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Modelling the soil microclimate: does the spatial or temporal resolution of input parameters matter?

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Abstract. The urgency of predicting future impacts of environmental change on vulnerable populations is advancing the development of spatially explicit habitat models. Continental-scale climate and microclimate layers are now widely available. However, most terrestrial organisms exist within microclimate spaces that are very small, relative to the spatial resolution of those layers. We examined the effects of multi-resolution, multi-extent topographic and climate inputs on the accuracy of hourly soil temperature predictions for a small island, generated at a very high spatial resolution (<1 m²) using the mechanistic microclimate model in NicheMapR. Achieving an accuracy comparable to lower-resolution, continental-scale microclimate layers (within about 2–3°C of observed values) required the use of daily weather data as well as high resolution topographic layers (elevation, slope, aspect, horizon angles), while inclusion of site-specific soil properties did not markedly improve predictions. Our results suggest that large-extent microclimate layers may not provide accurate estimates of microclimate conditions when the spatial extent of a habitat or other area of interest is similar to or smaller than the spatial resolution of the layers themselves. Thus, effort in sourcing model inputs should be focused on obtaining high resolution terrain data, e.g., via LiDAR or photogrammetry, and local weather information rather than *in situ* sampling of microclimate characteristics.

Keywords. Environmental niche, global climate layers, mechanistic microclimate model, species distributions, soil temperature, terrain data.

Introduction

Predicting the impacts of environmental variation on species is of primary concern in ecology, especially for examining population viability and predicting range shifts within the context of modern climate change and habitat modification (Porter et al. 2000, Pearson and Dawson 2003, Thuiller 2004, Guisan and Thuiller 2005, Kearney and Porter 2004). The low spatial resolution at which environmental variables are typically sampled in situ (Kearney and Porter 2004, Kearney et al. 2014b), relative to the microenvironment actually experienced by an organism (Geiger et al. 2003), is an important limitation on the predictive capacity of a niche model (Dormann et al. 2012). Ideally, environmental inputs have been obtained from (1) weather stations, which collect multiple data types (e.g., air temperature, humidity, wind speed, rainfall) long-term at a single point that is geographically near to a population of interest and (2) measurements collected instantaneously or over a pre-determined time period (e.g. with dataloggers) within the known habitat of a population (Porter et al. 2002, Kearney and Porter 2004, Austin 2007, Ashcroft and Gollan 2012).

The highest-resolution interpolated, gridded climate data currently available for a global extent are the WorldClim climate layers, which are freely available at horizontal spatial resolutions of 30" and 10' (approximately 1 km and 20 km) and contain mean monthly terrestrial rainfall and mean, minimum, and maximum monthly air temperatures (Hijmans et al. 2005). The datasets most recently developed by the Climatic Research Unit

(CRU CL 2.0) include monthly precipitation, mean temperature, relative humidity, sunshine hours, ground frost and 10 m mean monthly wind speed data for the 1961–1990 normal period at a 10' spatial resolution (New et al. 2002). A global-extent set of gridded microclimate surfaces ('microclim') is also available at a horizontal resolution of approximately 15 km (Kearney et al. 2014a).

Both the WorldClim and CRU CL 2.0 datasets are widely employed in the development of species distribution models (SDMs) (Guisan and Zimmerman 2000, Guisan and Thuiller 2005, Elith et al. 2006) and predictive climate models (Jeffrey et al. 2001, Wood et al. 2004, Tait et al. 2006, Smith et al. 2007, Tait et al. 2012), which are subsequently used to inform conservation-focused research and applications in biodiversity management (Loiselle et al. 2003, Brooks et al. 2006, Kerhoulas et al. 2013). However, most organisms experience their environment within a geographical extent much finer than that of any of the available surfaces (Hutchinson and MacArthur 1959, Porter et al. 2002, 2010, Geiger et al. 2003, Potter et al. 2013, Hannah et al. 2014). Additionally, the spatial resolution of underlying terrain layers can significantly affect the strength of modelled relationships with climate variables (Leempoel et al. 2015). If all known occurrences of a species are bounded within a few 1 km² cells, then very little of the underlying variation that describes that species' realised niche (or that underlies its fundamental niche) may be captured by a coarse-scale distribution model. For some applications, predicting bounded possibilities in potential microclimates, such as modelling distributional limits based on the range of environments that are available to an organism at a variety of depths below ground, may be highly informative. However, predictions at a higher spatial and temporal resolution are required to answer questions about responses to extremes (Kearney et al. 2012) or to quantify habitat configuration explicitly (Sears et al. 2011). Increasing the resolution of a derived climate surface requires either (i) improvement of interpolation methods or (ii) collection of additional measurements of relevant covariates in the field, which may be constrained by practical considerations (e.g., restricted site access or limited availability of research funding, sampling equipment, or personnel).

In contrast to climate surfaces interpolated from direct measurements, mechanistic climate and microclimate models derive environmental variables as the outcomes of atmospheric and soil thermodynamic processes (Porter et al. 1973, 2002). Soil temperature profiles are predicted as a function of the flow and storage of energy that is conducted below the soil surface, after emitted solar radiation that reaches the outer atmosphere is reduced by atmospheric scattering and absorption (e.g., by clouds and greenhouse gasses) and by low-altitude reflection (e.g., by vegetation and the soil surface) (McCullough and Porter 1971, Porter et al. 1973, Geiger et al. 2003). Soil temperature is a model output, rather than an input, and the spatial resolution of the model is limited by the spatial resolution of input GIS layers, rather than the sampling resolution of in situ temperature data.

