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Felix Fornoff, Julia Lanner, Michael Christopher Orr, Tingting Xie, Shikun Guo, et al.. Home-and-away comparisons of life history traits indicate enemy release and founder effects of the solitary bee, *Megachile sculpturalis*. *Basic and Applied Ecology*, 2024, 76, pp.69-79. 10.1016/j.baae.2024.02.008 . hal-04593761

HAL Id: hal-04593761

<https://amu.hal.science/hal-04593761>

Submitted on 30 May 2024

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RESEARCH PAPER

Home-and-away comparisons of life history traits indicate enemy release and founder effects of the solitary bee, *Megachile sculpturalis*

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ARTICLE INFO

Keywords:

Intergular distance
Mating strategy
Nest architecture
Environmental filter
Phenology
Trap nest

ABSTRACT

Occurrences of introduced and invasive pollinators are increasing worldwide. To predict the potential impacts of exotic bees on native ecosystems we need to understand their ecological interactions. Life history traits are fundamental for understanding ecological interactions and often help to explain the spread of exotic species. We conducted home-and-away comparisons of life history traits of the first invasive bee in Europe, the sculptured resin bee *Megachile sculpturalis* Smith 1853. We compiled information on nest architecture, offspring, natural enemies, body size and phenology using published literature, museum specimen, data from citizen science initiatives, field observations and reared specimen. *Megachile sculpturalis* uses a broad variety of nesting materials for brood cell construction, including even plastic at the exotic range. Body size at warm temperate climate was similar in the native and exotic ranges, but phenology shifted forward by about one month (28.9 ± 3.3 SE days) in the exotic ranges. The abundance of natural enemies was similar between native and exotic ranges but specialist enemies were missing in the exotic ranges. These trait shifts may be explained by founder effects or ecological filtering. The comparison of life history traits in native and exotic ranges sheds light on the ecological-evolutionary process of this quickly spreading species and provides a better understanding of invasion processes in solitary bees.

Introduction

Bees (Anthophila) are among the most economically and ecologically important pollinators (Klein et al., 2007; Ollerton et al., 2011). Even solitary bee species like the alfalfa leafcutting bee *Megachile rotundata* (F.), which was purposefully introduced into the US, can provide

economic value in pollination services (Barthell et al., 1998; Pitts-Singer & Cane, 2011; Schlaepfer et al., 2011; Groutsch et al., 2019). Besides the known benefits (Debnam et al., 2021), introduced bees are widely considered a threat to biodiversity and ecosystem functions (Barthell et al., 1998; Russo, 2016; Aizen et al., 2020; Pyšek et al., 2020). Exotic bees can negatively impact native fauna and flora, by competing with

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<https://doi.org/10.1016/j.baae.2024.02.008>

Received 5 April 2023; Accepted 20 February 2024

Available online 21 February 2024

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native pollinators, influencing native pollination networks, or altering the seed set of native plants by decreased or increased flower visitation (Russo, 2016). Additionally, exotic species are potential vectors of introduced parasites and pathogens, which can spread to native species (Goulson, 2003; Aizen et al., 2014; David et al., 2017; Russo et al., 2021). If the presence of exotic species exhibits negative effects on the economy or the natural ecosystem components of the exotic range, they are classified as invasive species (Catford et al., 2009; Bradshaw et al., 2016; Diagne et al., 2021). Most research has focused on deliberately introduced and managed bees like *Apis mellifera* L. or *Bombus terrestris* (L.), but there is a lack of knowledge on accidentally introduced and solitary bee species (Paini, 2004a; Dafni et al., 2010; Goulson, 2010; Morales et al., 2013; Russo, 2016; Geslin et al., 2017).

Understanding invasion biology of bees, as well as other insects, relies on the knowledge of the ecology and life history traits of individual species to predict the ecological consequences of range expansions (Goulson, 2003; Bradshaw et al., 2016). In turn, impacts of invasive bees depend on species-specific life history traits (LHTs), including dispersal ability, number of offspring, nesting and foraging mode, phenology and sociality (Phillips et al., 2010; Jarošík et al., 2015; Russo, 2016; Valdovinos et al., 2018; Kharouba et al., 2019; Poulsen & Rasmussen, 2020). For example, previous studies found that social aculeates (bees and wasps) and solitary generalist bees are more successful in invading new environments than solitary specialized species (Aizen et al., 2008; Downing & Liu, 2012; Vanbergen et al., 2018). Consequently, LHTs can determine the invasiveness, as well as the severity of impacts of introduced species (Valdovinos et al., 2018; Gippet et al., 2019). Furthermore, species-specific traits can explain why some exotic aculeate species become successful invaders (Beggs et al., 2011; Fournier et al., 2021). However, traits of one species might differ between its native and exotic ranges and also between disconnected exotic ranges. Ecological filtering, selecting for species-specific trait expressions during range expansion and founder effects, for example the introduction of only very few genotypes could be responsible for this mismatch. Besides traits, missing interaction partners like antagonists can influence invasion success, a mechanism called ‘enemy release’ (Elton, 1958). Moreover, mean trait values of a species might not remain stable, but shift post-invasion (Phillips et al., 2010). For these reasons, it is important to compile comprehensive knowledge on LHTs through home-and-away comparisons, which is the foundation for research that aims to reveal trait shifts and identify enemy release which may determine invasion success (Elton, 1958; Van Kleunen et al., 2010).

The Sculptured resin bee, *Megachile sculpturalis* Smith 1853, is native to Eastern Asia and the first invasive wild bee established in Europe in 2008 (Vereecken & Barbier, 2009); previously, it was recorded in the US in 1994 (Mangum & Brooks, 1997). *M. sculpturalis* is invasive in some European and North American regions due to its direct competition for nesting sites, resulting in negative effects on native solitary bee species (Laport & Minckley, 2012; Roulston & Malfi, 2012; Geslin et al., 2020; Lanner et al., 2020b; Straffon Díaz et al., 2021). The species likely arrived in Europe via maritime trading routes, through accidental transportation of nesting individuals, in cavities of dead wood (Vereecken & Barbier, 2009; Le Féon et al., 2018). From its putative point of introduction (Allauch, France), it has spread to many European countries (Switzerland, Amiet, 2012; Italy, Quaranta et al., 2014; Hungary, Kovács, 2015; Germany & Austria, Westrich et al., 2015; Serbia, Četković & Plečaš, 2017; Spain, Aguado et al., 2018, Ortiz-Sánchez et al., 2018; Slovenia, Gogala & Zadavec, 2018; Ukraine, Ivanov & Fatergya, 2019; Liechtenstein, Lanner et al., 2020a; Romania, Bulgaria, Montenegro, Croatia, Bosnia & Herzegovina, Bila Dubaić et al., 2022; Greece, <https://www.inaturalist.org/observations/130109721> 2022). Besides further introduction events (Lanner et al., 2021), its ongoing intracontinental colonization is remarkably fast (Lanner et al., 2020a; Bila Dubaić & Lanner, 2021; Le Féon et al., 2021) and anthropogenically assisted by roads allowing accidental transport and human settlements providing ornamental host plants (Lanner et al., 2020a; Lanner et al.,

2022). According to the literature, it is considered a polylectic (generalist for pollen host plants) species, using a wide variety of plants for provisioning its larva with pollen (Mangum & Brooks, 1997; Parys et al., 2015; Le Féon et al., 2018; Ruzzier et al., 2020).

