



HAL
open science

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

Valentin Journé, Jean-Yves Barnagaud, Cyril Bernard, Pierre-André Crochet,
Xavier Morin

► **To cite this version:**

Valentin Journé, Jean-Yves Barnagaud, Cyril Bernard, Pierre-André Crochet, Xavier Morin. Correlative climatic niche models predict real and virtual species distributions equally well. *Ecology*, 2020, 101 (1), pp.e02912. 10.1002/ecy.2912 . hal-02399969

HAL Id: hal-02399969

<https://hal.science/hal-02399969>

Submitted on 29 Aug 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

TITLE:

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

4

VALENTIN JOURNÉ^{1,2,4}, JEAN-YVES BARNAGAUD³, CYRIL BERNARD¹, PIERRE-
6 ANDRÉ CROCHET^{1†} AND XAVIER MORIN^{1†}

8

¹ *CEFE, CNRS, University of Montpellier, University Paul Valéry Montpellier 3, EPHE-PSL,*
10 *IRD, Montpellier Cedex 5, 34293, France.*

² *INRA UR 629, Ecologie des Forêts Méditerranéennes (URFM), Avignon Cedex 9, 84914*
12 *France.*

³ *CEFE, EPHE-PSL, CNRS, University of Montpellier, University Paul Valéry Montpellier 3,*
14 *IRD, Montpellier Cedex 5, 34293, France.*

[†] *These authors contributed equally to this paper.*

16

⁴ **Corresponding author:** valentin.journe@inra.fr

18

Running head: Climate modelling of virtual species

20 4 Figures, 1 Table, 1 Supporting Information

22

ABSTRACT

24 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
26 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
28 predictive abilities with current conditions, irrespective of the studied taxon. However, cSDMs
rely on statistical association between species' presence and environmental conditions and have
30 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
32 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
34 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
36 independent from climate. We found that i) for real species, the performance of cSDMs varied
principally with range size, rather than with taxonomic groups and ii) cSDMs did not predict the
38 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
40 autocorrelation in climatic and distributional data and does not necessarily reflect causal
relationships between climate and species distributions. Thus, high predictive performance of
42 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
44 predictions on future range shifts in response to climate change.

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

48 INTRODUCTION

Climate is one of the main drivers of global diversity patterns along latitudinal and elevation
50 gradients (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,
52 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
54 observations of range shifts in response to climate change (e.g. Walther et al. 2002, Parmesan et
al. 2003). However, a complex array of factors interacts with climate to shape actual species
56 distributions. Biotic interactions, dispersal, micro-habitat availability, disturbances (including
anthropogenic habitat changes or local species extirpation) all contribute to displace boundaries
58 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
60 the sense of Hutchinson 1957) and its geographic realization (Gaston 2003).

Deciphering the links between climate and species distributions are more crucial than ever:
62 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
64 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
66 straightforward for species whose range limits are known to be affected by climate, but they
require a cautious examination in most cases because non-climatic drivers may be important (Guo
68 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
70 particularly challenging (Coreau et al. 2009).

Various approaches have sought to identify the determinants of range limits in plants and
72 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
74 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
76 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.
78 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
80 responses (eg. 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
82 (e.g. Kearney & Porter 2009), emphasizing the role of acclimation to cold temperatures (Leinonen
1996), phenology (Chuine 2000), or metabolic rates (Kearney and Porter 2004). However, these
84 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
86 are difficult to collect.

The vast majority of studies aiming at predicting species range shifts in response to climate
88 change have therefore used cSDMs based on climatic variables (Guisan and Thuiller 2005,
Pacifiçi et al. 2015). These “climatic cSDMs” predict local presence probabilities of a species
90 from correlations between distribution data (occurrences in most cases, sometimes abundances)
and climatic variables (Elith and Leathwick 2009) and are relatively straightforward to calibrate.
92 Non-climatic 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, Boulangéat
94 et al. 2012, Palacio and Girini 2018), but these examples are the exception rather than the rule.
However, the ability of climatic cSDMs to properly identify and quantify the role of climate on
96 species distributions is challenged increasingly often. The forecasting abilities of cSDMs can be
tested by comparing their predictions of range shifts between past and current distributions –

98 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
100 mixed results so far: Sofaer et al. (2018) reported that modelling was poor at predicting observed
range change in North American birds, while Fordham et al. (2018) concluded the opposite in
102 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-
104 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
106 to correctly predict observed range shifts despite high spatial model accuracies during model
training. Another widely used approach to evaluate predicting abilities of cSDMs is to compare
108 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
110 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.
112 (2010, plants); Early and Sax (2014, plants); Goncalves et al. (2014, plants) or Hill et al. (2017,
insects) found opposite conclusions.

114 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-
116 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,
118 2003, 2004, and see review by Elith & 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,
120 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
122 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
124 that they cannot be externally validated since they are typically tested by resampling the dataset
of available occurrences (Dormann et al. 2012).

126 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).
128 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
130 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,
132 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
134 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
136 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
138 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
140 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
142 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
144 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
146 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

148 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
150 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
152 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
154 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.

156 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
158 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
160 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,
162 we generated 10 virtual species distributions with spatial cohesion. We hypothesized that the
predictive power of cSDMs varies across each taxonomic group due to their contrasted ecologies.
164 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
166 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-
168 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 i) assessed the
170 sensitivity of our analysis to range size and ii) compared accuracy of cSDM results on real species
distributions between the five species groups, then iii) compared the accuracy of climatic cSDM

172 suitability maps obtained for these virtual species distributions to those obtained for the real
species, across the five groups of taxa.

