

Predictor weighting and geographical background delimitation: two synergetic sources of uncertainty when assessing species sensitivity to climate change

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Abstract An accurate estimation of the expected consequences of climate change requires the proper quantification of the effect of climate on current species distributions. Several interrelated sources of uncertainty may affect the likelihood of species distribution models (SDMs) to determine the relative importance of climate. Our aim was to assess the relationship between the influence of geographical background (GB) delimitation and that of subtracting the non-climate effects from the weight of climatic predictors to estimate the combined influence of these two factors on predictions in climate change scenarios. The distribution of 40 endemic mammals in Western Europe have been modeled by (i) using the whole territory of Western Europe as the GB and also specifically delimiting the GB with a geographical criterion and (ii) considering climatic predictors in addition to other non-climatic variables in order to extract the pure effect of climate. The models were used to quantify species' sensitivity to new climate scenarios. Results showed discrepancies among the analytical approaches. Changes in distribution obtained by considering the pure effect of climate were lower than those obtained by considering the apparent effect, and GB-delimited models yielded higher changes than those

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trained in Western Europe. We evidence that climate weighting and GB delimitation have dramatic influences on the projections of models when transferred to new scenarios. We emphasize that scientific studies and derived adaptation policies based on SDMs without an explicit consideration of the GB and the weighting of the climate-related variables may be misleading and in need of revision.

Keywords European wild mammals · Extent · Historical factors · Spatial factors · Spatial structure · Species distribution models

1 Introduction

Over the last two decades, species distribution models (SDMs) have become relevant tools for conservation biology (Peterson et al. 2011; Guisan et al. 2013). These spatially explicit models provide hypotheses on the processes modulating both actual and potential species geographical ranges and produce cartographic representations of the ecogeographical favorability for species occurrence (Guisan and Thuiller 2005). In applied biogeography, SDMs can be transferred to new territories and new time periods in order to predict environmental potential for the species in unsampled territories and environmental change scenarios (e.g., Werkowska et al. 2017). Nevertheless, crucial ecological (e.g., biotic interactions) and evolutionary processes (e.g., glacial refuges) determining species distributions are usually poorly represented in SDMs (e.g., Soberón 2010; Barve et al. 2011; Hortal et al. 2012; Fordham et al. 2013; Acevedo et al. 2015), and methodological uncertainties (e.g., delimitation of the study area, predictor selection, and model complexity) emerge at each step and propagate throughout the modeling procedure (e.g., Beaumont et al. 2007; Buisson et al. 2010; Rocchini et al. 2011; Wenger et al. 2013; Lobo 2016). Both of these issues hamper the reliability of the predictions and their usefulness as regards deriving sound management actions (e.g., Real et al. 2010).

Accurately determining the relative contribution of the factors that may govern species distributions is primordial when using SDMs in applied biogeography, but it is not straightforward (Dormann et al. 2013) because it depends on several methodological aspects with non-independent implications. Previous studies have highlighted the importance of delimiting the geographical extent or geographical background (GB) for SDM calibration explicitly and in a clear way since it dramatically affects the relative weight of the different ecogeographical predictors (VanDerWal et al. 2009; Acevedo et al. 2012a) and, as a consequence, the derived suitability maps. This is so especially as a consequence of the enlargement in the environmental conditions at which the species is absent (Lobo et al. 2010); the larger the geographical extent, the higher the chance of obtaining response curves conditioned by environmental circumstances which lie far apart from the accessible area (sensu Barve et al. 2011). On the other side, predictions from models based on partial information about the response of the species to relevant environmental gradients could produce biased weights of the predictors and therefore may yield wrong suitability maps (Thuiller et al. 2004; Sánchez-Fernández et al. 2011). Consequently, when projected to new environmental scenarios, model predictions carried out considering different GBs may provide different results (VanDerWal et al. 2009; Anderson and Raza 2010; Barve et al. 2011; Vale et al. 2013). In this context, Barve et al. (2011) argued that the appropriate GB for modeling should comprise the set of localities that are accessible to the species via dispersal over relevant periods of time, i.e., the territory in which the species has probably achieved distributional equilibrium. Several

procedures were described to delimit this dynamic area (e.g., Barve et al. 2011; Niamir et al. 2016). The trend surface analyses (TSA) was proposed as a practical procedure to minimize the probability of including regions that are suitable for the species, but are uninformative for an ecological model due to their spatial remoteness from the current geographical range, and it was shown that this procedure was able to improve model performance (see details in Acevedo et al. 2012a).

