




## RESEARCH ARTICLE OPEN ACCESS

# Climatic Predictors of Long-Distance Migratory Birds Breeding Productivity Across Europe

Jan Hanzelka<sup>1,2</sup>  | Tomáš Telenský<sup>1,3</sup> | Jaroslav Koleček<sup>1,2</sup>  | Petr Procházka<sup>2</sup> | Robert A. Robinson<sup>4</sup> | Oriol Baltà<sup>5</sup> | Jaroslav Cepák<sup>6</sup> | Gabriel Gargallo<sup>5</sup> | Pierre-Yves Henry<sup>7,8</sup> | Ian Henshaw<sup>9</sup> | Henk van der Jeugd<sup>10</sup> | Zsolt Karcza<sup>11</sup> | Petteri Lehikoinen<sup>12</sup> | Bert Meister<sup>13</sup> | Arantza Leal Nebot<sup>14</sup> | Markus Piha<sup>15</sup> | Kasper Thorup<sup>16</sup> | Anders P. Tøttrup<sup>16</sup> | Jiří Reif<sup>1,17</sup> 

<sup>1</sup>Faculty of Science, Institute for Environmental Studies, Charles University, Prague 2, Czech Republic | <sup>2</sup>Institute of Vertebrate Biology, Czech Academy of Sciences, Brno, Czech Republic | <sup>3</sup>Center for Theoretical Study, Charles University and the Czech Academy of Sciences, Prague, Czech Republic | <sup>4</sup>Euring and British Trust for Ornithology, The Nunnery, Thetford, UK | <sup>5</sup>Catalan Ornithological Institute, Nat-Museu de Ciències Naturals de Barcelona, Barcelona, Spain | <sup>6</sup>Bird Ringing Centre, National Museum, Prague 10, Czech Republic | <sup>7</sup>Mécanismes adaptatifs et évolution (MECADEV UMR 7179), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Brunoy, France | <sup>8</sup>Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France | <sup>9</sup>Department for Environmental Research and Monitoring, Swedish Bird Ringing Centre, The Swedish Museum of Natural History, Stockholm, Sweden | <sup>10</sup>Vogeltrekstation—Dutch Centre for Avian Migration and Demography, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands | <sup>11</sup>Hungarian Bird Ringing Centre, BirdLife Hungary, Budapest, Hungary | <sup>12</sup>The Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland | <sup>13</sup>Grimma, Germany | <sup>14</sup>SEO/BirdLife, Ciencia Ciudadana, Madrid, Spain | <sup>15</sup>Natural Resources Institute Finland, Helsinki, Finland | <sup>16</sup>Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark | <sup>17</sup>Department of Zoology, Faculty of Science, Palacký University, Olomouc, Czech Republic

**Correspondence:** Jan Hanzelka ([jan.hanzelka@natur.cuni.cz](mailto:jan.hanzelka@natur.cuni.cz))

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## ABSTRACT

**Aim:** Ongoing climate changes represent a major determinant of demographic processes in many organisms worldwide. Birds, and especially long-distance migrants, are particularly sensitive to such changes. To better understand these impacts on long-distance migrants' breeding productivity, we tested three hypotheses focused on (i) the shape of the relationships with different climate variables, including previously rarely tested quadratic responses, and on regional differences in these relationships predicted by (ii) mean climatic conditions and (iii) by the rate of climate change in respective regions ranging from Spain to Finland.

**Location:** Europe.

**Time Period:** 2004–2021.

**Major Taxa Studied:** Long-distance migratory passerine birds.

**Methods:** We calculated breeding productivity from constant effort ringing sites from 11 European countries covering 34° of latitude, and extracted temperature- and precipitation-related climate variables from E-OBS and NASA MODIS datasets. To test our hypotheses, we fitted GLMM and Bayesian meta-analytic models.

**Results:** We revealed hump-shaped responses of productivity to temperature, growing degree-days, green-up onset date, and precipitation anomaly, and negative responses to intense and prolonged rains across the regions. The effects of March temperature

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and April growing degree-days were more negative in cold than in warm regions, except for the region with the highest accumulated heat, whereas increasing June precipitation anomalies were associated with higher productivity in both dry and wet regions. Productivity responses to climate were unrelated to the rate of climate warming.

**Main Conclusions:** The influence of climate on bird productivity proved to be frequently nonlinear, as expected by ecological theory. The rate of climate change is less important than regional interannual variability in climate (which is predicted to increase), but this may change with the progression of climate change in the future. Productivity declines in long-distance migratory songbirds are particularly expected if out-of-norm water excess increases in frequency or strength.

## 1 | Introduction

The ongoing climate change has been exerting increasing pressure on organisms through the rapid alteration of environmental conditions worldwide (Cui, Liang, and Wang 2021; Elsen et al. 2022; Hoegh-Guldberg and Bruno 2010). To understand the impacts of the recent global climate change on populations of organisms, we need to gain insights into the mechanisms by which climate affects organisms' vital rates over large spatial and temporal scales. In this regard, birds serve as an important model taxon due to the existence of extensive datasets whose analyses may provide such insights (Morrison et al. 2021; Saracco et al. 2006). One of the most important vital rates determining bird population trends is breeding productivity (Morrison et al. 2016), defined as the total number of fledged chicks per adult produced in the breeding period. When climate strongly and continuously impacts breeding productivity, bird populations can be exposed even to local extinctions (Szabo et al. 2012; Wiens 2016).

Climatic conditions during the breeding period represent the most fundamental environmental constraint of productivity at both local (Morrison et al. 2021, 2022) and large spatial scales (Halupka et al. 2023). Notably, in the Northern temperate zone, the breeding season starts later at higher latitudes than at lower latitudes (Baker 1939) due to a later onset of vegetation development and a shorter growing season (Chmielewski and Rötzer 2001; Hut et al. 2013). This indirect climate effect forces the birds to have lower breeding productivity in the north, where they raise fewer broods per season compared to the south (Böhning-Gaese et al. 2000). Climate can limit breeding of birds also in the south. For instance, the poor water availability at lower latitudes can have a considerable influence on insect performance and survival (Chown, Sørensen, and Terblanche 2011), which could consequently limit food availability for birds during breeding. Due to these climatic constraints in both cold and warm regions, the highest breeding productivity is observed at midlatitudes (Eglington et al. 2015). Climate warming may affect productivity variably in different regions, resulting in decreases in warm areas (Auer and Martin 2013; Barras et al. 2021), but increases in colder, boreal areas (Meller et al. 2018). Additionally, climate variables can show unpredictable annual fluctuations, which can have a dramatic negative impact on productivity due to smaller clutches and very low breeding success (Gładalski et al. 2022; Pipoly et al. 2013; Whitehouse et al. 2013).

Long-distance migrants (LDMs) may be particularly affected by climate; while resident birds can track the climate changes on nearby breeding sites, migrants likely arrive without direct experience of the prebreeding climatic conditions, and their

time of arrival may be driven by conditions *en route* (Ambrosini et al. 2011; Robson and Barriocanal 2011; Samplonius et al. 2018; Søraker et al. 2022). However, the responses of LDMs to spring onset (vegetation green-up) can vary based on the speed of spring migration or the location of their breeding sites (Briedis, Hahn, and Bauer 2024; Mayor et al. 2017; Youngflesh et al. 2021, 2023).

Climate primarily affects breeding land birds through temperature and water availability. Temperature and growing degree-days (GDD) influence the phenology of birds, causing them to start breeding earlier during warmer springs (Sockman and Courter 2018). Moreover, they facilitate the growth of organisms at lower trophic levels that constitute birds' food sources, that is, insects (Cayton et al. 2015) and plants (Anandhi 2016). For all these groups, the start of the growing season (green-up onset date) is an important phenological milestone. With the onset, the availability of fresh foliage surges, boosting resources across the trophic cascade.

Concerning the effect of water availability, birds can typically cope well with regular fluctuations in rainfall (Radford et al. 2001), but excessive precipitation may reduce the activity and availability of their insect food (Cox et al. 2019; Schöll et al. 2016). Birds may not be able to compensate for this shortfall (Riggio et al. 2023; Schöll and Hille 2020; Siikamäki 1996), especially during breeding when they require additional resources. This can result in lower breeding productivity as fewer chicks survive to fledging due to limited food sources (Fischer 1994; Halliwell et al. 2023; Öberg et al. 2015; Zuckerberg, Ribic, and McCauley 2018). Moreover, sudden episodes of intense rainfall can wash the insects off vegetation (Shrestha 2019), further reducing food availability. Similarly, prolonged periods of consecutive rainfall days can hinder insect recovery, negatively affecting food provisioning for nestlings (Radford et al. 2001; Schöll and Hille 2020) and subsequently negatively impacting breeding productivity.

To our knowledge, no study has tested the relative importance of all the climatic factors mentioned above in concert across latitudes. To fill this knowledge gap, we utilised a unique bird ringing dataset collected by a long-term monitoring scheme employing a standardised technique in 11 European countries. This dataset enables the estimation of breeding productivity in 23 species of common LDMs. By the investigation of the relationships between LDMs' breeding productivity and various climate variables describing the conditions on breeding grounds (Table 1) we aimed (i) to identify the shapes of the responses of breeding productivity of LDMs in different European regions to respective climate variables over the period of 2004–2021, and (ii) to explain possible differences in these responses between the regions by regional mean climatic conditions and the rate of

**TABLE 1** | Concise definitions of climate variables characterising climate in the breeding grounds of long-distance migratory birds.