174

METHODS

Study area and climatic variables

The study area corresponds to the Western Palearctic ecozone, including the European region of
178 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
180 area of 33,152,400 km² (i.e. 331,524 pixels of 5 arc-minutes resolution) when excluding oceans
and large water bodies. Using a finer resolution would have been relevant regarding the resolution
182 of species distribution. Because pixels are different around the shores to the Caspian Sea, we
redefined the Caspian Sea with a specific mask
184 (<http://www.natureearthdata.com/downloads/50m-physical-vectors/>). We downloaded 19
climatic variables from the WORLDCLIM database (see Table S1 in Supporting Information, see
186 Hijmans et al. 2005 for more details, downloaded in February 2016 from www.worldclim.org,
version 1.4) and added elevation (downloaded from <https://lta.cr.usgs.gov/SRTM>) because it
188 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
190 variables. The first six axes of a PCA on all 20 original variables explained *ca.* 97% of the variance
of the data set (Table S1) and were retained as predictors in all subsequent modeling analyses.
192 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.

194

Real species distribution data

196 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
198 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).
200 For these four taxonomic groups, species distributions were downloaded from the IUCN Red List
website (<http://www.iucnredlist.org>). If a distribution was not available for a given species, we
202 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 EUFORGEN
204 (<http://www.euforgen.org>, San-Miguel-Ayanz et al. 2016). We removed areas of non-native
presence (if any) and non-breeding range for birds, as well as parts of the range located outside
206 the study area. We then rasterized species distribution maps into presence-absence data at a 5-
minute resolution to match climatic data. Because some of the selected species had small ranges
208 (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
210 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
212 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
214 of 244,492 pixels on 331,524 land pixels, see Metadata S1).

216 *Null models*

For each real species, we generated 10 virtual species distributions with the same range size
218 (prevalence) as the real species (Fig. S1, Fig. 1). We chose to generate spatially cohesive
distributions for virtual species, i.e. the virtual distributions were formed of a single block rather
220 than multiple isolated pixels with occurrence data (see discussion). We developed an algorithm

under the R environment (R Core Team 2016) to generate these virtual species distributions using
222 a diffusion model approach (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
224 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 selected within a large water
226 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 mid-domain effect (Colwell and
228 Lees 2000), where most distributions would be located in the center of the study area.

230 *Distribution modeling*

All cSDMs were fitted with the R package BIOMOD2 (Thuiller et al. 2009). We used the same
232 modeling workflow for real and virtual distributions (Fig. S1). We used two kinds of algorithms
to fit the cSDMs. First we built generalized additive models (GAMs; Wood 2006) to describe the
234 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
236 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 dataset of
238 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 six to 244,492
240 presences depending on the species), considering all pixels outside species’ distributions as
absences.

242 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
244 random subsample of the dataset of observed presences or presences-absences different from the
subsample of data used for model calibration. Calibration and validation based on random samples

246 of presence-absence data can underestimate the errors when dependence structures are present in
the data (Roberts et al. 2017), as it is the case with climatic data. In fact, defining separate blocks
248 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
250 issues. As recommended by Roberts et al. (2017), we defined two non-randomly chosen blocks
of data, one for cSDM calibration and another one for cSDM validation. To do so, we split the
252 study area in two according to the mean latitude of species distribution. We then sampled 5000
absences in each block to insure a minimal value of 10,000 absences in total for the study site
254 (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, i.e. with and without cross validation, for
256 GAM algorithm. Our general methodology is summarized in Figure S1.

As GAMs are prone to overfitting and may produce response functions that are difficult to
258 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
260 obtained with MAXENT were qualitatively similar to those obtained with GAMs and are not
detailed here (see Appendix A1 in Supporting Information). Note that overfitting can also affects
262 machine learning methods or MAXENT (Elith et al. 2006, Elith and Graham 2009).

264 *Models evaluation and statistical analysis*

We used the two most common evaluation methods (Fourcade et al. 2018) to calibrate and validate
266 GAMs, the Area Under the Receiver Operating Curve (AUC) criterion and the TSS. AUC is
independent from the threshold value used to convert probabilities of presence per pixel into
268 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, while a value of 0.5 corresponds to
270 random prediction of a species presence in a given cell.

To better check whether our conclusions are sensitive to the evaluation metrics used, we also used
272 a threshold-dependent metric with the GAM algorithm, the True Skill Statistics (TSS, Allouche
et al. 2006). The TSS is an alternative metric used in cSDMs studies that is not influenced by the
274 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
276 a threshold value maximizing sensibility and specificity as recommended by Liu et al. (2013).
Two real species and 49 virtual species were not predicted due to the low number of presences
278 used to calibrate the model, but the results yielded the same conclusions than the AUC (see Figure
3).

280 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
282 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, i.e. rank 1, while if it was found to have the
284 lowest AUC (or TSS) it was assigned the last rank, i.e. rank 11. We then compared the rank
distribution of the real species to the expected distribution under the null hypothesis that AUC (or
286 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
288 of variances I to test if real and virtual species had AUC (or TSS) of equal variance (Stats package
in R).

290 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
292 prior to analysis to reduce non-normality and group was defined as random. We started with the
complete model $AUC \text{ (or TSS)} = \log(\text{prevalence}) + \text{group} + \text{group} * \text{prevalence}$.

