



Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Predicting the invasion risk by the alien bee-hawking Yellow-legged hornet *Vespa velutina nigrithorax* across Europe and other continents with niche models

Claire Villemant^{a,*}, Morgane Barbet-Massin^b, Adrien Perrard^a, Franck Muller^a, Olivier Gargominy^c, Frédéric Jiguet^b, Quentin Rome^a

^a Muséum National d'Histoire Naturelle, UMR7205, CP 50, 45 rue Buffon, 75005 Paris, France

^b Muséum National d'Histoire Naturelle, UMR7204 MNHN-CNRS-UPMC, CP 51, 55 rue Buffon, 75005 Paris, France

^c Muséum National d'Histoire Naturelle, Service du patrimoine naturel, 57 rue Cuvier, 75005 Paris, France

ARTICLE INFO

Article history:

Received 17 September 2010

Received in revised form 1 April 2011

Accepted 4 April 2011

Available online 11 June 2011

Keywords:

Beekeeping

Invasive species

Native range

Niche modelling

Vespidae

Social Hymenoptera

ABSTRACT

Vespa velutina nigrithorax, an Asian bee-hawking hornet, has been unintentionally introduced in south-western France before 2004 and is currently widely spreading across the country. Its arrival in northern Spain was reported in 2010. The potential invasion risk of the species is assessed using climatic suitability models. We used eight different modelling techniques within an ensemble forecast framework to show that the invasion success in south-western France could have been predicted using data from the native Asian range of the species, while we further used data from both the native and invaded ranges (including a recently established population in Korea) to better predict its potential invasion range across all continents. Results are discussed in terms of the interest of ecological niche modelling for invasion biology, realised niche of the invasive wasp, potential threats to native entomofauna and economic impacts of this new predator. A particular attention is paid to beekeeping activities that are nowadays already threatened by a wide panel of adversary factors.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Biological invasions by alien species are widely recognised as a significant component of human-caused global environment change and the second most important threat to biodiversity (DAISIE, 2009). By definition, alien invasive species are taxa introduced outside their native range either intentionally or unintentionally, showing high growth rate and quick range expansion, with noticeable consequences on human activities and environmental conservation (IUCN, 2000; Wittenberg and Cock, 2001; Kenis et al., 2008; Roques et al., 2009). Social insects, such as ants, wasps and bees, are among the most successful invaders of new habitats worldwide, their reproductive and dispersal strategies making them fierce antagonists of native biota (Hingston and McQuillan, 1999; Chapman and Bourke, 2001; Holway et al., 2002; Paine and Dale Roberts, 2005; Inoue et al., 2008). They sometimes become major urban and agricultural pests or permanent additions to invaded natural communities (Beggs, 2001; Matthews et al., 2001; Holway et al., 2002). Several social Vespidae, mainly wasps of the genera

Vespula (yellow jackets) and *Polistes* (paper wasps), have been introduced during the 19th century from European continental area into various European islands (Roques et al., 2009; Rasplus et al., 2010) or remote countries of the world (Carpenter and Kojima, 1997; Beggs et al., in press).

Vespa species have also been introduced beyond their native range, mostly unsuccessfully. *Vespa velutina* was recorded in Yemen, *Vespa simillima* in British Columbia, Canada, and *Vespa orientalis* in Madagascar (Carpenter and Kojima, 1997). Recently, *V. orientalis* was also reported from Mexico (Dvorak and Landolt, 2006), but none of these introductions led to a successful establishment confirmed in the peer-reviewed literature. A successful acclimatisation of a hornet wasp outside its native range relates to *Vespa crabro* intentionally released in the USA to control forest caterpillar outbreaks (Shaw and Weidhaas, 1956). The European hornet was first recorded in 1840 in the state of New York and is now naturalised across eastern United States and in Ontario, Canada (Carpenter and Kojima, 1997). In France, the recent introduction and establishment of *V. velutina*, the Yellow-legged hornet, represents the first successful invasion of an exotic Vespidae into Europe (Haxaire et al., 2006; Villemant et al., 2006; Rasplus et al., 2010).

V. velutina, which occurs in 12 colour variants in his native area, is naturally distributed from Afghanistan to eastern China, Indochina and Indonesia (Carpenter and Kojima, 1997), where it is

* Corresponding author. Tel.: +33 1 40 79 38 41; fax: +33 1 40 79 56 79.

E-mail addresses: villemant@mnhn.fr (C. Villemant), barbet@mnhn.fr (M. Barbet-Massin), perrard@mnhn.fr (A. Perrard), fmuller@mnhn.fr (F. Muller), gargominy@mnhn.fr (O. Gargominy), fjiguet@mnhn.fr (F. Jiguet), rome@mnhn.fr (Q. Rome).

known as an active predator of honey bees (Abrol, 1994; Tan et al., 2007). The first field record of the variant *Vespa velutina nigrithorax* was obtained in Lot-et-Garonne department in 2005, while locally collected data documented that it was present there as early as 2004 (Haxaire et al., 2006). Since then, this hornet has spread rapidly across south-west of France (Villemant et al., 2006; Rome et al., 2009). Furthermore, the bonsai producer who first saw hornets and nests near his property regularly imports potteries from China. These data suggest that hibernating founder queens could have been accidentally imported in Aquitaine before 2004 through horticultural trade (Villemant et al., 2006). The invaded area reached about 190,000 km² in 2010 (see Fig. S1 in ESM). The hornet was also very recently reported from Basque Country in Spain (Castro and Pagola-Carte, 2010).

Many hornet species hunt honey bees – among various other invertebrate preys – to provide their brood with protein sources. Only a few of them focus their attacks on hives (Van der Vecht, 1957; Matsuura and Yamane, 1990), though the Yellow-legged hornet does. Apart from the Giant hornet *Vespa mandarinia* which attacks hives in group, other species are bee-hawking hornets that predate bees individually (Matsuura and Yamane, 1990). *V. velutina* is considered as a fierce enemy of honey bees colonies in Kashmir (Shah and Shah, 1991; Abrol, 2006), Nepal (Ranabhat and Tamrakar, 2008) and China (Tan et al., 2007), as well as in Korea where the variant *nigrithorax* became established near Busan in the 2000s (Kim et al., 2006; Jung et al., 2008). In Asia, which is considered as the centre of hornet evolutionary diversification (Matsuura and Yamane, 1990), native honey bees like *Apis cerana* or *Apis dorsata* are able to defend their colonies against hornet attacks (Ono et al., 1995; Tan et al., 2007; Kastberger et al., 2008), while introduced European honey bees *A. mellifera* exhibit less efficient defence strategies (Abrol, 2006). In the same way, *A. mellifera* in France seems unable to withstand the attack of this new predator (Rortais et al., 2010; Arca et al., unpubl. data). Apart from reported damages to hives, little is known on the biology of *V. velutina* throughout its native Asian range (Matsuura, 1973; Martin, 1995; Nakamura and Sonthichai, 2004). In the invaded range, the impact of *V. v. nigrithorax* on the diversity and biomass of the invertebrate fauna is under study, while preliminary results reported a diversified diet varying among seasons and habitat types (Villemant et al., 2011). However, the size of the hornet colonies as well as the duration of their period of activity leads us to predict a significant impact on local entomofauna. Such impacts on domestic bees and native insect community could locally challenge beekeeping economics and affect pollination services. Thus, modelling the potential invasion extent of *V. v. nigrithorax* appears necessary to predict regions at risk, hence to help with planning future surveys of invaded range expansion and possible dedicated control measures, a prerequisite for replacing the reactive nature of current solutions with a proactive, predictive approach.

