

Environmental niche and global potential distribution of the giant resin bee *Megachile sculpturalis*, a rapidly spreading invasive pollinator

Carlo Polidori ^{a, b, *}, David Sánchez-Fernández ^c

^a Instituto de Ciencias Ambientales (ICAM), Universidad de Castilla-La Mancha, Avenida Carlos III, s/n, 45071, Toledo, Spain

^b Dipartimento di Scienze e Politiche Ambientali, Università Degli Studi di Milano, Via Celoria 26, 20133, Milan, Italy

^c Departamento de Ecología e Hidrología, Universidad de Murcia, Campus de Espinardo, 30100, Murcia, Spain

ARTICLE INFO

Article history:

Received 21 May 2020

Received in revised form 26 October 2020

Accepted 10 November 2020

Keywords:

Megachilidae

Invasive bees

Environmental niche

Niche shift

Potential distribution

ABSTRACT

Since alien species may threaten native ecosystems when becoming invasive, one of the main challenges is try to predict their potential spread. Despite bees are essential pollinators and provide important ecosystem services in their native areas, outside these areas they could represent a risk for the local bee fauna, e.g. by competing for resources or by transmitting pathogens, as it was observed for species of *Megachile*, the bee genus with the highest number of recorded alien species. Here, using two complementary methods (Multidimensional Envelope procedure (MDE) and the Maximum Entropy algorithm (MaxEnt)), we aim to explore environmental niche as well as to identify potential worldwide distribution of the giant resin bee *Megachile sculpturalis*, native to Asia and recently introduced in North America and Europe. The two methodological approaches predict an important expansion for the species and reveal a preference for areas of Palearctic and Nearctic regions with reduced temperature fluctuations and moderate precipitation regimes. The Southern hemisphere seems not having good conditions for this species. Estimations for the future (2070) predict a further, though limited expansion to northern areas in the North hemisphere. However, during roughly 25 years of spreading outside its native range, *M. sculpturalis* clearly expanded the range of inhabitable environmental conditions, which may increase its potential invasiveness in a pattern difficult to predict using only correlative methods. Physiological and ecological data are necessary to better assess the potential niche of this bee species and in consequence to better predict its future spreading dynamics.

© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Alien species, i.e. those species which establish outside their native range after a deliberate (e.g. as a managed crop pollinator or a pest control agent) or accidental (e.g. through trade routes) introduction, may become invasive (i.e. problematic for biodiversity in the occupied areas) under certain conditions (Williamson 1996; Levine and D'Antonio 2003; Colautti and MacIsaac 2004; Blackburn et al., 2014). Typically, with a high growth rate, a fast range expansion, and a

*Corresponding author. Dipartimento di Scienze e Politiche Ambientali, Università Degli Studi di Milano, via Celoria 26, 20133, Milan, Italy
E-mail address: carlo.polidori@unimi.it (C. Polidori).

prominent competitive ability, these invasive species greatly impact native biological communities, causing serious problems for the environment and society (Wittenberg and Cock 2001; Clavero and García-Berthou 2005; Lockwood et al., 2007; Roques et al., 2009).

For this reason, a key challenge for ecologist is to understand the potential spread of alien species and predict the patterns of range expansion in order to plan prevention strategies (Hastings et al., 2005; Arim et al., 2006). Such studies are mainly based on species distribution models (SDMs, also known as ecological niche models; Guisan et al., 2013). SDMs consist in a set of methods widely used to forecast the potential distribution of species spanning many different organisms (e.g. Peterson et al., 2003; 2007; Broennimann et al., 2007; Ward 2007; Guareschi et al., 2013). Since abiotic factors are central in determining the survival of a species in a given territory, climate and other environmental variables, such as altitude and land use, are extensively used in building such potential distributions (Araújo and Guisan 2006; Peterson et al., 2011).

SDMs have their limitations, which largely depend on data accuracy, the type of applied modelling procedure, and niche stability of the studied species (Jiménez-Valverde et al., 2008). In particular, since SDMs are correlative models which relate species occurrences (i.e. the response variable) to environmental predictors (i.e. predictor variables), their output could be more reliable when assuming that the current species distribution is limited by the environmental factors we are using in the model and the species has already reached all suitable areas within the native range and is absent from all unsuitable sites (i.e., the equilibrium assumption). Furthermore, SDMs would finely predict the potential distribution of a species when their ecological niche was stable in space and time (niche conservatism: the environmental conditions where the species lives are the same in the native and the invaded areas) (Guisan and Thuiller 2005). However, this equilibrium assumption is often violated, since alien species may either show niche unfilling (the niche of the invaded area is only a sub-space of the niche of the native area) or, even more problematic, niche shift (a new environmental space is occupied in the invaded range) (Broennimann et al., 2012; Guisan et al., 2014; Polidori et al., 2018). However, SDMs are extremely useful tools to rapidly estimate the spreading patterns of alien species (Peterson et al. 2003, 2007, 2011).

In this study, we focus on potential distribution of bees (Hymenoptera: Apoidea). To date, over 80 species of both domestic (honeybees, bumblebees) and wild bees have established outside of their native ranges (reviewed in Russo 2016). Some were imported in non-native areas to increase crop production, while others enter non-native territories accidentally (Russo 2016), and in both cases benefits from their pollination service arise together with potential negative effects on the occupied ecosystems. Indeed, while bees are arguably the most efficient pollinators at a global scale, providing important ecosystem services and guaranteeing more than 30% of global crop production (Biesmeijer et al., 2006; Klein et al., 2007), some of the alien bee species distributed around the world were observed, or at least suggested from observations on their behaviour, to have negative impacts on local fauna. For example, alien bees could affect the local bee fauna through competition for food resources and nesting sites, transmission of pathogens, and reproductive disruption via interspecific hybridization (Goulson 2003; Traveset and Richardson 2006; Morales 2007; Stout and Goulson 2000; Stout and Morales, 2009; Norfolk et al., 2018).

Most of the alien wild bee species recorded to date belong to Megachilidae (Russo 2016), suggesting that bees of this family possess biological and/or ecological traits that make them more likely to successfully persist in non-native areas. For example, most species nest in tunnels in wood (Michener 2007; Danforth et al., 2019), which increases the probability of accidental introduction via commercial trade (Polidori et al., 2018). Furthermore, males of many species aggressively defend mating territories on plants, which may limit flower exploitation by native species (Strange et al., 2011). Within Megachilidae, *Megachile* is well represented, with >10 species recorded outside their native ranges (Russo 2016; Bortolotti et al., 2018). Species of this genus provide some evidence of competition with native bee fauna. For example, Barthell and Frankie (1998) found the alien *Megachile apicalis* Spinola 1808 and *Megachile rotundata* Fabricius 1787 occupying more trap-nests than native bees in California, and *Megachile sculpturalis* Smith 1853 was observed to compete with species of *Xylocopa* and *Osmia* for nesting sites (Laport and Minckley 2012; Parys et al., 2015; Le Féon et al., 2018). Furthermore, transmission of pathogens from alien to native *Megachile* species is known (Goerzen et al. 1990, 1992). Females of very large *Megachile* species can also damage flowers during foraging (Mangum and Sumner 2003). Thus, it is important to try to predict where alien *Megachile* species may spread, based on their ecological niches.

This study represents the first attempt to estimate potential areas, at a global scale, of invasion of the alien giant resin bee *M. sculpturalis* (Fig. 1A and B) using species distribution models. Since prevention of invasions is the most cost-effective way to avoid biodiversity loss and nature conservation problems (Leung et al., 2002), the obtained information could be considered as a useful tool to understand and prevent further spreads of this alien species. Apart from an earlier study on *M. sculpturalis* confined to North America (Hinojosa-Diaz et al., 2005), no investigations attempted to estimate the potential distribution of this species at a global scale.

Specifically, we aim to 1) estimate the environmental space (based on bioclimatic data) occupied by the species, 2) identify areas of the world that could potentially be invaded by the species under the current environmental conditions, 3) evaluate if *M. sculpturalis* is conserving, unfilling or shifting its environmental niche in the invaded areas, and 4) identify the potential distribution of the species under future scenarios of climate change.

