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The need for large-scale distribution data to estimate regional changes in species richness under future climate change

Nicolas Titeux[1,2,3,4] (iD) | Dirk Maes[5,6] (iD) | Toon Van Daele[5] (iD) | Thierry Onkelinx[5] (iD) |
Risto K. Heikkinen[7] | Helena Romo[8] (iD) | Enrique García-Barros[8] (iD) |
Miguel L. Munguira[6,8] (iD) | Wilfried Thuiller[9] (iD) | Chris A. M. van Swaay[6,10] (iD) |
Oliver Schweiger[3] (iD) | Josef Settele[3,4,6] (iD) | Alexander Harpke[3] | Martin Wiemers[3,6] |
Lluís Brotons[1,2,11] (iD) | Miska Luoto[12] (iD)

[1]Forest Sciences Centre of Catalonia (CEMFOR-CTFC), InForest Joint Research Unit (CSIC-CTFC-CREAF), Solsona, Catalonia, Spain

[2]Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Cerdanyola del Vallés, Spain

[3]UFZ, Department of Community Ecology, Helmholtz Centre for Environmental Research, Halle, Germany

[4]iDiv, German Centre for Integrative Biodiversity Research, Halle-Jena-Leipzig, Leipzig, Germany

[5]Research Institute for Nature and Forest (INBO), Brussels, Belgium

[6]Butterfly Conservation Europe, Wageningen, the Netherlands

[7]Finnish Environment Institute, Natural Environment Centre, Helsinki, Finland

[8]Departamento de Biología, Edificio de Biología, Universidad Autónoma de Madrid, Madrid, Spain

[9]CNRS, Laboratoire d'Ecologie Alpine (LECA), University of Grenoble Alpes, Grenoble, France

[10]Dutch Butterfly Conservation, Wageningen, the Netherlands

[11]Consejo Superior de Investigaciones Científicas (CSIC), Cerdanyola del Vallés, Spain

[12]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

Correspondence
Nicolas Titeux, Forest Sciences Centre of Catalonia, Solsona, Catalonia, Spain.
Email: nicolas.titeux@ctfc.es

Abstract

Aim: Species distribution models built with geographically restricted data often fail to capture the full range of conditions experienced by species across their entire distribution area. Using such models to predict distribution shifts under future environmental change may, therefore, produce biased projections. However, restricted-scale models have the potential to include a larger sample of taxa for which distribution data are available and to provide finer-resolution projections that are better applied to conservation planning than the forecasts of broad-scale models. We examine the circumstances under which the projected shifts in species richness patterns derived from restricted-scale and broad-scale models are most likely to be similar.

Location: Europe.

Methods: The distribution of butterflies in Finland, Belgium/Netherlands and Spain was modelled based on restricted-scale (local) and broad-scale (continental) distribution and climate data. Both types of models were projected under future climate change scenarios to assess potential changes in species richness.

Results: In Finland, species richness was projected to increase strongly based on restricted-scale models and to decrease slightly with broad-scale models. In Belgium/Netherlands, restricted-scale models projected a larger decrease in richness than

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broad-scale models. In Spain, both models projected a slight decrease in richness. We obtained similar projections based on restricted-scale and broad-scale models only in Spain because the climatic conditions available here covered the warm part of the distributions of butterflies better than in Finland and Belgium/Netherlands.

Main conclusions: Restricted-scale models that fail to capture the warm part of species distributions produce biased estimates of future changes in species richness when projected under climatic conditions with no modern analogue in the study area. We recommend the use of distribution data beyond the boundaries of the study area to capture the part of the species response curves reflecting the climatic conditions that will prevail within that area in the future.

1 | INTRODUCTION

Climate change is affecting the physiology, phenology and distribution of organisms (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Robinet & Roques, 2010). Short-lived, ectothermic invertebrates, such as butterflies, are expected to respond rapidly (Devictor et al., 2012; Parmesan, 2006; Thomas et al., 2004). Butterflies are a useful model system because their ecology, taxonomy and distributions are well documented (e.g., Forister et al., 2010). They have already responded to climate change, for example, through latitudinal shifts (Eskildsen et al., 2013; Pöyry, Luoto, Heikkinen, Kuussaari, & Saarinen, 2009), altitudinal shifts (Konvička, Maradova, Beneš, Fric, & Kepka, 2003; Wilson, Gutiérrez, Gutiérrez, & Monserrat, 2007) and phenological changes (Altermatt, 2012; Van Dyck, Puls, Bonte, Gotthard, & Maes, 2015).

Species distribution models are a popular tool to project future distributions of climatically suitable conditions under a changing climate (e.g., Barbet-Massin & Jetz, 2014; Franklin, 2013; Titeux et al., 2016). Many models have employed species and climate data covering large spatial extents, often continents, to capture the full range of climatic conditions used by species (Pearson & Dawson, 2003; Sánchez-Fernández, Lobo, & Hernandez-Manrique, 2011). Failing to do so may lead to an unreliable estimation of species response curves and biased projections of distribution shifts (e.g., Barbet-Massin, Thuiller, & Jiguet, 2010; Fernández, Jordano, & Fernández Haeger, 2015; Hannemann, Willis, & Macias-Fauria, 2016; Randin et al., 2009; Thuiller, Brotons, Araújo, & Lavorel, 2004).

For conservation and management, broad-scale models have, however, two important shortcomings. First, a major problem is that broad-scale distribution data are usually available for some species groups only (e.g., plants, butterflies, mammals, birds—Hudson et al., 2014). A multitaxa approach is, however, needed in climate change impact assessments or for implementing anticipatory conservation strategies, because different species groups (Hickling, Roy, Hill, Fox, & Thomas, 2006) and species traits (Pöyry et al., 2009) may respond

contrastingly to climate change. Second, applying the projections of broad-scale models to practical conservation planning may be problematic due to their coarse spatial resolution (Franklin et al., 2013; Guisan et al., 2013). Conservation practitioners are generally interested in potential future changes over a small extent and at fine resolution. Downscaling procedures (Araújo, Thuiller, Williams, & Reginster, 2005; Keil, Belmaker, Wilson, Unitt, & Jetz, 2013) or methods that integrate information at different scales (Talluto et al., 2016) have been proposed, but often involve sophisticated modelling approaches that are not easy to implement or understand for practitioners (Addison et al., 2013).

National or regional distribution data covering a wider range of taxa than those for which broad-scale data are available can in principle be used to develop models over smaller spatial extents. As there is a strong conservation interest in projecting future species distributions at this level (e.g., Regos et al., 2016), a critical question is to identify the factors that lead to notable differences in the estimation of species response curves when using restricted-scale data instead of adopting a broad-scale modelling approach and then downscaling its outputs. If, under certain circumstances, the projections based on both approaches are similar, useful assessments of the potential shifts in species richness could be performed based on restricted-scale data (Thuiller, 2004). Moreover, if the factors that affect the credibility of restricted-scale models are identified, it might also become possible to extend the assessments to other taxa for which distribution data exist at the restricted scale only. However, there is no consensus on the main factors that affect the level of congruence between the projections derived from restricted-scale and broad-scale models (Hannemann et al., 2016).

We expected that one important factor when using restricted-scale data is the difference between the climatic conditions used to calibrate the models and the conditions experienced by the species across their entire distribution range (Thuiller et al., 2004). Restricted-scale data often cover only a fraction of the conditions used by the species across their range, but importantly they may also represent a biased sample of these conditions. Depending on the geographical

location of the study area and the species of interest, the warm part of the distribution of species (i.e., towards the retracting edge of their range) and/or the cold part of their distributions (i.e., towards the expanding edge) may be systematically truncated. As climate will become warmer in the future, we hypothesized that the truncation of the warm part of the distributions will produce more severely biased projections than the truncation of the cold part.

