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A warmer world will reduce tree growth in evergreen broadleaf forests: evidence from Australian temperate and subtropical eucalypt forests

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ABSTRACT

Aims Understanding how tree growth is influenced by climate is vital for predicting how forests will respond to climate change, yet there have been few studies of tree growth spanning macroclimatic gradients. The aim of this study is to correlate growth of a single lineage of broadleaf evergreen trees with continental-scale variability in climate.

Location Australia's temperate mesic eucalypt forests, spanning latitudes from 23 to 43° S and longitudes from 115 to 153° E.

Methods We compiled and analysed a dataset containing around half a million measurements of growth in eucalypt tree diameter, collected from 2409 permanent forestry plots. These plots spanned a range of 558–2105 mm mean annual precipitation and 6–22 °C mean annual temperature. Generalized additive models were used to study the relationship between growth in tree diameter and several temperature and water availability variables.

Results Tree growth increased with precipitation, but with a diminishing response above a mean annual precipitation of 1400 mm. There was a peaked response to temperature, with maximum growth occurring at a mean annual temperature of 11 °C and maximum temperature of the warmest month of 25–27 °C. Lower temperatures directly constrain growth. High temperatures primarily reduced growth by reducing water availability, but they also appeared to exert a direct negative effect. Our best model, which included maximum temperature of the warmest month and the ratio of precipitation to evaporation, explained 28% of the deviance.

Main conclusions The productivity of Australia's temperate eucalypt forests could decline substantially as the climate warms, given that 87% of these forests currently experience a mean annual temperature above 11 °C, where the highest growth rates were observed. This will reduce carbon sequestration and slow recovery after catastrophic disturbances such as wildfire.

Keywords
Climatic gradients, macroecology, precipitation, temperature, tree growth, water availability.

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INTRODUCTION

Forests are a critical component of the global carbon cycle, yet there is surprisingly little information on how tree growth and forest biomass respond to climate change (Bowman *et al.*, 2013b). Existing studies suggest that global warming may increase tree growth in forests in cold climates but cause declines in warmer climates, especially where water is limiting (Mäkinen
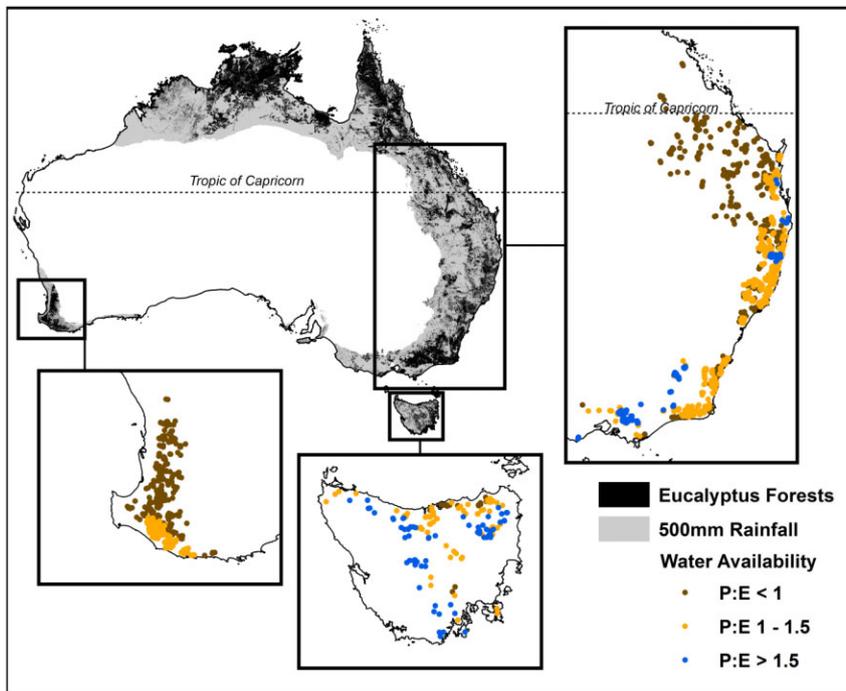
Figure 1 Australia's mesic eucalypt forests and location of the permanent plots. Mesic forests (Black on the main map) were considered those in areas receiving > 500 mm mean annual precipitation (grey on main map). Insets show location of the permanent plots, with the brown, yellow and blue dots representing sites with low, medium and high water availability, respectively. Water availability is the ratio of mean annual precipitation to evaporation (P:E).

