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Article in *Science of The Total Environment* · March 2022

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On the road: Anthropogenic factors drive the invasion risk of a wild solitary bee species



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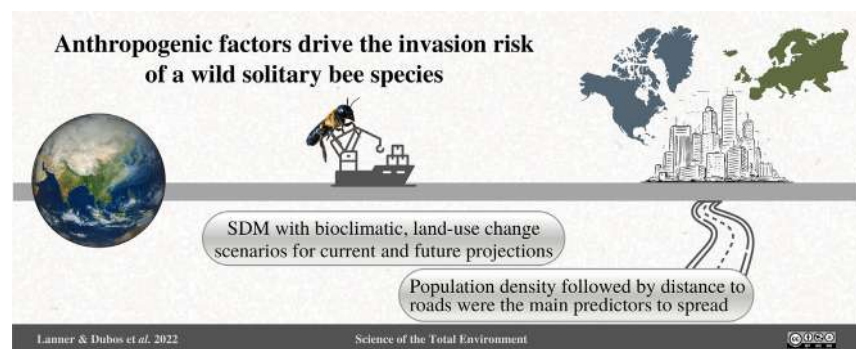
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HIGHLIGHTS

- Our models represent an invasive pollinator currently in global range expansion.
- Human activity is a primary factor influencing invasion dynamics.
- Climate change scenarios differ in habitat suitability for two non-native regions.
- Regional differences indicate an early invasion stage in Europe.

GRAPHICAL ABSTRACT



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ARTICLE INFO

Article history:

Received 22 October 2021

Received in revised form 20 February 2022

Accepted 26 February 2022

Available online 01 March 2022

Editor: Rafael Mateo Soria

Keywords:

Invasive pollinator

Species distribution modelling

Human-mediated spread

Disturbance effects

Megachile sculpturalis

Direct and indirect drivers of change in biodiversity

ABSTRACT

Complex biotic networks of invaders and their new environments pose immense challenges for researchers aiming to predict current and future occupancy of introduced species. This might be especially true for invasive bees, as they enter novel trophic interactions. Little attention has been paid to solitary, invasive wild bees, despite their increasing recognition as a potential global threat to biodiversity. Here, we present the first comprehensive species distribution modelling approach targeting the invasive bee *Megachile sculpturalis*, which is currently undergoing parallel range expansion in North America and Europe. While the species has largely colonised the most highly suitable areas of North America over the past decades, its invasion of Europe seems to be in its early stages. We showed that its current distribution is largely explained by anthropogenic factors, suggesting that its spread is facilitated by road and maritime traffic, largely beyond its intrinsic dispersal ability. Our results suggest that *M. sculpturalis* is likely to be negatively affected by future climate change in North America, while in Europe the potential suitable areas at-risk of invasion remain equally large. Based on our study, we emphasise the role of expert knowledge for evaluation of ecologically meaningful variables implemented and interpreted for species distribution modelling. We strongly recommend that the monitoring of this and other invasive pollinator species should be prioritised in areas identified as at-risk, alongside development of effective management strategies.

1. Introduction

Accidental or deliberate introductions of species outside their native ranges can generate biological invasions, causing severe ecological and socio-economic impacts (Bradshaw et al., 2016; Diagne et al., 2021; Sakai et al., 2001). Biological invasions are now recognised as one of the most important drivers of biodiversity loss worldwide (Bellard et al., 2016a, 2016b, Potts et al., 2010), while species are continuously introduced across the world (Seebens et al., 2017). Indeed, multiple anthropogenic drivers foster biological invasions, such as growth of international trade, increasing human population densities, and associated urbanisation. These drivers might provide new opportunities for invaders to spread and establish (Bellard et al., 2018; Pyšek et al., 2010; Rounsevell et al., 2018; Seebens et al., 2015). Additionally, climate change may act as an invasion driver (Keeler et al., 2021; Sentis et al., 2020; Tabor and Koch, 2021), potentially opening colonization opportunities as the world warms (Chen et al., 2011).

Human-mediated deliberate or accidental transportations play a fundamental role in the introduction of bees to new environments (Russo, 2016). Invasion by bees requires special attention due to their important role as pollinators, and their potential impact on that ecosystem service. Invasive bees can display competitive behavior for floral and nesting resources against native species, disturb pollination networks, decrease phylogenetic diversity by facilitating extinction events or vector newly introduced pathogens and parasites (Aizen et al., 2014; Goulson, 2003, 2010; Russo et al., 2021; Veron et al., 2018). The invasion success of some aculeate species might be associated with their social life history traits (Beggs et al., 2011). Social species have the potential to reproduce and spread rapidly, attain high densities, exploit large amounts of a wide variety of resources, have well-defended colonies and, in general, are formidable competitors (Geslin et al., 2017; Russo et al., 2021). However, there are about 80 social and solitary bee species documented to occur outside of their native range (Russo, 2016), most of them introduced accidentally, receiving little to no attention.

Only a few species have been deliberately introduced. Foremost the social honey bee (*Apis mellifera*, L. 1758), a few social bumblebees (*Bombus* sp.) and the solitary alfalfa leaf-cutting bee (*Megachile rotundata*; Pitts-Singer and Cane, 2011) were translocated for crop pollination and the majority of research focuses on such highly managed bees (Aizen et al., 2014; Debnam et al., 2021; Fontúrbel et al., 2021; Hung et al., 2018; Morales et al., 2017; Strange et al., 2017; Valido et al., 2019).

A solitary bee species accidentally introduced to new environments has now spread far outside its native range in East Asia. *Megachile sculpturalis* Smith, 1853 was first recorded in the US on the east coast in 1994 (Mangum and Brooks, 1997), then quickly expanded its range across the eastern US, from Florida to Canada, and also to many mid-western states

like Iowa and Kansas (Mangum and Sumner, 2003; Paiero and Buck, 2003; Parys et al., 2015). Across the sea, it was first recorded in France in 2008 by Vereecken and Barbier (2009), and *M. sculpturalis* has since colonised much of the European continent within only a decade: Switzerland, Italy, Germany, Hungary, Slovenia, Austria, Liechtenstein, Serbia, Spain and the Crimean peninsula (Aguado et al., 2018; Amiet, 2012; Četković and Plečaš, 2017; Gogala and Zadravec, 2018; Ivanov and Fateryga, 2019; Kovács, 2015; Le Féon et al., 2018; Ortiz-Sánchez et al., 2018a; Quaranta et al., 2014; Ribas-Marquès and Díaz-Calafat, 2021; Ruzzier et al., 2020; Westrich et al., 2015; Westrich, 2017). Today, this non-managed solitary bee species occupies the second largest range outside its natural environment after *Anthidium manicatum*, another wild, non-managed megachilid bee species native to Eurasia and North Africa, accidentally introduced to the Americas (Strange et al., 2011), New Zealand (Soper and Beggs, 2013) and Australia (Walker et al., 2020).

This intracontinental spread of *M. sculpturalis* happened within a remarkably short period and its expansion is ongoing: in Europe, where the invasion is the most recent, it was estimated that its spectacular range expansion was associated with a ten-fold increase in records after 2014 (Bila Dubaić et al., 2021; Lanner et al., 2020a). Several authors have indicated that *M. sculpturalis* could impact native bees through interspecific competition (sensu Blackburn et al., 2014). Geslin et al. (2020) found a significant negative correlation between the appearance of *M. sculpturalis* and native cavity nesters at managed nesting sites. Field records of citizen scientists and researchers documented direct and indirect competition observing nest evictions and fatal encounters with native bee species (Lanner et al., 2020b, 2020a; Laport and Minckley, 2012; Roulston and Malfi, 2012). Additionally, a recently published study reported high numbers of cohabited cavities, where *M. sculpturalis* females positioned brood cells in front of native mason bee cells (*Osmia cornuta*, Latreille 1805) blocking the exit and dooming newly-hatching *Osmia* bees to die (Straffon Díaz et al., 2021). However, further research needs to be conducted to estimate the population- and community-level impacts on native bees as well as its pollination-function in regard to native plant communities (Fründ et al., 2013).