To test this hypothesis, we used the European butterfly database (Kudrna, 2002; Settele et al., 2008) as a source of broad-scale distribution data ("continental" data) and the butterfly databases from three biogeographically and climatically contrasting regions of similar but restricted spatial extent in Europe ("local" data): SW Finland, Belgium/Netherlands and NE Spain (Figure 1). As butterfly assemblages and climatic conditions are very different in SW Finland, Belgium/Netherlands and NE Spain, local distribution data in these three regions were expected to differently represent the climatic conditions used by the species across their range in Europe. Hence, we predicted that the warm and the cold parts of the distribution of the species would be contrastingly truncated when using local data in these three regions. We developed species distribution models based on local ("local" models) or continental ("continental" models) distribution data. We tested whether the projected shifts in species richness under future climate change differed between both types of models. We describe to what

extent the local models developed in the three regions captured an adequate part of the species response curves to project distribution shifts under future climate. Based on this, we discuss the important factors that affect the relevance of using restricted-scale data to project the effects of climate change on local species richness.

2 | METHODS

2.1 | Study areas

The climate of Finland is both oceanic and continental and it is subject to Atlantic, Arctic and Siberian influences, with a decrease in rainfall and temperature from the south-western hemi-boreal zone (mean annual temperature ca. 5°C and mean annual precipitation 600–700 mm) to the subarctic region in northernmost Finland (−2°C and 400 mm) (http://en.ilmatieteenlaitos.fi/climate). The climate of Belgium and the Netherlands is temperate with a mean annual temperature of ca. 8°C and an annual rainfall of ca. 800 mm (http://www.meteo.be/meteo/view/fr/65657-Climat.html). Peninsular Spain has a diverse climate with higher rainfall and colder temperatures in the north-west (annual rainfall between 800 and 1500 mm and mean annual temperature of ca. 11°C) than in eastern and southern areas (250 – 600 mm and ca. 15°C) (http://www.aemet.es).
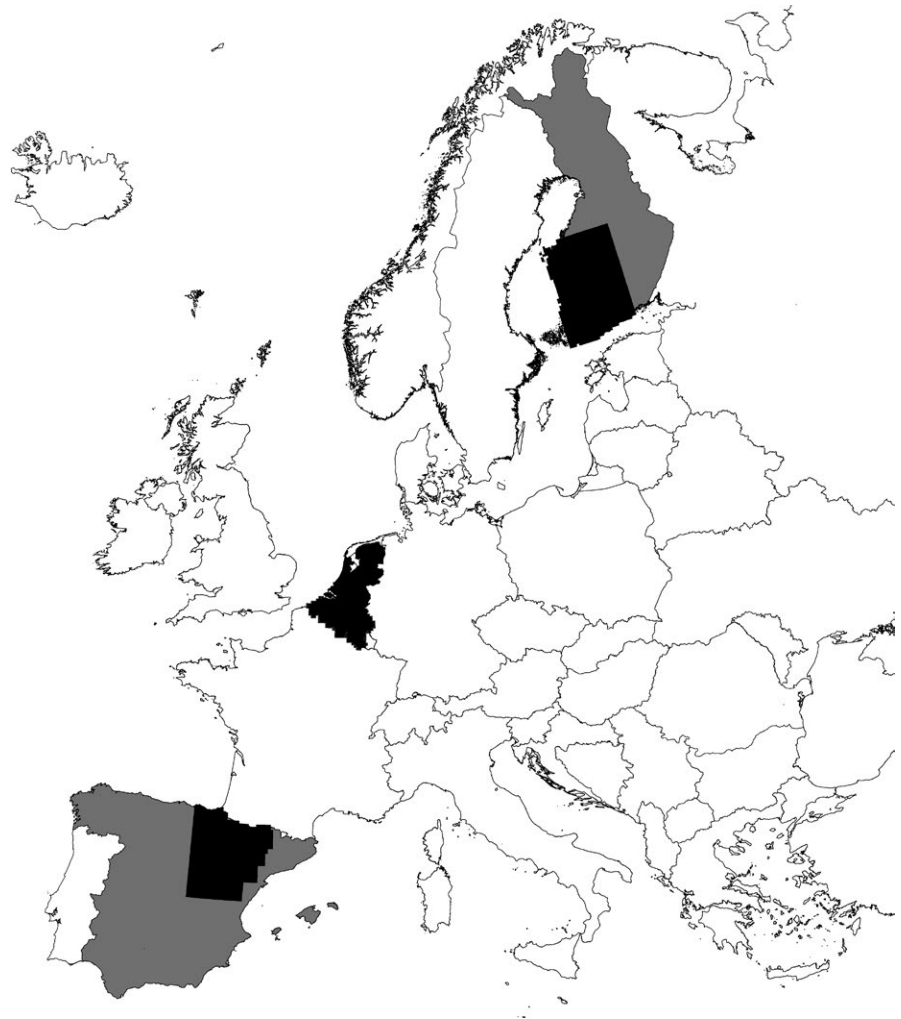

FIGURE 1 Location of the three study areas in Europe: SW Finland, Belgium/Netherlands and NE Spain. Based on local expert opinion on the best-surveyed areas in the whole of Finland and Spain (grey colour), we focused on SW Finland and NE Spain to analyse local butterfly data at a similar spatial scale as in Belgium/Netherlands (black colour)

2.2 | Butterfly data

European butterfly data were compiled from the Mapping European Butterfly project (Kudrna, 2002; Settele et al., 2008). Data from the period 1981–2002 were available for 419 species and 1 985 squares at 50-km resolution, and recorded using the Universal Transverse Mercator (UTM) projection (total number of squares in Europe: $N = 2\,811$). Butterfly data in Finland, Belgium/Netherlands and Spain were extracted from different sources (Table 1) and matched to squares at 10-km resolution using the UTM projection. Only species with resident breeding populations were used in the analyses.

2.3 | Completeness of butterfly data

As the total number of squares was different in the three study areas (Table 1), we selected regions in Finland and Spain with a number of squares similar to that in Belgium/Netherlands (i.e., the smallest region). Based on local expert opinion on the best-surveyed areas, we focused on SW Finland and NE Spain (black areas in Figure 1). For clarity, we hereafter refer to these regions as "countries" (Finland, Belgium/Netherlands and Spain).

As survey intensity and potential species richness differed across Europe and among and within countries, we determined the completeness of butterfly distribution data in each square both in Europe (50-km resolution) and in the countries separately (10-km resolution). We considered that a square included sufficient data when butterfly presence was reported for at least 20% of the species that were present in the biogeographical area in which the square was located (Appendix S1 in Supporting Information). In subsequent analyses, we only used these squares with sufficient butterfly data, that is, 434 squares in Finland, 770 in Belgium/Netherlands, 420 in Spain and 983 in Europe.

Among the species observed in each country, we removed those that were too rare (i.e., present in <20 squares with sufficient data) or too common (i.e., absent from <20 of these squares). We used 65 species in Finland, 72 in Belgium/Netherlands and 174 in Spain. In total, 192 different species were used to build the local models in the three countries altogether and this same subset of species was used to build the continental models.

2.4 | Climate data and climate change scenarios

Climate data were obtained from the Climatic Research Unit (Mitchell, Carter, Jones, Hulme, & New, 2004; New, Lister, Hulme, & Makin, 2002). To match butterfly data in Europe, climate variables for the period 1971–2000 (i.e., present-day climate) were aggregated from the original 10-min resolution to the 50-km resolution by calculating the centroid of each 10-min resolution square and then averaging the values of the squares for which the centroids fall inside the 50-km resolution squares. To match the local distribution data in the different countries, we converted the climate data to the 10-km resolution squares by calculating the centroid of each 10-min resolution and 10-km resolution square and then averaging the values of the four 10-min resolution squares that are closest to each 10-km resolution square using inverse distance weighting.

