

Title

Accounting for inter-annual variability alters long-term estimates of climate suitability

Running Title

Estimating long-term climate suitability

Author information

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Abstract

Aim: Species respond to environmental conditions and so reliable assessments of climate suitability are important for predicting how climate change could alter their distributions. Long-term average climate data are often used to evaluate climate suitability of an area, but in these aggregated climate datasets, interannual variability is lost. Due to non-linearity in species' biological responses to climate, estimates of long-term climate suitability from average climate data may be biased and so differ from estimates derived from the average annual suitability over the same period (average response). We investigate the extent to which such differences manifest in a regional assessment of climate suitability for 255 plant species across two 17-year time periods.

Location: Cornwall in South-West England provides a case study.

Taxon: Plantae

Methods: We run a simple mechanistic climate suitability model and derive quantitative estimates of climate suitability for 1984-2000 and 2001-2017. For each period, we run the model using climate data representing average monthly values for that period. We then run the model for each year using monthly climate data for that year and average the annual suitability scores across each period (average response). We compare estimates of climate suitability from these two approaches.

Results: Average climate data gave higher estimates of suitability than the average response, suggesting bias against years of poor suitability in temporally aggregated climate datasets. Differences between suitability estimates were larger in areas of high climate variability and correlated to species' environmental requirements, being larger for species with small thermal niches and narrow ranges of precipitation tolerance.

Main Conclusions: Incorporating interannual variability into climate suitability assessments or understanding the extent to which average climate data might obscure this variance will be important to predict reliably the impacts of climate change on species distributions and should be considered, even when using mechanistic species distribution models.

Key words

Climate change; climate suitability model; climate variability; Ecocrop model; species distribution model; temporal aggregation

Introduction

Recent climate change has driven shifts in the geographic ranges of species (e.g. Kelly and Goulden, 2008, D'Andrea et al., 2009, Zorio, Williams and Aho, 2016) and further range shifts are expected as the climate continues to warm and weather patterns become more variable (Leemans and Solomon, 1993, Collins et al., 2011). Tools to predict how a changing climate might alter species distributions have been applied widely in studies of biogeography, ecology, and conservation biology and for species in both natural and cultivated systems. Inter alia, this information has helped to suggest how habitat suitability may be altered (Bunn et al., 2015, Dyderski et al., 2018), the risks posed by invasive species (Paini et al., 2016, Petitpierre et al., 2016) and where conservation efforts may experience conflict with changing land uses, including agricultural production (Hannah et al., 2013). The reliability of these predictions therefore has bearing on measures taken to limit biodiversity loss, ensure food security and maintain the ecosystem functions upon which human society depends.

Methods to predict species' responses to climate change often begin with the characterisation of a 'suitable climate'. By understanding a species' environmental requirements (a mechanistic or physiological approach) or by drawing statistical relationships between presence/absence records and the climate in these locations (a correlative approach), we might hope to identify the areas where conditions might be favourable in the future. The spatial and temporal resolution of climate data used in these assessments can affect how reliably suitable climate is identified (and for correlative approaches these factors can also affect the accuracy of the definition of a suitable climate) (e.g. Austin and Van Niel, 2011). Potter et al. (2013), for example, show how grid cell sizes (spatial resolution) of the climate data used in species distribution models (SDMs) are often far larger than the plants or animals being studied and this may be problematic if cell average climate variables are dissociated from physical and biological processes and become poor predictors of species persistence (Bennie et al., 2014). Kearney et al. (2012) show that high temporal resolution data may be required to get closer to the temporal scale that catches variability relevant to biological and ecological processes and to predict climatic impacts on species' survival, growth, and reproduction. If the spatial or temporal resolution of climate data is inappropriate, we may be unable to reconstruct effectively the climate conditions imposing constraints on organism performance, and the resulting predictions of where suitable climate might be found may be unreliable.

How the temporal resolution of climate data may affect predictions of climate suitability has received far less attention than has the effects of using climate data at different spatial

resolutions (e.g. Gillingham et al., 2012, Lembrechts et al., 2019), but it is generally considered that accuracy is improved by using variables that capture short-term climate variation (e.g. Nadeau et al., 2017). However, the issue of temporal resolution extends beyond the variables used initially to define a species' climatic niche, and how proximal these are to the temporal scales at which organisms respond to their environment, to the way in which these variables are then applied to assess long-term suitability.

Standard approaches to climate change modelling use climate variable datasets averaged over periods of c.30 years (Elith et al., 2006, Serra-Diaz et al., 2014) to predict how species distributions may change according to altered averages between a baseline (current) and projected (future) period. Gardner et al. (2019), for example, find that the most widely used climate dataset in the SDM literature is WorldClim, which provides temperature and precipitation variables for 1970-2000 and projections for four future 20-year climate periods under different representative concentration pathways (RCPs) (Hijmans et al., 2005). By averaging conditions over multiple years, aggregation bias may accrue even if the original variables are measured over a short time period (e.g. daily). This is because biological (and therefore species') responses to climate are often non-linear, such that the mean response to climate cannot be taken to be the same as the response to mean climate (Bütikofer et al., 2020).

Most species complete an annual cycle, so climate conditions over the course of a year are often most relevant. When aiming to predict climate suitability over multiple years, the use of aggregated climate datasets can obscure year-to-year variability and extreme values and therefore bias results. During short periods (e.g. a single year) of unfavourable climate, local extinctions may occur even if conditions, on average, remain suitable (Briscoe et al., 2016) or the overall trend is increasing climatic suitability (Vasseur et al., 2014). Equally, short periods of favourable climate that might allow a species to move into a new area may be missed. Some plant species, for example, remain dormant as seeds until a favourable season and during these 'good years' could expand their range (Walck et al., 2011). Thus, species may be present in areas that average data would consider climatically unsuitable, or absent from areas that average data would consider climatically suitable.

While it has been shown previously that incorporating climate variability into species distribution models can improve predictions of species occurrences (Bateman et al., 2016) and niche characterisation (Perez-Navarro et al., 2021), these are rare insights into the effects of inter-annual climatic variability on long-term suitability estimates. To date, no study has examined this effect when using a mechanistic species distribution model. This is important to test, because mechanistic models are thought to give robust estimates of

suitability due to their proximate links to species' physiology (Jackson et al., 2009). Indeed, there is increasing emphasis in the species distribution modelling literature on the benefits of using mechanistic models, and particularly, how their physiological basis means that the results from these models can be extrapolated to predict reliably suitability over space and time (Austin, 2002). However, it is possible that when average climate data are used, even if the variables constructed hold physiological relevance, that this averaging causes sufficient dissociation between species responses and climate that model outcomes are affected. Thus, incorporating interannual variation may be necessary to gain the fundamental ecological and biogeographical understanding that might otherwise be assumed to be achieved simply by using a mechanistic approach to species distribution modelling (Jackson et al., 2009).

The physiological basis of mechanistic models means that they are preferred when aiming to predict suitability over space and time (Kearney and Porter, 2009). However, if predictions of climate suitability from mechanistic models based on average climate data cause important gaps in a species' climate path to be missed (Early and Sax, 2011), this could mask species' vulnerability to climate change (Reside et al., 2010) or downplay the impacts of climate change on their distributions (Bateman et al., 2012), depending on the extent of a species' response to climate, whether it is occupying the warmer or cooler edge of its range margin, and the overall suitability of the climate in any given year. Any benefit derived from incorporating interannual variability into a correlative SDM may not compensate for the fact that results will remain difficult to extrapolate into novel environments (Strasburg et al., 2007). Therefore, we need to know how mechanistic models are affected by the use of average climate data to ensure we can answer some of the most important questions in ecological research, namely, how climate change may affect climate suitability for species in the future.

In this study, we explore the potential for average climate data to affect long-term estimates of climate suitability from a mechanistic model. For this, we use information on the environmental tolerance ranges of 255 species, as documented in the FAO Ecocrop database (FAO, 2000), to run the climate suitability model Ecocrop (Hijmans et al., 2017). Ecocrop takes temperature and precipitation data as inputs and considers species' tolerance thresholds for these parameters throughout their growing season to return an estimate of climatic suitability for an area. We run the Ecocrop model with average climate data for 1984-2000 and 2001-2017 (average climate) and then run the model for each year 1984-2017 before averaging the annual model outputs across the same two periods (average response). We compare estimates of suitability for each period considering the climatic variability within these periods.

Ecocrop has been used to predict how agriculture may be impacted by climate change (e.g. Jarvis et al., 2012, Rippke et al., 2016, Hunter and Crepso, 2019) and has been shown to provide reliable results (Ramirez-Villegas et al., 2013). Nevertheless, we emphasise that we do not seek to provide robust estimates of climate suitability for the modelled species. Rather, we assess whether temporal aggregation of climate data affects these estimates, not the estimates *per se*.

Materials and Methods

Study area

Climate suitability was assessed across Cornwall and the Isles of Scilly in south west England, as an example, at 100m spatial resolution. Temperature and precipitation in the region vary spatially (Maclean et al., 2015), but also temporally (Figure 1a-1c). Annual mean and minimum temperatures have increased in the 20th and 21st centuries and anticipated further climate change is likely to have major implications for biodiversity (Kosanic et al., 2014). Indeed, species with low temperature requirements have already suffered losses in west Cornwall due to rising temperatures (Kosanic et al., 2018).

A strong maritime influence on the regional climate results in a narrow range in mean annual temperature and mild winters, with some places remaining frost-free throughout the year (Met Office, 2016). This means that Cornwall and the Isles of Scilly could become one of the first places in the UK to be colonised by species characteristic of Mediterranean-type climates as their potential ranges expand northwards. On the Lizard Peninsula in southern Cornwall, for example, species composition has shifted recently in favour of those with higher temperature and lower moisture requirements (Maclean et al., 2015). Cornwall and the Isles of Scilly therefore provides an ideal study system for examining how estimates of climate suitability may be affected by the aggregation of climate data.

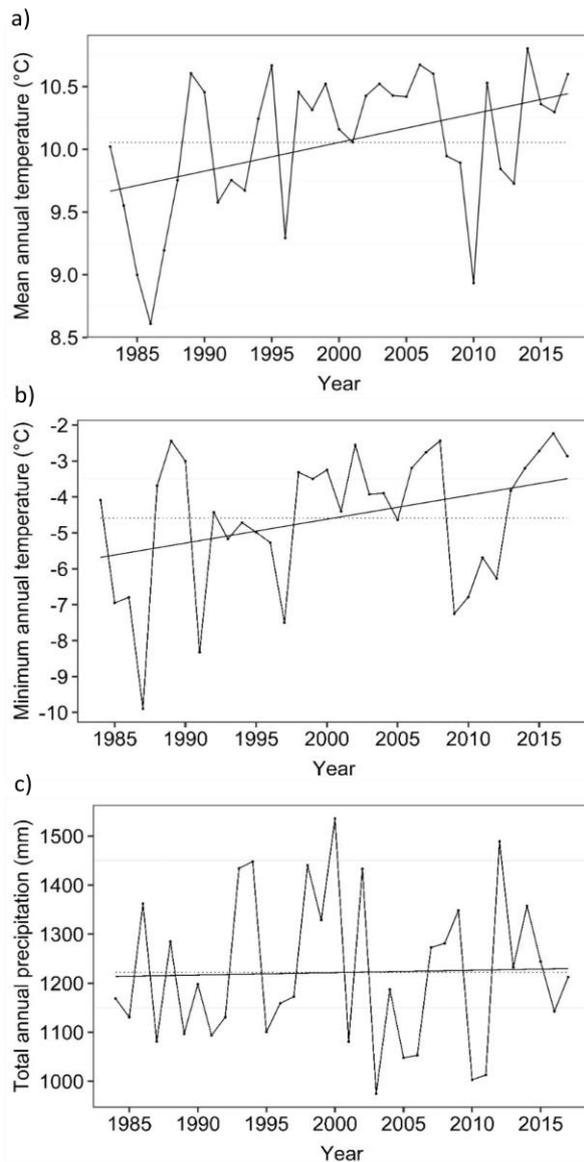


Figure 1: Mean annual temperature (a), minimum annual temperature (b) and total annual precipitation (c) trends for Cornwall and the Isles of Scilly (1984-2017). Black dots indicate mean values in each year, solid line represents the linear trend, dotted line indicates the mean value across all years. All values are the mean across the full study region and calculated from the hourly temperature and daily precipitation data derived to run the Ecocrop model.

Climate data

The Ecocrop model requires as inputs values for monthly mean and minimum temperature and total monthly precipitation. We calculated monthly mean and minimum temperature from hourly values at 100m spatial resolution, thus ensuring that temperature minima and spatial variation in suitability could be captured effectively.

