



UNIVERSITY
OF WOLLONGONG
AUSTRALIA

University of Wollongong
Research Online

Faculty of Science, Medicine and Health - Papers

Faculty of Science, Medicine and Health

2012

Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 x 300 km) and diverse region

Michael B. Ashcroft

Australian Museum, ashcroft@uow.edu.au

John R. Gollan

Australian Museum

Publication Details

Ashcroft, M. B. & Gollan, J. R. (2012). Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 x 300 km) and diverse region. *International Journal of Climatology*, 32 (14), 2134-2148.

Research Online is the open access institutional repository for the University of Wollongong. For further information contact the UOW Library:
research-pubs@uow.edu.au

Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 x 300 km) and diverse region

Abstract

The development of fine-resolution climate grids is an important priority in explaining species' distributions at the regional scale and predicting how species may respond to variable and changing climates. Recent studies have demonstrated advantages of producing these grids using large networks of inexpensive climate loggers, as the resulting grids can capture local climatic variations over a range of environments. In this study we extend these methods to develop innovative fine-resolution (25 m) climate grids for a large region (~200 x 300 km) of New South Wales, Australia. The key aspects of these grids is that they: (1) are based on near-surface (5 cm) observations to better reflect where many species live; (2) cover a wide variety of habitats including forests, woodlands and grasslands so that they are broadly applicable; (3) include both temperature and humidity, the latter of which has often been neglected in similar studies; (4) are developed using a variety of climate-forcing factors rather than relying only on elevation and geographic location; and (5) they focus on the extreme temperatures and humidities regardless of when these occur. Analyses showed that elevation was the dominant factor explaining mild temperatures (low maximums, high minimums), but cold air drainage, distance from coast, canopy cover and topographic exposure had more effect on the extreme maximum and minimum temperatures. Humidities were predominately determined by distance to coast, elevation, canopy cover and topography; however, the relationships were nonlinear and varied in both shape and effect size between dry and moist extremes. Extreme climates occur under specific weather conditions, and our results highlight how averaging climates over seasons or periods of consecutive days will include different weather patterns and obscure important trends. Regional-scale climate grids can potentially be further improved through a better understanding of how the effects of different climate-forcing factors vary under different weather conditions.

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

Publication Details

Ashcroft, M. B. & Gollan, J. R. (2012). Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 x 300 km) and diverse region. *International Journal of Climatology*, 32 (14), 2134-2148.

Fine-resolution (25m) topoclimatic grids of near-surface (5cm) extreme temperatures and humidities across various habitats in a large (200 × 300 km) and diverse region

Short title: Fine resolution topoclimatic grids

Ashcroft, Michael B.* Email: Mick.Ashcroft@austmus.gov.au

Gollan, John R. Email: John.Gollan@austmus.gov.au

Australian Museum, 6 College St, Sydney, NSW, Australia, 2010.

* Corresponding author. Phone x-61-2-9320 6475. Fax x-61-2-9320 6021

Research sponsored by NSW Environmental Trust – grant number GER-08-AM01, through the Great Eastern Ranges Conservation initiative.

Research is continuing under Australian Research Council Linkage Grant

LP100200080, in conjunction with the University of New South Wales, the NSW Office of Water, and the Central West Catchment Management Authority.

ABSTRACT

The development of fine-resolution climate grids is an important priority to explain species' distributions at the regional scale and predict how species may respond to variable and changing climates. Recent studies have demonstrated advantages of producing these grids using large networks of inexpensive climate loggers, as the resulting grids can capture local climatic variations over a range of environments. In this study we extend these methods to develop innovative fine-resolution (25m) climate grids for a large region (~200km by 300km) of New South Wales, Australia. The key aspects of these grids is that they: 1) are based on near-surface (5cm) observations to better reflect where many species live; 2) cover a wide variety of habitats including forests, woodlands and grasslands so that they are broadly applicable; 3) include both temperature and humidity, the latter of which has often been neglected in similar studies; 4) are developed using a variety of climate-forcing factors rather than relying only on elevation and geographic location; and, 5) they focus on the extreme temperatures and humidities regardless of when these occur. Analyses showed that elevation was the dominant factor explaining mild temperatures (low maximums, high minimums), but cold air drainage, distance from coast, canopy cover and topographic exposure had more effect on the extreme maximum and minimum temperatures. Humidities were predominately determined by distance to coast, elevation, canopy cover and topography, however the relationships were non-linear and varied in both shape and effect size between dry and moist extremes. Extreme climates occur under specific weather conditions, and our results highlight how averaging climates over seasons or periods of consecutive days will include different weather patterns and obscure important trends. Regional scale climate grids can potentially be further

improved through a better understanding of how the effects of different climate-forcing factors vary under different weather conditions.

KEY WORDS canopy cover; climate variability; coastal influence; cold air drainage; microclimate; regional climate; synoptic patterns; topoclimate

1. Introduction

Climate change in the 21st century is expected to lead to dramatic shifts in species' distributions and increased extinction risks (Thomas *et al.*, 2004; IPCC, 2007; Thuiller *et al.*, 2008). However, these risks may currently be overestimated, as predictions are typically based on coarse-scale climate grids that ignore microrefugia where species can persist despite unfavourable regional conditions (Pearson, 2006; Ashcroft, 2010; Austin and Van Niel 2011). A growing number of studies are therefore developing fine-resolution climate grids that are more suitable for landscape and regional scale climate change analysis (e.g. Fridley, 2009; Bennie *et al.*, 2010; Shoo *et al.*, 2010), and are at a more appropriate scale for environmental planning and management (Ferrier *et al.*, 2002).

A number of studies have downscaled coarse-scale climate grids based only on elevation and geographic location (e.g. Trivedi *et al.*, 2008; VanDerWal *et al.*, 2009), however temperatures are also affected by other climate-forcing factors that become increasingly important at finer resolutions (Daly, 2006). Cold air drainage, topographic exposure, canopy cover and coastal influences are four examples of factors that can dramatically affect climate at fine scales, and indeed, a number recent studies have found that the effects of these factors can dramatically reduce correlations between temperature and elevation (Ashcroft *et al.*, 2008; Fridley *et al.*, 2009; Suggitt *et al.*, 2011). The quality of climate data is often overlooked as a source of error in studies that explain or predict species distributions (Soria-Auza *et al.*, 2010), and as the quality of fine-resolution climate grids cannot be assessed by resolution alone, more attention needs to be given to climate-forcing factors other than elevation (Daly, 2006).

1.1 Issues of instrumentation and recording

The first problem that arises when catering for a wider variety of climate forcing factors is that standardised weather station networks (i.e. sparsely distributed Stevenson screens placed ~1.5–2 m above the surface of flat, cleared areas) are designed to reduce the effects of many of these factors, and are therefore unsuitable (Geiger, 1971; Daly, 2006). For example, weather stations are biased against areas of high topographic shelter (i.e. shading from winds or radiation) and canopy cover, and therefore standardised weather stations cannot be used to determine the effects of these factors or predict the climate in environments such as sheltered gullies or forests. While habitat variables such as these have been considered separately to climatic factors when predicting species distributions, this is insufficient when there are complex interactions between habitat preferences and climate. For example, Suggitt *et al.* (2011) provide numerous examples of species that occupy different habitats within their range to maintain a suitable climate, and differences in climatic variability between different habitats can also affect community structure (Retana and Cerdá, 2000). It is therefore more appropriate to deal with interactions between topography, habitat and climate when the climate grids are produced, rather than treat climate and habitat independently (Gutiérrez Illán *et al.*, 2010; Suggitt *et al.*, 2011).

The second issue with standardised weather stations is that the number of stations needed to establish relationships increases sharply as the number of climate-forcing factors considered increases (Vanwallegem and Meentemeyer, 2009). While a low density of standardised weather stations may be sufficient to produce coarse-scale climate grids based only on elevation and geographic location, they are insufficient to determine the effects of many factors at fine-resolutions. Standardised weather stations

are also typically expensive, and therefore cost hinders the deployment of large networks of standardised weather stations covering a broad range of habitats.

These problems with standardised weather stations have been partially addressed by the recent availability of relatively inexpensive temperature loggers (e.g. Lookingbill and Urban, 2003; Ashcroft, 2006). The small size of these sensors allows them to be placed in a variety of environments, and the lower cost allows scientists to increase sample size and determine the effects of a wider variety of climate forcing factors. Historical studies of microclimate were often non-spatial, focusing on statistical summaries in a limited number of locations or environments (Geiger, 1971; Chen *et al.*, 1999). However, the low cost of these microclimatic sensors have more recently allowed spatial grids of topoclimate to be produced (e.g. Lookingbill and Urban, 2003; Ashcroft, 2006).

One issue that remains to be resolved is the method of protecting these devices from direct solar radiation. For example, while some have used the shade of trees to provide shelter (e.g. Lookingbill and Urban, 2003; Lundquist and Huggett, 2008), this also limits the environments where temperatures can be recorded. In the same way that standardised weather stations in flat, cleared areas cannot predict the climate in forests, sensors placed exclusively under forests cannot predict the climate in open areas. The goal of developing climate surfaces that consider interactions between climate, habitat and topography requires sensors in a variety of environments, and therefore sensors must be sheltered in a way that is not specific to any environment. Recently, sensors have been wrapped in foil (Suggitt *et al.*, 2011), although it is not clear how much protection this offers, or how it affects observations.

The second issue with low-cost loggers concerns the variables that should be recorded to accurately capture the climate of a location. Inexpensive loggers have generally only been used to record temperature, while standardised weather stations also capture other factors that are relevant for species, such as rainfall, humidity and wind. Moisture availability is a particularly important aspect of climate, and given that inexpensive humidity loggers are also available, including humidity in studies is an important priority. Humidity also has some advantages over the rainfall predictors frequently used in ecological studies, as rainfall only acts indirectly to determine the moisture available to species. Moisture availability is also influenced by factors such as topographic run-on and run-off, soil texture and drainage, and variations in evapotranspiration due to temperature and canopy cover.

A final instrumental issue that warrants discussion is the height at which observations are made. While atmospheric meteorologists sometimes refer to the standardised height of 1.5–2 m as ‘near-surface’ (e.g. Dobrowski *et al.*, 2009), it is well known that the climate at this height can differ substantially from the actual ground surface (Wolfe, 1945; Geiger, 1971). Indeed, the standardised height for Stevenson screens was deliberately chosen to minimise the effects of many climate-forcing factors that act nearer the surface (Geiger, 1971), yet these factors still influence species distributions. Obtaining climate observations nearer the surface is obviously important for ground dwelling plants and animals, but is also of interest for trees or arboreal species that may occur there while they are immature and therefore more susceptible to climate extremes (Kennedy, 1997).

