The sensitivity of topoclimatic models to fine-scale microclimatic variability and the relevance for ecological studies

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Abstract Microclimatic loggers are increasingly used to collect data from various habitats and interpolate ecologically meaningful landscape-scale topoclimatic grids. However, it is unknown how sensitive these grids are to finer-scale variations in microclimate. We performed a sensitivity analysis using three microclimatic loggers at 27 sites for 5 months in a semi-arid region of Western Australia. We partitioned the within- and between-site variance in temperature and produced 100 different topoclimatic models using a random sensor from each site. For the coldest temperatures, we found within-site variance was negligible (3 %), and models were strong ($r^2=0.74$) and the coefficients consistent. However, for the hottest temperatures, there was substantial within-site variance (39 %), and models were weaker ($r^2=0.27$) and more sensitive. We concluded that careful site design is needed to maximise the reliability of topoclimatic grids, including using large sample sizes, ensuring there is low predictor collinearity and sampling full environmental gradients.

1 Introduction

It is widely accepted that climate affects the distribution of biodiversity. As such, ecologists regularly make direct use of climatic data from the nearest standardised weather station (i.e. Stevenson screens ~1.5–2 m above flat, cleared

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areas) or estimate climate using macroclimatic surfaces that have been interpolated from these observations (e.g. Hijmans et al. 2005). However, many have questioned the appropriateness of using such observations for understanding biodiversity–climate relationships (Wolfe 1945; Kennedy 1997; Lookingbill and Urban 2003; Ashcroft et al. 2008; Suggitt et al. 2011; Graae et al. 2012). Criticisms include (1) standardised weather stations shelter instruments from conditions that most organisms experience (Wolfe 1945); (2) observations are made at a height of 1.5–2 m and do not reflect the conditions relevant for ground-dwelling fauna, germinating seeds, tender saplings or ecological processes (Geiger 1971; Ashcroft et al. 2008; Graae et al. 2012); (3) observations are made on largely flat, unvegetated land and do not reflect the environments (e.g. gorges/forests) that many species actually live in (Geiger 1971; Kennedy 1997; Suggitt et al. 2011) and (4) neither standardised weather station data nor interpolated macroclimatic grids capture the fine-scale climatic variations that actually occur at regional and landscape scales (Wolfe 1945; Lookingbill and Urban 2003; Dixit and Chen 2011; Scherrer and Körner 2011; Ashcroft and Gollan 2012).

To address these four criticisms, there has been a surge in studies placing large numbers of microclimatic data loggers across different environments and interpolating topoclimatic grids. These grids have grain sizes as fine as 5–100 m and consider a broad range of fine-scale climate-forcing factors such as cold air drainage, topographic exposure and canopy cover (Lookingbill and Urban 2003; Ashcroft et al. 2008; Fridley 2009; Vanwalleghem and Meentemeyer 2009; Dixit and Chen 2011; Shoo et al. 2010; Holden et al. 2011; Ashcroft and Gollan 2012). While the intent is to produce climatic grids that better capture ecologically meaningful fine-scale variations in climate, it is worth considering the degree to which the above four criticisms are actually overcome. For example, microclimatic loggers have been placed

on the shady side of trees (Lookingbill and Urban 2003; Fridley 2009), wrapped in foil (Suggitt et al. 2011) or placed inside polyvinyl chloride (PVC) containers or other radiation shields (Lundquist and Huggett 2008; Vanwalleghem and Meentemeyer 2009; Dixit and Chen 2011; Shoo et al. 2010; Holden et al. 2011; Ashcroft and Gollan 2012). Therefore, the fine-scale grids are still produced using sensors that are protected from the conditions that many organisms experience. Similarly, these requirements for shelter can also introduce a bias in the environments where sensors are placed (e.g. only forests if you rely on shade from trees), so they still may not reflect the climate in all species' habitats. Finally, sensors are also placed at a variety of heights including 1–2 cm below the soil surface (Ashcroft et al. 2008; Graae et al. 2012), 5 cm above the surface (Ashcroft and Gollan 2012) and 1–2 m above the surface (Lookingbill and Urban 2003; Fridley 2009; Vanwalleghem and Meentemeyer 2009; Shoo et al. 2010; Holden et al. 2011). If ground level observations are important for most species and processes (as suggested by Geiger 1971; Graae et al. 2012), then, many grids are still based on observations at other heights.