Climatic suitability models are widely used to predict the potential geographic distribution of animal and plant species (Guisan and Thuiller, 2005; Elith et al., 2006) with ensemble forecast predictions accounting for model variability by returning the central tendency of the distributions (Araújo and New, 2007). Besides their use in predicting potential impacts of global change on species extinction risk (Thomas et al., 2004; Thuiller et al., 2005a), in reserve planning (Wilson et al., 2005; Marini et al., 2009) or in identifying unknown distributional areas of rare species (Guisan et al., 2006), climatic suitability models can be used to predict invasion risk (Peterson and Vieglais, 2001; Peterson, 2003; Peterson et al., 2003; Thuiller et al., 2005b; Chen et al., 2007; Ficetola et al., 2007; Roura-Pascual et al., 2009). In this paper, we use climatic suitability models within an ensemble forecast framework to assess the potential invasion risk of *V. v. nigrithorax*. We first consider presence data from the native Asian range only, using eight

different modelling techniques, to test if the invasion risk could have been predicted in France. Second, we used data from both the native range and the invaded range to better predict the invulnerable range across all continents.

2. Material and methods

2.1. Presence data from the native range

We collected presence data of *V. v. nigrithorax* in its native Asian range by gathering information on museum specimens (held by the Muséum National d'Histoire Naturelle in Paris, France – MNHN, Natural History Museum in London, UK – NHM, and University of Zhejiang, Hangzhou, China), published records (Van der Vecht, 1957, 1959; Kim et al., 2006; Nguyen et al., 2006; Tan et al., 2007), and hornet sampling performed in China (Zhejiang, Jiangsu) in summer 2010 by some of the authors, thus totalling 69 different georeferenced record localities. Among them, six were not originally attributed to *nigrithorax* but were supposed to refer to this variant as having been obtained within the native expert-known distribution of that variant. These record localities are reported in Fig. 1.

2.2. Presence data from the invaded range

The Korean record locality of *V. v. nigrithorax* was considered as non-native, so within the subset of localities where the species has been introduced. The recent records obtained in Spain were not included because they have not yet been subject to the validation process applied to the French records. The records from France were stored on an online biodiversity database held by the MNHN (<http://inpn.mnhn.fr/>; INPN, 2010). This database aggregates all validated records within the country, including all nests found between 2004 and 2009 in south-western France. Nest record registration for 2010 is still in course but provisional data related to newly invaded French *départements* were added to the analysis (Fig. 2). Information on nests are collected by naturalists and beekeepers networks, state and regional services, firemen and municipal services, private wasp controllers and individual public warnings (Rome et al., 2009). During the current year, the local

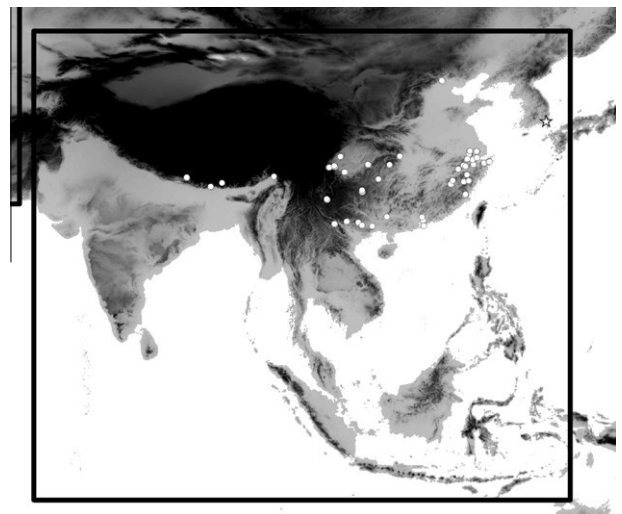


Fig. 1. Localities where *Vespa velutina nigrithorax* has been recorded in its native Asian range (dataset used in the models). The star represents the introduced Korean population. The geographical area included in the box was the one used to calibrate the niche models developed with the native data. Altitude is represented in grey shades.

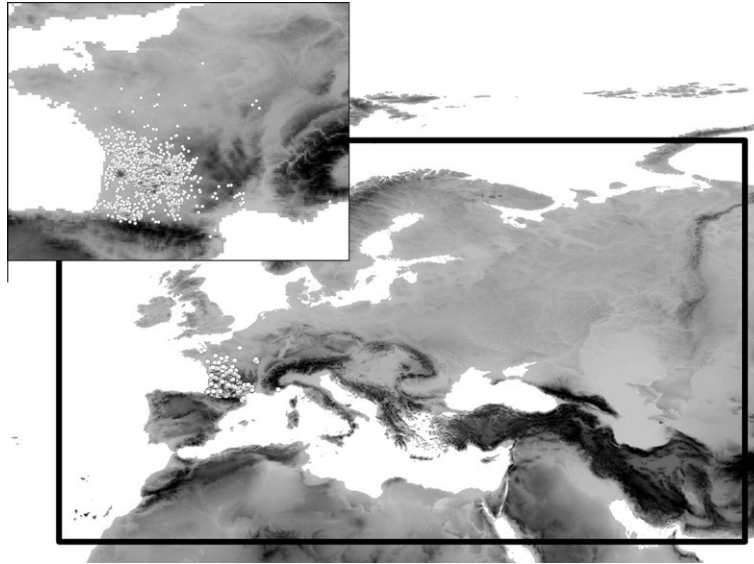


Fig. 2. Localities where *Vespa velutina nigrithorax* has been recorded in its invaded French range. The geographical area included in the box was the European area used to calibrate the niche models developed with the complete data in addition to the Asian area depicted in Fig. 1. The window provides better details of the location of French data used in the models. Altitude is represented in grey shades.

occurrences of *V. v. nigrithorax* workers are also recorded as presences in regions where nests have not yet been found. Before being registered in the database, any record is checked to validate the specific identification. The GPS locations of the nests are registered, but if unavailable, the position of a nest inside a given French district (*commune*) is attributed to the centroid of the district. We get 4165 available georeferenced records. Such data obtained by volunteers has already served to predict the potential distribution of an invasive bumblebee (Kadoya et al., 2009). Details on the recent colonisation and range expansion in France can be found in the Electronic Supplementary Material (ESM).

As the species range is still expanding, 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 minimize the contribution of the most recent colonisation events. Therefore, we decided to randomly draw two 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 to obtain replicates of presence data. Each of the final 10 datasets used for modelling the global invasion risk included all records from the native range, the Korean introduced population and one of the set of 69 French locations.

