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Post-fire development of faunal habitat depends on plant regeneration traits

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Abstract

The concept that vegetation structure (and faunal habitat) develops predictably with time since fire has been central to understanding the relationship between fire and fauna. However, because plants regenerate after fire in different ways (e.g. resprouting from above-ground stems vs. underground lignotubers), use of simple categories based on time-since-fire might not adequately represent post-fire habitat development in all ecosystems. We tested the hypothesis that the post-fire development of faunal habitat structure differs between ecosystems, depending on fire regeneration traits of the dominant canopy trees. We measured 12 habitat components at sites in foothill forests (n = 38), heathy woodlands (n = 38) and mallee woodlands (n = 98) in Victoria, Australia and used generalised additive models to predict changes in each variable with time since fire. A greater percentage of faunal habitat variables responded significantly to time since fire in mallee woodlands, where fires typically are stand-replacing, than in foothill forests and heathy woodlands, where canopy tree stems generally persist through fire. In the ecosystem with the highest proportion of epicormic resprouters (foothill forests), only ground cover and understorey vegetation responded significantly to time since fire, compared with all but one variable in the ecosystem dominated by basal resprouters (mallee woodlands). These differences between ecosystems in the post-fire development of key habitat components suggest there may also be fundamental differences in the role of fire in shaping the distribution of fauna. If so, this challenges the way in which many fire-prone ecosystems are currently categorised and managed, especially the level of dependence on time since fire and other temporal surrogates such as age-classes and successional states. Where time since fire is a poor surrogate for habitat structural development, additional complexity (e.g. fire severity, topography, prior land-use history) could better capture processes that determine faunal occurrence in fire-prone ecosystems.

Key words

Ecosystem, epicormic resprouting, eucalypt, faunal habitat, post-fire succession, plant regeneration traits, time since fire.

Introduction

Fire-prone ecosystems have evolved under particular temporal and spatial patterns of fire occurrence (Bond and Keeley 2005, Archibald et al. 2018, Pausas and Parr 2018). Consequently, plants have regeneration strategies that help them survive and reproduce after fire, such as resprouting from dormant buds and fire-cued germination (Pausas and Keeley 2014). However, in many regions fire regimes are changing. First, with climate change, many regions are becoming hotter and drier, increasing the likelihood of more frequent and severe wildfires in many forests and woodlands (Bradstock 2010, Stephens et al. 2013). Second, contemporary fire-management activities such as fire suppression and prescribed burning may be incongruous with natural or historic regimes (Giljohann et al. 2015, Connell et al. 2017). Third, humans have altered ignition patterns and the spread of fire through land-use changes (Bowman et al. 2011). In the face of such changes, understanding the relationships between fire, plant regeneration and faunal habitat development is essential to conserve faunal diversity while also achieving other management goals.

Fire can affect the distribution of fauna directly by removing individuals, and indirectly by changing vegetation composition and structure and, therefore, the available habitat (Fox et al. 2003, Pausas and Parr 2018). Understanding how habitat changes through time in fire-prone ecosystems can help ecologists and land managers to better predict the impact of fire on fauna and identify species that could potentially be at risk due to changing fire regimes (Haslem et al. 2011). Indeed, the time between fires is widely used as a surrogate for animal and plant distributions, an idea captured by related terms in the fire ecology literature including ‘age-classes’ and ‘successional states’ (Cohn et al. 2015, Giljohann et al. 2015).

A common management paradigm is based on the idea that post-fire vegetation development follows a successional pathway that facilitates faunal occupancy associated with different successional states. Support for this approach has come from studies of taxa in a range of ecosystems: for example, small mammals in shrubby heathlands in Australia (Fox 1982) and in savannas of the Brazilian Cerrado (Briani et al. 2004); reptiles in semi-arid woodlands in Australia (Nimmo et al. 2012); and birds in boreal forests in Canada (Haney et al. 2008) and in shrublands in the European Pyrenees (Pons and Clavero 2010). In each of these systems, the association of faunal species with post-fire successional states is linked to changes in vegetation structure that enhance faunal habitat. An emphasis on post-fire succession underpins current fire management in our study region, the state of Victoria, Australia. Landscape-scale fire management is guided by two main measures: Tolerable Fire Interval (TFI) and Vegetation Growth Stage Structure (GSS) (York and Friend 2016). Tolerable fire intervals are determined for stands of vegetation based on the minimum and maximum intervals between fires that will prevent plant species loss (Cheal 2010). Vegetation Growth Stages are time-since-fire categories assumed to represent distinct assemblages of flora, fauna and habitat attributes (Cheal 2010). Fire management aims to maintain desirable combinations of Growth Stages in landscapes to conserve biodiversity. The applicability of these measures requires that biodiversity values develop predictably with time since fire.

Ecosystems may vary in the way in which vegetation structural changes correspond to time since last fire. In some ecosystems, such as those listed above, fires typically are ‘stand-replacing’: above-ground vegetation is removed, and regeneration occurs from the ground-up (et al. 2005, Clarke et al. 2010). In others, such as Pinus canariensis woodlands on Canary Island (Pausas and Keeley 2017) and stringybark eucalypt forests in Australia (Burrows 2013), canopy tree stems generally persist through fire and regeneration occurs rapidly, facilitated by epicormic buds. Thus, the role of time since fire in the long-term development of vegetation structure (and faunal habitat) may differ fundamentally between ecosystems: for example muted influence of time since fire on vertebrates in temperate eucalypt forests (Kelly et al. 2017) compared to a strong influence on fauna in stand-replacing ecosystems (e.g. Pons and Clavero 2010, Watson et al. 2012,). If this is true, there may be a need to re-think the way in which some fire-prone ecosystems are currently categorised and managed. For example, if faunal habitat does not change predictably with time since fire in all ecosystems, then management strategies could be more effective by concentrating on the actual habitat features that influence fauna.

We sampled vegetation structural attributes across a chronosequence of time since fire in three eucalypt-dominated ecosystems in Victoria, south-eastern Australia: foothill forests, heathy woodlands and mallee woodlands to compare the post-fire dynamics of faunal habitat structure. These three ecosystems are dominated by Eucalyptus species with contrasting fire regeneration traits. The thick-barked canopy trees in foothill forests generally survive fire and regenerate rapidly from protected epicormic buds along the trunk and branches (Fig. 1a – c). Canopy trees in heathy woodlands may survive fire and regenerate from epicormic buds, or basally from lignotubers (Fig. 1d – e). Fires in mallee woodlands typically are stand-replacing: the above-ground vegetation is consumed by fire and the canopy trees resprout basally from lignotubers, such that the system regenerates from the ground-up (Fig. 1f – g).

