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Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia

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Abstract

Drought and heat-induced forest dieback and mortality are emerging global concerns. Although Mediterranean-type forest (MTF) ecosystems are considered to be resilient to drought and other disturbances, we observed a sudden and unprecedented forest collapse in a MTF in Western Australia corresponding with record dry and heat conditions in 2010/2011. An aerial survey and subsequent field investigation were undertaken to examine: the incidence and severity of canopy dieback and stem mortality, associations between canopy health and stand-related factors as well as tree species response. Canopy mortality was found to be concentrated in distinct patches, representing 1.5% of the aerial sample (1,350 ha). Within these patches, 74% of all measured stems (> 1cm DBHOB) had dying or recently killed crowns, leading to 26% stem mortality six months following the collapse. Patches of canopy collapse were more densely stocked with the dominant species, *Eucalyptus marginata*, and lacked the prominent midstorey species *Banksia grandis*, compared to the surrounding forest. A differential response to the disturbance was observed among co-occurring tree species, which suggests contrasting strategies for coping with extreme water stress. These results suggest that MTFs, once thought to be resilient to climate change, are susceptible to sudden and severe forest collapse when key thresholds have been reached.

Keywords

Climate change, die-off, forest mortality, density-dependent, *Eucalyptus marginata*, *Corymbia calophylla*

Introduction

Catastrophic forest damage resulting from extreme drought and heat is increasingly being reported from around the world (Ganey and Vojta 2011; Granzow-de la Cerda et al. 2012). A recent review by Allen et al. (2010) outlined 88 documented episodes of forest damage resulting from drought and/or heat events since the early 1970's, illustrating the vulnerability of forests to extreme climate conditions worldwide. Long periods of drought result in chronic stress, causing growth reductions (Barber et al. 2000), crown dieback (Fensham and Holman 1999), and tree decline (Starkey et al. 2004). For example, during five years of experimental drought conditions, the diameter increment of *Quercus ilex* L. was reduced by 41% (Ogaya and Peñuelas 2007). In contrast episodes of extreme drought, leading to severe stress, can result in sudden large-scale forest canopy collapse (dieback and die-off). Over 12,000 km^2 of temperate pine forests died in the southwestern U.S. following severe droughts in 1996 and 2002 (Breshears et al. 2005). Such a rapid and mass collapse of forests have the potential to alter the composition (Mueller et al. 2005), structure, and functioning of forests, causing the loss of ecosystem services (Guardiola-Claramonte et al. 2011) including sequestered carbon (Huang et al. 2010).

A variety of site and stand factors may interact with sudden and extreme drought conditions to result in forest tree losses (Bowker et al. 2012; Breshears et al. 2005; Worrall et al. 2008). Recently, edaphic factors were found to be the primary driver of juniper (*Juniperus monosperma* [Engelm] Sarq.) mortality during forest collapse in the southwestern U.S. (Bowker et al. 2012), while stand density may have influenced mortality of the dominant species *Pinus edulis* Engelmann (Greenwood and Weisberg 2008). Massive mortality of trembling aspen (*Populus tremuloides* Michx.) occurred following acute drought stress in boreal forests in Western Canada (Hogg et al. 2002) and montane forests of Colorado, USA (Worrall et al. 2008). In the latter, an array of site and stand factors, including low elevation, southern aspects, and stand maturation were found to predispose forest areas to drought, while biotic pests contributed in killing weakened trees (Worrall et al. 2008). Finally, a sudden and severe drought in the western Mediterranean (NE Spain) in 1994 caused complete canopy dieback in up to 76% of the dominant tree species, *Q. ilex* L. (Lloret et al. 2004). The incidence of the canopy dieback was strongly associated with edaphic factors, including soil compaction and the ability for roots to penetrate soil substrates. These examples illustrate how site and stand factors can interact with sudden and severe drought to affect canopy dieback and tree mortality patterns.

Mediterranean-type forests (MTFs) experience a mediterranean-type climate characterized by cool, wet winters followed by a distinct hot and dry summer period during which they may be exposed to seasonal drought conditions (Gentilli 1989). Additionally, MTFs have historically experienced dramatic interannual fluctuations in precipitation and temperature (Nicault et al. 2008), which has, in part, selected for highly resilient species (Dell et al. 1986) with a unique range of adaptations to disturbance (Zavala et al. 2000). Despite these adaptations, MTFs have been plagued by chronic stress during recent periods of protracted drought conditions (Carnicer et al. 2011). This has translated to extensive crown dieback (Lloret et al. 2004) and declines in both growth (Jump et al. 2006; Sarris et al. 2007) and tree health (Raftoyannis et al. 2008) in the Mediterranean basin. Many dominant tree species within MTFs in the South-West of Western Australia (SWWA) have shown similar symptoms in recent decades (Archibald et al. 2005; Auclair 1992; Hooper 2009), corresponding with a long-term decline in rainfall (Fig. 1a)(Bates et al. 2008). Despite this, large-scale tree mortality resulting from sudden and severe drought has largely not been observed until this point.

The SWWA experiences a typical mediterranean-type climate that has been rapidly changing since the 1970's (Suppiah et al. 2007). More specifically, the region has experienced a pronounced shift in rainfall since the 1970's (Fig. 1b). Meanwhile average temperatures have risen at a rate of 0.15°C per decade over the same time period (Bates et al. 2008). The long-term drying and warming trends culminated in a record dry (40-50% below average rainfall) and hot year in 2010, made possible by a record dry summer (December-February), winter (June-August), and below average spring (September-November) rainfall (BOM 2011a). It was also the hottest year on record for most of the Perth Metropolitan area, with annual mean maximum temperatures of 1 to 1.5°C above average (BOM 2011a). This trend continued into 2011, with the Perth Metropolitan area experiencing the third hottest February on record (BOM 2011b). Decreases in precipitation have corresponded with significant decreases in streamflow and groundwater levels in forested catchments (Croton and Reed 2007; Kinal and Stoneman 2011). Formerly perennial streams are now ceasing to flow for considerable periods each year (Petrone et al. 2010), while groundwater levels have fallen up to eleven meters in some regions since 1975 (Croton and Reed 2007).

