The effect of spatial resolution on projected responses to climate warming.

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Running Title: Future habitat suitability varies with resolution.

(A) ABSTRACT

(B) Aim

To determine how changing the resolution of modelled climate surfaces can affect estimates of the amount of thermally suitable habitat available to species under different levels of warming.

(B) Location

Lake Vyrnwy RSPB Reserve, which covers around 9,700 hectares of a topographically diverse landscape in Wales.

(B) Methods

A recently published microclimate model was used to predict maximum, minimum and mean temperatures at 5 x 5 m resolution for the study site, under current and possible future conditions. These temperature surfaces were then averaged to produce coarser resolution surfaces, up to a maximum of 1 x 1 km resolution. Ground beetles were collected using pitfall traps between May and August 2008. GLMs were fitted to the temperature surfaces to predict the amount of landscape suitable for a northerly-distributed ground beetle, *Carabus glabratus*, and the most southerly distributed ground beetle found at the site, *Poecilus versicolor*, under current and possible future conditions.

(B) Results

A wider range of temperatures are expected within our site when temperature is modelled at finer resolutions. Fitting GLMs at different resolutions resulted in the inclusion of different temperature variables in the best models. Coarser resolution models tended to have higher prediction error, and different resolution models predicted that different amounts of the landscape would remain or become suitable in future. There was less agreement between models for *C. glabratus* than for *P. versicolor*.

(B) Main Conclusions

In our example system, different resolution analyses result in different predictions about the ability of populations to survive climatic warming. Higher resolution analyses are not only likely to provide more accurate estimates of expected patterns of change, but also to highlight potential microclimatic refugia for the conservation of species that otherwise might appear to be threatened with regional or global extinction.

(B) Keywords

Carabus glabratus, Climate change, Coleoptera, conservation, distribution models, extinction, *Poecilus versicolor.*

(A) INTRODUCTION

Many studies use climatic variables such as temperature to define the range of conditions that species can occupy. At large spatial extents, such climatic variables are commonly found to be associated with the presence and absence of species (Peterson, 2001). Environmental “niche” or “bioclimate” models, which are based on the associations of species’ distributions with climatic variables, are often then used to predict changes in the area available to species following future climatic change (e.g. Huntley *et al.*, 1995; Leathwick *et al.*, 1996; Peterson *et al.*, 2001; Thomas *et al.*, 2004; Elith & Leathwick, 2009; Kearney *et al.*, 2010; Bellard et al

2012) and changes in species' richness within an area following climatic warming (Hannah *et al.,* 2005; Menéndez *et al.,* 2006; Huntley *et al.,* 2007). In the past, these climate envelope studies have normally considered the associations between climate and species’ distributions at relatively coarse resolutions (usually 1 km^2 or coarser; commonly around 100 km^2 resolution in Britain, or 2500 km^2 in Europe). This corresponds to the availability of species' distribution data (e.g. National Biodiversity Network, NBN, http://data.nbn.org.uk) and/or of climate surfaces; and gives the capacity to run models quickly for large geographic areas. It also corresponds to resolution at which climate is perceived to be an important factor when determining distributions (McGill, 2010). However, a recent study suggested that climate can be important at finer resolutions (Gillingham *et al.,* 2012). In addition, some distribution records are submitted with greater spatial precision and climate surfaces are increasingly downscaled to finer resolutions (Guan *et al.,* 2009) as computational power continues to increase. This makes the prospect of producing fine-resolution bioclimate models increasingly realistic (e.g. Montoya *et al.,* 2009; Seo *et al.,* 2009). Here we consider the implications of modelling distribution change at different spatial resolutions.

A number of previous studies suggest that the spatial resolution of analysis could affect estimates of species declines and extinction. Thomas & Abery (1995) found that the observed decline rates of 12 British butterfly species were 35 % higher when estimated using a 4 km^2 grid than when based on a 100 km^2 grid. For *Plebejus argus,* the loss of 90 % of the local populations resulted in a loss of only 56 % of 4 km^2 grid squares. Similarly, Thomas *et al.,* (2006) found that much higher rates of retraction at low latitude/elevation range boundaries were detected when they were measured using a 1 km^2 grid than when using a 100 km^2 grid. This may be a particular issue in mountainous regions, where coarse-resolution grid cells may contain a wide range of environments and population densities (Shoo *et al.,* 2006). Within such a grid square, there is likely to be a wide range of microclimatic conditions (Ashcroft *et al.*, 2009), potentially resulting in the presence of locally-suitable conditions for species at their thermal margins, the existence of which might not be apparent at a coarser resolution. Many species are associated with locally suitable microclimates at their range margins, where the coarser-scale mean climate is less suitable than at the centres of their ranges (Thomas *et al.*, 1999; Bryant *et al.*, 2002; Lennon *et al.*, 2002; Stefanescu *et al.*, 2004). Thus, models that utilise fine resolution data should be more accurate than those using coarse resolution climate data (Ferrier *et al.*, 2002) in areas of high relief and for predicting the likely persistence of species in small areas such as individual nature reserves.

These resolution issues mean that estimates of rates of decline under climatic change may be either too high or too low when using coarse resolution data and model projections. There is a possibility that coarse resolution models will overestimate the area available to species (Trivedi *et al.*, 2008) if, for example, a species only lives in the coldest 1 % of a coarse-grained grid cell, which contains a heterogeneous mix of different microclimatic conditions, but statistically appears to be able to inhabit the mean temperature of the grid square. Under modest climate warming, the coldest 1 % may become unsuitable for the species, even if the average temperature of the grid square still appears to remain suitable. Under this circumstance, a coarse resolution model may be slow to predict the disappearance of thermal refugia, and may therefore underestimate the rate of decline. Alternatively, however, fine resolution models may predict the persistence of these thermal refugia for longer into the future with climatic warming than do low resolution models (Randin *et al.*, 2009). So far, there are very few studies that have attempted to discover whether over- or under-estimation of declines is likely to be projected using coarse resolution models. Those that have been attempted have been restricted to plants, which, being sessile, might be expected to have a different propensity to survive in spatially restricted thermal refugia than more mobile organisms.

