Patterns of decline of small mammal assemblages in vegetation communities of coastal south-east Australia: identification of habitat refuges

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Abstract.   Since European settlement Australian native mammals have experienced significant extinctions and severe declines in the range and abundance of populations. Longitudinal studies are required to identify declines and activate timely management. Population studies of native small mammal communities were conducted across the eastern Otway Ranges during 1975–2007; however, their subsequent status was unknown. We aimed to: compare the current occurrence and abundance of species and communities (2013–18) to those in previous decades across major vegetation communities (heathy woodland, low forest, sand heathland, headland scrub, coastal dunes and estuarine wetland), and identify change characteristics and management priorities. Live trapping was employed to assess mammals at 30 sites across seven vegetation communities. In total, 67% of sites exhibited large to severe decreases in abundance and only 3% of sites had more than four species compared to 27% in earlier decades. Declines occurred following wildfire and drought, with drivers likely to be multifactorial. While regional declines were significant, higher mammal abundance (two- to six-fold) and native species richness were recorded at coastal dune sites, indicating that this community provides important mammal refuges. Identification of refuges across the landscape and their protection from inappropriate fire and predators should be management priorities.

Additional keywords: conservation, fire, marsupial, population declines, rainfall, refuges, rodent.

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Introduction

The extinction of ~200 vertebrate species worldwide in the last 100 years has been identified as a sixth mass extinction episode (Ceballos *et al.* 2015, 2017). Several major drivers of worldwide fauna extinctions such as habitat loss, introduced species, changed fire regimes and disease have been identified (Cardillo *et al.* 2005; Davidson *et al.* 2009). Australian ground-dwelling mammals have experienced one of the world's worst extinction rates since European settlement, consisting of 30 species (Burbidge and McKenzie 1989; Johnson 2006; McKenzie *et al.* 2007; Burbidge *et al.* 2008; Woinarski *et al.* 2014, 2015). In addition to the extinctions, more than one-fifth of extant species have declined significantly and are now also threatened with extinction (Woinarski *et al.* 2014, 2015). The threatening processes leading to declines are broadly recognised and include introduced feral predators, rainfall deficits, loss of habitat, inappropriate fire regimes and introduced plant pathogens (Burbidge and McKenzie 1989; Wilson 1991*b*; McKenzie *et al.* 2007; Woinarski *et al.* 2010; Bilney 2014). However, the interactions between several threats and the characteristics of

different sites mean that causation of individual population changes are difficult and costly to assess (Woinarski *et al.* 2015; Doherty *et al.* 2015).

Effective long-term monitoring has been recognised as essential for assessing ecological responses to drivers of ecosystem change over prolonged periods (Krebs *et al.* 2001; Lindenmayer *et al.* 2012, 2014). Longitudinal data allows changes or declines in fauna populations to be detected in appropriate timeframes to inform evidence-based policy, management decisions and conservation activities (Krebs *et al.* 2001; Burgman *et al.* 2012; Lindenmayer *et al.* 2012, 2014). Long-term studies are important because they can enable identification of overall trends that are not revealed in cross - sectional studies particularly where there is a prolonged lag period, sometimes decades, for expression of fundamental trends (Likens 1989; Lindenmayer *et al.* 2012, 2018).

Although long-term monitoring of mammal assemblages in Australia to quantify changes in abundance and distribution have been somewhat limited, several important studies have provided evidence for declines in the abundance and distribution

of mammals. In forests of south-eastern Australia, declines of arboreal mammals have been recorded (Lindenmayer *et al.* 2013, 2018). Long-term surveys in Tasmania have identified extensive declines for many species such as the eastern quoll (*Dasyurus viverrinus*) (Driessen and Hocking 1992; Fancourt *et al.* 2013; Fancourt 2016) and declines of mammals in the Victorian Grampians were recorded in the mid-2000s (Hale *et al.* 2016). In arid and semiarid Australia, where long-term monitoring of mammal assemblages have been conducted, population trends were more difficult to discern from short-term fluctuations associated with marked variation in rainfall conditions (Dickman *et al.* 2010; Greenville *et al.* 2012). Monitoring in the forests of south-west Australia identified multiple species declines of seven native mammal species (80–100%) since the mid-1990s (Wayne *et al.* 2017*a*). In northern Australia a marked decline in the abundance of very small, small and medium-sized mammal species was recorded in tropical savannas and open woodlands of Kakadu National Park from the 1980s through to 2009 (Braithwaite and Muller 1997; Woinarski *et al.* 2010).

There is growing evidence that regional persistence of small mammal populations in times of decline is reliant on the presence of refuge habitats or patches into which populations contract during dry periods and in the face of climate change (Milstead *et al.* 2007; Letnic and Dickman 2010; Keppel and Wardell-Johnson 2012; Wilson *et al.* 2012; Greenville *et al.* 2013; Pavey *et al.* 2014, 2017). The refuge areas enhance the resistance of the biota by providing more favourable environmental conditions (temperature, moisture) or higher resource availability and act as a source of animals when recolonisation occurs during and after subsequent resource increases across the landscape (Brandle and Moseby 1999; Milstead *et al.* 2007; Letnic and Dickman 2010; Dickman *et al.* 2011; Greenville *et al.* 2013; Pavey *et al.* 2014, 2017; Reside *et al.* 2019).

In the eastern Otway Ranges of south-east Australia long-term research investigating the population ecology, habitat requirements and reproduction of small mammal species communities was conducted between 1975 and 2007. They considered the impacts of threats including fragmentation (Wilson *et al.* 2001), fire (Wilson 1990, 1991*a*, 1996; Wilson *et al.* 1990, 2001; Lock and Wilson 1999) reduced rainfall (Wilson *et al.* 2007; Magnusdottir *et al.* 2008; Sale *et al.* 2008), introduced predators (feral cats and foxes) (Hutchings 1996, 2000; Wilson and Wolrige 2000; Wilson *et al.* 2001, 2017*a*, 2017*b*) and vegetation degradation due to the introduced plant pathogen *Phytophthora cinnamomi* (Wilson *et al.* 1990; Laidlaw and Wilson 2006; Annett 2008).

In 2013 the status of the mammal communities and species in the region was unclear and it was recognised that a reassessment was required. A focus of the re-evaluation was the current status of two nationally threatened species in the region, namely the swamp antechinus (*Antechinus minimus maritimus*) and the New Holland mouse (*Pseudomys novaehollandiae*) (Wilson *et al.* 2017*b*, 2018*b*; Burns 2018, 2020). The swamp antechinus was recorded at only six sites compared to previous records at 25 sites, and trapping failed to record the New Holland mouse at any sites, including eight where the species was previously extant (Wilson *et al.* 2001, 2017*b*, 2018*b*). Long-term declines were recorded following wildfire, and during periods of below-average rainfall and drought,
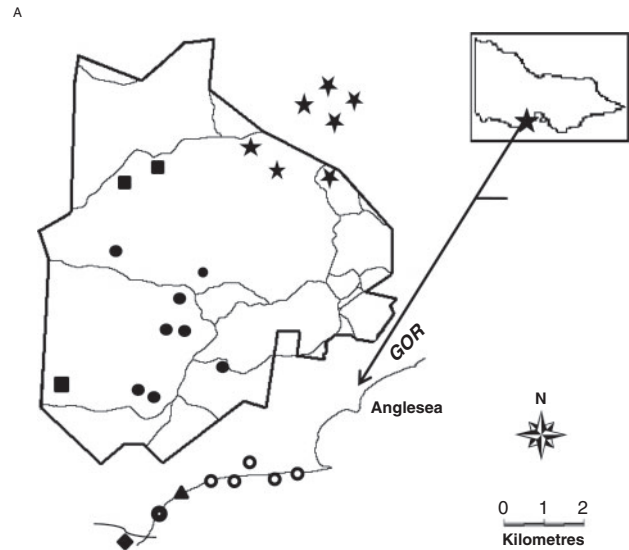
Fig. 1.   Study area in the eastern Otways showing long-term trapping sites. ●, HWW (heathy woodland west); ★, HWE (heathy woodland east); ▲, SH (sandy heath); ■, HLF (heathy low forest); ◆, EW (estuarine woodland); ◉, CHS (coastal headland scrub); ○, CS (coastal scrub); GOR, Great Ocean Road.

especially during the 'millennium drought' (1996–2010) where much of the south-east of Australia experienced persistent drought (CSIRO and Australian Bureau of Meteorology 2015). Recently we also identified multiple species declines at 19 long-term study sites in the eastern Otway ranges (Wayne *et al.* 2017*b*). Differences in the species richness, and abundance trends of mammal communities were also noted between the major vegetation communities and provided some evidence that declines may not be uniform across the landscape.

The aims of this paper were thus to: (1) compare the current occurrence and abundance of mammal species and communities (2013–18) to those of previous decades across major vegetation communities (heathy woodland, heathy low forest, sand heathland, coastal headland scrub, coastal dune scrub and estuarine wetland), (2) evaluate the characteristics of population and community changes and (3) provide information to support effective management and recovery programs for small mammal communities.

