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## Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation

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### Abstract

Current predictions of how species will respond to climate change are based on coarse-grained climate surfaces or idealized scenarios of uniform warming. These predictions may erroneously estimate the risk of extinction because they neglect to consider spatially heterogeneous warming at the landscape scale or identify refugia where species can persist despite unfavourable regional climate. To address this issue, we investigated the heterogeneity in warming that has occurred in a 10 km × 10 km area from 1972 to 2007. We developed estimates by combining long-term daily observations from a limited number of weather stations with a more spatially comprehensive dataset (40 sites) obtained during 2005–2006. We found that the spatial distribution of warming was greater inland, at lower elevations, away from streams, and at sites exposed to the northwest (NW). These differences corresponded with changes in weather patterns, such as an increasing frequency of hot, dry NW winds. As plant species were biased in the topographic and geographic locations they occupied, these differences meant that some species experienced more warming than others, and are at greater risk from climate change. This species bias could not be detected at coarser scales. The uneven seasonal nature of warming (e.g. more warming in winter, minimums increased more than maximums) means that climate change predictions will vary according to which predictors are selected in species distribution models. Models based on a limited set of predictors will produce erroneous predictions when the correct limiting factor is not selected, and this is difficult to avoid when temperature predictors are correlated because they are produced using elevation-sensitive interpolations. The results reinforce the importance of downscaling coarse-grained (~50 km) temperature surfaces, and suggest that the accuracy of this process could be improved by considering regional weather patterns (wind speed, direction, humidity) and topographic exposure to key wind directions.

### Disciplines

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**Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation**

Running title: Climate change at the landscape scale

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**Abstract** Current predictions of how species will respond to climate change are based on coarse-grained climate surfaces or idealised scenarios of uniform warming. These predictions may erroneously estimate the risk of extinction because they neglect to consider spatially heterogeneous warming at the landscape scale or identify refugia where species can persist despite unfavourable regional climate. To address this issue, we investigated the heterogeneity in warming that has occurred in a 10 km by 10 km area from 1972 to 2007. We developed estimates by combining long-term daily observations from a limited number of weather stations with a more spatially comprehensive dataset (40 sites) obtained during 2005-2006. We found that the spatial distribution of warming was greater inland, at lower elevations, away from streams, and at sites exposed to the NW. These differences corresponded with changes in weather patterns, such as an increasing frequency of hot, dry NW winds. As plant species were biased in the topographic and geographic locations they occupied, these differences meant that some species experienced more warming than others, and are at greater risk from climate change. This species bias could not be detected at coarser scales. The uneven seasonal nature of warming (e.g. more warming in winter, minimums increased more than maximums) means that climate change predictions will vary according to which predictors are selected in Species Distribution Models. Models based on a limited set of predictors will produce erroneous predictions when the correct limiting factor is not selected, and this is difficult to avoid when temperature predictors are correlated because they are produced using elevation sensitive interpolations. The results reinforce the importance of downscaling coarse-grained (~50 km) temperature surfaces, and suggest that the accuracy of this process could be improved by considering regional weather patterns (wind speed, direction, humidity) and topographic exposure to key wind directions.

## Introduction

Current predictive modelling of the response of species to climate change produces highly variable results according to variations in the Global Climate Model (GCM, Beaumont *et al.* 2007) and statistical technique used (Araújo *et al.* 2005). These differences raise questions regarding the usefulness of the models (Araújo *et al.* 2005), and highlight a need to improve methodologies.

Much discussion on methodology has concerned the choice between mechanistic process-based models of plant demographics and bioclimatic models based on the correlation between climatic factors and the current distribution of species. Both approaches have advantages and disadvantages (Loehle & LeBlanc 1996; Pearson & Dawson 2003, 2004), yet there are a number of problems common to both that are associated with the climate data used. First, climatic data is typically either from coarse-grained (e.g. 50km) GCMs, or from an idealised scenario of a fixed and uniform increase in temperature (see Beaumont *et al.* 2007 for a comprehensive list of examples). Both cases are unable to distinguish fine-scale heterogeneity in climate change, and this may introduce a bias in predictions (Loehle & LeBlanc 1996; Araújo & Rahbek 2006). Temperature increases will vary across microclimates (Beaumont & Hughes 2002), and species respond to spatially heterogeneous regional climates rather than global averages (Walther *et al.* 2002). Local scale effects of climate change have been poorly explored (del Barrio *et al.* 2006), and further investigation is needed to identify refugia from apparently unfavourable conditions at coarser scales (Pearson 2006). These refugia are a known problem with coarse-scale models, and may mean that predictions of extinctions are exaggerated (Thuiller *et al.* 2005; Anciães & Peterson 2006; Pearson 2006; Botkin *et al.* 2007).

The second issue is that seasonal temperatures are often reduced to a limited and predefined set of variables prior to modelling species distributions—most commonly mean annual temperature, winter minimum, and either summer maximum or an estimate of growing degree-days (e.g. Araújo *et al.* 2005; Thuiller *et al.* 2005; Anciães & Peterson 2006; Beaumont *et al.* 2007). While these variables have been selected based on the general physiological response of species, this a priori selection of predictors will lead to erroneous predictions for species that are limited by temperatures during other seasons. Some seasons have warmed more than others, and minimum temperatures have increased by more than maximum and average temperatures (Loehle & LeBlanc 1996). Seasonal fine-tuning of climatic variables has been shown to improve bird models (Heikkinen *et al.* 2006), and this may be true for plants as well.

The third issue concerns the accuracy of temperature predictions. Errors in temperature estimates are usually stated as being less than 5% (e.g. Beaumont & Hughes 2002), but the absolute magnitude of these errors can still be in the order of 1°C when temperatures are approximately 20°C. In addition, there can be variations of up to 33.8°C within one 50 km cell (mean 1.8°C, Hijmans *et al.* 2005), and errors of this magnitude are significant for many species. For example, Hughes *et al.* (1996) found that 41% of eucalypts in Australia had a mean annual temperature range of less than 2°C, and 25% less than 1°C.

