



HAL
open science

Predicting species distribution combining multi-scale drivers

Alice Fournier, Morgane Barbet-Massin, Quentin Rome, Franck Courchamp

► **To cite this version:**

Alice Fournier, Morgane Barbet-Massin, Quentin Rome, Franck Courchamp. Predicting species distribution combining multi-scale drivers. *Global Ecology and Conservation*, 2017, 12, pp.215-226. 10.1016/j.gecco.2017.11.002 . hal-02457121

HAL Id: hal-02457121

<https://hal.science/hal-02457121>

Submitted on 1 Apr 2021

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.



Original Research Article

Predicting species distribution combining multi-scale drivers

Alice Fournier^{a,*}, Morgane Barbet-Massin^a, Quentin Rome^b,
Franck Courchamp^a

^a Ecologie, Systématique et Evolution, Univ. Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, Paris, 91400 Orsay, France

^b UMS 2006 Patrimoine Naturel – AFB, CNRS, MNHN – Muséum national d'Histoire naturelle, CP50, 57 Rue Cuvier, 75235, Paris Cedex 05, France



ARTICLE INFO

Article history:

Received 28 September 2017

Received in revised form 9 November 2017

Accepted 10 November 2017

Keywords:

Climatic variables

Spatial scale

Environmental filtering

Habitat

SDM

Yellow-legged hornet

ABSTRACT

Species Distribution Models (SDMs) are often used to predict the potential range of invasive species. Unfortunately, most studies do not evaluate variables relevance before selecting them to fit their models. Moreover, multiple variables such as climate and land use may drive species distribution at different spatial scales but most studies either use a single type of drivers, or combine multiple types without respecting their operating scale. We propose a three steps framework to overcome this limitation. First, use SDMs to select the most relevant climatic variables to predict a given species distribution, at continental scale. Then, characterize the species-habitat relationships, at a local scale, to produce species and area specific habitat filters. Finally, combine both information, each obtained at a relevant scale, to refine climatic predictions according to habitat suitability. We illustrate this framework with 14,794 Asian hornet (*Vespa velutina nigrithorax*) records. We show that integrating multiple drivers, while still respecting their scale of effect, produced a potential range 55.9% smaller than that predicted using the climatic model alone, suggesting a systematic overestimation in many published predictions. This general framework illustrated by a well-documented invasive species is applicable to other taxa and scenarios of future climate and land-cover changes.

© 2017 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Species distribution models (SDMs) are regularly used to generate predictions of species presence; they rely on correlations between environmental variables and geo-localized species records to understand the environmental variables that drive species presences (Blach-Overgaard et al., 2010) and delineate potential species distributions (Araújo and Guisan, 2006; Araújo and Peterson, 2012). An extensive number of environmental datasets are available nowadays for fitting SDMs; but only a limited number of them should be included when running SDMs. Indeed, although increasing the number of predictors increases the chance of having ecologically relevant ones, it also inflates the risk of overfitting the model (Merow et al., 2014) and of collinearity issues between variables (Dormann et al., 2013a). Restricting the number of variables and choosing only the most appropriate ones for a species is thus crucial to maximize the performance of SDMs and the accuracy of the predictions (Araújo and Guisan, 2006; Araújo and Peterson, 2012; Barbet-Massin and Jetz, 2014; Braunisch et al., 2013). Ideally, this choice should rely on expert knowledge concerning the ecological requirements of the species, but such knowledge is

* Corresponding author.

E-mail address: alice.fournier@u-psud.fr (A. Fournier).

hardly ever available. Predictor selection thus remains a key challenge when running SDMs (Araújo and Guisan, 2006), and despite its proven and important effect on the predictions, has received too little attention (Austin and Van Niel, 2011; Syphard and Franklin, 2009; Tulloch et al., 2016).

Another challenge of SDMs, linked to the selection of the most appropriate variables, is to combine multiple variables that may drive species distribution at different spatial scales. Niche modelling has always lacked unifying theories and methods to bring together multi-scale drivers, which reduces their accuracy and their appropriateness for conservation planning. Notably, studies integrating climatic and land use variables at different scales remain extremely rare, despite evidences of their necessity (Sirami et al., 2016). Most biodiversity scenarios focus on climatic models and fail to integrate other environmental filters, which also have significant impacts on species distributions (Sirami et al., 2016; Titeux et al., 2016), or mix all predictors at the same resolution (Bucklin et al., 2014; Gallardo et al., 2015). These filters may be related to climate, topography, primary production or land use (Milbau et al., 2009). Furthermore, many studies have now come to the agreement that species–environment relationships are strongly scale dependent; species presence results from an interplay between climate, which governs their distributions at continental scales (Blach-Overgaard et al., 2010), and for instance habitat, which drives species' occupancy at finer spatial resolution (Luoto et al., 2007; Monceau and Thiéry, 2017; Virkkala et al., 2005). Each of these drivers, acting as a filter that shapes the species distribution as a special spatial scale, must thus be identified and included in the model at the appropriate resolution (Cabra-Rivas et al., 2015; Luoto et al., 2007; Milbau et al., 2009; Pearson et al., 2004, 2003). Very few studies have provided theoretical bases to bring together climate and habitats predictors in a hierarchical manner (Kelly et al., 2014; Milbau et al., 2009; Pearson et al., 2003; Sirami et al., 2016). They represent valuable theoretical starting points, but methods carefully selecting the regional habitat filters to be considered and put this theory into practice are needed to improve the accuracy of climate-driven models (Thuiller et al., 2004; Zhu et al., 2017). Therefore, a key challenge now is to develop a practical method to integrate multi-scale predictors and capture more accurately their environmental niche (Virkkala et al., 2005).

We present here a framework to select the most relevant climatic variables, at a global scale, build species-specific habitat suitability filters, at a local scale, and combine both information to produce refined suitability maps. We illustrate this framework with the case of the invasive Asian hornet, *Vespa velutina nigrithorax*. The crucial step of variable selection has never been addressed to predict this species potential range, and previous predictions have been obtained with climatic variables only. The Asian hornet arrived accidentally in France from China in 2004 (Arca et al., 2015), and since then has invaded almost the whole of France and other European countries (Spain, Portugal, Italy, Belgium Germany and UK). Due to its predatory behavior on insects, and particularly honey bees (Monceau et al., 2014), there are great concerns about its potential impacts on the native biodiversity (Choi et al., 2012), on the beekeeping industry and on pollination services overall (Monceau et al., 2014). It is necessary to develop tools to better predict its future invasion range and help stop its spread and reduce its impacts efficiently. The method is generalizable to any other taxa, and can be used to combine as many environmental layers as needed, as it provides tools to deal with both continuous and categorical layers.