To properly gauge the global invasive risk of *M. sculpturalis*, it is essential to achieve a better understanding of the relative contribution of different biotic and abiotic factors driving its spread. To this end, analytical approaches such as species distribution modelling (SDM) have the potential to identify and classify factors that were key drivers in the recent invasion of a species and that could play a pivotal role in accounting for its present and future distribution under scenarios of global change (Louppe et al., 2019, 2020). For example, the extent of areas at-risk of invasion can be projected by calibrating models with native and non-native occurrences (Broennimann et al., 2012; Broennimann and Guisan, 2008; Jiménez-

Valverde et al., 2011). Likewise, previous studies on invasive species have shown that anthropogenic and environmental factors can explain areas at risk of invasion and help predict potential areas at-risk of invasion in the future (Bellard et al., 2016b; Hill et al., 2017; Soberon and Nakamura, 2009). Particularly for invasive insects, human-associated factors, e.g., urbanisation and general human ecological footprint, have ranked among the most important drivers of range expansion (Gallardo et al., 2015; Sanderson et al., 2002).

Thus, our objective here is to predict the current and future areas at-risk of invasion by the invasive bee *M. sculpturalis*. Existing studies on the distribution of *M. sculpturalis* were limited to climate predictors only (Hinojosa-Diaz et al., 2005; Polidori and Sánchez-Fernández, 2020), which make them unsuitable to estimate the areas at-risk of invasion, because they miss important habitat predictors as well as socio-economic correlates of invasion risks. We address all these points here. In addition, we compiled a dataset of 2000 global occurrences for this species, a 3-fold increase including data of its current range expansion compared to a former study of Polidori and Sánchez-Fernández (2020). More specifically, we used species distribution modelling (SDM) as an analytical approach (i) to identify and classify factors that were key in the recent spread of a species, with a procedure accounting for sampling bias, and (ii) to project the extent of areas at-risk of invasion at the worldwide scale by calibrating models with native and non-native occurrences under different climate and land-use change scenarios following former studies using drivers of propagule pressure to explain the areas at-risk of invasion (e.g., Alaniz et al. (2021) Cameron and Bayne (2009)). Moreover, anthropogenic factors might be key drivers for the current observed colonization. We discuss the extent to which *M. sculpturalis* might turn out to rank among “winner” species under a warming climate and changing habitats, particularly in Europe.

2. Material and methods

2.1. Study organism – *Megachile sculpturalis*

Megachile sculpturalis is a member of the subgenus *Callomegachile* (Michener, 2007). The bee is sexually dimorphic in body size (females measure 21–27 mm and males measure 12–19 mm; Fig. 1) and nests in pre-existing cavities in dead wood. Most likely, developing individuals were accidentally transported by timber trade (Geslin et al., 2020; Quaranta et al., 2014; Zandigiacomo and Grion, 2017). It is considered a polylectic species

in its native environment (Kakutani et al., 1990; Mangum and Brooks, 1997). However, initial pollen analyses indicate that females might be mostly associated with the Asian ornamental trees *Styphnolobium japonicum* Schott, 1830 and *Ligustrum* spp. L., 1753 often found in urban green spaces (Aguado et al., 2018; Andrieu-Ponel et al., 2018). In addition, the species has been found to nest preferentially in urban areas and might have developed synanthropic affinities (Lanner et al., 2020), similarly to *A. manicatum* (Strange et al., 2011).

2.2. Occurrence data collection

We gathered presence data from the native range (N native range = 200) of *M. sculpturalis* from three sources: the specimens information stored at the Institute of Zoology, Chinese Academy of Sciences (Beijing); previously published literature (Lee and Ryu, 2013); and public data platforms GBIF Download (2021) (Global Biodiversity Information Facility, Copenhagen, 2011; GBIF Download: *Megachile sculpturalis* 2222 occurrences included in download,” 2021; <https://doi.org/10.15468/dl.9ht545>). We used occurrence data after 1970 for this study, because this corresponds to the starting date of our climate data. Since the environment may have changed during the past (both climate and land use), recent environmental variables may not accurately reflect past conditions during which older data were collected (Baines and Folland, 2007; Bartomeus et al., 2011; Warren et al., 2001).

We collected presence data from its non-native range (N non-native range = 1749) as observations over the course of several European citizen science projects and the literature (Fig. 2: Europe: Aguado et al., 2018; Amiet, 2012; Četković and Plečaš, 2017; Dillier, 2016; Gogala and Zdravec, 2018; Guariento et al., 2019; Ivanov and Fateryga, 2019; Kovács, 2015; Lanner et al., 2020a, 2020b; Le Féon et al., 2021, 2018; Liu et al., 2019; Poggi et al., 2020; Quaranta et al., 2014; Vereecken and Barbier, 2009; Westrich, 2020; Zandigiacomo and Grion, 2017; North America: Ascher, 2001; Batra, 1998; Hinojosa-Diaz et al., 2005; Kondo et al., 2000; Maier, 2005; Mangum and Brooks, 1997; Mangum and Sumner, 2003; O'Brien and Craves, 2008; Paiero and Buck, 2003; Parys et al., 2015; Tonietto and Ascher, 2008; Wolf and Ascher, 2008) and natural history platforms (GBIF, [observations.org](https://www.gbif.org), [naturgucker.de](https://www.naturgucker.de), Le Monde des Insectes, Spipoll, Faune-France, INPN Espèces). Data collection for modelling was terminated on 30th of October 2020. Wild bee experts verified each occurrence based on pictures or videos, museum specimens and

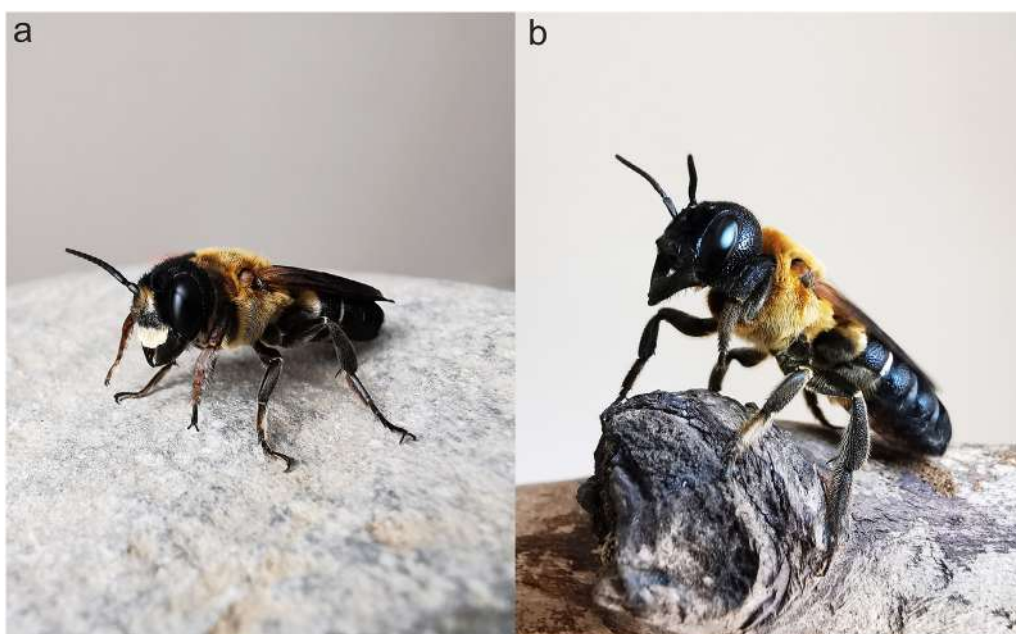


Fig. 1. Male (right) yellow sup-clypeal hair and female (left) with scopal hair for pollen collection of *Megachile sculpturalis*.