Geiger (1971) referred to the standardised climate at 1.5 m as ‘human climate’ and the near-surface climate as ‘habitat climate’, however habitat will inevitably vary

from species to species. Determining the climate in specific habitats such as under rocks, inside tree hollows etc is largely a species-specific issue. For climate grids to be broadly applicable over a range of species, the climate in any particular grid cell should be based on the general environment, topography and habitat, not a specific microclimate within that cell. Throughout this article we therefore use ‘macroclimate’ to refer to the general trend in climate based only on elevation and geographic location, ‘microclimate’ to refer to the climate in a specific microhabitat (e.g. under a rock), and ‘topoclimate’ to refer to the intermediate climate grids that are not specific in microhabitat, but which consider a broad range of climate forcing factors. Note that none of these definitions is based on scale. This is because increased computing power increasingly allows finer resolution grids to be produced over larger areas, however a fine-resolution climate grid based only on elevation and geographic location still reflects macroclimate rather than topoclimate or microclimate.

1.2 Describing climatic patterns

Climate can be represented spatially as raster grids of factors such as mean annual temperature and precipitation, or average summer maximum and winter minimum temperatures. However, the climate of an area is not simply its long term average, but rather the array of conditions that are possible and how often those conditions occur (McGregor, 2006). For example, two locations with the same long-term average summer maximum temperature and rainfall may vary according to how frequently extremely hot or dry conditions occur, and extreme conditions can have an important influence on species distributions (Mitikka *et al.*, 2008; Adler *et al.*, 2009; Beever *et al.*, 2010; Giesecke *et al.*, 2010).

One method to cater for this variability is to use bioclimatic predictors such as BioClim (Houlder *et al.*, 2003) and WorldClim (Hijmans *et al.*, 2005), which include some additional grids that estimate daily and seasonal variability. However, there are still limitations on how well these can predict inter-annual changes in climate. For example, a static map of summer maximum temperature that is produced based on an elevation sensitive interpolation does not provide any information on which climate forcing factors influenced that distribution. It is therefore impossible to predict how the pattern would change in future years if the frequencies of cloudy days, wet weather, westerly winds, etc varied.

Recently, studies have differentiated between climatic patterns under different weather conditions, as determined using synoptic patterns, or wind speed and direction (Lundquist and Cayan, 2007; Milionis and Davies, 2008; Ashcroft *et al.*, 2009). If we know the frequency of different weather conditions and the spatial distribution of climate under each, then these can be combined to produce seasonal averages and spatially variable estimates of change. In contrast, seasonal averages cannot be separated into individual weather patterns, and therefore spatial variations in climate change due to changing weather patterns are uncertain and often idealised as uniform warming across a landscape (e.g. see examples in Beaumont *et al.*, 2007).

While climatic grids based on weather patterns therefore have some advantages, it is difficult to describe these patterns in large regions where different conditions may be present in different locations. An alternative we explore in this article is to focus on the extreme conditions at each location, that is, the hottest, coldest, driest and moistest. These are the conditions that are most likely to be physiologically limiting for species, so they are of great ecological interest. By focusing on the extreme observations at each

site, we are indirectly focusing on the weather conditions that drive those observations, even though these conditions may occur on different days at different locations. In contrast, focusing on a predefined season or group of consecutive days will inevitably include different weather patterns (they typically only last a few days; Stahl *et al.*, 2006a) and confound which climate-forcing factors are most important for extreme conditions.

It is worth stressing that describing climate patterns is not an exercise in determining which factors significantly affect climate. The climate-forcing factors are already generally well known. Indeed, the main problem addressed when producing climate grids is quantifying the magnitude of the effect each factor has, and these effects typically vary both spatially and temporally. For example, temperature generally decreases at approximately 6°C/1000m, however it may be as low as 3–4°C/1000m in winter and for minimum temperatures, and up to 10°C/1000m in summer and for maximum temperatures (Lookingbill and Urban, 2003; Stahl *et al.*, 2006b; Ashcroft *et al.*, 2008). Temperature inversions are even possible under still, anti-cyclonic conditions (Milionis and Davies, 2008; Dobrowski *et al.*, 2009; Daly *et al.*, 2010). Similarly, the effects of radiation and canopy cover are lower during cloudy conditions (Bennie *et al.*, 2008; Suggitt *et al.*, 2011), and the effect of exposure varies according to wind speed and direction (Lundquist and Cayan, 2007; Ashcroft *et al.*, 2009). Demonstrating differences in climate between different environments is rather trivial. It is more relevant and challenging to quantify how those differences vary in space and time, and this is crucial to understanding climate variability and change.

1.3 Objectives of this study

The main objective of this study was to develop innovative fine-resolution (25m) climate grids for a large region of New South Wales (~200km by 300km) that were suitable for explaining and predicting species' distributions. The key aspects of these climate grids is that they: are 1) based on near-surface (5cm) observations to better reflect where many species live (Kennedy, 1997); 2) cover a wide variety of habitats including cleared pastures, rainforests, eucalypt forests, woodlands, coastal dune communities and upland swamps so that they are broadly applicable; 3) include both temperature and humidity, the latter of which has often been neglected in similar studies; 4) are developed using a variety of climate-forcing factors rather than relying only on elevation and geographic location; and, 5) they focus on the extreme temperatures and humidities regardless of when these occur. We did however examine the timing of extreme conditions to assess how well they could be captured by seasonal averages.

While inexpensive climate loggers have already been used to produce climate grids in other studies, we are not aware of any publications that have used these grids to comprehensively predict current or future distributions for a wide range of species. We suggest that this is because they have focused on too narrow a range of environments, been at too small an extent to be broadly applicable, or have neglected moisture. We hope that by overcoming these limitations we will encourage ecologists to use climate grids that are potentially more biologically meaningful than simplistic interpolations from standardised weather stations. While it is sometimes assumed that climate is unimportant to species distribution at fine scales (Pearson and Dawson, 2003), this is not the case when accurate topoclimatic grids are used (Gutiérrez Illán *et al.*, 2010).

2. Material and methods

2.1 Study area and observation locations

The study was centred on a large coastal catchment (~60,000km²) of New South Wales (NSW; 31.4–33.4°S, 149.4–152.6°E; Fig. 1) known as the Hunter Valley. The eastern boundary was the coastline of mainland Australia, while the northern, southern and western boundaries were selected to ensure the quality of the climate data gathered. That is, to accurately capture the effect of each climate forcing factor it is crucial that the survey locations are chosen to minimise correlations between predictors, ensure that the full range of each factor is sampled, and to ensure that samples are not spatially auto-correlated (e.g. by having all high elevation sites on the same mountain). In our case, we chose the study area to ensure there were four distinct areas where elevation exceeded 1000m, low-elevation sites were not clustered in the central valley of the study area, and the correlation between elevation and distance from coast was minimised as much as possible.

The mean annual temperatures of the study area range from 10°C atop the highest mountains, to 18°C on the coastal plains, while average annual precipitation varies from 650mm on the inland plains to 1300mm on the coast (Hijmans *et al.*, 2005). Rainfall is higher during the summer months, and although snow occasionally occurs at inland and high elevation sites, to our knowledge there was no snow during the duration of this study.

The study area was diverse in terms of topography and land use. Much of the study area had been cleared for agriculture and open-cut mining, but there were also many national parks and managed forests. Common land uses included cattle grazing and vineyards. Vegetation was diverse, including coastal dune shrublands, grasslands,

upland swamps, eucalypt forests and woodlands, with rainforests in coastal, high elevation and sheltered topographic locations.

2.2 Environmental data

The fourteen potential climate-forcing factors considered as part of this study were: latitude; distance to coast; elevation; two estimates of canopy cover; exposure to the northwest, northeast and south; distance to water body; locally averaged flow accumulation; the relative elevation within a 500m radius; and the percentage of ground surface within 1m of the sensors that was bare soil, rock or live vegetation.

Longitude was not considered as it was correlated with distance from coast, with the latter considered to be a more direct predictor of climate (continentality effects; Daly, 2006). A topographic estimate of incoming solar radiation was not considered directly, despite the fact that radiation is a key driver of climate (Geiger, 1971). We omitted it because the radiation reaching the ground is influenced by cloud cover, canopy cover, topography and latitude, and we could not adequately estimate and validate the spatial and seasonal variations in radiation over such a large area considering all these factors. In addition, while clear sky radiation typically displays a north-south trend, trends in vegetation and climate are typically northwest-southeast (southern hemisphere) or southwest-northeast (northern hemisphere) due interactions between time-of-day and radiation, or exposure to winds (Ashcroft *et al.*, 2008; Bennie *et al.*, 2008). Indeed, in cloudy or windy locations the east-west effect of winds can be greater than the north-south effect of radiation (Pepin and Lundquist, 2008). Finally, it is not universally true that temperatures increase with radiation, as for example, radiation increases with elevation while temperatures decrease (Körner, 2007). Due to

these factors, similar studies have found that topographically derived estimates of clear-sky radiation often have a limited effect on the distribution of climate (e.g. Lookingbill and Urban, 2003; Ashcroft *et al.*, 2008; Vanwallegem and Meentemeyer, 2009). Therefore, the exclusion of a radiation predictor is probably of little consequence given that latitude and canopy cover were included directly as predictors, cloud cover was assumed to be a function of elevation and distance to coast, and topography was considered by the exposure predictors.

Latitude was taken directly from a GPS where our sensors were placed. Elevation was obtained from a 25m-resolution drainage-enforced digital elevation model (DEM) derived from 10m contours by the NSW Dept. of Lands. Canopy cover at a 25m resolution was taken from the interim foliage projected cover (FPC) data for NSW prepared using remote sensing (DECC, 2008).

Exposure to the northeast, south and northwest (azimuths of 30° , 180° and 300° respectively) were derived from the DEM using the methods of Ashcroft *et al.* (2008). This method estimates the exposure to wind using the hillshade command of ArcGIS at different altitudes. Higher values indicate a more sheltered location. Azimuths were selected based on the most influential wind directions in an adjacent study area in New South Wales (Ashcroft *et al.*, 2008). Note that while aspect and slope are more commonly used in ecological studies, these are inadequate because they fail to consider topographic shading (Pierce Jr. *et al.*, 2005) and are sensitive to DEM errors (Van Niel *et al.*, 2004). For example, a flat area may be exposed to many directions if it is on a hilltop, but sheltered if it is in a gully. While it has been suggested that exposure predictors may be unnecessary (Shoo *et al.*, 2010), this recommendation was based on air temperatures at a height 1.5m, an 80m resolution DEM, and only a 10° range of

altitude. Exposure is expected to have more effect nearer the surface, at finer resolutions and over a larger range of altitudes, and has been shown to be a dominant predictor of summer maximum soil surface temperatures under these circumstances (Ashcroft *et al.*, 2008).