294

RESULTS

296 *Comparison between real and virtual species*

The distributions of the real species were generally accurately predicted without cross-validation
298 (hereafter “CV”) with AUC values ranging from 0.899 to 1.00 ($\mu_{\text{AUC}} = 0.972$, $\sigma_{\text{AUC}} = 0.02$), while
AUC values with blocked CV ranged from 0.308 to 0.99 ($\mu_{\text{AUC-CV}} = 0.675$, $\sigma_{\text{AUC-CV}} = 0.179$,
300 Figure 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 ($\mu_{\text{TSS-CV}} = 0.323$, $\sigma_{\text{TSS-CV}} = 0.278$, Figure S3). The AUC and TSS
302 values of cSDMs for virtual species distribution were also higher without CV ($\mu_{\text{AUC}} = 0.975$, σ_{AUC}
 $= 0.05$; $\mu_{\text{TSS}} = 0.848$, $\sigma_{\text{TSS}} = 0.20$), than with blocked CV ($\mu_{\text{AUC-CV}} = 0.741$, $\sigma_{\text{AUC-CV}} = 0.16$; $\mu_{\text{TSS-}}$
304 $\text{CV} = 0.432$, $\sigma_{\text{TSS-CV}} = 0.28$). The goodness-of-fit values of models fitted without CV were similar
between virtual and real species (GAM AUC, *t*-test, $t = -1.27$, $df = 283.62$, $p = 0.206$; GAM TSS,
306 *t*-test, $t = -0.39$, $df = 200.16$, $p = 0.691$). However mean values were different between real and
virtual species distribution fitted with blocked CV (GAM AUC-CV, *t*-test, $t = -4.36$, $df = 1450$, p
308 < 0.0001 ; GAM TSS-CV, *t*-test, $t = -4.20$, $df = 1450$, $p < 0.0001$), with virtual species showing
higher AUC and TSS values on average.

310 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; $F_{131, 1319} = 4.88$, $p < 0.00001$; TSS: *F*-test of
312 equality of variances; $F_{131, 1319} = 2.39$, $p < 0.00001$). However, these differences disappeared with
blocked CV (AUC-CV: *F*-test of equality of variances; $F_{131, 1319} = 0.832$, $p = 0.14$; TSS-CV, *F*-
314 test of equality of variances; $F_{131, 1319} = 1.04$, $p = 0.75$).

Most real species distributions had a lower rank than virtual species distributions, and only eight
316 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
318 distributions (Fig. 2, Fig. 3-a & 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
320 “status” (i.e. real or virtual): under random expectations, one out of 11 real species should show

a better fit than its 10 associated virtual species, i.e. a total of 12 (132/11) real species ranked first
322 by chance. The results were similar regardless the metric and the methodology used (Fig. 3-b, c,
d & Metadata S1) or the algorithm (Figure S2 & Metadata S1). We can thus conclude that real
324 and virtual species' distribution were predicted with the same accuracy.

326 *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
328 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
330 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).

332

DISCUSSION

334 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,
336 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
338 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
340 calls for a greater caution when using cSDMs to make predictions about future changes in species
distributions in response to climate change.

342

Prevalence and taxonomic groups did not affect our conclusions

344 We expected the increase size of the distribution (or prevalence, see Stockwell and Peterson 2002,
Proosdij et al. 2016) increase the accuracy of cSDMs, as previously found in invertebrates

346 (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
348 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,
350 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
352 cSDMs in birds would become significant with a larger sample size per taxonomic group (approx.
25 real species per group in our study), as expected if birds, being endotherms, are less constrained
354 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,
356 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
358 pattern does not depend on the size of the distribution group and also appears consistent regardless
the ecological characteristics of the real species investigated.

360

Spatial auto-correlation of climatic variables is the most likely culprit to explain our finding

362 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
364 autocorrelation of environmental variables could generate spurious relationships with species
distributions, while Chapman (2010) simulated climatic gradients to demonstrate that the spatial
366 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
368 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
370 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
372 variable with a strong geographic structure (spatial autocorrelation) can accurately predict the
distribution of a species.

374 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
376 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
378 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
380 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
382 to Beale et al. (2008) but i) using a novel and more rigorous evaluation of models (i.e. blocked
cross-validation) and ii) attaining more generality by incorporating species with more contrasted
384 range sizes and ecologies, we confirmed that the spatial structure of climatic predictors allows the
accurate modelling of almost any spatially coherent distribution with a cSDM. In fact, there seems
386 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
388 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
390 accuracy of cSDMs.

392 *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
394 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

396 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
398 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
400 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.

402 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'
404 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
406 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
408 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
410 cannot inform us on the causal link between climate and species occurrence, which possibilities
can be envisaged? Possible alternative approaches include mechanistic models linking
412 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).

414 Although some of the processes embedded in these mechanistic approaches may be sometimes
modelled partly through correlations (for instance if a process relies on bioclimatic thresholds
416 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,
418 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
420 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 directly
422 test the impact of climate on species distribution (Kerr et al. 2007). Whenever actual changes in
range limits as a response to climate change match the predictions of climatic cSDMs, the causal
424 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
426 and upward range shifts and it is likely that the direct contribution of climate to range limits vary
between taxonomic groups and/or biogeographic regions (see Lenoir and Svenning 2015).
428 Unfortunately, none of these alternative approaches is as easy to use or as general as correlative
SDMs.

430

Comparisons with previous studies and the need for repeatability in ecology

432 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).
434 However, we wish to point out here the novel aspects of our study.

Firstly, the most original aspect of this work is clearly the comparison of several taxonomic groups
436 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
438 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,
440 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
442 than questioning the bases of correlative climatic niche modelling. We are not aware of any study
comparing the performance of cSDMs on virtual and real species for such a wide range of taxa
444 (ie., 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)

446 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
448 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.

450 Secondly, validation practices rapidly evolve in niche modelling and low performance of cSDMs
compared to null models has also been linked to failure of validation tools. The study by Fourcade
452 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
454 - in addition to the commonly used AUC - and we showed that our conclusions did not change
with the validation tools.