2. Materials & methods

2.1. Distributional data

We used the GPS records from the INPN biodiversity database (<http://inpn.mnhn.fr>), maintained by the French National Natural History Museum, and based on a participative science program (<http://frelonasiatique.mnhn.fr>), as in Barbet-Massin et al. (2013). The database totaled to 14,794 records of Asian hornet colonies, from the invaded range (France, Italy, Germany, Spain & Portugal, Belgium), spanning from 2004 to 2016. We did not include presence data from the native range for two reasons. Firstly, this invasion results from a single introduction event (Arca et al., 2015), of one female only, that gave rise to the whole European population of Asian hornets. A single organism cannot encompass the whole population genetic and phenotypic diversities. Furthermore, altered species–climate relationships during invasion are recurrent for insects, due to their ability to respond quickly to novel environments (Hill et al., 2017). The niche conservatism assumption is highly unlikely to be met and the niche overlap between native and invasive ranges expected to be poor (Early and Sax, 2014; Medley, 2010). In this context, a conservative framework is favored, which consists in using only invasive occurrences to build the model. A recent study on the Asian hornet showed that the predictive accuracy of the SDM was significantly better when models were calibrated with invasive data only, excluding native data (Barbet-Massin et al., unpublished results). Secondly, there were only 68 occurrences available from its native range, some of which of uncertain and unequal quality compared to the invasive range data. For these reasons, we preferred to rely on invasion occurrences only.

2.2. Environmental data

We used a set of 19 climatic variables (averaged from 1950 to 2000) available from the worldclim database (<http://www.worldclim.org/>) at 2.5 arc min (~4 km) resolution (Hijmans et al., 2005). These variables represent a combination of means, extremes, variability and seasonality of temperature and precipitation data that are known to influence species distribution (Root et al., 2003).

We used the CORINE (Coordination of Information on the Environment) Land Cover 2006 dataset to study the suitability of each habitat for the hornet (The European Environment Agency (EEA), 2010). This dataset is characterized by its high-spatial

(100 m resolution) and thematic resolution. It is composed of 44 different land cover classes (hereafter habitat), each belonging to one of the four following broad categories: artificial surfaces (urban, roads, industrial units, etc.), agricultural areas (non-irrigated arable land, pastures, fruit trees, etc.), natural areas (coniferous forest, bare rocks, etc.) and wetlands and marine areas (estuaries, salines, etc.). We considered that both of these datasets (Worldclim between 1950 & 2000, and CORINE 2006 dataset) are representative of current climatic and land use conditions.

2.3. Species distribution modelling

Ranking of climatic variable. The first step of our framework was to select the most relevant climatic variables to predict the hornet's distribution (Fig. 1-A). To avoid running models using correlated variables, we separated the 19 variables into two uncorrelated groups; the temperature variables group and the precipitation one. Any variable from one of them is uncorrelated to any variable from the other. We then run a series of models, testing all possible combinations of two variables, with one variable from the temperature and the other from the precipitation group. This totaled to 88 possible combinations (eleven temperature variables times eight precipitation variables). For each model, we used seven different SDM algorithms within the 'biomod2' package (Thuiller et al., 2014), using the R platform (R Development Core Team, 2013): Generalized Linear Model (GLM), Flexible Discriminant Analysis (FDA), Artificial Neural Network (ANN), Random Forest (RF), Generalized Boosting Model (GBM), Classification tree analysis (CTA) and Multiple Adaptive Regression Splines (MARS) (Fig. S7 for the models parameters and pseudo absences selection procedure). These seven algorithms were used to build an ensemble model, to account for the variability between the seven SDMs and provide the central tendency (Araújo and New, 2007). The ensemble model, or final consensus distribution, was the weighted mean, proportional to the accuracy evaluation, of the seven modelling techniques.

Two metrics were used to evaluate the accuracy of each SDM; the True Skill Statistics (TSS) (Allouche et al., 2006) and the Area Under the receiver operating characteristic Curve (AUC) (Fielding and Bell, 1997). AUC has been criticized (Lobo et al., 2008) because of its dependence on the prevalence and the spatial extent, but it was used here to compare models with a constant prevalence and geographical extent (only the sets of predictors varied). The TSS accounts for both sensitivity (i.e., correctly predicted presences/[correctly predicted presences + predicted absences]) and specificity (i.e., correctly predicted absences/[correctly predicted absences + predicted presences]) of the model. To calculate TSS and AUC, we used a random subset of 70% of the data to calibrate the model and the remaining 30% to evaluate it. We chose the threshold that maximizes the TSS for its calculation. The data splitting approach was repeated five times. We ranked the climatic variables according to the mean TSS and AUC measures of all ensemble models run with each variable.

2.4. Projection of potential climatically suitable range

The next step of the framework was to select, among the variables with better predictive accuracy, the ones that were not correlated to avoid collinearity issues and overfitted models (Dormann et al., 2013b). We measured the correlation between our 19 bioclim variables similarly to Bellard et al. (2016) method (S1, A). It is a hierarchical classification method based on a distance metric (Pearson's correlation coefficient) at a threshold of 0.7. This resulted in nine "correlation groups" (S1); nine was thus the maximum number of variables that could be chosen for the final climatic prediction. Based on our ranking of climatic variables (section above), we identified the most relevant variables from each of the nine groups of correlated variables. But because using a small number of variables in SDM reduces the risk of overfitting and collinearity issues, we looked for a tradeoff between fewer variables and a highly accurate prediction. We compared the accuracy and the output of the ensemble models run with either the best 9, 8, 7 or 6 variables (Fig. S3) to see how this modified the predictions. These models were all as accurate (similar TSS and AUC values) and produced similar spatial projections (Pearson's correlation between the maps comprised between 1 and 0.97, Figs. S3–C). There was, however, a slight drop in AUC and TSS when using 6 variables (Figs. S3–B). Therefore, for the final climatic suitability prediction we choose to use only the 7 most powerful and uncorrelated variables (TSS > 0.8) (Fig. S1). This final subset of seven variables enabled us to produce a robust ensemble forecast (TSS = 0.907 and AUC = 0.990), which gave us the climatic suitability for the hornet, in each 2.5 arc min grid cell, under current conditions in Europe. It is noteworthy that the approach presented here is the most complete and robust for variable selection. One could want a different time-quality tradeoff by selecting good variables but not necessarily the best ones. This could be done simply by forming the correlation groups from the start, automatically taking the variables that are not correlated with others, and thus reducing the number of variables combinations to test.