Climate variable	Units	Definition
Temperature ( $T$ )	Degree Celsius	Mean monthly $T$ for each site
Growing degree-days (GDD10)	Degree-days	Monthly accumulated GDD10 for each site, $T_{\text{base}} = 10^{\circ}\text{C}$
Green-up onset date (GOD)	Day of year	A day in year when the reflectance of specific wavelengths of light from vegetation surface crosses 15% of the reflectance maximum of the current vegetation season
Precipitation anomaly ( $\Delta R$ )	Millimetre	Mean monthly $\Delta R$ for each site calculated as a deviation of the sum of monthly precipitation from the long-term average for period 1991–2020
Heavy rain days ( $R10$ )	Number of days	Number of days when daily precipitation is $\geq 10$ mm for each site
Very heavy rain days ( $R20$ )	Number of days	Number of days when daily precipitation is $\geq 20$ mm for each site
Consecutive rain days 1 mm ( $R1c$ )	Number of days	Maximum number of consecutive rain days when the daily sum of precipitation is $\geq 1$ mm for each site
Consecutive rain days 2 mm ( $R2c$ )	Number of days	Maximum number of consecutive rain days when the daily sum of precipitation is $\geq 2$ mm for each site

Note: Values of each climate variable were calculated for each site and year in months of March, April, May, and June in each study region, except for green-up onset date. For details on the calculations of these variables refer to the Supplementary Material 2.

climate warming. To achieve this, we tested three hypotheses with one or two predictions for each (Table 2).

## 2 | Methods

### 2.1 | Bird Data

Our study is based on bird ringing data collected under a standardised protocol in 11 European countries from 2004 to 2021. These data consist of the counts of individual adult and juvenile birds at each site in respective years produced by the European Constant Effort Sites programme (Euro-CES). We define breeding productivity as the proportion of the abundance of juveniles to adults at each site. Euro-CES is a large-scale and long-term bird ringing programme running in several European countries (e.g., Morrison et al. 2021; Robinson 2023), focusing on the investigation of demographic rates in bird populations. Skilled voluntary bird ringers follow a standard protocol requiring a constant capture effort at each site and producing data comparable across sites and years (Robinson, Julliard, and Saracco 2009). Three-meter-high mist-nets mostly target small passerines from shrubby, understorey or wetland habitats. Nine to 12 capture sessions take place throughout the breeding season, which spans from March to September. The span is usually confined to a shorter period reflecting the local breeding season in respective countries. We obtained data from Euro-CES schemes in 11 countries, and we merged or split some of them to obtain 11 regions covered by a comparable number of sites (Figure 1). If enabled by the number of sites, we also took climatic conditions into account in this procedure by delimitating regions that differ in climatic conditions from the others (e.g., south-eastern vs. north-western France). Such a division into regions enabled us to present results related to traditional and well-known spatial units broadly corresponding to countries, and also allowing for slight methodological differences between particular Euro-CES schemes (e.g., Robinson, Julliard, and Saracco 2009). We covered the period 2004–2021,

with the exceptions of France, from which we excluded the years 2020 and 2021 due to very low ringing effort resulting from COVID-19 restrictions, and Czechia excluding the year 2013 due to a large flooding event occurring during the breeding season. Our measure of productivity was the ratio of the total number of (free-flying) juveniles caught on a site in a year to the total number of adults. Although not all the prescribed visits were completed in every season, this does not have a substantial effect on the estimated indices (Miles et al. 2007).

In each region, we selected bird species meeting the following conditions: the individuals of a species were captured on at least five sites in each region every year, species were not gregarious (i.e., species like barn swallow *Hirundo rustica* were excluded), and species were sub-Saharan long-distance migrants. Altogether, we selected 23 bird species (7–16 species per region, Table 3).

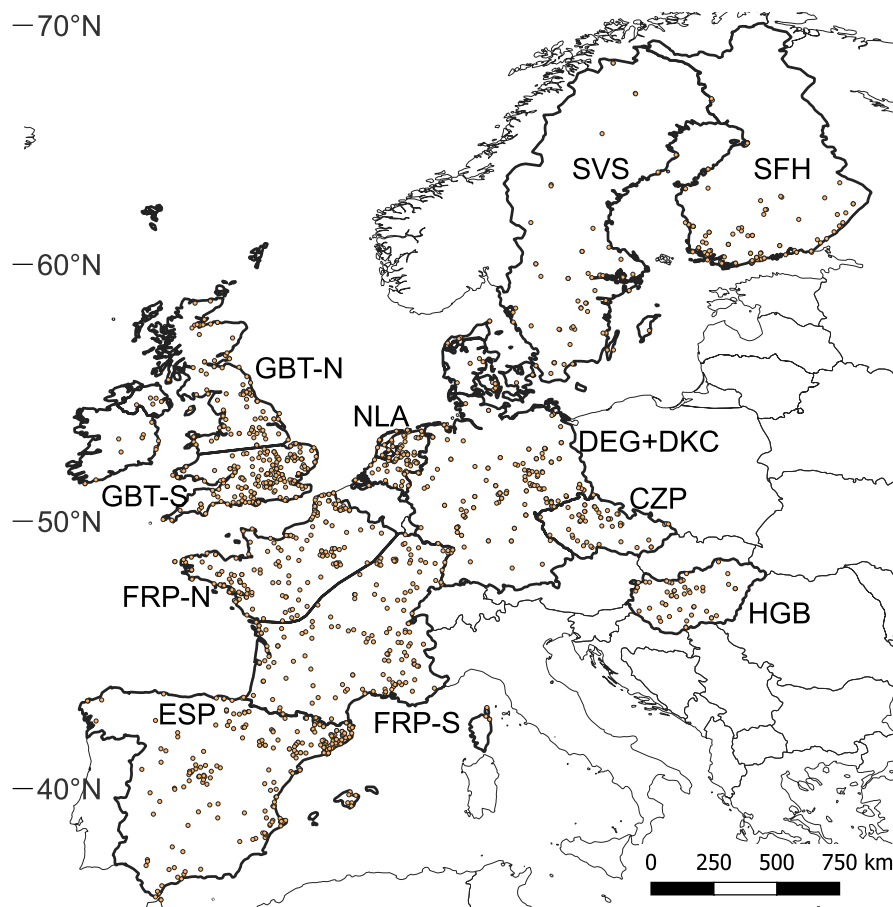
Relationships between breeding productivity and climate variables can be affected by climate on wintering grounds via carry-over effects (Harrison et al. 2011). Among various climate variables, we focused on water availability since it is considered the most important: higher water saturation of ecosystems during wintering in Africa could positively affect productivity in the subsequent breeding season (Zwarts, Bijlsma, and Van Der Kamp 2023). To take this into account, we defined the wintering grounds of the selected species based on ecoregions (<https://ecoregions.appspot.com>, Dinerstein et al. 2017) and the locations of nonbreeding areas provided by BirdLife International (2017). We defined the following seven regions covering sub-Saharan Africa: NW arid, NW humid, NE arid, E arid, C humid, S humid, and S arid (Figure 2). We used data on ring recoveries from Africa available in the EURING Data Bank (du Feu et al. 2009), Dutch Bird Migration Atlas (VogeltrekAtlas, <https://vogeltrekAtlas.nl>), Hungarian Bird Atlas (Magyarország madarai, <https://www.mme.hu/magyarorszagmadarai>) and various literature sources covering geolocator and GPS-tag studies (Hahn et al. 2013, 2014;

**TABLE 2** | Summary of the tested hypotheses, related predictions and their rationale, and climate variables related to respective predictions.

Hypotheses	Predictions	Climate variables	Justifications	References
H1: The highest breeding productivity is at optimal values of climate variables	P1a: Hump-shaped relationships between breeding productivity and temperature-related climate variables and precipitation anomaly. Optimal values of climate variables = average values	<i>T</i> , GDD10, GOD, $\Delta R$	Both high and low temperatures or water availability limit breeding productivity. Temperature: high values in early spring = trophic mismatch connected with decreased food availability for chicks; high values in late spring = vegetation senescence, speeding-up of summer onset; low values throughout season = poor breeding conditions; Precipitation: high values = limited insect activity and availability, low values = droughts, vegetation senescence, decreased food sources	Carleton et al. (2019), Finch et al. (2023), Halupka and Halupka (2017), Schöll and Hille (2020), Socolar et al. (2017), Youngflesh et al. (2023)
H2: Limitation of breeding productivity by climate depends on regional climate characteristics	P1b: Negative linear relationships between breeding productivity and an excessive or prolonged rainfall. Optimal values of climate variables = low values P2a: More negative effects of temperature and growing degree-days on the breeding productivity in colder than in warmer regions P2b: More positive effects of precipitation anomaly in drier than in wetter regions	<i>R10</i> , <i>R20</i> , <i>R1c</i> , <i>R2c</i>  <i>T</i> , GDD10  $\Delta R$	Heavy rains cause poor breeding conditions (limited food availability, higher energetic costs)  Higher climatic seasonality in colder regions underpins stronger trophic mismatch in years with higher temperature  Higher water availability in drier regions results in more food resources for breeding birds, while such a water limitation is relaxed in wetter regions	Chen et al. (2019), Keller and van Noordwijk (1994), Schöll and Hille (2020)  Vega, Fransson, and Kullberg (2021), Zhemchuzhnikov et al. (2021)  Howard et al. (2015)
H3: Responses of breeding productivity to climate are stronger in regions with higher warming rate	P3: The effects of early and late spring temperature-related variables on breeding productivity will be more negative and positive, respectively, in regions experiencing faster climate warming during 2004–2021	<i>T</i> , GDD10, GOD and main principal components derived from these variables	Higher early spring climate change velocity results in stronger trophic mismatch; higher late spring climate change velocity results in improved conditions for breeding	Kwon et al. (2019)

*Note:* See Table 1 for concise definitions of the climate variables.

Abbreviations: GDD10, growing degree-days; GOD, green-up onset day; *R10*, heavy rain days; *R20*, very heavy rain days; *R1c*, consecutive rain days 1 mm; *R2c*, consecutive rain days 2 mm; *T*, temperature;  $\Delta R$ , precipitation anomaly.



