (*Lagorchestes leporides*) as ‘tolerably abundant’ on the plains of southern Australia in the 1840s and Krefft (1865a) found it ‘common’ on the plains around the Murray–Darling junction in the 1850s. The last record in Victoria was from Mt Hope 1867 (Menkhurst 1995). The last record in NSW (1892) was from the Riverina near where TO-LM continued to 1880 (Allen 1983). The Eastern Hare-wallaby’s diet and the reasons for its rapid disappearance prior to European settlement remain unknown. However, its association with tussock grasslands implies reliance on TO-LM (Gould 1863; Jones 1923; Strahan 1998b). It was hunted by Traditional Owners using fire (and nets) in country between the Darling and Lachlan Rivers, where it was ‘as thick as rabbits’, similarly for the Mala (*Lagorchestes hirsutus*) (Berndt 1947; Allen 1983).

The Mala is the western equivalent of the Eastern Hare-wallaby and has sub-fossil remains in Victoria. In Central Australia, Finlayson (1935a,b) observed sophisticated Mala hunting using fire (covering around 5 km²): ‘it might be thought that such a fire would wipe out every living thing in its path, but that this is by no means so, can be seen from inspection of the ground afterwards, when fresh mammal tracks are in plenty; it follows also from the fact that the whole business has been carried out systematically for untold generations and over enormous areas.’

In WA, the Mala was common food for the Martu in the 1950s. It preferred nutritious post-fire forbs and grasses with high water content (Johnson & Burbidge 1998; Bird et al. 2013). In Central Australia, the last two populations of Mala used ≥10 year-old *Triodia* for shelter and travelled 150 m to feed on fire-recovery plants in burnt areas (Bolton & Latz 1978). If shelters were burnt there were movements of 0.5 km to older *Triodia*, a patch burning adaptation. Large bushfires adversely affected these populations and it is now being reintroduced to the Tanami Desert where a ‘tight mosaic of vegetation in various stages of recovery that provided structural and floristic diversity favourable to the species’ is being re-implemented within predator-proof fencing (Bolton & Latz 1978; Johnson & Burbidge 1998; Richards 2012a).

Rodents

Recent taxonomic revision found the Shark Bay Mouse (*Pseudomys fieldi*) to be conspecific with *P. gouldii*, so this species is not universally extinct (Roycroft et al. 2021) but is certainly so in our study region. This study found that all the Australia rodents that became extinct were genetically diverse and robust at the time of European settlement. Genetic impoverishment or other aspects of ‘lack of fitness’ of native species, sometimes used by proponents of the ‘additions’ argument, appear to have little or no explanatory value.

Compared with arid and mesic environments, the semi-arid zone supports low species richness of rodents. Nevertheless, our study area has the highest percentage of rodent species’ extinctions (Watts & Aslin 1981). In 1829, on their way to the lower Darling, Sturt’s party saw hundreds of *Leporillus* sp. nests, each estimated to contain 6–10 rats (Allen 1972). Krefft (1865a) found that the Greater Stick-nest Rat (*Leporillus conditor*) fed on seeds, bulbous roots and insects and that it had disappeared south of the Murray River well before 1856 (Table 3) (Robinson 1998). The smaller, but more aggressive, Lesser Stick-nest Rat (*Leporillus apicalis*) had a broader diet, including smaller mammals and bird eggs and remained in ‘great numbers’ on both sides of the Murray River (Krefft 1865a). Modern assessments suggest both species of *Leporillus* favoured succulents, some common species of which benefit from fire, e.g. *Carpobrotus modestus* (Table 3) (Parsons 1997). Traditional Owners ate these stick-nest rats and TO patch burning would have benefited food availability and protected nests from bushfires (Allen 1972) (Figure 11, Tables 1 & 2). The tighter diet preferences of the Greater Stick-nest Rat suggest greater dependence on a productive pulse and thus its more rapid disappearance.

Most of the *Pseudomys* species, including four once common in the region (Table 3), are predominantly granivorous, but also eat herbage, insects and seasonal fungi. *Pseudomys* spp. also appear to exploit post-fire pulses. Most arid–semi-arid species are associated with grasslands (tussock and spinifex hummock), using grass for communal nesting. *P. desertor* occurred in the region, disjunct from its continental range, and is the most herbivorous of the species feeding on rhizomes and succulent shoots, suggesting a post-fire association (Kerle 1998) (Table 3). Bolam’s Mouse (*Pseudomys bolami*), once common, remains but is rare in the region, with data too few to determine food preferences (Kelly et al. 2011). These rodents respond to wetter years but distributions within ranges appear sporadic (Watts & Aslin 1981). Landscape decline of the fire-induced grassland pulse with its enhanced supply of autumn-winter food,