456 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
458 much caution: cSDMs are more widely used than ever, and the limits of this modelling technique
and philosophy are almost never acknowledged. Like in many other fields, it will take at least a
460 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
462 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
464 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 cSDMs validation
466 represents a significant step in this direction.

468 *Methodological issues and perspectives of our study*

The methods used in this study differ from the classical way of fitting cSDMs in several aspects.
470 Firstly, 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
472 occurrence data instead, resulting in a mixture of presence and pseudo-absence data inside the
distribution range of species. Such an approach assumes that i) pseudo-absence data inside the
474 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 ii) that the environmental factors used
476 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
478 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
480 database), as most of the variables used for modelling certainly do not vary at the spatial scale
corresponding to the spatial resolution of the presence and pseudo-absence data. In other words,
482 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
484 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
486 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
488 done in many empirical studies (e.g. Araújo et al. 2005, Barbet-Massin et al. 2012, Elith and
Graham 2009). Using various proportion of presence data did not alter our results and our
490 conclusion that real species distributions are not predicted with stronger accuracy than virtual
species distributions therefore remains valid (see Appendix A1 in Supporting Information).

492 Secondly, the size of the study area is known to affect the accuracy of modelling results
of cSDMs (Thuiller et al. 2005). If the study area is too large relative to the species distribution,
494 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

496 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
498 accuracy. In this work, we did not adjust the size of the study area to be proportional to each
distribution (Fig. 1, Metadata S1) because defining a specific study area for every real and virtual
500 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
502 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.

504 Thirdly, 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
506 independence between calibration and validation datasets than usually done in cSDMs-based
studies with random cross-validation. Doing so also strengthened the robustness of our results.

508 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
510 distributions obtained through a diffusion model, while real species may have disjointed
distributions, especially those located in mountains and/or at high latitude. It has been shown that
512 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
514 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 to design fragmented distributions, in order to compare
516 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,
518 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 Figure S4), and because,
520 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
522 limitation about the level of fragmentation of the virtual distributions.

524 *Combining various approaches to better predict the impact of climate change*

Forecasting distributions (e.g. projecting climate change impact on species distribution) is
526 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
528 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
530 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
532 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
534 introduction and earlier in the discussion. Our results further emphasize that forecasting
distributions with cSDMs should be done with caution: correlative species distribution models
536 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.
538 (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
540 the fact that the physiology of many insect species (phenology, survival rates) is strongly
dependent on climate (Chuine and Régnière 2017). Since current distributions are not necessarily
542 limited by climatic factors, recent developments of cSDMs have tried to incorporate non-climatic
factors such land use, interspecific interactions or dispersal abilities to improve the modelling
544 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 non-climatic

546 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 than in classic
548 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
550 classical cSDMs.

Given these limitations, how can we obtain robust predictions of the impact of climate
552 change on species distributions? As written above, although the use of process-based or
experimental approaches is currently expending, they are not straightforward to develop. A first
554 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
556 distributions and validation with current distributions (Kerr et al. 2007) or to invasive species
whose invasive areas have been well predicted - although both approaches brought contrasted
558 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
560 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.
562 2010), and to select those climatic variables that are biologically meaningful prior to the modelling
steps of cSDMs. Yee-Law et al. (2016) nicely illustrates how climatic cSDMs can provide
564 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
566 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
568 experiments was not supported. An even more mixed pattern emerges from studies using human-
mediated species translocations as quasi-experiments (see Introduction section), so a direct link
570 between climate and current range limits cannot always be taken for granted.

572 **CONCLUSION**

Disentangling the role of climate and other factors in shaping species ranges overreaches
574 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
576 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
578 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
580 change on species range. While 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
582 crucial for conservation and climate change impact issues. It will allow the development of more
realistic forecasting models incorporating dispersal, biotic interactions, actual relationships
584 between climate and fitness, and non-climatic environmental factors.

586 **ACKNOWLEDGEMENTS**

We are grateful to Georges Kunstler, Nicolas Martin-St Paul, Cédric Perret, Estelle Barbot, Volker
588 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.
590 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
592 no. 11-PDOC-030-01).

REFERENCES

- 594 Aguirre-Gutiérrez, J., L. G. Carvalheiro, C. Polce, E. E. van Loon, N. Raes, M. Reemer, and J.
C. Biesmeijer. 2013. Fit-for-Purpose: Species Distribution Model performance depends on
596 evaluation criteria - Dutch hoverflies as a case study. PLoS ONE 8.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution
598 models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology
43:1223–1232.
- 600 Anderson, R. P., and A. Raza. 2010. The effect of the extent of the study region on GIS models
of species geographic distributions and estimates of niche evolution: Preliminary tests with
602 montane rodents (genus *Nephelomys*) in Venezuela. Journal of Biogeography 37:1378–
1393.
- 604 Araújo, M. B., R. G. Pearson, W. Thuiller, and E. Markus. 2005. Validation of species–climate
impact models under climate change. Global Change Biology 11:1504–1513.
- 606 Ay, J.-S., J. Guillemot, N. Martin-StPaul, L. Doyen, and P. Leadley. 2017. The economics of
land use reveals a selection bias in tree species distribution models. Global Ecology and
608 Biogeography 26:65–77.
- Bahn, V., and B. J. McGill. 2007. Can niche-based distribution models outperform spatial
610 interpolation? Global Ecology and Biogeography 16:733–742.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences
612 for species distribution models: How, where and how many? Methods in Ecology and
Evolution 3:327–338.

