

# Changes in structure of over- and midstory tree species in a Mediterranean-type forest after an extreme drought-associated heatwave

EMMA J. STEEL,<sup>1\*</sup>  JOSEPH B. FONTAINE,<sup>1</sup> KATINKA X. RUTHROF,<sup>1,2</sup> TREENA I. BURGESS<sup>1</sup> AND GILES E. ST. J. HARDY<sup>1</sup>

<sup>1</sup>*Environment and Conservation Science, College of Science, Health, Engineering and Education, Murdoch University, Murdoch, Western Australia, 6150 (Email: emma.steel@murdoch.edu.au); and*

<sup>2</sup>*Department of Biodiversity, Conservation and Attractions, Kensington, Western Australia, Australia*

**Abstract** Worldwide, extreme climatic events such as drought and heatwaves are associated with forest mortality. However, the precise drivers of tree mortality at individual and stand levels vary considerably, with substantial gaps in knowledge across studies in biomes and continents. In 2010–2011, a drought-associated heatwave occurred in south-western Australia and drove sudden and rapid forest canopy collapse. Working in the Northern Jarrah (*Eucalyptus marginata*) Forest, we quantified the response of key overstory (*E. marginata*, *Corymbia calophylla*) and midstory (*Banksia grandis*, *Allocasuarina fraseriana*) tree species to the extreme climate event. Using transects spanning a gradient of drought impacts (minimal (50–100 m), transitional (100–150 m) and severe (30–60 m)), tree species mortality in relation to stand characteristics (stand basal area and stem density) and edaphic factors (soil depth) was determined. We show differential mortality between the two overstory species and the two midstory species corresponding to the drought-associated heatwave. The dominant overstory species, *E. marginata*, had significantly higher mortality (~19%) than *C. calophylla* (~7%) in the severe zone. The midstory species, *B. grandis*, demonstrated substantially higher mortality (~59%) than *A. fraseriana* (~4%) in the transitional zone. *Banksia grandis* exhibited a substantial shift in structure in response to the drought-associated heatwave in relation to tree size, basal area and soil depth. This study illustrates the role of climate extremes in driving ecosystem change and highlights the critical need to identify and quantify the resulting impact to help predict future forest die-off events and to underpin forest management and conservation.

**Key words:** *Banksia grandis*, canopy, die-off, *Eucalyptus marginata*, mortality.

## INTRODUCTION

The unprecedented extent and intensity of human influence on the biosphere has precipitated the designation of a new geologic era, the Anthropocene (Pachauri *et al.* 2014; Lewis & Maslin 2015). Among the most wide-reaching and profound changes, humans have triggered are shifts in the earth's climate and, in turn, climate-driven impacts on ecosystems. These changes are often manifested via extreme climatic events such as heatwaves, droughts and storms (Seneviratne *et al.* 2012; Reichstein *et al.* 2013; Frölicher & Laufkötter 2018) or combinations of chronic, long-term changes and extreme events (Matusick *et al.* 2018). These climatic events can have significant consequences for taxa across ecosystems (Ruthrof *et al.* 2018). For example, forest die-off events are increasing in frequency, severity and duration on regional and continental scales (Breshears *et al.* 2009; Allen *et al.* 2010; Williams *et al.*

2013). Concurrently, background mortality in old, unmanaged forests has increased and is driving decreases in basal area and carbon stocks (Van Mantgem *et al.* 2009). The vulnerability of these major terrestrial carbon pools to climate change presents a wide range of risks at many levels, for example, runaway positive feedbacks, loss of ecosystem services and biodiversity loss (Reichstein *et al.* 2013).

Future climate predictions are for continued warming globally, a further increase in the frequency of extreme climatic events, and increasingly widespread forest mortality (McDowell & Allen 2015). For example, of the world's major climate types, Mediterranean-type ecosystems (MTEs) are experiencing both warming and drying, whereas other climate types (i.e. portions of tropics, higher latitudes) are anticipated to become warmer and wetter (Diffenbaugh & Field 2013). A predicted increase in drought severity in MTEs will drive losses in net primary production and carbon sequestration (Rolinski *et al.* 2015; Walden *et al.* 2019), as well as increased species loss directly (i.e. drought-driven mortality) and indirectly, for example, through increased fire

\*Corresponding author.

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frequencies (Enright *et al.* 2015), in regions such as south-western Australia (Enright *et al.* 2014).

Forest die-off events induced by drought and heatwaves have been well documented (Phillips *et al.* 2009; Van Mantgem *et al.* 2009; Allen *et al.* 2010; Carnicer *et al.* 2011; Peng *et al.* 2011; Matusick *et al.* 2013). Heatwaves exacerbate die-off during a drought; even a slight increase in temperature creates a multiplicative elevation of vapour pressure deficit (VPD, the evaporative demand on the plant) (Breshears *et al.* 2013; Eamus *et al.* 2013). Disentangling the relative contributions to tree mortality from meteorological components, such as heat and drought, is difficult; however, it is also important to understand the ecosystem-level drivers and consequences of extreme climatic events. To do this, we need to investigate how stand structure and local edaphic factors (such as soil depth and landscape position) interact with drought and heat events to trigger particular responses (McDowell *et al.* 2013; Merlin *et al.* 2015; Clark *et al.* 2016). For example, stand structure, and hence competition, has been shown to be very important in forest responses to drought; Guillemot *et al.* (2015) showed that high stem densities increased mortality in *Cedrus atlantica* during a drought in southern France. Soil depth is an indication of potential water storage capacity in the vadose zone; it dictates moisture available to vegetation and is a variable affecting tree mortality and health (Jackson *et al.* 1996; Harper *et al.* 2009). Shallower soils, and hence access to water resources during drought, have been linked with a higher probability of forest mortality in the Sierra Nevada (Paz-Kagan *et al.* 2017), and increases in soil depth have been associated with higher survival probabilities in *Quercus ilex* in NE Spain (Galiano *et al.* 2010).

