



A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling

Morgane Barbet-Massin^{1,2*} and Walter Jetz¹

¹Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA, ²Muséum National d'Histoire Naturelle, UMR 7204 MNHN-CNRS-UPMC, Centre d'Ecologie et de Sciences de la Conservation, Paris, France

ABSTRACT

Aim Species distribution models (SDMs) are increasingly used to address numerous questions in ecology, biogeography, conservation biology and evolution. Surprisingly, the crucial step of selecting the most relevant variables has received little attention, despite its direct implications for model transferability and uncertainty. Here, we aim to address this with a continent-wide, evaluation of which climate predictors provided the most accurate SDMs for bird distributions.

Location Conterminous United States.

Methods For 243 species, we used yearly data since 1971 (from the North American Breeding Bird Survey) to run SDMs (six different algorithms) with combinations of six relatively uncorrelated climate predictors (selected from 22 widely used climate variables). We then estimated the importance of each predictor – both spatially and over a 40-year time period – by comparing the accuracy of the model obtained with or without a given predictor.

Results Three temperature-related variables (annual potential evapotranspiration, mean annual temperature and growing degree days) produced significantly more accurate SDMs than any other predictors. Among precipitation predictors, annual precipitation provided the most accurate results. Albeit only rarely used in SDMs, the moisture index performed similarly strongly. Interestingly, predictors that summarize average annual climate produced more accurate distributions than seasonal predictors, despite distinct seasonal movements in most species considered. Encouragingly, spatial and temporal (over 40 years) evaluation of variables yielded very similar results.

Main conclusions The approach presented here allowed us to identify the statistically most relevant predictors for birds in the USA and can be applied to other taxa and/or in different parts of the world. Appropriately selecting the most relevant predictors of species distributions at large spatial scale is vital to identifying ecologically meaningful relationships that provide the most accurate predictions under climate change or biological invasions.

Keywords

Bioclim variables, model transferability, spatial evaluation, species distribution models, temporal evaluation, variable importance.

*Correspondence: Morgane Barbet-Massin, Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New Haven, CT 06520, USA.
E-mail: morgane.barbet-massin@yale.edu

INTRODUCTION

Species distribution models (SDMs) relate species presence/absence data to environmental variables based on statistically or theoretically derived response surfaces (Guisan &

Zimmermann, 2000). They are increasingly used to address numerous questions in ecology, biogeography, conservation biology and evolution (Guisan & Thuiller, 2005). SDMs have been used to test biogeographical, ecological and evolutionary hypotheses (Graham *et al.*, 2004; Carnaval & Moritz,

2008; Vega *et al.*, 2010), to predict species' invasion and proliferation (Broennimann & Guisan, 2008; Villemant *et al.*, 2011), to discover new populations or unknown species (Raxworthy *et al.*, 2003; Bourg *et al.*, 2005; Guisan *et al.*, 2006), to assess the potential impact of climate, land use and other environmental changes on species distributions (Thuiller *et al.*, 2005; Lawler *et al.*, 2009; Hof *et al.*, 2011; Barbet-Massin *et al.*, 2012b) and to support conservation planning and reserve selection (Williams *et al.*, 2005; Marini *et al.*, 2009; Araújo *et al.*, 2011).

There is, however, increasing appreciation for the limits to the accuracy and transferability of SDMs (Menke *et al.*, 2009; Anderson & Raza, 2010; Dormann *et al.*, 2012; Heikkinen *et al.*, 2012). These include the prediction variability stemming from the choice of modelling algorithm (Elith *et al.*, 2006; Buisson *et al.*, 2010), which lead to the use of ensemble forecast methods (Araújo & New, 2007; Marmion *et al.*, 2009) that emphasize the central tendency of several models. Additionally, given that confirmed absences are usually difficult to obtain, especially for mobile species (Mackenzie & Royle, 2005), pseudo-absences are widely used, adding yet another source of uncertainty (Chefaoui & Lobo, 2008; VanDerWal *et al.*, 2009; Wisz & Guisan, 2009; Barbet-Massin *et al.*, 2012a). In climate change applications of SDMs, these issues are exacerbated by the uncertainty related to the choice of general circulation model and emission scenario (Thuiller, 2004; Barbet-Massin *et al.*, 2009; Lawler *et al.*, 2009; Buisson *et al.*, 2010). One additional, significant and to date surprisingly little-tackled source of error-affecting inference and prediction is predictor selection (Synes & Osborne, 2011; Braunisch *et al.*, 2013).

Identifying the most appropriate variables is a crucial step to maximize the performance of species distribution modelling and its projection in space or time (Austin, 2002; Araújo & Guisan, 2006; Elith & Leathwick, 2009; Menke *et al.*, 2009; Araújo & Peterson, 2012). Predictions obtained with inappropriate variables are more likely to exhibit patterned residuals than predictions obtained with more proximal variables (Leathwick & Whitehead, 2001). As pointed out by Austin (Austin, 2002), 'species distribution models will have only local value for either prediction or understanding when using distal variables. Models based on proximal resource and direct gradients will be the most robust and widely applicable'. Overlooking potential ecological mechanisms or processes is therefore a limiting factor in the application of species distribution modelling. However, the crucial step of selecting the most relevant variables has received little attention compared with the choice of the modelling method (but see Ashcroft *et al.*, 2011; Synes & Osborne, 2011; Watling *et al.*, 2012; Williams *et al.*, 2012). Previous work has assessed whether climate variables or land use variables should be considered in SDMs (Luoto *et al.*, 2007; Menke *et al.*, 2009). However, the question of the more relevant climate variables remains open despite its proven influence on SDMs results (Syphard & Franklin, 2009; Synes & Osborne, 2011). Ideally, the choice of climate variables to include