2.3. Climatic variables

We used eight climatic variables for the niche modelling, extracted from the BIOCLIM database as 5 arc min grids (<http://www.worldclim.org/>; Hijmans et al., 2005). We considered: the annual mean temperature (T_{avg}), the temperature seasonality (T_{sd}), the maximum temperature of the warmest month (T_{wm}), the minimum temperature of the coldest month (T_{cm}), the annual precipitation (P_{avg}), the precipitation of the wettest month (P_{wm}), the precipitation of the driest month (P_{dm}) and the precipitation seasonality (coefficient of variation; P_{sd}). Climatic variables are supposed to be 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 scale closely matching the scale of the French districts where presence records were available.

2.4. Representation of the data in climatic space

A first visual way to see if the use of the data from both the invaded and the native ranges leads to an extension of the species climatic niche is to geographically plot the data in the climatic space. In order to obtain a 2D visualisation, a principal component analysis (PCA) was run to represent the positions of occurrences in the climatic space for both datasets of occurrence. Because the number of data was biased towards the invaded range, we weighted all data from the native range equally to that from the invaded range.

2.5. Niche modelling and worldwide projections

Climatic suitability of *V. v. nigrithorax* was modelled by running eight different niche-based modelling techniques using the BIO-MOD platform (Thuiller et al., 2009). These models are: (1) generalised linear model (GLM), (2) generalised additive model (GAM), (3) classification tree analysis (CTA), a classification method running a 50-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance, (4) artificial neural networks (ANN), a machine learning method, with the mean of three runs used to provide predictions and projections, as each simulation gives slightly different results, (5) multivariate adaptive regression splines (MARS), (6) mixture discriminant analysis (MDA), a classification method that uses MARS function for the regression part of the model, (7) generalised boosting model (GBM), a machine learning method which combines a boosting algorithm and a regression tree algorithm to construct an 'ensemble' of trees, and (8) Random Forest (RF), a machine learning method which is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all trees in the forest. 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). The SRE model is a niche-based modelling technique performed with BIOMOD (Thuiller et al., 2009) that does not require absences. For the model computed with only the data from the native range, pseudo-absences were only chosen in the south-east part of Asia, whereas for the model computed with data from both the native range and the invaded range, pseudo-absences were chosen in both Europe and South-East Asia. In both cases, 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). Both models were then projected onto the whole world map.

2.6. Ensemble forecast

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). For the distribution computed with data from both the native and invaded ranges, the models 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 sum of the sensitivity and the specificity obtained with the threshold maximising the TSS value (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 (Fielding and Bell, 1997; Allouche et al., 2006). For each dataset used we also calculated the weighted standard deviation between models, in order to distinguish between areas where the models give similar predictions and areas where they give different predictions. For the full dataset, the final map was then obtained by calculating the mean probability between the 10 runs.

3. Results

Distribution of both Asian and European datasets of *V. v. nigrithorax* occurrence in the climatic space are represented by their projection on the first plan of the PCA (Fig. 3). Results emphasise that the area of invasion is globally discriminated from most of the Asian occurrences by its higher levels of precipitations during the driest month of the year.

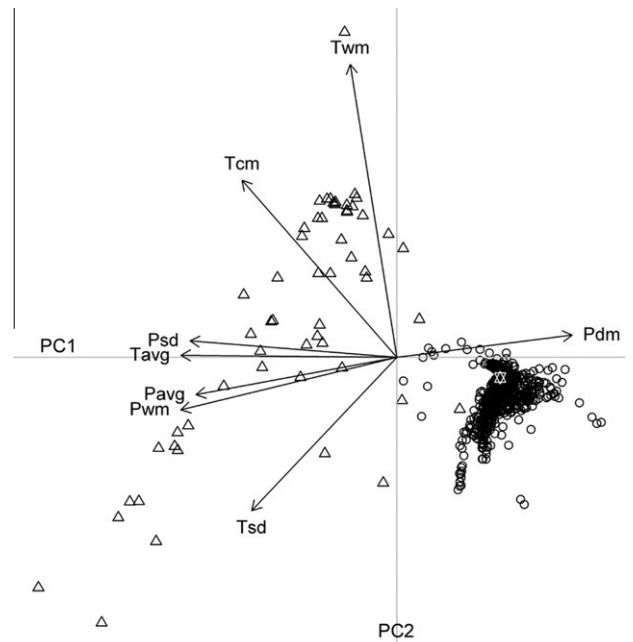


Fig. 3. Projection in the climatic space, represented by the first plan of the principal component analysis, of *Vespa velutina nigrithorax* occurrences – data from the native range (triangles) were weighted equally to that from the invaded range (circles). The white star represents the location of the first nests discovered in France. T_{avg} : annual mean temperature; T_{sd} : temperature seasonality; T_{wm} : maximum temperature of the warmest month; T_{cm} : minimum temperature of the coldest month; P_{avg} : annual precipitation; P_{wm} : precipitation of the wettest month; P_{dm} : precipitation of the driest month; P_{sd} : precipitation seasonality (coefficient of variation).

We obtained a high value of weighted mean AUC (0.904) and of TSS (0.778) for models computed with native data. The corresponding distribution obtained from the ensemble technique (Fig. 4) identifies an area of high climatic suitability of *V. v. nigrithorax* in China and southern Korea, but also in Japan, an archipelago where the species is absent (Matsuura and Yamane, 1990). It also reveals other worldwide areas with non-negligible suitability values. The climatic suitability of the location where the first hornet nest was discovered in France (Lot-et-Garonne) is estimated at 0.308, which is within the range of suitability values associated with presence points in the native range. Indeed, from this model, the mean \pm s.d. climatic suitability of presences from the native range was 0.641 ± 0.172 (range 0.046–0.879), while it was 0.392 ± 0.054 (range 0.241–0.525) for the presences from the invaded range. The model based on data from the native range only could have predicted the invasion success in south-western France, where the climatic suitability was among the highest in Western Europe.

In turn, all areas of medium climatic suitability were those exhibiting the highest variability between models, due to heterogeneous climatic suitability predicted by the different models (cf. Fig. S2 in ESM).

We obtained a high value of weighted mean AUC (0.977) and of TSS (0.909) for models computed with data from both native and invaded ranges. The corresponding distribution obtained from the ensemble technique reveals a roughly similar pattern (Fig. 5) to the one obtained with native only data (Fig. 4). The main difference is that many areas (outside Asia) which exhibited medium to high presence probability, now exhibit a higher presence probability. The second difference is that the most suitable area 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

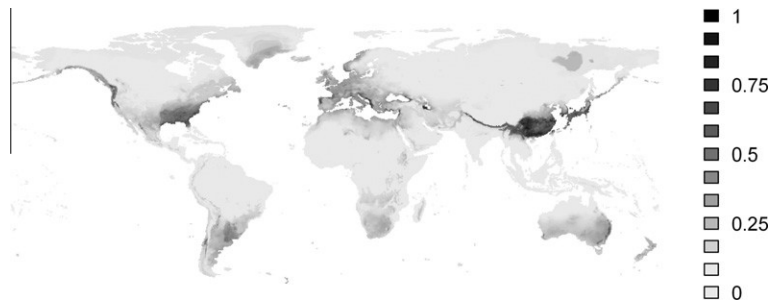


Fig. 4. Predicted climatic suitability distribution map for *Vespa velutina nigrithorax*, obtained with presence data from the native range of the species. The suitability probability is increasing from pale to dark grey.