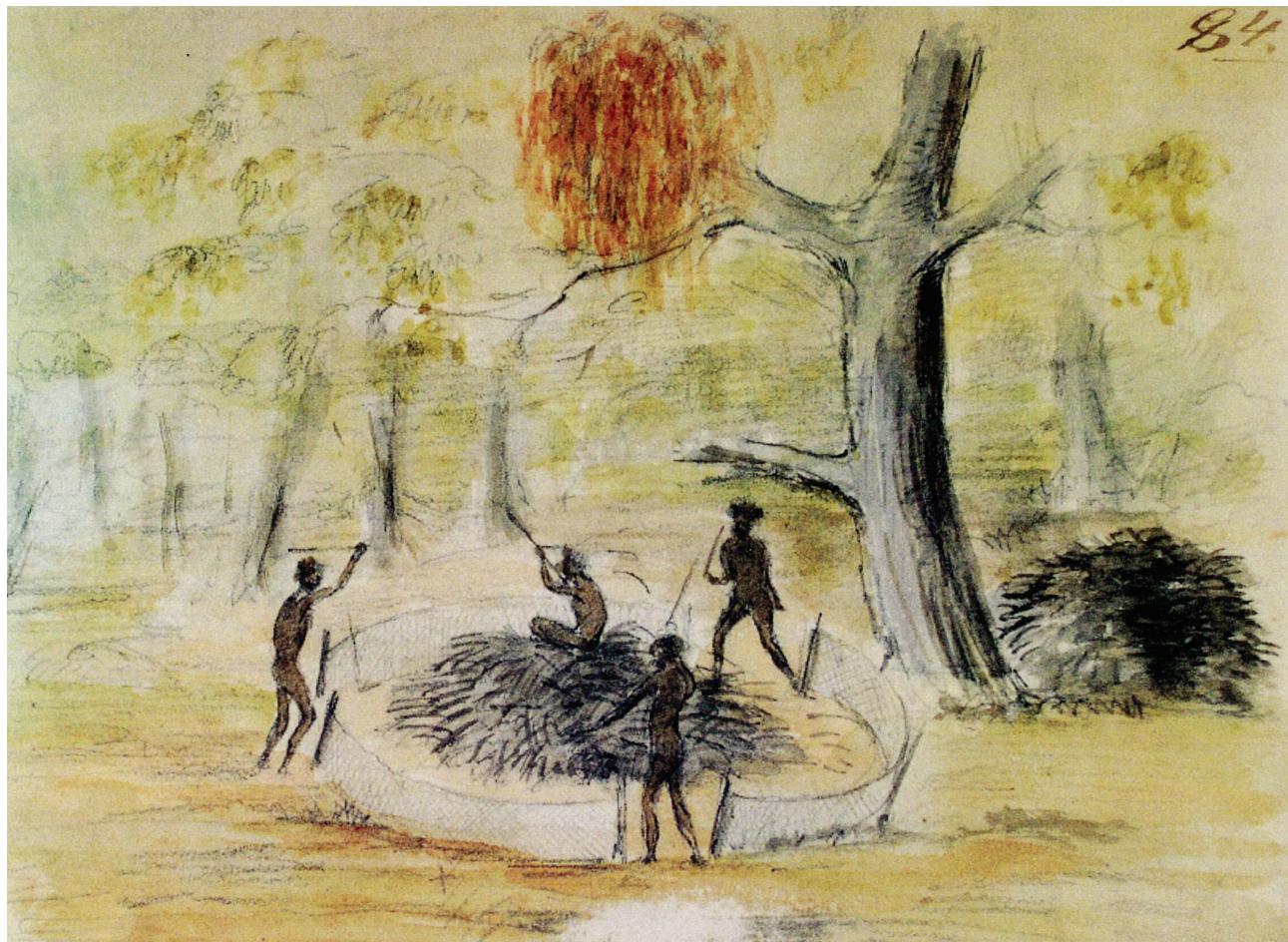


Figure 11: Gerard Krefft — Natives catching the Building Haplotsis (species of native rat); detail from an illustration of *Leporillus conditor*, Blandowski Collection, Museum für Naturkunde, Humboldt University, Berlin. (Drawings of mammals from the Blandowski Expedition are provided in: Allen 2009, Menkhorst 2009 and Allen et al. 2010.)

provides a feasible explanation for the drastic reductions of populations across this genus.

Notomys spp. have an association with grasses; however each species had distinct habitat, and direct association with the productive pulse is unclear (Table 3). Gilbert, Gould's collector, found that the favourite haunt of the Long-tailed Hopping-mouse (*Notomys longicaudatus*) was a stiff clay soil, whereas *N. mitchelli* favoured sandy substrates. Traditional Owner patch burning appears to accommodate such subtleties, as Stefferson (2020) shows substrates may determine application (if any) of fire. The Fawn Hopping Mouse (*N. cervinus*) and Dusky Hopping Mouse (*N. fucus*) may have occurred in the region as their perceived ranges occur very close to the northwest of our study area (see Strahan 1998a). The Long-tailed Hopping Mouse appears to have become rapidly extinct in our study area. The last specimen was collected in the Northern Territory in 1901–2. The Long-tailed Hopping Mouse is twice the size of *N. fucus* (30–50 g), yet Sturt observed Traditional Owners with a catch of 150 to 200 of the smaller species for eating (Watts 1998; Krefft 1865b). Mammals as small as 30 g were harvested and the Traditional Owners

knew where and when to harvest. The Barkindji travelled great distances for these foods (Allen 1972; Krefft 1865b).

