

Does woodland condition influence the diversity and abundance of small mammal communities?

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Abstract. Loss of mammal species in Australia in the last 200 years has been attributed to many factors including habitat removal and altered fire regimes. Decline in tree condition could contribute further to the ongoing decline of mammals. *Eucalyptus wandoo* trees are currently undergoing a decline in condition that can result in a loss of canopy and other changes to the habitat. This paper examines the relationships between *E. wandoo* tree condition, habitat characteristics and small mammal species richness and abundance. Live-capture trapping was conducted at 24 *E. wandoo* sites at Dryandra State Forest and Wandoo Conservation Park, Western Australia. Condition and microhabitat variables of *E. wandoo* were recorded for each site. Generalised additive mixed models revealed a range of habitat and tree condition characteristics that influenced small mammal abundance and species richness, including site litter cover, crown dieback, understorey vegetation cover and tree density. The availability of coarse woody debris played a large role in explaining the abundance of *Cercartetus concinnus* and *Antechinus flavipes*, along with other microhabitat and tree condition variables, such as tree leaf litter and crown dieback. Epicormic growth, crown density and the distance to the drift fence from *E. wandoo* trees were the common variables in the best model for the abundance of *Sminthopsis griseoventer*. The decline in condition of *E. wandoo* and the subsequent modifications to the microhabitat are correlated with changes in the small mammal community. A better understanding of how the decline of *E. wandoo* impacts small mammal communities could improve management practices in *E. wandoo* woodlands.

Additional keywords: *Antechinus*, *Cercartetus*, *Eucalyptus wandoo*, microhabitat, *Sminthopsis*.

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Introduction

The distribution and abundance of small mammals is often linked to habitat structure, including crown density, understorey cover, coarse woody debris and leaf litter cover (Knight and Fox 2000; Catling *et al.* 2001; Holland and Bennett 2007). These habitat structures contribute to overall habitat complexity and provide small mammals with nesting and foraging resources (McElhinny *et al.* 2006; Mac Nally and Horrocks 2008) and refuge from predators and extreme weather conditions (Bos and Carthew 2003). An emerging phenomenon that is altering habitat structure of forests and woodlands globally is the decline in tree condition (Allen *et al.* 2010). Although tree decline can be attributed to multiple causes (e.g. drought: Allen *et al.* 2010; pathogens: Stone *et al.* 1998), the death of upper portions of the tree canopy is an increasingly common phenomenon in forests and woodlands (Manion and Lachance 1981; Close and Davidson 2004). Loss of the foliage creates an open canopy, directing more sunlight to

the understorey, altering herb communities, bare ground, leaf litter and understorey vegetation density (due to greater isolation, changes in soil moisture, and pH). These changes will alter available habitat for small mammals (Loyn and Middleton 1980; Jurskis 2005). The effects of tree decline on small mammals are not well understood, though a decline in tree condition could result in a major loss of habitat and resources for them (Catling and Burt 1995; Williams *et al.* 2002; McKenzie *et al.* 2007).

Of all continents, Australia has recorded the most mammal extinctions over recent centuries. Seventeen Australian mammal species have been lost over the last 200 years, which is approximately half the total number of mammal species extinctions worldwide (Short and Smith 1994; Cardillo and Bromham 2001; Woinarski *et al.* 2010). Mammal decline and extinction in Australia are highest in Western Australia's farming and cropping area (Burbidge and McKenzie 1989), where land

clearing has led to a loss of more than 90% of native vegetation (Hobbs 1993). During the early colonisation of Western Australia, 43 mammal species (excluding bat species) were present in the farming region. However, by the 1970s, only 12 species were moderately common in the region (Kitchener *et al.* 1980). Today a large number of threatened mammals persist in patches of remnant vegetation (Yates *et al.* 2000) and a decline in the condition of remnant vegetation may contribute to further regional extinctions. *Eucalyptus wandoo*, a smooth-barked tree, once covered most of the greater agricultural area of the south-west region of Western Australia. Following clearing of the wheatbelt area, only 40% of *E. wandoo*-dominated woodlands remain, largely as small remnant patches (Mattiske Consulting Pty Ltd and Havel Land Consultants 1998; Wandoo Recovery Group 2006). Ten years ago it was noted that trees within two of the three largest patches, the Wandoo Conservation Park and the Dryandra State Forest, were showing signs of decline with symptomatic retraction or loss of canopy (Wandoo Recovery Group 2006; Brouwers *et al.* 2013). Declines of this eucalypt occur heterogeneously, where healthy trees can be adjacent to declining trees (Brouwers *et al.* 2013; Moore *et al.* 2013), differing from other eucalypt decline where large-scale canopy loss occurs (e.g. *Eucalyptus marginata*, jarrah) (Matusick *et al.* 2012).

