The interaction between a drying climate and land use affects forest structure and above-ground carbon storage

6 authors, including:

Joanne M Bennett
Australian National University
59 PUBLICATIONS   1,922 CITATIONS

Shaun C. Cunningham
Deakin University
58 PUBLICATIONS   2,828 CITATIONS

Christine Connelly
Deakin University
4 PUBLICATIONS   109 CITATIONS

Rohan H Clarke
Monash University (Australia)
182 PUBLICATIONS   2,595 CITATIONS

RESEARCH PAPER

The interaction between a drying climate and land use affects forest structure and above-ground carbon storage

Joanne M. Bennett*, Shaun C. Cunningham, Christine A. Connelly, Rohan H. Clarke, James R. Thomson and Ralph Mac Nally

Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

ABSTRACT

Aim Climate change has been linked to negative effects on vegetation, including drought-induced dieback. Large-scale dieback not only leads to considerable carbon emissions but often leads to loss of ecological resources. We investigated whether, and how, the structure, composition and carbon content changed over a period of extended drought (the 'Big Dry') in a much-modified forest ecosystem. We explored whether landscape configuration, management practice or soil type influenced vegetation change.

Location The Box-Ironbark forests of south-eastern Australia.

Methods In 2010, we remeasured 120 forest transects that had first been measured in 1997 by using identical field methods. Vegetation structure and composition were quantified. We used allometric growth models to estimate the expected increase in above-ground carbon (AGC) storage between 1997 and 2010; these estimates were compared with observed values.

Results Forest structure was systematically different between the two periods. Canopy cover, shrub cover and litter decreased between the 1997 and 2010 surveys, whereas total basal area of dead trees, dead trees in all size classes and saplings increased between the two surveys. Climate, fragment size and their interaction were the major predictors of change in most of the measured vegetation characteristics. By comparing measured AGC in 2010 and estimates from growth models, we estimated that 5.6 ± 2.1 SE t C ha^{-1} may have been foregone over the Big Dry.

Main conclusions Our findings add to the evidence linking climate change to negative effects on vegetation, including mortality, canopy dieback and reduced carbon sequestration. These effects may be amplified in fragmented vegetation because of greater water and heat stress. If the carbon sequestration deficit of *c.* 5.6 t C ha^{-1} were to apply across the extant Box-Ironbark forests of Victoria (*c.* 255,400 ha), then 1.43 Mt of carbon sequestration may not have occurred during the Big Dry.

Keywords

Carbon sequestration, climate change, dieback, forest futures, vegetation change, vegetation fragmentation.

*Correspondence: Joanne Margaret Bennett, Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Clayton, Vic. 3800, Australia.
E-mail: joanne.bennett@monash.edu

INTRODUCTION

Human-induced increases in atmospheric CO_2 have been linked to rising global temperatures, changes in the spatial patterns of precipitation and increases in the frequency and severity of extreme weather events (IPCC, 2007). There is growing evidence linking climate change to adverse effects on vegetation, including dieback (Allen *et al.*, 2010) and impaired regeneration

(Suarez & Kitzberger, 2010). The effects may lead to considerable shifts in the distribution of vegetation, which may induce large-scale changes in land use as natural systems respond and agriculture and other human activities are reorganized (Capon et al., 2013).

Vegetation dieback and reduced tree growth may produce a net release of stored carbon (Schaphoff et al., 2006). The role of emissions from terrestrial ecosystems in the carbon (C) cycle is not fully understood (Schaphoff et al., 2006). There has been increasing focus on forest-based carbon storage and its relationship to biodiversity values. Forests accumulate and store carbon in soils, living biomass and fallen wood. Protecting existing and restoring structurally complex forests could result in the storage of carbon and promote biodiversity (Hatanaka et al., 2011).

Dieback events caused by increases in the frequency of extreme droughts may produce large-scale changes in vegetation distribution that may be more severe than effects of gradual shifts from mean climate conditions (Hoffmann et al., 2011). Forest dieback under recent severe droughts or high temperatures have been recorded in Europe (Bréda et al., 2006), North America (van Mantgem et al., 2009) and Australia (Brouwers et al., 2013), highlighting the possibility that recent climate change may already be causing changes in forest structure (Allen et al., 2010).

Since 1960, south-eastern Australia has experienced substantial warming, with a 1 °C increase in mean maximum temperature, which is consistent with global circulation models (Timbal et al., 2010). From 1997, the region experienced a 13-year severe drought, 'The Big Dry' (Verdon-Kidd & Kiem, 2009), during which rainfall deficits were the highest recorded (Gergis et al., 2011). There has been widespread clearance of forests in the south-east since European settlement in Australia, with the extent of woody vegetation halved (McAlpine et al., 2009). The effects of the Big Dry may have been exacerbated by loss of extensive tree cover, which decreases evapotranspiration and modifies atmospheric and soil moisture cycles, with flow-on effects to regional climate (McAlpine et al., 2009). These processes potentially lead to further forest degradation, producing a negative climate-feedback mechanism (McAlpine et al., 2009).

Land use change resulting in the loss, fragmentation and degradation of habitat has been the most significant driver of recent biodiversity decline (Swift & Hannon, 2010). Habitat loss and fragmentation directly reduce local population sizes and increase spatial isolation, often increasing the probability of extirpation (Cushman et al., 2012). In addition, fragmentation alters conditions, reducing health and seedling recruitment in many plants (Barbeta et al., 2011). Fragmented vegetation may be more exposed to climate change due to regional shifts in the distribution of precipitation, local drying and increased fire frequency and severity (Brook et al., 2008). Climate change may overtake land use change as the most important negative influence on biodiversity (Mantyka-Pringle et al., 2012). There has been growing speculation on how climate change will affect biological populations and how it will interact with other major stressors (Mantyka-Pringle et al., 2012). In the Amazonian rainforests, positive feedbacks among fire, drought, forest fragmen-

tation and climate change may already have led to irreversible changes in vegetation (Nepstad et al., 2008).