A valuable opportunity to study forest die-off was presented by an extreme drought-associated heatwave event in south-western Australia (Ruthrof *et al.* 2018). In the summer of 2011, the region experienced nine days over 35°C in late February, following an acute drought in 2010, and resulted in mass canopy collapse of the Northern Jarrah (*Eucalyptus marginata*) Forest (NJF). Patches of canopy collapse contained the two dominant overstory species (*E. marginata* and *Corymbia calophylla*), but lacked the key midstory species, *Banksia grandis*. At sites where *B. grandis* did occur, its mortality seemed to precede that of the overstory species (Matusick *et al.* 2013). However, more information was needed about the factors contributing to these patterns. Thus, the objective of this study was to describe and quantify the pattern of responses of key overstory and mid-story species, and their stand and site characteristics, following a drought-associated heatwave and forest collapse. Our specific research questions were as follows:

- What are the overstory and midstory responses along transects encompassing a gradient of drought-associated heatwave impact zones (minimal, transitional and severe)?
- What are the associations between overstory and midstory responses, stand characteristics (stem density, stand basal area) and edaphic factors (soil depth) across the drought-associated heatwave impact zones?

## METHODS

### Site description

South-western Australia is one of five Mediterranean-type climate biodiversity hotspots worldwide (Myers *et al.* 2000). Among the major vegetation types present in south-western Australia, is the Jarrah (*E. marginata*) Forest, forming an extensive natural forest system on the Darling Plateau, east of Perth, Western Australia, and spanning over 3 million ha between longitude 115°01'E and 117°48'E and latitude 31°50'S and 34°57'S (Specht *et al.* 2012). The northern part of the Jarrah Forest (NJF) contains over 860 flora species, with many more still undescribed (Hopper & Gioia 2004). Rainfall in the NJF ranges from 1100 mm annually at the south and western margins, to 650 mm annually at the north and eastern margins. Temperatures vary from a daily mean of 11.4°C in winter and 22.4°C daily mean in summer (BOM 2017). Seasonal drought (in summer, but also including spring and autumn) frequently lasts up to seven months (Gentilli 1989).

The NJF is located on the undulating north-western part of the Darling Plateau with crests at an elevation of 280–320 m, and valley floors are 50–100 m lower (Churchward & Dimmock 1989). The Darling Plateau is an old and complex system of deeply weathered soil and landforms, rock outcrops are common and slopes are irregular. In the upper layers of the profile, the high content of sesquioxides of iron and aluminium is often extremely weathered and/or indurated forming a lateritic duricrust (Anand & Paine 2002). A sandy pisolithic (nodular material) soil overlies a prominent 'hard cap' or duricrust, about a metre in thickness. The nodular material decreases in hardness, size and abundance, and the earthy matrix transitions into a pallid zone of clay at 0.6–3 m below the duricrust which overlies un-weathered granite or dolerite bedrock (Churchward & Dimmock 1989).

The NJF is dominated by an overstory of *E. marginata* Sm. (Myrtaceae) and the less common *C. calophylla* Lindl. K.D.Hill & L.A.S. Johnson (Myrtaceae) (typical canopy height ~25 m), with the midstory comprised of smaller trees *B. grandis* Willd. (Proteaceae) (~12 m tall), *Allocasuarina fraseriana* L.A.S. Johnson (Casuarinaceae) (~15 m) and *Persoonia* species (Proteaceae) (~8 m) (Bell & Heddle 1989). Frequent fire is a primary disturbance in most MTEs (Keeley *et al.* 2011), including the NJF, and has been for thousands of years (Burrows *et al.* 1995). Contemporary managed fire intervals are targeted at 8–10 years, and there is some debate over whether historic fire intervals ranged from very short (3 years) to longer (81 years)

(Enright *et al.* 2012). *Eucalyptus*, *Allocasuarina* and some *Banksia* species have adapted to fire and seasonal drought with the ability to re-sprout from adventitious buds or a below-ground lignotuber (Bell *et al.* 1989). The below-ground lignotuber stores water and carbon and develops during the seedling stage, ensuring survival through the early stages of growth (Clarke *et al.* 2013). If the original bole is damaged from fire or drought and cannot produce epicormic shoots, coppice shoots regenerate from the lignotuber (Crombie 1997).

### Site selection and study design

During the austral autumn of 2011, following an historic, winter drought and summer heatwave (BOM 2011), there was a sudden and severe collapse of overstory and midstory tree crowns in the NJF (Matusick *et al.* 2018). The annual mean for 2011 was 1.1°C warmer, and the summer 2010–2011 maximum temperatures were 1.4°C warmer than the means over recent decades (1981–2010) (Evans & Lyons 2013). Annual precipitation in the year before the mortality began was 69% less than the mean of 1981–2010 (Evans & Lyons 2013). Importantly, the drought-associated heatwave was superimposed on long-term warming (increase of 0.4°C) (Bates *et al.* 2008) and drying (15–20% less than mean rainfall) since the 1970s (Petrone *et al.* 2010). The incidence and severity of canopy die-off and stem mortality corresponding to the drought-associated heatwave were investigated by Matusick *et al.* (2013). Drought impact was marked by total defoliation of distinct patches of forest (0.3–85.7 ha in size; see Matusick *et al.* 2013, 2016; for more extensive descriptions). Patches were mapped through an aerial survey and subsequent field investigation and a subset selected for study (Matusick *et al.* 2013). Plots for that study were located inside and outside the drought-affected sites; however, no transects were established.