In the mallee vegetation in the Mallee region, Kelly et al. (2011) studied the response of three surviving small mammals and *Mus musculus* in relation to fire history (1–105 years). These were not Traditional Owner burns and there were no native species directly associated with short fire intervals (all were extinct – Table 3). These results are consistent with our contention. The Mallee Ningaui (*Ningaui yvonneae*) favoured mature unburnt mallee. The Western Pygmy-possum (*Cercartetus concinnus*) and the Common Dunnart appeared to have habitat preferences with no strong association to time since fire. Fox (1998) found the Common Dunnart did have a post-fire association in his study area (not in our subject region). Each study area probably experienced fires with different, e.g. extent, intensity and seasonality. Predictably, the exotic House Mouse showed a preference for recently burnt habitat, as do at least some *Pseudomys* spp., which, where present, often displace the House Mouse as vegetation ages (Kelly et al. 2011; Fox and Pople 1994).

Box 1: Environmental change over deep time

Basic vegetation types (and habitat) are expressions of soil, climate, available genetic plant and fungi material, fire and grazing regimes (fauna) over time. Whatever the combination of causes of the extinction of Australia's herbivorous megafauna (climate, human, fire) around that time, the continent's vegetation transitioned to become more fire-tolerant sclerophyllous. Grasses (Poaceae) and tuber-forming taxa (Asteraceae) have been a feature of the southern Victorian plains for over 30 000 years, with lower biological activity under cooler, drier conditions, and fauna contracted to refugia (Canning 2009). Mammal distributions and abundances also changed to reflect habitat availability — periods of refugia and radiation — which continued during massive changes in the climate, rainfall and vegetation of the Holocene (see text). TO-LM adapted patch burning to maintain and create more predictable food resources which reduced extensive bushfires, all of which advantaged mammals and maintained higher population levels (Bliege Bird et al. 2008; Bird et al. 2013; see text). Empirical data indicate such landscape management can be accomplished even at very low densities of TO populations (Bird et al. 2013).

By 7000 y BP, the Barkindji diet was 40% cereals — the lacustrine economy of Mungo Man (c. 42 000 y BP) had changed to riverine-grassland (Allen 1972). Regeneration of grasslands with fire created grains and productivity pulses for a suite of mammals; this niche creation meant increased populations of mammals and additional food (Table 3, Figure 4). In the south, tubers were more important food than grains but mosaic burning achieved the same for tuberous species (Gott 2005, 2008) (Table 2). Over the millennia, TO populations with the 'fundamental human cognitive ability to utilise entire landscapes and the ability to schedule resources' (Canning 2009) used fire to conserve and make predictable food resources. TO burning could maintain extensive grasslands—grassy field layers where landscape-scale edaphic factors favoured its persistence (e.g. geology, self-mulching clays, flooding regimes), grassy woodlands where eucalypt invasion could be ameliorated; and elsewhere in smaller patches (e.g. in swales) where micro-edaphic factors allowed fire assisted persistence of grasses. Within these broad environments, continual patch burning created habitat heterogeneity and increased the availability and efficiency of on-foot small game foragers in arid and semi-arid environments (Bliege Bird et al. 2008; Bird et al. 2013). These processes would have been continual, yet adaptive. TO-LM grasslands could be maintained across the Mallee and elsewhere providing productive pulses that supported meta-populations of smaller mammals (see text; Burch 2020) (Figures 1a & 5–8).

Over time, direct observation would reveal that fire could be used for multiple objectives. Burning in patch-mosaics would enhance grassland productivity and food predictability across all trophic levels, but very important for small game (Bliege Bird et al. 2008); slow the encroachment of trees and shrubs (Figure 4) (Stefferson 2020); help avoid extensive bushfires; create habitats as species (including mammals) moved through the landscape, e.g. migration out from drought refugia (Newsome 1980); ameliorate drought; and conserve mature vegetation and refugia. Cumulative observational knowledge could be preserved, incorporated into TO lore, and passed down through dreamtime stories, ceremony, totems etc. into a fully integrated world view.

Numbat

The predominantly termite diet of the Numbat (*Myrmecobius fasciatus*) does not appear to fit into the grassland pulse model and the impacts of patch burning on termites are largely unknown (Friend 1998). Krefft (1865a) reported one place it was common about 20 miles northwest of Mildura (Wakefield 1966), probably in grassy woodland. Platform termites (*Drepanotermes* spp.) consume grasses with densities reflecting the productivity of grasses (Sluiter pers. comm 2021). Along the Murray River, termites are abundant in forests that are infrequently inundated (Yen et al. 2002). As a recent planned burn controversy in WA indicates, fire was used by Traditional Owners in the management of Numbat habitat, often in order to avoid large bushfires (Stefferson 2020; ABC 2021; Parletta 2021).