To avoid overfitting and collinearity between variables, we restricted the number of predictors to three climate variables reflecting the primary limitations on butterfly growth and survival (e.g., Heikkinen et al., 2010; Hill et al., 2002; Luoto, Heikkinen, Pöyry, & Saarinen, 2006): (1) annual daily temperature sum above 5°C (GDD5; surrogate for the development threshold for butterfly larvae), (2) mean temperature of the coldest month (MTCO; related to overwintering survival) and (3) water balance (WB; moisture availability for both larvae and adult butterflies). WB was calculated as the sum of the monthly differences between precipitation and potential evapotranspiration (Holdridge, 1967). Variables were standardized prior to analysis.

The projected values of the climate variables for two future time periods (2021–2050 and 2051–2080) were computed in each 10-km

TABLE 1 Detailed information on butterfly data in Finland, Belgium/Netherlands and Spain: sources of national or regional data, sampling or monitoring period, total number of species recorded, number of 10-km squares for each country (total), number of 10-km squares with butterfly data for each country (covered) and relevant references for additional details

Country	Data sources	Period	Number of species	Number of squares		References
				Total	Covered	
Finland	National Butterfly Monitoring Scheme	1991–2003	112	3779	1499	Saarinen, Lahti, & Marttila (2003)
Belgium/Netherlands	Belgium: Flemish Butterfly Atlas	Belgium: 1991–2006	107	844	832	Maes & Van Dyck, (2001), Maes et al., (2016), Fichefet et al. (2008)
	Walloon Butterfly Atlas					
	Netherlands: Dutch Butterfly Atlas	Netherlands: 1995–2003				Bos et al. (2006)
Spain	Iberian Butterfly Atlas	1980–2000	220	5419	3355	García-Barros et al. (2004), Romo & García-Barros (2005), Romo, García-Barros, & Lobo (2006)

Numbers relate to the entire countries (Finland, Belgium/Netherlands and Spain) before restricting the analysis to SW Finland, Belgium/Netherlands and NE Spain (see "Completeness of butterfly data" and Figure 1).

resolution square covering the three countries using the same procedure as described above. Three different climate change scenarios described potential future climate based on the IPCC storylines (Nakicenovic et al., 2000): BAMBU (Business As Might Be Usual, A2 storyline), GRAS (GRowth Applied Strategy, A1FI storyline) and SEDG (Sustainable European Development Goal, B1 storyline) (Settele, Carter, Kuhn, Spangenberg, & Sykes, 2012). Figure 2 shows the present-day variation in the climate variables in Europe and in the three countries along with their projected future variation according to the most severe scenario (GRAS). These scenarios were developed by the EU FP6 project ALARM (Settele et al., 2012) and have been employed in several in-depth European-wide climate change impacts studies on butterflies (e.g., Schweiger et al., 2012; Settele et al., 2008) or other pollinators (Settele, Bishop, & Potts, 2016); to ensure comparability with these earlier studies, we used the three ALARM scenarios instead of the latest RCP scenarios (van Vuuren et al., 2011).

2.5 | Data analysis

To interpret potential differences in the projections derived from local and continental models, we quantified the climatic niche of each butterfly species in Europe (Appendix S2): (1) "marginality," estimated as the difference between the mean climatic conditions that are available for and used by the species in Europe, and (2) "tolerance," reflecting the fraction of the climatic conditions available across Europe that are used by the species. For the different species, we also examined whether the climatic conditions prevailing in the different countries have the potential to represent the conditions they experience across the whole of Europe (Appendix S2).

We used generalized additive models (GAMs) (Hastie & Tibshirani, 1987) with four splines (k = 5) to model species distributions in the *biomod2* R-package (Thuiller, Georges, Engler, & Breiner, 2016). We calibrated two types of models: (1) local models, using the butterfly distribution and climate data in the 10-km resolution squares within each
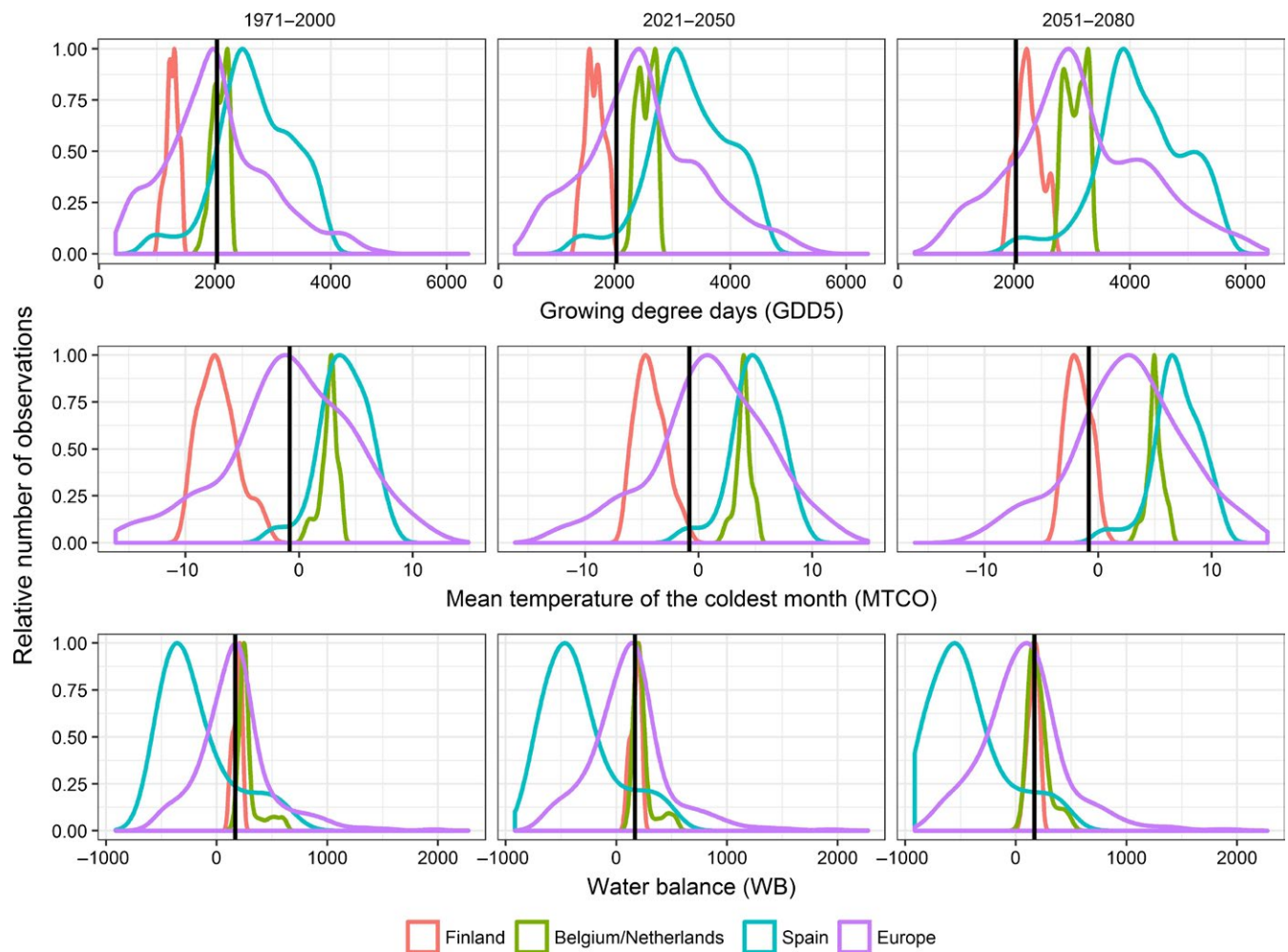

FIGURE 2 Present-day (1971–2000) and future (2021–2050 and 2051–2080 under the GRAS scenario) frequency distribution of climate variables (GDD5, MTCO and WB) in the different countries at 10-km resolution and in the whole of Europe at 50-km resolution. The black vertical line represents the average present-day conditions in Europe. The relative number of observations (i.e., number of squares) was calculated as a kernel density estimate using the *geom_density* function in the *ggplot* package in R. The percentage of overlap between the present-day and future kernel density estimates for each variable in each country is provided in Table 2. [Colour figure can be viewed at wileyonlinelibrary.com]

country separately, and (2) continental models, using the European distribution and climate data in the 50-km resolution squares. Models were calibrated 10 times using a random sample of 70% of the data (calibration sets) and subsequently evaluated against the remaining 30% (evaluation sets). We applied the local models to predict the distribution of the species in the 10-km resolution squares in the three countries and downscaled the predictions of the continental models from 50-km to 10-km resolution in each country to spatially match the predictions of the local models (Araújo et al., 2005). In each case, the models were used to predict species distributions for the present-day period (1971–2000) and to project the distributions in the future (2021–2050 and 2051–2080) under the three climate change scenarios.