For this study, five sites were chosen in the NJF (Fig. 1), each exhibiting stem mortality and canopy die-off induced by the drought-associated heatwave and typical of the documented collapse (Andrew *et al.* 2016; Matusick *et al.* 2013). All five sites were located in the high rainfall portion (~930 mm year<sup>-1</sup>) of the NJF (Gentilli 1989). Sites had similar logging and fire histories (time since last fire > 5 years). The ecology and management of the Jarrah Forest is widely affected by the pathogen *Phytophthora cinnamomi* which inflicts damage on a diverse host range of susceptible plants (Colquhoun & Hardy 2000). Candidate sites with symptoms of *Phytophthora* infection or other signs of disturbance such as logging stands, roads or trails were excluded. The presence of *Phytophthora* susceptible (indicator) plant species and soil baiting for *Phytophthora* was used to confirm the absence of *Phytophthora* (data not included here).

At each site, four to five permanent belt transects were installed, giving a total of 24 transects. Transects originated from a single point at the centre of each collapse patch (site) (Fig. 1). The direction of each transect was chosen randomly, although azimuths were restricted to avoid extended patches of mortality and instead capture the transition from severely impacted, through the transitional zone, to minimally impacted forest. Sites were demarked *a*

*priori* into impact zones based on observed tree mortality (Fig. 1). Typically, transects spanned 30–60 m of severely impacted zone, 100–150 m of transitional vegetation and finally 50–100 m of minimally impacted forest (Table 1). A randomly chosen side (using digital random number generator) of each transect consisted of a belt of consecutive plots, 3 m wide × 10 m long in which measurements were taken. A total of 577 3 m × 10 m plots were sampled across the five sites (Table 1).

### Vegetation: stand and individual tree assessment

Sites were surveyed from August to November 2012 (15–18 months post-heatwave) with overstory and midstory mortality, composition, structure and abundance quantified in each plot for a total of 3445 trees. Overstory trees recorded were *E. marginata* and *C. calophylla* and midstory were *A. fraseriana* and *B. grandis*. Trees were often multi-stemmed (20% of stems measured were multi-stemmed trees); therefore, every tree stem was measured, diameter at breast height (130 cm; DBH), species and mortality (live, dead) were recorded, and stem density and stand basal area were calculated. There were only two instances (*E. marginata*) where multi-stemmed trees consisted of both living and dead stems, in all other cases stems were either all alive or all dead. Trees <130 cm height were counted as regeneration and not included in this study. When the crown of a stem was dead but there was basal or epicormic growth on the stem or crown, stems were recorded as alive. Since this study was initiated 15 months after the collapse event, differentiation was not made between dead and stems dead prior to the drought-associated heatwave of 2011, as determining long dead stems from recent dead stems was difficult. In an earlier study, immediately following the collapse, long dead stems were found to make up between 12 and 16% of all stems surveyed within what we have called the severe and transitional zones in the present study (Matusick *et al.* 2013).

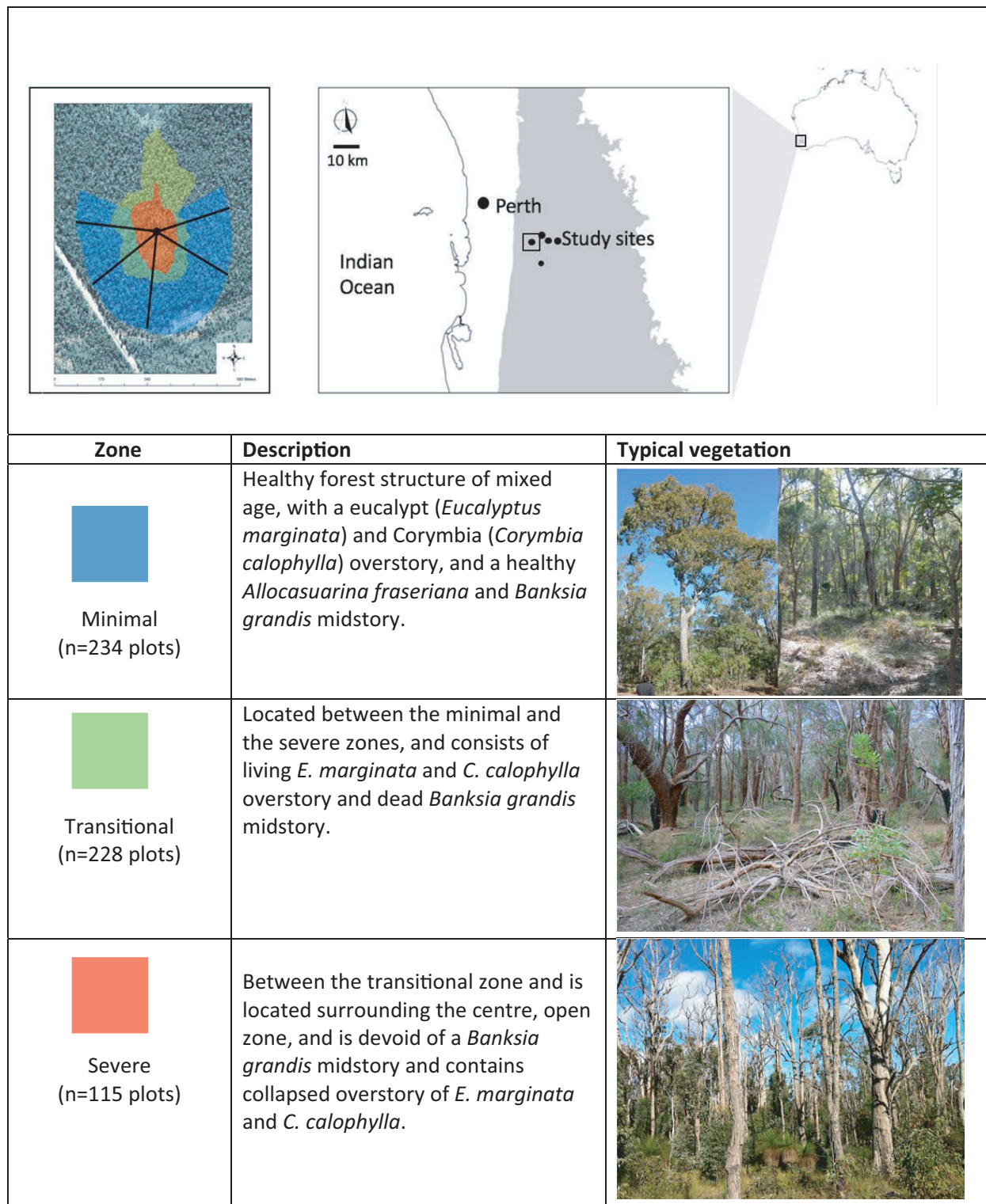
### Edaphic characteristics

To quantify potential soil water resources available to trees at a plot scale, soil depth to the mostly impenetrable lateritic mantle was measured. This was investigated, at each plot (3 × 10 m), by driving a 1-cm-diameter steel rod into the ground until underlying bedrock impeded it, or the depth exceeded 180 cm indicating the limit of the steel rod.