within SDMs should be based on prior knowledge regarding the variables' ecological relevance for a species. Unfortunately, such information is rarely available. As climate data – both nationally and globally (e.g. Hijmans *et al.*, 2005; Di Luzio *et al.*, 2008) – proliferate, an increasing variety of climate predictors becomes available for inclusion in SDM. The greater the set of variables used in a SDM, the more likely is it that ecologically relevant predictors are also included, but unfortunately, this also increases the risk of overfitting (Beaumont *et al.*, 2007). A greater number of predictors also increases collinearity, a potentially severe problem when a model is trained on data from one region or time, and predicted to another with a different or unknown structure of collinearity (Dormann *et al.*, 2013). Limiting SDMs to a minimal set of predictors seems therefore to be the best alternative to avoid these issues. This leaves the choice of final climatic predictors a key remaining challenge for species distribution modelling (Araújo & Guisan, 2006; Ashcroft *et al.*, 2011; Williams *et al.*, 2012).

Here, we use an almost continental, yet spatially detailed and standardized dataset for birds to develop and demonstrate a comprehensive approach for identifying the climatic predictors providing greatest model accuracy. Specifically, we assess predictor strength not only spatially, but also with regard to temporal model transferability over a 40-year period. We argue that in absence of prior ecological knowledge or additional data, cautious variable selection is most likely to identify process-based constraints on distributions and provide ecologically sound models. We use the North American Breeding Bird Survey (BBS) data which offer many advantages for this work. It is possible to develop a representative, yet geographically expansive subset of spatial samples (routes) which has a spatial resolution (c. 40-km length) at which climate effects are expected (Luoto *et al.*, 2007) and have been shown to dominate (Jiménez-Valverde *et al.*, 2011). Finally, the survey started more than 40 years ago allowing training and evaluating the model with different time periods and thus offering a temporally independent evaluation that is often missing from SDM studies. For 243 species, we used yearly data to run SDMs (six different algorithms) with many combinations of six relatively uncorrelated climate predictors (from 22 widely used climate variables). We then estimated the importance of each predictor – both spatially and temporally – by comparing the accuracy of the model obtained with or without a given predictor.

METHODS

Species data

Presence/absence data of North American birds were derived from the North American Breeding Bird Survey (BBS; USGS Patuxent Wildlife Research Centre, <http://www.pwrc.usgs.gov/bbs/>). Each year during the height of the avian breeding season, June for most of the USA, participants skilled in

avian identification collect bird population data along roadside survey routes. Each survey route is 39.4-km long with 50 stops at 0.8-km intervals. At each stop, a 3-min point count is conducted. During the count, every bird seen within a 0.3-km radius or heard is recorded. Surveys start one-half hour before local sunrise and take about 5 h to complete. We considered a given species to be present at a route in a given year if it was observed at least once; otherwise, the species was considered absent. The spatial resolution of our study is therefore 39.4×0.6 km as a BBS route is the unit of analysis. Currently, 4100 survey routes are located within the continental USA, but not all were surveyed yearly or since programme onset in 1967. Here, we considered only the routes which were surveyed at least three times in each of the following 5-year period: 1971–1975, 1976–1980, 1981–1985, 1986–1990, 1991–1995, 1996–2000, 2001–2005, 2006–2010. The potential predictors of bird distributions we explore in this study are all climatic which limits our ability to account for effects of habitat change. We therefore identified and removed from our analysis all BBS routes which may have experienced significant changes in vegetation or land cover over the study period. US-wide high-resolution land cover information is lacking for the early part of the study period, but National Land Cover Datasets allowed an assessment for 1992, 2001 and 2010 (Vogelmann *et al.*, 2001; Homer *et al.*, 2007; Fry *et al.*, 2011). These datasets consist of a 16-class land cover classification that has been applied consistently across the USA at a spatial resolution of 30 m. We used them to select the BBS routes for the study in which more than 95% of the 30-m pixels within a 300-m buffer along the route had no change in land cover class among the three time periods. Overall, 427 routes were considered for this study (Fig. 1). Within these 427 routes, 473 species were observed at least once, and for modelling purposes, we considered only the 243 species (see Appendix S1 in Supporting Information for the list of species) that had at

least 10 observed presences between 1971 and 1975 (excluding water birds, raptors and nocturnal species).

Climate data and climatic variables

Climate data were obtained from the PRISM Climate Group (Oregon State University, <http://prism.oregonstate.edu>). These data consist of monthly maximum and minimum temperature and monthly precipitation yearly from 1890 at 2.5-arcmin resolution (*c.* 4 km). For each of the 427 routes, we extracted values from pixels intersecting the 300-m buffered route and calculated the weighted average of these pixels (weighted by the percentage of the pixel intersecting the buffered route). From all potential monthly climatic measures, we selected the 19 'bioclim' variables (Busby, 1991), growing degree days above 5 °C (GDD), potential evapotranspiration (PET) and the moisture index (MI) (Table 1) as predictors with greatest use and relevance for birds (Hijmans & Graham, 2006; Huntley *et al.*, 2008; Peterson & Nakazawa, 2008; Gregory *et al.*, 2009; Barbet-Massin *et al.*, 2012b). The 'bioclim' variables cover annual trends, seasonality and extreme or limiting environmental factors related to temperature and precipitation per se. To these 'bioclim' variables, we added GDD, PET and MI as they are regarded as determinants of physiological processes limiting plant distributions (Prentice *et al.*, 1992) that could have an indirect effect on bird distributions. The 19 bioclim variables were calculated yearly (1971–2010) using the biovars function within the 'dismo' package. GDD, PET and MI were calculated (1971–2010) following Synes & Osborne (2011). All variables were calculated yearly from 1971 to 2010, so as to match our yearly presence/absence data. However, as the routes were mostly surveyed in June, the 1971 dataset (matching presence/absence from 1971) was calculated using June 1970–May 1971 monthly data instead of the calendar year, and so forth for all other years.