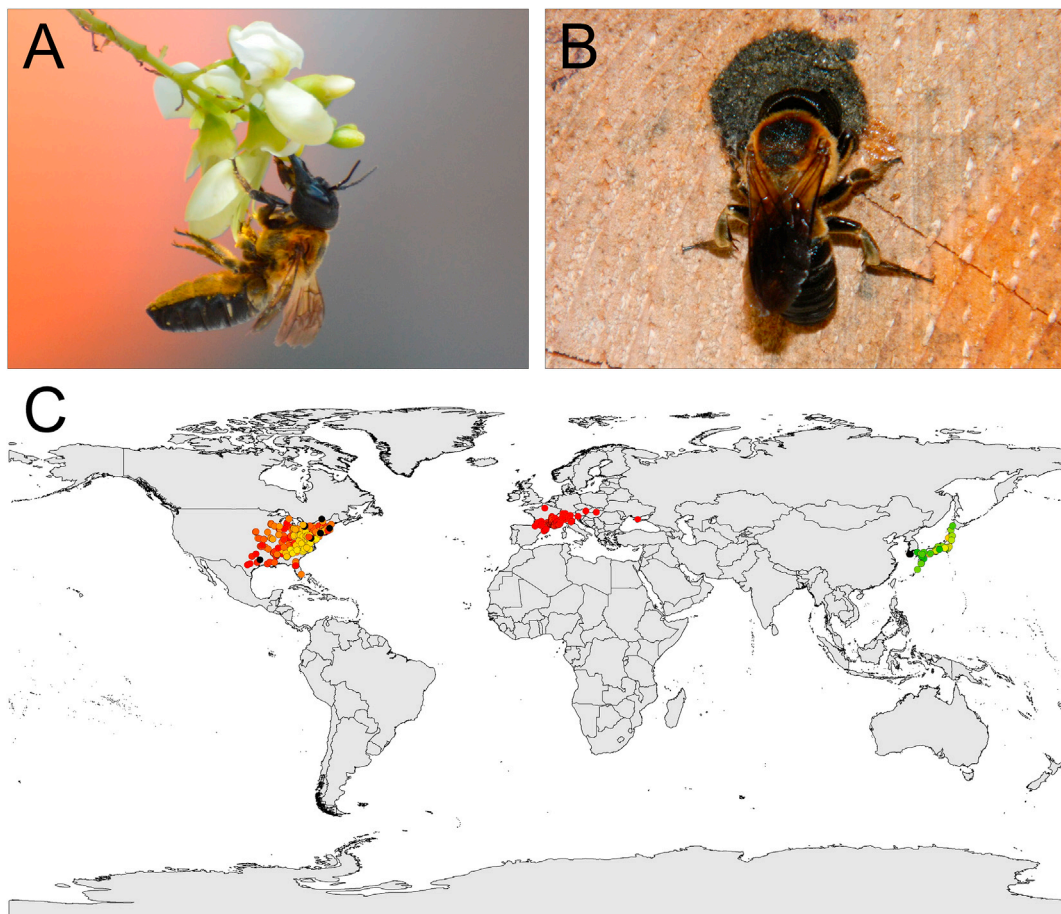


Fig. 1. (A) A female *M. sculpturalis* while foraging on *Sophora japonica* in Italy (credit: Laura Bortolotti); (B) A female *M. sculpturalis* at a nest entrance in wood in Italy (credit: Angelo Sommaruga); (C) Actual distribution of *M. sculpturalis*, based on published records (see Table A1). Occurrence records are from yellow to green (increasing year of record) for the native areas, and from yellow to red (increasing year of record) for the invaded areas. Black dots indicate records with no available year. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2. Materials and methods

2.1. Study species and origin of data

The native distribution range of *M. sculpturalis* covers eastern Asia (Japan, China, Korea, Taiwan) (Iwata 1933; Hirashima 1974; Okada, 1995; Lee and Ryu 2013). *Megachile sculpturalis* established first in North America at least since 1994 and it now occupies many areas of America and Europe (Hinojosa-Díaz et al., 2005; Vereecken and Barbier 2009; Amiet 2012; Quaranta et al., 2014; Westrich et al., 2015; Parys et al., 2015; Le Féon et al., 2018). This large (body length 17–27 mm) species belongs to the subgenus *Callomegachile*. The species is easily to recognize by the large body, the infuscated wings and the bright orange hairy thorax (Fig. 1A and B). Females nest in hollow stems or pre-existing cavities in dead wood and thus are placed above the ground level (Fig. 1B). Nests are composed of a number of brood cells, where a single egg in each is laid (Amiet 2012; Quaranta et al., 2014; Aguado et al., 2018). The walls between the brood cells are made with mud, while the lateral walls and the nest entrances are capped with resin (Hinojosa-Díaz et al., 2005; Parys et al., 2015; Westrich et al., 2015). The pollen to feed the immature brood is collected from plant species spanning many families, often from non-native species (Fig. 1A) (Batra 1998; Michener 2007; Praz 2017; Laport and Minckley 2012; Quaranta et al., 2014; Aguado et al., 2018; Le Féon et al., 2018). *Megachile sculpturalis* is a protandrous species, i.e. males emerge earlier than females within a flying season that starts in late June-early July and ends in mid-September (Hinojosa-Díaz et al., 2005; Quaranta et al., 2014).

The current distribution of *M. sculpturalis* was retrieved from published studies (articles, books, official reports), from GBIF (Global Biodiversity Information Facility) (GBIF.org, 2019) and confirmed observations in entomological websites (Table A1). Although we cannot exclude that we missed some records, for example available in Museums collections which were not inspected or available in large monographies on regional entomofauna, the complete dataset used in this study essentially represents the whole current distribution of the species. We obtained 625 georeferenced points (49 native and 576 invaded)

(Table A1). We associated each distribution record to its geographical coordinates (latitude and longitude), and to a binary code identifying if it refers to either the native or the invaded area. Then, we created a database at a spatial resolution (grid cell size) of 0.4° . In order to minimize spatial bias in the niche modelling procedure, we used a spatial thinning approach on the points to make sure they are all at minimum 10 km distance from one another.

2.2. Estimation of the environmental niche

We refer in our study to the “environmental potential distribution”, which is the geographical representation of the environmental niche from a climatic perspective. We focus on environmental niche because available information in the literature suggests that biotic limitations for this bee species in invaded areas (i.e. in finding resources) may be very weak. First, the species was observed to be largely polylectic in their pollen use (Iwata 1933; Batra 1998; Quaranta et al., 2014); second, the species was observed to nest in different types of galleries, including bamboo reeds, tunnels in wood excavated by other insects and trap-nests prepared by researchers (Praz 2017; Quaranta et al., 2014).

To estimate the abiotic environmental niche of *M. sculpturalis*, we used climate information obtained from the 19 layers in the current climate available in WorldClim database version 1.4 (<http://www.worldclim.org>). Spatial resolution was the same as that of the occurrence data (0.4°). These layers present data on seasonality trends, average and extreme values of temperatures and precipitation over the period 1950–2000 (Fig. A1).

Since many of these environmental variables were strongly inter-correlated, and because we were unaware of which of them could be particularly important for the niche of the studied bee species, we performed a Principal Component Analysis (PCA) to reduce the number of variables to few ones that are not correlated (the PCA factors). The two first PCA factors (which explained the 72.2% of the total variance) were selected and then the variables that most strongly correlated with these two factors were identified (see Fig. A1) (Broennimann et al., 2012; Silva et al., 2014). The PCA factor 1 was positively correlated mostly with Mean diurnal temperature range [mean of monthly (max temp – min temp)] (BIO2) and secondarily negatively correlated with Mean temperature of driest quarter (BIO9). The PCA factor 2 was mostly negatively correlated with Temperature seasonality (standard deviation*100) (BIO4) and secondarily positively correlated with Precipitation of driest quarter (BIO17). A plot with these PCA factors as axes was built to represent the global environmental space occupied by *M. sculpturalis*.

We calculated the native and invaded range overlap to test if *M. sculpturalis* is experiencing niche conservatism, niche unfilling or niche expansion in the invaded area (Wiens and Graham 2005; Broennimann et al., 2012; Guisan et al., 2014). In particular, the niche overlap between native and invaded range was calculated using Schoener's *D* index (Schoener 1970), which varies from 0 (no overlap between niches) to 1 (whole overlap). We then followed the procedure of Broennimann et al. (2012) to test niche equivalency (i.e. whether the niche overlap is constant when randomly reallocating the occurrences of both entities among the native and invaded areas) and similarity (i.e. whether the overlap between observed niches in native and invaded ranges is different from the overlap between the observed niche in one range and niches selected at random from the other range). The null hypothesis of niche equivalency cannot be rejected if the observed value of *D* falls within the density of 95% of 100 simulated values, while the species occupies environments in both of its ranges that are more similar to each other than expected if the observed overlap is greater than 95% of 100 simulated values (Broennimann et al., 2012). These statistical analyses were performed using the *ecospat* package (Di Cola et al., 2017) in R v3.3.1 (R Core R Development Core Team, 2015).

2.3. Potential distribution under current climate conditions

We estimated the global potential distribution of *M. sculpturalis* (i.e. the geographic area in which the abiotic environment is suitable to live; see Jiménez-Valverde et al. (2011)) through two methods largely used in biological invasion studies. Both methods were based on the two variables best correlated with the first two PCA factors (BIO2 and BIO4). Because these two variables were highly correlated respectively with BIO9 and BIO17, the role of the latter can be then also discussed. Besides, we decided to use simple methods and as few variables as possible in order to be conservative, avoiding overfitting models to predict potential distributions of invasive species.

