Macroclimate data over-estimate species range shifts in response to climate change

Ilya Maclean (✉ I.M.D.Maclean@exeter.ac.uk)

University of Exeter   https://orcid.org/0000-0001-8030-9136

Regan Early

University of Exeter, Penryn Campus

Abstract

The expectation that places with suitable climate will lie outside the current range of many species has shaped 21st century conservation policy and led to predictions of numerous extinctions. We show that the magnitude of range shifts is often overestimated because the climate data typically used do not reflect the microclimatic conditions that many organisms experience. We model the historic (1977–1995) distributions of 302 plant taxa using both macro- and microclimate data and project these distributions forward to present day (2002–2020). Whereas macroclimate models predicted major range shifts (mean: 9.2 km per decade), microclimate models predicted localised shifts into favourable microclimate (mean: 88 m per decade) that more closely match observed patterns of establishment and extinction. In consequence, improving protecting of refugial populations within species' existing geographic range is likely to be more effective for many species than assisted translocations and overhaul of protected area networks.

Main

It is widely predicted that places with suitable climate will soon lie outside the current range of many species[1–3], and in consequence, that their survival over the next 100 years depends on how rapidly populations can move[4]. Many organisms are thought to face insurmountable range-shift barriers, leading to the conclusion that the only viable option to prevent extinctions is thus to translocate them to places where the climate is suitable[5], or create habitat corridors that allow them to get there of their own accord[6]. However, the expectation that species will have to undergo major range shifts to avoid range loss is founded on the assumption of strong and smooth geographic gradients in climate. These gradients would mean that temperature or precipitation changes make swathes of species' current ranges unsuitable and create swathes of suitable habitat elsewhere, further along the climatic gradient. While clear climatic gradients occur at coarse spatial resolution, at finer resolutions topography, soil conditions and vegetative shading exert great influence on local climatic conditions, resulting in considerable localised heterogeneity, particularly near the ground[7,8]. These fine-resolution variations can exceed the variability that occurs over continents in coarse-resolution climate, and greatly exceed the magnitude of climate change expected over the next 100 years[9]. For the most part organisms experience and respond to climate at resolutions where topography, soil, and shading determine conditions, and which are orders of magnitude finer than the scales at which shifts are measured and modelled[10]. Despite this, there is little consensus on the extent to which microclimate matters for species range shifts. On the one hand, it has been proposed that microclimate data may overestimate the thermal tolerances of species, and hence under-estimate the loss of suitable climate, as they fail to pick-out the localised warm microclimates in which species are driven to extinction. In contrast, it has also been suggested that microclimate heterogeneity may buffer species against climate change by providing locally suitable climatic conditions[11], and hence over-estimate loss of suitable climate. Measurements of observed range shifts could in theory resolve this uncertainty, but in practise the majority of observed distribution shifts are of range expansions[12,] and are almost invariably assessed using coarse-resolution data. At a coarse

grid scale, all populations must go extinct from a region for that grid cell to become newly unoccupied, whereas the occurrence of just one new individual is enough to ensure that it would be considered as newly occupied[16]. In consequence, range loss at coarse resolutions would appear to be much slower than range expansion, and will therefore be observed less often. Moreover, recent comprehensive meta-analyses of observed range shifts provide no support for their being a widespread phenomenon in terrestrial environments[13]. Here we show that macroclimate data, defined as data interpolated from weather stations at 1.5–2 m above-ground and at grid resolutions of 1 km or more, frequently over-estimate range shifts.

Why Range Shifts May Be Overestimated

To illustrate the mechanism by which ranges may be over-estimated by macroclimate data, we first consider a hypothetical example. In Fig. 1a, mean annual temperature, measured with macroclimate, decreases with latitude. Each coarse grid cell is assumed to contain a range of microclimatic conditions both cooler and warmer than the mean temperature of the grid-cell. A hypothetical species with a true thermal tolerance range of 5–10°C is assumed to occupy all coarse grid cells with at least some suitable microclimate, and the thermal tolerance, estimated from macroclimate data, is thus over-estimated by 10°C: the range of conditions present within each cell. When uniform warming of 2°C is applied to all cells, macro- and microclimate data thus yield exactly the same predicted range shift. Grid cells predicted by macroclimate data to be climatically unsuitable for that species, are also those that lose suitable microclimatic conditions and thus, there is a near linear relationship between macroclimate suitability and microclimate availability in both periods. In Fig. 1b, the outcome is shown for a hypothetical species with the same distribution as in Fig. 1a, when near-ground temperatures are decoupled from macroclimate across latitudes. This phenomenon is widely observed, and arises because near-ground temperatures are influenced more strongly by solar radiation at lower latitudes[7]. Therefore, at lower latitudes the offset between ground and air temperatures is higher at lower latitudes. While the thermal tolerance range estimated from macroclimate data is again 0–15°C the species' true thermal range in this case is actually 7.2–16.7°C. In Fig. 1b, macroclimate data over-estimate thermal tolerance limits to a lesser extent than in Fig. 1a. With uniform warming of 2°C the shift in the microclimate is less than the shift in macroclimate, suggesting that the species would persist in parts of its range predicted by macroclimate data to be unsuitable. Thus, the range shift predicted by temperatures the species actually experiences is less than would be predicted when using macroclimate data derived from weather stations. Figure 1 therefore shows that the major flaw in using macroclimate derived from weather stations, is the geographic pattern in the discrepancy between macroclimate and near-ground microclimate (and not necessarily the climate grid size *per se*). Given that there is also greater spatial heterogeneity in near-ground temperature than in macroclimate, the resulting effects on projected range shifts could be profound.