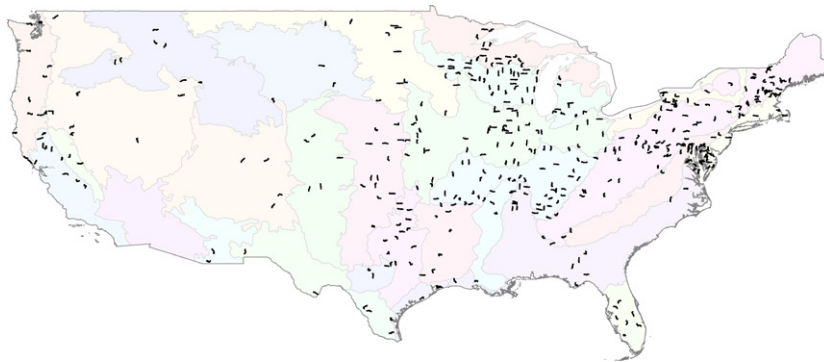


Figure 1 Breeding Bird Survey routes used in the study. These routes did not experience significant changes in vegetation or land cover over the study period and were surveyed at least three times during each of the following 5-year period: 1971–1975, 1976–1980, 1981–1985, 1986–1990, 1991–1995, 1996–2000, 2001–2005, 2006–2010. Bird Conservation Regions (BCRs) are depicted in different colours. BCRs are ecologically distinct regions in North America with similar bird communities, habitats and resource management issues.

Table 1 List of climatic predictors used in the study with their abbreviation and the ‘correlation group’ they were included in.

Abbreviation	Correlation group	Climatic predictor
bio1	temp	Annual mean temperature
bio3	temp	Isothermality (bio2/bio7)
bio4	temp	Temperature seasonality (standard deviation)
bio5	temp	Max temperature of warmest month
bio6	temp	Min temperature of coldest month
bio7	temp	Temperature annual range (bio5-bio6)
bio9	temp	Mean temperature of driest quarter
bio10	temp	Mean temperature of warmest quarter
bio11	temp	Mean temperature of coldest quarter
GDD	temp	Growing degree days
PET	temp	Potential evapotranspiration
bio12	prec	Annual precipitation
bio13	prec	Precipitation of wettest month
bio14	prec	Precipitation of driest month
bio15	prec	Precipitation seasonality (coefficient of variation)
bio16	prec	Precipitation of wettest quarter
bio17	prec	Precipitation of driest quarter
bio19	prec	Precipitation of coldest quarter
bio2	bio2	Mean diurnal range [mean of monthly (max temp–min temp)]
bio8	bio8	Mean temperature of wettest quarter
bio18	bio18	Precipitation of warmest quarter
MI	MI	Moisture Index

Estimating predictors relevance for species distribution

To estimate the relevance of each predictor for bird species distribution in North America, we ran a variety of species distribution models using different predictors and assessed how the accuracy of these models varied with the predictor used.

Many of the 22 selected predictors were highly correlated with one another (Fig. 2). We therefore split them up into ‘correlation groups’ such as each predictor from one group has a Pearson’s correlation < 0.7 with each variable in any other group (Dormann *et al.*, 2013). This resulted in six ‘correlation groups’ (Table 1 & Fig. 2), four of them holding only one predictor: bio2 (mean diurnal range), bio8 (mean temperature of wettest quarter), bio18 (precipitation of warmest quarter) and MI (moisture index). The fifth group included the 11 remaining predictors related to temperature, whereas the sixth group included the seven remaining predictors related to precipitation. Note that two predictors can

have a correlation < 0.7 with one another and still belong to the same group because they both have a correlation > 0.7 with a third predictor.

For each species, we used six different SDMs with the ‘biomod2’ package (Thuiller *et al.*, 2009): two regression methods (GLM – Generalized Linear Model and GAM – Generalized Additive Model), one classification method (FDA – Flexible Discriminant Analysis) and three machine learning methods (ANN – Artificial Neural Network, BRT – Boosted Regression Trees and RF – Random Forest) within an ensemble framework (Araújo & New, 2007), considering the median climate suitability value for each route. For each species, presences and absences were given different weights so that the total weight of presences would be equal to the total weight of absences (therefore ensuring the same 0.5 prevalence for all species). In order to correct for a potential spatial bias in the coverage of BBS routes (Fig. 1), each route was weighted so that each Bird Conservation Region (U. S. North American Bird Conservation Committee, 2000) would have the same overall weight. Bird Conservation Regions (BCRs) are ecologically distinct regions in North America with similar bird communities, habitats and resource management issues. To limit the collinearity among predictors used for the SDMs, only one predictor within a ‘correlation group’ was used – six predictors overall. For each species, models were run with all 77 possible combinations (11 predictors in the ‘temp’ group \times seven predictors in the ‘prec’ group, all other groups containing only one predictor). To assess the accuracy of the different models obtained using different sets of predictors, we used a threshold-independent method, the area under the relative operating characteristic curve (AUC) (Fielding & Bell, 1997). AUC has been recently criticized (Lobo *et al.*, 2008) because of its dependence on parameters such as the prevalence and the spatial extent to which models are carried out, but in this study, it is only used to compare models obtained with different predictors for each species (the prevalence and the geographical extent are therefore constant). We assessed model accuracy by projecting both spatially and temporally. We calculated seven ‘spatial’ AUCs values by fitting the models with a random 50% subset of the 427 routes (using the yearly data for 1971–1975) and projecting them into the 50% remaining routes (during the same 5-year timeframe) for evaluation. We acknowledge that under this procedure (and lack of fully suitable alternatives), spatial autocorrelation will inflate absolute AUC values. We expect, however, the effect if this issue for relative AUC values (differences between variables) to be minimal. For the temporal evaluation, the models were fitted using the yearly data for 1971–1975 and projected into seven different 5-year timeframes: 1976–1980, 1981–1985, 1986–1990, 1991–1995, 1996–2000, 2001–2005, 2006–2010. Seven ‘temporal’ AUCs were calculated by comparing the projections obtained for each timeframe to the actual data surveyed. These AUC measures allow us to assess how model accuracy differs between different predictors within a group. To assess model accuracy of each correlation group, each