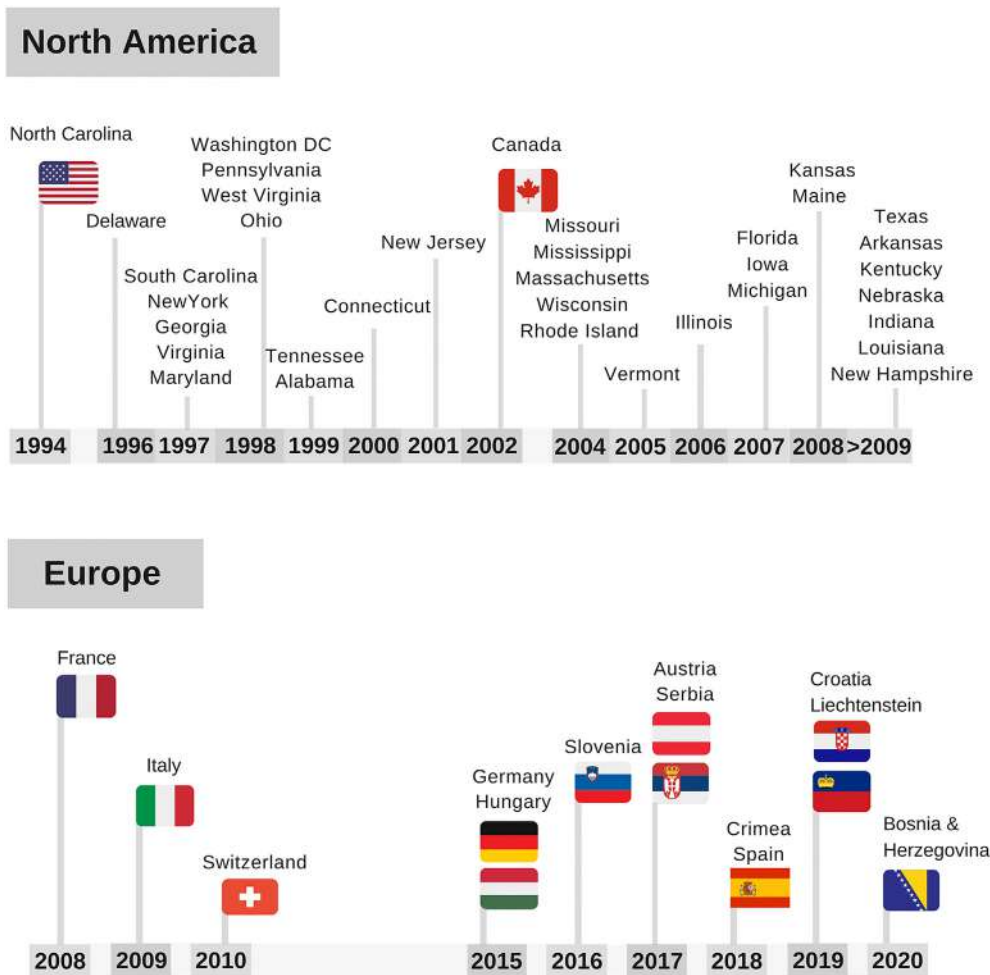


Fig. 2. Timeline of the North American and European invasion history of *Megachile sculpturalis*. Although [Batra \(1998\)](#) describes two intercepted specimens in 1968 and 1976 at US ports, the first established colony outside its native range was found in 1994 in North Carolina ([Mangum and Brooks, 1997](#)). References presenting the species for the first time in a US state or country are listed in the text.

collected specimens. We aggregated the occurrence data at the resolution of the environmental data as bioclimatic variables have a resolution of 10 km and due to the degree of uncertainty of several data points derived from public platforms (i.e., 10 km spatial thinning; [Steen et al., 2021](#); [Vollering et al., 2019](#)); keeping one occurrence per pixel of the environmental

variables to avoid duplicate records resulting in biased outputs towards oversampled regions. We further applied a sample bias correction technique (see [Section 2.4](#)). We included 1219 global occurrences for modelling after aggregation to the resolution of our environmental variables.

Table 1

Variables used as potential descriptors in distribution models for *M. sculpturalis*, grouped as climate, biotic and anthropogenic variables. Variables marked with * are the most important according to our output models.

Climate variables			
Bio1	Annual Mean Temperature	Bio11	Mean Temp. of Coldest Quarter
Bio2	Mean Diurnal Range	Bio12	Annual Precipitation
Bio3	Isothermality	Bio13	Precipitation of Wettest Month
Bio4	Temperature Seasonality	Bio14	Precipitation of Driest Month
Bio5	Max Temperature of Warmest Month	Bio15*	Precipitation Seasonality
Bio6	Min Temperature of Coldest Month	Bio16	Precipitation of Wettest Quarter
Bio7	Temperature Annual Range	Bio17	Precipitation of Driest Quarter
Bio8	Mean Temperature of Wettest Quarter	Bio18	Precipitation of Warmest Quarter
Bio9	Mean Temperature of Driest Quarter	Bio19	Precipitation of Coldest Quarter
Bio10	Mean Temperature of Warmest Quarter		
Vegetation cover variables		Anthropogenic variables	
NET_tem	needleleaf evergreen tree - temperate	global road data*	distance to road
BET_tem	broadleaf evergreen tree - temperate	human population density*	
BDT_tem	broadleaf deciduous tree - temperate	global port and airport data	distance to ports and airports
BDS_tem	broadleaf deciduous shrub - temperate		

2.3. Environmental data

We included bioclimatic variables at 5 arc-minutes (approximately 10 km) resolution of the current climate data and of the 2070 projections from Chelsea version 1.2 (Karger et al., 2017). Variable sub-setting is detailed in a following paragraph. We used four General Circulation Models (GCMs – i.e., GFDL-ESM2M, IPSL-CM5A-LR, MIROC5, NorESM1-M) and four socio-economic pathway scenarios (SSP1/RCP2.6; SSP2/RCP4.5; SSP4/RCP6.0; SSP5/RCP8.5) to construct future scenario models. For anthropogenic variables and major vegetation forms, we used data from the Land Use Harmonization dataset version 2 at a 0.05° resolution (Chen et al., 2020). We included the habitat categories, corresponding to vegetation cover, that are found in temperate climates, which were the most relevant to the biology of this species (Tables 1 and 2). For future projections of landuse, we used the same GCMs, SSPs and time horizons as for climate data.

To account for the risks of introduction and spread in our model predictions, we used anthropogenic predictors that we assumed to be related to the propagule pressure and spread of this species. Because the species was most likely accidentally introduced with the transport of goods, we used three categories of drivers of propagule pressure (number of individuals released to new environment) and factors of spread. First, we used distance to port and airports as a proxy for propagule pressure. Port data was downloaded from the World Port Index (<https://msi.nga.mil/Publications/>

Table 2

Biological explanation for seven selected variables treated as factors and based on our knowledge on the species.

Selected variable	Mean variable importance	Ecological meaning
Temperature of warmest month (bio 5)	0.06	Aspect of temperature as factor for species occurrence. The species requires a certain temperature to develop from prepupal stage (hibernating stage) to full imagines, which happens within 7 until 10 days. Species of summer months that forage preferably during hot and dry months. At this time of the year only few other foraging bees remain in Mediterranean environments.
Precipitation of coldest quarter (bio 19)	0.07	Aspect of precipitation as factor for species occurrence, avoidance of extreme cold-dry regions.
Precipitation of wettest month (bio 13)	0.08	Aspect of precipitation as factor for species occurrence, indication for the distribution of precipitation over the year. Activity depends on dry weather condition. Exotic plants such as <i>Styphnolobium japonicum</i> flourish during dry months. Physiologically it is costless to fly under warm weather conditions and to develop in dry and warm environments.
Needleleaf + Broadleaf evergreen tree - temperate	0.08	Cavity-nesting bee species depend on whole in dead wood or plant stems (bamboo) with a minimum diameter of 8 mm. Females use resin for brood cell architecture. Main foraging (pollen) resources are trees.
Distance to (air-)ports	0.12	Introduction gateways for propagules, wood storage and transportation.
Precipitation seasonality (bio 15)	0.14	Activity depends on dry weather conditions similar bio 13
Distance to roads	0.19	Intracontinental transportation pathways for propagules, wood material and therefore shelter of nests and ornamental plants providing foraging resources on highways gas stations.
Human population density	0.22	Proxy for introduction and dispersal risk providing nesting opportunities (e.g., artificial nests called "bee hotels"), ornamental trees and bushes (<i>Styphnolobium japonicum</i> , <i>Ligustrum</i> sp.) as foraging resources; cities are in general close to ports/airports and a dense road net.