Relationships Between Macro- And Microclimate Suitability

In order to investigate the combined effects of using both fine-resolution and near-ground temperature on the accuracy of range-shift projections, we modelled associations between multiple climate variables and the distributions of 302 higher plant taxa (Table S1). Species distribution models (SDMs) were constructed and projected at three scales: across Europe at 0.5°, the United Kingdom (UK) at 5 km, and the Lizard Peninsula, southwest UK at 100 m. To test the accuracy of range-shift projections, we modelled associations between historic species distributions and climate (1977–1995), projected range-shifts to the present day (2002–2020), and compared projected climate suitabilities measured at each spatial resolution to observed distribution changes. To ensure our results were not biased by peculiarities of the climate of the Lizard Peninsula, we also modelled, at 100 m resolution, the historic and current distributions of one of these species, *Melittis melissophyllum* (Bastard Balm), at 72 4 km^2 localities across Europe and compared this with results obtained by modelling changes in the European distribution at 0.5°. This species was selected as its global range is almost entirely confined to Europe and adequate data were available at each of the chosen sites for model calibration and validation.

The historic suitability predicted by macroclimatic SDMs in the 0.5° or 5 km grid-cell(s) that encompass the Lizard were reasonably correlated with the area predicted to be suitable at 100m resolution (0.5° slope = 0.425, r^2 = 0.235, 5 km slope = 0.570, r^2 = 0.324), and at 100m resolution for *M. melissophyllum* across Europe (slope = 2.46, r^2 = 0.327). However, as hypothesised by our illustrative example, the slope of the relationship was shallower, and the correlation weaker when probability of occurrence was projected forward to current conditions (0.5° slope = 0.337, r^2 = 0.228; 5 km slope = 0.493, r^2 = 0.234; *M. melissophyllum* slope = 0.862, r^2 = 0.048; Figs. 2 and 3). Most importantly, the discrepancy in the relationship between macroclimatic suitability and microclimate availability over the two periods was greatest for those species for which macroclimate suitability was low. For example, a species with very low (0.001) predicted probability of occurrence at 0.5° resolution would be predicted to have approximately 3.6 (Europe) to 3.7 (UK) times more suitable microclimate under recent climatic conditions than under historic conditions (Fig. 2). In consequence, a species that experienced a reduction in predicted probability of occurrence derived from macroclimate data will not necessarily lose climate at fine-resolution. Indeed, though 0.5° European models implied the extirpation of 37 species from the Lizard Peninsula, and 5 km UK models 29 species, no extirpations were predicted by fine-resolution models (or indeed observed). For *M. melissophyllum* the results were similar (Fig. 3), though extirpation was predicted by microclimate models at some locations. Nevertheless, at localities with low (0.1) predicted probability of occurrence at 0.5° resolution in either period, *M. melissophyllum* was predicted to have 24.9 times the area under recent climatic conditions than under historic conditions. Whereas 0.5° resolution models predicted extirpation from 29 of the 72 localities, 100m resolution models predicted extirpations from just 16. The breakdown in the relationship between macro and microclimate suitability over just a few decades calls into question the accuracy of range projections made using macroclimate data.