- 614 Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J.
Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche
616 modeling and species distribution modeling. *Ecological Modelling* 222:1810–1819.
- Beale, C. M., J. J. Lennon, and A. Gimona. 2008. Opening the climate envelope reveals no
618 macroscale associations with climate in European birds. *Proceedings of the National
Academy of Sciences* 105:14908–14912.
- 620 Beale, C. M., J. J. Lennon, and A. Gimona. 2009. European bird distributions still show few
climate associations. *Proceedings of the National Academy of Sciences* 106:E41–E43.
- 622 Beaumont, L. J., R. V. Gallagher, W. Thuiller, P. O. Downey, M. R. Leishman, and L. Hughes.
2009. Different climatic envelopes among invasive populations may lead to
624 underestimations of current and future biological invasions. *Diversity and Distributions*
15:409–420.
- 626 Bombi, P., D. Salvi, L. Vignoli, and M. A. Bologna. 2009. Modeling Bedriaga’s rock lizard
distribution in Sardinia: An ensemble approach. *Amphibia Reptilia* 30:413–424.
- 628 Boucher-Lalonde, V., and D. J. Currie. 2016. Spatial autocorrelation can generate stronger
correlations between range size and climatic niches than the biological signal - A
630 demonstration using bird and mammal range maps. *PLoS ONE* 11:1–15.
- Boulangéat, I., D. Gravel, and W. Thuiller. 2012. Accounting for dispersal and biotic
632 interactions to disentangle the drivers of species distributions and their abundances.
Ecology Letters 15:584–593.
- 634 Breeman, A. M. 1988. Relative importance of temperature and other factors in determining
geographic boundaries of seaweeds: Experimental and phenological evidence. *Helgoländer
636 Meeresuntersuchungen* 42:199–241.

- Broennimann, O., U. A. Treier, H. Müller-Schärer, W. Thuiller, A. T. Peterson, and A. Guisan.
638 2007. Evidence of climatic niche shift during biological invasion. *Ecology Letters* 10:701–
709.
- 640 Cabral, J. S., and F. M. Schurr. 2010. Estimating demographic models for the range dynamics of
plant species. *Global Ecology and Biogeography* 19:85–97.
- 642 Chapman, D. S. 2010. Weak climatic associations among British plant distributions. *Global
Ecology and Biogeography* 19:831–841.
- 644 Chen, I., J. K. Hill, R. Ohlemüller and Thomas, C. D.. 2011. Rapid Range Shifts of Species.
Science 333:1024–1026.
- 646 Chuine, I. 2000. A unified model for budburst of trees. *Journal of Theoretical Biology* 207:337–
347.
- 648 Chuine, I., and E. G. Beaubien. 2001. Phenology is a major determinant of tree species range.
Ecology Letters 4:500–510.
- 650 Chuine, I., and J. Régnière. 2017. Process-based models of phenology for plants and animals.
Annual Review of Ecology, Evolution and Systematics 48:159–82.
- 652 Colautti, R. I., and S. C. H. Barrett. 2013. Rapid Adaptation to Climate Facilitates Range
Expansion of an Invasive Plant. *Science* 342:364–366.
- 654 Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: Geometric constraints on the
geography of species richness. *Trends in Ecology and Evolution* 15:70–76.
- 656 Coreau, A., G. Pinay, J. D. Thompson, P.-O. Cheptou, and L. Mermet. 2009. The rise of
research on futures in ecology: rebalancing scenarios and predictions. *Ecology Letters*
658 12:1277–1286.

- Diamond, S. E., L. M. Nichols, N. McCoy, C. Hirsch, S. L. Pelini, N. J. Sanders, A. M. Ellison,
660 N. J. Gotelli, and R. R. Dunn. 2012. A physiological trait-based approach to predicting the
responses of species to experimental climate warming. *Ecology* 93:2305–2312.
- 662 Dormann, C. F., S. J. Schymanski, J. Cabral, I. Chuine, C. Graham, F. Hartig, M. Kearney, X.
Morin, C. Römermann, B. Schröder, and A. Singer. 2012. Correlation and process in
664 species distribution models: Bridging a dichotomy. *Journal of Biogeography* 39:2119–
2131.
- 666 Early, R., and D. F. Sax. 2014. Climatic niche shifts between species' native and naturalized
ranges raise concern for ecological forecasts during invasions and climate change. *Global*
668 *Ecology and Biogeography* 23:1356–1365.
- Elith, J., and C. H. Graham. 2009. Do they? How do they? Why do they differ? on finding
670 reasons for differing performances of species distribution models. *Ecography* 32:66–77.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F.
672 Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G.
Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J.
674 Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M.
S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species'
676 distributions from occurrence data. *Ecography* 29:129–151.
- Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological explanation and
678 prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*
40:677–697.

- 680 Fordham, D. A., C. Bertelsmeier, B. W. Brook, R. Early, D. Neto, S. C. Brown, O. Sébastien,
and M. B. Araùjo . 2018. How complex should models be ? Comparing correlative and
682 mechanistic range dynamics models. *Global Change Biology* 24:1357–1370.
- Fourcade, Y., A. G. Besnard, and J. Secondi. 2018. Paintings predict the distribution of species,
684 or the challenge of selecting environmental predictors and evaluation statistics. *Global
Ecology and Biogeography* 27:245–256.
- 686 Francis, A. P., and D. J. Currie. 2003. A Globally Consistent Richness-Climate Relationship for
Angiosperms. *The American Naturalist* 161:523–536.
- 688 Gallagher, R. V., L. J. Beaumont, L. Hughes, and M. R. Leishman. 2010. Evidence for climatic
niche and biome shifts between native and novel ranges in plant species introduced to
690 Australia. *Journal of Ecology* 98:790–799.
- Gaston, K. J. 2003. *The Structure and Dynamics of Geographic Ranges*. Page (Oxford
692 University Press, Ed.). New-York.
- Geerts, A. N., J. Vanoverbeke, B. Vanschoenwinkel, W. Van Doorslaer, H. Feuchtmayr, D.
694 Atkinson, B. Moss, T. A. Davidson, C. D. Sayer, and L. De Meester. 2015. Rapid evolution
of thermal tolerance in the water flea *Daphnia*. *Nature Climate Change* 5:665–668.
- 696 Gogol-Prokurat, M. 2011. Predicting habitat suitability for rare plants at local spatial scales
using a species distribution model. *Ecological Applications* 21:33–47.
- 698 Goncalves, E., I. Herrera, M. Duarte, R. O. Bustamante, M. Lampo, G. Velásquez, G. P.
Sharma, and S. García-Rangel. 2014. Global invasion of *Lantana camara*: Has the climatic
700 niche been conserved across continents? *PLoS ONE* 9.
- Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. *Ecology* 14:368.