2.5. Identification of suitable habitat

Our next aim was to combine the climatic suitability (obtained above) with the habitat related requirements of the species. To measure the suitability of each of the 44 habitats for the hornet, we compared the observed number of *V. v. nigrithorax* nests in a given habitat to the number expected by chance, if the nests were randomly distributed (Fig. 1-B). We also measured the across-all-habitats suitability of each of the four groups of habitats (artificial surfaces, agricultural areas, forests & natural areas and wetlands & water bodies) following the same method. To obtain the expected number of nests in any given habitat, we did a bootstrap; i.e. repeated 10,000 random samplings of 14,794 points (the same number as hornet's presences) and counted the number of random points sampled in each habitat (Fig. 1-B). Following this method, we built the density plots of

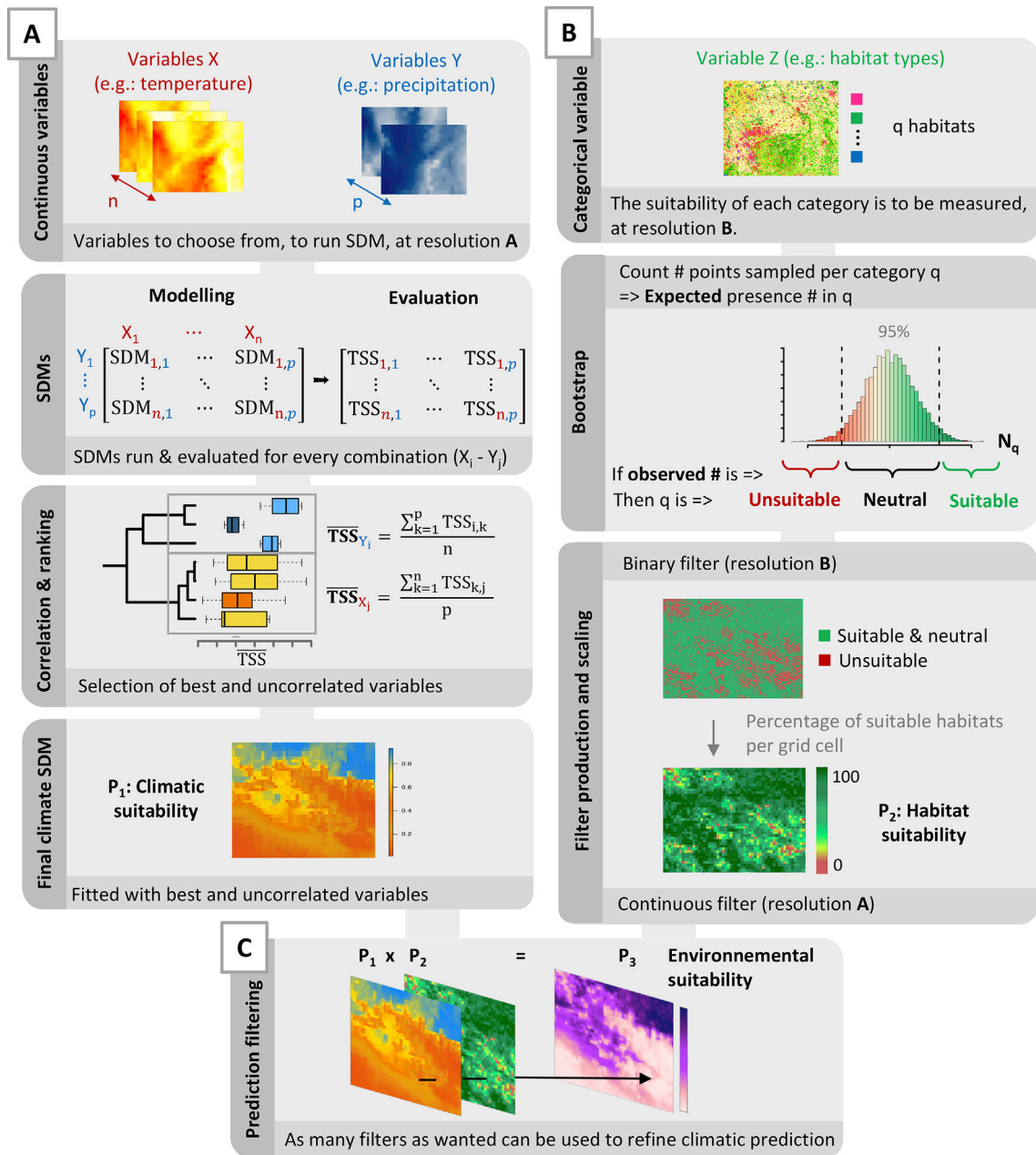


Fig. 1. Computational framework to refine species distribution predictions using multiscale filters. (A) **Continuous variable selection.** Any number of groups of variables can be tested (here; two), where variables from one group are uncorrelated with those in the other groups. We propose to run a SDM with every possible combination of two variables, evaluate the accuracy of the models (TSS), and use each variable TSS to rank them (Fig. S1). Only the best variable from each correlation group is finally retained for the climatic suitability ensemble modelling. (B) **Filter construction from categorical variables.** A bootstrap gives us the number of presences expected by chance in each category (Fig. 2 and Fig. S4), to which we compare the observed presences, to estimate each category suitability for the species. We produce binary filters, at the resolution that is the most relevant for this variable, and then upscale them to match the coarser climatic variables resolution. (C) **Filters combination.** As many filters can be multiplied, each of them representing independent probabilities, to refine initial climatic predictions (Fig. 3).

expected number of presence in each of the 44 habitats (Fig. 2 & Fig. S4). The habitat analysis concerned only the habitats present in the climatically suitable part of Europe (climatic suitability > 0.5, i.e. area in which the probability to find a hornet is greater than random). This geographical restriction relied on the assumption that climate and habitat drivers interact in a hierarchical manner; climate drives the species presence at a broad scale, and then, within the climatically suitable area, the habitat drives the species settlement locally (Milbau et al., 2009).

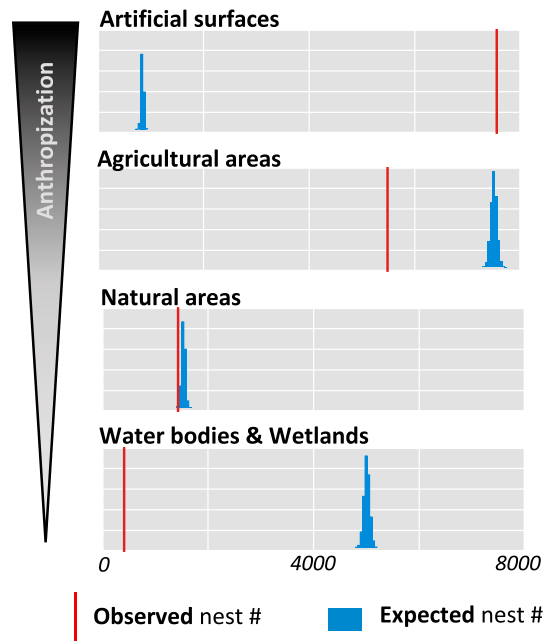


Fig. 2. Identification of habitat-type suitability for the hornet. Histograms showing, in each habitat-type, the number of nests expected if the hornet was randomly distributed (blue bars) and the observed number of nests (red vertical line). Random samplings were repeated 10,000 times, with the same number as hornet's nests ($n = 14,791$) drawn each time. Similar figures depicting the density plots for each of the 44 habitat are available in Fig. S4. Habitat-types where the hornet's number of nests is in the upper (resp. lower) 2.5% of the random distribution, are suitable (resp. unsuitable). Artificial surfaces are highly suitable for the hornet and probably play a major role in shaping its distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For each of these density plots, we analyzed in which quantile of the expected distribution the actual number of hornet presences occurred. If the hornet's number of presences was in the upper (resp. lower) 2.5% of the distribution, we classified this habitat as suitable (resp. unsuitable). When the observed number of nest was comprised between 2.5 and 95.5% of the distribution, it was not significantly different from the random distribution, and thus qualified as neutral for the species. This method is illustrated in Fig. 1-B.