We obtained hourly 100m spatial resolution temperature data using microclimate modelling techniques and functions in the R package 'microclima' (Maclean et al., 2019). The steps involved are described below.

We first downloaded and extracted for our study region the following coarse resolution climate data for the years 1984-2017:

1. Daily minimum and maximum temperature at 1km grid resolution from the UK Met Office (Met Office, 2018);
2. Six-hourly sea-level pressure, wind speed and wind direction, and specific humidity available at ~200km grid resolution from the National Weather Service National Centres for Environmental Prediction (NOAA-NCEP; Kanamitsu et al., 2002);
3. Hourly surface incoming shortwave (SIS), and direct normal (DNI) radiation available at 5km grid resolution from the EUMETSAT Satellite Application Facility on Climate Monitoring (CMSAF; Posselt, Müller, Trentmann, Stockli, and Liniger, 2014);
4. Daily mean sea surface temperatures at 25km grid resolution from the National Oceanic and Atmospheric Administration (NOAA; Reynolds et al., 2007).

We then processed these coarse resolution data to provide the inputs necessary to run the microclimate model as follows.

Cloud fractional cover was estimated from radiation data using the 'cloudfromrad' function. Six-hourly specific humidity and pressure data and daily sea-surface temperature data were interpolated to hourly using the native 'spline' function of R (R Core Team, 2019) and hourly diffuse radiation was calculated from hourly incoming shortwave radiation and direct normal radiation multiplied by the solar index. We then derived initial hourly temperature values with the 'hourlytemp' function in 'microclima', which took as inputs the hourly values for direct and diffuse radiation, hourly humidity and pressure and daily maximum and minimum temperature data.

We adjusted these initial hourly temperature values to account for mesoclimate effects, including elevation, wind sheltering and cold-air drainage. To do this, easterly and northerly wind vectors were derived from wind speed and wind direction, which were spline interpolated to hourly before back-calculating hourly wind speed and direction. Wind speed

at 1m height above the ground was calculated using the 'windcoef' function, which applies a topographic shelter coefficient, using elevation, to wind data. Elevation data were sourced using the 'get_dem' function. We then generated an array of land-sea ratios in each of 36 directions and used these data to calculate an index of total and upwind coastal exposure as described in Maclean et al (2019). We then fitted thin plate models to the hourly differences between land and sea temperature data at 1 km resolution with coastal exposure and elevation as covariates and applied these models at 100 m to estimate the land-sea temperature differences, and hence also land temperatures at that resolution, using the same procedure described and validated in Maclean et al (2019).

Finally, we ran the microclimate model using 'runmicro'. Following Maclean et al (2019), the procedure therein models the local difference in near-ground temperature from ambient temperatures as a linear function of net radiation, with the slope of this relationship determined by wind speed. Model coefficients were derived automatically using procedures described in Kearney et al. (2020). Net radiation is assumed to be affected by terrain and sky-view and was downscaled using the 'shortwavetopo' function in microclima. Final hourly microclimate temperatures were calculated by addition of temperature anomalies to the land temperature values predicted by the thin-plate spline models.

From the final hourly temperature values, we calculated monthly mean and minimum temperature values for each year and the average monthly values for these variables across the periods 1984-2000 and 2001-2017 to use as inputs to the Ecocrop model.

We calculated monthly total precipitation from daily values at 100m spatial resolution. Total daily 1 km gridded precipitation data for years 1984-2017 were downloaded from the Met Office HadUK dataset (Met Office, 2018) and cropped to our study area. We resampled precipitation values to 100m spatial resolution using the 'resample' function (Hijmans et al., 2015). We then applied elevation corrections to these data by calculating the total monthly precipitation, fitting a thin-plate spline model to these data with 1km gridded elevation as a covariate and then applying the model at a 100m spatial resolution using gridded elevation data. This provided higher resolution elevation adjusted estimates of total monthly precipitation for each year. We also calculated the average total precipitation for each month over periods 1984-2000 and 2001-2017.

Running the Ecocrop model

We ran the mechanistic climate suitability model Ecocrop as implemented through the R package 'dismo' using the function 'ecocrop' (Hijmans et al., 2017). When supplied with values of monthly mean and minimum temperature and total monthly precipitation, the model calculates a climatic suitability index score based on where conditions fall within optimal and

absolute ranges of tolerance (as documented in the FAO Ecocrop database referenced within the package) for the 12 possible growing seasons in a year. Suitability scores range from 0 (unsuitable) to 1 (optimally suitable). Values above 0 but less than 1 indicate suboptimal, but permissible suitability, meaning that both temperature and precipitation remain within bounds of absolute tolerance, but are above or below the optimal values during the growing season period (see Ramirez-Villegas, Jarvis and Läderach (2013) for a detailed explanation of the Ecocrop model).

We ran the 'ecocrop' function 36 times under default settings for each of the 1631 unique plant species for which environmental tolerance data are provided in the 'dismo' package. All species included have been identified to have human use, for example as food, fodder, or for energy or industrial purposes. In each model run, we changed the climate data (monthly mean and minimum temperature and total monthly precipitation) used as inputs as follows: on the first and second model runs, we used average climate data for 1984-2000 and 2001-2017, respectively, to estimate average suitability for each period. This meant, for example, that to calculate suitability for 1984-2000, the model was supplied with the average values of monthly mean and minimum temperature and total monthly precipitation across the 17-year period. Therefore, using average climate data we obtained estimates of average suitability for the two periods after two model runs. The third to 36th model runs represented annual model runs for each year, 1984-2017. Each model was supplied with monthly mean and minimum temperature and monthly precipitation values from that year. For each species, we calculated average suitability for each period as the mean of the yearly suitability scores for 1984-2000 and 2001-2017. For example, to calculate average suitability for 1984-2000, we calculated the mean of all yearly suitability scores across this 17-year period. In this way, the average suitability scores for each period represent each species' 'average response' and capture interannual variability in climate suitability. In all runs, both model inputs (climate data) and model outputs (suitability scores) were in raster format.

We retained for further analysis the results for 255 species with average suitability estimates above 0.5 in at least one location in at least one period (please see Appendix 1, Table A1 for a list of the 255 species). A threshold of 0.5 was chosen because below this value the climate is considered marginal (Ramirez-Villegas et al., 2013) and 255 species provided a sample size large enough to draw conclusions without dilution of results by very low suitability scores.

We produced a raster stack of model outputs for all 255 species from average climate data for 1984-2000 and 2001-2017 and took the mean across each stack. We repeated this process for the suitability scores from average response data.

Analysis of results

For each 17-year period, we compared estimates of average suitability from average climate and average response data. We then tested statistically whether differences between estimates for each period were correlated with the interannual variability in climate (coefficient of variation in mean monthly temperature, minimum monthly temperature, and total monthly precipitation) during the period. Interannual variability in temperature and precipitation variables was measured using the coefficient of variation (CV) to follow measurements of climate variability used commonly in species distribution models (e.g. ANUCLIM; Xu and Hutchinson, 2011). As a standardised measure CV gives a comparable value of climate variability for two time periods with different mean values for each climate variable and thus allows for the effects of climate variability on suitability scores to be assessed in a comparable way. We tested for correlations using spatially lagged dependent variable (SLX) models run on random subsets of 10% of the full dataset to reduce spatial autocorrelation. We created a spatial weights matrix for the nearest neighbours within 5 km of the centroid of each pixel before running a spatially lagged dependent variable (SLX) model using the 'lmSLX' function in the R package 'spdep' (Bivand and Wong, 2018). We built and plotted correlograms of the SLX model residuals at different multiples of the nearest neighbour distance (up to 50 km) and determined the distance at which Moran's I was ≤ 0 (indicating no spatial autocorrelation) (see Appendix A, Figure A5 for example correlograms). We repeated this process five times with different subsets of the dataset and took the mean distance at which Moran's I was ≤ 0 . This distance was found to be 20 km for both periods. We created a new spatial weights matrix of nearest neighbours within 20 km from each pixel centroid and re-ran the SLX model 200 times on different subsets of 10% of the full dataset. We used the 'impacts' function in 'spdep' to determine the total effects for each model and report the mean coefficient, mean standard error and mean p value across all 200 model runs.

Differences in suitability estimates as predicted by climatic requirements

We examined whether differences in suitability estimates could be explained by species' climatic requirements, namely their maximum (GMAX) and minimum (GMIN) growing season length requirements, optimal (TOPMX) and absolute (TMAX) mean temperature tolerance thresholds, optimal (TOPMN) and absolute (TMIN) minimum temperature tolerance thresholds, and optimal (ROPMX) and absolute (RMAX) maximum precipitation and optimal (ROPMN) and absolute (RMIN) minimum precipitation tolerance thresholds. To do this, we used a generalised linear model (GLM) with quasi-binomial error distribution and logit link function. For each species, we calculated the mean difference in suitability

estimates between average climate and average response data across both periods. The absolute values of this mean difference were the response variable in the GLM and each species' corresponding threshold values for each of the climate variables were the explanatory variables. Sample size in the GLM was therefore 255 (species). We tested all explanatory variables for multicollinearity by assessing Variance Inflation Factors (VIF) using the 'vif' function in the 'car' R package (Fox and Weisberg, 2018). All variables had a VIF value of <4 and so multicollinearity was not deemed as a threat to the results of our analysis (Lavery et al., 2019). Finally, we tested the GLM outcomes against the null model using the 'anova' function in R and specifying an F test. We report these results to evidence the overall significance of the model.

All data analyses were carried out in R (R Core Team, 2019).

Results

For the period 1984-2000, average climate data gave higher estimates of suitability than average response data for 245 species (Figure 2; Appendix 1, Table A1). Mean climate suitability across all 255 species (over the full study region) was 0.67 for average climate data and 0.58 for average response data (Appendix A, Figure A1a-b).

For the period 2001-2017, average climate data gave higher estimates of average climate suitability than average response data for 240 species (Figure 2; Appendix 1, Table A1). Mean climate suitability across all 255 species (over the full study region) was 0.71 for average climate data and 0.64 for average response data (Appendix A, Figure A1c-d).

Differences between suitability estimates across average climate and average response data varied spatially. For 1984-2000, some of the largest differences were in the north-east, whereas western coastal areas in the south had some of the smallest differences (Figure 3). A similar pattern was observed for 2001-2017, although differences between scores were slightly lower overall.

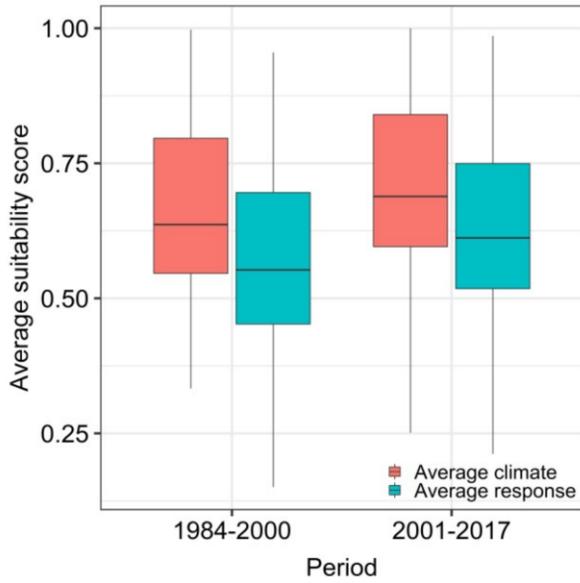
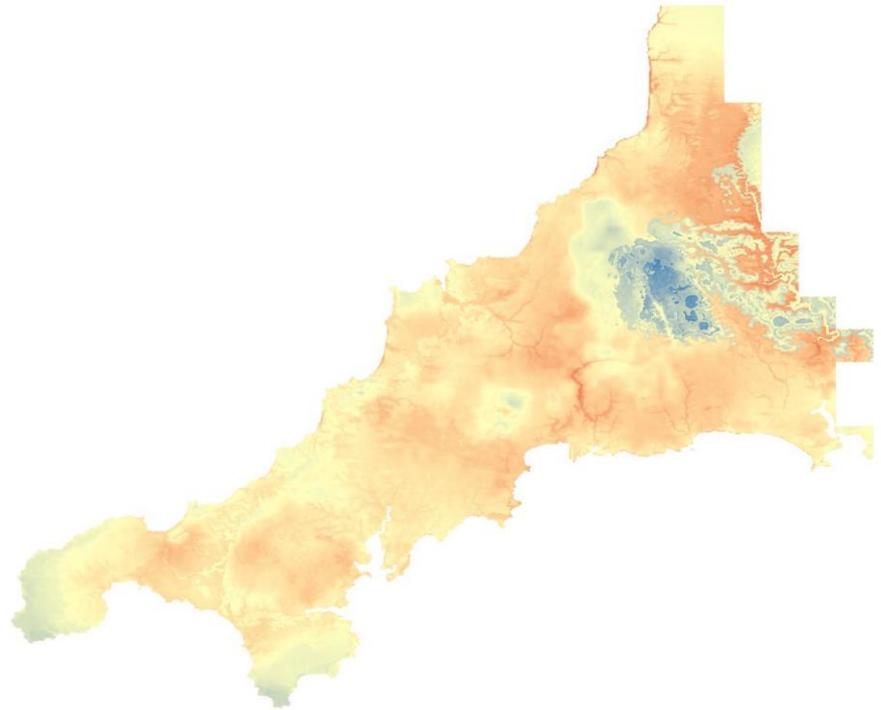
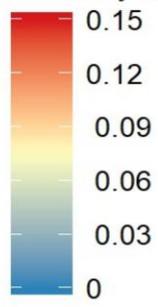