The predictive performance of the models was evaluated based on the present-day model predictions in the evaluation sets using the area under the curve (AUC) of receiver operating characteristic (ROC) plots (Huang & Ling, 2005; Swets, 1988). We tested for AUC differences between local and continental models in the three countries separately, using repeated-measures ANOVA with species as repeated factor.

The importance of the three climate variables in local and continental models was calculated for each species. The values of each climate variable were randomized among the squares and this procedure was replicated 20 times. For each replicate, a score was calculated as 1 minus the correlation coefficient between the predictions based on the shuffled data and on the original data. The mean scores among the different replicates were rescaled relative to the sum of the scores across all the variables to derive the relative importance of each variable (Thuiller, Lafourcade, Engler, & Araujo, 2009).

Finally, we tested whether the projected changes in butterfly richness within the 10-km resolution squares from 1971–2000 to 2021–2050 and from 1971–2000 to 2051–2080 differed between local and continental models (Appendix S3). All modelling and statistical analyses were carried out in R 3.2.3 (R Core Team, 2015).

3 | RESULTS

The range of climatic conditions available in Spain during 1971–2000, 2021–2050 and 2051–2080 is much larger than that available in Finland and Belgium/Netherlands for the three climate variables (Figure 2). The present-day climate in Spain covers a large fraction of the future conditions that will prevail in this country, whereas future

temperatures (GDD5 and MTCO) in Finland and Belgium/Netherlands have almost no modern analogue in these countries (Figure 2, Table 2).

The climatic marginality and tolerance of butterfly species in Europe vary considerably among the subsets of species present in each country (hereafter Finnish, Belgian/Dutch and Spanish butterflies) (Figure 3). Finnish butterflies show an opposite marginality compared to that of the Spanish butterflies and their climatic tolerance in Europe is similar to that of the Belgian/Dutch butterflies. Spanish butterflies exhibit a more pronounced marginality and use a smaller range of climatic conditions in Europe than in Belgian/Dutch butterflies.

The climatic conditions available in Finland and Belgium/Netherlands cover a very small fraction of the conditions used by Finnish and Belgian/Dutch butterflies across Europe (Figure 4). The climate in Finland is much colder than the mean temperatures (GDD5 and MTCO) experienced by Finnish butterflies in Europe. The climate available for the species in Belgium/Netherlands is warmer (MTCO) and wetter (WB) than the climatic conditions used by Belgian/Dutch butterflies across their entire range. In Spain, the mean values of the three climate variables only differ slightly from the climate experienced by Spanish butterflies in Europe and, when compared to the other two countries, the available climate covers a much larger fraction of the conditions used by these species in Europe.

Average predictive performance of local models varied from poor to good (Table 3). The downscaling of continental models resulted in significantly lower mean AUC values in the three countries (Table 3). In Finland, variable importance was higher for GDD5 than for MTCO in local models, but an opposite pattern was found in continental models (Figure 5). Here, variable importance was very low for WB in both types of models. In Belgium/Netherlands and in Spain, variable importance was higher for MTCO in the local models, but GDD5 and WB were most important in the continental models.

Projected changes in mean butterfly richness differed significantly between local and continental models in Finland and Belgium/Netherlands, but not in Spain (Figure 6, Table 4). Local models in Finland projected a strong increase in future species richness, while continental models projected a slight decrease. In Belgium/Netherlands, butterfly richness was projected to decrease slightly or to remain stable based on continental models, but the decrease was projected to be much stronger with the local models. In Spain, butterfly richness was projected to decrease slightly or to remain stable according to both the local and continental models. A sensitivity analysis indicated that the threshold used to select

TABLE 2 Climatic similarity between 1971–2000 and 2021–2050 (2000–2050) and between 1971–2000 and 2051–2080 (2000–2080) based on the GRAS scenario in the different countries. The percentage of overlap between the present-day and future kernel density estimates of Figure 2 was calculated using the *overlap* package in R for each climate variable in each country

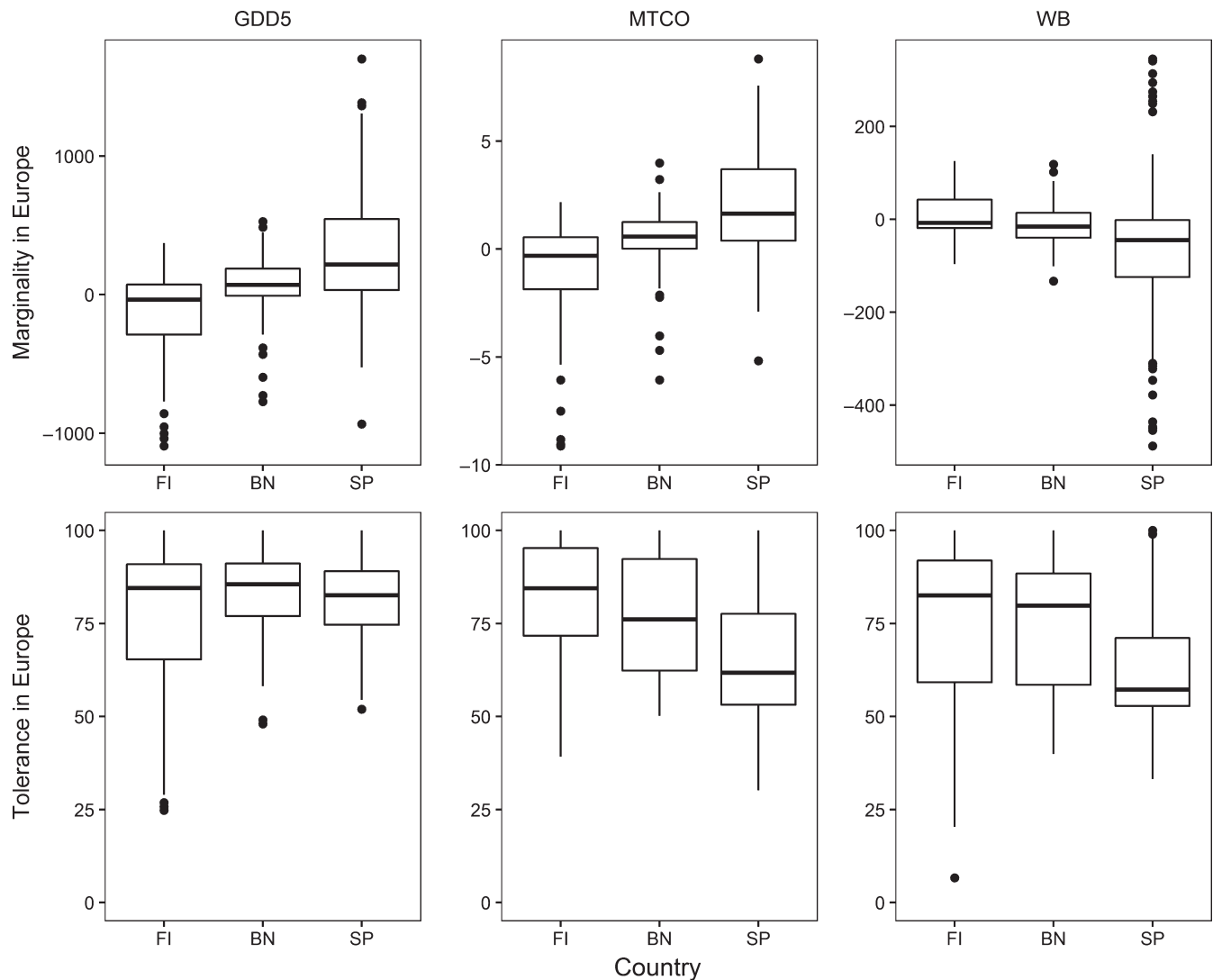|	Overlap (%)					
	Finland		**Belgium/Netherlands**		**Spain**	
Variable	**2000–2050**	**2000–2080**	**2000–2050**	**2000–2080**	**2000–2050**	**2000–2080**
GDD5	12.7	0	6.5	0	64.3	28.9
MTCO	32.5	6.7	30.5	7.6	78.6	46.1
WB	88.5	75.6	63.1	52.8	77.5	62.3