Therefore, at least three of the above four criticisms of macroclimatic grids can still be directed at many fine-scale topoclimatic grids produced using large networks of microclimatic loggers. However, topoclimatic grids will still be an improvement if they better capture ecologically meaningful variations in climate at landscape or regional scales (the fourth criticism). An outstanding issue in this respect is how much variability is captured by topoclimatic grids with grain sizes of 5–100 m and how much variability is not captured because it still occurs at finer scales within these cells. For example, in a global study, Hijmans et al. (2005) suggested 30 arc second (~1 km) cell sizes were better than 10 arc minute (~20 km) cells because there could be up to 33.8 °C difference in mean annual temperature (mean 1.8 °C) within the larger cells sizes. However, assessing ~1-km cells using ~25-m resolution topoclimatic grids in a large (300 km by 200 km) and topographically complex (e.g. elevational range of ~1,400 m) temperate landscape in eastern Australia (Ashcroft and Gollan 2012) shows that there are still large variations in climate within 1-km grid cells. For example, in terms of the hottest temperatures, there was up to 14.2 °C variation within 1-km cells (mean 4.6 °C), and in terms of the coldest temperatures, there was up to 11.2 °C variation (mean 4.5 °C). Ashcroft and Gollan (2012) suggested that there were still microclimatic variations within their 25-m cells, and moving all sensors a few metres would change observations noticeably at some individual sensors (see also Scherrer and Körner (2011) for an analysis of fine-scale microclimatic variations). However, these variations would not affect the overall topoclimatic models if the relationships between climate and climate-forcing factors were unchanged. In effect, fine-scale variation

might affect the residuals (errors) in topoclimatic models but have little effect on the models themselves. This is an important issue to address, as it is important for understanding the usefulness and accuracy of the resulting topoclimatic grids and assessing whether it is sufficient to place one sensor at each site as all topoclimatic studies we are aware of to date have done.

The objective of this study was to quantify how sensitive topoclimatic grids are to within-cell variations in microclimate. The specific aims were (1) to quantify the variation in microclimate within topoclimatic cells relative to the overall variations between sites, (2) to determine how fine-scale variability affects the coefficients and performance of topoclimatic models and (3) to determine the effect of random variations in predictor variables, as fine-scale variation in the predictors themselves may also affect topoclimatic models. In essence, the focus of this article is on sensitivity analysis (how much do models vary) rather than on producing one best model.

2 Methods

2.1 Study area and data

Our study was conducted across a ~10 km by 6 km area near the town of Newman in the Pilbara bioregion, Western Australia (~23.5°S, 119.5°E). The Pilbara is within a zone characterised by a hot and semi-arid climate. The climate at the nearby Bureau of Meteorology weather station at Newman Airport (~18 km to the east of the study area) is dry (mean annual rainfall of 310 mm) and hot (mean daily maximum temperature of 31.4 °C). The elevation varies from ~550 to 800 m (Fig. 1). The landscape is dominated by rocky hills and stony plains, with stony soils and shallow red loams (Hamersley Plateau Zone in Tille 2006).

Grazing is the dominant (~60 % by area) land use in the Pilbara bioregion (Fisher et al. 2004), but it is also rich in several minerals including iron ore. Large-scale developments worth billions of dollars are either underway or proposed for the region, and the ecology of the region has a large influence on land management decisions. Short-range endemic invertebrates are a particularly important group of fauna, as development proposals are thoroughly scrutinised by state government agencies to ensure their protection. These range-restricted species favour isolated, moist, cool patches in the landscape (Harvey 2002), and it is important to understand fine-scale variations in climate in this region in order to quantify and locate these microrefugia (e.g. Ashcroft et al. 2012).

Three microclimatic loggers were placed at each of 27 sites within the study area (Fig. 1), which is typical of the number of sites used by other topoclimatic studies (e.g. Lookingbill and Urban 2003; Ashcroft et al. 2008; Dixit

