

# ECOGRAPHY

## Research

### Climate extreme variables generated using monthly time-series data improve predicted distributions of plant species

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Extreme weather can have significant impacts on plant species demography; however, most studies have focused on responses to a single or small number of extreme events. Long-term patterns in climate extremes, and how they have shaped contemporary distributions, have rarely been considered or tested. BIOCLIM variables that are commonly used in correlative species distribution modelling studies cannot be used to quantify climate extremes, as they are generated using long-term averages and therefore do not describe year-to-year, temporal variability. We evaluated the response of 37 plant species to base climate (long-term means, equivalent to BIOCLIM variables), variability (standard deviations) and extremes of varying return intervals (defined using quantiles) based on historical observations. These variables were generated using fine-grain (approx. 250 m), time-series temperature and precipitation data for the hottest, coldest and driest months over 39 years. Extremes provided significant additive improvements in model performance compared to base climate alone and were more consistent than variability across all species. Models that included extremes frequently showed notably different mapped predictions relative to those using base climate alone, despite often small differences in statistical performance as measured as a summary across sites. These differences in spatial patterns were most pronounced at the predicted range margins, and reflect the influence of coastal proximity, continentality, topography and orographic barriers on climate extremes. Species occupying hotter and drier locations that are exposed to severe maximum temperature extremes were associated with better predictive performance when modelled using extremes. Understanding how plant species have historically responded to climate extremes may provide valuable insights into our understanding of contemporary distributions and help to make more accurate predictions under a changing climate.

Keywords: climate extremes, climate variability, plant species, species distribution modelling, time-series



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## Introduction

Extreme weather events are short in duration but can have significant impacts upon plant demography (Walter et al. 2013). The global increase in heatwave and drought related mortality events since the start of the century (Allen et al. 2015) has highlighted how extreme weather events can shape the abundance and distribution of plant communities (Allen and Breshears 1998, Breshears et al. 2009, Brouwers et al. 2013, Wernberg et al. 2013, Duke et al. 2017, Brown et al. 2018, Thomsen et al. 2019). Extremes of low temperature (i.e. frost events) can cause dieback (Cavanaugh et al. 2014, Matusick et al. 2014) and limit the poleward distribution of plants (Cavanaugh et al. 2014, 2015, Osland and Feher 2020, Osland et al. 2020). Observed declines in frost events have facilitated the expansion of frost sensitive species to cooler climates (Cavanaugh et al. 2014) while increases in hot and dry conditions are contributing to plant dieback at regional and global scales (Mitchell et al. 2014, Allen et al. 2015). Changes to the frequency and magnitude of extremes, and variability in climatic conditions more generally, are expected to promote more drastic shifts in species distributions than those expected by changes in mean climate (Adams et al. 2009, Vasseur et al. 2014, Bailey and van de Pol 2016).

Weather and climate extremes can initiate demographic events that are not in equilibrium with long-term average conditions, leading to mortality and dieback in plant communities (Law et al. 2019). Mitchell et al. (2016) estimated that in southeast Australia, short-duration extremes in water deficit every 1–2 years can lead to recruitment failures while more intense but rarer (every seven years) events could lead to tree dieback and mortality. Seasonal and annual variations in temperature and soil moisture are important determinants of recruitment success in plants (Ibáñez et al. 2007) and changes in recruitment ability due to these variations can lead to changes in landscape-scale distributions of plants (Mok et al. 2012), particularly at their range margins (Zimmermann et al. 2009). Mortality of adult plants under extremes are driven by physiological thresholds that prevent maintenance of water relations (Adams et al. 2009, Breshears et al. 2009) or photosynthetic function (Cavanaugh et al. 2015). At a broad temporal scale, climate extreme driven demographic events can expose maladaptation of species and genotypes to average climate conditions. Benito-Garzón et al. (2013) found that a 1-in-60 year extreme frost event ( $-22^{\circ}\text{C}$ ) triggered widespread mortality of Iberian sourced *Pinus pinaster* individuals planted 35 years prior at a site in France. The Iberian population was sourced from a region in Spain with the same number of winter frost days as the French site but with a different frequency and magnitude of extreme frost events. In this case, the 1-in-10 year ( $-10^{\circ}\text{C}$ ) and 1-in-20 year ( $-15^{\circ}\text{C}$ ) extreme frost events were not enough to cause mortality but the 1-in-60 year event pushed Iberian individuals past a critical threshold for survivorship. Understanding the frequency and or magnitude of climate extremes that push species past these critical thresholds is key to understanding how these events shape species demography and

distributions (Cavanaugh et al. 2015, Mitchell et al. 2016, Law et al. 2019).

The importance of extreme events in shaping plant species demography and distributions is well established; however, the incorporation of extremes into predictive models lags behind this understanding. Many modelling studies that aim to predict species distributions under current and future climates use statistical correlations between species observations and long-term climatic means (i.e. calculated over 30 years or greater), and therefore few consider the potentially significant impacts of extremes and variability (Vasseur et al. 2014, Lawson et al. 2015, Bailey and van de Pol 2016). Zimmermann et al. (2009) showed that incorporating inter-annual variability around climate averages improved the predictive power of species distribution models (SDMs) for common tree species in central Europe. Cavanaugh et al. (2015) incorporated a metric that encapsulated extremes in frost days to model the distribution of mangroves in Florida, based on the annual average of extreme events. Law et al. (2019) developed an SDM based on experimental work that linked mortality to thresholds in plant available soil moisture. They used this model to explore how changes in the average frequency of extreme drought events could increase tree mortality events. Brown et al. (2018) developed SDMs based on a single extreme event that lead to *Quercus douglasii* dieback in California. These studies have improved upon the limitations that can arise when calibrating models using average climate metrics. However, they have not directly assessed how the frequency and magnitude of extremes, based on historical observations, have shaped contemporary plant distributions. For example, Zimmermann et al. (2009) did not consider extremes per se but variability in climate, Brown et al. (2018) modelled dieback to a single event, while Cavanaugh et al. (2015) focused on long-term average extremes.