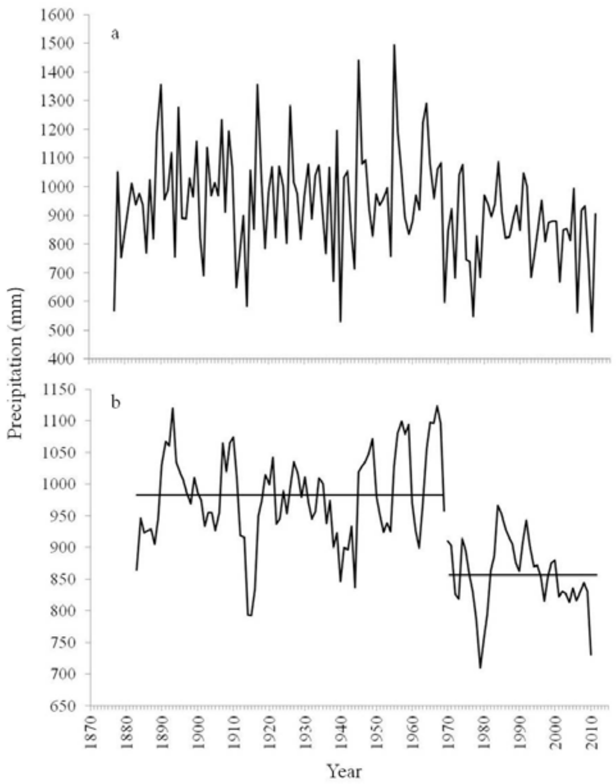

Fig 1 Precipitation trend since 1877 for Pinjarra, Western Australia (see Fig. 3 for location), station number 9596. Total annual precipitation (**a**) and annual values smoothed with five-year running mean (**b**) and fitted with means from 1877-1969 and 1970-2011 illustrating a climate shift described in Bates et al. 2008

Corresponding with a prolonged heatwave (nine days greater than 35°C) in late February 2011(BOM 2011b) midstorey and overstorey tree crowns suddenly began dying (collapsing) in several ecosystems in SWWA (Matusick et al. 2012). This paper addresses the recent canopy collapse in the Northern Jarrah Forest (NJF) and aims to: 1) estimate the incidence (spatial scale) and severity of canopy collapse across the NJF; 2) define associations between canopy collapse and forest stand variables; and, 3) investigate the variation in crown collapse and regrowth in relation to tree species and size.

Methods

Study area

The NJF is located in the Southwest Botanical Province of Western Australia and covers an area of 1,127,600 ha (Havel 1975), representing the northern section of the *E. marginata*-dominated forest-type (Fig 2). It ranges from a tall, open, and dry sclerophyll forest in the north to a tall closed forest in the south (Dell and Havel 1989). The NJF harbours over 850 known vascular plant species (in addition to many unnamed) contributing to SWWA being one of the 35 global biodiversity hotspots (Mittermeier et al. 2011). This study is focused on upland sites, which are dominated by *E. marginata*, with *Corymbia calophylla* (R. Br.) K.D. Hill & L.A.S. Johnson (marri) as the primary co-dominant.

Allocasuarina fraseriana (Miq.) L.A.S. Johnson (sheoak), *Banksia grandis* Willd. (bull banksia), and *Persoonia* spp. are also commonly found throughout the midstorey. The NJF overlies Archaean granite and metamorphic rocks capped by an extensive lateritic duricrust, which is interrupted by occasional granite outcrops in the form of isolated hills (Churchward and Dimmock 1989). The soils are some of the oldest on the planet. They are characterized by extremely low fertility and are highly leached (Mulcahy 1960). The lateritic plateau has an average elevation of 300 meters. The climate of the NJF is a Mediterranean-type, with most (~80%) rainfall falling between April and October (Bates et al. 2008), and a seasonal drought that may last from 4 to 7 months (Gentilli 1989). There is a strong west-east rainfall gradient across the forest, ranging from >1100 mm/yr on its western edge (Darling Scarp) to ~700 mm/yr in the east and north (Gentilli 1989). Historically, the NJF has played a significant role in timber production (Havel 1989) and continues to provide high-value timber for a range of uses, including flooring and furniture. Other dominant land uses include water production, mining, plantation forestry, and recreation (Abbott and Loneragan 1986).

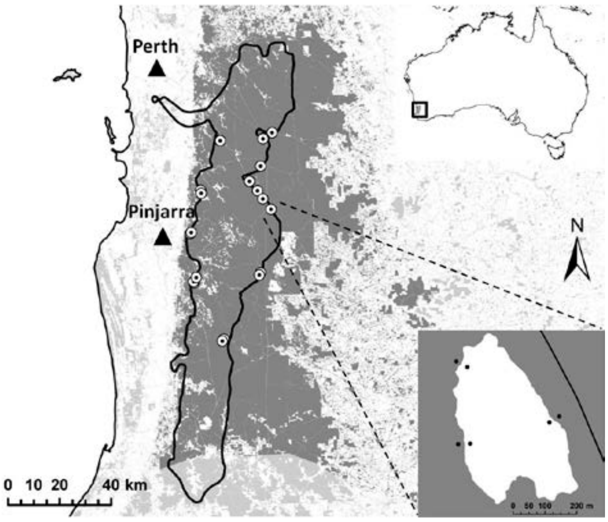

Fig 2 Aerial flight path (black line) traversing the vegetation of the Northern Jarrah Forest (dark grey) and locations of the 20 field sites (white/black dots), each containing three sets of paired affected and control plots (map detail)

Site selection

The earliest observations of significant crown collapse in overstorey trees (*E. marginata* and *C. calophylla*) were made the week of 28 February 2011, coinciding with a prolonged heatwave (nine days greater than 35°C). Two sites experiencing crown collapse were visited approximately bi-weekly between late February and early May 2011. Observations of tree crown dieback were noted during visits.

In response to the early field observations of canopy damage, an aerial survey of the NJF was conducted in late May 2011 using a Cessna 172 fixed-wing aircraft. The flight path roughly traversed two transects, spanning the north to south distribution of the NJF (Fig. 2).

Since collapsed forest canopy was found to be concentrated in distinct patches, two DSLR digital cameras (Nikon D90, Nikon Corporation, Tokyo, Japan and Sony A55, Sony Corporation, Tokyo, Japan) were used to capture approximately 2500 oblique, georeferenced, aerial photos, including all damaged patches greater than 0.3 ha along the flight path. Identifiers, including landform, roads, cleared land, granite outcrops, and other landmarks, were used to link oblique photos with vertical orthorectified images to enable delineation and digitization of areas representing collapsed forest canopy using OziExplorer GIS mapping software (version 3.95.5, Brisbane, Australia). Midstorey canopy collapse, where present, extended well beyond overstorey canopy collapse. However due to inherent difficulties with accurately detecting midstorey collapse confined beneath a green and healthy overstorey canopy, the survey was limited to areas experiencing overstorey canopy collapse only. A total of 236 independent forest patches experiencing canopy collapse were delineated from the survey. In order to estimate the area of the NJF that was sampled, the distance between the edges of each polygon and the actual flight path was determined. The ten greatest and shortest distances were averaged separately to provide an estimate of the greatest and shortest distance from the flight path, resulting in a "strip" of sampled forest parallel to the flight path. The estimated sampled area and area of collapsed forest canopy were determined using ArcGis 10 software (ESRI, Redlands, CA).