Besides this, little is known about other fundamental LHTs of *M. sculpturalis*, including phenology, reproduction, sex ratio, development and potential natural enemies from the native and the exotic ranges. To fill this gap, we generate new knowledge on LHT of this species in a home-and-away comparison. By comparing data of the LHTs gathered in its original habitat and post-invasion, we aimed to i) identify traits potentially enhancing invasion success and ii) identify trait shifts that potentially relate to founder effects or ecological filtering. We statistically compare LHTs, in particular body size and phenology, nesting and reproductive traits and natural enemies to highlight the differences between the native and exotic range by testing the following hypotheses:

- A) Phenology of *M. sculpturalis* changed post-invasion. Recent studies showed that multifactorial environmental influences (most importantly local temperature regimes) and species-specific traits affect bee phenology (Stemkovski et al., 2020; Forrest, 2016).
- B) Intertegular distance (ITD) of *Megachile sculpturalis* is larger within the exotic range. Larger ITD could act as an indirect proxy for dispersal ability, as bees with larger body size tend to have greater flight capacities (Zurbuchen et al., 2010). High flight capacity should be beneficial for individuals arriving at the exotic range, as it may facilitate reaching suitable resources and increases the home-range in which it can forage and nest.
- C) Natural enemies of its larvae are less specialized and species-rich in the exotic compared to the native range. Reproductive success may be increased by enemy release in the exotic habitat.
- D) Nesting traits such as number of brood cells per cavity, or total offspring, increase in the exotic range. The new environment may release the species from ecological filters including enemies that are present at the native range, leading to nesting trait changes that increase reproductive success.

Materials and methods

Data collections

We compiled a data set of life history traits of *M. sculpturalis*, including phenology, intertegular distance, fecundity, mortality, sex ratio, nesting traits, larval development, nesting activity and natural enemies’ abundances and identities based on own observations and measurements, complemented by online databases, data from scientific publications and citizen science initiatives. Specimen data and observations for each of the following collections are listed in Table 1.

Collection 1 (ITD data—native)

All specimen of *M. sculpturalis* available at the insect collection of the Institute of Zoology (IOZ) at the Chinese Academy of Science (Beijing, China). Specimens were georeferenced with GaoDe (gaode.com) to complement existent date information with spatial coordinates.

Collection 2 (nest and natural enemy data—native)

Megachile sculpturalis specimens reared from giant reed internodes exposed as trap nests in 88 plots at the subtropical tree diversity experiment (BEF-China) in southeast China (Xingangshan, Jiangxi, China). We sampled all trap-nesting insects and natural enemies, including *M. sculpturalis*, monthly from August 2014 to September 2015. We recorded information on nesting phenology, number of brood cells, date and number of male and female offspring, abundance and identity of natural enemies and development mortality. Details on the experimental set up and the sampling method at this location are described in Fornoff et al. (2021).

Table 1

Summary of collections and data origins used for different analysis. The US collection 4 included specimens from Florida, Ohio, Maryland, Missouri, Mississippi (Stoneville-USDA; some of these records were previously recorded in Parys et al. (2015)), Museum of Natural History at Auburn University located in Auburn, Alabama, USA (AUEM/AUMNH), National Pollinating Insects Collection located in the Pollinating Insect—Biology, Management, Systematics Research Unit in Logan, Utah, USA (BBSL-USDA ARS), Clemson University Arthropod Collection located in Clemson, SC, USA (CUAC), Mississippi Entomological Museum at Mississippi State University in Mississippi State, Mississippi, USA (MEM/ UMIC) Russo Lab at the University of Tennessee Knoxville (RUSSO); Institute of Zoology, Chinese Academy of Sciences, Beijing (IOZ). Abbreviations: Collection (C); inter tegula distance (ITD); Data compilation from Germany, Austria and Switzerland (D-A-CH); Data from south France (SFR); male (m); female (f); Germany (D); Austria (A).

	Collection 1	Collection 2	Collection 3	Collection 4	Collection 5
Description	ITD–native specimen	native nests reared to specimen	D-A-CH SFR observed and reared	ITD–NA specimen	GBIF data base
Data type					
Origin of samples	South-east Asia	Jianxi/China	Serbia, Switzerland, Liechtenstein, Hungary, Italy, Spain, Austria, Germany and France	North America	Global
Location of samples	IOZ	IOZ	Bern/CH (D-A-CH) Marseille/FR (SFR)	Stoneville, AUEM/AUMNH, CUAC, MEM/ UMIC, RUSSO, BBSL-USDA ARS	GBIF
Study period	1970–2010	2014–2015	2016–2020	2001–2020	1970–2020
Phenology [# observations]					1188
ITD [# individuals]	283	20	356	148	
Natural enemies & parasitism [# brood cells infected/non-infected]		75/361	54/498 D-A-CH 44/285 SFR		
Nest traits [# nests] # brood cells, materials, diameter, length		232	204 D-A-CH 120 SFR		
Nesting phenology [# nests]		232	204		
Mortality [# brood cells]		361	498		
Male vs. female phenology [# individuals]		253			
Male-ratio [# individuals]		253	86 D-A-CH 105 SFR		
Activity, mating and behavior [#female #male]			3f 3 m D 2f 2 m A		

Collection 3 (behavior, activity, nest and natural enemy data—exotic EU)

We collected life history trait and behavioral observations, e.g. mating and behavioral patterns, on *M. sculpturalis* from citizens that were engaged in citizen science projects (www.beeradar.info and <https://srbee.bio.bg.ac.rs/english>) from Switzerland, Liechtenstein and Austria (exotic D-A-CH) from 2018 to 2020, and in Serbia from 2019 to 2020 (Lanner et al., 2020a, 2020b; Bila Dubaić et al., 2021, 2022; Bila Dubaić & Lanner, 2021). These citizens were familiar with species identification from previous work in the projects and reported behavioral observations to us. Additionally, we recorded diel activity and behavioral patterns of three females at one location in Germany in 2020 (exotic D-activity).