Second, to control that our sampling was not biased towards human-dense areas (where observations may be more likely), we performed the same analysis in an area where the hornet's nests were exhaustively searched for (i.e., where we had true absences) (Fig. S5). This study area, in the North of Chizé, is a research facility managed by the CEBC research unit (*Zone Atelier Plaine et Val de Sèvre, Centre d'Études Biologiques de Chizé*, 46°15'N, 0°30'W). This 45,000 ha, area gave us complementary information on some of the land use type where hornets were present and absent. It enabled us to strengthen our conclusions regarding habitats suitability and avoid a possible observer bias.

2.6. Combining climate and habitat

The final step of the framework was the combination of the climatic and habitat suitabilities into a unique and refined prediction of environmental suitability (Fig. 1-C). We constructed a habitat filter, as the percentage of suitable and neutral habitats per grid cell, at the same resolution as the climatic suitability map. This filter corresponds to the probability to find a suitable habitat in each grid cell. We included the neutral habitats when building the filter, in order to make our prediction as conservative as possible. The climatic suitability and the percentage of suitable habitats per grid cell are two independent events, so we multiplied these two probabilities, which gave us the environmental suitability, i.e. the probability of presenting both a suitable climate and habitat. This multi-filter combination can be done with as many filters as required, according to the species, to increase the accuracy of the prediction.

3. Results

3.1. Climatic variables selection

The TSS of all models were comprised between 0.735 and 0.859, and AUC between 0.932 and 0.978 (Fig. S2). The rankings obtained either with the TSS and the AUC were similar (Figs. S2–A). Variables related to temperature or precipitation performed similarly; the mean TSS of all temperature variables (0.805, ± 0.029) and the mean TSS of all precipitation variables

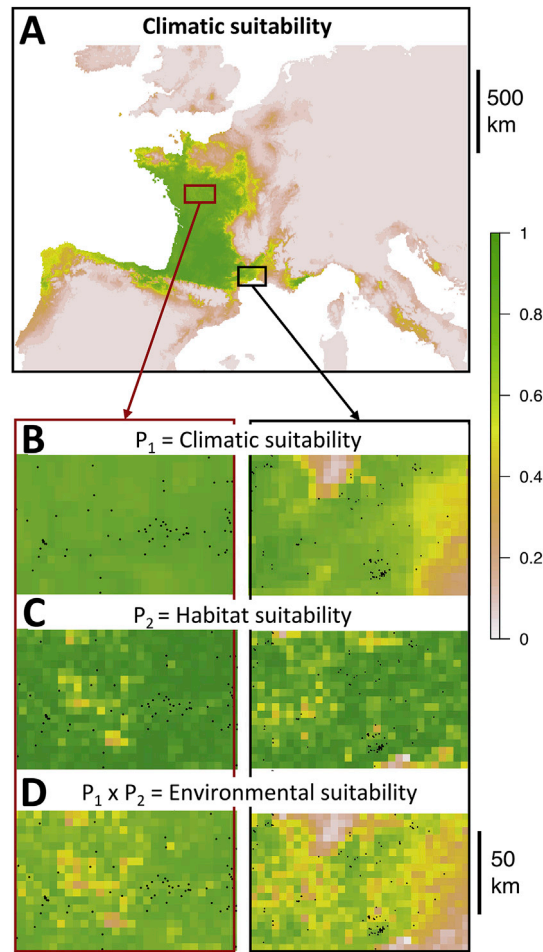


Fig. 3. Two-filters approach applied to *V. velutina* to refine its environmental suitability prediction. (A) Predicted current climate suitability for *V. velutina* in Western Europe (ensemble consensus across eight SDM algorithms), (B) climatic suitability zooms in, located in the middle and on the edge of the distribution, (C) corresponding habitat suitability (percentage of suitable habitat per grid cell). The multiplication P_1 and P_2 is the probability of both of them occurring in each grid cell, called here environmental suitability (D). Black dots represent hornet nests.

(0.803, ± 0.030) were not significantly different (ANOVA; $F_{1, 175} = 0.067$, $P = 0.796$). Using temperature or precipitation variables is equally relevant to predict the Asian hornet's distribution.

Variable performances among the precipitation group were not significantly different from one another (ANOVA; $F_{7, 80} = 0.793$, $P = 0.595$); all precipitation variables seemed to perform similarly in predicting the hornet's distribution. Precipitation variables formed three groups of correlation (Fig. S1). Choosing any three precipitation variables, one from each correlation group, would provide similarly accurate hornet's distributions, while reducing collinearity problems.

On the contrary, variables performances among the temperature group were significantly different (ANOVA; $F_{11, 77} = 38.6$, $P < 0.001$); the choice of the temperature variable used in the model has an impact on the accuracy of the distribution. Bio1 (annual mean temperature) performed significantly better than all other predictors in the temperature group (post hoc Tukey test, $P < 0.005$). Bio1 was highly correlated with bio 6, 9 and 11 (temperature maximum of warmest month, mean temperature of driest quarter and mean temperature of coldest quarter); although these three other variables provided accurate predictions, they could not be used jointly with bio1 in a SDM. So bio1 was retained as a relevant variable to predict the hornet's distribution, and bio6, 9 and 11 were left out. The final set of relevant and uncorrelated variables retained were bio1,3,4,10,12,15 and 17 (Fig S1 and S2-B).

The most climatically suitable areas (suitability values > 0.7) were mainly located in France and in the western part of Southern Europe: Spain, Italy and Portugal (Fig. 3-A). These climatically highly suitable areas represented 28.96% of France.

3.2. Habitat suitability

Our analysis of the four habitat groups showed that the artificial surfaces (group with highest level of anthropization) were significantly more attractive than the agricultural areas, forest and natural areas and wetlands, which did not, overall, enable the settling and persistence of hornets' nests (Fig. 2).