Historically, the spatial and temporal resolution of climate datasets has presented a barrier to characterising extremes at ecologically relevant scales. The widely-adopted BIOCLIM variables (Xu and Hutchinson 2011), many of which are available globally at fine grain (approx. 1 km) as part of the WorldClim (Hijmans et al. 2005, Fick and Hijmans 2017) and CHELSA (Karger et al. 2017) datasets, are summaries of long-term average climate over periods of 30 years or greater. BIOCLIM variables include measures of temperature and moisture seasonality (e.g. BIO4, BIO15, BIO31) that describe month-to-month variability in long-term averages; however, they do not describe year-to-year variability which is necessary for examining temporal trends in extreme conditions. For example, variables such as maximum temperature of the hottest month (BIO5) and minimum temperature of the coldest month (BIO6) describe the long-term average over several decades and therefore cannot describe how these variables fluctuate from year-to-year. Conversely, global time-series climate datasets such as those developed by the Climatic Research Unit (Harris et al. 2020) can describe year-to-year variability but tend to be much coarser in spatial resolution (approx. 55 km), which can limit suitability for species distribution modelling, particularly in topographically

complex terrain (Guisan et al. 2007, Franklin et al. 2013). Downscaling and blending techniques (Kriticos et al. 2012) can be used to increase both the spatial and temporal grain of climate datasets, meaning that increasingly the component inputs needed for estimating extremes are available (Karger and Zimmermann 2018). However, there are many ways that extremes may be quantified and identifying how best to summarise their properties remains both a challenge and an opportunity (Sofaer et al. 2017, Suggitt et al. 2017).

The objective of this study was to explore the long-term influence of extreme weather, that is known elsewhere to have significant impacts on plant species demography, on contemporary distributions of plants in southeast Australia. We developed extreme variables using monthly time-series data to describe the observed frequency and magnitude of events that are hotter, colder or drier than typically expected. Spatial patterns in these variables can identify regions that are prone to being exposed to the most severe conditions and thus characterise important survival thresholds. We address a key research gap by taking a climatological view of extremes that considers weather over many years, rather than a small number of specific events that have been the focus of most previous studies (Bailey and van de Pol 2016). Base climate variables, analogous to standard BIOCLIM variables, are used as a baseline for comparison with extremes and year-to-year variability. Hence this study both showcases relevant methods for characterising extremes and tests their explanatory power for plant distributions in southeast Australia.

## Material and methods

### Study region

Species distribution models were developed for select plant species across the state of Victoria ( $141^{\circ}$ – $150^{\circ}$ E,  $34^{\circ}$ – $39^{\circ}$ S), southeast Australia. Elevations reach approximately 2000 m above sea level in the alpine regions in the northeast of the state, where mean annual temperature (MAT) is typically  $10^{\circ}$ C or below and precipitation (MAP) typically greater than 1400 mm. The landscape in the west of the state is generally much flatter, hotter (MAT up to  $18^{\circ}$ C) and drier (MAP of 600 mm or less) than the heavily forested and topographically complex regions to the east (Stewart and Nitschke 2017a, Fedrigo et al. 2019). Record-breaking heatwaves and droughts have impacted the region in recent years (Bureau of Meteorology 2009, van Dijk et al. 2013), and are expected to increase in both severity and duration in the future (Herold et al. 2018, Trancoso et al. 2020).

### Climate and extreme variables

Fine grained (approx. 250 m) monthly temperature (Stewart and Nitschke 2017a, b, 2018) and precipitation (Stewart et al. 2020a) datasets, specifically developed for ecological modelling across Victoria, provided our foundational data. While the component datasets are available at a daily frequency, we

decided to use monthly data to represent extremes, as this is the temporal frequency which is most likely to be available at fine spatial grain to species distribution modellers. Precipitation was expressed as a three-month rolling sum to represent cumulative seasonal dryness. Further details on how these datasets were generated, their availability and the associated cross validation statistics are provided in the Supporting information.

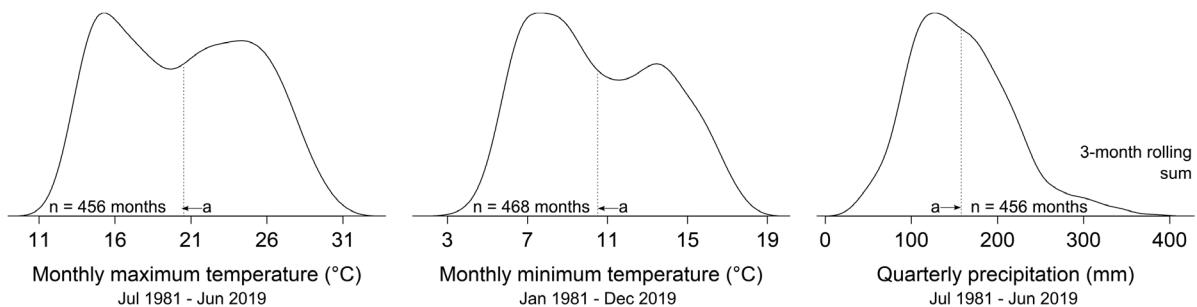
Variables representing extremes, and specifically the spatial and temporal distribution of the hottest, coldest and driest conditions, were developed. We focused on hottest, coldest and driest because it is these that quantify the stresses on plant populations, and the extremes in these could characterise the defining events in plant demography. The workflows for generating these variables are illustrated for a single location in Fig. 1 and a tutorial using spatial data with R code is provided in the Supporting information. Monthly time-series of maximum temperature, minimum temperature and precipitation were first collated for the period between 1981 and 2019 (top row, Fig. 1). The maximum temperature of the hottest month (TMXH), minimum temperature of the coldest month (TMNC) and precipitation of the driest quarter (PRDR) was then calculated for each year in the time series (middle row, Fig. 1). As our study site is in the southern hemisphere, annual periods were evaluated between July and June for TMXH and PRDR to avoid splitting years mid-summer. Finally, each of the annual values were collated (bottom row, Fig. 1), and used to calculate spatial predictors. The series of annual mapped values for TMXH, TMNC and PRDR were used to quantify the base climate that can be expected on a typical year, variability that occurs across years, and the frequency with which extreme events of a specific magnitude have occurred (i.e. the expected return interval based on historical observations). Base climate variables were calculated as the mean across all available years, and are equivalent to those estimated using the BIOCLIM approach (known as BIO5, BIO6 and BIO17; Xu and Hutchinson 2011). Variability was represented using the standard deviation to quantify spread around the base climate variables. Extremes were defined as the difference between base climate and the quantiles of annual values in our datasets corresponding to return intervals of between 5 and 30 years (Fig. 1, bottom row). For example, a 1-in-20 year extreme extracted from historical observations corresponds to the 95th percentile for TMXH and the 5th percentile for both TMNC and PRDR. This approach characterises the relative magnitude of extremes, that often have heavily-tailed distributions, while greatly reducing collinearity. The sets of variables used for species modelling (Table 1) included base climate alone ( $n=1$ ) and base climate in conjunction with either variability ( $n=1$ ) or extremes ( $n=6$ ).

