

Correlative climatic niche models predict real and virtual species distributions equally well

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Citation: Journée, V., J.-Y. Barnagaud, C. Bernard, P.-A. Crochet, and X. Morin. 2019. Correlative climatic niche models predict real and virtual species distributions equally well. Ecology 00(00):e02912. 10.1002/ecy.2912

Abstract. Climate is one of the main factors driving species distributions and global biodiversity patterns. Obtaining accurate predictions of species' range shifts in response to ongoing climate change has thus become a key issue in ecology and conservation. Correlative species distribution models (cSDMs) have become a prominent tool to this aim in the last decade and have demonstrated good predictive abilities with current conditions, irrespective of the studied taxon. However, cSDMs rely on statistical association between species' presence and environmental conditions and have rarely been challenged on their actual capacity to reflect causal relationships between species and climate. In this study, we question whether cSDMs can accurately identify if climate and species distributions are causally linked, a prerequisite for accurate prediction of range shift in relation to climate change. We compared the performance of cSDMs in predicting the distributions of 132 European terrestrial species, chosen randomly within five taxonomic groups (three vertebrate groups and two plant groups), and of 1,320 virtual species whose distribution is causally fully independent from climate. We found that (1) for real species, the performance of cSDMs varied principally with range size, rather than with taxonomic groups and (2) cSDMs did not predict the distributions of real species with a greater accuracy than the virtual ones. Our results unambiguously show that the high predictive power of cSDMs can be driven by spatial autocorrelation in climatic and distributional data and does not necessarily reflect causal relationships between climate and species distributions. Thus, high predictive performance of cSDMs does not ensure that they accurately depict the role of climate in shaping species distributions. Our findings therefore call for strong caution when using cSDMs to provide predictions on future range shifts in response to climate change.

Key words: blocked cross-validation; climate change; model evaluation; null models; range shift; spatial autocorrelation; species distribution models.

INTRODUCTION

Climate is one of the main drivers of global diversity patterns along latitudinal and elevation gradients (von Humboldt 1807, Merriam 1894, Francis and Currie 2003, Willig et al. 2003) and is unquestionably a major determinant of species distributions regardless of taxa (Woodward 1987, Kearney and Porter 2009), as shown by paleoecological data (e.g., Williams et al. 2004), experimental approaches (e.g., Pigott and Huntley 1980, Rehfeldt et al. 2002), or current observations of range shifts in response to climate change (e.g., Walther et al. 2002, Parmesan and Yohe 2003). However, a complex array of factors interacts with climate to shape actual species distributions. Biotic interactions, dispersal,

microhabitat availability, and disturbances (including anthropogenic habitat changes or local species extirpation) all contribute to displace boundaries of species ranges away from the limits of their climatic niche (Sexton et al. 2009) and generate differences between the climatic requirements of a species (i.e., its fundamental climatic niche in the sense of Hutchinson 1957) and its geographic realization (Gaston 2003).

Deciphering the links between climate and species distributions is more crucial than ever: Robust predictions of species range shifts in response to climate change is a priority for the conservation of biodiversity and its functions (Coreau et al. 2009, Mouquet et al. 2015), but climate-based predictive models of species distributions rely on crucial assumptions on the role of climate in setting species distribution boundaries (Sexton et al. 2009). These assumptions are straightforward for species whose range limits are known to be affected by climate, but they require a cautious examination in most cases because nonclimatic drivers may be important (Guo

Manuscript received 23 January 2019; revised 12 July 2019; accepted 16 September 2019. Corresponding Editor: Hannah Buckley.

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2003). In fact, disentangling the relative influence of climate and other ecological factors on species distribution, and understanding how these drivers determine species range limits, remains particularly challenging (Coreau et al. 2009).

Various approaches have sought to identify the determinants of range limits in plants and animals (Gaston 2003, Sexton et al. 2009). Among these, frameworks based on correlations between species distributions and climatic variables have a long history (Merriam 1894). Building on this legacy, correlative species distribution models (cSDMs; see Jarnevich et al. 2015) represent the most popular approach by far and have been applied to a wide range of taxa and geographic scales (e.g., Thomas et al. 2004, Pereira et al. 2010, Thuiller et al. 2011). Experiments permit a more direct assessment of the causal role of climatic factors on species distributions (e.g., Breeman 1988, Loehle 1998, Morin et al. 2007a), but they are difficult to carry out at large spatial scales and for all organisms. Mechanistic modeling approaches relying on explicit species responses (e.g., growth, survival, reproduction, phenology) to climate variables have also been developed in the last two decades, for plant (e.g., Chuine and Beaubien 2001) and animal species (e.g., Kearney and Porter 2009), emphasizing the role of acclimation to cold temperatures (Leinonen 1996), phenology (Chuine 2000), or metabolic rates (Kearney and Porter 2004). However, these process-based models have been restricted to a small number of species (see, e.g., Morin et al. 2007b, Sinervo et al. 2010, Diamond et al. 2012) because the data needed to implement such tools are difficult to collect.

The vast majority of studies aiming at predicting species range shifts in response to climate change have therefore used cSDMs based on climatic variables (Guisan and Thuiller 2005, Pacifici et al. 2015). These “climatic cSDMs” predict local presence probabilities of a species from correlations between distribution data (occurrences in most cases, sometimes abundances) and climatic variables (Elith and Leathwick 2009) and are relatively straightforward to calibrate. Nonclimatic predictors can also be used in cSDMs (e.g., land cover: Thuiller et al. 2004, Ay et al. 2017; dispersal and biotic interactions: Heikkinen et al. 2007, Cabral and Schurr 2010, Boulangeat et al. 2012, Palacio and Girini 2018), but these examples are the exception rather than the rule. However, the ability of climatic cSDMs to identify and quantify the role of climate on species distributions properly is challenged increasingly often. The forecasting abilities of cSDMs can be tested by comparing their predictions of range shifts between past and current distributions—assessed with historical occurrence data—based on observed climate change with actual range shifts. Although there are still few examples (Elith and Leathwick 2009), this approach yielded mixed results so far: Sofaer et al. (2018) reported that modeling was poor at predicting observed range change in North American birds, and Fordham et al. (2018) concluded the opposite

in British birds (but with considerable variation in predictive abilities among species; see, e.g., fig. 3 in Fordham et al. 2018). For butterflies, Kharouba et al. (2009) showed that climate-change–induced range shifts of North American species could be well predicted by SDMs for most of the 160 species tested, but also reported a large variation between species in the abilities of the models to predict observed range shifts correctly, despite high spatial model accuracies during model training. Another widely used approach to evaluate predicting abilities of cSDMs is to compare predicted and observed distribution in invasive areas. Again, this approach produced contrasted conclusions. For instance, Peterson et al. (2003, plants), Petitpierre et al. (2012, plants), or Ramírez-Albores et al. (2016, plants) reported good abilities of cSDMs in predicting invasive ranges, but Broennimann et al. (2007, plants), Beaumont et al. (2009, plants), Gallagher et al. (2010, plants), Early and Sax (2014, plants), Gonçalves et al. (2014, plants), or Hill et al. (2017, insects) found opposite conclusions.