WPI, accessed December 2020) and airport data was downloaded from the OpenFlights Airport database (<https://openflights.org/data.html>, accessed December 2020). Second, we used distance to main roads and highways as an indicator of potential spread facilitation based on former studies identifying roads as used pathways for invasive species (Gippet et al., 2019). We calculated distance from roads using the Global Roads Inventory Project (GRIP4) dataset (Meijer et al., 2018). We selected the first two categories regarding the size of roads (highways, primary roads). For both distance to ports and airports, and distance to roads, we could not include future scenarios of change as such data are unavailable – hence our future scenarios do not account for potential changes in these variables. Third, we used human population density as a proxy for both introduction and expansion risks, as observations suggest that *M. sculpturalis* may be associated with areas of moderate to high population density (Lanner et al., 2020a). We obtained human population density data for the current period and all four future scenarios from (Gao, 2020) with an original data resolution of 1 km². We projected all data in Mollweide WGS84 at a 10 km² resolution; for raster data, we used bilinear interpolation to make the projection. All climatic, anthropogenic and vegetation cover variables used in the model are listed in Table 1.

2.4. Species distribution modelling (SDM)

We modelled and projected species distributions with the Biomod2 R package (Thuiller et al., 2009), using 10 modelling techniques: generalised linear model (GLM), generalised additive model (GAM), classification tree analysis (CTA), artificial neural network (ANN), surface range envelop (SRE), flexible discriminant analysis (FDA) and random forest (RF), Multiple Adaptive Regression Splines (MARS), Generalised Boosting Model (GBM) and Maximum Entropy (MaxEnt). For all models, we generated five different sets of 10,000 pseudo-absences down-weighted for a 0.5 prevalence (Barbet-Massin et al., 2012). The calibration area is the world, excluding Antarctica (we used a 5-fold block cross validation, with four folds used for calibration and one for evaluation; see below).

As our data collection contained presence-only data, we generated artificial absences (pseudo-absences) at locations where the species was never detected (Sillero and Barbosa, 2021). First, pseudo-absences were generated without sample bias correction (hereafter “uncorrected models”) and secondly by accounting for sample biases (hereafter “corrected models”). In the corrected models, we accounted for sample biases by generating pseudo-absences sharing the same biases as our presence points, following the original concept proposed by Phillips et al. (2009). This method seems appropriate in the case of invasive species that are still expanding their range, because it helps reducing the down-weighting of important variables in unreached areas. To do so, we generated null geographic models computed with the geoDist function of the dismo R package (Hijmans et al., 2015). This model produced a mask of values that are proportional to the proximity to presence points (Fig. S1). We weighted the probability of pseudo-absence selection by the null geographic model so that pseudo-absences are more concentrated around presence points. When based on presence-only data, the effect of sample bias correction on species distribution models cannot be reliably assessed by comparing classic performance metrics (Dubos et al., 2021b). Therefore, we used an approach that quantifies the effect of correction relative to within-model variability. We used the Relative Overlap Index (ROI) (Dubos et al., 2021b), which quantifies the degree of information in common (i.e., Schoener's D overlap) between corrected and uncorrected models, corrected by a measure, which indicates whether this effect is of higher or equivalent magnitude that the effects of model settings (cross-validation runs, pseudo-absence runs).

To select the predictors best explaining the distribution of *M. sculpturalis*, we applied a variable selection protocol (Bellard et al., 2016a, 2016b; Leroy et al., 2014). We tested for correlations among all predictors and selected one variable per group of inter-correlated variables to avoid collinearity (Pearson's $r > 0.7$) using the removeCollinearity function of the virtualspecies R package (Leroy et al., 2016). We used the variable importance procedure as implemented in biomod2 to select the best predictors. This procedure evaluates the importance of each variable by

randomising its values (i.e., permutation) and comparing the correlation in model predictions between non-randomised and randomised runs. We analysed the importance of all uncorrelated variables (i.e., one per inter-correlated variable group, plus all non-correlated variables) with 10 repetitions per modelling technique and pseudo-absence set (total = 500) for each variable. To identify the most important variables, we chose those that were considered important by the ecology of the species and by output models for at least 50% of models (those with a median relative importance >0.1 across all models). We also checked the correlations in variable importance values among variables, to ensure that there were no negative interactions in the selection of variables. Finally, among the most important predictors (Table 1), we selected the variables that were the most relevant to the ecology and invasion history of this species (Table 2).

We calibrated our final models with the selected variables, and we computed the response curves for each variable using the evaluation strip method (Elith et al., 2006). We evaluated our models with a block-cross-validation procedure to reduce autocorrelation between calibration and evaluation datasets, using the blockCV R package (Roberts et al., 2017; Valavi et al., 2018). We chose a five-fold cross-validation (i.e., spatial partitioning); for each fold we used 80% of data for calibration and 20% for evaluation (each presence point was evaluated once). We chose a block size of 500 km for the block cross-validation as a trade-off between the autocorrelation range of variables and balanced folds. We assessed the reliability of our models with a procedure adequate for presence-only models, the Boyce index (Hirzel et al., 2006; Leroy et al., 2018). A value of 1 indicates projections which perfectly predicted the presence points, a value of 0 indicates that projections were not better than random, and a value of -1 indicates a counter prediction.

Finally, we built a consensus map (ensemble prediction) based on the average of all individual models, excluding all poorly performing models (Boyce <0.5) from the ensemble prediction. We then evaluated the uncertainty in our ensemble models assessed the inter-model variability (as an index of uncertainty) of our projections by computing the standard deviation of the suitability scores between all model runs for current and future projections separately (Kujala et al., 2013).

We investigated the current and future areas at-risk of invasion posed by the species. We define the risk of invasion as the chance a species will pass multiple filters of the invasion process (introduction, establishment, spread), following Blackburn et al. (2014). To test for areas at-risk of invasion, we compared the ratio between areas already invaded and all areas deemed as at-risk of invasion by models for each non-native region. To estimate the area already invaded, we calculated the extent of invasive occurrence within each non-native region (Europe, North America). We computed the extent of occurrence using alpha hull polygons with the SpatialEco R package (version 1.3-6; Evans and Murphy, 2021; Fig. S2). We recovered the distribution of suitability scores for both non-native regions (Europe and North America). We also provided the proportion of total suitability inside the non-native area relative to the total suitability scores. We preferred to consider the total suitability scores rather than values beyond a given threshold of suitability because the latter suggests binary transformations, which are generally misleading and inappropriate for presence-only data (Muscatello et al., 2021). In addition, we tested for niche overlaps computing a PCA approach between native and non-native American and native and non-native European ranges based on climate variables solely (bio13, bio15 and bio19) following the methodology proposed by Warren et al. (2008), and further developed by Broennimann et al. (2012).

3. Results

Models better predicted the presence points when corrected for sample bias (mean Boyce index (corrected) = 0.91 versus 0.84 for uncorrected models; Fig. S6). The ROI was 0.289 on average across all 10 modelling techniques, indicating a strong effect of sample bias correction compared to within-model variability. We chose to base our inferences on corrected models, because the uncorrected model appeared

mostly driven by distance to roads, which taken alone suggests a strong effect of sampling bias.