### Species data

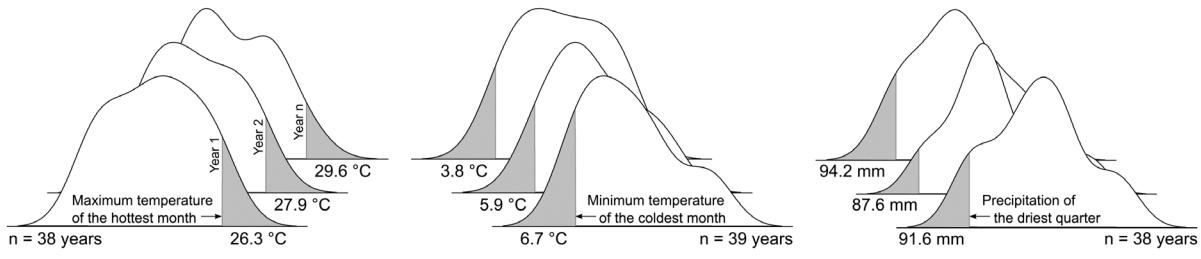
Comprehensive vegetation surveys were collated from 1864 sites within naturally occurring forested ecosystems across Victoria between 2006 and 2017 (Supporting information).

## Distribution of monthly values

Mean (a)



## Extremes extracted for each year in the time series



## Distribution of annual extremes and summary variables

Base = mean annual extreme (b)

Variability = standard deviation of annual extremes ( $\sigma$ )

Extremes = 1 in 5 year extreme (c); 1 in 30 year extreme (d)

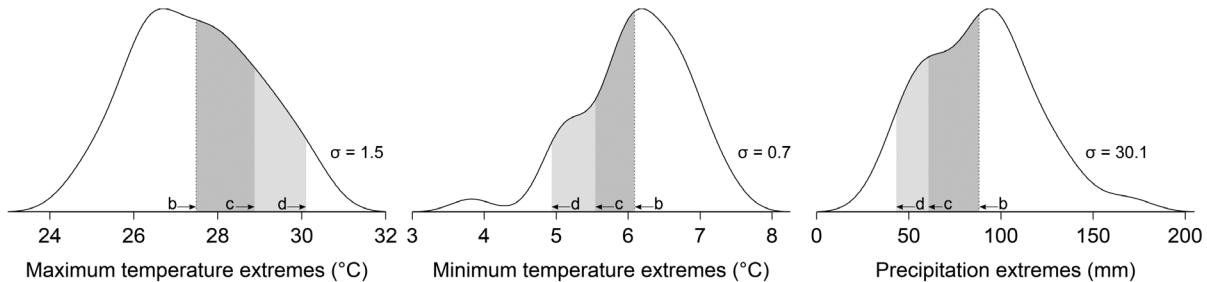


Figure 1. Workflow for generating variables describing base climate, variability and extremes using monthly maximum temperature, minimum temperature and precipitation data at a single location approximately 7 km east of Melbourne, Australia.

Surveys from the Victorian Forest Monitoring Program (Haywood et al. 2018) provided a large, systematically sampled, state-wide dataset representing a broad range of environmental conditions and plant species. The remaining datasets were typically focused on specific, but distinct, forested regions across the state. Plant species ( $n=37$ ) were selected for modelling based on the following criteria: 1) being capable of reaching at least 3 m in height (to maximise detection probability); 2) having at least 80 presence records available (to ensure sufficient numbers for reliable modelling

and evaluation); 3) comprising a variety of prevalent canopy and understory species (to represent an assortment of functional traits and levels of exposure to climatic conditions); and, 4) covering a range of realised distributions with varying spatial configurations (to ensure contrasting gradients in base climate, variability and extremes). An exception to criterion 1 was made for *Xanthorrhoea minor* (growing to approximately 1 m above ground but with a branching subterranean stem; Conn 1994) to provide contrast against a second grass tree species, *Xanthorrhoea australis*.

Table 1. Sets of climate variables used for modelling species distributions.

Set	Climate variables <sup>a</sup>	n variables
Base climate <sup>b</sup>	Mean maximum temperature of the hottest month (TMXH), minimum temperature of the coldest month (TMNC) and precipitation of the driest quarter (PRDR)	3
Variability	Base climate and variability (standard deviation) of TMXH, TMNC and PRDR	6
Extremes	Base climate and extremes <sup>c</sup> of increasing magnitude and decreasing frequency for TMXH, TMNC, PRDR	6

<sup>a</sup> Calculated using monthly maximum temperature (July 1981–June 2019), monthly minimum temperature (January 1981–December 2019) and quarterly precipitation (calculated as three-month rolling sum; July 1981–June 2019).

<sup>b</sup> Base climate variables are equivalent to BIOCLIM variables (Xu and Hutchinson 2011) BIO5 (TMXH), BIO6 (TMNC) and BIO17 (PRDR) calculated using long-term averages.

<sup>c</sup> Extremes are calculated as the difference between the base climate and magnitude of extremes observed at a frequency of once every n years (where n=5, 10, ..., 30) based on quantiles of historical observations.

## Modelling and analysis

Distribution models for 37 plant species were fitted with boosted regression trees (Elith et al. 2008) using the gbm.step function from the *dismo* package (Hijmans et al. 2017) in R. A total of eight models were fitted for each species using the variable sets described in Table 1. Models were fitted with a learning rate of 0.004, tree complexity of six and a bag fraction of 0.75, ensuring that the final models contained enough trees (> 1000) for stable predictions. Model performance was assessed using the area under the receiver operating characteristic (AUC) and the proportion of deviance explained ( $D^2$ ) on data held out for evaluation.