**FIGURE 1** | Distribution of Constant Effort Sites used for collecting data on long-distance migrants' breeding productivity across eleven study regions in Europe. CZP, the Czech Republic (50 sites); DEG + DKC, Germany and Denmark (181 sites); ESP, Spain (262 sites); FRP-N, northern part of France (182 sites); FRP-S, central & southern part of France (168 sites); GBT-N, northern parts of the UK—Wales, England, Scotland and Northern Ireland—and Ireland (118 sites); GBT-S, southern parts of the UK—England and Wales (203 sites); HGB, Hungary (54 sites); NLA, the Netherlands (78 sites); SFH, Finland (106 sites); SVS, Sweden (64 sites).

Horns et al. 2016; Koleček et al. 2016, 2018; Lerche-Jørgensen et al. 2017; Ouwehand et al. 2016; Procházka et al. 2018; Stach et al. 2012; Tøttrup et al. 2017) to delimit the most probable wintering regions (from those seven mentioned above) for each species. This approach also allowed for the possibility of different wintering quarters in a species breeding in different European regions (Supplementary Material 1). Additionally, we selected six main land cover types widely distributed in sub-Saharan Africa (Figure 2 and Table S2), and assigned them to each species as the most probable habitats the species occupy in the wintering grounds (Supplementary Material 1), based on data provided by Birds of the World (Billerman et al. 2023) and Glutz von Blotzheim (2001).

## 2.2 | Climate Data

We related bird breeding productivity to a set of eight climate variables characterising the breeding grounds and one characterising wintering grounds. For the breeding grounds, we selected the following variables: Temperature ( $T$ ), Growing degree-days ( $10^{\circ}\text{C}$ ) (GDD10), Green-up onset date (GOD), Precipitation anomaly ( $\Delta R$ ), Heavy rain days (R10), Very heavy rain days (R20), Consecutive rain days 1 mm (R1c), and

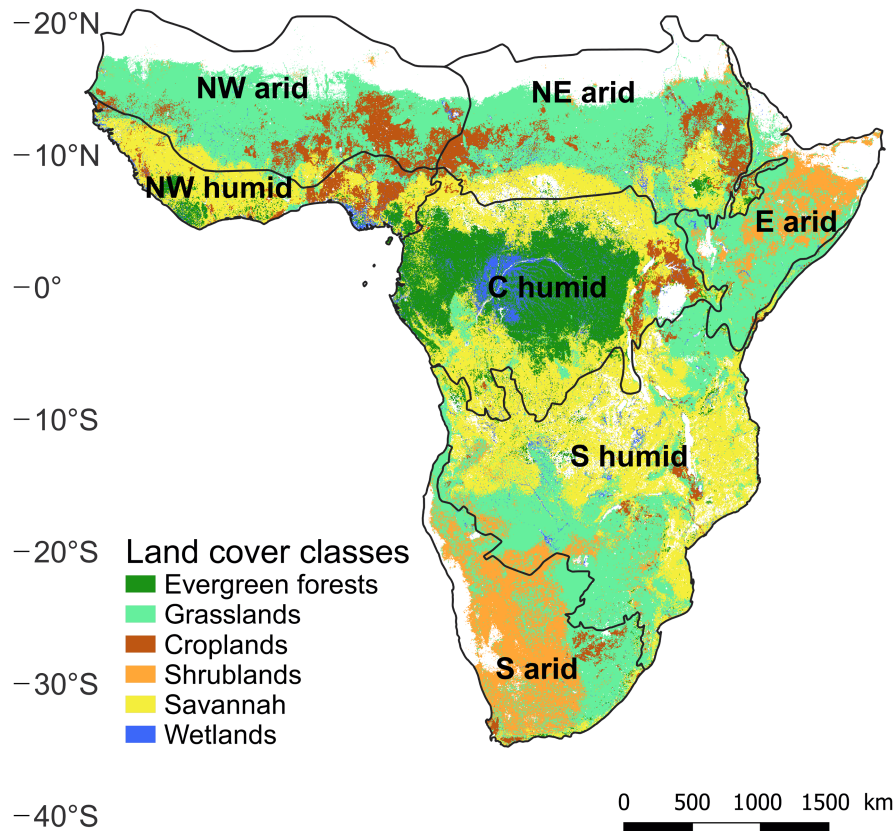
Consecutive rain days 2 mm (R2c) (Table 1), which represent the effects of temperature- and precipitation-related variables. Except for GOD, which is expressed on annual basis by definition, we obtained values for months March, April, May, and June for each variable, because these months cover prebreeding and breeding periods of the investigated LDMs in Europe (Billerman et al. 2023) and we can expect their impacts on LDMs' breeding productivity. Climate data were extracted from the E-OBS datasets v 23.1e (resolution  $0.1^{\circ} \times 0.1^{\circ}$ , R10 and R20 variables) and v 25.0e (resolution  $0.1^{\circ} \times 0.1^{\circ}$ ,  $T$ , GDD10,  $\Delta R$ , R1c and R2c variables) (Cornes et al. 2018) and MODIS MCD12Q2v061 datasets (resolution  $\sim 0.004^{\circ} \times 0.004^{\circ}$ , GOD variable; Friedl, Gray, and Sulla-Menashe 2022). Values of each climate variable were calculated for each site and year in respective months in each study region. To provide an idea of the regional climatic conditions, we present mean values of the climate variables in each month and region (Figures S1–S6). For details on the calculations of the variables, refer to the Supplementary Material 2.

To characterise conditions on the wintering grounds, we expressed *water availability* as the ratio of actual evapotranspiration (ETa) to potential evapotranspiration (PET), hereafter called ETr. In this ratio, ETa is the amount of water evaporated from soil surfaces and canopies, and transpired by plants,

**TABLE 3** | List of European long-distance migratory bird species selected for breeding productivity analyses in each region.

Common name	Scientific name	CZP	DEG + DKC	ESP	FRP-N	FRP-S	GBT-N	GBT-S	HGB	NLA	SFH	SVS
Great reed warbler	<i>Acrocephalus arundinaceus</i>	×	×	×					×			
Marsh warbler	<i>Acrocephalus palustris</i>	×	×		×	×			×	×	×	
Common reed warbler	<i>Acrocephalus scirpaceus</i>	×	×	×	×	×	×	×	×	×	×	×
Sedge warbler	<i>Acrocephalus schoenobaenus</i>	×	×	×	×	×	×	×	×	×	×	×
Tree pipit	<i>Anthus trivialis</i>										×	×
Greater whitethroat	<i>Curruca communis</i>	×	×	×	×	×	×	×	×	×	×	×
Lesser whitethroat	<i>Curruca curruca</i>	×	×		×	×	×	×	×	×	×	×
Western subalpine warbler	<i>Curruca iberiae</i>			×								
Pied flycatcher	<i>Ficedula hypoleuca</i>		×	×					×	×	×	×
Icterine warbler	<i>Hippolais icterina</i>		×							×		
Melodious warbler	<i>Hippolais polyglotta</i>			×	×	×						
Red-backed shrike	<i>Lanius collurio</i>	×	×			×		×			×	
Woodchat shrike	<i>Lanius senator</i>			×								
Savi's warbler	<i>Locustella luscinioides</i>	×	×							×		
Common grasshopper warbler	<i>Locustella naevia</i>	×	×		×		×	×		×		
Thrush nightingale	<i>Luscinia luscinia</i>										×	×
Common nightingale	<i>Luscinia megarhynchos</i>		×	×	×	×	×	×	×	×		
Spotted flycatcher	<i>Muscicapa striata</i>		×	×		×				×	×	
Eurasian golden oriole	<i>Oriolus oriolus</i>			×								
Common redstart	<i>Phoenicurus phoenicurus</i>		×							×		×
Western Bonelli's warbler	<i>Phylloscopus bonelli</i>			×								
Willow warbler	<i>Phylloscopus trochilus</i>	×	×	×	×	×	×	×		×	×	×
Garden warbler	<i>Sylvia borin</i>	×	×	×	×	×	×	×		×	×	×

Abbreviations: CZP, the Czech Republic; DEG + DKC, Germany and Denmark; ESP, Spain; FRP-N, northern part of France; FRP-S, central & southern part of France; GBT-N, northern parts of the UK—Wales, England, Scotland and Northern Ireland—and Ireland; GBT-S, southern parts of the UK—England and Wales; HGB, Hungary; NLA, the Netherlands; SFH, Finland; SVS, Sweden.



**FIGURE 2** | Wintering grounds of the long-distance migrants in sub-Saharan Africa and land cover classes in the regions. NW arid, Northwest arid region; NW humid, Northwest humid region; NE arid, Northeast arid region; E arid, East arid region; C humid, Central humid region; S humid, South humid region; S arid, South arid region. The extent of relevant land cover classes as derived from MODIS MCD12Q1v061 layers (Friedl and Sulla-Menashe 2022) in the year 2004 is shown. Details on the land cover classes are in Table S2.

while PET is the extent of evapotranspiration that would have occurred in a fully water-saturated ecosystem (Mu, Zhao, and Running 2011). We calculated ETr for the area covered by six land cover types (see chapter 2.1 Bird data) in each wintering region (Figure 2 and Table S2) for the period of September to April in each winter preceding the breeding season in each year (starting from 2003/2004). Evapotranspiration data were extracted from the MODIS MOD16A2GFv061 dataset (resolution 500m per pixel; Running et al. 2021), land cover data from the MODIS MCD12Q1v061 (resolution 500m per pixel; Friedl and Sulla-Menashe 2022) and the CIFOR Global Wetland V3b dataset (resolution upscaled from originally 231 to 500m per pixel; Gumbricht et al. 2017). For details on the calculation of ETr, refer to Supplementary Material 2.