Fig. 1 The topography of the study area in the Pilbara bioregion of western Australia (~23.5°S, 119.5°E). *Black dots* illustrate the locations of 27 sites where three microclimatic loggers were installed
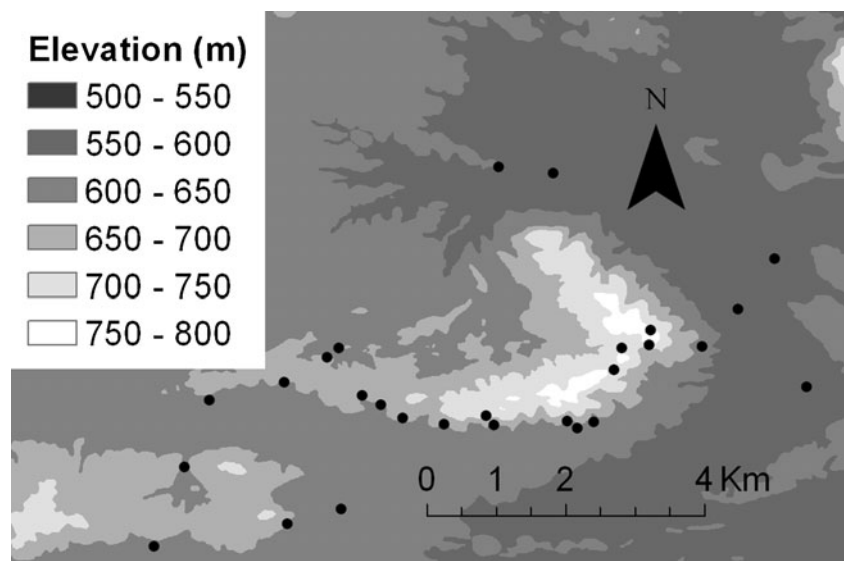
and Chen 2011; Shoo et al. 2010 all use between 21 and 50 sites). While larger sample sizes should be beneficial and have become more common (e.g. Vanwalleghem and Meentemeyer 2009; Holden et al. 2011; Ashcroft and Gollan 2012 use hundreds of sites), all these studies have only used one sensor per site. Placing multiple sensors per site allowed us to examine the amount and effects of within-cell variation in microclimate and examine the inherent trade-off between the number of sensors per site and the number of sites that can be used for a given budget. While the number of sites is lower than some of the more recent studies mentioned above, this was beneficial to the present study as it would better highlight the sensitivity of models.

Sites spanned broad habitat types that were present across the study area and the region as a whole. Habitat types included floodplain woodlands, deep and densely forested gullies and gorges, steep slopes with various aspects and sparsely vegetated ridges. Common canopy trees included mulga (*Acacia aneura*) and snappy gum (*Eucalyptus leucophloia*), shrubs included hop bush (*Dodonia* spp.) and low-growing *Acacia* species, and the understorey was dominated by spinifex (*Triodia* spp.). A range of topographic positions and habitat types were selected to capture the broad range of climates experienced by biota within the region.

Sensors at each site were separated by 10–20 m and were placed within the same habitat type. Some sensors failed or were disturbed by wildlife, leaving three sites with one sensor, six sites with two sensors and 18 sites with three sensors. The sensors were DS1923 hygrochron iButtons (Maxim/Dallas) that were housed ~5 cm above the soil surface inside PVC shelters according to the methodology of Ashcroft and Gollan (2012). Sensors recorded hourly temperature and humidity from 17 March to 9 August 2010. Temperature data were software corrected using internally stored calibration data and were accurate to within 0.5 °C between −10 and 65 °C.

As observations were made near ground level, minimum temperatures could be lower those reported by standardised weather stations, and maximum temperatures could be as much as 10–20 °C higher (Geiger 1971; Campbell and Norman 1998). Humidity observations saturate under moist conditions and can exceed 100 %. Based on 3 years of observations at 250 sites in eastern Australia (Ashcroft and Gollan 2012), it is clear that the amount of saturation varies in different iButtons. We, therefore, applied a correction whereby we calculated the 95th percentile of daily maximum humidities for each sensor and then linearly scaled humidity observations such that 100 % humidity corresponded with the top 5 % of maximum humidities. This correction reduced bias between iButtons and will be valid whenever there is occasional rainfall or sharp declines in overnight temperatures such that the air saturates at each site.

We calculated the daily maximum and minimum temperature and humidity for each sensor and then calculated the 95th percentile of maximum temperatures as an indication of the hottest conditions, the fifth percentile of minimum temperatures as an indication of the coldest conditions and the fifth percentile of minimum humidity as an indication of the driest conditions. Extreme conditions occur under specific weather conditions, and percentiles allow a focus on those extreme conditions even if they do not occur simultaneously or on consecutive days (Ashcroft and Gollan 2012).

A wide variety of climate-forcing factors can be influential at fine scales (Daly 2006), but given the low number of sites in our study (*n*=27), we were cautious to include no more than three climate-forcing factors per model. As the coast was more than 350 km away, coastal influences were not expected to have a significant effect and were not considered. Exposure to cold air drainage was estimated as the difference between the elevation at a site and the minimum elevation within 500 m of a site. Sites that are near the

local topographic minima are exposed to cold air pooling, while perched sites are not exposed because the cold air can drain away downhill. This 'relative elevation' predictor has been shown to be a good method of predicting cold air drainage elsewhere (Daly et al. 2007; Bennie et al. 2010; Ashcroft and Gollan 2012). Elevation and cold air drainage were highly correlated (r^2=0.92) in this study area. Given that elevation has a stronger effect on maximum temperatures and minimum humidities than cold air drainage (Ashcroft and Gollan 2012), we used only elevation in models for these factors. Cold air drainage was used in the models for minimum temperatures as this has a stronger effect than elevation.

