

# Metabarcoding reveals global variation in pollen collecting behavior of the invasive bee *Megachile sculpturalis* (Hymenoptera: Megachilidae)

J. Lanner

julia.lanner@plus.ac.at

University of Salzburg

S. Mader

BOKU University

C. Rupprecht

BOKU University

J. Bila Dubaić

University of Belgrade

J. Raičević

University of Belgrade

C. M. Orr

Stuttgart Naturkundemuseum

P. Nikolić

University of Banja Luka

F. Fornoff

University of Freiburg

M. Martini

University of Freiburg

C. Hernandez-Castellano

Czech University of Life Sciences Prague

S. Dötterl

University of Salzburg

H. Meimberg

BOKU University

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## Article

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# Abstract

Invasive species are proliferating globally. The establishment success depends on resource availability, such as pollen for bee foraging and larval development. Trophic flexibility—ranging from exploiting novel floral resources to maintaining preferences for co-evolved hosts and even mutual facilitation with invasive plants—can promote invasion success.

*Megachile sculpturalis* is an East Asian solitary bee, introduced to Europe and North America. Although it has become a model organism for studying invasive pollinators, data on its pollen sources remain scarce. Here, we provide the first global data for diet composition and consistency applying DNA metabarcoding to over 250 pollen samples collected globally.

We identified 14 in its native range and 28 plant taxa in the bee's non-native range including trophic relationships with two invasive plant species: *Lythrum salicaria* in North America and *Pueraria montana* in Europe. The species exhibited a generalist foraging strategy in its non-native range, typical for successful invaders. European pollen profiles, however, were frequently dominated by a single East-Asian ornamental tree *Styphnolobium japonicum*.

The widely planted trees may have unintentionally facilitated the establishment of *M. sculpturalis*. Prioritizing native flora and avoiding mass plantings of exotics in urban spaces could help mitigate the spread and impacts of invasive pollinators while promoting native fauna.

## 1. Introduction

Invasive species are a key driver of biodiversity decline, alongside climate change, habitat loss, and chemical pollution [cf. 1]. Globalization and the expansion of international trade and travel have led to more frequent introductions of non-native species, including pollinators [2, 3]. While only a small subset of introduced species becomes invasive, those that do can cause significant ecological and economic harm [4]. Invasive species are a threat to species communities and local ecosystems: outcompete native species, co-introduce pathogens, alter ecosystem functioning and disrupt ecological networks. In pollination systems, invasive pollinators can interfere established mutualisms and interaction networks by competing for floral resources or altering interaction patterns, leading to declines in native pollinator populations and reduced plant reproductive success [10–12].

The success of establishment and survival of invasive pollinators increases with the availability of resources [13], such as floral hosts. Collecting knowledge on the diet composition and consistency of invasive bees is important, as it provides predictive power of their invasive potential [14, 15]. Until now, however, only few studies have investigated trophic interactions and how floral resources facilitate the establishment of invasive pollinators, focusing predominantly on social honey and bumble bees [16–19].

Basically, three non-mutually exclusive scenarios are possible: First, the invaders adapt to novel environmental conditions, including previously unknown foraging sources [20–22]. Examples of such generalists are honey bees or bumble bees often intentionally introduced to pollinate crops [6, 17, 21]. This ability to respond flexibly to novel situations promotes invasiveness [23]. Second, according to the 'native preference hypothesis' [18, 24], invasive pollinators locate and use floral hosts in the new environment that co-occur in their native ranges and were also introduced to the new ecosystems [25–27]. Examples of introduced bees displaying a preference for co-evolved plants, thereby supporting the native preference hypothesis, include the social *Apis mellifera* L. 1758 in South America, *Bombus terrestris* (L. 1758) in New Zealand and Tasmania [16, 28, 29] and *Anthidium manicatum* L. 1758 in New Zealand [30]. Third, according to the 'invasional meltdown' scenario, which is closely related to the native preference hypothesis, the invaders visit invasive floral hosts with a reciprocal benefit [31, 32]. These mutualistic interactions among invaders

create positive feedback loops that accelerate invasion processes of both partners, for example plants and their pollinators. Liu & Pemberton (2009) found proof for an invasive mutualism in the buzz-pollination by the unintentionally introduced solitary species *Euglossa viridissima* Friese, 1899 and the weed *Solanum torvum* in Florida.

One especially noteworthy invasive pollinator is *Megachile sculpturalis* Smith 1853, a solitary wild bee native to East Asia. It was first documented outside of its native range in the United States in 1994 [34], and later in Europe in 2008 (South France) [35]. It is categorized as a moderately competitive invasive species [36] exhibiting aggressive behavior for nesting space and material against native bee species [37–40]. However, its broader impact on native bees, plant communities, and their interactions remains unclear.

Side-selective European palynological studies present a contrasting picture of its pollen collection behavior compared to reports from its native range [41–46]: In East Asia, *M. sculpturalis* is known as a generalist species, collecting pollen from species of several plant families [47–50]. In contrast, the bee appears to prefer the ornamental *Styphnolobium japonicum* in Europe [42–44] (Suppl. Material A Tab. S1), which co-occurs with *M. sculpturalis* in its native range. To ultimately understand the ecological role of *M. sculpturalis* and to evaluate which scenario is likely, it is essential to investigate its dietary composition and consistency in its introduced range.