The Box-Ironbark forests of south-eastern Australia are a prime example of a fragmented and much-modified ecosystem in which the effects of fragmentation and climate change may be synergistic (Mac Nally et al., 2009b). These forests generally are open woodland in character and were once widely distributed in areas now mostly used for agriculture, and there are many reports of deleterious effects on the biota of the region.

As part of the work on understanding the biotic effects of land use change in this region, detailed information on vegetation structure was collected in the late 1990s, in the early stages of the Big Dry (Mac Nally et al., 2000). The availability of these data allowed us to explore how land use (especially forest fragmentation) and climate change might interact in influencing vegetation structure.

We assessed differences in vegetation structure after the Big Dry by revisiting exactly the same sites and repeating the vegetation measures using identical field methods. Direct comparisons in such a before–after setting, spanning extended periods of time, are scarce in the literature (Horner et al., 2009), so these provide a rare opportunity to assess temporal changes in vegetation and the factors that influence those changes.

We expected that the Big Dry, whose occurrence is consistent with climate-change models that predict drought events of increasing duration and intensity into the 21st century, would cause widespread forest degradation. Resultant canopy dieback and tree mortality were predicted to be highest in areas with larger reductions in precipitation or larger increases in temperature (Allen et al., 2010). These effects may be exacerbated in smaller remnants because of increased micro- or meso-climatic stresses, such as greater exposure to windthrow and relatively higher evapotranspiration (Mantyka-Pringle et al., 2012). We asked three main questions. First, did the structure, composition and carbon content of the Box-Ironbark forests differ between 1997 and 2010? Second, which, if any, vegetation characteristics changed across the region over the duration of the Big Dry? Third, if there were major vegetation changes, did these differ in relation to landscape configuration, management practice or soil type?

METHODS

The Box-Ironbark forests of south-eastern Australia occur on the inland slopes of the Great Dividing Range, from southern Queensland to western Victoria (ECC, 2001). In the 200 years since European settlement, the Box-Ironbark forests of central and northern Victoria have been reduced by 83% of their once > 3 M ha (ECC, 2001). The ecosystem has been much disturbed by human activities, including gold mining, timber felling and clearing for agriculture since European settlement, and few large (6000–40,000 ha) remnants remain (ECC, 2001). There are many remnants scattered in the agricultural landscape. Only 2% of the existing forest is thought to be 'old growth', with characteristics such as large, hollow-bearing trees. Remaining native vegetation is predominantly regrowth from wholesale clearance

during in the 1850s gold rush, and ongoing management for timber production has maintained the forests in a non-mature state; these woodlands are characterized by small stems that occur at high densities (ECC, 2001).

Mean annual rainfall historically ranged from 400 to 700 mm, falling mostly in winter and spring (Mac Nally *et al.*, 2000). Mean annual rainfall decreased from 537 ± 111 SD mm yr^{-1} for 1984–96 to 430 ± 87 SD mm yr^{-1} for 1997–2009. The declines in rainfall were disproportionately large in autumn and early winter (Verdon-Kidd & Kiem, 2009). Temperature anomalies are based on a historical baseline (1961–90), with a daily mean of 14.7 °C, a daily mean maximum of 20.6 °C and a daily mean minimum of 8.8 °C. Temperature anomalies over this period were +0.7 °C for daily mean, +0.7 °C for mean daily maximum, +0.4 °C for mean daily minimum. Between 1997 and 2010, mean temperature increased by 0.65 °C. Among sites between 1997 and 2010, cumulative temperature anomaly ranged from +0.33 °C to +0.92 °C and cumulative rainfall anomaly from −754 mm to −2023 mm. Across the domain, there was little evidence of a gradient in climate data (either from east to west or from north to south).

The spatial configuration of Box-Ironbark forests allows one to differentiate between the effects of fragmentation and habitat loss per se (Parker & Mac Nally, 2002). 'Actual' remnants of *c.* 10, 20, 40 and 80 ha in area were compared with replicate 'pseudoremnants' of notionally the same areas. Remnants have a relatively long history of isolation (> 50 years) and are distributed around four regional centres in north-central Victoria: St Arnaud, Dunolly, Bendigo and Rushworth (Mac Nally *et al.*, 2000). Pseudoremnants were positioned within three extensive (> 10,000 ha) forest blocks in the vicinity of St Arnaud, Dunolly and Rushworth. There were 31 actual remnants (17 of 10 ha, eight of 20 ha, three of 40 ha and three of 80 ha) and 30 pseudoremnants (12 of 10 ha, six of 20 ha, six of 40 ha and six of 80 ha), which were each referred to as 'sites' (hence 61 sites containing 120 transects). To ensure representative areal coverage, survey transects were replicated within each site: (1) one transect in each 10 ha site; (2) two in each 20 ha site; (3) three in each 40 ha site; and (4) four in each 80 ha site (Mac Nally *et al.*, 2000). Sixty-one of the 68 sites established in 1997 (Mac Nally *et al.*, 2000) were included in the 2010 survey; of the remainder, two 40-ha remnants and one 80-ha remnant had been largely cleared and access was no longer granted by owners at the other remnants.