FIGURE 3 Marginality and tolerance of butterfly species relative to the climatic conditions available in Europe (Appendix S2). Marginality (top row) and tolerance (bottom row) of butterfly species in Europe were synthesized (box plots) for the different climate variables and for the different subsets of species present in each country separately: Finland (FI): *N* = 65, Belgium/Netherlands (BN): *N* = 72, and Spain (SP): *N* = 174. Marginality (top row): positive / negative marginality indicates that the mean value of the climate variable among the squares occupied by the species in Europe is higher / lower than the mean value of the same climate variable among all squares available in Europe. Tolerance (bottom row): tolerance close to 0 / 100 indicates that the range of climatic conditions used by the species in Europe is restricted / similar compared to that available in Europe

squares with sufficient data did not affect the observed differences between local and continental models (Appendix S4). In order to validate that our findings do not emerge solely due the selected modelling approach, we also used other modelling algorithms for projecting butterfly richness under climate change. However, the main results reported above for GAMs were very similar for the different algorithms (Appendix S5).

4 | DISCUSSION

Forward-looking approaches that explore future changes in species distributions and richness in a range of species groups are essential anticipatory tools in conservation planning (Franklin, 2013; Titeux et al., 2016). Apart from being useful at large scales, there is

a growing interest in applying such tools in geographically restricted areas of conservation relevance and at fine spatial resolutions that closely match the scale of decision-making processes for local conservation practitioners (Maes et al., 2010). Although our results in Spain indicate that local models may produce estimates of future changes in species richness that are similar to the outcomes of continental models, projections based on local models in Finland and Belgium/Netherlands deviate strongly from those derived from the continental models. Below, we use the results in these three countries to describe the capability of local models to adequately capture the response curves of the species for projecting distribution shifts under future climate. Based on this, we shed light on the conditions under which local models might be useful to project future changes in species richness.
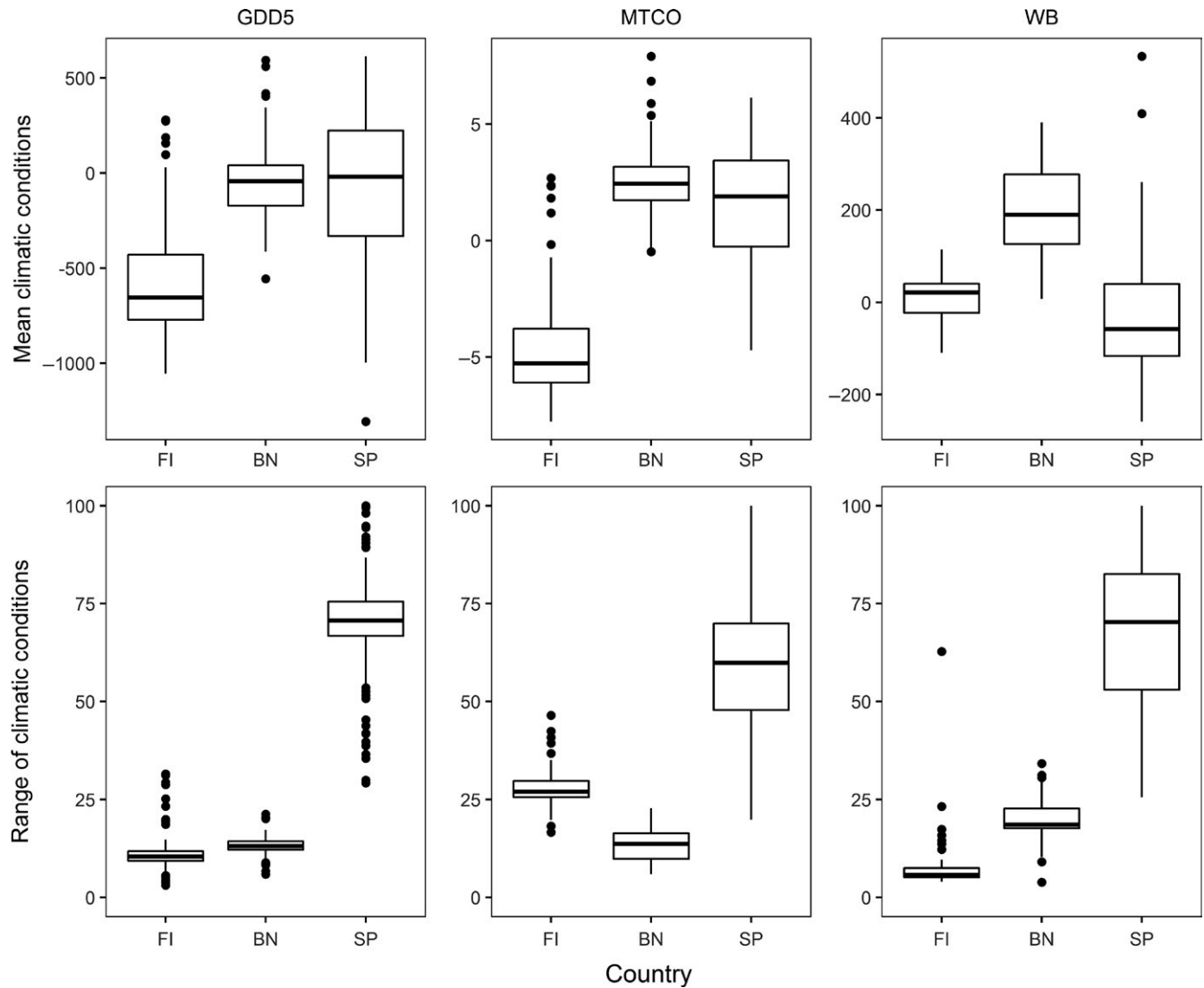
FIGURE 4 Differences between the climatic conditions that are available for the butterfly species in the different countries and the conditions that these species use across their European range (Appendix S2). The differences were synthesized (box plots) separately for the different climate variables and for the different subsets of species present in each country: Finland (FI): *N* = 65, Belgium/Netherlands (BN): *N* = 72, and Spain (SP): *N* = 174. Mean climatic conditions (top row): positive / negative difference indicates that the mean value of the climate variable among all the squares in the country is higher / lower than the mean value of the same climate variable among the squares occupied by the species in Europe. Range of climatic conditions (bottom row): values close to 0 / 100 indicate that the range of climatic conditions in the country is restricted / similar compared to the range of conditions used by the species in Europe

TABLE 3 Average performance of the generalized additive models (mean AUC values and standard deviation) across all butterfly species modelled in each country and in Europe

	Country			
	Finland	Belgium/Netherlands	Spain	Europe
Model	(*n* = 65)	(*n* = 72)	(*n* = 174)	(*n* = 192)
Local model	0.674 ± 0.121	0.820 ± 0.123	0.782 ± 0.107	
Continental model	0.610 ± 0.112***	0.625 ± 0.173***	0.636 ± 0.152***	0.844 ± 0.067

Significant differences between local and continental models (repeated-measures ANOVA) are indicated as follows: ***$p < .001$; **$p < .01$; *$p < .05$. The number of species used in each country is indicated in parentheses.