We use the term 'spatial resolution' to refer to the area represented by a single pixel of gridded climate or terrain data, as distinct from 'spatial scale,' which we use to refer to both the area of a terrestrial microclimate of interest (e.g., the home range of an organism) and the area over which microclimates are aggregated (e.g., the distribution of a species or a study area). The term 'geographical extent' refers to the entire area represented by a gridded climate or terrain dataset and is independent of both spatial resolution and scale (Whittaker et al. 2001). Whether a microclimate surface can be reasonably labeled as 'high resolution' is relative to the geographic extent of an area of interest. A horizontal spatial resolution of 30", or approximately 1 km, can be considered very high resolution for a global or continental model (Hijmans et al. 2005, Kearney et al. 2014a, b) but would be extremely low-resolution if the area being represented is a small island. Similarly, a 1 km² gridded surface could be labeled as highresolution, relative to the home range of a large mammal, but would capture little of the heterogeneity within the habitat of a small, soil-dwelling invertebrate.

Few studies have developed soil temperature estimates at a spatial resolution that is biologically meaningful. The accuracy of one processexplicit model, NicheMapR, has been tested at a 5 km spatial resolution, continent-wide for Australia (Kearney et al. 2014b) and for regions of North America (Kearney et al. 2014a). A spatially explicit model of soil temperatures has been tested at a horizontal resolution of 5 m but is currently limited to predicting temperatures for a single topsoil layer (Bennie et al. 2008). A model of hourly soil temperatures generated using Niche Mapper™ (Porter et al. 1973, Porter and Mitchell 2006) at a 0.5 m horizontal resolution was used to predict hatchling sex ratios in a population of tuatara (Sphenodon punctatus), a long-lived, New Zealand -endemic reptile (Mitchell et al. 2008). The latter study captured the topographic influences of slope and aspect on soil temperatures but did not explicitly test the effects of microsite-scale variation (e.g., soil properties, wind speed) on model accuracy.

From the perspective of predictive ecology, the selection of appropriate model parameters is critical for examining the potential for range shifts and for identifying barriers to population dispersal, particularly under novel environmental conditions (Bean et al. 2014). However, the resolution of model parameters, i.e., the size and period of time represented by each value of an input, may itself affect the accuracy of predictions. We used NicheMapR, an R-implementation of Niche Mapper™, to examine how the resolution of microclimate parameters affects the accuracy of modelled

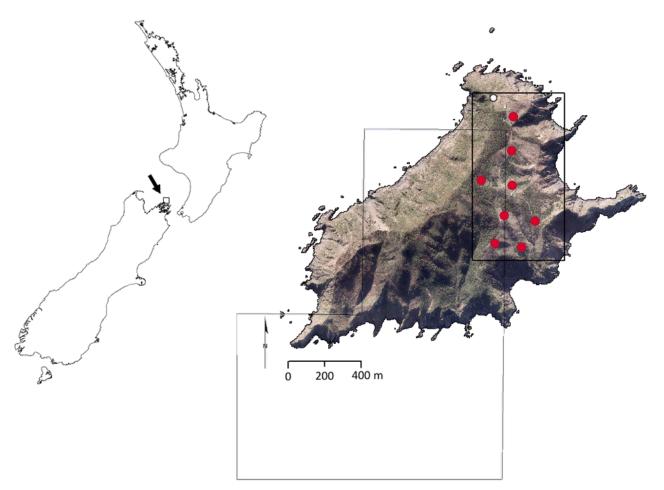


Figure 1. Map of the study site, with the arrow indicating the location of the island of Takapourewa relative to the main North and South islands of New Zealand (https://data.linz.govt.nz/). The black rectangle overlaid onto the island shows the area accessible to researchers, with soil temperature sampling locations indicated by red dots; the white dot approximates the location of the permanent weather station and logging anemometer. The larger polygon shows the area (comprised of three pixels) covered by the WorldClim 30" dataset¹.

¹ http://www.worldclim.org/tiles.php?Zone=411

soil temperatures within a small geographical extent. We tested the effects of topography, soil thermal properties, shade availability and wind speed on the accuracy of microsite soil temperature predictions to determine (1) whether microclimate-level parameter values improve predictions of soil temperatures over those generated using broad-scale, mean values and/or (2) whether local, time-specific weather data improve prediction accuracy compared to predictions generated using periodic climate means.

Methods

Microclimate model structure

We modelled soil temperatures for the year 2011 for the island of Takapourewa (also known as Stephens Island), a 150 ha offshore Nature Reserve located in Cook Strait, New Zealand [approx. 40°40'S 174°00'E] (Fig. 1). We used NicheMapR (Kearney et al. 2014a, b), a global-extent implementation of the Fortran Niche Mapper™ mechanistic microclimate model (McCullough and Porter 1971, Porter and Mitchell 2006), written to be called from the R-environment. To model soil temperatures, NicheMapR uses a one-dimensional, finite-difference algorithm (Carslaw and Jaeger 1959, McCullough and Porter 1971, Porter et al. 1973) to solve heat-mass balance equations for ten specified soil depths at a given location and through the given period of time.

The input data include topographic parameters (e.g., elevation, slope, aspect, horizon angle) for calculating clear-sky solar radiation using the integrated SOLRAD radiation model (McCullough and Porter 1971, Porter et al. 2002); daily maximum and minimum values of seasonally dynamic climate variables (e.g., wind speed, air temperature, humidity, rainfall, cloud cover); and values for relatively constant, site-specific environmental variables (e.g., physical properties of soils, shade availability). Values of soil properties can optionally be modified, e.g., to simulate a layer of organic topsoil. NicheMapR also incorporates scattering of solar radiation due to atmospheric aerosols (Kearney et al. 2014a, b; Fig. 2).

We modified the NicheMapR global functions to allow user-supplied input of local environmental variables at any spatial and temporal (e.g., daily, hourly) resolution. Daily observations of rainfall (resolution 0.2 mm), relative humidity (resolution 1.0%), minimum and maximum air temperatures (resolution 0.1°C), and minimum and maximum wind speeds (resolution 0.1 ms⁻¹) for the study period were obtained from the NIWA CliFlo database for the weather station on Takapourewa [Station No. 26169]. Observations of relative humidity recorded at 9:00 a.m. were assumed to represent daily maxima. We estimated humidity minima by splining the lowest maximum daily value by month across 365 days. We estimated cloud cover for the study period as the difference between maximum possible (i.e., total daylight hours, regardless of cloud cover) and recorded daily sunshine hours (resolution 0.1 hr), expressed as a percentage, using sunshine data from the Blenheim Research weather station [NIWA Station No. 12430] approximately 95 km from Takapourewa, the nearest location at which sunshine hours were recorded in 2011.