Another key aspect that hampers the identification of the relative role played by different predictors is the usually high collinearity existing among them, making it hard to separate the independent effects of each one (Fox 1997; Williams et al. 2012; Nyström Sandman et al. 2013). When using SDMs to assess species' sensitivity to changes in climate (i.e., the amount and direction of change in species distributions when projected onto new climate scenarios; Thomas et al. 2004), the proper quantification of the effect of climate on current geographic ranges is a must if the expected consequences are to be accurately estimated (Braunisch et al. 2013). Under the assumption that climatic factors are the main determinants of species' geographic ranges (at least on large spatial scales; Pearson and Dawson 2003; Thomas 2010), climatic variables are usually the only predictors used during modeling (Thuiller et al. 2004). Some authors have argued against this procedure, since the effect of climate can only be adequately estimated in the context of the other influential factors that may covariate with climate (e.g., Márquez et al. 2011). The real climatic effect on species distributions might therefore be masked (under or overrated) by confounding correlated factors, which become evident only when the effects of non-climatic factors, and principally spatially structured factors, are subtracted (see Lobo et al. 2001; Péres-Neto and Legendre 2010) from the weights of the climatic predictors (e.g., Lavergne et al. 2005; Real et al. 2013; Record et al. 2013). Real et al. (2013) employed variation partitioning procedures to estimate the so-called pure climatic effect (i.e., not affected by the covariation with non-climatic—mostly spatial—factors included in the model) and the “apparent” climatic effect (i.e., including shared effects between climate and non-climatic factors). Using correlative models, it is not possible to precisely disentangle what proportion of the variation explained by the combined effect between climatic and non-climatic factors is due to climate; and therefore, both the pure and apparent fractions could be interpreted as the lower and upper bounds of a range of possible scenarios. This approach produces a more realistic and honest picture of the effects of climate than those obtained with traditional approaches only based on the apparent effect of climate (Real et al. 2013).

Previous studies have considered the effects of predictor weighting when assessing species sensitivity to climate change, but to the best of our knowledge the possible synergetic effects of GB delimitation and predictor weighting have not been explored. Thus, the main objective of this study is to examine the relationship between the influence of GB delimitation and that of subtracting or not the non-climate effects from the weight of climate predictors, to estimate the combined influence of these two factors on predictions in future climate change scenarios. To do that, SDMs were calibrated for several mammal species using the entirety of Western Europe as a common geographical background territory, and also specifically delimiting the geographical extent to the accessible area as proposed by Acevedo et al. (2012a). SDMs were calibrated in each GB considering climatic predictors (apparent effect of climate) in addition to other non-climatic variables in order to extract the pure effect of climate (following Real et al. 2013). All of these models were extrapolated to future climate scenarios and the impact of the different approaches on the geographic projections was evaluated. Even when the study is presented in a context of predicting species response to future scenarios of climate, the

obtained results are interpretable in all cases in which SDMs are transferred to either past or future scenarios.

2 Methods

2.1 Species data

The distribution data were extracted from *The Atlas of European Mammals* (Mitchell-Jones et al. 1999). This information refers to UTM 50 km × 50 km squares (the territorial units employed for modeling purposes). Only those UTM squares in which at least one mammal species has been reported were considered (see Acevedo et al. 2012b). This criterion left us with 2557 UTM squares (Appendix S1 in Supporting Information). The species to be included in the analyses were selected on the basis of two criteria: (1) only those species endemic to Western Europe were considered in order to account for the full response of the species to the environment (Thuiller et al. 2004; Sánchez-Fernández et al. 2011); (2) species with less than ten records were excluded so as to avoid poorly performing models resulting from low sampling sizes (Stockwell and Peterson 2002). The 40 species selected are listed in Appendix S2 in Supporting Information.