In recent years, DNA metabarcoding has emerged as a powerful tool for analyzing plant-pollinator interactions [51, 52]. By sequencing short taxonomically informative regions of the DNA, metabarcoding enables identification of plant species from mixed pollen samples, e.g. obtained from nest provisions of the bees, with high accuracy and taxonomic resolution [53, 54]. It is a sensitive, efficient, and reproducible method for investigating foraging behavior of bees [55, 56], such as *M. sculpturalis*.

With this study we provide first global insights on the pollen usage of the invasive bee, *M. sculpturalis*, by applying DNA metabarcoding. We analyse diet composition and consistency using pollen samples from female scopae and nest provisions collected across the introduced European and North American ranges, supplemented by preliminary samples from the native range. We expect that the bee is an opportunistic forager and uses more host plants in Europe than previously known. We further hypothesize that there is geographic variation in the plants used within and among continents, as the plants available to the bee varies among regions. We also expect the bee to use both newly encountered plants in the invaded environments (scenario one) and plants that co-occur with the bee in its native range (scenario two).

## 2. Material and Methods

### 2.1. The study organism – *Megachile sculpturalis*

*Megachile sculpturalis* is a solitary, univoltine bee active from summer to early autumn [23, 39]. Individuals of *Megachile sculpturalis* have likely been introduced via maritime trading networks from East Asia to several areas on the northern hemisphere [35, 57]. Several independent accidental introductions facilitated the establishment in Europe, followed by rapid range expansion with spread rates estimated up to 87 km/year [58, 59]. Spatial distribution modeling indicates that the bee is still in range expansion utilizing, at least partly, human transportation networks [60]. Females nest in cavities (often wooden cavities or reed stems provided with trap nests), with at least 8 mm in diameter. As the common name sculptured resin bee suggests, the brood cells are constructed mainly from resin, although females were observed using alternative materials, including artificial materials such as plastics [23] (unpublished data; Lanner 2026) or grafting wax [61]. Females collect pollen as provision for the brood cells with dense ventral scopal hairs (Fig. 1). *Megachile sculpturalis* is the first invasive bee reported on the European continent and has been added to the IUCN list of invasive species [62].

## 2.2. Sample collection and processing

In total, 252 pollen samples were collected from the female scopa or nest provisions of *M. sculpturalis* in Europe (n = 233), the USA (n = 19), and its native range (n = 3). One sample per bee or nest was collected to prevent pseudo-replications. Pollen was either directly scraped off the living bee's scopa using a cotton swab (scopal pollen, n = 117) or collected from the brood cells of nests (provisioned pollen, n = 135). European samples were collected between February 2019 and November 2021 across nine countries: Austria, Germany, Switzerland, France, Italy, Hungary, Serbia, Spain and Bosnia & Herzegovina (Fig. 2). Nests from Austria, Germany, Switzerland, and France were mainly provided by citizen scientists participating in the *BeeRadar* project ([www.beeradar.info](http://www.beeradar.info);[39]). All 19 USA samples were retrieved from individuals stored in ethanol collected in four states: North Carolina, Mississippi, Michigan, and Florida.

Most samples (n = 203) were stored in Eppendorf tubes at -20°C after collection, while 49 samples (including all USA samples) were stored in absolute ethanol at 4°C. Detailed information on processed samples is listed in the Suppl. Material B Tab. S1.

Laboratory procedures from DNA extraction through PCR, indexing, and library preparation followed standard protocols and are described in detail in the Suppl. Material A (S1.1. and Tab. S2). The amplicon library was sent for Illumina MiSeq sequencing at the technical University of Munich, Germany. Bioinformatic sequence processing approach, including database construction and taxonomic assignment, is also described in the Suppl. Material A S1.2.

Additionally, raw sequences from three pollen samples collected in its native range were included as these samples provide the first insights to its diet composition in China. These samples consisted of provisioned pollen loads collected from brood cells located within a subtropical forest of Jiangxi province. These samples were amplified using a shorter ITS2 fragment (ITS-S2F/ITS4), compared to the longer ITS-S2F/ITS2R amplicon [63] used for the European and USA samples. However, this inconsistency of the marker length should not affect the conclusions made as the Chinese samples were used for preliminary qualitative comparisons.

## 2.3. Data preparation

We employed a multi-marker metabarcoding approach using three genetic markers: rbcL, ITS2, and trnL. This strategy was chosen to provide complementary taxonomic coverage [64, 65]. Our primary focus is on ITS2 due to its higher species-level resolution resulting from greater sequence variability [66]. Additionally, we included rbcL for its broad taxonomic coverage, and trnL as a complement. This multi-marker approach maximizes taxonomic coverage and detection sensitivity, although direct comparisons across markers remain challenging due to differences in resolution and amplification biases. Marker concordance analysis and results are provided in the Suppl. Material. A Figure S3 and S4, D and E.

Quantitative results obtained through barcoding (relative abundances of material proportionally to generated sequence reads) have been controversially discussed in the literature [51, 67, 68].

Samples with zero reads were excluded (n = 31). A total of 49 samples (Serbia n = 46; Austria n = 2, Spain n = 1) were excluded as they were collected from the scopa while the bee was foraging to prevent biased sequencing results. In cases when species assignment failed, we labeled them as 'unidentified\_reads' and excluded them from statistical analysis.