To test the effects of climate changes on breeding productivity (Hypothesis 3, Table 2), we needed to acquire temporal trends in climate variables in the breeding regions. We used the main gradients of temperature-related variables ( $T$ , GDD10, GOD) obtained by Principal Component Analysis (PCA), instead of calculating temporal trends of individual climate variables. This approach enabled us to analyse the complex effects of climate warming, comprising both direct (temperature per se) and indirect temperature-related variables (e.g., our variables GDD10, GOD), using a single variable (PC gradient). We employed the PCA separately for each month (from March to June) and each year to obtain the gradients of climatic variables. For further

analysis, we considered only PC1 (accounted for 77%–92% of variance explained, depending on the month and year), which described a gradient from cold regions with delayed spring onset to warm regions with early spring onset (Figure S7). We then extracted PCA scores for each site from the main PC gradient and calculated the means of the scores for each region, month, and year. Then we employed a linear model  $PCA\ scores \sim Year$  separately for each region and month to derive the temporal trend in warming in a given region (Figure S8); we did not consider nonlinear trends as they were not expected to occur during our period of study. In cases where we detected temporal autocorrelation using the *check\_autocorrelation* test in the ‘performance’ R-package (Lüdecke et al. 2021), we employed a generalised least squares (GLS) model  $PCA\ scores \sim Year + AR1(Year)$  with an AR(1) correlation structure to account for temporal autocorrelation in the data. Trend coefficients (see Supplementary Material 3) were extracted from the GLS models if they outperformed the linear models with a  $\Delta AICc > 2$ .

### 2.3 | Data Analyses

To investigate the responses of bird breeding productivity to climate variables in different breeding regions (Hypothesis 1, Table 2), we built a model, which had two variants, Model 1a and Model 1b. The first variant contained both the linear and quadratic (polynomial) terms (Model 1a) and the second variant

contained solely the linear terms (Model 1b). In both variants, we employed generalised mixed-effects models (GLMM) with a binomial distribution of errors and a logit link function using the *glmmTMB* function from the R-package 'glmmTMB' (Brooks et al. 2017). For each month, we fitted separate models relating climate variables to breeding productivity. Model notation can be described as follows:

$$\begin{aligned} \text{Productivity} \sim & \text{Clim}_1^* \text{Reg} + \dots + \text{Clim}_n^* \text{Reg} + \text{Clim}_1^{2*} \text{Reg} + \dots \\ & + \text{Clim}_n^{2*} \text{Reg} + \text{ETr}^* \text{Reg} + \text{Ad\_abund}^* \text{Reg} + \\ & (1 + \text{Clim}_1^* \text{Reg} + \text{Clim}_1^{2*} \text{Reg} + \dots + \text{Clim}_n^* \text{Reg} + \text{Clim}_n^{2*} \text{Reg} \\ & + \text{Ad\_abund} \mid \text{Species: Site: Reg}) + (1 \mid \text{Species: Year: Reg}) \\ & + (1 \mid \text{Species: Reg}). \end{aligned} \quad (\text{Model 1a})$$

$$\begin{aligned} \text{Productivity} \sim & \text{Clim}_1^* \text{Reg} + \dots + \text{Clim}_n^* \text{Reg} + \text{ETr}^* \text{Reg} \\ & + \text{Ad\_abund}^* \text{Reg} + (1 + \text{Clim}_1^* \text{Reg} + \dots + \text{Clim}_n^* \text{Reg} \\ & + \text{Ad\_abund} \mid \text{Species: Site: Reg}) \\ & + (1 \mid \text{Species: Year: Reg}) + (1 \mid \text{Species: Reg}). \end{aligned} \quad (\text{Model 1b})$$

The response variable (*Productivity*) was the proportion of the abundance of juvenile to adult birds in a given site, year and region for each species. The explanatory variables included eight climate variables in the breeding grounds (*Clim*<sub>1</sub>, *Clim*<sub>2</sub>, ...*Clim*<sub>n</sub>), water availability in the wintering grounds (*ETr*), and abundance of adults (*Ad\_abund*). During model composition, we checked the relationships between climate variables (*Clim*), and the variables with Pearson's correlations  $|r| > 0.70$  (Figure S9) were not used in the same model for a given month. Therefore, Model 1a and Model 1b contained several submodels consisting of only weakly correlated climate variables. Sometimes we also excluded the less correlated climate variables to maintain a consistent model structure for March and April (two submodels for each month), and for May and June (two submodels for Model 1a and eight submodels for Model 1b for each month); see Table 4 for the specific variables included in each submodel. We centred *Clim* to zero mean for each site and region to remove the spatial variation of climate across sites and regions. *ETr* is the ratio of actual to potential evapotranspiration (water availability) in the wintering grounds in each year. *Ad\_abund* is the abundance of adults for each site, year and region, included to control for known negative density-dependent responses in breeding productivity (e.g., Jørgensen et al. 2016; Meller et al. 2018; Telenský et al. 2020), standardised to zero mean and unit *SD* for each site and species to obtain relative site-specific abundances of each species. Random slopes for *Clim* allow for species-, site- and region-specific responses of productivity to climate, resulting from potentially different sensitivity of particular species to climate effects. The random slope for *Ad\_abund* controls for the assumed variability in site-dependent regulation of abundance in each species and region, resulting from possibly varying relative quality of the sites (Rodenhouse, Sherry, and Holmes 1997), independent of the climate conditions in these sites. The random intercept for *Species:Year:Reg* allows for species- and region-specific interannual variability in the responses of breeding productivity, and the random intercept for *Species:Reg* allows for species- and region-specific variability of responses. The models

converged successfully, and the random effects explained a significant proportion of the variance, which supports the complex model structure of Model 1a and Model 1b. We checked for the presence of model overdispersion using *check\_overdispersion* test from the R-package 'performance'; overdispersion was not present in any of the models. The variables *Clim*, *ETr*, and also the already site- and species-standardised *Ad\_abund* were standardised to zero mean and unit *SD* across the whole dataset to facilitate model convergence.

Because we fitted more than one model for some of the climate variables (Table 4), we performed model averaging using the R-package 'MuMIn' (Bartoń 2018) for inference. We set Akaike weights to 1 for each model before averaging to assign them equivalent performance, as we did not search for the set of the best performing climate variables. We obtained the averaged coefficients for each climate variable and region using a function *emtrends* from the R-package 'emmeans' (Russell 2022). We present support for the hump-shaped patterns (Hypothesis 1, prediction P1a; Table 2) based on the statistical significance ( $p < 0.05$ ) of respective climate effects in Model 1a. When hump-shaped patterns in Model 1a and linear relationships in Model 1b were both statistically significant, we present both relationships in the plots, because averaged models cannot be compared by common metrics like AIC or R-squared. Support for linear effects of climate variables (Hypothesis 1, prediction P1b; Table 2) was assessed by their statistical significance in Model 1b.

We investigated whether bird responses to climate differed between regions, expecting different responses in different climatic conditions (Hypothesis 2, Table 2). To do so, we fitted Bayesian meta-analytic models using the function *brm* in the 'brms' R-package (Bürkner 2021) to take into account the standard errors of the coefficients describing breeding productivity responses to climate in each region. The structure of the models was  $\text{Reg\_coef} \mid \text{SE\_reg\_coef} \sim \text{Clim}$  and  $\text{Reg\_coef} \mid \text{SE\_reg\_coef} \sim \text{Clim} + \text{Clim}^2$ . The response variable *Reg\_coef* is regression coefficients describing the linear or second-order (quadratic) polynomial responses of birds' productivity to climate in each region derived from Model 1b or Model 1a, respectively, separately for each climate variable and month of March, April, May, and June. *SE\_reg\_coef* is the measurement error of the response variable represented by the standard errors of the regression coefficients. *Clim* and *Clim*<sup>2</sup> represent the mean values of *T*, *GDD10*, or  $\Delta R$  climate variables (i.e., climate variables relevant for testing of Hypothesis 2) in respective regions, included as linear or quadratic forms into the models, respectively. The models were run with 4000 warmup and 5000 total iterations for each of the four Markov chains. Priors were set to Normal(0, 0.5) distribution for the climate effects and to Cauchy(0, 0.5) distribution for sigma parameters. To eliminate divergent transitions during model fitting, we increased *adapt\_delta* to 0.95 or set 5000 warmup and 6000 total iterations per chain when needed. We considered statistical evidence of the climate effects when the proportion of the posterior distribution of the climate effect in ROPE was <3%. ROPE is the region of practical equivalence corresponding to the range of values with negligible magnitude, here defined as 100% of the highest density interval (HDI). When calculating the range of ROPE, we set limits to  $\pm 0.1 * \text{SD}(\text{response variable})$  following Kruschke (2018). For climate variables showing a

**TABLE 4** | Climate variables included in Model 1a and Model 1b (see chapter 2.3 Data analyses for their definitions) used to test Hypothesis 1 (Table 2).

Month	Submodel #	Climate variables	
		Model 1a	Model 1b
March	Submodel 1	$T, T^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$T, \text{GOD}, \Delta R$
	Submodel 2	$\text{GDD}10, \text{GDD}10^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$\text{GDD}10, \text{GOD}, \Delta R$
April	Submodel 1	$T, T^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$T, \text{GOD}, \Delta R$
	Submodel 2	$\text{GDD}10, \text{GDD}10^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$\text{GDD}10, \text{GOD}, \Delta R$
May	Submodel 1	$T, T^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$T, \text{GOD}, \Delta R, R1c$
	Submodel 2	$\text{GDD}10, \text{GDD}10^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$T, \text{GOD}, R10, R1c$
	Submodel 3		$\text{GDD}10, \text{GOD}, \Delta R, R1c$
	Submodel 4		$\text{GDD}10, \text{GOD}, R10, R1c$
	Submodel 5		$T, \text{GOD}, \Delta R, R2c$
	Submodel 6		$T, \text{GOD}, R20, R2c$
	Submodel 7		$\text{GDD}10, \text{GOD}, \Delta R, R2c$
	Submodel 8		$\text{GDD}10, \text{GOD}, R20, R2c$
June	Submodel 1	$T, T^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$T, \text{GOD}, \Delta R, R1c$
	Submodel 2	$\text{GDD}10, \text{GDD}10^2, \text{GOD}, \text{GOD}^2, \Delta R, \Delta R^2$	$T, \text{GOD}, R10, R1c$
	Submodel 3		$\text{GDD}10, \text{GOD}, \Delta R, R1c$
	Submodel 4		$\text{GDD}10, \text{GOD}, R10, R1c$
	Submodel 5		$T, \text{GOD}, \Delta R, R2c$
	Submodel 6		$T, \text{GOD}, R20, R2c$
	Submodel 7		$\text{GDD}10, \text{GOD}, \Delta R, R2c$
	Submodel 8		$\text{GDD}10, \text{GOD}, R20, R2c$

Note: Both models consisted of several different submodels in each month to avoid including climate variables with strong correlations to each other into a single model (Figure S9). The submodels contained different climate variables allowing to test predictions P1a and P1b (see Table 2). The effects of climate variables included in more than one submodel for a given month were averaged across respective submodels. Quadratic (polynomial) terms are indicated by upper index (e.g.,  $T^2$  for quadratic effect of temperature).