Vegetation characteristics

Twenty-one vegetation variables (Table 1) were measured using exactly the same methods as were used in 1997 (Mac Nally *et al.*, 2000). To minimize potential observer differences between surveys, measurement techniques were calibrated in situ with G. F. B. Horrocks, who conducted the 1997 surveys. The species, diameter at breast height (DBH) and number of all trees and shrubs were recorded within an 80 × 100 m transect, as were the number of hollow-bearing trees and stumps. Trees were assigned to four size classes: 10–39 cm DBH (small), 40–59 cm

DBH (medium), 60–79 cm DBH (large) and ≥ 80 cm DBH (very large); the diameters of the latter were measured, whereas the others were allocated by inspection. Trees with < 10 cm DBH were classified as saplings and were excluded from basal area estimates, as in the original study. An exception was the green mallee *Eucalyptus viridis*, which was included in basal area estimates because it has a multi-stemmed growth form and was considered mature regardless of stem diameter. Cover estimates were from randomly placed quadrats: two 5 × 5 m quadrats for groundcover, two 25 × 25 m quadrats for shrub cover and one 10 × 50 m quadrats for fallen timber. Canopy cover was estimated at four random locations in each transect by holding a transparent grid of 30 × 20 cm, partitioned into 2 × 5 cells parallel to the ground to estimate the percentage of cells overlain by canopy.

Estimation of carbon storage

Carbon makes up *c.* 50% of a tree dry mass, and carbon stocks can be estimated from DBH (Grierson *et al.*, 1992). Live and dead carbon biomass at a site (t C ha^{-1}) were estimated using the allometric equation for grey box (*E. microcarpa*), a dominant Box-Ironbark species within the study region (Hamilton *et al.*, 2005). The study sites within the Box-Ironbark of Victoria have a relatively uniform species composition, which is dominated by three species: *E. microcarpa*, *E. tricarpa* and *E. leucoxylon*. All tree species in this region grow to a height of *c.* 25 m. The allometric equation for *E. microcarpa* was used for all species because this was the only published relationship based on trees growing in native forests within the study region and not on plantation trees in more productive regions elsewhere. This is important because climate, soils and management are major determinants of tree growth. The equation used measurements of stem cross-section as a function of volume and wood density to estimate biomass. Biomass of standing dead trees was calculated using the same allometric equations but by excluding leaves. Fallen dead timber and stump biomass was calculated using an equation developed for the river red gum (*E. camaldulensis*), which occurs within the region; the equation converted volumetric measurements into mass (Robinson, 1997), from which C content can be calculated. The Box-Ironbark forest experienced wholesale clearance 150 years ago, followed by continued selective logging of large trees up until the last decade. This repeated removal has stopped the recruitment of large trees, so that the forest cannot be considered mature. A mature tree would be at least 2 m in diameter, yet only two live trees were recorded across the 120 study transects that approached maturity (*c.* 190 cm in diameter), and no standing dead trees of this size were recorded. The majority of trees were much smaller. As such, 'background' mortality, due to senescence, was expected to be negligible and was excluded from estimates for biomass projections. Shrub biomass was calculated to be negligible < 0.007 t C ha^{-1} and was excluded.

The Victorian State Department of Sustainability and Environment (DSE) forestry timber resource assessment involved measurements of incremental growth within mixed-species

Table 1 Vegetation characteristics used to compare differences among transects between the two survey periods and between 'actual' remnants and pseudoremnants.

Abbreviation	Description
Floristic variables	
Shrub richness	Number of shrub species
Tree size class distribution	Distribution of trees by size class for each species (ha^{-1}) (DBH: 10–39 cm (small), 40–59 cm (medium), 60–79 cm (large), $\geq$ 80 cm (very large), and 10–$\geq$ 80 cm (total). Grey box *Eucalyptus microcarpa*, red box *E. polyanthemos*, yellow box *E. melliodora*, white box *E. albens*, river red gum *E. camaldulensis*, yellow gum *E. leucoxylon*, red ironbark *E. tricarpa*, long-leaved box *E. goniocalyx*, red stringybark *E. macrorhyncha*, green mallee *E. viridis*, buloke *Allocasuarina luehmannii*, drooping sheoak *A. verticillata*, cherry ballart *Exocarpos cupressiformis*
Golden wattle density	Density of golden wattle *Acacia pycnantha* shrubs (ha^{-1})
Structural variables	
Dead trees	Total basal area of dead trees (summed over size-classes): m^2 ha^{-1}.
Live trees	Basal areas of tree species per size-class (DBH: 10–39 cm (small), 40–59 cm (medium), 60–79 cm (large), $\geq$ 80 cm (very large), and 10 to > 80 cm (total) (m^2 ha^{-1}; trees exceeding 10 cm DBH)
Live sapling density	Number of live *Eucalyptus* saplings (ha^{-1})
Dead sapling density	Number of dead *Eucalyptus* saplings (ha^{-1})
Hollows	Number of trees with hollows (ha^{-1})
Coppices	Density of coppices (ha^{-1})
Stumps	Density of stumps (ha^{-1})
All shrubs density	Density of all shrubs (ha^{-1})
Density of logs	Density of logs (ha^{-1})
Volume of logs	Fallen timber volume (fallen timber > 10 cm diameter) (m^3 ha^{-1})
Canopy cover	Canopy cover (%)
'Tall' shrub cover	Shrubs > 2 m high (%)
'Low' shrub cover	Shrubs $\leq$ 2 m high (%)
Rock cover	Rock coverage (area of rocks > 100 cm^2) (%)
Bare ground cover	Bare ground (%)
Coarse-litter cover	Cover of coarse litter (%)
Fine-litter cover	Cover of fine litter (%)
Live carbon	Total live tree carbon biomass summed across all species (t C ha^{-1})
Dead carbon	Total dead tree carbon biomass (t C ha^{-1})

stands for several species of *Eucalyptus* in open forest and woodlands within the Box-Ironbark region. We used an incremental growth rate of 0.38 cm yr^{-1}, which was calculated over a period in which rainfall was considered to be average (DSE, 1998). This figure was used to project growth from the 1997 DBH measurements to estimate potential carbon sequestration in 2010 in the absence of the Big Dry (i.e. with average growth rates). Projected carbon growth was then compared with actual live carbon in 2010 to estimate differences between expected and observed carbon storage at sites between 1997 and 2010.