Affected sites that were deemed inaccessible were discounted for future field investigations, including those restricted to private property and those more than 3 km from roads. From the remaining population of affected sites, 28 were randomly chosen for ground delineation. Each of the sites was visited and delineated using a differential GPS (Pathfinder Pro XRS receiver, Trimble Navigation Ltd., Sunnyvale, CA). The size of aerially-and ground-derived delineations were compared in ArcGIS10 to determine the error associated with the aerial survey technique. Finally, from the 28 sites that were accurately delineated, a random sub-sample of 20 sites was chosen for further field investigations using a paired-plot design (Fig.2).

Plot establishment

Plots were established between 21 June and 12 July 2011. Within each affected site three six metre radius plots (0.011 ha each) were randomly selected on a 20m x 20m grid using fGIS forestry cruise software (Wisconsin DNR-Division of Forestry). Paired control plots, representing areas which did not experience canopy collapse, were located approximately 20 m outside the affected site boundary at the shortest straight-line distance from each affected plot. A total of 20 affected sites were sampled with six plots at each site (three affected/three control see Fig. 2), totalling 120 plots.

Since many eucalypts, including *E. marginata* and *C. calophylla*, have the propensity to produce multiple stems per individual, measurements were made on all stems greater than 1cm diameter at breast height over bark (DBHOB) within each plot. The species were recorded and total stem heights were measured using a digital clinometer (Haglof HEC, Langsele, Sweden). Stem crown conditions fell into the four crown health classes described by Worrall et al. (2008), including “healthy”, characterised by predominately green turgid foliage, “dying”, characterised by predominately dry and discoloured foliage, “recently killed”, characterised by predominately red and dead foliage, and “long dead” characterised by a lack of leaves, fine twigs, and the presence of slipping bark. An estimate of previous crown dieback (%) was made based on the amount of previous crown retraction, which was estimated from the abundance and size of long dead branches. For all tree species, regeneration was assessed by counting the number of stems on the plot (stem ≤ 1 cm DBHOB), the average height, and the predominant crown health class (as above). Density measures, including trees/ha (individuals/ha), stems/ha, and basal area/ha were derived from the plot data.

Plot re-assessment

In October and November 2011, following the wet winter season, all plots were revisited in order to assess stem response to the collapse. Each stem was inspected for crown health changes and evidence of re-sprouting. Stem mortality was estimated at this time including only those stems with recently killed crowns that lacked evidence of re-sprouting. The percentage of stems re-sprouting per plot, number of sprouts per re-sprouting stem, and the percentage of each stem that remained living (i.e. maximum height of sprouts/total height of original tree) were recorded. Additionally, canopy cover was assessed at the centre of each plot by taking the average of four measurements (facing aspects north, east, south, west), using a spherical densiometer (Lemmon 1956).

Statistical analyses

All variables were assessed for normality using Q-Q plots and Anderson-Darling tests. For variables found to be non-normally distributed following transformation, nonparametric methods (Mann-Whitney *U*-test/Kruskal-Wallis tests) were used to determine differences between groups. For all other quantitative variables, mixed effects models, using site as a random factor, were used. The Chi-square goodness-of-fit tests were used to assess categorical variables. All analyses were performed using SAS statistical software (SAS Institute, 9th ed., Cary, NC).

Differences in crown health between control and affected plots were investigated. Tree crowns falling within dying and recently killed crown health classes were combined to specifically examine the percentage of stems affected by the disturbance in 2011. The mean percentage of stems within each crown health class, affected stems, stem mortality, canopy cover, and previous crown dieback were assessed between control and affected plots using Mann-Whitney *U*-tests in the npar1way procedure in SAS.

Subsequently, the percentage of affected stems and stem resilience patterns were investigated between diameter classes and tree species, using only data from affected plots. Stem diameters were divided into 10 cm size classes and those stems greater than 60 cm DBHOB were pooled due to low numbers in these larger diameter classes. With the exception of previous crown dieback, nonparametric statistics (Mann-Whitney *U*-tests /Kruskal Wallis) were used for testing hypotheses, since percentage data were not normally distributed despite arcsin-square-root transformations. Previous crown dieback was analysed using ANOVA (GLM procedure in SAS), including site and either stem diameter class or tree species in models, followed by Tukey’s multiple comparison test to differentiate groups. To determine the relative rates of affected stems and stem mortality between stem diameter classes, only those plots represented by a given diameter class were used for analyses. Similarly, for re-sprout rates among diameter classes, only those diameter classes/plots with dying or recently killed crowns were used. For tree species comparisons, *E. marginata*, present on all plots, was compared with co-dominants *C. calophylla* and *A. fraseriana* separately, using only those plots in which three or more co-dominant stems were measured. Comparisons of the mean number of re-sprouts per re-sprouting stem and percentage of re-sprouting stems remaining alive were made between *E. marginata* and *C. calophylla* only, given that a limited number of *A. fraseriana* stems were found re-sprouting during the re-assessment.

Stem diameter distributions were produced for control and affected plots, and differences within each class were examined using Mann-Whitney *U*-tests. Stem density (stems/ha) and basal area (m^2) per plot were derived for all measured *E. marginata* and *C. calophylla* stems. Additionally, the density of multi-stemmed trees and stem regeneration was computed. Comparisons for these variables were made between control and affected plots using mixed effects models (MIXED procedure in SAS), including site as a random factor following either square-root or log transformations to improve normality.

Results

Early field observations

Crown changes were first observed during January 2011 in *B. grandis,* the primary midstorey tree species on upland NJF sites in the western forest. Large patches of *B. grandis* crowns rapidly discoloured and died over periods as short as five days. Shortly following in February 2011, many overstorey and understorey *E. marginata* and *C. calophylla* crowns also discoloured and died within two weeks. Canopy discoloration generally began within one branch, and then appeared to spread rapidly throughout the crown (Fig. 3a). Discoloured foliage was notably dry and was associated with drying of conductive tissues, determined from limited destructive sampling. By the middle of June many branches up to 1 cm had abscised from affected canopies (Fig. 3b). Stems with incomplete crown discolouration present along the periphery of each affected site in late June, maintained their condition throughout the winter (June-August) period before losing affected foliage in the spring (September-November).