Previous studies that explored the implications of using models at different spatial resolutions interpolated fine-resolution climate surfaces using lapse rates (i.e., adjusting local temperatures to take account of the local elevation; Trivedi *et al.,* 2008; Randin *et al.,* 2009). However, variation in aspect and slope can have even larger effects than elevation on local temperature (Suggitt *et al*., 2011). Given this uncertainty, and contrasting conclusions in the literature, it is not clear whether fine-resolution analysis is expected to predict reduced (Trivedi *et al.*, 2008) or increased (Randin *et al.*, 2009) persistence, compared to coarse-resolution analyses. Here, we present the first study to compare the effects of different resolution models on predicted landscape suitability for a species where the effects of slope, aspect, hill-shading and elevation on local temperatures are included.

In this study, we sampled the abundance of ground beetles from within a single 10 x 10 km square (Figure 1). Because ground beetles are predatory, they should not be directly limited to particular vegetation types, although some preferences may be caused due to the microclimate experienced under different canopies. The study site is an area with substantial topographic variation, which thus gives a range of predicted temperatures depending on the resolution of the data (Figure 2), and sampled 1 km grid squares sometimes contained both sample locations where species were present and those where they were absent (e.g. see Figure 1). Because our records have a spatial precision of 5 m and include abundance data rather than presence/absence data, we were able to use them to answer several questions: 1) How does the spatial resolution used when modelling alter our perceptions of the temperatures of topographically diverse areas?

2) Does the projected percentage of a landscape that will remain suitable northern or southern species following climatic change vary with the resolution of the distribution model?

(A) METHODS

(B) Field Sampling

Ground beetles were collected by pitfall trapping from the start of May to the end of August 2008. Trapping took place on the Royal Society for the Protection of Birds (RSPB) Lake Vyrnwy reserve.

Lake Vyrnwy is situated adjacent to Snowdonia National Park in Wales (52° 47′ 09″ N, 03° 30′ 49″ W) and covers around 9,700 hectares. It contains several different vegetation types, but all trapping was undertaken in heathland dominated by *Calluna vulgaris* (heather) that occurs mainly on peaty soils. This heathland is actively managed for wildlife with a combination of mowing, burning and grazing being employed to maintain a mosaic of heather and grassland. The lowest areas of the reserve are around 350 m a.s.l., with the highest around 620 m a.s.l. The location and elevational range of the site means that it is at the southern range margin of many species with northerly distributions within the UK.

Stratified random sampling was used to select 40 locations. A 5 x 5 m grid was laid across the landscape, then grid cells were stratified into twelve categories on the basis of combinations of slope, aspect and elevation, with a thirteenth category for areas at the lowest elevations; three sampling locations were then randomly positioned within each of the first 12 strata, and four in the last. This ensured that the full range of microclimates present at the site was sampled. Sample points were georeferenced in the field using a handheld Global Positioning System (Garmin GPS 60). At each sample location, five pitfall traps were deployed in a circle of 2 m diameter. Traps consisted of two standard plastic vending cups of 7 cm diameter nested together and sunk into the soil so that the rim of the inner cup was flush with the soil surface. Each trap was filled to a 2.5 cm depth with ethylene glycol antifreeze. Traps were covered with a lid made up of a terracotta coloured plastic saucer suspended 11 cm above the ground and trap using galvanised wire. This served the dual purpose of limiting liquid loss by evaporation and limiting flooding from rainfall. A surround of chicken wire (mesh diameter 20 mm) completed the lid, with the aim of excluding small mammals from the trap.

Traps were emptied at monthly intervals, with the antifreeze solution being replaced when necessary. Catch was pooled for all five traps across the entire sampling season for each location, providing a total of 18,795 trap-hours across the entire landscape. All carabid beetles were identified to species. One northerly-distributed ground beetle, *Carabus glabratus* and the most southerly distributed ground beetle, *Poecilus versicolor*, were selected as examples for distributional modelling. *C. glabratus* might be expected to decline under climate change, whilst *P. versicolor* is expected to benefit from climate change. Both species fulfilled modelling criteria used in previous studies (see Gillingham *et al.*, 2012).

(B) Microclimate modelling

A recently published microclimate model, which has been ground-truthed and found to perform well when predicting vegetation surface temperatures in two different topographically heterogeneous landscapes (Bennie *et al.*, 2008), and additionally verified for this landscape (Gillingham, 2011) was coded into C++ (Programme available on request from PKG). Wind speed, air temperature and radiation data was obtained for the Vyrnwy meteorological station (52º 45′ 25″ N, 03º 38′ 45″ W) from the British Atmospheric Data Centre (BADC, www.badc.rl.ac.uk). A digital elevation model (DEM) at 5 x 5 m resolution (hereafter referred to as 5 m resolution) and 1 m vertical precision for the site was obtained from the NERC Earth Observation Data Centre (NEODC, neodc.nerc.ac.uk). Slope and aspect values for each 5 m cell were calculated using standard functions in ArcMap. The microclimate model used this information to generate hourly predicted temperatures at vegetation surface height at 5 m resolution from the start of September 2007 until the end of August 2008.

The microclimate model adjusted the temperature values from the Vyrnwy meteorological station to take account of the elevation difference between the met station and each point in the landscape, as well as differences in direct and indirect radiation associated with different slopes and aspects at different times of the day and year (including effects of hill-shading, and assuming homogenous cloud cover across the entire site; Bennie *et al.*, 2008). From these hourly surfaces of predicted temperature at vegetation height, annual mean temperature, maximum temperature in July (T_{max}) and minimum temperature in December (T_{min}) were extracted for use in the distribution model at 5 m resolution.

We used interpolated, rather than directly-measured, temperatures in the present study because: (a) much of the value of distribution models arises from their ability to generalise from sample points to other locations (in the present and future), and hence this requires the use of climatic surfaces that can be extrapolated in space and time, (b) ground beetles can move over short distances (see below), and so will experience temperatures over a larger spatial scale than single point measurements (logger temperatures at fixed points under a heather canopy are variable), and (c) we placed five pitfall traps within each sample location, so some measure of the expected “average condition” of such an area is more relevant to our sample data than the temperature at a single point. Resources were not available to place multiple loggers in each sample location.