Materials and methods

Study area

The study area in the eastern Otway Ranges is 100 km south-west of Melbourne, Victoria and covers ∼22 000 ha of predominantly public land, including the Great Otway National Park (Fig. 1). Within the study area is the Anglesea Heath (7141 ha) which was, before the establishment of the park, leased for brown coal extraction over an area of 400 ha (1961–2015). The Anglesea Heath is recognised for its biodiversity, and a Land Management Cooperative Agreement was established to protect those values (McMahon and Brighton 2002). The vegetation communities comprise a diverse mosaic of predominantly eucalypt forests, woodlands and heathlands, interspersed with dense wet shrublands (Land Conservation Council Victoria 1985;

Wark *et al.* 1987). The rich mammal assemblage in the study area consists of 15 small to medium-sized mammal species (Kentish 1983; Land Conservation Council Victoria 1985; Laidlaw and Wilson 1989, 2006; Wilson 1991*a*, 1996; Wilson *et al.* 1986, 1990, 2001). The mammals include several threatened species listed under the Federal *Environment Protection and Biodiversity Conservation Act 1999* (EPBCA) and the Victorian *Flora and Fauna Guarantee Act 1988* (FFGA): the New Holland mouse (*Pseudomys novaehollandiae*) – Vulnerable (EPBCA), Threatened (FFGA); the Southern Brown Bandicoot (*Isoodon obesulus obesulus*)- Endangered (EPBCA), Threatened (FFGA); the long-nosed potoroo (*Potorous tridactylus*) Vulnerable (EPBCA), Threatened (FFGA); the swamp antechinus (*Antechinus minimus maritimus*) – Vulnerable (EPBCA), Threatened (FFGA); the white-footed dunnart (*Sminthopsis leucopus*) – Threatened (FFGA).

The most extensive recent fire in the area, the 'Ash Wednesday 'wildfire (1983), burnt 40 000 ha and left few unburnt small patches of vegetation in the study area (Wilson *et al.*1990). Fire management and fuel reduction burns have been undertaken since 1986, currently by the Department of Environment, Land, Water and Planning (2018) and an increase in fuel reduction burning is being implemented as a result of recommendations arising from the 2009 Victorian Bushfires Royal Commission (Parliament of Victoria 2010; Department of Environment and Primary Industries 2014). Regular baiting for fox control has occurred since 2005, and before this on a less regular basis (Antos and Yuen 2014; Parks Victoria 2015). Significant areas have been infected with *Phytophthora cinnamomi* (Wilson *et al.* 2000, 2003; Laidlaw and Wilson 2003; Annett 2008) however management to minimise its spread has been limited.

General trapping methods

Trapping was undertaken using Elliott traps ($325 \times 90 \times 100$ mm) baited with universal bait (peanut butter, rolled oats, honey) across all trapping periods. Traps were set for three or four nights. Species, sex, reproductive condition, bodyweight (g), and body measurements, including head length (mm), head-body length (mm), tail length (mm) and pes length (mm), were recorded for each individual animal. Captured individuals were identified or marked before release at capture point. At most sites 30 Elliott traps were set in transect formation in lines of 10 at 10–15 m intervals or 10×10 grids at 10–15 m intervals, however, at four sites only 4–10 traps were set due to the very small area of the habitat patches.

Description of study sites, communities and trapping at long-term sites (1975–2018)

The sites were located in heathy woodland, heathy lowland forest, sandy heathland, estuarine woodland, coastal headland scrub and coastal dune scrub (Table 1, Fig. 1, Supplementary Fig. S1*a–g*). On the basis of differences identified in the topography and vegetation between the heathy woodland sites located in the west and east of the study area we identified two communities: heathy woodland west (HWW) and heathy woodland east (HWE) (Table 1, Fig. S1*a–b*). The differences were also found to be reflected in the different mammal compositions of the two communities

Detailed accounts of the study areas and monitoring protocols are presented elsewhere (Wilson *et al.* 1986, 1990, 2001, 2017*b*, 2018*b*; Wilson 1990, 1991*a*, 1996; Lock and Wilson 1999, 2017; Laidlaw and Wilson 2006; Annett 2008; Magnusdottir *et al.* 2008; Sale *et al.* 2008). The long-term monitoring results collated in this paper derive from studies at 30 sites conducted between 1975 and 2018 (Table 2).

The HWW sites ($n = 8$) were located west of the Anglesea River and across the Bald Hills, on mainly inland southern slopes (Table 1, Figs 1, S1*a*). Trapping at these sites was conducted on 19–64 occasions between 1975 and 2007 (Table 2) with recent trapping conducted between 2013 and 2018. The HWE sites ($n = 7$) were distributed along the eastern ridge of the study area on flat to undulating topography (Table 1, Figs 1, S1*b*). Trapping was conducted from 1983 to 2004 on 13–42 sessions, and recently from 2013 to 2018 (Table 2). One sandy heathland site (Urquhart) was located on a coastal southern slope (Table 1, Figs 1, S1*c*). Trapping was conducted at the sites on 35 occasions between 1998 and 2007 and recent trapping between 2013 and 2018 (Table 2). Four sites located in heathy low forest were distributed across the northern ridge of the study area (Table 1, Figs 1, S1*d*). Trapping was conducted annually from 1984 until 2004 and recent trapping was completed between 2014 and 2015 (Table 2). One estuarine wetland site was located on the Painkalac Creek (Table 1, Figs 1, S1*e*). Trapping was conducted between 1999 and 2003 on 15 occasions, and recently between 2015 and 2017 (Table 2). Trapping in coastal headland scrub was conducted at the Aireys Inlet locality in six small patches located along coastal cliff-tops (Table 1, Figs 1, S1*f*). Trapping commenced in March 1997 and continued until 2003 on 30 occasions with recent trapping conducted between 2014 and 2017 (Table 2). Five sites were established in coastal scrub, between Anglesea and the Urquhart site, following the 1983 wildfire (Table 1, Figs 1, S1*g*). Trapping was undertaken on 17 occasions between 1983 and 2004 and recently between 2014 and 2018.

Assessment of abundance trends at long-term trapping sites

Although mark–recapture and other analyses have been used to derive estimates of populations (number of individuals known to be alive; density) for several species (the swamp antechinus, the agile antechinus, the New Holland mouse, the swamp rat, the southern bush rat) at particular sites (Wilson *et al.* 1986, 1990, 2001; Wilson 1991*a*; Lock and Wilson 1999, 2017; Annett 2008; Magnusdottir *et al.* 2008; Sale *et al.* 2008) this precise population information was not available at several important survey sites or for data series at sites. To ensure consistent comparison across years we used trapping rate as a standard measure of abundance:

$$\text{Trap success} = (\text{total captures}/\text{total number of trap} - \text{nights}) \times 100$$

(see Wayne *et al.* 2017*a*, 2017*b*).

The total abundance of mammals and species (trap success), and species richness for the long-term data were calculated and trends at sites compared. Changes in abundance in each of the vegetation communities were estimated on a baseline

Table 1.   Summary description of long-term study sites

Vegetation communities: HWW, heathy woodland west; HWE, heathy woodland east; SH, sandy heathland; HLF, heathy lowland forest; EW, estuarine woodland; CHS, coastal headland scrub; CS, coastal scrub. Ecological vegetation class is the standard unit for classifying vegetation types in Victoria, based on floristics, lifeforms and ecological characteristics

Vegetation community	No. of sites	Ecological vegetation class	Description, dominant plant species
HWW	8	Heathy woodland, lowland forest, riparian scrub	Inland south valley. *Eucalyptus obliqua* (messmate stringybark), dense wet areas of *Leptospermum continentale* (prickly tea-tree) (4 m); low heath *Banksia marginata* (silver banksia), *Danthonia penicillata*, *Dillwynia glaberrima* (smooth parrot-pea), *Epacris impressa* (common heath), *Gahnia radula* (thatch saw-sedge), *Pteridium esculentum* (austral bracken), *Leptospermum myrsinoides* (silky tea-tree), *Xanthorrhoea australis* (austral grass-tree).
HWE	7	Heathland, low open-forest, scrub.	Inland flat to undulating, hillside. *E. obliqua*, *Eucalyptus willissii*, *Eucalyptus aromaphloia* (7–11 m), *E. impressa*, *Acacia pycnantha*, *Acacia myrtifolia*, *Leptospermum juniperinum*, *L. myrsinoides*, *G. radula*, *Lepidosperma semitieres.*
SH	1	Sandy heathland	Coastal south slope. Upper storey *E. obliqua*, *L. continentale*; mid–understorey *G. radula*, *L. myrsinoides*, *Acrotriche serrulata* (honey pots), *Hibbertia riparia* (erect guinea-flower), *Lepidosperma filiforme* (common rapiers-sedge); valley dominated by *L. continentale* (~1 m).
HLF	4	Heathy lowland forest	Flat inland sites. *E. obliqua*, *Eucalyptus baxteri* (20–390 m); understorey dominated by *L. filiforme*, *E. impressa*, *Poa sieberiana*, *L. semitieres*, *Helichrysum scorpiodes.*
EW	1	Estuarine wetland	Grassland (~1 m). *Poa labillardieri* (common tussock-grass), *Lepidosperma gladiatum* (coast sword-sedge), *Ficinia nodosa* (knobby club rush); herbfields *Phragmites australis* (common reed), *P. esculentum*, *Eleocharis acuta* (common spike-rush), *Juncus kraussii* (sea rush).
CHS	4	Coastal headland scrub	Coastal cliffs, fragmented vegetation. Scrub (~3 m) dominated by *Melaleuca lanceolata* (moonah), *Allocasuarina verticillata* (drooping sheoak), *Leptospermum laevigatum* (coast tea-tree); low open woodland, dense understorey *L. continentale*, *L. myrsinoides*; heathland (<1.0 m) dominated by *Spyridium vexilliferum* (propellor plant), *Leucopogon parviflorus* (coast beard heath), *Lasiopetallum baueri* (slender velvet bush); tussock grassland (<0.5 m), *Poa* spp., *Themeda triandra* (kangaroo grass).
CS	5	Heathy woodland, damp heathy mosaic	Dune, interdune scrub. Dense *L. laevigatum*, *L. parviflorus* (~2 m), understorey *B. marginata*, *P. esculentum*, *Poa* sp., *L. parviflorus* (coast beard-heath), *Carex apressa* (tall sedge), *Acaena anserinifolia* (bidgee widgee), *Olearia argophylla* (musky daisy bush), *Agrostis billardieri* (coast blown-grass), *Pelargonium australis* (austral storks-bill), *L. gladiatum*, *F. nodosa.*