We aimed to capture elements of the ground cover, understorey vegetation and canopy structure (Table 1) that represent important habitat attributes for faunal species in forests and woodlands (Table 2). For example, leaf litter and understorey shrubs provide foraging substrate, shelter and nesting sites for birds, invertebrates, reptiles and terrestrial mammals (Fox et al. 2003, McElhinny et al. 2006, Kelly et al. 2011, Nimmo et al. 2012); and large trees provide resources such as den sites, nest hollows and foraging substrates for arboreal mammals and hollow-nesting birds (McElhinny et al. 2006, Bennett 2016). Understanding the post-fire dynamics of these habitat attributes will provide insight into how time since fire influences the distribution of faunal species within fire-prone ecosystems.

We hypothesised that the post-fire development of faunal habitat structure differs between ecosystems, depending on the extent to which fire is stand-replacing for the dominant canopy trees, or whether canopy tree stems persist and recover rapidly. Specifically, we address the following predictions: (1) the number and breadth of habitat structural components that respond to time since fire will be greater in ecosystems in which fires typically are stand-replacing than in ecosystems where canopy tree stems persist through fire; (2) in ecosystems in which canopy tree stems persist through fire, components of the ground layer structure will be driven by time since fire, but not components of the canopy structure; and (3) in ecosystems in which fires are stand-replacing, the development of all main habitat structural components will be driven by time since fire.

Methods

Study location and ecosystems

We studied three eucalypt-dominated ecosystems in Victoria, Australia: foothill forests, heathy woodlands and mallee woodlands (Fig. 2). A key difference between these distinct ecosystems is the proportion of epicormic resprouting trees vs. basal resprouting trees. Related differences, such as local climate, topography and fire regimes are described below.

Climate and topography

The generic term 'foothill forests' refers to temperate eucalypt forests that occur on the lower- to mid-slopes of the Great Dividing Range, covering ~ 75 000 km^2 in Victoria. The climate is temperate with a mean annual rainfall of ~ 850 mm. The highest rainfall occurs in winter (August) and the hottest month is February (mean daily maximum ~ 29°C) (Lake Eildon, station no. 083023; http://www.bom.gov.au/). Foothill forests occur on mountainous terrain, often with steep slopes and densely-vegetated gullies. Elevation in the study area ranges between ~ 450 and 950 m above sea-level.

Heathy woodlands occur sparingly throughout coastal areas of south-eastern Australia on nutrient-poor, deep sandy soils of quartzite gravel. The climate in the heathy woodlands study area is also temperate with a mean annual rainfall ranging from 540 – 895 mm. The highest rainfall occurs in winter (August) and the hottest month is February (mean daily maximum 28°C) (Mount Gellibrand, station no. 090035l, Cape Otway lighthouse, station no. 090015; http://www.bom.gov.au/). The topography in the heathy woodlands study area is gently undulating with elevation ranging between ~ 40 and 250 m above sea-level.

Mallee woodlands cover an area of ~ 100 000 km^2 in the semi-arid zone of south-eastern Australia. Summers are hot and dry, and winters are mild. Mean annual rainfall is ~ 290 mm. The highest rainfall occurs in spring and the hottest month is January (mean daily maximum ~ 32°C) (Mildura Airport, station no. 076031; http://www.bom.gov.au/). Mallee woodlands occur on low-lying ($\leq$ 100 m above sea-level) terrain with little topographic variation. An extensive dune-swale system characterises the region with sandy dunes receding to clayey swales.

Vegetation

Foothill forests are the tallest of the three ecosystems, with canopy trees reaching heights of 30 – 60 m, often accompanied by a secondary tree layer of Acacia spp. The term 'foothill forests' encapsulates several similar but distinct vegetation communities, ranging from wetter forest-types in gullies to drier forest-types on ridge tops and steep north-facing slopes. To avoid inherent differences in vegetation composition and structure between gullies and ridges, sites in this study were limited to a single Ecological Vegetation Class (EVC): 'herb-rich foothills forest' (Victorian Government Department of Sustainability and Environment 2004a). The dominant canopy species at these sites were messmate stringybark (Eucalyptus obliqua), broad-leaved peppermint (E. dives), narrow-leaved peppermint (E. radiata), and mountain grey-gum (E. cypellocarpa). Small trees and shrubs constitute the understorey, including blackwood (Acacia melanoxylon), prickly currant-bush (Coprosma quadrifida), common cassinia (Cassinia aculeata), and ferns such as austral bracken (Pteridium esculentum). The ground layer consists of a rich cover of herbs.

In heathy woodlands, a low canopy ($\leq$ 10 m) of eucalypts occurs over a diverse array of ericoid-leaved shrubs that form a dense understorey over time, following disturbance. The dominant canopy species are brown stringybark (E. baxteri) and western peppermint (E. fasciata). The main understorey shrubs include austral grass tree (Xanthorrhoea australis), heath tea-tree (Leptospermum myrsinoides), prickly tea-tree (L. continentale) and silver banksia (Banksia marginata) (Victorian Government Department of Sustainability and Environment 2004b). Fire regeneration traits of understorey species vary: tea trees resprout from basal lignotubers, austral grasstree resprouts apically, and silver banksia regenerates from seed.

Mallee woodlands are characterised by a low ($\leq$ 6 m) canopy of multi-stemmed Eucalyptus species. Three broad vegetation types have been described in this system; Triodia Mallee, Chenopod Mallee and Heathy Mallee, based on their floristic and structural differences (Haslem et al. 2010). We limited this study to Triodia Mallee because responses of both flora and fauna to fire can differ between vegetation types (Haslem et al. 2011). The low canopy is generally dominated by dumosa mallee (E. dumosa) and grey mallee (E. socialis). The understorey is dominated by porcupine grass (Triodia scariosa) and Acacia spp.