3.1. Status and trends of invasive range

The two main predictors for corrected models were population density and distance to roads, followed by precipitation seasonality (bio15), precipitation of wettest month (bio13), precipitation of coldest quarter (bio19), forest cover and maximum temperature of warmest month (bio5; Fig. S3b, S5). Outputs for corrected and uncorrected models are available in the appendix (Fig. S3 and S6). We eventually selected seven variables, which had high importance, and were relevant to this species and its invasion (Table 2). We removed 34 poorly performing models from ensemble maps.

Potential areas at-risk of invasion were predicted from a combination of bioclimatic, vegetation cover and anthropogenic variables (Fig. 3). The predicted suitability in the non-native regions was higher than that of the native region overall (Fig. 3). Our models predicted that the species is only at the onset of its invasion in Europe: low suitability areas with <25%, moderate suitability areas between 25% and 75% and high suitability areas with >75% have been invaded (Fig. 4a). In Europe, we observed several areas still without any reports of the species (southern UK, Turkey), but with great room for further spread in northern and eastern regions (Fig. 6). Conversely, in North America, the species has already invaded most suitable areas: between 25 and 75% of moderate suitability areas and over 75% of high suitability areas have already been invaded (Fig. 4b). Currently uninvaded and suitable areas in North America are located in relatively temperate parts of the West Coast (almost entirely disjunct from the East, Fig. 6). Overall, if we integrate all moderate to high suitability classes (i.e., from 250 to 1000 suitability), we found that 74.4% and 35.3% of environmental suitability is still not occupied in Europe and America, respectively.

We additionally identified potential suitable areas at-risk of invasion in South America between Rio de Janeiro and Buenos Aires, as well as in South Africa and in Australia along their respective south-eastern coasts (Fig. 3).

Niche overlap for the native and non-native North American range performed with a Schoener's D value = 0.07691436 and for the native and non-native European range a Schoener's D value = 0.06000983 (See Fig. S7).

3.2. Future projections

We predict a gradual decrease from 2050 to 2070 and a 6.2% global decrease in suitability by 2070 (based on total suitability scores; Figs. 5 and 6; S8, S9). The impact of environmental change will vary with the respective region, with an average decrease of environmental suitability in North America and Asia (-10.4% and -9.9% suitability by 2070, respectively), and a slight extension in Europe (+0.3%). In the worst-case scenario (SSP585), environmental suitability will decrease by 13.9%, 14.8% and 1.9%, respectively for the aforementioned regions. We identify for Europe an overall expansion of potential areas at-risk of invasion especially in the North (e.g., UK and Baltic countries), and a slight decrease in suitability around the Mediterranean region (e.g., Italy and Greece). All GCMs and scenarios were consistent overall (Figs. S8, S9). Most discrepancies are in large cities (see 'Uncertainty' panel on Fig. 5). In North America, highly suitable areas will shift poleward, largely leaving the US southern states, e.g., Florida and Texas, less suitable but with a more continuous scale comparing the distinct patches with higher peaks in current projections. Low suitability areas connect eastern, already occupied, and western, unoccupied areas in the US. Suitable areas contract towards coastal areas in South America, e.g., Brazil. A similar pattern is reflected for its native range in East Asia: suitable areas shift towards coastal areas and poleward.

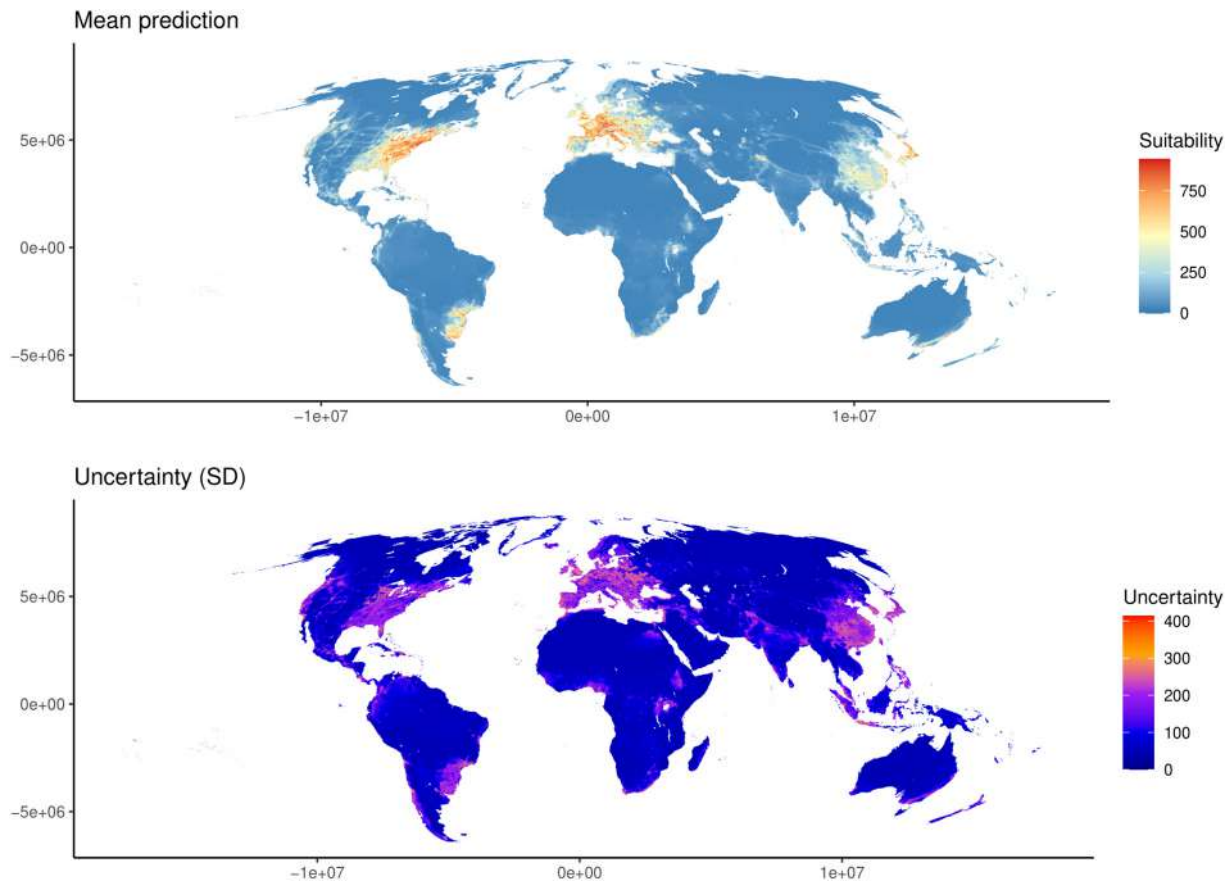


Fig. 3. Global current potential areas at-risk of invasion for *M. sculpturalis* after sample bias correction. The top panel shows the mean prediction across high-performing models (Boyce > 0.5). The bottom panel shows the variability between model replicates (Uncertainty inferred from standard deviation SD). X and Y axes represent coordinates in Mollweide WGS84 (in meter).