To determine whether local weather data improved the accuracy of soil temperature estimates over that obtained using global-scale climate information, we also parameterised the microclimate model with monthly climate data interpolated to a 10' latitude/longitude resolution for the World Meteorological Organization standard normal period 1961-1990 (New et al. 2002) from the University of East Anglia Climatic Research Unit CL 2.0 database³ (Online supplementary documentation). We extracted monthly minimum and maximum relative humidity and air temperatures and wind speed data from the global database and splined them to daily resolution. We spread total monthly rainfall evenly across the number of rainy days (i.e., the number of days with > 0.1 mm of rainfall) per month. We assumed that daily maximum air temperature and wind speed and minimum relative humidity and cloud cover occurred one hour after local solar noon and that daily minimum air temperature and wind

² http://www.cliflo.niwa.co.nz

³ http://www.cru.uea.ac.uk/cru/data

speed and maximum relative humidity and cloud cover occurred at local sunrise (Kearney et al. 2014a, b). Data on atmospheric aerosols were obtained from a modified version of the Global Aerosol Data Set (GADS) (Koepke et al. 1997).

Terrain data

We extracted topographic data in ArcMap™ Desktop v 10.1 software (Environmental Systems Research Institute [Esri] ArcGIS: Redlands, CA, USA 2012) from a 0.5 m resolution gridded digital elevation map (DEM) of the study site (Aerial Surveys Ltd., Auckland, NZ 2011). We obtained values for latitude, longitude, and elevation directly from the DEM, calculated slope as the ratio of maximum change in elevation to horizontal distance from each pixel to its eight nearest neighbours and aspect as the maximum change in slope from each pixel to its eight nearest neighbours (Online supplementary documentation). To correct solar radiation values for complex topography, we calculated solutions.

lated twenty-four horizon angles for each pixel of the DEM using the r.horizon function in GRASS v 6.4 (GRASS Development Team 2012).

Soil physical and thermal properties

The physical and thermal properties of soils influence the amount of energy that is transferred and the rate of transfer from the surface to subsequent depths (i.e., the soil heat flux). Heat conduction through soils is described primarily by thermal conductivity and specific heat (de Vries 1963). While soil thermal properties are relatively stable across temperature changes (de Vries 1963), both physical and thermal properties of soils, especially moisture content, can vary throughout the soil matrix and can affect heat transfer (Campbell 1985, Ochsner et al. 2001, Kearney et al. 2014b). The inclusion of local soil bulk density and moisture content in an Australiawide test of NicheMapR did not significantly improve model performance (Kearney et al. 2014a,

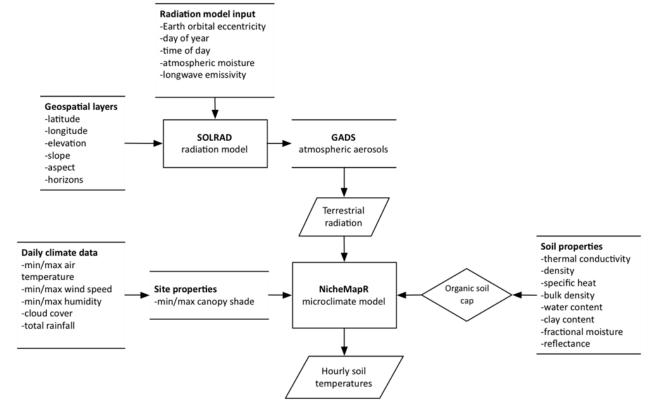


Figure 2. Flow chart summarising the environmental inputs used by the NicheMapR microclimate model to calculate soil heat-energy balances and estimate hourly sub-surface temperatures (adapted with permission from Porter et al. 1973, Porter & Tracy 1983, Porter et al. 2006). Semi-enclosed rectangles designate model inputs, enclosed rectangles are model algorithms, parallelograms are outputs, and the diamond is the optional 'organic cap' soil parameter, which did not improve model accuracy and was not included in the 'best' set of models.

b); however, the effects of site-specific soil thermal properties on prediction accuracy have not been examined. For this study, we experimentally determined thermal conductivity, bulk density, and fractional soil moisture and density of soil minerals (details below) for the soil types and type composites (n = 10) present on Takapourewa (Ward 1961). We estimated specific heat of soil minerals, soil reflectance, and clay content from other soil properties. Soil moisture content and conductivity were adjusted with depth inside the model subroutine (Kearney et al. 2014a, b).

To define locations for soil sampling, we manually georeferenced a hard-copy map of soil types (Ward 1961) to a high-resolution aerial photo of the study location (Aerial Surveys 2011) and transformed the digitisation to the 2000 New Zealand Transverse Mercator/NZ Geodetic Datum 2000 coordinate system in ArcMap[™] using a cubic spline. We defined control points for the transformation until the root mean squared error (RMSE) between congruent points on the soil map and aerial photo was < 0.0001 m. The quality of the original map was low relative to the aerial photo, so we defined locations for soil sampling at random points at least 20 m from the edges of each stratified soil polygon to minimise the potential for confusion of soil types. Soil cores were collected between 15–20 November 2012, at least 12 hours following rainfall to avoid inflation of soil moisture content. After removing surface vegetation, one core sample (volume ≈ 1455 ml) was collected from 20 mm below the surface to a depth of around 200 mm at each sampling location (n = 10) using a hand-held stainless steel soil corer and a striking plate (Materials Advisory Testing Service, Stokes Valley, NZ). Samples were double-bagged and stored out of direct sunlight until testing (Sheppard and Addison 2006).