Furthermore, we collected nests from balconies and gardens in Switzerland, Austria, Hungary, Germany, Italy and Spain within the mentioned citizen science projects and provided by commercially circulated trap nests with customers in France and Switzerland. The nests were reared at outside temperatures in Bern (Switzerland).

Within the framework of an experiment investigating the natural enemies of *M. sculpturalis* in southern France, we reared individuals from artificial cavities (trap nests) under lab conditions at 25 °C and 50 % relative humidity. These so-called SFR samples were collected in Marseille, one putative point of introduction to EU and, hence, the oldest known population (Vereecken & Barbier, 2009). Due to this and the very high sample size at this location we treated it distinct from all other EU samples, in the analysis of number of cells per nest. Effects rearing, handling and cultivation temperatures might have influenced larval development; therefore, we excluded this data for mortality rate and sex-ratio calculation.

Collection 4 (ITD—exotic NA)

Specimens from North American insect collections were obtained for ITD measurement covering 10 US states.

Collection 5 (phenology—world-GBIF)

For phenology comparison, records of *M. sculpturalis* listed at the

Global Biodiversity Facility (GBIF) were downloaded in September 2020 (“GBIF Occurrence Download Asia, 2020”; “GBIF Occurrence Download Europe, 2020”; “GBIF Occurrence Download North America, 2020”). The retrieved records were from a range of sources including museum collections but mostly observations (60 %) submitted to public nature platforms like ‘iNaturalist’ (© California Academy of Science 2016).

Species identification

Specimens of *M. sculpturalis* were identified by the authors, including all iNaturalist observations. Natural enemy identifications from the native range were conducted mainly through comparison with reference specimens at the Institute of Zoology in Beijing (IOZ), as described in Fornoff et al. (2021). Natural enemies found in nests of *M. sculpturalis* in SFR (exotic SFR) were sent for Sanger sequencing to confirm their identity (LGC Genomics, Berlin, Germany). The standardized CO1 barcoding regions were targeted in a PCR reaction, and the PCR products were purified before sequencing. To identify species, generated sequences were blasted on BOLD (Ratnasingham & Hebert, 2007). Information on DNA barcoding procedure including DNA isolation, amplification and sequencing is provided, see Appendix A: Tables S1–S4. Parasitism rates and mortality rates were calculated as the number of nest cells affected either by a natural enemy or by other causes of mortality, respectively, relative to all nest cells within each dataset.

Phenology, intertegular distance and temperature data

To approximate the activity period (phenology) of *M. sculpturalis* individuals we used the day of record that was reported for each sample (Julian date between 1 and 365) within the GBIF record. GBIF data did not include the sex of the specimen, however, we assumed no sex biases between continents or temperature ranges.

Intergular distance (ITD) was measured as the shortest distance between the tegulae. For native bees of data collections 1 and 2, ITD was

measured using a reticle eyepiece on a Motic SMZ-161-BLED microscope. European and American specimens of data collections 3 and 4 were measured using a digital microscope (Leica S8AP0 exotic SFR samples, and Keyence VHX-7000x for all other samples).

Phenology and ITD may vary with climatic conditions, for example insect body size with temperature (Chown & Gaston, 2010). Measures of climatic conditions like temperature and relative humidity are commonly correlated (for example, Fornoff et al. 2021), therefore we only use temperature. We calculated mean spring (March–May), mean summer (June–August), mean autumn (September–November), mean winter (December–February) and mean annual temperature based on the WorldClim database (Fick & Hijmans, 2017), corresponding temperature maps were visualized in Fig. 1. Temperature data of each location used in phenological or ITD analysis were extracted using the ‘raster’ package in R (Hijmans, 2020). The database provides monthly temperature values as average of the period from 1970 to 2000 at a maximum resolution of 1 km² across all land surfaces. Monthly mean temperature values were averaged to calculate the respective seasonal and annual mean temperatures and plotted as reference information for phenological analysis (Appendix A: Fig. S1). Pearson’s correlation coefficient showed high correlation between the different temperature groupings, therefore only mean annual temperature was used for analysis.

Statistical analysis

All analyses were conducted in R 3.6.1 (R Core Team 2021). We used two linear mixed models one for phenology and one for ITD to test the difference in phenology and ITD between continents (native range: Asia, exotic ranges: Europe and North America) and included annual mean temperature as a co-variable including the interaction between continent and temperature using the function ‘lme’ from the ‘nlme’ package (Pinheiro et al., 2021). For ITD analysis we added sex as a further predictor. Non-significant terms that did not improve the model were compared via AIC scores (lower AIC scores indicate better model fit), were dropped in the final models.

For the ITD analysis, all samples of collections 1, 3 and 4 were used and 20 individuals from collection 2, for which ITD measurements could

be taken (Table 1). ITD was measured by the same method but by different persons and using different microscopes. Therefore, we corrected for a potential systematic measurement bias by including “person” as a random effect in the ITD model.

For the phenology analysis, samples of collection 5 were used as they included unique occurrence observations. To further restrict potential influence of climatic differences between continents we compared phenology within the same climate zone across continents. To do so, we followed the Köppen–Geiger climate classification and included only locations of warm temperate climate, with mean annual temperature >3 °C and <18 °C (Kottek et al. 2006).

Year was included as a random effect to capture potential temporal changes, such as climate change, in both models. However, no further temporal correction term was implemented, as observations were random across space and time, reducing a potential temporal dependence of data points. Moreover, phenology and ITD samples were spatially clustered, therefore we controlled for spatial autocorrelation by including a spatial correlation structure based on Euclidean distances between geographic coordinates of all samples. The best fitting spatial correlation structure (Linear, Gaussian, Exponential, Spherical or Rational quadratic spatial correlation structure) and the most parsimonious set of predictors was identified by the lowest AIC value for both models (Pinheiro et al., 2006).

The effect of the predictors was tested using an analysis-of-deviance (Chambers & Hastie, 1992). A subsequent post-hoc z-test, implemented in the Tukey HSD test from the ‘multcomp’ package (Hothorn et al., 2016), tested differences between multi-categorical variables, such as continents.