Table 2.   Summary of trapping and sampling periods at study sites

HWW, heathy woodland west; HWE, heathy woodland east; SH, sandy heathland; HLF, heathy lowland forest; EW, estuarine woodland; CHS, coastal headland scrub; CS, coastal scrub

Vegetation community	No. of sites	Years (sampling events)	Base years (trap-nights)	Final years (trap-nights)
HWW	1	1975–2017 (64)	1986–87 (600)	2014–17 (195)
	1	1988–2018 (37)	2002 (600)	2013–18 (910)
	1	1990–2017 (22)	2002 (600)	2013–17 (637)
	3	1983–2014 (15)	1986–87 (600)	2014–16 (450)
	2	1981–2016 (19)	1986–87 (960)	2016 (180)
HWE	1	1983–2018 (42)	1986–87 (360)	2013–18 (480)
	1	1983–2018 (16)	1987 (540)	2014–18 (370)
	1	1991–2015 (13)	1992 (600)	2014–15 (253)
	4	1995–2018 (27)	1995–96 (960)	2013–18 (935)
SH	1	1998–2018 (39)	2002 (400)	2013–18 (325)
HLF	4	1983–2015 (15)	1986–87 (600)	2014–15 (450)
EW	1	1999–2017 (13)	1999–2000 (180)	2015–17 (180)
CHS	4	1997–2017 (33)	1998 (600)	2014–17 (370)
CS	5	1983–2018 (16)	1986–87 (540)	2015–18 (373)

of the maximum success recorded between 1975 and 2007 compared to the years 2013–18 (Table 2). Mean abundance and species richness was compared for each community using two-sample T-tests, with arcsine-transformation for non-normal distribution. Percentage change in abundance was calculated as $(V_2 - V_1 / V_1) \times 100$. Trends were categorised as either severe decrease (>80% reduction in abundance), large decrease (50–80%) decline (30–80% reduction in abundance) or increase.

The total abundance of individual species (trap success) were calculated and trends at sites compared. Percentage changes and

trends were categorised as above. The percentage of sites occupied by each species was calculated for 5–6-year periods between 1981 and 2018.

Fire history and rainfall patterns

The fire history (time since last burnt, number, area and type of burn) at individual sites was acquired, and the fire history (area and percentage area burnt) of the major Ecological Vegetation Divisions was obtained (Department of Environment, Land, Water and Planning, Victoria 2019 unpublished data).

Long-term rainfall data were obtained from stations in the eastern Otways at Anglesea and Aireys Inlet (Bureau of Meteorology 2019).

Assessments of site-specific threats

Assessments of threats at sites were compared using the historical data and recent surveys. An estimate of extent of fragmentation of sites was based on the habitat patch size delineated by roads or tracks. The presence of weeds, the plant pathogen *P. cinnamomi* and introduced species (the rabbit (*Oryctolagus cuniculus*), the dog (*Canis lupus familiaris*), deer and humans) were based on site observations, while the presence of predators (the red fox (*Vulpes vulpes*) and the cat (*Felis catus*)) were based on camera results and site observations from a concurrent camera-trapping study. The degree of the threat was categorised as none, low, medium or high, e.g. the impact of *P. cinnamomi* was rated as none if no vegetation damage was observed, low (<30% of vegetation impacted), medium (31–50% of vegetation impacted) or high (>50% of vegetation impacted).

Results

Comparison of total trapping success and species richness in vegetation communities

The mean maximum abundance of small mammals in the 2013–18 period was significantly lower than that for the 1975–2007 period in HWW ($t = 8.568$, d.f. $= 14$, $P = 3.05 \times 10^{-7}$), HWE ($t = 5.864$, d.f. $= 12$, $P = 3.83 \times 10^{-5}$), heathy low forest ($t = 3.823$, d.f. $= 6$, $P = 0.004$) and coastal scrub communities ($t = 2.928$, d.f. $= 8$, $P = 0.0095$) (Fig. 2). The maximum abundances at the coastal headland site, the estuarine wetland and sandy heath sites were lower in the 2013–18 period than in the 1975–2007 period (Fig. 2).

Of the 30 sites surveyed since 2013, six had no native mammals detected, 20 exhibited decreases (50–80% reduction) or severe decreases (>80% reduction) in total native mammal abundance compared to previous years (Supplementary Table S1). Decreases at sites in HWW and heathy low forest were predominantly large to severe. In the HWE community declines were also severe to large with three sites recording no native mammals. Decreases at the sandy heathland, estuarine wetland and coastal headland scrub were severe (>80%). In coastal scrub declines were less pronounced (7%) (Table S1).

The mean species richnesses of small mammals in the 2013–18 period were all significantly lower than in the 1975–2007 period for HWW ($t = 5.239$, d.f. $= 14$, $P = 0.00012$), HWE ($t = 4.18$, d.f. $= 12$, $P = 0.00127$) and heathy low forest communities ($t = 3.464$, d.f. $= 6$, $P = 0.00133$) (Fig. 3). The species richnesses at the coastal headland site, the estuarine

wetland and sandy heath sites were lower in the 2013–18 period than in the 1975–2007 period (all 2 : 3). Mean species richness in the coastal scrub in the 2013–18 period was not significantly different ($t = 0.365$, d.f. $= 8$, $P = 0.72$) from that in the 1975–2007 period (Fig. 3).

Comparison of total trapping success and site occupancy for mammal species

Between 1975 and 2007 the highest maximum trapping success for the agile antechinus was recorded in coastal scrub, HWW, HWE and heathy lowland forest (6.7–26.7 captures per 100 trap-nights). Recently, the species was recorded in low abundance in HWW and HWE (1.1, 0.17 captures per 100 trap-nights) and in higher abundance in heathy low forest (4.4 captures per 100 trap-nights). The species declined by 44–100% with minimum decline (44%) in heathy lowland forest (Table 3). The highest maximum trapping success for the swamp antechinus (1975–2007) was recorded in coastal headland scrub (34.0 captures per 100 trap-nights), sand heathland (20.7 captures per 100 trap-nights), with lower success in HWW and estuarine woodland (7.7–13.3 captures per 100 trap-nights) and the lowest success in coastal scrub dunes (4.4 captures per 100 trap-nights). During the recent study the species was recorded at low abundance in HWW (0.7 captures per 100 trap-nights) and coastal scrub (2.2 captures per 100 trap-nights). Maximum declines (83–100%) were recorded in HWW, sand heathland, estuarine woodland and coastal headland scrub, with a lower decline (33%) in coastal scrub (Table 3). The highest maximum trapping success for the white-footed dunnart (1975–2007) was recorded in HWW, and HWE (8.3, 8.0 captures per 100 trap-nights) with lower success (1.1–3.0 captures per 100 trap-nights) in other communities. The species was not captured in the recent surveys.

The southern bush rat occurred in maximum abundance in coastal scrub (22.0 captures per 100 trap-nights), HWW (14.7 captures per 100 trap-nights) and heathy lowland forest (11.0 captures per 100 trap-nights) between 1975 and 2007. During the recent study the species was recorded in low abundance in HWW (1.1 captures per 100 trap-nights), HWE (2.2 captures per 100 trap-nights); heathy low forest (1.1 captures per 100 trap-nights), sand heathland (1.3 captures per 100 trap-nights), coastal headland scrub (5.1 captures per 100 trap-nights) and coastal scrub (10.0 captures per 100 trap-nights). The southern bush rat exhibited increases in HWE and coastal headland scrub and declines in other communities (56.0–100%) (Table 3). Between 1975 and 2007 the swamp rat occurred in high abundance in coastal scrub (25.0 captures per 100 trap-nights), HWW (16.4 captures per 100 trap-nights), coastal headland scrub (11.1 captures per 100 trap-nights), heathy low forest (12.2 captures per 100 trap-nights) and estuarine woodland (12.0 captures per 100 trap-nights). This species exhibited high declines (67–100%) in all vegetation communities recently (Table 3). Between 1975 and 2007 the New Holland mouse was recorded only in HWE at maximal abundance (21.1 captures per 100 trap-nights) and the species was not captured in the recent surveys.