Distance to coast was calculated as a Euclidean distance in metres using ArcGIS. This was obviously sensitive to how the coastline was defined—especially considering that climate can change more rapidly nearer the coast (see results). The coastline could have been defined in a number of ways by including or excluding coastal lakes and estuaries (some of which are intermittently open to the ocean), and by how far up the mouths of rivers the coastline was defined. We elected to define the coastline as areas where the DEM did not define an elevation. This meant that lakes and estuaries were included as part of the coastline, as well as the mouths of large rivers up to a maximum distance of ~20km.

Cold air drainage is a key driver of minimum temperatures, yet it is unclear how it should best be captured to produce climate grids. We therefore tested three different methods. First, we used the average log flow accumulation (determined using the DEM and the hydrology commands of ArcGIS) with a five cell radius (Chung *et al.*, 2006). Second, we calculated the distance to water bodies. Distance to streams has been shown to be an important predictor of minimum temperatures (Lookingbill and Urban, 2003), but we calculated the minimum distance to a lake, stream or the coast, as these also have effects (Daly, 2006). Both the flow accumulation and distance to streams predictors try to estimate where cold air converges, whereas the amount of pooling is also influenced by how well it drains away (Lundquist *et al.*, 2008). We therefore used a third predictor, designed to predict how well air would drain away from a location. This ‘relative

elevation' predictor was simply the difference between the elevation of a site and the minimum elevation within a 500m radius (Bennie *et al.*, 2010; and see Daly *et al.*, 2007 for a similar methodology at coarser resolution). A high value indicated a perched location where air could drain away. A low value indicated it was either a valley or flat area where air could pool. Note that while the former two predictors produced highly channelised results, the latter predictor produced both pools and channels in different locations.

In February 2010 we recorded the percentage of the ground surface (within 1m of sensors) that was bare soil, rock, live vegetation, or leaf litter. These summed to 100%, so only the former three were considered (the fourth would not have been independent). We also recorded the canopy cover of both trees and shrubs in August 2009, November 2009 and February 2010. The shrub and canopy layers were estimated independently, so they could sum to more than 100%. We summed the shrub cover and tree cover and averaged over the three periods to produce an estimate of canopy cover that ranged from 0 to 138%. Canopy cover is spatially and temporally variable, and the relevance of different canopy and subcanopy layers is unclear. In addition, the effective canopy cover would be influenced by seasonality and the path of the sun, and our estimate does not consider this. There are important unresolved issues regarding how canopy cover should be meaningfully recorded, and we do not imply that our method is optimal.

The first ten factors mentioned (latitude; distance to coast; elevation; remotely sensed canopy cover; flow accumulation; distance to water bodies; relative elevation; and exposure to northwest, northeast and south) were each available as GIS layers, and could therefore be used to extrapolate results spatially to unobserved locations and

produce climate grids. By including the amount of soil, rock and vegetation within 1m, and replacing the remotely sensed canopy cover with the observed canopy cover, a set of 13 factors was available for producing non-spatial models. The non-spatial models give an indication of how much the accuracy of climate predictions could be improved if better GIS layers or site specific environmental data were available.

2.3 Climate observation

We placed DS1923 iButton sensors (Maxim) at 150 selected sites (Fig. 1), covering a broad range of each environmental factor including distance to coast (ranging between 200 m and 224 km), elevation (ranging between 2 m and 1428 m) and remotely sensed canopy cover (ranging between 0 and 100%). Sites were selected to minimise correlations between the 10 spatial predictors. Only 6 of the 45 combinations had correlations (r^2) greater than 0.1, and only 1 greater than 0.3. The highest correlation was between distance to water bodies and flow accumulation ($r^2 = 0.41$), although these factors were seldom selected in our models and this correlation is unlikely to have impacted results. The second highest correlation was between elevation and distance from coast ($r^2 = 0.28$), which we minimised but could not avoid completely as elevation was generally higher at inland locations. While this correlation was undesirable, it was unlikely to be strong enough to have a direct detrimental effect on results. However, it was strong enough to hinder the use of interaction terms such as elevation \times distance to coast. For example, although the correlation (r^2) between elevation and distance to coast was only 0.28, the interaction term had much higher correlations with these two terms ($r^2 = 0.71$ and $r^2 = 0.66$ respectively). Therefore, we did not include interaction terms in this study, although we acknowledge that interactions may exist. Minimising

correlations between predictors and ensuring the full range of conditions is sampled is critical to these types of studies, as the representativeness of climate data can be more important than the interpolation method employed (Lundquist *et al.*, 2008).

The DS1923 iButtons were housed inside white PVC jars, approximately 10 cm in diameter, 15 cm high, and 1 mm thick. The jars were inverted and secured to the ground using tent pegs. Wooden stakes were erected around sensors where it was necessary to protect them from cattle or other disturbances. Holes (9mm diameter) drilled in the side of the jars allowed free passage of air, water was free to drain out the bottom as the lids were removed, and the containers provided some protection against direct sunlight and rainfall. The DS1923 iButtons were suspended in netting inside the containers such that they were approximately 5cm above the ground and not in contact with the container. Photos and further usage information are included in section S1 in Supporting Information.

As the protection from radiation would obviously differ from more expensive radiation screens, such as Gill-type shields, we wanted to validate that the observations were reliable. This was not straight forward as we were making observations at a different height to standardised weather stations and therefore expected to record higher maxima and lower minima. Indeed, we wanted and expected our stations to give different readings to standardised weather stations because we were recording climate in different environments. To address this issue we placed DS1921G (temperature only) iButtons 1cm below the soil surface at 34 selected sites and recorded hourly temperature over the summer months (December to February; see section S2 in Supporting Information for detailed results). Results were consistent with theory (Campbell and Norman, 1998) and previous studies (Likso, 2006; Bennie *et al.*, 2008) in that the 5cm

maximum air temperatures at open sites (up to 55.7°C) were ~10°C higher than nearby Bureau of Meteorology observations at ~1.5m (up to 43.2°C), but ~10°C lower than the soil surface temperatures (up to 68.5°C). There was no evidence that the plastic containers were causing maximum temperatures at exposed locations to be markedly higher than observed soil surface temperatures or expected 5cm air temperatures, and other studies have reported that the bias between Gill shields and PVC shields can be as little as 1°C (Daly *et al.*, 2007). Therefore, the 5 cm sensors gave a plausible approximation of near-surface air temperatures, and provided a standardised environment that could be deployed in a wide range of environments. Our observations of maximum temperatures would be cooler than the conditions that exposed grasses and ground surface dwelling fauna experience, but warmer than the conditions experienced by organisms that take refuge under rocks or deep beneath the soil surface. These potential errors are discussed further in section 3.9.

Sensors were initially deployed in May 2009, and programmed to make hourly records at high resolution (0.0625°C, 0.04% Humidity) for 85 days from 1st June 2009 to 24th August 2009 inclusive. As it took 7 days to drive around the sites to download data and reprogramme the devices, subsequent recording was done from 2nd September to 25th November 2009, 3rd December 2009 to 25th February 2010, and 5th March 2010 to 28th May 2010. Both the temperature and humidity observations were manually corrected using internal calibration data. Temperature is accurate to 0.5°C. Humidity is less accurate, as the devices saturate when humidity is greater than ~70% and give artificially high readings. The correction supplied by the manufacturer is insufficient to correct this bias (see section S1 in Supporting Information), and therefore the humidities

reported in this study can exceed 100%. The humidities reported in this article should be interpreted as a relative moisture index rather than a strict percentage.

For each 85 day period, we successfully obtained data from between 140 and 147 of the 150 sensors. Data were discarded when plastic containers were dislodged from the ground by animals or sensors failed or gave spurious data (e.g. negative humidities). Note that this loss rate is much lower than reported in other grazed areas (e.g. Suggitt *et al.*, 2011), so the tent pegs and wooden stakes proved effective.

2.4 Analysis of extreme temperatures and humidities

For each of the 127 sites where we had a complete record of climate, we determined the daily minimum and maximum humidity and temperature for each of the 340 days. We then calculated the 5th and 95th percentile of each of these four factors at each site to create 8 response variables (5th percentile of minimum temperature, 95th percentile of maximum humidity, etc). For example, the 5th percentile of minimum temperature indicates only 5% of days (17 days) had a lower minimum temperature at that site, and this provides an estimate of extreme cold.

One potential problem with the multiple linear regression technique that we applied (see below) is that it is sometimes possible to extrapolate climates well outside the observed range if some locations have unique combinations of predictor variables, and this can lead to unrealistic climate grids. To avoid this, we transformed each response variable using a logit transform ($y = -\ln((1 - x) / x)$). Similarly to how the logit transform is commonly used in presence-absence studies (logistic regression) to restrict predictions to the range of 0 to 1, it can also be used to, for example, restrict humidities to a range of 0 to 100%, or restrict temperatures to the observed range. Therefore, for

each of the eight response variables we calculated the range of observations, and increased this by 10% to allow predictions slightly outside our observed range. We then scaled the observations to between 0 and 1 and used the logit function to calculate the transformed response variables.

We originally produced a Generalised Additive Model (GAM) for each response variable using the 13 non-spatial predictors. We used these GAMs to examine the shape of each partial response curve and transform the predictors where necessary to achieve linearity. Generally, it was only possible to confidently identify transforms for the more significant predictors (see results), with linear responses assumed for the less significant factors. Once the appropriate transforms were identified, we conducted stepwise linear regression using all 13 predictors and the standard parameters in S-Plus v8.0.4 for Windows to produce a non-spatial model. We examined the partial response plots of the selected model to confirm linearity and normally distributed errors. We then produced a spatial model by removing the site variables that could not be used to produce spatial maps and substituting the remotely sensed canopy cover for the canopy cover observed at the site. This spatial model was used to develop grids of the transformed response variables in ArcMap. These were passed through a sigmoid function ($y = 1 / (1 + \exp(-x))$) to reverse the logit transform performed originally, and scaled back to the original range of values.