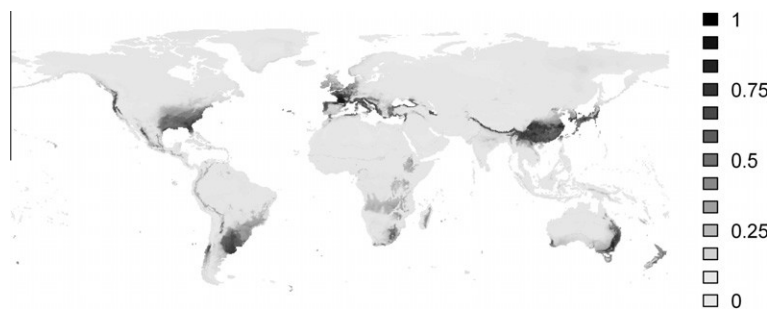


Fig. 5. Predicted climatic suitability distribution map for *Vespa velutina nigrithorax*, obtained with presence data from the native and invaded ranges. The suitability probability is increasing from pale to dark grey.

Mediterranean basin appears less suitable. With this model, the mean \pm s.d. climatic suitability of presences from the native range was 0.642 ± 0.183 (range 0.046–0.862), so very similar to that obtained when modelling with native data only. For the presences from the invaded range, the mean \pm s.d. was 0.874 ± 0.110 (range 0.093–0.963), clearly higher than that obtained when modelling with the native data only.

As for models obtained from the native data, the variability between models computed with data from both the native and invaded ranges is higher for the areas of medium or high climatic suitability, showing that predictions of the different models are not totally concordant (see Fig. S3 in ESM). This underlines the importance of using an ensemble forecast technique instead of only one modelling technique.

4. Discussion

4.1. Ecological niche models in invasion biology

Vespa velutina is part of the Chinese hornet diversity, which may comprise up to 11 species locally (Fig. 6). Among the three variants present in China, *V. v. nigrithorax* is the most widely distributed under temperate to subtropical climates. The prediction map based on Asian native records only (see Figs. 1 and 4) confirms that there was a noticeable probability for *V. v. nigrithorax* to succeed in establishing populations in south-east Korea and to a lesser extent in south-western France and northern Spain, where its invasive presence is currently attested. The Basque country, in south-western France, was indeed one of the most suitable areas for the species in Western Europe, but the suitability there did not reach the average value associated with a presence in the native range. Ecological niche modelling can identify suitable areas susceptible to future invasions, providing an important preventative management tool (Peterson, 2003). The classical approach to predict the geographical extent of potential or putative invasions

consists of training models in the native range and projecting them in distinct, potentially invulnerable areas.

However, this classical approach is hampered by potential changes in the realised climatic niche, allowing invasive species to spread into areas that are climatically distinct from those occupied in the native range (Medley, 2010). Indeed, current *V. v. nigrithorax* occurrences in Europe are characterised by a higher level of precipitation during the driest month of the year compared to the native area (Fig. 3), suggesting that range expansion would be easier along coastal margins of the potentially invaded countries (Fig. 5). Therefore, in our study, predictions of invulnerable areas was improved by using data from both the native and the invaded range (Broennimann and Guisan, 2008), in order to better capture dimensions of the realised niche. Besides providing the central tendency of different modelling techniques, the use of ensemble forecast allowed us to estimate the variability between modelling techniques, which explicitly points out where limitations of the predictions can be made (see Figs. S2 and S3 in ESM).

4.2. Realised niche and potential invasion risks

Releases from biotic and abiotic constraints such as the absence of competitors, predators or pathogens, may well lead to a shift in the realised niche (Mitchell and Power, 2003; Torchin et al., 2003; Callaway and Maron, 2006; Mitchell et al., 2006; Snyder and Evans, 2006; Medley, 2010). Indeed, taking into account the richness of potential competitive species as a limiting factor could help capturing the realised niche. Thus, though introduction probably occurred at the same period (the 2000s) in both countries, *V. v. nigrithorax* appeared to have spread much more rapidly in France (Rome et al., 2009; Villemant et al., 2011) than in Korea (Jung et al., 2008). In Korea, indeed, the invasive hornet is confronted to six *Vespa* species versus only one, *V. crabro*, in France. Moreover, one of the Korean hornet (*V. mandarinia*) is not only a fierce predator of social wasps and bees but also the most dominant when

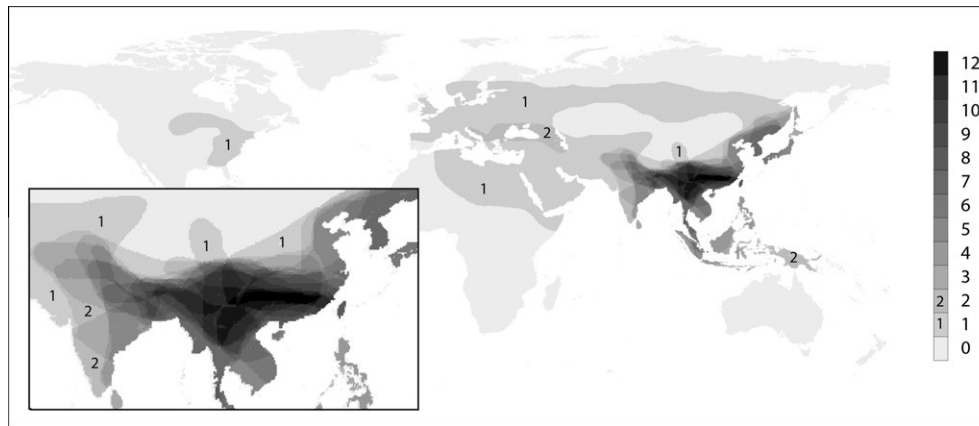


Fig. 6. Geographical distribution of specific diversity in the genus *Vespa*, established from the distribution range of the 22 species. The grey scale represents the local species richness.

competing for food with other hornet species (Matsuura and Yamane, 1990; Yoshimoto and Nishida, 2009). In addition to the suitable climatic conditions and the abundance of one of its main food source (honey bees), the low level of interspecific competition that *V. v. nigrithorax* faces in Europe may thus have facilitated its rapid spread in France (see Fig. S1 in ESM).

When considering all known occurrences of *V. v. nigrithorax* in the native and invaded ranges, models revealed that many countries of Western Europe exhibit a high probability of being invaded with a higher risk along the Atlantic and northern Mediterranean coasts. Coastal areas of the Balkan Peninsula, Turkey and Near East appear also suitable and could potentially be colonised later. The other parts of the world that show high climatic suitability for this species may also be potentially threatened by the invasive hornet since the scenario of introduction through international trade – as it occurred in France – could well be repeated. Moreover, when they happen to shelter in goods that get shipped, hibernating wasp funders have a relatively low probability of being detected with standard protocols used for custom inspection (Work et al., 2005; Kenis et al., 2007). However, in Hawaii, there has been some success cutting down on yellowjacket queen introduction through a combination of shaking and pesticide application in Christmas tree shipments (Hollingsworth et al., 2009).