Alteration in vegetation structure and microhabitat availability caused by a decline in tree condition of *E. wandoo*-dominated woodlands may affect the availability of resources for small mammals and influence their presence and abundance. This study explores the influence of decline in *E. wandoo* canopy condition and associated structural and microhabitat changes on mammalian species richness and abundance. We ask two questions: (1) is small mammal abundance and species richness associated with *E. wandoo* canopy condition; and (2) what other habitat characteristics (e.g. time since last fire, site litter cover and understorey density), potentially associated with canopy decline, are reflected in the abundance and species richness of small mammals in *E. wandoo* woodlands.

Methods

Site description

Study sites were located in Dryandra State Forest (32°48'S, 116°53'E) and Wandoo Conservation Park (31°54'S, 116°27'E) 160 km south-east and 75 km east of Perth, respectively. *E. wandoo* woodlands within these reserves have an open canopy (<30% canopy cover), a grassy herb layer and a patchy understorey of small shrubs including *Gastrolobium* spp., *Macrozamia riedlei* and *Xanthorrhoea preissii* (although sites with high *X. preissii* numbers were avoided as they are classified as another habitat type) (Mercer 1991). These two reserves were chosen as they are some of the largest areas of remnant *E. wandoo* woodlands in the Western Australian farming region. Despite their differences in tenure (Department of Conservation and Land Management 1980), the two reserves have similar histories of land clearing, stock grazing, timber harvesting, and prescribed fire management. A total of 24 sites were chosen within these reserves using Landsat imagery (1990–2009) and Vegmachine (CSIRO 2010) (vegmachine calculates the changes in vegetation cover over a landscape using Landsat imagery) to identify sites

with predominately healthy or declining *E. wandoo* trees (12 of each condition, six of each per reserve) at least 500 m away from the edges of remnant native vegetation. Initially, this project was not focussed on the fire history of the reserves and therefore matching fire ages were not considered in the planning stages of the research project. Similarly, the sites varied in terms of understorey vegetation, litter cover, tree density and the density of coarse woody debris.

Trapping design

Trapping grids consisted of three 20-L buckets, two 45-cm lengths of PVC pipe and four Elliott traps. Buckets and PVC tubes were arranged along a 29-m drift fence with ~6 m between traps, beginning and ending 3 m from each end of the drift fence. Elliott traps were located in the understorey 5 m diagonally from the end of each drift fence and baited with universal bait (i.e. peanut butter, sardines and rolled oats). Styrofoam trays and leaf litter were placed inside the buckets and PVC tubes and Elliott traps were lined with shredded tissue paper as shelter and nesting for captured animals. Buckets and PVC tubes were installed in late August and early September to allow the traps to settle in the ground before trapping commenced. Twelve sites were trapped over four consecutive nights in September/October 2009, November 2009, December 2009 and March/April 2010 within each location (12 sites in both Dryandra State Forest and Wandoo Conservation Park). A total of 16 nights trapping per site gave a total of 3456 trap-nights (24 sites × 16 nights × 9 traps per site). All 24 sites could not be monitored simultaneously due to distance and logistics. All Elliott traps were set, baited and positioned, and buckets and PVC tube lids opened on the afternoon preceding the four trapping nights, checked morning and afternoon for the four days and all traps were closed or removed on the last morning. All animals captured were weighed, sexed, ear notched and head-body length measured and released immediately after processing.