Errors in temperature estimates are partially due to the assumption that temperature can be interpolated based only on elevation. While elevation is the dominant factor controlling the distribution of most seasonal temperatures, coastal influences and exposure to wind are more important in some seasons—especially the extreme temperatures that are limiting for many species (Ashcroft *et al.* 2008).

Incorporating these other factors into temperature predictions changes the spatial distribution of seasonal temperature estimates and dramatically affects model predictions.

This paper addressed these issues with the temperature data used in climate change models by estimating the fine-scale spatial heterogeneity in warming that has occurred between 1972 and 2007 in an approximately 10 km by 10 km area. A better understanding of these past changes in temperature assists us to improve our predictions of future changes. We used the estimates of past warming to investigate whether some locations were potential refugia because they had warmed by less than others. The reduced warming in refugia could act to prevent extinctions, or at least slow the rate at which climate change affects species. We estimated the average amount of warming that 37 plant species had experienced to determine if any species was at more risk because of the bias in the topographic and geographic locations they occupied.

## **Materials and methods**

### *Overview of approach*

The approach we adopted combined 35 years of data from Bureau of Meteorology (BoM) weather stations with one year of personal observations of soil-surface temperatures. BoM weather stations provided a good record of historical climate change, but were not sufficient to make fine-grained predictions of warming as there were not enough stations, they were too sparsely distributed, and they did not cover the full range of microclimates in our study area. By recording soil temperatures at 40 sites for one year, and determining the relationship between the air temperatures at the BoM stations and the soil temperatures at each site, we could estimate the spatial fine-grained spatial distribution of temperatures for the whole period of interest (1972-2007). This was based on the assumption that the soil-air temperature relationships were temporally stable. The relationships between BoM air temperatures and site soil temperatures were determined separately for each weather pattern (e.g. wind speed and direction, humidity) as these factors can affect the spatial distribution of soil temperatures (Ashcroft *et al.* 2008).

### *Temporal changes in weather patterns*

The study was conducted on approximately 12000ha of the Illawarra Escarpment and Woronora Plateau (34.4°S, 150.9°E), approximately 80km south of Sydney, Australia (Fig. 1). The study area was selected because it contains a complex mosaic of vegetation (NPWS 2002), and the patterns cannot be easily explained using common



predictors such as elevation and geology. We suspected that elevation may have been a poor surrogate for temperature in this area, and have subsequently shown that this is the case for the extreme temperatures (winter minimums, summer maximums) that have a strong influence on the distribution of species (Ashcroft *et al.* 2008).

Long-term weather data from the Bureau of Meteorology ([www.bom.gov.au](http://www.bom.gov.au)) was only available for one weather station within the study area (Wollongong University). Therefore, we also obtained data from the five nearest long-term stations in a variety of directions (Fig. 1). Data for the period of March 1972 to February 2007 was obtained for all six stations, although the Nowra and Point Perpendicular data was actually a combination of two stations for different periods.

Hierarchical cluster analysis (using JMP, Ward method) was performed to group days with similar weather patterns. There were 48 variables used, eight for each of the six weather stations. The eight variables were northerly wind component at 9am and 3pm, easterly wind component at 9am and 3pm, humidity at 9am and 3pm, and the relative minimum and maximum temperatures. The northerly and easterly wind components were calculated as  $\text{wind speed} \times \sin/\cos(\text{wind direction})$ . The relative minimum and maximum temperatures were the difference between each station and the average of all stations. The relative temperatures were used so that uniform spatial warming within and between years would not cause the weather pattern to change. Clusters would only be affected if there were changes in wind speed, wind direction or humidity, or some stations had larger temporal differences in temperature than others. A small number of observations were missing from each weather station, but these could be estimated using linear regression and the data from other stations. Any errors introduced by this process are considered negligible due to the small amount of

missing data relative to the 48 variables considered for each day (8 variables  $\times$  6 stations), and the high correlations that we observed between data at different stations.

Cluster analysis was used to group all individual days from March 1972 to February 2007 into one of eight groups—each representing a different weather pattern. The number of groups was selected as a trade-off between more groups (less data in each group to establish relationships between air and soil temperatures) and less groups (more variable weather conditions within each group). We could just have validly used more or less than 8 groups, and the implications of this trade-off are included in the discussion.

The number of days of each weather pattern in each calendar year (1973–2006) was regressed against years to determine if there was an increase or decrease in the frequency of different weather patterns. We also calculated the percentage of days in each calendar month that belonged to each weather pattern to determine if there was a seasonal trend. We assessed selected statistics for each weather pattern by calculating the mean (and standard deviation) of daily variables using all days in all years that were part of that pattern. Daily variables were northerly and easterly wind component at 3pm and 9am, humidity at 3pm and 9am, and minimum and maximum temperatures. All variables were the average of the respective values at the six weather stations. Note that relative temperatures were used to produce clusters (see above), but weather patterns were assessed using actual temperatures.

#### *Relationships between air and soil temperatures*

The weather station data used above was only available at 6 locations, and was therefore insufficient to determine the fine-grained spatial distribution of warming. To

counter this problem, we obtained soil temperatures at 40 locations (Fig. 1) for the period September 2005 to August 2006, and determined the relationship between soil and air temperatures for this period. These relationships were used to predict minimum and maximum soil temperatures at all 40 sites for each day that BoM data was available (1972-2007, as above).

Soil temperatures were recorded using DS1921G iButton temperature loggers (Dallas Semiconductor/MAXIM), which were placed 1cm below the surface and recorded hourly temperatures (Ashcroft *et al.* 2008). Linear regression was used to relate the daily minimum and maximum air temperatures (the average of the six BoM stations) with the respective minimum and maximum soil temperatures from the iButtons for the period September 2005 to August 2006. We used the average of six stations, rather than simply the one station that was recorded within the study area, because we wanted to relate the soil temperatures to the average air temperature and weather pattern of the region. Individual weather stations vary in factors such as distance to coast and exposure to key wind directions, and therefore have greater potential to be biased. Using the regional temperature and weather pattern means the method has greater potential to downscale course-grained GCM data.