Figure 2: Average climate suitability scores for 1984-2000 and 2001-2017 using average climate (red) and average response (blue) data. Data presented are mean suitability scores across the study region for the 255 species analysed. Boxes capture the first (25th percentile), second (median) and third (75th percentile) quartiles of the data. Upper and lower whiskers extend to the maximum and minimum values, respectively.

a)

Difference in
suitability score



b)

Difference in
suitability score

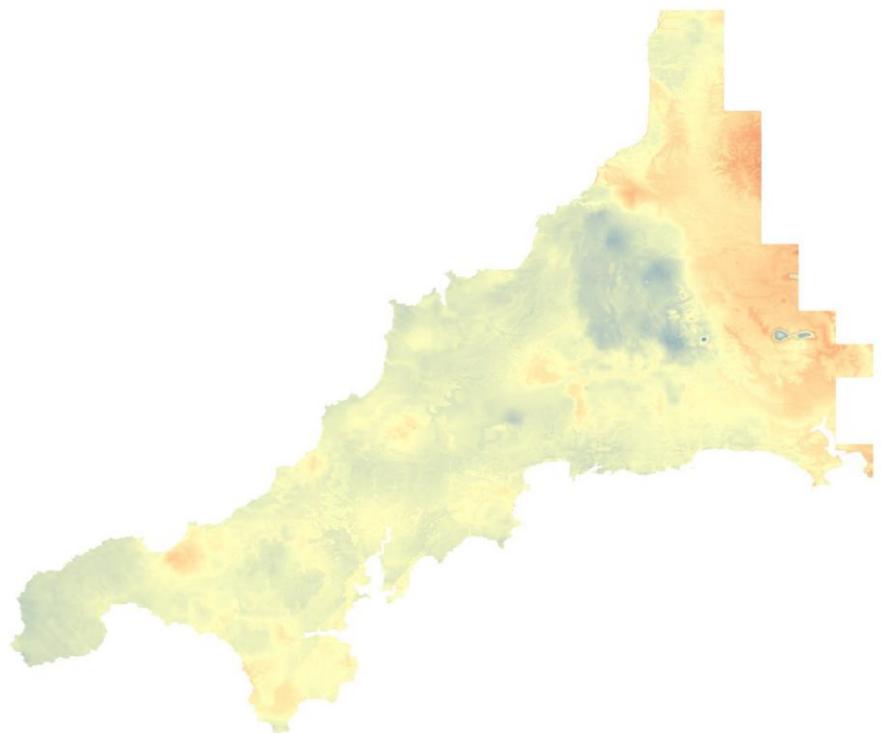
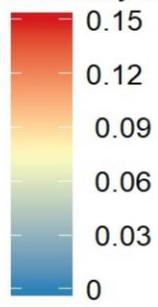


Figure 3: Difference in average suitability scores between average climate and average response data (average climate minus average response) for a) 1984-2017; and b) 2001-2017. Values presented are mean differences across all 255 species.

Differences in suitability estimates as predicted by climatic variability

Minimum temperatures across Cornwall and the Isles of Scilly showed a positive trend in warming from 1984-2017 but inter-annual variability was also high, with any particular year not necessarily experiencing higher minimum temperatures than the previous one (Figure 1a and 1c). Although total annual precipitation did not change significantly from 1984-2017, inter-annual variation was also evident (Figure 1c).

For both periods, differences between estimates of suitability from average climate and average response data were larger in areas more variable in total annual precipitation and minimum and mean annual temperature (Table 1). This trend is evident, for example, around Land's End (west Cornwall), where interannual variability, particularly in mean annual temperature and total annual precipitation was low and differences between scores were ~0.01 (Figure 2; Appendix A, Figure A2-A4).

Table 1: Predictors of the effect of the interannual coefficient of variation (%) in total precipitation, mean annual temperature and minimum temperature on differences between suitability scores for each period (average climate data minus average response data). Statistical significance is shown (* $p < 0.05$; ** $p < 0.01$; * $p < 0.001$).**

Period	Climate variable (coefficient of variation, %)	Total coefficients
1984-2000	Precipitation	0.0065 ($\pm 4.0 \cdot 10^{-4}$)***
	Minimum temperature	0.017 (± 0.003)***
	Mean annual temperature	0.84 (± 0.06)***
2001-2017	Precipitation	0.0026 ($\pm 2.4 \cdot 10^{-4}$)***
	Minimum temperature	0.0075 (± 0.009)*
	Mean annual temperature	0.049 (± 0.03)*

Differences in suitability estimates as predicted by climatic requirements

Differences in estimates of suitability change were larger for species with longer growing seasons and higher minimum temperature and minimum precipitation requirements but lower maximum precipitation requirements (Table 2 and Appendix 1, Figure A6). When the average climate was closer to optima (>0.6), we observed that differences between scores were greater (Appendix A, Figure A7).

There was a strong negative correlation between the range of temperature tolerance (absolute maximum temperature threshold (TMAX) minus absolute minimum temperature threshold (TMIN)) and the differences between estimates (GLM, $F_{1,253}=16.93$, $P < 0.001$) (Appendix 1, Figure A8). Therefore, differences were larger for species with smaller thermal niches. There was a strong negative correlation between the range of precipitation tolerance (absolute maximum precipitation threshold (RMAX) minus absolute minimum precipitation threshold (RMIN)) and the differences between estimates (GLM, $F_{1,253}=32.32$, $P < 0.001$) (Appendix 1, Figure A8). Therefore, differences were larger for species with smaller ranges of precipitation tolerance.

Table 2: Analysis of variance using F test for generalised linear models exploring the difference between suitability estimates as predicted by species' tolerance thresholds. Statistical significance indicated as * $p < 0.05$; ** $p < 0.01$; * $p < 0.001$; and .0.1).**

Variable reference	Variable full name	F statistic
GMIN	Minimum growing period length	54.28***
GMAX	Maximum growing period length	2.78
TMIN	Absolute minimum temperature threshold	12.94***
TOPMN	Optimal minimum temperature threshold	29.29***
TOPMX	Absolute maximum temperature threshold	1.05
TMAX	Optimal maximum temperature threshold	3.22
RMIN	Absolute minimum precipitation threshold	39.04***
ROPMN	Optimal minimum precipitation threshold	0.65
ROPMX	Optimal maximum precipitation threshold	28.52***
RMAX	Absolute maximum precipitation threshold	5.28*

Discussion

It is common to average climate variables over multiple years to predict climatic suitability for species within and between periods of time and to estimate how climate change may alter their future distributions (e.g. Carter et al., 1996, Byju et al., 2018). However, suitability can vary substantially year-to-year in response to climatic variation (Diffenbaugh and Scherer, 2013). Due to the non-linearity of biological responses to climate, suitability estimates derived from average climate can be biased, and therefore differ from predictions made using the average response. In our analysis, we tested the extent to which estimates of

suitability across two 17-year periods could be affected by using temporally aggregated climate data in a mechanistic climate suitability model. For our study region, we found that average climate data was likely to overestimate climate suitability, which could lead ultimately to less accurate predictions of species' distributions.

In a previous study, Bateman et al. (2016) reported that models based on short-term variability rather than long-term average climate covariates predicted more accurately the current breeding distributions of bird species in the United States. The authors attributed this to average climate data overlooking the negative impacts of short-term environmental variation. Similarly, we found that there were larger differences between suitability estimates in areas of high climatic variability; scores were biased positively by average climate data in these locations, indicating that the negative impact of years of poor suitability were not captured by aggregated climate datasets. Our findings carry additional importance, however, as we use a mechanistic model to show this effect, whereas Bateman et al (2016) use a correlative (maximum entropy) model. Whilst the limitations of correlative models are widely reported and understood, it is generally considered that mechanistic models are a robust way to determine climate suitability because they are based on physiological constraints limiting a species' distribution and abundance (Kearney and Porter, 2009). However, given the differences we observe between suitability estimates with average climate and average response data, we conclude that some proximality is lost when interannual variation is not specifically incorporated into the model. This is important to understand as it could reduce model accuracy and give misleading predictions about species' responses to environmental change.

Climate change and extremes

Climate change is expected to increase both the frequency and severity of extreme events (Jentsch et al., 2007, Coumou and Rahmstorf, 2012) and so it could become increasingly important to account for the impacts of climate variability when making predictions for future periods (Jan et al., 2017). Morán-Ordóñez et al. (2018), for example, demonstrate that although models based on long-term averages can show similar performance to models that incorporate extremes in current data, they predict dramatically different future geographic ranges for species under 2070 climate scenarios.

Climate change is also likely to alter average environmental conditions (Collins et al., 2013), which can affect the distribution and population dynamics of species (Parmesan et al., 2000, Jentsch et al. 2007, Jentsch and Beierkuhnlein 2008). When changes to long-term averages and short-term climate variability are experienced together, the ecological effects of extreme conditions can be exacerbated by a change in the distribution of a related parameter. For

example, extreme hydrologic drought, coupled with a changing mean in atmospheric drought, can lead to an increase in the number of tree die-off events compared with when these changes occur in isolation (Law et al., 2018). As such, it could be necessary to account for both the influence of a changing mean and changing variability in climate to predict accurately the possible effects on species' distributions. In our study area, this could mean that it would be most important to consider interannual variation in suitability in areas that are both climatically variable and experiencing high levels of climate change.

Species in marginally suitable areas

Climatic variability increases the likelihood of climatic conditions passing lethal thresholds for survival (Ni et al., 2006) and this means that species occupying areas near their mean requirements can be less sensitive to the same level of climatic variability than species at the edge of their range (Swihart et al., 2003). Navarro et al. (2018), for example, observed how species closer to their climatic tolerance limit were more vulnerable to extreme drought. Species are more likely to be living close to their physiological limits at range margins (Parmesan et al., 2000, Thuiller et al., 2008, Brook et al., 2009), and they can therefore be more sensitive (Thomas et al., 2004) and respond more strongly (Bateman et al., 2016) to short-term climatic variability. The tendency for average climate data to underestimate climatic variability could result in poorer suitability predictions for individuals in these locations.

It may also be important to account for temporal patterns in suitability when assessing species' migration potential (Thuiller et al., 2008). At expanding range margins, climate variability may influence strongly the opportunity for species to move into new areas (Higgins et al., 2000) and 'gaps' in the climate path, which could limit successful colonisation, may be missed if variability in climate change is unaccounted for (Early and Sax, 2011). Equally, temporally aggregated climate data could overlook opportunities for establishment. Serra-Diaz et al. (2016), for example, found that 30-year average estimates of seedling survival greatly underestimated the potential for establishment for three tree species under climate change scenarios compared to estimates considering survival rates over a three-year period. In our study, differences in suitability estimates were high for species with long growing seasons and higher minimum temperature requirements. Examples include saffron (*Crocus sativus* L.) and quince (*Cydonia oblonga* Mill.), which are not currently widespread in Cornwall or the Isles of Scilly, or indeed in the UK, being more commonly associated with areas at lower latitudes where temperatures are warmer. These species demonstrate the

importance of considering inter-annual variability in climate in areas beyond the dominant range of species and where conditions can easily become limiting.

Species with narrow tolerance thresholds

It may be preferable to account for interannual variability when assessing suitability for species with narrow climatic tolerances. The likelihood that species' absolute thresholds of tolerance will be breached will rise with increasing climatic variability, even if mean conditions remain favourable (Ni et al., 2006, Vasseur et al., 2014). Species with small climatic niches are therefore predicted to be more vulnerable to increasing climatic variability due to climate change (Foden et al., 2009) and to experience greater changes in their distributions because they have less capacity to cope with these fluctuations (Van de ven et al., 2007). Trends in climatic suitability can be captured with annual data and, as we show here, average climate data were more likely to overestimate suitability for species with narrow tolerance thresholds.