Effects Of Resolution On Range Shifts

Whether macroclimate or microclimate data are used to predict species distribution shifts also affected expectations of how far species' ranges would have to shift in order to track changes in climate. We calculated the mean of the distances between each grid cell predicted to be occupied historically and the nearest location with climatically suitable conditions under recent conditions. To track climate change at 0.5° resolution, species would have had to shift between 0.56 and 259 km, with a mean of 23.0 km. At 5 km resolution, species would have had to shift between 2 m and 306 km, with a mean of 5.93 km. When assessed using microclimate data, species would have had to have shifted between just 0 m and 3.15 km, with a mean of 220 m, equating to just 8.8 m per year (Table S1). Therefore, the rate at which taxa must move in order to keep pace with climate, is likely to be within the dispersal capability of even slow-growing sessile species[14]. The shorter distances predicted by microclimate models appear to be more accurate than the longer distances predicted by macroclimate models. Whereas microclimate SDMs were able to predict extinctions and establishments with reasonable accuracy (extinctions median: 78%, establishments median 76%: macroclimatic predictions of extinctions and establishments were worse than would be expected by chance (0.5° European models, establishments median: 49%, extinctions median: 34%; 5 km UK models, establishments median: 16%, extinctions median 9%; Table S3).

Our findings were not sensitive to methods used to construct species distribution models, nor to assumptions about variation in recorder effort. While models built with different techniques or subsets of the data yielded slight differences in projected distributions, the overall finding, that the magnitude of projected range is much lower when predicted with microclimate data held true regardless of the approach used (Table S1).

Our results demonstrate that the projections of species range shifts may systematically underestimate the importance of microclimatic refugia, and over-estimate range contractions, largely because spatial gradients in temperature were underestimated and thermal tolerances over-estimated when using macroclimate data. Warmer localities were those with higher solar irradiance — either poleward-facing slopes or those at lower latitudes — where the angle of incidence between the sun and the earth's surface is closer to perpendicular[15]. Variation in solar irradiance has a more pronounced effect on near-ground temperatures than on air temperature 1.5-2 m above ground, as the majority of radiation is transmitted through air without appreciably warming it[16]. In consequence, the loss of suitable microclimate is less than would be expected given the degree of ambient warming. The microclimate model we used to estimate climate suitability at fine-resolution incorporated the effect of exposure to varying degrees of solar radiation, so represented near-ground temperatures more accurately than temperatures derived from weather stations[9,16]. Combined with the existence of considerable local spatial heterogeneity in microclimate, and likely slower rates of warming of microclimatic refugia[9], microclimate models thus predict greater persistence and more localised shifts that more closely match observed patterns of establishment and extinction.

It is possible that we found such a striking difference between macro- and microclimate projections because the majority of the study species are associated with grassland and heathland, for which the

greater effects of solar irradiance on near-ground temperatures are particularly pronounced. This may not hold true for species associated with densely forested environments, where tree canopy functions as a thermal insulator and buffers sub-canopy microclimatic conditions[17]. Nevertheless, the study species have widely divergent distributions and associations with climate variables. The conclusions we reached are therefore likely to be representative of non-forest species from other taxa and regions.

These problems in range-shift forecasts have probably gone unnoticed for so long for three reasons. First observed range expansions have been mistakenly interpreted as range shifts (i.e. retractions and expansions). Studies frequently document the mean of shifts in species range centroids or do not clearly differentiate between range expansions and retractions[12] and in consequence the strength of empirical evidence for contraction of warm range-margins is far weaker than is commonly perceived (see also[13]). Second, almost all studies of projected shifts to date have used climatic and biological data with grid cell sizes several orders of magnitude larger than species under study[10]. It is only recently that methods for generating fine-resolution climate datasets have been developed[18], and very rarely have these been used to project species range shifts[19]. The coarse-gridded data are almost always generated using measurements obtained from weather stations. These stations have design criteria which deliberately limit local climatic influences[20] and hence reduce fine-scale variability in climate. Lastly, the most common way to test the performance of SDMs is to use cross-validation techniques within species current, observed distributions. Such approaches suffer from the problems associated with autocorrelation, thus increasing the likelihood that SDM ability to project future distribution is over-estimated[21]. This issue is illustrated well with our own coarse-scale models. Standard cross-validation metrics suggested good performance (Table S2), but their ability to predict extinctions and establishments was worse than would be expected by chance (Table S3).

Conclusions

Our findings do not suggest that climate does not pose a threat to species. Indeed, despite marked differences in predicted range shift distances, the mean and median change in the area of suitable climate was broadly similar across scales (Fig S2), with approximately half of the species predicted to lose suitable climate space irrespective of the resolution of climate data used. Rather our results suggest that in the near future many species distribution changes in responses to climate in terrestrial environments are likely to be localised and difficult to infer using coarse-resolution data. These localised shifts could fragment populations, alter demography and affect community composition and ecosystem function. However, we caution against assuming long-distance range shifts will occur as an immediate response to climate, and hence that the redesign of protected area networks[10,11] and assisted colonisations[27] are the most pressing conservation priorities. Finite conservation resources and competing land-uses in many instances render such approaches impractical, emphasising the need for robust measures for carrying-out conservation *in situ*[22]. Rather, we emphasise the need to implement measures that sustain viable populations of species within their current geographic extent, Conservation

at locations with high microclimatic heterogeneity could provide a practical and cost-effective means of reducing extinction threat because this can be targeted at specific suitable locations.