Note that these models estimated the climate based only on the conditions at each site. In reality, the conditions at neighbouring sites can also have an influence. For example, edge effects near forests boundaries can cause gradual transitions in climate rather than abrupt boundaries (Chen *et al.*, 1999; Pohlman *et al.*, 2009). To prevent unrealistically sharp transitions in climate and cater for edge effects, we followed a

similar method to Ashcroft (2006). That is, we performed a neighbourhood average of the spatial predictions using radii of 50m, 100m, 200m, 400m, 600m, 800m, 1000m and 1500m. This created smoother transitions in climate, and simulated edge effects near sharp boundaries. We selected the radius that maximised the correlation between the predicted climate and actual observations. The final climatic grids we produced are therefore a combination of the conditions at the site, as well as the average conditions in the surrounding area.

One downside of the logit transform we used is that model coefficients cannot be directly used to estimate lapse rates or the effect size of each predictor (model coefficient \times range of respective predictor). Therefore, the effect sizes were estimated using both the model coefficients as well as the relationships between transformed and untransformed response variables. Note that the coefficients of each factor cannot be directly compared because they have different units (e.g. $6^{\circ}\text{C}/1000\text{m}$ elevation cannot be compared with $1^{\circ}\text{C}/10\%$ canopy cover), and do not give an indication of which factors had the strongest influence on results as this also depends on the range of each factor (e.g. elevation may have little effect on results in a study area with an elevational range of only 200m, but might be dominant in an area with a 3000m range). Therefore, we focus only on effect sizes rather than coefficients throughout the remainder of this article.

2.5 Timing of extreme conditions

To examine the timing of extreme events we calculated the number of sites that exceeded the 95th percentile or fell below the 5th percentile for each of the 8 response variables for each day of observation. Results were related to the average rainfall

recorded on each day at the 38 Bureau of Meteorology weather stations in the study area.

3. Results and discussion

3.1 Extreme cold

The 5th percentile of minimum temperatures was an indication of extreme cold, and the observed range varied from -8.6°C to 9.3°C. The best predictor of extreme cold was the relative elevation predictor used to reflect cold air drainage. Elevation, distance to coast and canopy cover were also influential, while ground vegetation within 1m and latitude had minor effects on the non-spatial model. Results were similar in the spatial model (Fig. 2), but the correlation was lower (non-spatial model $r^2 = 0.81$; spatial model $r^2 = 0.72$). The effect size of relative elevation (8.6°C over range of 263 m) was 46% greater than the effect size of distance to coast (5.9°C over range of 224 km), 49% greater than that the effect size of elevation (5.8°C over range of 1428 m; lapse rate 4.1°C/1000m), and 159% greater than the difference between 0% and 100% remotely sensed canopy cover (effect size of 3.3°C).

Neighbourhood averages suggested the best model was produced using a radius of 50 m. The final climate grid produced for the 5th percentile of minimum temperatures (Fig. 3a) had a correlation (r^2) of 0.74, and an RMS error of 1.67°C (Fig. 4a). The coldest locations were generally inland, cleared, low lying areas where cold air could pool (blue areas in Fig. 3a). The least cold locations were coastal forests, where high humidity and canopy cover will have reduced long-wave radiation losses (Geiger, 1971). Although temperatures were predicted to decrease with elevation (there was no inversion *per se*), the higher canopy cover and less cold air pooling at most upland sites

led to apparent temperature inversions in some locations. Nevertheless, the coldest site was an upland swamp at high elevation that had low canopy cover and was subject to cold air pooling.

The flow accumulation and distance to water bodies predictors were not selected in models, and were not able to capture cold air drainage as well as the relative elevation predictor. This can be attributed to at least three factors. Firstly, both these former predictors predict channelised flow of cold air, where cold air drainage can actually form non-channelised pools in low lying areas. Secondly, streamlines or valleys do not necessarily result in cold air pooling if the valley is steep and wide enough to allow the cold air to drain away (Lundquist *et al.*, 2008). Finally, while distance to streams has been a successful predictor in small, rugged study areas (e.g. Lookingbill and Urban, 2003), it is difficult to scale this to large regions where ‘streams’ can be anything from major rivers to intermittent creeks, and valleys can vary dramatically in the width of the surrounding flood plain. The dominant performance of the relative elevation predictor shows it has great potential to capture cold air drainage, but it may still be possible to improve it further. For example, the 500m radius was chosen arbitrarily based on the results of Bennie *et al.* (2010), while larger radii have also performed well at coarser resolutions (Daly *et al.*, 2007).

In terms of current climate change, winter minimum temperatures have been found to be increasing faster than maximum or other seasonal temperatures (Hughes, 2000; Lundquist *et al.*, 2008; Ashcroft *et al.*, 2009). Given that we found extremely low temperatures were largely determined by cold air drainage (even when distance to coast, elevation and canopy cover varied widely), this reinforces the suggestion that predicting the frequency and magnitude of cold air pooling events is crucial to understanding the

potential impacts of climate change and identifying potential microrefugia (Dobrowski, 2011). Cold air pools are decoupled from the free atmosphere, and affected areas will not respond to climate change in the same manner as other locations (Daly *et al.*, 2010). The errors introduced by not considering cold-air drainage in climate grids has previously been reported as between 3°C and 13°C (Daly *et al.*, 2007; Lundquist *et al.*, 2008), with our effect size of 8.6°C falling near the middle of this range. Any of these estimates is larger than many estimates of 21st century climate change (IPCC, 2007), once again highlighting the importance of predicting the magnitude and frequency of cold air pooling events.

3.2 Mild minimum temperatures

The 95th percentile of minimum temperatures provided an indication of when overnight temperatures remained high, and the observed range varied from 12.4 to 21.7°C. These conditions are expected on cloudy nights in late summer, when long wave radiation losses are low (Geiger, 1971). The models for mild minimum temperatures were strong (non-spatial model $r^2 = 0.86$, spatial model $r^2 = 0.84$; $r^2 = 0.89$ and RMS error of 0.48°C after inverting transform and neighbourhood average of 50m), and dominated by elevation (effect size 7.5°C; lapse rate 5.3°C/1000m; all other effect sizes < 1.6°C; see Fig. S10 in Supporting Information). This is consistent with previous studies showing that the effects of factors such as canopy cover and distance to coast are negated to a large extent when it is cloudy (e.g. Pepin and Lundquist, 2008; Suggitt *et al.*, 2011).

3.3 Extreme heat

The 95th percentile of maximum temperature provided an indication of extreme heat, and the observed range varied from 26.6 to 53.2°C. There was a notable difference between the non-spatial ($r^2 = 0.65$) and spatial ($r^2 = 0.53$) models due to the difference in canopy cover predictors. Canopy cover recorded at the sites was the most influential factor in the non-spatial model, while remotely sensed canopy cover was only the third most influential predictor in the spatial model behind distance to coast and elevation (Fig. S11 in Supporting Information). It is important to note that the canopy cover predictor was highly non-linear, with little difference between an observed canopy cover of 0 and 90%, and then a sharp drop in temperatures between 90% and 138% (Fig. 5). We made it a linear relationship using a canopy cover 3 predictor (Fig. 5), although this did not work as well with the remotely sensed canopy cover predictor (Fig. S11). Indeed, the remotely sensed canopy cover was less accurate in the upper range (DECC, 2008), and did not necessarily reflect both tree and shrub canopy layers. This led to overestimation of the maximum temperatures in rainforests in the spatial model (low temperatures in Fig. 4b), with similar errors absent from the non-spatial model. Given the differences in shading between tree and shrub canopies (Breshears and Ludwig, 2010), our results highlight the importance of capturing the complete canopy architecture. Improving the accuracy of the canopy cover layer is crucial to improving estimates of extreme heat in forests.

While canopy cover (effect size 7.8°C), elevation (effect size 13.3°C; lapse rate of 9.3°C/1000m) and distance to coast (effect size 13.7°C) were the factors most affecting extremely hot temperatures, exposure to northwesterly winds, (effect size 5.2°C), southerly winds (effect size 2.5°C) and latitude (effect size 5.5°C) were also important. As expected, sites exposed to the northwest were warmer than sheltered sites,

and sites exposed to the south were cooler (Ashcroft *et al.*, 2008). While the effects of exposure predictors were smaller than other factors, they were still comparable to the predicted effects of climate change (IPCC, 2007) and are crucial for rainforest species that favour topographically sheltered locations where maximum temperatures are low (Ashcroft *et al.*, 2008, 2011). The trend in latitude was opposite to expected, with warmer temperatures in more poleward locations. This trend is plausible for the duration of our study as there were hot, dry conditions and bushfires in the southwest of the study area during November and December. However, it is not clear if this trend would be repeated every year, and there would obviously be dangers in extrapolating this elsewhere.

The optimal radius for neighbourhood averages was 100 m, and the resulting model had a correlation (r^2) of 0.58, and an RMS error of 3.42°C (Fig. 4b). The locations with the least exposure to extreme heat were coastal and high elevation forests, especially where they had suitable topographic shelter (Fig. 3b). These locations were characterised by rainforests and moist eucalypt forests. The warmest locations were inland, low elevation pastures, although even inland forests are predicted to be warm because the canopy covers observed at our sites rarely exceeded the threshold of 90%. Our results are consistent with a recent study showing that the typically open understoreys beneath eucalypt forests provide little protection from solar radiation (Breshears and Ludwig, 2010).

3.4 Mild maximum temperatures

The 5th percentile of maximum temperatures provided an indication of conditions when daytime temperatures remained low, and our observations ranged from 9.3 to 22.0°C.

Similarly to mild minimum temperatures, these were determined predominately by elevation (effect size 12.1°C; lapse rate 8.5°C/1000m), although canopy cover (effect size 4.9°C), distance to coast (effect size 3.6°C), flow accumulation (effect size 2.0°C) and exposure to the northwest (effect size 2.1°C), south (effect size 2.3°C) and northeast (effect size 0.4°C) winds were also selected in the spatial model (Fig. S12 in Supporting Information), in addition to soil within 1m in the non-spatial model. Mild maximum temperatures could be estimated more accurately than extremely hot conditions (non-spatial $r^2 = 0.77$; spatial $r^2 = 0.73$; $r^2 = 0.77$ and RMS error = 1.49°C after inverting transform and neighbourhood average over 50m).

Our results confirm those of Ashcroft *et al.* (2008), where mild maximum and minimum temperatures were well correlated with elevation, but extreme temperatures were not. Given that rare, extreme climatic events can have a strong influence on species distributions (Mitikka *et al.*, 2008; Adler *et al.*, 2009; Beever *et al.*, 2010; Giesecke *et al.*, 2010) more attention should be given to climatic processes and factors driving extreme maximum and minimum temperatures.