et al., 2002; Intergovernmental Panel on Climate Change, 2006; Reich & Oleksyn, 2008; Mu *et al.*, 2011), but there have been few studies across wide temperature and rainfall gradients to test this proposition. Such macroecological studies are an attractive approach for investigating relationships between tree growth and climate, because geographic gradients capture a greater range of climate variation than occurs at specific locations. Importantly, this approach can quantify climatic effects on the growth of forest trees, which are impractical to study through experimental manipulation. Networks of strategically located permanent plots can be used to track regional trends in tree growth over large geographic scales (Malhi *et al.*, 2004; Bowman *et al.*, 2013b). Accordingly, we analysed almost half a million observations of tree growth from 2409 permanent plots established by forest management agencies in Australia's temperate mesic forests (Prior *et al.*, 2011; Prior & Bowman, 2014). These plots are located between latitudes 23.5 and 43° S, and experience climates ranging from cool temperate wet to subtropical dry (*sensu* Holdridge, 1947) (Fig. 1). The forests are naturally regenerating and are dominated by eucalypts with a range of co-dominant *Acacia*, *Callitris* and rain forest species. Our analysis considered only eucalypts (*Eucalyptus* and the allied genera *Corymbia* and *Angophora*) in order to avoid gross phylogenetic differences in growth between families and genera. Eucalypts are a valuable model system for macroecological investigations of tree growth because they span very wide climate gradients, dominating forests in all but the driest areas of the Australian continent, and have comparable photosynthetic and water-use physiologies to other evergreen broadleaf trees (Wright *et al.*, 2004).

The aim of our study was to quantify eucalypt growth in relation to climate, and in particular to water availability and temperature. The interpretation of temperature responses is complicated due to indirect effects on water availability via evaporation as well as direct metabolic effects. While plant growth is suppressed by cold temperatures, respiration increases more rapidly than photosynthesis as temperature increases, leading to higher tissue maintenance costs and lower net primary productivity (NPP) at high temperatures (Zhang *et al.*, 2009; Larjavaara & Muller-Landau, 2012). In eucalypts, leaf temperatures higher than *c.* 35 °C can depress photosynthesis independently of the effect on stomatal conductance (Prior *et al.*, 1997), and temperatures > 45 °C can lead to extensive foliar damage (Groom *et al.*, 2004). Statistical modelling was therefore used to tease apart the direct and indirect effects of temperature and rainfall, and demonstrate whether both apparently contribute to lower growth rates at hotter sites. We also tested whether the overall response of eucalypt growth to climate was similar within and among species or was driven by species replacement: in other words, whether fast-growing species occur only in particular climates and that species able to survive in other climates have inherently slower growth. Finally, we calculated the likely change in growth resulting from projected climate change during this century.

METHODS

Tree growth data

Permanent growth plots have been established to monitor tree growth in these forests by Australian state government forestry organizations since the 1930s. Our study focused on permanent plots located in temperate mesic (> 500 mm mean annual precipitation) eucalypt forests (Fig. 1). The data were compiled as

Table 1 Summary of the final dataset.

	Mean	Minimum	Maximum
Plot area (m²)	1451	100	8280
Measurement date	31/01/1984	1/02/1930	29/10/2009
Measurement interval (years)	4.0	1.0	37.6
Mean annual precipitation (mm)	1117	558	2105
Mean annual temperature (°C)	14.8	6.4	22.4
Maximum temperature of warmest month (°C)	26.3	16.3	34.4
Minimum temperature of coldest month (°C)	4.0	-3.0	12.2
Pan evaporation (mm)	1008	563	1649
Water availability (ratio precipitation: evaporation)	1.18	0.38	2.96
Elevation (m)	514	3	1371
Initial stand basal area (m² ha⁻¹)	31.3	10	93.6
Initial DBH (cm)	34.8	10.4	133
DBH increment (cm year⁻¹)	0.39	-0.50	1.94

The data presented here are based on plot means rather than individual trees, after filtering according to the criteria specified in the Methods section.

part of a research programme to understand the effects of climate change on Australia's forests, which are used for timber production (Prior *et al.*, 2011).

The plots are naturally regenerating, often with a pulse of recruitment following disturbance (typically wildfire). Tree age is not known, as plots were generally set up in established forest, and eucalypts are very difficult to age using dendrochronology. Forests are generally multi-aged. Approximately one-third of plots were monospecific with respect to eucalypts > 10 cm diameter.

The tree growth data consisted of repeated measurements of the diameter at breast height (d.b.h.) of individually identified trees within marked plots of known area and location, with measurement intervals averaging 4.0 years (range 1–44 years) (Table 1). In most cases, all trees > 10 cm d.b.h. within a plot were measured, but in some plots only large trees (e.g. > 50 cm d.b.h.) were measured over the entire plot, and smaller trees measured in subplots of known area. The stand basal area of each plot (an indicator of intertree competition) was calculated by summing the cross-sectional area of each tree stem then dividing by the ground area. Where subplots were used, basal area was calculated for each size class individually, then summed to give total stand basal area for the plot. Diameter increments were annualized, and to avoid anomalous observations arising from measurement error or extreme situations we included only data complying with the following conditions: measurement interval ≥ 1 year; plot size ≥ 100 m² and stand basal area 10–100 m² ha⁻¹; eucalypts with d.b.h. from 10–150 cm and diameter increments from −0.5–2.5 cm year⁻¹ (or the 95th percentile for the one species where this was > 2.5 cm year⁻¹; Fox *et al.*, 2010). After filtering, the dataset comprised records

from 2409 plots, and 499,161 tree-intervals and > 100 species or subspecies (Table 1 and Appendix S1 in Supporting Information).