(B) Statistical Modelling

Abundance (number of individuals trapped across the season) of *C. glabratus* and *P. versicolor* were the response variables to which predictor variables were fitted using a Generalised Linear Model (GLM) with Negative Binomial error structure and a log link function. The annual mean (T_{mean}), July maximum (T_{max}) and December minimum (T_{min}) temperatures as calculated by the microclimate model were included as predictor variables. Trapping effort, corresponding to the proportion of the trapping effort that was lost to damage at each location (e.g., loss of two of the five pitfall traps at a given location in one month), was included as a log-offset in all models to allow for variations in catch caused by damage to pitfall traps. An indication of model fit was calculated using the function cv.glm in the boot package in R. The default leave-one out cross validation was used to calculate adjusted prediction error. To give an indication of how informative our models were, delta-AIC was calculated by subtracting AIC of the intersect-only model from AIC of the selected model. All possible models were fitted, and as the models were to be used to illustrate predicted scenarios, the best model was selected as the one with lowest prediction error. However, because there is co-linearity within our explanatory variables (see Table S1 in Supporting Information), we fitted models in three additional ways to increase confidence in our conclusions. We additionally removed correlated variables (see Tables S2-S3 and Figures S1-

S2), we selected the best model using Multimodel Inference (see Tables S4-S5 and Figures S3-S4) and we selected the best model by backwards stepwise regression using AIC (see Tables S6-S7 and Figures S5-S6). These methods have been found to be effective when dealing with correlated explanatory variables (Smith *et al.*, 2009). All statistical analyses were carried out in R version 2.9.0 (R Development Core Team, 2008).

Coarser resolution temperature surfaces were generated by blocking up the data in 100 m increments using the mean value of the enclosed 5 m cells, to a maximum of 1 km resolution (for examples see Figure 2, note that resolution refers to the length of the side of each cell, such that 100 x 100 m cells are referred to as “100 m resolution”). GLMs were refitted to these lower resolution layers as before. Where more than one sampling location fell within a given coarse resolution cell, both abundance and trapping effort values were pooled to create one value for each variable per cell, such that coarse resolution cells containing more than one trapping location had much higher values for trapping effort. The trapping effort offset was retained in all models *because* it reflects the way the data were collected and manipulated.

We used 5 m resolution grids as the finest resolution considered for several practical and biological reasons: (a) this is the finest resolution at which elevational data are widely available; (b) this resolution seems relevant to the short-distance (daily, weekly) movements of adults and large larvae (*P. versicolor* has been found to move 7 m per day in heathland, whilst adults of other ground beetle species have been observed to move less than one metre over 48 hours; Brouwers & Newton, 2009); (c) the entire durations of eggs, pupae, and probably early larval instars will be contained within such an area. However, it should be noted that population persistence and abundance for our example organism may also be determined by larger-scale processes (e.g., average suitability at 100 m or coarser resolution), and hence we should not conclude that the finest-resolution analysis is the only one of relevance.

(B) Future Projections

The microclimate model was used to predict hourly temperature surfaces for the site for temperature increases in half degree steps to 6 ºC, which is the central estimate of the maximum predicted by 2085 for the UK under the maximum emissions scenario (http://ukclimateprojections.defra.gov.uk). This resulted in slightly uneven warming across the site, with cooler areas warming slightly more than hotter ones, thus reducing the range of available temperatures within the site. This approach was used in order to compare the effects of data resolution on future predictions and it is not within the remit of our study to comment on the likelihood of future scenarios of climatic change.

The 5 m resolution future temperature surfaces were again blocked to the resolutions previously used, and the respective model equations derived previously were applied to these future surfaces to predict the abundance of *C. glabratus* and *P. versicolor*. A threshold of one or more individuals predicted to be present within a cell given a maximum sampling effort of 4 months of continuous capture in five pitfall traps (which corresponds to our sampling season with no damage to traps) was used to estimate the percentage of the total landscape that is expected to be climatically suitable for the species with each temperature increase, based on these models. This corresponds to our ability to detect the species at any particular location, if it is present. One individual present in a trap would be likely to indicate larger numbers present in the immediate environment, as pitfall traps do not trap 100% of individuals present, rather provide an indication of activity density (Baars, 1979). We have an important caveat here. Our purpose is to illustrate the role of spatial resolution on projections, and not to make a specific prognosis for *C. glabratus* or *P. versicolor*. The latter would require the inclusion of more sample points and species-specific data (e.g., spatial scales of movement and persistence, see above; additional prey or habitat data and a quantified relationship between population density and detection probability), and testing of the predictive accuracy of the regression models over a number of years. It is not within the remit of this study to discover the relationship between the number of trapped individuals and whether a population is viable, as this information is not available for the majority of species for which climate envelope modelling is undertaken.

(A) RESULTS

(B) Microclimate surfaces

The microclimate surfaces are illustrated using July maximum temperatures ($T_{max,}$ see Figure 2). The range of T_{max} values that appeared to exist within the landscape decreased greatly as one moved from a 5 m resolution analysis (11.2 ºC range; 22.4 ºC to 33.6 ºC) to 1000 m resolution (3.9 ºC range; 26.1 ºC to 30.0 ºC). This compares to the maximum temperature of 23.5 °C recorded at the Lake Vyrnwy meteorological station for July 2008 (this temperature is within a Stevenson screen at 1.5 m height, and hence tends to be lower than average T_{max} values estimated for the vegetation surface). In general, as the resolution of the analysis became coarser, the range of temperatures declined, with the coolest observable locations being warmer and the highest observable temperatures being cooler, although this effect was much less marked for T_{mean} and T_{min} (Figure 3).

(B) Current Distributions

For the northern species, *C. glabratus*, T_{max} was the only independent variable apart from trapping effort to be retained in the best model at 5 m resolution. It showed a negative effect ($\beta = -0.91$, $n = 40$, $p < 0.0001$) on the abundance of *C. glabratus*. There were fewer *C. glabratus* in areas with warmer summer (July) T_{max} temperatures, as expected for a species at the southern limit of its distribution. Comparable results were obtained when fitting models at 200 m, 600 m, and 900 m resolution.

Using the 100 m resolution temperature surface yielded a different result. Annual mean temperature had a negative effect ($\beta = -1.21$, $n = 40$, $p < 0.0001$) on the abundance of *C. glabratus* Comparable results were achieved when fitting models at 700m and 800m resolutions. The overall relationship between abundance and the three temperature variables was negative at most resolutions (i.e. increasing abundance in cooler locations). However, at 400 m, 500 m and 1 km resolution, a positive relationship was found between temperature and abundance. The coefficients fitted show a large standard error compared to the effect size, so at these resolutions an effect of temperature was not seen, despite the comparatively low prediction error associated with the 500 m resolution model. In addition, these models all predicted the entire landscape to be suitable under current conditions, which is not the case (see figure 1).

