



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

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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 the climate suitability of an area, but in these aggregated climate datasets, inter-annual 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 with species' environmental requirements, being larger for species with small thermal niches and narrow ranges of precipitation tolerance.

Main Conclusions: Incorporating inter-annual 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 when using mechanistic species distribution models.

KEYWORDS

climate change, climate suitability model, climate variability, ecocrop model, species distribution model, temporal aggregation

1 | INTRODUCTION

Recent climate change has driven shifts in the geographic ranges of species (e.g. D'Andrea et al., 2009; Kelly & Goulden, 2008; Zorio et al., 2016) and further range shifts are expected as the climate continues to warm and weather patterns become more variable (Collins et al., 2013; Leemans & Solomon, 1993). 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 & 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 and 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 inter-annual 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 & 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 & 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 inter-annual 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. Hunter & Crespo, 2019; Jarvis et al., 2012; Rippke et al., 2016) 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.

2 | MATERIALS AND METHODS

2.1 | Study area

Climate suitability was assessed across Cornwall and the Isles of Scilly in south-west England, as an example, at 100 m spatial resolution. Temperature and precipitation in the region vary spatially (Maclean et al., 2015) and also temporally (Figure 1a–c).

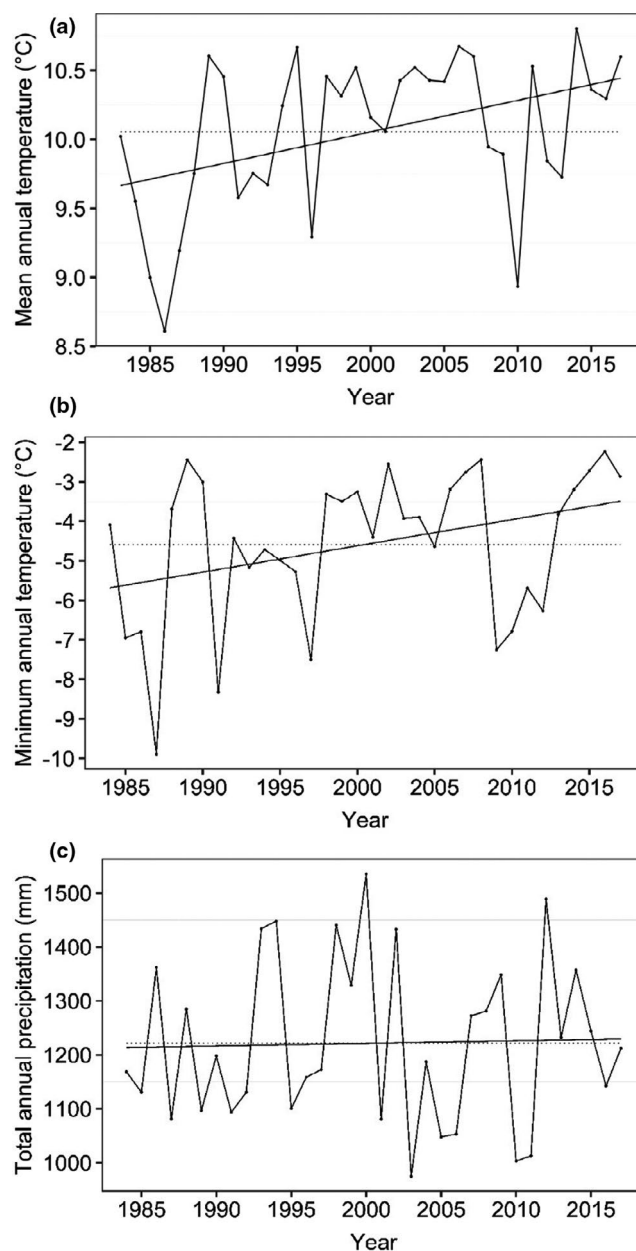


FIGURE 1 Mean annual temperature (a), minimum annual temperature (b) and total annual precipitation (c) trends for Cornwall and the Isles of Scilly (1984–2017). Black dots indicate mean values in each year, solid line represents the linear trend and dotted line indicates the mean value across all years. 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

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 (Kosanec et al., 2014). Indeed, species with low-temperature requirements have already suffered losses in west Cornwall due to rising temperatures (Kosanec 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, provide an ideal study system for examining how estimates of climate suitability may be affected by the aggregation of climate data.

2.2 | 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 100 m spatial resolution, thus, ensuring that temperature minima and spatial variation in suitability could be captured effectively.