Direction of the effect of aggregated climate data on suitability estimates

Overall, differences between suitability estimates will depend on how close the mean climate of a region is to species' optima. If the mean climate is close to the climatic optima for species, and their climatic tolerance range is quite low, then averaging climate data is likely to result in higher apparent suitability than averaging the response. On the other hand, if the average climate is marginal, and only suitable in a handful of years, then averaging the response will give higher suitability scores. It should be considered how close the mean climate is to species' upper or lower limits of climatic tolerance, and therefore whether average climate data may risk over- or under-estimating climatic suitability, in any cases where biologically significant inter-annual variability in climate conditions might exist within the period of interest. For the temperate Cornwall climate, we expect that suitability was more likely to be negatively affected by a cold year than positively affected by a warm year, thus explaining why average climate led to higher estimates of suitability in our study (by overestimating minimum temperatures).

Further work

The Ecocrop model considers the favourability of climatic conditions during a growing season to calculate a suitability score. Therefore, for annual plants, with a single growing season, the model can effectively estimate whether a full life cycle is completed. For perennial plants, however, the model is limited in that suitability of a single year's growing season may impact growth and survival in subsequent years. Whereas this is not problematic for the purposes of our study, as precise estimates of suitability were not

required or necessary to make our comparisons, this limitation should be acknowledged or addressed in any other studies where this is not the case. We might suppose, however, particularly given our finding here that differences in suitability estimates were larger for species with longer growing seasons, that as average climate data cannot capture the impacts of climate variability across multiple years, differences between suitability estimates derived from average climate and average response data would be amplified in longer-lived species. We hope that such an effect can be investigated in the future, but also that analyses like ours can be extended into other areas and for different taxa to develop understanding of the species and circumstances under which negative impacts of climate data aggregation on model accuracy are likely to be greatest.

Conclusion

Climate change will alter species distributions in both natural (Thomas et al., 2004) and cultivated (Leemans and Solomon, 1993) systems. Recent trends in global warming and altered precipitation patterns (event number, frequency, and intensity) will continue, regardless of any mitigation strategy to reduce anthropogenic greenhouse gas emissions (Collins et al., 2013), and it is therefore timely that we enhance the ability to predict how future climate change may affect global biodiversity. We show that a mechanistic model run with temporally aggregated climate data may fail to capture the effects of inter-annual variation on estimates of climate suitability. We suggest that, because species responses to climate are often non-linear, average response data are used wherever possible. However, this could be particularly important for species in areas where the climate is highly variable, especially if mean conditions are favourable, for species living at the upper or lower limits of their climatic range, and for species with narrow tolerance thresholds. Estimating climatic suitability in a way that can account for inter-annual trends could help to predict more reliably how climate change may affect species distributions.

Data availability

The 'microclima' R package release relevant to this paper has been stored at DOI: [10.5281/zenodo.4636409](https://doi.org/10.5281/zenodo.4636409). All raw climate data detailed in the main text are open access and available for download from the referenced sources. Using functions 'get_NCEP' and 'dailyprecipNCEP' in the 'microclima' R package it is also possible to download the climate data required to run the Ecocrop model for anywhere on earth.

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Biosketch

The authors are interested in conducting and applying ecological research to find practical solutions to environmental problems. They hope to advance species distribution modelling techniques to bear on important issues in ecology and conservation biology such as land use strategies. Current research includes the study of climate change impacts on plant distributions and the associated risks and benefits this may bring to the agricultural industry. Author contributions: I.M.D.M. and K.J.G. led manuscript conception and design. A.S.G. ran the analysis and led writing of the manuscript. All authors contributed significantly to drafts and gave final approval for publication.

Appendices

Appendix 1: Supplementary results

Appendix 1: Supplementary Results

Table A1: List of 255 plant species with suitability >0.5 in at least one location, in at least one period. Averaged climate data means that the Ecocrop model was run with climate data representing the average monthly values for minimum and mean temperature and total precipitation over the modelled period (1984-2000 or 2001-2017). Averaged response data means that, for the period of interest, the Ecocrop model was run for each year in that period using monthly values for minimum and mean temperature and total precipitation experienced in that year, and then annual suitability scores were averaged across the full period. Suitability scores are the mean across the full study region.

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Salt wattle	Acacia ampliceps B.R.Maslin	0.59	0.50	0.66	0.61
Silver wattle	Acacia dealbata Link	0.49	0.43	0.55	0.49
Prickly wattle	Acacia victoriae Benth.	0.59	0.44	0.70	0.55
Sugar maple	Acer saccharum	0.63	0.52	0.67	0.56
Istle	Agave lecheguilla Torrey	0.48	0.35	0.61	0.46
Thickspine wheatgrass	Agropyron dasystachyum	0.85	0.79	0.89	0.86
Grenar wheatgrass	Agropyron intermedium Host	0.53	0.47	0.58	0.53
Quarkgrass	Agropyron repens (L.)Beauv.	0.93	0.83	0.95	0.86
Streambank wheatgrass	Agropyron riparium Scribn.	0.67	0.61	0.73	0.66
Western wheatgrass	Agropyron smithii Rydb.	0.95	0.88	0.95	0.92

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Velvet bentgrass	Agrostis canina L.	0.93	0.87	0.95	0.90
Common bentgrass	Agrostis gigantea Roth.	0.83	0.76	0.90	0.83
Creeping bentgrass	Agrostis stolonifera L.	0.92	0.87	0.95	0.91
Colonial bentgrass	Agrostis tenuis Sibth.	0.89	0.82	0.91	0.87
Agrostis trinii	Agrostis trinii Turcz.	0.72	0.56	0.66	0.61
Ailanthus	Ailanthus altissima (Mill.)	0.54	0.44	0.60	0.51
Onion	Allium cepa L. v cepa	0.93	0.90	0.95	0.94
Chives	Allium schoenoprasum L.	0.99	0.84	0.99	0.89
Creeping foxtail	Alopecurus arundinaceus Po.	0.73	0.72	0.76	0.72
Meadow foxtail	Alopecurus pratensis L.	0.95	0.89	0.96	0.90
European beachgrass	Ammophila arenaria (L.)Link	0.74	0.57	0.70	0.60
American beachgrass	Ammophila breviligulata F.	0.54	0.42	0.52	0.47
Big bluestem	Andropogon gerardii Vitman	0.69	0.72	0.80	0.78
Sand bluestem	Andropogon hallii Hack.	0.50	0.36	0.62	0.44
Garden angelica	Angelica archangelica L.	0.96	0.84	0.90	0.80
Chervil	Anthriscus cerefolium L.	0.57	0.47	0.64	0.55

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Horseradish	Armoracia rusticana P.Gaer.	0.55	0.48	0.62	0.55
Meadow oat grass	Arrhenatherum elatius (L.)	0.86	0.76	0.91	0.84
Southernwood	Artemisia abrotanum L.	0.81	0.64	0.86	0.73
Tarragon	Artemisia dracunculoides L.	0.79	0.68	0.86	0.75
Arundinella hirta	Arundinella hirta (Thunb) K	0.67	0.63	0.72	0.70
Custard banana	Asimina triloba (L.) Dunal	0.51	0.44	0.53	0.46
Cicer milkvetch	Astragalus cicer L.	0.63	0.57	0.69	0.65
Shadscale	Atriplex confertifolia (T.)	0.48	0.46	0.25	0.53
Gardner saltbush	Atriplex gardneri	0.92	0.85	0.86	0.84
Mediterranean salt	Atriplex halimus L.	0.75	0.77	0.81	0.82
Garden oarch	Atriplex hortensis L.	0.92	0.79	0.97	0.87
Old man saltbush	Atriplex nummularia Lindl.	0.56	0.54	0.63	0.60
Bladder saltbush	Atriplex vesicaria Heward	0.52	0.44	0.59	0.52
Red oat	Avena byzantina K. Koch	0.51	0.41	0.54	0.45
Wild oat	Avena fatua L.	0.84	0.78	0.88	0.82
Oats	Avena sativa L.	0.49	0.44	0.54	0.49

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Sloughgrass	Beckmannia syzigachne (St.)	0.97	0.77	0.98	0.85
Sugar beet	Beta vulgaris L. v vulgaris	0.57	0.40	0.61	0.46
Borage	Borago officinalis L.	0.58	0.50	0.63	0.55
Yellow bluestem	Bothriochloa ischaemum (L.)	0.50	0.39	0.55	0.45
Side-oats grama	Bouteloua curtipendula (M.)	0.74	0.68	0.79	0.75
Blue grama	Bouteloua gracilis (Willd.)	0.96	0.88	0.98	0.92
Browntop millet	Brachiaria ramosa (L.)Stapf	0.45	0.26	0.53	0.35
Rutabaga	Brassica napus L. Napobras.	0.60	0.50	0.66	0.57
Black mustard	Brassica nigra L.	0.97	0.89	0.97	0.92
Collards	Brassica oleracea L.v acep.	0.57	0.55	0.62	0.61
Cauliflower	Brassica oleracea L.v botr.	0.66	0.56	0.65	0.60
Cabbage	Brassica oleracea L.v capi.	0.73	0.62	0.79	0.72
Mountain brome	Bromus carinatus Hook.&Arn.	0.99	0.88	0.99	0.91
Brome grass	Bromus inermis Leys.	0.87	0.82	0.91	0.87

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Russian brome grass	Bromus tomentellus Boiss.	1.00	0.96	1.00	0.99
Rescue grass	Bromus unioloides Kunth	0.60	0.50	0.66	0.56
Buffalo grass	Buchloe dactyloides (Nutt.)	0.71	0.65	0.76	0.72
Calamagrostis epigei.	Calamagrostis epigeios L.	0.97	0.89	0.99	0.92
Cowslip	Caltha palustris L.	0.68	0.58	0.74	0.65
Rampion	Campanula rapunculus L.	0.49	0.39	0.58	0.46
Hemp	Cannabis sativa L.	0.63	0.55	0.70	0.63
Pecan nut	Carya illinoensis Wangenh.	0.55	0.43	0.60	0.49
Fat hen	Chenopodium album L.	0.75	0.58	0.79	0.63
Wormseed	Chenopodium ambrosioides L.	0.58	0.50	0.62	0.55
Canihua	Chenopodium pallidicaule H.	0.97	0.81	0.97	0.85
Quinoa	Chenopodium quinoa Willden.	0.70	0.67	0.75	0.71
Persian insect flower	Chrysanthemum coccineum W.	0.52	0.32	0.58	0.39
Chick pea	Cicer arietinum L.	0.64	0.57	0.70	0.64

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Colchicum	Colchicum autumnale L.	0.55	0.42	0.63	0.48
Coriander	Coriandrum sativum L.	0.71	0.67	0.76	0.71
European hazelnut	Corylus avellana L.	0.57	0.41	0.60	0.44
Seakale	Crambe maritima L.	0.67	0.60	0.72	0.67
Saffron	Crocus sativus L.	0.69	0.39	0.69	0.45
Sunn hemp	Crotalaria juncea L.	0.49	0.42	0.53	0.47
Buffalo gourd	Cucurbita foetidissima HBK	0.50	0.43	0.55	0.50
Quince	Cydonia oblonga Mill.	0.36	0.22	0.51	0.31
Chufa	Cyperus esculentus L.	0.85	0.75	0.90	0.83
Orchard grass Mediter.	Dactylis glomerata hispani.	0.63	0.56	0.70	0.63
Orchard grass	Dactylis glomerata L.	0.95	0.85	0.98	0.91
Carrot	Daucus carota L.	0.54	0.45	0.57	0.51
Deyeuxia angustifolia	Deyeuxia angustifolia Vick.	0.48	0.41	0.52	0.47
Foxglove, Common	Digitalis purpurea L.	0.85	0.67	0.89	0.72
Barnyard millet	Echinochloa crus-galli (L)	0.58	0.54	0.61	0.59
Eleusine africana	Eleusine africana Kennedy-O	0.52	0.50	0.56	0.52
Goose grass	Eleusine indica (L.) G. in.	0.45	0.35	0.51	0.42