Fire regimes

In all three ecosystems, wildfires typically occur in summer (Dec – February), whereas prescribed burns are undertaken in autumn and spring months. Large wildfires (> 10 000 ha) have occurred within the wider foothill forests region in 1939, 1962, 1983, 2003, 2005, 2006, 2009 and 2014 (Victorian Government Department of Environment, Land, Water and Planning 2015), and in the mallee woodlands region they occur approximately decadally (Avitabile et al. 2013). Prescribed burning is undertaken in all three ecosystems to achieve management goals relating to fuel reduction and ecosystem resilience. Minimum tolerable fire intervals are used to guide the timing of prescribed burns: these are 15 years for foothill forests, 12 years for heathy woodlands and 25 years for mallee woodlands (Cheal 2010). In foothill forests, but not heathy woodlands, prescribed burns typically do not scorch the canopy (Gill 2012). In mallee woodlands, both wildfires and prescribed burns typically are stand-replacing.

Study design

We employed a space-for-time approach in each ecosystem to compare the post-fire development of key faunal habitat components. Sites were selected to span a chronosequence from one (foothill forest and heathy woodlands) or two years (mallee woodlands) to 80 years post-fire, and to cover a range of post-fire successional states based on the Vegetation Growth Stages described by Cheal (2010) (see Appendix S1).

We sampled foothill forests from 38 sites positioned on slopes at least 100 m from a gully and 50 m from a ridge top within an ~ 320 km^2 area of the Highlands Southern Fall (-37.516 S, 146.042 E), heathy woodlands from 38 sites within an ~ 100 km^2 area of the Great Otway National Park and Forest Park (-38.608 S, 143.346 E), and used data collected from 98 sites within a 4 200 km^2 area of the Murray-Sunset and Hattah-Kulkyne National Parks (-34.757 S, 141.628 E) in north-west Victoria (Fig. 2).

There were a greater number of sites in the mallee woodlands as these were surveyed as part of a project that investigated the responses of multiple taxa to fire mosaics across the whole Murray-Mallee region, covering parts of Victoria, New South Wales and South Australia (Haslem et al. 2012, Nimmo et al. 2012, Watson et al. 2012). To reduce the influence of rainfall and temperature gradients on vegetation structure (Kenny et al. 2018), this study was restricted to mallee sites within Victoria. There were disproportionately more sites in the 11-35 years-since-fire category, so we took a random sample of 21 sites from this growth stage to ensure even coverage of the chronosequence (Appendix S1).

Fire history

The fire history of foothill forests and heathy woodlands sites was determined by using spatial data maps of fire history supplied by the Victorian Department of Environment, Land, Water and Planning, and analysed using the software ArcMap (ESRI 2011). The mapped time since fire was ground-truthed at each site by looking for signs of charring on eucalypt bark and other structural features of the vegetation.

The fire history of sites in mallee woodlands was ascertained in two ways. For sites burnt post 1972, Landsat imagery and existing fire mapping were used to determine the exact year of the last fire (Avitabile et al. 2013). For sites burnt prior to 1972, time since fire was deduced by using regression models of the relationship between stem diameter and tree age (time since fire) (Clarke et al. 2010).

Fires of different severity can affect habitat structural components differently in some vegetation types (Bassett et al. 2017). Prescribed burns, undertaken for fire management in cooler periods, are usually of a lower intensity than wildfires and tend not to reach the canopy in foothill forests. To control for fire severity in foothill forests, fire-type of the last fire was limited to prescribed burns at all sites, except for the oldest time since fire. Prescribed burns were not used routinely in fire management until the 1970s, so sites burnt prior to this were last burnt during a 1939 wildfire. Because of recent large wildfires in the study area, limiting fire-type to wildfire while covering an adequate range of age-classes was not possible without introducing effects of climate and environmental gradients. Previous work in foothill forests found that fire-type had a relatively minor influence on the distributions of species at temporal scales similar to that used here (Kelly et al. 2017).

Heathy woodlands were sampled at sites burnt either during prescribed burns or wildfires as there were insufficient sites available within a single fire-type. Based on observations of resprouting eucalypts, fire severity does not vary greatly between prescribed burns and wildfires in heathy woodlands because both fire-types typically reach the canopy. In mallee woodlands, both prescribed burns and wildfires also generally reach the canopy, consume above-ground vegetation and are stand-replacing (Haslem et al. 2011); as such, both fire-types were included for these two systems.

Data collection

We sampled faunal habitat structural components in each ecosystem covering three broad categories: (i) ground cover, (ii) understorey vegetation and (iii) canopy structure (Table 1).

The type of ground cover and the depth of leaf litter (cm) were recorded at 1 m intervals along a 50 m transect, and these data were used to calculate percentage cover of different ground cover types and mean litter depth, respectively. At each point (1 m interval) the number of intercepts of living vegetation in different height categories was recorded using a 2 m ranging pole and these data were used to estimate the precent cover of understorey vegetation.

To assess the canopy structure in each ecosystem, we recorded the number and diameter at breast height (DBH) of living eucalypt trees at each site. In foothill forests, we used the point-centred quarter method (PCQM) (Cottam and Curtis 1956). At each site, two parallel transects were established 40 m apart that ran perpendicular to the slope. At 10 points at 20 m intervals along each transect (total of 20 points per site) we measured the DBH and distance to the nearest tree in each quarter of 360 degrees (total of 80 stems per site). A minimum of 20 points (80 stems) is required to estimate canopy tree density in forests (Ruch et al. 2008). In heathy woodlands a 4 m × 250 m quadrat, and in mallee woodlands a 4 m × 50 m quadrat were used to record canopy trees. To compare the post-fire development of habitat structural components between ecosystems, we then calculated 12 variables considered to be important for fauna within each ecosystem (Table 1). Differences between ecosystems in the size categories for certain variables represent inherent differences in vegetation structure.

Data analysis

We used generalised additive models (GAMs) to determine the relationship between faunal habitat structure variables (Table 1) and time since fire (years). From visualisation of the observed data and consultation with the literature, GAMs were deemed appropriate as they model both linear and non-linear relationships and are useful when responses are unknown a priori. Generalised additive modelling is a regression modelling technique that uses a smoothing term to fit response curves to predictor variables (Wood 2017). We used a mixed-model approach (GAMM) for mallee woodlands as these data were collected from points clustered in landscapes (Haslem et al. 2011). Mixed models were fitted with landscape unit (1 – 12) as a random effect to account for spatial autocorrelation among sampled sites. Residual plots were examined to assess adherence to assumptions of normality of variance prior to analysis. Degrees of freedom (K) for the smoothing term was initially set at four for all variables. However, model exploration indicated better models were fitted when K was set to three for the following variables: bare ground cover, mean diameter of large trees, and maximum tree diameter.