STATISTICAL ANALYSES

Vegetation change

Non-metric multidimensional scaling (NMDS) was used to ordinate the vegetation data. The NMDS was based on Bray–Curtis dissimilarities to quantify differences in vegetation characteristics among transects between the two survey periods (Table 1). Vegetation data were range standardized (subtract minimum and divide by range), and dissimilarities were calculated using the *vegdist* function in the *vegan* package of R

(Oksanen *et al.*, 2010). We used the *smacofSym* function in the *smacof* package of R to fit the NMDS ordination (de Leeuw & Mair, 2009). The statistical significance of changes in vegetation characteristics between 1997 and 2010 was analysed using the *Adonis* function of the *vegan* package. The NMDS ordination was fitted with correlation vectors for each variable using the *envfit* function of the *vegan* package to determine if any vegetation characteristics were correlated strongly with the overall vegetation change (Oksanen *et al.*, 2010).

Environmental predictors

Individual vegetation characteristics that were strongly correlated with the overall change in vegetation structure were related to potential environmental predictors. Climate characteristics, soil and management predictors were derived using a Geographic Information System (GIS) (ESRI, 2010) for each site in 1997 and 2010. Climate predictors were extracted from spatial data modelled for 500 m^2 grids from the Bureau of Meteorology Data Library (BoM, 2012). Rainfall and temperature data were obtained from mean rainfall and temperature data from the 6 years prior to the surveys (1991–96 and 2003–09). Soil data were

derived from airborne gamma ray spectrometry (Pracilio *et al.*, 2006). Gamma radiation emitted from potassium (K), uranium (U) and thorium (Th) radioisotopes in the top 30 cm of the soil are related to source elements, which are correlated with soil surface properties, such as clay content and potassium (Pracilio *et al.*, 2006). We used gamma U:Th (γU:Th) as an indicator of clay content, which affects water-holding capacity of soil and gamma K (γK) as a indicator of plant available potassium, which is important for plant growth and drought and heat tolerance of plants (Pracilio *et al.*, 2006). Predictors including tenure (public or private), years since logging and years since fire were collated from the DSE Corporate Spatial Data Library (DSE, 2010).

We used hierarchical Bayesian models to identify environmental factors (e.g. climate, soil type, years since fire and logging) that were predictors of individual vegetation characteristics. For each vegetation variable that showed temporal trends in the NMDS ordination (i.e. *envfit* vectors were correlated strongly with time vector), we fitted:

$$y_{ij} = (\alpha_{1997} + \delta I_{2010}) + X_{ij}(\beta_{1997,j} + \lambda_j I_{2010}) + \varepsilon_{\text{site}} + \varepsilon_{\text{transect}}.$$

The model related the measured values of the response y on transect i in year j to environmental variables X. The term $(\alpha_{1997} + \delta I_{2010})$ is the intercept for variable y and consists of a value for 1997 and a deviation from that value for 2010. The term $X_{ij}(\beta_{1997,j} + \lambda_j I_{2010})$ relates the variable y to the environmental variables X, allowing for time-dependent functional relationships between y and each environmental variable. There is a matrix of linear coefficients for 1997 plus an interaction matrix for the change to 2010. $\varepsilon_{\text{site}}$ is a site-based random effect, and $\varepsilon_{\text{transect}}$ is a transect-based random effect (nested within site). All random effect parameters were assigned 'exchangeable' (Gelman *et al.*, 1995) normal prior distributions [$\varepsilon_{\text{site}} \sim N(0, \sigma_{\text{site}}^2)$; $\varepsilon_{\text{transect}} \sim N(0, \sigma_{\text{transect}}^2)$]. Intercept parameters (α and δ) were assigned independent, uninformative normal prior distributions [$N(0,1000)$]. Slope parameters (β and λ) were assigned uninformative, exchangeable prior distributions:

$$\beta, \lambda \sim N(0, \tau_{\beta,\lambda}); \tau_{\beta,\lambda} \sim Uniform(0, \tau_{\beta,\lambda;\text{max}}); \tau_{\beta,\lambda;\text{max}} = SD_y/1.96.$$

where SD_y is the standard deviation of the variable y.

We used Bayesian model averaging with reversible-jump Markov chain Monte Carlo (MCMC) to estimate all model parameters and to calculate the posterior probability that each environmental variable was a predictor of the response variable (Lunn *et al.*, 2009). We fitted the model twice for each response variable: once with only linear effects and once allowing for nonlinear effects, implemented by replacing the matrix of predictor variables X with a basis matrix for linear splines (Lunn *et al.*, 2009). We calculated posterior probabilities that each predictor variable had linear and nonlinear associations with each response variable. All models were fitted in WinBUGS 1.4 developed by the MRC Biostatistics Unit, Cambridge, UK (Spiegelhalter *et al.*, 2003) with three MCMC chains of 100,000 iterations after 20,000 iteration burns-in. Examination of
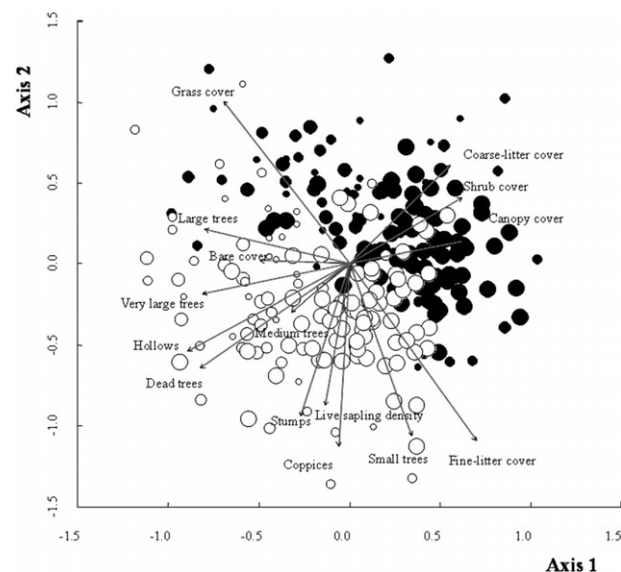
Figure 1 Non-metric multidimensional scaling (NMDS) ordination (stress = 0.07) of vegetation characteristics for 1997 (black) and 2010 (white), based on a Bray-Curtis dissimilarity matrix. Point size indicates the fragment size class of transects. Fitted vectors show correlations between NMDS axial scores and individual vegetation characteristics ($P < 0.001$). The length of a vector is proportional to strength of the correlation, and the direction indicates the direction of the correlation.