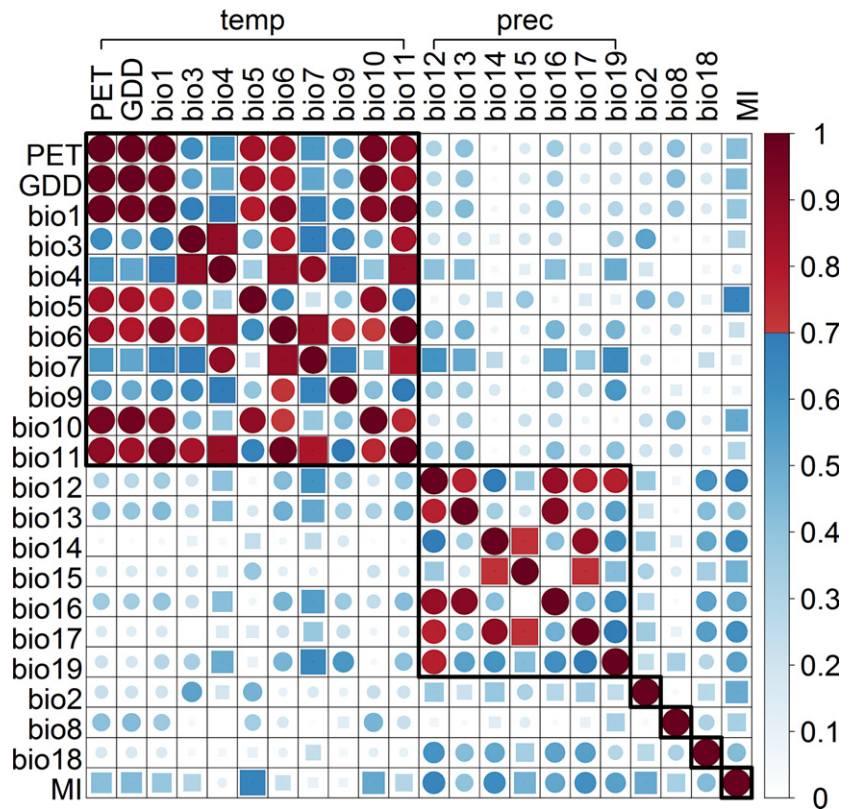


Figure 2 Correlation matrix of all potential climatic predictors. Positive correlations are represented by circles, and negative correlations are represented by squares. Values above 0.7 are depicted in red and were used to split the predictors into ‘correlation groups’ (defined as any two predictors from two different groups having a Pearson’s correlation < 0.7). The six groups that were identified – ‘temp’, ‘prec’, bio2, bio8, bio18 and MI from the upper left corner to lower right corner – are bounded by black lines.

model that was run with a given set of predictors was run six more times by removing one of the predictors in turn. This then allowed us to infer the importance of each group by comparing spatial and temporal AUC obtained with or without a variable of a given correlation group.

RESULTS

Among the 243 evaluated bird species, the developed species distribution models including six climatic predictors (one from each group) generally show very good predictive accuracy, with a mean spatial AUC of 0.917 (± 0.076) (prediction in space) and a mean temporal AUC of 0.896 ± 0.090. Prediction in time, as expected, yielded a slightly lower, but still strong average AUC.

We use the difference in AUC resulting from a predictor’s omission in the multipredictor model to illustrate relative variable importance. As expected given the similarity of the models compared within a species (same presence/absence data and five common predictors), these absolute differences are usually quite small (< 0.03). However, they usually represent statistically highly significant differences (see Fig. S1 for the statistical multiple mean comparisons). For the spatial assessment, we find that predictors in the ‘temp’ group (Figs 3a & S1a for statistical multiple mean comparisons) perform strongest, with MI next in relevance, followed by bio2. Then bio18 and predictors in the ‘prec’ group perform similarly, and the bio8 variable appears less relevant. Interestingly, this ranking is very similar for the temporal evalua-

tions (Figs 3b, 4 & S1b for statistical multiple mean comparisons), except that bio18 performs better than bio2 (which still performs better than predictors in the ‘prec’ group).

With both spatial and temporal assessments, we are able to further differentiate predictor relevance among the ‘temp’ and the ‘prec’ groups. Among ‘temp’ predictors, PET, bio1 and GDD were consistently more relevant, both spatially and temporally (Figs 4 & S1c,d), while in the ‘prec’ group bio12 performed significantly better (Figs 4 & S1e,f) (see Fig. S2 for statistical multiple mean comparisons for both). Among the ‘temp’ group, four predictors (bio3, bio4, bio7 and bio9) emerge as not highly correlated with PET, bio1 or GDD (the most relevant within the group) (Fig. 2). Among those four predictors, bio4 is the most relevant (Figs 4 & S1c,d) for statistical multiple mean comparisons). Despite ranking low within the group, it still appears to be more relevant than any other predictor outside the ‘temp’ group (Fig. 4). Similarly, bio9 (not highly correlated with PET, bio1, GDD or bio4) appears to be more relevant than any other predictor outside the ‘temp’ group (Fig. 4). Further, even though the ‘prec’ group overall does not appear very important, bio12 is a stronger predictor than bio18 and bio2. Therefore, the predictors that appear to provide the most accurate bird distributions while being minimally collinear include: (1) either PET (the potential evapotranspiration) or bio1 (annual mean temperature), (2) bio4 (temperature seasonality), (3) bio9 (mean temperature of the driest quarter), (4) MI (moisture index), (5) bio12 (annual precipitation), (6) bio2 (mean

