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**Early-phase colonization by introduced  
sculptured resin bee (Hymenoptera, Megachilidae,  
*Megachile sculpturalis*) revealed by local floral resource  
variability**

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Ćetković

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2 **Megachilidae: *Megachile sculpturalis*) revealed by local floral resource variability**

3

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11 **Running title:** Early-phase colonization by *Megachile sculpturalis*

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19

## 20 Abstract

21

22 There is a growing interest to document and better understand patterns and processes involved  
23 in non-native bee introductions and subsequent colonization of new areas worldwide. We  
24 studied the spread of the East Asian bee *Megachile sculpturalis* in Serbia and southeastern  
25 Europe; the bee was earlier established in the USA (since 1994) and western Europe (since  
26 2008). Its establishment in Serbia remained dubious throughout most of 2017–2019, following  
27 the first detection. We herewith report about its establishment and spreading, that was  
28 corroborated in 2019 under specific circumstances. Owing to the exceptionally poor blooming  
29 of *Styphnolobium japonicum*, we recorded high activity density of *M. sculpturalis* concentrated  
30 on a scarce key food resource. We presented a novel quantitative approach for the improved  
31 early detection of *M. sculpturalis*, based on the interplay between the bee's local occurrence  
32 pattern and dynamics of key food-plant(s) availability. The approach seems particularly  
33 effective during the early-phase colonization, at initially low population density of introduced  
34 bees. We addressed the importance of integration of the genuine plant usage patterns with  
35 context-specific bee assessment options, for establishing the effective monitoring. Yet, no  
36 comprehensive approach exists for the effective quantification of its wider spatial trends,  
37 various interactions and their effects; hence, further research is needed for evaluation of bee's  
38 invasiveness potential. Our improved understanding of *M. sculpturalis* local dynamics and  
39 detectability triggered an extension of the study scope to the regional-scale context: the early  
40 colonization of SE-Europe. With a more insightful interpretation of *M. sculpturalis*  
41 introduction into Serbia, we suggest that a diffusive mode of spreading now seems the more  
42 plausible scenario (than the seemingly more likely long-distance jump). The two-scale study  
43 outcomes further advanced the evidence base and relevant efforts for the development of  
44 standardized monitoring protocols.

45

46 **Keywords:** colonization scenarios, invasive pollinators, monitoring, non-native bees, Serbia,  
47 southeastern Europe, *Styphnolobium japonicum*

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49

## 50 Introduction

51

52 Among the continually growing number of introduced species being discovered around the  
53 world (Seebens et al. 2017; Pyšek et al. 2020), bees as a group (Hymenoptera: Apoidea:  
54 Anthophila) may count as moderately large. About 80 species were recently listed as non-  
55 native worldwide (Russo 2016) representing a small share of an estimated total of more than  
56 20,000 extant bee species (Michener 2007; Ascher and Pickering 2020). The majority of non-  
57 native bees (around 73%) were established following accidental introductions, with a  
58 remarkable number of those that are cavity-nesters, principally in various types of wooden  
59 material or hollow plant stems (Russo 2016; Poulsen and Rasmussen 2020). Most of the  
60 introductions happened in North America (around 69%), while Europe could be currently  
61 regarded as a comparatively “coldspot” of alien bee species richness. Of only three fully  
62 confirmed non-native bee species in Europe, two are still known from quite restricted areas:  
63 *Megachile disjunctiformis* Cockerell, 1911 in central Italy (only Bologna) and *Xylocopa*  
64 *pubescens* Spinola, 1838 in southern Greece and southern Spain (Rasmont et al. 2017;  
65 Bortolotti et al. 2018). So far, *Megachile sculpturalis* Smith, 1853 is the only alien bee widely  
66 established and continuously spreading across Europe.