Online Method

Climate data

Monthly global gridded 0.5 degree gridded climate data for the period 1979–2020 were obtained from the Climatic Research Unit[23] and the data for Europe extracted from this. Monthly gridded 5 km climate data for the UK were obtained from the Met Office[24]. Monthly 100 m gridded temperature data for the Lizard Peninsula were obtained by aggregating the hourly outputs from a microclimate model previously developed for the study region[25]. To derive 100m resolution temperature data for the 71 *M. melissophyllum* locations across Europe, we used the R[26] package microclima[16], which automatically downscales sub-daily climate data from the National Centres for Environmental prediction[27], using high-resolution digital elevation data[28]. Monthly 100m gridded rainfall data for the Lizard Peninsula were derived by spatially interpolating 5 km gridded rainfall data using a thin-plate spline, with 100m resolution elevation data[28] included as an additional covariate. Interpolation was performed using the fields package[29] for R[26]. The same procedure was used to downscale rainfall at 71 locations across Europe, though using rainfall data Climatic Research Unit. Monthly data were used to reconstruct, for two study periods (1977–1995) and (2002–2020), the 19 widely used "Bioclim" variables presented in Hijmans *et al*[30].

Species distribution data

Records of vascular plants across the Lizard Peninsula were obtained from Environmental Records in Cornwall Automated (ERICA) database, a compilation of verified local biodiversity records curated by members of the Cornwall and Isles of Scilly Federation for Biological Recorders, comprising more than 3 million plant records[31]. Records georeferenced to a precision of >100m were removed and the remaining data used to determine the presence of species within each 100m grid cell in each of two study periods. The 302 taxa present in at least 50 grid cells in the historic period were selected for all subsequent analysis. Plant records from across the United Kingdom were obtained from the Botanical Society of the British Isles[32], and the presence in 5 km grid cells determined in the same two periods. Plant records from across Europe were obtained were downloaded from the Global Biodiversity Information Facility (GBIF), supplemented by data from the Atlas Flora Europaea[33], for those species for which such data were available, and used to establish presence in each 0.5 degree grid cell during the two time periods. For the fine-resolution *M. melissophyllum* analyses, only records georeferenced to ≤ 100 m were used.

Modelling species distribution

We used climate envelope models[34] to predict species distribution shifts. Because the 'bioclim' variables were correlated with one another, and to ensure greater transferability between regions or time periods[35], we performed Principal Components Analyses, and used the first 7 components, which together explained > 99% of the variance, as climatic predictors of species distributions. In each instance we constructed the model using historic distribution and climate data and projected distributions forward to the present day, thus permitting robust empirical validation. To account for spatial biases in recording, we repeatedly subsampled the data in a manner proportional to the log-transformed number of visits to each square such that presences were more likely to be generated from grid cells with low visit coverage and absences from grid cells with high observer coverage. The number of visits to each square was calculated as the number of unique date, observer and location name combinations in each grid cell. Each sub-sample was obtained by randomly selected $n/10$ presences and absences, where n is the total number of occupied grid cells. Where fewer than 100 grid cells were occupied $n/5$ presences and absences were generated. To account for methodological uncertainties in models, we generated species distribution using three varied, but widely used model classes, namely Maxent[36], General Additive Models[37] and random forests[38]. For each species and method, 20 distribution models were constructed using separate sub-sampled data. To account for possible spatial autocorrelation in model coefficients, we spatially-kriged the residuals of each distribution model using inverse-distance squared weightings and creating new distribution models with same sub-sampled distribution data, but with this variable included as an autocovariate[39]. The results provided in the main text are from a final probabilistic weighted (by cross-validation True Skill Statistic, TSS) ensemble distribution of the 60 distributions for each species and period, constructed using the Biomod2 package[40] for R[26]. Additionally, we investigated whether our results could be caused by 100m resolution models, based only on data from the Lizard, underestimating species' full climate envelope. To do so, we used the models derived from the two sets of macroclimate data to project species distributions using the 100m climate data.

Model validation

We independently evaluated the ensemble models by computing sensitivity and specificity and determining the number of times they correctly predicted establishments and extinctions between time periods. Probabilistic projections of species distributions were thus converted to binary outputs using a predicted probability of occurrence threshold set separately for each model and species, that ensured that 90% of observe presences occurred in grid cells with suitable climate. To account for incomplete observer coverage, and hence the likelihood that an apparent absence in either period is a false absence, we computed the number of cells in which establishment, extinction, persistence and absence (in both periods) were predicted by each ensemble model. We then generated an equivalent number of each possibility randomly and assessed model performance in the same way. The randomisation process was repeated 10,000 times, and the proportion of times the model performed better than random assessed. To ensure our results were robust to the method for thresholding suitable climate, we re-ran our analysis using 0.5 for all species, and found qualitatively similar results.