Interestingly, the potential world wide distribution of *V. v. nigrithorax*, as predicted here, significantly matches the current distribution of another invasive social wasp, the German yellow jacket, *Vespula germanica* (Fig. 7). This species is widely distributed in Eurasia and was, as several other invasive wasps, unintentionally but successfully introduced in many regions of the world

(Beggs et al., in press). Indeed, invasive wasps (yellow jackets and paper wasps) proved to be efficient invaders in the past decades (Moller, 1996). Documented cases show that they are able to adapt their life cycles (Harris, 1996; Wilson et al., 2009) and out-compete native wasps as well as other arthropods and even birds, for the use of local resources (Stahlhut et al., 2006; Beggs and Wardle, 2006). In some cases the arrival of an additional wasp even led to displacement of a congeneric native or invasive species, suggesting that Vespidae communities can be strongly structured by inter-specific competition (Beggs et al., in press).

4.3. Potential threats to native entomofauna

During the reproductive season, invasive vespine wasps prey intensively on invertebrates to feed their larvae, so that vulnerable prey species may become threatened (Beggs, 2001; Harris, 1991; Thomas et al., 1990). In New-Zealand, for example, the amount of preys killed by *Vespula vulgaris* and *V. germanica* has been considered to be similar to that consumed by the entire insectivorous bird fauna (Harris, 1991). Social wasps being already part of the European fauna, the arrival of *V. v. nigrithorax* in France may not be as deleterious on insect fauna as observed after European yellow jackets' introduction in social wasps-free areas. However, *V. v. nigrithorax* occurs in France in highly humanized and disturbed areas and, although not being a new kind of predator, it may yet seriously impact the local entomofauna due to the size and increasing number of its colonies. A particular attention must be paid to its impact on yellow jackets and honey bee colonies which it actively predate in urbanised areas (Perrard et al., 2009;



Fig. 7. Native (in grey) and invasive (in black) ranges of *Vespula germanica* (see Beggs et al. (in press) for references on the current species distribution).

Villemant et al., 2011). Another indirect impact of this hornet on biodiversity can be suspected considering that pollinators (bees but also syrphids) represent a noticeable part of its prey spectrum (Villemant et al., 2011). Such a potential impact must however be carefully assessed. Drawing conclusions about effects on arthropod populations must rather be based on a comparison of faunas of the same areas before and after invasion than by comparing faunas of invaded versus similar un-invaded areas (Holway et al., 2002). Being able to predict the risk of acclimatisation of *V. v. nigrithorax* in a given region will thus greatly help with planning where to survey pollinators in a before/after invasion design, in order to provide insights into a wide variety of impacts associated with such invasions.

We can also raise the question of competition between *V. v. nigrithorax* and the European hornet, *V. crabro*, its unique congeneric species in Western Europe. Such competition, if occurring, could rise a further conservation problem as *V. crabro* is already considered as threatened in several European countries (Erlandson, 1988). The two hornet species have yet different nesting habits: *V. v. nigrithorax* preferentially builds its nests in the tree canopy (Rome et al., 2009; Villemant et al., 2011; see also ESM), while *V. crabro* almost exclusively nests in protected spaces such as underground cavities and tree hollows (Spradbery, 1973). *V. crabro* is bigger than *V. v. nigrithorax* (Rortais et al., 2010) and thus not concerned by direct predation by its invasive congener. However, largest colonies of *V. v. nigrithorax* can produce more than 15,000 individuals in a season (Villemant et al., 2011), which represents three times the size of the largest *V. crabro*'s colonies (Archer, 2008). The European hornet may thus hardly compete with the huge colonies of the Yellow-legged hornet which are able to remove a considerable biomass of arthropods (Villemant et al., 2011). Further studies are required to assess the prey overlap between the two species and find out if *V. v. nigrithorax* predation activity may impact *V. crabro* European populations.

Furthermore, as a consequence of this invasion, beekeepers and citizens react by actively searching for *V. v. nigrithorax* nests. As a by-side effect, they also encounter and destroy a greater number of *V. crabro* and other Vespidae (*Vespula* or *Dolichovespula* spp.) colonies than in the past. Such thoughtless reactions may increase the threats due to *V. v. nigrithorax*'s predation and competition. Moreover, until research to develop an effective control method against this hornet succeeds, the uncontrolled mass trappings and wasp colony destructions performed every year in France, in and outside the invaded area, might even be more deleterious to the entomofauna than the pest problem itself. Traps and poisoned baits kill a huge number of non-target insects (Dauphin and Thomas, 2009; Rome et al., 2011) while nests filled with insecticides and left on site may threaten birds that intensively feed on brood of poisoned colonies (Villemant et al., 2010).

4.4. Economic impacts

Damages on crops and fruits have been reported after invasions by *Vespula* species, but the main impact of social wasps on human production concerns beekeeping (Clapperton et al., 1989). By their predation on honey bees, social wasps disturb beekeeping activities and can lead to the death of beehives. Hornets like *V. velutina* are even more important predators of bees; their impact on honey bee colonies is well established in the native range (Abrol, 1994, 2006) and could be amplified in the invaded ranges.

Since several decades, American and European managed honey bees are in decline, though information for Europe remains patchy and localised (Potts et al., 2010). In France, colony number is greater today when compared to 1961 populations, but has constantly decreased after reaching a peak in 2000 (VanEngelsdorp and Meixner, 2010). A wide panel of adversary factors, such as pests

and diseases, pesticides, loss of forage or beekeeping practices are involved in this phenomenon throughout Europe (Bacandritsos et al., 2010; Ellis et al., 2010; Genersch et al., 2010; Higes et al., 2010; Neumann and Carreck, 2010). The invasion of *V. v. nigrithorax* adds to this long list a new protagonist that will undoubtedly focus its attack on weakened bee colonies.

Comparing the map of invasion risks (Fig. 5) with an estimated density of bee colonies in each country (ratio between number of managed hives and surface of agricultural land in each country; data from FAO (2010) and agricultural resources or Apiservices' database (<http://www.apiservices.com/>; see Fig. S4 in ESM), show that many European countries, and notably the Balkan Peninsula and Turkey, exhibit high level of beekeeping activity with a great risk of *V. v. nigrithorax* acclimatisation. Though arriving at the fourth rank in Europe with more than 1 million of registered hives (FAO, 2010), France does not show as a whole a high level of beehive density due to the extend of its agricultural lands. However, when considering the previous ratio at the regional level (data 2004; see Fig. S5 in ESM), it appears that – in addition to the whole South-West of France – the Rhone valley, Corsica and Alsace gather the greatest managed beehive numbers with the highest risks of *V. v. nigrithorax* arrival. Moreover, Spain that counts the greatest number of beehives (more than 2.5 millions) in Europe just underwent the arrival of the bee-hawking hornet in the Basque country, colonising from the French invasive population. From our models, this area faces a high invasion risk. On another hand, the expansion risk of *V. v. nigrithorax* in Albania, Greece and Turkey could be hampered by the presence of a congeneric competitor (Snyder and Evans, 2006); indeed *V. orientalis* inhabits these regions and is another active bee-hawking hornet (Papachristoforou et al., 2007; Rortais et al., 2010).