## 2.4. Statistical Analyses

Statistical analysis was conducted in RStudio version 2023.12.0 [69] and data was prepared using the tidyverse package [70]. Species richness was quantified for EU and USA samples using iNEXT (datatype = "individual-based

abundance") for Hill numbers of order  $q = 0$  [71] and generated coverage-based rarefaction/extrapolation curves, plotting species diversity versus sample coverage ( $n_{boot} = 500$  and confidence intervals = 95%). The coverage-based rarefaction curves indicated near-complete sampling for both sample sets (Suppl. Material C Fig. S1). We used relative read abundances (RRA) for statistical analyses [72]. Before testing for differences on multiple scales, species composition between sources (bee scopa and provisioned pollen) was analysed by applying a Permanova and a non-metric multidimensional scaling (NMDS) based on the RRA per species per samples with Morisita-Horn distances ( $dist = horn$ ) and `seed.set` (123) implemented in `vegan`. As tests showed no significant differences ( $R^2 = 0.0$ ,  $F = 0.49$ ,  $p = 0.67$ ) and species composition overlapped except for a single sample (Suppl. Material C Fig. S2), we did not further account for differences between sources in our analyses.

We assigned growth type ('tree', 'shrub', 'herb' and 'climber' following [55]) and origin status ('East-Asian' for taxa occurring in the original habitat with the bee vs. 'non-Asian') to the identified plant species. Analyses are based on the relative abundance of reads per species and families per sample.

Differences in the species richness between non-native ranges (Europe vs. USA) was tested with a Wilcoxon rank sum test (`wilcox.test`), implemented in `vegan`. We tested for different community compositions A) on a global scale between continents (Europe vs. USA) and B) on a continental scale between European countries by applying a non-metric multidimensional scaling (NMDS) approach by Morisita-Horn distances ( $dist = horn$ ) with `seed.set` (123) implemented in `vegan`. We fitted species and family vectors to the ordination using `envfit` (`vegan`), with 999 permutations. Further, we calculated a Permanova with the `adonis2` function, also with `seed.set` (123) and 10 000 permutations to support the results from the NMDS. Homogeneity of multivariate dispersion among groups was assessed with `betadisper`, also implemented in `vegan` [73]. Pairwise differences in dispersion were evaluated with Tukey's Honest Significant Difference applied to the `betadisper` model (`TukeyHSD`). Results from the dispersion tests are included in the Suppl. Material C S2.

Then the pollen composition of four nests located in an urban landscape ( $n = 22$ ; Vienna, Austria) was analysed C) on a local scale. We compiled a list of all tree species present within a 1 km radius (compare *Megachile spp.* foraging distance in [74]) from the municipal tree inventory using QGIS 3.8 [75] for each of the four local nest locations. This approach was chosen to investigate the surrounding tree compositions and consequently available pollen sources for the bee. Finally, we studied the pollen composition D) between brood cells within nests (number of nests: Austria 6, France 2, Switzerland 6) The composition of provisioned pollen samples within nests were again analysed and differences calculated based on Morisita-Horn distances.

### 3. Results

A total of 557,305 reads were retained across all three markers for the European and USA dataset, and 102,954 reads for the Chinese ITS data; detailed statistics are provided in the Suppl. Material A 1.2.

#### 3.1. Pollen composition

To investigate whether *M. sculpturalis* is a generalist forager, we analysed the sequencing results at the family level and detected pollen from 16 families. Samples from the non-native range contained one to six different families. Fabaceae pollen was frequently identified in 210 pollen samples in its non-native range (Fig. 3 B). In the three pollen samples from the native range, we detected a minimum four and maximum seven families. Also, pollen from Fabaceae plants was most abundant by RRA (relative read abundance; Fig. 4 B).

On species level, we detected 28 species in the pollen samples from the non-native range of *M. sculpturalis* ( $n = 173$ ). Minimum number of taxa was one ( $n = 116$ ), and maximum number was nine species (EU sample = MSNTe1: *Ligustrum*

*lucidum*, *S. japonicum*, *Robinia pseudoacacia*, *Koeleria paniculata*, *Wisteria sinensis*, *Brassica napus*, *Pueraria montana*, *Cucumis sativus*, *Brassica oleracea*). Of the 116 single species samples, 113 contained *S. japonicum*, one sample *Pueraria montana* (USA sample = USFL12D5) and another sample *Lagerstroemia indica* (USA sample = UFL010). The most abundant taxon by read count and across all samples was *S. japonicum* (58750 reads, present in 149 samples = 86.13%), followed by *Lathyrus sylvestris* (4805 reads, in 14 samples = 8.09%), and *P. montana* (1915 reads, in 16 samples = 9.25%, Fig. 3 A).

In European samples we found nine plant species of East-Asian origin (45% of all detected species) (Suppl. Material C Tab. S4), and nine (52.9%) East-Asian species in USA samples (Suppl. Material C Tab. S5). Due to the high prevalence of *S. japonicum*, one or more East-Asian plant species were detected in 186 European samples (74.7%), and 34 USA samples (63%). Regarding growth type, there were five (25%) trees, one (5%) shrub, nine (45%) herbs, and five (25%) climbers counted in the EU dataset (compare Table 1). In the USA pollen samples, we assigned species to five (24.9%) trees, two (11.8%) shrubs, four (23.5%) herbs, and six (35.3%) climbers.

Within the three native range samples, we identified 14 taxa. Reads were most frequently assigned to *Ilex memecylifolia*, followed by *Triadica cochinchinensis* and *Actinidia lanceolata*, all were present in one sample (Fig. 4 A). Families exclusively detected in Asian pollen samples were: Aquifoliaceae, Euphorbiaceae, Rutaceae, Actinidiaceae, Lamiaceae, Myrtaceae, whereas families exclusively detected in pollen from its non-native range were: Lythraceae, Oleaceae, Brassicaceae, Malvaceae, Anacardiaceae, Boraginaceae, Cucurbitaceae, Asteraceae, Ranunculaceae.