Soil testing was conducted in a climate-controlled laboratory (Geotechnics Ltd., Auckland, NZ) from 2–8 December 2012. Thermal conductivity was determined using a calibrated non-steady-state thermal probe (Bristow 1998) and digital thermal resistivity meter (TP09/MTN01; Hukeseflux Thermal Sensors, Delft, The Netherlands). We modified the protocol (ASTM 2008) in two ways to

allow for testing of very low-density soils: (1) remoulded samples were wrapped with an A4-size sheet of transparent polyethylene terephthalate (PET) and supported by a circle of fine steel mesh to maintain sample integrity and (2) the thermal probe was suspended above soils that were of sufficiently low density to cause the needle to sink into the sample. To prevent excessive temperature increases during testing of relatively dry or low-density soils, we set the thermal probe heating voltage at 2V for samples with a calculated density ≤ 0.0012 Mgm⁻³ and at 2.5V for samples with a density > 0.0012 Mgm⁻³. The thermal conductivity (WmK⁻¹) of each sample was measured over 600 seconds to a standard deviation of < 0.10. Two fractions of each soil sample, one sieved and one un-sieved, were also weighed, oven-dried for 24 hours at 108°C (Contherm Scientific Thermotec™ 2000 Series drying oven) and re-weighed to determine moisture content and confirm calculated dry densities (Sheppard and Addison 2006). We calculated fractional soil moisture as the ratio of the mass of water (g) in each sample to the sample dry mass.

We calculated the density of the mineral component of soils (kgm⁻³) as the ratio of sample mass to the sample volume, with sample mass corrected for the masses of water, carbon (Ward 1961), and organics. Specific heat (MJm⁻³-K) of the mineral component was estimated by calculating the volumetric specific heat of each soil sample and solving for the mineral component, given the volume fractions of each component (de Vries 1963, Campbell 1985, Campbell and Norman 1998). We estimated the organic component using a ratio of carbon to organic matter of 0.5 (de Vries 1963, Campbell 1985) and estimated soil reflectance using the Munsell colour values (Escadafal 1989, Post et al. 2000) previously reported for soils on Takapourewa (Ward 1961). Clay content was estimated as 20% for all soil types following textural classification (Shirazi and Boersma 1984, Hendrickx et al. 2003, FAO 2006; Online supplementary documentation).

Cliffs surrounding the island, which were not included in historical surveys (Ward 1961) or sampled for this study, were assigned mean values of soil properties. Volumetric water content at saturation was specified as 0.26 m³m⁻³ of soil, and surface roughness (i.e., the size of soil particles) was set at 0.004 m for all simulations (Kearney et al. 2014a). We compared the accuracy of models run using spatially-explicit, experimentally-derived soil properties with that of models run using parameter values for the mineral fraction of a generalised soil (Kearney et al. 2014a, b).

Shade cover

Shading by vegetation affects the proportion of total solar radiation that reaches the soil surface and, consequently, soil temperature (Geiger et al. 2003). Using gap-light analysis of hemispherical photography (Frazer et al. 1999), we estimated near-ground, microsite shade availability on Takapourewa at around 95% under the forest canopy and between 20-60% at most non-forested sampling locations, regardless of vegetation type (Carter unpub. data). Because vegetation type did not predict percent-shading, microsite shade values could not be generalised to non-sampled points based on vegetation class, and temperature predictions were instead generated using shade values of 0%, 20% (the approximate minimum calculated shade), 45% (the approximate mean non-forest shading), and 60% (the approximate upper range of shade at non-forested locations) for all sites. We also modelled soil temperatures for each site using a random integer value for canopy shading of between 20-60%.

Simulated wind speeds

The exposed maritime environment of the study site increased the likelihood that wind would significantly impact soil temperatures. Single-point wind station data were not expected to reflect the effects of highly variable local topography on wind (Mitchell et al. 2008), so we used a separate turbulence velocity model to simulate wind speeds across the island. We modelled wind speeds on Takapourewa using WindStation™ v 4.0.1 software (Lopes 2003), which incorporates a Navier-Stokes turbulence equation solver (CANYON) (Lopes et al. 1995) and a kinematic model

(NUATMOS) (Ross et al. 1988) to simulate wind flow over complex terrain. The goal of this study was not to generate accurate, microsite-resolution values for wind speed, which would have been an unrealistic expectation of the simulator (Ross et al. 1988, Lopes 2003), but to determine whether modelled temperature predictions were sensitive to the effects of wind speed at a microsite scale.

We installed a logging anemometer (Inspeed Vortex Wind Sensor and Madgetech Pulse 101A datalogger) at a height of 2 m directly below the island's permanent anemometer at a mast height of 10 m (180m asl), which recorded wind speed at two-minute intervals for approximately one year (Fig. 1). Wind speed and direction data recorded at hourly intervals during the same period by the permanent weather station were obtained from the NIWA climate database². The permanent station at the study site is located in a relatively open, exposed area, so the wind direction at a height of 2 m was assumed to be equal to the direction at 10 m.

Wind flow simulations required two terrain-defining datasets: elevation and roughness, which includes both the 'bumpiness' inherent in local topography and the heights of above-ground elements such as vegetation, rocks, and artificial structures (Lopes 2003, 2011). We extracted elevation data at a horizontal resolution of 2 m from a re-sampled DEM of the study site. We recorded approximate maximum vegetation height measurements in November 2011 and 2012 at random sites, stratified by vegetation type, and assigned broad roughness values between 0.5-4.0 m to a categorical land cover classification map of the island (Carter unpub. data). Hourly wind field simulations were run inside a gridded bounding box with a horizontal resolution of approximately 25 m and converted to daily maximum and minimum values (summarised in Online supplementary documentation). We interpolated modelled wind data to the spatial resolution of the terrain layers using a distance -minimising algorithm in ArcMap[™] software.