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Basin wildrye	Elymus cinereus Scrib.&Merr	0.86	0.80	0.90	0.86
Giant wildrye	Elymus condensatus Presl.	0.66	0.56	0.71	0.63
Blue wildrye	Elymus glaucus Buckl.	0.84	0.75	0.87	0.79
Teff	Eragrostis tef (Zucc.) Trot	0.53	0.47	0.56	0.52
Bano	Eragrostis tremula (Lam.) S	0.54	0.53	0.57	0.56
Sand love grass	Eragrostis trichodes	0.57	0.47	0.63	0.56
Garden rocket	Eruca sativa Miller	0.69	0.55	0.77	0.67
European beech	Fagus sylvatica L.	0.94	0.78	0.96	0.87
Tall fescue	Festuca arundinacea Schreb.	0.54	0.47	0.60	0.54
Idaho fescue	Festuca idahoensis Elmer	0.84	0.76	0.89	0.81
Hard fescue	Festuca longifolia Thuill.	0.64	0.60	0.69	0.67
Sheep fescue	Festuca ovina L.	0.96	0.89	0.98	0.92
Meadow fescue	Festuca pratensis Huds.	0.80	0.71	0.83	0.75
Chewing's red fescue	Festuca rubra L v commutata	0.96	0.88	0.98	0.92
Red Fescue	Festuca rubra L. v. rubra	0.85	0.83	0.91	0.89

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Virginia strawberry	Fragaria virginiana Duch.	0.75	0.54	0.78	0.60
Dyer's-greenwood	Genista tinctoria L.	0.56	0.35	0.61	0.42
Licorice, Common	Glycyrrhiza glabra L.	0.84	0.72	0.90	0.81
Licorice, American	Glycyrrhiza lepidota Pursh	0.37	0.32	0.63	0.36
Sulla rose	Hedysarum carnosum Desf.	0.73	0.63	0.74	0.66
Spanish sainfoin	Hedysarum coronarium L.	0.67	0.61	0.72	0.67
Sulla epineux	Hedysarum spinosissimum L.	0.73	0.63	0.74	0.66
Sunflower	Helianthus annuus L v macro	0.61	0.54	0.65	0.60
Jerusalem artichoke	Helianthus tuberosus L.	0.55	0.50	0.61	0.56
Hierochloe odorata	Hierochloe odorata L.Beauv.	0.57	0.50	0.62	0.56
Galleta grass	Hilaria jamesii (Torr.) Be.	0.67	0.44	0.63	0.55
Sea buckthorn	Hippophae rhamnoides L.	0.52	0.49	0.58	0.56
Sea buckthorn	Hippophae salicifolia D. D.	0.52	0.49	0.58	0.56
Hordeum brevisubulatum	Hordeum brevisubulatum (T.)	0.46	0.39	0.50	0.44
Bulbous barley	Hordeum bulbosum L.	0.79	0.72	0.85	0.80

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
California b. walnut	Juglans hindsii Jeps.	0.47	0.43	0.54	0.51
Black walnut	Juglans nigra L.	0.72	0.49	0.74	0.55
Heartnut	Juglans sieboldiana	0.54	0.36	0.57	0.42
Koeleria cristata	Koeleria cristata Griseb.	0.92	0.88	0.94	0.92
Hyacinth bean	Lablab purpureus Medik.	0.50	0.41	0.53	0.45
Rough pea	Lathyrus hirsutus L.	0.50	0.38	0.53	0.42
Grass pea	Lathyrus sativus L.	0.98	0.91	1.00	0.96
Lentil	Lens culinaris Medikus	0.58	0.58	0.63	0.65
Lovage	Levisticum officinale Koch	0.62	0.54	0.68	0.61
White meadowfoam	Limnanthes alba	0.57	0.15	0.64	0.21
Linseed	Linum usitatissimum L.	0.72	0.62	0.77	0.70
Italian ryegrass	Lolium multiflorum Lam.	0.70	0.65	0.75	0.70
Perennial ryegrass	Lolium perenne L.	0.59	0.46	0.64	0.52
Rigid ryegrass	Lolium rigidum Gaud.	0.61	0.58	0.68	0.65
Birdsfoot trefoil	Lotus corniculatus L.	0.62	0.57	0.66	0.62
Esculent birdsfoot trefoil	Lotus edulis L.	0.48	0.39	0.55	0.49

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Narrowleaf trefoil	Lotus tenuis Wald. & Kit.	0.59	0.46	0.64	0.54
Big trefoil	Lotus uliginosus Schkuhr	0.62	0.56	0.66	0.61
White Lupine	Lupinus albus L.	0.58	0.52	0.63	0.60
Blue lupine	Lupinus angustifolius L.	0.85	0.85	0.91	0.91
Lupinus pilosus	Lupinus pilosus	0.79	0.79	0.88	0.88
Spotted burclover	Medicago arabica (L.) Huds.	0.58	0.47	0.62	0.53
Sickle medick	Medicago falcata L.	0.67	0.66	0.71	0.71
Black medic	Medicago lupulina L.	0.67	0.60	0.72	0.65
Burr medic	Medicago polymorpha L.	0.59	0.48	0.63	0.53
Variegated alfalfa	Medicago varia Martyn.	0.63	0.52	0.66	0.55
White sweetclover	Melilotus alba Medik.	0.76	0.71	0.79	0.76
Indian melilot	Melilotus indica (L.) All.	0.58	0.48	0.62	0.53
Yellow sweetclover	Melilotus officinalis Lam.	0.81	0.77	0.89	0.84
Sweet clover	Melilotus suaveolens Ledeb.	0.70	0.53	0.76	0.58
Corn mint	Mentha arvensis v piperasc.	0.65	0.60	0.74	0.69
European pennyroyal	Mentha pulegium L.	0.66	0.54	0.73	0.65

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Oriental tobacco	Nicotiana spp	0.52	0.41	0.61	0.52
Tobacco	Nicotiana tabacum L.	0.71	0.59	0.78	0.69
Black cumin	Nigella sativa L.	0.63	0.46	0.71	0.54
Sainfoin	Onobrychis viciifolia Scop.	0.48	0.45	0.52	0.49
Ricegrass	Oryzopsis holciformis (M.B)	0.59	0.32	0.61	0.46
Smilgrass	Oryzopsis miliacea (L.) As.	0.47	0.28	0.58	0.42
Scarlet poppy	Papaver bracteatum Lindl.	0.77	0.62	0.82	0.69
Opium poppy	Papaver somniferum L.	0.61	0.54	0.65	0.59
Vasey grass	Paspalum urvillei Steud.	0.53	0.42	0.48	0.45
Parsnip	Pastinaca sativa L.	0.75	0.63	0.82	0.71
Bulb canarygrass	Phalaris aquatica L.	0.68	0.59	0.79	0.69
Reed canarygrass	Phalaris arundinacea L.	0.56	0.51	0.60	0.55
Canary grass	Phalaris canariensis L.	0.57	0.54	0.61	0.58
Scarlet runner bean	Phaseolus coccineus L.	0.33	0.39	0.51	0.45
Bean, Common	Phaseolus vulgaris L.	0.42	0.45	0.48	0.52
Timothy	Phleum pratense L.	0.61	0.55	0.64	0.60

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Pinus tabulaeformis	Pinus tabulaeformis Carr.	0.53	0.39	0.57	0.46
Pea	Pisum sativum L.	0.52	0.45	0.49	0.46
Annual bluegrass	Poa annua L.	0.83	0.74	0.88	0.80
Bulbous bluegrass	Poa bulbosa L.	0.49	0.44	0.55	0.50
Mutton bluegrass	Poa fendleriana (Steud.) V.	0.42	0.28	0.51	0.36
Smooth meadow grass	Poa pratensis L.	0.54	0.50	0.60	0.55
Sinai meadow grass	Poa sinaica Steud.	0.55	0.54	0.59	0.60
Rough bluegrass	Poa trivialis L.	0.96	0.84	0.97	0.89
Yacon	Polymnia sonchifolia P. & E.	0.59	0.35	0.64	0.40
Almond	Prunus amygdalus Batsch.	0.43	0.31	0.57	0.37
Wildrye, Russian	Psathyrostachys juncea (F.)	0.99	0.91	1.00	0.93
Bullamon lucerne	Psoralea patens Lindl.	0.51	0.39	0.56	0.47
Garden rhubarb	Rheum rhaponticum L.	0.54	0.39	0.58	0.45
Hairy gooseberry	Ribes hirtellum	0.82	0.69	0.83	0.73
Red currant	Ribes rubrum	0.78	0.64	0.79	0.66
Common red ribes	Ribes sativum	0.86	0.72	0.92	0.80

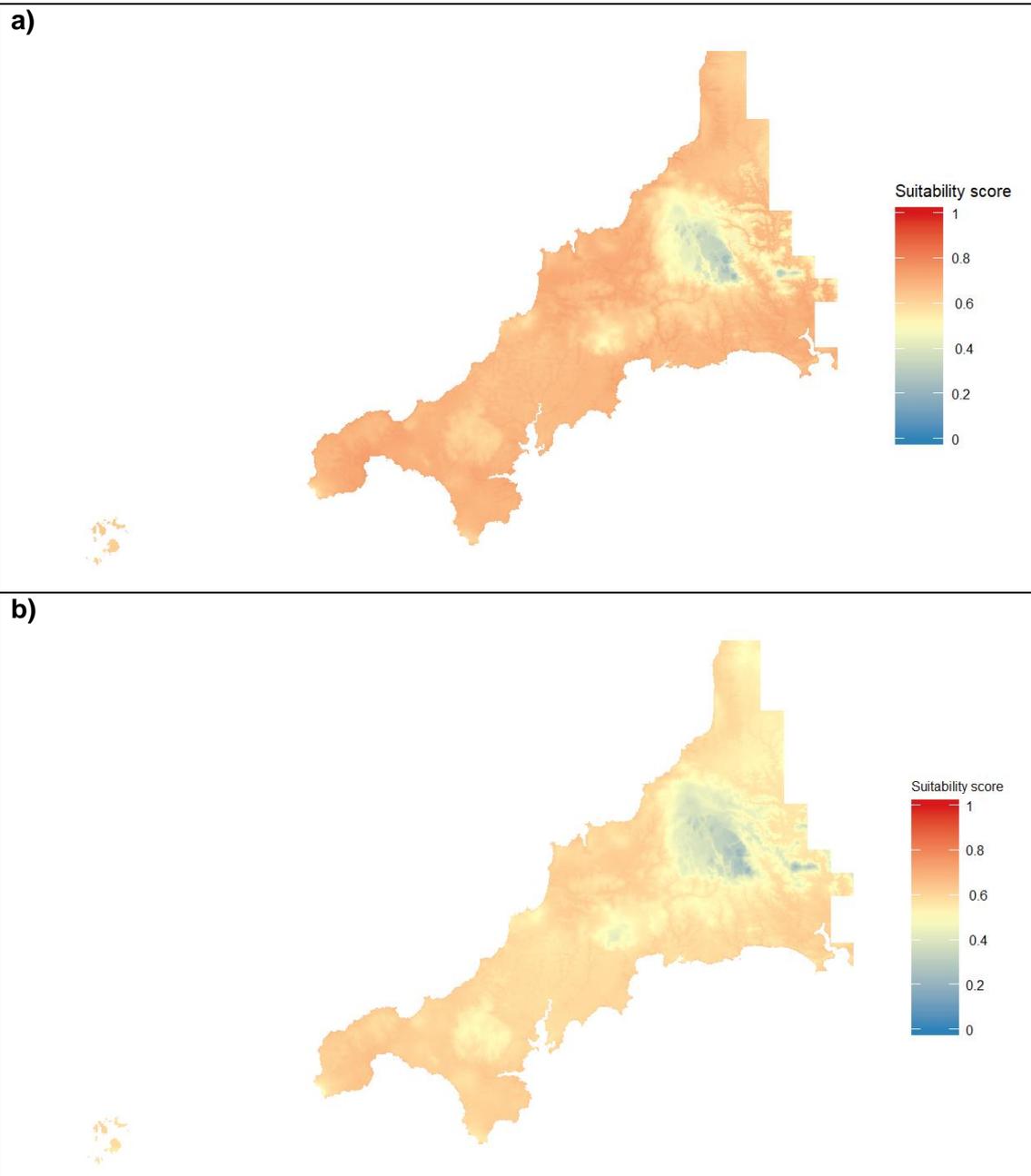
Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
False acacia	Robinia pseudoacacia L.	0.49	0.41	0.54	0.46
Red raspberry	Rubus idaeus L.	0.47	0.46	0.51	0.51
Black raspberry	Rubus occidentalis L.	0.62	0.59	0.67	0.63
Purple raspberry	Rubus occidentalis x idaeus	0.59	0.55	0.64	0.60
Sage	Salvia officinalis L.	0.55	0.44	0.60	0.49
Eastern elderberry	Sambucus canadensis L.	0.68	0.62	0.74	0.68
Burnet	Sanguisorba minor	0.88	0.77	0.94	0.84
Rye	Secale cereale L.	0.55	0.43	0.60	0.49
Italian millet	Setaria italica (L.) Beauv.	0.65	0.59	0.70	0.64
Mustard, White	Sinapis alba L.	0.73	0.53	0.80	0.61
Potato	Solanum tuberosum L.	0.74	0.64	0.80	0.73
Potato, Bitter	Solanum x juzepczukii	0.82	0.72	0.88	0.75
Spanish broom	Spartium junceum L.	0.55	0.42	0.59	0.47
Spinach	Spinacia oleracea L.	0.53	0.51	0.51	0.51
Spodiopongo sibiricus	Spodiopongo sibiricus Trin	0.51	0.42	0.59	0.51
Alkali sacaton	Sporobolus airoides Torr.	0.50	0.38	0.54	0.44
Needler grass	Stipa barbata Desf.	0.52	0.47	0.57	0.53