Climatic variables

Climatic data were derived using the latitude and longitude of the plot and digital elevation data, with a resolution of 5 arcmin used throughout. Gridded data were obtained from the WorldClim dataset (Hijmans *et al.*, 2005) for the BIOCLIM variables of mean annual precipitation (P), mean annual temperature (T), mean daily maximum temperature of the warmest month (MaxWarm) and mean daily minimum temperature of the coldest month (MinCold). Pan evaporation (E) was derived from ANUCLIM 6.1 (Australian National University, Canberra), and the ratio P : E was used as a proxy for water availability (Ellis & Hatton, 2008).

Data analyses

Initial inspection of the raw data showed that the relationships between diameter increments and the climatic variables were nonlinear, so generalized additive models (GAMs) were used to evaluate these relationships. GAMs are semi-parametric extensions of generalized linear models and provide a smooth response to the explanatory variables, without imposing a particular type of relationship (e.g. linear, quadratic, power, logarithmic) (Crawley, 2002). The smoothness of the curve can be varied by adjusting the parameters of the GAM fitting algorithm, thereby avoiding over-fitting. Cubic regression splines were used, and we specified smoothers with up to three effective degrees of freedom for all variables, which produced biologically sensible response curves. The GAMs were evaluated by the percentage deviance they explained and the associated Akaike information criterion (AIC) (Burnham & Anderson, 2002). The raw data were spatially and temporally autocorrelated because there were multiple measurements on each plot. GAMs have limited capacity to incorporate random effects, so to overcome this autocorrelation, all measurements, including d.b.h. increment, were averaged over all measurement intervals for each plot, and plot means were used in the analyses. The statistical software R was used for all analyses (R Development Core Team, 2013), and the package mgcv (v.1.6-2) was used for the generalized additive modelling.

Climatic variables were strongly intercorrelated (Appendix S1). In developing models of eucalypt growth patterns we therefore grouped the variables into two suites, those related to temperature (T, MaxWarm and MinCold) and those related to water availability (P, E and P : E), and compared the explanatory power of the variables within each suite. We reasoned that the indirect effect of temperature mediated through water availability would be subsumed by a water availability term, but that a strong correlation with both temperature and water availability would indicate an additional, direct, effect of temperature on metabolism. Further, we expected the diameter increment to be more closely related to MaxWarm or MinCold than to T if

extremes of heat or cold, respectively, were driving the negative relationship between growth and temperature.

The relationships between diameter increment and climate were explored using GAMS to (1) test which of the water availability variables P, E or P : E is the best predictor of growth, individually and in combination with temperature variables; and (2) compare the explanatory power of the temperature variables T, MaxWarm and MinCold, individually and in combination with water availability variables. This analysis suggested that there is statistical support for a direct effect of temperature in addition to its effect through water availability, an aspect that was explored further by examining the response to temperature within five P : E classes individually.

We estimated the likely impact of climate change on tree growth by using the model based on mean annual temperature only, because estimates of T are much more reliable than those for P and E. Full details are given in Appendix S1. Briefly, diameter increment was calculated for T in the temperate mesic eucalypt forests currently, and for the projected T in 2070. Future climate projections for temperate eucalypt forests were based on the CSIRO_mk3, a2a scenario (Ramirez & Jarvis, 2008). Diameter increments were converted to above-ground biomass (AGB) increments for an average-sized tree (d.b.h. = 34.8 cm) using the relationship developed for native sclerophyll forest in southern Australia (Keith *et al.*, 2000).

Intraspecific growth responses to water availability were tested using a linear mixed effects model, with P : E the fixed effect and tree within plot the random effect. The P : E effect was considered statistically important if this model received an AIC weight > 0.73 relative to the null model (Richards, 2005).

RESULTS

Eucalypt diameter growth was related to temperature and water availability to a similar degree, with the best variables in both suites explaining 21% of the deviance (Table 2). The growth response to temperature was peaked, being maximal around a T of 11 °C and a MaxWarm of 25–27 °C, but there was a poor relationship with MinCold (Fig. 2; Table 2). Compared with the mean diameter growth rate of 0.53 cm year^{-1} at a T of 11 °C, diameter growth was 14% lower at 8 °C, 18% lower at 14 °C and 56% lower at 20 °C. These growth rates suggest that a tree of diameter 100 cm growing under a T of 11 °C would be 187 years old while a similar sized tree growing under 20 °C would be 430 years old.