Analysis was performed separately for each of the eight weather patterns and 40 sites (320 regressions for maximum and minimum temperature), as air temperature may have a different effect on soil temperature at different sites according to wind direction or humidity. In addition, different sites are affected differently according to the exposure to those wind directions (Ashcroft *et al.* 2008). The established relationships between air and soil temperatures were used to estimate the soil temperatures at each of the 40 iButton sites for each day from March 1972 to February 2007.

We investigated a number of factors that had the potential to affect the relationships between soil and air temperatures. First, the average slopes of the air-soil relationships for the eight weather patterns were regressed against their average humidity, average minimum and maximum temperatures, and average northerly and easterly wind components. Second, the average slopes of the air-soil relationships for the 40 sites were regressed against their elevation, distance to coast, distance to streams, and exposure to different directions. The ‘exposure’ predictors were topographically derived estimates of exposure to wind based on the angle to the horizon in a given direction (Ashcroft *et al.* 2008). Exposure has a number of advantages over aspect, and has been shown to be important for the spatial and temporal variations in temperature (Ashcroft *et al.* 2008).

#### *Estimating spatial variations in temperature change from 1972 to 2007*

The average seasonal minimum and maximum temperatures for each site in each of the 35 years (from March 1972–February 1973 to March 2006–February 2007) were calculated by averaging the respective daily temperatures. Seasons conformed to those of the southern hemisphere. That is, summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). For each site, the 35 years of seasonal average minimum and maximum temperatures were regressed against years to determine the trend in temperatures. The amount of warming was estimated as the slope of the regression  $\times 34$  (the difference in years between the start and end dates). The four respective seasonal estimates of warming at each site were averaged to estimate the annual warming in minimum and maximum temperatures. In total, there were 10 estimates of warming for each of the 40 sites—minimum and

maximum temperatures for four seasons plus an annual average. The averages across the 40 sites were used to estimate the amount of warming in each season that had occurred between 1972/3 and 2006/2007.

The factors influencing the spatial distribution of warming were examined by regressing the warming at the 40 sites (10 separate regressions—one for each of the seasonal temperatures above) against elevation, distance from coast, distance from streams and exposure. These predictors are known to influence the distribution of temperatures in this study area (Ashcroft *et al.* 2008). The selected direction of the exposure predictor was the one that maximised the  $r^2$  of the regression.

The relative contribution that each environmental factor made to the amount of warming was compared with other factors by multiplying the coefficient of each predictor with its range. This estimated its overall ‘influence’ in degrees Celsius, and allowed predictors with different units and ranges to be directly compared (Ashcroft *et al.* 2008).

### *Estimating the impact of climate change on plants*

The established relationships, between the amount of warming at a site and the respective environmental variables, were used to generate ‘warming surfaces’ for the whole landscape in a GIS. These warming surfaces were then used to estimate the amount of warming at each of 600 sites where a vegetation survey was conducted (Fig. 1).

The study area contains a complex mosaic of moist and dry rainforests, moist eucalypt forests, tall open eucalypt forests, upland swamps and woodlands (NPWS 2002). Each site (20m by 20m) was surveyed for presence or absence of 37 species

that were common in these communities (NPWS 2002), of which the majority were trees (Table 1). Previous results have shown that the distributions of these species are explained well by models with landscape scale soil temperatures (Ashcroft *et al.* 2008).

For each species, we averaged the amount of warming in the 10 seasonal temperature gradients using only the sites where that species was found. This produced 10 estimates of warming for each species—each representing the average amount of warming for that species in terms of that seasonal temperature. We determined the potential bias in course-grained climate models by determining the difference in warming that different species experienced on each gradient. If there were no bias in course grained models, then all species should experience the same amount of warming. Differences in the amount of warming could occur if species were biased in the topographic and geographic locations they occupied within the landscape.

For each of the 10 seasonal temperatures, we ranked all species using a linear scale from 0% (experienced the least amount of warming) to 100% (experienced the most amount of warming). We calculated the mean and standard deviation for each species across the 10 seasonal temperatures to determine if they consistently experienced a similar amount of warming relative to the other species. This was used to determine whether the bias in warming for each species was predictor specific, or whether the bias was consistent across all temperature predictors.

## Results

### *Temporal changes in weather patterns*

The eight weather patterns that were identified using cluster analysis each favoured different seasons during the year. Winter was dominated by group 7 conditions, which were characterised by low temperatures, intermediate humidity, and light west to northwest winds (Fig. 2). Group 7 days decreased in frequency from approximately 64 to 46 days per year over the period of interest. Group 8 and group 4 were also common in early and late winter respectively. Group 4 days were characterised by strong westerly winds, low temperatures, and low humidity. They increased from approximately 33 to 38 days per year. Group 8 days were characterised by light NE to NW winds, low temperatures, but relatively high humidity. They decreased in frequency from 35 to 18 days per year, the largest percentage drop of any of the weather patterns (Fig. 2f). All of the three groups that were common in winter had similar average temperatures, but the higher humidity groups (7, 8) decreased in frequency, and were replaced by group 4 (lower humidity, stronger westerly winds) and an increasing frequency of spring conditions (see group 2 below). This suggested a change towards drier and/or shorter winters.

The most common conditions in summer were group 5 and group 6. Both were characterised by high temperatures and moderate humidity, but group 5 had northeast winds, while group 6 had southeast winds. Both increased in frequency, with group 5 increasing from 60 to 67 days per year, and group 6 from 48 to 50. This suggested an increase in the frequency and/or length of summer conditions.

Spring and autumn were transition periods where both winter and summer conditions were observed. However, spring also contained the peak of group 2 days. Group 2 was characterised by high temperatures and low humidity under the influence of westerly winds. These conditions are desiccating for moist rainforest plants, and pose bushfire hazards (Fuller 1995). They increased in frequency from 20 to 36 days per year, which was the biggest increase in frequency of all the weather patterns (Fig. 2f).

The final two groups (1 and 3) were observed over the whole year, but were more common in summer than winter. Both had moderate temperatures, low diurnal ranges, and high humidity, suggesting they occurred during rainy periods. Group 1 was characterised by strong southerly winds and increased from 55 to 66 days per year. Group 3 was characterised by light easterly winds, and decreased from 50 to 44 days per year.