To compare the number of brood cells between the native and the exotic range we used only nests that were constructed in bamboo. Additionally, we compared the number of brood cells between cavity materials (wood vs. bamboo). For both, we used samples of reared individuals from collection 2 (native) and 3 (exotic). As the response variable was presence-only data, we implemented a truncated Poisson distribution using the package ‘glmmTMB’ (Magnusson et al., 2021). In these models the sampling location was used as random effect to account for pseudo-replication. The fit of all statistical models was evaluated using the diagnostics implemented in the ‘DHARMA’ package (Hartig &

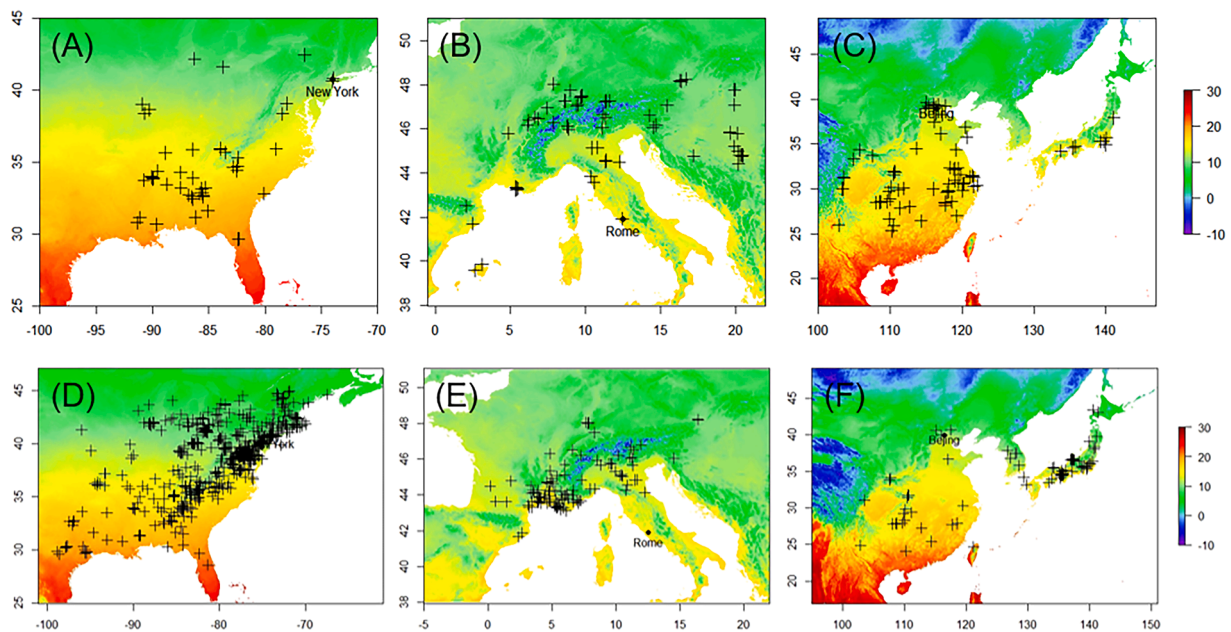


Fig. 1. Locations of *M. sculpturalis* records; (A–C): specimens including ITD information that were used for analysis, from North America, Europe and Asia, respectively. (D–F) occurrences with phenology information provided by GBIF, from North America, Europe and Asia, respectively. Map colors show annual mean temperature.

Lohse, 2021).

Results

Phenology and ITD at the native vs. exotic range

The final model for phenology included continent and temperature, the ITD model temperature and sex as predictors, all other parameters did not improve the model fit.

The phenology, measured as day of record, was significantly earlier at higher mean temperature (estimate = -2.35 ± 0.32 SE, $F = 55.9$, $p < 0.001$) and significantly different between continents ($F = 57.3$, $p < 0.001$; Fig. 2). In Asia, bees occurred significantly later (28.9 ± 3.3 SE days) than in Europe and North America (median day of record EU 199 and NA 200 (July), Asia 230 (August), EU—Asia, estimate = -28.97 ± 3.53 SE, $z = -8.2$, $p < 0.001$; NA—Asia, estimate = -28.89 ± 3.04 SE, $z = -9.5$, $p < 0.001$), while there was no significant difference between Europe and North America.

ITD was not different between continents, but significantly increased with mean temperature across continents (estimate = 0.02 ± 0.01 SE, $F = 16.3$, $p < 0.001$; Fig. 3(A)) and male ITD was significantly smaller than female ITD (estimate -0.89 ± 0.03 SE, $F = 1031.0$, $p < 0.001$; Fig. 3(B)).

Not statistically tested but calculated for one location in China, males occurred on average 6.4 days earlier than females (day 155.6 ± 17 , day 162 ± 32 , respectively).

Fecundity, mortality and sex ratio

Cavity diameters used for nesting varied between 9 and 23 mm (exotic SFR), 8–12 mm (exotic D-A-CH); 6–17 mm (native CN) and 8 mm (native JPN; Ishihara, 1994). Cavity length was 30 cm (exotic FR), 12–30 cm (exotic D-A-CH); 10–20 cm (native CN) and 25 cm (native JPN; Ishihara, 1994). Within each nesting cavity, across all nesting materials, brood cells were linearly ordered, the number of brood cells per nest ranged from 1 to 16 (Table 2).

In the rather comparable material bamboo, the number of brood cells per nest cavity was significantly higher in Europe than at one location in China (D-A-CH, collection 3, mean = 1.88, estimate = 0.45 ± 0.17 SE, $Z = 2.57$, $p = 0.010$ and SRF, collection 4, mean = 2.32, estimate = 0.76 ± 0.18 SE, $Z = 4.02$, $p < 0.001$ compared to China collection 2, mean = 1.56, Fig. 4(A)). The number of brood cells per nest cavity was significantly higher in wood (mean = 3.18) than in bamboo cavities (mean = 1.84, estimate = 0.69 ± 0.16 SE, $Z = 4.31$, $p < 0.001$, Fig. 4(B)), in

samples from different places of the EU (D-A-CH).

Parasitism rate in the native range varied between 14.1 % (Japan) and 20.8 % (China) and in the exotic range between 11 % (D-A-CH) and 15.8 % (SRF collection 4). Mortality of developing eggs and larvae was comparable at 8–9 % across locations (Table 2), mortality rate in SRF collection 4 was at 25.9 % and excluded from interpretations due to expected impacts of larval rearing in air sealed Petri dishes.

The number of brood cells per female (eggs/female) was higher in the exotic range (Exotic D-A-CH, 9 females, mean eggs \pm SD: 24.1 ± 5.6) than was reported by Sasaki and Maeta (2018) for the native range (Native JPN; year 1, 8 females, mean eggs 9.3; year 2, 11 females, mean eggs 18.8; year3, 13 females, mean eggs 8.8). At the exotic range, a female bee constructed 21 brood cells in 2019. In the next generation three marked females which were collected to obtain ITD measures after 24, 33 and 54 days of activity, constructed in total 72 brood cells. Assuming that all females had lived up to 54 days, then each would have built 35 brood cells. At this location, individuals needed on average three days to complete (construct, provision, egg placement, closing) two brood cells.