Measuring tree condition and other habitat characteristics

Seven characteristics (Table 1) were measured on six trees (termed 'site trees') at each of the 24 sites. Site trees were those (diameter at breast height >20 cm) closest to the trapping line. Whitford tree condition index is a semiquantitative measure that rates tree canopy condition holistically on a pictorial scale to provide a categorical value. USDA tree condition index (Schomaker *et al.* 2007) includes a range of tree characteristics originally designed for use by USA foresters assessing tree condition of *Pinus* spp. Some of these indices can be adapted to measure a range of tree types depending on the growth form. Those that were the most appropriate indices for *E. wandoo* were crown density, crown dieback and uncompact live crown ratio. Lastly, epicormic growth, canopy cover and the percentage of dead branches were recorded for each tree as the individual characteristics have been deemed important in other studies that have investigated tree condition and fauna (Wentzel 2010). In addition to these tree characteristics and indices, six habitat characteristics were recorded for each site (Table 2). One sampling characteristic, distance to the drift fence, was recorded as trapping grids were opportunistically installed in more open areas and subsequently there were differences in the distance

Table 1. Tree characteristics

Details of tree condition variables estimated on *Eucalyptus wandoo* trees in Dryandra State Forest and Wandoo Conservation Park. Each tree characteristic was visually assessed; canopy cover was measured using a spherical densitometer

Tree characteristic	Definition
Whitford tree condition index	Whitford index rates trees 1 to 6 (1 = healthy and 6 = declining) and was specifically designed for <i>E. wandoo</i> trees (Whitford <i>et al.</i> 2008).
Crown density (%)	Percentage of crown that contains foliage, branches, and reproductive structures (Schomaker <i>et al.</i> 2007).
Crown dieback (%)	Percentage of crown that has undergone recent dieback. Crown dieback is often an early indication of stress (Schomaker <i>et al.</i> 2007).
Uncompacted live crown ratio (%)	Percentage of live crown to above-ground tree length (i.e. ratio of crown to tree trunk). Uncompacted means crown length is not reduced to compensate for gaps between live crown base and live top of the tree. Trees that are older should have smaller ratios (Schomaker <i>et al.</i> 2007).
Dead branches (%)	Percentage of all major branches (diameter >20 cm) that are senescent.
Epicormic growth (%)	Percentage of foliage in the canopy that is epicormic growth: the new growth from eucalypts recovering from a decline episode (Podger 1980; Stone 1999).
Canopy cover (%)	Four canopy cover measurements were taken 1.5 m from the base of each tree at north, south, east and west facings using a spherical densitometer. They were averaged for the tree to give a single canopy cover value for each tree.

Table 2. Habitat and sampling characteristics

Habitat and sampling characteristics recorded in each of the 24 trapping sites at Dryandra State Forest and Wandoo Conservation Park

Characteristic	Definition
Habitat characteristics	
Time since last fire (years)	Database: Years since last burn maps; Custodian: Department of Parks and Wildlife (Hills and Great Southern Districts).
Understorey vegetation <1 m (%)	Visually assessed for 16 quadrats (each 1 m ²) at each site and averaged to create a value for the site.
Site litter cover (%)	Visually assessed for 16 quadrats (each 1 m ²) at each site and averaged to create a value for the site. Site litter cover was significantly correlated with the percentage of bare ground ($r = -0.88, P < 0.001$), so the inverse relationship is assumed for bare ground.
Tree leaf litter cover (%)	Measured at the base of the six site trees within two 1-m ² quadrats, then averaged across each site.
Coarse woody debris density (number/ha ²)	Count of all logs (diameter >20 cm) in a 1-ha area around the drift fence.
Tree density (number/ha ²)	Calculated from the nearest-neighbour method (Barbour <i>et al.</i> 1987) from distance measures collected from the six site trees to the nearest tree.
Sampling characteristic	
Distance to the drift fence (m)	Measured from each trap to the closest <i>E. wandoo</i> tree (this averaged 9.3 ± 3.7 m across all 24 sites).

from trees to the trapping grids between sites (Table 2). All percentage cover values were arcsine-square-root transformed and tree density values were log-transformed to meet the assumptions of ANOVA and Pearson's correlations (Zar 1998).

