Climate change increases the risk of invasion by the Yellow-legged hornet

Morgane Barbet-Massin [a,b], Quentin Rome [c], Franck Muller [c], Adrien Perrard [c], Claire Villemant [c], Frédéric Jiguet [a,*]

[a] Muséum National d'Histoire Naturelle, UMR 7204 MNHN-CNRS-UPMC, CP51, 55 Rue Buffon, 75005 Paris, France
[b] Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA
[c] Muséum National d'Histoire Naturelle, UMR 7205 MNHN-CNRS, CP50, 45 Rue Buffon, 75005 Paris, France

ABSTRACT

The Yellow-legged hornet *Vespa velutina nigrithorax* has established viable populations in France since an unintentional introduction before 2004, and the potential invasion risk of this bee-hawking hornet was estimated by modelling the species climatic suitability worldwide. By further projecting such models under 2100 future climate scenarios, we here estimated the predicted trends in invasion risk related to climate change. We performed eight different modelling techniques within an ensemble forecast framework using presence data from the native and the invaded ranges. We predicted an increase in the climatic suitability for the species in the Northern hemisphere, especially close to the already invaded range in Europe, in Spain and in Central and Eastern Europe – from Switzerland to Hungary up to Southern Sweden. Climate change should also increase the invasion risk in the United States except along the Eastern coast. Scenarios for future climates include predictions from five global circulation models and three special reports on emission scenarios. Standard deviations of the results obtained from the 13 different climate scenarios confirmed the low uncertainty of models to predict an increase in invasion risk across Central and Eastern Europe, close to the already invaded European range. These regions hold among the highest densities of bee-hives in Europe, and could suffer from the potential predation of the putative invading hornet on pollinators.

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1. Introduction

Predicting the current and potential future distributions of introduced invasive species is of central importance to plan adaptation and management strategies. Within the framework of species distribution modelling (Guisan and Thuiller, 2005), correlational approaches based on ecological niche modelling are widely used even for invasive taxa (Chen et al., 2007; Peterson, 2003; Ficetola et al., 2007; Peterson et al., 2003; Peterson and Vieglais, 2001; Roura-Pascual et al., 2009; Thuiller et al., 2005a) and can be useful for invasion risk assessment (Jiménez-Valverde et al., 2011). Climatic suitability models are useful to forecast future distributions of various taxa under climate change scenarios, e.g. plants (Thuiller et al., 2005b) and animals (reptiles: Araújo et al., 2006; mammals: Levinsky et al., 2007; and birds: Jetz et al., 2007; Barbet-Massin et al., 2011). In the case of introduced and invasive species, spatial predictive modelling of current invasion risk can be coupled with projections under future climate scenarios, in order to forecast

potential trends in invasible probability ensuing from predicted climatic changes (Bourdôt et al., 2012; Bradley et al., 2010; Régnière et al., 2009).

The Yellow-legged hornet *V. velutina* is naturally distributed in Asia, from Afghanistan to Eastern China, South to Indochina and Indonesia (Carpenter and Kojima, 1997). Within its native range, it actively predates honeybees (Tan et al., 2007) and attacks colonies (Abrol, 1994). Introduced in Korea, the variant *nigrithorax* became established near Busan in the 2000s (Kim et al., 2006; Jung et al., 2008), while the same variant was discovered in France in 2004. Since its unintentional introduction in South–Western France, the species has widely spread across the country (Villemant et al., 2011a) so that the invaded range covered about 190,000 km² in 2010, with a recent expansion to Northern Spain (Castro and Pagola-Carte, 2010). The potential invasion risk of the species was recently assessed using climatic suitability models under current climatic conditions (Villemant et al., 2011a), while the same study reported the potential ecological and economical impacts of the invasive hornet across Europe. Indeed, the predation of pollinators could impact pollination of wild and cultivated plants, so pollination services, while the predation of bee hives could impact honey production and pollination services too (Villemant et al., 2011a). As climatic models were efficient in

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* Corresponding author. Tel.: +33 1 40 79 30 80; fax: +33 1 40 79 38 35.
  E-mail addresses: barbet@mnhn.fr (M. Barbet-Massin), rome@mnhn.fr (Q. Rome), fmuller@mnhn.fr (F. Muller), villeman@mnhn.fr (C. Villemant), fjiguet@mnhn.fr (F. Jiguet).