All analyses were conducted using the R statistical environment (R Development Core Team 2013) and the mgcv package (Wood 2018) and source scripts adapted from Elith et al. (2008) to calculate model deviance.

Results

There were differences between ecosystems in the percentage of faunal habitat structure variables that responded to time since fire. In foothill forests, 33% (4/12) of variables had a significant response (i.e. p-values of regression models < 0.05) to time since fire, compared with 58% (7/12) in heathy woodlands and 92% (11/12) in mallee woodlands (Fig. 3).

Foothill forests

In foothill forests, two of the four ground cover variables, litter cover ($P < 0.001$) and litter depth ($P < 0.001$), increased significantly with time since fire (Fig. 3). Litter cover increased rapidly, reaching a peak at < 20 years since fire, whereas litter depth increased linearly across the chronosequence. Both lower- ($P < 0.001$) and upper-midstorey ($P < 0.01$) vegetation cover increased with time since fire. However, none of the canopy structure variables showed a significant response to time since fire.

Heathy woodlands

In heathy woodlands, three of the four ground cover variables, bare ground cover ($P < 0.001$) litter cover ($P < 0.001$) and litter depth ($P < 0.001$), responded to time since fire (Fig. 3). Bare ground cover decreased rapidly to almost zero in late-successional states. Litter cover increased rapidly until ~ 20 years since fire, after which it plateaued. Litter depth increased until ~ 25 years since fire and then decreased before plateauing. Both lower- ($P < 0.01$) and upper-midstorey ($P < 0.001$) vegetation cover responded to time since fire. Lower-midstorey vegetation increased until ~ 25 years since fire, then decreased to plateau at ~ 60 years since fire. Upper-midstorey vegetation cover plateaued at ~ 50 years since fire. Two of the five canopy structure variables, basal area ($P < 0.05$) and maximum tree diameter ($P < 0.01$) increased moderately with time since fire.

Mallee woodlands

All but one of the faunal habitat structure variables that were modelled in mallee woodlands responded significantly to time since fire (Fig. 3). Bare ground cover ($P < 0.001$) decreased with time since fire until ~ 40 years post-fire. Litter cover ($P < 0.001$) and litter depth ($P < 0.01$) both increased linearly with time since fire. Plant cover increased with time since fire, but this was not significant ($P = 0.283$). Lower-midstorey vegetation cover decreased with time since fire ($P < 0.01$). Upper-midstorey vegetation cover showed a bell-shaped response, peaking at ~ 30 years since fire ($P < 0.01$). The size, density and distribution of large trees all increased, whereas tree density ($P < 0.01$) decreased linearly with increasing time since fire.

Model outputs can be found in Appendix S2.

Discussion

This study shows that the post-fire development of habitat structural variables differs between ecosystems, and that these patterns are consistent with the fire regeneration traits of the dominant tree species. In mallee woodlands, where fires typically are stand-replacing, more structural components were driven by time since fire than in foothill forests and heathy woodlands, where stands of canopy trees generally persist though fire. The shape of the fire-response curve for most structural components also differed between ecosystems. For faunal species that respond to these habitat structural components, there may be fundamental differences between ecosystems in the role of fire in shaping distributional patterns. These findings have implications for the way in which ecosystems are categorised and managed for biodiversity conservation, which we discuss in the sections below.

Temporal development of faunal habitat structure

Most notably, the three ecosystems differed in the post-fire development of canopy structure. In mallee woodlands, all variables measuring canopy structure responded to time since fire. Overall, the observed pattern was for large trees to increase in mean diameter, occur at a higher density and constitute a greater proportion of all canopy trees, in later successional states. In mallee woodlands, the above ground component of canopy trees typically is killed by fire and resprouts basally from lignotubers, and so stands of canopy trees take decades following fire to grow to maturity (Clarke et al. 2010). Resprouting from basal buds is the most common form of post-fire resprouting, globally (Pausas and Keeley 2017). This trait is especially prevalent in drier biomes of lower productivity where crown fires are experienced (Clarke et al. 2013), like semi-arid woodlands.

In recently burnt mallee woodlands, the density of live stems was high because of vigorous resprouting but decreased over time as canopy trees grow. Some resources that large trees provide for faunal species, such as tree hollows, take many decades to develop and are not present until later successional states (~ 60 years since fire) (Haslem et al. 2012). As a result of the slow development of these and other resources (e.g. hummock grass), many faunal species in mallee woodlands are associated with mid-later successional vegetation (Kelly et al. 2012, Connell et al. 2017).

By contrast, in foothill forests, where stands of canopy trees survive fire and resprout epicormically, none of the canopy variables we modelled responded to time since fire. These structural variables are proxies for important resources for animals provided by the forest canopy. For example, the availability of tree hollows that provide essential nesting and shelter sites for arboreal mammals and hollow-nesting birds is directly related to the distribution of large trees (Lindenmayer et al. 1993, Remm and Lõhmus 2011). In foothill forests, large canopy trees were still present immediately after fire and throughout the chronosequence, thus serving as biological legacies (Pulsford et al. 2016) that do not depend on time since fire. Further, the percentage of trees in the canopy stratum that were 'very large' was generally modest (~ 25%) across the range of successional states. This suggests that canopy tree regeneration in foothill forests happens continually and does not follow a clear post-fire successional pathway.

Globally, epicormic resprouting is rare in ecosystems that experience high-intensity crown-fire regimes, such as Mediterranean-type and warm-temperate forests and woodlands (Pausas and Keeley 2017). Taxa that resprout epicormically, additional to Eucalyptus species, include Pinus canariensis on Canary Island, Protea nitida in South Africa, Quercus agrifolia, Q. kelloggii in California and Q. suber in the Mediterranean Basin (Pausas and Keeley 2017). This adaptation enables rapid canopy regeneration and makes these species and their associated habitat features resilient to most fire regimes. Epicormic resprouting is also widespread in tree species in grassy-savanna ecosystems (e.g. in northern Australia) that experience frequent grass-fuelled fires. In such savanna ecosystems, fire frequency, fire season and fire severity are more influential fire parameters for biota than simply the time since last fire (Murphy et al. 2010, Andersen et al. 2012). These ecosystems represent examples of situations where simple classifications based on time since fire may not be sufficient to capture fire-driven dynamics for faunal species.