Wombats

Both species of hairy-nosed wombat (*Lasiorhinus* spp., weighing c. 30 kg.) were marginal to the region and also

soon became extinct therein (not included in Table 3). Their size and diets are similar to the large grazing macropods (e.g. *M. fuliginosus*, *M. giganteus*). As grass eaters they would have benefited from TO-LM of grasslands, but it is unlikely they were reliant upon the productivity pulse (Figure 2). Their larger body mass and denning habit enabled use of a less nutrient-rich diet (QDES 2021). The eastern limit of the Southern Hairy-nosed Wombat extended to around Euston (north of the Murray River). By the turn of the nineteenth century, persecution and rabbits were implicated in its demise (Swinbourne et al. 2017). However, a population remains at Dunedin Park Station east of Lake Victoria, in far southwest NSW. The Northern Hairy-nosed Wombat (*Lasiorhinus krefftii*) persisted in at least three isolated populations (NSW and Queensland) at the time of European contact, one of which occurred around Jerilderie (eastern border of our region), with satellite populations at Barooga on the Murray River where they were 'in their thousands'. These large grazers required a year-round supply of grass and deep sandy soils,

Box 2: A history of other iconic biota associated with TO-LM grasslands in the Murray–Darling Basin

Murnong (Yam Daisies, *Microseris* spp.) were a staple food of the TOs, more so in the south of our region areas where tubers were a more significant part of TO diet (Gott 2005). Three recognized species remain extant, all threatened — none having a particularly large tuber (Walsh 2016). However, the complex of *M. walteri* is being further reviewed with a distinctive semi-arid ‘form’ having much enlarged tubers (Walsh 2016; Ian Sluiter and Walsh pers. comm., 2021). It is likely that TO created cultivars of the plant; they traded seeds and there are numerous historical accounts of managed yam grounds (Curr 1883; Gott 2008; Mansergh & Cheal 2019). Abundance was linked to the grassland-fire system and such tuberous species feature in a suite of mammalian and insect diets (Table 3). Over-abundant large macropods may deplete Murnong but were not common where this yam daisy was prolific (Curr 1883; Sluiter, pers. obs., 2021). Even under a depleted TO fire regime, extensive areas of TO-LM grasslands remained to be targeted by sheep and Murnong were very rapidly eliminated across the landscape (Mitchell, 1834; Curr, 1883; Gott, 2005).

A tetraploid variant of *Themeda triandra* has characteristics of semi-arid and drought adaptations: taller, less tussocky, prolonged and multiple seed set (Morgan and Bryceson, pers. comm., May 2021). It was more widespread north of the Great Dividing Range, most likely the tussock grass observed by Curr (1883) but its range drastically reduced (sheep, hot summer fires competition of annuals etc.). A remnant population persists around Terrappee Cemetery (Dja Dja Wurrung country, near Boort, Vic) which has provided a century-long refugium. Presence in northern grasslands and grassy mallee would have provided additional seed sources (emergency food) and predictable, more flammable fuel for TO burning. The mass depletion of this variant and the Murnong indicates the large-scale changes in species and processes since cessation of TO-LM. Early expansion of native annuals (*Austrostipa* etc.) readily expanded into TO-LM grasslands with changed grazing–fire regimes brought by the pastoralists (McIvor 2005; Allen 1983).

Bogong Moths (*Agrotis infusa*) have their natal sites in the self-mulching soils (grasslands) of southern Queensland, western NSW and Victoria and occur in their billions (Green et al. 2021). They (larvae and adults) provided food for TOs and a suite of mammals in Table 3. The larvae eat roots of forbs (e.g. yam daisies) rather than grasses so were advantaged under TO-LM (Figure 3). Survival was assisted by prey-switching and they became an agricultural pest (Common 1954). The massive annual migration to the alps persisted until recently when agricultural intensification and pesticides have caused populations to crash (Mansergh & Heinze 2019; Warrant et al. 2016; Green et al. 2021).



Murnong – Yam Daisy (*Microseris walteri*). Rare, undescribed semi-arid ‘forms’ have much expanded tubers. Photograph: Neville Walsh (RBGV).



Kangaroo Grass (*Themeda triandra*). Note: A remnant semi-arid tetraploid form persists at Terrappee cemetery, Dja Dja Wurrung. Photograph: ANBG.



Bogong Moth (*Agrotis infusa*). Summer aestivation at Mt Higginbotham. Photograph: Ian Mansergh.

the latter for burrowing. Significantly, they survived sheep grazing but were later exterminated as their burrows were havens for rabbits, which arrived in 1879 (>1000 wombats were killed on one property in one year) (Swinbourne et al. 2017). The last specimen was collected at Jerilderie in 1884.