Table 1. Seven basic microclimate model parameterisations and corresponding sources of input data: 'global' mean data were downloaded from the CRU 2.0 global climate database and represent the 1961–1990 standard normal period; 'local daily' climate data were obtained from weather stations for the year 2011; 'gridded' wind data were generated using a turbulence velocity model; 'local' soil properties were determined empirically; and 'generalised' soil properties were based on published values.

model #	model name	terrain data	climate data	soil data	wind data
1	global	global database	global mean	generalised	global mean
2	high-res	microsite	global mean	generalised	global mean
3	weather_1	microsite	local daily	generalised	local daily
4	weather_2	microsite	local daily	generalised	gridded
5	soils_1	microsite	global mean	local	global mean
6	soils_2	microsite	local daily	local	local daily
7	micro	microsite	local daily	local	gridded

Soil temperature data

To provide field data for comparison with predicted soil temperatures, we used 31 temperature dataloggers [23x Thermochron™ DS1921H iButtons (resolution: 0.5/0.125°C, accuracy: ± 1°C) and 8x Onset HOBO™ Pro v2 U23-002 (resolution: 0.02°C, accuracy: ± 0.21°C)] to measure hourly soil temperature data at random points, stratified among previously studied sites in the eastern part of the island, which is the only portion accessible to researchers (Fig. 1). To maintain consistency between studies (Mitchell et al. 2008) and, because most temporal variation in soil temperature dissipates at around 200 mm below the soil surface (Geiger et al. 2003), we measured soil temperatures at depths of 100 mm and 200 mm. Each iButton collected approximately 1,400 observations over three months, and each Pro v2 datalogger collected approximately 8,350 observations over one year from late November 2011.

Model selection

To determine whether the resolution of topographic variables, soil thermal properties, shade availability or wind speed affected the accuracy of predicted soil temperatures within a small geographic extent, we tested a series of unique microclimate models. We generated hourly temperature predictions at 100 mm and 200 mm at every microsite (defined by a unique latitude/longitude) using seven different baseline models, each parameterised to increasing complexity (Table 1). With the exception of the 'global' imple-

mentation, models were run using unique terrain data for all datalogger sites, and each microsite was defined by, at a minimum, a unique combination of topographic parameters (i.e., the 'high_res' model).

We ran all seven models using the five scenarios of percent-shading: 0, 20, 45, 60, and random [20:60] to generate 35 baseline sub-models. We then modified and re-ran each of the 35 submodels to examine the effects of key soil properties on the accuracy of temperature predictions. We examined the effects of moisture on soil temperatures for all models by simulating evaporative cooling of the soil surface on days that received at least 1.5 mm of rainfall (Kearney et al. 2014b). We also examined the effects of (1) near-surface biousing a 50 mm 'organic soil turbation, cap' (Kearney et al. 2014b) and (2) shallow soils, using a simulated rock substrate (Kearney et al. 2014a). The models parameterised with experimentally derived soil properties ('soils_1,' 'soils_2', 'micro') were run using generalised values for thermal conductivity and density of soil minerals. Models parameterised with local weather data ('weather_1,' 'weather_2,' 'soils_2,' 'micro') were run using both daily observations and splined mean monthly cloud cover data.

We generated predictions of hourly soil temperatures for one year and calculated values for the coefficient of determination (R²), root-mean-squared deviation (RMSD), and normalised RMSD (nRMSD) for each comparison of predicted hourly soil temperatures with the corresponding observed values at each datalogger location, with

lower values indicating better agreement between observed and modelled soil temperatures. We calculated RMSD using the 'rmse' function in R package hydroGOF (Zambrano-Bigiarini 2014). We calculated nRMSD as the RMSD value divided by the range of observed hourly soil temperatures (i.e., maximum - minimum temperature) for each comparison between predicted and corresponding observed values as well as modelled and observed daily maxima and minima (Horton and Corkrey 2011, Kearney et al. 2014b). We used the accuracy of lower-resolution, larger-extent implementations of NicheMapR, within around 2–3°C of observed soil temperatures (Kearney et al. 2014a, b), as a high-quality benchmark for assessing models.

Results

Model selection

Neither simulation of evaporative cooling nor inclusion of a 50 mm organic soil cap increased the accuracy of predicted soil temperatures from the baseline set of models. Simulating a rock substrate instead of soil had no effect on either RMSD or R² values. In contrast, models run using generalised

values for soil thermal conductivity and mineral density and experimentally-derived values for other soil properties generated more accurate temperature predictions than those run using only experimentally-derived values. Substitution of statistically smoothed, mean monthly cloud cover data for daily observed values decreased RMSD values across all models parameterised with local weather data.

Except for the 20%, 45%, and 60% shading scenarios of 'high-res' and 'soils_1,' RMSD values were lower at 200 mm compared to 100 mm for the same models. Only the 0% and 20% shading scenarios of 'soils_2' and the 20% shading scenario of 'micro' had RMSD values < 3.0°C. Of all models tested, the 0% shading scenario of the 'soils_2' model had the lowest RMSD and nRMSD values at both 100 mm and 200 mm depths. The 'weather_1' models had the highest R² values at 100 mm. The 0% and 20% shading scenarios of the 'weather_1' and 'soils_2' models had the highest R² values at 200 mm depth (Fig. 3).

The accuracy of site-specific, daily minimum soil temperature predictions was similar across