First, we used a multidimensional envelope procedure (MDE), which is based on the minimum and maximum values of the two variables extracted from the PCA factors (Beaumont et al., 2005). MDE is an approach directed at maximizing the capacity to represent geographically the potential distribution of species when they are only based on distributional data (Broennimann and Guisan 2008; Jiménez-Valverde et al., 2011; Sánchez-Fernández et al., 2011), under the assumption that occurrence points reflect a subset of the suitable conditions under which a species can survive. The Mahalanobis distance (a type of multidimensional non-Euclidean distance) between each grid cell and the centroid of the hyper-volume of the selected variables was used to obtain continuous values for environmental suitability within the potential distribution of *M. sculpturalis* (Farber and Kadmon 2003; Calenge et al., 2008; Guareschi et al., 2013). These statistical analyses were performed in Statistica 8.0 (Statsoft, 2008).

Second, we used the maximum entropy algorithm (MaxEnt v3.3.0), which also uses presence-only data (Elith et al., 2006; Phillips et al., 2006; Phillips and Dudik 2008; Merow et al., 2013). As for MDE, also in MaxEnt both continuous and categorical environmental data can be used as input variables. Maximum entropy modelling is a machine-learning method that estimates an organism's potential distribution by finding the probability distribution using maximum entropy (i.e. the highest

uniformity), given the constraint that the expected value of each environmental predictor under this estimated distribution matches the empirical average of sample locations. Default values for the convergence threshold, and the cloglog output format to generate response curves and Jackknife results were selected (see Phillips et al., 2017). Finally, 25 replicates were run, and MaxEnt output a single average model. The final map obtained shows the probability of occurrence according to a 0–1 scale. In each replicate, eighty percent of the records were used for model training and the remaining twenty percent for validation. To evaluate model performance, the Area Under the receiver operating characteristic Curve (AUC) was used (Elith et al., 2006). This analysis provides a single measure of model performance and ranges from 0.5 (randomness) to 1 (perfect discrimination). Thuiller (2003) established a scale to enable interpretation of AUC values and for model validation: 0.90 to 1.00 = excellent; 0.80 to 0.90 = good; 0.70 to 0.80 = average; 0.60 to 0.70 = poor; 0.50 to 0.60 = insufficient. Additionally, a Jackknife analysis was adopted to estimate which variables were most important for model building. In the case of generating binary maps we were conservative using the Minimum training presence as threshold.

2.4. Potential distribution under future climate conditions

Effects of climate change on the potential distribution were predicted considering the IPCC5 climate projections using the CCSM4 global climate model for 2070 (average for 2061–2080), and two extreme representative concentration pathways which reflect two possible changes in future anthropogenic (i.e., human) greenhouse gas (GHG) emissions. One pathway concentration was RCP 2.6, which assumes that global annual GHG emissions (measured in CO₂-equivalents) will peak before 2100 and then declines; the other scenario was RCP 8.5, which assumes that global annual GHG emissions will continue to rise throughout the twenty-first century. The layers with the future climatic data were obtained from Worldclim 1.4. (<http://www.worldclim.org>) (Hijmans et al., 2005), with the same spatial resolution of the occurrence data (0.4°). Future potential distributions under such scenarios were estimated through both MDE and MaxEnt.

3. Results

Megachile sculpturalis currently lives exclusively in the Northern hemisphere. The native range is confined to eastern Asia (Table A1), while the invaded range include both areas of North America and of Europe (Fig. 1C). In America, this bee species rapidly expanded from North Carolina (where was first detected in 1994) to Alabama, Wisconsin, Maine, Kansas, Texas and other US states, as well as to Canada (Table A1). In Europe, after the first detection in France (2008), the species reached Italy, Switzerland, Germany, Hungary, Slovenia, Austria, Spain and Crimea (Table A1).

By plotting the first two PCA factors obtained from the environmental variables, we found that *M. sculpturalis* occupies areas with moderate values of PCA factor 1, which is strongly correlated with BIO2 and BIO9 (Fig. 2). This suggests that this species occupies climates with reduced diurnal temperature fluctuations (BIO2) and areas with moderate temperature during the driest months (BIO9). Furthermore, *M. sculpturalis* mostly occupies areas with moderate values of PCA factor 2. This suggests an occupation of areas with moderate temperature seasonality (BIO4) and moderate precipitation in the driest months (BIO17). Thus, overall *M. sculpturalis* mostly occupies areas with temperate climatic regimes.

Despite such preference for temperate climate can be clearly observed in both the Asian native and invaded European and North American areas, in the latter two continents *M. sculpturalis* both enlarged and shifted its environmental niche after invasion (Fig. 2, Table 1). Indeed, both niche expansion and (even with higher values) niche unfilling were considerable, particularly for Europe (Table 1), and *D* value (niche overlap) was small. No significant results were found for both niche equivalency test (although higher in Europe than in North America) and niche similarity test (similar values in both invaded continents; see Table 1).

Both used methods (MDE and MaxEnt (AUC: 0.94–0.99, see Table A2)) provided very similar outputs predicting an important expansion in many areas still not occupied (Fig. 3A and B). In Europe, *M. sculpturalis* could easily establish further in the Iberian Peninsula, which showed high climatic suitability in most of its area excluding Portugal; some unoccupied areas of Italy, France and other central-eastern countries have climatic conditions that fall within the climatic niche suitable for the species (Fig. 3A and B). New European areas that could be potentially be invaded by the species include, among others, Scandinavia, Balkans and Greece (Fig. 3A and B). In North America, *M. sculpturalis* could potentially expand its invaded range within the United States and Canada, including far western areas not occupied yet, though it would not survive in central areas of North America (Fig. 3A and B). The MaxEnt outputs also showed that this alien bee species prefers area with reduced diurnal temperature fluctuations (BIO2) and low to moderate temperature seasonality (BIO4) (Fig. 3C).

We identified also new areas out of the already reached continents that could be potentially invaded by *M. sculpturalis*. These include central-southern Asia (e.g. India), Northern Africa (including Arabic peninsula) and, to a weaker extent of suitability, few areas in Australia and South America. In general, the species would not establish at optimum conditions in any countries of the southern hemisphere, where most areas were completely unsuitable (Fig. 3). The effect of the observed niche expansion and niche shift after invasion in *M. sculpturalis* is also clearly visible when the potential distribution is built using either using occurrence data only from the native areas, only from European invaded area and only from North America invaded area, since these three predicted distributions greatly varied (Fig. A2).

Under climate change, the species may show a further, though limited spread. While MDE predicts a limited distribution expansion towards North in the North America and towards North-East from Europe into Asian territories (Fig. 4A–C), MaxEnt predicts even lesser expansion, essentially in Europe, into regions like Northern Germany and Northern France, but

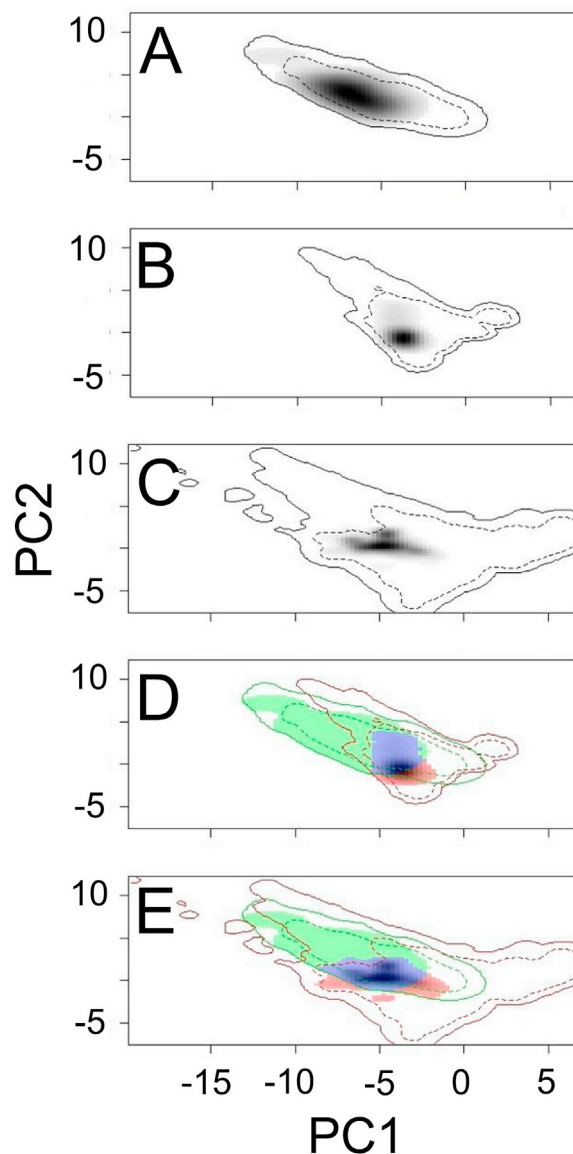


Fig. 2. Comparison of climatic niches of *M. sculpturalis* in its native range (A), European invaded range (B) and American invaded range (C), and niche shifts between native range and the two invaded ranges ((D) Europe, (E) America)). Colours indicate niche expansion (red), stability (blue), and unfilling (green). Darker shading indicates higher density of species occurrences in the invaded area; solid contour lines enclose all available environments for each range; dashed contour lines, 90th percentile of the background environment for both ranges. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Niche expansion and niche unfilling of *M. sculpturalis* in the native range and two invaded areas (Europe and North America), and results of niche overlap (Schoener's *D*), niche equivalency test and niche similarity test for the native vs. the invaded areas. Measures of niche expansion and unfilling are based on the 90th percentiles of the common environment between ranges. Niche overlap (Schoener's *D*) values of native populations are compared with 1000 simulated data sets for both Europe and North America.