5. Conclusion

Like ants, social wasps represent a particularly destructive and successful group of invasive invertebrates. Their sociality, including a number of unique mechanisms enhancing survival and reproduction, is certainly the key factor that substantially contributes to their success as invaders (Moritz et al., 2005). Their main general advantage may be the flexibility arising from having both individual and colony responses (Moller, 1996), as is the case in invasive ants (Holway et al., 2002; Roura-Pascual et al., 2009). This confers them a remarkable efficiency to compete and exploit food sources, buffering against environmental changes. They develop populous colonies with an effective predator defence and producing numerous founders that provide large dispersal capacity (Moller, 1996; Davidson, 1998).

Given the potential economic and biological impacts of the invasive *V. v. nigrithorax*, future developments should focus on better understanding the invasion dynamics by developing modelling approaches to predict the rate of range expansion, which is necessary for a temporal risk assessment and the further implementation of effective management strategies (Hastings et al., 2005; Kadoya and Washitani, 2010).

Acknowledgements

This work was supported by France AgriMer (Programme communautaire pour l'Apiculture, 2008–2011), MEDDTL (Ministère de l'Ecologie, du Développement Durable, des transports et du Logement) and FRB (Fondation pour la Recherche sur la Biodiversité; programme Wasprey 2010–2011). We are most thankful to all persons and organizations that provided records of hornet nests in France (their list is available on the INPN website). Special thanks are due to Dr. Gavin Broad that helped us to get records

from the NHM collection as well as Prof. Chen Xue-xin and Dr. Tan Jiang-li from the University of Zhejiang (Hangzhou, China), for their kind help during our trip in China, a mission funded by the MNHN (ATM Forms). We are grateful to two anonymous reviewers whose valuable comments improved the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.biocon.2011.04.009.

References

- Abrol, D.P., 1994. Ecology, behaviour and management of social wasp, *Vespa velutina* Smith (Hymenoptera: Vespidae), attacking honeybee colonies. Korean J. Apic. 9, 5–10.
- Abrol, D.P., 2006. Defensive behaviour of *Apis cerana* F. against predatory wasps. J. Apic. Sci. 50, 39–46.
- 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.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47.
- Archer, M.E., 2008. Taxonomy, distribution and nesting biology of species of the genera *Provespa* Ashmead and *Vespa* Linnaeus (Hymenoptera, Vespidae). Entomol. Month. Mag. 144, 69–101.
- Bacandritsos, N., Granato, A., Budge, G., Papanastasiou, I., Roinioti, E., Caldon, M., Falcaro, C., Gallina, A., Mutinelli, F., 2010. Sudden deaths and colony population decline in Greek honey bee colonies. J. Invertebr. Pathol. 105, 335–340.
- Beggs, J., 2001. The ecological consequences of social wasps (*Vespa* spp.) invading an ecosystem that has an abundant carbohydrate resource. Biol. Conserv. 99, 17–28.
- Beggs, J.R., Wardle, D.A., 2006. Keystone species: competition for honeydew among exotic and indigenous species. In: Allen, R.B., Lee, W.G. (Eds.), Biological Invasions in New Zealand. Springer-Verlag, Berlin Heidelberg.
- Beggs, J., Brockerhoff, E., Corley, J., Kenis, K., Masciocchi, M., Muller, F., Rome, Q., Villemant, C., in press. Ecological effects and management of invasive Vespidae. In: Roy, H., Ware, R., Handley-Lawson, L., De Clercq, P., Wajnberg E. (Eds.), Invasive Arthropod Predators and Parasitoids: An Ecological Approach. Biocontrol.
- Broennimann, O., Guisan, A., 2008. Predicting current and future biological invasions: both native and invaded ranges matter. Biol. Lett. 4, 585–589.
- Callaway, R.M., Maron, J.L., 2006. What have exotic plant invasions taught us over the past 20 years? Trends Ecol. Evol. 21, 369–374.
- Carpenter, J.M., Kojima, J., 1997. Checklist of the species in the subfamily Vespinae (Insecta: Hymenoptera: Vespidae). Nat. Hist. Bull. Ibaraki Univ. 1, 51–92.
- Castro, L., Pagola-Carte, S., 2010. *Vespa velutina* Lepeletier, 1836 (Hymenoptera: Vespidae), recolectada en la Península Ibérica. Heteropterus Rev. Entomol. 10, 193–196.
- Chapman, R.E., Bourke, A.F.G., 2001. The influence of sociality on the conservation biology of social insects. Ecol. Lett. 4, 650–662.
- Chen, P.F., Wiley, E.O., McNyset, K.M., 2007. Ecological niche modeling as a predictive tool: silver and bighead carps in North America. Biol. Invas. 9, 43–51.
- Clapperton, B.K., Alspach, P.A., Moller, H., Matheson, A.G., 1989. The impact of Common and German wasps (Hymenoptera: Vespidae) on the New Zealand beekeeping industry. N. Z. J. Zool. 16, 325–332.
- Dauphin, P., Thomas, H., 2009. Quelques données sur le contenu des “Pièges à frelons asiatiques” posés à Bordeaux (Gironde) en 2009. Bull. Soc. Linn. Bordeaux 144, 287–297.
- Davidson, D.W., 1998. Resource discovery versus resource domination in ants: breaking the trade-off. Ecol. Entomol. 23, 484–490.
- Dvorak, L., Landolt, P.J., 2006. Social wasps trapped in the Czech Republic with syrup and fermented fruit and comparison with similar studies (Hymenoptera Vespidae). Bull. Insectol. 59, 115–120.
- Eliith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.
- Ellis, J., Evans, J., Pettis, J., 2010. Colony losses, managed colony population decline and colony collapse disorder in the United States. J. Apic. Res. 49, 134–136.