Large macropods

The more generalist grazers, large macropods (Red Kangaroo *Macropus rufus*, Grey Kangaroo *M. giganteus*, Black-faced Kangaroo *M. fuliginosus* and Euro *M. robustus*) exploited TO-LM grassland burning but were not dependent on the productivity pulse (Figure 2). Indeed,

they may have had their ‘own country’ under TO-LM (Newsome 1980). As noted by Mitchell (1834) Traditional Owners burnt grasslands around rocky outcrops and escarpments (Euro habitat) and kangaroos could be absent on some plains and obvious on others. After the cessation of TO-LM (and predation) and persecution of the other apex predator, the Dingo (*Canis dingo*), populations went from rare to abundant (e.g. Curr 1883). By 1860, which was well before the arrival of rabbits, extensive overgrazing and the proliferation of water points (wells and dams after 1870) led to massive increases in kangaroo numbers throughout the inland (Krefft 1865a; Frith 1973; Rolls 1969; Allen 1983; Strahan 1998a). This sudden rise of the large generalist grazers would have eliminated any remaining areas of grassland productivity pulses, as trophic level changes cascaded across the landscape (Ripple & Beschta 2003).

Special places

However, all the subject species were Traditional Owner food resources and connected to their lore and rites (e.g. Bird et al. 2013; Sutton & Walshe 2021). Newsome (1980) showed the deep ecological understanding behind the Arunta’s sacred site and song lines of the totemic Red Kangaroo (drought refugia and repopulation routes). Bird et al. (2013) concluded that through their dreaming, fire management of grasslands and hunting, the Martu people could create niches that supported persistence of species on country. Most species listed in Table 3, and other biota associated with the productive pulse (e.g. Yam daisies, Bogong moth; Howitt 1904) were totems of some resident Traditional Owners and each would have benefited from consequent land management obligations and imperatives.

Totems of the southern semi-arid Wotjobaluk included both *Dasyurus* spp., Dingo, possum, bandicoot, red and grey kangaroos and fire (Howitt 1904). The *D. viverrinus* (as Yung) remains the spirit (totem) of the Yung Balug people in the Boort area (Dja Dja Wurrung country). There were probably many of these totemic places of importance in lore spread across the region (individuals had multiple totems, with numerous clans in each of the language groups). Lack of management of these totemic places probably accelerated landscape ecological decline. Before arrival of the fox and rabbit, Daisy Bates recorded the mass depletion and extinction of the Jinyila clans and their associated mammal totems (= clan name) from Point Malcolm across the Nullarbor into South Australia (Bates 1985; Bolam 1926).

DISCUSSION

Williams et al. (2015) and Mooney et al. (2011) explored the relationship between Aboriginal population indices and fire in Australia, at both continental and regional levels over the last 20 000 years. They found weak statistical correlation between these factors at both scales but short-lived synchronous responses (around 10–7 ka, 5–4 ka and 1.2–0.8 ka) could be explained by climate. They argued that, at the macro scale, there were no long-lasting impacts on the biota that required an explanation by human agency. However, they did not discount the possibility of systematic or deliberate manipulation of the fire regimes *at local scales*. Williams et al. (2015) concluded that ‘further empirical research is required to explore the relationship between known fire events of different scale and intensity and the contemporary charcoal record’. We concur.

Although the decline of the mammals of the mid-Murray–Darling region has been extensively assessed by numerous authors, all essentially concluded that the primary cause was the additions of the European invasion (ungulates, rabbits, cats, foxes etc.). The role of the loss of TO-LM was generally ignored or dismissed (Bennett et al. 1989; Dickman 1994; Menkhorst 2009). Menkhorst (2009), using the postulate of Allen (1983), thought the hypothesis of cessation of TO-LM as a primary cause of these regional extinctions was plausible. Nevertheless, he rejected it as it did not explain either the rapidity of declines (using the time for vegetation to evolve to new seral stage) or the lack of evidence that mosaic burning was undertaken across the landscape. In contrast, our results show that it was the subtraction (c. 1830) of TO-LM mosaic burning of grasslands and loss of the productive pulse that best explains the initially rapid collapse of mammalian populations across the landscape. Those mammals most dependent on this pulse decreased first. Across these degrading and out-of-balance ecosystems many species were in extinction vortices. Any remnant or refugial mammalian populations became increasingly vulnerable to consequent changes, such as over-grazing (ungulates and larger macropods), novel predators and clearing. The evidence above shows that TO-LM, including the careful use of targeted fire across the entire landscape, kept the invading eucalypts at bay, lessened extensive bushfires (thus conserving mature vegetation) and provided food across otherwise less hospitable environments.