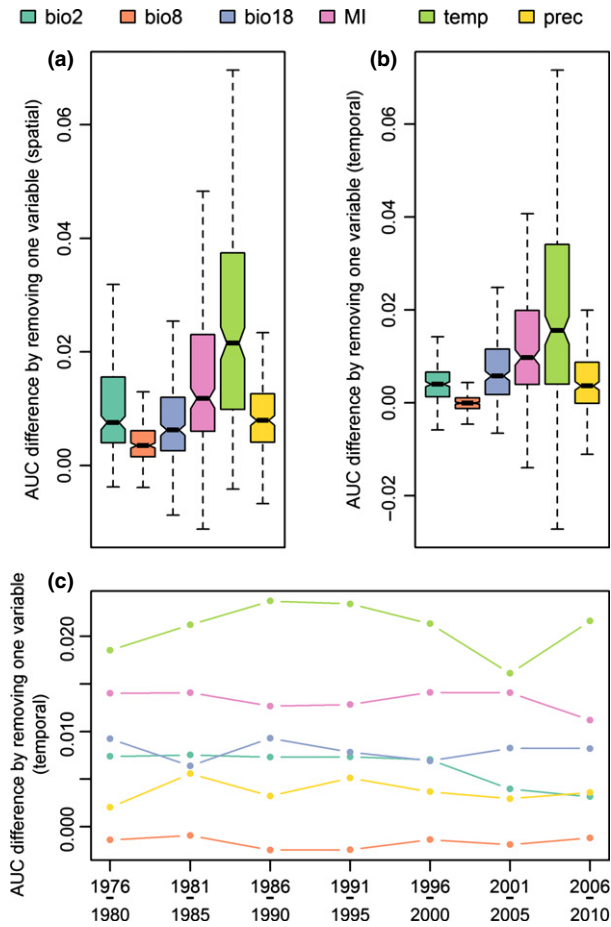


Figure 3 Importance of each ‘correlation group’ to provide better accurate SDMs. This importance was assessed by comparing the AUC of the model obtained with all six predictors (one from each correlation group) to the AUC of the model obtained with all but one predictor. The higher the difference, the more important the predictor. (a, b) Boxplots (showing variability among species) of AUC difference by removing the predictor from one of the six ‘correlation groups’, evaluated either spatially (a) or temporally (b). (c) Details of the different temporal evaluations (Models were calibrated with data from 1971–1975 and projected to each of the following 5-year periods. Each of these projections was then evaluated by comparison with the actual data from the corresponding period). The colour legend stands for all three panels, as well as for Fig. 4. Similar figures depicting the importance of predictors within the ‘temp’/‘prec’ groups are available in the Supporting Information (Fig. S2).

diurnal range) and (7) bio18 (precipitation of warmest quarter).

All above results were derived from evaluation metrics (AUC) calculated by comparing observed data with a predicted distribution that was calculated as the median of all six SDM model predictions. Interestingly, when calculating AUCs separately for each modelling technique, we find little variance among most of these (FDA, GAM, GBM and GLM, Figs S3 & S4). ANN shows greatest discrepancy, especially

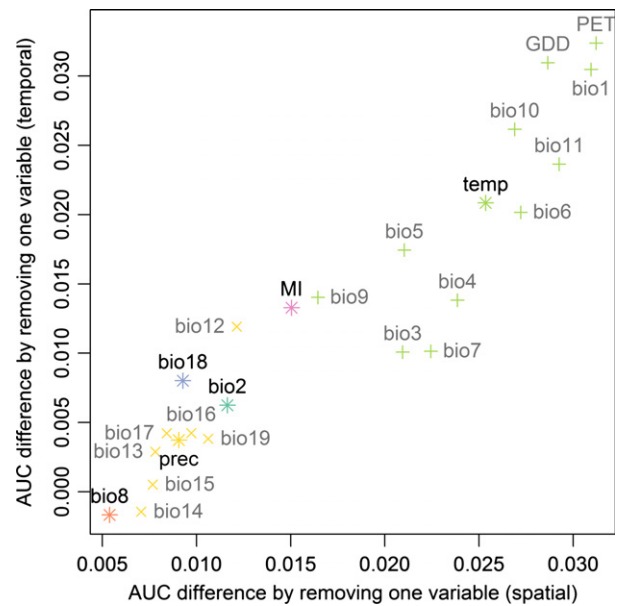


Figure 4 Importance of each climate predictor to provide more accurate SDMs. This figure depicts AUC differences that were estimated both from spatial evaluation (x-axis) and from temporal evaluation (y-axis). The mean AUC difference that was observed when the predictor from a given correlation group was removed is depicted with an asterisk (with the same colour code as for Fig. 3). The AUC difference actually differs according to which predictor was used initially in either the ‘temp’ group or the ‘prec’ group. These individual values are depicted with a green ‘plus’ symbol for the ‘temp’ group and with a yellow cross for the ‘prec’ group. These are the mean results for the 243 species. Results from statistical multiple comparisons are presented in Fig. S1 in the Supporting Information.

with the ranking of predictors within ‘prec’, as bio12 is not detected as being a relevant predictor for this modelling technique. Results from RF are quite consistent except for the fact that the AUC difference is five times higher for the spatial evaluation than for the temporal evaluation (and higher than evaluation from other modelling techniques). This probably results from a tendency of RF to overfit the data or to perform not as well when extrapolation is necessary (Heikkinen *et al.*, 2012; Dormann *et al.*, 2013). We note that for the spatial evaluation, the training/testing split is 50/50. Despite the random assignment, the climate space covered by the evaluation data is thus bound to have slight differences to that of the training data. This is different to the temporal evaluation, where the same routes are considered for training and evaluation. Further, climate variability among time intervals is less strong than that within a time interval (among years). As a consequence, we expect that actual extrapolation in climate space is more prevalent for the spatial evaluation than the temporal evaluation.