2.2 Ecogeographical data

Nineteen potential predictors related to spatial location and climate were used to calibrate the models (Table 1). With regard to the spatial factor, the third-degree polynomial of latitude and longitude (trend surface analysis; nine predictors) was considered in order to account for any spatial trend in the occurrence data (Legendre and Legendre 1998). With regard to climate, ten bioclimatic predictors for the present time were obtained from the WorldClim project database version 1 (Hijmans et al. 2005).

The models calibrated for the present study were projected into the future by replacing the values of the current bioclimatic predictors with those which, according to the CGCM2 circulation model from the Canadian Climate Centre for Modeling and Analysis, and the A2 emissions scenario, are expected for 2080 (Nakicenovic et al. 2000). Only one scenario was

Table 1 Variables used to model the distribution of wild mammals in Western Europe

Third-degree polynomial of the trend surface analysis	Bioclimate variables
Mean latitude (°N) [LA]	Annual mean temperature
Mean longitude (°E) [LO]	Mean diurnal range (mean of monthly (maximum temperature–minimum temperature))
$LALO = LA \times LO$	Isothermality (mean diurnal range/temperature annual range) (×100)
$LOLA^2 = LO \times LA^2$	Temperature seasonality (standard deviation ×100)
$LO^2LA = LO^2 \times LA$	Annual range of temperature (maximum temperature of the warmest month–minimum temperature of the coldest month)
$LA^2 = LA \times LA$	Mean temperature of the warmest quarter
$LO^2 = LO \times LO$	Mean temperature of the coldest quarter
$LA^3 = LA^2 \times LA$	Annual precipitation
$LO^3 = LO^2 \times LO$	Precipitation of the driest month
	Precipitation seasonality (coefficient of variation)

used, since our principal objective was to assess differences among the climate weighting approaches, and not the effect of different global circulation models or emissions scenarios.

2.3 Estimation of the sensitivity to climate change

As a general scheme of work, multiple logistic regressions (MLRs) were parameterized (Hosmer and Lemeshow 1989) to inductively explain the species distribution ranges based on the locations in which they are present and absent (dependent variable) and a set of ecogeographical variables (independent variables). The most relevant ecogeographical predictors were selected by following a forward–backward stepwise procedure based on the Akaike Information Criteria (AIC; Akaike 1974). For each species and extent, we performed stepwise selection procedures instead of using a fixed set of predictors in order to improve the performance of the models. More details about the modeling procedure can be found in Acevedo et al. (2012a).

Apparent and pure climatic effects were estimated for each species by using variation partitioning procedures, first by modeling species distributions in Western Europe (WE models; without GB delimitation), and second by modeling species distribution after GB delimitation (GB models). Four predictions of sensitivity to climate change were therefore estimated for each species. Analyses were carried out in R v. 2.15.2 (R Core Team 2012).

First, a complete MLR model in Western Europe, considering all the predictors described in Table 1, was calibrated for each species. Partial models were also calibrated (i.e., models in which only the predictors related to each factor—climatic or non-climatic—were included). Values of the deviance explained by the complete model (D_{WE}) and those explained by the partial models ($D_{WE\ clim}$ and $D_{WE\ Nclim}$) were subjected to subtraction rules (see Alzaga et al. 2009) in order to split the deviance explained by the pure effect of climate ($D_{WE\ pclim}$):

$$D_{WE\ pclim} = D_{WE} - D_{WE\ Nclim}$$

Second, for each species, the territory for model training was delimited by subjecting species distribution data to a TSA (Legendre and Legendre 1998; this is equivalent to the partial non-climatic model). The GB for the models therefore included only those localities with TSA-estimated values that were higher than the minimum TSA value assigned to a presence (for further details, see Acevedo et al. 2012a). This could be considered an approximation to the actual range of the different species (see Appendix S3); the area that is spatially accessible to the species and, thus, where the probability of obtaining realistic response curves to climatic conditions is maximized (Austin 2007; Halvorsen 2012). The deviance accounted for by these GB-delimited models (D_{GB}) was partitioned by following the rules described previously in order to obtain the apparent effect of climate within the new GB ($D_{GB\ clim}$) and the pure effect of climate ($D_{GB\ pclim}$).