When looking at each habitat separately, we found that 22 (out of 44) habitats are suitable for the hornet, i.e. there are significantly more hornets within these habitats than if the nests were randomly distributed (Table 1, Table 2 and Fig. S3). 68% of these suitable habitats belong to the most anthropized categories of habitats, according to CORINE classification (i.e. artificial surfaces and agricultural areas). Only two habitats were neutral (mineral extraction sites and construction sites), that is, the number of nest was not significantly different from the one expected by chance. Finally, 14 habitats appeared as unsuitable by the hornet (Table 2), and only two of them were anthropized. There remained six extremely rare habitats (ex: Coastal lagoons, burnt areas, glaciers ...) for which we had no suitability information (no nest in them and none of the 10,000 bootstraps sampled points fell in them). Overall, the suitable habitats for the hornet represent 72.60% of Western Europe.

Not all habitats were present in the exhaustively studied zone of Chizé (Table S1). But those present enabled us to confirm the result obtained Europe wide (same habitats found as suitable or unsuitable), and also reject any observer structural bias in favor of areas with dense human population (S5 and Table S1).

3.3. Combining climatic and habitat suitabilities

Areas with a high (>0.7) environmental suitability (combining climate and habitat) were located mainly in France (except in the mountainous areas) and in the North of Italy, Spain and Portugal (Fig. S6). They represented 16.20% of the French territory. Therefore, this refining led to a reduction of the predicted highly suitable area (>0.7) by 55.9%. The areas the most concerned by this filtering were the pine forest in the south west of France and the Cantabria region of Spain.

4. Discussion

In this study, we suggest and illustrate a framework to select and combine continuous (e.g.: climatic) and categorical (e.g.: habitat) variables, while respecting their scale of effect. This approach enabled us to select the seven most relevant climatic variables to predict our species distribution, and identify 22 suitable habitats for this species. These habitats represent 72.6% of Europe. We refined the climatic suitability map, using the habitat filter we constructed, which reduced the predicted suitable area of the species by 55.9%.

4.1. Climatic drivers of the hornet

The choice of variables has an important impact on the predictions obtained when using SDM (Araújo and Peterson, 2012; Austin and Van Niel, 2011; Braunsch et al., 2013). However, our study is the first to compare the accuracy of the predictions obtained with different sets of climatic variables, while controlling for collinearity between them, to assess their relative importance for the Asian hornet. Most studies simply rely on commonly used sets of variables in the literature, without examination of their power in predicting their species distribution (Bessa et al., 2016; Medley, 2010; Villemant et al., 2011) and therefore risk major overestimation of predictions. Our framework is thus highly valuable and applicable to any studies relying on SDMs. The reliability of our ranking is further reinforced by the fact that it was similar for both accuracy measures (TSS and AUC, Figs. S2–A) and across all modelling techniques used (Figs. S2–C). One must be careful when interpreting the variables in terms of ecological meaning though; a powerful variable may be a proxy for another relevant variable, not included in the model. Yet, this method enabled us to select the climatic predictors that produce the most accurate predictions, and which are likely to influence key phases of the life cycle of *V. v. nigrithorax*. Further tests could be done to assess how well the climatic variables performances can be extrapolated spatially (in other continents) and temporally (in the future).

It is noteworthy that this species being invasive, it may not be at equilibrium with its environment, which may result in an underestimated potential range (Gallien et al., 2012). Yet, it does not alter the climatic variables selection process. Our method, that refines climatic prediction according to habitat suitability, is thus especially valuable in the context of biological invasions. It enables the improvement of SDMs, which already provide conservative predictions of invasive species distribution, and allows for more effective monitoring programs for these invasions. There are no such issues when modelling non-invasive species distribution, which are considered at equilibrium with their environment, but our method remains nonetheless valuable to improve these predictions.

4.2. Habitat drivers for the hornet

Our framework also includes a method to construct habitat suitability filters for the studies species. Applying this to the Asian hornet, we demonstrated the high suitability of anthropized environments for this species. This result is in accordance with previous works, showing a positive correlation between the degree of urbanization and the abundance of *V. v. nigrithorax* (Choi et al., 2012). But previous studies either failed to study the hornet-habitat relationship at a local scale or did not consider

Table 1

Ranking of the 21 suitable habitats for *Vespa velutina nigrithorax*. The ranking is based on the ratio between the observed number of nests and the number expected by chance (obtained by random sampling). The higher the ratio, the more suitable the habitat. The Level of anthropization corresponds to first level of classification of the Corine Land Cover database categories. The higher the level, the most anthropized the habitat (and the darker the shade); (1) Water bodies; (2) Forests and natural areas, (3) Agricultural areas and (4) Artificial surfaces. Most of the suitable habitats are from the categories 3 and 4; human mediated habitats seem crucial to shape the distribution of the Asian hornet.

Land cover type	Observed		Expected		Observed Expected	Level of anthropization
	Count	% ^a	Count ^b	% ^c		
Continuous urban fabric	391	2,64	1	0,01	391	4
Vineyards	150	1,01	0	0,00	150	3
Green urban areas	55	0,37	0	0,00	55	4
Annual & permanent crops	36	0,24	0	0,00	36	3
Water courses	105	0,71	3	0,02	31	1
Fruit trees and berry plantations	80	0,54	3	0,02	25	3
Discontinuous urban fabric	6841	46,24	448	3,03	15	4
Natural grasslands	47	0,32	5	0,03	10	2
Sclerophyllous vegetation	8	0,05	0	0,00	8	2
Permanently irrigated land	7	0,05	0	0,00	7	3
Port areas	7	0,05	1	0,01	5	4
Industrial or commercial units	355	2,40	73	0,49	5	4
Road and rail networks	23	0,16	6	0,04	4	4
Sport and leisure facilities	129	0,87	34	0,23	4	4
Burnt areas	3	0,02	0	0,00	3	2
Airports	10	0,07	3	0,02	3	4
Agriculture, with significant areas of natural vegetation	497	3,36	245	1,66	2	3
Olive groves	2	0,01	0	0,00	2	3
Complex cultivation patterns	2769	18,72	1415	9,56	2	3
Transitional woodland-shrub	124	0,84	75	0,51	2	2
Mixed forest	189	1,28	162	1,09	1	2
Broad-leaved forest	758	5,12	675	4,56	1	2

^a Percentage of all recorded presences found in this habitat.

^b Mean count averaged over the 10000 random samplings.

^c Percentage of all randomly drawn points found in this habitat.

a sufficiently high thematic resolution to make it applicable for management planning, or did not have access to enough occurrences to identify general hornets-habitat patterns (Bessa et al., 2016; Choi et al., 2012; Monceau and Thiéry, 2017).