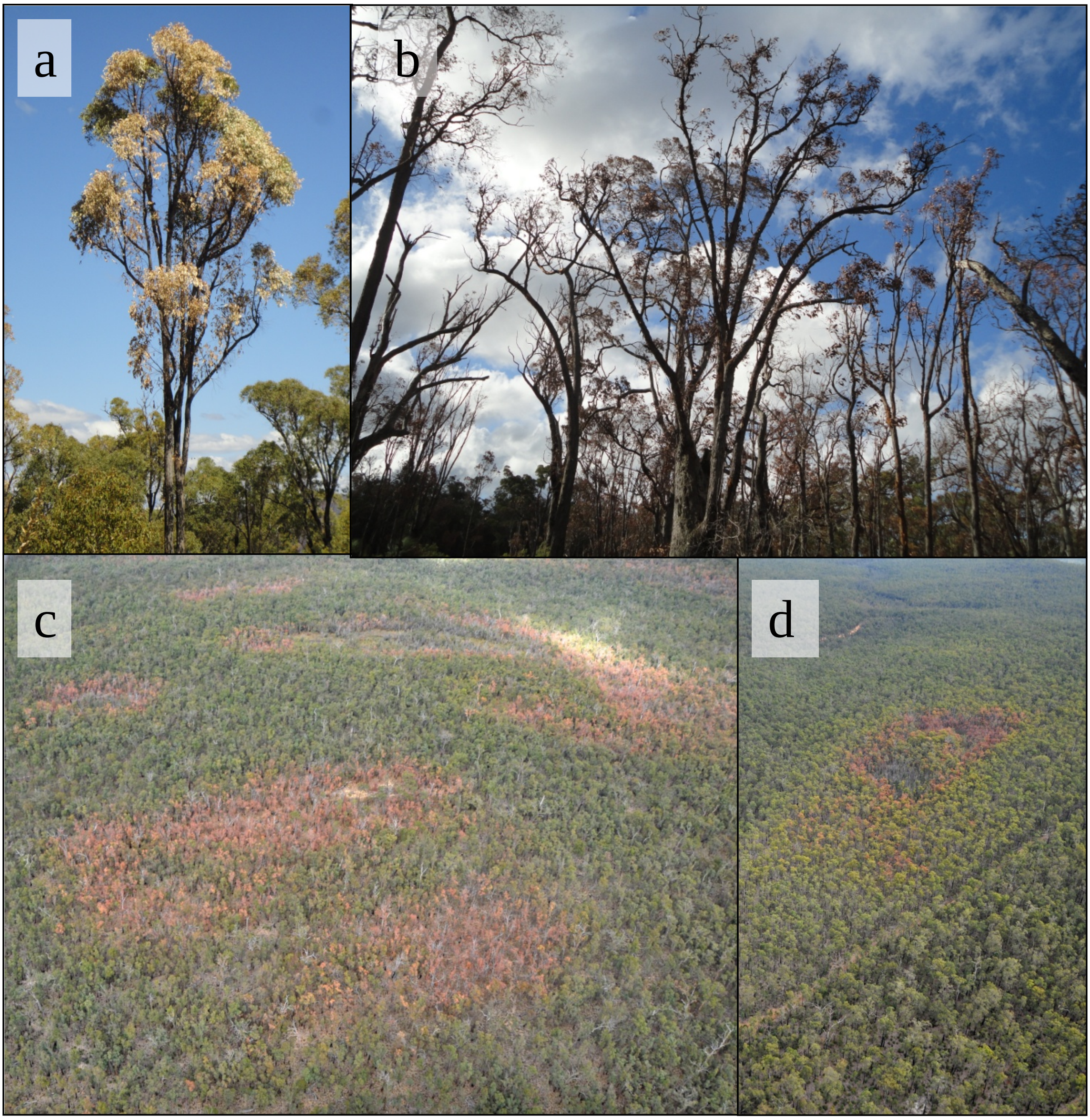

Fig 3 (a) Discoloured and dying *E. marginata* crown (5 March 2011). (b) Trees abscising small branches and foliage (23 June 2011). (c) Forest damage was concentrated in patches scattered across the landscape (25 May 2011). (d) Strongly chlorotic forest canopy radiating from severely affected forest patches (25 May 2011).

Damage incidence and severity

An estimated 92,181 ha of native forest was sampled during the aerial survey, representing 8.2% of the NJF. Observations confirmed canopy collapse occurred in clearlydefined patches (Fig. 3c) scattered across a wide geographical area. A total of 236 affected patches, ranging from 0.3 ha to 85.7 ha, were delineated. The aerially-derived delineations were found to be, on average, 14.4% larger than the field delineations, indicating an overestimation of the area exhibiting canopy collapse using the aerial delineation technique as described. This percentage overestimation was used to correct the estimate of area exhibiting canopy collapse. The collapsed forest patches totalled 1,350 ha and 1.5% of the sample area. Although the sample was weighted toward the central and western NJF, a projection across the NJF suggests that 16,515 ha of native forest experienced canopy collapse. Large areas of strongly chlorotic forest canopy radiated from many collapsed forest patches (Fig. 3d); however this was not quantified.

The majority of tree crowns on affected plots were dying or recently killed (Fig. 4), including 74% (±3%) (mean [±SE]) of all stems that were living prior to the collapse (>1cm DBHOB), as opposed to only 11% (±2%) in paired control plots (Mann Whitney *Z*=8.88, *P*<0.0001). Following re-assessment in late spring (October/November) 2011, stem mortality resulting from the disturbance was found to be 26% (±3%) (mean [±SE]) on affected plots compared to 5% (±1%) on controls (Mann Whitney *Z*=5.77, *P*<0.0001). Forest canopy cover was found to be 20% (±2%) (mean[±SE]) on affected plots compared to 57% (±2%) on controls (Mann Whitney *Z*=-8.52, *P*<0.0001). When considering overstorey eucalypts (*E. marginata* and *C. calophylla*) only, the percentage of long dead stems (Mann Whitney *Z*=3.36, *P*=0.0004) and previous crown dieback (Mann Whitney *Z*=2.86, *P*=0.0021) were greater on affected plots compared to control plots (Fig. 5), suggesting that affected plots had experienced substantial crown dieback and stem mortality prior to 2011.

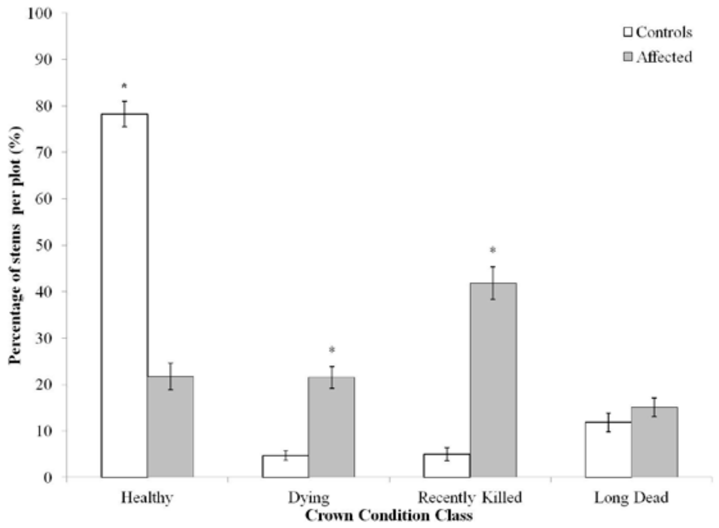

Fig 4 The mean percentage of all stems falling within all four crown health classes on control and affected plots (*n=120*). Columns within each crown health class with asterisks are significantly different at alpha=0.05 from Mann Whitney *U*-tests. Error bars represent the standard error of the mean