modelling the species distribution in Asia and its potential invasion range in Europe, we propose here to project the climatic models under future climate scenarios, in order to assess the potential trends in invasion risk from climate change. We used eight different modelling techniques within an ensemble forecast framework (Thuiller et al., 2009) to model the current species distribution across all continents, using presence data from the native and the invaded ranges. We further projected the modelled distribution worldwide under future climatic conditions using an ensemble forecast approach to obtain predictions from scenarios for 2100 of the IPCC fourth assessment (IPCC, 2007). Scenarios for future climates include predictions from five global circulation models (GCMs) and three special reports on emission scenarios (SRES), totalling 13 different scenarios. The results are further discussed in terms of the predicted changes in climatic suitability in the native range, in Europe especially close to the currently spreading invaded range and in other areas where the species could succeed in establishing populations if it was to be introduced.

2. Material and methods

2.1. Presence data from the native and invaded ranges

We used collected presence data of *V. v. nigrithorax* in its native Asian range as available in Villemant et al. (2011a), totalling 69 different georeferenced record localities. We further considered localities where the species was established in the invaded ranges, in Korea and in France. The records from France were stored in a database aggregating all validated national records, including nests but also presences of workers in regions where nests have not yet been found. We had 4165 available georeferenced French records (Villemant et al., 2011a). As the species range is still expanding in France, we have clearly more data from the central part of the current distribution, whereas some yet un-invaded areas could be climatically suitable. If considering all detected presences in the models, we would overweight the importance of the central range, and minimise the contribution of the most recent colonisation events. Therefore, we decided to randomly draw 2 localities within each of the 39 French *départements* where the species has been recorded, except for the nine *départements* where only one nest was reported, to build up a dataset of 69 occurrences. This selection was repeated ten times on the original complete dataset to obtain replicates of presence data. Each of the final 10 datasets used for modelling the global invasion risk included the 69 records from the native range, the Korean introduced population and one of the set of 69 French locations. Therefore, we had no sampling bias towards the native or the invaded range.

2.2. Climatic variables

We used the same eight climatic variables as in Villemant et al. (2011a) for the niche modelling, as they proved efficient to model the species distribution. We extracted these variables from the BIOCLIM database as 5 arc-min grids (http://www.worldclim.org/ ; Hijmans et al., 2005). We considered: (1) annual mean temperature, (2) mean temperature of the warmest month, (3) mean temperature of the coldest month, (4) temperature seasonality, (5) annual precipitation, (6) precipitation of the wettest month, (7) precipitation of the driest month, and (8) precipitation seasonality. The seasonality is the coefficient of variation of the monthly means. Climatic variables are probably the main contributors to species niche delimitation at large scale (Luoto et al., 2007) and these variables have previously been used for insect niche modelling (Medley, 2010). We used a spatial resolution closely matching

the scale of the French districts where presence records were available.

Future climate projections (for 2100) were derived from five general circulation models (GCMs; BCM2, ECHAM5, HADCM3, MIROC3_2-HI and MK3) and three recent special reports on emission scenarios (SRES) (A1B, B1 and A2 when available), using monthly mean predictions taken from IPCC (2007), resulting in 13 future climate projections for this species (A2 was not available for two GCMs). Monthly mean predictions were only available at coarse resolutions (IPCC, 2007; http://www.ipcc-data.org/), so we down-scaled the anomalies (differences between predicted future values and actual values) to the 5 arc-min grid using a bilinear interpolation.