One of the main reasons for the success of climatic cSDMs undoubtedly lies in the strong accuracy of their results when compared to observed species distributions. Such high goodness of fit under current climatic conditions is often interpreted as evidence for the ability of cSDMs to represent a causal link between climatic variables and species range (e.g., Pearson and Dawson 2003, 2004, and see review by Elith and Leathwick 2009) or as a way to identify key specific climatic variables driving species range limits (e.g., Bombi et al. 2009, Gogol-Prokurat 2011, Javanbakht et al. 2017). However, several studies have questioned the ability of cSDMs to identify accurately the role of climate in determining species range (Loehle and LeBlanc 1996, Bahn and McGill 2007, Beale et al. 2008, Lozier et al. 2009, Fourcade et al. 2018, Rich and Currie 2018). A key criticism is that cSDMs rely on correlations that do not necessarily have a causal basis, and that they cannot be externally validated because they are typically tested by resampling the data set of available occurrences (Dormann et al. 2012).

Null models represent a more appropriate way to assess the capacity of species distribution models to detect the causal relationship between species and climate (Gotelli and Graves 1996). Only a handful of studies have used null models to assess the robustness of climatic cSDMs in the past, either by comparing the output of cSDMs obtained on actual species distributions and on virtual species distributions (Bahn and McGill 2007, Beale et al. 2008, Jiménez-Valverde et al. 2011) or by using randomized environmental predictors (Boucher-Lalonde and Currie 2016, Fourcade et al. 2018). These null model approaches have yielded mixed results. For instance, Beale et al. (2008) concluded that species–climate associations found by cSDMs were no better than chance in a majority of European bird species, while Jiménez-Valverde et al. (2011) found the

opposite conclusion for North American birds. However, most of these studies questioning the actual robustness of cSDMs have focused on bird species, and no study that we know of has used null models to assess the goodness of fit of cSDMs across several taxonomic groups, i.e., to test whether the robustness of cSDMs may depend on the group of taxa considered.

In this study, we used real species from five taxonomic groups and virtual species distributions of the same range size to test whether or not the accuracy of cSDMs calibrated with climatic variables reflect the role of climate in shaping species distribution. By doing so, we assessed the extent to which cSDMs can actually capture the processes linking climate and species distributions. A key requirement of our approach is the design of appropriate null models. We used random diffusion models, unconstrained by climatic gradients, to build virtual species distributions that have no causal link to climate, then compared the performance of climatic cSDMs when predicting real and virtual species distributions. We selected real species in five groups differing in their ecology and dispersal abilities, which excludes that our findings are explained by biological traits specific to a given group of organisms. Our aim was to answer the following question: can the distribution of virtual species be predicted with a similar accuracy as real species? Doing so, we do not question the role of climate as a major driver of species distributions (see Merriam 1894, Walther et al. 2005, Chen et al. 2011), or that cSDMs can be useful for assessing climate change impacts whenever climate is the main factor limiting a species range. Instead, what we precisely question is the use of cSDMs to assess the importance of climate on species distributions and consequently their use in predicting range shifts in response to climate change in species where the link between climate and range limits has not been clearly established.

We focus this study on the Western Palearctic region (Europe, North Africa, and the Middle East) because species distributions there are known with greater accuracy than in most other areas and can be associated with reliable climatic data. We selected two plant functional groups (herbaceous plants and trees), and three vertebrate groups, two ectotherms (reptiles and amphibians), and an endotherm (birds). We randomly picked 25 species (hereafter “real species”) of widely variable range size (i.e., prevalence) in each of these five groups. For each real species, we generated 10 virtual species distributions with spatial cohesion. We hypothesized that the predictive power of cSDMs varies across each taxonomic group because of their contrasted ecologies. For example, one may expect that plants, amphibians, and reptiles could be more influenced by the variation in climate variables than warm-blooded species such as birds (Gaston 2003). We also expect that the predictive accuracy of cSDMs decreases with increasing species range size, because larger distributions tend to sample broader arrays of climatic conditions than restricted-range

species. Furthermore, we used a newly proposed rigorous evaluation of models’ outcomes (Roberts et al. 2017) to strengthen the scope of our findings. We therefore (1) assessed the sensitivity of our analysis to range size and (2) compared accuracy of cSDM results on real species distributions between the five species groups, then (3) compared the accuracy of climatic cSDM suitability maps obtained for these virtual species distributions to those obtained for the real species, across the five groups of taxa.

METHODS

Study area and climatic variables

The study area corresponds to the Western Palearctic ecozone, including the European region of Eurasia together with North Africa (north of the Sahara) and the Middle East (Fig. 1). It is located roughly between the latitudes of 30° to 72° N and the longitudes of 12° W to 68° E and covers an area of 33,152,400 km² (i.e., 331,524 pixels of 5-arcmin resolution) when excluding oceans and large water bodies. Using a finer resolution would have been relevant regarding the resolution of species distribution. Because pixels are different around the shores to the Caspian Sea, we redefined the Caspian Sea with a specific mask.⁵ We downloaded 19 climatic variables from the WORLDCLIM database⁶ (Appendix S1: Table S1; see Hijmans et al. 2005 for more details) and added elevation⁷ because it strongly correlates with local climatic conditions in the study area. We used a principal-component analysis (PCA) to reduce the number of predictors to a smaller number of uncorrelated synthetic variables. The first six axes of a PCA on all 20 original variables explained ca. 97% of the variance of the data set (Appendix S1: Table S1) and were retained as predictors in all subsequent modeling analyses. This was sufficient for our purpose, as we did not aim to identify the most relevant climatic variables influencing the range of a given species.

Real species distribution data

We first built a species list for birds, amphibians, reptiles, and herbaceous plants occurring in Europe, retaining only species native to Europe that have most of their breeding range within Europe. We further excluded seabirds and other strictly coastal or insular bird species. Once the lists were completed, we randomly selected 25 species for each of these taxa (100 species in total). For these four taxonomic groups, species distributions were downloaded from the International Union for Conservation of Nature (IUCN) Red List website (IUCN 2017).