MCMC chain histories and Gelman-Ruben-Brooks statistics (Brooks & Gelman, 1998) confirmed adequate MCMC mixing and convergence.

RESULTS

Overall change in vegetation

There was a distinct clustering of sites from the 1997 and 2010 surveys in the NMDS ordination (Fig. 1). There was a significant difference in vegetation characteristics between the 1997 and 2010 surveys (Adonis $P \sim 0.002$) and among the fragment size classes (Adonis $P \sim 0.001$), but there was no important interaction between survey and fragment size (Adonis $P \sim 0.915$).

Change in individual vegetation characteristics

Several vegetation characteristics were correlated strongly with the overall shift in vegetation structure and composition between the 1997 and 2010 surveys (Fig. 1). These characteristics changed systematically across the region: canopy cover, low shrub cover, high shrub cover, coarse litter load and litter depth all decreased between the 1997 and 2010 surveys (Fig. 1). Bare ground, total basal area of dead trees, basal area of dead trees in all size classes, basal area of live trees in all size classes, number of stumps, and number of live and dead saplings increased

Table 2 Comparison of the changes in individual vegetation characteristics with spatial environmental predictors derived from Bayesian model comparison of all possible additive models using reversible jump Markov chain Monte Carlo (MCMC). Maximum linear and nonlinear posterior probabilities of inclusion (Pr) with Pr > 0.75 supporting a positive coefficient (in bold) and regression coefficients (β) are shown (full table in supplementary material Appendix S1)

	Fragment Size		Rainfall		Mean temperature		Logging		γU:Th		γk		Private	
	β	Pr	β	Pr	β	Pr	β	Pr	β	Pr	β	Pr	β	Pr
Decreased overall														
Canopy cover	**−2.59**	**0.87**	0.26	0.46	−0.06	0.40	−0.04	0.39	−0.03	0.32	−0.83	0.54	−1.37	0.60
Litter depth	**−0.15**	**0.79**	0.05	0.51	0.02	0.43	0.02	0.46	0.01	0.35	0.01	0.34	−0.09	0.58
High shrub cover	**−0.89**	**0.87**	0.19	0.47	−0.02	0.39	0.03	0.42	−0.01	0.30	−0.04	0.32	−0.01	0.46
Coarse litter	**3.25**	**0.99**	−0.31	0.47	−1.01	0.65	0.14	0.41	−0.06	0.30	−0.90	0.64	0.04	0.40
Increased overall														
Small trees	0.25	0.51	**2.06**	**0.96**	0.03	0.32	−0.52	0.72	0.00	0.21	0.02	0.26	−0.04	0.40
Medium trees	−0.04	0.53	0.06	0.49	0.00	0.38	0.05	0.42	**0.44**	**0.98**	−0.05	0.37	0.06	0.46
Large trees	−0.02	0.60	0.03	0.49	0.00	0.38	0.01	0.41	**0.12**	**0.92**	−0.01	0.35	0.02	0.48
Very large trees	**−0.18**	**0.99**	0.02	0.45	0.02	0.41	0.03	0.44	0.01	0.31	0.00	0.30	0.00	0.45
Coppice	**16.89**	**0.99**	**28.47**	**0.94**	−1.13	0.36	−1.31	0.34	0.41	0.25	0.64	0.29	−1.15	0.39
Hollow	**−2.56**	**0.96**	**9.34**	**0.98**	**4.00**	**0.90**	0.48	0.37	−1.11	0.58	**−2.38**	**0.85**	**4.13**	**0.84**
Dead basal	**−4.43**	**0.85**	13.01	0.60	10.15	0.59	7.58	0.57	4.26	0.45	−11.88	0.71	−4.72	0.51
Dead saplings	1.26	0.51	**10.68**	**0.91**	1.12	0.45	**−5.29**	**0.82**	−0.14	0.33	1.90	0.51	0.06	0.43
Stump	**2.58**	**0.75**	1.90	0.58	0.51	0.41	−0.90	0.50	**3.11**	**0.86**	−0.13	0.38	0.46	0.47
Dead C	0.10	0.51	1.22	0.73	0.63	0.63	0.07	0.35	**0.69**	**0.76**	−0.44	0.61	−0.14	0.43
Live C	0.62	0.39	**23.69**	**1.00**	1.52	0.45	−0.31	0.40	0.24	0.22	0.13	0.19	−0.47	0.34

γK, gamma K; γU:Th, gamma U:Th.

between the two surveys (Fig. 1). All tree and shrub species were affected similarly and species relative composition remained the same between 1997 and 2010.

Vegetation characteristics

Climate and fragment size were probable predictors of change in several vegetation characteristics in the Box-Ironbark forests over the study period (Table 2). In 1997, sites with higher rainfall had more live saplings and higher shrub richness (see Appendix S1 in Supporting Information). The number of small trees and dead saplings increased relatively more at sites with higher rainfall in 2010 (Table 2). The number of hollows increased relatively more on sites with higher mean temperature (Table 2). Sites with a high soil γU:Th ratio had a larger relative increase in stumps, medium and large trees compared with sites with lower soil γU:Th (Table 2).