#### *The relationships between soil and air temperatures*

The 640 correlations (40 sites, 8 weather patterns, minimum and maximum temperatures) between soil and air temperatures were strong (mean  $r^2 = 0.83$ , s.d. = 0.10), however the slope of the regressions varied dramatically from 0.30 to 1.35 (mean = 0.71, s.d. = 0.15). This illustrates that, on average, a 1°C increase in average air temperatures across the six weather stations corresponded with a 0.71°C rise in soil temperatures on the Illawarra Escarpment, but there were noticeable variations.

There were large differences in the average slope of the air-soil temperature relationships between the eight different weather patterns (mean = 0.71, s.d. = 0.12,  $n = 8$ ), which were best explained in terms of humidity ( $r^2 = 0.54$ ,  $P < 0.05$ , Fig. 3). The



weather patterns with low average humidity (groups 2, 4, 7) were less sensitive to changes in air temperature than those with high humidity.

There were smaller differences in average slope of the air-soil relationships between the 40 different sites (mean = 0.71, s.d. = 0.07, n = 40), but these were significantly correlated with exposure to the WNW ( $r^2 = 0.14$ ,  $P < 0.05$ ). Exposed sites had higher regression slopes, indicating that a 1°C change in air temperature had more affect on ‘west facing’ slopes than ‘east facing’ slopes.

#### *Estimating the spatial distribution of warming from 1972 to 2006*

The amount of warming (averaged over the 40 sites) that was estimated to have occurred over the last 34 years was higher in winter and spring than summer and autumn, and was higher for minimum temperatures than maximum temperatures (Fig. 4). The 10 estimates of warming (minimum and maximum temperatures for the four seasons and annual period) at the 40 sites were explained using multiple regressions against environmental factors (mean  $r^2 = 0.39$ , s.d. = 0.07).

Distance from coast was, on average, the most influential predictor of warming, with inland sites warming by more than coastal sites in all ten models. The magnitude of the effect varied from 0.06°C to 0.30°C, with highest influence on winter minimums. Distance from streams was the least influential predictor, but there was more warming away from streams in all ten models. The effect ranged from 0.01°C to 0.11°C. Elevation was the most influential predictor of warming in minimum temperatures, but was less influential than exposure and distance to coast for maximum temperatures. All ten models suggested there was more warming at lower elevations, and the difference ranged from 0.02°C to 0.37°C. Exposure was the

most influential predictor for maximum temperatures, but was less significant than elevation and distance from coast for minimum temperatures. The effect ranged from 0.05°C to 0.20°C. Annual minimums, and autumn and winter temperatures were best explained using an exposure direction of S to SE, with exposed sites warming by less than sheltered sites. Annual maximums and spring and summer temperatures were best explained using exposure to the W to NW or N to NE, with exposed sites warming by more than sheltered sites. These directions were consistent with more warming at sites exposed to the warm-dry NW winds, and less warming at sites exposed to cold SE sea breezes (Fuller 1995; Ashcroft *et al.* 2008).

The different contributions of environmental factors in different seasons meant that the surfaces for warming displayed different spatial patterns (Fig. 5). For example, summer maximums only displayed a small amount of warming (< 0.35°C), and were heavily influenced by distance to coast. In contrast, spring maximums displayed a high level of warming (0.4–1.0°C), with exposure to the WNW the dominant factor. This was consistent with the increasing frequency of the group 2 weather pattern (westerly winds in spring) noted above. Finally, winter minimums had the most warming (0.4–1.4°C), and were influenced by both distance to coast and elevation.

#### *Effect of warming on vegetation*

The difference in warming between species on the same temperature gradient varied from 15% to 197% (Table 2). For the less extreme temperature gradients (winter maximums and spring and summer minimums), there was less than 16% difference in warming between all 37 species. For the more extreme temperatures (winter

minimums and summer, autumn and annual maximums), there was more than 30% difference between species (Table 2).

Most species had a similar amount of warming relative to other species over all ten temperature gradients (Fig. 6). Species that were only found at inland sites, and typically on drier slopes exposed to the west and northwest, experienced a relatively high amount of warming on all ten gradients. These species included *Eucalyptus cypellocarpa* (MGG), *E. piperira* (SPM), *Acacia binervata* (TVH) and *A. mearnsii* (GW). In contrast, species that experienced a relatively low amount of warming on all ten gradients included moist and dry rainforest species (e.g. *Acmena smithii* (LP), *Doryphora sassafras* (SF), *Toona ciliata* (RC) and *Cassine australis* (ROP)) as well as species that were predominately restricted to the sheltered slopes of the escarpment (e.g. *Syncarpia glomulifera* (TT) and *Eucalyptus pilularis* (BB)). The species that did vary in relative warming (high standard deviation in Fig. 6) were typically those that were common on the Hawkesbury sandstone peaks (e.g. *Eucalyptus sieberi* (SA) and *Corymbia gummifera* (RB)) and dry rainforest species from the foothills and coastal plain (e.g. *Croton verreauxii* (NC) and *Melicope micrococca* (HLD)). The former two species (SA and RB) were below the 30<sup>th</sup> percentile in terms of relative warming for winter minimum, but above the 70<sup>th</sup> percentile in terms of summer maximum. The latter two species (NC and HLD) were below the 16<sup>th</sup> percentile in terms of summer maximum, but above the 80<sup>th</sup> percentile in terms of winter minimum.

## Discussion

### *The importance of weather patterns for climate change predictions*

The results of this study provide further evidence that the spatial distributions of landscape scale soil temperatures are heavily dependent on weather patterns such as the speed and direction of prevailing winds (Ashcroft *et al.* 2008). This is an important finding with respect to climate change studies, because any change in weather patterns could dramatically change the spatial distribution of temperatures, and cause large differences in the temperature changes that different locations experience. Locations where there is less warming could act as refugia, and prevent extinctions that are typically predicted by coarse-scale models, or at least reduce the rate at which climate change affects different species.