⁵ <http://www.naturalearthdata.com/downloads/50m-physical-vectors/>

⁶ www.worldclim.org, version 1.4

⁷ <https://lta.cr.usgs.gov/SRTM>

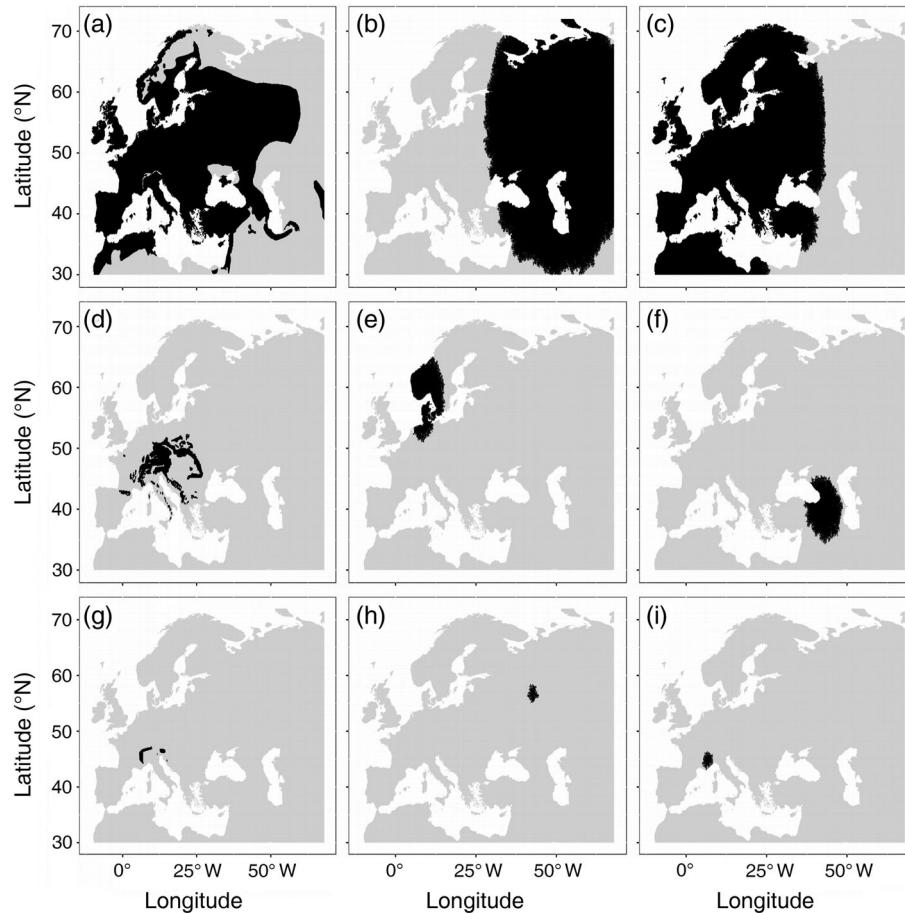


FIG. 1. Distribution of (a) *Chloris chloris* (bird), (d) *Abies alba* (tree) and (g) *Eryngium alpinum* (herbaceous plant), and two examples of virtual distributions for each of these three species [(b) and (c) for *C. chloris*; (e) and (f) for *A. alba*; (h) and (i) for *E. alpinum*].

If a distribution was not available for a given species, we randomly picked another species of the same group in our list. For trees, we downloaded the distributions of all 26 available species (at the time of the study in 2016) from EUFORGEN⁸ (San-Miguel-Ayán et al. 2016). We removed areas of nonnative presence (if any) and nonbreeding range for birds, as well as parts of the range located outside the study area. We then rasterized species distribution maps into presence–absence data at a 5-min resolution to match climatic data. Because some of the selected species had small ranges (i.e., less than 100 pixels), we anticipated difficulties to fit accurately a distribution model (as illustrated in other studies, e.g., Stockwell and Peterson 2002). We therefore added three supplementary species of amphibians and herbaceous plants to circumvent this issue. In total, we gathered data for 132 species distributions of five taxonomic groups. The distributions of 88 species were entirely included within our study zone. The distributions retained for the final analyses vary from local endemics

(minimum of six pixels) to continent-wide presence (maximum of 244,492 pixels on 331,524 land pixels; see Data S1 and Metadata S1).

Null models

For each real species, we generated 10 virtual species distributions with the same range size (prevalence) as the real species (Fig. 1; Appendix S1: Fig. S1). We chose to generate spatially cohesive distributions for virtual species, that is, the virtual distributions were formed of a single block rather than multiple isolated pixels with occurrence data (see Discussion). We developed an algorithm under the R environment (R Development Core Team 2016) to generate these virtual species distributions using a diffusion model approach (Data S2 and Metadata S2). We started by randomly selecting one pixel in the study area. The virtual distribution was then extended gradually by colonizing adjacent pixels in a direction chosen randomly at each step, until the final range size was reached (i.e., the same range size as the corresponding real species). Whenever a pixel was

⁸ <http://www.euforgen.org>

selected within a large water body, it was exchanged with the closest unoccupied pixel in land. This procedure guaranteed that sea basins were not a barrier to “colonization” and avoided the middomain effect (Colwell and Lees 2000), where most distributions would be located in the center of the study area.

Distribution modeling

All cSDMs were fitted with the R package BIOMOD2 (Thuiller et al. 2009). We used the same modeling workflow for real and virtual distributions (Appendix S1: Fig. S1). We used two kinds of algorithms to fit the cSDMs. First we built generalized additive models (GAMs; Wood 2006) to describe the relationships between presence–absence data and the six climatic predictors. GAMs are commonly used in species distribution modeling because they handle complex responses and are robust to data quality as well as to the number of absence data (Barbet-Massin et al. 2012).

As our main aim was to compare real with virtual species, we did not need to split the data set of observed presences as commonly done to test for the validity of the fitted model. Thus we first fitted GAMs by including all the pixels in our study area (331,524 pixels, from 6 to 244,492 presences depending on the species), considering all pixels outside species’ distributions as absences.