Species' sensitivity to climate change is usually estimated as the amount of either contraction or expansion of geographic ranges when SDMs are projected into future climate scenarios (Thomas et al. 2004; Randin et al. 2006). The favorability function was used for this purpose, since its combined use with fuzzy logic operations increases the possibilities of making comparisons between models (Real et al. 2010). The probabilities yielded by the MLR models were converted into favorability values using the function proposed by Real et al. (2006) (see also Acevedo and Real 2012; Real et al. 2016). For each species, favorability values for the future according to the apparent effect of climate were obtained by replacing the current

climatic values in the favorability models with those values expected according to the A2 emissions scenario for 2080 ($F_{WE \cdot clim}$ and $F_{GB \cdot clim}$ for Western Europe and GB-delimited models, respectively). Future favorability values according to the pure effect of climate were estimated by following the procedure described in Real et al. (2013). Briefly, for the Western Europe models, the proportion of the apparent climatic effect represented by the pure climatic effect ($\hat{\partial}_{WE}$) was calculated as:

$$\hat{\partial}_{WE} = \frac{D_{WE \cdot pclim}}{D_{WE \cdot clim}}$$

The future favorability according to the pure effect of climate ($F_{WE \cdot pclim}$) was then estimated as:

$$F_{WE \cdot pclim} = F_{WE \cdot present} + \hat{\partial}_{WE} \times (F_{WE \cdot clim} - F_{WE \cdot present}),$$

where $F_{WE \cdot present}$ is the favorability for present time in Western Europe. This rationale was also used to estimate the favorability for the future according to the apparent and pure effects of climate determined from GB-delimited models ($F_{GB \cdot clim}$ and $F_{GB \cdot pclim}$, respectively).

Favorability values for the present and future were used to estimate species’ sensitivity to climate change according to the fuzzy increment index (I ; Real et al. 2010). This index indicates the positive or negative increment (net loss) of a favorable area for the species. The calculation of I was restricted to the actual species range (i.e., the area delimited by the TSA) in order to avoid a possible bias resulting from the extrapolation of GB-delimited models to overall Western Europe and to work in the area in which the ecological factors really affect the occurrence of the species. Four increment indices, one for each procedure, were estimated for each species. For each species and approach, I was estimated as:

$$\text{Western Europe model} \left\{ \begin{array}{l} I_{WE \cdot clim} = \frac{cF_{WE \cdot clim} - cF_{WE \cdot present}}{cF_{WE \cdot present}} \rightarrow \text{Apparent effect of climate} \\ I_{WE \cdot pclim} = \frac{cF_{WE \cdot pclim} - cF_{WE \cdot present}}{cF_{WE \cdot present}} \rightarrow \text{Pure effect of climate} \end{array} \right\}$$

$$\text{GB-delimited model} \left\{ \begin{array}{l} I_{GB \cdot clim} = \frac{cF_{GB \cdot clim} - cF_{GB \cdot present}}{cF_{GB \cdot present}} \rightarrow \text{Apparent effect of climate} \\ I_{GB \cdot pclim} = \frac{cF_{GB \cdot pclim} - cF_{GB \cdot present}}{cF_{GB \cdot present}} \rightarrow \text{Pure effect of climate} \end{array} \right\}$$

where c is the cardinality of each fuzzy set of localities favorable for the species (i.e., the sum of the favorability values of all the localities).

2.4 Estimation of the independent and synergetic effects of climatic predictor weighting and GB delimitation

General linear mixed models (Zuur et al. 2009) were used to explore the effect on the absolute values of I of two potential factors: the delimitation of the GB and the subtraction of the non-climatic effect. The interaction between these factors was also explored. “Species” was included as a random factor because the I values were not independent (four I values were calculated for each species). Scatterplots of raw I values for pairs of different approaches were

explored in order to detect uncertainty and opposite trends for a given species (i.e., an increment predicted with one approach but a net loss predicted with another). Statistical analyses and plots were performed with R v. 2.15.2 (R Core Team 2012) and the “lme4” package (Bates et al. 2012).

3 Results

The deviance explained by both the apparent effect of climate and the pure climatic effect, for WE and GB-delimited models, and the number of localities selected after GB delimitation are shown in Appendix S2. After TSA, half of the species GB-delimited models included less than 8.5% of Western Europe squares, and less than 20% of squares for 75% of the species.