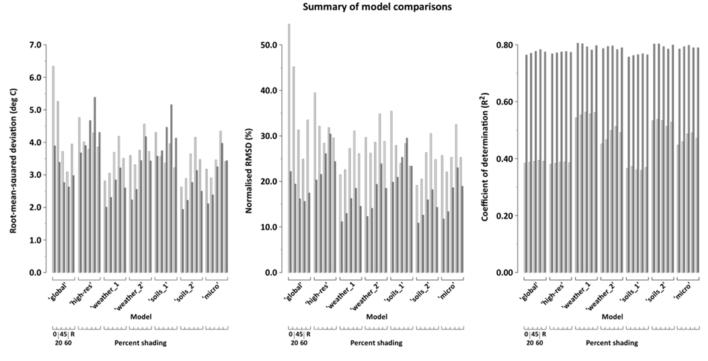
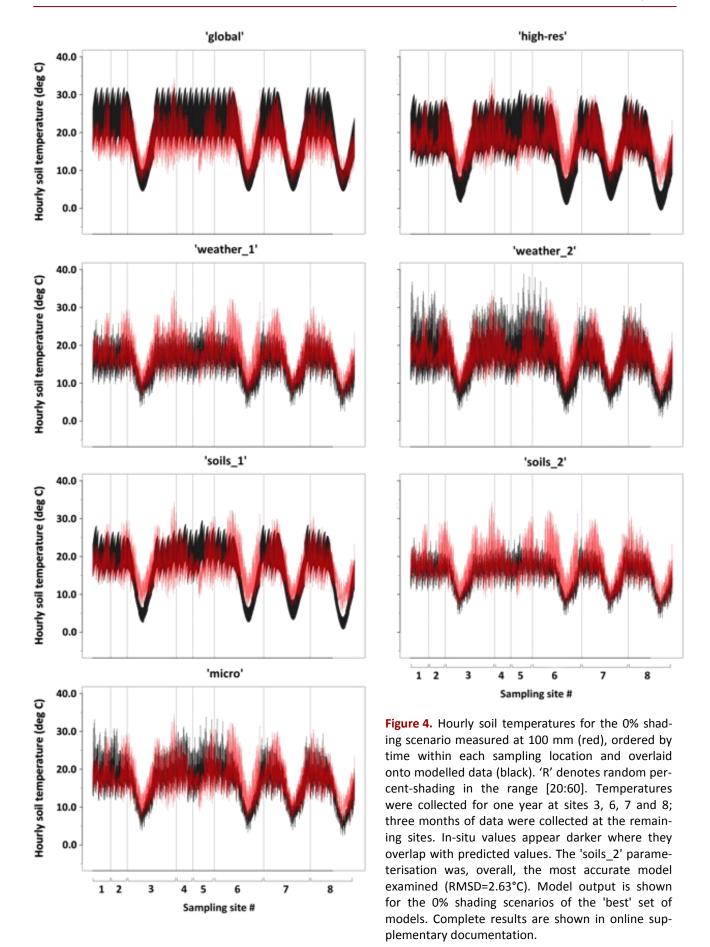
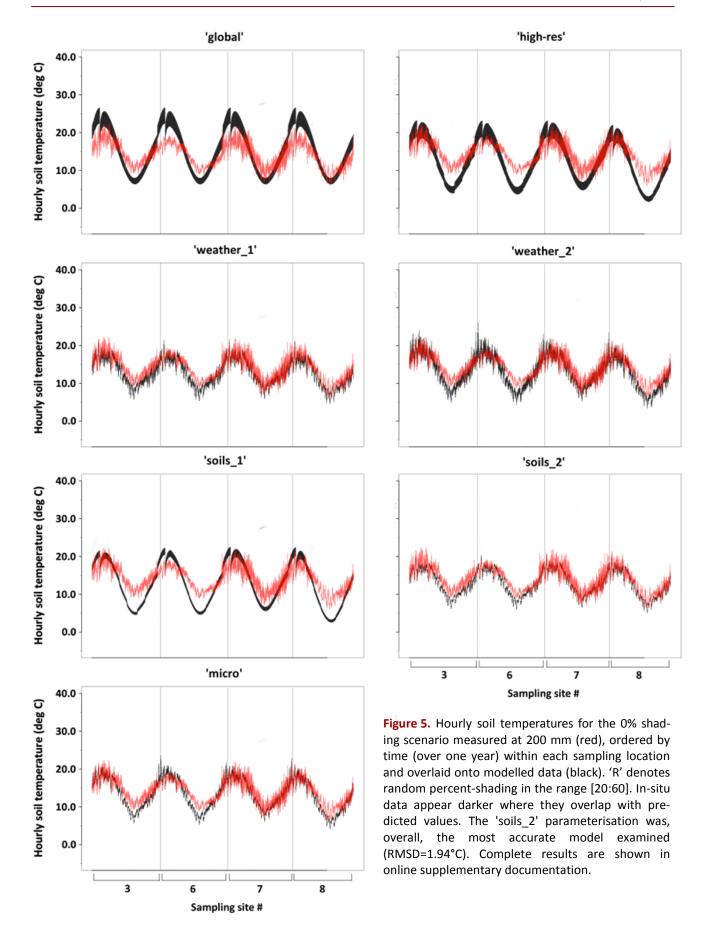


Figure 3. Summary statistics comparing observed and modelled hourly soil temperatures. Light gray bars show comparisons between temperatures at 100 mm; dark gray bars show comparisons at 200 mm depth. Each of the seven models was run using five scenarios of percent-shading: 0, 20, 45, 60, and random [20:60], denoted 'R'. All statistics were averaged across 27 sites at 100 mm (approx. 1,400 values per site) and 4 sites at 200 mm (approx. 8,350 values per site). Comparisons are shown for the 'best' overall set of models only.





models; however, the rank performance of models at 100 mm and 200 mm was reversed, relative to hourly predictions. The ability of any model to predict site-specific, daily maximum soil temperatures was lower. Normalised RMSD values were similar to the lowest nRMSD values calculated across all soil temperature predictions. We present complete summary statistics for all shading scenarios of the set of models with the overall lowest values of RMSD: the 'soils_2' model, simplified with smoothed cloud cover data and generalised values for soil minerals density and thermal conductivity but parameterised with experimentally-derived values for other soil properties (Fig. 3).

Maximum daily air temperature records were better predictors of maximum daily soil temperatures at 100 mm, but not at 200 mm, when compared with modelled values. The accuracy of predicted maxima was much lower at 100 mm, with a mean discrepancy just under 6.5°C, than at 200 mm, at which the mean discrepancy was within 3.5°C of observed values. Predicted minimum daily soil temperatures were more accurate than air temperature minima, within a mean of 3°C of observations at both 100 mm and 200 mm for most of the models examined.