Abbreviations: GDD10, growing degree-days; GOD, Green-up onset date; R10, heavy rain days; R20, very heavy rain days; R1c, consecutive rain days with 1 mm precipitation; R2c, consecutive rain days with 2 mm precipitation; T, temperature;  $\Delta R$ , precipitation anomaly.

significant pattern of the responses across the regions (support for Hypothesis 2), we also compared the responses between regions using the function *cld* from R-package ‘multcomp’ (Hothorn, Bretz, and Westfall 2008). For this test, we applied a correction for multiple comparisons using a multivariate t-test in the function *emtrends* from the R-package ‘emmeans’.

We tested whether the temporal trends in warming in respective regions affected the relationships between breeding productivity and climate variables (Hypothesis 3, Table 2). For this analysis, we fitted Bayesian meta-analytic models with the structure  $\text{Reg\_coef} | \text{SE\_reg\_coef} \sim \text{Trend}$ . The response variables *Reg\_coef* and its measurement error *SE\_reg\_coef* are the same as in the Bayesian models testing Hypothesis 2 (see the previous paragraph), and *Trend* are the regression coefficients quantifying the temporal trends in warming in the respective breeding regions. These trends were calculated by regressing PCA scores (obtained by PCAs that summarised all temperature-related variables into a single component, see chapter 2.2 Climate data) over years in each region (see Supplementary Material 3).

The models were run with 4000 warmup and 5000 total iterations for each of the four Markov chains. Priors were set to Normal(0, 0.5) distribution for the temporal trend effects and to Cauchy(0, 0.5) distribution for sigma parameters. To eliminate divergent transitions during model fitting, we increased *adapt\_delta* to 0.95 or set 5000 warmup and 6000 total iterations per chain when needed.

We calculated the proportion of temporal variability in breeding productivity explained by each climate variable (*R2\_var*), while taking into account the effect of water availability in wintering grounds, according to Grosbois et al. (2008; their equation 7). The values of *R2\_var* were calculated using each model (see Table 4), since the random effects necessary for the calculation were not present in the final averaged models. All models were fitted using R statistical software v4.3.1 (R Core Team 2023), and all figures, including maps, were created using QGIS v3.32.2 (QGIS.org 2023). Fitting the models can be reproduced using an R-script available at Dryad (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.fxpnvx0zt>).

### 3 | Results

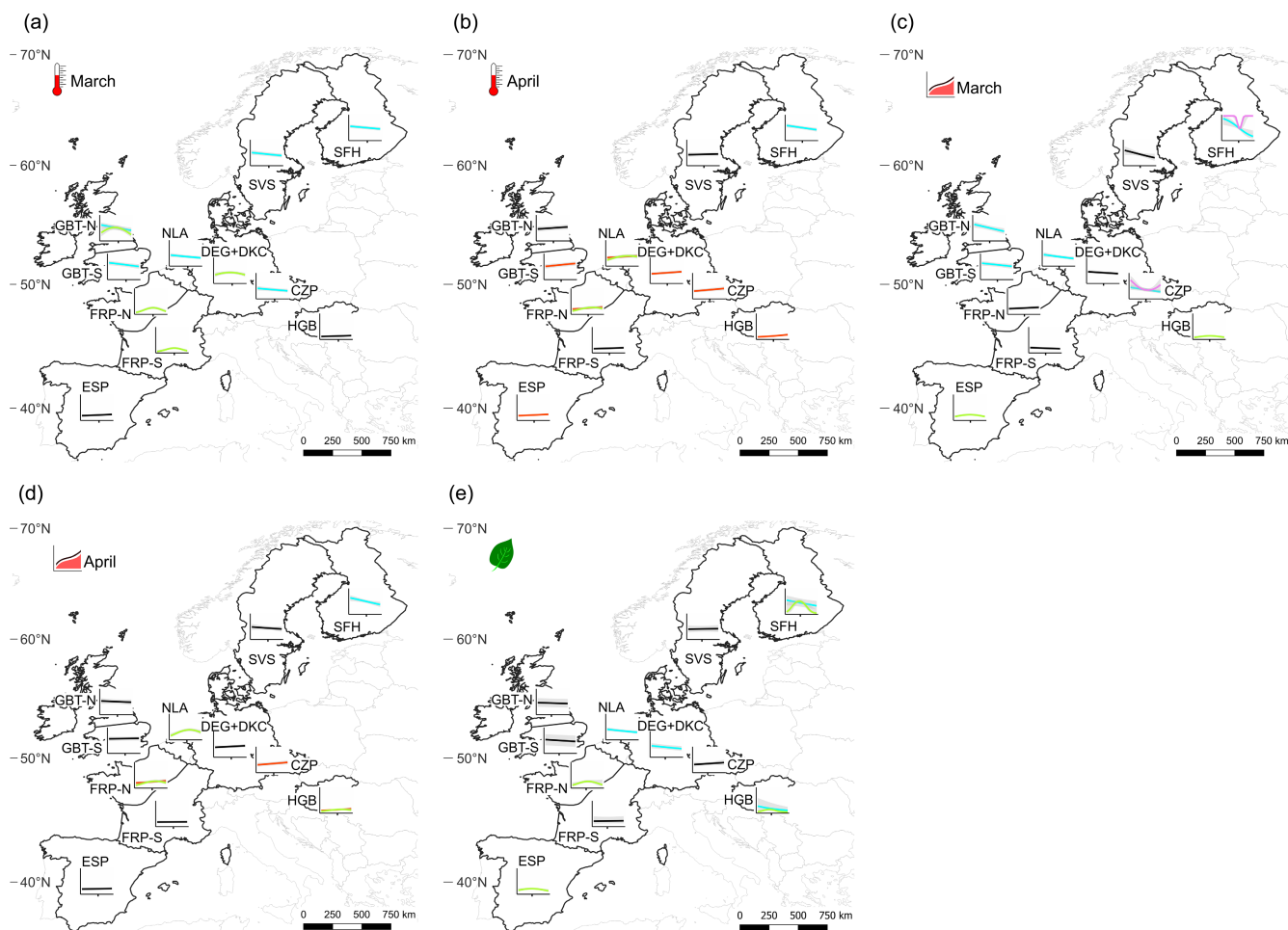
#### 3.1 | Hypothesis 1: Shape of Productivity Responses to Climate

In the case of temperature-related variables, Prediction 1a regarding hump-shaped relationships between breeding productivity and climate (see Table 2) was partially supported. We found the expected hump-shaped relationships with temperature, GDD10, and green-up onset date (GOD) in many regions, where these relationships accounted for more than 25% of all responses to temperature-related variables. However, positive and negative linear responses were more common, accounting for almost 30% and 20% of all responses, respectively, and even four *U*-shaped responses appeared (Figures 3 and 4). The number of hump-shaped responses to temperature and GDD10 did not differ between early (March and April) and late spring (May and June) (Figures 3 and 4).

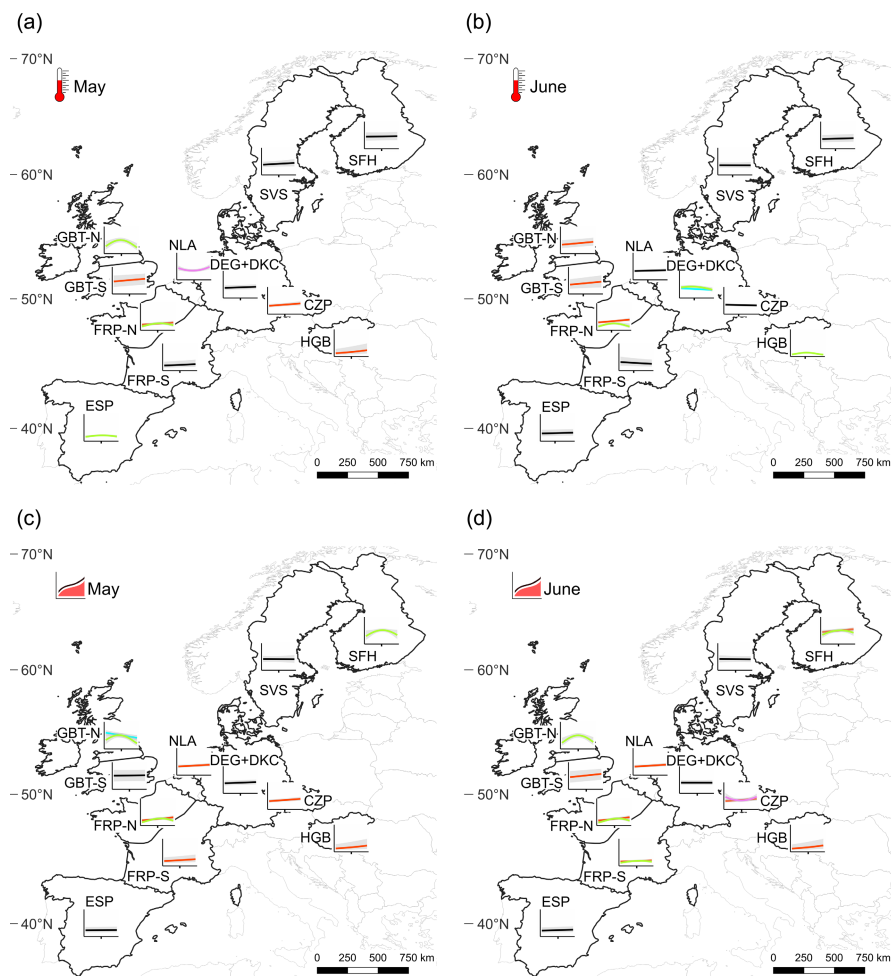
Prediction 1a was supported by only six hump-shaped relationships (out of 44) in the case of the effects of the early and