## 3.2. Global scale comparative pollen consistency

NMDS (Fig. 5 A + B) and PERMANOVA revealed significant differences in plant species and family composition between the European and USA ranges (Morisita-Horn dissimilarities species level:  $F = 129.52$ ,  $R^2 = 0.43$ ,  $p < 0.01$ ; family level:  $F = 85.79$ ,  $R^2 = 0.33$ ,  $p < 0.01$ ; Suppl. Material C Fig. S3 A + B). Species and family richness was significantly different between pollen samples collected in Europe and Asia, according to a Wilcoxon rank sum test  $p < 0.01$  (Fig. 5C + D; Table 1).

## 3.3. European scale comparative pollen consistency

Results of a Permanova indicate statistically significant differences in overall sample composition between countries ( $F = 11.344$ ,  $R^2 = 0.26$ ,  $p < 0.01$ ; permutation test  $p < 0.01$ ; Suppl. Material C Fig. S3 C and Tab S9). Highest heterogeneity within a county is in Switzerland (betadisper  $p = 0.17$ ), Germany (betadisper  $p = 0.26$ ), and Hungary (betadisper  $p = 0.03$ ), while other countries present identical compositions (Suppl. Material C Tab S10).

Switzerland contained the highest species richness with 18 taxa, and the largest number of unique species. Further, we detected a single unique species in a Bosnian sample (*Sedum hispanicum*; detailed results in Suppl. Material C Fig. S7 and Tab. S11).

## 3.4. Local urban scale and within nest pollen consistency

We compared the pollen consistency between four nests collected at a local scale (Vienna, Austria). All samples ( $n = 22$ ) contained pollen of a single taxon: *S. japonicum*. According to the municipal tree inventory, *S. japonicum* accounted for  $< 1\%$  (1,740 trees) of all trees within a 1000 m radius around the nest locations.

We analysed the pairwise correlations of provisioned pollen samples within 14 nests ( $2.79 \pm 1.05$  samples per nest) to investigate the larval diet composition at the species level. The Morisita-Horn dissimilarity indices (0 highly dissimilar and 1 highly similar) ranged from 0.12 to 1. Three nests from the same location (Ticino, Switzerland) showed lower similarity levels and more diversity than all other analysed nests (Suppl. Material C Fig. S12).

## 4. Discussion

Here we present first insights into the pollen collection behavior of the invasive bee, *M. sculpturalis*, on a global scale. Metabarcoding uncovered significant spatial variation in the usage of foraging sources and the usage of invasive plant species suggesting the potential of an invasional meltdown between pollination partners.

Traditionally, the pollen collection behavior of bees has been categorized as monolectic (single host plant species), oligolectic (up to a few host plant families), or polylectic (foraging on more than three host plant families) based on plant taxonomy [76].

The foraging behavior of *M. sculpturalis* varies significantly across its geographic range. This pattern may reflect differences in the surrounding environment (e.g., high abundance of a floral resource) and/or genetic or phenotypic (e.g., elongated proboscis) variation among populations [77]. Considering the full geographic coverage of our dataset, *M. sculpturalis* exhibits a broad taxonomic host spectrum consistent with generalists or a polylectic forager. Although we acknowledge that only three samples from the native range were available, the observed cross-continent patterns strengthen this pattern.

However, pollen hosts and composition varied across ranges significantly as European samples were less diverse than the relatively fewer samples collected in the USA. The bee presented a strong ecological specialization in Europe for a single Fabacean species, *S. japonicum*, and therefore could be classified as mesolectic or narrow polylectic [76]. In Europe, all samples from Serbia contained exclusively *S. japonicum* pollen and was highly abundant in Austrian (43 out of 46), Bosnian (seven out of eight), and Italian (eight out of nine) samples. The same pattern repeated when testing the diet composition of nests at a local scale: although the nests were surrounded by different urban land-use contexts (allotments, public park, private garden), and located at a gradient from urban to suburban, the only pollen source was *S. japonicum*.

While most prevalent in European samples, we did not detect *S. japonicum* in any of the samples collected in the USA. A comparable example for another mesolectic species established outside its home range is *Osmia cornifrons* Radoszkowski 1887. Introduced outside its native range, it has established widely in North America and collects pollen from five plant families [18]. However, these categories often do not fully capture the complexity or dynamics of bee foraging behavior, and additional concepts of specialization linked to the ecology, morphology, or evolution of flower visitors have been described [77].

The Japanese pagoda tree is highly abundant in many European settlements from small villages to highly urbanized areas, and at the gas stations on highways (personal observations). It is one of the last blooming large-flowered pollen sources of the season in Europe, relatively easy to cultivate, and therefore an ideal choice for landscape planners. Furthermore, it is an important foraging resource for *A. mellifera* and has therefore been promoted by beekeepers [78, 79]. Consistent with this, *S. japonicum* was also one of the most abundant pollen sources collected by *A. mellifera* according to a Viennese melissopalynological study [79]. According to records on iNaturalist platform, *S. japonicum* has been documented at one of our four USA sampling locations (Durham, North Carolina), although it was not detected by barcoding. Additional samples from areas with abundant *S. japonicum* trees (e.g., New York City) might reflect the results gained by European samples. The broad and repeated availability of *S. japonicum* likely increased encounter rates for *M. sculpturalis* and may have facilitated its establishment and spread, at least in Europe [80]. This indicates a management issue of urban green spaces and the necessity to promote regional biodiversity.