Effects of parameter values and resolution

Inclusion of high-resolution topographic parameters (i.e., elevation, slope, aspect, and horizon angles) in 'high-res' improved accuracy of modelled soil temperatures over predictions generated with 'global' only when simulated shade at microsites was relatively low. RMSD values were lower for the 0%, 20%, and random [20:60] shading scenarios at 100 mm and the 0% shading scenario at 200 mm. RMSD values increased at both depths for other shading scenarios (Fig. 3).

Inclusion of local, daily climate data (i.e., maximum/minimum air temperatures, maximum relative humidity, maximum and minimum wind speeds, daily rainfall) in 'weather_1' improved the accuracy of predictions generated with 'high-res' for all shading scenarios and decreased RMSD values more at 200 mm than at 100 mm. Inclusion of experimentally-derived, local soil properties (i.e., specific heat, bulk density, fractional soil moisture,

reflectance) in 'soils_1' decreased RMSD values for soil temperatures modelled using 'high-res' more at 100 mm than at 200 mm (Fig. 3).

Parameterisation of 'weather 1' with modelled wind speed data decreased the accuracy of soil temperature predictions, increasing RMSD values. Overall, inclusion of both daily weather data and experimentally-derived soil properties in 'soils_2' increased the accuracy of modelled soil temperatures generated using 'soils_1.' RMSD values decreased under the 0 and 20% shading scenarios but increased under 45%, 60%, and random [20:60] shading scenarios at 100 mm. RMSD values decreased under all shading scenarios at 200 mm. Overall, inclusion of modelled wind data in 'micro' decreased the accuracy of soil temperature predictions. With the exception of the 45% shading scenario, RMSD values increased at 100 mm. RMSD values increased at 200 mm under all shading scenarios for 'micro,' compared with 'soils 2' (Fig. 3). Comparisons between measured and predicted hourly soil temperatures for the 0% shading scenarios are shown in Figs. 4 and 5. Measured and predicted soil temperatures for all shading scenarios are provided in the online supplementary documentation.

Discussion

Summary of major findings

In this study, we generated hourly soil temperatures at a sub-meter spatial resolution with accuracy comparable to lower-resolution implementations of NicheMapR, i.e., within 2-3°C of observed values. Within the small spatial extent modelled here, marked improvements in prediction accuracy were only facilitated by the inclusion of high resolution terrain layers and local, time-series weather data. Overall, the models examined were better predictors of soil temperatures at 200 mm than at 100 mm depth, reflecting the reduction in temperature variance that occurs with soil depth. Modelled temperatures were consistently lower than observed values, regardless of the shading scenario. Data collected over a full year revealed a seasonal pattern in accuracy at three of the four sites in which we installed higher-capacity dataloggers, with soil temperatures slightly underpredicted in the austral winter, compared to other seasons. All but two of the modelled scenarios generated hourly soil temperatures within 5°C of observed values, and most were accurate to within 3–4°C of soil temperatures observed at 100 mm depth. Normalised RMSD values of the two most accurate models (i.e., the 0% shading scenarios of 'weather_1' and 'soils_2') indicated that the minimum residual variance across all sites was within only about 20% of observed values at 100 mm and within about 10% of observed values at 200 mm. Similarly, R² values across all models suggested that the ability to explain variance in observed values at 100 mm compared to 200 mm was reduced by almost 30% (Fig. 3).

The simulation of surface-level vegetation shading improved model accuracy only when climate inputs were sourced from the global database. Only the 60% shading scenario of the 'global' model, however, generated soil temperatures within approximately 3°C of observed values. Inclusion of experimentally derived soil properties did not markedly improve the accuracy of models parameterised with local weather data. Inclusion of high-resolution, modelled minimum and maximum wind speed data slightly decreased model accuracy relative to scenarios driven by local, daily maximum wind speeds. The most accurate model developed in this study, 'soils_2,' only improved upon the second-best model, 'weather_1,' by about 0.2°C, an increase in accuracy that is unlikely to impact the predictions of ecological niche models in a biologically relevant way. In addition, parameterisation of 'weather_1' requires no in situ data collection, which reduces the time and financial resources required for model implementation and largely eliminates any environmental impacts of habitat access.

Methodological limitations

Simulation of site-specific soil properties only slightly improved the accuracy of predicted soil temperatures relative to models parameterised with generalised values (Figs. 3, 4), although the spatial resolution of experimentally determined values of soil properties was coarse, relative to the resolution of terrain data. Determination of

soil properties in situ, using a higher-resolution, stratified sampling grid might reduce the amount of unexplained variation in soil temperatures and improve model predictions. The error in predicted soil temperatures may also be inflated due to the resolution of measured values. However, physical and thermal properties vary little within broad soil classifications, and the data obtained for this study are consistent with published values for their respective classes (de Vries 1963). Likewise, collecting empirical measurements of soil thermal properties is costly and time-consuming. Moreover, the accuracy of models parameterised using location-specific soil values in this and previous studies (Kearney et al. 2014a, b) was not improved over that of models that simulated a generalised sandy soil. More research is needed to determine if different patterns occur at sites with highly organic soils, which are less thermally conductive than sandy soils (de Vries 1963, O'Donnell et al. 2009).

Increasing the simulated canopy shading to levels representative of mean shade reduced accuracy of predicted soil temperatures, relative to that of temperatures modelled under the assumption of 0% shade. The current implementation of NicheMapR does not incorporate the insulating effect (Oliver et al. 1987) of low-growing plants, so vegetation can only reduce modelled soil temperatures via a shading mechanism. At lower spatial resolutions, e.g., on the order of km², canopy shading greater than 0% may accurately represent the mean shading over the area represented by each pixel. As the spatial resolution of a microclimate surface increases, however, the shading of a single pixel is less likely to be accurately represented by a mean value. Rather than specifying 'true' shade at ground-level, therefore, canopy shading for very high-resolution microclimate surfaces may be more accurately characterised as a binary variable signifying whether each site is or is not shaded.