late spring precipitation anomaly  $\Delta R$  (Figure 5a–d). The other responses were negative (12), positive (4), *U*-shaped (6) or non-significant (18). The Prediction 1b of the negative effects of intense (R10) and prolonged rains (R1c) (see Table 2) received slightly better support, as 10 out of 44 relationships were negative in May and June (Figure 5e–h). The other responses were positive (2) and nonsignificant (32). A similar result of 11 negative responses out of 44 was found even when considering the related variables of very heavy rain days (R20) and prolonged rain days with at least 2 mm of daily rainfall (R2c) in these months (Figure S10).

The temporal variance of breeding productivity ( $R2\_var$ ) explained by climate variables, while taking into account the effect of water availability in wintering grounds, varied between 0 and 15% for temperature, 1% and 12% for GDD10, and 3% and 12% for GOD, while precipitation anomaly  $\Delta R$  explained between 1% and 11% of the variance, R10 and R20 between 2% and 8%, and R1c and R2c between  $-1\%$  and 4% (Table S3). Note that the negative values of  $R2\_var$  suggest that the model might not adequately explain breeding productivity or that the



**FIGURE 3** | Responses of long-distance migrants' breeding productivity to early spring (March and April) (a, b) temperature and (c, d) GDD10, and (e) green-up onset dates in the study regions. Positive (red line), negative (cyan line), polynomial hump-shaped (quadratic; lime curve) and *U*-shaped (magenta curve), and nonsignificant (black line) responses are shown. Polynomial (quadratic) and linear responses of breeding productivity to climate are shown overlapping if both were statistically significant in a given region. The tick on the *x*-axis of each region-specific plot shows a value of 0 for the respective standardised (mean = 0,  $SD = 1$ ) climate variables. Note that due to many zero values of GDD10 in March in SFH, the shape of the corresponding quadratic response is distorted. Refer to Figure 1 for an explanation of the region abbreviations.



**FIGURE 4** | Responses of long-distance migrants' breeding productivity to late spring (May and June) (a, b) temperature and (c, d) GDD10 in the study regions. Positive (red line), negative (cyan line), polynomial hump-shaped (quadratic; lime curve) and *U*-shaped (magenta curve), and nonsignificant (black line) responses are shown. Polynomial (quadratic) and linear responses of breeding productivity to climate are shown overlapping if both were statistically significant in a given region. The tick on the x-axis of each region-specific plot shows a value of 0 for the respective standardised (mean = 0,  $SD = 1$ ) climate variables. Refer to Figure 1 for an explanation of the region abbreviations.

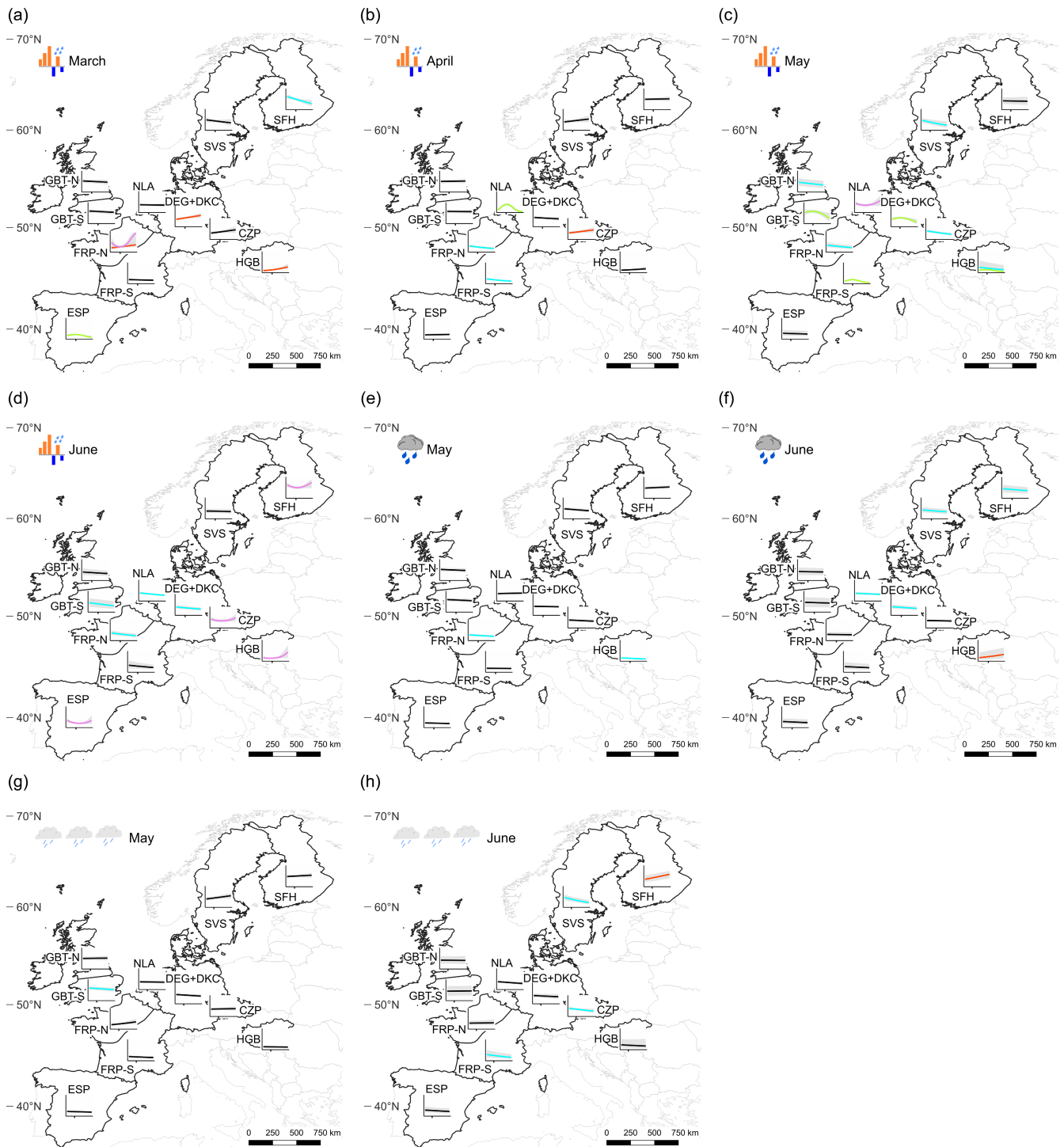
climate effects are very minimal, leading to limited capability of  $R2\_var$  in capturing the temporal variance of breeding productivity.

### 3.2 | Hypothesis 2: Differences in Productivity Responses to Climate Variables Between Regions

We found statistical evidence ( $\%ROPE < 3\%$ ) for three relationships between the linear regression coefficients derived from Model 1b and the mean values of the corresponding climate variables across the study regions (Figure 6). Two relationships corresponded to the patterns expected from Prediction 2a, that is, more negative effects of temperature-related variables in colder than warmer regions (see Table 2). We found that linear responses of breeding productivity to early spring temperatures (April) were more positive in warmer regions compared to colder regions (Figure 6a). The comparison of the responses to April temperatures between regions has shown that the responses in Finland were markedly more negative than those in all other regions except Sweden (Figure 7a). The effects of April GDD10 on breeding productivity were more

positive towards the regions with higher accumulated heat, but the hump-shaped pattern across regions suggested that too much accumulated heat may decrease breeding productivity (Figure 6b). Specifically, we found that in regions with higher accumulated heat, such as Czechia, the northern part of France, and Hungary, the responses were more positive than in regions with the lowest GDD10, such as Finland, but we did not find different responses to the region with the highest GDD10, that is, Spain (Figure 7b).

Prediction 2b, that is, the more negative effects of precipitation anomalies in drier than wetter regions (see Table 2), was partially supported by a *U*-shaped relationship of breeding productivity to June precipitation anomaly  $\Delta R$  (Figure 6c). The pattern suggests that breeding productivity was higher in regions with low  $\Delta R$ , such as Sweden and Czechia, than in regions with average  $\Delta R$ . However, in regions with high  $\Delta R$ , like Hungary, the breeding productivity increased. The comparison of the responses to June  $\Delta R$  between regions has shown that breeding productivity was significantly higher in Hungary compared to regions with different levels of  $\Delta R$ , such as the Netherlands, the northern part of France, and the southern part of the UK (Figure 7c).