For evaluating the models, a spatially blocked k-fold cross validation design was used to ensure a robust analysis of model performance that reflects the ability of models to extrapolate into new space (Roberts et al. 2017, Valavi et al. 2019). Spatial blocks were assigned using the blockCV package (Valavi et al. 2019) in R. A block size of 0.5° (approximately 50 × 50 km) was selected based on patterns of spatial autocorrelation in the predictor variables and species observations (*spatialAutoRange* function, blockCV package). The number of folds in the blockCV varied from 4 to 10, depending on the amount and distribution of presence records for any given species. The blockCV package allocates blocks to folds, choosing an arrangement that balances prevalence in training and test sets as well as possible. A random 10-fold cross validation was also run to provide an estimate of interpolation error. Statistical comparisons of model performance were conducted using two-sided Welch's t-tests with p values adjusted for multiple comparisons using the method of Holm (1979).

In order to explore the drivers of model performance, we fitted a regression model with change in cross-validated  $D^2$  as the response (n=37; 1 row per species, modelled with 1-in-15 year extremes for consistency) and climate, maximum species height (indicative of hydraulic functioning; Liu et al. 2019, Stovall et al. 2019), and species prevalence as explanatory variables. Climate variables included the mean base climate and 1-in-15-year extremes for TMXH, TMNC and PRDR at all sites with presence records for individual species. This analysis was performed to help identify the characteristics of species and their recorded climatic niche that are associated with stronger predictive performance. Boosted

regression trees were used as the regression method, with a tree complexity of 2 to allow for limited interactions. Partial dependence plots (i.e. holding all other variables equal) were generated to understand the modelled responses.

## Results

The spatial distribution of the base climate and 1-in-15 year extremes across Victoria are illustrated in Fig. 2. The base climate variables show strong dependence upon topography, reflecting the methods used to create our foundational climate variables (Supporting information). Spatial patterns in extremes show how temporal variability in climate is influenced by coastal proximity, continentality, topography and orographic barriers.

Under the spatially blocked cross validation design, significant ( $p < 0.05$ ) improvements in cross-validated  $D^2$  and AUC were achieved across all species when either variability, or extremes at return intervals of 1-in-10 years or greater were added to the base variables as predictors of species distributions. This is shown in Fig. 3 which compares model performance changes for each data set (Table 1) with the base climate variables as a baseline. Extremes with a 1-in-15 year return interval were associated with the largest improvement in performance overall ( $\Delta D^2 = 0.030 \pm 0.015$ ;  $\Delta AUC = 0.017 \pm 0.007$ ); however, return intervals corresponding to the optimal model performance varied from species to species. Inclusion of variability as a predictor led to significant, but smaller, improvements in performance across species ( $\Delta D^2 = 0.016 \pm 0.013$ ;  $\Delta AUC = 0.011 \pm 0.006$ ). Model performance was low overall when using 1-in-5 year extremes ( $\Delta D^2 = 0.011 \pm 0.009$ ;  $\Delta AUC = 0.002 \pm 0.006$ ), with no significant changes in AUC compared with models with base climate only. When the evaluation design did not enforce spatial separation of training and testing sets (i.e. CV), near-universal performance improvements were achieved for all variable sets (Fig. 3, right panels).

Focusing now on individual species, the median change in model performance with extremes relative to base climate models was positive for 24 of 37 species (Fig. 4) under the spatially blocked cross validation design, including 19 that were statistically significant when considering all return intervals.

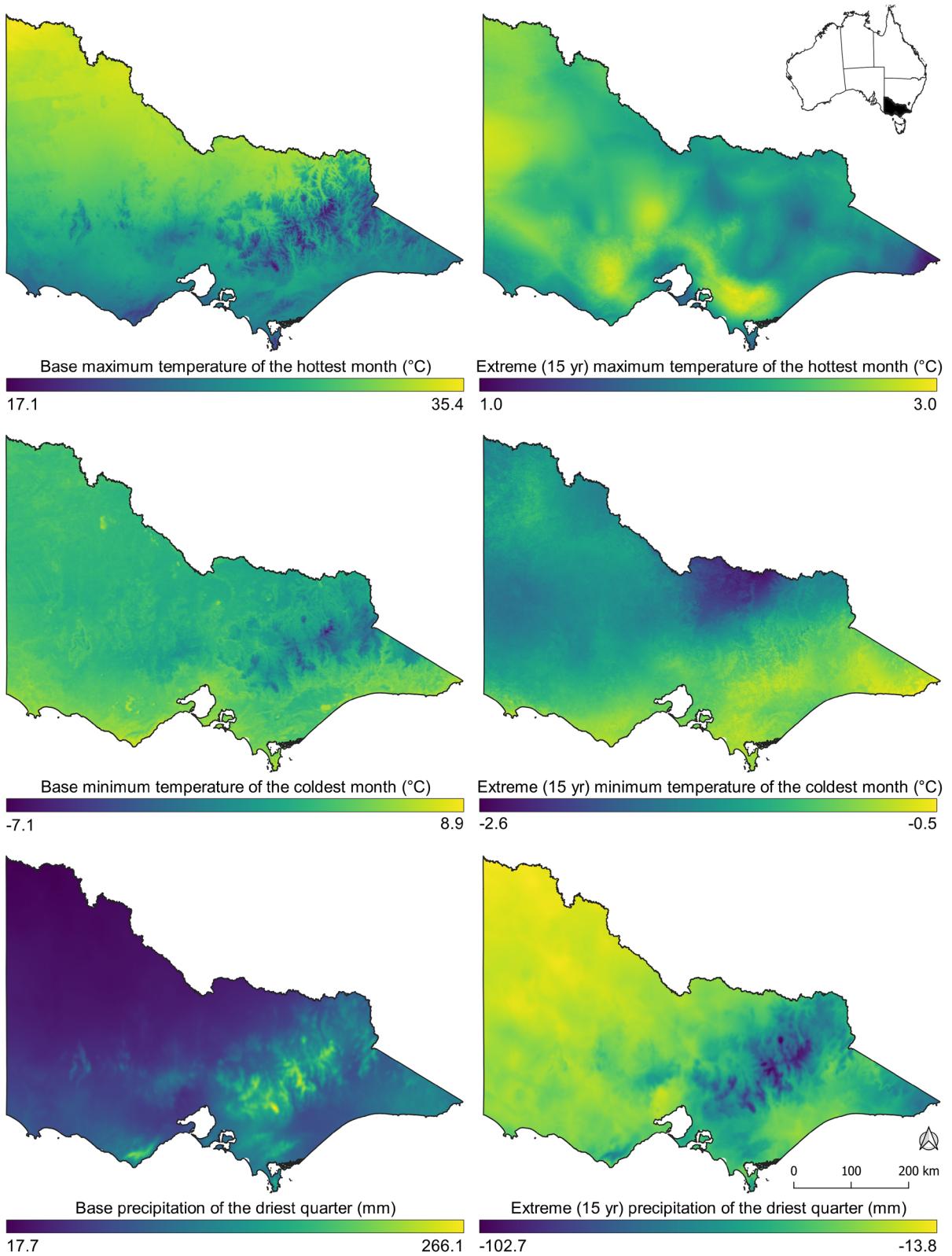


Figure 2. Base climate (mean) and the magnitude of extremes (relative to mean) expected once every 15 years based on historical observations across Victoria, southeast Australia.