- 702 Guisan, A., and W. Thuiller. 2005. Predicting species distribution: Offering more than simple
habitat models. *Ecology Letters* 8:993–1009.
- 704 Guo, Q. 2003. Plant abundance: The measurement and relationship with seed size. *Oikos*
101:639–642.
- 706 Gutiérrez, A. G., R. S. Snell, and H. Bugmann. 2016. Using a dynamic forest model to predict
tree species distributions. *Global Ecology and Biogeography* 25:347–358.
- 708 Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are Species' Range Limits Simply
Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range. *The*
710 *American Naturalist* 183:157–173.
- Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J. H. Körber. 2007. Biotic
712 interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology*
and *Biogeography* 16:754–763.
- 714 Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution
interpolated climate surfaces for global land areas. *International Journal of Climatology*
716 25:1965–1978.
- Hill, M. P., B. Gallardo, and J. S. Terblanche. 2017. A global assessment of climatic niche shifts
718 and human influence in insect invasions. *Global Ecology and Biogeography* 26:679–689.
- Humboldt, A. von. 1807. *Essai sur la géographie des plantes*. Schoell et Tübingue, Paris.
- 720 Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative*
Biology 22:415–427.
- 722 IUCN 2017. *The IUCN Red List of Threatened Species*. Version 2016-1.
<<http://www.iucnredlist.org>>. Downloaded on January 2016.

- 724 Jarnevich, C. S., Stohlgren, T. J., Kumar, S., Morisette, J. T., Holcombe, T. R. 2015. Caveats for
correlative species distribution modeling. *Ecological Informatics* 29:6–15.
- 726 Javanbakht, H., F. Ihlow, D. Jablonski, P. Šíroký, U. Fritz, D. Rödder, M. Sharifi, and P.
Mikulíček. 2017. Genetic diversity and Quaternary range dynamics in Iranian and
728 transcaucasian tortoises. *Biological Journal of the Linnean Society* 121:627–640.
- Jiménez-Valverde, A., N. Barve, A. Lira-Noriega, S. P. Maher, Y. Nakazawa, M. Papeş, J.
730 Soberón, J. Sukumaran, and A. T. Peterson. 2011. Dominant climate influences on North
American bird distributions. *Global Ecology and Biogeography* 20:114–118.
- 732 Kharouba, H. M., A. C. Algar, and J. T. Kerr. 2009. Historically calibrated predictions of
butterfly species' range shift using global change as a pseudo-experiment. *Ecology*
734 90:2213–2222.
- Kearney, M., and W.P. Porter. 2009. Mechanistic niche modeling: Combining physiological and
736 spatial data to predict species' ranges. *Ecology Letters* 12:334–350.
- Kearney, M., and W. P. Porter. 2004. Mapping the fundamental niche: Physiology, climate, and
738 the distribution of a nocturnal lizard. *Ecology* 85:3119–3131.
- Kelly, C. D. 2006. Replicating empirical research in behavioral ecology: How and why it should
740 be done but rarely ever is. *The Quarterly Review of Biology* 81:221–236.
- Kerr, J.T., H. M. Kharouba, and D. J. Currie. 2007. The macroecological contribution to global
742 change solutions. *Science* 316:1581–1584.
- Lee-Yaw, J.A., H. M. Kharouba, M. Bontrager, C. Mahony, A. A. M. Csörgő, A. M. E. Noreen,
744 Q. Li, R. Schuster, and A. L. Angert 2016. A synthesis of transplant experiments and
ecological niche models suggests that range limits are often niche limits. *Ecology Letters*
746 19:710–722.

- 748 Leinonen, I. 1996. A simulation model for the annual frost hardiness and freeze damage of Scots
Pine. *Annals of Botany* 78:687–693.
- 750 Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts - a global multidimensional
synthesis and new research directions. *Ecography* 38:15–28.
- 752 Liu, C., M. White, and G. Newell. 2013. Selecting thresholds for the prediction of species
occurrence with presence-only data. *Journal of Biogeography* 40:778–789.
- 754 Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for
trees. *Journal of Biogeography* 25:735–742.
- 756 Loehle, C., and D. LeBlanc. 1996. Model-based assessment of climate change effects on forests:
a critical review. *Ecological Modeling* 90:1–31.
- 758 Lozier, J. D., P. Aniello, and M. J. Hickerson. 2009. Predicting the distribution of Sasquatch in
western North America: Anything goes with ecological niche modeling. *Journal of
Biogeography* 36:1623–1627.
- 760 Merriam, C. H. 1894. Laws of temperature control of the geographic distribution of the
terrestrial animals and plants. *National Geographic* 6:229–238.
- 762 Morán-Ordóñez, A., J. J. Lahoz-Monfort, J. Elith, and B. A. Wintle. 2017. Evaluating 318
continental-scale species distribution models over a 60-year prediction horizon: what
764 factors influence the reliability of predictions? *Global Ecology and Biogeography* 26:371–
384.
- 766 Morin, X., T. Améglio, R. Ahas, C. Kurz-Besson, V. Lanta, F. Lebourgeois, F. Miglietta, and I.
Chuine. 2007a. Variation in cold hardiness and carbohydrate concentration from dormancy
768 induction to bud burst among provenances of three European oak species. *Tree Physiology*
27:817–825.