67

68 A growing number and geographical extent of alien bee introductions worldwide raises  
69 concerns regarding their potential to cause negative environmental impacts. Documented or  
70 predicted impacts include: decline of native bee populations through competition (for floral or  
71 nesting resources) or pathogen and parasite transmission, degradation of native flower-  
72 pollinator networks, reduced pollination of native and crop plants, facilitation of alien weeds  
73 and invasive plants (Goulson 2003; Russo 2016; Morales et al. 2017; Vanbergen et al. 2018;  
74 Aizen et al. 2020). So far, it was clearly established in relatively few cases that alien bees have  
75 caused detrimental effects – principally the representatives of social bees: *Apis mellifera* L. and  
76 *Bombus* spp. (Russo 2016; Morales et al. 2017). Much less common are studies which  
77 quantitatively document possible negative impact of solitary alien bees (MacIvor and Packer  
78 2015; Fitch et al. 2019; LeCroy et al. 2020), including the recent survey on *M. sculpturalis*  
79 (Geslin et al. 2020). Although these results were mostly based on correlational evidence, the  
80 lack of indisputable interaction among native and non-native bees should not be interpreted as  
81 lack of impact (Stout and Morales 2009). In the case of *M. sculpturalis*, its most worrying  
82 feature is an unusually aggressive and/or destructive behavior exerted while competing with  
83 native solitary bees for nesting cavities (summarized in: Le Féon et al. 2018; Lanner et al.

84 2020a; Lanner et al. 2020b; Straffon-Díaz et al. 2021). This competition may be both direct  
85 (aggressive repelling, or even destruction of brood of other bees in already closed nests) or  
86 indirect (preemptive usage), including the elements of amensalism (e.g., killing of co-occurring  
87 species which are using the cavities of different size-classes, i.e., not being in competition).  
88 However, there are still no exact and straightforward estimates of its extended impact on  
89 affected taxa, i.e., the conclusive evidence of causative effects on population trends. Following  
90 the environmentalists' precautionary principle, it may be best considered as a potentially  
91 invasive alien species (Bila Dubaić et al 2021), pending further studies. In this context, we use  
92 the term “invasive” in its restricted conservationist sense, i.e., to denote a subset of all  
93 established alien species which cause substantial negative impact on native biota and/or  
94 ecosystems (e.g. Russo 2016; Vanbergen et al. 2018; IUCN 2020). In some other studies on  
95 this bee, the term was used somewhat more loosely or in a wider sense – according to the  
96 approach to include all alien species which rapidly/extensively expand in non-native range,  
97 regardless of impact (cf. Blackburn et al. 2011; Hui and Richardson 2017; for conceptual and  
98 terminological controversies in invasion biology see also: Hoffmann and Courchamp 2016;  
99 Courchamp et al. 2017).

100

101 *Megachile sculpturalis* belongs to the subgenus *Callomegachile* Michener, which is distributed  
102 principally in the Old World tropics (Michener 2007; Ascher and Pickering 2021). As a rare  
103 extratropical member, *M. sculpturalis* range stretches across eastern Asia: from Taiwan and  
104 eastern mainland China, through Korean Peninsula to Japan (Batra 1998; Wu 2006; Ascher  
105 and Pickering 2021). It is a bee of distinctive appearance – quite large, parallel-sided black  
106 body, 21–27 mm long in females and 12–22 mm in males (Hinojosa-Díaz et al. 2005; Aguado  
107 et al. 2018), wings transparent with dark tips (a comprehensive description is available in  
108 Sheffield et al. 2011). Females make nests in existing cavities in dead wood or hollow plant  
109 stems and seal them with resin-like material (Hinojosa-Díaz et al. 2005; Maeta et al. 2008;  
110 Quaranta et al. 2014; Westrich et al. 2015), hence the colloquial name initially coined for this  
111 bee in North America: “giant resin bee”; here we adopted a more appropriate alternative name:  
112 “sculptured resin bee” (from: iNaturalist.org). It is assumed that long-distance overseas  
113 introductions of this cavity nester have happened *via* inadvertent importation of timber goods  
114 or other suitable nesting materials (Mangum and Brooks 1997; Quaranta et al. 2014; Russo  
115 2016; Le Féon et al. 2018). Similar mechanism (passive, human-assisted transportation) is  
116 expected to contribute to secondary introductions within colonized continents, as long- or  
117 short-distance jumps (Westrich et al. 2015; Lanner et al. 2020a). Due to a large size, contrasting

118 dark and bright color-pattern, vivid nesting activity and frequent visitation of some commonly  
119 available ornamental plants, this bee is readily spotted and recognized, hence, expectedly easy  
120 to be detected as soon as it appears in new areas (Quaranta et al. 2014; Lanner et al. 2020a).