4. Discussion

Megachile sculpturalis is a successful invader in two continents, and the first invasive solitary bee in mainland Europe. We found that anthropogenic variables (distance to roads and human population) were the most

important drivers of *M. sculpturalis* distribution and invasion risks, outperforming climate and vegetation cover variables. Hence, the invasion risk of introduction for certain areas will remain high even if future environmental changes decrease areas at-risk of invasion for the species. As a pollinator, *M. sculpturalis* will influence complex biotic networks by adding

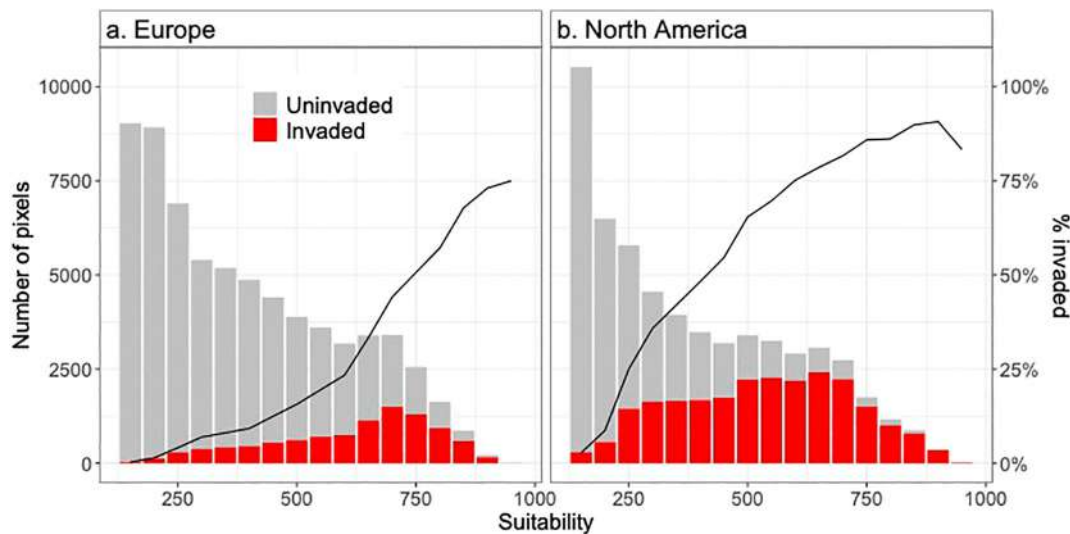


Fig. 4. Histograms of environmental suitability (left axis) for *Megachile sculpturalis* in Europe (a) and North America (b), with the area occupied by the species shown in red. Black lines indicate the proportion of pixel invaded for each bin (right axis). Suitability values range from 0 (unsuitable environments) to 1000 (highly suitable environments). We excluded from this graph the lowest suitability classes (i.e., suitability < 125) which dwarfed the other classes because of pixel counts over 130,000. See Fig. S2 in supporting information for spatially explicit distributions.

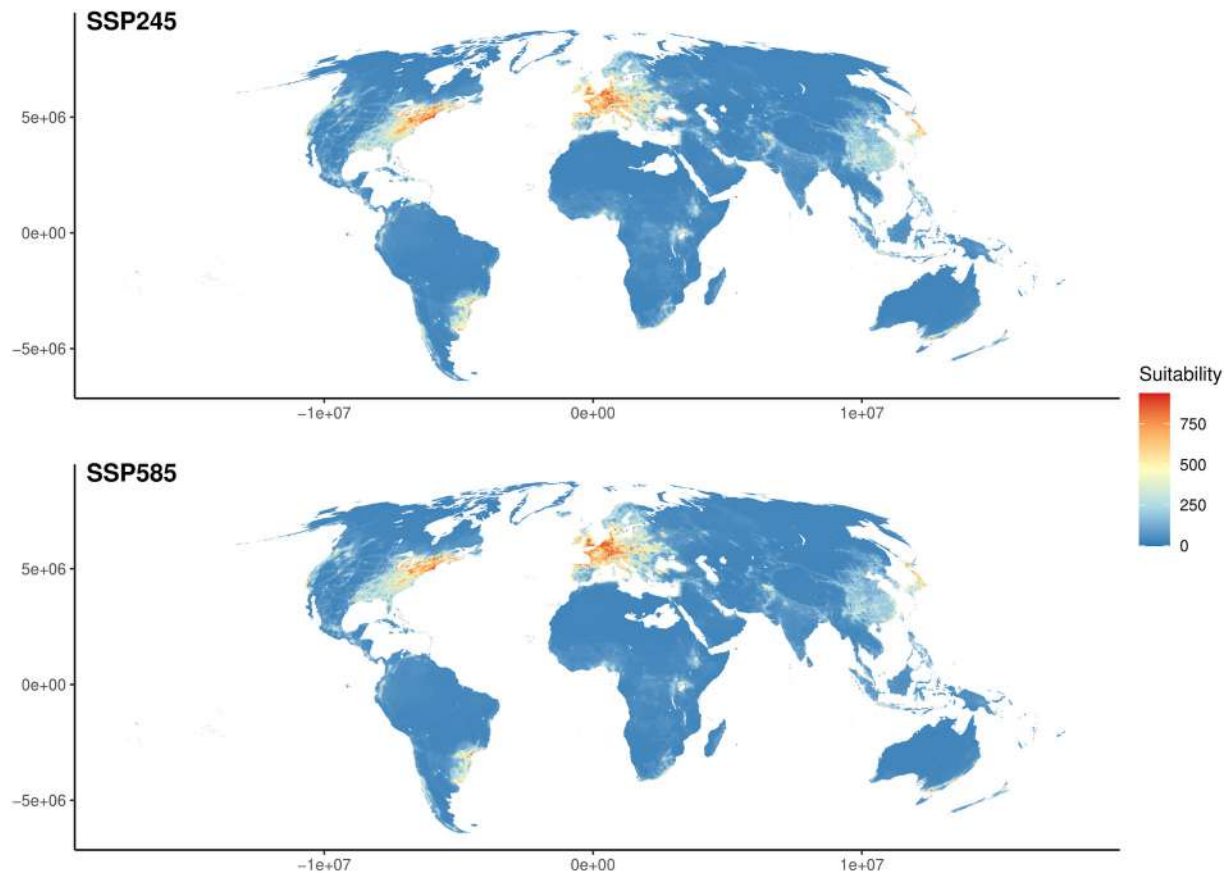


Fig. 5. Predicted future (2070) environmental suitability of *Megachile sculpturalis* for two Shared Socio-economic Pathways (SSP245 and SSP585). We show the mean prediction across high-performing models (Boyce >0.5) and four GCMs.

new interactions, facilitating exotic species, or replacing others (Simberloff and Holle, 1999; Vanbergen et al., 2018), potentially leading to host-plant co-extinctions and important losses of phylogenetic diversity (Veron et al., 2018). This is associated with a potential set of dangers for the newly-inhabited environment, e.g., outcompeting native species, spreading pathogens and/or parasites (Geslin et al., 2017; Goulson, 2003; Russo, 2016; Russo et al., 2021).

4.1. Areas at risk of invasion and future scenarios

Based on our models, *M. sculpturalis* can be characterised as a synanthropic species of the temperate zone, with preferences for moderate precipitation and intermediate temperatures and close proximity to human settlements. According to these projections, most suitable areas in North America have already been colonised since the first record in 1994. Most suitable areas are occupied in North America, except for the US Southwest coast. This is of particular interest as the region appears to be a bee hotspot due to its Mediterranean landscape (Orr et al., 2021; Ropars et al., 2020). This contrasts with its distribution in Europe, where our models resolved large areas at risk of invasion without observations. These projections are congruent with the rapid range expansion of the species. Since the first European observation in 2008, the species reached about 20.4% of the potential areas at-risk of invasion there. In particular, northern, south-western coastal and south-eastern regions are projected as likely expansion fronts. To date, we have observed range expansion towards multiple directions on the European continent (Bila Dubaić et al., 2022; Bila Dubaić and Lanner, 2021; Lanner et al., 2020a; Ruzzier et al., 2020).

Further potential areas at-risk of invasion are indicated on all continents in the southern hemisphere without any documented observations of the species to this date. This possibility is maintained when considering future projections. With a global suitability loss of 10.1% by 2070 on average

across scenarios, the invader might be slowed, at least in North America. However, in Europe, suitability scores remain similar. This output might be influenced by two patterns observed: in North America there are many occurrences filling almost the full potential of areas at-risk of invasion, while in Europe there is a rapid range expansion. As the invasion is ongoing, it may be that future projections cannot fully account for likely further range increases under current and near-term conditions.