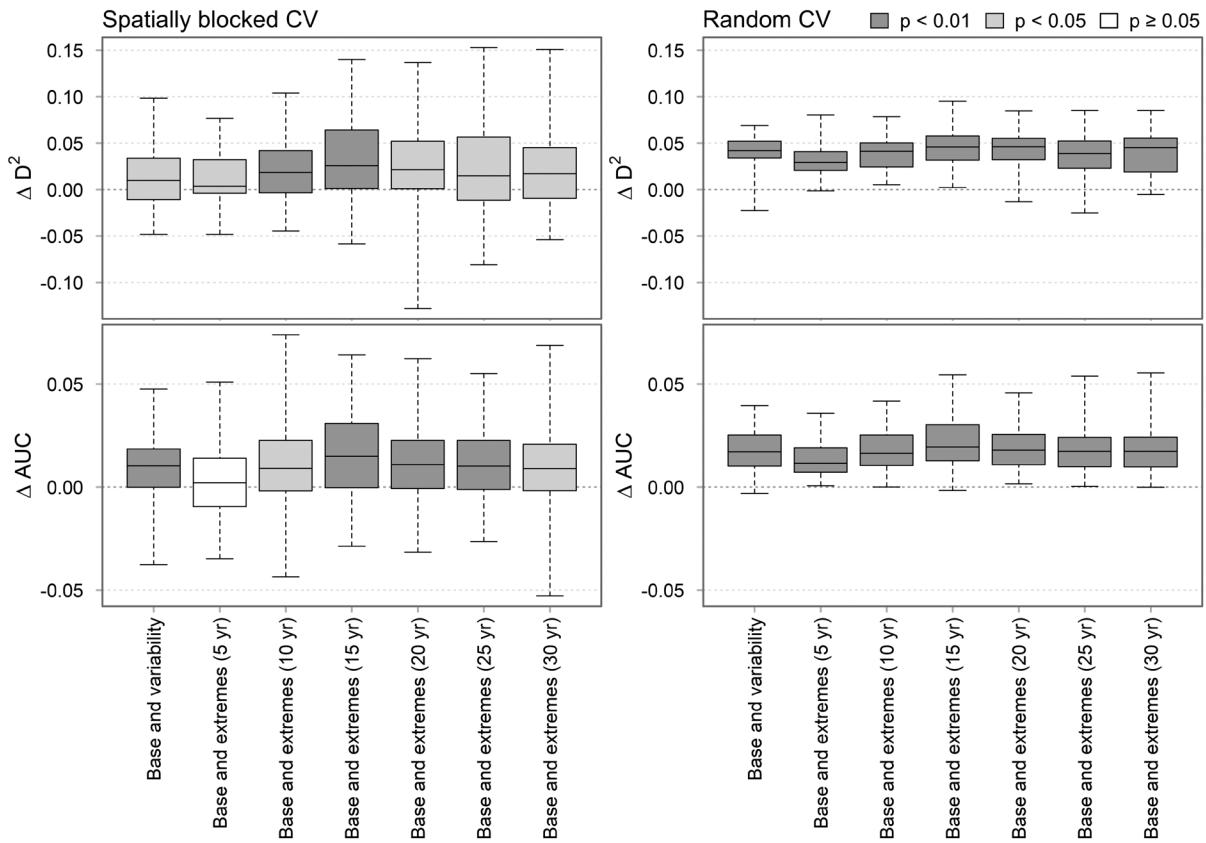


Figure 3. Pairwise comparisons of spatially blocked and random cross-validation performance for species distributions ( $n = 37$ ) modelled using base climate and either variability or extremes at varying observed return intervals relative to base climate alone.  $p$  values indicate statistical significance relative to base climate models. Boxes correspond to interquartile range, whiskers to minimum and maximum values.

Only 3 of 37 species showed a statistically significant decrease in  $D^2$  when modelled using extremes relative to base climate alone. The random cross validation results showed significant performance improvements for 34 of 37 species (top panel, Fig. 4). Cross validation statistics for all models are tabulated for each species in the Supporting information.

Most (14 of 18) species capable of reaching a height above 20 m performed better with the inclusion of 1-in-15 year extreme variables (Supporting information). The four species not responsive to 1-in-15 extremes are largely found within the coldest or most arid areas of the study region. *Eucalyptus delegatensis* and *Eucalyptus regnans* are montane species which persist in cooler, wetter environments. *Eucalyptus globoidea* and *Eucalyptus polyanthemos* both persist in some of the hottest and driest locations occupied by our study species. Prevalence was 0.1 or less for most species (7 of 9) with models that did not improve in response to extremes (Supporting information).

The regression model exploring correlates of model performance explained 39.4% deviance in the data. Extreme TMXH was the most important explanatory variable, comprising 53.4% of the total relative variable importance (Fig. 5), followed by base TMXH (15.1%), base PRDR (9.2%) and

maximum species height (8.4%). Improved model performance was associated with hot (increasing extreme and base TMXH) and dry (decreasing base PRDR) conditions as measured at presence sites, and increasing species height. Models explained more deviance for species with less severe PRDR extremes (Fig. 5, bottom right panel); however, the PRDR extremes are restricted in dry environments as they already receive little rainfall.

The spatial distribution of predictions varied considerably when modelled using base climate and extremes relative to base climate alone (Fig. 6). Relative changes in predictions typically showed strong spatial autocorrelation, with large spatially contiguous trends in model divergence often at the periphery of the modelled range. These trends were frequently associated with coastal proximity and positioning relative to topographic features in the landscape that are reflected in climate extreme variables (Fig. 2). For example, patterns in the predicted distribution of *Eucalyptus obliqua* were associated with strong TMXH and moderate PRDR extremes. Patterns in TMNC extremes associated with coastal proximity and PRDR extremes associated with topography influenced the predicted distribution of *Eucalyptus dives*.