2.3. Distribution modelling under current climatic conditions

Climatic suitability of *V. v. nigrithorax* was modelled by running eight different niche-based modelling techniques using the BIOMOD platform under R (Thuiller et al., 2009). These models are: (1) generalised linear model (GLM), (2) generalised additive model (GAM), (3) classification tree analysis (CTA), (4) artificial neural networks (ANN), (5) multivariate adaptive regression splines (MARS), (6) mixture discriminant analysis (MDA), (7) generalised boosting model (GBM), and (8) Random Forest (RF) (see details in the BIOMOD manual available within the dedicated R package or at http://www.will.chez-alice.fr/pdf/BiomodTutorial.pdf). In order to evaluate the predictive performance of a species distribution model, we used a random subset of 70% of the data to calibrate every model, and the remaining 30% for the evaluation. Models were evaluated using a relative operating characteristic (ROC) curve and the Area Under the Curve (AUC) (Fielding and Bell, 1997). We replicated the data splitting five times and calculated the average AUC of the cross-validations, which gives a more robust estimate of the predictive performance of each model. The potential problems raised by Lobo et al. (2007) on the use of AUC as a measure of model performance were considered as minor here because AUC was used to rank models obtained from the same dataset and within the same geographical area, according to their predictive performance. The final calibration of every model for making predictions uses 100% of the data available. All models used in this study need information about presences and absences to determine the suitable conditions for a given species, so virtual absences (pseudo-absences) were considered. Because only a few data were available in the Asian area, pseudo-absences were chosen outside the suitable range predicted by the surface range envelope (SRE) model, in order to decrease the potential number of false absences among the pseudo-absences (Maitre et al., 2008; Barbet-Massin et al., 2012). The SRE model is a niche-based modelling technique performed with BIOMOD (Thuiller et al., 2009) that does not require absences. The SRE model identifies minimum and maximum values for each environmental variable from the localities where the species is present, and the predicted distribution then includes any site with all variables falling between these minimum and maximum limits. Pseudo-absences were chosen in the South–East part of Asia and in Europe, as illustrated in Villemant et al. (2011a). We used 5000 pseudo-absences, with the total weight of presences (the sum of all presence weights) being equal to the total weight of pseudo-absences (the sum of all pseudo-absence weights) (Barbet-Massin et al., 2012). All models were further projected onto the whole world map.

2.4. Ensemble forecasts and modelling under future climatic conditions

To obtain a consensus distribution under current climatic conditions, we used an ensemble forecast technique which aims to take into account the variability among species distribution mod-

els, climate models and climate scenarios (Araújo and New, 2007). In order to get the central tendency of the models for each presence dataset, we calculated the weighted mean of the probability distributions (Marmion et al., 2008). Each model is ranked according to the evaluation score (AUC), and a decay of 1.6 gives the relative weights (Thuiller et al., 2009). Distributions were computed for 10 different presence data combinations. Therefore, after calculating the ensemble forecast for each of the 10 runs, we calculated the mean probability distribution.

The weighted AUC and TSS (True Skill Statistic) for the current ensemble forecast distributions were calculated as accuracy measures of modelling performance. The TSS is the threshold maximising the sum of the sensitivity and the specificity (Allouche et al., 2006). Sensitivity and specificity are statistical measures of the performance of a binary classification test. Sensitivity measures the proportion of actual presences which are correctly predicted as such. Specificity measures the proportion of negatives which are correctly predicted. Models with AUC higher than 0.9 and TSS higher than 0.8 are usually considered very accurate (Allouche et al., 2006; Fielding and Bell, 1997).

All models obtained with the 10 different presence data combinations were further projected under future climatic conditions using the 2100 climatic layers and the ensemble forecast parameters were again applied to the future predicted distributions for each combination of GCM and SRES. Because different modelling tools can provide different results, we aimed at obtaining a consensus as the central tendency of all distributions (models), accounting for variations among modelling techniques. The consensus future distribution was obtained by calculating the mean distribu-

tions across the climate change scenarios. We also calculated the standard deviations between scenarios, in order to distinguish between areas where climatic scenarios give similar predictions and areas where they give different predictions.

3. Results

We obtained a high value of weighted mean AUC (0.977) and of TSS (0.909) of the models developed with current climatic datasets. The corresponding potential world distribution obtained from the ensemble technique is reported in Fig. 1a. Most suitable areas in Europe expands to the neighbouring countries of France, mainly along the Atlantic coast, the Mediterranean coast and the Southern coasts of Black and Caspian Seas, while the South–Eastern part of the Mediterranean basin appears less suitable. Most suitable areas outside Europe include the Eastern and Western coasts of North America, Southern Argentina, South coast of South Africa and of Australia, and New Zealand. With this model, the mean ± s.d. climatic suitability of presence points from the native range was 0.642 ± 0.183 (range 0.046–0.862). For the presence points in the invaded French range, the mean ± s.d. was 0.874 ± 0.110 (range 0.093–0.963).