The ratio P : E, a proxy for water availability, had more explanatory power than its components P or E, both in single-variable models and in combination with temperature terms (Table 2). Growth increased as the ratio of P : E increased to about 1.8, after which there was little response (Fig. 2). A similar pattern was evident for P, with a diminishing response to P above 1400 mm (Fig. 2). Conversely, growth declined with increasing E (Fig. 2).

Models containing both temperature and water availability terms performed better than single-factor models (Table 2). For example, adding MaxWarm to the P : E model increased the

Table 2 Comparison of generalised additive models used to analyse d.b.h. increment. The explanatory power of each of the terms mean annual precipitation (P), mean annual temperature (T), mean daily maximum temperature of the warmest month (MaxWarm), mean daily minimum temperature of the coldest month (MinCold), evaporation (E) and P:E (the ratio of precipitation to evaporation, an indicator of water availability) in describing tree diameter growth was determined for each factor individually. Predictions of the best model, indicated by bold type, are plotted in Fig. 3 (*n* = 2409 plots).

	%Dev. expl.	AIC	Delta AIC
Single-variable models – temperature			
MaxWarm	21.0	313	206
T	14.2	512	405
MinCold	9.3	646	539
Single-variable models – water availability			
P : E	21.0	314	207
E	18.2	397	290
P	9.2	648	541
Combining water availability terms and T			
P : E + T	24.2	217	110
P + T	21.9	292	185
E + T	19.9	352	245
Combining water availability terms and MaxWarm			
P : E + MaxWarm	**27.6**	**107**	**0**
P + MaxWarm	25.5	178	71
E + MaxWarm	24.3	214	107
Combining water availability terms and MinCold			
P : E + MinCold	23.2	252	145
E + MinCold	19.8	355	248
P + MinCold	18.6	390	283

%Dev. expl. is the amount of deviance explained by the model, and is analogous to R^2 in a linear model. AIC is the Akaike information criterion, which balances model fit and simplicity (the lower the value, the better the model). Delta AIC is the difference in AIC relative to that of the best model.

deviance explained from 21% to 28%, suggesting that temperature has a direct effect on eucalypt growth in addition to the one it exerts via increased evaporation. Much of this additional temperature effect is due to slow growth in cooler areas (MaxWarm < 20 °C), but growth is also slower in hotter areas (MaxWarm > 25 °C), even when P : E is controlled for in the model (Fig. 3). Investigating the growth response to temperature within individual P : E classes, we found that within the three classes that spanned a large temperature range (i.e. P : E between 0.8 and 2.0), growth decreased when T exceeded 14 °C or MaxWarm exceeded 26 °C (Fig. 4). (The temperature range of the driest and wettest classes was insufficient to draw conclusions.) GAMs showed that growth decreased as MAT exceeded 10–12 °C (P : E < 1.2) or 14–15 °C (P : E 1.2–2.0) (Appendix S2). For plots with P : E > 2, the MAT range was only 7–12 °C,
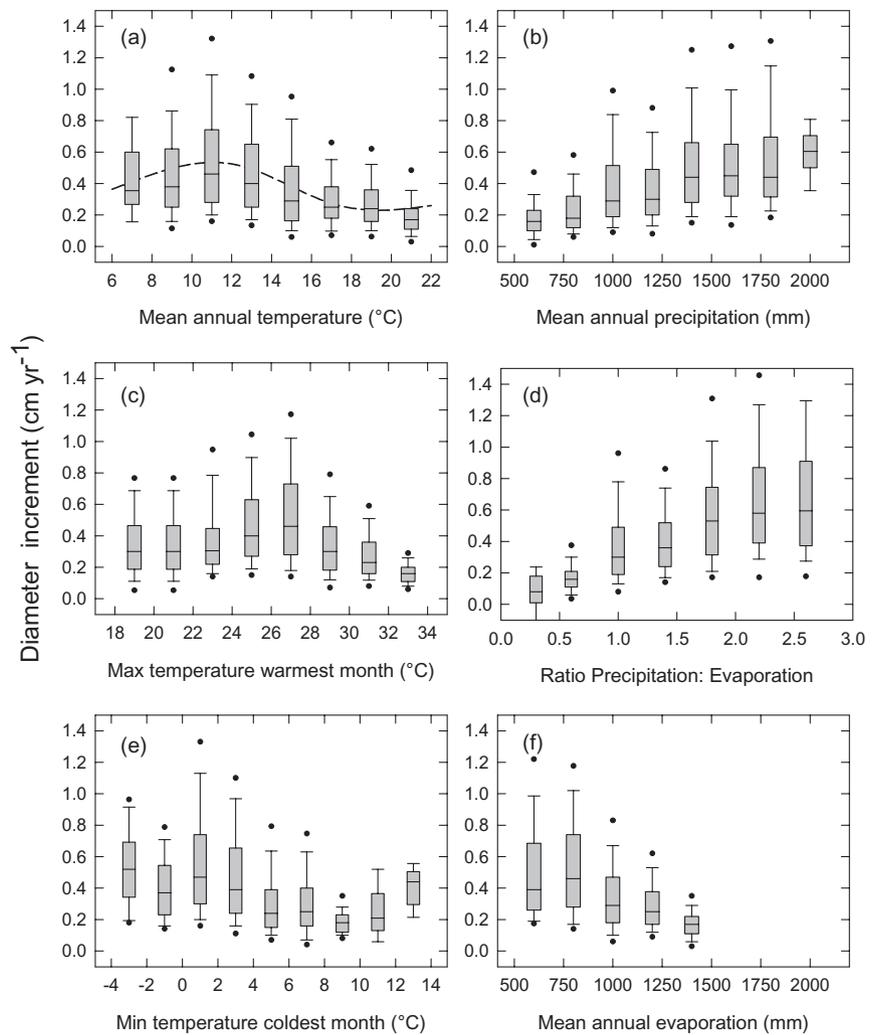
Figure 2 Tree diameter increment in relation to (a) mean annual temperature, (b) mean annual precipitation, (c) maximum temperature of the warmest month, (d) the ratio of precipitation to evaporation, (e) minimum temperature of the coldest month and (f) mean annual evaporation. For presentation, raw data are grouped into 200-mm precipitation classes, 0.4 precipitation:evaporation classes and 2 °C temperature classes. Boxes indicate the median and upper and lower quartiles, with whiskers showing 10th and 90th percentiles and circles 5th and 95th percentiles. Fitted values for the diameter increment versus temperature model are indicated by the dashed line in (a). This model was used to predict the effects of climate change on forest carbon sequestration. The line is derived independently of the boxplot, although based on the same data.