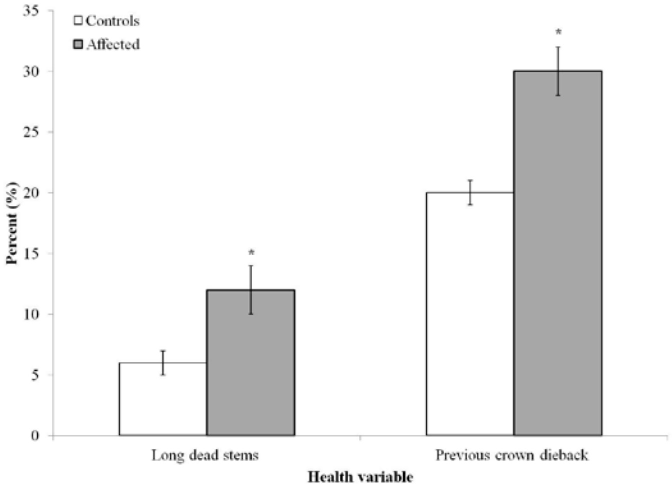

Fig 5 The mean percentage of long dead stems and previous crown dieback using only *E. marginata* and *C. calophylla* stems in control and affected plots (*n=120*). Columns within each health variable with asterisks are statistically different at alpha=0.05 and determined from Mann-Whitney *U*-tests. Error bars represent the standard error of the mean

Crown mortality and stem mortality were observed during the first and second survey, respectively. Crown mortality was defined as 100% foliage death during the initial survey, whereas stem mortality was determined based on the lack of re-sprouting in stems with recently killed crowns during the second survey in spring 2011(October and November). The relative percentage of dying or recently killed crowns observed in the first survey varied between stem diameter classes (Kruskal-Wallis χ^2 =19.56, *P*=0.0033) on affected plots, though high crown mortality (>60 %) was observed in all classes (Fig. 6). This trend suggests that crowns within the middle stem diameter classes (20-60 cm) were more impacted than smaller stems, with variable results for the few trees in the largest diameter class. Stem mortality did not differ among stem diameter classes (Kruskal-Wallis χ^2 =4.00, *P*=0.6763) (Fig. 6). Despite wide variation in re-sprouting between size classes (affected plots only)(i.e. from 33% in the >60cm class to 61% in the 40-50cm class),the relative percentage of stems which re-sprouted was not significantly associated with stem diameter size class (Kruskal-Wallis χ^2 = 12.00, *P*=0.0620)(Fig. 7). On average across all affected plots, 52% (±3.6%) (mean[±SE]) of stems that were initially judged to have dying or recently killed crowns were found to be re-sprouting during the second assessment in November 2011. Mean previous crown dieback on affected plots varied by stem diameter class (ANOVA *F*=2.79, *P*=0.0125) with stems in the largest diameter class having more previous dieback than stems in smaller classes (Fig. 8).

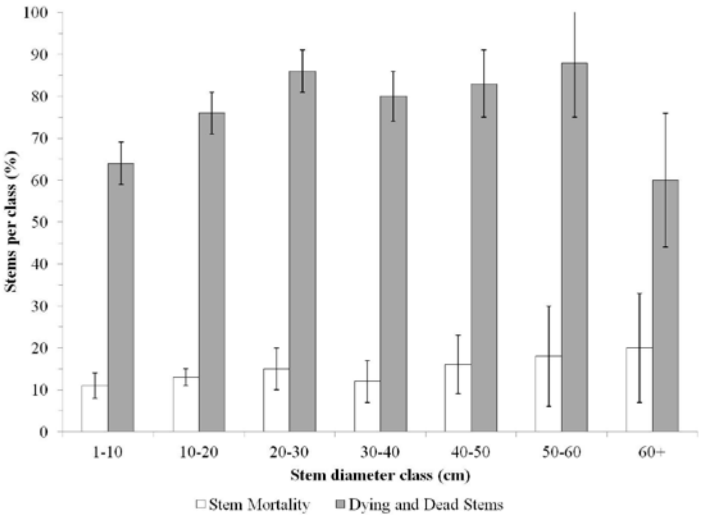

Fig 6 Relative percentage of stems observed within each diameter class with dying and dead stems following disturbance in June/July 2011 was found to be different between classes (Kruskal-Wallis χ^2 = 19.5607, *P*= 0.0033). The relative percentage of stem mortality determined following the second survey was not statistically significant between classes. Error bars represent the standard error of the mean.

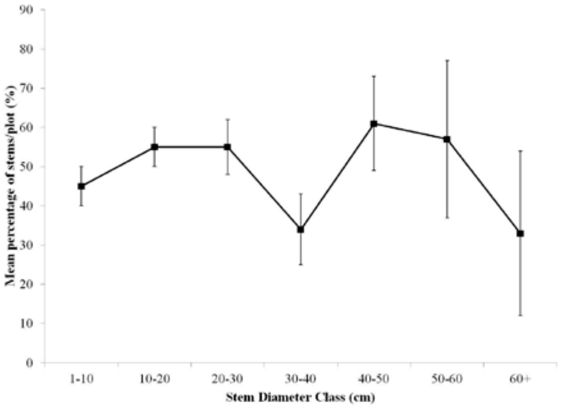

Fig 7 The percentage of dying or recently killed stems found to be re-sprouting within each diameter class following the second survey in November 2011. The relative percentage of stems which re-sprouted is not significantly different among stem diameter class at alpha=0.05 from Kruskel-Wallis test. Error bars represent standard error of the mean.

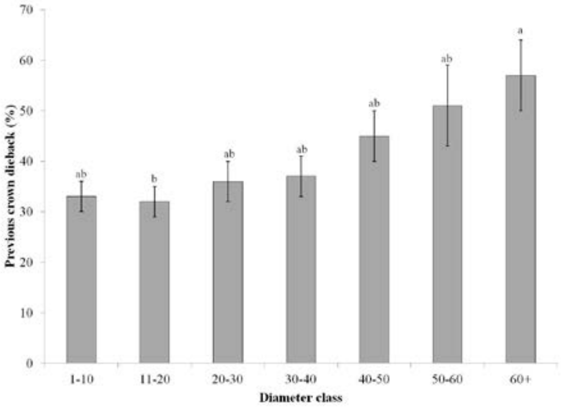

Fig 8 Previous crown dieback (occurring prior to 2011) in all stems within seven diameter classes on affected plots only (*n=60*). Columns with the same letter are not statistically different at alpha=0.05 and represent the results of Tukey's multiple comparison tests. Error bars represent the standard error of the mean.