Distribution shifts

To calculate the distance over which species must move to keep pace with climate, we again converted the probabilistic projections of species distributions to binary output. European projections of probability of occurrence were resampled to a UTM equal area projection prior to calculation. Then, for each historically occupied grid cell, we calculated the centre-to-centre distance between that grid cells and the nearest location with climatically suitable location under present day conditions, setting this distance at zero if the grid cell was to be occupied in both periods.

References

1   Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15, 365-377 (2012).

2   Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C. & Mace, G. M. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53-58 (2011).

3   Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* 427, 145 (2004).

4   Loarie, S. R. *et al.* The velocity of climate change. *Nature* 462, 1052 (2009).

5   Thomas, C. D. Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution* 26, 216-221 (2011).

6   Heller, N. E. & Zavaleta, E. S. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142, 14-32 (2009).

7   Bramer, I. *et al.* in *Advances in Ecological Research* 58, 101-161 (2018).

8   Maclean, I. M. D, Bennie, J. J., Scott, A. J. & Wilson, R. J. A high-resolution model of soil and surface water conditions. *Ecological Modelling* 237, 109-119 (2012).

9   Maclean, I. M. D., Suggitt, A. J., Wilson, R. J., Duffy, J. P. & Bennie, J. J. Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology* 23, 256-268 (2017).

10   Potter, K. A., Woods, H. A. & Pincebourde, S. Microclimatic challenges in global change biology. *Global Change Biology* 19, 2932-2939 (2013).

11   Suggitt, A. J. *et al.* Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change* 8, 713-717 (2018).

12   Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024-1026 (2011).

13   Lenoir, J. *et al.* Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution* 4, 1044-1059 (2020).

14   Stevens, V. M., Turlure, C. & Baguette, M. A meta-analysis of dispersal in butterflies. *Biological Reviews* 85, 625-642 (2010).

15   Maclean, I. M. D., Suggitt, A. J., Wilson, R. J., Duffy, J. P. & Bennie, J. J. Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Global change biology* 23, 256-268 (2017).

16   Maclean, I. M., Mosedale, J. R. & Bennie, J. J. Microclima: An r package for modelling meso-and microclimate. *Methods in Ecology and Evolution* 10, 280-290 (2019).

17   Haesen, S. *et al.* ForestTemp–Sub-canopy microclimate temperatures of European forests. *Global Change Biology* 27, 6307-6319 (2021).

18   Lembrechts, J. J. & Lenoir, J. Microclimatic conditions anywhere at any time! *Global Change Biology* 26, 337-339 (2020).

19   Gillingham, P., Huntley, B., Kunin, W. & Thomas, C. The effect of spatial resolution on projected responses to climate warming. *Diversity and Distributions* 18, 990-1000 (2012).

20   Jarraud, M. Guide to meteorological instruments and methods of observation (WMO-No. 8). *World Meteorological Organisation: Geneva, Switzerland* (2008).

21   Araújo, M. B. *et al.* Standards for distribution models in biodiversity assessments. *Science Advances* 5, eaat4858 (2019).

22   Greenwood, O., Mossman, H. L., Suggitt, A. J., Curtis, R. J. & Maclean, I. M. D. Using in situ management to conserve biodiversity under climate change. *Journal of Applied Ecology* (2016).

23   Harris, I., Osborn, T. J., Jones, P. & Lister, D. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data* 7, 1-18 (2020).

24   Jenkins, G. J. *The climate of the United Kingdom and recent trends*. (Exeter: Met Office Hadley Centre, 2007).

25   Mosedale, J. R., Abernethy, K. E., Smart, R. E., Wilson, R. J. & Maclean, I. M. Climate change impacts and adaptive strategies: lessons from the grapevine. *Global Change Biology* 22, 3814-3828 (2016).

26   R Development Core Team. (ISBN 3-900051-07-0, 2016).

27   Kalnay, E. *et al.* The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society* 77, 437-472 (1996).

28   Farr, T. G. *et al.* The shuttle radar topography mission. *Reviews of Geophysics* 45, 1-33 (2007).

29   Nychka, D., Furrer, R., Paige, J. & Sain, S. *"fields: Tools for spatial data."* http://doi.org/10.5065/D6W957CT (2015).

30   Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *International journal of Climatology* 25, 1965-1978 (2005).