The suitability of urban areas can be explained by the fact that buildings provide shelter for primary nest establishment (Franklin et al., 2017), and that the hornet is an opportunistic forager attracted by food scraps (bins, market places with seafood ...) available in urban areas (Monceau and Thiéry, 2017). Previous studies pointed out to the fact that honeybees represent at least a third of *V. velutina* diet (Monceau et al., 2014). One hypothesis could be that the recent phenomenon of placing high densities of beehives in cities increases the suitability of this habitat for the hornet, by providing it with abundant

Table 2

Ranking of the 16 land cover types unsuitable by *Vespa velutina nigrithorax*. The ranking is based on the ratio between the observed number of nests and the number expected by chance (obtained by random sampling). The higher the ratio, the more suitable the habitat. The Level of anthropization corresponds to first level of classification of the Corine Land Cover database categories. The higher the level, the most anthropized the habitat (and the darker the shade): (1) Water bodies; (2) Forests and natural areas, (3) Agricultural areas and (4) Artificial surfaces. Only two of the unsuitable habitats belong to the artificial surfaces habitat groups; the others are either agricultural or natural habitats.

Land cover type	Observed		Expected		Observed Expected	Level of anthropization
	Count	% ^a	Count ^b	% ^c		
Construction sites	5	0,03	2	0,02	2,5	4
Mineral extraction sites	20	0,14	20	0,14	1	4
Pastures	1115	7,54	1610	10,88	0,7	3
Moors and heathland	16	0,11	31	0,21	0,5	2
Inland marshes	6	0,04	12	0,08	0,5	1
Water bodies	11	0,07	28	0,19	0,4	1
Coniferous forest	84	0,57	387	2,62	0,2	2
Non-irrigated arable land	947	6,40	4505	30,45	0,2	3
Estuaries	2	0,01	12	0,08	0,2	1
Intertidal flats	2	0,01	5024	33,96	0	1
Beaches, dunes, sands	0	0,00	4	0,03	0	2
Salt marshes	0	0,00	9	0,06	0	1

^a Percentage of all recorded presences found in this habitat.

^b Mean count averaged over the 10000 random samplings.

^c Percentage of all randomly drawn points found in this habitat.

food sources. Our result is in accordance with [Cabra-Rivas et al. \(2015\)](#) and [Monceau and Thiéry \(2017\)](#) work, which highlight the relevance of including human mediated disturbances when modelling invasive species distribution.

Agricultural areas were also mostly suitable for *V. v. nigrithorax*: especially complex and heterogeneous cultivation patterns and fruit crops. These types of agricultural areas are mainly composed of small-sized fields associated with agroforestry units (suitable nesting support and wood fibers for nest construction), and the types of crops grown on them - vineyards, fruits and berry plantations - represent valuable food sources for the colony. Indeed, sugar and nectar are essential carbohydrates sources for the founder queens, the workers and the males ([Richter, 2000](#)). Furthermore, these habitats have been proven to host the great diversity and abundance of wild pollinators ([Deguines et al., 2012](#)), which also represent significant food sources for the larvae. This result goes along with [Franklin et al. \(2017\)](#) observation that >75% of primary nests are found on man-made structures, and 73% of the secondary nests are located in trees.

A strength of our result is that it is unlikely to be affected by observation biases. Indeed, we used data from two complementary sampling protocols: a large-scale, citizen-based database and a local exhaustive search for nests in Chizé. Data analyses from both sampling methods were concordant and showed the same habitats as suitable for the hornet. This enabled us to conclude that the suitability of anthropized habitats, identified Europe wide, was unlikely due to a greater detection probability in those areas. Yet, this analysis would benefit from complementary nest search to re-evaluate some habitats suitabilities for the hornet. Altogether, these results provide a valuable management tool; knowing the suitability of each habitat for the Asian hornet will help to efficiently detect nests, at a very local scale, and take action to mitigate this invasion.

4.3. Relevance of the multi-scale framework

Our method enabled us to filter the climatic prediction according to the suitability and availability of habitats present locally; both drivers are complementary and combining these information is crucial to identify areas where special attention is needed. SDMs that do not consider species–habitat relationships may produce unrealistic and overestimated predictions

(Hattab et al., 2014). None of the previous studies on *V. velutina* distribution considered the species-habitat relationships, which is particularly important at the scale at which the species can be monitored; the local scale (Barbet-Massin et al., 2013; Hattab et al., 2014; Villemant et al., 2011). One hypothesis is that its dispersion results from a trade-off between the climate, which operates at continental scale, and the habitat, which operates at local scale by regulating the availability of nesting and foraging resources (Bucklin et al., 2014; Luoto et al., 2007; Sohl, 2014). From this perspective, it is critical to identify each driver at the scale at which it significantly influences the distribution of the species; several kilometers for climate and around a hundred meters for nesting and foraging resources (Milbau et al., 2009; Pearson et al., 2003).

Our framework considerably improves the accuracy of the prediction, which is highly valuable for invasive species management planning, in order to efficiently measure local vulnerabilities, prioritize areas for early detection and control, and limit their impact. The framework we propose here to integrate multi-scales filters goes beyond the simple description of each driver's importance (Roura-Pascual et al., 2011), as it uses and combines them to refine the species distribution prediction. It has a broad range of possible applications; it can be applied anywhere else, under current and future conditions, for other species (invasive or not), to generate accurate maps of potential establishment. It can be used with as many predictors as wanted, continuous or categorical, each relevant at a different resolution, to better suit the focal species. In this paper, we illustrate the framework by upscaling the habitat filter to match the resolution of the climatic prediction (Fig. 1-B). According to the management strategy, one could also do the opposite, and downscale the climatic suitability map, to match that of the habitat filter. All filters, as long as they are built using information at the most relevant scale for the species distribution, can be up- or down-scaled to be combined. For instance, instead of the percentage of favorable habitats per grid cells, one could use other landscape metrics if these are more relevant regarding the biology of the suited species (connectivity of the patches, Shannon's Diversity Index, heterogeneity of the landscape ...). Another application of our method could be to include biotic interactions to refine the predictions; additional filters representing hosts, preys or predators could easily be combined to the existing framework, or Bayesian networks could be coupled to SDMs (Staniczenko et al., 2017). Further analyses could also consider species dispersal and demographic parameters (Keeling et al., 2017; Robinet et al., 2016) to refine the predictions. Finally, combining future climate and land use changes (Rounsevell et al., 2006) datasets would be interesting, in order to evaluate how the interplay between the two drivers will impact the focal species.

5. Conclusion

Following the recommendation of Milbau et al. (2009) to study invasibility at different scales, we propose a framework to identify various drivers, respecting the scale at which they operate, and combine them to produce environmental suitability maps. We used this framework to identify, for the first time, the most relevant climatic variables and the most suitable habitats for the Asian hornet. This gave us a more comprehensive picture of the species environmental requirements in its invasion range, and led to a refining of the predicted highly suitable areas by ~56%. Our method is generalizable to any taxa, any scenarios of global change, and can be used to combine as many environmental layers as needed, by providing tools to deal with both continuous and categorical layers. It takes us a step closer to capturing species full ecological niche, and produce significantly more accurate distribution maps.

Data accessibility

All environmental layers (climate and habitat) are available publicly.