- Erlanson, S., 1988. The distribution of the hornet (*Vespa c. crabro* L.) in northwestern Europe. Entomol. Tidskrift 109, 155–159.
- FAO, 2010. Faostat/Production/Live Animals. <<http://faostat.Fao.Org>> (accessed 09.07.10).
- Ficetola, G.F., Thuiller, W., Miaud, C., 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. Divers. Distrib. 13, 476–485.
- Fielding, A.H., Bell, J.F., 1997. A review methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
- Genersch, E., Ohe, W. von der, Kaatz, H., Schroeder, A., Otten, C., Büchler, R., Berg, S., Ritter, W., Mühlen, W., Gisder, S., Meixner, M., Liebig, G., Rosenkranz, P., 2010. The German bee monitoring project: a long term study to understand periodically high winter losses of honey bee colonies. Apidologie 41, 332–352.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.
- 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. Conserv. Biol. 20, 501–511.
- Harris, R.J., 1991. Diet of the wasps *Vespa vulgaris* and *V. Germanica* in honeydew beech forest of the south island. N. Z. J. Ecol. 18, 159–170.
- Harris, R.J., 1996. Frequency of overwintered *Vespa germanica* (Hymenoptera: Vespidae) colonies in scrubland-pasture habitat and their impact on prey. N. Z. J. Zool. 23, 11–17.
- Hastings, A., Cuddington, K., Davies, K., Dugaw, C., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B., Moore, K., Taylor, C., Thomson, D., 2005. The spatial spread of invasions: new developments in theory and evidence. Ecol. Lett. 8, 91–101.
- Haxaire, J., Bouguet, J.-P., Tamisier, J.-P., 2006. *Vespa velutina* Lepeletier, 1836, une redoutable nouveauté pour la faune de France (Hym., Vespidae). Bull. Soc. Entomol. Fr. 111, 194.
- Higes, M., Martín-Hernández, R., Martínez-Salvador, A., Garrido-Bailón, E., González-Porto, A.V., Meana, A., Bernal, J.L., Noza, M.J. del, Bernal, J., 2010. A preliminary study of the epidemiological factors related to honey bee colony loss in Spain. Environ. Microbiol. Rep. 2, 243–250.
- 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.
- Hingston, A.B., McQuillan, P.B., 1999. Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). Aust. J. Zool. 47, 59–65.
- Hollingsworth, R.G., Chastagner, G.A., Reimer, N.J., Oishi, D.E., Landolt, P.J., Paull, R.E., 2009. Use of shaking treatments and preharvest sprays of pyrethroid insecticides to reduce risk of yellowjackets and other insects on Christmas trees imported into Hawaii. J. Econ. Entomol. 102, 69–78.
- Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D., Case, T.J., 2002. The causes and consequences of ant invasions. Ann. Rev. Ecol. Sys. 33, 181–233.
- DAISIE, 2009. Handbook of Alien Species in Europe. Invading Nature, Springer Series in Invasion Ecology, vol. 3. Springer-Verlag, Berlin.
- Inoue, M.N., Yokoyama, J., Washitani, I., 2008. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). J. Insect Conserv. 12, 135–146.
- INPN, 2010. *Vespa velutina*. Inventaire National du Patrimoine Naturel. <<http://inpn.mnhn.fr/>>.
- IUCN, 2000. Guidelines for the prevention of biodiversity loss caused by alien invasive species. SSC Invasive Species Specialist Group, IUCN, The World Conservation Union, Gland, Switzerland.
- Jung, C., Kim, D.-W., Lee, H.-S., Baek, H., 2008. Some biological characteristics of a new honeybee pest, *Vespa velutina nigrithorax* Buysson 1905 (Hymenoptera: Vespidae). Korean J. Apic. 24, 61–65.
- Kadoya, T., Washitani, I., 2010. Predicting the rate of range expansion of an invasive alien bumblebee (*Bombus terrestris*) using a stochastic spatio-temporal model. Biol. Conserv. 143, 1228–1235.
- Kadoya, T., Ishii, H.S., Kikuchi, R., Suda, S.I., Washitani, I., 2009. Using monitoring data gathered by volunteers to predict the potential distribution of the invasive alien bumblebee *Bombus terrestris*. Biol. Conserv. 142, 1011–1017.
- Kastberger, G., Schmelzer, E., Kranner, I., 2008. Social waves in giant honeybees repel hornets. PLoS ONE 3 (9), e3141. doi:10.1371/journal.pone.0003141.
- Kenis, M., Rabitsch, W., Auger-Rozenberg, M.A., Roques, A., 2007. How can alien species inventories and interception data help us prevent insect invasions? Bull. Entomol. Res. 97, 489–502.
- Kenis, M., Auger-Rozenberg, M.-A., Timms, L., Péré, C., Cock, J.W., Settele, J., Lopez-Vaamonde, C., 2008. Ecological effects of invasive alien insects. Biol. Invas. 11, 21–45.
- Kim, J.-K., Choi, M., Moon, T.-Y., 2006. Occurrence of *Vespa velutina* Lepeletier from Korea, and a revised key for Korean *Vespa* species (Hymenoptera: Vespidae). Entomol. Res. 36, 112–115.
- Lobo, J.M., Jiménez-Valverde, A., Real, R., 2007. AUC: a misleading measure of the performance of predictive distribution models. Global Ecol. Biogeogr. 17, 145–151.
- Luoto, M., Virkkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models depends on spatial resolution. Global Ecol. Biogeogr. 16, 34–42.
- Maitre, D.C.L., Thuiller, W., Schonegevel, L., 2008. Developing an approach to defining the potential distributions of invasive plant species: a case study of *Hakea* species in South Africa. Global Ecol. Biogeogr. 17, 569–584.
- Marini, M.A., Barbet-Massin, M., Lopes, M.E., Jiguet, F., 2009. Major current and future gap of Brazilian reserves to protect Neotropical savanna birds. Biol. Conserv. 142, 3039–3050.
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2008. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15, 59–69.
- Martin, S.J., 1995. Hornets (Hymenoptera: Vespinae) of Malaysia. Malaysian Nat. J. 49, 71–82.
- Matsuura, M., 1973. Nesting habit of several species of the genus *Vespa* in Formosa. Kontyu 41, 286–293.