In south-eastern Australia, recent large wildfires in foothill forests have reduced the temporal range of post-fire successional states associated with wildfire. Consequently, to cover the breadth of age-classes without introducing effects of vegetation type, climate and environmental gradients, it was necessary to sample prescribed burns for age-classes <80 years since fire. A limitation is that we may have underestimated the potential effects of severe fires on habitat structure. However, Haslem et al. (2016) showed that the main effect of fire severity in foothill forests is on canopy cover, and this effect diminishes rapidly (after ~ 10 years since fire). The interacting effects of fire severity and time since fire on habitat structure would be a fruitful area for further research.

In general, the cover of understorey vegetation responded positively to time since fire in all three ecosystems, except for lower-midstorey vegetation in mallee woodlands which responded negatively. However, the shapes of the responses differed: in foothills forests upper-midstorey cover increased rapidly and peaked earlier than in both heathy woodlands and mallee woodlands. Similar patterns to those shown here have been observed previously in temperate eucalypt forests (Swan et al. 2015, Haslem et al. 2016) and mallee woodlands (Haslem et al. 2011). Understorey vegetation provides nesting, foraging and shelter sites for many bird and mammal species typical of these and similar ecosystems (Ford et al. 1986, Fox et al. 2003, Simonetti et al. 2013, Swan et al. 2015, Verdon et al. 2019). Consequently, the temporal responses of such faunal species to fire are likely to be positively influenced by these post-fire trajectories in habitat suitability (e.g. Fox 1982, Watson et al. 2012). However, early post-fire succession can also create short-term opportunities for species that favour more-open habitats and which decline in occurrence as understorey vegetation recovers (e.g. Watson et al. 2012).

Biomass allocation in plants (i.e. habitat structure for animals) depends on environmental factors as well as disturbance regimes (Clarke et al. 2013). Factors, such as climate, soils and productivity influence development of habitat structural components: plant growth rate is higher in mesic than semi-arid biomes. Environmental influences will be most evident when comparing structural components that are removed by fire and regenerate from the ground-up (e.g. rate of increase in understorey vegetation). However, plant regeneration traits are fundamental in explaining the differences we observed between ecosystems, as they provide the mechanism that determines whether or not key structures are present within certain successional states.

Fire regeneration traits and ecosystem succession

Support for the idea that, following fire, vegetation development follows a successional pathway that facilitates faunal occupancy has mainly come from studies of stand-replacing ecosystems (Briani et al. 2004, Haney et al. 2008, Pons and Clavero 2012, Watson et al. 2012). In such stand-replacing ecosystems, categories based on time since fire have proved useful for predicting landscape-scale impacts of fire on faunal species (Connell et al. 2017, Regos et al. 2018). In contrast, in epicormic-resprouting systems, in which canopy tree stems generally persist though fire, the successional pathway is not reset to ‘time-zero’ by burning. Rather, the occurrence and distribution of some key structures, such as large trees tend to be a legacy from past disturbances rather than a product of the time since the last fire. If key components of habitat structure, such as large trees and their associated resources, do not show strong temporal patterns of post-fire development, the fauna that rely on those components are less likely to be associated with distinct successional stages. In epicormic resprouting ecosystems such as the foothill forests, the resources provided by canopy trees in forests and woodlands (e.g. foliage, hollows, bark, large limbs, flowers: Table 2), are important for a wide range of faunal species (McElhinny et al. 2006). Consequently, in such ecosystems, categorising landscapes into successional states is likely to be less useful for predicting the landscape-scale impacts of fire.

Implications for fire management

The primary finding of this study, that post-fire development of faunal habitat components differs between ecosystems, has implications for the way in which fire-prone ecosystems are understood and subsequently managed. The habitat components studied here are surrogates for important resources for fauna, so differences in their pattern of post-fire development are likely to influence the fire-responses of species that rely on them. Clearly, an important next step is to directly test the relative influence of time-since-fire on faunal species in these disparate ecosystems.

If differences between ecosystems in the fire-response of habitat components reflect real differences in the role of time since fire in shaping faunal distributions, then it will be necessary to rethink how some landscapes are understood and categorised for fire management. For example, fire managers often aim to maintain mosaics of post-fire vegetation age-classes (surrogates of time since fire) across the landscape (Bradstock et al. 2005). This approach is likely to be more effective in maintaining biodiversity values in ecosystems in which vegetation age-classes are structurally and functionally distinct, and support distinct faunal assemblages (Kelly et al. 2012, Watson et al. 2012). Where there is less difference between age-classes, and factors such as pre-fire structure and environmental gradients are influential (e.g. in foothill forests), a more nuanced approach that recognisees both time since fire and the biological legacy of historical disturbance regimes, is required.

We recommend that when using a patch mosaic approach in landscape-scale fire management, the ‘patches’ incorporate the most ecologically meaningful fire regime and environmental parameters. For example, in grassy savanna ecosystems of northern Australia (Davies et al. 2018) and conifer forests of western U.S.A. (Tingley et al 2016), management strategies that aim to maintain patch mosaics based on fire frequency and fire severity, rather than simply time since fire, are understood to benefit biodiversity across landscapes. In foothill forests, an approach that similarly incorporates additional complexity (beyond time since fire) could improve conservation management outcomes for fauna. A key question to address is ‘how do other aspects of the fire regime (e.g. fire severity) and environmental conditions (e.g. topography) interact with time since fire to influence faunal species at the landscape scale’?

Conclusions and future directions

Incorporating the needs of fauna into fire management remains a challenge in fire-prone regions worldwide. Our finding that the regeneration traits of the dominant canopy species in wooded ecosystems influences the development of key habitat components, suggests there are fundamental differences in the mechanisms underpinning fire-habitat-fauna dynamics between disparate ecosystems. In systems where fire is not stand-replacing, the persistence of pre-fire structural attributes (e.g. tree size, tree density) as post-fire legacies can mediate the influence of temporal post-fire succession. The next step is to directly examine how the coupling of time since fire and habitat structural development influences the distribution of faunal species in disparate ecosystems, to test whether observed differences in habitat dynamics equate to real influence on the occurrence and status of faunal species.