Vespa Velutina presence points are available by filling in the request form available at <https://inpn.mnhn.fr/contact/contacteznous?lg=en> and aggregated data (number of nests by 10 × 10 km grid cells) are freely available.

The output of our model, i.e. the environmental suitability in each grid cell in Europe. It is available at: http://max2.ese.u-psud.fr/epc/conservation/pages/Franck/docs/env_suitability.csv.

Acknowledgments

We are most thankful to all persons and organizations that provided records of hornet nests in France and the SPN (Service du Patrimoine Naturel, MNHN) who supported the process. The records from Chizé proceed from a project funded by the European Community program (797/2004) for French beekeeping coordinated by the French Ministry of Agriculture (convention FranceAgriMer 14-03R). We thank Claire Villemant, Fabrice Requier, Benoît Geslin, Damien Decante for their useful advice and discussions concerning *Vespa Velutina* biology. We are also thankful to Céline Bellard for her essential help and suggestions to improve this work. This work was supported by grants from the ANR (14-CE02-0021-01), the Fondation BNP Paribas (INVACOST), BiodivERsA Eranet (FFII) and the French Ministry of Ecology.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2017.11.002>.

References

- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>.
- Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* 33, 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>.
- Araújo, M.B., Peterson, A. T., 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93, 1527–1539. <https://doi.org/10.1890/07-1861.1>.
- Arca, M., Mougél, F., Guillemaud, T., Dupas, S., Rome, Q., Perrard, A., Muller, F., Fossoud, A., Capdevielle-Dulac, C., Torres-Leguizamon, M., Chen, X.X., Tan, J.L., Jung, C., Villemant, C., Arnold, G., Silvain, J.F., 2015. Reconstructing the invasion and the demographic history of the yellow-legged hornet, *Vespa velutina*, in Europe. *Biol. Invasions* 17, 2357–2371. <https://doi.org/10.1007/s10530-015-0880-9>.
- Austin, M.P., Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. *J. Biogeogr.* 38, 1–8. <https://doi.org/10.1111/j.1365-2699.2010.02416.x>.
- Barbet-Massin, M., Jetz, W., 2014. A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. *Divers. Distrib.* 20, 1285–1295. <https://doi.org/10.1111/ddi.12229>.
- Barbet-Massin, M., Rome, Q., Muller, F., Perrard, A., Villemant, C., Jiguet, F., 2013. Climate change increases the risk of invasion by the Yellow-legged hornet. *Biol. Conserv.* 157, 4–10. <https://doi.org/10.1016/j.biocon.2012.09.015>.
- Barbet-Massin, M., Rome, Q., Villemant, C., Courchamp, F., unpublished results. Can species distribution models really predict the expansion of invasive species?. *PLoS One*.
- Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. *Biol. Lett.* 12, 20150623 <https://doi.org/10.1098/rsbl.2015.0623>.
- Bessa, A.S., Carvalho, J., Gomes, A., Santarém, F., 2016. Climate and land-use drivers of invasion: predicting the expansion of *Vespa velutina nigrithorax* into the Iberian Peninsula. *Insect Conserv. Divers.* 9, 27–37. <https://doi.org/10.1111/icad.12140>.
- Blach-Overgaard, A., Svenning, J.C., Dransfield, J., Greve, M., Balslev, H., 2010. Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography (Cop.)* 33, 380–391. <https://doi.org/10.1111/j.1600-0587.2010.06273.x>.
- 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 (Cop.)* 36, 971–983. <https://doi.org/10.1111/j.1600-0587.2013.00138.x>.
- Bucklin, D.N., Basille, M., Benscoter, A.M., Brandt, L.A., Mazzotti, F.J., Romanach, S.S., Speroterra, C., Watling, J.L., 2014. Comparing species distribution models constructed with different subsets of environmental predictors. *Divers. Distrib.* 21, 1–13. <https://doi.org/10.1111/ddi.12247>.
- Cabra-Rivas, I., Saldaña, A., Castro-Díez, P., Gallien, L., 2015. A multi-scale approach to identify invasion drivers and invaders' future dynamics. *Biol. Invasions* 18, 411–426. <https://doi.org/10.1007/s10530-015-1015-z>.
- Choi, M.B., Martin, S.J., Lee, J.W., 2012. Distribution, spread, and impact of the invasive hornet *Vespa velutina* in South Korea [WWW Document]. *J. Asia. Pac. Entomol.* <https://doi.org/10.1016/j.aspen.2011.11.004>.
- Deguines, N., Julliard, R., de Flores, M., Fontaine, C., 2012. The whereabouts of flower visitors: contrasting land-use preferences revealed by a country-wide survey based on citizen science. *PLoS One* 7, 1–9. <https://doi.org/10.1371/journal.pone.0045822>.
- 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., 2013a. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop.)* 36, 027–046. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- 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., 2013b. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop.)* 36, 027–046. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Early, R., Sax, D.F., 2014. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Glob. Ecol. Biogeogr.* 23, 1356–1365. <https://doi.org/10.1111/geb.12208>.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49. <https://doi.org/10.1017/S0376892997000088>.
- Franklin, D.N., Brown, M.A., Datta, S., Cuthbertson, A.G.S., Budge, G.E., Keeling, M.J., 2017. Invasion dynamics of Asian hornet, *Vespa velutina* (Hymenoptera: Vespidae): a case study of a commune in south-west France. *Appl. Entomol. Zool.* <https://doi.org/10.1007/s13355-016-0470-z>.
- Gallardo, B., Zieritz, A., Aldridge, D.C., 2015. The importance of the human footprint in shaping the global distribution of terrestrial, freshwater and marine invaders. *PLoS One* 10, 1–17. <https://doi.org/10.1371/journal.pone.0125801>.
- Gallien, L., Douzet, R., Pratte, S., Zimmermann, N.E., Thuiller, W., 2012. Invasive species distribution models - how violating the equilibrium assumption can create new insights. *Glob. Ecol. Biogeogr.* 21, 1126–1136. <https://doi.org/10.1111/j.1466-8238.2012.00768.x>.
- Hattab, T., Albouy, C., Lasram, F.B.R., Somot, S., Le Loc'h, F., Leprieux, F., 2014. Towards a better understanding of potential impacts of climate change on marine species distribution: a multiscale modelling approach. *Glob. Ecol. Biogeogr.* 23, 1417–1429. <https://doi.org/10.1111/geb.12217>.
- 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. *Int. J. Climatol.* 25, 1965–1978. <https://doi.org/10.1002/joc.1276>.
- Hill, M.P., Gallardo, B., Terblanche, J.S., 2017. A global assessment of climatic niche shifts and human influence in insect invasions. *Glob. Ecol. Biogeogr.* <https://doi.org/10.1111/geb.12578>.
- Keeling, M.J., Franklin, D.N., Datta, S., Brown, M.A., Budge, G.E., 2017. Predicting the spread of the Asian hornet (*Vespa velutina*) following its incursion into Great Britain. *Sci. Rep.* 7, 6240. <https://doi.org/10.1038/s41598-017-06212-0>.
- Kelly, R., Leach, K., Cameron, A., Maggs, C. a., Reid, N., 2014. Combining global climate and regional landscape models to improve prediction of invasion risk. *Divers. Distrib.* 20, 884–894. <https://doi.org/10.1111/ddi.12194>.
- Lobo, J.M., Jiménez-valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* 17, 145–151. <https://doi.org/10.1111/j.1466-8238.2007.00358.x>.
- Luoto, M., Virkkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models depends on spatial resolution. *Glob. Ecol. Biogeogr.* 16, 34–42. <https://doi.org/10.1111/j.1466-8238.2006.00262.x>.
- Medley, K. a., 2010. Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Glob. Ecol. Biogeogr.* 19, 122–133. <https://doi.org/10.1111/j.1466-8238.2009.00497.x>.
- Merow, C., Smith, M.J., Edwards, T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, W., Wuest, R.O., Zimmermann, N.E., Elith, J., 2014. What do we gain from simplicity versus complexity in species distribution models? *Ecography (Cop.)* 37, 1267–1281. <https://doi.org/10.1111/ecog.00845>.
- Milbau, A., Stout, J.C., Graae, B.J., Nijs, I., 2009. A hierarchical framework for integrating invasibility experiments incorporating different factors and spatial scales. *Biol. Invasions* 11, 941–950. <https://doi.org/10.1007/s10530-008-9306-2>.
- Monceau, K., Bonnard, O., Thiéry, D., 2014. *Vespa velutina*: a new invasive predator of honeybees in Europe. *J. Pest Sci.* (2004) 87, 1–16. <https://doi.org/10.1007/s10340-013-0537-3>.
- Monceau, K., Thiéry, D., 2017. *Vespa velutina* nest distribution at a local scale: an 8-year survey of the invasive honeybee predator. *Insect Sci.* 24, 663–674. <https://doi.org/10.1111/1744-7917.12331>.
- Pearson, R.G., Dawson, T.P., Liu, C., 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography (Cop.)* 27, 285–298. <https://doi.org/10.1111/j.0906-7590.2004.03740.x>.
- Pearson, R.G., Dawson, T.P., Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of Species: are bioclimate envelope models Useful. *Glob. Ecol. Biogeogr.* 12, 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x/pdf>.