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Stripa baicalensis	Stripa baicalensis Roshev	0.85	0.63	0.86	0.74
Stripa breviflora	Stripa breviflora Griseb.	0.61	0.54	0.55	0.55
Stripa gobica	Stripa gobica Roshev.	0.80	0.65	0.57	0.69
Fine stem stylo	Stylosanthes guianensis int	0.51	0.39	0.55	0.42
Dandelion	Taraxacum officinale Weber	0.84	0.74	0.90	0.82
Kangaroo grass	Themeda australis (R.Br.) S	0.61	0.61	0.66	0.68
Wild thyme	Thymus serpyllum L.	0.68	0.53	0.75	0.58
Thyme	Thymus vulgaris L.	0.55	0.48	0.58	0.54
Salsify	Tragopogon porrifolius L.	0.75	0.59	0.79	0.67
Hop clover	Trifolium agrarium L.	0.68	0.57	0.75	0.65
Egyptian clover	Trifolium alexandrinum L.	0.57	0.53	0.61	0.57
Kura clover	Trifolium ambiguum Bieb.	0.66	0.54	0.68	0.55
Rabbitfoot clover	Trifolium arvense L.	0.75	0.57	0.79	0.59
Large hop clover	Trifolium campestre Schreb.	0.44	0.33	0.55	0.40
Small hope clover	Trifolium dubium Sibth.	0.44	0.33	0.55	0.40
Strawberry clover	Trifolium fragiferum L.	0.75	0.55	0.80	0.63

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Alsike clover	Trifolium hybridum L.	0.69	0.66	0.73	0.69
Crimson clover	Trifolium incarnatum L.	0.66	0.59	0.70	0.65
Zigzag clover	Trifolium medium L.	0.62	0.49	0.67	0.52
Red clover	Trifolium pratense L.	0.48	0.52	0.57	0.59
White clover	Trifolium repens L.	0.64	0.56	0.69	0.62
Persian clover	Trifolium resupinatum L.	0.76	0.69	0.81	0.76
Kenya white clover	Trifolium semipilosum Fres.	0.50	0.42	0.54	0.47
Subterranean clover	Trifolium subterraneum L.	0.60	0.51	0.63	0.55
Wolly trefoil	Trifolium tomentosum	0.54	0.43	0.63	0.55
Fenugreek	Trigonella foenum-graecum L.	0.58	0.53	0.61	0.58
Wheat, common	Triticum aestivum L.	0.55	0.42	0.59	0.47
Wheat, club	Triticum compactum Host	0.93	0.77	0.95	0.81
Emmer	Triticum diococcon Schrank	0.62	0.61	0.66	0.67
Spelt	Triticum spelta L.	0.83	0.70	0.88	0.76
Lowbush blueberry	Vaccinium angustifolium Ait	0.71	0.58	0.76	0.65
Cranberry	Vaccinium macrocarpon Ait.	0.56	0.52	0.60	0.58

Common Name	Scientific Name	Suitability score - averaged climate data (1984-2000)	Suitability score - averaged response data (1984-2000)	Suitability score - averaged climate data (2001-2017)	Suitability score - averaged response data (2001-2017)
Broad bean	Vicia faba L.	0.57	0.51	0.61	0.57
Bard vetch	Vicia monantha Retz.	0.91	0.71	0.94	0.79
Narbonne vetch	Vicia narbonensis L.	0.97	0.84	0.98	0.90
Hungarian vetch	Vicia pannonica Crantz	0.87	0.72	0.92	0.78
Blackpod vetch	Vicia sativa L. s. nigra	0.81	0.69	0.86	0.73
Common vetch	Vicia sativa L. s. sativa	0.61	0.53	0.66	0.59
Woolypod vetch	Vicia villosa Roth	0.81	0.69	0.85	0.74
Cardyne vetch	Vicia villosa Roth. s dasy.	0.87	0.67	0.91	0.76

Average suitability



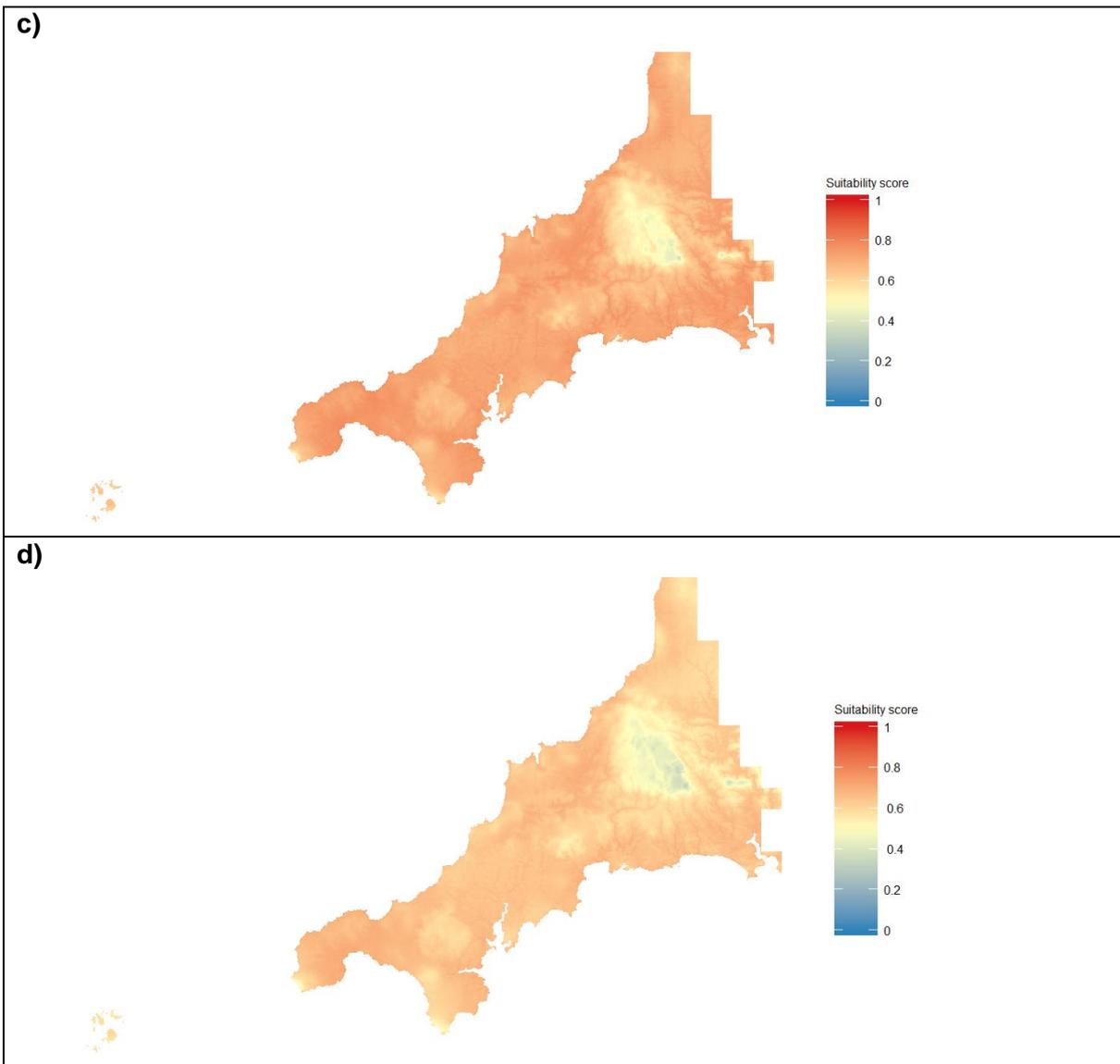


Figure A1: Average suitability estimates a) averaged climate data 1984-2000; b) averaged response data 1984-2000; c) averaged climate data 2001-2017; d) averaged response data 2001-2017.

Climate variability

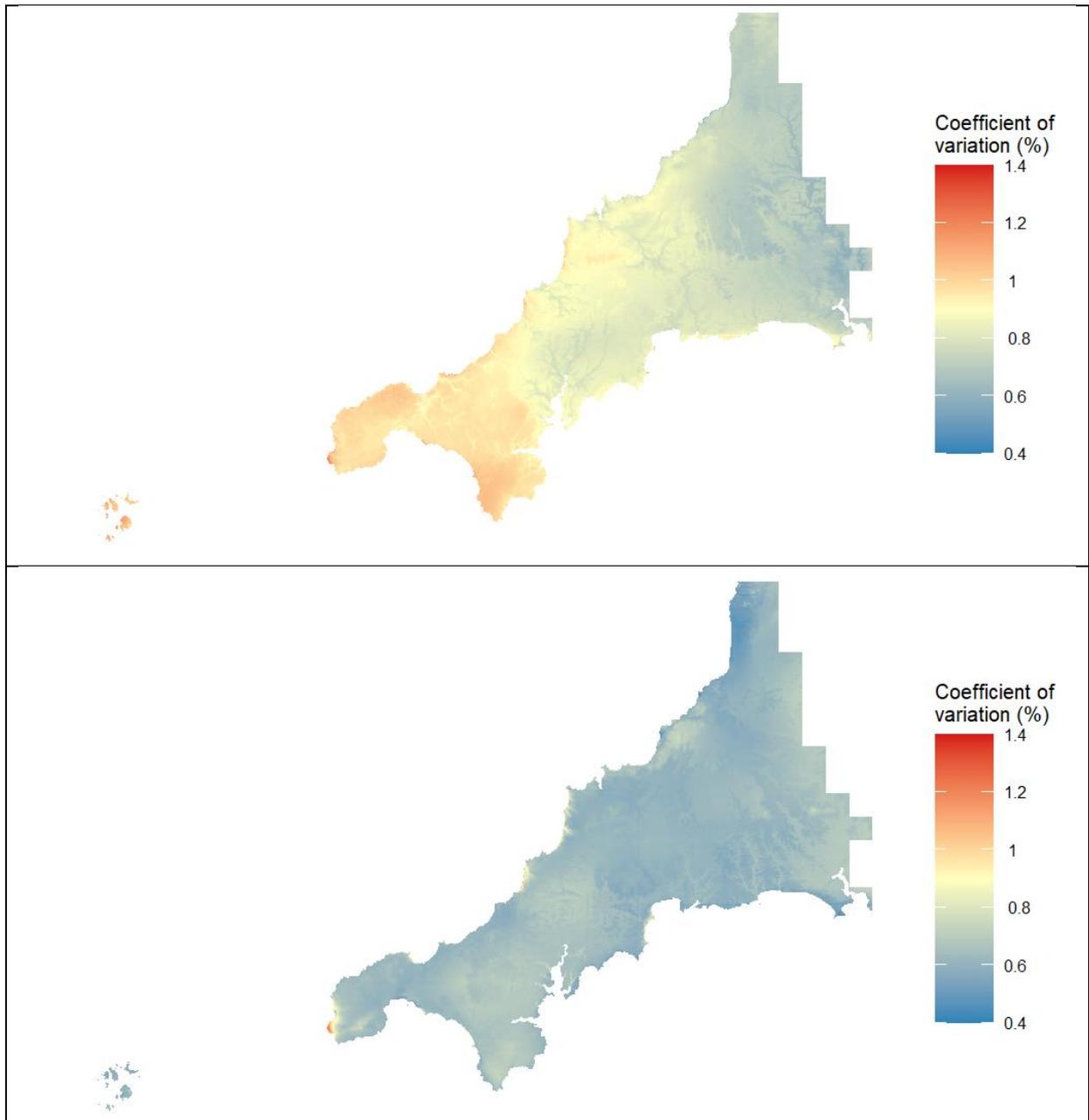


Figure A2: Mean coefficient of variation (%) in minimum annual temperature a) 1984-2000; b) 2001-2017. Temperature values were converted to degrees Kelvin to avoid having to divide by zero.