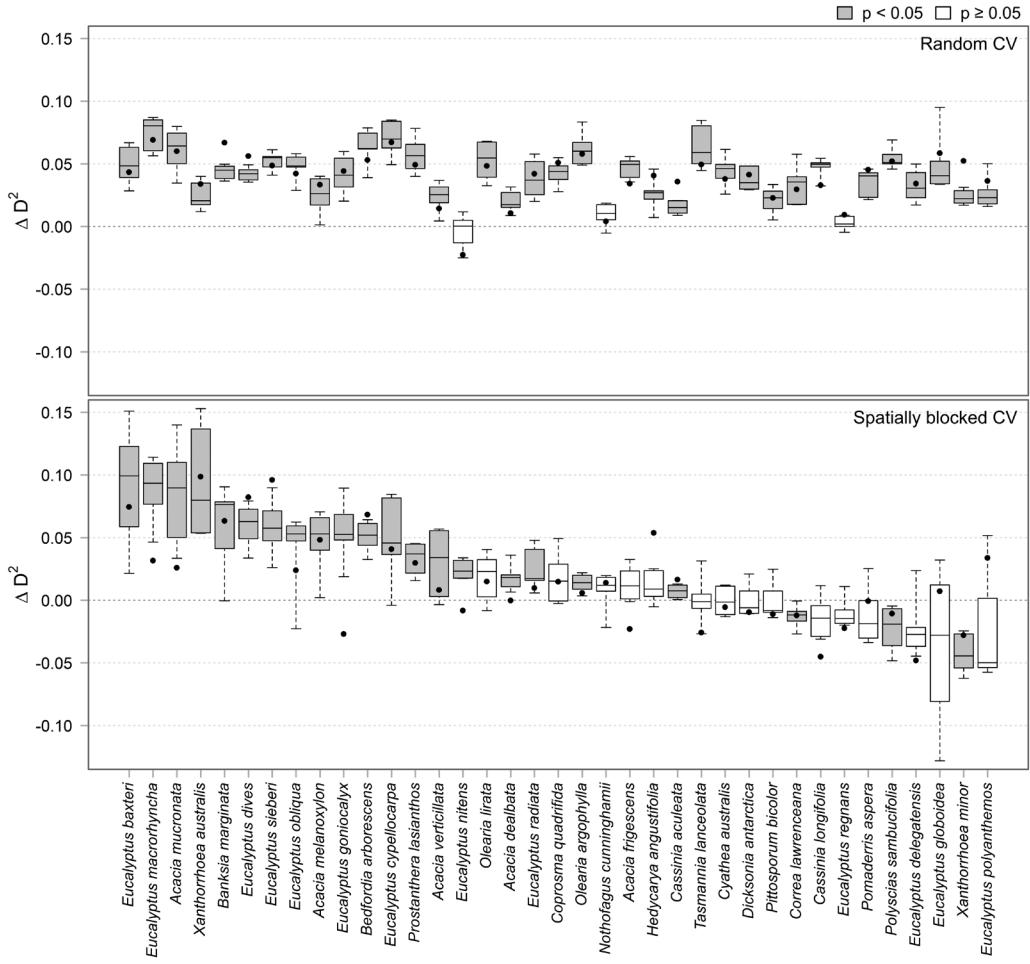


Figure 4. Pairwise comparisons of cross-validated change in the proportion of deviance explained for species distributions modelled using base climate and extremes (boxplots; 1-in-5 to 1-in-30-year return intervals) or base climate and variability (points) relative to base climate alone. p values indicate statistical significance of base climate and extremes relative to base climate alone. Boxes correspond to interquartile range, whiskers to minimum and maximum values.

## Discussion

Our results highlight that climate extremes have shaped the contemporary distributions of plant species in our study region. Extremes with a fixed expected frequency (e.g. 15 years) remained effective across most species, despite differences in the statistically optimal return interval, indicating that meaningful, parsimonious summaries of climate extremes can be produced using our methods. The main findings support but also build on the work by Zimmermann et al. (2009) and Cavanaugh et al. (2015) that considered climate variability and average extremes, respectively, to improve SDMs. Improvements in model performance, even where small, lead to considerable differences in predicted distributions. Changes in the modelled distribution of plant species were most pronounced at the range margins, indicating that the improvements in model performance are ecologically meaningful (Pulliam 1988, Zimmermann et al. 2009, Ratajczak et al. 2017, Osland et al. 2020).

Our findings have potentially significant ramifications for modelling species distributions under future climate change as increases in the frequency and magnitude of extreme weather events are expected in many parts of the world (Rahmstorf and Coumou 2011, Diffenbaugh et al. 2017, Mann et al. 2017), irrespective of mean conditions (Orlowsky and Seneviratne 2012). Neglecting to account for environmental variability, in this case climate extremes, can confound responses to changing mean conditions (Lawson et al. 2015). Our approach represents the frequency and magnitude of extremes that have historically been observed and allows for the skewed nature of extreme series to be represented using quantiles. This means that the extreme variables developed can be linked to projected climate change scenarios where both the mean and variability of extremes may change. Note, however, that there are considerable challenges and uncertainties in downscaling climate projections to such fine spatial grain (Chen et al. 2011, Baker et al. 2017), and therefore these efforts need to be treated with a large degree of caution. Provided suitable downscaling techniques are applied at