### Data analysis and calculations

The objective of this study was to describe and quantify the pattern of responses of key overstory and midstory species, and their stand and site characteristics. To do this, we first describe the stand characteristics for each impact zone (minimal, transitional and severe). The covariates (stem density, stand basal area, soil depth) were first quantified in





**Fig. 1.** Site and impact zone description showing location within Australia, delineation and vegetation of drought-associated heatwave impact zones and sampling design, Northern Jarrah Forest, south-western Australia. Note that yellow shading denotes an area of midstory mortality that was not sampled due to the large distance needed to reach healthy forest. Black lines represent transects.

**Table 1.** Summary of study design in the Northern Jarrah Forest, south-western Australia, describing site, number of transects, transect length (m), number of plots per transect and number of plots per impact zone (minimal, transitional and severe)

Site	Number of transects	Transect length (range, m)	Number of plots per transect (range)	Number of plots per impact zone		
				Minimal (range)	Transitional (range)	Severe (range)
A	5	240–260	24–26	0–20	3–23	3–6
B	5	220–320	22–32	5–12	7–12	3–13
C	4	190–320	19–32	3–10	4–20	4–11
D	5	200–270	20–27	0–19	2–16	2–6
E	5	170–200	17–20	6–15	4–10	1–3
Total	5	24	577	234	228	115

each ( $3 \times 10$  m) plot. ANOVA with Welch's correction for unequal variances was performed on variables (stem mortality, stem density, stand basal area and soil depth) to determine differences between impact zones. Basal area of a tree ( $\text{m}^2$ ) =  $(\text{DBH}/200)^2 \times 3.142$ , and for stand basal area ( $\text{m}^2 \text{ ha}^{-1}$ ), the sum of the basal area of each tree in the plot was divided by the area (ha) of the plot. All statistics were performed in R (R Core Team 2017), and all figures were created in ggplot2 (Wickham 2009). To facilitate interpretation, data were graphically summarised with mean and 95% confidence intervals reported.

To investigate which of the stand characteristics are associated with stem mortality for each of the overstory and midstory species, individual stem mortality was used as the response variable. Predictor variables were identified *a priori* and consisted of individual stem size (DBH), and plot-scale measures of soil depth, stem density and stand basal area. Data exploration (outliers, normality, homogeneity, independence, collinearity, relationships between predictors, interactions between predictors, zero problems) was carried out according to Zuur *et al.* (2010). To model the mortality as a function of covariates (predictor variables), a binomial generalised linear mixed model with a logit link function and optimiser bobyqa for glmer control in R package lme4 (Bates *et al.* 2014) was used for each species (Eqn ). Fixed covariates included DBH (continuous: individual tree scale) and plot-scale measures of impact zone (categorical with three levels), stem density (continuous), stand basal area (continuous) and soil depth (continuous). To incorporate the dependency among observations, site, transect and plot were included in the model as nested random intercepts.

$$\begin{aligned}
 \text{Mortality}_{ijk} &\sim \text{Bin}(1, p_{ijk}) \text{logit}(p_{ijk}) \\
 &= \alpha + \beta_1 \times \text{zone}_{ijk} + \beta_2 \times \text{DBH}_{ijk} \\
 &\quad + \beta_3 \times \text{soil depth}_{ijk} + \beta_4 \times \text{stand basal area}_{ijk} \\
 &\quad + \beta_5 \times \text{stem density}_{ijk} + \text{site effect}_i \\
 &\quad + \text{transect within site effect}_{ij} \\
 &\quad + \text{plot within transect within site effect}_{ijk} \\
 \text{Site}_i &\sim N(0, \sigma_i^2) \\
 \text{transect}_{ij} &\sim N(0, \sigma_{ij}^2) \\
 \text{plot}_{ijk} &\sim N(0, \sigma_{ijk}^2)
 \end{aligned} \tag{1}$$

where  $\text{count}_{ijk}$  is the  $k$ th observation in  $\text{plot}_{ijk}$  in transect  $ij$  within site  $i$ , and  $i = 1, \dots, 577$ , and  $\text{plot}_{k}$  is the random

intercept, which is assumed to be normally distributed with mean 0 and variance  $\sigma^2$ . All covariates were standardised before fitting the model for each species. The models for *A. fraseriana* and *C. calophylla* failed to converge, and all variables were incorporated into separate univariate models. To verify that the models complied with underlying model assumptions, residuals were plotted against fitted values for each covariate in the model and not in the model. The residuals were assessed for spatial and temporal dependency. For models, standardised estimates and their SEs,  $Z$  and  $P$  values are reported.

## RESULTS

### Impact zones and stand variables

Mortality levels of the overstory and midstory species confirmed the demarcation of *a priori* zone divisions were accurate (Table 2). The dominant overstory tree (*E. marginata*) showed significantly higher per cent mortality ( $F = 10.5$ , d.f. = 2.0, 332,  $P < 0.001$ ) in the plots in the severe zone (Fig. 2a), with a mean mortality per plot of ~19% (Table 2). Mortality of the dominant midstory tree (*B. grandis*) was highest in the transitional zone ( $F = 45.8$ , d.f. = 2.0, 280,  $P < 0.001$ ) (Fig. 2a), with a mean mortality of 59% per plot (Table 2). Only three plots in the severe zone contained the dominant midstory tree *B. grandis*. For the less common species (*C. calophylla*, *A. fraseriana*), there was moderate evidence of higher mortality in the severe zone than in the minimal zone, though this was not significant due to high variance in plots (Table 2, Fig. 2a). Trees of *Persoonia* species were rarely encountered (<30) and so excluded from the study.