Less warming has occurred at sites that are nearer the coast, closer to streams, at higher elevations, exposed to cold S to SE winds, or sheltered from warm, dry, W to NW or N to NNE winds. Species are biased in the topographic and geographic positions they occupy, and therefore different species have experienced different amounts of warming over the last 34 years. For example, moist rainforest species are typically found in locations that are sheltered from the warm, dry W to NW winds. Therefore, these species have experienced less warming than species such as *Eucalyptus cypellocarpa*, *E. piperita* and *E. saligna*X*botryoides*, which are often found at inland sites exposed to these winds. In this context, moist rainforest species are already restricted to refugia within the landscape.

The topographic and geographic biases in species distributions are not unique to this study area. For example, rainforest species are restricted to sheltered gullies at

other locations along the east coast of Australia (e.g. Van Niel & Austin 2007), and eucalypts have consistent biases in the topographic positions they favour (e.g. Austin & Meyers 1996). Therefore, although our study has only determined the species-specific bias in warming in one study area, it is possible that these biases result in consistent over or underestimates across the whole range. If this were the case, then it would represent a consistent bias in each cell of course-grained SDMs.

Our results highlight the need to improve the accuracy of methods that are used to downscale course-grained temperature surfaces. Currently, course-scale bioclimatic models are downscaled using elevation as a surrogate for temperature (Trivedi *et al.* 2008), or SDMs consider fine-scale heterogeneity by including the elevational range of each cell as an extra predictor (Luoto & Heikkinen 2008). The accuracy of these approaches could be improved by considering the regional weather pattern (wind speed, direction, humidity) and the topographic exposure to key wind directions. To successfully implement this over large geographic regions, it will be necessary to develop general rules as to how regional weather patterns relate to fine scale temperature distributions. This will require applying our methods (or similar) to numerous other study areas, and determining whether generally applicable relationships can be established.

Further research is also needed to confirm how the fine-grained spatial variability of climate change, and the species-specific biases, affects the results of Species Distribution Models. However, it is already known that climate change predictions vary substantially according to variations in the GCM (Beaumont *et al.* 2007) and statistical technique (Araújo *et al.* 2005), and the results of SDMs vary when fine-grained spatial variability in temperature is considered (Ashcroft *et al.*

2008). Therefore, it is likely that new methods to downscale temperature data would dramatically change climate change predictions from SDMs.

### *Selecting the correction temperature predictors in models*

While spatial variations in temperature change caused small differences (up to 0.22°C, Table 2) in the average warming each species experienced on the same temperature gradient, these differences were small when compared to the difference between different temperature gradients (0.68°C–0.81°C). For example, minimum temperatures increased almost twice as much as maximum temperatures (except in spring), and winter and spring temperatures increased approximately twice as much as those in summer and autumn. Therefore, an important area for climate change studies is determining which seasonal temperatures are limiting the distribution of each species. Modelling species with the wrong seasonal temperature estimate will dramatically alter estimates of extinction risk.

Determining the seasonal temperatures that are limiting each species is not a simple task. Many seasonal temperatures are highly correlated (especially if they are all derived using only elevation and location), and there may be little difference in model performance using temperature estimates from different seasons. The wrong predictors can easily be selected, and this can drastically alter predictions if they are in different seasons than the true limiting factors. One of the advantages of deriving fine-grained temperature estimates using distance to coast, distance to streams, exposure to key wind directions and elevation, is that it reduces the correlation between alternative temperature predictors. This reduces the probability that the wrong predictor will be

selected, although it does not eliminate it completely when multiple seasons have a similar spatial distribution of temperature.

#### *The relationship between soil and air temperatures*

An unexpected and interesting result from this study was that the relationship between soil and air temperatures varied according to the humidity of the weather pattern and the exposure of the site to the WNW. Humidity was low when winds were from the west (groups 2, 4, 7), and a 1°C difference in air temperature made an average difference of 0.53-0.64°C to soil temperatures under these conditions. In contrast, for the other weather patterns, a 1°C difference in air temperature made an average difference of 0.71-0.86°C to soil temperatures.

The reason that humidity affects the relationship between soil and air temperatures is not clear, but there are at least two possibilities. Firstly, the high specific heat of water may affect the transfer of heat between soil and air. That is, it may be more efficient to transfer heat to the soil when the air is humid and the soil is dry, than when the air is dry and the soil is moist. Secondly, this result may reflect a bias in the locations of the iButtons relative to the broader study area covered by the weather stations. The study area where the iButtons were placed is near the coast, and many of the sites are sheltered from the westerly winds by the escarpment. These possibilities require further investigation.

Understanding the interactions between soil and air temperatures is important, as both may be important for determining the response to climate change. More data is available from the BoM on air temperatures, but soil temperatures are more spatially heterogeneous and may be better able to explain the patchy nature of

vegetation (Ashcroft *et al.* 2008). Our results suggest that a change in humidity may affect soil temperatures, and therefore the distribution of species, even if there is no change in mean air temperatures.

### *Assumptions and limitations*

The primary assumption of this study is that the relationships between soil and air temperatures are temporally stable. This assumption needs to be tested to ensure that there has been no bias in the relationships introduced by climate change. The primary limitation is that the study is restricted to one 10 km by 10 km study area, and further research is needed to determine if the results are indicative of other areas.

We selected eight weather patterns to conduct our analysis. This ensured that we had sufficient data to determine the air-soil temperature relationships, but meant we only had eight points (Fig. 3) when determining which factors affected the slope of the regressions. Increasing the period (one year) over which soil temperatures were recorded would provide extra data, and this would allow more weather patterns to be analysed without compromising the strength of relationships between soil and air temperatures.

### **Conclusions**

Spatial variations in temperature are influenced by the prevailing weather pattern (wind direction, wind speed, humidity), and geographic and topographic factors such as distance to coast and exposure to winds. Climate change has altered the frequency of different weather patterns and this has led to fine-grained spatial differences in the



amount of warming. As species are biased in the topographic and geographic locations they occupy, these spatial variations in warming mean that some species are at more risk of extinction than others, and these differences can not be detected by coarse-grained models. Determining which seasonal temperatures affect each species' distribution and improving the accuracy of temperature distributions will improve the accuracy with which models can predict the response of species to climate change.