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Table 1. Habitat structure variables calculated for three eucalypt-dominated ecosystems (foothill forests, heathy woodlands, mallee woodlands) in south-eastern Australia. The range of values for each variable in each ecosystem is given, together with a description of the variable.

Habitat category	**Variable**	**Foothill forests**	**Heathy woodlands**	**Mallee woodlands**	**Description**
Ground cover	Bare ground cover	0-70	0-76	4-94	Percent (%) cover of bare ground
	Litter cover	28-100	20-98	0-90	Percent (%) cover of leaf litter
	Litter depth	0.4-9.4	0.13 -4.1	0-2.7	Mean depth of leaf litter (cm)
	Plant cover	0-32	0-32	0-28	Percent (%) cover of plants (includes shrubs, herbs and ferns)
Understorey	Lower-midstorey	21-89	42-96	0-54	Percent (%) cover of vegetation 0 – 1 m (FF, HW), 0 – 0.5 m (MW)
	Upper-midstorey	0-33	6-67	0-39	Percent (%) cover of vegetation 1 – 4 m (FF, HW), 0.5 – 2 m (MW)
Canopy	Basal area	23-76	0.37-2.22	0-6.9	Basal area cover of canopy trees (m^2/ha)
	Density of large trees	147-324	200-1280	0-1800	Density (live stems/ha) of canopy trees with diameter greater than the median for that ecosystem (>25 cm FF; >8 cm HW; >4 cm MW).
	Maximum tree diameter	50-200	16-60	0-30	Diameter (cm) of the largest tree within the sample area
	Mean diameter of large trees	34-59	11.4-22.5	0-15.5	Mean diameter (cm) of trees with diameter greater than median for the ecosystem (>25 cm FF; >8 cm HW; >4 cm MW)
	Percentage of very large trees	11-45	3-76	0-100	Percent (%) of trees in the canopy stratum with diameter in the upper quartile for the ecosystem (>39 cm FF; >12 cm HW; >7 cm MW)
	Tree density	270-750	500-2900	150-2850	Density of canopy trees (live stems/ha)

FF = foothill forests, HW = heathy woodlands, MW = mallee woodlands.

Table 2. Key habitat attributes used by seven faunal groups, their associated resources and functions, and the habitat surrogate category used in our assessment. Adapted from a review by McElhinny et al. 2006 of fauna-habitat associations in Australian forests and woodlands.

Taxonomic group	Habitat attribute (McElhinny et al. 2006)	Associated resources/function (McElhinny et al. 2006)	Habitat surrogate category (present study)
Amphibians	Vegetation cover	Shelter, moist microclimate	Ground cover, understorey
	Ground debris	Shelter, refuge, foaging	Ground cover
Arboreal mammals	Foliage	Edible material	Canopy
	Flowers	Nectar, pollen	Understorey, canopy
	Bark	Exudates, invertebrates	Canopy
	Tree hollows	Den/nest sites, water	Canopy
Birds	Foliage	Exudates, invertebrates	Understorey, canopy
	Flowers	Nectar, invertebrates	Understorey, canopy
	Bark	Exudates, invertebrates	Canopy
	Ground layer	Invertebrates, small vertebrates	Ground cover
	Air spaces	Invertebrates	Understorey, canopy
	Tree hollows	Nest sites, shelter	Canopy
Bats (insectivorous)	Foliage	Invertebrates	Understorey, canopy
	Canopy space	Invertebrates	Understorey, canopy
	Hollows, decorticating bark	Roost/nest sites	Canopy
Ground mammals	Shrubs	Shelter	Understorey
	Litter	Nesting, invertebrates, fungi	Ground cover
Invertebrates	Foliage	Edible material, sap, shelter	Understorey, canopy
	Flowers	Nectar, pollen	Understorey, canopy
	Bark	Shelter, exudates, prey	Understorey, canopy
	Shrubs	Foliage, flowers, shelter	Understorey
	Litter, woody debris	Food, prey, shelter	Ground cover
Reptiles	Basking sites	Temperature regulation	Ground cover
	Litter	Invertebrates, cover	Ground cover
	Shrubs	Cover, invertebrates	Understorey