Impact zone categories showed significantly shallower soil ( $F = 14.9$ , d.f. = 2, 528,  $P < 0.001$ ) and a higher stem density ( $F = 45.8$ , d.f. = 2, 528,  $P < 0.001$ ) in the transitional zone than in the minimal and severe zones (Table 2, Fig. 2b,c). Stand basal area was significantly higher in the minimal

**Table 2.** Summary statistics for variables, stem density (stems per hectare), stand basal area ( $\text{m}^2 \text{h}^{-1}$ ), stem mortality for each tree species (*Eucalyptus marginata*, *Corymbia calophylla*, *Allocasuarina fraseriana*, *Banksia grandis*) (% per plot) and soil depth (cm), for impact zones (minimal, transitional and severe). Variables were assessed at the plot level

Variable	Minimal zone		Transitional zone		Severe zone	
	Range	Mean (CI 95%)	Range	Mean (CI 95%)	Range	Mean (CI 95%)
Stem density (stems per hectare)						
All species combined	333–5667	2737 (74.4)	333–7333	3220 (86.8)	333–5333	2632 (113)
<i>Eucalyptus marginata</i>	0–5667	803 (80.0)	0–7333	1289 (99.7)	0–5333	1956 (139)
<i>Corymbia calophylla</i>	0–5667	109.5 (33.2)	0–7333	195 (45.1)	0–4333	135.5 (55.6)
<i>Banksia grandis</i>	0–5667	1289 (94.8)	0–7333	1305 (98.8)	0–4000	45.9 (36.4)
<i>Allocasuarina fraseriana</i>	0–5333	535 (60)	0–7333	431 (57)	0–5333	494 (55)
Stand basal area ( $\text{m}^2 \text{h}^{-1}$ )						
All species combined	0–739	81.8 (6.18)	0–690	65.6 (3.97)	0–298	65.5 (5.65)
<i>Eucalyptus marginata</i>	0–739	26.3 (4.43)	0–690	29.6 (3.27)	0–298	44.0 (4.67)
<i>Corymbia calophylla</i>	0–600	2.19 (1.15)	0–595	4.21 (1.61)	0–192	3.65 (1.73)
<i>Banksia grandis</i>	0–739	29.2 (4.02)	0–595	19.4 (2.45)	0–192	2.20 (0.89)
<i>Allocasuarina fraseriana</i>	0–739	24.1 (3.82)	0–267	12.4 (1.98)	0–298	15.7 (4.53)
Species mortality (%)						
<i>Eucalyptus marginata</i>	0–50	2.70 (1.78)	0–100	3.14 (1.91)	0–100	19.0 (6.90)
<i>Corymbia calophylla</i>	0–100	2.70 (5.48)	0–100	3.16 (3.98)	0–100	7.14 (10.9)
<i>Banksia grandis</i>	0–100	19.7 (5.07)	0–100	58.9 (6.55)	60–100	86.7 (57.4)
<i>Allocasuarina fraseriana</i>	0–100	1.80 (1.93)	0–100	3.90 (3.29)	0–100	12.1 (11.8)
Soil depth (cm)	8–187	49.6 (1.44)	0–129	45.0 (1.20)	0–167	50.0 (2.21)

zone ( $F = 10.318$ , d.f. = 2, 528,  $P < 0.001$ ) than in the severe or transitional zones (Fig. 2d).

### Stand variables associated with species-specific response

Mortality in the dominant overstory species *E. marginata* showed a weak association with higher stem diameter and was more pronounced in plots with lower basal area (Table 3). Covariates significantly associated with high levels of stem mortality of the common midstory species *B. grandis* were DBH, soil depth and stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ) (Table 3). Specifically, larger *B. grandis* trees (approximately >20 cm) growing in plots with low basal area and shallow soil were more likely to die (Fig. 3a–c). Mortality in the less common tree species (*C. calophylla*, *A. fraseriana*) was not linked to explanatory variables in this study, possibly due to low numbers sampled, which caused high variance and non-convergence in statistical models.