The projection of these models under future climatic scenarios is illustrated in Fig. 1b. We further mapped the difference between the current and the future climatic suitability in Fig. 2, with an insertion focusing on Europe, close to where the species was introduced and established recently. Climatic suitability is predicted to increase globally across Eurasia, especially so in Eastern Europe, and also in central North America and along the Western coast of
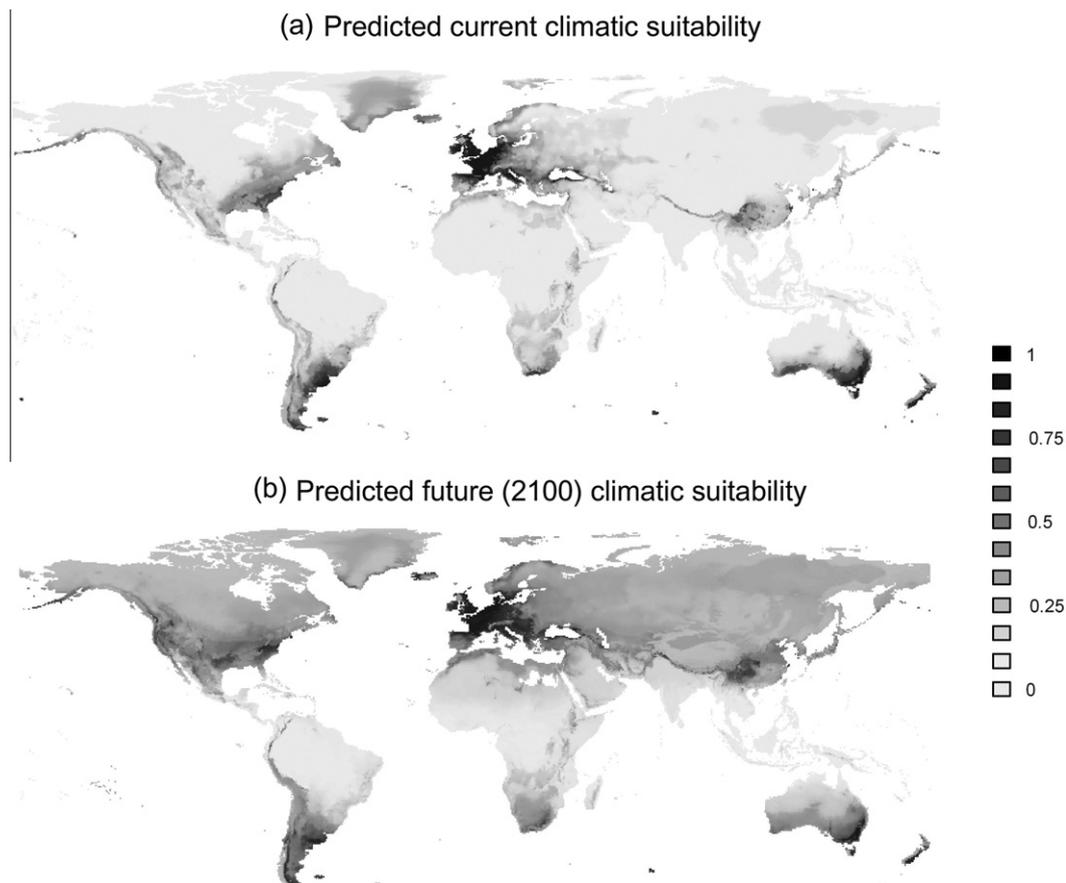
Fig. 1. Predicted consensus distributions of *V. v. nigrithorax* under (a) current climatic conditions and (b) 2100 future climatic predictions (obtained using 13 different climatic dataset combining 5 GCMs and 3 SRES). The suitability probability is increasing from pale to dark grey.