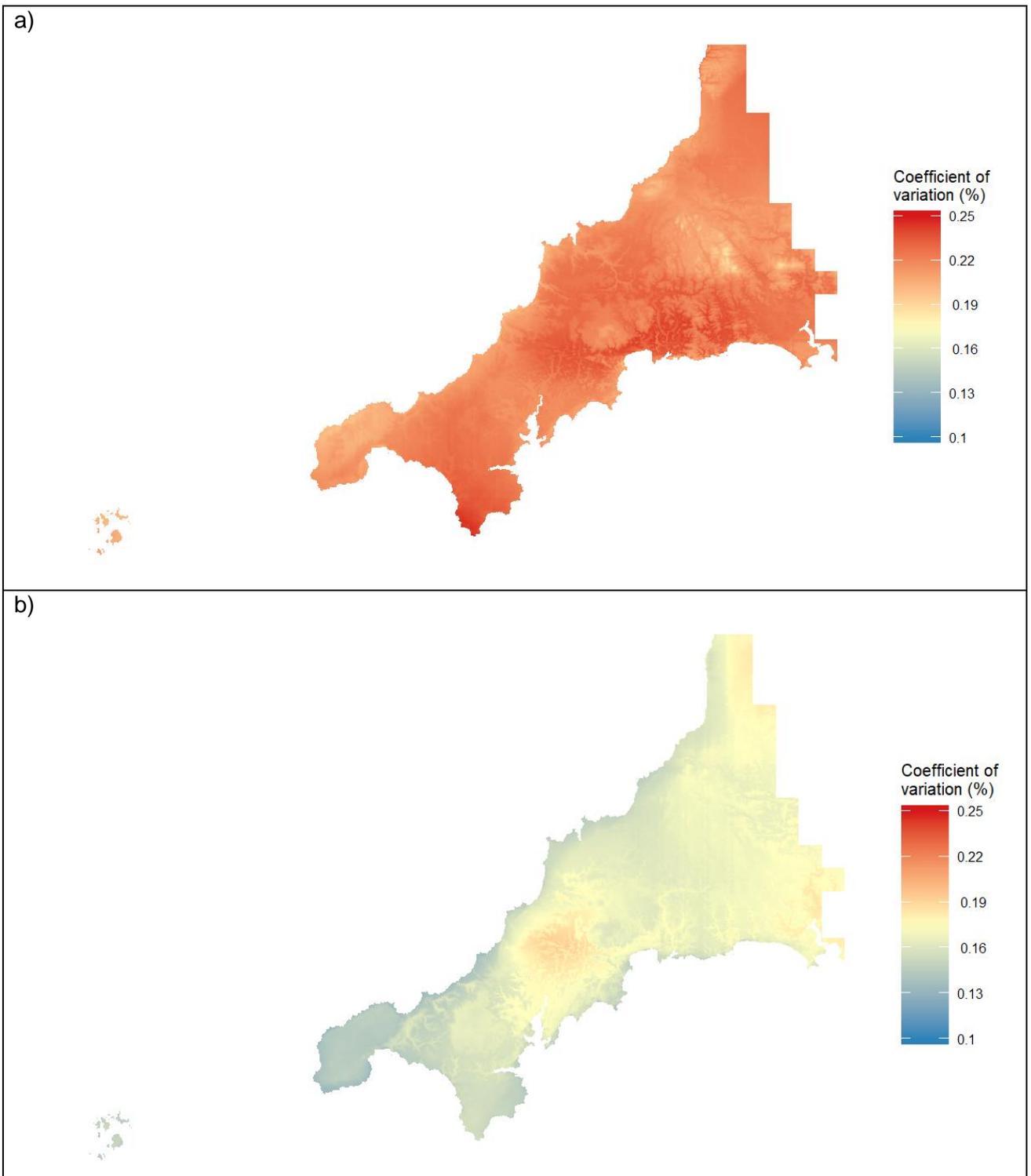


Figure A3: Mean coefficient of variation (%) in mean annual temperature a) 1984-2000; b) 2001-2017. Temperature values were converted to degrees Kelvin to avoid having to divide by zero.

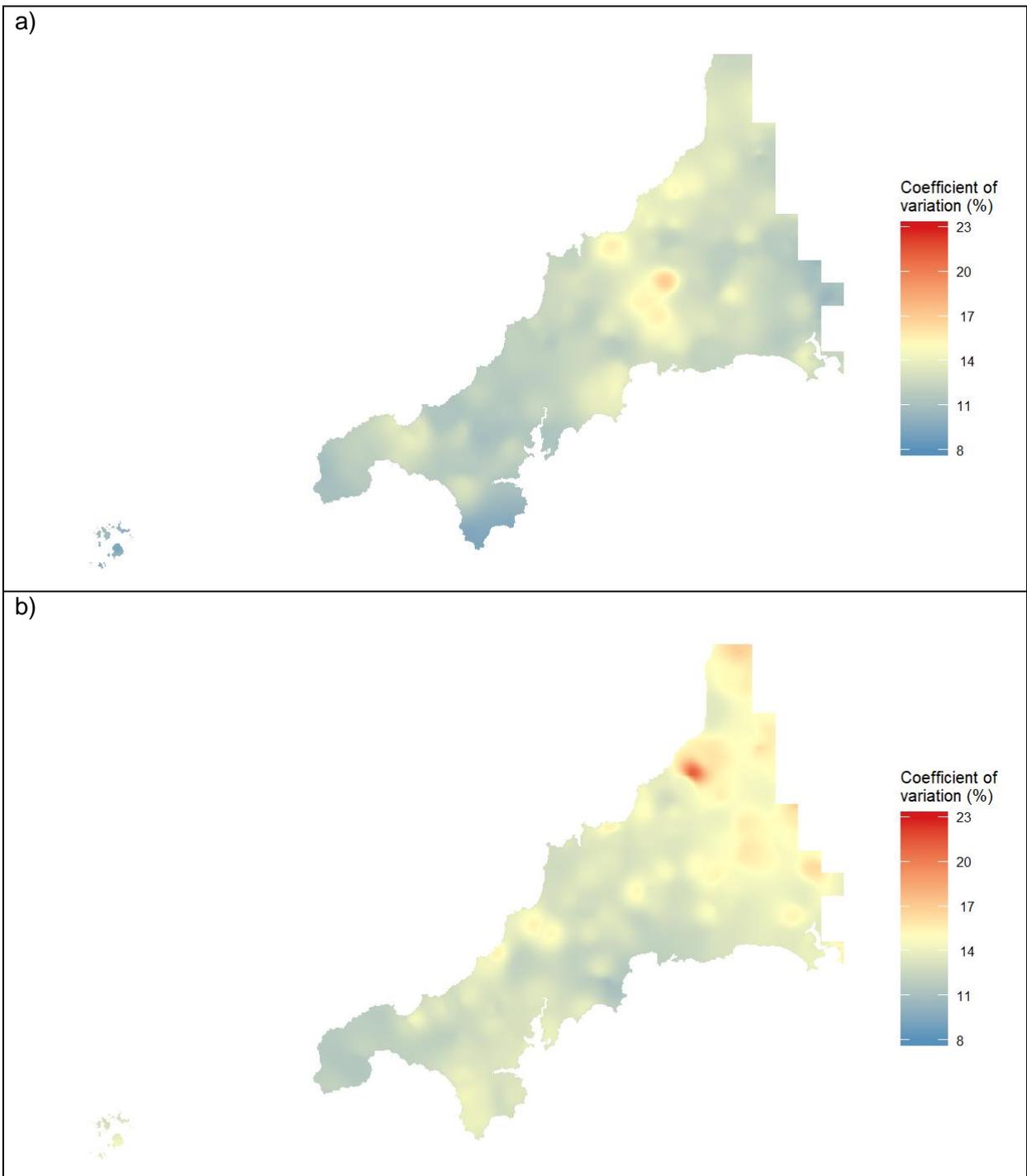
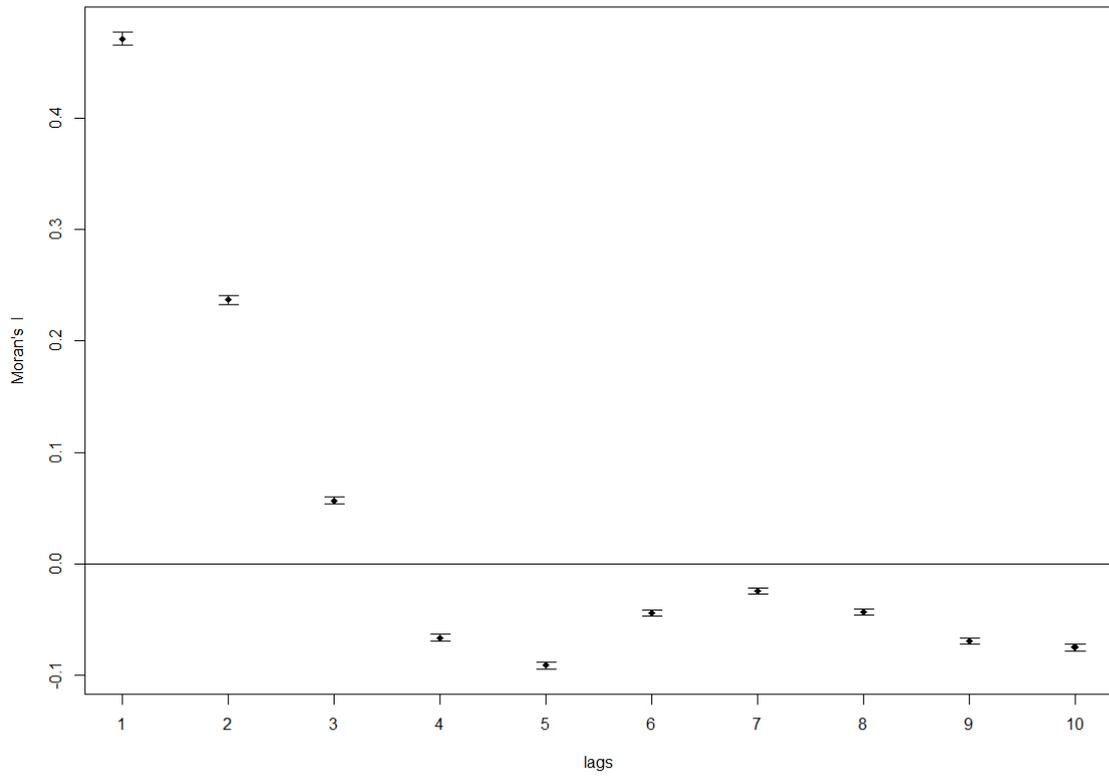


Figure A4: Mean coefficient of variation (%) in total annual precipitation a) 1984-2000; b) 2001-2017.

a)



b)

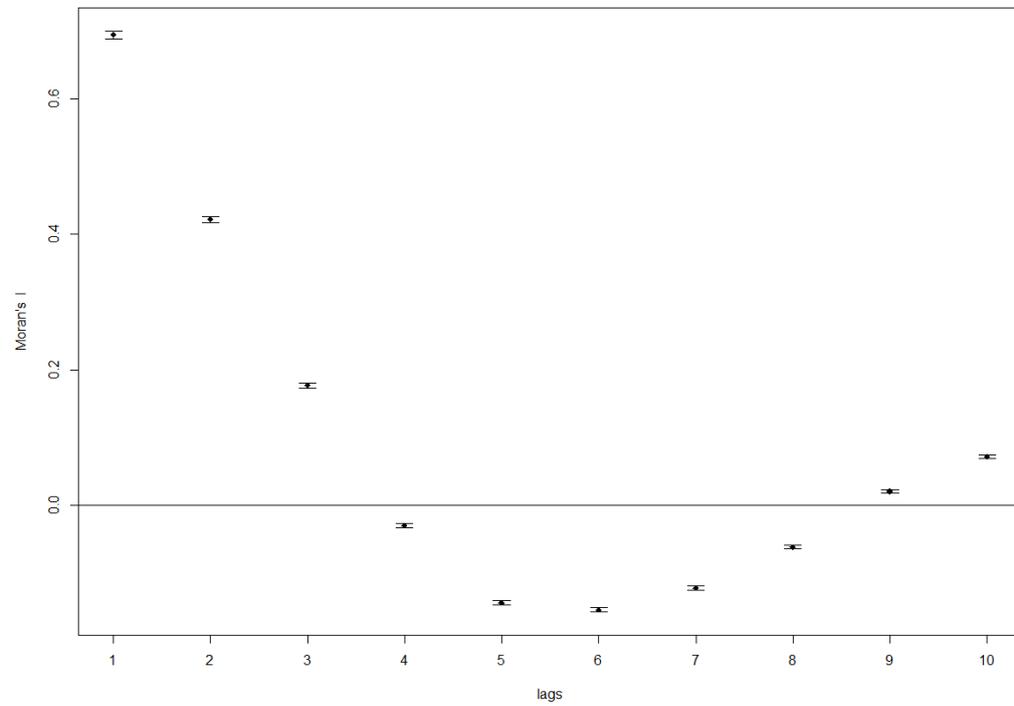


Figure A5: Correlogram at lag values up to a value of 10 (50km) for a) 1984-2000; b) 2001-2017.