- 770 Morin, X., C. Augspurger, and I. Chuine. 2007b. Process-based modeling of species'
distributions: What limits temperate tree species' range boundaries? *Ecology* 88:2280–
772 2291.
- Mouquet, N., Y. Lagadeuc, V. Devictor, L. Doyen, A. Duputié, D. Eveillard, D. Faure, E.
774 Garnier, O. Gimenez, P. Huneman, F. Jabot, P. Jarne, D. Joly, R. Julliard, S. Kéfi, G. J.
Kergoat, S. Lavorel, L. Le Gall, L. Meslin, S. Morand, X. Morin, H. Morlon, G. Pinay, R.
776 Pradel, F. M. Schurr, W. Thuiller, and M. Loreau. 2015. Predictive ecology in a changing
world. *Journal of Applied Ecology* 52:1293–1310.
- 778 Nagakawa, S. and T. H. Parker. 2015. Replicating research in ecology and evolution: feasibility,
incentives, and the cost-benefit conundrum. *BMC Biology* 13:88.
- 780 Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R.
Scheffers, D. G. Hole, T. G. Martin, H. R. Akçakaya, R. T. Corlett, B. Huntley, D.
782 Bickford, J. A. Carr, A. A. Hoffmann, G. F. Midgley, P. Pearce-Kelly, R. G. Pearson, S. E.
Williams, S. G. Willis, B. Young, and C. Rondinini. 2015. Assessing species vulnerability
784 to climate change. *Nature Climate Change* 5:215–225.
- Palacio, F. X., and J. M. Girini. 2018. Biotic interactions in species distribution models enhance
786 model performance and shed light on natural history of rare birds: a case study using the
Straight-billed Reedhaunter (*Limnortyx rectirostris*). *Journal of Avian Biology*. In press.
- 788 Palmer, A. R. 2000. Quasi-replication and the contract of error: lessons from sex ratios,
heritabilities and fluctuating asymmetry. *Annual Review of Ecology and Systematics*
790 31:441–80.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts
792 across natural systems. *Nature* 421:37–42.

- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the
794 distribution of species: Are bioclimate envelope models useful? *Global Ecology and
Biogeography* 12:361–371.
- Pearson, R. G., and T. P. Dawson. 2004. Bioclimate envelope models: what they detect and
796 what they hide - response to Hampe (2004). *Global Ecology and Biogeography* 13:471–
798 473.
- Pereira, H. M., P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-
800 Manjarres, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D.
Cooper, E. L. Gilman, S. Guenette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T.
802 Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, and M. Walpole. 2010.
Scenarios for Global Biodiversity in the 21st Century. *Science* 330:1496–1501.
- Peterson, A. T., M. Papes, and D. A. Kluza. 2003. Predicting the potential invasive distributions
804 of four alien plant species in North America. *Weed Science* 51:863–868.
- Petitpierre, B., C. Kueffer, O. Broennimann, C. Randin, C. Daehler, and A. Guisan. 2012.
806 Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science* 335:1344–1348.
- Phillips, S. B., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of
808 species geographic distributions. *Ecological modeling* 190:231–259.
- Pigott, C. D., and J. P. Huntley. 1980. Factors controlling the distribution of *Tilia cordata* at the
810 Northern limit of its geographical range. II. History in North-West England. *New
812 Phytologist* 84:145–164.
- Proosdij, A. S. J. van, M. S. M. Sosef, J. J. Wieringa, and N. Raes. 2016. Minimum required
814 number of specimen records to develop accurate species distribution models. *Ecography*
39:542–552.

- 816 R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for
Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 818 Ramírez-Albores, J. E., R. O. Bustamante, and E. I. Badano. 2016. Improved predictions of the
geographic distribution of invasive plants using climatic niche models. *PLoS ONE* 11:1–14.
- 820 Rehfeldt, G. E., N. M. Tchebakova, Y. I. Parfenova, W. R. Wykoff, N. A. Kuzmina, and L. I.
Milyutin. 2002. Intraspecific responses to climate in *Pinus sylvestris*. *Global Change*
822 *Biology* 8:912–929.
- Rich, J. L., and D. J. Currie. 2018. Are North American bird species' geographic ranges mainly
824 determined by climate? *Global Ecology and Biogeography* 27:461–473.
- Roberts, D. R., V. Bahn, S. Ciuti, M. S. Boyce, J. Elith, G. Guillera-Arroita, S. Hauenstein, J. J.
826 Lahoz-Monfort, B. Schröder, W. Thuiller, D. I. Warton, B. A. Wintle, F. Hartig, and C. F.
Dormann. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or
828 phylogenetic structure. *Ecography* 40:913–929.
- San-Miguel-Ayanz, J., D. de Rigo, C. G., T. Houston Durrant, A. Mauri, W. Tinner, D. Ballian,
830 P. Beck, H. J. B. Birks, E. Eaton, C. M. Enescu, S. Pasta, I. Popescu, C. Ravazzi, E. Welk,
R. Abad Viñas, J. C. Azevedo, A. Barbati, J. I. Barredo, S. E. Benham, R. Boca, C. Bosco,
832 M. C. Caldeira, S. Cerasoli, G. Chirici, A. Cierjacks, M. Conedera, F. Da Ronch, M. Di
Leo, J. I. García-Viñas, A. Gastón González, F. Giannetti, N. Guerrero Hue, N. Guerrero
834 Maldonado, M. J. López, R. Jonsson, P. Krebs, D. Magni, S. Mubareka, G. Mulhern, P.
Nieto Quintano, S. Oliveira, J. S. Pereira, M. Pividori, M. Rätty, F. Rinaldi, S. Saura, R.
836 Sikkema, T. Sitzia, G. Strona, C. Vidal, L. Vilar, and B. Zecchin. 2016. European atlas of
forest tree species. Page (A. San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston
838 Durrant, T., Mauri, Ed.). European Commission.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of
840 species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.