Predicted future increases in climatic suitability
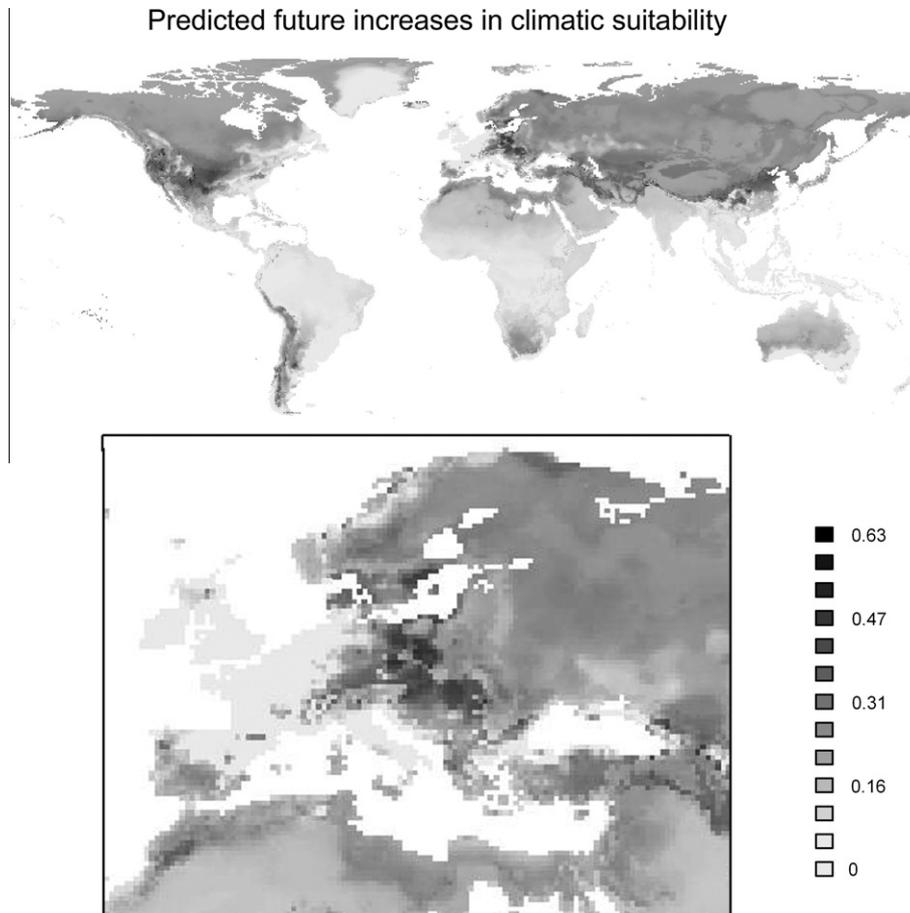
Fig. 2. Increases in climatic suitability for *V. v. nigrithorax* as obtained by comparing data used to draw the maps presented in Fig. 1. The window provides finer details of the trends over Europe so close to the French established invasive population. The suitability probability is increasing from pale to dark grey.

South America in Chile. The native range could expend northwards, the invaded Korean range should not be under pressure from climate change, and the invaded European range could expand northward to Southern Scandinavia and eastwards to, e.g. Hungary, Poland, and Belarus. While climatic suitability is not predicted to increase along the Eastern coasts of North America, it is predicted to increase on the West coast and inland, but less strongly at arctic latitudes.

In Europe, areas where predictions are more variable between different climate change scenarios are not those where we predicted an increase in climatic suitability, except in the Balkans. In France, the largest variations between climatic scenarios are obtained in already invaded areas where the average climatic suitability is not predicted to increase. In Asia, projections were more variable at the Northern edge of the current distribution range, from Inner Mongolia to Beijing, potentially challenging the predicted possible northward shift of the species native range.

4. Discussion

4.1. Climatic suitability models for the Yellow-legged hornet

Climate has been reported to influence the fate of social wasps (Dejean et al., 2011), hence the interest of modelling the distribution of the Yellow-legged hornet using bioclimatic variables, as proposed here. Among the variants of the Yellow-legged hornet in Asia, *V. v. nigrithorax* is widely distributed under temperate to subtropical climates, and is the only one that has established pop-

ulations outside its native range, in Korea and in France. The prediction map based on Asian and French records indicates a high probability for *V. v. nigrithorax* to succeed in establishing populations in Western Europe, where its invasive presence is already attested in France, Northern Spain (Castro and Pagola-Carte, 2010), with further recent observations in Portugal, Belgium and Italy. Ecological niche modelling can identify suitable areas susceptible to future invasions, providing an important preventive management tool (Peterson, 2003). In South–Western France, the hornet first colonised the Aquitaine region, which is indeed one of the most suitable areas for the species in Western Europe. In our study, predictions of invisible areas were obtained by using occurrence data from both the native and the invaded range (Villemant et al., 2011a), in order to better capture dimensions of the species fundamental niche. In a non native range, invasiveness can be promoted by favourable changes in the outputs of interspecific interactions such as competition, predation, parasitism or mutualism (Andonian and Hierro, 2011; Mitchell and Power, 2003; Mitchell et al., 2006; Torchin et al., 2003), so that a species realised niche can extend or shift compared to the native niche (Broennimann and Guisan, 2008). Here, by using presence data from both native and invaded ranges, we actually increased our knowledge about the species fundamental niche, since the absence of enemies in one range allows the species to occupy suitable abiotic conditions from which it was excluded in the native range. Distribution models have also some limitations, even if they are produced with appropriate environmental variables and presence/absence datasets. First, projecting distribution models under future climatic conditions supposes a strong niche conservatism. Also, a range