Canopy cover was estimated as a percentage based on visual observations at each of the 27 sites. This is a commonly used approach, and although there can be a large variation between observers, all our observations were made by the same person (JG), and this method is sufficiently accurate for our purposes as most observers rank sites in similar order (Gorrod and Keith 2009; Gollan et al. 2012). Radiation was estimated using the Area Solar Radiation tool of ArcMap 9.3 (ESRI) and based on Julian days 76–86, corresponding with the hotter temperatures near the start of our observations. Exposure to the north-west was calculated using the method of Ashcroft et al. (2008), with an azimuth of 315° used as this is the direction that has been associated with the cool, moist habitats that terrestrial short-range endemic invertebrates are reported to favour (Harvey 2002). There were moderate correlations between radiation and the other two of these predictors (canopy cover r^2=0.38, t=−3.88, P=0.0007; exposure to north-west r^2=0.34, t=−3.57, P=0.001), and we cautiously preferred canopy cover and exposure to north-west in models as they were slightly less correlated (r^2=0.20, t=2.51, P=0.019). Therefore, the models we used were

$$T_{min} = a_0 + a_1.\text{cad} + a_2.\text{canopy} + a_3.\text{expNW} + \text{err}$$

$$H_{min} \text{ or } T_{max} = a_0 + a_1.\text{elev} + a_2.\text{canopy} + a_3.\text{expNW} + \text{err}$$

where T_{min}, T_{max} and H_{min} represent the fifth percentile of minimum temperatures, 95th percentile of maximum temperatures and fifth percentile on minimum humidities, respectively; a_0 to a_3 are the coefficients in the regional regression models; err is the error term; and, cad, canopy, expNW and elev represent cold air drainage, canopy cover, exposure to the north-west and elevation, respectively. We also produced models with radiation instead of expNW to test the effect of including predictors with higher collinearity.

2.2 Analysis

We first examined how much of the variation in our observations could be attributed to within-site microclimatic variability rather than topoclimatic differences between sites. For each of the three response variables (fifth percentile minimum temperatures, 95th percentile maximum temperatures, fifth percentile minimum humidities), we conducted an ANOVA with the 69 samples (27 sites×3 sensors per site—12 missing samples) to determine if site had a significant effect on observations and to partition the variance into within- and between-site variance.

We then examined how much intra-site climatic variability affected model performance and coefficients by selecting one sensor at random from each of the 27 sites and producing topoclimatic models for each of the three response variables using the models detailed above. We repeated this process 100 times using different random combinations of sensors and calculated the mean, standard deviation and range of model performance (r^2 of regional regressions detailed below) and coefficients (examined as the effect size=coefficient×range of predictor so that different predictors could be directly compared). The intent was not to produce one best model but to assess how sensitive the models were.

The models were produced using a regional regression approach (Lookingbill and Urban 2003; Daly 2006; Ashcroft and Gollan 2012), with the response modelled as a linear combination of the three selected predictor variables (as detailed above). The cold air drainage predictor was transformed as log(relative elevation×1,000) to ensure linearity, whereas the other predictors could be used directly as relationships were already linear.

We then tested the effect of small variations in two arbitrarily selected predictor variables, using cold air drainage and minimum temperatures as one example and exposure to the north-west and maximum temperatures as the other. Response variables were calculated as the average of the 1–3 sensors at each site. Errors in the predictor variables were introduced using a normal distribution (mean=0, standard deviation (s.d.)=0.1), where 0.1 represented 6.2 and 6.7 % of the range of the respective predictor variables above. We have observed differences approximately of this magnitude when comparing predictors generated using different digital elevation models (DEMs) in another study area (unpublished data). We repeated the process 100 times using randomly generated errors in the predictors and once again noted the effects on the variability of model performance and coefficients as above.

3 Results

3.1 Within-site variation

The observed fifth percentile of minimum temperatures ranged from 5.8 to 14.8 °C (mean 12.0 °C; s.d.=2.4 °C). The average within-site variation was comparatively low (mean s.d.=0.45 °C; Fig. 2a), and the ANOVA showed that within-site variance accounted for just 3.4 % of the total