Basal area of dead trees and number of hollows and very large trees increased relatively more in remnants than in pseudoremnants (Table 2). In pseudoremnants, canopy cover and tall shrub cover decreased relatively more than in remnants, whereas coppices increased relatively more (Table 2). In 1997, pseudoremnants had higher canopy cover, litter depth and shrub cover than actual remnants and remnants had more course woody debris and very large trees (> 80 cm) (Appendix S1). During the study period, years since fire had little effect on vegetation characteristics. In recently logged sites < 20 years, there was a larger increase in dead saplings compared with long-unlogged sites (> 90 years).

Carbon content

Live carbon in 1997 was 42.2 ± 1.4 SE t C ha⁻¹. Projected live carbon by 2010 was calculated to be 62.3 ± 2 SE t C ha⁻¹. Actual live carbon stock in 2010 was 56.7 ± 2.4 SE t C ha⁻¹, giving a mean carbon growth deficit of 5.6 ± 2.1 SE t C ha⁻¹. Higher mean rainfall was associated positively with standing live carbon (Table 2). Mean standing dead carbon increased from 3.8 ± 0.3 SE t C ha⁻¹ in 1997 to 7.5 ± 0.4 SE t C ha⁻¹in 2010. Sites with a high soil γU:Th ratio had a greater increase in dead carbon.

DISCUSSION

Even under the more conservative emission scenarios, which seem increasingly unlikely, the frequency and severity of Big Dry-like droughts are predicted to increase (IPCC, 2007). In our region, reductions in precipitation seen in the Big Dry probably reflect a long-term shift to a drier climate, which is the projection for the region (Gergis et al., 2011) rather than being just one, albeit severe, drought. Increases in the frequency and intensity of extreme events may produce severe effects on the biota (Thompson et al., 2013); there are reports of declines in birds (Mac Nally et al., 2009b), amphibians (Mac Nally et al., 2009a) and freshwater invertebrates (Thomson et al., 2012) in the region over this period.

Forest structure

The structure of the Box-Ironbark forests of central Victoria changed substantially between 1997 and 2010 following the Big

Dry (Fig. 1), in which autumn and early winter rainfall was reduced by 10–20% and there was a 0.7 °C increase in mean annual maximum temperatures across south-eastern Australia (Gergis *et al.*, 2011). There were systematic changes in vegetation characteristics that indicated that the forests were very different in character between the two periods.

Greater numbers of saplings were dead at sites with higher rainfall than at sites with lower rainfall (Table 2). This somewhat counter-intuitive result may relate to higher initial densities (in 1997) of saplings in these sites (Appendix S1) and intensified competition for water during the Big Dry. Saplings probably were disadvantaged relative to mature trees because of saplings' greater reliance on surface soil moisture. High stem densities induce greater competition for water and light (Dwyer *et al.*, 2010), which may leave tree stands more vulnerable to drought (Ciais *et al.*, 2005).

Dieback and regeneration partly may be related to soil properties (Fensham & Fairfax, 2007). Soil γU:Th is an indicator of clay content, and clay soils have greater water-holding capacities than sandy soils, but once dry, such soils may not readily rehydrate (Pracilio *et al.*, 2006). Sites with higher soil γU:Th had greater standing dead carbon and medium and large trees (Table 2). Higher mortality can occur on favourable soils when trees have shallow root systems (Fensham & Fairfax, 2007).

There was an interaction between land use (in this case, forest fragmentation) and survey period such that increases in mortality were highest in actual remnants while reductions in canopy cover were highest in pseudofragments (Table 2). The higher mortality in fragments is consistent with global dieback trends that indicate that climate change may exacerbate water and heat stress in smaller remnants of native vegetation due to higher surface roughness and albedo of agricultural lands in which smaller remnants are embedded (McAlpine *et al.*, 2009; Allen *et al.*, 2010; Mantyka-Pringle *et al.*, 2012). Reduced canopy cover, litter depth and tall shrub cover in pseudoremnants may be due to higher initial levels in pseudoremnants than actual remnants (Appendix S1). The higher initial canopy cover in pseudoremnants suggests that they had experienced less water stress and, therefore, had not reduced their leaf area as much as the more exposed smaller remnants. During the chronic stress of the Big Dry, many trees within the remnants may have reduced their leaf area to the point of mortality.

Carbon dynamics

The above-ground live C biomass in 2010 was much lower than the projected value for 2010 (Table 2). Small-tree recruitment was much less in the 2010 surveys than in 1997 (Table 2). Although tree growth may be enhanced by higher temperatures, water stress probably will counter this relationship. If mortality increases and lowered growth rates occur in response to increases in the frequency and severity of drought, then forests will become net carbon emission sources, contributing to future warming through positive feedback (Chapin *et al.*, 2008).

Widespread increases in tree mortality would be a considerable source of carbon emissions, and many forests may become net carbon sources. Moreover, fewer living trees would sequester less carbon per unit area compared with previous conditions. The extant Box-Ironbark forests of Victoria cover *c.* 255,400 ha. If the carbon sequestration deficit of 5.6 ± 2.1 SE t C ha^{-1} were to apply across this entire area, then 1.43 Mt of carbon sequestration may not have occurred during the Big Dry. The Box-Ironbark forests are part of 7 Mha of 'Eucalypt Open Forest' in south-eastern Australia; much of this area was affected by the Big Dry, and if our results were representative across the region, then up to 40 Mt of carbon may not have been sequestered over that severely arid period.

Without direct measures of soil and root carbon stocks and fluxes, we have no information on the dynamics of below-ground C stocks. However, root and microbial activity in the soil is reduced markedly during dry periods (Ciais *et al.*, 2005). Decreased root growth would decrease the rate of carbon accumulation in the soil, whereas decreased microbial respiration and decomposition would reduce carbon losses from the soil, so the effects may have been marginal.