4.2. Strengths and limitations of SDMs

Previous studies on this species exclusively considered bioclimatic variables to estimate potential and future species ranges (Hinojosa-Diaz et al., 2005; Polidori and Sánchez-Fernández, 2020). Here, we provided estimations of areas at-risk of invasion, which require integrating the multiple drivers of invasion, which include both environmental requirements (bioclimatic niche, habitat variables) and drivers pertaining to the invasion itself (introduction risk, spread). Model accuracy depends on appropriate sample size (Liu et al., 2019) and sample bias correction (Dubos et al., 2021b). Compared to Polidori and Sánchez-Fernández (2020), our data collection included over three times more occurrences (1950 vs. 625 data points included in the work of Polidori and Sánchez-Fernández, 2020) from its global range compared to relatively few native records (200 from China, Taiwan, South Korea, and Japan vs. 49 from South Korea and Japan after Polidori and Sánchez-Fernández, 2020) and includes data from novel expansion fronts, like the Balkan peninsula.

We circumvented issues derived from data gathered by opportunistic surveys, which result in imperfect detection and are biased towards accessible and frequently visited locations (Guillera-Arroita et al., 2015; Hughes et al., 2021). We addressed this issue by applying a sample bias correction technique that prevented overfitting and model inflation (Hijmans, 2012; Hui and Richardson, 2017; Louppe et al., 2020), as biased and

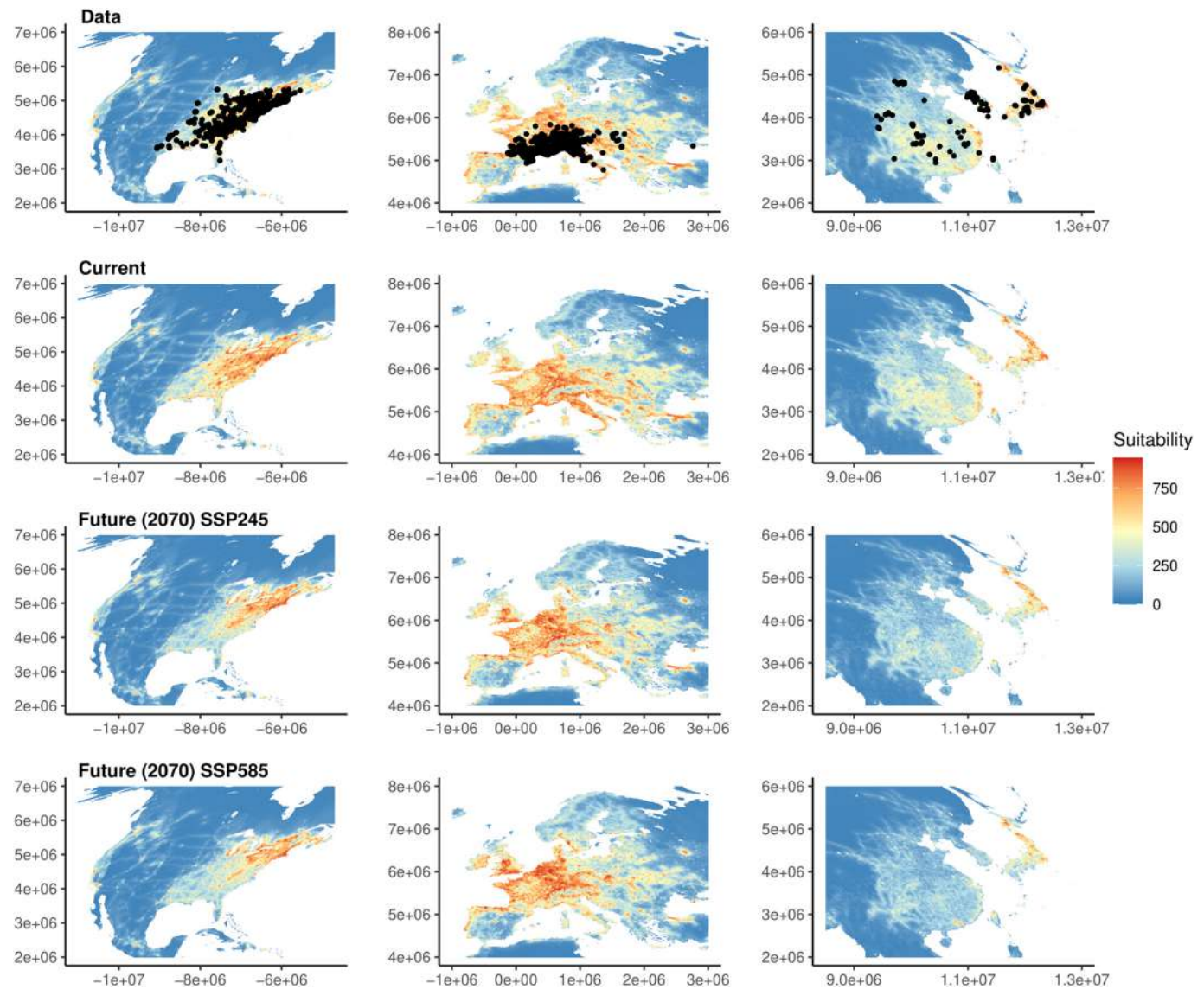


Fig. 6. Comparison of model output for input data (black dots, top), current corrected (middle) and future (bottom) suitable environments for *M. sculpturalis*. In Europe, we observe large areas at-risk of invasion yet unoccupied and a stable prediction of environmental suitability for the year 2070, whereas in North America suitable environments are almost fully occupied. Projected future suitable areas shrink by 2070 in its exotic North American and native East Asian habitat. X and Y axes represent coordinates in Mollweide WGS84 (in meter).

uncorrected input data can result in misleading models (Boria et al., 2014; Hijmans, 2012; Louppe et al., 2020). We generated pseudo-absences, emulating the bias of the presence points included (Phillips et al., 2009). In our case, sampling biases might differ between the native and the non-native range. Occurrence records were more scattered in the native range, where it is more widespread (Michael C. Orr, pers. Com.). Therefore, the correction, which consists in concentrating pseudo-absences around the presence points, may have generated more pseudo-absences in locations that may be occupied by the species. This may have downplayed the natural drivers of species occupancy and decreased the predicted environmental suitability in the native range.

Finally, we affirm prior suggestions that the inclusion of bioclimatic, habitat and anthropogenic factors enable convincing modelling outputs to test for current and future areas at-risk of introduction (Graham and MacLean, 2018; Miranda et al., 2021; Soberon and Nakamura, 2009). Often, variables related to human activities are the most relevant factors for (invasive) species distribution (Gallardo et al., 2015; Helmus et al., 2014). Our model outputs reinforce the necessity of incorporating socio-economic factors for predictions of invasion areas at risk now and in the

future. In addition to bioclimatic variables, one must select biologically meaningful variables and interpret model outputs in light of biological traits (Dubos et al., 2021b; Fourcade et al., 2018; Graham and MacLean, 2018), ideally with expert input (Sutherst, 2014). Consequently, methodological enhancements circumvent misinterpretations regarding habitats identified as potentially suitable (e.g., Arabic peninsula for a species living in the temperate zones; see Polidori and Sánchez-Fernández (2020) and unsuitable (e.g., European coastal areas and islands mentioned; also see Polidori and Sánchez-Fernández, 2020), though recent findings highlight the potential for invasion of the latter (Aguado et al., 2018; Le Féon et al., 2018; Ortiz-Sánchez et al., 2018; Ruzzier et al., 2020). Our models clearly showed that coastal areas with ports and heavily trafficked sea routes may play crucial roles in trafficking species and need to be taken into consideration.

In our case, we assumed vegetation cover and human population density to represent proxies for plant-bee interactions, since the bee is wood-dependent for nesting and often associated with ornamental plants (Aguado et al., 2018; Andrieu-Ponel et al., 2018). Females mainly construct their brood cells, and entrance plugs, from resin (Maeta et al., 2008). The

biological relevance of needleleaf trees were reflected by the models, even if dense forests with over 75% coverage by needleleaf trees were recovered less suitable (most likely because foraging resources are limited in dense needleleaf forests; Orr et al., 2021; Taki et al., 2007, 2013).