However, considering all pixels may inflate goodness-of-fit values and thus level differences between real and virtual species. In most cSDMs-based studies, model validation is assessed on a random subsample of the data set of observed presences or presences–absences different from the subsample of data used for model calibration. Calibration and validation based on random samples of presence–absence data can underestimate the errors when dependence structures are present in the data (Roberts et al. 2017), as is the case with climatic data. In fact, defining separate blocks for training and testing model represents a new opportunity to limit effect of spatial structure for climate and species distribution (Roberts et al. 2017). Block cross-validation can address these issues. As recommended by Roberts et al. (2017), we defined two nonrandomly chosen blocks of data, one for cSDM calibration and another one for cSDM validation. To do so, we split the study area in two according to the mean latitude of species distribution. We then sampled 5,000 absences in each block to ensure a minimal value of 10,000 absences in total for the study site (Barbet-Massin et al. 2012). When it was impossible to split the study area according to latitude, we used longitude. We present results for both methods, that is, with and without cross-validation, for GAM algorithm. Our general methodology is summarized in Appendix S1: Fig. S1.

As GAMs are prone to overfitting and may produce response functions that are difficult to interpret biologically (Wood 2006), we also used MAXENT (v3.3.3,

Phillips et al. 2006, using only presence data) to assess the robustness of our findings to changes in algorithm. The results obtained with MAXENT were qualitatively similar to those obtained with GAMs and are not detailed here (see Appendix S1: Section S1). Note that overfitting can also affect machine learning methods or MAXENT (Elith et al. 2006, Elith and Graham 2009).

Model evaluation and statistical analysis

We used the two most common evaluation methods (Fourcade et al. 2018) to calibrate and validate GAMs, the area under the receiver operating curve (AUC) criterion and true skill statistics (TSS). AUC is independent from the threshold value used to convert probabilities of presence per pixel into presence–absence data (Elith and Leathwick 2009) and is one of the most popular criteria to evaluate cSDMs. An AUC value of 1 means a perfect fit, and a value of 0.5 corresponds to random prediction of a species presence in a given cell.

To check whether our conclusions are sensitive to the evaluation metrics used, we also used a threshold-dependent metric with the GAM algorithm, the TSS (Allouche et al. 2006). The TSS is an alternative metric used in cSDMs studies that is not influenced by the distribution size. It is based on presence–absence data and varies between -1 (poor fit) and 1 (perfect fit). To convert the probabilities of presence into presence–absence data for TSS, we used a threshold value maximizing sensitivity and specificity as recommended by Liu et al. (2013). Two real species and 49 virtual species were not predicted because of the low number of presences used to calibrate the model, but the results yielded the same conclusions than the AUC (see Fig. 3).

To compare the accuracy of cSDMs results for virtual and real species distributions, we assigned a rank to each real species based on its AUC (or TSS) value compared with the AUC (or TSS) values of its 10 corresponding virtual species: if the real species was found to have the highest AUC (or TSS) it was assigned the first rank, that is, rank 1, whereas if it was found to have the lowest AUC (or TSS) it was assigned the last rank, that is, rank 11. We then compared the rank distribution of the real species to the expected distribution under the null hypothesis that AUC (or TSS) values did not differ between real and virtual species. We also used a *t*-test to test whether AUC (or TSS) values of cSDMs differed between real and virtual species and an *F*-test of equality of variances to test if real and virtual species had AUC (or TSS) of equal variance (Stats package in R).

Last, we ran a general linear model in Statistica version 10 (StatSoft 2011) to examine the effects of group and prevalence on AUC (or TSS) for real species only. Prevalence was log-transformed prior to analysis to reduce nonnormality and group was defined as random. We started with the complete model $\text{AUC (or TSS)} = \log(\text{prevalence}) + \text{group} + \text{group} * \text{prevalence}$.

RESULTS

Comparison between real and virtual species

The distributions of the real species were generally accurately predicted without cross-validation (hereafter CV), with AUC values ranging from 0.899 to 1.00 ($\mu_{\text{AUC}} = 0.972$, $\sigma_{\text{AUC}} = 0.02$), and AUC values with blocked CV ranged from 0.308 to 0.99 ($\mu_{\text{AUC-CV}} = 0.675$, $\sigma_{\text{AUC-CV}} = 0.179$, Appendix S1: Fig. S3). The TSS values ranged from 0 to 0.99 without CV ($\mu_{\text{TSS}} = 0.844$, $\sigma_{\text{TSS}} = 0.129$) and from 0 to 0.98 with blocked CV ($\mu_{\text{TSS-CV}} = 0.323$, $\sigma_{\text{TSS-CV}} = 0.278$, Appendix S1: Fig. S3). The AUC and TSS values of cSDMs for virtual species distribution were also higher without CV ($\mu_{\text{AUC}} = 0.975$, $\sigma_{\text{AUC}} = 0.05$; $\mu_{\text{TSS}} = 0.848$, $\sigma_{\text{TSS}} = 0.20$), than with blocked CV ($\mu_{\text{AUC-CV}} = 0.741$, $\sigma_{\text{AUC-CV}} = 0.16$; $\mu_{\text{TSS-CV}} = 0.432$, $\sigma_{\text{TSS-CV}} = 0.28$). The goodness-of-fit values of models fitted without CV were similar between virtual and real species (GAM AUC, *t*-test, $t = -1.27$, $\text{df} = 283.62$, $P = 0.206$; GAM TSS, *t*-test, $t = -0.39$, $\text{df} = 200.16$, $P = 0.691$). However, mean values were different between real and virtual species distribution fitted with blocked CV (GAM AUC-CV, *t*-test, $t = -4.36$, $\text{df} = 1,450$, $P < 0.0001$; GAM TSS-CV, *t*-test, $t = -4.20$, $\text{df} = 1,450$, $P < 0.0001$), with virtual species showing higher AUC and TSS values on average.

The AUC and TSS values of cSDMs for virtual species distribution were more variable than for real species (AUC: *F*-test of equality of variances; $F_{131,1,319} = 4.88$, $P < 0.00001$; TSS: *F*-test of equality of variances; $F_{131,1,319} = 2.39$, $P < 0.00001$). However, these differences disappeared with blocked CV (AUC-CV: *F*-test of equality of variances; $F_{131,1,319} = 0.832$, $P = 0.14$; TSS-CV, *F*-test of equality of variances; $F_{131,1,319} = 1.04$, $P = 0.75$).