Fig. 2 The mean temperatures and humidities recorded by one to three microclimatic sensors at 27 sites in the Pilbara region of Western Australia. *Error bars* show within-site standard deviation, with *larger error bars* in panels **b** and **c** due to greater within-site climatic variability
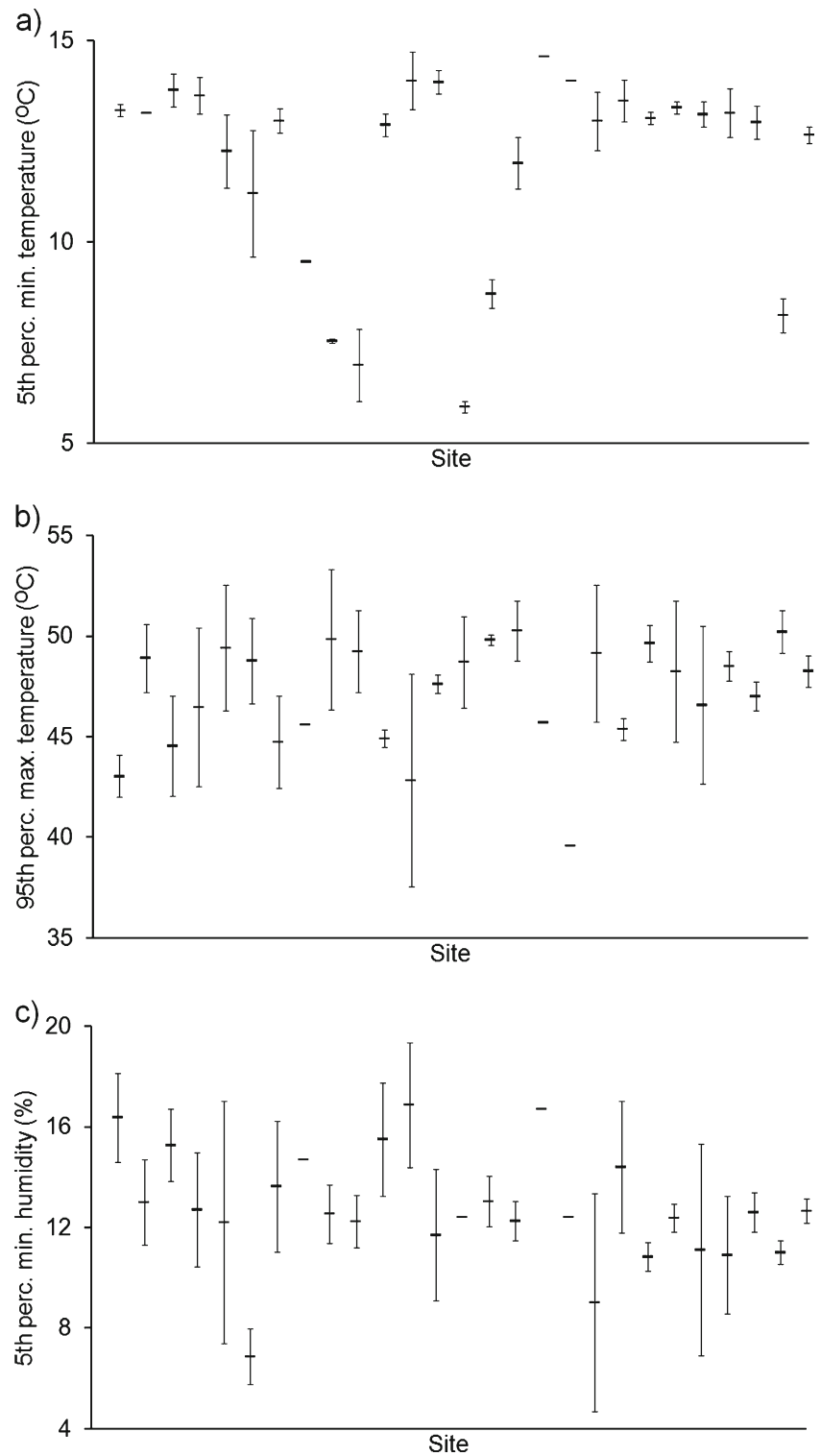
variance (total variance=403.5; within-site variance 13.8; between-site variance 389.7; F=45.7; degrees of freedom (d.f.)=26, 42; $P<0.0001$).

In contrast, there was far more within-site variation in both the 95th percentile of maximum temperatures and the fifth percentile of minimum humidities (Fig. 2b, c). The 95th

percentile of maximum temperatures ranged from 36.8 to 53.8 °C (mean 47.3 °C; s.d.=3.1 °C), with an average within-site standard deviation of 2.0 °C. Within-site variance accounted for 39.2 % of total variance (total variance=659.2; within-site variance=258.4; between-site variance=400.8; F= 2.51; d.f.=26, 42; P=0.004). The fifth percentile of minimum

humidities ranged from 4.0 to 19.7 % (mean 12.6 %; s.d.= 2.8 %) with an average within-site standard deviation of 1.8 %. Within-site variance accounted for 37.1 % of total variance (total variance=547.7; within-site variance=203.0; between-site variance=344.7; F=2.74; d.f.=26, 42; P=0.002).