Analysis

Mammal variables of interest were mammal species richness, overall mammal abundance and abundances of individual mammal species. These variables are measures of individual captures and do not include recaptures. Data from 16 trap-nights from all three trap types were pooled for each site to estimate these dependent variables and then square-root-transformed to meet the assumptions of parametric statistics (Zar 1998).

Generalised additive mixed models (GAMMs) are powerful statistical analyses that allow blending of generalised linear models and additive models (non-parametric models). Generalised additive mixed models (REML – restricted maximum likelihood) were used to explore the relationships between the dependent and independent variables. The dependent variables were mammal species richness, mammal abundance (number of individuals) and the abundance of the three most common mammal species (*Cercartetus concinnus*, *Antechinus*

flavipes and *Sminthopsis griseoventer*); independent variables were tree condition and habitat characteristics (Tables 1 and 2). Location (Dryandra State Forest or Wandoo Conservation Park) was present in all models as a random factor. The number of independent variables in each model ranged from 1 to 5 to avoid overfitting models (Burnham and Anderson 2002).

A total of 447 models were created for each dependent variable, to capture combinations of the independent variables. To avoid autocorrelation between variables, a Pearson's correlation matrix of tree and habitat characteristics was constructed (Microsoft Excel) and variables that were correlated ($r \geq 0.35$) were not included in the same models. Independent variables included time since last fire (years), site litter cover, understorey vegetation <1 m cover, tree litter cover, coarse woody debris density, tree density, crown density, crown dieback, uncompacted live crown ratio, dead branches, epicormic growth, canopy cover, Whitford tree condition index, since each species could respond to one aspect of tree condition independently of other indices. The only relationship found was between time since last fire and tree litter ($r = 0.57, P < 0.05$), so these two variables were not included in the same model.

positive relationships with site litter cover (Fig. 1a) and negative relationships with crown dieback, understorey vegetation cover, and tree density (Table 3). There were four well supported models for mammal species richness (Tables 3 and 4); these included positive relationships with site litter cover (Fig. 1b), distance to drift fence, crown density, crown dieback and epicormic growth, but negative relationships with canopy cover, coarse woody debris and time since last fire (Table 4). Some tree condition variables were not included in any of the best models, including percentage of dead branches and uncompact live crown ratio.

Relationships between tree and microhabitat characteristics and individual species

There were two well supported models for the abundance of *C. concinnus* ($n=25$ individuals) (Table 3), which included positive relationships with tree litter cover (Fig. 2a), crown dieback (Fig. 2b) and coarse woody debris and a negative relationship with crown density. The abundance of *A. flavipes* ($n=12$ individuals) had five well supported models that included a range of variables: positive relationships with Whitford tree condition indices (Fig. 2c), understorey cover, epicormic growth, crown dieback, tree litter cover, time since last fire, distance to drift fence, crown density and negative relationships with coarse woody debris (Fig. 2d; Tables 3 and 4). However, the model weights of the five models were low, indicating that each model has little explanatory power in terms of the abundance of *A. flavipes*. The abundance of *S. griseoventer* ($n=20$ individuals) was best explained by two models that included positive relationships with epicormic growth (Fig. 2e), crown density (Fig. 2f) and distance to drift fence (Tables 3 and 4). Model weights for all other measures of the mammal community had adequate explanatory power.

Discussion

This study investigated the relationships between small mammals, *E. wandoo* decline and the microhabitat. Relationships indicated that not only *E. wandoo* condition, but also understorey habitat, were strongly correlated with the small mammal community, highlighting that management should include

preservation of *E. wandoo* trees and the understorey microhabitat necessary for shelter and food resources by small mammals, as seen in other studies (Stephens *et al.* 2012). It should be noted that generalising results over the two locations can be difficult; however, the heterogeneous nature of the *E. wandoo* decline (and the microhabitat) (Brouwers *et al.* 2013; Moore *et al.* 2013) meant there was habitat variability within a site, as well as a location.