3.5 Extreme dry

The 5th percentile of minimum humidity provided an indication of extremely dry conditions, and observations varied from 13.7 to 62.2%. Distance from coast had the largest effect on results (effect size 38.1%; Fig. S13 in Supporting Information). Similarly to extreme heat, canopy cover was non-linear, with increases in humidity only noticeable once the observed canopy cover was greater than approximately 90% (Fig. 5). The effect was even more pronounced than that for extreme heat, and we used a transformed canopy cover 5 predictor to ensure linearity. Results in the spatial model

also suffered due to the errors in the remotely sensed canopy cover layer (non-spatial $r^2 = 0.81$; spatial $r^2 = 0.73$). Nevertheless, remotely sensed canopy cover was still the second most important factor (effect size 19.7%), with latitude (effect size 14.3%) and elevation (effect size 17.4%) having moderate influence, and flow accumulation and exposure to the south and northwest having minor effects (Fig. S13). Vegetation within 1 m was included in the non-spatial model, but had less effect than the spatial factors. Similarly to extreme heat, the latitude effect suggested it was drier in the southwest of our study area where the bushfires occurred.

Our estimates of extreme dry were not improved using neighbourhood averages, and the final correlation (r^2) and RMS errors of our model were 0.72 and 5.8% respectively (Fig. 4c). Note that the r^2 between the predicted and actual humidities can differ slightly from that in the spatial model itself because of the logit transform we used in the models.

3.6 Moist days

The 95th percentile of minimum humidity provided an indication of when the air remained moist during the day, and observations ranged from 78.3 to 108.3%. Both the non-spatial ($r^2 = 0.67$) and spatial models ($r^2 = 0.72$) were dominated by distance from coast (effect size 33.5%) and elevation (effect size 30.5%), with canopy cover (effect size 13.6%), flow accumulation (effect size 14.3%), and exposure to northwesterly (effect size 7.5%) and southerly (effect size 3.2%) winds also selected (Fig. S14 in Supporting Information). Like the 5th percentile of minimum humidity, neighbourhood averages did not improve results, and the final model after inverting the logit transform had a correlation (r^2) of 0.72 and an RMS error of 4.0%.

Although the factors affecting the 5th (dry) and 95th (moist) percentiles of minimum humidities were similar, variations to the effect sizes of each factor and the transformations that were applied to cater for non-linear relationships resulted in very different spatial patterns. Under dry conditions, most sites had low humidities (Fig. 3c, 4c), with high humidities only in coastal locations that were high in canopy cover, at higher elevation, or in sheltered topographic locations. In contrast, under moist conditions most sites had high humidities, with only a few inland, low elevation, cleared sites having low humidities (Fig. 3d, 4d).

3.7 Maximum humidities

Maximum humidities could not be predicted as well as the other response variables, probably because maximum humidities frequently approached 100%, and the saturation of iButtons introduced noise that obscured the underlying trends. The 95th percentile of maximum humidities was observed to range from 104.6 to 112.2%, demonstrating this saturation. Indeed, models for the 95th percentile were especially poor (non-spatial $r^2 = 0.21$, spatial $r^2 = 0.16$), with higher humidities at higher elevation, nearer the coast, where there was higher flow accumulation, or higher canopy cover (Fig. S15 in Supporting Information).

The models for the 5th percentile of maximum humidities were better than those for the 95th percentile, but were largely determined by the amount of soil and live vegetation within 1m of the sensors. Hence, the spatial model performed noticeably worse than the non-spatial model (non-spatial $r^2 = 0.72$; spatial $r^2 = 0.57$). Humidities were higher near the coast, where the relative elevation was low (cold air pooling),

where the flow accumulation was high, or at higher elevations (Fig. S16 in Supporting Information).

Neighbourhood averages improved the models for the 5th percentile of maximum humidity (RMS error = 5.3%; final $r^2 = 0.57$; radius = 200m) but not those for the 95th percentile (final $r^2 = 0.19$; RMS error = 1.2%).

3.8 Timing of extreme events

The timing of extreme temperatures had a distinct seasonal trend, with highest minimum temperatures in the summer months (December–February) and lowest in the winter months (June–August; Fig. 6). However, the extreme conditions were clustered on discrete days within these seasons and were not evenly distributed. Given that synoptic patterns generally only last a day or two (Stahl *et al.*, 2006a), it is the conditions on these days that are of interest rather than the average conditions for each season. Extreme maximum temperatures preceded the minimum temperatures by approximately a month, and generally occurred in November–January and May–July respectively.

The timing of extreme humidity events was associated more with rainfall events than seasons (Fig. 6). While the driest extremes (5th percentiles) occurred mostly in spring and summer, these were interspersed with extremely humid conditions (95th percentiles). This trend may be common in locations where higher rainfall occurs in the warmer months, and highlights the shortcomings of moisture indices built on seasonal averages. The average humidity for the summer months would not detect that it is both extremely humid and extremely dry during this season.

3.9 Errors

The first source of errors in this study is the observation of climate variables by the iButton sensors. Humidity is obviously overestimated in this study due to the saturation of the iButtons. Although this results in a bias in the observations, the iButtons should still be reliably distinguishing between the least and most humid sites. The biggest danger is that the saturation is higher in winter, when humidities are generally higher, and this could result in a systematic bias between summer and winter humidities. Given that extreme humidities were observed throughout the year, this is unlikely to have a large effect, but it is possible.

It is also possible that housing the iButtons inside plastic containers close to the ground may have added to the saturation by creating an artificially high humidity environment for the sensors. Once again, this may have added to the bias in our results, but would not prevent the observations being used as a relative moisture index. However, it should be stressed that humidities of approximately 100% are not unreasonable observations given the frequency of frosts, dews and rainfall in the study area, and the fact that the Bureau of Meteorology often reports humidities of more than 90% at height of 1.5–2m.

Temperatures recorded by iButtons are generally within 0.5°C of more precise instruments, but errors in either Stevenson screens or our containers may approach 2°C under still conditions when they are not aspirated (Lundquist and Huggett, 2008). A qualitative comparison between our observations and other observations at 5cm (Likso, 2006; Bennie *et al.*, 2008) suggests our instruments are accurate to within a 2–3°C (less for minimums), and similar studies have reported errors of only 1°C between PVC shelters and Gill screens (Daly *et al.*, 2007). However, the apparent errors will be larger

when the climate grids are applied to specific species. For example, both Stevenson screens and our containers protect instruments from conditions that many organisms face (Wolfe, 1945), while other species may be even more sheltered if they take refuge deep in the soil, under rocks, or inside tree hollows. Temperatures at the surface of plants may differ from the atmosphere depending on vegetation structure (Grace, 1987), and temperatures 1 cm below the ground surface can exceed those we recorded at 5cm by more than 10°C on hot days (see section S2 in Supporting Information). The relationship between soil and air temperatures at different heights varies according to the habitat characteristics and prevailing weather (Geiger, 1971; Ashcroft *et al.*, 2009; section S2), so there is no straight forward way to convert temperatures at a given height to any other height. Therefore, the difference between the microhabitat of species and the housing of sensors is probably the biggest source of error when the climate grids are applied to model species' distributions. For example, butterflies that fly ~1.5m above grasslands may be more accurately modelled using climate grids based on standardised weather stations, while grids based on our observations may be more appropriate for ground cover plants and ground dwelling arthropods. Further research is needed to confirm which climate grids are best able to explain species distributions.

The second major source of error is misspecification of the multiple linear regression models used to predict the climate at unobserved locations. The RMS errors we reported in this study reflect a combination of instrumentation errors discussed above, fine scale variability in climate and model misspecification errors. Climate can vary appreciably over short distances, and moving all our sensors a few metres in a random direction would probably change results noticeably at some individual sites. However, the overall trends between climate-forcing factors and climate variables

should be similar, and therefore the resulting grids would be almost identical. The RMS errors reported for our models in this article reflect this fine scale variability to some extent, and are not totally due to model misspecification.

Model misspecification errors could result from inappropriate transforms of predictor variables, missing climate forcing factors, inaccurate GIS layers of climate forcing factors, or errors due to correlated predictors or poorly sampling the range of a climate forcing factor. It is difficult to quantify the effect of each of these factors, but the large drop in model performance when using remotely sensed canopy cover suggests that the accuracy of GIS layers is a crucial factor. We believe that improving the accuracy of canopy cover, cold air drainage, distance to coast and topographic exposure predictors would be the best way to reduce errors. Including interactions is also an important priority, but is difficult when interaction terms are highly correlated with individual factors.

A third potential source of errors is the limited time frame of this study. Indeed the dry November/December of 2009 is in stark contrast to the floods the area experienced at the same time during 2010, and examining variability over a number of years would be beneficial. Factors such as distance from coast and latitude may capture geographic differences in where the extremes occurred in any particular year, and therefore these factors may change appreciably between years. Factors such as cold air drainage, topographic exposure and canopy cover are more important for extreme temperatures, and a year with even more extreme conditions may exacerbate the effects of these factors even more. Indeed, our definition of extremes based on the 5th and 95th percentiles meant that ~17 days had more extreme conditions during our study period,

and if we examined the 1st and 99th percentiles the effects of these factors may be even higher still.

4. Conclusions

The development of fine-resolution climate grids is an important priority to explain species distributions at the regional scale and predict how they may respond to variable and changing climates. There are many advantages to developing these grids using large networks of inexpensive climate loggers, as these can be placed over a range of environments and record near-surface conditions in habitats where many species live. While many studies have focused on 21st century temperature changes, it is also crucial to understand moisture availability given its relevance to many species. Temperature and moisture are also linked through evaporative cooling and thermal inertia (Lookingbill and Urban, 2004; Lu *et al.*, 2009), and moisture may help buffer sites from the effects of climate change (Fridley *et al.*, 2009).

Our study focused on the extreme conditions that have a strong influence on species distributions. These extremes are associated with distinct weather patterns, and focusing on individual days with these conditions is potentially more relevant for species than the average climate over seasons that may contain many different weather patterns. For example, we found that summer months contained both extremely moist and extremely dry conditions, and averaging over the season would conceal these extremes. Similarly, mild temperatures are determined mainly by elevation, while extreme temperatures are determined more by cold air drainage, canopy cover and topographic exposure. If we examined temperatures over a predefined period that

included a variety of weather conditions, then this would obscure the importance of the factors affecting extreme temperatures.

We found that maximum temperatures could not be predicted as well as minimum temperatures, and was particularly sensitive to canopy cover. We suggest that improving the accuracy of the canopy cover predictor, as well as the GIS layers of other climate forcing factors, is probably the best way to improve climate predictions, although it is also important to refine the non-linear relationships for some factors. For example, the distance to coast and canopy cover predictors were highly influential in many of our models, yet the results were non-linear and variable in both effect size and response shape between models. Regional scale climate grids could be further improved through a better understanding of these relationships, and by understanding how the effects of different factors are affected by different weather conditions.