Management

The reduction in above-ground carbon sequestration and increased tree mortality suggest that the Box-Ironbark forests, and ones similar to them in eastern Australia and on other continents, may become poorer overall sequesterers of carbon under climate change. What options are there to lessen these effects? From the perspective of landscape management, the largest relative gains might be achieved by investing in restoration activities that ameliorate the heat and water stresses experienced by remnant vegetation. Revegetating adjacent to remnants seems desirable, particularly if there are concomitant positive effects on population viabilities of the fauna and flora (Lambeck, 1997). Revegetating remnants in areas of higher precipitation and soil fertility (Vesk & Mac Nally, 2006) will be especially advantageous in generating higher growth rates of trees and more rapid carbon sequestration. Soil fertility and access to moisture promote flowering in eucalypts, which provides an important food resource for many animals (Mac Nally *et al.*, 2009b). Carbon-emission reduction schemes might be a source of revenue to influence land-holders to enact land use change. In situ management might include thinning, which reduces mortality and results in higher carbon accumulation in flood plain forests of south-eastern Australia (Horner *et al.*, 2010). However, there is little evidence that these effects hold for drier, upland and plains forests such as the Box-Ironbark, and its implementation is likely to damage understory plants and soil structure.

Overview

We found an increase in mortality and canopy dieback over an extended period of severe drought, which adds to evidence linking climate change to negative effects on vegetation (Allen *et al.*, 2010; Suarez & Kitzberger, 2010). Few studies have examined the importance of land use and climate change on long-

term vegetation trends, but in the few cases that have done so, disentangling which stressor is the major contributor to change has been difficult (Allen *et al.*, 2010; Mantyka-Pringle *et al.*, 2012). At present, it is generally believed that habitat loss and fragmentation outweigh the effects of climate change (Mantyka-pringle *et al.*, 2012). Moreover, spatial information of environmental condition is often lacking, making it difficult to determine which climate variables, including precipitation and temperature, induce forest dieback (Allen *et al.*, 2010). The spatial and temporal configuration of our study allowed us to draw links between mortality and dieback to causal climate and landscape effects. We found less mortality in larger remnants in higher rainfall areas. Fragmented vegetation may be more susceptible to extended drought than more extensive stands of woodland because of probable greater water and heat stress in smaller fragments.

ACKNOWLEDGEMENTS

REFERENCES

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Barbeta, A., Penuelas, J., Ogaya, R. & Jump, A.S. (2011). Reduced tree health and seedling production in fragmented Fagus sylvatica forest patches in the Montseny Mountains (NE Spain). *Forest Ecology and Management*, **261**, 2029–2037.

BoM (2012) *Australian climate variability & change*. Available at: http://www.bom.gov.au/cgi-bin/climate/change/timeseries.cgi? (accessed 16 May 2013).

Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, **63**, 625–644.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, **23**, 453–460.

Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434–455.

Brouwers, N., Matusick, G., Ruthrof, K., Lyons, T. & Hardy, G. (2013) Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem. *Landscape Ecology*, **28**, 69–80.

Capon, S., Chambers, L., Mac Nally, R., Naiman, R., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D., Stewardson, M., Roberts, J., Parsons, M. & Williams, S. (2013) Riparian ecosystems in the 21st century: hotspots for climate change adaptation? *Ecosystems*, **16**, 359–381.

Chapin, S.F.I., Randerson, J.T., McGuire, A.D., Foley, J.A. & Field, C.B. (2008) Changing feedbacks in the climate-biosphere system. *Frontiers in Ecology and the Environment*, **6**, 313–320.

Ciais, P., Reichstein, M., Viovy, N. *et al.* (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Cushman, S., Shirk, A. & Landguth, E. (2012) Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. *Landscape Ecology*, **27**, 369–380.

DSE (1998) Box-Ironbark Timber Assessment Project. In: *Bendigo Forest Management Area and Pyrenees Ranges*. Department of Natural Resources and Environment, Victoria.

DSE (2010) Victorian spatial data directory, DSE, Melbourne. In: Department of Sustainability and Environment, Melbourne, Victoria.

Dwyer, J.M., Fensham, R.J., Fairfax, R.J. & Buckley, Y.M. (2010) Neighbourhood effects influence drought-induced mortality of savanna trees in Australia. *Journal of Vegetation Science*, **21**, 573–585.

ECC (2001) *Box-Ironbark forests and woodlands investigation*. Environment Conservation Council, Melbourne.

ESRI (2010) *ArcGIS 10.0 geographic information system*. Environmental Systems Research Institute, Redlands, CA.

Fensham, R.J. & Fairfax, R.J. (2007) Drought-related tree death of savanna eucalypts: species susceptibility, soil conditions and root architecture. *Journal of Vegetation Science*, **18**, 71–80.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (1995) *Bayesian data analysis*. Chapman and Hall, London.

Gergis, J., Gallant, A.J.E., Braganza, K., Karoly, D.J., Allen, K., Cullen, L., D'Arrigo, R., Goodwin, I., Grierson, P. & McGregor, S. (2011) On the long-term context of the 1997–2009 'Big Dry' in South-Eastern Australia: insights from a 206-year multi-proxy rainfall reconstruction. *Climatic Change*, **111**, 923–944.

Grierson, P.F., Adams, M.A. & Attiwill, P.M. (1992) Estimates of carbon storage in the aboveground biomass of Victorias forests. *Australian Journal of Botany*, **40**, 631–640.

Hamilton, S., Brodie, G. & O Dwyer, C. (2005) Allometric relationships for estimating biomass in grey box (*Eucalyptus microcarpa*). *Australian Forestry*, **68**, 267–273.