There was a combination of reasons why the southeast region was the first to suffer such catastrophic losses. The former faunal complement included arid and mesic species, some at the edges of their ranges. The Murray River area supported among the highest densities of Aborigines on the continent and the landscape was managed to support these populations (Mulvaney 1971; Burch 2017; Williams

et al. 2015). The flat and relatively uniform topography of the plains country supported no large refugial areas. Reed beds (along rivers and in deflation lake-basins) lost TO-LM and were depleted by pastoralists (e.g. Curr 1883). Dowling (1997 & 2021) documented the impact of a series of infectious diseases leading to massive depopulation of Traditional Owners, effectively and rapidly ending millennia-long TO-LM (including mosaic burning), and initiating an ecologically traumatic event with no recovery once Europeans invaded to exploit their grasslands.

In the Pilliga–Coonabarabran region, to the immediate northeast of our study area, Rolls (1981) described the extent and ecological effects of Traditional Owner burning and its cessation on native vegetation, leading to increases in large fires and expansion of forests. His assessments and disdain for the previous scientific discountenance of Traditional Owner burning are in accord with our postulates.

In analysing the twentieth-century attrition and extinction of species in WA (and across Australia) Burbidge and McKenzie (1989) attributed the loss of native fauna to the loss of available productivity, most pronounced in Critical Weight Range mammals that had relatively high metabolic requirements (c.f. reptiles) and lesser mobility (c.f. birds). They also noted that many mammal disappearances broadly followed Traditional Owners leaving country and recognized that changed fire regimes may have contributed (Burbidge 1985; Burbidge et al. 1988; Burbidge & McKenzie 1989). Our investigations indicate that Traditional Owner patch burning maintained and enhanced available productivity in a closed self-reinforcing regenerative system, also resulting in elevated populations of the associated fauna (Figure 2, Table 3). The subtraction of this ecological agency best explains the progressive mammalian population collapses in this landscape. These collapses were first manifest in the Murray–Darling basin. Acknowledging this as the primary cause does not diminish the extent of the consequent loss of productivity caused by the degradation and export of nutrients resulting from the addition of sheep and cattle, and other associated changes.

In 1953, many Martu people left their country in WA. In 1964, the last traditional nomads of the northern Martu were finally ‘cleared out’ of country for the Woomera rocket testing (Davenport et al. 2005a,b). Yuwait, a 16-year-old at the time, recorded that they always carried fire sticks, burning country as they went, which produced larger numbers of food-bearing plants and significantly more food and game (Davenport et al. 2005a,b; Latz 1995a,b). The Martu had captured Bilbies, Boodies and Mala by burning mature spinifex (*Triodia* spp.) grassland in the cool-dry season (Bird et al. 2013). The Martu returned to country in 1984

and the Boodies and Mala were gone. The Greater Bilby, a dietary generalist, was able to persist but was rare (see Table 3). Populations of the Martu’s major food source, the Sand Goanna (*Varanus gouldii*), had dramatically declined but tight mosaic burning restored abundances (Bird et al. 2013). Bird et al. (2013) also concluded that Martu land management (including fire and hunting) increased the abundance of Sand Goannas and created niches that could maintain the presence (and increase abundance) of species in their country when environmental conditions would otherwise be less favourable.

The extinction patterns of decline in this and other species across the semi-arid and arid zones in WA, SA and NT (e.g. Western-barred Bandicoot, Bilby and Lesser Bilby) broadly correlate with cessation or degradation of TO-LM (see species accounts in Bates 1985; Hercus 1985; Burbidge & McKenzie 1989; Strahan 1998a; Richards 2012a,b; Bird et al. 2013; Peasley 2009). Coincidence or consequence?

The landscape and vegetation of the mid-Murray–Darling which the mammals inhabited, that the explorers saw and to which the squatters were attracted (Figure 1) were modified and managed by TO-LM fire for millennia. The grassland food base (attractive to Europeans) was maintained, eucalypt and woody shrub invasion managed and the risk of large bushfires minimized (Tindale 1959; Williams 1962). Over the millennia, mammal distributions and abundances and TO-LM would have responded to previous gross vegetation changes, e.g. the expansion of mallee shrublands (Luly 1990; Cupper 2005). New mammalian food sources in clan areas in the semi-arid zone are known from historical times (Bates 1985). Martu land management kept country habitable despite having among the lowest population densities on the continent. When they left country (1953) the mean size of all fires increased dramatically (about five orders of magnitude) and the extent of all kinds of mature vegetation was substantially lessened (Bird et al. 2013). Such bushfires hastened the demise of remnant populations, e.g. of Mala (Johnson & Burbidge 1998). Environmental modelling in arid and tropical savanna environments confirms that the persistence of mature vegetation is an emergent quality of landscape patch burning (Letnic & Dickman 2010; Trauernicht et al. 2015.)