121

122 The first confirmed establishment outside of its native range was in 1994 in North Carolina,  
123 USA (Mangum and Brooks 1997), followed by rapid expansion across eastern half of North  
124 America (Mangum and Sumner 2003; Hinojosa-Diaz et al. 2005; Parys et al. 2015). In Europe,  
125 it was first detected in 2008, in southeastern France (Vereecken and Barbier 2009), soon  
126 followed by records in northwestern Italy in 2009, and southeastern Switzerland in 2010  
127 (Amiet 2012; Quaranta et al. 2014). Documented spreading in the period 2011–2014 was  
128 mostly confined to these areas (Westrich et al. 2015; Le Féon et al. 2018; Ruzzier et al. 2020).  
129 Since 2015 a more dynamic range extension took place: around the Alps in Switzerland,  
130 southern Germany, Slovenia, Austria and Liechtenstein (Westrich et al. 2015; Dillier 2016;  
131 Gogala and Zadavec 2018; Lanner et al. 2020a; Westrich 2020), much more widely in France  
132 and Italy (Le Féon and Geslin 2018; Le Féon et al. 2018; Poggi et al. 2020; Ruzzier et al. 2020),  
133 south-westwards into NE-Spain (Aguado et al. 2018; Ortiz-Sánchez et al. 2018) and most  
134 recently across the Mediterranean Sea, reaching the island of Mallorca as the southernmost  
135 point in Europe so far (Ribas Marquès and Díaz Calafat 2021). In contrast with this, largely  
136 continuous spreading (comprising also few smaller jumps), range establishment east of the  
137 Alps (2015–2019) represents more remote, arguably long-distance dispersal events of yet  
138 unclear origin and mechanism: into northeastern Hungary (Kovács 2015), northeastern Austria  
139 (Westrich 2017), northern Serbia (Ćetković and Plećaš 2017), southern Croatia (Resl 2018;  
140 “pitrusque” 2019), Crimea (Ivanov and Fateryga 2019), southern Romania (Hymenopterists  
141 Forum 2019), and northern Bosnia & Herzegovina in 2020 (Nikolić 2020). Range expansion  
142 within Europe for the reference period (2008–2019) is presented schematically with the series  
143 of phase-maps and summarizing review of its dynamic distribution (Ćetković et al. 2020;  
144 Suppl. material 1).

145

146 Following its remarkable non-native spreading, evidence was accumulated about sculptured  
147 resin bee interactions with numerous plant genera and families (Quaranta et al. 2014; Parys et  
148 al. 2015; Le Féon et al. 2018; Ruzzier et al. 2020), showing more diverse spectrum than  
149 currently available for its native area. Accordingly, *M. sculpturalis* is often referred to or  
150 assumed to be polylectic (Mangum and Brooks 1997; Maeta et al. 2008; Quaranta et al. 2014;  
151 Parys et al. 2015; Westrich et al. 2015; IUCN 2020; Ribas Marquès and Díaz Calafat 2021),

152 but without clear evaluation of the documented visitation pattern, e.g., the share of pollen vs.  
153 only nectar foraging. Based on numerous sources (cf. Četković et al. 2020; an ongoing  
154 analysis), *M. sculpturalis* shows particularly strong preference for the pollen of Fabaceae  
155 (Batra 1998; Mangum and Sumner 2003; Maeta et al. 2008; Westrich et al. 2015; Campbell et  
156 al. 2016; Dillier 2016; Hall and Avila 2016; Aguado et al. 2018; Andrieu-Ponel et al. 2018; Le  
157 Féon and Geslin 2018; Le Féon et al. 2018; Guariento et al. 2019; Ruzzier et al. 2020; Westrich  
158 2020; Ribas Marquès and Díaz Calafat 2021), principally of large-flowered members of the  
159 subfamily Faboideae. Within the European range, most frequently documented pollen-source  
160 is the ornamental Japanese pagoda tree, *Styphnolobium japonicum* (L.) Schott. In contrast with  
161 this growing evidence, the loosely repeated “wide polylecty” might represent a biased or  
162 uncritical perception, which ignores often remarkably narrow effective dietary preferences of  
163 *M. sculpturalis*. The patterns of genuine plant usage of this bee are yet to be thoroughly  
164 evaluated, taking into account floral resource availability, variability of plants phenology and  
165 suitability of different habitat types across the colonized areas.