Figure 3 Diameter increment in relation to water availability (the ratio of mean annual precipitation to evaporation) and mean maximum temperature of the warmest month, predicted from our most strongly supported generalized additive model, which explained 28% of the deviance. The growth responses to each variable are shown holding the other variable constant at the average value. The solid line is the smoothed model fit, the dotted lines are 95% confidence interval bands.
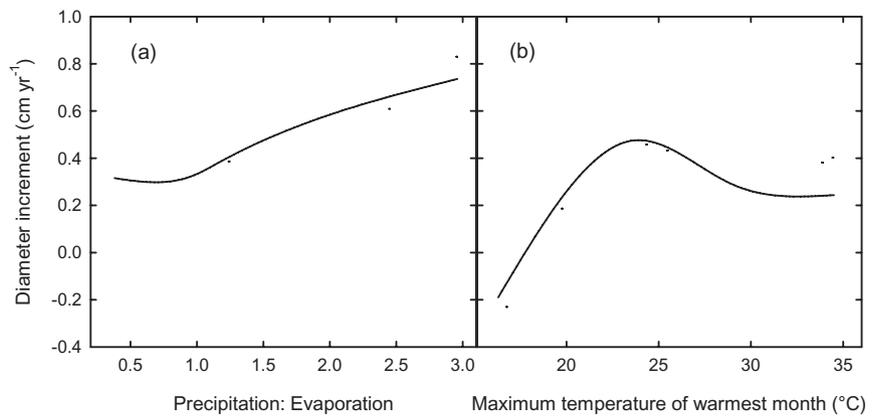
but growth appeared to plateau at around 12 °C. GAMs also indicated a decline in MaxWarm values higher than 23 to 26 °C for all P : E classes (except P : E > 2, where the highest MaxWarm value was 25 °C).

Our modelling predicted that as a result of a warming climate, the average diameter increment in temperate Australian eucalypt forests would decrease from a current value of 0.41 to

0.32 cm year^{-1} in 2070, equivalent to a 22.4% decrease in biomass increment (details in Appendix S4). This equates to a decrease of approximately 90 Mt C year^{-1} over the 333,000 km^2 of Australian eucalypt forest estate that receives a mean annual precipitation of more than 500 mm.