Acknowledgements

This project was initially funded by a NSW Environmental Trust Grant as part of the Great Eastern Ranges conservation initiative, and is continuing under ARC linkage grant LP100200080. Special thanks to more than 100 landowners who granted us permission to position sensors on their properties, and to Jessica Lundquist for comments on an earlier draft.

References

Adler PB, HilleRisLambers J, Levine JM. 2009. Weak effect of climate variability on coexistence in a sagebrush steppe community. *Ecology* **90**: 3303–3312.

- Ashcroft MB. 2006. A method for improving landscape scale temperature predictions and the implications for vegetation modelling. *Ecological Modelling* **197**: 394–404.
- Ashcroft MB, Chisholm LA, French KO. 2008. The effect of exposure on landscape scale soil surface temperatures and species distribution models. *Landscape Ecology* **23**: 211–225.
- Ashcroft MB, Chisholm LA, French KO. 2009. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Global Change Biology* **15**: 656–667.
- Ashcroft MB. 2010. Identifying refugia from climate change. *Journal of Biogeography* **37**: 1407–1413.
- Ashcroft MB, French KO, Chisholm LA. 2011. An evaluation of environmental factors affecting species distributions. *Ecological Modelling* **222**: 524–531.
- Austin MP, Van Niel KP. 2011. Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* **38**: 1–8.
- Beaumont LJ, Pitman AJ, Poulsen M, Hughes L. 2007. Where will species go? Incorporating new advances in climate modelling into projections of species distributions. *Global Change Biology* **13**: 1368–1385.
- Beever EA, Ray C, Mote PW, Wilkening JL. 2010. Testing alternative models of climate-mediated extirpations. *Ecological Applications* **20**: 164–178.
- Bennie J, Huntley B, Wiltshire A, Hill MO, Baxter R. 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling* **216**: 47–59.

- Bennie JJ, Wiltshire AJ, Joyce AN, Clark D, Lloyd AR, Adamson J, Parr T, Baxter R, Huntley B. 2010. Characterising inter-annual variation in the spatial pattern of thermal microclimate in a UK upland using a combined empirical-physical model. *Agricultural and Forest Meteorology* **150**: 12–19.
- Breshears DD, Ludwig JA. 2010. Near-ground solar radiation along the grassland-forest continuum: tall-tree canopy architecture imposes only muted trends and heterogeneity. *Austral Ecology* **35**: 31–40.
- Campbell GS, Norman JM. 1998. *An Introduction to Environmental Biophysics*. Springer-Verlag: New York.
- Chen J, Saunders SC, Crow TR, Naiman RJ, Brosofske KD, Mroz GD, Brookshire BL, Franklin JF. 1999. Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience* **49**: 288–297.
- Chung U, Seo HH, Hwang KH, Hwang BS, Choi J, Lee JT, Yun JI. 2006. Minimum temperature mapping over complex terrain by estimating cold air accumulation potential. *Agricultural and Forest Meteorology* **137**: 15–24.
- Daly C. 2006. Guidelines for assessing the suitability of spatial climate data sets. *International Journal of Climatology* **26**: 707–721.
- Daly C, Smith JW, Smith JI, McKane RB. 2007. High-resolution spatial modeling of daily weather elements for a catchment in the Oregon Cascade Mountains, United States. *Journal of Applied Meteorology and Climatology* **46**: 1565–1586.
- Daly C, Conklin DR, Unsworth MH. 2010. Local atmospheric decoupling in complex topography alters climate change impacts. *International Journal of Climatology* **30**: 1857–1864.

- DECC. 2008. *NSW Interim Native Vegetation Extent (2008-Version 1)*. Report and data prepared by NSW Department of Environment and Climate Change for the National Land and Water Resources Audit.
- Dobrowski SZ, Abatzoglou JT, Greenberg JA, Schladow SG. 2009. How much influence does landscape-scale physiography have on air temperature in a mountain environment? *Agricultural and Forest Meteorology* **149**: 1751–1758.
- Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**: 1022–1035.
- Ferrier S, Watson G, Pearce J, Drielsma M. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodiversity and Conservation* **11**: 2275–2307.
- Fridley JD. 2009. Downscaling climate over complex terrain: high finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). *Journal of Applied Meteorology and Climatology* **48**: 1033–1049.
- Geiger R. 1971. *The Climate Near the Ground*. Revised edn. Harvard Univ. Press: Cambridge.
- Giesecke T, Miller PA, Sykes MT, Ojala AEK, Seppa H, Bradshaw RHW. 2010. The effect of past changes in inter-annual temperature variability on tree distribution limits. *Journal of Biogeography* **37**: 1394–1405.
- Grace J. 1987. Climatic tolerance and the distribution of plants. *New Phytologist* **106**: (Suppl.) 113–130.

- Gutiérrez Illán J, Gutiérrez D, Wilson RJ. 2010. The contributions of topoclimate and land cover to species distributions and abundance: fine-resolution tests for a mountain butterfly fauna. *Global Ecology and Biogeography* **19**: 159–173.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.
- Houlder D, Hutchinson M, Nix H, McMahon J. 2003. *ANUCLIM 5.1 user's guide*. Australian National University: Canberra.
- Hughes L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* **15**: 56–61.
- IPCC. 2007. *Climate change 2007: the physical science basis, AR4 synthesis report*. Intergovernmental Panel on Climate Change. Available at: <http://www.ipcc.ch> (accessed 18 December 2009).
- Kennedy AD. 1997. Bridging the gap between general circulation model (GCM) output and biological environments. *International Journal of Biometeorology* **40**: 119–122.
- Körner C. 2007. The use of 'altitude' in ecological research. *Trends in Ecology and Evolution* **22**: 569–574.
- Likso T. 2006. Estimation of air temperature at 5cm above grassland at the Zagreb-Maksimir Observatory. *Theoretical and Applied Climatology* **85**: 217–225.
- Lookingbill TR, Urban DL. 2003. Spatial estimation of air temperature differences for landscape-scale studies in montane environments. *Agricultural and Forest Meteorology* **114**: 141–151.

- Lookingbill T, Urban D. 2004. An empirical approach towards improved spatial estimates of soil moisture for vegetation analysis. *Landscape Ecology* **19**: 417–433.
- Lu S, Ju Z, Ren T, Horton R. 2009. A general approach to estimate soil water content from thermal inertia. *Agricultural and Forest Meteorology* **149**: 1693–1698.
- Lundquist JD, Cayan DR. 2007. Surface temperature patterns in complex terrain: daily variations and long-term change in the central Sierra Nevada, California. *Journal of Geophysical Research* **112**: D11124.
- Lundquist JD, Huggett B. 2008. Evergreen trees as inexpensive radiation shields for temperature sensors. *Water Resources Research* **41**: W00D04.
- Lundquist JD, Pepin N, Rochford C. 2008. Automated algorithm for mapping regions of cold-air pooling in complex terrain. *Journal of Geophysical Research* **113**: D22107.
- McGregor GR. 2006. Climatology: its scientific nature and scope. *International Journal of Climatology* **26**: 1–5.
- Milionis AE, Davies TD. 2008. The effect of the prevailing weather on the statistics of atmospheric temperature inversions. *International Journal of Climatology* **28**: 1385–1397.
- Mitikka V, Heikkinen RK, Luoto M, Araújo MB, Saarinen K, Pöyry J, Fronzek S. 2008. Predicting range expansion of the map butterfly in Northern Europe using bioclimatic models. *Biodiversity and Conservation* **17**: 623–641.
- Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Global Ecology and Biogeography* **12**: 361–371.

- Pearson RG. 2006. Climate change and the migration capacity of species. *Trends in Ecology and Evolution* **21**: 111–113.
- Pepin NC, Lundquist JD. 2008. Temperature trends at high elevations: patterns across the globe. *Geophysical Research Letters* **35**: L14701.
- Pierce Jr. KB, Lookingbill T, Urban D. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. *Landscape Ecology* **20**: 137–147.
- Pohlman CL, Turton SM, Goosem M. 2009. Temporal variation in microclimatic edge effects near powerlines, highways and streams in Australian tropical rainforest. *Agricultural and Forest Meteorology* **149**: 84–95.
- Retana J, Cerdá X. 2000. Patterns of diversity and composition of Mediterranean ground and communities tracking spatial and temporal variability in the thermal environment. *Oecologia* **123**: 436–444.
- Shoo LP, Storlie C, VanDerWal J, Little J, Williams SE. 2010. Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Global Change Biology* **17**: 186–193.
- Soria-Auza RW, Kessler M, Bach K, Barajas-Barbosa PM, Lehnert M, Herzog SK, Böhner J. 2010. Impact of quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia. *Ecological Modelling* **221**: 1221–1229.
- Stahl K, Moore RD, McKendry IG. 2006a. The role of synoptic-scale circulation in the linkage between large-scale ocean-atmosphere indices and winter surface climate in British Columbia, Canada. *International Journal of Climatology* **26**: 541–560.

- Stahl K, Moore RD, Floyer JA, Asplin MG, McKendry IG. 2006b. Comparison of approaches from spatial interpolation of daily air temperature in a large region with complex topography and highly variable station density. *Agricultural and Forest Meteorology* **139**: 224–236.
- Suggitt AJ, Gillingham PK, Hill JK, Huntley B, Kunin WE, Roy DB, Thomas CD. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* **120**: 1–8.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004. Extinction risk from climate change. *Nature* **427**: 145–148.
- Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **9**: 137–152.
- Trivedi MR, Berry PM, Morecroft MD, Dawson TP. 2008. Spatial scale affects bioclimatic model projections of climate change impacts on mountain plants. *Global Change Biology* **14**: 1089–1103.
- VanDerWal J, Shoo LP, Williams SE. 2009. New approaches to understanding late Quaternary climate fluctuations and refugial dynamics in Australian wet tropical rain forests. *Journal of Biogeography* **36**: 291–301.
- Vanwallegem T, Meentemeyer RK. 2009. Predicting forest microclimate in heterogeneous landscapes. *Ecosystems* **12**: 1158–1172.

Van Niel KP, Laffan SW, Lees BG. 2004. Effect of error in the DEM on environmental variables for predictive vegetation modelling. *Journal of Vegetation Science* **15**: 747–756.

Wolfe JN. 1945. The use of weather bureau data in ecological studies. *Ohio Journal of Science* **45**: 1–12.