Predictors differ strongly among the 243 species in the consistency of their relevance (Figs 5 & S5 for results for individual species). As expected, the most important predictors overall are also the ones most relevant for the greater

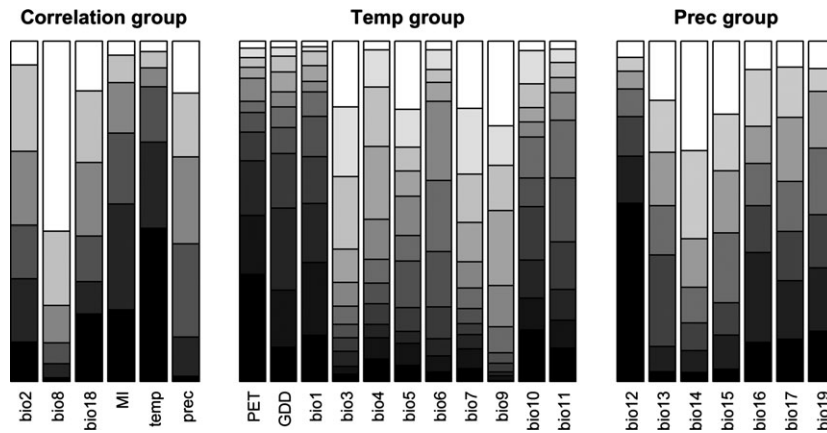


Figure 5 Variability in predictor ranking among species. Within each vertical bar, sections of different grey intensity represent the different ranking (higher rankings, that is, higher relevance for darker bars), their lengths being proportional to the number of species concerned. Rankings from spatial and temporal evaluations are combined here. Only species for which at least two groups or two predictors were significantly different were considered ($n = 241$ for spatial evaluation and $n = 243$ for temporal evaluation within the correlation group ranking; $n = 193$ for spatial evaluation and $n = 236$ for the temporal evaluation for the predictor ranking within the ‘temp’ group; $n = 187$ for spatial evaluation and $n = 232$ for the temporal evaluation for the predictor ranking within the ‘prec’ group).

number of species. For example, while in the ‘temp’ group some predictors, such as PET or bio1, were vital for providing the most accurate SDMs for a majority of species, this was not the case for others, such as bio3 and bio9 (Fig. 5). All correlation groups were shown to be either the most or the least relevant for at least some species, although the number of species concerned greatly differs. Similarly each predictor within the ‘temp’ group (or the ‘prec’ group) is the most or the least relevant for at least a few species.

DISCUSSION

Although many studies previously discussed the various sources of uncertainty in SDMs (Araújo *et al.*, 2005; Buisson *et al.*, 2010; Elith *et al.*, 2010), the focus has mainly been on algorithms and climate scenarios. However, a few recent studies (Synes & Osborne, 2011; Braunisch *et al.*, 2013) have highlighted that the choice of the environmental predictors to include in the models is very important. Our study is in line with these results, as we show that models obtained with different (but correlated) sets of variables can give very different predictions (Fig. S6). Ideally, only the predictors that are ecologically most pertinent for a species should be included within SDMs. However, such a priori information is rarely available, and the number of climate variables that could potentially be used to predict species distribution is almost infinite. Unfortunately, there is often a high level of collinearity among the potential predictors. Thus, variable selection becomes an issue because of the difficulties in assessing the relative importance of collinear variables. Very few studies have attempted to identify the most relevant predictors of species distributions at large spatial scale for a wide group of species, leaving the modeller to make a subjective yet crucial choice of predictors to include in its model.

We assessed the relative importance of 22 climate predictors for bird distribution in the USA while controlling for collinearity among predictors. For example, among the bioclim variables related to precipitation, the use of the annual precipitation clearly led to more accurate results than any other precipitation variable. Despite being significant, such a result still has to be interpreted carefully with regard to its ecological meaning. Given that the models remain correlative, the causality remains uncertain. For instance, annual precipitation might actually be a proxy for yet another, more relevant variable not considered. Even though we were able to differentiate most of the temperature-related variables, we could not distinguish whether PET or the mean annual temperature was the most likely to have a direct effect on bird distribution. Although we are unable to infer what predictors have a direct (mechanistic) effect on bird distributions, it is interesting to note that ‘annual’ predictors (such as annual PET, temperature seasonality and annual precipitation) produce more accurate distributions than predictors addressing a specific season, even though most of the species considered in this study are migratory. Another interesting result is that the moisture index (ratio of annual precipitation over PET) appears to roughly equally important as annual precipitation, although it is only rarely considered as a predictor in SDMs. Our results further underline how different the predictions can be when different variables are selected within the same group (despite being correlated), all other variables being the same (Fig. S6). A better accuracy can be achieved by choosing a specific variable within each group as it was strongly emphasized by our results: models accuracy significantly depends on the variable that was used in both the ‘temp’ group and the ‘prec’ group (Fig. 4).

The spatial evaluations were undertaken on a random subset of the data. A potential problem with random subsets is that spatial autocorrelation may inflate absolute AUC values.

A way to get closer to non-independence would be to use spatial filters or striped or checkerboard designs (Munson *et al.*, 2010), but this would in turn very likely lead to a truncated estimation of the climatic niche and therefore an underestimation of the projected distribution (Barbet-Massin *et al.*, 2010). However, we estimated the importance of predictors with AUC difference, which makes the absolute AUC value less crucial for the study. Besides, we were interested in the relative importance of the predictors, regardless of the actual performance of the models. For all these reasons, the spatial random subsetting (replicated seven times) seemed the most appropriate here. Even though the spatial evaluation replicates were independent from each other, it is not true for the temporal evaluation replicates which can be ordered chronologically. Temporal autocorrelation is likely to inflate the absolute AUC value, especially for the first time periods. The temporal AUC values actually slightly decrease when the models are projected further in time. However, the relative importance (estimated through AUC difference) of the 'correlation groups', as well as the relative importance of predictor within the 'temp' group and the 'prec' group is consistent through time (Figs S2a3,b3 & S3c).