	Niche expansion (%)	Niche unfilling (%)	Niche overlap (<i>D</i>)	Niche Equivalency (<i>P</i>)	Niche Similarity (<i>P</i>)
Europe	36.3	76.6	0.19	1	0.38
North America	13.9	57.5	0.31	0.27	0.37

not in North America. Additionally, MaxEnt estimates that areas currently weakly suitable, like certain mountain areas of the Alps, the Apennines and the Spanish central system, will increase their suitability. However, such further spreads will be likely

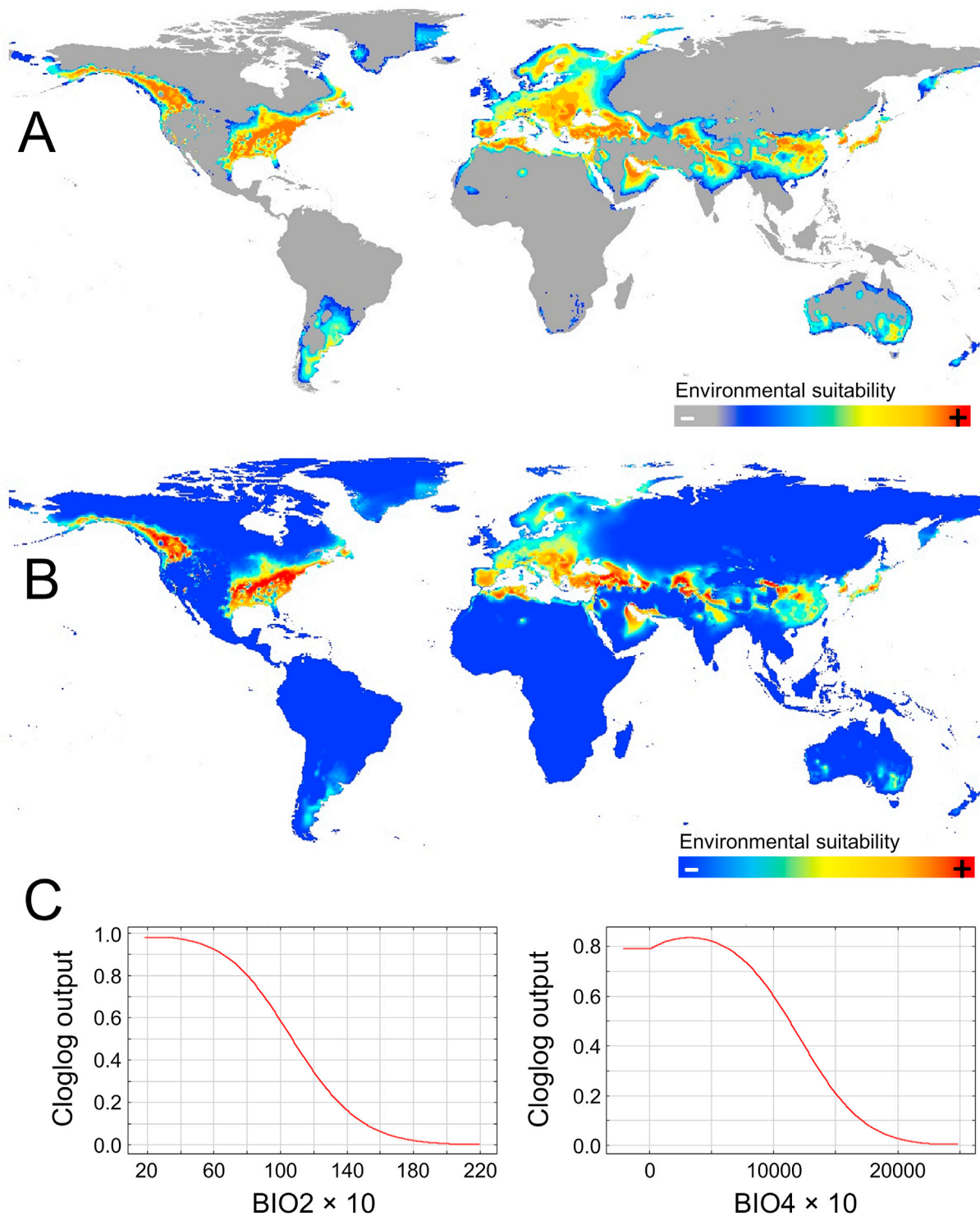


Fig. 3. Potential distribution of *M. sculpturalis*, based on the multidimensional envelope procedure (MDE) (A) and on MaxEnt algorithm (B) using all occurrence data, highlighting the degree of suitability (calculated through Mahalanobis distance method) for the species survival (increasing from grey to red in A and increasing from blue to red in B). (C) Relationships, as obtained with MaxEnt, between climatic variables (BIO2 and BIO4) and occurrence suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

only under the most extreme scenario of climate change (RCP 8.5), since under the RCP 2.6 scenario differences with current conditions are almost unappreciable (particularly as obtained with MaxEnt) (Fig. 4B).

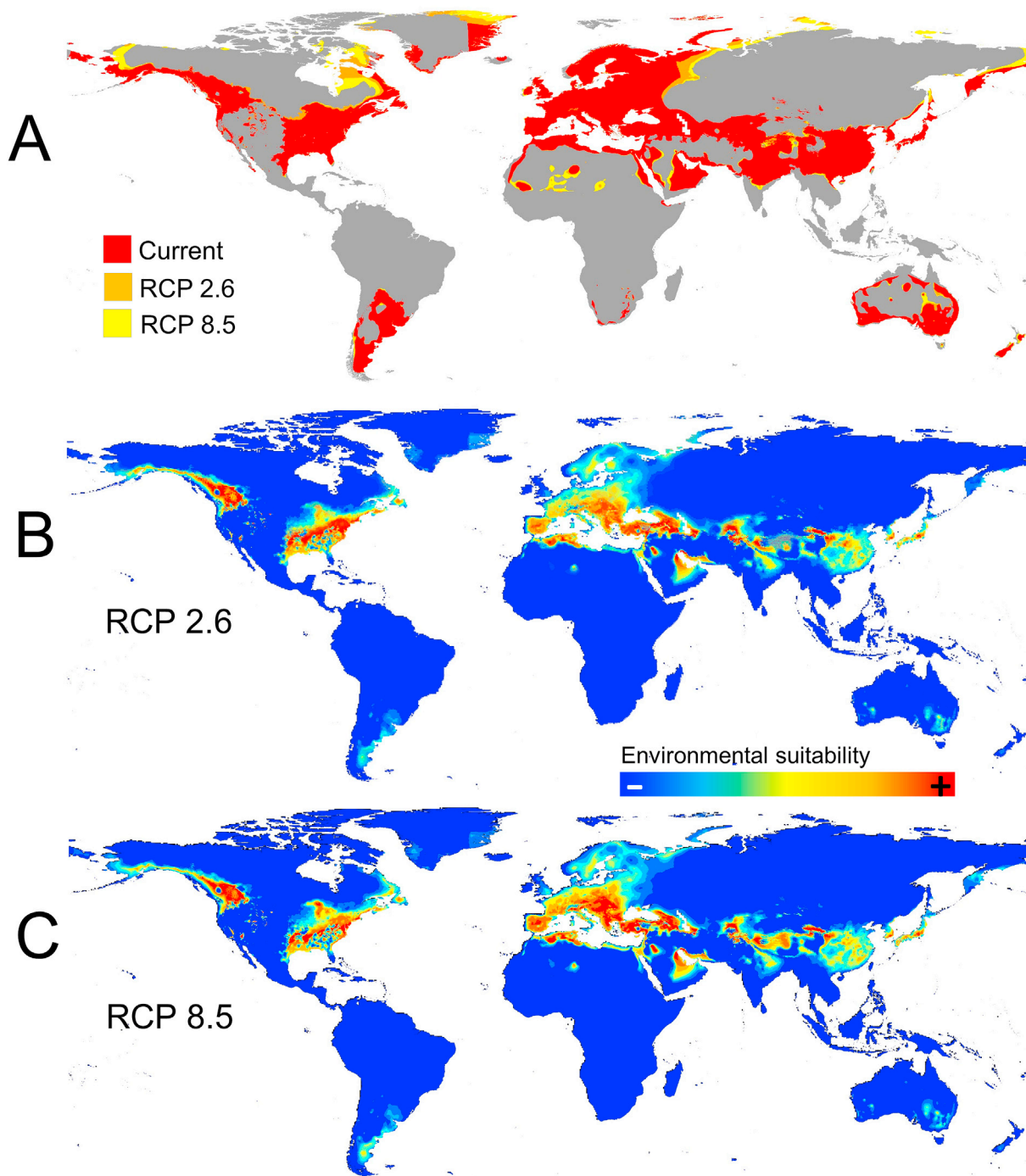


Fig. 4. Estimate of the future potential distribution of *M. sculpturalis*, under IPCC5 climate projections using the CCSM4 global climate model for 2070, and considering two concentration pathways (RCP 2.6 and RCP 8.5). (A) Estimate of the potential dynamics of invasion risk areas through time (i.e., combining current and future model outputs), based on multidimensional envelope procedure (MDE); (B–C) Estimate of the future potential spread based on MaxEnt algorithm (B: RCP 2.6 concentration pathway; C: RCP 8.5 concentration pathway).