In Finland, GDD5 was the most important climate variable in the local models (Figure 5). GDD5 in Finland is much lower than its mean value in Europe and its range of values is strongly restricted compared to that available across Europe (Figure 2). Finnish butterflies use a large spectrum of GDD5 that is on average slightly lower than the mean GDD5 in Europe (Figure 3). This pattern exerted two effects
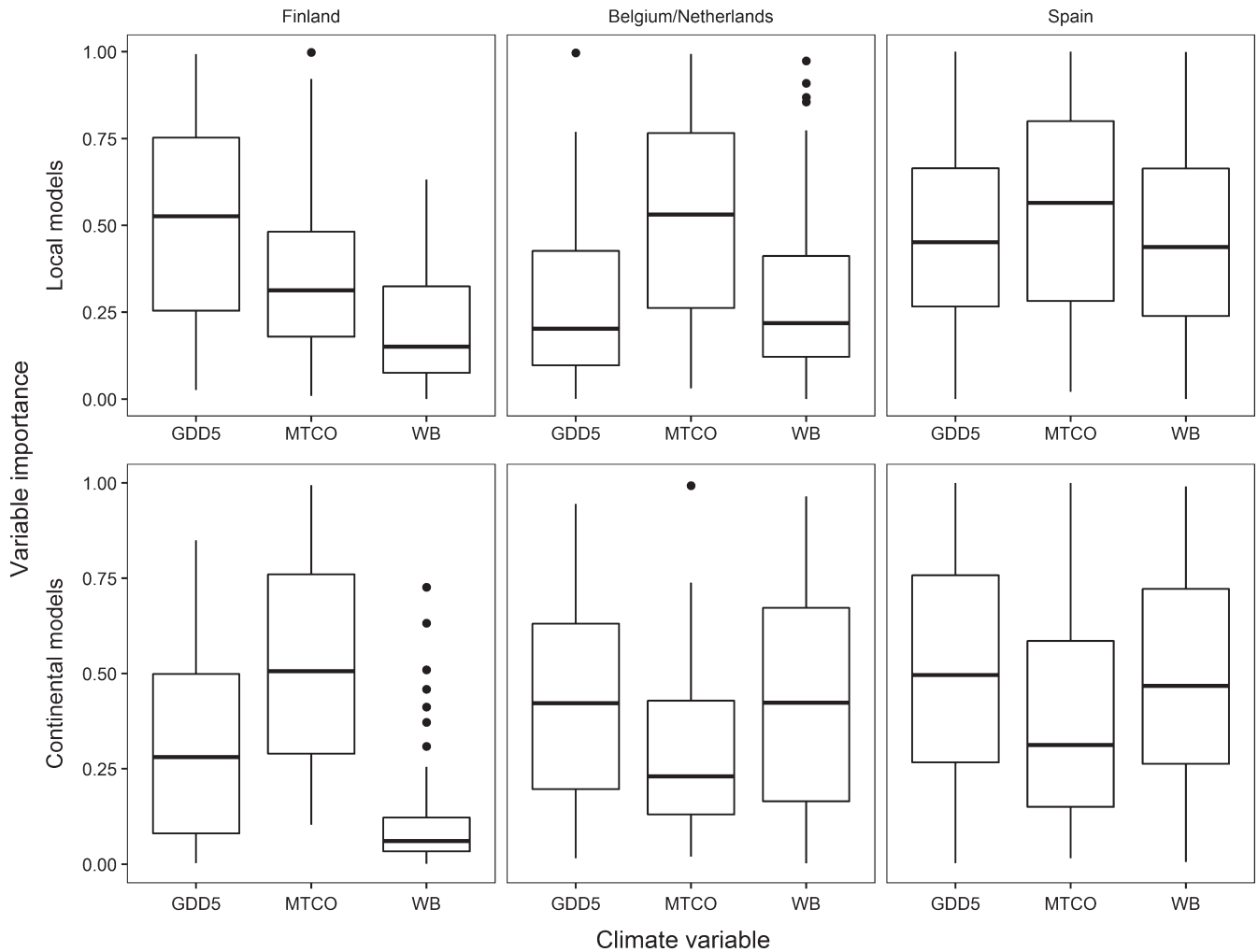
FIGURE 5 Relative importance of the different climate variables in the calibration of the local models (top row) and the continental models (bottom row) for the different subsets of species occurring in each country separately (Finland: *N* = 65, Belgium/Netherlands: *N* = 72, and Spain: *N* = 174)

on the local models. First, they failed to capture the entire response curves of Finnish butterflies because the range of GDD5 in Finland is strongly restricted compared to the range of values experienced by Finnish butterflies across Europe (Figure 4). Second, the fraction of the response curves captured by the local models was biased because the mean GDD5 in Finland is much lower than the mean GDD5 used by Finnish butterflies across Europe (Figure 4). The fraction of the bell-shaped response curves that describes decreasing suitability for the species with increasing GDD5 (i.e., the warm part of the distributions of the species towards their retracting edge) was truncated in the local models (Figure 7). Hence, these models in Finland captured only the fraction of the curves that describes increased climatic suitability with increasing GDD5. As temperatures are projected to increase in the future (Figure 2) and to strongly deviate from the present-day conditions (Table 2), extrapolating the truncated response curves beyond the range of values used to develop the local models (Fitzpatrick & Hargrove, 2009) projected a marked increase in the number of occupied squares for most Finnish butterflies. In contrast, continental models captured response curves more completely and they dealt with the

fact that beyond an optimal value, the climatic suitability for butterflies decreases with increasing temperatures (Figure 7). Importantly, this warm part of the distributions of the species includes climatic conditions that will become increasingly prevalent in Finland in the future. As continental models downscaled to Finland entirely covered this fraction of the response curves, they predicted a moderate decrease in future species richness.