31   Bennallick, I. *et al. Red Data Book for Cornwall and the Isles of Scilly*. 2 edn,   (Croceago Press, Praze-an-Beeble, 2009).

32   Preston, C. D., Pearman, D. & Dines, T. D. *New Atlas of the British & Irish flora*. (Oxford University Press, 2002).

33   Kurtto, A., Sennikov, A. & Lampinen, R. *Atlas florae europaeae*. (The Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo. 2016).

34   Pearson, R. G. & Dawson, T. P. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12, 361-371 (2003).

35   Petitpierre, B., Broennimann, O., Kueffer, C., Daehler, C. & Guisan, A. Selecting predictors to maximize the transferability of species distribution models: Lessons from cross-continental plant invasions. *Global Ecology and Biogeography* 26, 275-287 (2017).

36   Phillips, S. J. & Dudík, M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161-175 (2008).

37   Hastie, T. J. & Tibshirani, R. J. *Generalized Additive Models*. Vol. 43 (CRC Press, 1990).

38   Breiman, L. Random forests. *Machine Learning* 45, 5-32 (2001).

39   F Dormann, C. *et al.* Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609-628 (2007).

40   Thuiller, W., Georges, D., Engler, R., Georges, M. D. & Thuiller, C. W. Package 'biomod2'. (2012).
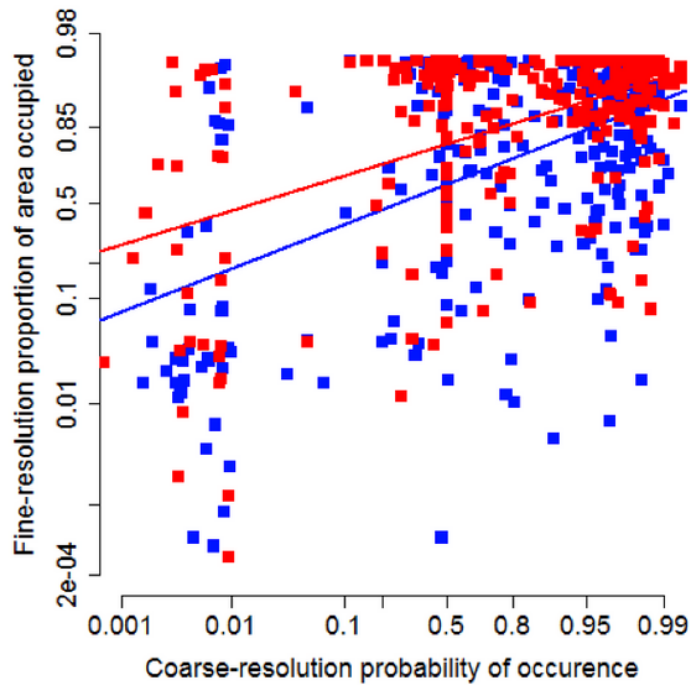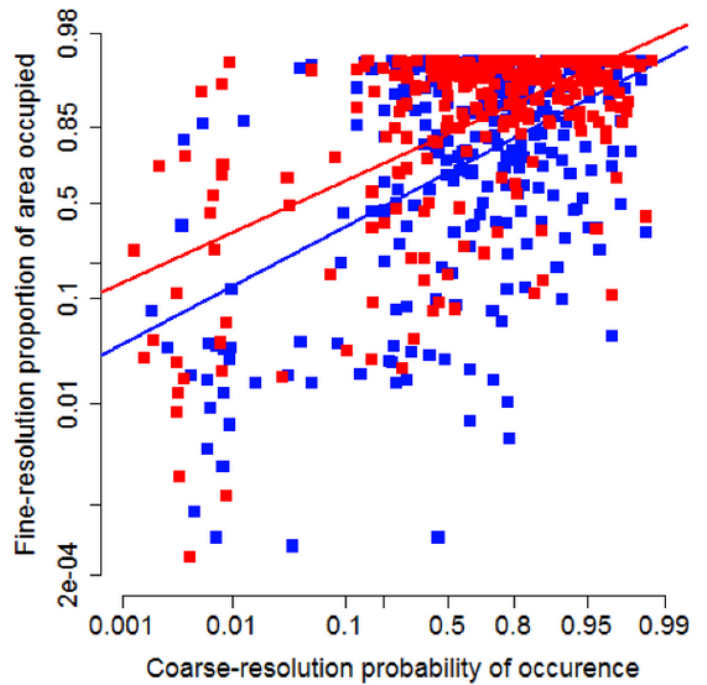
Figures
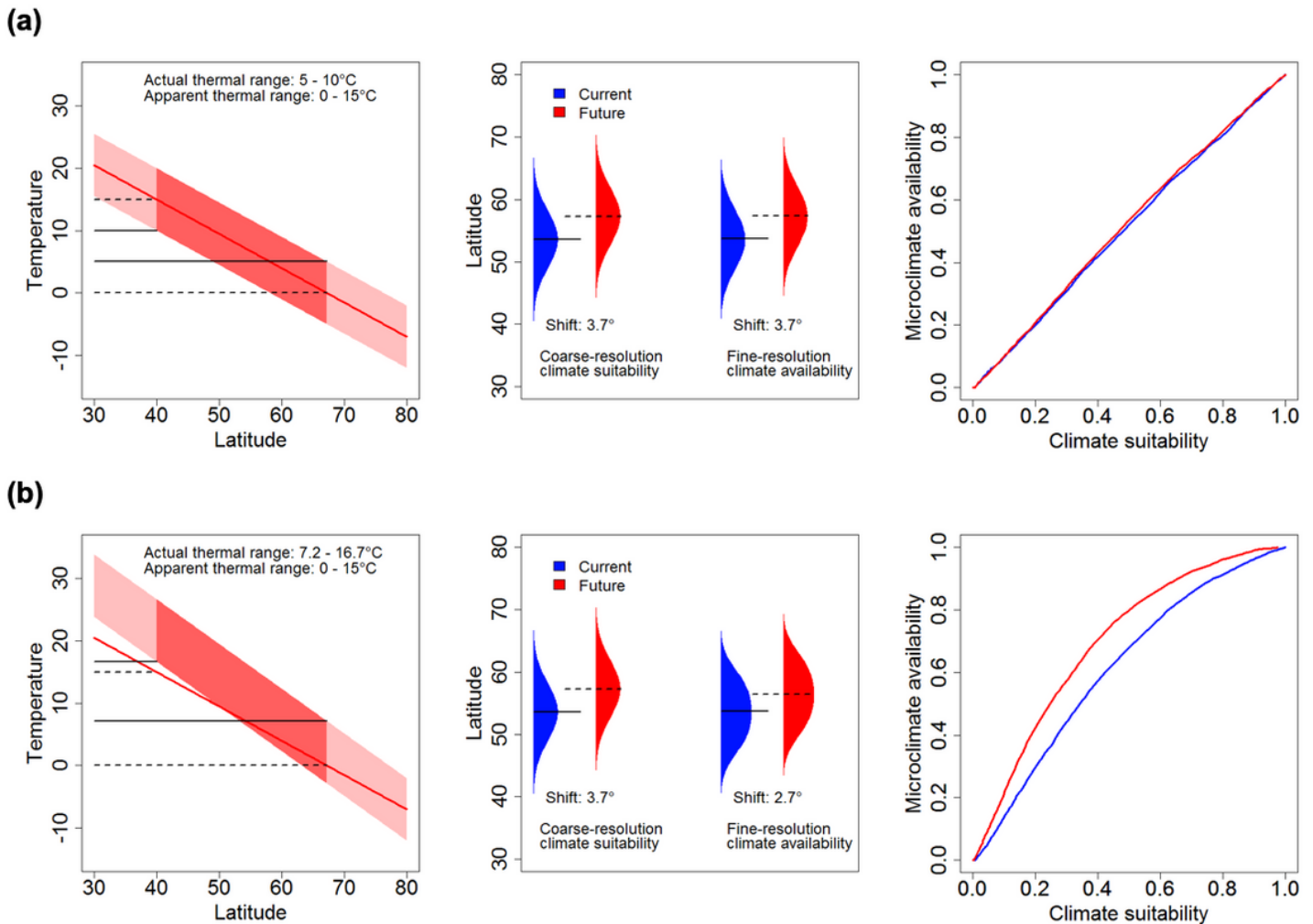
Figure 1

Microclimate and range shifts. In **(a)** mean annual temperature measured macroclimatically (i.e. derived at coarse-resolution, interpolated above ground from weather stations), varies with latitude, but microclimatic temperature conditions present within a grid cell range from -5 to +5°C from the mean of that cell. A hypothetical species with a thermal tolerance of 5 to 10°C is assumed to occupy all grid cells with at least some suitable microclimate, and the thermal tolerance, estimated from macroclimate data, is thus over-estimated by 10°C, the range of conditions present within each cell. When uniform warming of 2° is applied to all cells, coarse- and fine resolution data thus yield exactly the same predicted range shift. Grid cells predicted by macroclimate data to be climatically unsuitable for that species, are also those that lose suitable microclimatic conditions and there is this a near linear relationship between macroclimate suitability and microclimate availability in both periods. In **(b)** the same latitudinal relationship with macroclimate temperature is shown, but here near-ground temperatures are assumed warmer at lower-latitudes, and while the apparent thermal tolerance range is again 0 – 15°C the actual thermal range is resultantly 7.2-16.7°C. Because the thermal tolerance limits are over-estimated to a lesser extent by macroclimate data, the predicted range shift when using fine-scale data is less than would be predicted when using macroclimate data. Resultantly, the reduction in microclimate availability