The agile antechinus declined from occupancy rates of 52–61% (1983–95) to 19–30% (1996–2007) and occupied 43% of sites between 2013 and 2018 (Table 4). The swamp antechinus was present at 17% of sites (1983–88), 30% (2001–07) and 13% (2013–15). However, the species was not recorded in 2016–18.
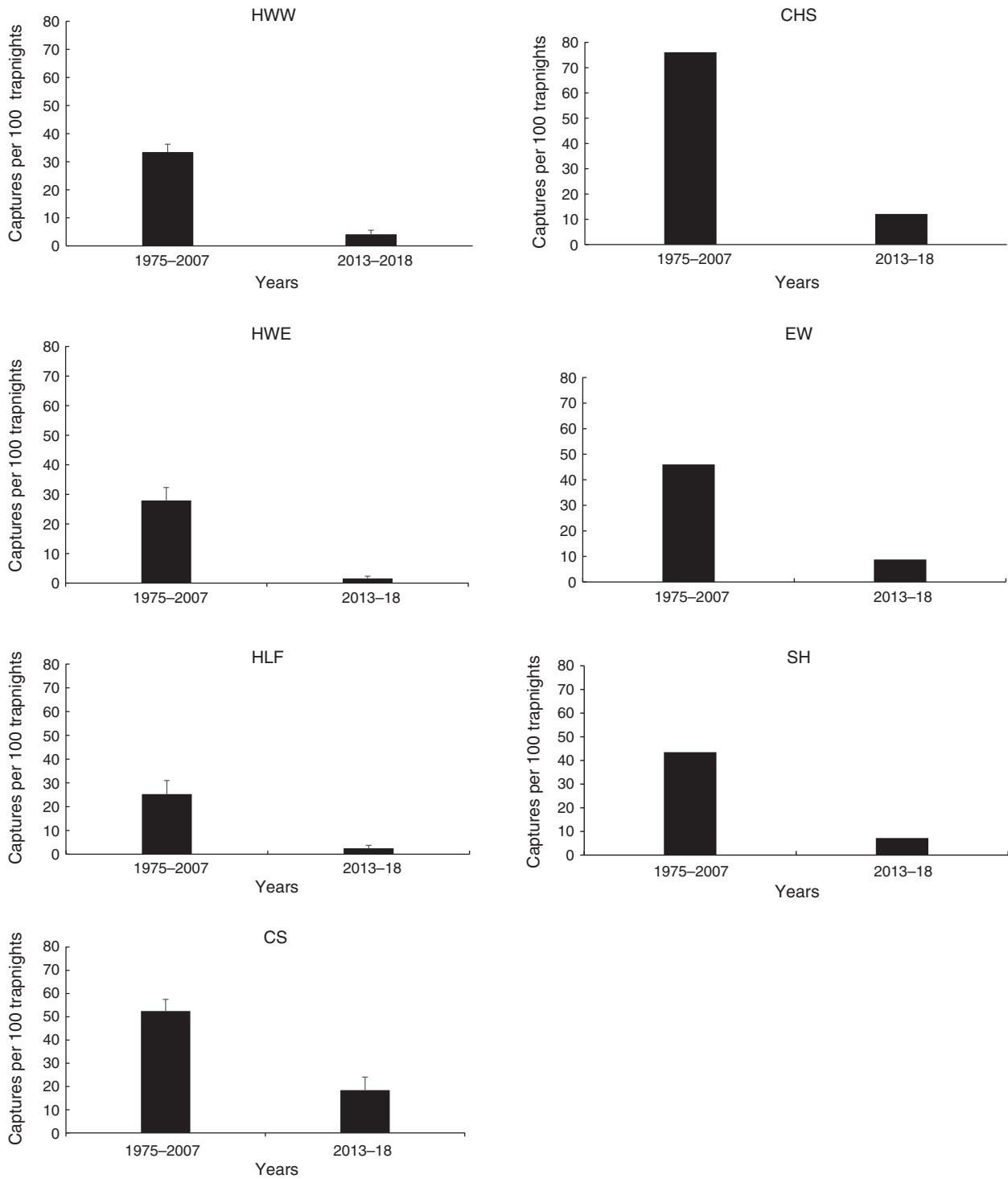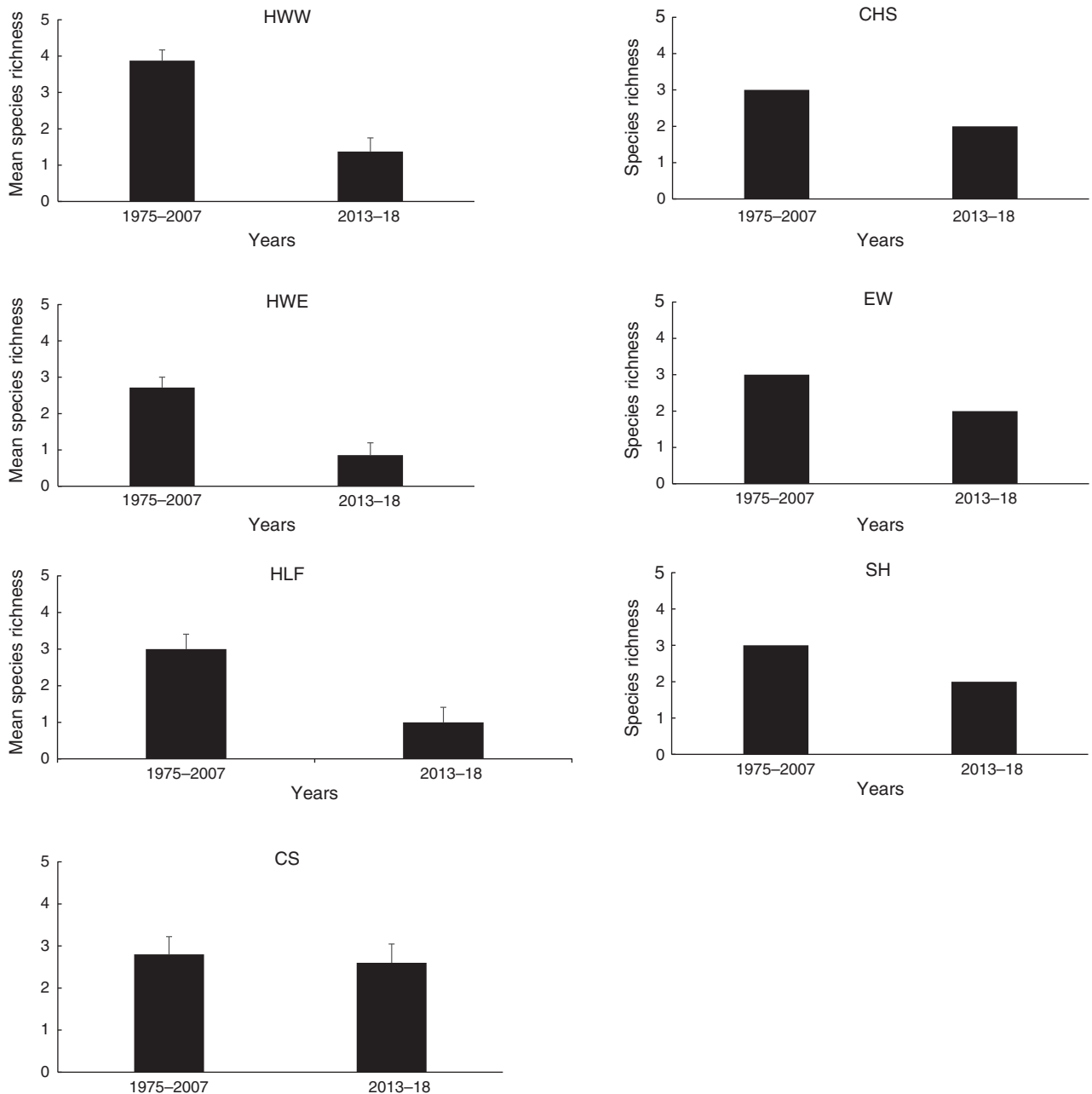
Fig. 2.   Mean maximum abundance ± s.e. (except for CHS, EW and SH, where $n = 1$) of small mammals in different vegetation communities during 1975–2007 and 2013–18 periods.

The white-footed dunnart declined from occupancy rates of 26–56% (1983–2007) but was not trapped between 2013 and 2018 (Table 4). The southern brown bandicoot was present at 44% of sites between 1983 and 1988 but was not captured from 1989 to 2007. It was trapped at 6.7% of sites in the recent 2013–18 period

(Table 4). The eastern pygmy possum was present at few sites (1983–88). It was trapped at 13% of sites during 1989–95 and was present at one site in the period 2013–18.

From 1983 to 2007 the bush rat occupied high numbers of sites (44–70%) with a similar percentage (60%) recently (2013–18)

Fig. 3.   Mean species richness ± s.e. (except for CHS, EW and SH, where *n* = 1) of small mammals in different vegetation communities during 1975–2007 and 2013–18 periods.

(Table 4). The swamp rat occupied a high percentage of sites from 1983 to 1995 (61–89%), declining to lower values (23–33%) during 1996–2007 and 20% in the recent period (2013–18). The New Holland mouse occupied few sites (0.1 to 0.2%) during 1983–2000 but was not captured subsequently.

Patterns of changes of mammal species abundance at selected sites

Between 1975 and 1981 the Harvey site (HWW) was dominated by populations of two dasyurids the agile antechinus and the swamp antechinus and two rodents, the southern bush rat and the

swamp rat (Fig. 4). Other species recorded intermittently included the white-footed dunnart, the southern brown bandicoot and the long-nosed potoroo (Wilson 1990; Wilson *et al.* 1986).