A greater percentage of *E. marginata* crowns were found to be dying or recently killed compared with *C. calophylla* within affected plots (Mann Whitney *Z* =-2.75, *P*=0.0030)(Fig. 9). Although crowns of *E. marginata* were highly affected, a higher proportion of stems re-sprouted in this species when compared to *C. calophylla* (Mann

Whitney Z=-2.87, P=0.0021). There were no differences between the species in the number of re-sprouts per stem (i.e. an average of 10 for both species), or the percentage of stem that remained alive (*E. marginata* 67% ± 3.8% (mean[±SE]), *C. calophylla* 56% ± 7.0%) (Mann Whitney Z=-0.88, P=0.1882). The percentage of stems with affected crowns was similar for plots where *E. marginata* and *A. fraseriana* co-occurred (Mann Whitney Z=1.38, P=0.0840), though only 11 plots could be used for this comparison since *A. fraseriana* was infrequently measured.

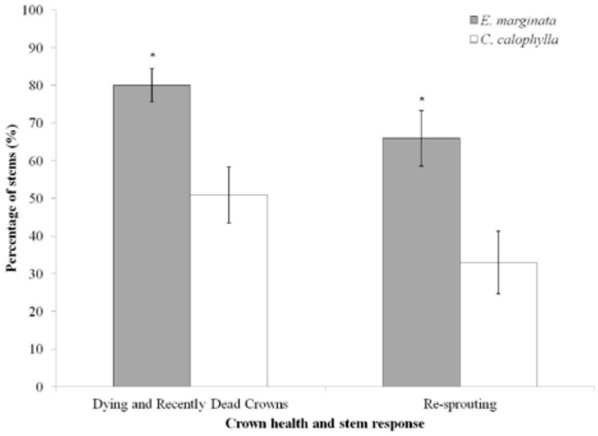

Fig 9 The mean percentage of *E. marginata* and *C. calophylla* stems per plot with dying and recently dead crowns, and percentage of stems per plot found re-sprouting for those plots in which both species co-occurred (*n=29*). Columns within each category with asterisks are different at alpha=0.05, resulting from Mann Whitney *U*-tests. Error bars represent the standard error of the mean.

Forest structure and damage

Eucalyptus marginata dominated the overstorey of both control and affected plots, while *C.calophylla* was the most common co-dominant (Table 1). The largest difference in forest composition between control and affected plots was the presence of *B. grandis* and *Persoonia longifolia* R.Br. in the midstorey, despite paired plots generally being in the same vegetation-type. *Banksia grandis* was found on 25% of control plots with an average stem density of 122 stems ha^{-1}, while it was found on only one affected plot. For those stands where *B. grandis* was present, control plots roughly fell within the dying front, where 64% of crowns were either dying or recently killed, and 32% of crowns were long dead. These results confirm field observations that the dying front for *B. grandis* precedes the dying front for overstorey eucalypts (*E. marginata* and *C. calophylla*).

Table 1 Tree composition and relative composition of tree species on control and affected plots (*n=120*). Relative values represent the percent of each species present within each treatment group (control and affected)

Species	Plot presence (%)	Stem Density (no. ha^{-1})	Relative Density (%)	Basal Area (m^2 ha^{-1})	Relative Basal Area (%)
Control plots					
Eucalyptus marginata	100	719 (63)	66.8 (3.5)	37.3 (3.8)	85.9 (11.9)
Corymbia calophylla	68	189 (28)	20.4 (2.8	8.9 (2.1)	21.6 (3.5)
Allocasuarina fraseriana	13	43 (19)	2.9 (1.5)	2.9 (1.5)	3.9 (1.9)
Banksia grandis	25	122 (41)	7.0 (2.1)	0.4 (0.1)	1.4 (0.7)
Banksia sessillis	2	68 (68)	1.4 (1.4)	0.1 (0.1)	< 0.1
Persoonia longifolia	13	22 (9)	1.6 (0.6)	0.2 (0.1)	0.7 (0.5)
Affected plots					
Eucalyptus marginata	100	1021 (89)	74.2 (3.2)	31.6 (3.5)	83.1 (3.3)
Corymbia calophylla	62	220 (33)	18.4 (2.8)	6.8 (1.9)	19.7 (5.2)
Allocasuarina fraseriana	18	85 (33)	5.4 (1.8)	2.7 (1.6)	4.0 (1.9)
Banksia grandis	2	3 (3)	0.2 (0.2)	< 0.1	< 0.1
Banksia sessillis	2	15 (15)	0.5 (0.5)	< 0.1	< 0.1
Persoonia longifolia	2	1 (1)	0.1 (0.1)	< 0.1	< 0.1

- Means and percentages are followed by the standard error of the mean

Pooled stem diameter distributions for both control and affected plots show a reverse J-shaped stem distribution (Fig. 10) which is characteristic of the NJF population structure (Abbott and Loneragan 1986). Affected plots had greater numbers of stems in the smallest diameter classes and were lacking stems in the largest diameter class, compared with controls. Affected plots were found to have higher stem densities overall than controls which were mainly due to *E. marginata* densities (Table 2). Tree densities on both control and affected plots were similar when considering all species, but were greater on affected plots when considering *E. marginata* alone. Additionally, greater numbers of multiple-stemmed trees were present in affected plots. Multiple-stem coppice regrowth commonly occurs in *E. marginata* following mortality of the main stem, which can result from timber harvest or severe disturbance (Abbott and Loneragan 1986; Peet and McCormick 1971). Most multiple-stemmed trees measured were *E. marginata* (78%) and were not the result of timber harvest, based on the presence of standing dead stags. This suggests that affected areas have experienced significant stem mortality in the past, followed by a period of regrowth. The four tallest trees on each plot were considered dominant overstorey trees, since a subset of measurements recorded an average of four overstorey dominants on each plot. Dominant trees were found to be shorter on affected versus control plots (mixed model F=6.56, P=0.0120), despite having similar mean diameters (mixed model F=1.18, P=0.2804).