166

167 The present survey of the sculptured resin bee introduction in Serbia is an event-driven case  
168 study of an early-phase colonization. First accidental encounter of a single specimen in 2017  
169 was interpreted as a likely long-distance chance dispersal of uncertain success (Četković and  
170 Plećaš 2017). Due to an extended lack of confirmation throughout the seasons of 2017–2018,  
171 the current study was initiated with the second find in the same area (the city of Belgrade),  
172 attained late in 2019 under specific circumstances. Namely, owing to an extremely reduced  
173 blooming of its preferred host plant (*S. japonicum*) in 2019, we managed to detect the vivid  
174 activity of still locally rare sculptured resin bees, temporarily concentrated on a scarce food  
175 source. We herewith explored the spatial relationships between bee activity patterns and local  
176 availability of key plant resources. We specifically evaluated the effects of variable floral  
177 resources on the bee detectability in 2017–2019. Despite a growing number of studies, a  
178 specified approach is still missing to quantify the sculptured resin bee distribution dynamics,  
179 population trends, its interactions with key plants and with native bees, hence ultimately, to  
180 assess its invasiveness potential. Until now, we lack an effective approach for early detection  
181 and the extended surveillance of its expansion. The presented quantitative assessment  
182 represents a step towards a more comprehensive monitoring. Our improved understanding of  
183 *M. sculpturalis* local dynamics and detectability triggered an extension of the research scope,  
184 which enabled inferences about possible origin(s) and modes of its dispersal within this part of  
185 Europe. The study of the wider, regional-scale context of this introduction (the colonization of

186 SE-Europe) enabled a better understanding of possible scenarios of *M. sculpturalis*  
187 introduction and early colonization. Therefore, the two-scale study outcomes further advanced  
188 the evidence base and relevant efforts for the development of standardized monitoring  
189 protocols.

190

191

## 192 **Material and methods**

193

194 The study of *M. sculpturalis* arrival and establishment in Serbia was mostly based on extensive  
195 fieldwork within the city of Belgrade, during the period of 2017–2019. The wider geographical  
196 and temporal context of this survey included principally the eastern Pannonian Plain, but we  
197 also considered the nearest known occurrences towards the west and to the east of this area  
198 (from Austria and Slovenia through the Crimean Peninsula), for the period of 2015–2019.