All species at the Harvey site declined rapidly or were extirpated after the 1983 wildfire (Fig. 4). The house mouse experienced a 'boom' increase in the first two years followed by decline. Native species recovery time and extent varied among species. The bush rat and the agile antechinus increased within the first year, the latter increasing rapidly in the third year. The white-footed dunnart recovered slowly after two years and the swamp rat took three years to re-establish and recover

Table 3.   Percentage changes in maximum trap success (captures per 100 trap-nights) for mammal species

Values are the changes from baseline (maximum two years recorded 1975–2007) to final (maximum two years recorded 2013–18). HWW, heathy woodland west; HWE, heathy woodland east; SH, sand heathland; HLF, heathy lowland forest; EW, estuarine woodland; CHS, coastal headland scrub; CS, coastal scrub; –, species not recorded at this site

Species	Community (total sites)						
	HWW (8)	HWE (6)	SH (1)	HLF (4)	EW (1)	CHS (4)	CS (5)
Antechinus agilis	−84	−98	−100	−44	–	–	−100
Antechinus minimus	−83	–	−100	–	−100	−100	−33
Sminthopsis leucopus	−100	−100	−100	−100	–	−100	−100
Isoodon obesulus	−100	–	–	−100	–	–	–
Cercartetus nanus	−100	−41	–	–	–	–	–
Pseudomys novaehollandiae	–	−100	–	–	–	–	–
Rattus fuscipes	−93	>23	−57	−84	−100	>35	−56
Rattus lutreolus	−75	−100	−67	−100	−73	−100	−91

Table 4.   Changes in percentage of sites occupied by species

No. of sites shown in parentheses.

Species	1975–81		1983–88		1989–95		1996–2000		2001–07		2013–18	
	(1)	%	(18)	%	(23)	%	(27)	%	(27)	%	(30)	%
Antechinus agilis	1	100	11	61	12	52	8	30	5	19	13	43
Antechinus minimus	1	100	3	17	2[A]	0.1	3	0.11	8	30	4	13
Sminthopsis leucopus	1	100	10	56	14	61	7	26	7	26	0	0
Isoodon obesulus	1	100	8	44	0	0	0	0	0	0	2	6.7
Perameles nasuta	1	100	0	0	0	0	0	0	0	0	0	0
Cercartetus nanus	0		1	0.1	3	13	0	0	2	7	1	3.3
Potorous tridactylus	1	100	0	0	0	0	0	0	0	0	0	0
Pseudomys novaehollandiae	0		2	0.1	5	0.2	4	0.15	0	0	0	0
Rattus fuscipes	1	100	11	61	16	70	12	44	13	48	18	60
Rattus lutreolus	1	100	16	89	14	61	7	23	9	33	6	20

[A]Reintroduced.

abundance, peaking five to six years after fire (Fig. 4). Species such as the southern brown bandicoot and the eastern pygmy possum were recorded intermittently in this post fire period however the swamp antechinus was not recorded (Wilson 1990; Wilson *et al.* 1990). In 1995 and 2002 only two species were recorded the bush rat and the swamp rat (Fig. 4). Trapping at the Harvey site in the recent survey period resulted in no small mammal captures (2014, 2015) with one bush rat and one agile antechinus captured in 2017 (Fig. 4).

The Forest (HWE) site was first trapped following the 1983 wildfire (Fig. 5). One species, the swamp rat, was recorded in 1984. The house mouse experienced a 'boom' increase in the second year and peaked in autumn until 1988 (Fig. 5). The New Holland mouse colonised the site in 1985 and maintained a population until 1988. The bush rat colonised the site at low abundance in 1985–86, and the swamp rat at higher abundance in 1986–88. Trapping in 1995 and 1998 resulted in no mammal captures and in the recent survey period the bush rat was the only species detected (Fig. 5).

The sandy heathland (Urquhart) site was dominated by the presence of the swamp antechinus from 1998 until 2007 (Fig. 6). In 2007 the species was present at lower abundance and no captures were recorded recently. Five other species (the agile antechinus, the white-footed dunnart, the bush rat, the swamp rat

and the house mouse) were recorded between 1998 and 2007 (Fig. 6). Recent trapping resulted in the capture of three species in low abundance (the agile antechinus, the bush rat and the swamp rat) (Fig. 6).

The coastal scrub was first trapped following the 1983 wildfire when no animals were trapped (Fig. 7). The house mouse peaked in abundance from 1984 to 1986 and then declined. Species such as the bush rat and the swamp rat established and increased in abundance from 1985 to 1988. In the recent surveys the abundance of the bush rat and the swamp rat were lower. The swamp antechinus was recorded intermittently in coastal scrub between 1984 and 2001 and was trapped recently in 2015 but not in 2017 (Fig. 7). The white-footed dunnart and the agile antechinus and the southern brown bandicoot were captured intermittently between 1987 and 2017.

Fire history and rainfall

All long-term sites were burnt in the 1983 'Ash Wednesday' wildfire (Table 5). The Harvey site was burnt twice subsequently by fuel-reduction burning, and Bald Hills Grids B and C once by fuel-reduction burning (Table 5).