4. Discussion

Despite it is not ascertained, *M. sculpturalis* was most probably transported to the currently invaded areas by trans-continental shipping inside wood, which is its nest substrate (Hinojosa-Díaz et al., 2005). This is not surprising given that

many invertebrates, including other Apoidea, which develop in wood, have colonized non-native areas in the last decades (Klapwijk et al., 2016; Polidori et al., 2018). It is actually unknown if *M. sculpturalis* colonized independently North America and Europe, or if the species arrived to Europe from North America, the latter pattern having been observed for other invasive insects through molecular analyses (Lombaert et al., 2014). What seems clearer is that this alien bee species is progressing remarkably fast from year to year expanding its area geographically, likely helped, at last in Europe, by jump-dispersal through the major traffic routes (Lanner et al., 2020). The fast rate of invasion of this bee species could be also favoured by its remarkably large body size, since this trait is known to affect flight distance in bees (Greenleaf et al., 2007).

While Mediterranean areas are known to be generally very suitable for alien Hymenoptera that occur today in Europe (Rasplus et al., 2010; Polidori et al., 2018), the potential distribution of *M. sculpturalis* suggests that this may be only partially true for this bee species. Indeed, while our data show that this species could likely expand through further areas of Europe, it will not find optimal conditions in many strictly Mediterranean zones, such as southern Italy and almost all Mediterranean islands. Furthermore, *M. sculpturalis* would not find optimal conditions in most coastal areas in Europe, converting it in a possible exception to the general observation that, at global scale, coastal areas, (together with islands) harbour the highest richness of already established alien species (Dawson et al., 2017). In North America, *M. sculpturalis* would likely reach and establish in vast highly suitable areas of the West coast, but to do so it should first establish in the central areas of North America, which are largely very weakly suitable. Thus, this bee species could only reach the West coast through a further accidental introduction by humans. Such predictions are similar to those resulting from a previous model of a smaller North American dataset (Hinojosa-Díaz et al., 2005).

Despite the great range expansion of *M. sculpturalis* predicted under current climatic conditions, predictions for future (in 50 years) potential range overall suggest that climate change may weakly further enlarge the suitable areas. This is interesting, since in general increased temperature and higher frequency of extreme climatic events (e.g. heat waves, hurricanes) are expected to greatly affect the establishment of alien species in new territories (Diez et al., 2012; Hulme 2017). An important increase in the extent of suitable areas under climate change scenarios was also predicted for other aculeate Hymenoptera (Bertelsmeier et al., 2015; Barbet-Massin et al., 2013; Polidori et al., 2018), including other bees (Dew et al., 2019). However, cases of bee species that are predicted to retract their ranges due to climate change are also known (Sirois-Delisle and Kerr 2018).

The potential spread of *M. sculpturalis* may have consequences on the local bee fauna. For example, this species was observed to compete for nesting resources with large native bees of the genus *Xylocopa* (Laport and Minckley 2012; Parys et al., 2015; Le Féon et al., 2018). In Europe, very high suitability areas for this invasive species correspond also with high density areas of *Xylocopa* populations (Southern-central Europe) (Terzo and Rasmont 2014), so that some level of competition is expected. In North America, *Xylocopa virginica* L., one abundant species that was seen to be displaced by *M. sculpturalis* (Laport and Minckley 2012), shows a distribution clearly overlapping with that of this alien bee (Western USA) (Skandalis et al., 2011). However, phenological differences between *M. sculpturalis* and *Xylocopa* (which, e.g., in Europe tends to start earlier their nesting activity in Spring) may mitigate such competition in certain periods of the year. Furthermore, both *M. sculpturalis* and species of the genus *Xylocopa* are largely generalists in the plant species used for pollen collection (Kearse 2010; Le Feón et al., 2018), suggesting that they may also overlap at least partially their diet and thus compete for food resources. However, it is also notable that this alien bee tends to collect pollen preferentially from exotic plants, such as *Sophora japonica* L. (Fabaceae) and *Ligustrum* sp. (Olaceae) (Quaranta et al., 2014; Andrieu-Ponel et al., 2018), which perhaps limits competition for pollen resources.

Recently, *M. sculpturalis* was the most abundant species that emerged from bee hotels (i.e. trap-nests) set up in Marseille (France) and, more worryingly, a negative correlation between the occurrence of this alien species in bee hotels and the presence of native bees emerged (Geslin et al., 2020). This alien bee was even observed actively removing all the content (e.g. wasps' prey, bee pupae) from nests of other bee and wasp species in order to use them to breed (Westrich 2018; Lanner et al., 2020). Hence, the territorial and aggressive behaviour of *M. sculpturalis* toward the nests built by native bees can even decrease the efficacy of conservation programs and biodiversity studies that heavily use bee hotels (e.g. Fortel et al., 2016; Dainese et al., 2018).

It is important to point out that our predictions on the potential distribution of the studied bee species give insights on the areas where these species are more likely to expand their range, but may be not powerful in assessing where these species could not establish. Indeed, the niche estimated from the invasive ranges greatly differ from the niche estimated from the native range, pointing to niche shift and niche expansion in the invaded areas. Furthermore, such niche changes differed between the two invasions (Europe and North America). This pattern indicates that the distribution of this species is not in equilibrium with the environmental conditions. Indeed, while niche conservatism (somehow *a priori* assumption for predicting potential invasion areas (Jiménez-Valverde et al., 2011)) limits the uncertainty associated with niche shifts from native to invaded areas (Peterson et al., 2011), niche shift and expansion imply that the species is plastic enough to adapt to novel conditions in an unpredictable way. This uncertainty could be at least partially due to two reasons. First, we considered only one portion of the fundamental niche of the species, i.e. climatic conditions, while it would be desirable to add also biotic (as well as additional abiotic) drivers of distributions in the models (e.g. food resources, interactions with other species, habitat type, land cover) (Soberón and Nakamura 2009; Biella et al., 2020). Second, physiological experiments devoted to ascertain which conditions the species are actually able to tolerate add precision to any prediction on potential distribution (Jiménez-Valverde and Lobo 2011; Arribas et al., 2012; Biella et al., 2020). Our result, however, is not really surprising, since observations of niche changes in invasive species are increasingly reported (Early and Sax 2014; Tingley et al., 2014; Hill et al., 2017).

In addition, the environmental niche of *M. sculpturalis* seems largely unfilled. This pattern seems more common in case of recent introductions (Strubbe et al., 2015; Polidori et al., 2018), and likely applies to this bee species. An alternative less plausible hypothesis is that niche shift and niche unfilling in *M. sculpturalis* are only apparent and due to its over-sampling in the invaded range compared with the native range.

When comparing with other invasive insect species, at first one notes that niche conservatism is rare and niche unfilling and niche expansion common (Hill et al., 2017). However, the degree of shift/expansion is extremely variable, with only five of the insect species analysed in that study showing conspicuous niche change (>30%). For *M. sculpturalis*, niche shift was 36.3% for European invasion and 13.9% for North American invasion, thus also reaching important values. Altogether, our results suggest that *M. sculpturalis* could reach in the future even some areas not predicted as highly suitable in our analysis. Thus, predictions resulting from environmental niche modelling should be taken with cautions for this bee species, given its possible important adaptation ability to new conditions. For this reason, our environmental niche modelling approach has to be considered as a base for future studied on the colonization patterns of *M. sculpturalis*. A similar conclusion was reached by Strange et al. (2011) while modelling the potential distribution of another invasive megachilid, *Anthidium manicatum* (Linnaeus 1758), for which the bioclimatic models show poor predictive capabilities, particularly for South America.