The confidence one can have in the results provided by this study is magnified by the fact that both spatial and temporal (over 40 years) evaluation provided highly similar results. This further means that the variables that are the most relevant in explaining current distribution of bird species are also the ones that ensure the best transferability in time of species distribution models. Even more importantly, the results were very similar across diverse modelling techniques (except for ANN) despite often being the main source of uncertainty for predictions (Buisson *et al.*, 2010). Even though ANN exhibited a good accuracy for most species in some studies (Thuiller, 2003), it appears to be less reliable than other modelling techniques regarding its ability to rank predictors according to their importance. Furthermore, this study did not rely on a single species that could have very specific climate factors driving its distribution. Obviously, the variable importance differed among the 243 species (Figs 5 & S5) and explaining this interspecific variability will require further exploration. Nevertheless, some predictors provided significantly more accurate results when considering all species, so it seems that most bird species in the USA have similar climatic drivers.

This study was carried out for birds over a large spatial extent and at an intermediate spatial resolution (*c.* 25 km²). Further work is needed to assess how well these results extend to other continents, other taxa or other spatial resolutions. We expect them to most strongly apply to bird species in other temperate regions. Further research and data of similar quality will be needed to perform similar assessments for other biomes, such as tropical regions. Likewise, it is unlikely that climate drivers of species distributions would be similar for other taxa, but it would be interesting to know at what phylogenetic level the climate drivers of species start to differ the most. We would expect precipitation variables to be

more important for plant species. For this group, other climatic variables such as seasonal precipitation or seasonal moisture index would be worth added to the pool of variables to be tested. However, the method we proposed here can be applied to presence/absence data from any taxa and in any part of the world, which would allow further comparisons.

ACKNOWLEDGEMENTS

We are grateful to Adam M. Wilson, Phoebe L. Zarnetske and Ben S. Carlson as well as all members of the Jetz lab, two anonymous referees and Risto Heikkinen for their constructive comments on this manuscript. We also acknowledge the contributions of the thousands of U.S. BBS participants who survey routes annually, as well as the work of dedicated USGS and CWS scientists and managers. The work benefited from the high-performance computing clusters provided by Yale University. MBM acknowledges funding from EU FP7-PEOPLE-2011-IOF project BIRDCHANGE. WJ acknowledges support from NSF grants DBI 0960550 and DEB 1026764 and NASA grant NNX11AP72G.

REFERENCES

- Anderson, R.P. & Raza, A. (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 montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography*, **37**, 1378–1393.
- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22**, 42–47.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484–492.
- Ashcroft, M.B., French, K.O. & Chisholm, L.A. (2011) An evaluation of environmental factors affecting species distributions. *Ecological Modelling*, **222**, 524–531.
- Austin, M. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157**, 101–118.
- Barbet-Massin, M., Walther, B.A., Thuiller, W., Rahbek, C. & Jiguet, F. (2009) Potential impacts of climate change on the winter distribution of Afro-Palaeartic migrant passerines. *Biology Letters*, **5**, 248–251.
- Barbet-Massin, M., Thuiller, W. & Jiguet, F. (2010) How much do we overestimate future local extinction rates

- when restricting the range of occurrence data in climate suitability models? *Ecography*, **33**, 878–886.
- Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012a) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3**, 327–338.
- Barbet-Massin, M., Thuiller, W. & Jiguet, F. (2012b) The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology*, **18**, 881–890.
- Beaumont, L.J., Pitman, A.J., Poulsen, M. & Hughes, L. (2007) Where will species go? Incorporating new advances in climate modelling into projections of species distributions. *Global Change Biology*, **13**, 1368–1385.
- Bourg, N.A., McShea, W.J. & Gill, D.E. (2005) Putting a cart before the search: successful habitat prediction for a rare forest herb. *Ecology*, **86**, 2793–2804.
- Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H. & Bollmann, K. (2013) Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. *Ecography*, **36**, 971–983.
- Broennimann, O. & Guisan, A. (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biology Letters*, **4**, 585–589.
- Buisson, L., Thuiller, W., Casajus, N., Lek, S. & Grenouillet, G. (2010) Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, **16**, 1145–1157.
- Busby, J.R. (1991) BIOCLIM - a bioclimate analysis and prediction system. *Plant Protection Quarterly*, **6**, 8–9.
- Carnaval, A.C. & Moritz, C. (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, **35**, 1187–1201.
- Chefaoui, R.M. & Lobo, J.M. (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling*, **210**, 478–486.
- Di Luzio, M., Johnson, G.L., Daly, C., Eischeid, J.K. & Arnold, J.G. (2008) Constructing retrospective gridded daily precipitation and temperature datasets for the conterminous United States. *Journal of Applied Meteorology & Climatology*, **47**, 475–497.
- Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B. & Singer, A. (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119–2131.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 027–046.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330–342.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Fry, J.A., Xian, G., Jin, S., Dewitz, J.A., Homer, C.G., Yang, L., Barnes, C.A., Herold, N.D. & Wickham, J.D. (2011) National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing*, **77**, 859–864.
- Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J., Moritz, C. & Cunningham, C. (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in Dendrobatid frogs. *Evolution*, **58**, 1781–1793.
- Gregory, R.D., Willis, S.G., Jiguet, F., Voříšek, P., Klvánová, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. & Green, R.E. (2009) An indicator of the impact of climatic change on European bird populations. *PLoS ONE*, **4**, e4678.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A. & Zimmermann, N.E. (2006) Using niche-based models to improve the sampling of rare species. *Conservation Biology*, **20**, 501–511.
- Heikkinen, R.K., Marmion, M. & Luoto, M. (2012) Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography*, **35**, 276–288.
- Hijmans, R.J. & Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hof, C., Araújo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–519.
- Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., VanDriel, J.N. & Wickham, J. (2007) Completion of the 2001 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing*, **73**, 337–341.