The long-term average rainfall for the eastern Otways was 664 mm (Fig. 8). Record levels of annual deficit rainfall (below average in 11 of 17 years) occurred during the 'millennium
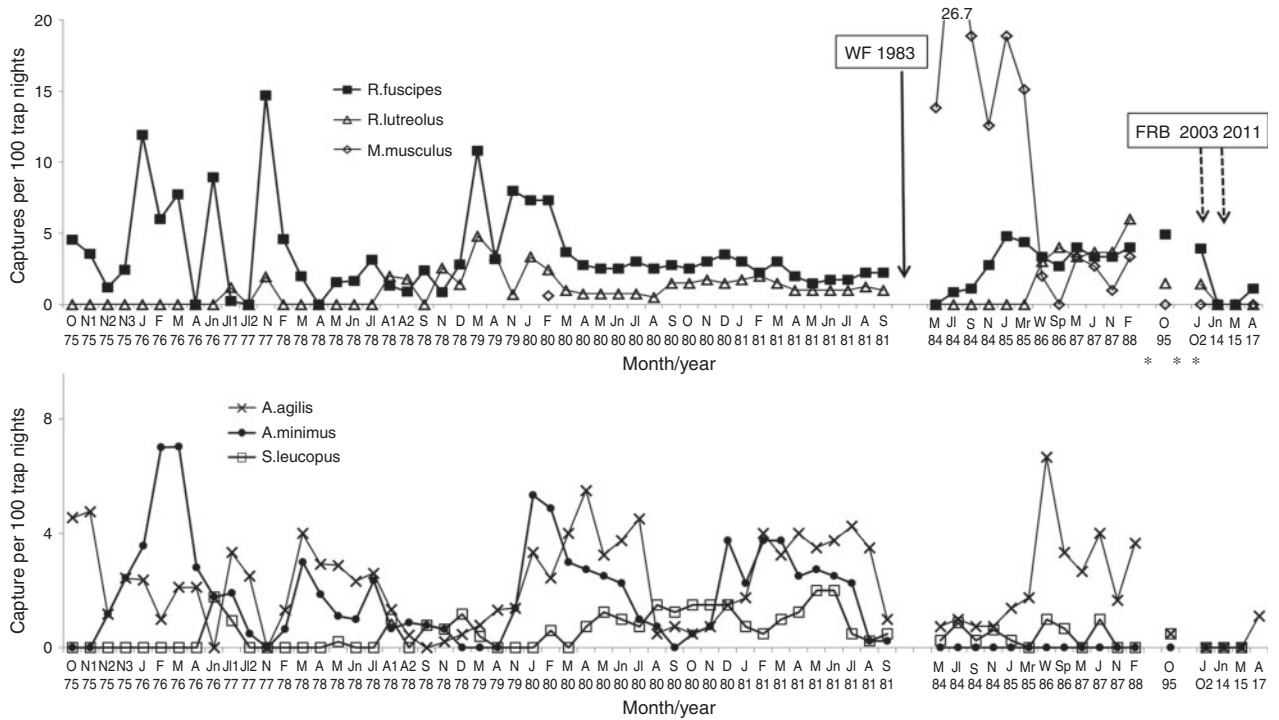
Fig. 4. Trapping success for small mammal species in heathy woodland (west) (HWW) at the Harvey site (1975–2017). WF, wildfire; FRB, fuel reduction burn; *, not surveyed 1989–94, 1996–2001, 2003–13.
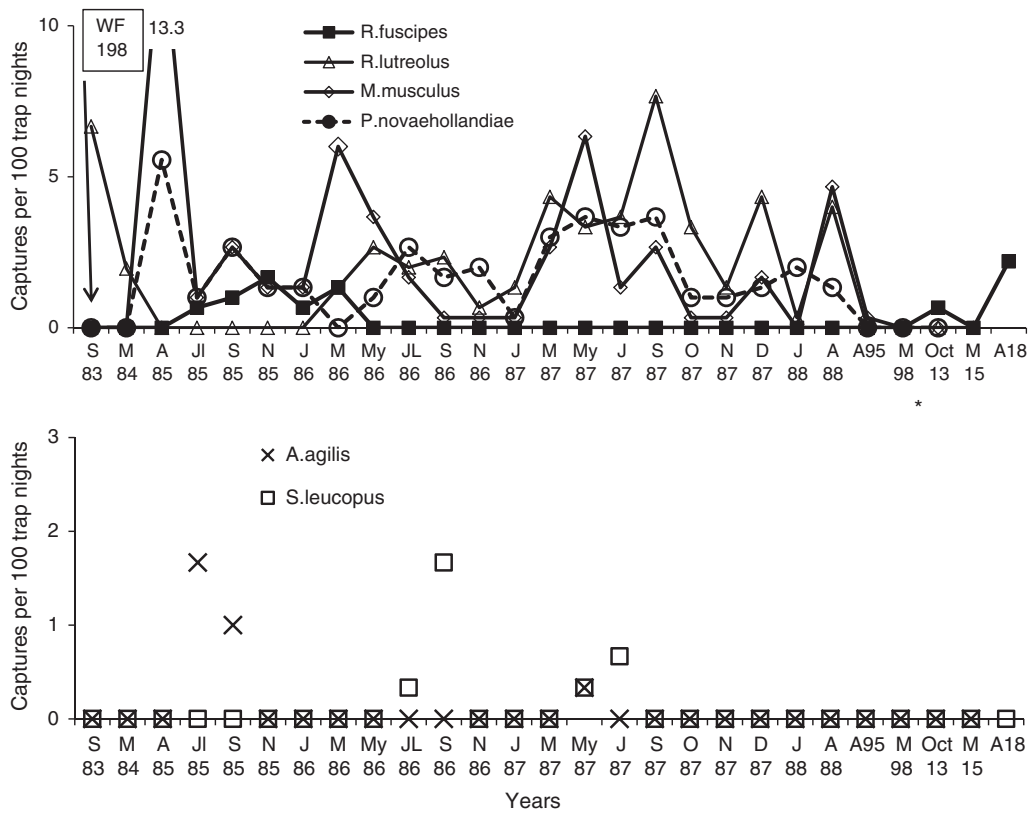
Fig. 5. Trapping success for small mammal species in heathy woodland (east) (HWE) at the Forest site (1983–2018). *, not surveyed 1999–2012.
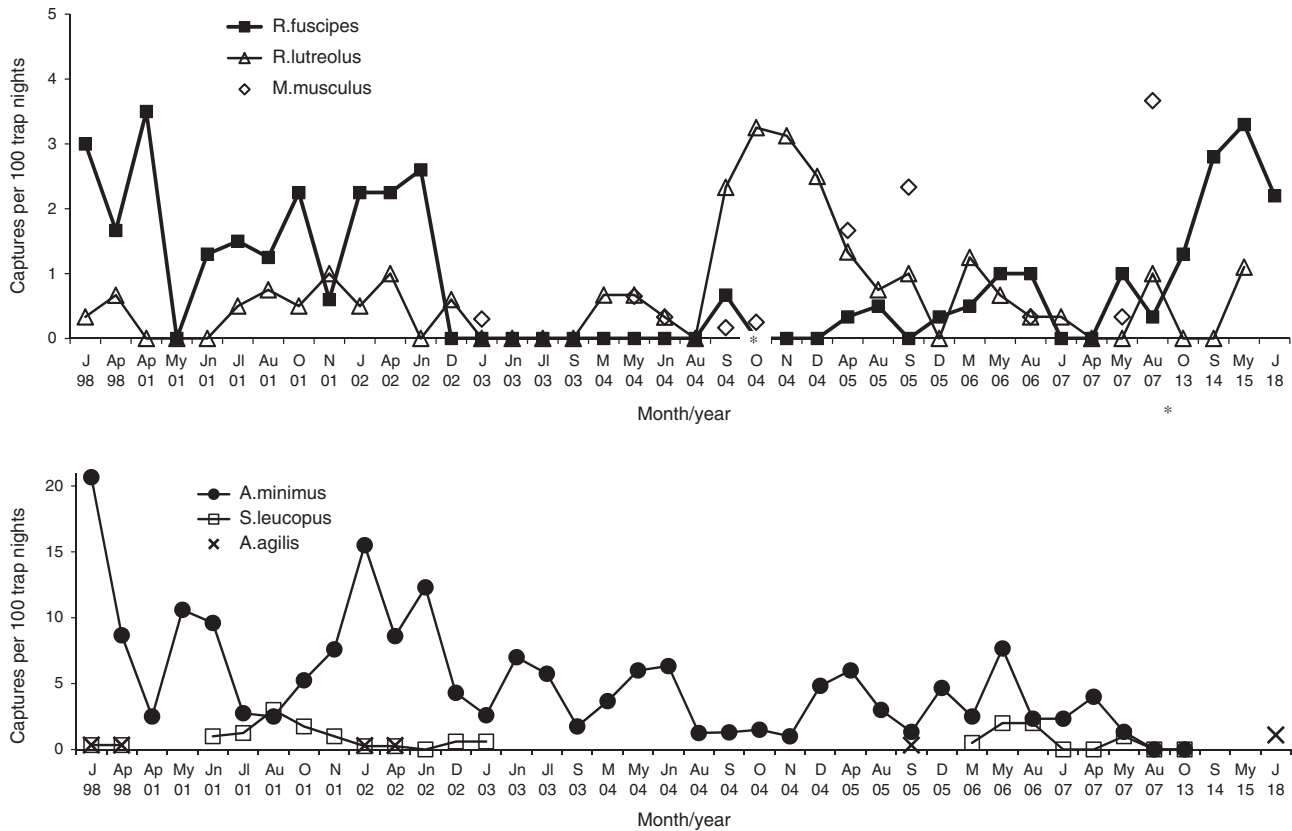
Fig. 6.   Trapping success for small mammal species in sandy heathland at the UB site (1998–2018). *, not surveyed 2008–12.

drought' (1996–2010) (Fig. 8) (CSIRO and Australian Bureau of Meteorology 2012). Accumulative declines were observed between 1994–99 and 2002–06 during this drought period, with the lowest annual rainfall of 445.8 mm in 2006. High rainfall (900 mm) occurred in 2001, 236 mm above the long-term average. Between 2010 and 2013 rainfall was long-term average; however, rainfall in 2014 (498 mm) and 2015 (448 mm) was very low (Fig. 8).

Assessments of threats at sites

Prior to 2007 the main processes identified as threatening populations at inland sites were inappropriate fire regimes, *P. cinnamomi* infestation and foxes, while at coastal sites they were habitat fragmentation, foxes and rabbits (Table 5). The processes identified in the recent surveys (2013–18) were similar with the addition of the presence of dogs, human activity and littering at coastal sites (Table 5).

Discussion

Small mammal declines in vegetation communities

Long-term repeat trapping studies at sites over 20- to 42-year periods have revealed significant declines in mammal assemblages across the eastern Otways. In the recent survey period 67% of sites exhibited decreases (50–80%) or severe decreases (>80% reduction) in native mammal abundance compared to previous years, and no native mammals were detected at six of

these sites. In the earlier decades 27% of the sites had 4–7 species, compared with 3% of sites in the recent period.

One limitation of the study may be variation in detection probability of species utilising live trapping across the habitats. While detectability of the swamp antechinus across the same habitats was 67% in 1997–98 it recently (2015) was low (38%) and may have resulted in some false negatives (Zhuang-Griffin 2015). Recent trapping has found that other species such as *Antechinus agilis* (99%) and *Rattus fuscipes* (91%) are highly detectable (Van der Heyden 2016).

The mean maximum abundance of small mammals during 2013–18 was significantly lower in most communities than during the 1975–2007 period; the extent of declines however varied between vegetation communities. There is evidence that the declines in the HWE community were more severe than in HWW with 43% of sites in the former recording zero native mammals in recent surveys. In contrast to the highly dissected landscape occupied by the HWW community, the east community occurs on dry flat to undulating topography, with no significant gullies (Wilson *et al.* 2015). The community may thus have lower capacity to retain moisture and dampness during drought and rainfall declines. Differences identified in the topography and vegetation between the heathy woodland sites located in the west and east of the study area were reflected in the different mammal compositions. While the sites in the east were historically dominated by the high abundance of the New Holland mouse and low abundance of the bush rat and the
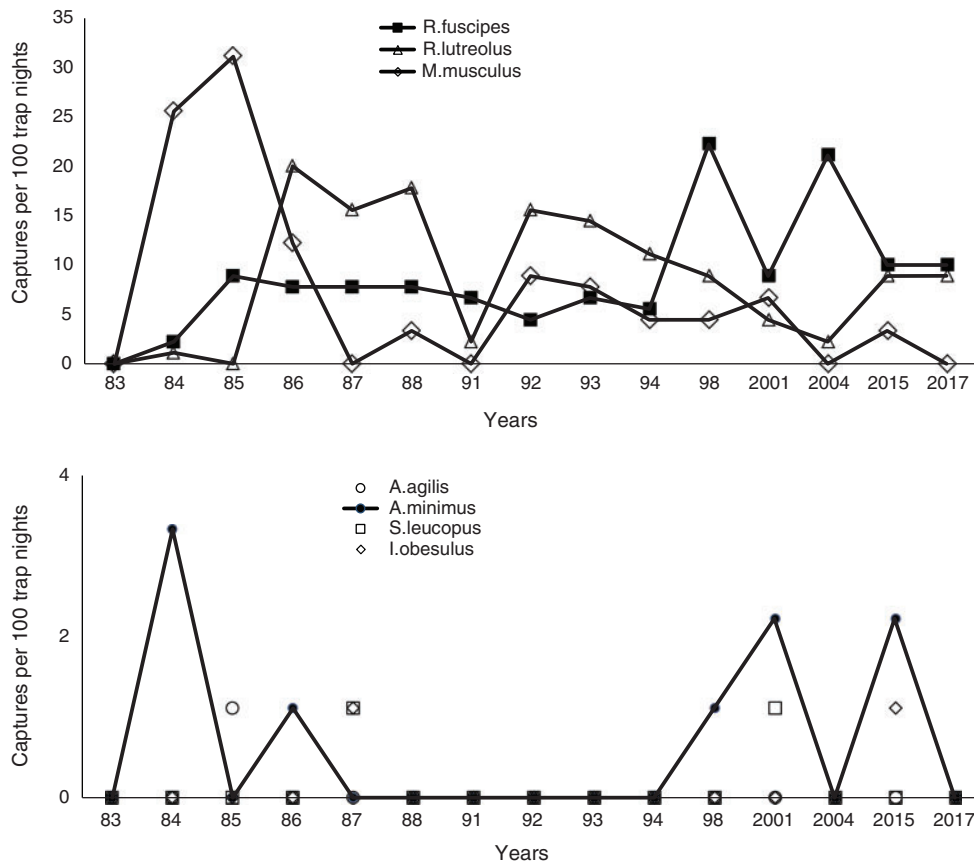
Fig. 7. Trapping success for small mammal species in coastal scrub at Site 36 (1983–2017). *, not surveyed 2008–12.