Due to the high prevalence of *S. japonicum*, species of East-Asian origin occurred in most European samples (74.7%). Comparably, *Megachile sculpturalis* was also found disproportionally abundant on East-Asian woody plant species (e.g., *T. daniellii* or *K. paniculata*) in the USA comparing the 63% we found the present data [19]. The authors emphasized the

limited selection of native woody plants blooming after the first of July used in urban landscaping and warned that these exotic ornamental plants could facilitate the establishment of non-native bees. Our samples collected in China presented a different species spectrum, containing, for example, three *Ilex* sp. or *Tetradium glabrifolium*, which was also found in low abundances in European samples (Switzerland). A shared genus across continents was *Vitex* with *Vitex negundo* detected in all three Chinese samples.

Future studies with enhanced sampling should account for planting density of different ornamental/East-Asian plants to explore the native preference hypotheses further. In addition, limiting factors for a confident conclusion on the native preference hypothesis include the lack of assured knowledge of utilized co-evolved plants and an experimental setup that offers native and exotic pollen sources simultaneously. For this reason, interpretations need to be made carefully, with explicit consideration of plant availability.

Two out of the 28 identified taxa – *Lythrum salicaria* and *Pueraria montana* – are of special ecological interest due to their invasive potential and showed relatively high read abundances in our samples (Fig. 3). *Lythrum salicaria* is an Euroasian Lythraceae species classified as invasive for North America, according to the Global Invasive Species Database [81]. We found this species in a single Austrian (Europe) sample, and in the scopal pollen of several samples collected in (USA). *Pueraria montana*, in contrast, is an East-Asian native Fabaceae species classified as invasive for America and Europe. It is listed as one of the 100 worst invasive species due to its rapid growth, suppression of native vegetation and the capacity to overgrow and damage infrastructure [82, 83]. We found pollen of the invasive *P. montana* in samples collected from nests located in southern Switzerland, and one sample collected directly from a bee's scopa in the USA states of North Carolina and Florida.

Sasaki & Maeta [48] described *P. montana* as the preferred pollen source of *M. sculpturalis* in its Japanese range. Interactions between *M. sculpturalis* and invasive plant species could contribute to the invasiveness of both. Although our results provide first indications of invasive relationships, the verification of the invasional meltdown hypothesis requires further investigations, especially to answer the question if *M. sculpturalis* is pollinating *P. montana* and consequently promoting the establishment in its non-native range.

## Conclusion and future prospective

Our results show that *M. sculpturalis* is an invasive generalist forager with significant regional selective patterns benefitting from exotic ornamentals, especially a large-flowered Fabaceae species, *S. japonicum*. In addition, our results suggest potential invasion facilitation between *M. sculpturalis* and *P. montana* and *L. salicaria*. Interactions between *M. sculpturalis* and co-evolved plants may contribute to invasion processes and require closer attention. Together, these findings reflect the multifaceted nature of an invasion process.

Given the accelerating movement of species via trade and transport, co-occurrence of invasive pollinators and ornamental exotics is likely to become more frequent, with potential consequences for the native biodiversity. Conservation and management should therefore prioritize diverse native plants in urban landscape planning and incorporate pollinator–plant interaction data into planning and risk assessment, particularly as urbanization has the power to influence the transition from benign to invasive dynamics [15].

Future work should investigate the foraging behavior of *M. sculpturalis* in its primary invaded range in North America and, more importantly, across the native East Asian range. Although the three analysed samples from China provided valuable first insights into the otherwise scarce knowledge of bee foraging behavior in its native range, broader geographic coverage and larger sample sizes are needed to draw meaningful conclusions. Finally, evaluating network level consequences of invasive organisms is of high conservation concern and calls for future studies.

# Declarations

## Ethics approval and consent to participate:

Not applicable

## Consent for publication:

Not applicable

## Data availability:

The sequences supporting the conclusions of this article will be made available on NCBI upon acceptance. The metadata and taxonomic information are included in the supplementary information.

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## Authors' contributions:

JL, SM and HM conceived the study. JL and SM processed the pollen samples in the lab; CR conducted the bioinformatic processing of the data. JL, SM and SD analyzed and interpreted the data. JL drafted the first version of the manuscript. JL, JBD, JR, FF, MM and MCO collected the samples. All authors contributed to and approved its final version. JL and SM contributed equally to the study.

## Competing Interests:

The authors declare that they have no competing interest.

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## Tables

Table 1

Alphabetically ordered species and families identified in both non-native ranges, only found in samples from the USA or European continent.

| Shared non-native range species | Exclusive USA species | Exclusive EU species    |
|---------------------------------|-----------------------|-------------------------|
| Cucumis sativus                 | Clematis vitalba      | Adonis annua            |
| Koeleria paniculata             | Firmiana simplex      | Brassica napus          |
| Lagerstroemia indica            | Lythrum salicaria     | Brassica oleracea       |
| Lathyrus sylvestris             | Rhus chinensis        | Cerinth minor           |
| Ligustrum lucidum               | Rudbeckia hirta       | Eupatorium cannabinum   |
| Pueraria montana                | Securigera varia      | Hedera helix            |
| Robinia pseudoacacia            | Tipuana tipu          | Ranunculus repens       |
| Trifolium repens                | Vigna unguiculata     | Sedum hispanicum        |
| Wisteria sinensis               |                       | Sinapis alba            |
|                                 |                       | Styphnolobium japonicum |
|                                 |                       | Tetradium glabrifolium  |
| Both range families             | Exclusive USA family  | Exclusive EU family     |
| Asteraceae                      | Anacardiaceae         | Araliaceae              |
| Cucurbitaceae                   | Malvaceae             | Boraginaceae            |
| Fabaceae                        |                       | Brassicaceae            |
| Lythraceae                      |                       | Crassulaceae            |
| Oleaceae                        |                       | Rutaceae                |
| Ranunculaceae                   |                       |                         |
| Sapindaceae                     |                       |                         |