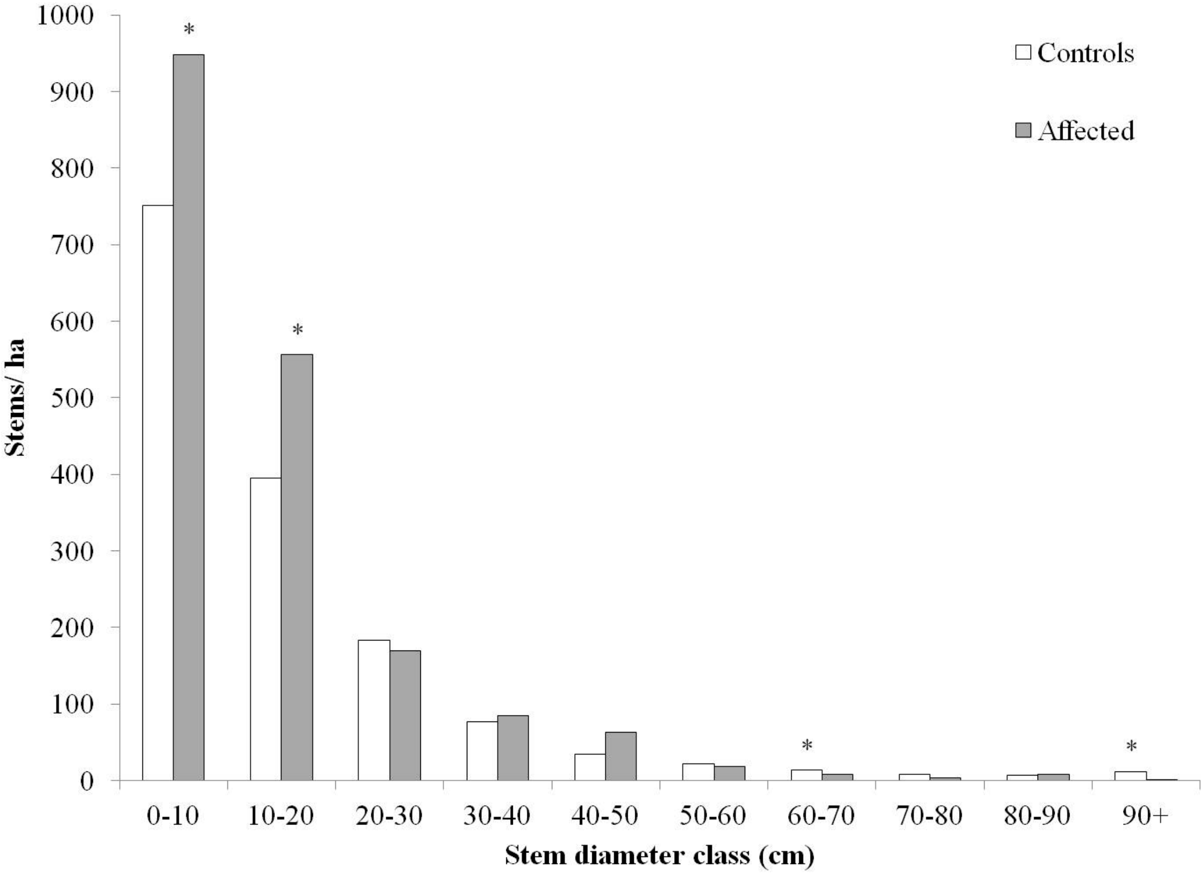

Fig 10 Pooled stem density by diameter class on control and affected plots (*n=120*). Columns within each diameter class with asterisks within each diameter class are statistically different at alpha=0.05 from Mann Whitney *U*-tests comparing control and affected plots.

Table 2 Stem and tree density measures for all *E. marginata*, and *C. calophylla* stems on control and affected plots (*n=120*). *F* and *P*-values represent the results of mixed effects models using site as a random factor (MIXED procedure in SAS)

		Control				Affected					
	Transformation	Mean	S.E.	Min	Max	Mean	S.E.	Min	Max	*F*-value	*P*-value
Stem density (stems ha^{-1})	square-root	1163	97	265	5040	1369	91	265	3537	3.47	0.0656
E. marginata (stems ha^{-1})	square-root	719	63	88	2122	1021	89	177	3537	**9.71**	**0.0024**
C. calophylla (stems ha^{-1})	square-root	189	28	0	973	220	33	0	884	0.08	0.7802
Tree density (trees ha^{-1})	square-root	881	84	265	4509	971	59	265	2653	2.00	0.1602
E. marginata (stems ha^{-1})	square-root	492	39	88	1238	713	61	88	2653	**12.32**	**0.0007**
C. calophylla (stems ha^{-1})	square-root	169	27	0	973	202	31	0	796	0.11	0.7461
Multiple-stemmed trees (trees ha^{-1})	square-root	172	19	0	619	258	29	0	1149	**5.42**	**0.0219**
Basal area (m^{2} ha^{-1})	log	47.5	4.3	6.4	164	38.1	3.7	5.9	164.8	2.28	0.1340
E. marginata (m^{2} ha^{-1})	log	37.3	3.8	0.4	152	31.6	3.5	1.4	149.2	0.04	0.8371
C. calophylla (m^{2} ha-^{1})	log	8.9	2.1	0	82.6	6.8	1.9	0	85.8	2.00	0.1608
Regeneration (stems ha^{-1})	square-root	1443	159	0	5659	1086	136	0	5128	2.91	0.0914
E. marginata (stems ha^{-1})	square-root	706	114	0	5570	685	118	0	5128	0.04	0.8490
C. calophylla (stems ha^{-1})	square-root	445	74	0	2918	296	64	0	2476	**5.14**	**0.0255**

- Bold values indicate significant relationships

Discussion

The canopy collapse reported here strongly contrasts with forest symptoms associated with extended drought conditions in MTFs around the world (Auclair 1992; Carnicer et al. 2011). Partial crown dieback, as well as declines in tree growth and health (Lloret et al. 2004; Ogaya et al. 2003) is commonly reported from MTFs during long-term periods of drought, including the recent period in SWWA (Archibald et al. 2005; Auclair 1992; Hooper 2009). However, evidence of large-scale complete crown dieback and stem mortality from sudden and severe drought conditions have been rare in MTFs (Allen et al. 2010). Trees in MTFs have evolved with frequent and extreme disturbance, including dramatic fluctuations in precipitation and temperature (Roberts et al. 2001), which has resulted in unique adaptations and survival abilities (James 1984). For example, background annual mortality rates in *E. marginata* are low, ranging from 0.02% per year in the humid zone to 2.42% per year in the subhumid (Abbott and Loneragan, 1983). Despite these adaptations, results presented here illustrate how unprecedented climate conditions can translate to sudden and dramatic changes in an MTF, including large-scale stem mortality.

Intraspecific competition is an important regulating mechanism in moisture limited forests, including MTFs (van Noort 1960; Vayreda et al. 2012). The majority of *E. marginata* mortality takes place shortly after seedling establishment (Stoneman et al. 1995). Groups of larger *E. marginata* trees are not known to self-thin. Instead, in the absence of severe disturbance, trees slow their growth and stagnate (Abbott and Loneragan 1986). It is hypothesized that stands can remain in this stagnant condition for centuries before any significant density-dependent mortality occurs (Abbott and Loneragan 1986). The current study shows affected plots were more densely stocked, with higher stem densities in the smallest diameter classes (1-10 cm and 10-20 cm). Recent research has indicated that forest structure can significantly affect forest transpiration rates in the NJF, such that forest areas with higher densities of small stems transpire larger volumes of water than stands of similar basal area comprising older trees (Macfarlane et al. 2010). Therefore, affected plots could have been using more water (through increased transpiration rates) than control plots prior to collapse. Alternatively, the epicormic response observed by many severely impacted trees coupled with higher densities of multi-stemmed trees in affected sites, may suggest higher stem densities are the product of canopy collapse rather than a contributing factor. The discrepancy in forest structure between affected and control plots may be the result of past canopy collapse (Batini 2007). Additional research is required to definitively explain the higher stocking levels on affected sites.