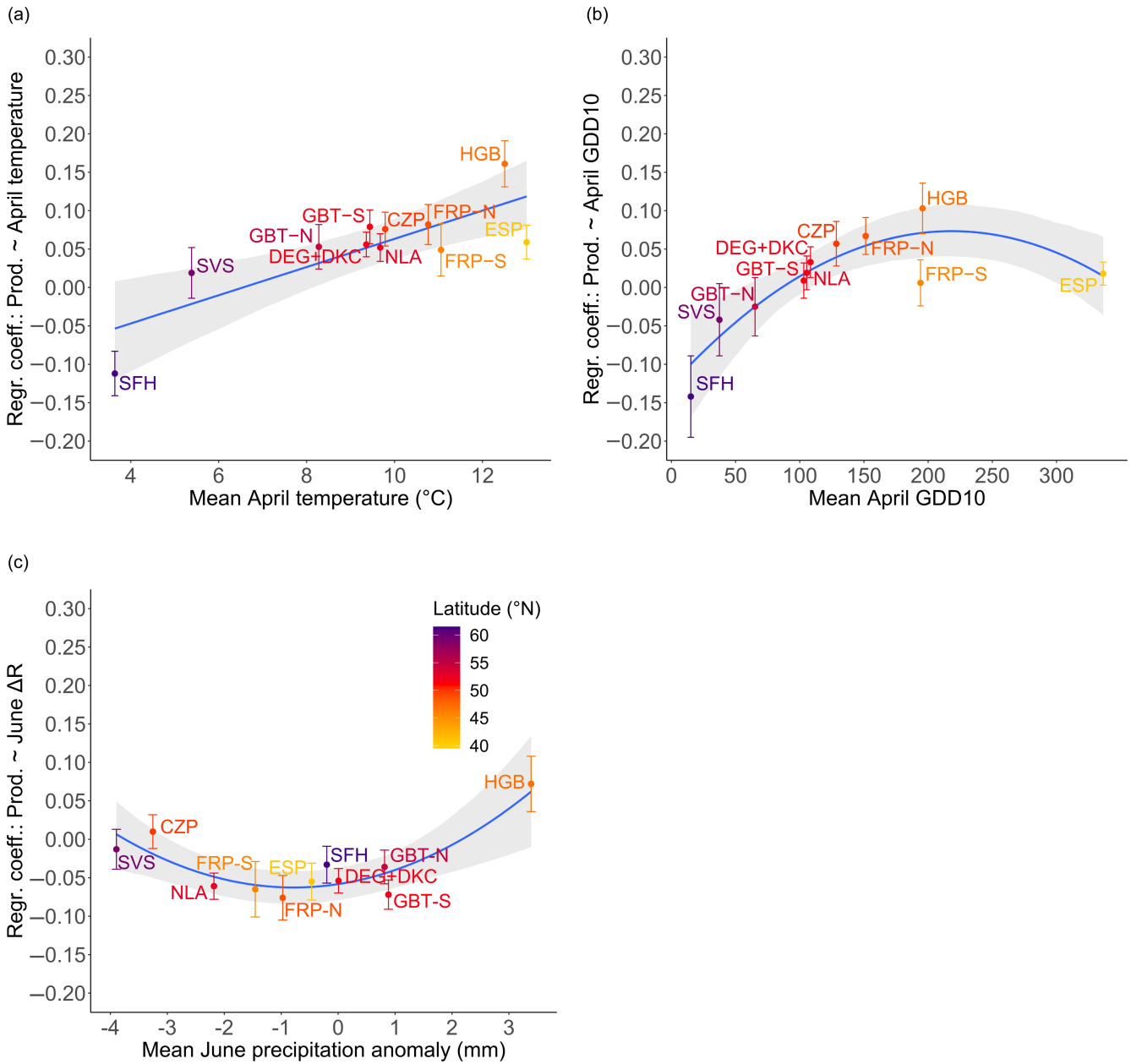


**FIGURE 5** | Responses of long-distance migrants' breeding productivity to early and late spring (March to June) (a–d) precipitation anomaly ( $\Delta R$ ), and late spring (May, June) (e, f) heavy rain days (R10), and (g, h) consecutive rain days (R1c) in the study regions. Positive (red line), negative (cyan line), polynomial hump-shaped (quadratic; lime curve) and *U*-shaped (magenta curve), and nonsignificant (black line) responses are shown. Polynomial (quadratic) and linear responses to climate are shown overlapping if both were statistically significant in a given region. The tick on the *x*-axis of each region-specific plot shows a value of 0 for the respective standardised (mean = 0, *SD* = 1) climate variables. Refer to Figure 1 for an explanation of the region abbreviations.

### 3.3 | Hypothesis 3: Effects of Temporal Trends in Climate Warming on Productivity

We did not find any statistical evidence (%ROPE < 3%) for effects of temporal trends in warming (Figure S8) in respective regions on

the relationships between breeding productivity and temperature-related variables (Supplementary Material 6). Therefore, Prediction 3a about more negative and more positive effects of early and late spring temperature-related variables, respectively, in regions experiencing faster climate warming, (see Table 2) was not supported.

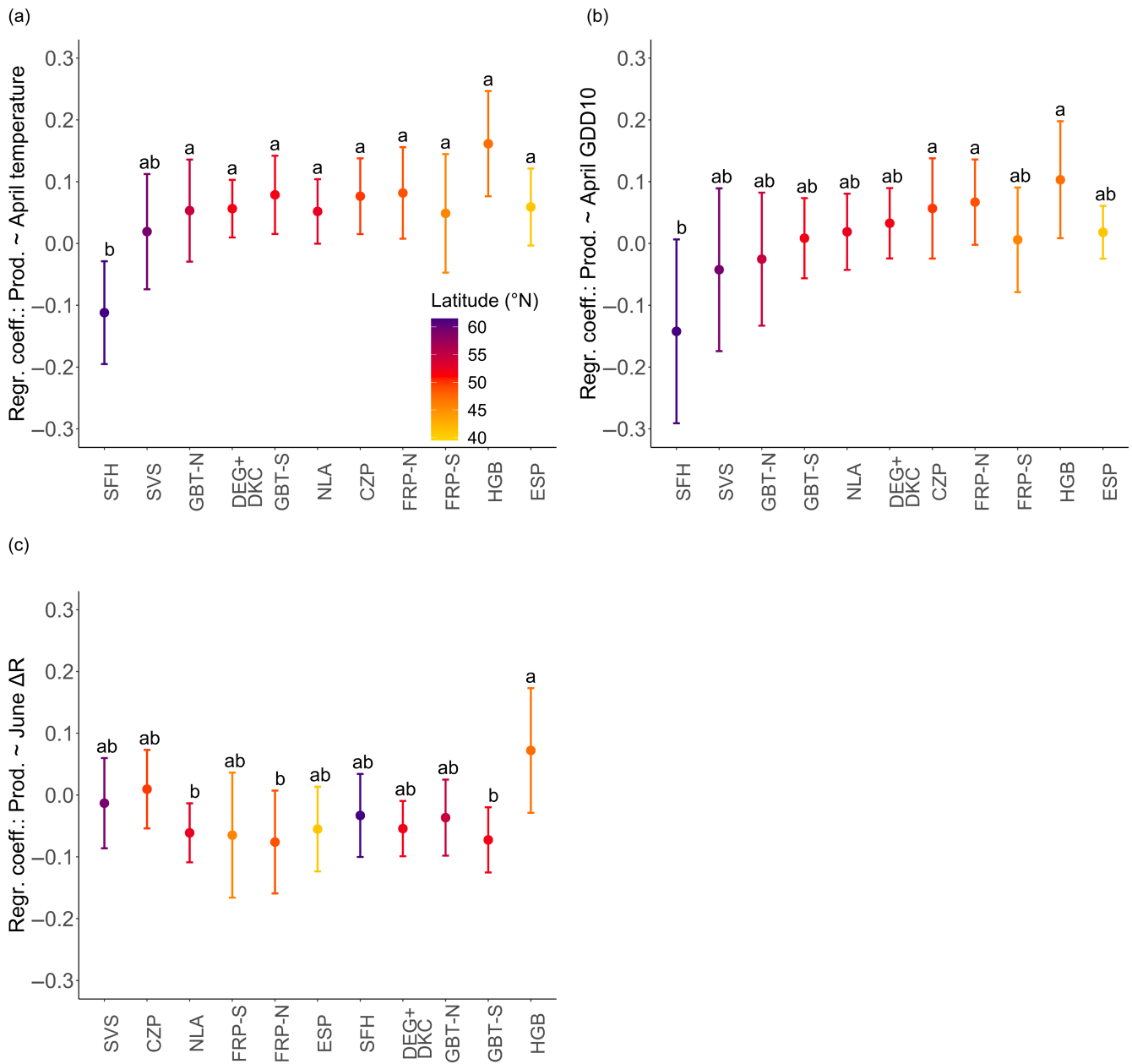


**FIGURE 6** | Relationships between the regression coefficients, derived from Model 1b, and mean values of (a) April temperature, (b) April GDD10, and (c) June precipitation anomaly across the study regions. Regression coefficients represent the responses (slopes) of breeding productivity to climate in each region (tested in Hypothesis 1) obtained from Model 1b. Error bars depict standard errors of the regression coefficients. Average latitude across all sites in each region is shown using a colour gradient. For a detailed model output see the Supplementary Material 7. Refer to Figure 1 for an explanation of the region abbreviations.