Sinervo, B., F. Méndez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. V. S. Cruz, R.
842 Lara-Resendiz, N. Martínez-Méndez, M. L. Calderón-Espinosa, R. N. Meza-Lázaro, H.
Gadsden, L. J. Avila, M. Morando, I. J. De La Riva, P. V. Sepúlveda, C. F. D. Rocha, N.
844 Iburgüengoytía, C. A. Puntriano, M. Massot, V. Lepetz, T. A. Oksanen, D. G. Chappie, A.
M. Bauer, W. R. Branch, J. Clobert, and J. W. Sites. 2010. Erosion of lizard diversity by
846 climate change and altered thermal niches. *Science* 328:894–899.

Sofaer, H. R., C. S. Jarnevich, and C. H. Flather. 2018. Misleading prioritizations from
848 modeling range shifts under climate change. *Global Ecology and Biogeography* 27:1–9.

StatSoft (2011). STATISTICA (logiciel d'analyse des données), version 10. www.statsoft.fr.

850 Stockwell, D. R. B., and A. T. Peterson. 2002. Effects of sample size on accuracy of species
distribution models. *Ecological Modeling* 148:1–13.

852 Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B.
F. N. Erasmus, M. Ferreira De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley,
854 A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L.
Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145–
856 148.

Thuiller, W., M. B. Araújo, and S. Lavorel. 2004. Do we need land-cover data to model species
858 distributions in Europe? *Journal of Biogeography* 31:353–361.

Thuiller, W., S. Lavorel, and M. B. Araújo. 2005. Niche properties and geographical extent as
860 predictors of species sensitivity to climate change. *Global Ecology and Biogeography*
14:347–357.

- 862 Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araùjo. 2009. BIOMOD - A platform for
ensemble forecasting of species distributions. *Ecography* 32:369–373.
- 864 Thuiller, W., S. Lavergne, C. Roquet, I. Boulangeat, B. Lafourcade, and M. B. Araùjo . 2011.
Consequences of climate change on the tree of life in Europe. *Nature* 470:531–534.
- 866 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C, J.-M. Fromentin,
O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change.
868 *Nature* 416:389–395.
- Walther, G. R., S. Berger, and M. T. Sykes. 2005. An ecological “footprint” of climate change.
870 *Proceedings of the Royal Society B: Biological Sciences* 272:1427–1432.
- While, G. M., J. Williamson, G. Prescott, T. Horváthová, B. Fresnillo, N. J. Beeton, B.
872 Halliwell, S. Michaelides, and T. Uller. 2015. Adaptive responses to cool climate promotes
persistence of a non-native lizard. *Proceedings of the Royal Society B: Biological Sciences*
874 282:1–9.
- Williams, J. W., B. N. Shuman, T. Webb, P. J. Bartlein, and P. L. Leduc. 2004. Late-Quaternary
876 vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological*
Monographs 74:309–334.
- 878 Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity:
patterns, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*
880 34:273–309.
- Wood, S. N. 2006. *Generalized additive models: an introduction with R*. Boca Raton 25.
- 882 Woodward, F. I. 1987. *Climate and plant distribution*. Cambridge University Press, Cambridge.

DATA ACCESSIBILITY STATEMENT

884 The data supporting the results will be archived in Dryad and the data DOI will be included at
the end of the article. The database and script have also been submitted with the present MS in
886 Supporting Information (Metadata S1 & S2).

TABLES

888

890 Table 1. Linear Mixed Model for the effects of group (random) and prevalence on evaluation
 891 metrics for GAM models with and without blocked cross-validation. The interaction term was
 892 removed from the final model when it was non-significant (p-values between 0.25 and 0.82 for
 the three models with non-significant interaction term). See text for detail.

	AUC - no CV			TSS - no CV			AUC - blocked CV			TSS - blocked CV		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
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
Ln (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 * Ln(Prev)	-			4, 122	4,44	0,002	-	-		-		-

894

896 **CAPTIONS AND FIGURES**

898 **Figure 1:** Distribution of *Chloris chloris* (a, bird), *Abies alba* (b, tree) and *Eryngium alpinum* (c, herbaceous plant), and two examples of virtual distributions for each of these three species (a1 and a2 for *C. chloris*; b1 and b2 for *A. alba* and c1 and c2 for *E. alpinum*).

902 **Figure 2:** Comparison of the AUC values without cross-validation (a) and with blocked cross-validation (b) for real species distributions and virtual species distributions, for each taxonomic group. Grey circles correspond to 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).

908 **Figure 3:** Ranks of metrics values (AUC & TSS) of all real species distributions modeled with GAM algorithm with all data (a-b) and with block cross validation (c-d). Metrics values of real species are compared with the 10 corresponding virtual species. (a) Ranks of AUC values for 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 due to 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).

920 **Figure 4:** Effect of taxonomic group and prevalence on AUC values.

SUPPORTING INFORMATION

922

Additional Supporting Information for this article, including supplementary tables and figures,

924 may be found online.