This evidence suggests that TO-LM affected and effected the configuration of grasslands, mature vegetation and thus availability of mammal habitat in our study region (Figures 4 & 5). Co-evolution of TO-LM and preferred faunal habitat has been described to explain the most rapid mammal extinction in Victoria, that of Tchuteba (*Conilurus albipes*) (Mansergh & Cheal 2019). Bird et al. (2013) concluded patch burning for forage-hunting created

finer-grained habitat mosaics, created niches for a range of species that would not otherwise persist in the arid Martu country and optimized the productivity and predictability of faunal populations. Despite misinterpretation of early adverse experimental results of patch burning (Short & Turner 1994; see Hiscock & Wallis 2005), some form of patch burning has been successfully used in recovery programs of over six endangered mammal species on the mainland (e.g. Johnson & Burbidge 1998; Richards 2012b). Traditional Owner societies managed the terrestrial mammal fauna through habitat manipulation, predation, niche creation and refugia protection (Newsome 1980; Bird et al. 2013). We conclude that the environment and the mammalian fauna (diversity and abundance) recorded by the first Europeans were an artefact of millennia of TO-LM (Tindale 1959; Gammie 2012) (Box 1).

Patch burning in these zones has been replaced by increased frequency of large bushfires over the twentieth century (Bradstock et al. 2002; Bird et al. 2013). Such changing fire regimes are leading to adverse decadal changes in soil carbon and nitrogen and ecosystem productivity (Pellegrini et al. 2018).

The date of arrival of feral cats in Australia is uncertain and may predate European settlement. We suggest their arrival in the semi-arid zone of southeastern Australia was late and did not involve high densities until recently (after European settlement) (Abbott 2002). Although not present in our region at the time of collapse, foxes and cats have been strongly implicated in the continental extinction and decline of the Critical Weight Range mammals and this has regrettably become a simplistic summary of this impact (Burbidge & McKenzie 1989). That cats and foxes can extinguish small, remnant or otherwise stressed populations of Critical Weight Range mammals is not disputed. There have been many successful rescue and recovery efforts based on predator exclusion. From the 1980s, populations of arid and semi-arid zone mammals (including some listed in Table 3) have been successfully introduced to fox- and cat-free islands (WA and SA, e.g. Strahan 1998a; Richards 2012a,b). From the mid-1990s, there have been successful releases into predator-proof enclosures, e.g. Scotia, Arid Recovery Reserve, Mt Rothwell Victoria, with many positive conservation outcomes (ARR 2021; Mt Rothwell 2021; Anon 2020).

A fundamental (but largely ignored) question for all recovery efforts is what role did the cessation of TO-LM have in the decline of the species? Or is what we now recognize as ‘natural habitat’ free of prior anthropogenic processes? At the broader level, asking these questions may also inform the official enquiries into why, after 30 years, both State and Commonwealth biodiversity legislation (respectively, Victorian *Flora & Fauna Guarantee Act*

1988 and the *Environmental Protection and Biodiversity Conservation Act 1995*) have failed to reverse ecosystem decline (see Victoria; Parliament 2021).

Our re-evaluation of this ecological history has woven lines of evidence derived from many disciplines and provides a reasonably comprehensive and coherent explanation of the collapse of the mammal fauna, and we contend one better than the ‘additions’ argument and its variants. As history, it remains unprovable. However, the perspective it provides allows interpretation (and design) of ongoing science-based actions under various land-management policies and species recovery plans (e.g. Richards 2012a,b). As patch burning and the mammals have been absent from the region for over 150 years and all environments are variously degraded, experimental design is difficult, but feasible. Focused research into the fundamental ecological drivers, fungi and invertebrates, of grasslands/grassy field layers and the productive pulse could test our basic thesis. Mammal exclosures (e.g. Arid Zone Recovery, Mt Rothwell) and other sites across the Victorian Mallee (e.g. Figure 7) are available and the increasing uptake of Traditional Owner mosaic burning, following Stefferson (2020), offers further opportunities.

The cosmology and economy of the Traditional Owner societies were rich and complex human endeavours (e.g. Tindale 1959; Bates 1985; Sutton & Walshe 2021). Traditional Owner persistence *in situ* over the millennia in an environment of changing drought, fire and flood regimes is a tribute to the knowledge, ingenuity and cultural strength of the Traditional Owners. They knew the ‘where, when, what and why’ of the mammal fauna. The ‘why’ was incorporated into their cosmology (lore, rites, totems) which embedded deep ecological understanding (Dawson 2009; Newsome 1980; Bird et al. 2013).

Under changing environmental conditions the mammal fauna adapted to, and benefited from, this ecological agency (TO-LM), which was brought to an abrupt end around 1830 in the mid-Murray–Darling catchment. Disappearance of the grassland pulse, probably within five years, was an ecologically traumatic event which rapidly cascaded through ecosystems. Productivity declined, food-chains (including predator-prey) degraded and mammal populations collapsed, many to extinction. Later extensive bushfires would further homogenize the environment. This subtraction opened the extinction vortex for the suite of mammals listed in Table 3. Subsequently, Europeans added further assaults on the ecosystems through the introduction of ungulates, feral predators and grazers, and persecution of the apex predator (*Dingo Canis dingo*), with additional adverse effects cascading through the ecosystems (Ripple & Beschta 2003).