#### 4 | Discussion

We investigated the relationships between the breeding productivity of 23 long-distance migratory bird species and temperature-related and precipitation-related climate variables in 11 European regions while controlling for the influence of climatic conditions in wintering grounds. We found hump-shaped relationships of breeding productivity to temperature-related variables ( $T$ , GDD10, GOD) and precipitation anomaly ( $\Delta R$ ) in some regions for March, April, May, and June. This pattern suggested that the highest breeding productivity was connected with values of climate variables around their local averages in

respective regions. The increased numbers of heavy rain days ( $R10$ ,  $R20$ ) and consecutive rain days ( $R1c$ ,  $R2c$ ) were associated with decreased breeding productivity in a small number of regions as well. In general, these patterns indicate some support for the predictions of Hypothesis 1 (Table 2), but this support was modest because various other kinds of relationships between productivity and the climate variables were found in our data. When comparing the analysed relationships between the regions, we observed that breeding productivity decreased with higher early spring temperature (April) in colder regions but increased in warmer regions, in line with the prediction of Hypothesis 2 (Table 2). This prediction was additionally partially



**FIGURE 7** | Comparison of breeding productivity responses to climate between particular regions considering the climate variables that have shown significant patterns across regions (Figure 6), that is, (a) April temperature, (b) April GDD10, and (c) June precipitation anomaly. Mean values of regression coefficients and 95% confidence intervals, adjusted for multiple comparisons using a multivariate *t*-distribution, are shown. Different letters above the bars indicate different responses for the given regions. For a detailed output of the comparisons, see the Supplementary Material 8. Refer to Figure 1 for an explanation of the region abbreviation.

supported by productivity responses to April GDD10, which showed that productivity decreased when GDD10 was high in regions with low accumulated heat. However, a decrease in productivity associated with higher GDD10 also occurred in the region with the highest accumulated heat. In the later spring, the relationship of breeding productivity to precipitation anomaly also partially supported Hypothesis 2. We found that the effects of June precipitation anomaly on productivity were more positive in relatively dry regions, but unexpectedly, productivity was positively affected by precipitation in relatively wet regions as well. Predictions of Hypothesis 3 (Table 2) about the effects of climate change velocity on the productivity-climate relationships were not supported.

#### 4.1 | Nonlinear, Positive, and Negative Responses of Productivity to Climate

The relationships between bird reproductive output and various climate variables have been widely studied across different climatic regions (Amano et al. 2020; Halupka et al. 2023; Vega, Fransson, and Kullberg 2021). However, only a minority of studies have focused on identifying the climatic conditions on breeding grounds that are connected with the highest breeding performance of birds, finding hump-shaped relationships between nest occupancy and rainfall (Rodríguez and Bustamante 2003), breeding productivity and temperature anomaly (Eglington et al. 2015), and population growth rate and

site temperature (Martay, Pearce-Higgins, et al. 2023). Here, hump-shaped patterns of responses emerged for spring temperature and GDD10. These patterns indicate that both excessively low and high temperatures occurring at the beginning as well as late in spring could decrease breeding productivity. Among possible mechanisms underpinning these effects, we can rank earlier peak of food abundance in warm springs, causing potential mismatch in food supply and demand (Burgess et al. 2018), or the cold spells responsible for increased mortality of adult migratory birds shortly after their arrival to breeding grounds (Newton 2007). In general, the presence of hump-shaped patterns emphasises the importance of investigating nonlinear responses in bioclimatological studies.

The frequent negative responses of productivity to March temperatures in various regions suggest that the increases of temperatures very early in the spring could contribute to earlier spring onset, associated with greater phenological asynchrony in birds and their food resources (Wood and Pidgeon 2015), leading to lower breeding productivity. This particularly applies to higher latitudes (Finland) where consistently negative effects of higher temperatures and accumulated heat in March and April on productivity were observed. In contrast, the positive responses to temperatures and accumulated heat observed later in the spring across regions indicate that the mismatch may not occur if the breeding period of migrants is already under way, and LDMs can indeed benefit from warmer springs. The benefits can be linked to ameliorated food supplies (Townsend et al. 2016), lower thermoregulatory costs (Dawson, Lawrie, and O'Brien 2005) or more frequent/successful supplementary breeding attempts (Halupka, Dyrcoz, and Borowiec 2008).

Spring onset is a critical point in the breeding season, as it is linked to the rapid emergence of resources in the food chain (Fernández-Tizón et al. 2020), where birds typically function as secondary consumers. Although an advancement or delay in spring onset can result in lower breeding productivity due to phenological mismatch (Lany et al. 2016; Visser et al. 2015), breeding productivity has shown statistically nonsignificant relationships with the green-up onset date in roughly half of the regions, and hump-shaped patterns appeared only in a few of them. This suggests, together with the positive effects of temperatures and accumulated heat later in the spring discussed above, that phenological mismatch may impact breeding productivity less significantly than it has been attributed (Martay, Leech, et al. 2023; Nater et al. 2023), probably due to the successful tracking of spring phenology (Jonzén et al. 2006; Klueen, Nousiainen, and Lehtikoinen 2017; Valtonen et al. 2017), or due to the adoption of various mechanisms to cope with the mismatch, such as adaptation to alternative insect food sources (Mallord et al. 2017) or shortening the interval between nest building and egg laying (Lany et al. 2016). On the other hand, regions characterised by nonlinear responses to the green-up onset date included areas at lower (Spain), middle (northern France, Hungary) and higher latitudes (Finland), which implies that LDMs may be negatively affected by both earlier and later onset of spring across latitudes. However, the negative effects of green-up onset dates found at middle and high latitudes could mean that slowing down the development of vegetation limited the food resources (insects) available to birds more severely, with a consequently greater negative impact on breeding productivity.

The negative effects of intense and prolonged rainfall on breeding productivity are in line with the detrimental impact of water excess during breeding, associated with a lack of food for nestlings (Anctil, Franke, and Bêty 2014; Schöll and Hille 2020). This pattern of negative responses found across the study regions and months indicated that birds did not benefit from heavy or persistent rainfall also in drier regions. Given that ongoing climate changes are likely to intensify precipitation (Trenberth 2011), birds may experience more severe consequences from excessive rains in the future (Cohen, Fink, and Zuckerberg 2020). In this context, we note that regular precipitation may have a different impact on productivity than strong rains because we found a positive effect of precipitation anomaly on productivity in both relatively dry and wet regions.

## 4.2 | Differences in Productivity Responses to Climate Variables Between Regions

The positive effects of increased early spring (April) temperatures and GDD10 on productivity in warm regions, though not in that with the highest accumulated heat, and the less positive or even negative effects of these climate variables in cold regions, could be associated with the earlier breeding onset at lower latitudes than higher latitudes. Many LDMs arrive much earlier on the breeding grounds in the south than in the north (Sullivan et al. 2009), which may enable them to utilise the increased temperatures and higher GDD10 early in the spring to start breeding earlier and increase their breeding productivity (Halupka et al. 2021; Hoover and Schelsky 2020). But note that such benefits of more available energy in the ecosystem may not be pronounced in the warmest regions because much more GDDs are needed to initiate spring onset at lower compared to higher latitudes (Fu et al. 2014). This is the reason for the less positive responses of productivity to GDD10 in Spain than would be expected for a linear trend of responses across latitudes. Additionally, we should remind that many LDMs breeding at higher latitudes do not arrive there by April (Sullivan et al. 2009), and thus they cannot directly respond to increased temperatures and GDD10 in these months. We found that LDMs can be negatively affected by higher prebreeding temperatures which can strongly advance spring onset in boreal regions (Montgomery et al. 2020) and subsequently increase phenological mismatch (Youngflesh et al. 2023). However, LDM's responses to spring onset date were both negative and hump-shaped in the coldest region. An intuitive explanation of these ambiguous effects in the north could be that different LDMs have different sensitivities to phenological mismatch or breeding temperatures, which may result in relationships we observe here. The alternative explanation for the negative effects of early spring temperatures on productivity in cold areas, presumably coming from a higher rate of climate warming in these regions, was not supported by our results. We did not find any support for the prediction that faster warming amplifies the negative impacts of phenological mismatch and consequently decreases productivity, although bird populations have been shown substantially declining in areas with the fastest rate of climate warming at a global scale (Spooner, Pearson, and Freeman 2018). However, it should be noted that Euro-CES schemes practically do not cover areas around the polar circle (Figure 1), where the rate of climate warming is the

highest (Rantanen et al. 2022). Lastly, some of the relationships between productivity and climate might be less clear due to a high influence of fledging and postfledging survival on breeding productivity (Ekman and Askenmo 1986). Unfortunately, additional data on nesting, not provided by Euro-CES datasets, would be needed to take survival effects into account.

The U-shaped pattern of the responses of breeding productivity to June precipitation anomaly ( $\Delta R$ ) across regions showed that increased rainfall in relatively dry regions increased breeding productivity. This increase could be due to the positive effect of water supply from precipitation on breeding productivity in dry environments (Skagen and Adams 2012). The unexpected positive effect of increased rainfall in the relatively wettest region (Hungary) could be a consequence of the joint effect of temperature and precipitation. Given this effect was observed in one of the warmest regions, high temperatures, which limit resources in ecosystems (mainly bird food), could be compensated for by increased rainfall, similarly to arid areas (Mares et al. 2017), although to a much smaller extent.

## 5 | Conclusions

Our findings reveal that the highest breeding productivity of LDMs can be related to local average values of climate variables, as demonstrated by the hump-shaped responses especially to direct (temperature itself) and indirect (growing degree-days, green-up onset day) effects of temperature. Given the general support for this pattern across regions, covering a large part of Europe, we recommend that future studies investigating the relationships between climate components and bird demographics also consider quadratic and other nonlinear responses. Although we did not find evidence for more pronounced impacts of climate on bird productivity in regions undergoing the most rapid climate changes, we did uncover consistent negative impacts of water excess manifested by consecutive rain days and very heavy rains. The importance of this climate aspect may increase in the coming decades or even years as global climate change progresses (Pörtner et al. 2022).

### Author Contributions

J.R., T.T., and J.H. designed and planned the study. O.B., J.C., R.A.R., G.G., P.-Y.H., I.H., H.v.d.J., Z.K., P.L., B.M., A.L.N., M.P., K.T., and A.P.T. curated Euro-CES datasets. J.H., J.K., and P.P. investigated the ringing data and determined wintering habitats in Africa. J.H. and T.T. designed the statistical models, performed the analyses, and interpreted the results. J.H. and J.R. wrote the first draft of the manuscript. All the authors contributed to the writing of this manuscript and approved the final version before submission.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The datasets generated during and/or analysed during the current study are available in the Dryad repository at <https://datadryad.org/stash/dataset/doi:10.5061/dryad.fxpnvx0zt>.

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## Supporting Information

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