with macroclimate suitability is lower when uniform warming of 2° is applied, suggesting that the species would persist in parts of its range predicting by macroclimate data to be unsuitable.
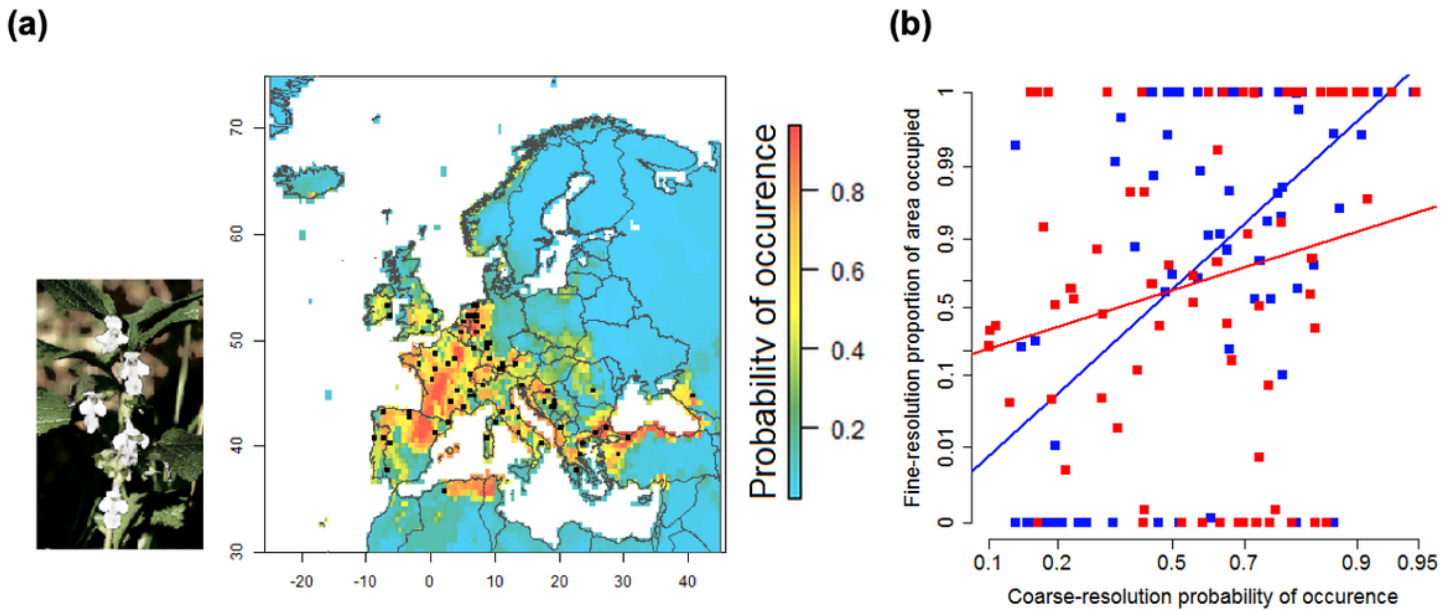

Figure 2

Relationships between macro- and microclimate suitability for 290 higher plant taxa on the Lizard Peninsula. Macroclimatic probability of occurrence was calculated from ensemble species distribution models constructed using 0.5° grid resolution European data (**a**) and 10 km grid resolution UK data (**b**), is compared to microclimate availability using historic (1977-1995; blue) and recent (1996-2014; red) data. Microclimate availability was calculated as the proportion of 100m grid cells with >0.5 probability of occurrence predicted from species distribution models constructed using 100 m grid resolution data.

Figure 3

Coarse- and fine-resolution climate suitability of *Melittis melissophyllum*. In **a** the probability of occurrence, predicted from an ensemble species distribution models constructed using 0.5° grid resolution European data, derived using climate data from 1977-1995 and projected forward to 1996-2014, is shown. In **b** the relationship between macroclimate (0.5°) probability of occurrence and microclimate availability at the 71 locations (black squares in **a**) is shown for both historic (1977-1995; blue) and current (1996-2014; red) periods. Microclimate availability was calculated as the proportion of grid cells with probability of occurrence above 0.388, thereby ensuring that 90% of observe presences occurred in grid cells with suitable climate.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SuppInfoFinal.docx