There was a wide range of diameter growth rates among species (Appendix S3). Of the species with more than 10
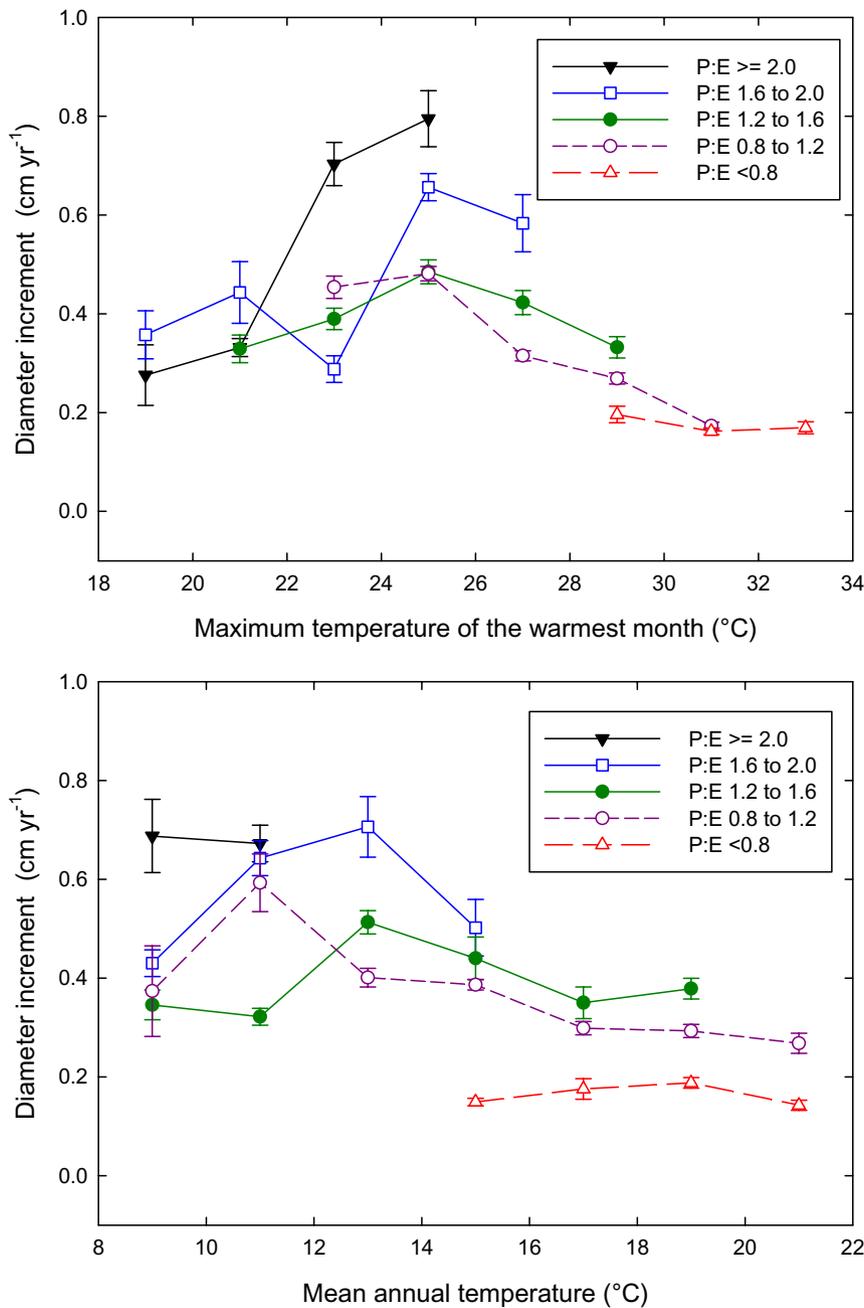
Figure 4 Diameter increment as a function of maximum temperature of the warmest month and mean annual temperature for five precipitation:evaporation (P:E) classes. For presentation, raw data are grouped into 0.4 P:E classes and 2 °C temperature classes. Points with fewer than 10 observations are omitted, and bars indicate standard errors.

observations, the three fastest growing were *Eucalyptus nitens* (0.87 cm year⁻¹), *Eucalyptus delegatensis* (0.67 cm year⁻¹) and *Eucalyptus fraxinoides* (0.61 cm year⁻¹) and the slowest-growing was *Eucalyptus drepanophylla* (0.04 cm year⁻¹). Differences among, rather than within, eucalypt species appeared to drive the positive relationship between diameter growth and water availability (Fig. 5a). All 15 major species with the fastest growth, but only one of the 12 species with the slowest growth, grew in forests where mean P : E was > 1. On the other hand, there was no significant relationship between growth and P : E within 15 of the major species, while two showed a negative relationship and 10 showed a positive one (Fig. 5b).