Indices of tree canopy condition were retained in the best models describing both mammal abundance and species richness. Less crown dieback, more epicormic foliage and overall healthier woodlands were related to increased mammal captures in *E. wandoo* woodlands. However, mammal species richness was negatively correlated with *E. wandoo* canopy cover, perhaps a result of the naturally open *E. wandoo* canopy (<30% canopy cover: Mercer 1991) and therefore low validity of this measure. Decline of *E. wandoo* alters the surrounding microhabitat, including changes in the build-up of litter cover and changes in the understorey vegetation from a loss of overhead foliage (Jurskis 2005); both of these factors are also correlated with overall mammal community composition. Site litter cover was the strongest predictor of small mammal abundance and species richness in this study, with the greatest abundance and diversity of mammals located at sites with more litter cover. Leaf litter is a productive foraging substrate and provides nesting sites and nesting material for small mammals (Mac Nally and Brown 2001; Mac Nally *et al.* 2001; McElhinny *et al.* 2006; Gresser 2009). Links between *E. wandoo* condition, the microhabitat and mammal abundance and species richness reinforce general findings in the literature that small mammal communities are strongly related to their habitat (Bowers and Dooley 1993; Lagos *et al.* 1995; Bos and Carthew 2003; Stokes *et al.* 2004; Torre and Diaz 2004; Stephens *et al.* 2012) and point towards a greater number and diversity of mammals at sites with healthier *E. wandoo* trees.

Cercartetus concinnus feeds on nectar and pollen, as well as insects, within both arboreal and terrestrial habitats (Pestell and Petit 2007; Marrant *et al.* 2010). In the present study, the abundance of *C. concinnus* was linked to the loss of canopy foliage and build-up of coarse woody debris and leaf litter, resulting from *E. wandoo* decline. A preference for open,

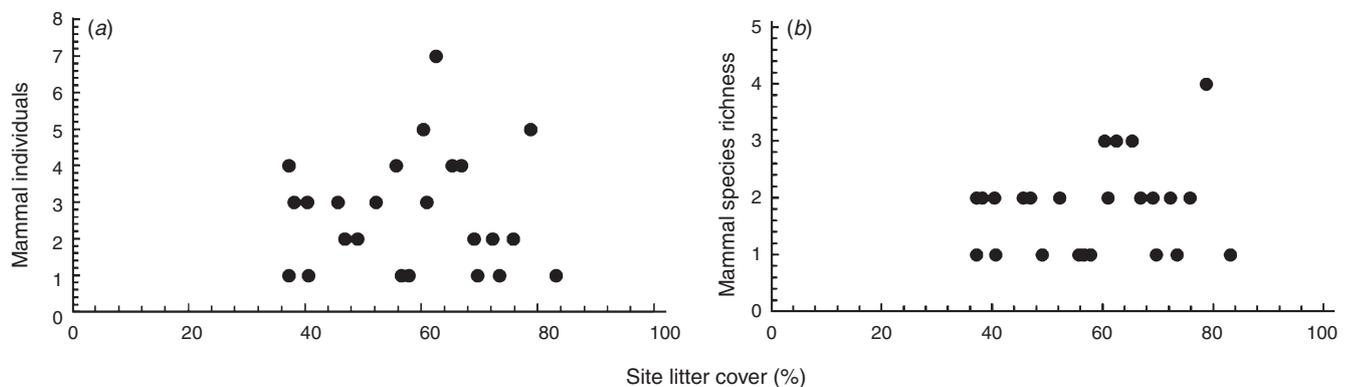


Fig. 1. The relationship between (a) site litter cover and overall mammal individuals and (b) mammal species richness and site litter cover. Each data point represents one of the 24 *Eucalyptus wandoo*-dominated sites. Note that some points overlap.