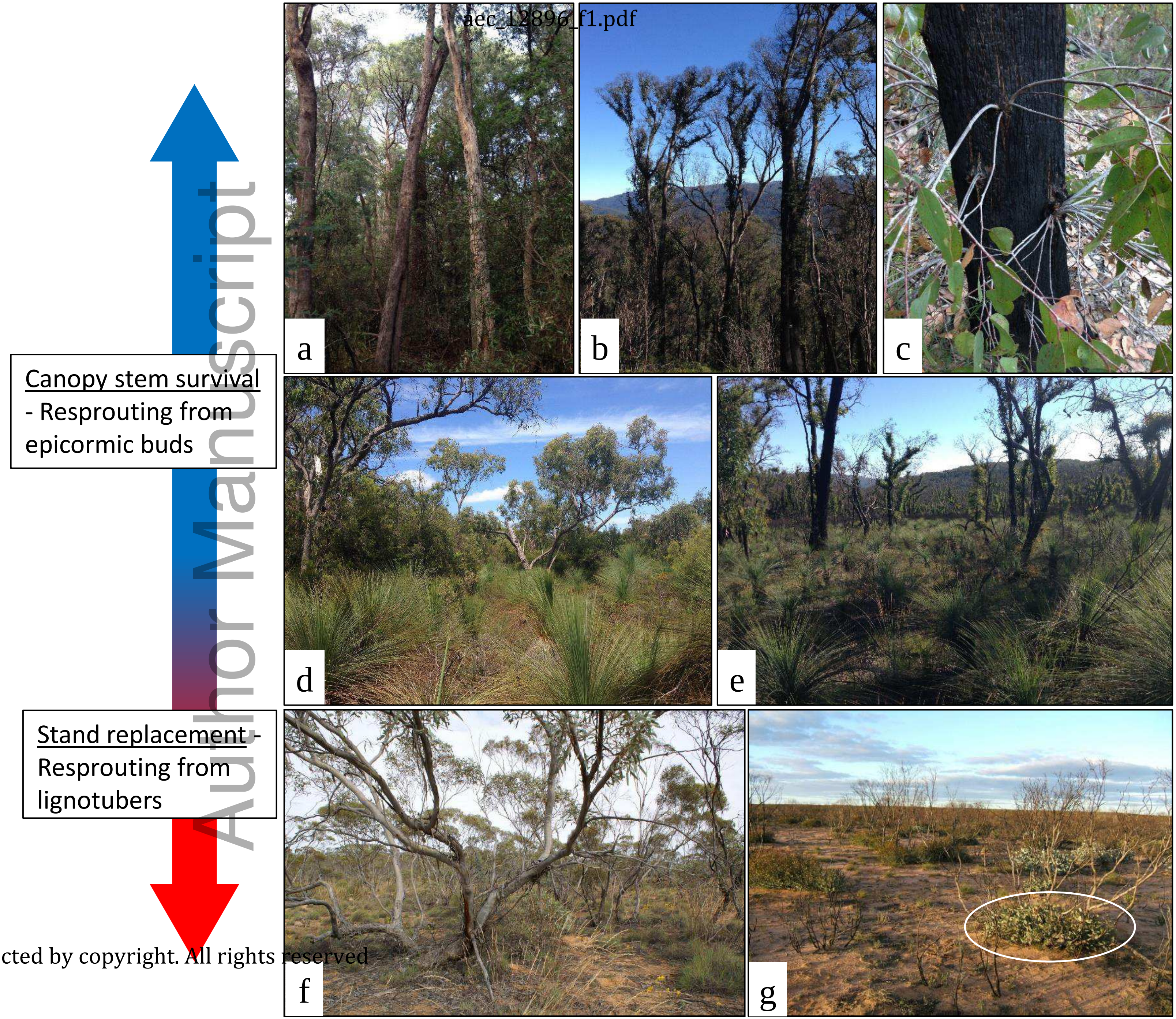
Figure captions

Figure 1. Vegetation of the study ecosystems. 1. Foothill forests: (a) long unburnt vegetation and (b - c) epicormic resprouting in recently burnt eucalypts. 2. Heathy woodlands: (d) long unburnt vegetation and (e) epicormic resprouting in recently burnt eucalypts. 3. Mallee woodlands: (f) long unburnt vegetation and (g) recently burnt eucalypts resprouting from

lignotubers. The blue and red arrow represents a gradient of stand-replacement (bottom) to stand-survival (top). Photo credits: FR (a – e), Mallee Fire and Biota Project (f – g).

Figure 2. Locations of study areas in foothill forests, heathy woodlands and mallee woodlands in Victoria, Australia, and the distribution of Ecological Vegetation Divisions (EVDs) that correspond to the three ecosystems studied: foothill forests (green; EVDs = foothills forest, forby forests), heathy woodlands (orange; EVD = heathland sands) and mallee woodlands (red; EVDs = chenopod mallee, hummock-grass mallee, lowan mallee) (Victorian Department of Environment, Land, Water and Planning).

Figure 3. Predicted patterns of post-fire temporal dynamics of faunal habitat components in foothills forests (solid green lines), heathy woodlands (orange dot-dashed lines) and mallee woodlands (red dashed lines). Lines are fitted smoothed terms from generalised additive models and shaded areas are 95% confidence intervals. Asterisks represent significance level of the smoothed term: * $P<0.05$, ** $P<0.01$, *** <0.001, ns = not significant. Lines with no shaded ribbon represent non-significant relationships. ‘Large’ and ‘very large’ trees refer to trees with trunk diameter above the median, and within the upper quartile for that ecosystem, respectively.