DISCUSSION

Growth rates in mesic Australian eucalypt forests are maximal at mean annual temperatures around 11 °C, and where MaxWarm is 25–27 °C. Our results suggest that high temperatures reduce growth largely through their effect on evaporation and water availability, with a smaller additional direct effect: a temperature effect was much weaker, albeit still present, in models that contained water availability terms (Table 2) and among plots with similar P : E. Mean annual temperatures less than 11 °C were suboptimal for growth, but higher temperatures also appeared to directly constrain growth: growth showed a decline once T
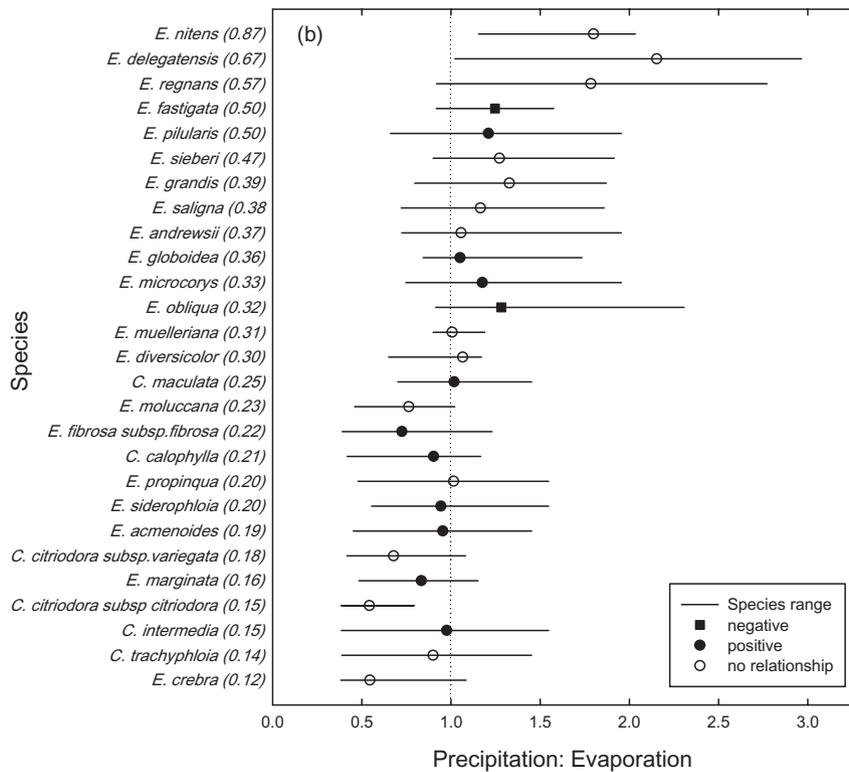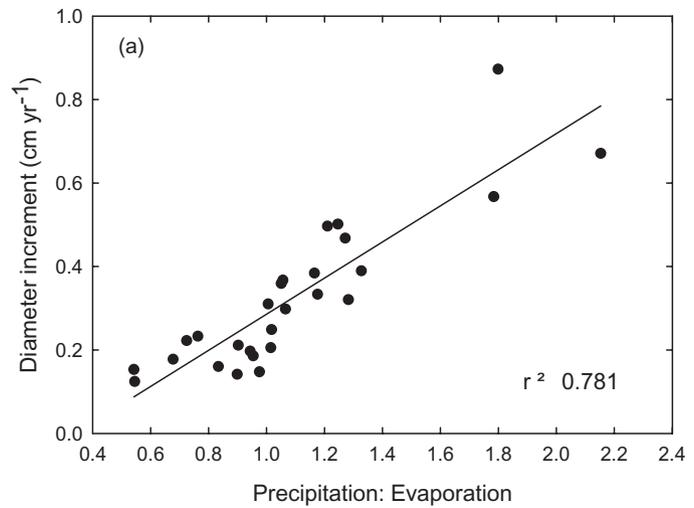
Figure 5 The relationship between diameter growth and water availability for the major eucalypt species. (a) The relationship between diameter growth and water availability (the ratio of precipitation to evaporation, P:E) for each of the 27 species with more than 2000 observations and (b) the range of P:E, indicated by the horizontal lines, for each of these 27 species, sorted by mean diameter increment, shown in brackets as cm year^{-1}. The dotted line indicates a P:E ratio of 1.0. Symbols indicate the mean P:E for each species: black circles represent species with a positive response to P:E, black squares those with a negative response, and open circles those without a statistically supported response.

exceeded 11–14 °C or MaxWarm exceeded 25 °C within the P : E classes that spanned the full temperature range. These findings are consistent with global meta-analyses showing that carbon use efficiency (the ratio of gross primary productivity to maintenance costs) and biomass accumulation are highest in cool temperate rather than tropical forests (Larjavaara & Muller-Landau, 2012). Higher gross primary production in tropical forests is apparently offset by higher autotrophic respiration than in temperate forests (Luyssaert *et al.*, 2007). In addition cool, high-rainfall environments (T of 10–15 °C, and P of 1200–2500 mm) (Midgley, 2001; Keith *et al.*, 2009), such as coastal California and south-eastern Australia, experience relatively infrequent disturbance and slow decomposition (Midgley, 2001; Keith *et al.*, 2009). Given that 87% of the area occupied by