swamp rat (see Fig. 5), those in the west were dominated by high-abundance mammal communities including species such as the swamp antechinus, the bush rat and swamp rat (see Fig. 4).

A significant finding of the study was that declines in abundance in the coastal scrub community were much less in 2013–18 in comparison to other communities, and mean species richness was not significantly different from the 1975–2007 period. The lower decline at coastal scrub sites indicates that this community may provide important refuges for mammals. Further, concurrent camera trapping studies have recorded additional mammal species including the long-nosed potoroo, the long-nosed bandicoot and the white-footed dunnart, which were not recorded during trapping (Wilson and Garkaklis 2016; Wilson *et al.* 2017a).

Long-term data (1983–2004) showed that the coastal scrub sites on dunes have consistently supported 5–7 native species including threatened species (the swamp antechinus, the southern brown bandicoot) and high-density populations (some two- to six-fold greater than in other communities) (Wilson *et al.* 1990, 2017a; Wilson and Garkaklis 2016). The results are important because they demonstrate that this community continues to support substantial mammal populations, while significant declines were recorded in all other woodland and forest communities.

Declines in species

Several native species that had been trapped previously were not captured during the recent surveys: the New Holland mouse, the

white-footed dunnart, the long-nosed potoroo, the long-nosed bandicoot and the sugar glider (*Petaurus breviceps*) (Wilson 1990; Wilson *et al.* 1990). A contemporaneous camera-trapping study at 18 of the 30 study sites did result in the record of the presence of three of these species; the white-footed dunnart the long-nosed potoroo and the long-nosed bandicoot at three, one and two sites respectively, confirming their continued presence in the study area *albeit* at few sites (Wilson and Garkaklis 2016; Wilson *et al.* 2017a).

The declines in numbers of the New Holland mouse and the swamp antechinus have been documented and discussed recently (Wilson *et al.* 2017b, 2018b; Burns 2018, 2020). Another species that exhibited high declines in abundance (67–100%) and distribution (61–89% in 1983–95 to 20% in 2013–18) was the swamp rat. This species is herbivorous, eating sedges and grasses, and prefers wet, high-density vegetation, with vegetation density of paramount importance for habitat selection (Fox and Monamy 2007).

There was evidence that two species (the agile antechinus and the bush rat) did not decline as precipitously as other species. The agile antechinus and the bush rat have also been recorded in recent trapping at other sites across the study area but predominantly in gullies (Van der Heyden 2016, Lees 2019; Watchorn pers. comm.). Recent habitat modelling of these two species found that areas with a probability of high occurrence had reduced significantly between the early 2000s (Wilson *et al.*

Table 5.   Summary of site-specific fire history, disturbance and threats

HWW, heathy woodland west; HWE, heathy woodland east; SH, sand heathland; HLF, heathy lowland forest; EW, estuarine woodland; CHS, coastal headland scrub; CS, coastal scrub; FRB, fuel reduction burn. Degree of threat or disturbance: –, none; *, low; **, medium; ***, high. Introduced species: r, rabbit; f, fox; c, cat; d, dog; dr, deer; dw, dog walking; old, off-leash dogs; mbr, motorbike riding; hr, horse riding

Vegetation community	HWW						HWE		SH	HLF	EW	CHS	CS
Location	Harvey	Bald Hills	Bald Hills	Batson A, C	Forest	Pipeline	Harrison	Flaxbourne	Urquhart	GumFlat	Painkalac	AInlet	Sanddune
Wildfire													
1975–2007	**	**	**	**	**	**	**	**	**	**	**	**	*/**
2013–18	–	–	–	–	–	–	–	–	–	–	–	–	–
FRB													
1975–2007	–	*	–	–	–	–	–	–	–	–	–	–	–
2013–18	**	–	–	–	*	–	*	*	–	–	–	–	–
Weeds													
1975–2007	–	–	–	–	–	–	–	*	–	–	*	**	*
2013–18	**	–	–	–	–	–	–	*	–	–	**	***	*
Phytophthora													
1975–2007	*	**	–	–	–	–	–	*	–	*	–	–	–
2013–18	**	**	–	–	–	–	–	*	–	*	–	–	–
Introduced spp.													
1975–2007	–	f*	–	–	f**	–	f**	f** r*	f** r*	f*	f* c*	f* r*	f* r*
2013–18	f**	f*	–	–	f* dr*	–	–	f* c* r*	f** r***	f*	f* c*	f* r**	f* c*r*
Fragmentation													
1975–2007	*	–	–	–	–	–	–	***	–	–	***	***	***
2013–18	*	–	–	*	**	–	–	***	–	–	***	***	***
Recreation													
1975–2007	–	–	–	–	–	–	mbr***	hr*	–	–	dw* old*	dw* old*	–
2013–18	d**	–	–	–	hr***	–	–	hr***	–	–	dw* old*	dw* old*	dw* old*
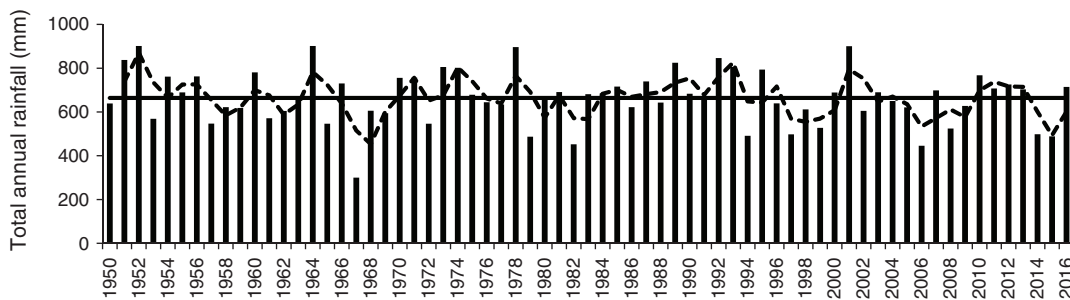
Fig. 8.   Total annual rainfall 1950–2016 with moving average line (dashed line) and long-term average (black line). (From Bureau of Meteorology.)

2001; Gibson *et al.* 2004) and 2016 (Van der Heyden 2016). The differences may relate to the recent model for the bush rat being a weaker model, or possibly due to an absence of habitat complexity as a model variable for both species in the recent models (Van der Heyden 2016). The behaviour and life-history attributes of these two generalist species may contribute to their apparent resilience. The agile antechinus is semiarboreal and thus capable of exploiting very diverse habitats, including understorey vegetation and trees in which to scavenge for food which is predominantly invertebrates (Green 1989; Goldingay 2000; Parrott *et al.* 2007). While the bush rat selects for dense cover of rushes and logs (Lunney and Ashby 1987; Catling 1991; Fordyce *et al.* 2016) it has a broad omnivorous diet of seeds,

fungi and invertebrates and is capable of breeding year-round (Parrott *et al.* 2007; Swan *et al.* 2016).

Patterns of declines

The sites reported on here were selected for specific studies into the ecology, life-history and reproduction of mammal species, not for long-term monitoring purposes. However, they are a good representation of environmental variation in the region and have provided valuable information on species and community population dynamics and patterns over time, at sites in different vegetation communities and across the landscape. If we had known the data were to be used for long-term monitoring our site selection may have included a process of hierarchical site

selection within each vegetation community and random location of sites within the communities.

The 1983 'Ash Wednesday' wildfire that burnt ~40 000 ha regionally and left only small patches of unburnt vegetation had a major impact on mammals in the study area (Wilson *et al.* 1990). Total abundance trends were similar for sites that were impacted by the wildfire (HWW, HWE, heathy forest, coastal scrub dunes) with very low abundance recorded in the first two years after fire. Recovery rates in the next two years resulted in high abundance in coastal scrub and HWW locations and lower abundance levels in HWE locations. Most native species recovered substantially, with recovery time and extent varying among species. Rainfall in the first three months and the first three years after fire was above average and contributed to rapid recovery of vegetation thus providing high vegetation cover and food resources including seeds, herbaceous material, fungi and invertebrates for mammals (Wark *et al.* 1987; Wilson 1990; Wilson *et al.* 1990). At least six inland populations of the swamp antechinus were extirpated by the wildfire and no recolonisation was recorded over a 15-year period (Wilson *et al.* 2001).