Most real species distributions had a lower rank than virtual species distributions, and only 8 of the 132 real species were ranked first in comparison to their virtual species. The majority of virtual species distributions were thus predicted with a stronger accuracy than real species distributions (Figs. 2 and 3a; Data S1 and Metadata S1). The proportion of real species ranked first is very similar to the expected proportion if species rank was randomly assigned, regardless of their “status” (i.e., real or virtual): under random expectations, 1 out of 11 real species should show a better fit than its 10 associated virtual species, that is, a total of 12 (132/11) real species ranked first by chance. The results were similar regardless the metric and the methodology used (Fig. 3b–d, Data S1 and Metadata S1) or the algorithm (Appendix S1: Fig. S2; Data S1 and Metadata S1). We can thus conclude that real and virtual species’ distribution were predicted with the same accuracy.

Effect of prevalence and taxon on the fit of the cSDMs for the real species

Prevalence strongly and negatively affected the cSDMs accuracy (AUC and TSS, without CV and with

blocked CV) for real species (Table 1). The group did not have a significant effect on AUC and on TSS with blocked CV, but it significantly affected TSS without CV (Table 1). In this last case, the interaction between prevalence and group was also significant. In all cases, AUC or TSS seemed to decrease more for birds than for the other groups when prevalence increased (Fig. 4).

DISCUSSION

Our main result is that SDMs based on climatic variables (cSDMs) predict equally well the distribution of real species and of virtual species whose distribution is independent of climate, regardless of the method used to fit cSDMs. Using a blocked cross-validation showed that virtual distributions may be even better predicted with cSDMs than real species distributions. Our findings therefore demonstrate that a strong predictive power of cSDMs should not necessarily be interpreted as an accurate depiction of the link between climate and species distribution, and thus calls for a greater caution when using cSDMs to make predictions about future changes in species distributions in response to climate change.

Prevalence and taxonomic groups did not affect our conclusions

We expected the increased size of the distribution (or prevalence; see Stockwell and Peterson 2002, van Proosdij et al. 2016) to increase the accuracy of cSDMs, as previously found in invertebrates (Aguirre-Gutiérrez et al. 2013) and tetrapods (mammals, reptiles, amphibians, and birds; Morán-Ordóñez et al. 2017). In agreement with these studies, we found that predictive accuracy of cSDMs decreased with increasing range size in real species. Contrary to our expectations, we did not find a significant variation of predictive performance of cSDMs between taxonomic groups, despite a tendency for weaker accuracies for birds (different slope of the AUC–prevalence relationships; Fig. 4). We might speculate that this tendency for a lower accuracy of climatic cSDMs in birds would become significant with a larger sample size per taxonomic group (approximately 25 real species per group in our study), as expected if birds, being endotherms, are less constrained by climate than ectotherms and plants (Gaston 2003). The main objective of including several taxonomic groups in our study was not to test for differences in accuracy among groups, however, but to ensure that our main conclusion was not dependent on the taxonomic group used. Therefore, virtual species distributions can be predicted as accurately as real species distributions, and this pattern does not depend on the size of the distribution group and also appears consistent regardless the ecological characteristics of the real species investigated.

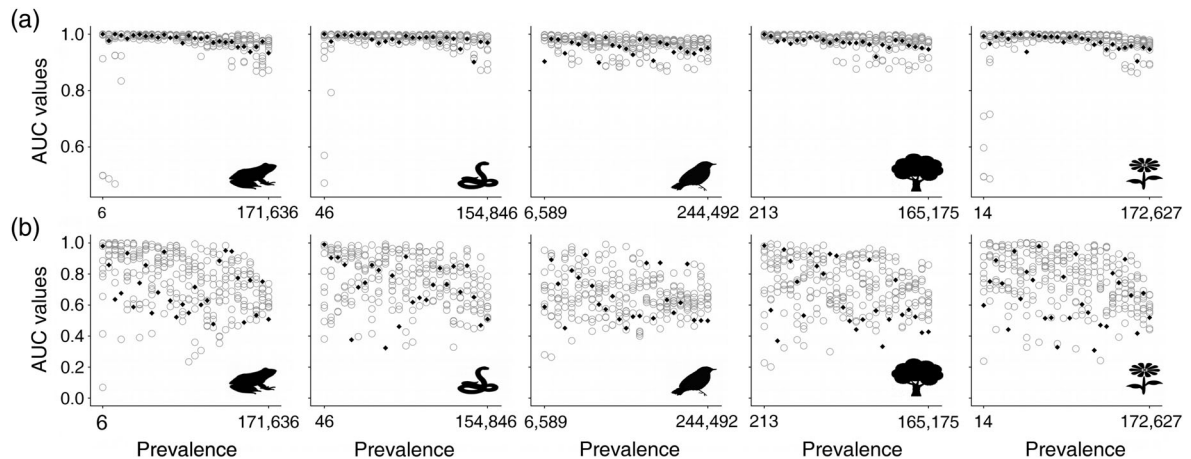


FIG. 2. Comparison of the AUC values (a) without cross-validation and (b) with blocked cross-validation for real species distributions and virtual species distributions, for each taxonomic group. Gray circles correspond to the area under the receiver operating curve (AUC) for virtual species, and black dots to the AUC for real species (amphibians, reptiles, birds, trees, herbaceous). Note that y-axis scale is different between (a) and (b).