Nest construction and developmental biology

Nests were observed in cavities of a variety of materials including bamboo stems, giant reed (*Arundo donax* L.) and wood. The nests contained organic and inorganic materials collected and stored by the bee: resin, mud, pebble stones, plant material like trichomes, dry grass, sawdust, bark and small twigs (Appendix A: Figs. S2–S4). Besides these natural materials, two females were observed to collect plastic foam, from a protective bumper on a trampoline in a garden, to use the artificial material for brood cell architecture (Appendix A: Fig. S4). The developmental stages of two of these brood cells, reared at constant room temperature, are shown in Appendix B. A comparison of larval development is given in the Appendix A: Table S5. Further behavioral observations of intraspecific competition of males and of mating are described in Appendix A: Results S1, and videos provided as Appendix C and D.

Interspecific competition for nest resources between *M. sculpturalis* in Europe and native bees was found four times out of 327 nests. These four nests were constructed in cavities already used as nests by native mason bees, and in two cases native mason bees used cavities occupied by *M. sculpturalis*. In all cases the exit of the primary nest was completely blocked by the second species (Appendix A: Fig. S3).

Diel activities of *M. sculpturalis* in its exotic range were recorded at

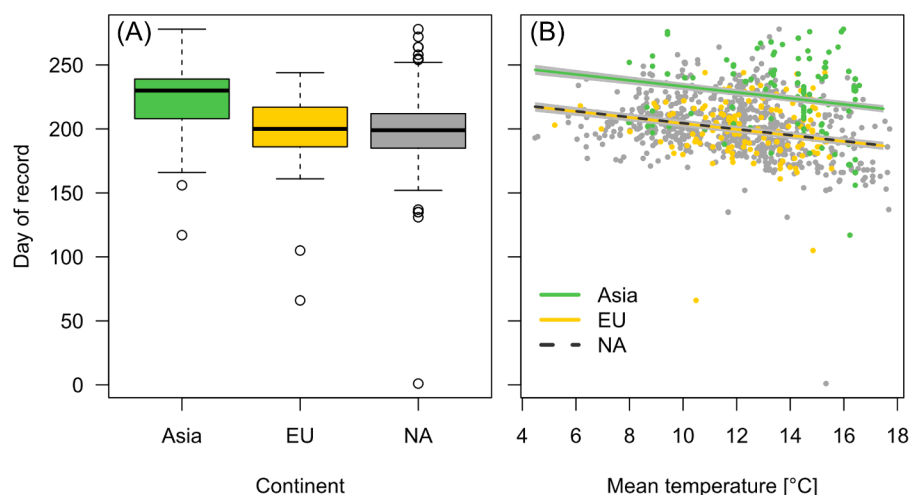


Fig. 2. (A) *Megachile sculpturalis* was recorded significantly later in the native (Asia) than in the exotic ranges (Europe—EU and North America—NA). Boxes and whiskers represent the data distribution about the median. (B) Individuals were recorded earlier at higher annual mean temperature. Model predictions (lines) and standard errors (shaded area).

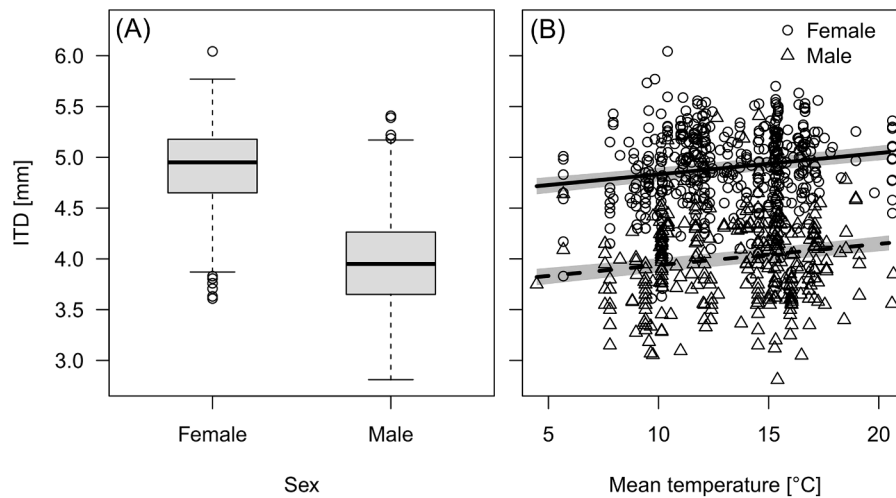


Fig. 3. (A) ITD was significantly lower for male compared to female individuals. Boxes and whiskers represent the data distribution about the median. (B) Across continents, Intertegular distance (ITD) increased significantly with increasing temperature in both sexes. Model predictions (lines) and standard errors (shaded area).

Table 2

Comparison of number of nests investigated (N nests), sum of brood cells per nest (N cells), mean number of brood cells per nest (Mean cells), minimal number of cells per nest (Min cells), maximal number of cells per nest (Max cells), parasitism rate of brood cells (% parasitism) and developmental mortality rate of brood cells excluding mortality caused by parasitoids (% mort). For reared adult specimens (CN $N = 253$; JPN $N = 44$ & 115 ; D-A-CH $N = 68$; SFR $N = 105$) sex of the offspring was recorded (% male). Nest material “bamboo” includes different bamboo species, giant cane (*Arundo donax*) and plume poppy (*Macleaya cordata*).

Location	Nest substrate	N nests	N cells	Mean cells	Min cells	Max cells	% parasitism	% mort	% male
Native CN	bamboo	232	361	1.6	1	4	20.8	9.1	80.2
Native JPN ^a	bamboo	454	4048	11.4	–	–	20.5	–	72.6
Native JPN ^b	bamboo	137	927	6.7	–	16	14.1	–	82.9
Native JPN ^c	bamboo	40	54	1.4	1	2	–	–	–
Native JPN ^d	bamboo	25	61	2.4	–	–	–	–	–
Exotic D-A-CH	bamboo/ wood	204	498	2.4	1	13	11	8.0	80.9
Exotic SFR	bamboo	120	285	2.4	1	7	15.8	–	76.2

^a Sasaki and Maeta (2018).

^b Maeta et al. (2008).

^c Ishihara (1994).

^d Endo and Hashimoto (1994).