There is strong evidence that rainfall deficit is a major contributing impact on declines of species such as the swamp antechinus and the New Holland mouse in the eastern Otways (Wilson *et al.* 2017*b*, 2018*b*). While low rainfall was proposed as a likely factor contributing to declines in populations of the swamp antechinus in the eastern Otways (Wilson *et al.* 2001) there is now strong evidence from several sites (e.g. Urquharts, Bald Hills) that rainfall does have a major impact on population dynamics (Annett 2008; Magnusdottir *et al.* 2008; Sale *et al.* 2008). Maximum population densities occurred after the highest total annual rainfall (901 mm) recorded for two decades. Features included increased survival of females into the breeding season, and of juveniles after weaning, and increased overall body weight following peak annual rainfall. In comparison, declines in population density were measured during periods of below-average rainfall and drought (2001–07) and were correlated with rainfall in the previous spring (Magnusdottir *et al.* 2008; Sale *et al.* 2008). The impacts of rainfall on the species are considered to result from bottom-up increases or declines in productivity of vegetation and associated dietary resources, particularly moth larvae and beetles (Sale *et al.* 2008; Sale and Arnould 2012). The swamp antechinus has a semelparous life-history strategy and females are monoestrous (Wilson 1986). The strategy, common to other dasyurid marsupials, has evolved in comparatively stable environments with a predictable spring flush of invertebrate food when the young are becoming independent (Braithwaite and Lee 1979). However, this strategy results in a high vulnerability to stochastic events, such as drought, as species are unable to delay breeding until conditions improve.

Significant relationships with drought and reduced body-weight, fecundity, survival and population size have been recorded for other small marsupial species such as the agile antechinus (*A. agilis*), the yellow-footed antechinus (*Antechinus flavipes*), the brush-tailed phascogale (*Phascogale tapoatafa*) and the honey possum (*Tarsipes rostratus*) (Rhind and Bradley 2002; Parrott *et al.* 2007; Bradshaw *et al.* 2007; Lunney *et al.* 2008; Lada *et al.* 2013).

The New Holland mouse has also been significantly influenced by rainfall, exhibiting a population irruption (15–20 individuals ha^{-1}) following six years of above-average rainfall and a precipitous decline to site extinction during subsequent drought (Lock and Wilson 2017; Wilson *et al.* 2018*b*). The decline was predominantly related to loss of adults before and during breeding seasons, together with an apparent decrease in survival of juveniles.

It is likely that declining rainfall during the 'millennium drought' (1996–2010), and exceptionally low rainfall in 2014 (498 mm) and 2015 (448 mm) have similarly impacted other small mammal species and communities across the landscape, although we do not have detailed population data for other species. During the recent study high rainfall in July 2016 followed by high spring rainfall was expected to result in increased survival and recruitment of small mammals. However, there was no increase in locations or trap success in 2017–19, providing no evidence of such responses. This indicates that following extended drought recovery may require longer periods of increased rainfall.

There is evidence that habitat fragmentation has contributed to population and community declines at some sites in the eastern Otways. The recent surveys found that populations of swamp antechinus that were previously identified to be at high risk from fragmentation impacts (Aireys Inlet, Urquhart), (Wilson *et al.* 2001; Magnusdottir *et al.* 2008) are now no longer extant. Since that time increased housing development has resulted in removal of habitat and increased fragmentation.

While several factors contributing to the decline of mammals in the eastern Otways have been identified, the relative impacts and their interactions are complex, and not well understood. Similarly, severe decline in terrestrial mammal assemblages of northern and south-western Australia and declines of terrestrial and arboreal mammals recorded in southern New South Wales, have been unable to identify clear mechanisms (Woinarski *et al.* 2010; Wayne *et al.* 2017*a*; Lindenmayer *at al.* 2018).

Several threats identified in the eastern Otways are likely to have complex synergistic interactions on the population dynamics of mammals. For example, wildfire or fuel-reduction management burns during drought conditions increase the risk of extirpation of small fragmented populations and decrease recovery opportunities. The recent evidence that the impacts of introduced predators on mammals are more severe in burnt areas (McGregor *et al.* 2014, 2015; Leahy *et al.* 2015; Hradsky *et al.* 2017) indicates that the impact of predators will be exacerbated under increased burning regimes. There is a need to understand further how these factors interact in order to develop recovery and management plans under predicted climate change.

Refuge locations and characteristics

The identification of mammal refuges in specific areas such as coastal scrub on sand dunes is significant. Further, during recent surveys captures of mammal species at many sites were found to be restricted to gullies (Wilson and Garkaklis 2016; Wilson *et al.* 2018*a*; Lees 2019; Watchorn pers. comm.). The contraction of mammals to these areas indicate that they represent important refuges. Evidence of contractions of small mammal populations into refuge habitats during drying periods and drought have been identified in arid, semi-arid and temperate environments (Milstead *et al.* 2007; Letnic and Dickman 2010; Keppel and

Wardell-Johnson 2012; Wilson *et al.* 2012; Greenville *et al.* 2013; Pavey *et al.* 2017). Attributes of refuge areas that enhance the resistance of the biota by providing more favourable environmental conditions or higher resource availability include topographic position and vegetation cover (Letnic and Dickman 2010; Greenville *et al.* 2013; Pavey *et al.* 2017; Reside *et al.* 2019).

It is possible that survival of threatened species and high-density populations of other small mammals in the coastal scrub dunes of the eastern Otways may be due to mammals benefiting indirectly from marine inputs such as seabird guano and other allochthonous marine nutrient inputs at these sites (Bancroft *et al.* 2005). Increased nutrient inputs have been linked to high food availability (invertebrates), dense vegetation cover, higher abundance of wildlife and increased reproductive success in island and coastal sites (Wolfe *et al.* 2004; Bancroft *et al.* 2005; Sale *et al.* 2008; Sale and Arnould 2012). Very-high density populations of the swamp antechinus that have been recorded on island habitats have also been shown to be supported in this way (Sale *et al.* 2008; Sale and Arnould 2012). A recent preliminary study in the eastern Otways did show that available plant nutrients were lower at inland forested and woodland sites than at coastal scrub dunes (Wilson *et al.* 2018a). In particular, the scrub dunes had several orders of magnitude higher available nitrogen and phosphorus than did inland sites (Wilson *et al.* 2018a).

Further, the vegetation in the coastal sand dunes is dense and structurally complex due to the absence of fire since 1983. The vegetation is likely to provide protection from predators such as cats and foxes which have been recorded by camera within this community (Wilson *et al.* 2017a). There is evidence that habitat structure can affect predation risk and prey behaviour; for example, vegetation cover can provide prey with a refuge to which it can escape, and also obscure a predator's search image, thus making hunting less efficient (Verdolin 2006; Dickman *et al.* 2010; Doherty *et al.* 2015).

Many refuge areas appear to occupy only a small portion of the landscape; for example, refuge habitats for rodents in Chile occupied only ~2% of the landscape studied (Milstead *et al.* 2007). The identification of locations that provide refuge from disturbances such as drought, increasing temperatures, fire and extreme weather events has thus been the focus of recent studies (Mackey *et al.* 2012; Robinson *et al.* 2013; Selwood *et al.* 2019). For example, landscape elements such as gullies and rocky outcrops provide physical protection from fire (Robinson *et al.* 2013), while mesic locations with high vegetation productivity, such as floodplains and riparian zones, support more stable animal assemblages during drought (Selwood *et al.* 2019; Nimmo *et al.* 2016). Management and protection of refuges is thus recognised as a conservation priority for fauna (Letnic and Dickman 2010; Pavey *et al.* 2017).

Recent research has aimed to identify refuges using remote sensing indices associated with high green vegetation cover (Mackey *et al.* 2012; Reside *et al.* 2013; Dubinin *et al.* 2018). Such cover is a characteristic of relatively humid conditions which can indicate potential refuges, high plant productivity, resource availability for animals, including food (seeds, fruit, foliage, prey), shelter and nesting resources (Albright *et al.* 2010; Mackey *et al.* 2012). Work is currently being undertaken to identify mammal fauna habitat refuges across the Otway Ranges utilising site topographical information, and satellite remote-sensed vegetation productivity data to characterise the refuge sites (Wilson *et al.* 2018a, 2019).

The projected rainfall declines over the study area under a high-carbon-emission scenario are from 25% to 45% by 2090 (Hope *et al.* 2015). Irrespective of the causal factors of mammal declines, more precise identification and better protection of refuges is considered crucial to increase resilience of mammal species and communities of the region, particularly with respect to wildfire, fuel-reduction burning and predator management (Robinson *et al.* 2013; Doherty *et al.* 2015; Wayne *et al.* 2017b; Wilson *et al.* 2017b, 2018a). The sand dune refuges should certainly be a focus of predator control, particularly after fire.

The long-term mammal research programs in this study were not established as monitoring programs, so were without defined population condition breakpoints that would prompt management responses (Burgman *et al.* 2012). There is a need to implement consistent monitoring of mammals that provides effective measures for management. Reporting on the effectiveness of fire management on public land to provide evidence that burning is delivering optimal habitat for mammals is also required (Department of Environment, Land, Water and Planning 2015).

Conflicts of interest

The authors declare no conflicts of interest.

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