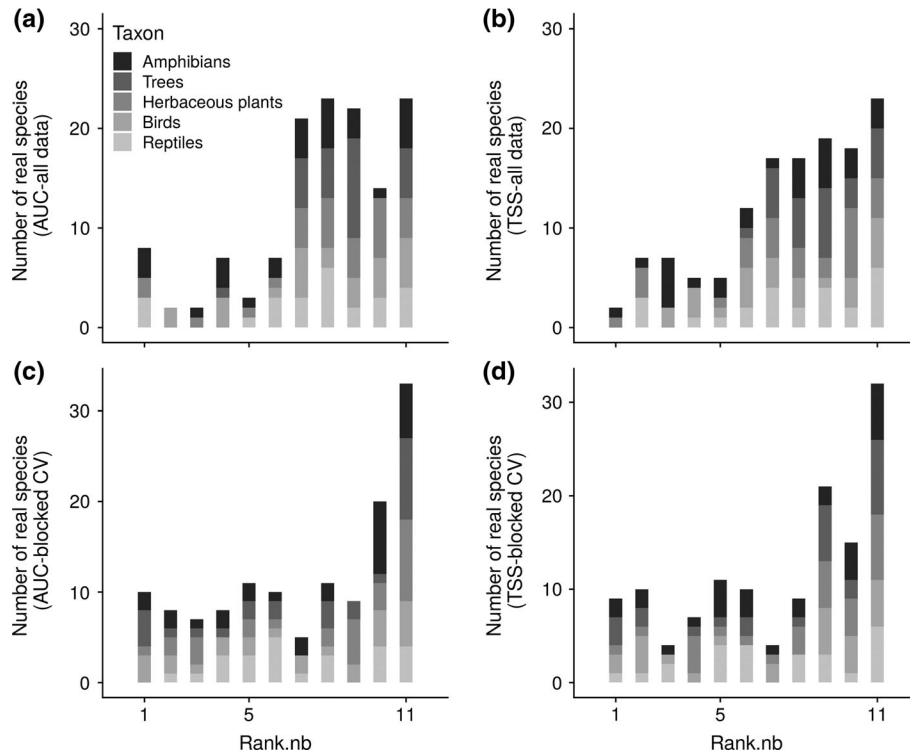


FIG. 3. Ranks of metrics values [area under the receiver operating curve (AUC) and true skill statistics (TSS)] of all real species distributions modeled with a generalized additive model (GAM) algorithm with (a), (b) all data and (c), (d) with block cross validation. Metrics values of real species are compared with the 10 corresponding virtual species. (a) Ranks of AUC values of all real species distributions modeled with GAM algorithm. (b) Ranks of TSS values of all real species distributions modeled with GAM algorithm. Note that two real species and 49 virtual species were not modeled because of the low number of presences used to calibrate the model. (c) Ranks of AUC values of all real species distributions modeled with GAM algorithm and a blocked cross-validation. (d) Ranks of TSS values of all real species distributions modeled with GAM algorithm and a blocked cross-validation. Results presented for (c) and (d) correspond to the validation block (AUC or TSS values of real species compared with the 10 corresponding virtual species).

TABLE 1. Linear mixed model for the effects of group (random) and prevalence on evaluation metrics for generalized additive models (GAM) with and without blocked cross-validation. The interaction term was removed from the final model when it was nonsignificant (P values between 0.25 and 0.82 for the three models with nonsignificant interaction term). See text for details.

	AUC–no CV			TSS–no CV			AUC–blocked CV			TSS–blocked CV		
	df	F	P	df	F	P	df	F	P	df	F	P
Group	4.126	1.98	0.101	4.122	5.69	<0.001	4.126	0.91	0.46	4.126	0.73	0.57
log (Prevalence)	1.126	46.69	<10 ^{−5}	1.122	0.33	0.59	1.126	13.26	<0.001	1.126	23.35	<0.001
Group * log (Prev)	–			4.122	4.44	0.002	–			–		

Note. AUC = area under the receiver operating curve; TSS = true skill statistics; CV = cross-validation.

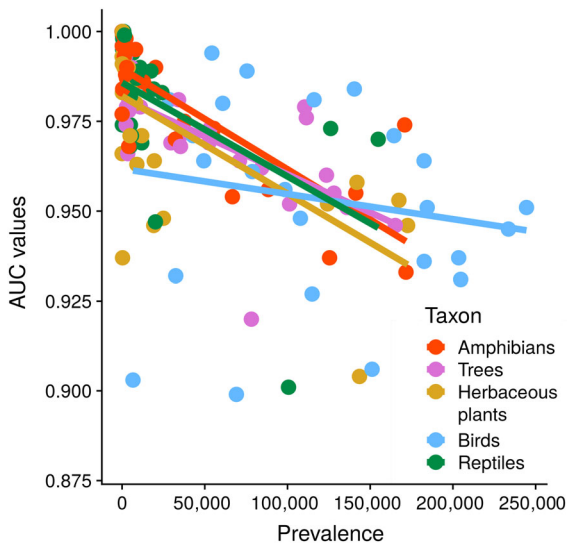


FIG. 4. Effect of taxonomic group and prevalence on the area under the receiver operating curve (AUC) values.

Spatial autocorrelation of climatic variables is the most likely culprit to explain our finding

How to explain that climatic variables can accurately predict a distribution range even when it is not linked to climate? Bahn and McGill (2007) already suggested that the spatial structure and autocorrelation of environmental variables could generate spurious relationships with species distributions, while Chapman (2010) simulated climatic gradients to demonstrate that the spatial structure of climate data drove the fit and the accuracy of cSDMs. Boucher-Lalonde and Currie (2016) removed all causal links between species distributions (here birds and mammals) and climate but retained the spatial autocorrelation structure of environmental variables. They found that the relation between climatic niche breadth and species range size could be adequately explained by the spatial autocorrelation of species ranges and climatic predictors. By using pseudo-predictors based on art paintings, Fourcade et al. (2018) recently demonstrated that any variable with a strong geographic structure (spatial autocorrelation) can accurately predict the distribution of a species.

In this study, we retained actual climatic variables (in contrast to Chapman 2010, Boucher-Lalonde and Currie 2016, Fourcade et al. 2018) but we generated virtual species distributions of the same size as real species but built without any causal relationships with climate (as done by Bahn and McGill 2007 or Beale et al. 2008 for birds). Our approach for generating virtual species distributions, using a random diffusion method, generated virtual distributions that had a more biologically realistic outline than previous studies based on simpler approaches (e.g., Bahn and McGill 2007) and retained the autocorrelation of species distributions necessary to build an appropriate null model, as rightfully advocated by Beale et al. (2008). With an approach similar to Beale et al. (2008) but (1) using a novel and more rigorous evaluation of models (i.e., blocked cross-validation) and (2) attaining more generality by incorporating species with more contrasted range sizes and ecologies, we confirmed that the spatial structure of climatic predictors allows the accurate modeling of almost any spatially coherent distribution with a cSDM. In fact, there seems always to be a combination of climatic variables that can describe a climatic envelope of a given distribution with a good accuracy, because of the strong latitudinal and longitudinal gradients of most climatic variables in Europe. A proper empirical test of this hypothesis would require altering the degree of spatial autocorrelation of climatic variables and examine how it affects accuracy of cSDMs.

Deciphering the role of climate on species distributions

Most studies that used null models to assess the ability of cSDMs to identify causal links between climate and species distributions concluded that climatic cSDMs did not perform generally better than alternative null models (Bahn and McGill 2007, Beale et al. 2008, Boucher-Lalonde and Currie 2016, Fourcade et al. 2018, Rich and Currie 2018; but see Jiménez-Valverde et al. 2011). Among these studies, some have argued that, because cSDMs based on climatic variables can predict null distributions with no relationship to climate as accurately as real species distributions, or because environmental variables added no predictive power beyond what spatial interpolation could provide, climate might not be the main

factor driving species distribution (e.g., Beale et al. 2008, Rich and Currie 2018). We do not share this view.