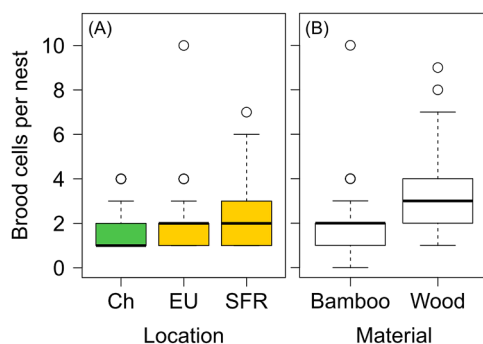


Fig. 4. (A) Number of brood cells in bamboo per nest cavity was significantly lower at one location in China (Ch, green) than at data sets from the EU (yellow, collection 4) and one location in southern France (SFR). (B) Number of brood cells was lower in cavities of bamboo (including giant cane) than in different wood cavities (Wood).

one nesting site in Germany. Females spent 48 % of their diel activity inside the nest, placing food, eggs or nesting material and 52 % outside for collecting food or nesting materials (Appendix A: Table S6). Bees were observed to be active for about 12 h on sunny days between 9 to 10 am and 9 to 10 pm. At night, female bees rested inside the cavity of their unfinished nests. In the exotic range, in Germany pollen and nectar collection took 19 min (Appendix A: Table S6), in other places within Europe citizen scientists recorded on average 7 min for this activity

(Appendix A: Table S7). At one location in Germany, resin collection took 4 min (Appendix A: Table S6) and citizen scientists across Europe reported on average 1 min (Appendix A: Table S7).

Natural enemies

In the native range, 75 out of 361 (21 %) brood cells hosted one of eight natural enemy species, which were supplemented by six further species listed in Sasaki and Maeta (2018) from Japan (Table 3). All these enemies were parasitoids or cleptoparasites, of which three were cuckoo bees (*Coelioxys fenestra*, *Euasps basalis*, *Euasps* sp.). In the exotic range of *M. sculpturalis*, 54 out of 498 (11 %) brood cells collected in D-A-CH and 44 out of 285 (15.8 %) from SFR hosted one of six natural enemy species (Table 3). These natural enemies included four generalist parasitoids (*Melittobia acasta*, *M. australica*, *Monodontomerus*, *Anthrax anthrax*) and one nest-predatory beetle (*Trichodes apiarius*) (Table 3). Only *Melittobia acasta* and potentially a *Monodontomerus* species occurred at native and non-native ranges. The phenology of *M. sculpturalis* and its parasitoids (*Euasps basalis*, *Coelioxys fenestrata* and *Anthrax aygula*) was synchronized in the native Chinese range. Only the generalist parasitoid *Leucospis japonica* Walker was not synchronized with the main peak of *M. sculpturalis* activity (Appendix A: Fig. S5, Ye et al., 2017).

Discussion

The sculptured resin bee, *M. sculpturalis* is the largest megachilid bee

Table 3

Infestation of brood cells of *M. sculpturalis* by natural enemies. Data for JPN¹ were taken from Maeta et al. (2008) and for JPN² from Sasaki and Maeta (2018), who provided mean values and for some natural enemies only occurrences without quantification (x). *Trichodes apiarius* is a predator attacking multiple brood cells of one or multiple nearby nests (Westrich 2018). Host specificity of species was assigned based on literature data (Westrich 2018; Michener 2007) and that of morphospecies was assigned based on common representatives within their genus.

Location	Family	Native range		Exotic range		SFR	Host specificity
		CN	JPN ¹	D-A-CH	JPN ²		
Total # of brood cells		361	760		674.7	498	285
Hymenoptera: Apoidea cuckoo bees							
<i>Coelioxys fenestrata</i>	Megachilidae	4.1 %	2.3 %		7.9 %		specialist on <i>Megachile</i> sp.
<i>Euasps basalis</i>	Megachilidae	8.6 %	1 %		2.6 %		specialist on <i>Megachile</i> sp.
<i>Euasps</i> sp.	Megachilidae	1.1 %					specialist on <i>Megachile</i> sp.
Hymenoptera: Chalcidoidea							
<i>Eurytoma</i> sp.	Eurytomidae	0.3 %					generalist
<i>Leucospis japonica</i>	Leucospidae	0.8 %			x		generalist
<i>Melittobia acasta</i>	Eulophidae				x	2.8 %	14.7 %
<i>Melittobia australica</i>	Eulophidae						0.8
<i>Melittobia</i> sp.1	Eulophidae	2.8 %					generalist
<i>Melittobia</i> sp.2	Eulophidae	0.8 %					generalist
<i>Monodontomerus</i>	Torymidae				x		0.4
Diptera							
<i>Anthrax anthrax</i>	Bombyliidae					0.2 %	generalist
<i>Anthrax cygula</i>	Bombyliidae	2.2 %			0.1 %		generalist
<i>Anthrax (Hemipenthes) jezoensis</i>	Bombyliidae				x		generalist
<i>Conops</i> sp.	Conopidae				x		generalist
<i>Physocephala</i> sp.	Conopidae				x		generalist
Coleoptera							
<i>Trichodes apiarius</i>	Cleridae					7.8 %	generalist
<i>Zonitis japonica</i>	Meloidae		8.2 %		9.9 %		generalist

species in its invaded ranges in Europe and North America. The origins of its human-assisted spread to North America and Europe are still not fully understood and the economic and ecological consequences remain uncertain (Lanner et al. 2021). With this synthesis and observational study, we show that natural history traits such as phenology and number of brood cells per nest potentially shifted and together with a lack of specialized enemies benefited this species in its ongoing spread across North America and Europe. We also showed how opportunistic the species is, for example, in its selection of nesting materials and cavities. Although antagonists may eventually slow the spread of this species, it will still remain a unique example for research in ecology and invasion biology, especially in terms of interaction network rewiring, genetic reconstruction of invasion history and potential founder effects.

Phenological shift

The phenology of the flight activity of *M. sculpturalis* shifted about one month forward in the exotic range. This shifted phenology was not associated with higher mean annual temperatures at the exotic range, as temperature was a covariable in the model, and the shift was observed in temperate regions. Phenological adaptation that matches host plant phenology might explain the observed shift. In its native range the species is considered a flower generalist (Kakutani et al., 1990; Maeta et al., 2008). In North America generalistic flower visitation was recorded (Parys et al. 2015), but not pollen collection. In the exotic range in the EU the bee is also observed on a variety of flowers but predominantly collects pollen from only a few plant species (Sasaki & Maeta, 1994; Westrich et al., 2015; Le Féon & Geslin, 2018) with relatively narrow flowering phenology. For example, in central Europe the species collects almost exclusively pollen from *Styphnolobium japonicum* (L.) Schott, a plant on which it is also observed in North America. Hence, at least in Europe *M. sculpturalis* individuals matching this plant phenology likely produce more offspring (Aguado, 2018).