For the southern species, *P. versicolor*, annual T_{mean} was the only independent variable apart from trapping effort to be retained in the best model at 5 m resolution. It showed a positive effect ($\beta = 4.44$, $n = 40$, $p < 0.0001$) on the abundance of *P. versicolor*. There were more *P.*

versicolor in areas with warmer mean temperatures, as expected for a species with a more southerly distribution. Comparable results were obtained when fitting models at 200 m, 400 m, 600 m, 800 m and 900 m resolution.

Using the 100 m resolution temperature surface again yielded a different result. T_{max} had a positive effect ($\beta = 1.44$, $n = 40$, $p = 0.0012$) on the abundance of *P. versicolor.* At 300 m and 700 m resolutions, T_{min} and T_{max} were both retained, showing a positive relationship with the abundance of *P. versicolor.* In all cases, the relationship between abundance and the three temperature variables was positive (i.e. increasing abundance in warmer locations).
For both species, prediction error varied with resolution (Tables 1 and 2). The greatest prediction errors were found for models fitted at 800m resolution or coarser.

(B) Future distributions

Each of the above models was then applied to the entire landscape, first for the current climate, and then for warming of up to 6 ºC. For the northern species, *C. glabratus*, the percentage of landscape perceived to be thermally suitable at current temperatures (i.e. we would expect to catch one individual or more in five pitfall traps over a four month period) varied from over 99 % at 100 m resolution to just over 90% at 200 m and 300 m resolutions. The area projected to remain thermally suitable, following climatic warming for *C. glabratus* within the study landscape, decreased in a non-linear fashion for all resolutions with informative models (see Figure 4). Different resolutions of data/models resulted in different rates of decline in the percentage of thermally suitable habitat associated with increasing temperatures (Figure 4). Following a 3 °C rise in temperature, one model predicted that < 1 % of the landscape would remain suitable (100 m resolution model), whilst one model predicted that 67 % of the landscape would remain suitable (800 m resolution model). The rate of decline was not predictable based on the resolution of the data used to fit models. However, the informative models based on different resolutions did agree on one point – almost the entire landscape would be thermally unsuitable following a 6 °C rise in temperature.

For the southerly-distributed *P. versicolor*, the percentage of the landscape predicted to be suitable increased in a non-linear manner at all resolutions (Figure 5). At current temperatures, between 29% (at 100m resolution) and just under 41% (at 900m resolution) of the landscape was predicted to be suitable. There was much more agreement between resolutions about the rate of increase of suitability for this species, and all models except the 400 m resolution model agreed that the entire landscape would be suitable following a 2 °C rise in temperature.

There is an important point to be made with regard to model selection, as different model selection methods resulted in different variables being retained for any one resolution for both species (see Tables S2-S7). For *P. versicolor* the retention of different variables had little effect on the model predictions, and agreement was high between all of the different methods (Figures S2, S4 and S6). However, for *C. glabratus* the results were very different at any one resolution depending on the model selection method used (Figures S1, S3 and S5). The most robust conclusion is that almost all resolution models, regardless of selection method, predicted that almost the entire landscape would be perceived as unsuitable following a 4 °C rise in temperature.

(A) DISCUSSION

In a landscape such as ours, topography can change markedly over a scale of tens to hundreds of metres, such that a coarser resolution cell may contain both north- and south-facing slopes, as well as several hundred metres of elevational range. These differences in topography and thus temperature conditions result in many coarse grid cells containing some areas that are much cooler and others that are much hotter than average (Figure 2). Our analyses showed that projections of future distributions are highly sensitive to this variation.

The statistical models (GLM) models that we fitted to the *current* distributions of our two study species were consistent, and sensible, in that the northerly distributed *C. glabratus* was mostly frequently encountered in the coolest parts of the landscape and that the southerly distributed *P. versicolor* was predominantly found in the warmest locations (at all resolutions). The finer resolution models generated the slowest rate of decline in the northern *C. glabratus* and the slowest predicted increase in the southern *P. versicolor* (although analyses for this species were far less sensitive to resolution). By modelling at resolutions far coarser than the environments that individuals actually experience, we apparently underestimated the capacity of northern *C. glabratus* to survive in small-scale refugia; a finding typical of other studies that have used fine-resolution models (Gottfried *et al.,* 1999; Williams *et al.,* 2003; Seo *et al.,* 2009), although these studies did not expressly compare model resolutions. For the southern *P. versicolor,* the coarsest 1 km resolution analysis may equally fail to identify warm microsites, and thereby under-estimate the potential for colonisation. However, it was not as simple as this because different temperature variables (annual mean, winter minimum, summer maximum) entered the models at different resolutions, and under different model selection methods. This resulted in *C. glabratus* appearing least sensitive to warming in some of the intermediate-resolution analyses. The most conservative conclusion we can make is that that projected sensitivities to climate warming are strongly dependent on the spatial resolution of analysis and the model selection method. Nonetheless, we were able to find some agreement in that almost all models predicted that the entire landscape would be perceived as unsuitable for *C. glabratus* following a 4 ºC rise in temperature.

There are two comparable studies, which reached opposite conclusions on the effect of resolution on the apparent suitability of a landscape following climatic change. Randin *et al.*, (2009) projected higher levels of persistence for high-resolution models of plant distributions in the Swiss Alps, whilst Trivedi *et al.*, (2008) found lower projected persistence in high resolution models of Scottish plants than in coarse resolution models. Both studies used elevation as the sole means for interpolating temperature to finer resolutions (i.e. colder at higher elevations), without considering the effects of slope and aspect. North and south facing slopes can differ by as much as 7 ºC (Suggitt *et al.*, 2011), so the coldest place within a landscape may be on a polewards-facing slope rather than at its highest point. However, topographic effects depend on the climatic variable considered (Suggitt *et al.*, 2011). Low elevation areas may experience lower minimum temperatures than mid-elevations due to cold air pooling (Geiger, 1973), and the highest maximum temperatures are commonly found on steep south facing hillsides (in the northern hemisphere) rather than at the lowest elevations (Bennie *et al.*, 2010; Suggitt *et al.*, 2011); whilst the lowest maxima (i.e. areas that are suitable refugia for species preferring cooler conditions) occur at moderate rather than high elevations in some landscapes (Ashcroft *et al.*, 2008), where some shelter is available from hot, dry winds. Hence we suggest that elevation-only models are insufficient for high resolution modelling of climatic effects on species' distributions. We suspect that the opposite results of Randin *et al.*, (2009) and Trivedi *et al.*, (2008) may arise partly because of the higher elevational, and hence temperature (based on lapse rate), range of Switzerland than Scotland. The microclimate model we used makes a step forwards by including the effects of radiation and wind speed, but there is scope for improvement by including effects such as cold air pooling. In any case, modelling at a range of different resolutions, rather than just coarse and fine resolution, highlighted the unpredictability of projections, with different resolution models predicting different rates of decline of a northern species. Therefore, the selection of different resolutions by the above-mentioned authors may be one potential source of their opposite results.