3.2 Effect of within-site variation on model coefficients and performance

The hundred different models for the fifth percentile of minimum temperatures performed consistently well (mean r^2=0.74; s.d.=0.02; range 0.68–0.77). Models were dominated by the cold air drainage term, which had a strong and consistent effect (mean effect size=6.6 °C; s.d.=0.34 °C; range 5.9–7.6 °C; Fig. 3a). Canopy cover (mean effect size= 1.8 °C; s.d.=0.54 °C) and exposure to the north-west (mean effect size=1.4 °C; s.d.=0.4 °C) had smaller but still relatively consistent effects. The relatively low standard deviations indicate that the 100 replicates produced similar models, and fine-scale climatic variability had little effect on the models for minimum temperature.

The hundred models for the 95th percentile of maximum temperatures (mean r^2=0.27; s.d.=0.09; range 0.10–0.56) and the fifth percentile of minimum humidities (mean r^2=0.26;

s.d.=0.12; range 0.07–0.58) were poorer and more variable than those for minimum temperatures. Both models were dominated by canopy cover (mean effects sizes −4.5 °C/4.9 % relative humidity (RH); s.d.=1.2 °C/1.3 % RH; Fig. 3b, c). The effect of elevation was small due to a low elevational range (mean effect sizes −2.2 °C/1.4 % RH; s.d.= 1.2 °C/0.8 % RH) and was very variable (ranges −5.0 to 0.3 °C/−0.5 to 3.6 % RH). The effect of exposure to the north-west was even smaller and more variable (mean effect sizes −1.3 °C/−0.4 % RH; s.d.=1.0 °C/0.9 % RH). The higher variability in the models for maximum temperatures and minimum humidities compared to those of minimum temperature indicated that they were more sensitive to which sensors were selected from each site, and therefore, the models were less reliable. That is, if we only placed one sensor at each site, as is usually the case, the models would be sensitive to the placement of those sensors within each site.

When radiation was included instead of exposure in models for the 95th percentile of maximum temperature, the variation in all coefficients was higher (Fig. 3c, d). This is likely due to the tendency for correlated predictors to lead to biased estimates of coefficients, and therefore, the models were less reliable, even though radiation had a larger effect than topographic exposure.
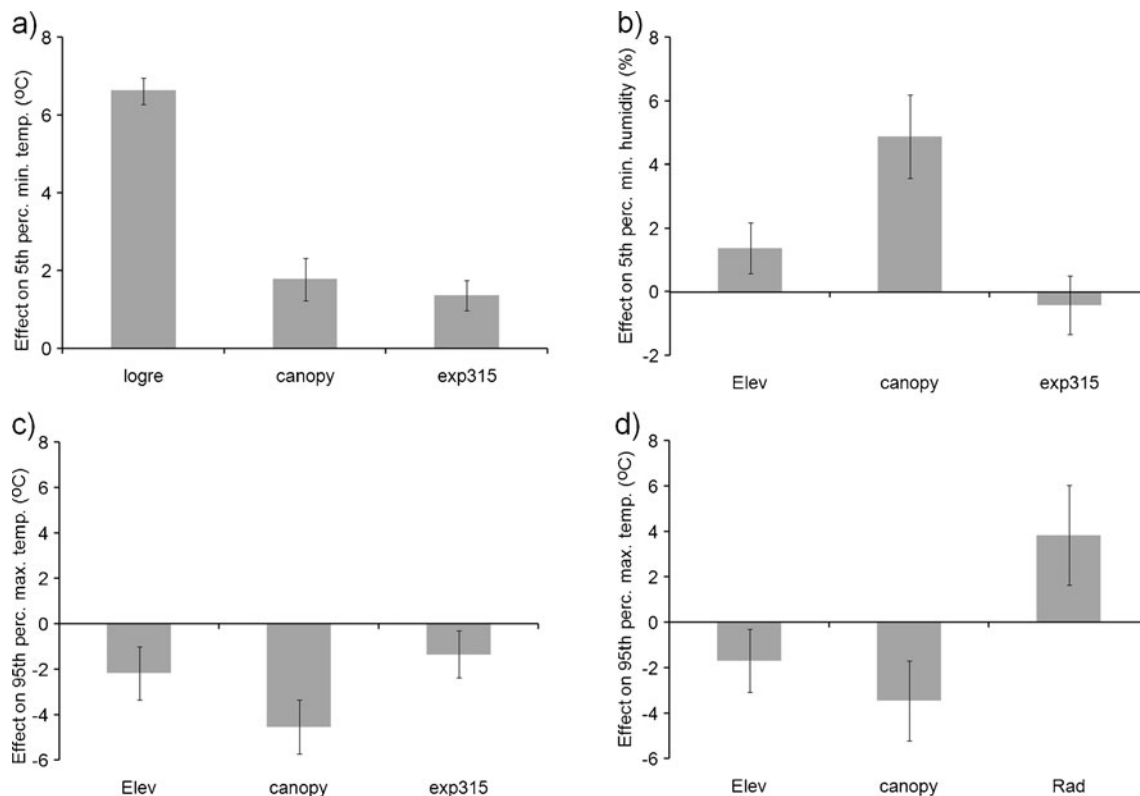
Fig. 3 The mean effect sizes (predictor range×coefficient) for 100 models produced using a randomly selected sensor from each of 27 sites. Predictors used were canopy cover (canopy), exposure to the north-west (exp315), elevation (Elev), radiation (Rad) and a cold air drainage term calculated using the log of relative elevation (logre). *Error bars* show standard deviation