## Figures



**Figure 1**

(A) *Styphnolobium japonicum* pollen grains collected by female *Megachile sculpturalis* as larval food. (B) A female *M. sculpturalis* collects pollen from *S. japonicum* (Japanese pagoda tree; picture by CC by 4.0 Petrović) with its scopal hairs at the abdomen. (C) *S. japonicum* represents an ornamental tree widely planted in European parks and avenues.

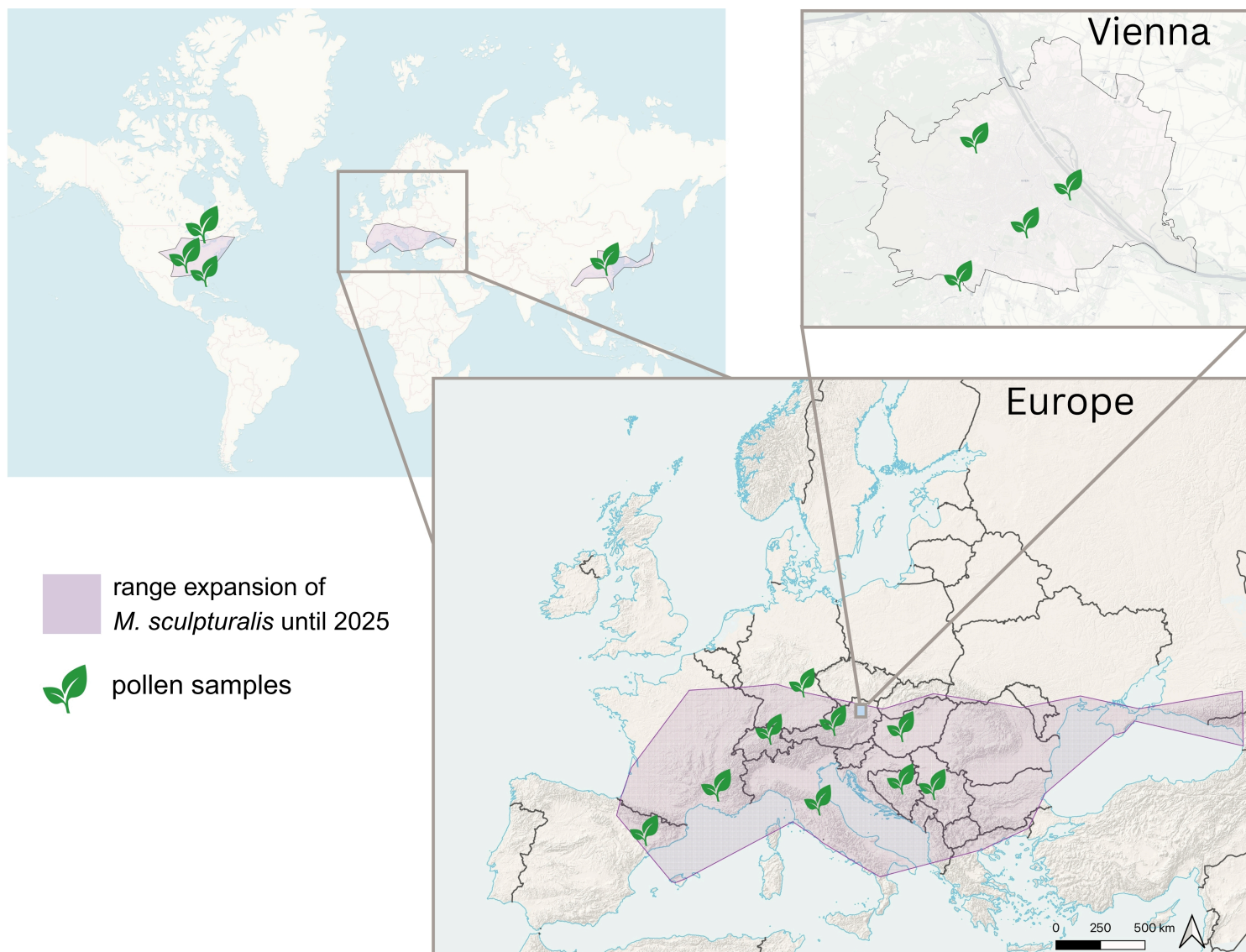


**Figure 2**

Global collection of *Megachile sculpturalis* pollen samples (indicated with a leaf symbol). The European map shows the extensive sampling collection from Spain, France, Switzerland, Germany, Austria, Italy, Hungary, Bosnia and Herzegovina, and Serbia, representing most countries colonized by the invasive bee. In Vienna (Austria) we studied the diet composition of provisioned pollen on a local scale. The purple polygons (alpha hull = 0.3) in A) and B) illustrate the broader range expansion based on occurrence records available up to December 2025. The map was created with QGIS 3.8.