Canopy stem survival - Resprouting from epicormic buds
Stand replacement - Resprouting from lignotubers
a
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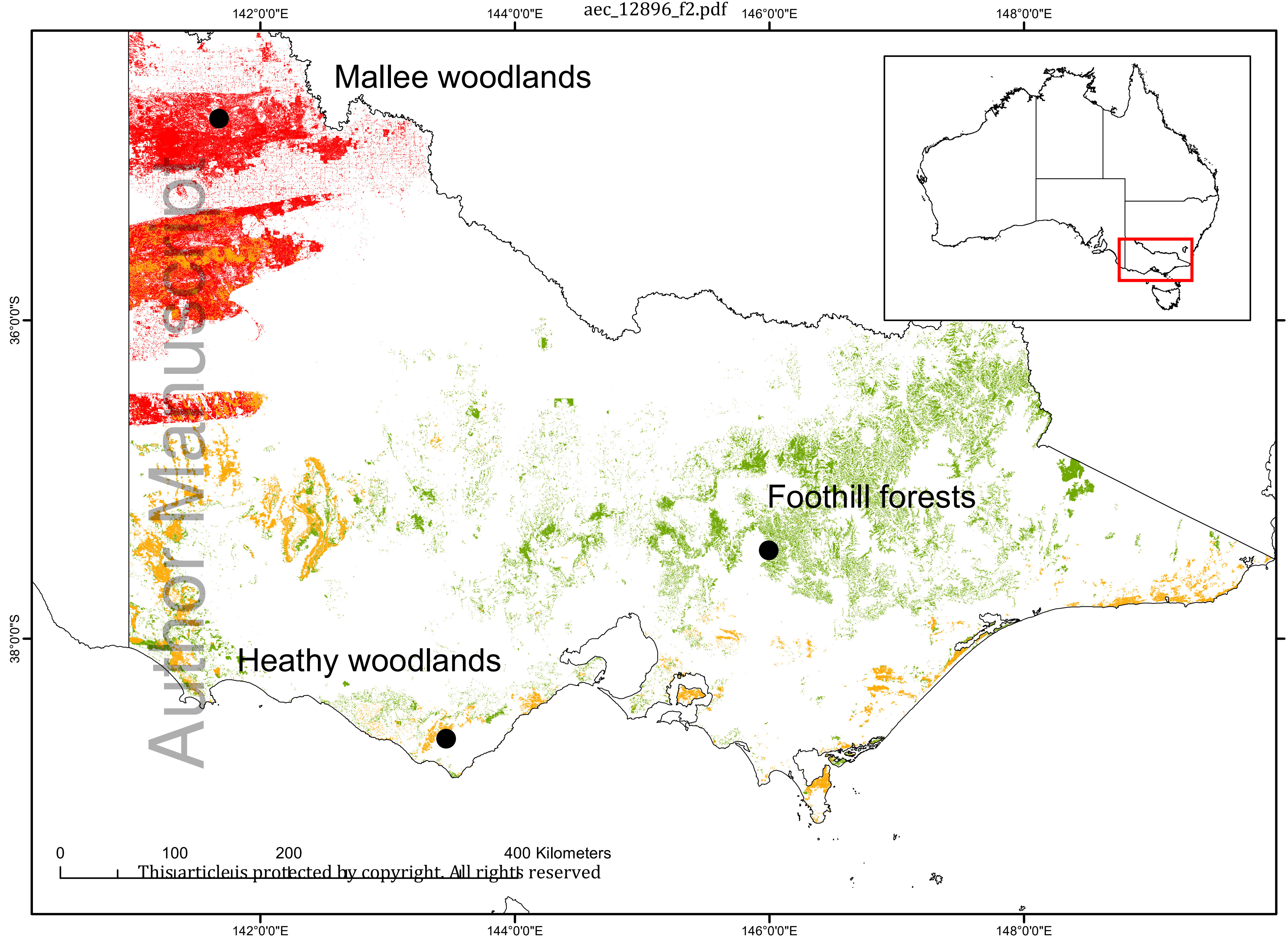
142°0'0"E
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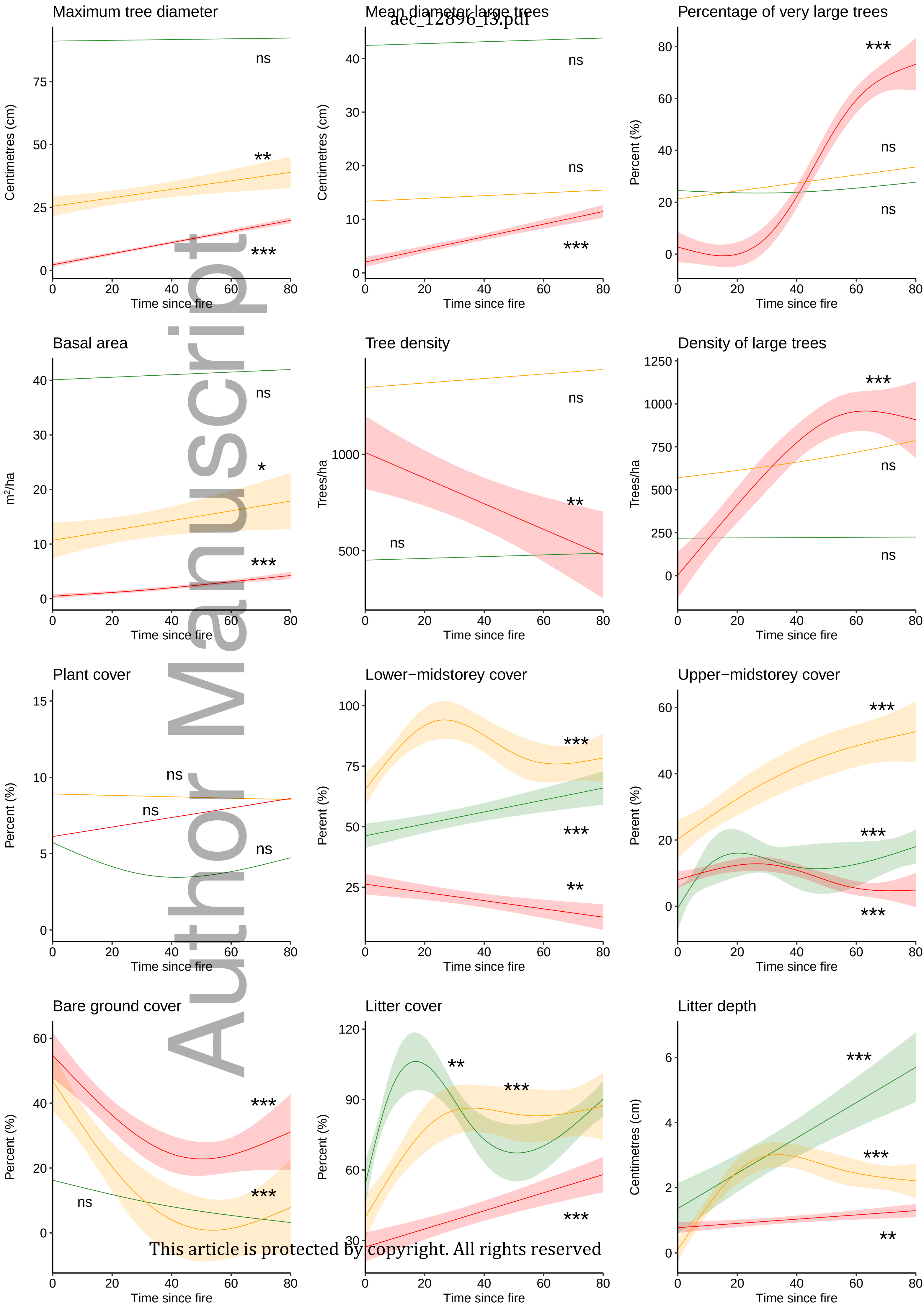
Mallee woodlands
Foothill forests
Heathy woodlands
0
100
200
400 Kilometers


Maximum tree diameter
Centimetres (cm)
0
25
50
75
ns
**
***
0
20
40
60
80
Time since fire
Mean diameter large trees
Centimetres (cm)
0
10
20
30
40
ns
ns
***
Time since fire
Percentage of very large trees
Percent (%)
0
20
40
60
80
***
ns
ns
Time since fire
Basal area
m²/ha
0
10
20
30
40
ns
*
***
Time since fire
Tree density
Trees/ha
500
1000
ns
**
ns
Time since fire
Density of large trees
Trees/ha
0
250
500
750
1000
1250
***
ns
ns
Time since fire
Plant cover
Percent (%)
0
5
10
15
ns
ns
ns
Time since fire
Lower−midstorey cover
Perent (%)
25
50
75
100
***
***
**
Time since fire
Upper−midstorey cover
Perent (%)
0
20
40
60
***
***
***
Time since fire
Bare ground cover
Percent (%)
0
20
40
60
***
ns
***
Time since fire
Litter cover
Percent (%)
30
60
90
120
**
***
***
Time since fire
Litter depth
Centimetres (cm)
0
2
4
6
***
***
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Time since fire