In Serbia at one location with cooler climatic conditions, we observed smaller and later emerging specimens compared to other locations in Serbia and the EU. These delayed individuals were still visiting flowers of also late blooming *S. japonicum* in 2020 and 2021 (Bila Dubaić et al., 2022). This observation is likely distinct from the report of Sasaki and Maeta (1994), who reported emerging individuals

in autumn that followed an earlier activity period at the same location, when their regional main floral resource (*Pueraria montana* var. *lobata* (Willd.) Maesen & S.M.Almeida ex Sanjappa & Predeep) already ended blooming. Phenological matching of host plant and solitary bee reproduction was shown in several studies (Forrest & Thomson, 2011; Stemkovski et al., 2020). Earlier summer in the exotic ranges could likely not explain the earlier phenology as shown by monthly temperature curves that overlaid for all continents. In contrast, due to the frequency of *S. japonicum* visitation reported for the species in the EU and the observation in Serbia we expect a reproductive benefit of a phenological match of *M. sculpturalis* individuals with the phenology of *S. japonicum*. This might indicate a floral host dependence of the bee species following the introduction to the new EU range. Thus, the distinct earlier phenology in its exotic range might be the synergistic result of selective filtering. However, we do not know if this is generalizable for the NA range as we don't know of any host plant specificity in the NA range. Future studies should investigate pollen in bee nests and phenological patterns at both exotic ranges, to evaluate the importance of host plants in shaping invasion dynamics of the bee species.

Body size increases with temperature

Our analysis showed that the ITD of *M. sculpturalis* individuals was not significantly increased at the exotic range. For bees, ITD is used as a proxy for body size and larger bee species have larger flight distance (Araújo et al., 2004; Greenleaf et al., 2007; Zurbuchen et al., 2010). Flight distance may affect dispersal by two mechanisms: First, it directly increases flight distance within a given time, for example to reach new suitable habitat. Second, it increases the tolerance to accept a habitat as suitable. This is because the home-range of a species, the area in which it nests and finds all other necessary resources, like pollen- and resin-providing plants, is higher (Cane, 1987; Zurbuchen et al., 2010). If dispersal ability was limiting the invasion success, a selective filter for larger individuals at exotic ranges could be expected but was not confirmed. Based on findings and latest results derived from species distribution modeling (Lanner et al., 2022), we conclude that dispersal is not a limiting factor, while other life history traits (e.g., reproduction rate, natural enemies) and its adaptative potential had more explainable

power for its invasion success.

We observed significantly larger individuals of *M. sculpturalis* in warmer locations. This contradicts a positive association between body size and latitude or colder environments of insects. The Bergmann's rule and similar rules (Angilletta & Dunham, 2003; Osorio-Canadas et al., 2016; Gérard et al., 2018) predict increasing body sizes at colder conditions and studies suggest that bees, especially large bees, follow Bergmann's rule (Osorio-Canadas et al., 2016; Gérard et al., 2018; Heinrich, 2004). Although body size increased significantly with temperature, the regression explained only a 0.3 mm increase in ITD while the ITD values varied by about 2.5 mm within each sex. Therefore, temperature is unlikely the only driver of body size and for example local phenotypes and food resource availability may play an important role in determining body size (Gérard et al., 2018; Chole et al., 2019). Potentially *M. sculpturalis* is more efficient at higher temperature regimes in finding food resources, or host plants produce more pollen, which might benefit its invasion success. Controlled experiments, for example, selecting individuals by traits or exposing multiple generations to altered temperature and food resources while accounting for potential genetic effects that alter plant traits are needed to test these factors (Maebe et al., 2021).

Flexible nest architecture

Nests were found in a variety of cavities in hard woods (e.g., cherry, plum or birch), reeds (e.g., *Arundo donax*), and bamboos from different species and can therefore be expected in a larger variety of suitably sized cavities. As the common English name already implies, the “Sculptured Resin Bee” always uses resin from coniferous trees, which is commonly used in mixture with other materials, for brood cell construction (Maeta et al., 2008). The materials for nest cell and closing plug construction were highly variable but mainly of natural origin. Using plastic for nest construction was reported only rarely for solitary bees. For example, the alfalfa bee, *M. rotundata*, used pieces of polyethylene-based plastics (Wilson et al., 2020) and *M. campanulae* used polyurethane-based plastics to form brood cells (MacIvor & Moore, 2013). The authors speculated that exploitation of artificial materials may generate selective advantages, which could also be true for *M. sculpturalis*. The utilization of resin for nest construction has several functionalities (e.g., defence, anti-microbial benefits; Chui et al., 2021), but a newly observed antagonist of *M. sculpturalis*, *Stelis costalis* Cresson, recognizes host nests by their resinous contents; as its native bee hosts in North America are also resin-using species (Neff, 2021). Usage of variable materials may hinder the evolution of nest recognition by natural enemies. Whether the use of plastic is advantageous or not, opportunism in this life history trait is likely beneficial for establishing in new environments (Farji-Br ener & Corley, 1998; Koch et al., 2021).

Natural enemies

We found exclusively generalist predators, parasitoids or cleptoparasites in *M. sculpturalis* nests collected from many European populations from three insect orders: Coleoptera (e.g., *Trichodes apiarius* L., Diptera (e.g., *Anthrax anthrax* Schrank) and Hymenoptera (e.g., *Melittobia australica* Girault). The cosmopolitan wasp, *M. australica* was reported in 2012 for the first time in Europe and is considered a generalist parasitoid of cavity-nesters (Cusumano et al., 2012). Our observations effectively quadrupled the number of natural enemies so far recorded in the European range by Straffon Díaz et al. (2021), but do not include *Cacoxenus indagator* Loew, as was recorded by Straffon Díaz et al. (2021). *Cacoxenus indagator* is an early flying parasitoid mostly of *Osmia cornuta* (Latreille) and *O. bicornis* (Linnaeus) active from March to June, that is, before the first *M. sculpturalis* occur. Therefore, we would treat their observation of *C. indagator* with caution until further confirmation. Furthermore, the spider beetle *Ptinus sexpunctatus* Panzer also mentioned by Straffon Díaz et al. (2021), may not be considered an

important natural enemy of *M. sculpturalis*. It is associated with cavity-nesting bees, with adults and larvae feeding on dead organic matter, including leftover pollen, insect exuviae or dead individuals (Majka et al., 2007). Additionally, *Stelis costalis* parasitizing larvae of *M. sculpturalis* outside its native range was reported from North America (Neff, 2021) and further generalist species can be expected in the exotic ranges.

The palette of generalist enemies found in its exotic range contrasts the specificity of enemies in its native range. We identified three cuckoo bee species in *M. sculpturalis* nests which occurred during the main breeding season in China, for example, the cuckoo bee *Coelioxys fenestratus* Smith. This species is also a common natural enemy of *M. sculpturalis* in Japan (Nagase, 2006), with high parasitism rates (7.9 % in Maeta et al., 2008; and 4.1 % in China).