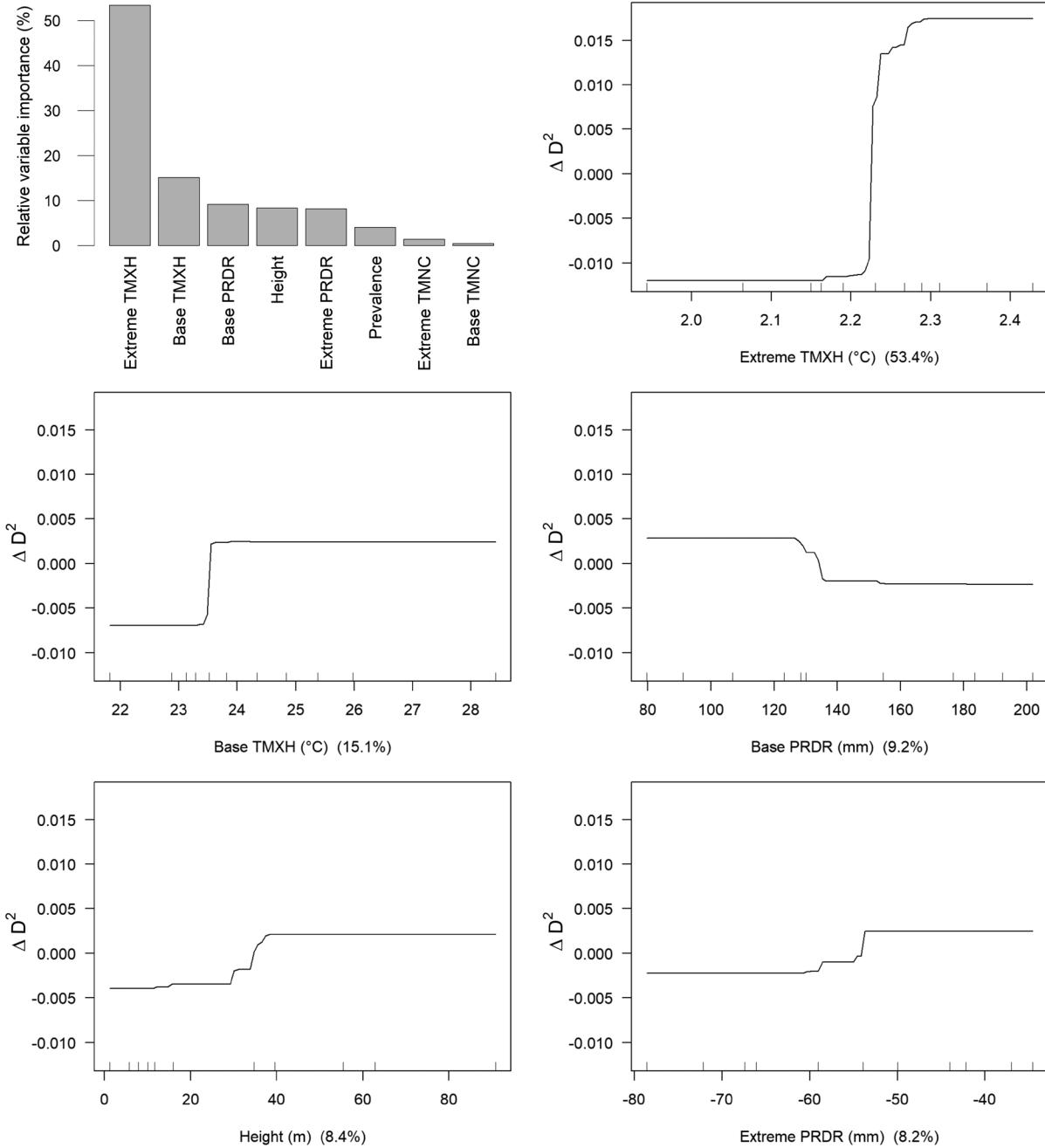


Figure 5. Relative importance and partial dependence plots of variables explaining the change in model performance when using 1-in-15-year extremes as predictors of species distributions.

appropriate spatial grain, these variables can be used to quantify not only how the distribution of extremes may change in the future but also how this will impact species persistence (Lloret et al. 2012) and productivity (Rypkema et al. 2019).

We used both spatially blocked and randomly sampled cross validation designs to evaluate both extrapolation and interpolation error, a distinction that is of critical importance given that the environmental niche of a species will likely shift in both space and time with climate. We also considered the observed frequency and magnitude of adverse climatic

conditions (i.e. hotter, colder or drier extremes) directly and tested the efficacy of a single (symmetrical) measure of variability. A near-universal improvement in model performance was achieved using base climate with any measure of variability or extremes when evaluated using a randomly sampled cross validation design, which was consistent with Zimmermann et al. (2009). The spatially blocked cross validation design, however, indicated that climate extremes provided an additional improvement in model performance over variability, particularly at an intermediate return interval of