The results of the statistical model used to explore for differences in species sensitivity (estimated with the fuzzy increment index in the species range) among approaches are summarized in Table 2 and Fig. 1. Absolute I values were higher when modeling the apparent effect of climate than when modeling the pure climatic effect, and they were also higher when the models were calibrated in a GB-delimited territory than when they were calibrated for Western Europe. The interaction between these factors had $p = 0.08$.

Scatterplots of raw I values from each pair of approaches reinforced the perception that relevant discrepancies were found (Fig. 2). Moreover, there were species for which an increment in a favorable area was predicted with one approach but a net loss was predicted with another (black points in Fig. 2).

4 Discussion

An understanding of the interactions among the many factors that determine species distributions is needed to obtain realistic estimations of the effect of climate change, an idea that has been pointed out by authors Pearson and Dawson (2003) and Márquez et al. (2011), among others. In correlative models, the GB used for model calibration and the consideration or non-consideration of other factors apart from climate—mainly spatially structured factors—conditions the relative contribution that will be assigned to each predictor. Unfortunately, although there is now abundant evidence of the effects of GB on several aspects of SDMs, such as model parameterization, validation, and comparison (e.g., VanDerWal et al. 2009; Anderson and Raza 2010; Barve et al. 2011; Acevedo et al. 2012a; Wang et al. 2012; Vale et al. 2013; Qiao et al. 2015), the GB is still frequently delimited by using geopolitical criteria with no biological justification (Meyer and Thuiller 2006). Moreover, it is well known that the

Table 2 Summary of the results of the general linear mixed model used to explore the effect of two potential factors, the delimitation of the geographical background (GB), and the subtraction of the non-climatic effect, on the estimations of species sensitivity to climate change (estimated with the fuzzy increment index, in absolute values) in the range of species distributions. “Species” was included as a random factor

Parameter	F -value	Significance
GB delimitation (f1)	33.816	$p < 0.001$
Non-climatic effect subtraction (f2)	42.187	$p < 0.001$
f1 \times f2	3.048	$p = 0.08$

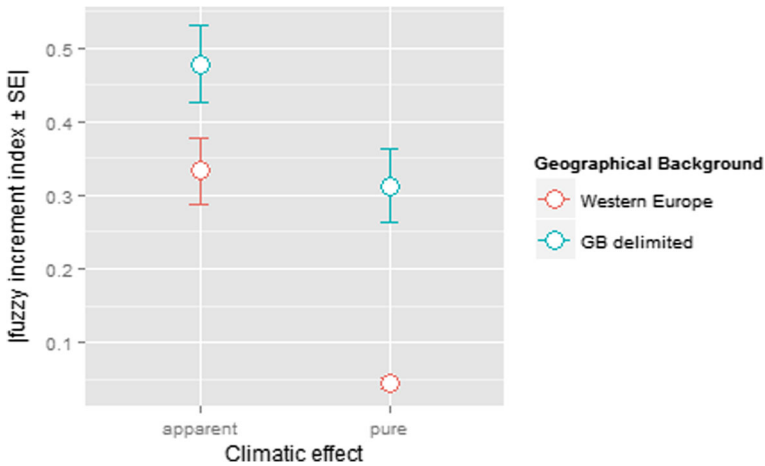


Fig. 1 Differences in the estimations of species' sensitivity to climate change (using the fuzzy increment index, in absolute values) in the range of species distribution in relation to the climatic effect (apparent versus pure; see text for details) and the geographical background (GB) used for model training (Western Europe versus GB delimited; see text for details)

coefficients of the predictors in a multiple statistical model depend on the inclusion or non-inclusion of other predictors, since each coefficient takes into account the variation explained by the other variables (Gotelli and Ellison 2004). Yet, it is general practice to employ only climate-related variables when using SDMs to forecast the effects of climate change (Real et al. 2013). In this study, considering the complete range of species distributions, it is shown that both aspects—GB delimitation and climate weighting—are interrelated and have dramatic influences on the geographic projections of the models when translated to other temporal scenarios, and that they consequently increase the uncertainty of the estimated trends of contraction or retraction.