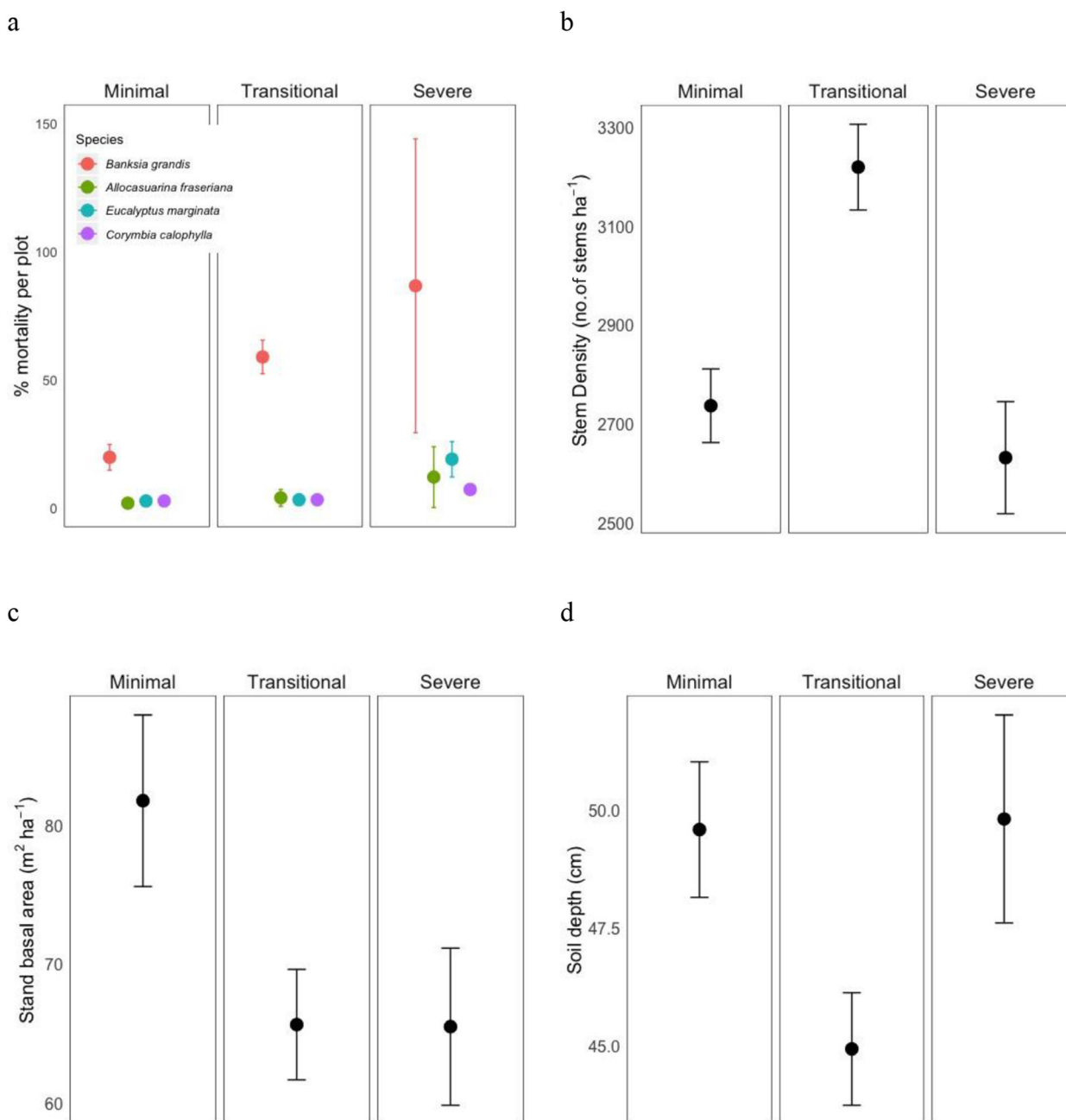
## DISCUSSION

This study has shown that the differential species response to the drought-associated heatwave leads to structural and compositional changes in the affected areas of the Northern Jarrah Forest, and key species were vulnerable because of stand and edaphic

characteristics. The dominant overstory species, *E. marginata*, responded to the drought-associated heatwave with the highest mortality in the severely affected zones at the centre of the collapse patches. The key midstory tree, *B. grandis*, showed elevated mortality in a transitional zone surrounding (but not including) the severe zone. High vulnerability to the drought-associated heatwave was demonstrated by *B. grandis*, as even in the minimally impacted zone, the mortality rate was high. Stand characteristics (basal area and tree size) and edaphic factors (soil depth) were strongly associated with *B. grandis* mortality. Specifically, larger *B. grandis* trees in plots with shallow soil already exhibiting low stand basal area had the highest mortality. Differential species mortality in response to drought has been demonstrated in semi-arid woodlands in Arizona (Mueller *et al.* 2005), in eucalypt savanna in NE Australia (Fensham & Fairfax 2007) and in MTE holm oak forest in NE Spain (Peñuelas *et al.* 2000; Lloret *et al.* 2004). In the present study, we confirm this type of differential species response and show how the drought-associated heatwave interacted with stand and edaphic conditions.

### Overstory mortality

The dominant overstory species (*E. marginata*) demonstrated higher mortality rates than the less common species (*C. calophylla*), and this is consistent



**Fig. 2.** Means (and 95% confidence intervals) for variables, (a) % stem mortality per plot of overstory species (*Eucalyptus marginata*, *Corymbia calophylla*) and midstory species (*Banksia grandis*, *Allocasuarina fraseriana*); (b) stem density (stems per hectare); (c) stand basal area (m<sup>2</sup> h<sup>-1</sup>); and (d) soil depth (cm) for impact zones (minimal, transitional and severe). For *B. grandis* % stem mortality per plot, there were only three values of data for the severe impact zone.

with a study by Ruthrof *et al.* (2015), where *C. calophylla* was found to exhibit stronger resistance traits than *E. marginata* to the same drought-associated heatwave. *Corymbia calophylla* employs a more conservative water use strategy by maintaining lower daily transpiration rates than *E. marginata* (Szota *et al.* 2011) and this may lead to lower mortality rates.

Competition via high stem density was not associated with overstory mortality in the present study. Self-thinning does not occur, or is very rare in the Jarrah Forest, and, as such, the forest may remain in a locked-up condition (at a high stem density) where poles stagnate until competition is reduced (Stoneman *et al.* 1989). In a previous study of die-off plots in the NJF, higher stem densities occurred on sites



**Table 3.** Estimated regression parameters, standard errors, z-values and P-values for binomial GLMM; stem mortality for dominant overstory (*Eucalyptus marginata*) and midstory (*Banksia grandis*) species modelled against diameter at breast height (130 cm), stem density (no. of stems per hectare), stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ) and soil depth (cm)