Site-related variables have been shown to act individually or in conjunction with density-dependent competition to influence drought-triggered tree mortality patterns (Guarín and Taylor 2005; Greenwood and Weisberg 2008). This is especially evident in MTFs (Lloret et al. 2004; Peñuelas et al. 2000). Recent evidence suggests site factors influenced the occurrence of canopy collapse in the NJF (Brouwers et al. 2013). Sites at elevated landscape positions, close to rock outcrops, low water-holding capacity soils were more likely to be affected (Brouwers et al. 2013). Factors related to variability in soil moisture, including soil depth and soil water storage capacity are known to predispose areas of forest to collapse in Mediterranean regions (Caspersen and Kobe 2011; Lloret et al. 2004; Peñuelas et al. 2000). In SWWA plantations of *Pinus pinaster* Aiton (McGrath et al. 1991) and *Eucalyptus globulus* Labill. (Harper et al. 2009) are predisposed to crown dieback and stem mortality by shallow soil depths during periods of extreme drought. *Eucalyptus marginata* is known to maintain relatively high transpiration rates during summer (December-February) (Colquhoun et al. 1984), which has been attributed to its deep root system and access to stored groundwater (Dell et al. 1983; Farrington et al. 1995). Trees on shallow soils however, have limited connection to groundwater during extended periods of drought (Dimmock et al. 1974; Reprecht and Schofield 1990). At a regional scale, the interaction between drought, soil water deficits, and shallow soils are thought to limit the distribution of *E. marginata* (Abbott and Loneragan 1986). The recent findings suggest that site and stand factors contribute independently and/or interact in predisposing drought and heat triggered canopy collapse in the NJF. A clearer understanding of these factors is required to better predict where future collapse events may occur.

Co-occurring tree species can respond differently to sudden and severe drought-triggered disturbances (Batista and Platt 2003). Peñuelas et al. (2001) found significant differential responses among co-occurring species following severe drought conditions in a MTF in Spain. Damage and recovery varied among functional types and genera with differing evolutionary histories, suggesting a strong genetic component (Peñuelas et al. 2001). Similarly, different degrees of damage and recovery were observed among tree species following the extreme conditions reported in this study. *Eucalyptus marginata* and the co-dominant *C. calophylla* appear to use different strategies for coping with extreme drought conditions. A higher percentage of *E. marginata* crowns experienced complete dieback, while retaining a relatively high capacity to re-sprout following the disturbance. In contrast, *C. calophylla* was more likely to maintain its crown, collapsing on only the most severely affected sites. However, affected *C. calophylla* were much less likely to re-sprout compared to *E. marginata*. These observations support recent experimental findings which illustrate contrasting physiological strategies during drought conditions, particularly on sites with low water holding capacity (Szota et al. 2011). *Corymbia calophylla* can likely tolerate drought conditions for longer periods, partially due to greater osmotic adjustment and to earlier stomatal closure (Szota et al. 2011). Despite this, physiological limitations of both *E. marginata* and *C. calophylla* make them highly vulnerable to drought-induced cavitation compared to other Mediterranean woody species in SWWA (Poot and Veneklaas 2012). The midstorey species *B. grandis* was likely the most susceptible tree to this drought-induced collapse event, based on our observations that its mortality precedes overstorey tree deaths. *Banksia grandis* and both co-occurring overstorey eucalypts exhibit dimorphic root morphologies (Abbott et al. 1989; Dawson and Pate 1996), extending sinker and tap roots through channels in the lateritic mantle deep into the soil profile (Dell et al. 1983), which is thought to sustain them over summer (December-February) drought periods (Crombie 1992). More research on the physiological, anatomical, and behavioural characteristics of *B. grandis* is needed to explain its relatively poor competitive ability on these upland NJF sites. Collectively, these results illustrate a differential response of co-occurring tree species to this disturbance with *C. calophylla* being the most resistant to complete crown dieback, *E. marginata* being less resistant, and *B. grandis* being the least resistant species.

The role of contributing stress agents in drought and heat-induced forest canopy collapses is poorly understood. In many forest ecosystems insect and disease pests are commonly associated with forest collapse events (Shaw et al. 2005; Worrall et al. 2008). These pests may either interact closely with climate to tip trees and forests past their thresholds (Negrón et al. 2009), or purely function as secondary factors (Worrall et al. 2008). Although the extreme climate conditions experienced in 2010-2011 are likely the driver of many of the observations made in the NJF, other biotic factors may be acting as predisposing, inciting, or contributing agents. For instance, the role of woodboring Coleoptera (family Cerambycidae), which have been observed in high numbers on some affected plots (Matusick, pers. observations), are poorly understood. Although *Phytophthora* dieback disease (caused by *P. cinnamomi* Rands) is associated with warm wet conditions in the NJF (Dell and Malajczuk 1989), its role in the observed disturbance is not completely understood. Preliminary sampling data suggests *Phytophthora* species are present and active on a small percentage of affected sites (Matusick et al. unpublished data). Future research should explore the potential role of root infection by *Phytophthora* species in predisposing or inciting drought and heat-triggered canopy collapse. Understanding the biology and ecology of these pests along with other potential contributing factors, will assist in determining their ultimate impact on the NJF, and other MTFs with continued climate change.

The long-term consequences of large-scale drought-induced mortality events are poorly understood in the NJF and other MTFs. Widespread crown mortality on affected sites has resulted in dramatic changes to site-level microhabitat characteristics including increased solar radiation, ground level temperatures and wind speed (Breshears et al. unpublished data). These changes are likely to have an impact on the remaining live trees, regeneration rates, understorey plant species, and fauna communities. Fire is an important disturbance agent in the NJF and other MTFs around the world (Burrows et al. 1995; Turner et al. 2008). The impact of this collapse on the quantity and distribution of fuels was considerable, with higher volumes of dead wood and debris on affected sites compared to the surrounding forest. The implications for how this higher fuel loading will influence fire frequency and intensity are likely to be significant. These effects should be explored further.

The forest damage reported here, resulting from an unprecedented disturbance event, could prove to represent a pivotal point in time for the Northern Jarrah Forest ecosystem. Many large trees that have survived on these sites for centuries were killed in 2011. Like other Mediterranean-type forests, the Northern Jarrah Forest is experiencing a long-term drying trend with pronounced extreme climate conditions (Bates et al. 2008). These trends are expected to continue and intensify in the coming decades (Suppiah et al. 2007). These forest ecosystems, once thought to be resilient to extreme fluctuations, may be reaching critical tipping points (Laurence et al. 2011). The recent disturbance impacts on Northern Jarrah Forest reported here exemplify how Mediterranean-type forests may transform through drought-driven processes in the coming decades with anticipated climate change.

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