Changes in species distribution (in absolute values) within the range of the species estimated by considering the pure effect of climate were the lowest, and GB-delimited models yielded higher range changes than models trained in Western Europe (Fig. 2), although in GB-delimited models the difference between considering the apparent or the pure effect of climate is less dramatic. These results are partly in accordance with the conceptual framework proposed by Real et al. (2013), in which the real effect of climate should be somewhere between the apparent and the pure climatic effects. Interestingly, our results show that models trained at biologically uninformative extents can underestimate the effect of climate in the core area of species distribution, even when considering the apparent effect of climate. This could be related to the capability of GB-delimited models to be better calibrated and, thus, to more accurately predict the species distribution within the range of the species (Acevedo et al. 2012a); the models on the Western Europe scale lack precision (most of the species range is simply predicted as highly favorable, which increases discrimination power but decreases calibration). This, in turn, limits the capacity of the models to accurately characterize the species' responses to climatic gradients at the most relevant geographical extent: the area that is accessible from the presently occupied localities. Interestingly, the pure climatic effect is much higher in GB-delimited models than in models trained in Western Europe (Fig. 1). This suggests that, at the continental scale, the apparent climatic variation can be also attributed to

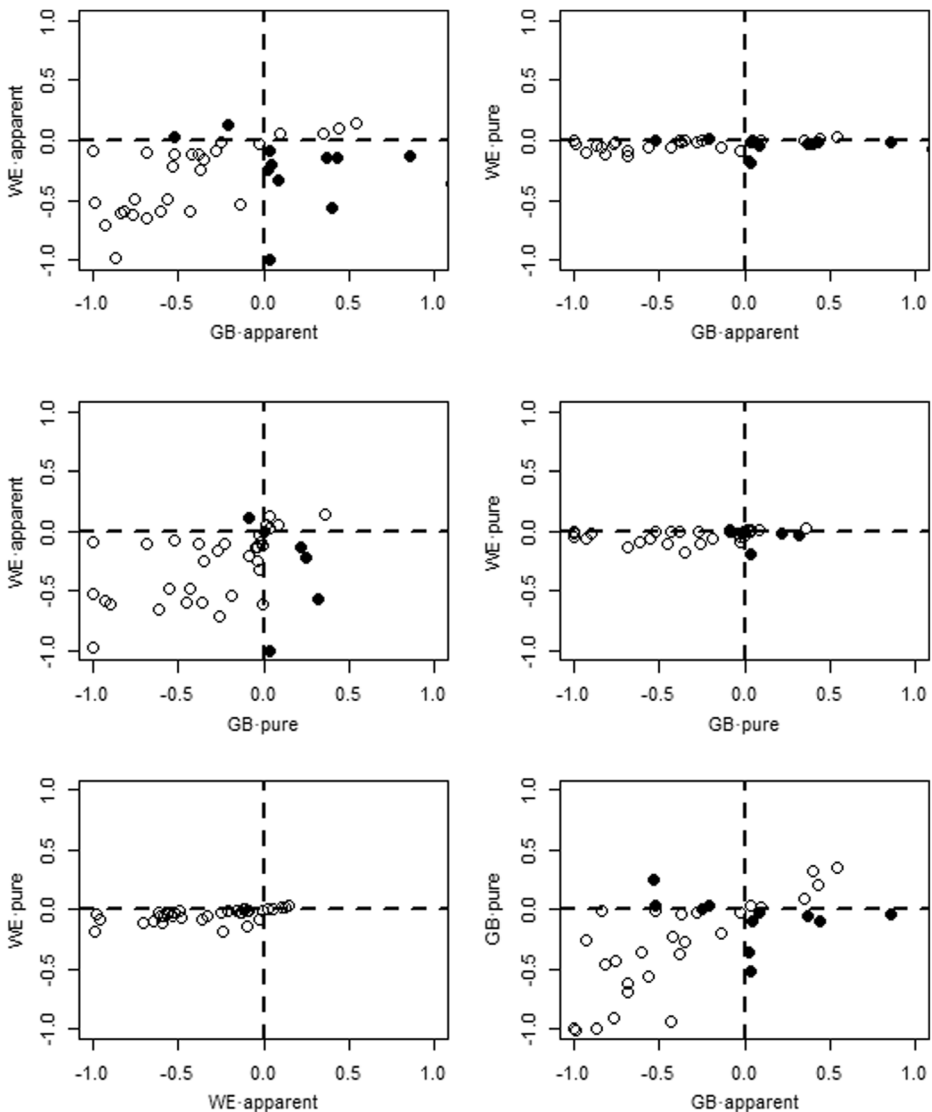


Fig. 2 Scatterplots of raw values of the fuzzy increment indices (estimated as proxies of species' sensitivity to climate change) for each pair of approaches tested. Two potential factors were combined: the geographical background, Western Europe (WE) versus a delimited geographical background (GB), and the climatic effect, apparent versus pure (see text for details). Black points represent species for which an increment in a favorable area was predicted with one approach but a net loss was predicted with another

other non-climatic gradients and that the risks to erroneously attribute to climate the role played by other spatially structured non-climatic factors increase with the extent. This result evidences that the effects of GB delimitation and predictor weighting on the predictions in climate change scenarios are mutually reinforcing and should be considered together. According to the conceptual framework behind GB delimitation using a geographical criterion, the accessible area from the species range is the most relevant territory for the species and is where

the species is able to effectively respond to environmental changes. Consequently, models aiming to explore the biogeographical response of the species to climatic conditions are more likely to be well calibrated if they are trained on this area (Appendix S3). We argue that by accounting for the precise response of the species to climatic gradients in this area, the assessment of species' sensitivity to climate change would, therefore, be more precise. It is worth mentioning that our results do not only apply to a climate change framework (i.e., temporal transferability of SDMs), they are also of concern in any other modeling exercise that implies a transfer in either time or space, for instance, in the assessment of invasion risk in new territories (Werkowska et al. 2017).