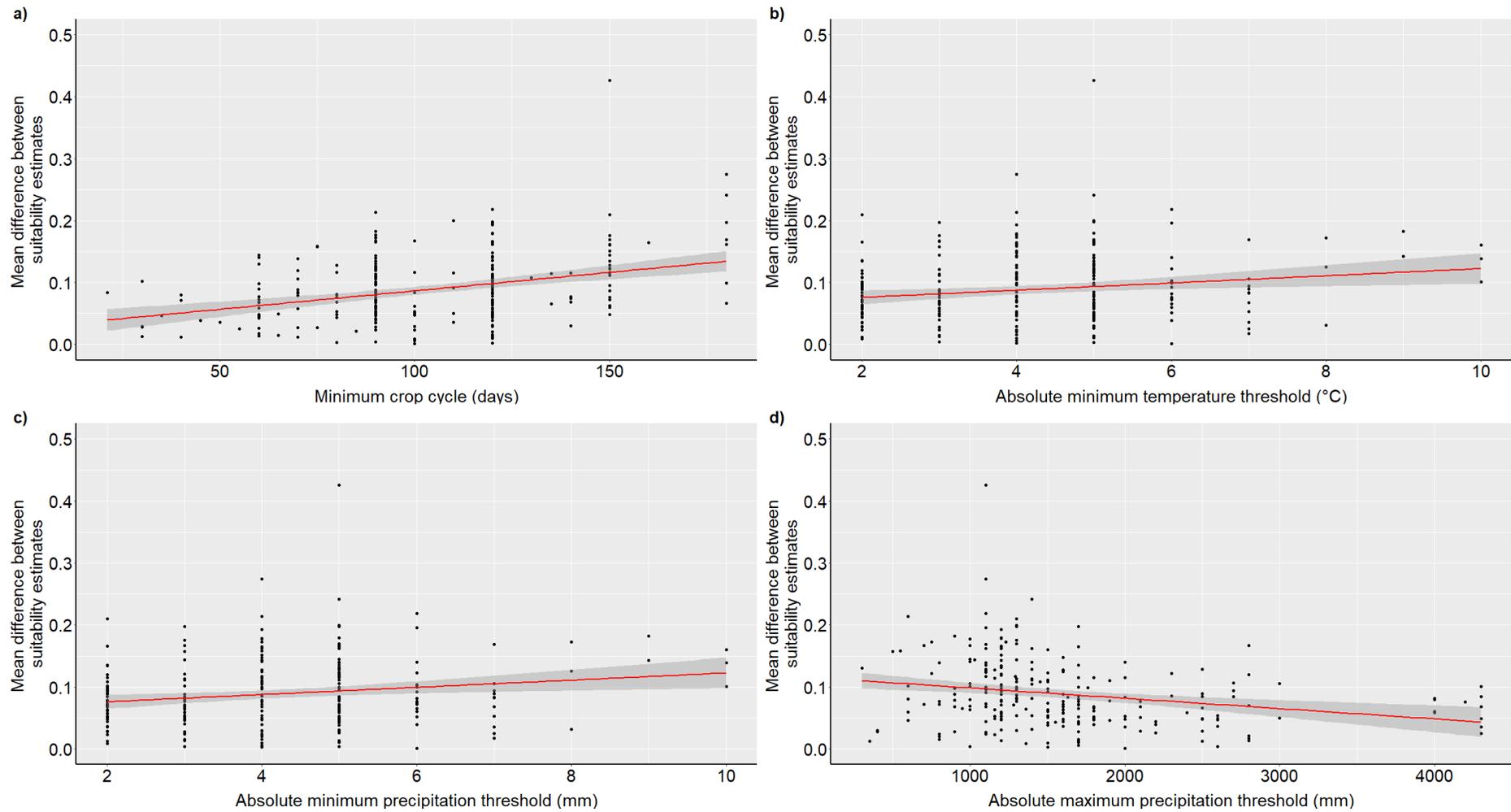


Figure A6: Correlation of a) minimum season length (GMIN); b) absolute minimum temperature (TMIN); c) absolute minimum precipitation (RMIN); and d) absolute maximum precipitation threshold (RMAX) to difference between suitability estimates from average climate and average response data.

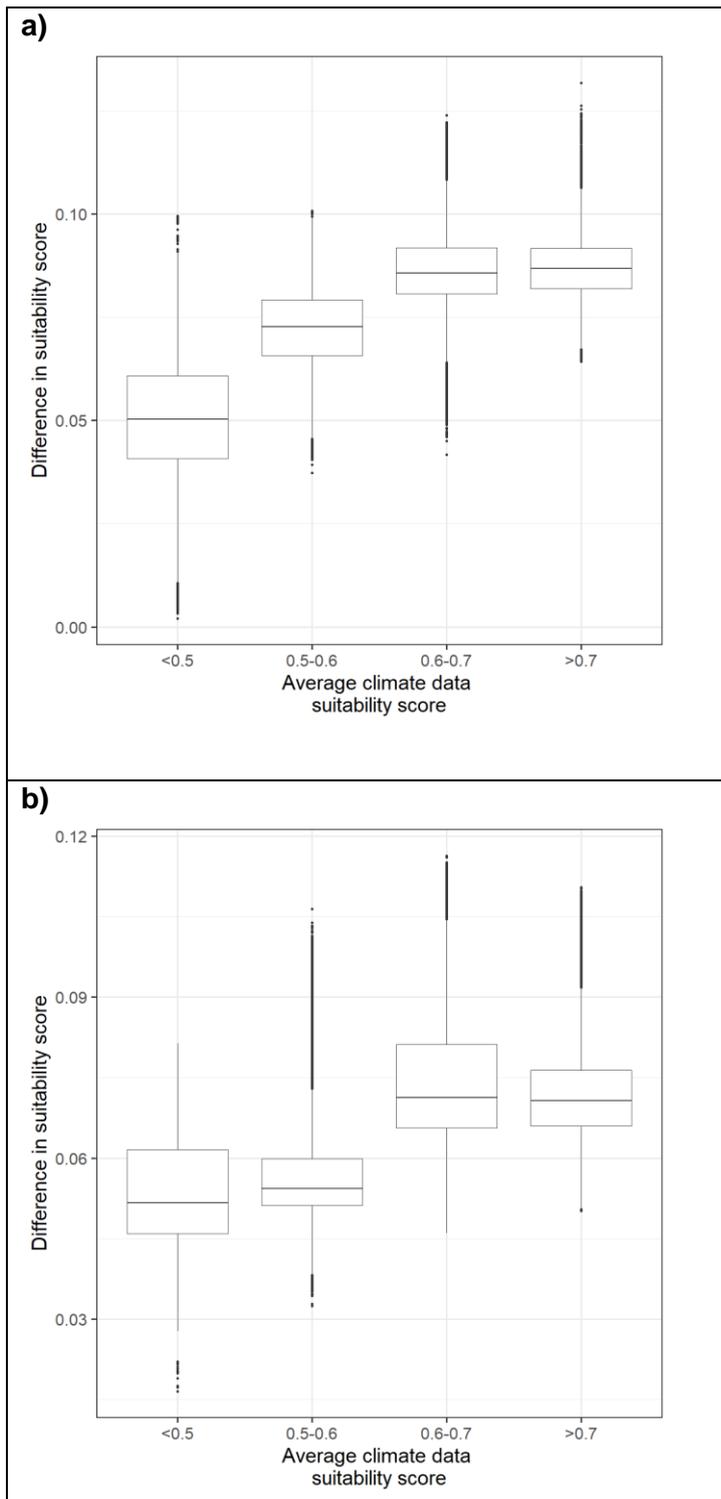
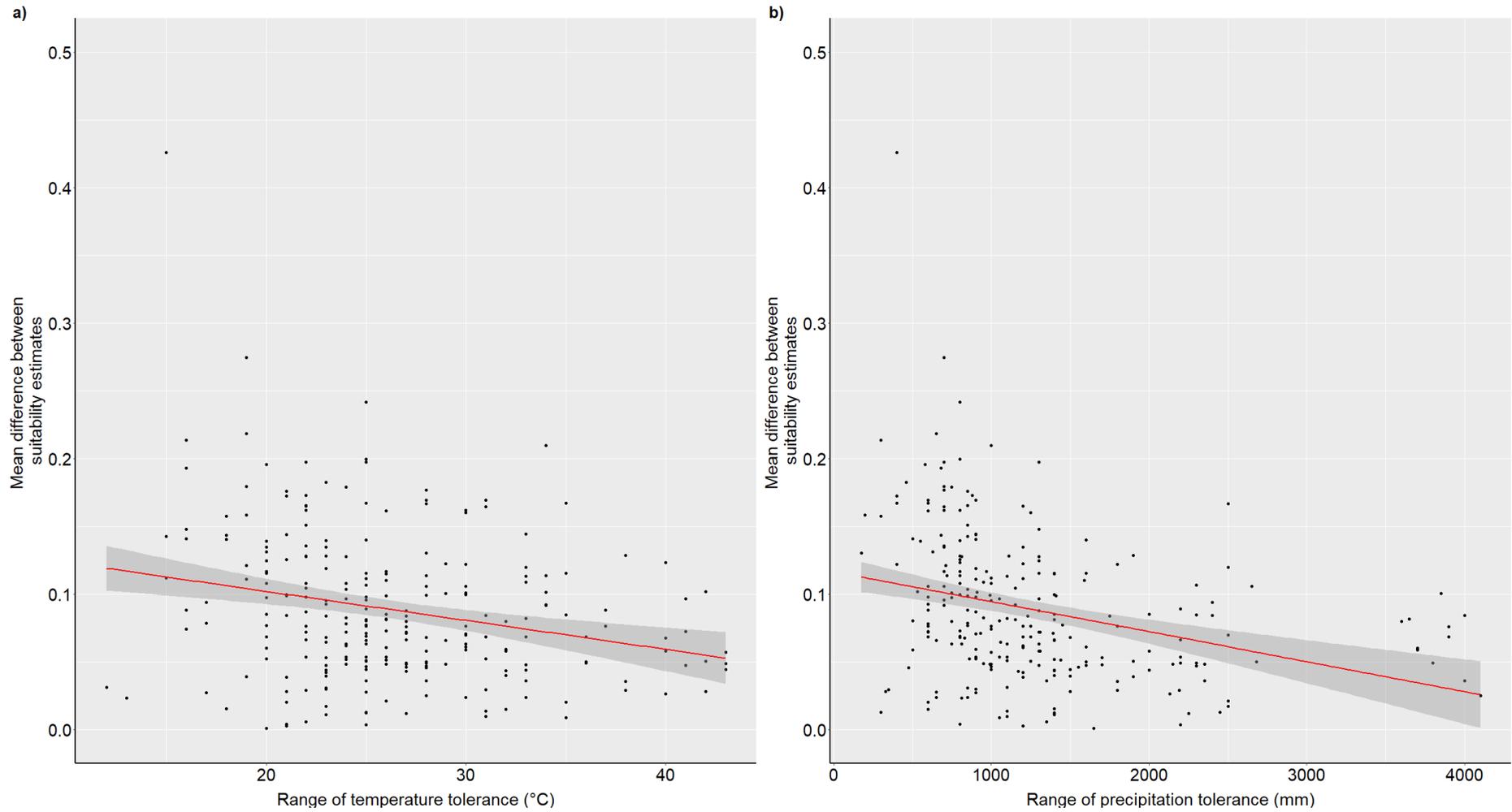


Figure A7: Difference in suitability scores between average climate and average response data at different values of climate suitability from average climate data: a) 1984-2000; b) 2001-2017



1

2 **Figure A8: Correlation of a) temperature tolerance range (TMAX - TMIN); b) precipitation tolerance range (RMAX-RMIN) to differences**
 3 **between suitability estimates from average climate and average response data.**

4