In Belgium/Netherlands, MTCO was the most important variable in the local models. Its mean value is higher and its range of variation is much more restricted than across Europe (Figure 2). Belgian/Dutch butterflies have a relatively high tolerance for MTCO in Europe and show a slightly positive marginality (Figure 3). In Belgium/Netherlands, the range of MTCO available is therefore strongly restricted and its mean value is only slightly higher compared to the MTCO values experienced by Belgian/Dutch butterflies across Europe (Figure 4). Hence, local models captured only a fraction of the entire species response curves that omitted the cold part of the distributions of most species but, also, the warmest part of their distributions (Figure 7). These models only focused on the fraction of the bell-shaped response curves
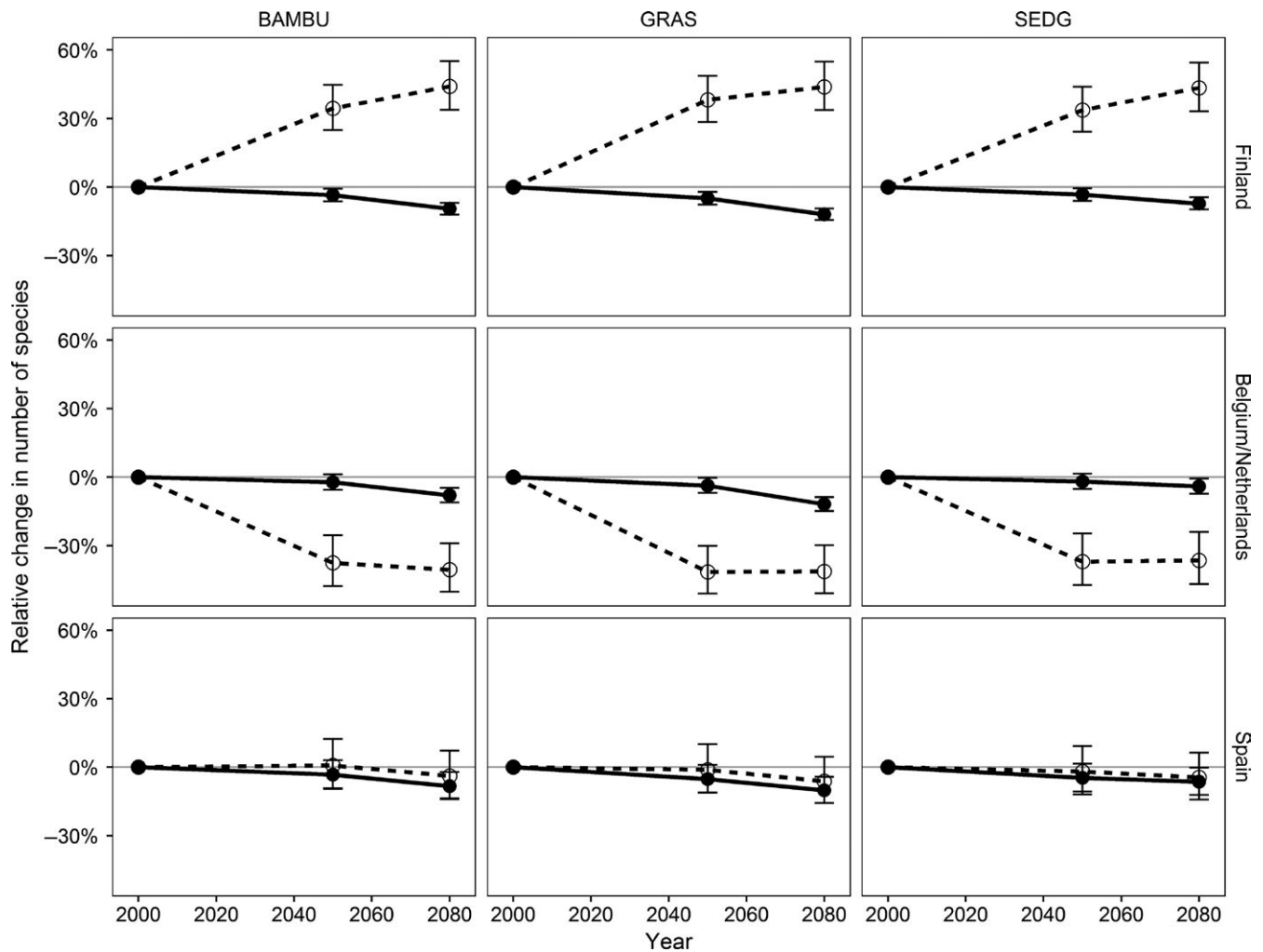
FIGURE 6 Predicted butterfly species richness per 10-km resolution square in Finland, Belgium/Netherlands and Spain in 1971–2000 (2000) and for three climate change scenarios (BAMBU, GRAS and SEDG) in 2021–2050 (2050) and 2051–2080 (2080). Mean predicted species richness in the future is transformed to percentages (± SE) relative to the baseline estimation for 1971–2000. Predictions based on local and continental generalized additive models (GAMs) are shown in open circles (dashed lines) and black dots (plain lines), respectively. See Supplementary Information for equivalent results based on different threshold of completeness in butterfly data (Appendix S4) or using other modelling algorithms (Appendix S5)

TABLE 4 Statistical differences (estimates and _p_-values) in projected butterfly richness changes between local and continental models (Appendix S3). Butterfly richness changes were estimated from 1971–2000 to 2021–2050 (2000–2050), from 1971–2000 to 2051–2080 (2000–2080) and in general from 1971–2000 to 2021–2080 (overall)

| | Year | | | | | |
| | 2000–2050 | | 2000–2080 | | Overall | |
Country	Estimate	_p_-value	Estimate	_p_-value	Estimate	_p_-value
Finland	0.366 (1.44)	<.001	0.477 (1.61)	<.001	0.421 (1.52)	<.001
Belgium/Netherlands	−0.440 (0.64)	<.001	−0.395 (0.67)	<.001	−0.420 (0.66)	<.001
Spain	0.042 (1.04)	.589	0.026 (1.02)	.877	0.034 (1.03)	.701

As butterfly species richness was modelled using the log scale, the exponentiation of the estimates is indicated in parentheses:
Exponentiation of the estimate >1: local models predict higher species richness than continental models.
Exponentiation of the estimate <1: local models predict lower species richness than continental models.
Exponentiation of the estimate = 1: local models predict the same species richness as continental models.
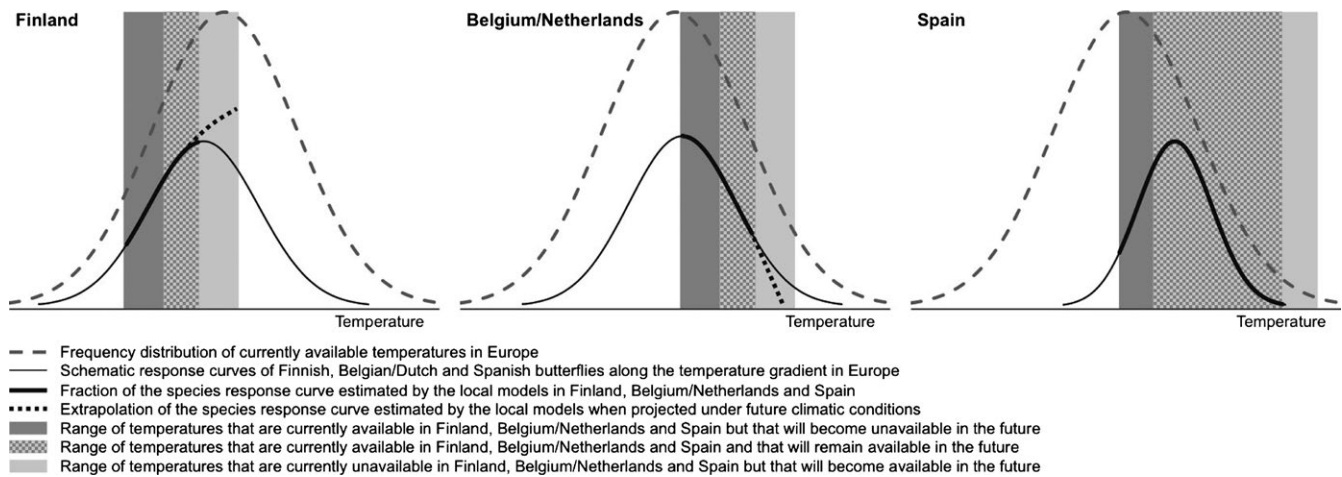
- - - Frequency distribution of currently available temperatures in Europe
—— Schematic response curves of Finnish, Belgian/Dutch and Spanish butterflies along the temperature gradient in Europe
—— Fraction of the species response curve estimated by the local models in Finland, Belgium/Netherlands and Spain
······· Extrapolation of the species response curve estimated by the local models when projected under future climatic conditions
▓ Range of temperatures that are currently available in Finland, Belgium/Netherlands and Spain but that will become unavailable in the future
▒ Range of temperatures that are currently available in Finland, Belgium/Netherlands and Spain and that will remain available in the future
▒ Range of temperatures that are currently unavailable in Finland, Belgium/Netherlands and Spain but that will become available in the future

FIGURE 7 Schematic bell-shaped curves representing the response of butterfly species to climatic conditions in Finland, Belgium/ Netherlands and Spain. Local models estimate the fractions of the response curves (bold part of the black lines) that overlap with the range of climatic conditions currently available in each country. When extrapolated to future climatic conditions that are not currently available (dotted black lines), the projections overemphasize increases (Finland) or decreases (Belgium/Netherlands) in species distributions and richness (Figure 6). When local models capture the part of the distributions of the species reflecting the climatic conditions that will prevail in the future (Spain), they produce projections that are more similar to those obtained from continental models (Figure 6)

that describes a strong decrease in climatic suitability for the species with gradually increasing MTCO. The fact that the cold part of the distributions was truncated had little influence on the projections because temperatures are projected to increase in the future and to deviate from the conditions experienced by the species towards the expanding edge of their range (Figures 2 and 7). In contrast, the warmest part describes a smaller decrease of climatic suitability with increasing MTCO and this part is important because it represents the climatic conditions that will prevail in the future in Belgium/Netherlands (Figure 7). As local models missed this part, they overemphasized the decreasing climatic suitability with increasing temperatures and, when extrapolated beyond the conditions used for calibration (Table 2), they projected a stronger decrease in future species richness than the continental models.