Geographic ranges have their own spatial cohesion (spatial structure), which is a product of historical, demographic, and dispersal limitation factors (analogous to the endogenous processes mentioned by Pères-Neto and Legendre 2010), but also can be induced by the environment (analogous to the exogenous processes; see Pères-Neto and Legendre 2010). The challenge would be to distinguish which part of the variation in species range explained by the climate can be assigned to these non-environmental processes. We argue that by delimiting the GB with a TSA, the confounding effects of these processes on the models are diminished because (i) the probability of overlooking spatial structures other than those caused by climatic factors is reduced; (ii) when working at the extent at which these processes that generate spatial cohesion operate, the likelihood of detecting the pure climatic response is increased; and (iii) the probability of recognizing the factors with a capacity to explain the boundary of species ranges is also increased.

The effect of GB delimitation was even more evident when raw *I* values were considered (Fig. 2). Previous studies suggest range reductions in future climate scenarios for most of the mammals endemic to Western Europe (e.g., Maiorano et al. 2011). However, our results show that discrepancies among methodological approaches are to be expected, which may even involve opposite trends—range increment versus range reduction—for the same species. This result evidences the high uncertainty in the assessment of the effects of climate change associated with the weighting of climatic factors in general (e.g., Braunisch et al. 2013) and with the delimitation of the GB in particular. In accordance with our results, other authors have shown that the geographical extent conditioned the importance assigned to the different explanatory factors and have questioned the application of fixed and general extents to understand biodiversity patterns (e.g., VanDerWal et al. 2009; Wang et al. 2012).

Since changes of local populations are expected to occur more acutely at the borders of species distribution (Gaston 2003), we suggest that the response of species to changing climates should be defined within the area accessible to the species, which is precisely where the models are best calibrated (Acevedo et al. 2012a), in order to ensure that the range borders are better delineated (Vale et al. 2013). Yet, various authors have recently warned that the SDMs customarily used have limitations as regards predicting range shifts under climate change (Real et al. 2010; Eskiildsen et al. 2013). We stress that further research is needed in order to assess the effect of GB on SDM-predicted—past and/or future—scenarios, and we emphasize that scientific studies and climate change adaptation policies based on the use of SDMs without an explicit and careful consideration of the GB and the weighting of the climate-related variables may be misleading and in need of revision.

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Author contributions P.A. and R.R. conceived the initial idea; P.A. carried out the statistical analyses; P.A., A. J.-V., J.M.L., and R.R. participated in the discussion of the results and wrote the manuscript.

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