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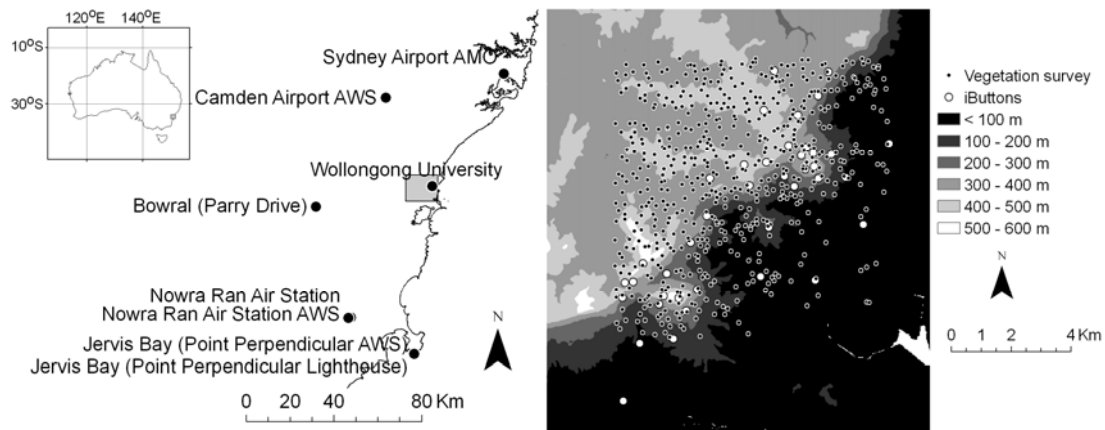
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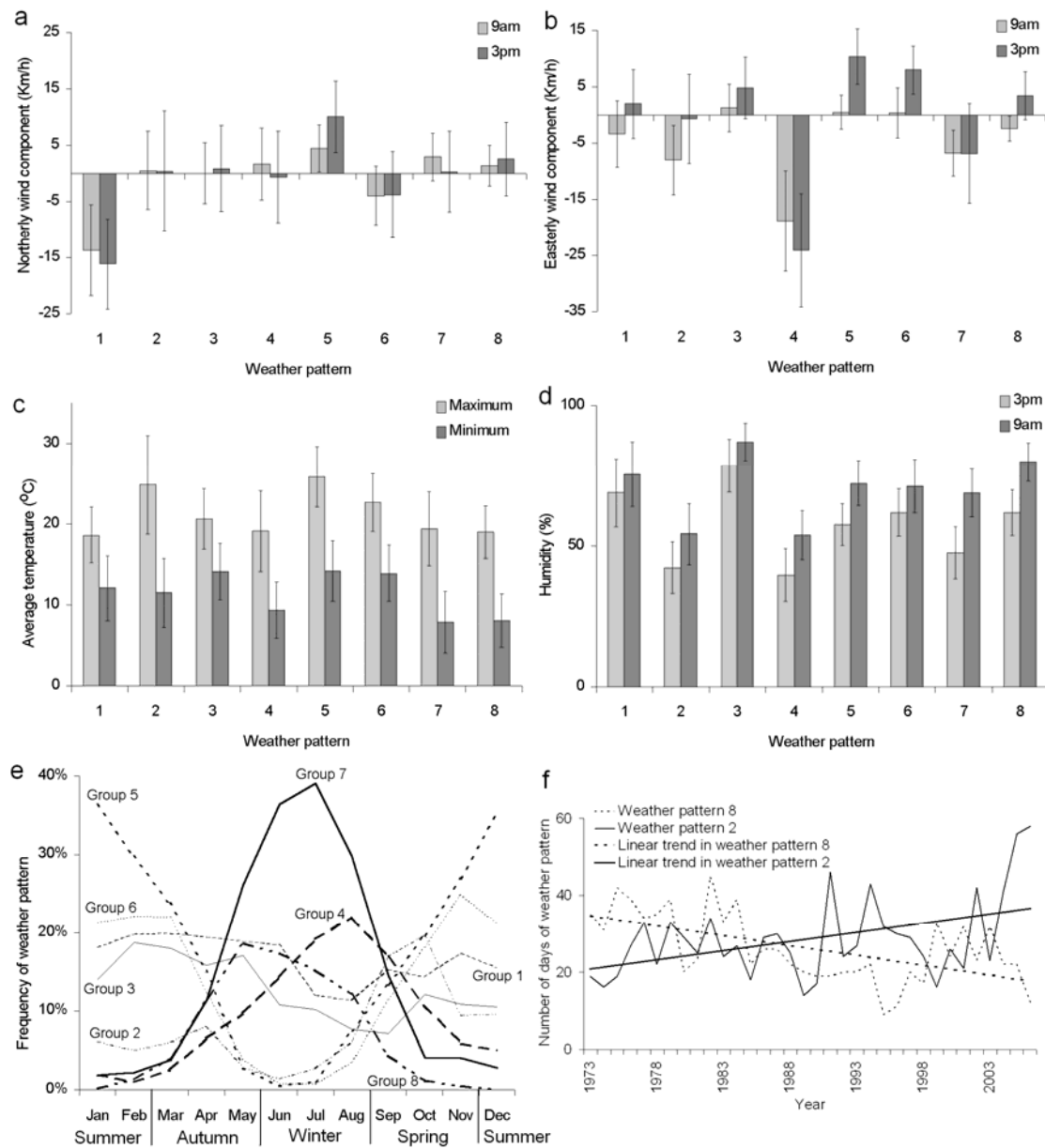
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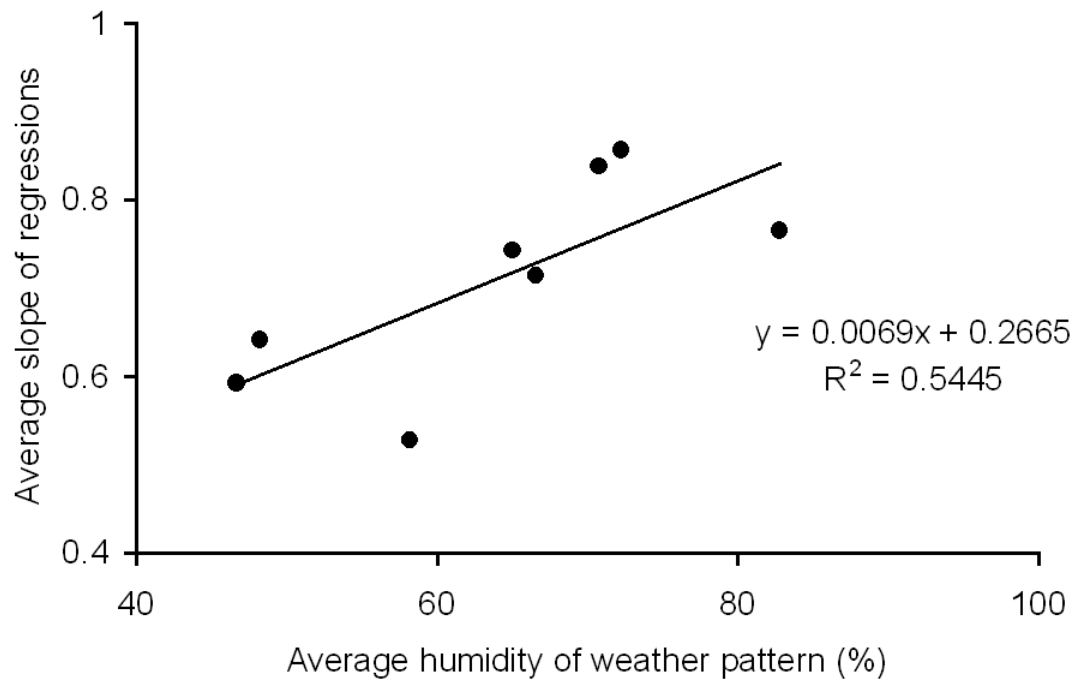
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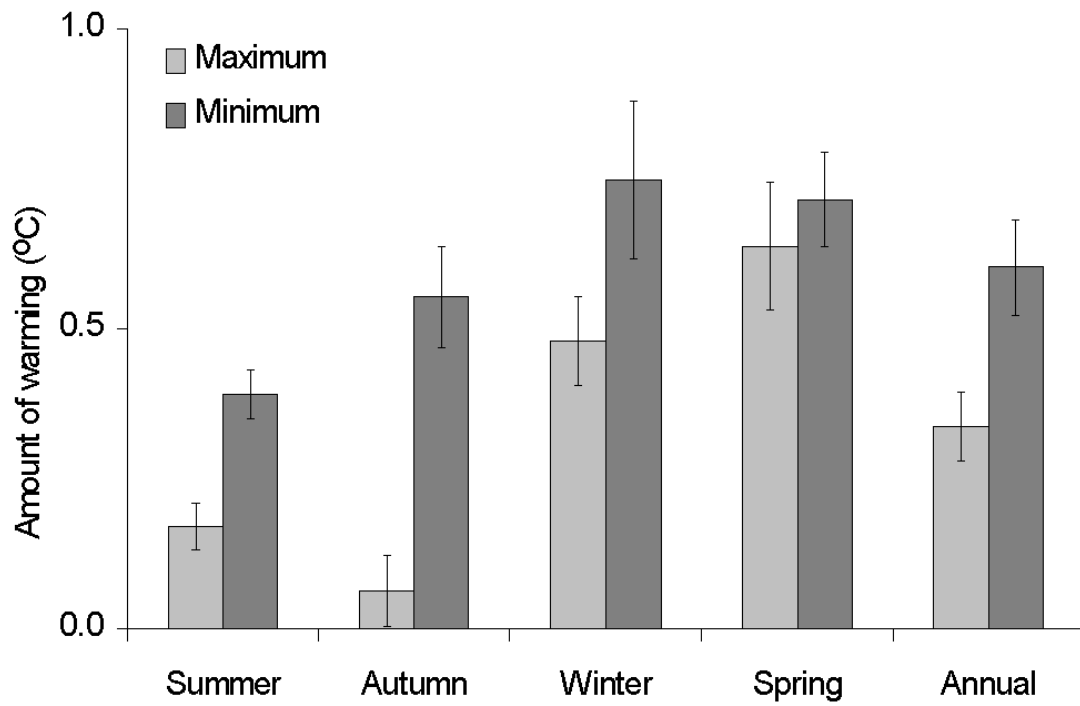
**Fig. 1:** The topography of the study area (right) as an elevation between 0 and 573 m. Superimposed are 40 locations where temperatures were recorded with iButtons, and 600 sites where a vegetation survey was conducted. Daily Bureau of Meteorology observations were obtained from six nearby locations (left).