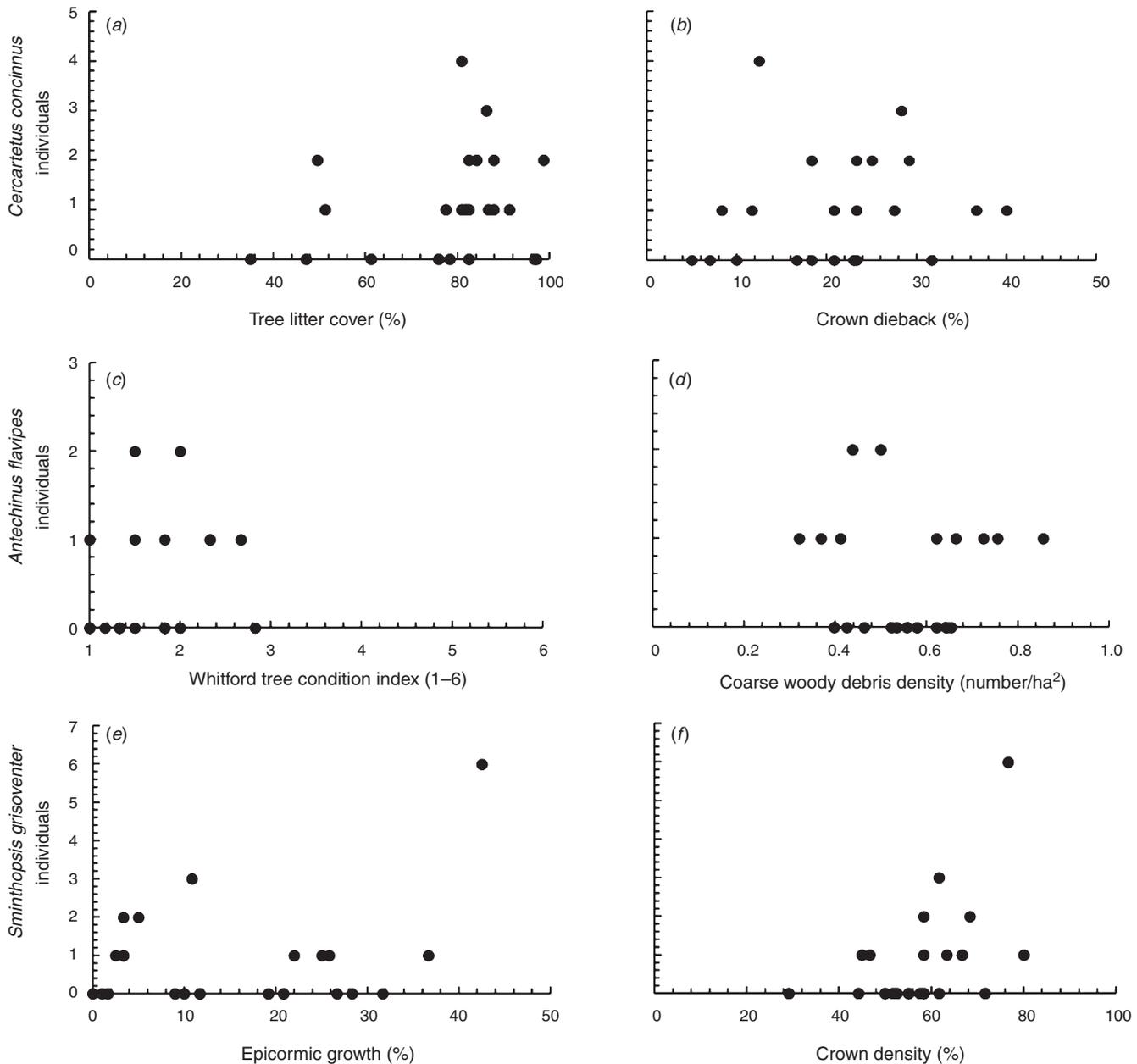


Fig. 2. Habitat factors that showed the strongest relationships with abundance of three of the most common mammal species: *Cercartetus concinnus* individuals and tree litter cover (a) and crown dieback (b); *Antechinus flavipes* individuals and Whitford tree condition index (c) and coarse woody debris density (d); and *Sminthopsis griseoventer* individuals and epicormic growth (e) and crown density (f). Each data point represents one of the 24 *Eucalyptus wandoo*-dominated sites; some points overlap.

declining *E. wandoo* canopies may reflect the use of terrestrial resources by these animals, since *Cercartetus* spp. use a range of microhabitat features for nesting and foraging (for invertebrate food resources), including woody debris (Sutherland *et al.* 2004; Tulloch 2004; Short *et al.* 2009) and leaf litter at the base of trees (Kemp and Carthew 2004; Tulloch 2004).