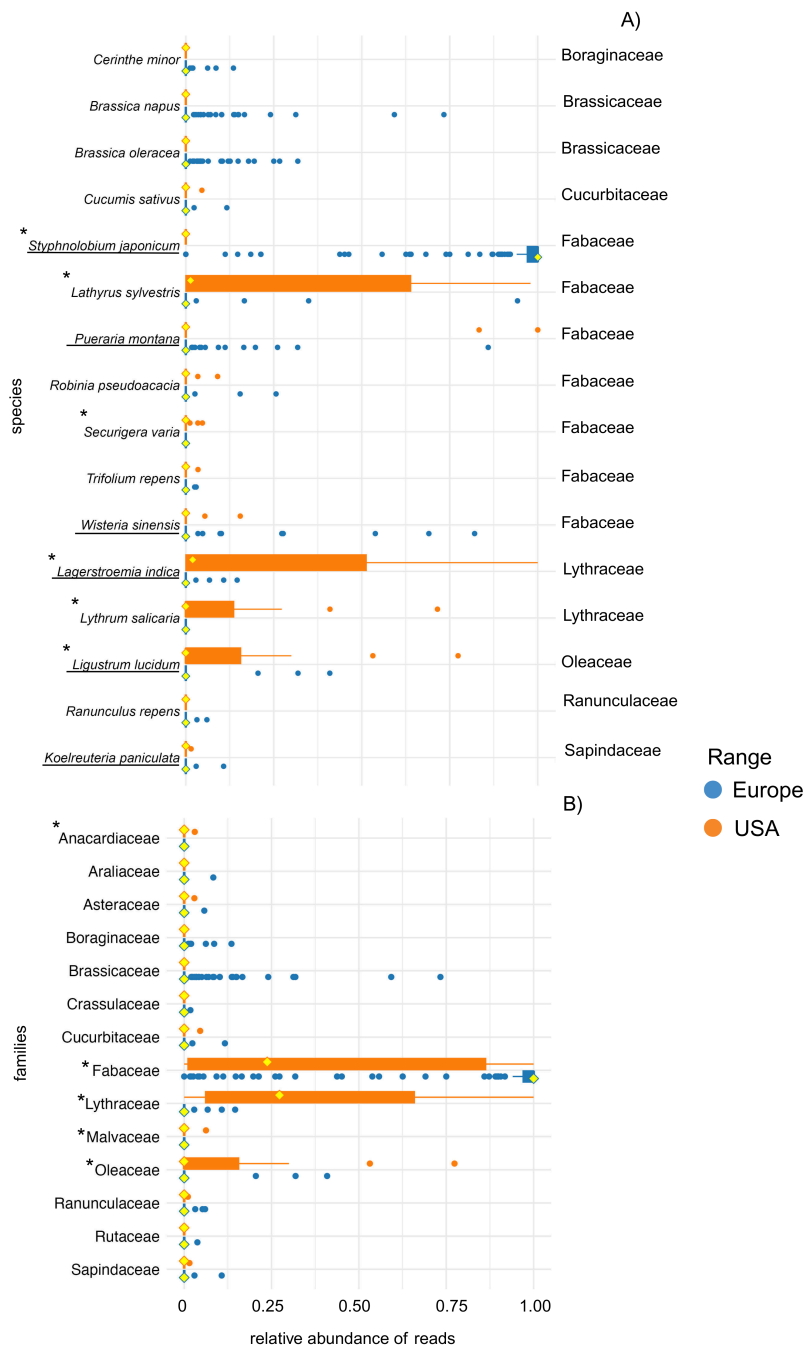


**Figure 3**

Relative read abundance of detected plant A) species and B) families in pollen collected by *M. sculpturalis* in its non-native ranges in Europe (blue; n = 173) and in the USA (orange; n = 19). Pollen was analysed using the ITS2 marker. The \* symbol marks significant differences ( $p < 0.05$ ) according to the pairwise Wilcoxon rank sum test for species between geographic ranges (Suppl. Material C Table S6). Underlined species indicate Asian origin, which is the same as the bee. The yellow diamond shape indicates the median of the RRA.