3.3 Effect of predictor error on model performance and coefficients

Introducing errors (mean=0; s.d.=0.1) to the cold air drainage predictor had a similar effect on models to the intra-site variability in temperature. The performance of models was still strong and consistent (mean r^2=0.73; s.d.=0.04), but the effect size of cold air drainage was slightly smaller (mean effect size=6.3 °C; s.d.=0.37 °C; Fig. 4a). The errors introduced to the exposure predictor had little effect on results for the 95th percentile of maximum temperatures (mean r^2=0.36; s.d.=0.01), and there was little variation in model coefficients (s.d. of effect sizes <0.3 °C; Fig. 4b).

4 Discussion

Our study produced mixed results on the amount and effects of fine-scale variability in climate. In terms of the coldest temperatures, there was little within-site variation in temperatures (3.4 % of total variance), and topoclimatic models were consistently strong (mean r^2=0.74) and dominated by cold air drainage (mean effect size 6.6 °C, effect of other predictors <1.8 °C). In this case, topoclimatic models adequately captured the trend in climate, and fine-scale microclimatic variation was relatively unimportant. This suggests that one sensor per site would be sufficient to capture topoclimatic trends in minimum temperatures and within-cell microclimatic variability could generally be ignored.

The dominant cold air drainage predictor we used in this study was based on the elevation relative to the minimum elevation within a 500-m radius. This predictor has been shown to be the dominant predictor of minimum temperatures in pre-alpine/arctic England (Bennie et al. 2010), temperate/sub-tropical eastern Australia (Ashcroft and Gollan 2012), and now semi-arid western Australia. The elevation relative to the mean elevation does not appear to work as well (Hjort et al. 2011). This demonstrates that even small elevational differences can have large effects on minimum temperatures (e.g. 6.6 °C in this study with sensors spanning ∼200 m) across a variety of biomes, and this effect operates at fine scales (i.e. 500-m radius) that are below the resolution of global datasets such as the 1-km resolution Worldclim climate grids (Hijmans et al. 2005). Therefore, climate grids with a grain size of approximately 25–100 m appear to be necessary for mapping minimum temperatures, although even finer resolutions may be needed where there are deep, narrow gorges (e.g. Holec and Wild 2011).

In contrast to minimum temperatures, there was more fine-scale variation in maximum temperatures and minimum humidities. Given maximum temperatures and minimum humidities are not completely independent (as temperatures rise the relative humidity generally falls) and the results for
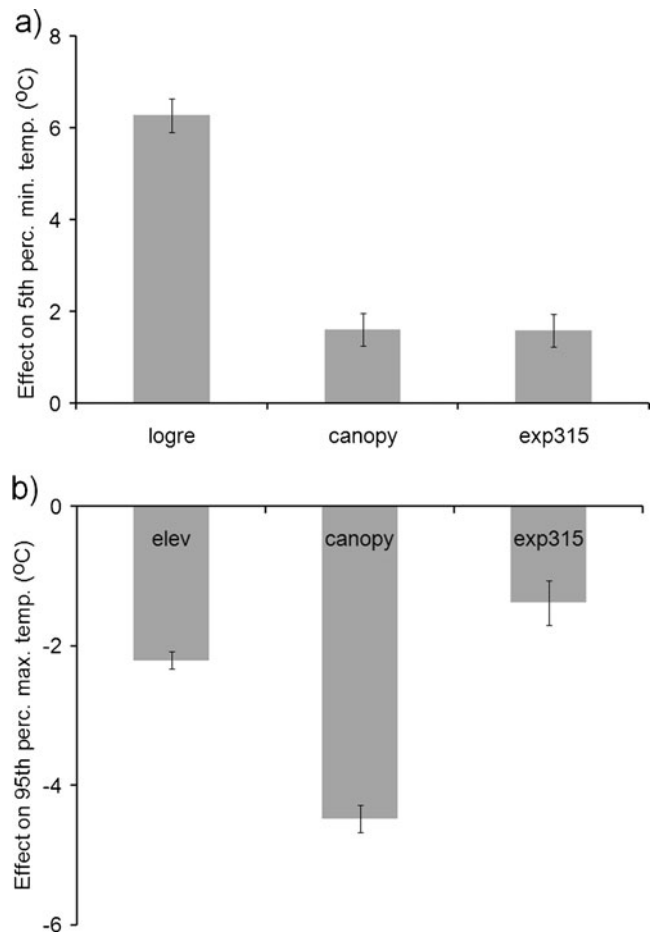
Fig. 4 The mean effect sizes (predictor range×coefficient) for 100 models produced with random errors added to the cold air drainage (**a**) and exposure to north-west (**b**) predictors at each of 27 sites. Predictors used were canopy cover (canopy), exposure to the north-west (exp315), elevation (elev) and a cold air drainage term calculated using the log of relative elevation (logre). *Error bars* show standard deviation