**Fig. 2:** Eight weather patterns were identified for the study area. Each weather pattern is represented as the average northerly (a) and easterly (b) components of the wind across the six BoM weather stations (wind speed  $\times$  sine/cosine of wind direction), average minimum and maximum temperatures (c), the average humidity at 9am and 3pm (d). Panel (e) illustrates the seasonal change in weather patterns using the percentage of days in each month that belonged to each of the eight weather patterns (average between 1973 and 2006). Panel (f) shows the inter-annual change in the annual number of days in weather patterns 2 and 8 over that period.

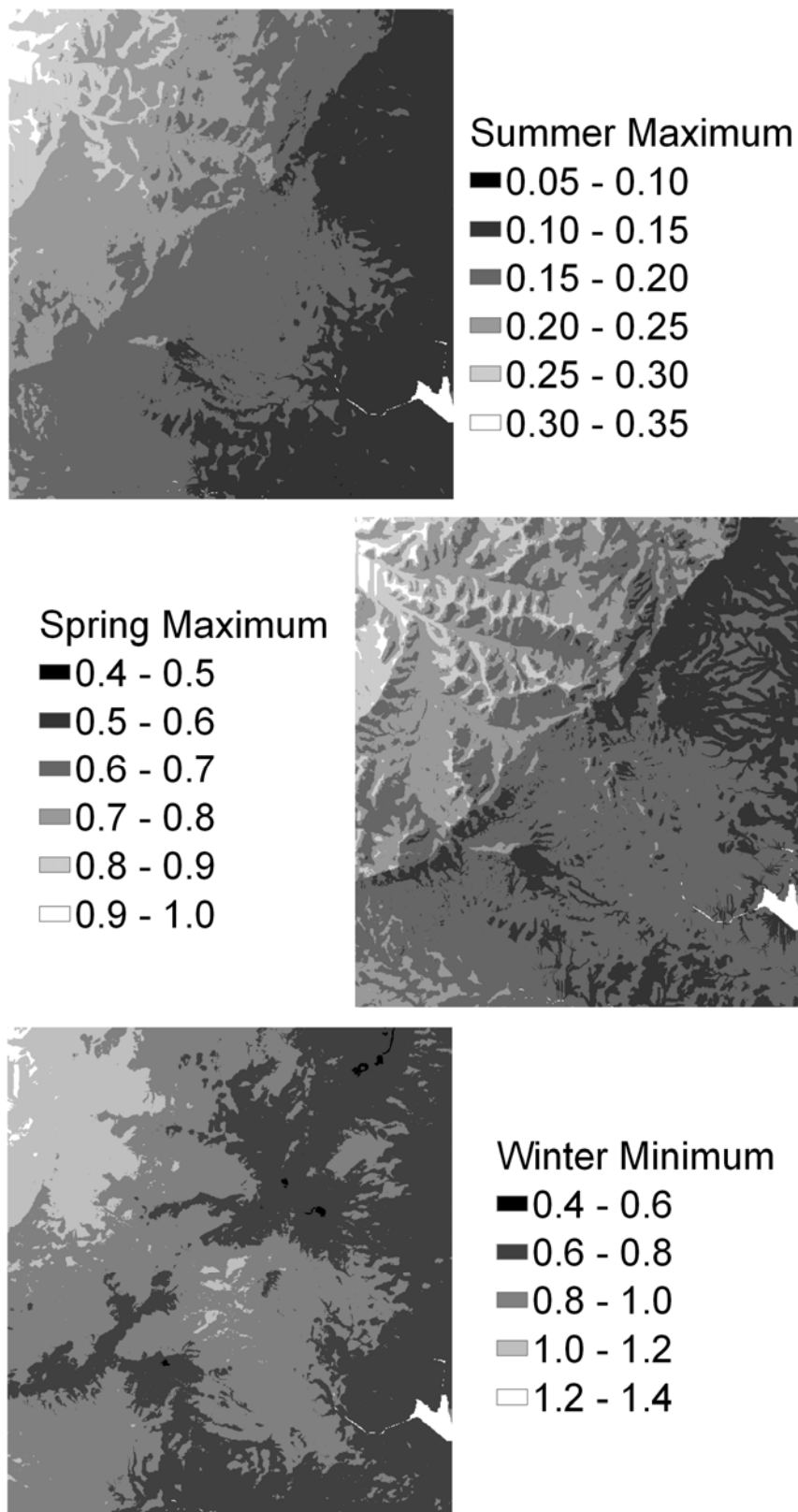


**Fig. 3:** The relationship between average slope of the air-soil temperature regressions and average humidity, where each point corresponds with one of the eight weather patterns used in this study.

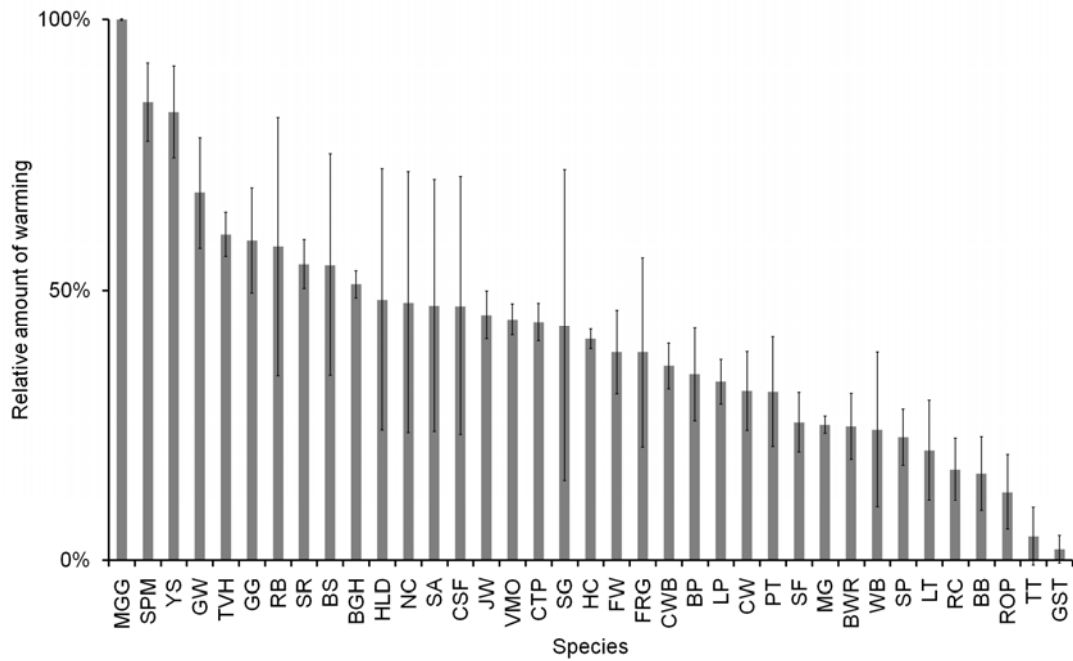


**Fig. 4:** The mean (and standard deviation) amount of warming (1972-2007) estimated at 40 sites where soil temperatures were recorded.





**Fig. 5:** The spatial distribution of warming (1972-2007) in the study area (Fig. 1) as estimated by regressing the amount of warming at the 40 sites where temperatures were recorded against environmental factors. All surfaces are in degrees Celsius.



**Fig. 6:** The average amount of warming (1972-2006) was estimated for 37 species (Table 1) using ten seasonal temperature gradients (Table 2). The relative warming for each species on each gradient was calculated on a linear scale from 0% (least warming of all species) to 100% (most warming of all species). This graph illustrates the mean (standard deviation) relative warming for each species over the ten gradients.