Large differences between the projections derived from local and continental models were found in Finland and in Belgium/Netherlands because the local climatic conditions cover a small and biased fraction of the conditions used by the species in Europe. These two countries provide examples where local models are only able to capture the fraction of the bell-shaped response curves describing either a strong increase (Finland) or a strong decrease (Belgium/Netherlands) in climatic suitability for the species (Figure 7). When these biased estimates of the response curves are projected under warming climate with no modern analogue in the study area, they overemphasize the future increase or decrease in climatic suitability for the species (Fitzpatrick & Hargrove, 2009).

The range of climatic conditions available in Spain is much larger than that in the other countries (Figure 2) and Spanish butterflies use a smaller range of climatic conditions in Europe than Finnish and Belgian/Dutch butterflies (Figure 3). As a result, available climate in Spain covers a large fraction of the conditions that Spanish butterflies experience in Europe (Figure 4). In addition, the mean climatic

conditions in Spain deviate only slightly from those used by these species in Europe (Figure 4). Therefore, local models captured a larger fraction of the response curves for most of the species, including the warmest parts of their distributions in Europe (Figure 7). Even if the cold part of the distribution for some species was slightly truncated, this effect was negligible for future projections under a warming climate. In comparison with the other two countries, future climatic conditions in Spain will also deviate less from the present-day climate (Table 2). For these reasons, local models provided projections of future butterfly species richness that more closely matched those of continental models (Figure 6).

Based on our results in the three countries, we conclude that local models failing to capture the warm part of the distributions of the species are likely to produce biased estimates of future changes in species richness when projected under future climatic conditions. We recommend the general use of distribution data in a way that models are able to include the part of the distributions of the species reflecting the climatic conditions that will prevail in the area of interest in the future. When considering the continental scale as a baseline reference, we found that this condition was only met in Spain for two main reasons. First, this country covered the retracting edge of the distribution range of many species. Second, the large climatic heterogeneity in that country limited the extrapolation to future conditions with no modern analogue. Our results in the other two countries show that distribution data are needed beyond the geographically restricted boundaries of the study area towards the retracting edge of the range of the species to represent climatic conditions that will prevail in the future in that area. If distribution data for particular taxa are only available within the area of conservation interest and if existing ecological knowledge is insufficient to ensure that the aforementioned conditions are met, we recommend avoiding their use for climate change impact assessments, even if such taxa are relevant to conservation decision-making.

Broad-scale models capture more adequately the part of the response curves that are relevant for future projections of the overall changes in the climatically suitable areas for the species (Heikkinen et al., 2010; Schweiger et al., 2012). This scale of analysis has also the potential to include those species that are not yet present in the area of interest but that are expected to become new native species as climate is warming. With respect to conservation planning, the drawback of such approaches is that they usually perform poorly when downscaling their outcomes to finer resolutions. Due to their coarse resolution, they might fail to capture climate details that correlate with the distribution of the species (Trivedi, Berry, Morecroft, & Dawson, 2008), especially in topographically heterogeneous areas (Franklin et al., 2013; Luoto & Heikkinen, 2008). It is, however, interesting to note that information is not necessarily needed at the whole continental extent to produce reliable models and projections. For instance, Johnston et al. (2013) projected spatial changes in bird species abundance within UK protected areas using abundance data from north-west Europe (i.e., Ireland, UK, France and the Netherlands) as such information was not readily available at fine spatial resolution for the whole of Europe. By doing so, they ensured that their models captured at least the part of the species response curves covering the climatic conditions that will prevail in the UK in the future.

It is also important to acknowledge that continental data and models can inadequately capture the climatic conditions used by the species across their full distribution ranges (i.e., the entire response curves of the species) for at least two other reasons. First, this large extent may be insufficient to cover the warmest parts of the distribution for some species, as was shown for birds in the Iberian Peninsula (Barbet-Massin et al., 2010). Some Mediterranean butterflies are also present in North Africa where they experience climatic conditions beyond those available in Europe (Numa et al., 2016). Hence, it is possible that even the continental models estimated a biased fraction of the entire response curves and truncated the warmest parts of the distributions for these species. This issue deserves further attention because, if this part of the response curves at least partly reflects the future climatic conditions that will prevail in Spain, the observed congruence between the projections derived from local and continental models would misinform on the reliability of using local models even in that region. Second, continental models typically ignore that the climatic niche of a species may vary within the geographical space it occupies (Gaston, 2003; Harte, Ostling, Green, & Kinzig, 2004; Hawkins, 2012). Recent studies have explicitly incorporated local adaptation in their modelling approach and reported that the projected distribution shifts under climate change might strongly deviate from the projections based on approaches that disregard within-species spatial niche variation (e.g., Bush et al., 2016). Most of these advanced methods use increasingly available information on genetic population structure, phenotypic plasticity or evolutionary adaptation to build and assemble a series of local models across the whole range of the species (Gotelli & Stanton-Geddes, 2015; Ikeda et al., 2017; Smith, Alsdurf, Knapp, Baer, & Johnson, 2017). Further research efforts are now needed to make this type of information increasingly available so that it would become possible to compare, for a large sample of species, the outcomes of such methods with the projections of models that ignore local adaptation.

Our results and recommendations highlight the need for distribution data beyond political boundaries. Biodiversity data have been collected for decades in long-term monitoring programmes and citizen-science projects (Schmeller et al., 2009). Such data are increasingly available from web-based portals and have been shown to be very useful for conservation (e.g., Devictor, Whittaker, & Beltrame, 2010; Maes et al., 2015; Sullivan et al., 2017; Supp et al., 2015). However, although the databases are increasingly implementing open access policy, their applicability may remain challenging because different databases often exist in heterogeneous systems that may differ across regions (Amano & Sutherland, 2013). Hence, we advocate strengthening international initiatives and collaboration efforts towards the development of innovative methods for the mobilization and integration of fine-resolution data over large spatial extents (Hoffmann et al., 2014; Robertson et al., 2014).

ORCID

Nicolas Titeux (iD) http://orcid.org/0000-0002-7719-7417

Dirk Maes (iD) http://orcid.org/0000-0002-7947-3788

Toon Van Daele (iD) http://orcid.org/0000-0002-1362-853X

Thierry Onkelinx (iD) http://orcid.org/0000-0001-8804-4216

Helena Romo (iD) http://orcid.org/0000-0002-5729-1342

Enrique Garcia-Barros (iD) http://orcid.org/0000-0003-2804-9626

Miguel L. Munguira (iD) http://orcid.org/0000-0002-1554-4380

Wilfried Thuiller (iD) http://orcid.org/0000-0002-5388-5274

Chris A. M. van Swaay iD http://orcid.org/0000-0003-0927-2216

Oliver Schweiger iD http://orcid.org/0000-0001-8779-2335

Josef Settele iD http://orcid.org/0000-0002-8624-4983

Lluís Brotons iD http://orcid.org/0000-0002-4826-4457

Miska Luoto iD http://orcid.org/0000-0001-6203-514

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BIOSKETCH

Nicolas Titeux is a researcher at the Forest Sciences Centre of Catalonia and at the German Centre for Integrative Biodiversity Research. The emphasis of his activities is on assessing and predicting the impact of global change on biodiversity across a range of spatial and temporal scales, combining structured and unstructured observation data to describe biodiversity dynamics, and understanding habitat selection patterns and processes in human-modified environments (https://nicolastiteux.wordpress.com).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.