the two were similar, we restrict our discussion here to maximum temperatures. The within-site variation in maximum temperatures was high (average within-site s.d.= 2.0 °C), and this made up 39.2 % of the total variance. Even if we reduced the spatial resolution of our topoclimatic grids dramatically, there are likely to be differences over distances of a few centimetres according to variations in shading from tree trunks and canopies and small variations in topographic exposure. Effects are likely higher than minimum temperatures due to higher radiation fluxes during daylight hours. Topoclimatic models for maximum temperatures have consistently been weaker than those for minimum temperatures (e.g. Lookingbill and Urban 2003; Ashcroft et al. 2008; Fridley 2009; Ashcroft and Gollan 2012), and the higher residual errors in these models probably reflect the greater within-site variations in maximum temperature. Topoclimatic models for maximum temperatures will still be capturing the overall climatic trend, but the

lower performance indicates there is substantial variation within each cell.

The models for maximum temperature were also more sensitive to the within-site variation in climate, with more variation in both model performance and coefficients (Fig. 3). This can be attributed to at least two factors. When model performance is low, the underlying relationships are weaker and more sensitive to the noise introduced by within-site variation in climate. Secondly, the models for maximum temperature were affected by predictor collinearity, especially when radiation was included instead of exposure to the north-west (Fig. 3). To reduce this sensitivity to within-site variation, it is important that sensors are placed wisely. As already suggested (Ashcroft and Gollan 2012), sensitivity will be reduced if the full range of predictors are sampled, spatial autocorrelation is minimised, predictor collinearity is reduced as far as possible, and large sample sizes are employed. Indeed, the low sample size ($n=27$ sites), high predictor collinearity (e.g. r^2 of 0.38 between canopy cover and radiation), and low elevational range (~200 m) in the present study probably meant that our results are a worst case-scenario, and indeed, the performance of our models for maximum temperature are lower than those reported elsewhere (Lookingbill and Urban 2003; Ashcroft et al. 2008; Ashcroft and Gollan 2012). Therefore, although within-site variation in maximum temperatures will affect all models to some extent, careful design can ensure models are less sensitive than indicated by this study. However, it should be noted that such careful design will only ensure that the mean temperature of cells can be predicted more accurately. Models will still not be capable of capturing within-cell climate range unless multiple sensors are placed at each site to estimate such variation.

Predictor accuracy can also be an issue that reduces model performance (e.g. McInerny and Purves 2011). Errors can be introduced by small positional inaccuracies or variations in the boundaries or resolutions of DEMs that change the perceived environmental factors at sites where sensors are located. We found that the variation introduced by these errors had similar but smaller effects to fine-scale climatic variations (Figs. 3 and 4), and efforts should also be made to minimise errors. For example, reducing the resolution of DEMs will help ensure the accuracy of predictors in small gorges (e.g. Holec and Wild 2011), where cold air drainage and topographic exposure can vary dramatically over short distances.

In conclusion, fine resolution (5–100 m) topoclimatic grids can capture landscape-scale climatic patterns more accurately than macroclimatic surfaces because they consider a broader range of fine-scale climate-forcing factors and are based on observations from a wider variety of habitats. However, there are still large within-cell variations in climate for topoclimatic grids of maximum temperature in particular. These fine-scale variations in microclimate can reduce model performance and affect model coefficients if care is not taken to reduce predictor collinearity, ensure samples span the full range of each predictor and obtain large sample sizes.

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