Hatanaka, N., Wright, W., Loyn, R.H. & Mac Nally, R. (2011) 'Ecologically complex carbon' – linking biodiversity values, carbon storage and habitat structure in some austral temperate forests. *Global Ecology and Biogeography*, **20**, 260–271.

Hoffmann, W.A., Marchin, R.M., Abit, P. & Lau, O.L. (2011) Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology*, **17**, 2731–2742.

Horner, G.J., Baker, P.J., Mac Nally, R., Cunningham, S.C., Thomson, J.R. & Hamilton, F. (2009) Mortality of developing floodplain forests subjected to a drying climate and water extraction. *Global Change Biology*, **15**, 2176–2186.

Horner, G.J., Baker, P.J., Mac Nally, R., Cunningham, S.C., Thomson, J.R. & Hamilton, F. (2010) Forest structure, habitat and carbon benefits from thinning floodplain forests: managing early stand density makes a difference. *Forest Ecology and Management*, **259**, 286–293.

IPCC (2007) Climate change 2007: the physical science basis. *Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), 996 pp. Cambridge University Press, Cambridge.

Lambeck, R.J. (1997) Focal species: a multi-species umbrella for nature conservation. *Conservation Biology*, **11**, 849–856.

de Leeuw, J. & Mair, P. (2009) Multidimensional scaling using majorization: SMACOF in R. *Journal of Statistical Software*, **31**, 1–30.

Lunn, D.J., Best, N. & Whittaker, J.C. (2009) Generic reversible jump MCMC using graphical models. *Statistics and Computing*, **19**, 395–408.

Mac Nally, R., Bennett, A.F. & Horrocks, G. (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7–29.

Mac Nally, R., Horrocks, G., Lada, H., Lake, P.S., Thomson, J.R. & Taylor, A.C. (2009a) Distribution of anuran amphibians in massively altered landscapes in south-eastern Australia: effects of climate change in an aridifying region. *Global Ecology and Biogeography*, **18**, 575–585.

Mac Nally, R., Bennett, A.F., Thomson, J.R., Radford, J.Q., Unmack, G., Horrocks, G. & Vesk, P.A. (2009b) Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, **15**, 720–730.

McAlpine, C.A., Syktus, J., Ryan, J.G., Deo, R.C. & McKeon, G.M. (2009) A continent under stress: interactions, feedbacks and risks associated with impact of modified land cover on Australia's climate. *Global Change Biology*, **15**, 2206–2223.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009) Widespread increase of tree mortality rates in the Western United States. *Science*, **323**, 521–524.

Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239–1252.

Nepstad, D.C., Stickler, C.M., Soares-Filho, B. & Merry, F. (2008) Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 1737–1746.

Oksanen, J.F., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H. & Wagner, H. (2010) *vegan: community ecology package*. R package version 2.0-4. Available at: http://CRAN.R-project.org/package=vegan (accessed 16 May 2013).

Parker, M. & Mac Nally, R. (2002) Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. *Biological Conservation*, **105**, 217–229.

Pracilio, G., Adams, M.L., Smettem, K.R.J. & Harper, R.J. (2006) Determination of spatial distribution patterns of clay and plant available potassium contents in surface soils at the farm scale using high resolution gamma ray spectrometry. *Plant and Soil*, **282**, 67–82.

Robinson, R. (1997) *Dynamics of coarse woody debris in floodplain forests: impact of forest management and flood frequency*. BSc Honours Thesis, Charles Sturt University, NSW, Australia.

Schaphoff, S., Lucht, W., Gerten, D., Sitch, S., Cramer, W. & Prentice, I. (2006) Terrestrial biosphere carbon storage under alternative climate projections. *Climatic Change*, **74**, 97–122.

Spiegelhalter, D., Thomas, A. & Best, N. (2003) WinBUGS version 1.4. Bayesian inference using Gibbs sampling. In: MRC Biostatistics Unit, Institute for Public Health, Cambridge, UK.

Suarez, M.L. & Kitzberger, T. (2010) Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. *Journal of Ecology*, **98**, 1023–1034.

Swift, T.L. & Hannon, S.J. (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews*, **85**, 35–53.

Thompson, R.M., Beardall, J., Beringer, J., Grace, M. & Sardina, P. (2013) Means and extremes: building variability into community-level climate change experiments. *Ecology Letters* (Epub Feb 2013 ahead of print).

Thomson, J.R., Bond, N.R., Cunningham, S.C., Metzeling, L., Reich, P., Thompson, R.M. & Mac Nally, R. (2012) The influences of climatic variation and vegetation on stream biota: lessons from the Big Dry in southeastern Australia. *Global Change Biology*, **18**, 1582–1596.

Timbal, B., Arblaster, J., Braganza, K., Fernandez, E., Hendon, H., Murphy, B., Raupach, M., Rakich, C., Smith, K.W. & Wheeler, M. (2010) Understanding the anthropogenic nature of the observed rainfall decline across South Eastern Australia. In: Centre for Australian Weather and Climate Research (CAWCR), Australia.

Verdon-Kidd, D.C. & Kiem, A.S. (2009) Nature and causes of protracted droughts in southeast Australia: comparison

between the Federation, WWII, and Big Dry droughts. *Geophysical Research Letters*, **36**, 1–6.

Vesk, P.A. & Mac Nally, R. (2006) The clock is ticking – revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. *Agriculture Ecosystems & Environment*, **112**, 356–366.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Comparison of the changes in individual vegetation characteristics with spatial environmental predictors derived from Bayesian model comparison.

BIOSKETCH

Author contributions: R.M. and S.C.C. conceived the research; J.M.B and C.A.C. collected the data; J.M.B. and J.R.T. analysed the data; J.M.B., S.C.C., R.H.C. and R.M. wrote the MS. More details from the group's web page http://monash.edu/science/about/schools/biological-sciences/staff/macnally/index.html.

Editor: Josep Penuelas