- Huntley, B., Collingham, Y.C., Willis, S.G. & Green, R.E. (2008) Potential impacts of climatic change on European breeding birds. *PLoS ONE*, **3**, e1439.
- Jiménez-Valverde, A., Barve, N., Lira-Noriega, A., Maher, S.P., Nakazawa, Y., Papeş, M., Soberón, J., Sukumaran, J. & Peterson, A.T. (2011) Dominant climate influences on North American bird distributions. *Global Ecology and Biogeography*, **20**, 114–118.
- Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, **90**, 588–597.
- Leathwick, J.R. & Whitehead, D. (2001) Soil and atmospheric water deficits and the distribution of New Zealand's indigenous tree species. *Functional Ecology*, **15**, 233–242.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology & Biogeography*, **17**, 145–151.
- Luoto, M., Virkkala, R. & Heikkinen, R.K. (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecology and Biogeography*, **16**, 34–42.
- Mackenzie, D.I. & Royle, J.A. (2005) Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, **42**, 1105–1114.
- Marini, M.Á., Barbet-Massin, M., Lopes, L.E. & Jiguet, F. (2009) Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. *Biological Conservation*, **142**, 3039–3050.
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59–69.
- Menke, S.B., Holway, D.A., Fisher, R.N. & Jetz, W. (2009) Characterizing and predicting species distributions across environments and scales: Argentine ant occurrences in the eye of the beholder. *Global Ecology and Biogeography*, **18**, 50–63.
- Munson, M.A., Caruana, R., Fink, D., Hochachka, W.M., Iloff, M., Rosenberg, K.V., Sheldon, D., Sullivan, B.L., Wood, C. & Kelling, S. (2010) A method for measuring the relative information content of data from different monitoring protocols. *Methods in Ecology and Evolution*, **1**, 263–273.
- Peterson, A.T. & Nakazawa, Y. (2008) Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecology and Biogeography*, **17**, 135–144.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.
- Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. & Peterson, A.T. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, **426**, 837–841.
- Synes, N.W. & Osborne, P.E. (2011) Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Global Ecology and Biogeography*, **20**, 904–914.
- Syphard, A.D. & Franklin, J. (2009) Differences in spatial predictions among species distribution modeling methods vary with species traits and environmental predictors. *Ecography*, **32**, 907–918.
- Thuiller, W. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, **10**, 2020–2027.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.
- Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.
- U. S. North American Bird Conservation Committee (2000) *North American bird conservation initiative: bird conservation region descriptions*. U.S. Fish and Wildlife Service, Arlington, VA, USA.
- VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling*, **220**, 589–594.
- Vega, R., Fløjgaard, C., Lira-Noriega, A., Nakazawa, Y., Svenning, J.-C. & Searle, J.B. (2010) Northern glacial refugia for the pygmy shrew *Sorex minutus* in Europe revealed by phylogeographic analyses and species distribution modelling. *Ecography*, **33**, 260–271.
- Villemant, C., Barbet-Massin, M., Perrard, A., Muller, F., Gargominy, O., Jiguet, F. & Rome, Q. (2011) Predicting the invasion risk by the alien bee-hawking Yellow-legged hornet *Vespa velutina nigrithorax* across Europe and other continents with niche models. *Biological Conservation*, **144**, 2142–2150.
- Vogelmann, J.E., Howard, S.M., Yang, L.M., Larson, C.R., Wylie, B.K. & Van Driel, N. (2001) Completion of the 1990s National Land Cover Data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. *Photogrammetric Engineering and Remote Sensing*, **67**, 650–662.
- Watling, J.I., Románach, S.S., Bucklin, D.N., Speroterra, C., Brandt, L.A., Pearlstine, L.G. & Mazzotti, F.J. (2012) Do bioclimate variables improve performance of climate envelope models? *Ecological Modelling*, **246**, 79–85.
- Williams, P., Hannah, L., Andelman, S., Midgley, G., Araújo, M., Hughes, G., Manne, L., Martinez-Meyer, E. & Pearson, R. (2005) Planning for climate change: identifying

minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, **19**, 1063–1074.

Williams, K.J., Belbin, L., Austin, M.P., Stein, J.L. & Ferrier, S. (2012) Which environmental variables should I use in my biodiversity model? *International Journal of Geographical Information Science*, **26**, 2009–2047.

Wisz, M.S. & Guisan, A. (2009) Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecology*, **9**, 1–13.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of the 243 species used in this study.

Figure S1 Mean comparisons of the AUC differences.

Figure S2 AUC differences for ‘temp’ and ‘prec’ predictors according to the seven different temporal evaluations.

Figure S3 Importance of each climate predictor to provide better accurate distributions for single SDMs.

Figure S4 Comparisons of results obtained from single SDMs predictions or ensemble forecast prediction.

Figure S5 Climate predictor relevance according to the species.

Figure S6 Climate suitability of the Carolina Chickadee predicted for 1971 and 2010.

BIOSKETCHES

Morgane Barbet-Massin is a postdoctoral researcher. Her research is at the interface of biogeography and climate change ecology, with a special interest for species distribution modelling.

Walter Jetz is an Associate Professors interested in biodiversity science.

Author contributions: M.B.M. conceived the ideas and collected the data; M.B.M. and W.J. analysed the data; and M.B.M. led the writing with help from W.J.

Editor: Risto Heikkinen