Mammal habitat and populations were manipulated and maintained without ‘domestication’ but what does this imply? Is this another version of ‘nomadic pastoralism’ *sensu* the Neolithic Britons (Harvey 2002)? Where does it fit in the current contentious debate about classification of Traditional Owner society as ‘aspects of agricultural’ (Pascoe 2014) or ‘hunter gatherer plus’ (Sutton & Walshe 2021)? Traditional Owner societies had a custodianship, cosmology and deep ecological understanding that manipulated the relatively harsh and variable environments of a unique continent. We have attempted to clarify the ecological ‘whats’ and ‘hows’ of the period and subsequent processes. The semantics are left to others.

CONCLUSION

Traditional Owner land management and the associated mammalian fauna adapted to changes in climate and vegetation. In the mid-Murray–Darling catchment, depopulation of the Traditional Owners from 1830, due to diseases, saw a disruption of landscape-scale management and it was subsequently extinguished by the early 1840s (Dowling 2011). The effect was rapid. Loss of the biological productivity pulse meant collapsing mammal populations, as observed by the Nyeri Nyeri and Krefft in 1856–7.

These declines were precipitous in this region and progressively continued across the continent into the next century, with progressive declines and extinctions of associated mammals (Burbidge & McKenzie 1989; Bird et al. 2013). Importantly, this fundamental ecological trauma began decades prior to standard explanations of continental scale mammalian decline (Gould 1863; Jones 1923; Troughton 1973; Ride 1970) and in this region (Dickman 1994; Menkhorst 1995; Bennett et al. 1989). It follows that many descriptions of ‘natural’ habitats were in reality of artefacts of intentional human intervention, as Edward Curr so long ago recognized (see also Mitchell 1838; Tindale 1959; Bird et al. 2013). The ecological agency of TO-LM has been ignored, neglected or restricted in the zoological and ecological literature. With very few exceptions, such denial continued after Tindale’s (1959) insightful recognition of Aboriginal ecological agency. Clear understanding and recognition of causal factors is a necessary precursor to better land management. Our analysis has been focused on ecology and mammals; however, our conclusions (and many references herein) suggest that the term ‘natural environment’, implying ‘free of human agency’, should be used much more cautiously. It is likely another colonial overhang. Without more rigour, conclusions reached and, most importantly, actions derived, from research of the ‘natural environment’ may be misleading.

Our current understanding, and thus efforts to ameliorate, ecosystem decline would be greatly improved by consideration of the subtractions rather than only the additions (notably of stock grazing and feral predators) of our history. The mammals were the most susceptible fauna to the loss of productivity (Burbidge & McKenzie 1989). Their declines were the first observed; however, that does not mean immunity for other groups and elsewhere. We consider the ‘window’ described here is applicable not only to other mammals (e.g. Bridled Nailtail Wallaby, Hairy-nosed Wombats, and the ‘perplexing’ declines of bandicoots — Opie et al. 1990) but also to avifauna (e.g. Australian Bustard in the south) and reptiles. The observations of Bird et al. (2013) on the decline of Sand Goanna are as cautionary as its recovery is inspiring and illuminating. Indeed, large-scale and long-term adverse trophic level ecological cascades can be reversed when the primary cause is identified and remedied (Ripple & Beschta 2003).

In Victoria, at the strategic and regional level, Traditional Owners themselves are re-asserting the need for traditional burning in restoring country and biodiversity (DDWCAC 2014; FVTOC 2019; O’Kane et al. 2019). This eco-history suggests that under future warming climates, re-institution of some form of TO-LM (in its broadest sense including fire, apex predator) would assist not only the biota but also with other major urgent national problems. The avoidance of increasingly catastrophic fires would lower CO₂ emissions and increase the capacity for carbon biosequestration in the arid semi-arid landscape (through an increase in the area of mature vegetation).

After 30 years, once-thought progressive legislation at State and Commonwealth levels is being reviewed, as ecosystems and species continue to decline. The catalogue of ‘whitefella’ additions to what was then regarded as *terra nullius* cannot be ignored in these continuing declines. But it never was *terra nullius*. Large parts of the ‘natural’ environment directly reflected human agency (Tindale 1959; Gott 2008). These additions have been blamed but there has been little acknowledgement of the subtraction of the millennia-long major ecological agent — Traditional Owner land management. Our explanation for the early demise of the suite of mammals from the Murray–Darling region, and subsequently across Australia, is that subtraction of Traditional Owner land management initiated these declines. From this perspective new approaches arise. Perhaps the basis of improved restoration of ecosystem health is best derived from an understanding of, respect for, and inclusion of the traditional knowledge that underpinned continental land management for millennia.

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‘There’s a crack, a crack in everything – that’s where the light gets in’ (L. Cohen).

Conflict of interest

The authors declare no conflicts of interest.

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