Species	Covariate	Estimate	Std error	z-Value	P-value
<i>Eucalyptus marginata</i>	Intercept	-4.53	1.32	-3.43	<0.001
	DBH (130 cm)	0.358	0.180	1.99	0.047
	Stem density (no. of stems per hectare)	0.317	0.337	0.940	0.347
	Stand basal area ( $\text{m}^2 \text{ha}^{-1}$ )	-0.609	0.307	-1.98	0.047
	Soil depth (cm)	0.164	0.302	0.545	0.586
<i>Banksia grandis</i>	Intercept	2.59	0.631	4.10	<0.001
	DBH (130 cm)	3.76	0.398	9.46	<0.001
	Stem density (no. of stems per hectare)	0.233	0.192	1.22	0.224
	Stand basal area ( $\text{m}^2 \text{ha}^{-1}$ )	-0.395	0.132	-3.00	0.003
	Soil depth (cm)	-0.38	0.163	-2.32	0.020

that collapsed, although basal area was not significantly different (Matusick *et al.* 2013). In contrast to Matusick *et al.* (2018) who investigated paired plots in sites of severe drought impact and healthy forest, plots in the present study covered a gradient of stem mortality and edaphic characteristics, and this difference in study design may explain the different results concerning stem density. Previous studies in other systems have reported high stem density associated with drought-induced tree mortality in *C. atlantica* forest in Southern French Alps (Guillemot *et al.* 2015) and Mediterranean *Quercus* woodlands in Northern Spain (Peñuelas *et al.* 2000; Lloret *et al.* 2004; Fernández-de-Uña *et al.* 2015). *Eucalyptus marginata* utilise root channels in the bedrock up to 40 m deep to access groundwater (Dell *et al.* 1983), and there is high competition for root channel access. Our results indicate the complex interactions between competition and soil depth should be acknowledged when determining forest structural changes resulting from a drought-associated heatwave.

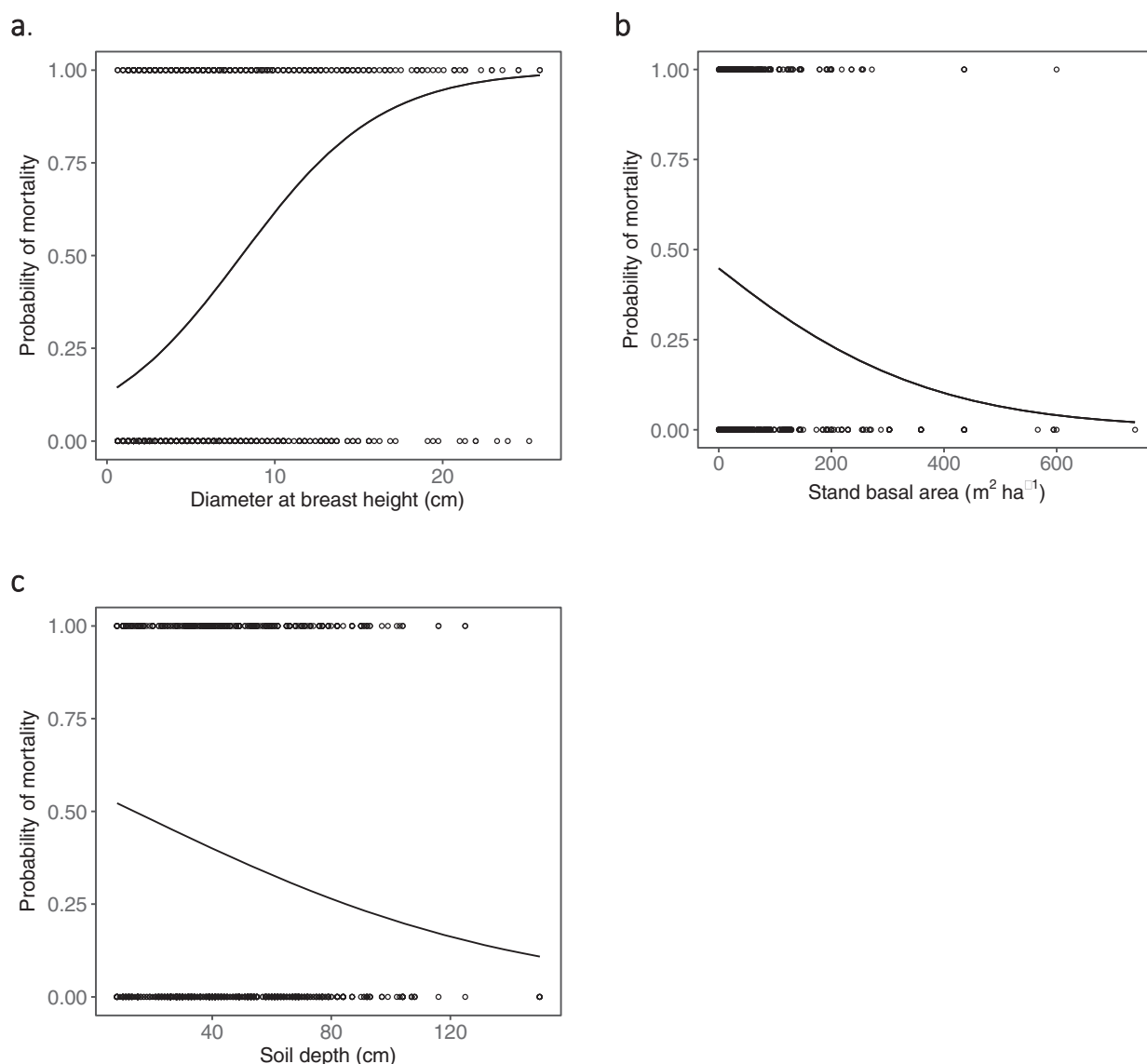
Mortality in *E. marginata* was weakly associated with larger stem diameter in plots with lower basal area, implicating the importance of site quality. More arid sites in the Jarrah Forest have been found to have a higher abundance of smaller stems and overall biomass than less arid sites (Pekin *et al.* 2009). Stands dominated by smaller trees have been found to have a lower leaf area:sapwood ratio than stands dominated by larger trees (Pekin *et al.* 2009) and thus an improved capacity to provide foliage with water without cavitation occurring (Delucia *et al.* 2000). As such, because smaller trees have proportionally more sapwood, it seems that larger *E. marginata* trees were more susceptible to mortality (through formation of an embolism when vapour pressure deficit exceeded thresholds) during the drought-associated heatwave. It is possible that the relationship between site quality and mortality may be predicted through the lower stand basal area found on low-quality sites. Variation in site quality

has been studied with respect to *E. marginata* seedling mortality, demonstrating that mortality is highest in low-quality sites during the first summer drought, thereby reducing stocking densities (Stoneman *et al.* 1994). A landscape-scale study on crown die-off in the NJF found crown die-off was most prevalent around rocky outcrops and in soils with poor water-holding capacity (Brouwers *et al.* 2013).