Australia's temperate eucalypt forests currently experiences MAT above 11 °C, at which the highest growth rates were observed, our results suggest that productivity of these forests will decline substantially as the climate warms. Based on the direct and indirect effects of MAT on diameter growth of eucalypts, we calculate that, without any change in precipitation, there will potentially be an overall reduction in tree growth of 22% resulting from projected temperature increases of around 3 °C for Australian forests by 2070 (calculations in Appendix S4). This is equivalent to a reduction in carbon uptake of about 90 Mt annually, or about 4% of current Australian total NPP (Haverd *et al.*, 2013). We note there are already suggestions of reduced terrestrial NPP from 2000 to 2009, attributed to high temperatures and water stress in the Southern Hemisphere

(Zhao & Running, 2010). Similarly, tree growth regionally in the south-western United States is positively correlated with winter rainfall and negatively correlated with summer temperature via its effect on vapour pressure deficit, and hence evaporative demand (Williams *et al.*, 2012). Thus, there is evidence to suggest that global warming will slow tree growth and reduce carbon sequestration in other warm temperate forests around the world.

Our findings suggest that the positive relationship between diameter growth and water availability was driven largely by differences among, rather than within, eucalypt species. There was no consistent relationship within species between growth rates and P : E. However, there was a clear relationship between growth rates and P : E averaged for the major species (Fig. 5), with the fastest-growing eucalypt species found in areas with the highest P : E. With P : E likely to decrease under future climate change, these species may gradually be replaced by less productive ones.

It is worth highlighting that our results represent the best possible case, where trees and species are adapted to the prevailing climate. In reality, existing trees may take time to acclimate to hotter climates, or may never do so. Given that most eucalypt species have a narrow thermal range (Hughes *et al.*, 1996), and a limited ability to adapt to warmer conditions (Crous *et al.*, 2013), it is likely that long-term changes in climate will lead to widespread local elimination of many eucalypt species accompanied by more limited replacement of these species by better adapted ones.

Increased CO_2 has been shown to increase the water-use efficiency of trees but this is unlikely to entirely offset the effects of increased water stress on tree growth (Leuzinger *et al.*, 2011). Indeed, recent increases in CO_2 have not prevented extensive drought-induced mortality in many parts of the world (Allen *et al.*, 2010), including in eucalypt forests in Australia (Fensham & Guymer, 2009; Brouwers *et al.*, 2013). We acknowledge that our macroecological approach can only provide a first approximation to partitioning the effects of temperature, drought and CO_2 on tree growth and mortality. Experimental and modelling approaches are critical but are beset by numerous practical challenges. For instance, the future climate projections are unable to provide details on P : E under specific CO_2 and temperature regimes. Direct experimentation on mature trees combining all these factors is obviously extraordinarily difficult.

Overall, our results are consistent with observations of recent increases in tree growth in cold-limited regions in the Northern Hemisphere, and predictions that it will decrease in warmer regions as a result of a warming climate (Mäkinen *et al.*, 2002; Reich & Oleksyn, 2008; Mu *et al.*, 2011). The broader effects of climate change on tree growth will depend on the interactions between elevated CO_2, increased temperature, changing amounts and patterns of rainfall and other factors affecting forest growth (Boisvenue & Running, 2006). For example, future drying and warming trends are expected to increase fire risk due to the increased number of extreme fire weather days and increased fuel loads from the shedding of drought-damaged foliage (Williams *et al.*, 2009). Reduced tree growth would

increase the vulnerability of forests dominated by obligate seeder species, such as *Eucalyptus regnans*, to catastrophic state shifts after bushfires (Bowman *et al.*, 2013a) because trees may be unable to mature quickly enough to set seed before the next fire. *Eucalyptus regnans* forests are amongst the tallest, most carbon-dense in the world (Keith *et al.*, 2009). Thus climate change may drive a positive feedback by increasing disturbance, reducing growth, causing change in vegetation composition and structure and increasing carbon emissions in the flammable eucalypt forest biome.

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Additional references may be found at the end of Appendix S4 in the online version of this article.

SUPPORTING INFORMATION

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

Appendix S1 Correlation coefficients between diameter increment and climatic variables.
Appendix S2 Growth response to mean annual temperature within water availability classes, derived using generalized additive models.
Appendix S3 Species growth summary.

Appendix S4 Calculation of above-ground biomass increment for an average tree under current conditions and in the year 2070.

BIOSKETCH

David Bowman holds a research chair in Environmental Change Biology in the School of Biological Sciences at the University of Tasmania. The primary motivation for his research is understanding the effects of global environmental change, natural climate variability and Aboriginal landscape burning on bushfire activity and landscape change across the Australian continent.

Author contributions: D.M.J.S.B. conceived and led the project and wrote the manuscript together with L.D.P.; L.D.P. also checked and analysed the data; G.J.W. constructed the dataset and performed the G.I.S. analyses; R.J.K. contributed to the conceptual development of the study, facilitated data acquisition and contributed to writing of the manuscript.

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