We obtained hourly 100 m 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 1-km-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 ~200-km-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 5-km-grid resolution from the EUMETSAT Satellite Application Facility on Climate Monitoring (CMSAF; Posselt et al., 2014); and
4. Daily mean sea surface temperatures at 25-km-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 1 m 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 100 m 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 re-sampled precipitation values to 100 m 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 1 km gridded elevation as a covariate and, then, applying the model at a 100 m 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.



2.3 | 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 et al. (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 3rd 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 inter-annual 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 Supporting Information 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.

2.4 | 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 inter-annual variability in climate (coefficient of variation in mean monthly temperature, minimum monthly temperature and total monthly precipitation) during the period. Inter-annual 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 & 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 & 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 Supporting Information Appendix A, Figure A5, e.g. 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.

2.5 | 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 & 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).

3 | RESULTS

For the period 1984–2000, average climate data gave higher estimates of suitability than average response data for 245 of 255 species (Figure 2; Supporting Information 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 (Supporting Information Appendix A, Figure A1a–b).

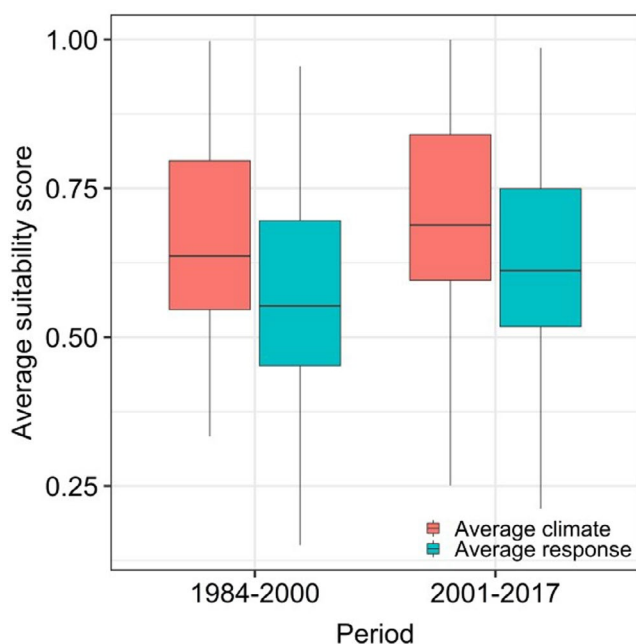


FIGURE 2 Average climate suitability scores for 1984–2000 and 2001–2017 using average climate (red) and average response (blue) data. Data presented are mean suitability scores across the study region for the 255 species analysed. Boxes capture the first (25th percentile), second (median) and third (75th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

For the period 2001–2017, average climate data gave higher estimates of average climate suitability than average response data for 240 of 255 species (Figure 2; Supporting Information 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 (Supporting Information 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.

3.1 | 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 to 2017 but inter-annual variability was also high, with any particular year not necessarily experiencing higher minimum temperatures than the previous one (Figure 1a,c). Although total annual precipitation did not change significantly from 1984 to 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 inter-annual variability, particularly in mean annual temperature and total annual precipitation was low and differences between scores were ~0.01 (Figure 2; Supporting Information Appendix A, Figure A2–A4).