The enemy release hypothesis (ERH) describes the benefit for population growth of exotic species at an exotic location as the absence of specialist antagonists at this location. The ERH specifies that: i) specialist enemies of an exotic species are missing in the new environment and ii) generalist enemies occurring in the exotic range have a greater ecological impact on native than exotic organisms (Keane, 2002; Enders et al., 2020). Accordingly, our investigation of almost 500 nests from the native and exotic ranges provides the primary requirements of the ERH, 1) a lack of specialist enemies and 2) an increase in generalist enemies at the exotic range compared to the native range. However, whether these changes are a relevant driver of the invasion success and of potential changes in other life history traits needs further investigation (Roy et al., 2011). Moreover, native and exotic antagonists may establish or adapt over time to the new species, as was observed for *M. rotundata* (Pitts-Singer & Cane 2011), which might reduce potential advantages in the future.

Reduced enemy pressure, as indicated in this study, might influence the species behavior. A lack of enemies could allow females to invest more in its offspring (Goodell, 2003) and enable more pollen and resin collection trips, resulting in more brood cells and increased fecundity. Our life history observations showed that females spent 45 % of their daily activities away from the nest. Brood cell protection by large vestibule may have become an unnecessary strategy to increased fitness under enemy release, which might explain the increased numbers of brood cells per nest, as we observed in SFR. Even though our behavioral data is lacking comparative data from its native range, the presence or absence of specialist and generalist enemies in its exotic range might play a crucial role in shaping the success of *M. sculpturalis* in Europe and North America.

Sex ratio and reproductive traits

We recorded the same 3 to 1 sex ratio of males to females from the native and the exotic ranges, matching rates observed in Japan by Maeta et al. (2008) and Sasaki and Maeta (2018). These results also confirm the sex ratios observed by Straffon Díaz et al. (2021) for the exotic, but contradict their findings for the native range. In general, sex ratios of cavity-nesting Hymenoptera including Megachilid bees are species-specific and can vary between generations, depending for example on food availability (for example, see Longair, 1981; Paine, 2004b; Zurbuchen et al., 2010). But, for *M. sculpturalis* a male bias should be accepted, given the rearing data from a multitude of native and exotic locations as presented in this study.

We observed slightly higher numbers of brood cells per nest in the exotic range and an increase by almost 50 % in SFR. This location is one putative origin of introduction to the EU with a large population, potentially currently adapting to the new range. Former studies have shown that range shifts can result in evolutionary pressure on specific life history traits including, for example, increased fecundity associated with population growth (Phillips et al., 2010). If the increased number of brood cells per nest is a result of these mechanisms it may also increase the number of offspring per female. Therefore, it is necessary to monitor

the ongoing population growth and the competitive potential with other solitary bee species (Laport & Minckley, 2012; Roulston & Malfi, 2012; Geslin et al., 2020; Lanner et al., 2020a, 2020b), which may call for invasive species management in the future.

Competitive behavior for nests and direct aggression of *M. sculpturalis* against the carpenter bee *Xylocopa virginica* (Linnaeus) have been described in North America (Roulston & Malfi, 2012; Laport & Minckley, 2012). If other wood-boring species at both exotic ranges are similarly affected is so far not documented. Straffon Díaz et al. (2021) documented 44 % blocked nests of cavity-nesting *Osmia* by *M. sculpturalis* from a single location, in contrast only 1 % of the nests we sampled across Europe contained blocked nests of other bee species. Blocking may prevent the former inhabitant from escaping through the resin walls, this is especially likely if the blocked species is not adapted to penetrating similarly structured cell walls, for example, many larger *Osmia* species that use only clay, or *Xylocopa* that use only wood (Cane et al. 2007). Conversely, we would expect *M. sculpturalis* to find a way to chew through a few thin clay walls of *Osmia* brood cells as *M. sculpturalis* is adapted to both clay and resin cell walls. However, these are observations documenting negative impacts on the individual, while impact at the population level of the affected species as well as potential competitive behavior for foraging resources remain to be further explored. Given these variable examples of direct competition for nesting sites, population monitoring of potential competitors is required to evaluate the impact of this species on its new environment.

Conclusion

Our home-and-away comparison revealed significant changes towards an earlier phenology, more brood cells per nest cavity and the lack of specialized natural enemies in the exotic range of the bee species *M. sculpturalis*. Thereby, synergistic effects of ecological filters or founder effects leading to a delayed flight period, potential enemy release and changes in reproductive traits might be the explanatory basis for the invasion success. In the exotic range, the species was opportunist for nesting cavities and nesting materials, using even plastic for nest construction. Taken together, behavioral and adaptive flexibility might be a key trait for passing filters during each step of the invasion process and for successful establishment (Renault et al., 2018). Although we cannot determine causation between life history traits and enemy release and invasion success, it is likely that some of the here documented life history traits promote the invasion success, while others resulted from the disconnection to the source population. With this, our study identified potential drivers of the invasion and provides a range of trait and behavioral information that shed light on the natural history of the species.

Funding

This study was partly funded by the Austrian Academy of Science DOC Fellowship Program supporting Julia Lanner, by BMBWF WTZ FR06/2022 supporting Julia Lanner and Benoît Geslin and by the German Research Foundation (DFG FOR 891/3, KL 1849/6-2) supporting Felix Fornoff.

This research was also supported in part by the U.S. Department of Agriculture, Agricultural Research Service. USDA is an equal opportunity provider and employer. Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

Funding source did not have any additional role in the study design, data collection and analysis, decision to publish or preparation of the manuscript.

Authors' contributions

Conceptualization JL, FF; Data curation JL, FF, MCO, TT, BG, GS, TX, SG, KP, AC, JBD and EG; Formal analysis FF, JL; Project administration JL, FF; Visualization FF; Writing - original draft JL, FF; Writing - review and editing JL, FF, MCO, TT, BG, GS, TX, SVS, SG, KP, AC, JBD, BP, HM, AMK and EG. JL and FF contributed equally to the study.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

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.

Data availability

The datasets supporting the conclusions of this article can be found, in the online version, at Appendix E–G.

Acknowledgments

We want to thank all participants of the ongoing Citizen Science Projects and Partner Institutions, which supported the project by providing nests, specimens or any other data necessary for this study: inatura Dornbirn, Naturschutzbund Österreich, Österreich Forscht, Schweiz Forscht, Entomologischer Verein Bern, Wildbiene + Partner, Mississippi State University, Clemson University, Auburn University, USDA PIRU, Laura Russo, Sam Droege, and Mike Arduser. Special thanks go to our colleagues Milan Plečaš and Jovana Raičević; and the Chinese Academy of Science.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.02.008.

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