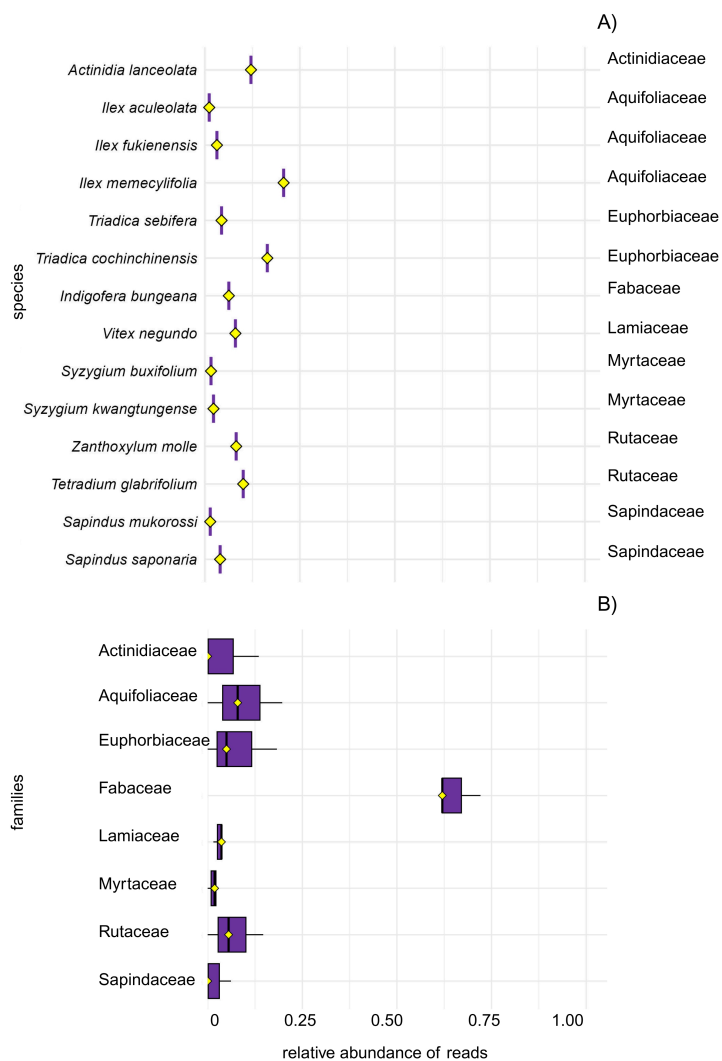


**Figure 4**

Relative read abundance of plants A) species and B) families detected by ITS2 metabarcoding in pollen collected by *M. sculpturalis* in its native range in Asia (n= 3). The yellow diamond shape indicates the median of the RRA.

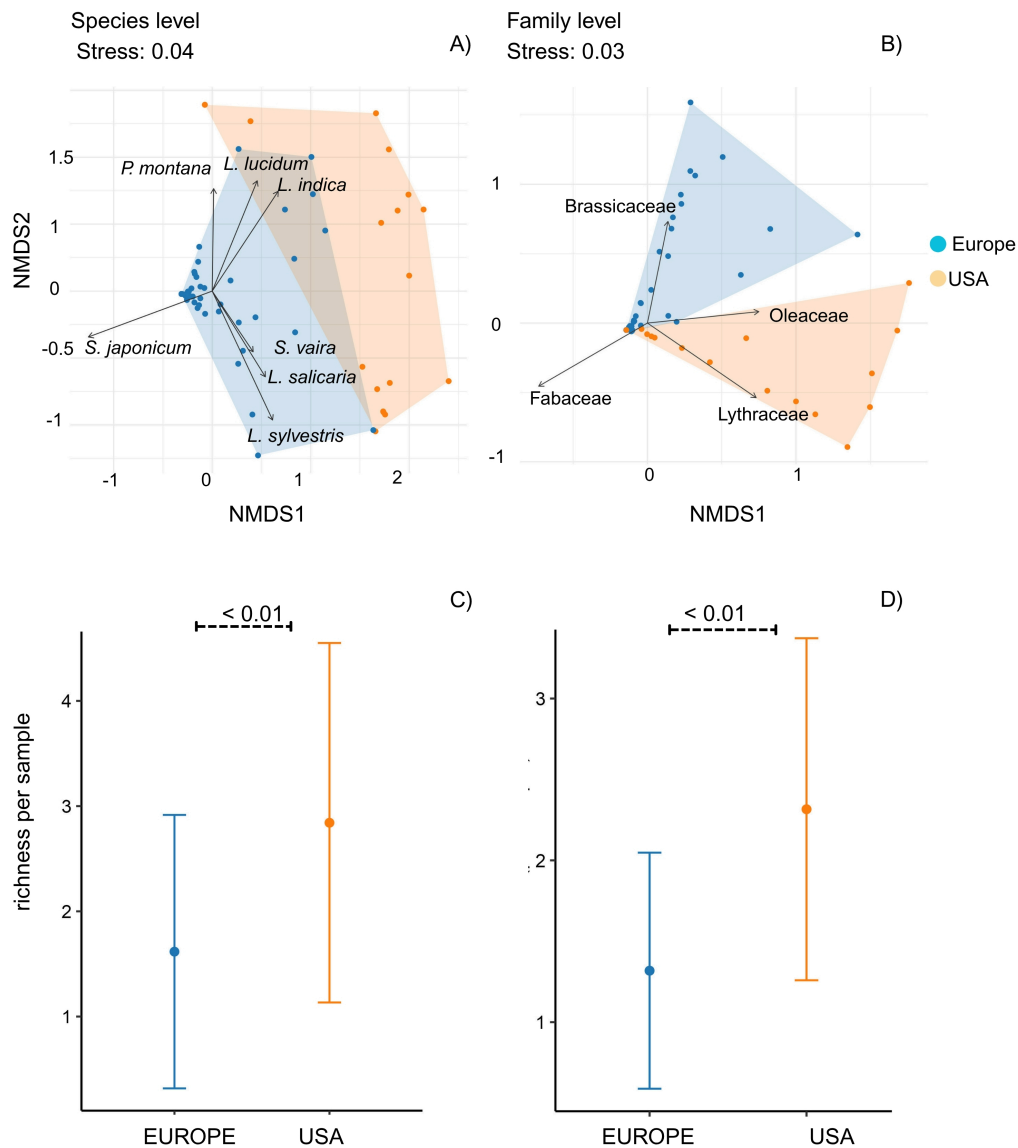


**Figure 5**

Identified plant community by metabarcoding of pollen samples collected by *M. sculpturalis* showed significant differences between non-native ranges in species A) composition and C) richness; and family B) composition and D) richness. (A) Vectors indicate the direction of increasing relative abundance plant species and families with envfit  $p < 0.01$ .

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Suppl.MaterialBTableS109082026.xlsx](#)
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