In our opinion, the ability of climatic cSDMs to model virtual species' distributions with the same accuracy as real species distribution tells nothing about the role of climate in shaping species distributions. These results simply demonstrate that fitting climatic cSDMs is not necessarily an appropriate tool to test for the role of climate in shaping species distributions. Because climatic cSDMs can and will accurately predict distributions that have no link to climate (Bahn and McGill 2007, Beale et al. 2008, our results), we need other approaches to investigate which species distributions are limited by climate or by other biotic or abiotic factors.

Testing the role of climate on species distributions is more crucial than ever. If fitting cSDMs cannot inform us on the causal link between climate and species occurrence, which possibilities can be envisaged? Possible alternative approaches include mechanistic models linking ecophysiological and/or demographic components to climatic variables on the basis of empirical and/or experimental data (Chaine and Beaubien 2001, Sinervo et al. 2010, Gutiérrez et al. 2016). Although some of the processes embedded in these mechanistic approaches may sometimes be modeled partly through correlations (for instance, if a process relies on bioclimatic thresholds inferred from presence-absence observed in distribution maps), the bias is certainly much weaker than for cSDMs that fundamentally depend on the species range size to be calibrated. Therefore, because they mostly rely on response functions that are a priori defined in experimental settings, they are not biased by spatial autocorrelation, and the effect of climate is directly tested. Another promising approach is the experimental manipulation of range limits (reviewed in Hargreaves et al. 2014). Last, the current level of climate change offers pseudo-experimental settings to test the impact of climate on species distribution directly (Kerr et al. 2007). Whenever actual changes in range limits as a response to climate change match the predictions of climatic cSDMs, the causal role of climate in determining distribution becomes well supported. As mentioned in the introduction, such approaches have yielded mixed responses within a general pattern of poleward and upward range shifts and it is likely that the direct contribution of climate to range limits varies between taxonomic groups and/or biogeographic regions (see Lenoir and Svenning 2015). Unfortunately, none of these alternative approaches is as easy to use or as general as correlative SDMs.

Comparisons with previous studies and the need for repeatability in ecology

Our work is not the first one to use virtual species distributions to assess the power of cSDMs to capture actual links between climate and species distributions

(see references in the introduction). However, we wish to point out here the novel aspects of our study.

First, the most original aspect of this work is clearly the comparison of several taxonomic groups of real species. Most previous papers using similar approaches focused on only one group of species (in most cases avian species), and it could be argued that their results were driven by a possible lack of response of birds to climate (in comparison with other kinds of organisms with physiological requirements more directly related to climate, like plants or ectotherms). In fact, one of the previous similar studies (Beale et al. 2008) concluded that “the distributions of most birds in our study are not strongly associated with the climate variables currently available,” rather than questioning the bases of correlative climatic niche modeling. We are not aware of any study comparing the performance of cSDMs on virtual and real species for such a wide range of taxa (i.e., the four main groups of terrestrial vertebrates and two functional groups of plants), thus comparing species strongly differing in dispersal abilities (from birds and trees to salamanders) and ecophysiology (endotherms vs. ectotherms and plants). We detected some differences between groups (consistent with the ecology of the groups), yet our conclusions draw a strong general trend. Therefore, with studies such as ours, it will be difficult to argue that the lack of power of cSDMs is restricted to the group(s) investigated.

Second, validation practices rapidly evolve in niche modeling, and low performance of cSDMs compared to null models has also been linked to failure of validation tools. The study by Fourcade et al. (2018) concluded on “the inability of current evaluation metrics to assess the biological significance of distribution models.” Here, we used the most stringent and recent validation tools—in addition to the commonly used AUC—and we showed that our conclusions did not change with the validation tools.

Last, we also wish to point out that in spite of the previous studies mentioned above, common practice has not changed much in the field, and cSDMs are still widely used for forecasting without much caution: cSDMs are more widely used than ever, and the limits of this modeling technique and philosophy are almost never acknowledged. Like in many other fields, it will take at least a series of independent studies by several teams (see Palmer 2000, Kelly 2006, Nagakawa and Parker 2015 on the need to repeat studies in ecology and evolution) before the cautionary message is heard. We thus think that it is important to publish independent studies reinforcing previous conclusions with different approaches and independent data sets. In that sense, we believe that our study, based on several groups of species, relying on spatially explicit virtual distributions (instead of randomizations) across Europe and using the most recent methods in cSDM validation represents a significant step in this direction.

Methodological issues and perspectives of our study

The methods used in this study differ from the classical way of fitting cSDMs in several aspects. First, we used polygons of distribution range as presence data, resulting in the spatial segregation of presence and pseudo-absence pixels. Many studies using cSDMs used actual occurrence data instead, resulting in a mixture of presence and pseudo-absence data inside the distribution range of species. Such an approach assumes that (a) pseudo-absence data inside the distribution range of species are more likely to correspond to real absences than to pixels where the species is actually present but has not been detected and (b) that the environmental factors used to model species occurrence differ between presence and pseudo-absence pixels. The first assumption might be realized in some species with high detectability in well-prospected areas, but is certainly not verified in most empirical studies that we know of. The second assumption seems unrealistic in climatic cSDMs based on broad-scale climatic variables (such as the WORLDCLIM data base), as most of the variables used for modeling certainly do not vary at the spatial scale corresponding to the spatial resolution of the presence and pseudo-absence data. In other words, it is highly unrealistic to use climatic variables varying over regional or continental scales to explain whether a species is present or absent in particular pixels of a local region. We are therefore confident that using polygons of distribution range as presence data does not undermine our work. We nevertheless checked the sensitivity of our results to this methodological choice by modeling real and virtual species distribution after removing 20, 40, 60, and 80% of the presence data and selecting pseudo-absence randomly inside and outside the species range, as done in many empirical studies (e.g., Araújo et al. 2005, Elith and Graham 2009, Barbet-Massin et al. 2012). Using various proportions of presence data did not alter our results, and our conclusion that real species distributions are not predicted with stronger accuracy than virtual species distributions therefore remains valid (Appendix S1: Section S1).

Secondly, the size of the study area is known to affect the accuracy of modeling results of cSDMs (Thuiller et al. 2005). If the study area is too large relative to the species distribution, there is a risk of overfitting (i.e., increased AUC values), leading to less realistic estimates of niche characteristics (Anderson and Raza 2010, Barve et al. 2011). This is simply because increasing the range of climate conditions spanned in a study area increases the ability of cSDMs to discriminate the range of conditions suitable for a given species, but at the cost of decreasing the accuracy. In this work, we did not adjust the size of the study area to be proportional to each distribution (Fig. 1; Data S1 and Metadata S1) because defining a specific study area for every real and virtual species distribution would distort the modeling procedure and would not allow a fair comparison for all

species. However, the key point was that real and associated virtual species always had the same range size. Furthermore, many real species selected had a large prevalence, so the effect of large study area relative to species range cannot be responsible for our main conclusion.