We did not take the dispersal capacity of the species (insect flight distance according to landscape characteristics) into account as it is not known yet. Our projections assumed an unlimited dispersal, which is acceptable given the aim of our study, i.e., identifying the areas at risk of invasion. Another possible limitation is single baseline climate data (i.e. CHELSA) as predictions can strongly differ between climate data sources (Baker et al., 2016; Dubos et al., 2021a). Here, we used a wide panel of GCMs and scenarios, which may represent a sufficient variability to produce robust uncertainty assessments.

Our models provided low D values for native and non-native niches indicating small overlaps for North America and Europe. However, these results are preliminary and need to be interpreted carefully as the species is in current range expansion at least in Europe and estimations on niche conservation or expansion might be misleading, suggesting the need for future research on this topic.

4.3. Incoming routes and post-introduction dispersal

Ports and airports are gateways for incoming species (Mangum and Brooks, 1997; Seebens et al., 2017), thus, maritime trade was most likely responsible for the transportation of nesting specimens of *M. sculpturalis* across large overseas distances (Mangum and Sumner, 2003; Vereecken and Barbier, 2009) and more recently to Mediterranean islands like Elba (Ruzzier et al., 2020) and Mallorca (Ribas-Marquès and Díaz-Calafat, 2021). *Megachile sculpturalis* could also arrive on other European islands for which suitable habitat is indicated by the model projections. These are mostly islands in the Mediterranean Sea and parts of the Canary Islands. Cargo-carrying ships transport by far the greatest volumes of commodities, and thereby non-native species, globally (Hulme, 2009). For bee species, cavity nesters, such as *M. sculpturalis*, are more likely to be passively dispersed to new habitats than species with different nesting behaviors, e.g., soil- or ground-nesting bees (Poulsen and Rasmussen, 2020). Consequently, all five detected non-native carpenter bees within Europe (*Xylocopa amadaei*, *X. pubescens*, *X. virginica*, *X. caffra*, and *X. nigrita*) as well as *Megachile disjunctiformis*, a second accidentally introduced *Megachilid* species, share this life history trait (Bortolotti et al., 2018; Rasmont et al., 2017). Although in contrast to *M. sculpturalis*, none of them have expanded their range to this degree.

Besides maritime routes, roads are assumed to be important invasion pathways, although accidental transportation is hard to detect (Meurisse et al., 2019). In our models, we identified distance to roads as the second most important variable. Roads are potential dispersal corridors and promote the spread of invasive species, entailing multiple types of vectors reaching disturbed habitats with high rates of human movement (Cameron and Bayne, 2009; Hill et al., 2017; Hulme, 2009). Human-associated vectors, e.g., cars and trucks, travelling on roads most likely transferred the species between countries and states creating biogeographic gaps of several 100 km during the early phases of invasion (Amiet, 2012; Bila Dubaić and Lanner, 2021; Lanner et al., 2021; Mangum and Brooks, 1997; Vereecken and Barbier, 2009). Although spatial biases along roads exist, a recent study indicated that non-opportunistic sampling is able to better circumvent accessibility biases (Hughes et al., 2021). During monitoring efforts within southern France, its putative point of introduction, a concentrated dispersal kernel was observed along the Rhône valley, one of the most frequently trafficked areas of France (as an example, the A7 highways that follow the Rhône valley host between 41,000 and 148,000 vehicles per day – data retrieved from the French ministry of Ecology; 2021). Another example for the importance of roads is on the island of Mallorca: monitoring has been limited to primary transportation routes, but with added effort researchers were still unable to find the bee in more remote areas of the island (Díaz-Calafat personal observation p person.). This result is in accordance with previous investigations of invasive species

unintentionally transported along roads (Cameron and Bayne, 2009; Carrasco et al., 2010; Liebhold et al., 2013).

4.4. Disturbed vs. natural habitats

Besides roads, population density could be another key factor influencing species invasions (Liebhold et al., 2013). Previous studies found non-native bees tend to naturalise more successfully in disturbed landscapes like urban areas, with high population densities and dense infrastructure (Fitch et al., 2019; Graham and MacLean, 2018; Gruver and CaraDonna, 2021). The synanthropic tendency of *M. sculpturalis* is supported by the importance of the variable ‘population densities’ in our models. The resource availability for bees within urban settlements is ensured via both nesting possibilities and well-maintained foraging resources. Raw data reflect a similar picture, with most observations gathered in urban areas (80%, 792 total); few existed in seminatural (13%), natural or rural (9%); and there were only two records (0,3%) in agricultural habitats in Europe most likely due to lack of suitable floral resources. However, interpretations need to be made cautiously due to the non-random sampling regime. Further investigations according to host plant interactions of *M. sculpturalis* are currently in preparation and will provide important knowledge to estimate its impact on native ecosystems.

5. Conclusions

The range of a species strongly depends on the regional climate, as well as its biotic interactions and dispersal ability. Given the dynamic nature of this calculus, predictions of future spread and impacts of invasive species are complex tasks for ecologists (Courchamp et al., 2017; Hui and Richardson, 2017).

Megachile sculpturalis may serve as a powerful model for invasive pollinator species and for answering ecological questions in the fields of invasion biology and risk management (Queffelec et al., 2020). The spatio-temporal dynamics of invasions captured with SDMs are crucial components of invasion biology. Meaningful modelling approaches rely on comprehensive data sets, model correction mechanisms and variables reflecting the underlying biotic interactions. Our models represent an invasive pollinator currently in global range expansion, and seemingly its intrinsic dispersal ability is the only thing limiting its current known distribution. Previous studies highlight human activity as a primary factor influencing invasion dynamics (Gallardo et al., 2015; Hill et al., 2017). Our results agree with these findings identifying human-associated variables (distance to roads, population densities) as the most significant drivers for the observed areas at risk of invasion of *M. sculpturalis*. Regional differences in patterns of spread indicate a relatively early invasion stage in Europe.

Based on our work, we recommend intensifying invasive species monitoring on both continents, especially in yet unoccupied regions. Monitoring programs of mobile organisms are transnational tasks and demand a dense network of experts working on the species. Here, established community science programs (e.g., www.beeradar.info, <https://oabeilles.net/projets/observatoire-abeilles-exotiques-2>) have been crucial for monitoring this distinctive bee and even provided most of the occurrence data used for SDMs. We recommend developing such programs in countries where the bee has not yet been found, and the intensification of current projects (Bila Dubaić and Lanner, 2021). In this way, citizen science programs combined with a respective transnational network of researchers will enable the assessment of this and other rapidly spreading species in newly colonised environments.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.154246>.

CRedit authorship contribution statement

JL and ND are co-first, and equally contributing authors. JL, BL, BG, ND, CHC and HM conceived the study. Except from these authors, all others are listed alphabetically and contributed as members of the international

consortium working on the species. The authors JL, BG, CHC, LB, ER, JBD, AČ, VLF, SF, MCO, NV, BP acquired the data. ND and BL conducted the modelling with preparatory work of JMM and model interpretations of JL, BG and HM. JL, ND, BL, BG and HM wrote the manuscript under the lead of JL. All authors contributed to the final manuscript and approved the content.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgements

We sincerely thank all participants of our citizen science programs and our colleagues Katharina Huchler, Philipp Meyer, Jovana Raičević, Milan Plečaš for sharing occurrence data. This study was partly funded by the DRF Pollinéco n°2058 (France), which provided support in the form of salaries for the author VLF. Further it was partly funded by the Austrian Academy of Science as the author JL is a recipient of the DOC fellowship program. Both funding sources did not have any additional role in the study design, data collection and analysis, decision to publish or preparation of the manuscript. Open access funding provided by University of Natural Resources and Life Sciences Vienna.

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