A range of variables were retained in the best models describing abundance of *A. flavipes*, including understorey vegetation, epicormic growth, crown dieback, tree litter cover, time since last fire and distance to drift fence. We expected the

abundance of *A. flavipes* to be related to a dense canopy, more coarse woody debris and leaf litter cover (for invertebrate prey, nesting sites and protection from predation) as other studies have noted (Braithwaite 1979; Newell 1998; Mac Nally *et al.* 2001; Holland and Bennett 2007; Lada *et al.* 2007, 2008; Armistead 2008). However, the strongest relationships for *A. flavipes* were with declining *E. wandoo* trees, sparse canopies and less coarse woody debris. Low model weights for *A. flavipes* abundance suggest that it may be responding to additional microhabitat features than those captured by this study.

Sminthopsis spp. forage nocturnally for insects in structurally complex terrestrial microhabitats (Stokes *et al.* 2004; Wilson and Aberton 2006; Finlayson *et al.* 2008). Abundance of *S. griseoventer* was related to changes in the canopy of *E. wandoo*, but, surprisingly, no links were seen with terrestrial microhabitat variables. Positive links between abundance of *S. griseoventer* and crown density, epicormic growth and distance from the drift fence to *E. wandoo* trees were noted in this study. Epicormic growth generally has a higher invertebrate load than older foliage on the same tree (Landsberg and Wylie 1983; Landsberg 1988, 1990). Although *S. griseoventer* is not an arboreal species, it is possible that the higher insect load of a recovering *E. wandoo* tree is not restricted to the canopy, and terrestrial abundance of insects and food resources for the small mammal may also be higher. Links between the abundance of *S. griseoventer* and higher crown densities may also reflect a response to the higher predation pressure in open canopy woodlands, since previous research (Bowers and Dooley 1993; Lagos *et al.* 1995) shows that a less complex habitat makes small mammals more susceptible to predation.

This study tested the relevance of a range of microhabitat measures to small mammal abundance and diversity. The holistic tree condition index (Whitford Index) was not common in the best supported models when compared with individual tree condition measures, highlighting that small mammals are likely to be responding to changes in microhabitat availability, rather than the decline of the woodland as a whole. Dead branches and uncompact live crown ratio were also not included in any of the best models for the small mammal community and individual species. Small mammals are not related to the loss of individual branches in the canopy, as seen by the lack of dead branches in the GAMMs, but rather the loss of canopy (branches, foliage, flowers and bark), as measured by crown density and crown dieback. Uncompact live crown ratio is a measure of tree size (trunk to canopy ratio). Perhaps as long as *E. wandoo* trees are still present in the woodlands, small mammals are not influenced by the size of the trees themselves.

Understanding relationships between small mammals and their habitat is important for reserve management (Flynn *et al.* 2011). This study demonstrated strong links between the small mammal community and their habitat, thus management actions, such as mosaic burning, should ensure the availability of healthy *E. wandoo* trees and microhabitat for small mammal shelter, nesting and food resources. Particularly, warmer temperatures and reduced rainfall are likely to exacerbate the decline of *E. wandoo*, further altering microhabitats for small mammals. In conclusion, future management needs to consider the decline in condition of *E. wandoo* and woodland microhabitats in the conservation of small mammal communities.

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Appendix 1. Captures

Total captures of mammal species in 24 sites in Dryandra State Forest and Wandoo Conservation Park over 3456 trap nights. Information on the sex ratios (male: female), average body mass of the species (g) and average head-body length (mm) is provided from the trapping data.

Species	Total captures	Sex ratio (M:F)	Average body mass (g)	Average head body length (mm)
<i>Antechinus flavipes</i>	12	3:9	21.4 ± 3.2	84.16 ± 10.35
<i>Mus musculus</i>	8	7:1	12.95 ± 2.92	65.70 ± 4.72
<i>Phascogale calura</i>	2	0:2	23 ± 0.42	87.77 ± 10.52
<i>Sminthopsis griseoventer</i>	20	9:11	12.1 ± 3.61	62.99 ± 5.87
<i>Sminthopsis gilberti</i>	4	1:3	12.1 ± 7.81	68.31 ± 7.21
<i>Cercartetus concinnus</i>	25	15:10	10.97 ± 3.20	67.88 ± 10.65