### Edaphic characteristics

It was expected the depth of soil to the lateritic mantle would occur on a gradient associated with *E. marginata* mortality. McGrath *et al.* (1991) and Harper *et al.* (2009) found that tree mortality in *E. globulus* plantations of south-western Australia was related to the soil volume available to the root system, and trees on shallower soils had greater mortality than those on deeper soils. However, in the present study the soil depth to the lateritic mantle was not a significant indicator of eucalypt overstory mortality. The NJF is comprised of a complex matrix of soil type and texture which transitions rapidly over short distances (Havel 1975; Churchward & Dimmock 1989). In a parallel study of the same sites in the NJF, dolerite dykes and associated fine-textured soils were observed to exist in some parts of the collapsed sites that we have called the severe zone in this study (W. Dunstan, unpubl. data, 2015). The available water in finer textured soils is more difficult to extract due to higher soil water potentials. The exacerbation of drought-induced tree mortality in fine-textured soils has also been demonstrated in semi-arid juniper woodlands in Arizona (Bowker *et al.* 2012), eucalypt savanna in NE Australia (Fensham & Fairfax 2007; Fensham *et al.* 2015), and in Mediterranean Scots pine forest in NE Spain (Galiano *et al.* 2010). Site quality and underlying edaphic conditions were important in drought-induced die-off in *Abies alba* in an MTE in southern





**Fig. 3.** Predicted probability stem mortality (with 95% confidence intervals) of midstory tree species *Banksia grandis* plotted against. (a) Diameter at breast height (cm); (b) stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ); and (c) soil depth (cm) from results of binomial generalised linear mixed-effects model.

France (Cailleret *et al.* 2014), and in Mediterranean Holm oak forest in NE Spain, die-off was more frequently associated with compact substrates (Lloret *et al.* 2004). To unravel the interactions surrounding the mortality of the dominant overstory species (*E. marginata*), further examination and research of physical, chemical and biological components of soil profiles in healthy and collapse areas are required (Gazol *et al.* 2018; Hopkins *et al.* 2018).

### Midstory mortality

High midstory mortality in *B. grandis* showed a significant relationship with tree size, soil depth and

stand condition; specifically, larger trees in shallow soils exhibited higher mortality in this drought-associated heatwave event. Thus, in comparison with the overstory trees, *B. grandis* may be more reliant on the soil depth and hence moisture available from this upper profile. In contrast to *B. grandis*, the less common midstory species, *A. fraseriana*, displayed resprouting and low mortality, with a high survival of individuals of all sizes. In studies of other *Banksia* species in south-western Australia following the same drought-heatwave event of 2011, mortality was also found to be size-dependent, with larger trees of *B. menziesii* and *B. attenuata* more susceptible to mortality (Bader *et al.* 2014; Challis *et al.* 2016). Size-dependent mortality has been observed in

pinyon pines in semi-arid woodlands in Arizona with higher mortality rates in larger reproductive-aged trees (Mueller *et al.* 2005) and in tropical forests in the Amazon (Nepstad *et al.* 2007). *Banksia grandis* in our study were more likely to survive in areas with higher overall stand basal area, indicating an overstorey canopy may have provided a facilitative effect on *B. grandis* during the 2011 heatwave event, by reducing heat stress through perhaps a reduction in temperature and increased humidity under the canopy. Previous studies of virgin and logged *E. marginata* forest demonstrated that shading from the canopy did not affect growth or survival of *B. grandis* (Abbott 1984, 1985a). However, these studies were completed over 30 years ago and may not account for the effects of subsequent long-term climate warming and decreased precipitation in south-western Australia on the growth and survival of *B. grandis*.

Predictive climate change models developed by Yates *et al.* (2010) project that in the most severe climate change scenario, which includes land transformation and zero seed dispersal, *B. grandis* will lose all its suitable habitat range. This is a substantive concern due to the serotinous nature of *B. grandis* and given that plants may take up to 30 years to reach reproductive maturity (Abbott 1985b). A shrinking spatiotemporal climate niche, coupled with increased rates of drought and fire, may very well act to squeeze *B. grandis* populations (Enright *et al.* 2015), leading to extirpation from many of the areas it now occupies. This would result in a change in species composition and also a shift in ecosystem functioning, given the extensive food supply the flower of this tree provides to a wide variety of fauna (Abbott & Heurck 1985).

## CONCLUSIONS

We described and quantified the pattern of responses of key overstorey and midstorey species, and their stand and site characteristics, following a drought-associated heatwave and forest collapse in south-western Australia. The dominant overstorey species, *E. marginata*, experienced higher mortality than *C. calophylla* in the severely impacted zone. The midstorey species, *B. grandis*, exhibited higher mortality than *A. fraseriana* in the transitional zone. *Banksia grandis* also exhibited a substantial shift in structure in response to the drought-associated heatwave in relation to tree size, stand basal area and soil depth. These results illustrate that changes in forest overstorey and midstorey structure are amplified by extreme climatic events and highlight the vulnerability of midstorey species (e.g. *B. grandis*) to drought-associated heatwaves. This information will assist in identifying

and monitoring vulnerable forest stands, informing management practices (such as controlled fire return intervals) in areas where midstorey *B. grandis* have not yet reached reproductive maturity. The continued change in climate trends, as is predicted, may lead to permanent changes in forest vegetation trajectories and, in turn, alter ecosystem composition, structure and function.

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