Third, we chose to assess the performance of the model through a blocked cross-validation (Roberts et al. 2017, Fourcade et al. 2018). This method provides a better spatial independence between calibration and validation data sets than usually done in cSDMs-based studies with random cross-validation. Doing so also strengthened the robustness of our results.

Lastly, the generated virtual distributions were on average less fragmented than the real species distributions (Fig. 1). This pattern arose because our null models relied on continuous distributions obtained through a diffusion model, whereas real species may have disjointed distributions, especially those located in mountains and/or at high latitude. It has been shown that the aggregation level may influence the goodness-of-fit of cSDMs, with species distribution with a high level of aggregation usually showing higher AUC values (Beale et al. 2009). Although this approach is likely to have a weak impact on our results, a relevant perspective to this work would be to create a diffusion model allowing the design of fragmented distributions, in order to compare real and virtual species' distributions with a similar level of spatial fragmentation and/or convolutions of distribution limits. However, we do not expect this to affect our main conclusion, because our set of real species also includes distributions that have simple shapes and they were not better predicted than virtual species distributions (for examples see Appendix S1: Fig. S4), and because, alternatively, some of the virtual distributions with a convoluted outline were adequately predicted by cSDMs. We are thus confident that the main finding of the present study is robust to this limitation about the level of fragmentation of the virtual distributions.

Combining various approaches to better predict the impact of climate change

Forecasting distributions (e.g., projecting climate change impact on species distribution) is conditioned by two assumptions: that current distributions are mainly limited by climatic variables and that climatic niches remain stable through time (this is called the "climatically constrained hypothesis" by Rich and Currie 2018). It is probably sensible to assume that evolutionary changes in climatic niche will be rare enough (i.e., be expressed in few species) or small enough (i.e., be of low magnitude) at contemporary time scales to have a limited effect on most forecasting attempts, even if contemporary adaptation to new climate has been documented before (e.g., Colautti and Barrett 2013, Geerts et al. 2015, While et al. 2015). However, assuming that all current species distributions are mainly limited by climatic

variables is highly questionable, as explained in the introduction and earlier in the discussion. Our results further emphasize that forecasting distributions with cSDMs should be done with caution: correlative species distribution models may be useful to predict changes in species distribution due to climate change whenever climate is the main factor determining range limits (Lee-Yaw et al. 2016). For instance, Kharouba et al. (2009) constructed cSDMs under historical conditions for butterfly species and predicted range shifts reasonably well when climate changed for many (but not all) species. This is consistent with the fact that the physiology of many insect species (phenology, survival rates) is strongly dependent on climate (Chuine and Régnière 2017). Because current distributions are not necessarily limited by climatic factors, recent developments of cSDMs have tried to incorporate nonclimatic factors such as land use, interspecific interactions, or dispersal abilities to improve the modeling tools (Thuiller et al. 2004, Cabral and Schurr 2010, Boulangeat et al. 2012). Such efforts have improved the fit of the models to current distributions and shed light on the role of nonclimatic drivers of species distributions, so they certainly represent a promising venue for forecasting the impact of climate change. The climatic part of these hybrid SDMs remain the same as in classic cSDMs in most cases, however, and their forecasting abilities should be rigorously evaluated, for example, using historical distribution data or out-of-range introductions, as has been done with classical cSDMs.

Given these limitations, how can we obtain robust predictions of the impact of climate change on species distributions? As mentioned previously, although the use of process-based or experimental approaches is currently expanding, these are not straightforward to develop. A first attempt to solve this issue may be to limit forecasting with cSDMs to species for which range shifts have been shown to be predicted with strong accuracy through calibration on historical distributions and validation with current distributions (Kerr et al. 2007) or to invasive species whose invasive areas have been well predicted—although these approaches had contrasting results, as reviewed in the introduction. Other possibilities may be to focus on species where the link between climate and the probability of presence is grounded on solid biological bases, such as experiments in controlled conditions (Rehfeldt et al. 2002, Chuine and Régnière 2017) or using measures of the effects of climate on life-history traits (Pigott and Huntley 1980, Sinervo et al. 2010), and to select those climatic variables that are biologically meaningful prior to the modeling steps of cSDMs. Lee-Yaw et al. (2016) nicely illustrates how climatic cSDMs can provide accurate information on niche limits and suitability in a given location when experimental data demonstrate a causal link between climate and fitness; this was the case for 31 of the 40 plant species investigated, so for nearly a quarter (9 out of 40) of the species investigated a link between suitability as

predicted by cSDMs and actual local persistence as assessed by transplant experiments was not supported. An even more mixed pattern emerges from studies using human-mediated species translocations as quasi-experiments (see Introduction), so a direct link between climate and current range limits cannot always be taken for granted.

CONCLUSION

Disentangling the role of climate and other factors in shaping species ranges overreaches fundamental ecology and has far-reaching consequences when trying to predict biodiversity responses to climate change. Fitting cSDMs using climatic variables and using them to predict range change in response to climate change rests on the untested hypothesis that climate determines where a species is found. Our study highlights that fitting correlative SDMs based on climatic variables to current species distributions is not enough to assess the effect of climate on species distribution. This especially calls for caution when forecasting the impact of climate change on species range. Although cSDMs remain an important tool in the emergence of predictive ecology (Mouquet et al. 2015), a better understanding of the drivers of species distribution is crucial for conservation and climate change impact issues. It will allow the development of more realistic forecasting models incorporating dispersal, biotic interactions, actual relationships between climate and fitness, and nonclimatic environmental factors.

ACKNOWLEDGMENTS

We are grateful to Georges Kunstler, Nicolas Martin-St Paul, Cédric Perret, Estelle Barbot, Volker Bahn, and Maxime Dubart for useful discussions and comments, Quentin Legros for his help in programming a first version of the diffusion model, and Timothée Bonnet for his statistical advice. We also thank two anonymous reviewers for their comments on previous versions of this manuscript. This study has been funded by the CNRS and by ANR project BioProFor (contract 11-PDOC-030-01). Authors Pierre-André Crochet and Xavier Morin contributed equally to this article.

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