- R Development Core Team, 2013. R: a Language and Environment for Statistical Computing, vol. 1. R Found. Stat. Comput., Vienna, Austria <https://doi.org/10.1017/CBO9781107415324.004>.
- Richter, M.R., 2000. Social wasp (hymenoptera: Vespidae) foraging behavior. *Annu. Rev. Entomol.* 45, 121–150.
- Robinet, C., Suppo, C., Darrouzet, E., Robinet, C., 2016. Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures. *J. Appl. Ecol.* 1–32. <https://doi.org/10.1111/1365-2664.12724>.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60. <https://doi.org/10.1038/nature01309.1>.
- Rounsevell, M.D.A., Reginster, I., Araújo, M.B., Carter, T.R., Dendoncker, N., Ewert, F., House, J.I., Kankaanpää, S., Leemans, R., Metzger, M.J., Schmit, C., Smith, P., Tuck, G., 2006. A coherent set of future land use change scenarios for Europe. *Agric. Ecosyst. Environ.* 114, 57–68. <https://doi.org/10.1016/j.agee.2005.11.027>.
- Roura-Pascual, N., Hui, C., Ikeda, T., Leday, G., Richardson, D.M., Carpintero, S., Espadaler, X., Gomez, C., Guenard, B., Hartley, S., Krushelnycky, P., Lester, P.J., McGeoch, M.A., Menke, S.B., Pedersen, J.S., Pitt, J.P.W., Reyes, J., Sanders, N.J., Suarez, A.V., Touyama, Y., Ward, D., Ward, P.S., Worner, S.P., 2011. Relative roles of climatic suitability and anthropogenic influence in determining the pattern of spread in a global invader. *Proc. Natl. Acad. Sci.* 108, 220–225. <https://doi.org/10.1073/pnas.1011723108>.
- Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., Martin, J.-L., 2016. Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. *Glob. Ecol. Biogeogr.* 1–10. <https://doi.org/10.1111/geb.12555>.
- Sohl, T.L., 2014. The relative impacts of climate and land-use change on conterminous United States bird species from 2001 to 2075. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0112251>.
- Staniczenko, P.P.A., Sivasubramaniam, P., Suttle, K.B., Pearson, R.G., 2017. Linking macroecology and community ecology: refining predictions of species distributions using biotic interaction networks. *Ecol. Lett.* 693–707. <https://doi.org/10.1111/ele.12770>.
- Syphard, A.D., Franklin, J., 2009. Differences in spatial predictions among species distribution modeling methods vary with species traits and environmental predictors. *Ecography (Cop.)* 32, 907–918. <https://doi.org/10.1111/j.1600-0587.2009.05883.x>.
- The European Environment Agency (EEA), 2010. Corine Land Cover 2006 raster data [WWW Document]. <http://www.Eea.Europa.Eu/Data-and-Maps/Data/Corine-Land-Cover-2006-Raster>.
- Thuiller, A.W., Georges, D., Engler, R., Georges, M.D., Thuiller, C.W., 2014. biomod2: Ensemble Platform for Species Distribution Modeling.
- Thuiller, W., Araújo, M.B., Lavorel, S., 2004. Do we need land-cover data to model species distributions in Europe? *J. Biogeogr.* 31, 353–361. <https://doi.org/10.1046/j.0305-0270.2003.00991.x>.
- Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H., Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. *Glob. Chang. Biol.* 22, 2505–2515. <https://doi.org/10.1111/gcb.13272>.
- Tulloch, A.I.T., Sutcliffe, P., Naujokaitis-Lewis, I., Tingley, R., Brotons, L., Ferraz, K.M.P.M.B., Possingham, H., Guisan, A., Rhodes, J.R., 2016. Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. *Biol. Conserv.* 199, 157–171. <https://doi.org/10.1016/j.biocon.2016.04.023>.
- 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. *Biol. Conserv.* 144, 2142–2150. <https://doi.org/10.1016/j.biocon.2011.04.009>.
- Virkkala, R., Luoto, M., Heikkinen, R.K., Leikola, N., 2005. Distribution patterns of boreal marshland birds: modelling the relationships to land cover and climate. *J. Biogeogr.* 32, 1957–1970. <https://doi.org/10.1111/j.1365-2699.2005.01326.x>.
- Zhu, G., Li, H., Zhao, L., 2017. Incorporating anthropogenic variables into ecological niche modeling to predict areas of invasion of *Popillia japonica*. *J. Pest Sci.* (2004) 90, 151–160. <https://doi.org/10.1007/s10340-016-0780-5>.