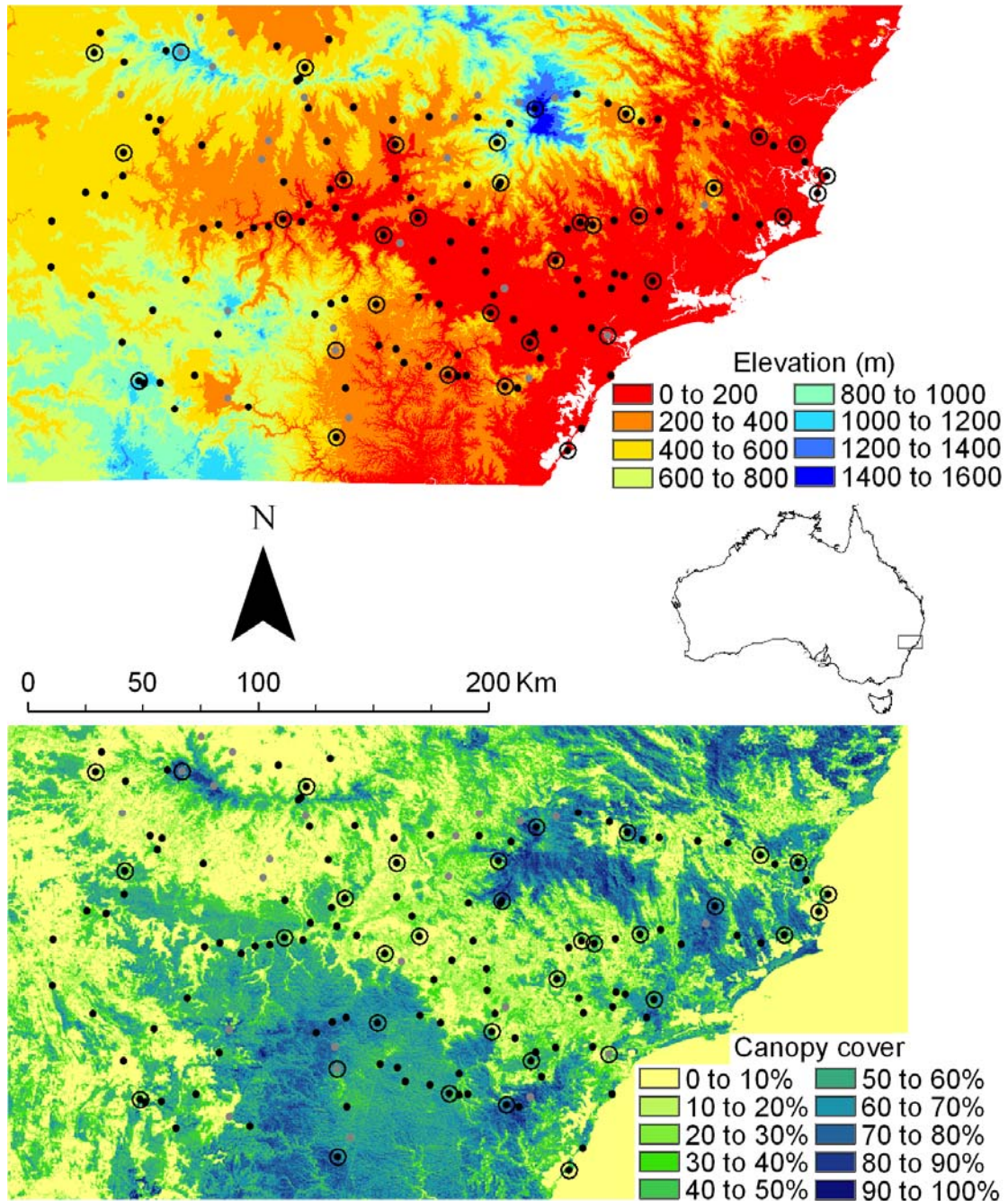


Fig. 1 The greater Hunter Valley region of New South Wales, Australia, where this study was conducted ($31.4\text{--}33.4^{\circ}\text{S}$, $149.4\text{--}152.6^{\circ}\text{E}$). Black dots indicate the 127 sites where a complete year of temperature and humidity data were available, while grey dots indicate partial data. Circles are around the locations where soil sensors were deployed over summer. Canopy cover is taken from DECC (2008).

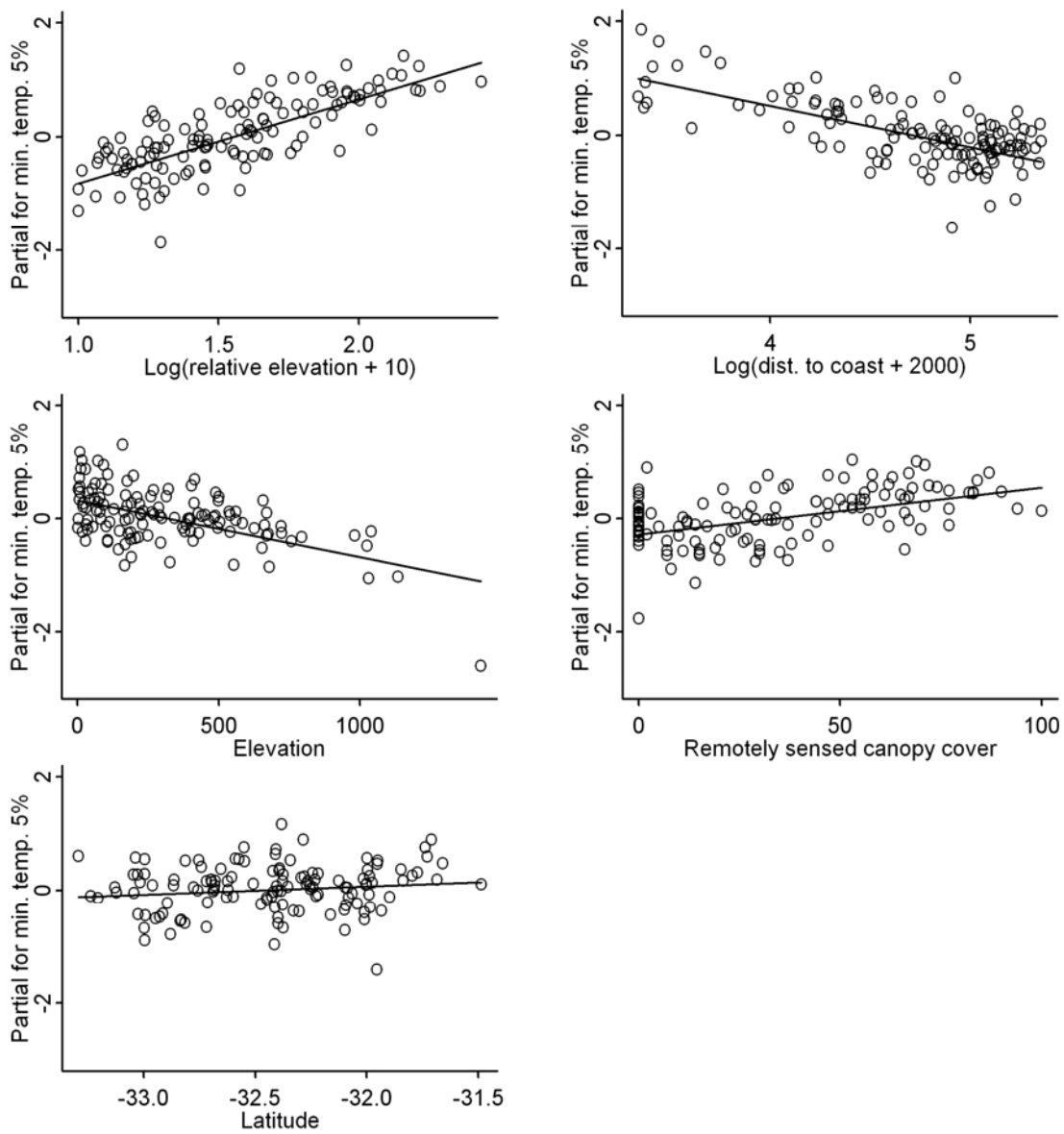


Fig. 2 Partial response graphs for the spatial model of 5th percentile of minimum temperature. The effect of each predictor can be gauged by the range of the Y-axis that each partial response line covers, such that relative elevation had the greatest effect and latitude the least.

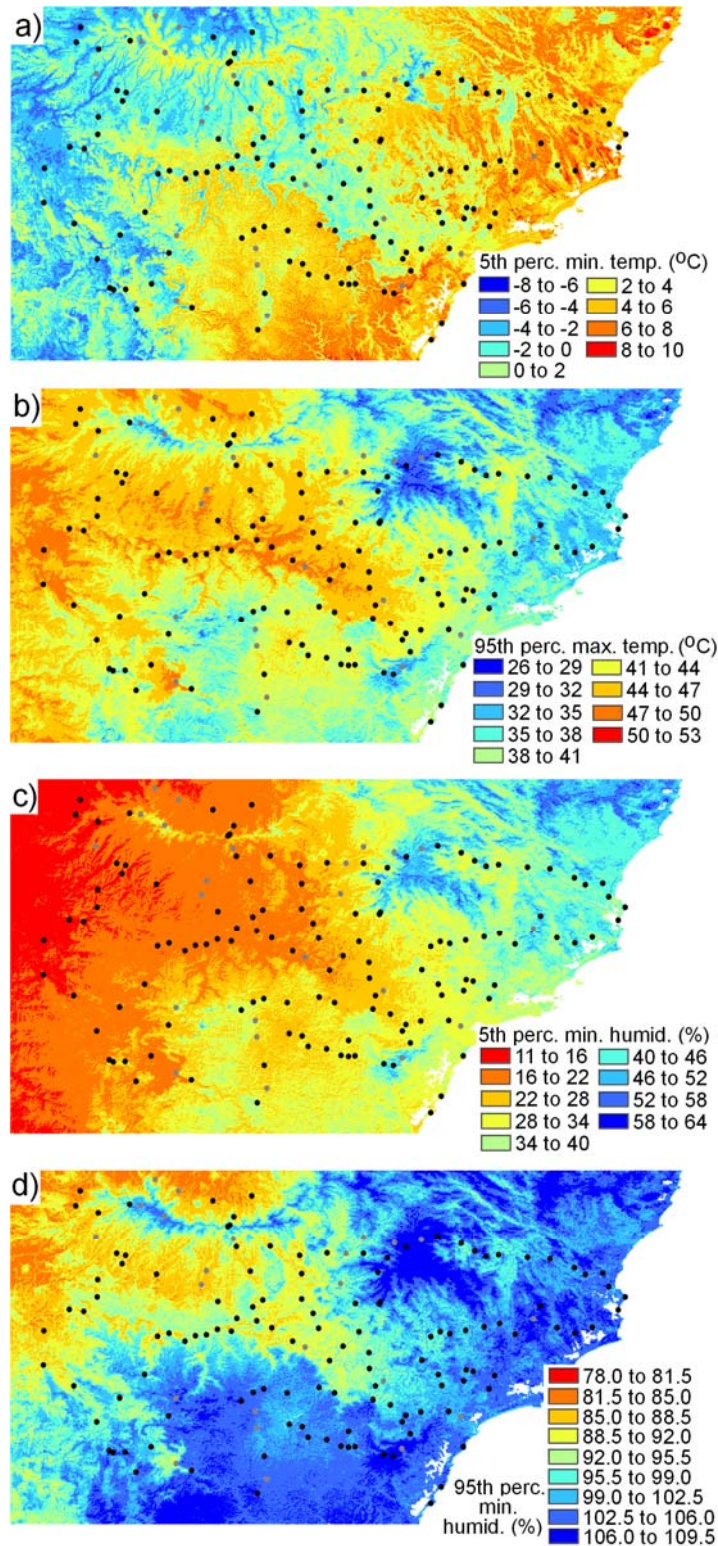


Fig. 3 Climate grids for extreme cold (a), extreme heat (b), extreme dry (c), and humid days (d) produced for the study area shown in Fig. 1. In all grids red refers to hotter and drier conditions, and blue to cooler and moister.