- Matsuura, M., Yamane, S., 1990. Biology of the Vespine Wasps. Springer-Verlag, Berlin.
- Matthews, R.W., Goodisman, M.A., Austin, A.D., Bashford, R., 2001. The introduced English wasp *Vespa vulgaris* (L.) (Hymenoptera: Vespidae) newly recorded invading native forests in Tasmania. *Aust. J. Entomol.* 39, 177–179.
- Medley, K.A., 2010. Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Global Ecol. Biogeogr.* 19, 122–133.
- Mitchell, C.E., Power, A.G., 2003. Release of invasive plants from fungal and viral pathogens. *Nature* 421, 625–627.
- Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloom, E.W., Torchin, M.E., Vazquez, D.P., 2006. Biotic interactions and plant invasions. *Ecol. Lett.* 9, 726–740.
- Moller, H., 1996. Lessons for invasion theory from social insects. *Biol. Conserv.* 78, 125–142.
- Moritz, R.F.A., Härtel, S., Neumann, P., 2005. Global invasions of the western honeybee (*Apis mellifera*) and the consequences for biodiversity. *Ecoscience* 12, 289–301.
- Nakamura, M., Sonthichai, S., 2004. Nesting habits of some hornet species (Hymenoptera, Vespidae) in northern Thailand. *Kasetsart J. Nat. Sci.* 38, 196–206.
- Neumann, P., Carreck, N., 2010. Honey bee colony losses. *J. Apic. Res.* 49, 1–6.
- Nguyen, L.T., Saito, F., Kojima, J., Carpenter, J.M., 2006. Vespidae of Viet Nam (Insecta: Hymenoptera) 2. Taxonomic notes on Vespinae. *Zool. Sci.* 23, 95–104.
- Ono, M., Igarashi, T., Ohno, E., Sasaki, M., 1995. Unusual thermal defense by a honeybee against mass attack by hornets. *Nature* 377, 334–336.
- Paini, D.R., Dale Roberts, J., 2005. Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (*Hylaeus alcyoneus*). *Biol. Conserv.* 123, 103–112.
- Papachristoforou, A., Rortais, A., Zafeiridou, G., Theophilidis, G., Garney, L., Thrasivoulou, A., Arnold, G., 2007. Smothered to death: hornets asphyxiated by honeybees. *Curr. Biol.* 17, R795–R796.
- Perrard, A., Haxaire, J., Rortais, A., Villemant, C., 2009. Observations on the colony activity of the Asian hornet *Vespa velutina* Lepeletier 1836 (Hymenoptera: Vespidae: Vespinae) in France. *Ann. Soc. Entomol. Fr.* 45, 119–127.
- Peterson, A.T., 2003. Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* 78, 419–433.
- Peterson, A.T., Vieglais, D.A., 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *Bioscience* 51, 363–371.
- Peterson, A.T., Papes, M., Kluz, D.A., 2003. Predicting the potential invasive distributions of four alien plant species in North America. *Weed Sci.* 51, 863–868.
- Potts, S., Roberts, S.P.M., Dean, R., Marris, G., Brown, M., Jones, R., Settele, J., 2010. Declines of managed honeybees and beekeepers in Europe. *J. Apic. Res.* 49, 15–22.
- Ranabhat, N.B., Tamrakar, A.S., 2008. Study on seasonal activity of predatory wasps attacking honeybee *Apis cerana* Fab. colonies in southern belt of Kaski district, Nepal. *J. Nat. Hist. Mus.* 23, 125–128.
- Rasplus, J.-Y., Villemant, C., Paiva, M.R., Delvare, G., Roques, A., 2010. Hymenoptera. In: Roques, A., Kenis, M., Lees, D., et al. (Eds.), *Arthropod Invasions in Europe*. doi:10.3897/biorisk.4.55 (Chapter 12).
- Rome, Q., Muller, F., Gargominy, O., Villemant, C., 2009. Bilan 2008 de l'invasion de *Vespa velutina* Lepeletier en France (Hymenoptera: Vespidae). *Bull. Soc. Entomol. Fr.* 114, 297–302.
- Rome, Q., Muller, F., Théry, T., Andrivot, J., Haubois, S., Rosenstiehl, E., Villemant, C., 2011. Impact sur l'entomofaune des pièges à bière ou à jus de cirier utilisés dans la lutte contre le frelon asiatique. In: Barbançon, J.-M., L'Hostis, M. (Eds.), *Proceedings of the Journée Scientifique Apicole – 11 February 2011*, Arles. ONIRIS-FNOSAD, Nantes, pp. 18–20.
- Roques, A., Rabitsch, W., Rasplus, J.-Y., 2009. Alien terrestrial invertebrates of Europe. In: Nentwig, W.H.P., Pysek, P., Vila, M.E. (Eds.), *Handbook of Alien Species in Europe*. Springer-Verlag, Berlin.
- Rortais, A., Villemant, C., Gargominy, O., Rome, Q., Haxaire, J., Papachristoforou, A., Arnold, G., 2010. A new enemy of honeybees in Europe: The Asian hornet *Vespa velutina*. In: Settele, J. (Ed.), *Atlas of Biodiversity Risks – from Europe to the Globe*, From Stories to Maps. Pensoft, Sofia, Moscow.
- Roura-Pascual, N., Brotons, L., Peterson, A.T., Thuiller, W., 2009. Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. *Biol. Invas.* 11, 1017–1031.
- Shah, F., Shah, T., 1991. *Vespa velutina*, a serious pest of honey bees in Kashmir. *Bee World* 72, 161–164.
- Shaw, F.R., Weidhaas, J., 1956. Distribution and habits of the giant hornet in North America. *J. Econ. Entomol.* 49, 275.
- Snyder, W.E., Evans, E.V., 2006. Ecological effects of invasive arthropod generalist predators. *Ann. Rev. Ecol. Evol. Syst.* 37, 95–122.
- Spradbery, J.P., 1973. Wasps: An Account of the Biology and Natural History of Solitary and Social Wasps with Particular Reference to Those of the British Isles. Sidgwick & Jackson, London.
- Stahlhut, K., Liebert, A.E., Starks, P.T., Dapporto, L., Jaenike, J., 2006. *Wolbachia* in the invasive European paper wasp *Polistes dominulus*. *Insect. Soc.* 53, 269–273.
- Tan, K., Radloff, S.E., Li, J.J., Hepburn, H.R., Yang, M.X., Zhang, L.J., Neumann, P., 2007. Bee-hawking by the wasp, *Vespa velutina*, on the honeybees *Apis cerana* and *A. mellifera*. *Naturwissenschaften* 94, 469–472.
- Thomas, C.D., Moller, H., Plunkett, G.M., Harris, R.J., 1990. The prevalence of introduced *Vespa vulgaris* wasps in a New Zealand beech forest community. *N. Z. J. Ecol.* 13, 63–72.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005a. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. USA* 102, 8245–8250.
- Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O., Rouget, M., 2005b. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biol.* 11, 2234–2250.
- Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. Biomod – a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373.
- Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., Kuris, A.M., 2003. Introduced species and their missing parasites. *Nature* 421, 628–630.
- Van der Vecht, J., 1957. The Vespinae of the Indo-Malayan and Papuan areas (Hymenoptera: Vespidae). *Zool. Verhand.* 34.
- Van der Vecht, J., 1959. Notes on Oriental Vespinae including some species from China and Japan (Hymenoptera, Vespidae). *Zool. Mededel.* 13, 205–232.
- VanEngelsdorp, D., Meixner, M.D., 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J. Invertebr. Pathol.* 103, S80–S95.
- Villemant, C., Haxaire, J., Streito, J.-C., 2006. Premier bilan de l'invasion de *Vespa velutina* Lepeletier en France (Hymenoptera, Vespidae). *Bull. Soc. Entomol. Fr.* 111, 535–538.
- Villemant, C., Rome, Q., Muller, F., 2010. *Vespa velutina nigrithorax* du Buysson, 1905 – Asian Yellow-legged Hornet (Hymenoptera, Vespidae). In: Roques, A., Lees, D. (Eds.), *Introductory Notes to Factsheets*. In: Roques, A., Kenis, M., Lees, D., et al. (Eds.), *Arthropod Invasions in Europe*. BioRisk. doi:10.3897/biorisk.4.55 (Chapter 14).
- Villemant, C., Muller, F., Haubois, S., Perrard, A., Darrouzet, E., Rome, Q., 2011. Bilan des travaux (MNHN et IRBI) sur l'invasion en France de *Vespa velutina*, le frelon asiatique prédateur d'abeilles. In: Barbançon, J.-M., L'Hostis, M. (Eds.), *Proceedings of the Journée Scientifique Apicole – 11 February 2011*, Arles. ONIRIS-FNOSAD, Nantes, pp. 3–12.
- Wilson, K.A., Westphal, M.I., Possingham, H.P., Elith, J., 2005. Sensitivity of conservation planning to different approaches to using predicted species distribution data. *Biol. Conserv.* 122, 99–112.
- Wilson, E.E., Mullen, L.M., Holway, D.A., 2009. Life history plasticity magnifies the ecological effects of a social wasp invasion. *Proc. Natl. Acad. Sci. USA* 106, 12809–12813.
- Wittenberg, R., Cock, M.J.W. (Eds.), 2001. *Invasive Alien Species: A Toolkit of Best Prevention and Management Practices*. CABI Publishing, Wallingford, Oxon, UK.
- Work, T.T., McCullough, D.G., Cavey, J.F., Komsa, R., 2005. Arrival rate of nonindigenous insect species into the United States through foreign trade. *Biol. Invas.* 7, 323–332.
- Yoshimoto, J., Nishida, T., 2009. Factors affecting behavioral interactions among sap-attracted insects. *Ann. Entomol. Soc. Am.* 102, 201–209.