Concerning niche overlap between native and invasive areas, our results on *M. sculpturalis* somehow differ from what observed in *A. manicatum*. In this European bee species, which colonized America, niche similarity (*D*) between the native and invasive models ranged from 0.69 (South American invasion) to 0.78 (North American invasion), revealing a moderate to high niche overlap and a low to moderate niche shift (Strange et al., 2011). Such values are much higher than those observed for *M. sculpturalis* in the present study (from 0.19 for European invasion to 0.31 for North American invasion), which indicates much lower niche overlaps, both due to large niche shift and considerable niche unfilling. On the other hand, the low niche overlap observed for *M. sculpturalis* seems closer to those observed for invasive social Hymenoptera, such as the bumblebee *Bombus terrestris* (L.), the honeybee *Apis florea* Fabricius, the wasps *Vespa velutina* Lepeletier and *Vespula germanica* (Fabricius) and several ant species (Villemant et al., 2011; Acosta et al., 2016; de Villiers et al., 2017; Hill et al., 2017; Silva 2019). However, conspicuous niche unfilling (57.5%–76.6%) as observed in *M. sculpturalis* seems rare in invasive Hymenoptera (only two ant species, *A. florea* and *I. mexicana* have niche unfilling >50%) (Hill et al., 2017; Polidori et al., 2018; Silva 2019), though only for *I. mexicana* this was not accompanied by a niche shift. Overall, these trends seem to suggest that invasive Hymenoptera tend, in general, to shift their niches rather than conserve their niches, during the colonization of non-native areas. However, cases of niche conservatism are also reported for bees expanding their range outside their native areas (Biella et al., 2020). At the moment, potential distribution and environmental niche were studied only for three alien solitary aculeate species (Strange et al., 2011; Polidori et al., 2018; this study), while more investigations were performed on alien social aculeate species (Ward 2007; Chen, 2005; Steiner et al., 2008; Acosta et al., 2016; de Villiers et al., 2017; Keeling et al., 2017; Sung et al., 2018; Silva et al., 2019; Biella et al., 2020). Thus, more studies are necessary to verify which factors, including social behaviour, may shape range extension patterns and niche changes in aculeate Hymenoptera.

5. Conclusions

In conclusion, our study suggests that *M. sculpturalis* has a strong potential to spread in new areas under current climatic conditions (with very limited further expansions under future conditions), possibly in a pattern not fully predictable. The fact that *M. sculpturalis* did not reach niche equilibrium (being its niche both unfilled and shifted in the invaded areas) represents an important aspect to consider while trying to predict its invasion patterns, and certainly shows a weak side of using SDMs solely based on the climatic conditions at the currently occupied areas. There are other limitations that merit attention. For example, our modelling procedures treats each record equally even if the bee abundance is very variable among sites, with the consequent overestimation of niche width and potential distribution (Gomes et al., 2018).

In any case it is important to invest in controls at ports and other trade nodes to minimize future dispersions, particularly when considered that the shuffling of bees across areas may both result in competition with local bee fauna and in the spread of novel bee pathogens and parasites (Gilliam et al., 1994; Goka et al., 2001; Goulson 2003; Colla et al., 2006; Schmid-Hempel et al., 2014). Both these adverse effects were reported for alien megachilids (Goerzen et al. 1990, 1992; Goerzen et al. 1990; Barthell and Frankie 1998; Laport and Minckley 2012; Parys et al., 2015; Le Féon et al., 2018). Greater investment in prevention rather than in management of alien species is warranted (Leung et al., 2002), and since this species nest in wood, control efforts should particularly be concentrated on commercial wood trades. Furthermore, the easy recognition of this alien bee species by citizens in the field supports early detections in still unreported localities via citizen-science programs (Lanner et al., 2020), that should be, in our opinion, promoted in both all colonized countries and not colonized countries where *M. sculpturalis* have environmental conditions predicted to allow its presence.

From an ecological point of view, our results on *M. sculpturalis* claims for further investigations on the many other alien bee species actually recorded over the world. For example, a comparative (phylogeny-corrected) approach can shed lights on the role of particular traits, such as body size, physiological thresholds (e.g. thermal tolerance), nesting habits, diet specialization, social behaviour and year of first establishment in the invaded area, on the spreading patterns of alien bees. This would also allow a better understanding on the reasons why megachilids are currently the most common among bees in non-native areas.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by Universidad de Castilla-La Mancha and the Universidad de Murcia [SECTI post-doctoral contracts to CP and DSF]; and Ministerio de Ciencia e Innovación (Spain) [CGL2017-83046-P]. We thank Davide Santoro (Victoria University of Wellington, New Zealand) for helping in checking the literature information. We are indebted to Laura Bortolotti and Angelo Sommaruga for kindly providing the pictures of *M. sculpturalis* shown in Fig. 1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01365>.

References

- Acosta, A.L., Giannini, T.C., Imperatriz-Fonseca, V.L., Saraiva, A.M., 2016. Worldwide alien invasion: a methodological approach to forecast the potential spread of a highly invasive pollinator. *PLoS One* 11, e0148295.
- Aguado, O., Hernández-Castellano, C., Bassols, E., Miralles, M., Navarro, D., Stefanescu, C., Vicens, N., 2018. *Megachile (Callomegachile) sculpturalis* Smith, 1853 (Apoidea: Megachilidae): a new exotic species in the Iberian Peninsula, and some notes about its biology. *Bull. Inst. Catal. Hist. Nat.* 82, 157–162.
- Amiet, F., 2012. Die blattschneiderbiene *Megachile sculpturalis* Smith, 1853 (Hymenoptera, apidae) nun auch in der Schweiz. *Entomol. Helvetica* 1853, 157–159.
- Andrieu-Ponel, V., Ponel, P., Le Féon, V., Geslin, B., Duvallet, G., 2018. A propos du comportement de butinage de *Megachile sculpturalis* Smith, 1853, en France méditerranéenne (Nîmes et Montpellier) (Hymenoptera, Megachilidae). *Bull. Soc. Entomol. Fr.* 123, 49–54.
- Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* 33, 1677–1688.
- Arim, M., Abades, S.R., Neill, P.E., Lima, M., Marquet, P.A., 2006. Spread dynamics of invasive species. *Proc. Natl. Acad. Sci. U.S.A.* 103, 374–378.
- Arribas, P., Abellan, P., Velasco, J., Bilton, D.T., Millan, A., Sanchez-Fernandez, D., 2012. Evaluating drivers of vulnerability to climate change: a guide for insect conservation strategies. *Global Change Biol.* 18, 2135–2146.
- 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.
- Barthell, J., Frankie, G., 1998. Invader effects in a community of cavity nesting megachilid bees (Hymenoptera: Megachilidae). *Environ. Entomol.* 27, 240–247.
- Batra, S.W.T., 1998. Biology of the giant resin bee, *Megachile sculpturalis* Smith, a conspicuous new immigrant in Maryland. *Md. Nat.* 42, 1–3.
- Beaumont, L.J., Hughes, L., Poulsen, M., 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecol. Model.* 186, 250–269.
- Bertelsmeier, C., Blight, O., Courchamp, F., 2015. Invasions of ants (Hymenoptera: formicidae) in light of global climate change. *Myrmecol. News* 22, 25–42.
- Biella, P., Četković, A., Gogala, A., Neumayer, J., Sároszpatáki, M., Šima, P., Smetana, V., 2020. North-westward range expansion of the bumblebee *Bombus haematurus* into Central Europe is associated with warmer winters and niche conservatism. *Insect Sci.* <https://doi.org/10.1111/1744-7917.12800>.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W. E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science* 313, 351–354.
- Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vilá, M., Wilson, J.R.U., Winter, M., Genovesi, P., Bacher, S., 2014. A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biol.* 12, e1001850.
- Bortolotti, L., Luthi, F., Flaminio, S., Bogo, G., Sgolastra, F., 2018. First record of the asiatic bee *Megachile disjunctiformis* in Europe. *Bull. Insectol.* 71, 143–149.
- Broennimann, O., Guisan, A., 2008. Predicting current and future biological invasions: both native and invaded ranges matter. *Biol. Lett.* 4, 585–589.
- Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T., Guisan, A., 2007. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* 10, 701–709.
- Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecol. Biogeogr.* 21, 481–497.
- Calenge, C., Darmon, G., Basille, M., Loison, A., Jullien, J.M., 2008. The factorial decomposition of the Mahalanobis distances in habitat selection studies. *Ecology* 89, 555–566.
- Chen, Y., 2005. Global potential distribution of an invasive species, the yellow crazy ant (*Anoplolepis gracilipes*) under climate change. *Integr. Zool.* 3, 166–175.
- Clavero, M., Garcia-Berthou, E., 2005. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* 20, 110.
- Colautti, R.I., MacIsaac, H.J., 2004. A neutral terminology to define 'invasive' species. *Divers. Distrib.* 10, 135–141.
- Colla, S.R., Otterstater, M.C., Gegear, R.J., Thompson, J.D., 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biol. Invasions* 129, 461–467.
- Dainese, M., Riedinger, V., Holzschuh, A., Kleijn, D., Scheper, J., Steffan-Dewenter, I., 2018. Managing trap-nesting bees as crop pollinators: spatiotemporal effects of floral resources and antagonists. *J. Appl. Ecol.* 55, 195–204.
- Danforth, B.N., Minckley, R.L., Neff, J.L., 2019. *The Solitary Bees: Biology, Evolution, Conservation*. Princeton University Press, Princeton.
- Dawson, W., Moser, D., van Kleunen, M., Krefth, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T.M., Dyer, E.E., Cassey, P., Scrivens, S.L., Economo, E.P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., García-Berthou, E., Casal, C., Mandrak, N.E., Fuller, P., Meyer, C., Essl, F., 2017. Global hotspots and correlates of alien species richness across taxonomic groups. *Nat. Ecol. Evol.* 1, 0186.
- de Villiers, M., Kriticos, D.J., Veldtman, R., 2017. Including irrigation in niche modelling of the invasive wasp *Vespa germanica* (Fabricius) improves model fit to predict potential for further spread. *PLoS One* 12, e0181397.
- Dew, R.M., Silva, D.P., Rehan, S.M., 2019. Range expansion of an already widespread bee under climate change. *Global Ecol. Cons.* 17, e00584.
- Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F.T., D'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R.G., Hordijk, W., Salamin, N., Guisan, A., 2017. Ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 40, 774–787.
- Diez, J.M., D'Antonio, C.M., Dukes, J.S., Grosholz, E.D., Olden, J.D., Sorte, C.J.B., Blumenthal, D.M., Bradley, B.A., Early, R., Ibañez, I., Jones, S.J., Lawler, J.J., Miller, L.P., 2012. Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.* 10, 249–257.
- 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. *Global Ecol. Biogeogr.* 23, 1356–1365.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, 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. McC., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R.,