Topography affected the wind profiles experienced at different points on the island. However, while simulated soil temperatures were sensitive to their inclusion, gridded wind speed data did not improve the accuracy of modelled soil

temperatures. Strong effects of wind speed on soil temperatures might be more apparent on the access-restricted, northwestern face of the study site, which is the least-sheltered area of the island and regularly exposed to gale-force winds (Ward 1961) (see Online supplementary documentation). Reducing the magnitude of wind speeds below measured values increased accuracy of modelled soil temperatures on nearby North Brother Island (Mitchell et al. 2008), which has a steep and exposed topography, relative to most of the area of Takapourewa. Alternatively, gridded wind data might improve model accuracy, if the uncertainty in soil properties or measured soil temperatures could be reduced or if gridded wind data were modelled using input data from multiple anemometers. Mean seasonal easterly-westerly wind speeds are predicted to vary in New Zealand by between -2.5 to +3.6 ms⁻¹ under climate change models for the next century (http:// ww.mfe.govt.nz). Changes in mean wind speeds may have a small effect on air temperatures near the soil surface and, thus, on soil temperatures. However, changes in macroclimate conditions should not affect accuracy of a mechanistic microclimate model.

Implications for model applications

We have shown that soil temperatures can be modelled mechanistically within a small spatial extent and at a very high spatial resolution (i.e., ≤ 1 m) with accuracy comparable to models parameterised using lower-resolution (i.e., 5-15 km) continental- or global-extent terrain layers (Kearney et al. 2014a, b). Importantly, predicting soil temperatures at our study site to within 2-3°C of observed values required that we parameterise the microclimate model both with micrositeresolution terrain data and local, daily weather information. Hourly soil temperatures predicted using the 'global' model, parameterised with topographic and climate inputs at approximately the same spatial resolution as the global-extent 'microclim' terrestrial climate layers (Kearney et al. 2014a), captured little microsite variation and were only accurate to within about 6°C of observed values. Our findings highlight the importance of considering within-pixel variation as a critical source of information and, in lower-resolution models, uncertainty.

Continental- and global-extent microclimate layers are unlikely to provide accurate estimates of microclimate conditions when the spatial scale of a study area is smaller than the resolution of the climate layer itself. Because the 'global' model in this study was parameterised using climate and topographic layers at a spatial resolution of 10' (~20 km), all 27 of our sampling sites were represented by a single pixel. The highest-resolution interpolated climate layers currently available (i.e., 30" or ~1 km) represent the entire island within three pixels. Very high-resolution layers are less likely to be available for study areas that are relatively isolated or uninhabited, e.g., protected wildlife reserves, especially those with a small geographical extent, such as small islands.

We did not explicitly examine whether reducing the spatial resolution of terrain data (e.g., from 0.5 m to 10 m or 20 m) affected the accuracy of soil temperature predictions. Increasing either the resolution or the extent of topographic layers increases the number of individual sites for which microclimate conditions are estimated and, as a result, markedly increases computation time. Determining the minimum spatial resolution of data required to accurately predict microclimate conditions at small scales or within a small geographical extent would be beneficial for minimising the resources necessary for developing very high-resolution microclimate surfaces.

The lower the spatial resolution of a microclimate surface, the more likely that a biophysical model would over-estimate the availability of suitable habitat for a species of interest. Likewise, biologically significant sources of environmental variation, e.g., relatively narrow dispersal barriers, can be masked by low-resolution microclimate surfaces. Barring practical limitations, e.g., the availability of terrain data or high-performance computing capability, the spatial resolution of a gridded microclimate surface should be informed both by the extent of the study area and by the size of an individual microclimate of interest. If the goal of a study is to predict range shifts by

modelling changes in the geographical extent of suitable habitat, the pixels that comprise a microclimate surface should be much smaller than the total area of habitat currently used by the organism. A higher-resolution microclimate surface is also more likely to predict expansion or contraction of a home range, if climate change affects the ability of an organism to meet its metabolic needs within its current habitat extent (McNab 1963, Gittleman and Harvey 1982, Mace et al. 1983). As producing a mechanistic microclimate surface is computationally intensive (Kearney et al. 2014a, b), a lower-resolution layer could be used first to delineate areas for which a higher-resolution surface should be generated. A management decision could then be informed by generating a very highresolution surface to provide a detailed assessment of the subset of larger areas identified as suitable future habitat.

As many components of a species' fundamental niche depend directly on microclimate conditions, the sensitivity of those components to model error should be examined at a very high spatial resolution to better quantify uncertainty in the boundaries between suitable and unsuitable sites. For example, for any species that deposits eggs underground, modelled soil temperatures that are 2-3°C cooler than reality would likely underestimate the total spatial area that is warm enough to facilitate hatching. Further, model error has important consequences at the organism or population level, where 2-3°C of model error may lead to under- or over-predicting of primary sex ratios in species with temperature-dependent sex determination (e.g., Stubbs et al 2014). However, the same magnitude of error could have no biologically relevant effect if macroclimate inputs are modified to simulate, e.g., extreme global warming. In such instances, the use of a higher resolution DEM would allow for identification of marginal areas that are misclassified as unsuitable or that should be targeted for field sampling under changing macroclimate conditions.

While comparisons between empirical and mechanistic predictions have previously been undertaken (Kearney and Porter 2004, Kearney et al. 2014a, b), the effects of parameter resolution on

prediction accuracy have only been extensively examined via comparison with in situ data at spatial resolutions similar to those of large-scale, empirical climate models (Porter et al. 1973, Kearney et al. 2014a, b). In contrast, the present study explicitly tested the accuracy of a mechanistic microclimate model at a very high spatial resolution and within a small geographical extent. Our findings suggest that site-specific, microsite-resolution climate and soil properties matter little to predictions of soil temperatures at an extremely high spatial resolution. From the perspective of predictive ecology, obtaining local, daily weather data and high resolution terrain data is more likely to improve model accuracy than comprehensive sampling of microclimate characteristics, such as soil properties.

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