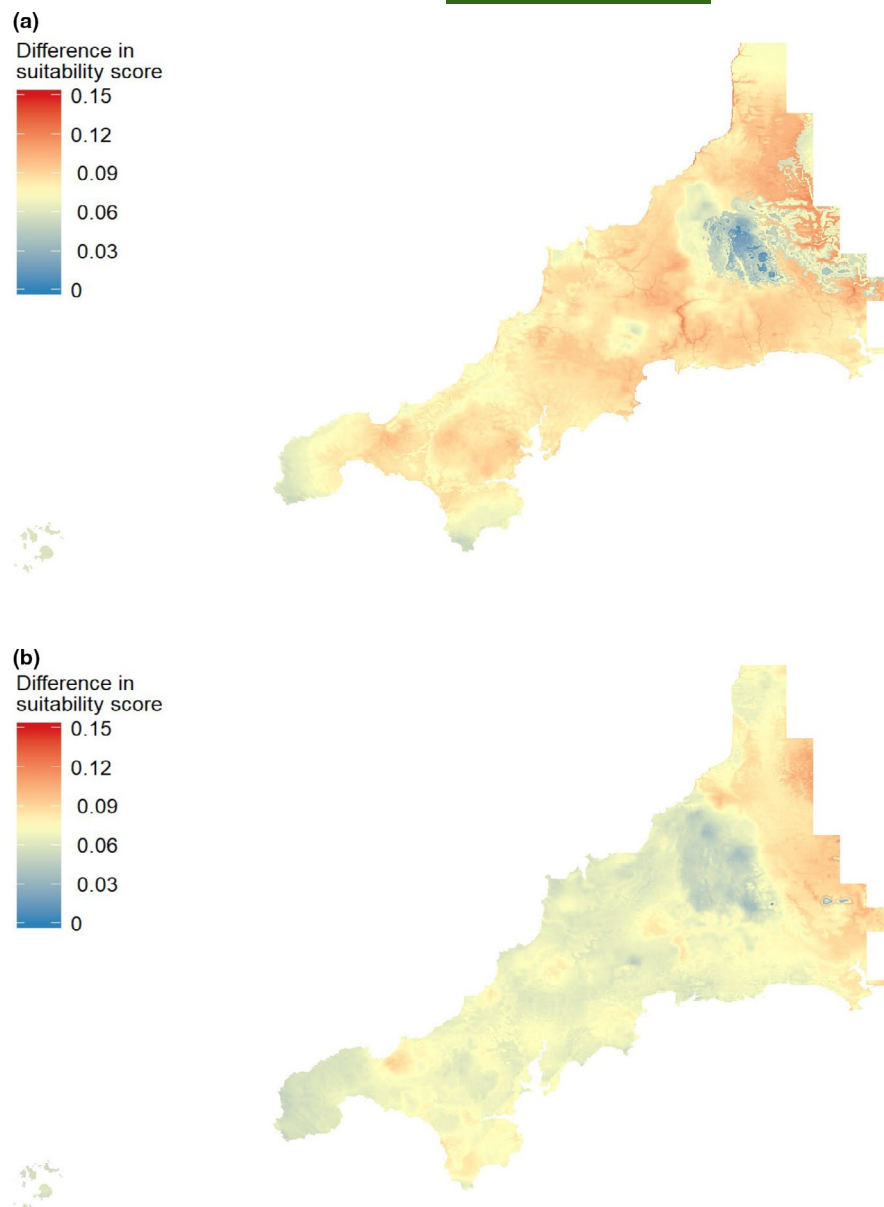
3.2 | Differences in suitability estimates as predicted by climatic requirements

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 Supporting Information Appendix 1, Figure A6). When the average climate was closer to optima (>0.6), we observed that differences between scores were greater (Supporting Information 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, $F_{1,253} = 16.93$, $p < 0.001$; Supporting Information 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)



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



minus absolute minimum precipitation threshold (RMIN)) and the differences between estimates (GLM, $F_{1,253} = 32.32$, $p < 0.001$; Supporting Information Appendix 1, Figure A8). Therefore, differences were larger for species with smaller ranges of precipitation tolerance.

4 | 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. Byju et al., 2018; Carter et al., 1996). However, suitability can vary substantially year to year in response to climatic variation (Diffenbaugh & Scherer, 2013). Due to the nonlinearity 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 were 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 was 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. While 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 & 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 inter-annual 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.

4.1 | Climate change and extremes

Climate change is expected to increase both the frequency and severity of extreme events (Coumou & Rahmstorf, 2012; Jentsch et al., 2007) 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 (Jentsch & Beierkuhnlein, 2008; Jentsch et al., 2007; Parmesan et al., 2000). 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 inter-annual variation in suitability in areas that are both climatically variable and experiencing high levels of climate change.

TABLE 1 Predictors of the effect of the inter-annual 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)

Period	Climate variable (coefficient of variation, %)	Total coefficients
1984–2000	Precipitation	0.0065 ($\pm 4.0\text{-e4}$)***
	Minimum temperature	0.017 (± 0.003)***
	Mean annual temperature	0.84 (± 0.06)***
2001–2017	Precipitation	0.0026 ($\pm 2.4\text{-e4}$)***
	Minimum temperature	0.0075 (± 0.009)*
	Mean annual temperature	0.049 (± 0.03)*

Note: Statistical significance is shown (* $p < 0.05$; *** $p < 0.001$).

4.2 | 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 (Brook et al., 2009; Parmesan et al., 2000; Thuiller et al., 2008), 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

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*

Note: Statistical significance indicated as (* $p < 0.05$; *** $p < 0.001$; and 0.1).

TABLE 2 Analysis of variance using F-test for generalised linear models exploring the difference between suitability estimates as predicted by species' tolerance thresholds



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 & 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 3-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.

4.3 | Species with narrow tolerance thresholds

It may be preferable to account for inter-annual 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.

4.4 | 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 are 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 underestimating 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).

4.5 | 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.

5 | CONCLUSION

Climate change will alter species distributions in both natural (Thomas et al., 2004) and cultivated (Leemans & 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 nonlinear, 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.

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DATA AVAILABILITY STATEMENT

The 'microclima' R package release relevant to this study has been stored at <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 from 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.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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