- Schapiro, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Farber, O., Kadmon, R., 2003. Assessment of alternative approaches for bioclimatic modelling with special emphasis on the Mahalanobis distance. *Ecol. Model.* 160, 115–130.
- Fortel, L., Henry, M., Guilbaud, L., Mouret, H., Vaissière, B.E., 2016. Use of human-made nesting structures by wild bees in an urban environment. *J. Insect Conserv.* 20, 239–253.
- Gbif.org, 1 November 2019. In: GBIF Occurrence Download. <https://doi.org/10.15468/dl.6ize1s>, 10.15468/dl.y0wswe.
- Geslin, B., Gachet, S., Deschamps-Cottin, M., Flacher, F., Ignace, B., Knoploch, C., Meineri, E., Robles, C., Ropars, L., Schurr, L., Le Féon, V., 2020. Bee hotels host a high abundance of exotic bees in an urban context. *Acta Oecol.* 105, 103556.
- Gilliam, M., Lorenz, B.J., Buchmann, S.L., 1994. *Ascospaera apis*, the chalkbrood pathogen of the honeybee, *Apis mellifera*, from larvae of a carpenter-bee, *Xylocopa californica arizonensis*. *J. Invertebr. Pathol.* 63, 307–309.
- Goerzen, D.W., Erlandson, M.A., Bissett, J., 1990. Occurrence of chalkbrood caused by *Ascospaera aggregata* skou in a native leaf-cutting bee, *Megachile relativata* cresson (Hymenoptera, Megachilidae), in saskatchewan. *Can. Entomol.* 122, 1269–1270.
- Goerzen, D.W., Dumouchel, L., Bissett, J., 1992. Occurrence of chalkbrood caused by *Ascospaera aggregata* skou in a native leaf-cutting bee, *Megachile pugnata* say (Hymenoptera, Megachilidae), in saskatchewan. *Can. Entomol.* 124, 557–558.
- Goka, K., Okabe, K., Yoneda, M., Niwas, S., 2001. Bumblebee commercialization will cause worldwide migration of parasitic mites. *Mol. Ecol.* 10, 2095–2099.
- Gomes, V.H.F., Ijff, S.D., Raes, N., Leão Amaral, I., Salomão, R.P., de Souza Coelho, L., et al., 2018. Species distribution modelling: contrasting presence-only models with plot abundance data. *Sci. Rep.* 8, 1003. <https://doi.org/10.1038/s41598-017-18927-1>.
- Goulson, D., 2003. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Systemat.* 34, 1–26.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationships to body size. *Oecologia* 153, 589–596.
- Guareschi, S., Coccia, C., Sánchez-Fernández, D., Carbonell, J.A., Velasco, J., Boyero, L., Green, A.J., Millán, A., 2013. How far could the alien boatman *Trichochirix verticalis verticalis* spread? Worldwide estimation of its current and future potential distribution. *PLoS One* 8, e59757.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.J., Regan, T.J., Brotons, L., McDonald-Madden, E., Matyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broenniman, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. *Ecol. Lett.* 16, 1424–1435.
- Guisan, A., Petitpierre, B., Broenniman, O., Daehler, C., Kueffer, C., 2014. Unifying niche shift studies: insights from biological invasions. *Trends Ecol. Evol.* 29, 260–269.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C., Thomson, D., 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecol. Lett.* 8, 91–101.
- 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.
- Hill, M.P., Gallardo, B., Terblanche, J.S., 2017. A global assessment of climatic niche shifts, and human influence, in insect invasions. *Global Ecol. Biogeogr.* 26, 679–689.
- Hinojosa-Díaz, I.A., Yáñez-Ordóñez, O., Chen, G., Peterson, A.T., Engel, M.S., 2005. The North American invasion of the giant resin bee (Hymenoptera: Megachilidae). *J. Hym. Res.* 14, 69–77.
- Hirashima, Y., 1974. Annotated check list of the Japanese species of the genus *Megachile* sensu lato (Hymenoptera, Megachilidae), with description of a new species. *Kontyu* 42, 174–180.
- Hulme, P.E., 2017. Climate change and biological invasions: evidence, expectations, and response options. *Biol. Rev.* 92, 1297–1313.
- Iwata, K., 1933. Studies on the nesting habits and parasites of *Megachile sculpturalis* Smith (Hymenoptera, Megachilidae). *Mushi* 6, 4–26 ([in Japanese]).
- Jiménez-Valverde, A., Lobo, J.M., 2011. Tolerance limits, animal. In: Simberloff, D., Rejmánek, M. (Eds.), *Encyclopedia of Biological Invasions*. University of California Press, Berkeley, CA, pp. 661–663.
- Jiménez-Valverde, A., Lobo, J.M., Hortal, J., 2008. Not as good as they seem: the importance of concepts in species distribution modelling. *Divers. Distrib.* 14, 885–890.
- Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P., Lobo, J.M., 2011. Use of niche models in invasive species risk assessments. *Biol. Invasions* 13, 2785–2797.
- Keasar, T., 2010. Large carpenter bees as agricultural pollinators. *Psyche* 2010, 927463. <https://doi.org/10.1155/2010/927463>.
- 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.
- Klapwijk, M.J., Hopkins, A.J.M., Eriksson, L., Pettersson, M., Schroeder, M., Lindelöw, Å., Rönnberg, J., Kesitalo, E.C.H., Kenis, M., 2016. Reducing the risk of invasive forest pests and pathogens: combining legislation, targeted management and public awareness. *Ambio* 45, 223–234.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. Roy. Soc. Lond. B* 274, 303–313.
- Lanner, J., Huchler, K., Pachinger, B., Sedivy, C., Meimberg, H., 2020. Dispersal patterns of an introduced wild bee, *Megachile sculpturalis* Smith, 1853 (Hymenoptera: Megachilidae) in European alpine countries. *PLoS One* 15 (7), e0236042.
- Laport, R., Minckley, R., 2012. Occupation of active *Xylocopa virginica* nests by the recently invasive *Megachile sculpturalis* in upstate New York. *J. Kans. Entomol. Soc.* 85, 384–386.
- Le Féon, V., Aubert, M., Genoud, D., Andrieu-Ponel, V., Westrich, P., Geslin, B., 2018. Range expansion of the Asian native giant resin bee *Megachile sculpturalis* (Hymenoptera, Apoidea, Megachilidae) in France. *Ecol. Evol.* 8, 1534–1542.
- Lee, H.-S., Ryu, D.-P., 2013. Insect Fauna of Korea, Volume 13, Number 4, Arthropoda: Insecta: Hymenoptera: Megachilidae. National Institute of Biological Resources, Ministry of Environment, Incheon, Republic of Korea.
- Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A., Lamberti, G., 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proc. Roy. Soc. Lond. B* 269, 2407–2413.
- Levine, J.M., D'Antonio, C.M., 2003. Forecasting biological invasions with increasing international trade. *Conserv. Biol.* 17, 322–326.
- Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2007. *Invasion Ecology*. Blackwell Publishing, Malden.
- Lombaert, E., Guillemaud, T., Lundgren, J., Koch, R., Facon, B., Grez, A., Loomans, A., Malausa, T., Nedvéd, O., Rhule, E., Staverlokk, A., Steenberg, T., Estoup, A., 2014. Complementarity of statistical treatments to reconstruct worldwide routes of invasion: the case of the Asian ladybird *Harmonia axyridis*. *Mol. Ecol.* 23, 5979–5997.
- Mangum, W.A., Sumner, S., 2003. A survey of the North American range of *Megachile (Callomegachile) sculpturalis*, an adventive species in North America. *J. Kans. Entomol. Soc.* 76, 658–662.
- Merow, C., Smith, M.J., Silander, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36, 1058–1069.
- Michener, C.D., 2007. *The Bees of the World*, second ed. Johns Hopkins University Press, Baltimore.
- Morales, C.L., 2007. Introducción de abejorros (*Bombus*) no nativos: causas, consecuencias ecológicas y perspectivas. *Ecol. Austral* 17, 51–65.
- Norfolk, O., Gilbert, F., Eichhorn, M.K., 2018. Alien honeybees increase pollination risks for range-restricted plants. *Divers. Distrib.* 24, 705–713.
- Okada, I., 1995. Behavioral characteristics of the giant leaf-cutter bee, *Megachile sculpturalis*. *Honeybee Sci.* 16, 111–112.
- Parys, K., Tripodi, A., Sampson, B., 2015. The giant resin bee, *Megachile sculpturalis* Smith: new distributional records for the mid-and gulf-south USA. *Biodivers. Data J.* 3, e6733 <https://doi.org/10.3897/BDJ.3.e6733>.