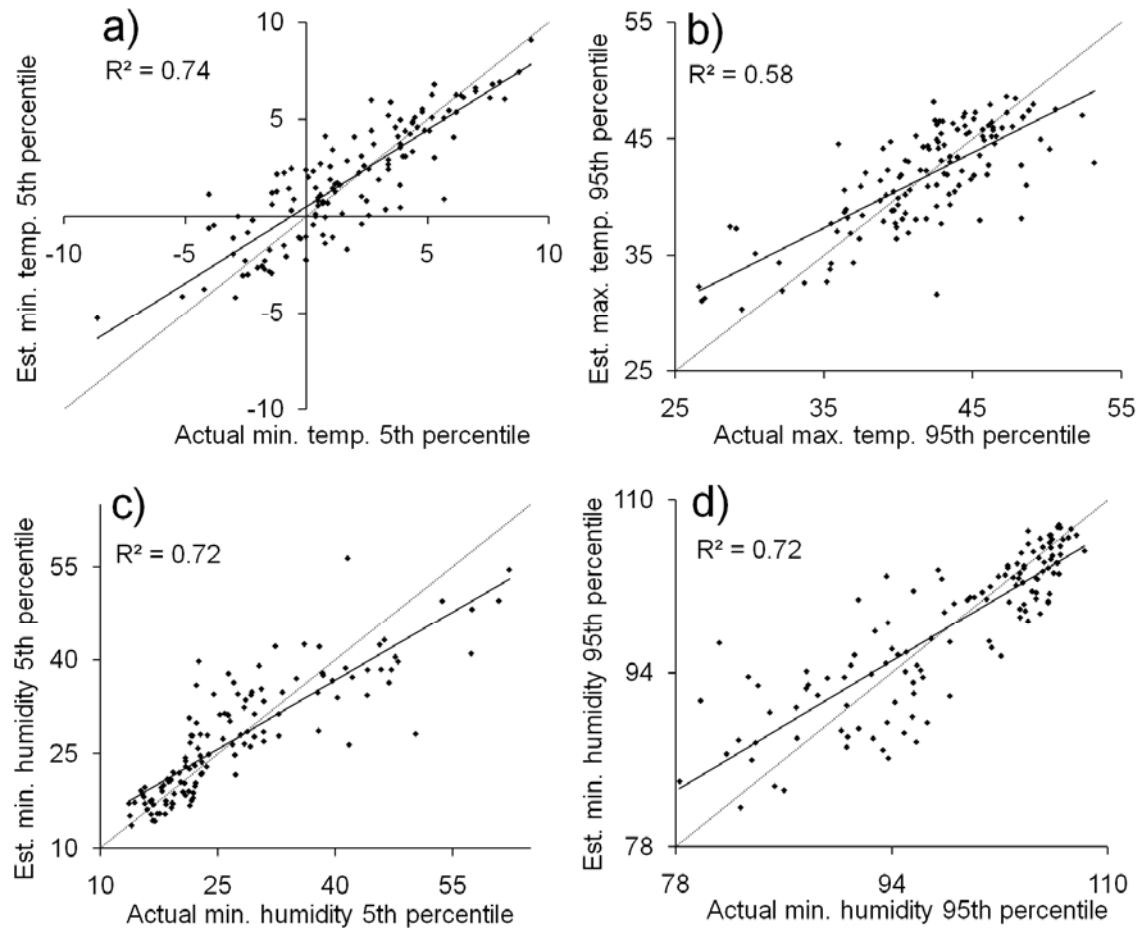


Fig. 4 Relationships between predicted and actual climate extremes, where the predicted values are based on the spatial model and neighbourhood averages.

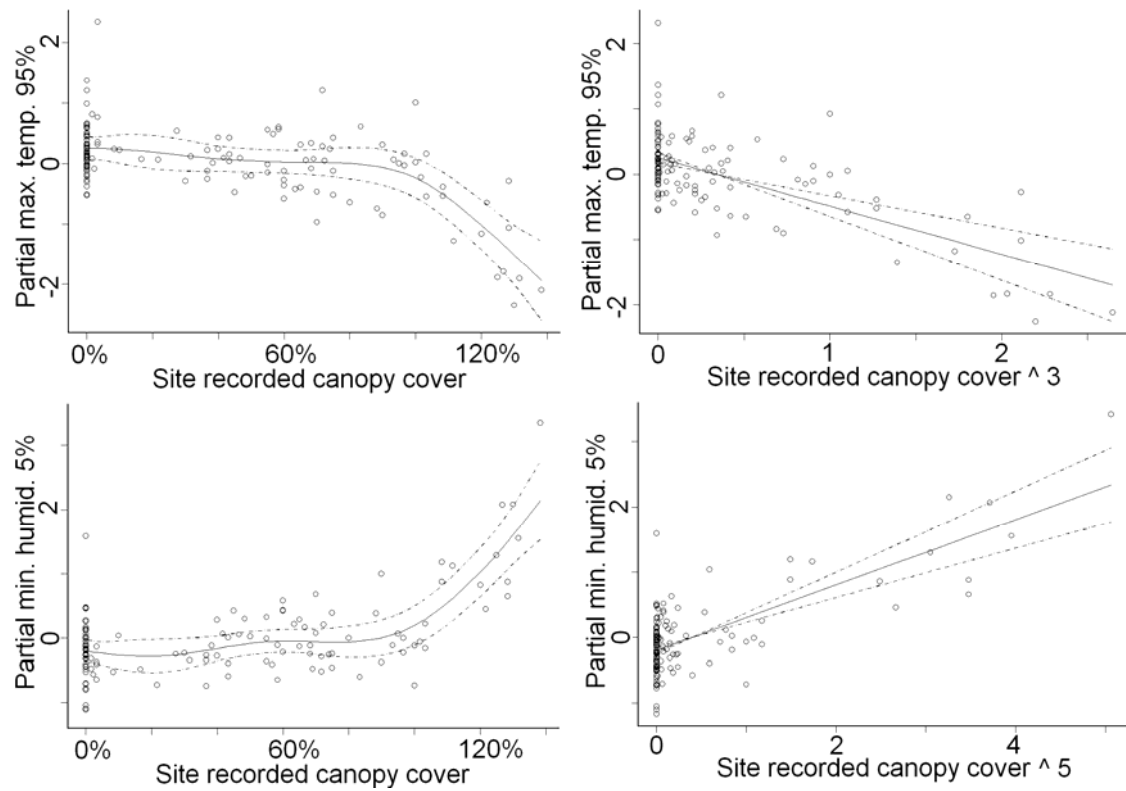


Fig. 5 Partial response graphs for generalised additive models for the 95th percentile of maximum temperature (top) and the 5th percentile of minimum humidity (bottom) in terms of the untransformed (left) and transformed (right) site observed canopy cover predictors.

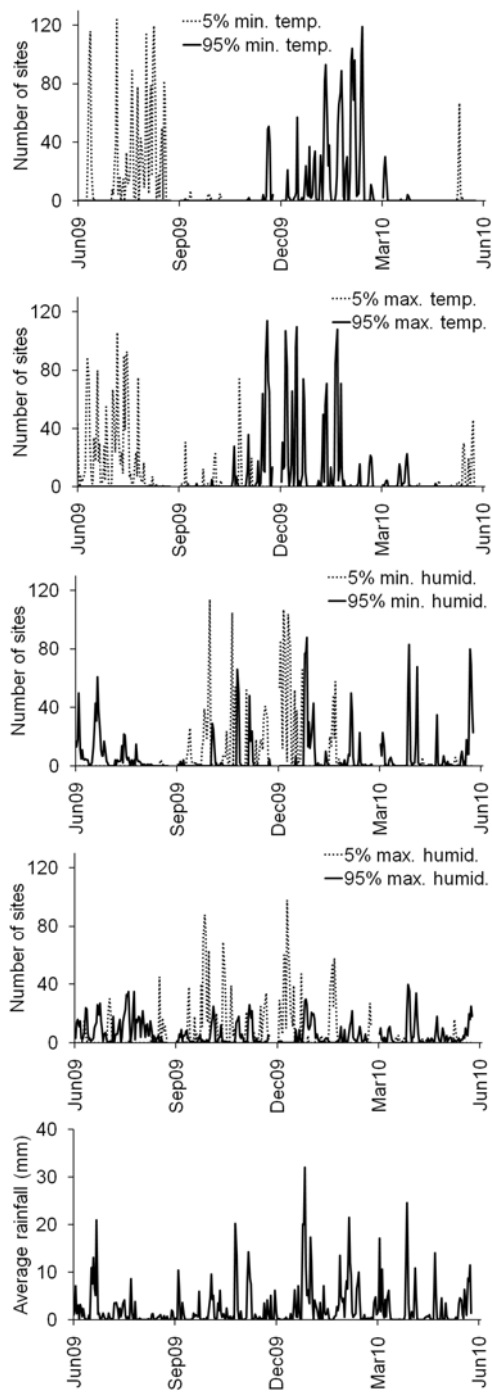


Fig. 6 The top four panels illustrate the number of sites that were above the 95th percentile or below the 5th percentile of minimum or maximum humidity or temperature on each day where we made observations. The bottom panel illustrates the average rainfall of the 38 Bureau of Meteorology weather stations in the study area.