The observed discrepancy between the perceptions of different resolution models, along with the fact that finer resolution models have been found to perform better than coarser ones in predicting species' distributions (Engler *et al.*, 2004), leads us to conclude that more modelling should be done at a range of resolutions across different taxa and regions, at least until we understand the circumstances leading to the prediction of higher or lower estimations of extinction when fine resolution data are used. Further research on the capacities of species from different taxonomic groups to persist in local microclimates is also needed. Small areas of suitable microclimates do not necessarily imply that sufficient area will survive to ensure long-term population persistence. There is also the question of which is the most appropriate resolution to model at for any given species. This will vary among species depending on the movement rates of individuals and the area required to support populations. Where such data do exist, individual-based mechanistic models (rather than the correlative ones used here) may be more appropriate as they provide a dynamic response to change based on well understood processes (e.g. Clark *et al.*, 2001; Wallentin *et al*., 2008). However, for the vast majority of species (as for the example species modelled in this study), such data do not exist. In these cases, comparing results from a range of resolutions to give a range of values for predicted suitability of landscapes is a step forward in representing the needs of the species more accurately.

A challenge is the need for high resolution analyses over large spatial extents, and a more systematic approach to sampling would be beneficial (Eyre *et al.*, 2005). To date, studies (including ours) often focus on relatively small geographical extents when modelling at a fine resolution. This is because it is impractical to collect distribution data at the fine resolution required for such studies throughout the whole of a species' range. However, the approach that we advocate may become increasingly feasible because: (a) as in this study, one only needs data from a sample of precisely georeferenced locations (it is not necessary to cover every cell); (b) many existing records are already at 100 m grid resolution (http://data.nbn.org.uk); and (c) cheap GPS units mean that many records are now submitted with location data that have a precision of < 20 m. Such records could be used to model species distributions at a fine resolution across whole countries in order to make a fair comparison between coarse and fine resolution models across large geographical extents. These models would then give conservation managers a better idea of the priority areas that should be managed for species of interest, both within single sites and on a national and international basis.

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Supporting Information

Table S1: Correlation coefficients between temperature variables

Table S2: Variable coefficients for *C. glabratus*, where T_{mean} has been removed

Table S3: Variable coefficients for *P. versicolor*, where T_{mean} has been removed

Table S4: Variables included in the best model selected by MMI for *C. glabratus*

Table S5: Variables included in the best model selected by MMI for *P. versicolor*

Table S6: Variables included in the best model selected by backwards stepwise regression on AIC for *C. glabratus*

Table S7: Variables included in the best model selected by backwards stepwise regression on AIC for *P. versicolor*

Figure S1: Model predictions for *C. glabratus* based on models in Table S2

Figure S2: Model predictions for *P. versicolor* based on models in Table S3

Figure S3: Model predictions for *C. glabratus* based on models in Table S4

Figure S4: Model predictions for *P. versicolor* based on models in Table S5

Figure S5: Model predictions for *C. glabratus* based on models in Table S6

Figure S6: Model predictions for *P. versicolor* based on models in Table S7

Biosketch

Phillipa Gillingham is interested in the ecology and conservation of upland ecosystems, as well as the effects of climate change on the distributions of species and how this will affect conservation in the future. She is currently based at Bournemouth University, where she is a lecturer in Biogeography. Author contributions: PKG and CDT conceived the idea with advice from BH and WEK. PKG collected and analysed the data with advice from CDT, BH and WEK. PKG led the writing, CDT, BH and WEK made extensive comments on all drafts.

Table 1: Summary of the Generalised Linear Models fitted at each resolution (Res), with number of sample locations N. Shown are the β-coefficient of the relationship between abundance of *Carabus glabratus* and annual mean temperature ($\beta\ T_{mean}$), winter minimum temperature ($\beta\ T_{min}$) and summer maximum temperature ($\beta\ T_{max}$) with standard errors in brackets, along with their associated p-values. A + in the Effort column indicates that the log trapping effort was included as an offset in the model. Delta AIC of the best model and prediction error (PE) are also shown.

Res	N	Effort	$\beta\ T_{mean}$	p	$\beta\ T_{min}$	p	$\beta\ T_{max}$	p	DeltaAIC	PE
5	40	+	-	-	-	-	-0.91 (0.23)	<0.0001	-11.09	143.83
100	40	+	-1.21 (0.71)	0.0879	-	-	-	-	-3.21	176.65
200	40	+	-	-	-	-	-1.05 (0.25)	<0.0001	-12.62	157.53
300	36	+	-	-	-	-	-1.17 (0.26)	<0.0001	-12.50	202.42
400	34	+	0.84 (0.90)	ns	-	-	-0.57 (0.31)	0.0709	-2.17	212.20
500	30	+	-	-	1.08 (0.83)	ns	-0.59 (0.27)	0.0296	-5.54	110.98
600	28	+	-	-	-	-	-0.92 (0.43)	0.0338	-2.21	366.30
700	25	+	-1.63 (0.98)	0.0950	-	-	-	-	-6.86	501.38
800	22	+	-0.82 (0.87)	ns	-	-	-	-	-3.22	532.21
900	20	+	-	-	-	-	-0.76 (0.40)	0.0608	-7.84	296.40
1000	20	+	-	-	0.07 (1.12)	ns	-	-	-3.12	530.38

Table 2: Summary of the Generalised Linear Models fitted at each resolution (Res), with number of sample locations N. Shown are the β-coefficient of the relationship between abundance of *Poecilus versicolor* and annual mean temperature (β T_{mean}), winter minimum temperature (β T_{min}) and summer maximum temperature (β T_{max}) with standard errors in brackets, along with their associated p-values. A + in the Effort column indicates that the log trapping effort was included as an offset in the model. Delta AIC of the best model and prediction error (PE) are also shown.