standard deviations of predictions obtained
with different climate change scenarios
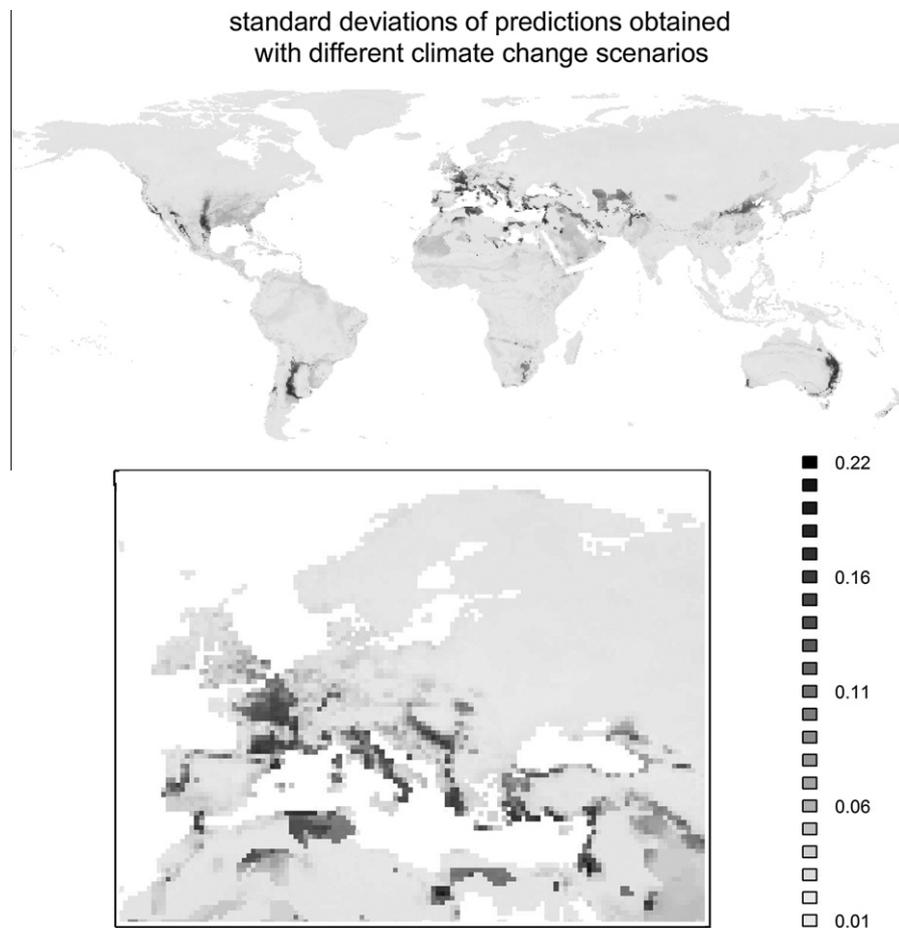
Fig. 3. Standard deviation of the climatic suitability predictions between the 13 future climate datasets used for the ensemble forecast. The window provides finer details of the uncertainty over Europe so close to the French established invasive population. The standard deviation is increasing from pale to dark grey.

expansion necessitates individuals able to disperse and colonise new areas. In this context, a species' dispersal ability is central (see an example for birds in Barbet-Massin et al. (2011)), while interactions with other species (prey, predators, competitors, or any other trophic association) are also important, so that population/community models can greatly improve distribution models if they can be combined together (Bellard et al., 2012; Swab et al., 2012).