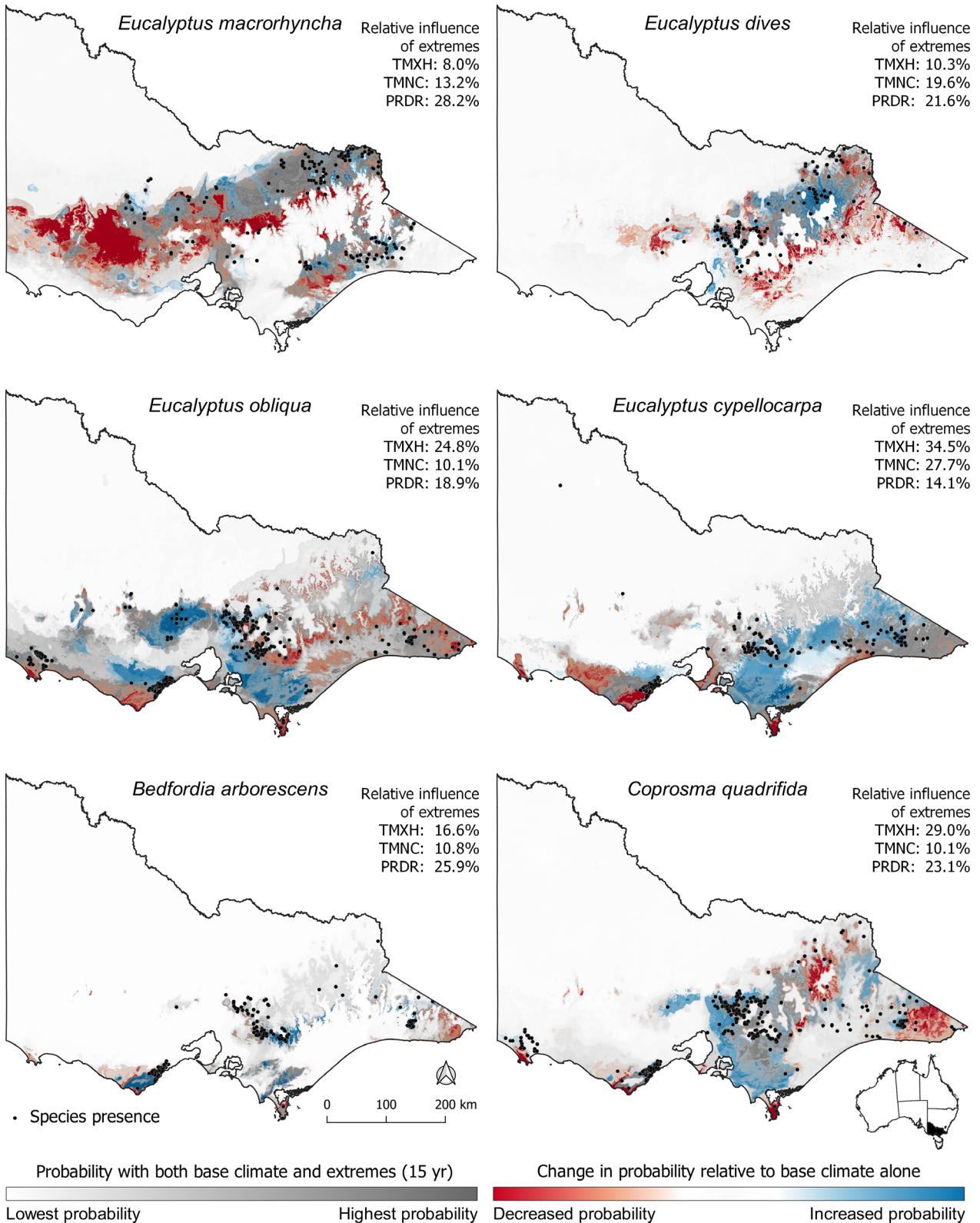


Figure 6. Difference in predicted distributions of species fitted with base climate and 1-in-15-year extremes, and base climate alone.

15 years. A simple, but probable, explanation for this is that the skewed distributions of extremes better capture the true constraints on plant species demography. This is supported by the results of the regression analysis, that indicated that hot and dry base climates and extremes as measured at presence sites were indicative of better statistical performance for our study species. By isolating the expected frequency and magnitude of the coldest winters, and the hottest and driest summers, we were thus able to characterise species responses to the extremes that limit their distributions.

Models for most (78%) species capable of growing to 20 m or taller were improved with the inclusion of 1-in-15 year extremes (Supporting information). Large trees can be highly sensitive to drought conditions and risk of mortality increases non-linearly with height due to hydraulic stress (Choat et al. 2012, Stovall et al. 2019). Four species capable of growing to 20 m in height were insensitive to extreme variables. *E. delegantesis* and *E. regnans* are montane species whose distributions do not appear to be limited by extreme maximum temperatures or very dry conditions relative to the remainder of the study region. *Eucalyptus globoidea* and *Eucalyptus polyanthemos* already occupy regions with the most severe maximum temperature and precipitation extremes across Victoria, resulting in fitted models that did not respond well to extremes.

Smaller species with a maximum height of 20 m also performed better in most cases (74%) when modelled using 1-in-15 year extremes. The results for these species were slightly more varied, potentially due to microclimatic effects that may attenuate the impacts of extreme weather events (Suggitt et al. 2011, Scheffers et al. 2014) or the potential for increased drought (Liu et al. 2019) or frost tolerance (Lim et al. 2017). For example, *Xanthorrhoea minor* which grows as a subterranean branching stem (potentially mitigating the impact of extreme weather) did not perform better with extremes, yet *Xanthorrhoea australis* which has a stem that grows above ground did. Due to the potential for microclimatic buffering or increased drought or frost tolerance of shorter species it could be expected that they would be much less responsive to extremes; however, our analysis did not strongly support this argument. From a hydraulic functioning perspective this may be due to the role of other traits such as wood density, sapwood-specific hydraulic conductivity and P50 (i.e. xylem tension where 50% loss of the maximum hydraulic conductivity occurs; Liu et al. 2019). Our results indicate that the trait of maximum height may be indicative, but not a dominant factor for determining if a species distribution has been influenced by extremes. Most importantly, it suggests that irrespective of plant height, extremes shape plant species distributions in southeast Australia.

The availability of suitable climate datasets (i.e. fine-grained in both space and time, to characterise both temporal patterns and spatial variability across complex terrain) has historically been a barrier to the implementation of these methods for describing extremes in SDM research. For this reason, we focused on developing extreme variables with monthly data so that the methods presented would be

compatible with datasets such as CHELSAcruts (Karger and Zimmermann 2018) that are currently available at fine spatial grain (approx. 1 km) globally. While extremes are likely to be important at finer temporal scales (e.g. daily), monthly surfaces are typically subject to fewer interpolation artefacts and are still capable of representing the spatial patterns of variability that are influenced by coastal proximity and terrain features. One limitation of our approach, however, is that we did not consider compound extremes (i.e. temporally autocorrelated events), and therefore we may not have detected the impacts that multi-year events such as drought (Mitchell et al. 2014) have contributed to the current spatial patterns in species distributions. Another limitation is that the analyses was limited to 39 years of monthly data. This may not have been long enough to suitably represent the distribution of extremes that have historically occurred, despite some of the most severe events on record across the study region having occurred within this time frame (Bureau of Meteorology 2009, van Dijk et al. 2013). We have focused on the long-term influence of extreme weather on plant species distributions in southeast Australia, however, there are many potential use-cases for extreme variables in SDM studies. Further opportunities remain to better define ecologically meaningful extreme events, and longer time series, consideration of temporal scale and autocorrelation are likely to be worth further examination.

## Data availability statement

All climate extreme variables and species distribution models are available from the CSIRO data access portal, <<https://doi.org/10.25919/b49k-9h77>> (Stewart et al. 2020b).

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*Data sources* – Species presence and absence records were collated from the following sources: Haslem et al. (2016), Leonard et al. (2016), Fairman et al. (2017), Kasel et al. (2017), Nelson et al. (2017), Chick et al. (2018), Haywood et al. (2018), Baker et al. (2019), Fedrigo et al. (2019). Species height were collated from the following sources: Conn (1994), Entwistle et al. (1996), Jeanes (1996), Puttock (1999), Aponte et al. (2020). Climate data and key supporting information presented in the supplementary materials not cited elsewhere were collated from the following sources: Hutchinson (1998), Sharples et al. (2005), Hutchinson et al. (2008), (2009), Hopkinson et al. (2012).

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