- Peterson, A.T., Papes, M., Kluza, D.A., 2003. Predicting the potential invasive distributions of four alien plant species in North America. *Weed Sci.* 51, 863–868.
- Peterson, A.T., Williams, R., Chen, G., 2007. Modeled global invasive potential of Asian gypsy moths. *Lymantria dispar*. *Entomol. Exp. Appl.* 125, 39–44.
- Peterson, A.T., Soberon, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M., Araujo, M.B., 2011. *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. *Ecography* 40, 887–893.
- Polidori, C., Nucifora, M., Sánchez-Fernández, D., 2018. Environmental niche unfilling but limited options for range expansion by active dispersion in an alien cavity-nesting wasp. *BMC Ecol.* 18, 36. <https://doi.org/10.1186/s12898-018-0193-9>.
- Praz, C.J., 2017. Subgeneric classification and biology of the leafcutter and dauber bees (genus *Megachile* Latreille) of the western Palearctic (Hymenoptera, Apoidea, Megachilidae). *J. Hym. Res.* 55, 1–54.
- Quaranta, M., Sommaruga, A., Balzarini, P., 2014. A new species for the bee fauna of Italy: *Megachile sculpturalis* continues its colonization of Europe. *Bull. Insectol.* 67, 287–293.
- R Core Development Core Team, 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rasplus, J.-Y., Villemant, C., Paiva, M.R., Delvare, G., Roques, A., 2010. Hymenoptera. In: Roques, A., Kenis, M., Lees, D., Lopez-Vaamonde, C., Rabitsch, W., Rasplus, J.-Y., Roy, D. (Eds.), *Alien Terrestrial Arthropods of Europe*. *BioRisk* 4, Berlin, pp. 669–776.
- Roques, A., Rabitsch, W., Rasplus, J.-Y., Lopez-Vaamonde, C., Nentwig, W., Kenis, M., 2009. Alien terrestrial invertebrates of Europe. In: *Delivering Alien Invasive Species Inventories for Europe (DAISIE)* (Eds.). *Handbook of Alien Species in Europe. Invading Nature*, vol. 3. Springer, Berlin, pp. 63–79. *springer series in invasion ecology*.
- Russo, L., 2016. Positive and negative impacts of non-native bee species around the world. *Insects* 7, E69. <https://doi.org/10.3390/insects7040069>.
- Sánchez-Fernández, D., Lobo, J.M., Hernández-Manrique, O.L., 2011. Species distribution models that do not incorporate global data misrepresent potential distributions: a case study using Iberian diving beetles. *Divers. Distrib.* 17, 163–171.
- Schmid-Hempel, R., Eckhardt, M., Goulson, D., Heinzmann, D., Lange, C., Plischuk, S., Escudero, L.R., Salathé, R., Scriven, J.J., Schmid-Hempel, P., 2014. The invasion of southern South America by imported bumblebees and associated parasites. *J. Anim. Ecol.* 83, 823–837.
- Schoener, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51, 408–418.
- Silva, D.P., Vilela, B., De Marco Jr., P., Nemésio, A., 2014. Using ecological niche models and niche analyses to understand speciation patterns: the case of sister neotropical orchid bees. *PloS One* 9 (11), e113246. <https://doi.org/10.1371/journal.pone.0113246>.
- Silva, D.P., Castro, A.C.F., Vilela, B., Ong, X.R., Thomas, J.C., Alqarni, A.S., Engel, M.S., Ascher, J.S., 2019. Colonizing the east and the west: distribution and niche properties of a dwarf Asian honey bee invading Africa, the Middle East, the Malay Peninsula, and Taiwan. *Apidologie*. <https://doi.org/10.1007/s13592-019-00711-x>.
- Sirois-Delisle, C., Kerr, J.T., 2018. Climate change-driven range losses among bumblebee species are poised to accelerate. *Sci. Rep.* 8, 14464. <https://doi.org/10.1038/s41598-018-32665-y>.
- Skandalis, D.A., Richards, M.H., Sformo, T.S., Tattersall, G.J., 2011. Climate limitations on the distribution and phenology of a large carpenter bee, *Xylocopa virginica* (Hymenoptera: apidae). *Can. J. Zool.* 89, 785–795.
- Soberón, J., Nakamura, M., 2009. Niches and distributional areas: concepts, methods, and assumptions. *Proc. Natl. Acad. Sci. U.S.A.* 106, 19644–19650.
- Statsoft, 2008. *Statistica for Windows (Data Analysis Software System)*, Version 8.0. 298 p. Computer Program Manual, Quick Reference. Statsoft, Inc., Tulsa.
- Steiner, F.M., Schlick-Steiner, B.C., VanDerWal, J., Reuther, K., Christian, E., Stauffer, C., Suarez, A.V., Williams, S.E., Crozier, R.H., 2008. Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. *Divers. Distrib.* 14, 538–545.
- Stout, J., Goulson, D., 2000. Bumblebees in Tasmania: their distribution and potential impact on Australian flora and fauna. *Bee World* 81, 80–86.
- Stout, J.C., Morales, C.L., 2009. Ecological impacts of invasive alien species on bees. *Apidologie* 40, 388–409.
- Strange, J.P., Koch, J.B., Gonzalez, V.H., Nemeika, L., Griswold, T., 2011. Global invasion by *Anthidium manicatum* (Linnaeus) (Hymenoptera: Megachilidae): assessing potential distribution in North America and beyond. *Biol. Invasions* 13, 2115–2133.
- Strubbe, D., Beauchard, O., Matthysen, E., 2015. Niche conservatism among non-native vertebrates in Europe and North America. *Ecography* 38, 321–329.
- Sung, S., Kwon, Y.S., Lee, D.K., Cho, Y., 2018. Predicting the potential distribution of an invasive species, *Solenopsis invicta* Buren (Hymenoptera: formicidae), under climate change using species distribution models. *Entomol. Res.* 48, 505–513.
- Terzo, M., Rasmont, P., 2014. *Atlas of the European Bees: Genus Xylocopa*. STEP Project, Atlas Hymenoptera, Mons, Gembloux. <http://www.zoologie.umh.ac.be/hymenoptera/page.asp?ID=214>.
- Thuiller, W., 2003. BIOMOD: optimising predictions of species distributions and projecting potential future shifts under global change. *Global Change Biol.* 9, 1353–1362.
- Tingley, R., Vallinoto, M., Sequeira, F., Kearney, M.R., 2014. Realized niche shift during a global biological invasion. *Proc. Natl. Acad. Sci. U.S.A.* 111, 10233–10238.
- Traveset, A., Richardson, D.M., 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol. Evol.* 21, 208–216.
- Vereecken, N.J., Barbier, E., 2009. Premières données sur la présence de l'abeille asiatique *Megachile (Callomegachile) sculpturalis* Smith (Hymenoptera, Megachilidae) en Europe. *Osmia* 3, 4–6.
- 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.
- Ward, D.F., 2007. Modelling the potential geographic distribution of invasive ant species in New Zealand. *Biol. Invasions* 9, 723–735.
- Westrich, P., 2018. Faszination wildbienen, forschungsprojekte: *Megachile sculpturalis*. Available at: <https://www.wildbienen.info/>.
- Westrich, P., Knapp, A., Berney, I., 2015. *Megachile sculpturalis* Smith 1853 (Hymenoptera, Apidae), a new species for the bee fauna of Germany, now north of the Alps. *Eucera* 9, 3–10.
- Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36, 519–539.
- Williamson, M., 1996. *Biological Invasions*. Chapman & Hall, London.
- Wittenberg, R., Cock, M.J.W. (Eds.), 2001. *Invasive Alien Species: a Toolkit of Best Prevention and Management Practices*. CABI Publishing, Wallingford.