4.2. Predicted trends in invasion risk under climate change scenarios

Areas with higher estimated invasion risk under current climatic conditions are similarly predicted as largely suitable under climate change scenarios, though often with lower suitability values in the Southern hemisphere. In Southern Australia, South Africa, Uruguay, and Northern Argentina, climatic suitability is maintained high but predicted to decrease, though it would still reach values within the range of current presence of the species in its native range. In the Northern hemisphere, climatic suitability for the Yellow-legged hornet is predicted to increase on average following climate change, with a global uniform increase all over Eurasia and Canada, without reaching suitabilities similar to the current presence ranges. The largest increases in suitability from climate change are expected to occur in Western and Central United States, from California to the Great Plains, North of the Asian native range, with a potential poleward shift of the species range (Parmesan et al., 1999), and in Europe. The situation in Europe is certainly one of the largest concern since the species already estab-

lished introduced populations in France (Villemant et al., 2011a) and Spain (Castro and Pagola-Carte, 2010). The largest increases in climatic suitability are predicted in Spain, Switzerland, Southern Germany, Denmark, Southern Sweden, Poland, North of the Adriatic Sea up to Hungary and Romania.

In addition to the suitable climatic conditions and the abundance of one of its main food source (honeybees), the low level of interspecific competition that *V. v. nigrithorax* faces in Europe may thus facilitate its spread in Europe while the ongoing climate changes should facilitate its spread to Eastern Europe. Vespidae communities can be strongly structured by interspecific competition (Beggs et al., 2011), so the Yellow-legged hornet might benefit from the release of such intraspecific competition in the introduced European range to invade successfully suitable areas.

Besides providing the central tendency of different modelling techniques, the use of ensemble forecast allowed us to estimate the variability between predictions obtained from the different climate scenarios, which explicitly points out where limitations of the predictions can be made (Fig. 3). This is more obvious to moderate the potential for the native range to shift northwards, but most European suitable areas were predicted with a great confidence, as the 13 climatic scenarios did not vary much in predicting an increase in climatic suitability across Eastern and Central Europe.

4.3. Potential threats associated with predicted invasion risk

The Yellow-legged hornet feeds on bees with potential impacts on bee-keeping activities and therefore domestic pollination. Be-

yond domestic bees, other wasps (yellow jackets) and pollinators (especially syrphids) represent a noticeable part of the hornet's prey spectrum (Perrard et al., 2009; Villemant et al., 2011b). According to the FAO (FAO, 2010), bee-hive densities are among the highest for European farmlands in Eastern countries (see Fig. S4 in Villemant et al. (2011a)). Countries with a high average hive density in farmland habitats are Switzerland, the Czech Republic, Croatia, Bulgaria, Greece (>100 hives per 10 km^2), with also Portugal, Spain, Austria, Slovenia, Hungary, Slovakia and Poland (>75 hives per 10 km^2). According to our predictions, all these countries should face large increase in climatic suitability for the invasive hornet from climate change. Indeed, climate change will increase the invasion risk in these countries, hence bee keeping activities and pollination could be at threat if the hornet was to colonise there (see Clapperton et al., 1989 for an example with wasps). This could be highly detrimental in a global context of ongoing declines of managed honeybees and beekeeper numbers in Europe (Potts et al., 2010) and an increasing risk of disruption in plant-pollinator mutualist interaction through global warming (Memmott et al., 2007).

5. Conclusions

The Yellow-legged hornet is currently spreading from its introduction across France (Villemant et al., 2011a) and now the North of the Iberian Peninsula (Castro and Pagola-Carte, 2010) and other countries adjacent to France and Spain. According to climatic models, this spread will face no climatic barrier to reach Portugal, Italy, the United Kingdom and Ireland, North–Western Germany and Denmark. Predictions under 2100 climate scenarios further predict an increase in climatic suitability so invasion risk in the Iberian Peninsula and across Central and Eastern Europe, where beekeeping activities are important and could suffer from the potential predation of the putative invader on pollinators. In France, nests have been found even 200 or 300 km from the known colonisation front (Rome et al., 2009), so the species is able to disperse long distances. Therefore, reaching the climatically suitable areas in Eastern Europe or Sweden within the next 90 years should not be constrained by the species dispersal ability. A putative invasion of the climatically suitable sites along the Eastern American coasts could lead to the invasion of the whole United States of America, as a consequence of increased suitability ensuing from future climate change.

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