Res	N	Effort	β T_{mean}	p	β T_{min}	p	β T_{max}	p	DeltaAIC	PE
5	40	+	4.44 (0.71)	<0.0001	-	-	-	-	-24.54	25.58
100	40	+	-	-	-	-	1.44 (0.44)	0.0012	-8.61	32.59
200	40	+	4.34 (0.82)	<0.0001	-	-	-	-	-19.38	30.54
300	36	+	-	-	4.30 (0.93)	<0.0001	0.60 (0.31)	0.0494	-15.98	25.43
400	34	+	4.06 (1.12)	0.0003	-	-	-	-	-10.07	39.23
500	30	+	4.29 (1.29)	0.0008	-	-	0.41 (0.46)	ns	-16.24	47.25
600	28	+	5.34 (1.83)	0.0035	-	-	-	-	-11.96	63.09
700	25	+	-	-	2.54 (1.78)	ns	1.65 (0.64)	0.0096	-7.65	9.99
800	22	+	4.25 (1.28)	0.0009	-	-	-	-	-9.67	60.18
900	20	+	3.57 (2.18)	ns	-	-	-	-	-3.28	93.82
1000	20	+	-	-	40.60 (1.59)	0.0038	-	-	-13.42	82.55

Figure legends

Figure 1: Locations within the landscape that were sampled for *Carabus glabratus*. Presences (black circles) and Absences (white circles) are shown on a 1 km resolution grid of cells with presence only (dark grey), absence only (pale grey) and containing both presence and absence records (mid grey)

Figure 2: The maximum temperature in July 2008 (T_{max}) across the Lake Vyrnwy field site, shown at four different resolutions a) 5 m b) 100 m c) 500 m d) 1000 m

Figure 3: The relationship between input data resolution and perception of various parameters at 2008 conditions; a) the maximum of T_{max} (black squares), minimum of T_{max} (black triangles), maximum of T_{mean} (grey squares), minimum of T_{mean} (grey triangles), maximum of T_{min} (open squares) and minimum of T_{min} (open triangles) in the landscape.

Figure 4: The proportion of the landscape predicted to remain thermally suitable for *Carabus glabratus* following climate warming based on the model with the lowest prediction error. Each line represents a different resolution model.

Figure 5: The proportion of the landscape predicted to become thermally suitable for *Poecilus versicolor* following climate warming based on the model with the lowest prediction error. Each line represents a different resolution model.

Figure 1:

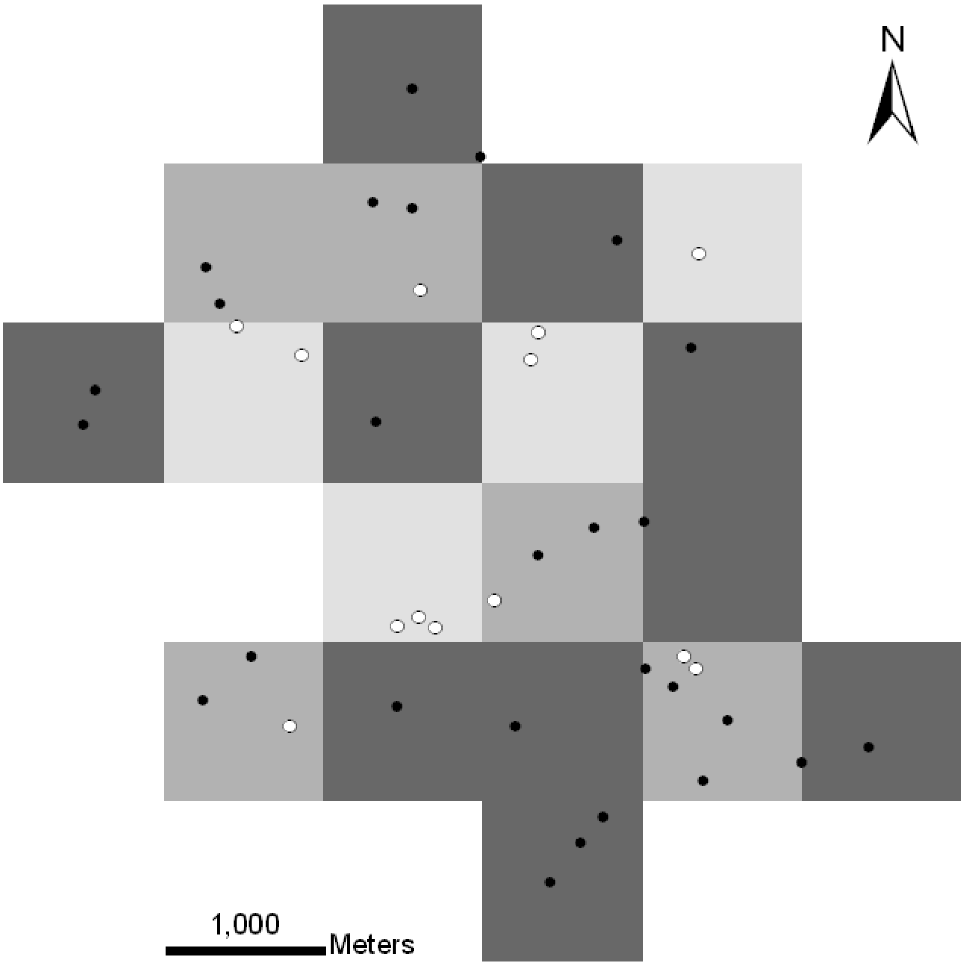


Figure 2:

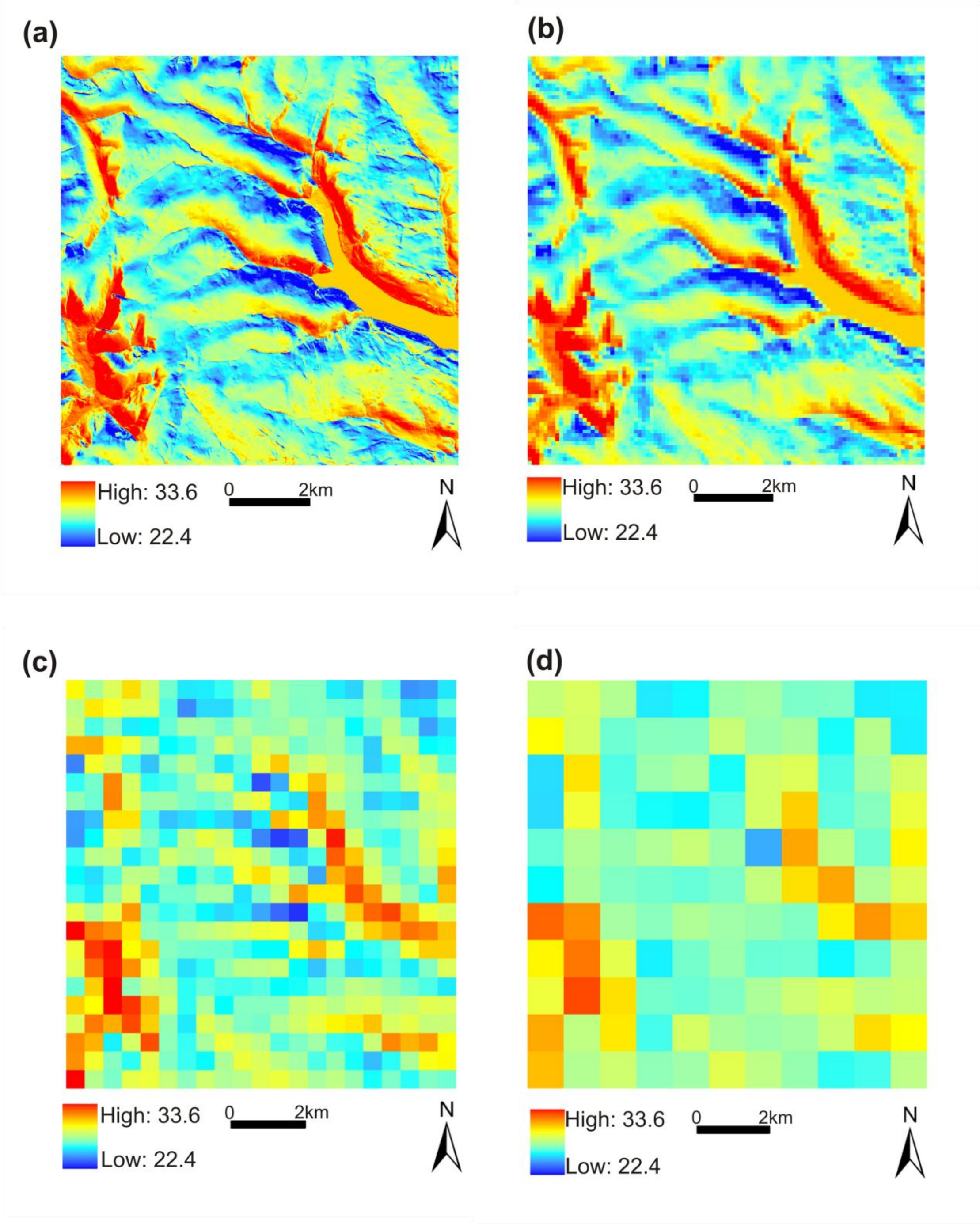

(a)
High: 33.6
Low: 22.4
0
2km
N
(b)
High: 33.6
Low: 22.4
0
2km
N
(c)
High: 33.6
Low: 22.4
0
2km
N
(d)
High: 33.6
Low: 22.4
0
2km
N

Figure 3:

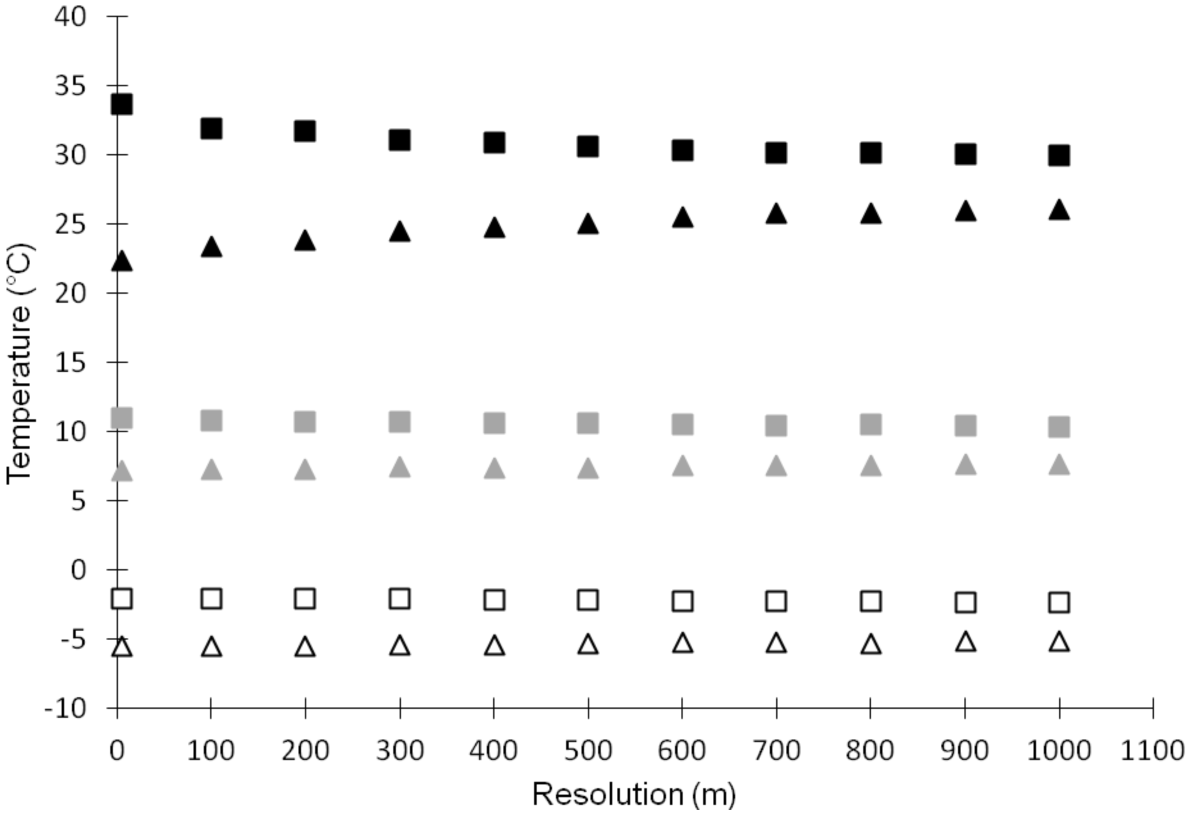


Figure 4:

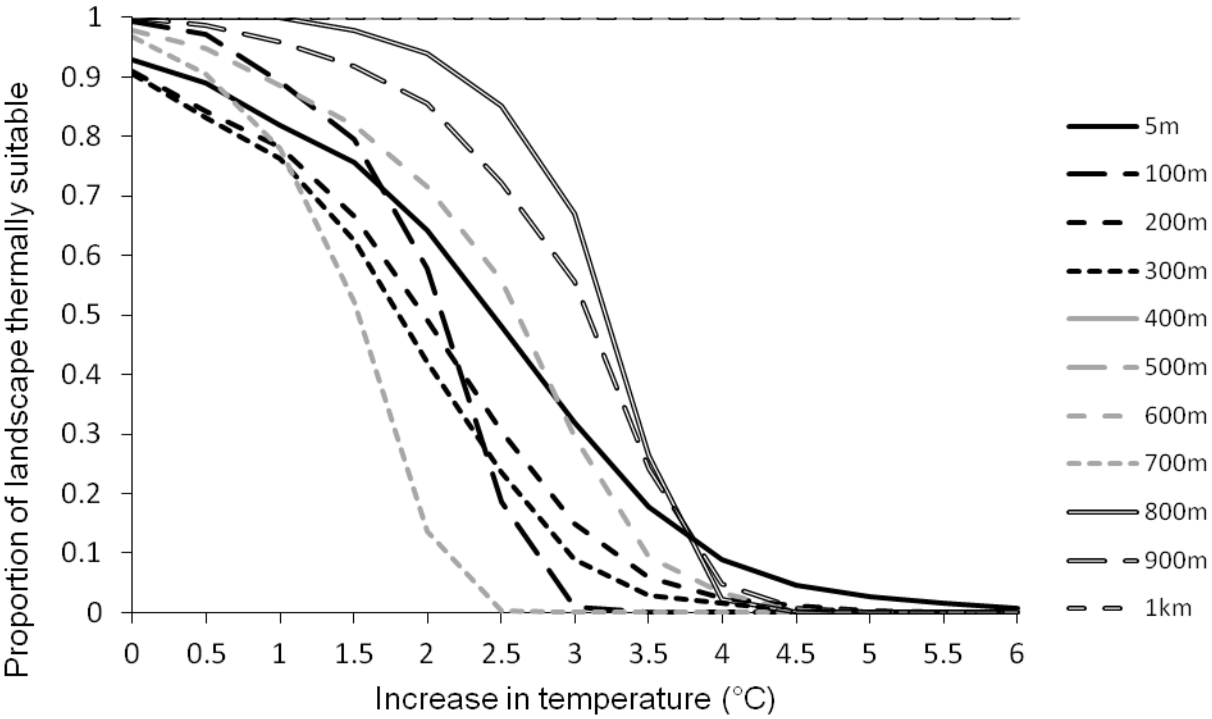
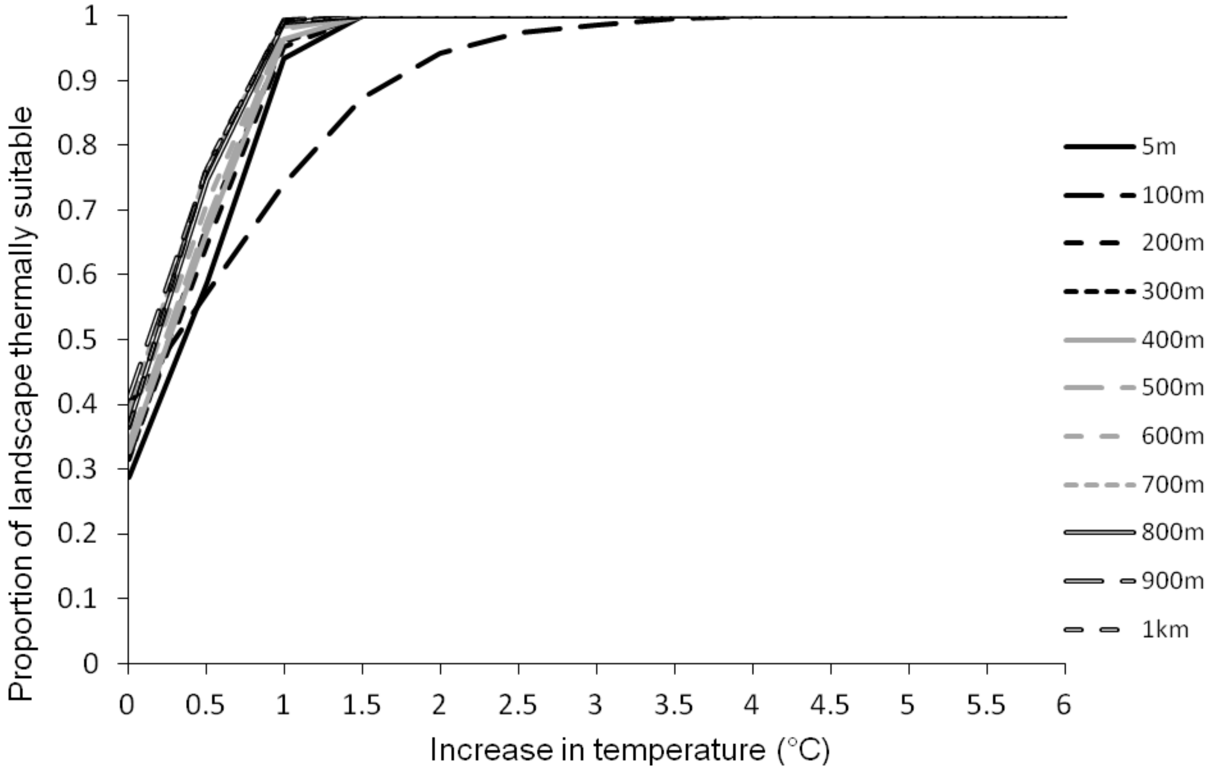

Proportion of landscape thermally suitable
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
Increase in temperature (°C)
5m
100m
200m
300m
400m
500m
600m
700m
800m
900m
1km

Figure 5:


Proportion of landscape thermally suitable
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
Increase in temperature (°C)
5m
100m
200m
300m
400m
500m
600m
700m
800m
900m
1km