199

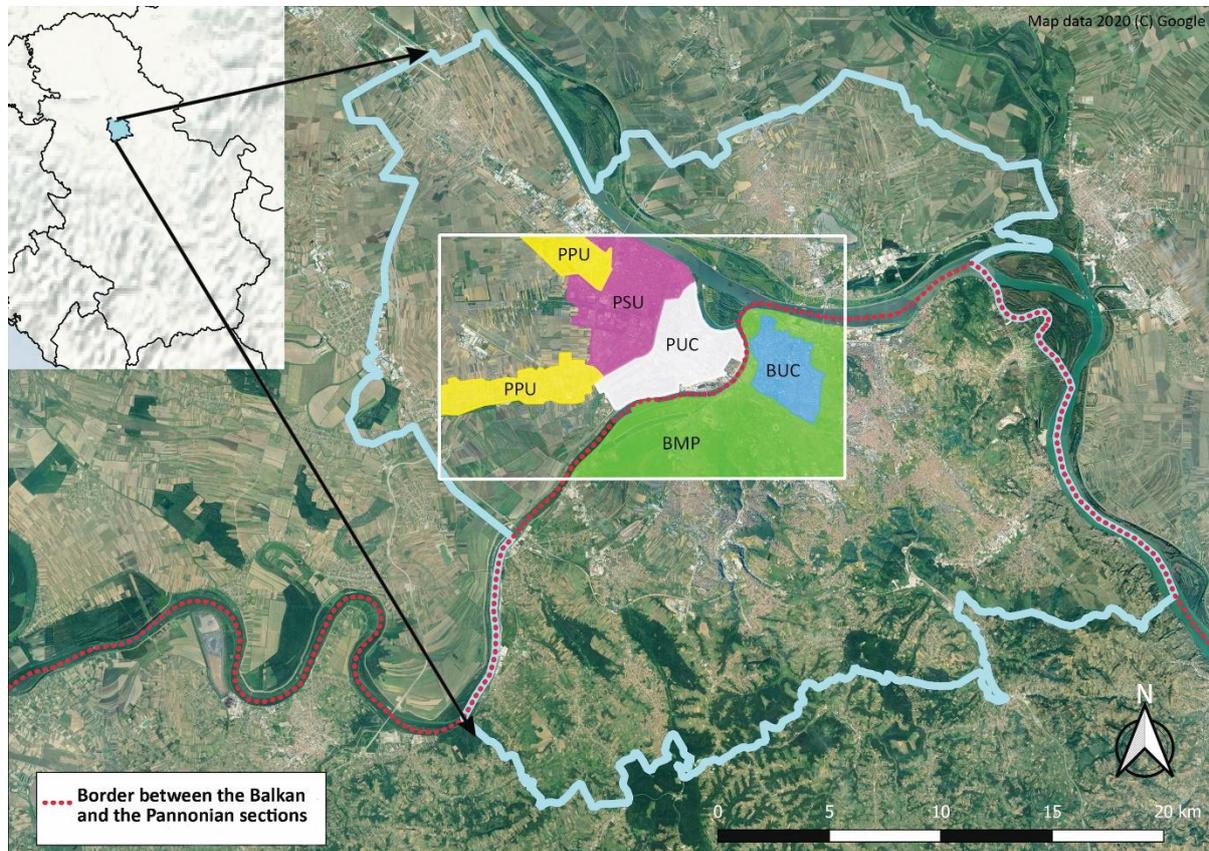
### 200 *Local scale: Belgrade as study area*

201

202 Belgrade is one of the largest cities in southeastern Europe (Belgrade “proper” administrative-  
203 urbanistic core area is nearly 776 km<sup>2</sup>, population >1.5 million), situated at the border between  
204 the two quite different geographical units: the predominantly hilly to mountainous Balkan  
205 Peninsula to the south, and the vast lowlands of the Pannonian Plain to the north. It is positioned  
206 in a climatically transitional zone between temperate-continental and more steppic regime, with  
207 a relief spanning the altitude range of 65–506 m. The Belgrade area encompasses more than  
208 50% of varied agricultural habitats as a matrix, with embedded mosaics of urban and rural  
209 habitats; two principal sections of Belgrade (the Balkan and the Pannonian – Fig. 1) are  
210 characterized with distinct spatial arrangement and contrasting types of settlements,  
211 agricultural systems and more natural habitats, owing to a largely different physiography and  
212 historical development. From the perspective of wild bee studies, various urbanistic areas may  
213 be characterized by differing types, extent and relative share of suitable habitats (e.g., from  
214 urban green to semi-natural). In order to consider possible coarse-scale effects of variability in  
215 key resources and other environmental features across urban gradients of Belgrade, we use a  
216 framework of wider “urbanistic zones” (Fig. 1). They are based on landscape scale  
217 characterization of available elements of physiography, land-cover, gradients of urbanization  
218 and management regime features. Some easily defined coarse-scale differences (e.g. varied  
219 urban temperature regimes or dominant management practice) might differently affect activity

220 patterns of plants and bees, potentially leading to dynamic shifts in bee local distribution and  
 221 resource usage. More details of the wider study area and operative aspects of zonation used in  
 222 this survey are available in Suppl. material 2 (ii–iii).

223



224

225 **Figure 1.** Urbanistic zonation of the study area in Serbia (18×11 km), within the Belgrade  
 226 proper (light blue outline; sections separated by the red dotted-line): BUC – Balkan Urban  
 227 Core; BMP – Balkan Mixed Periphery; PUC – Pannonian Urban Core; PSU – Pannonian Semi-  
 228 Urban; PPU – Pannonian Peri-Urban.

229

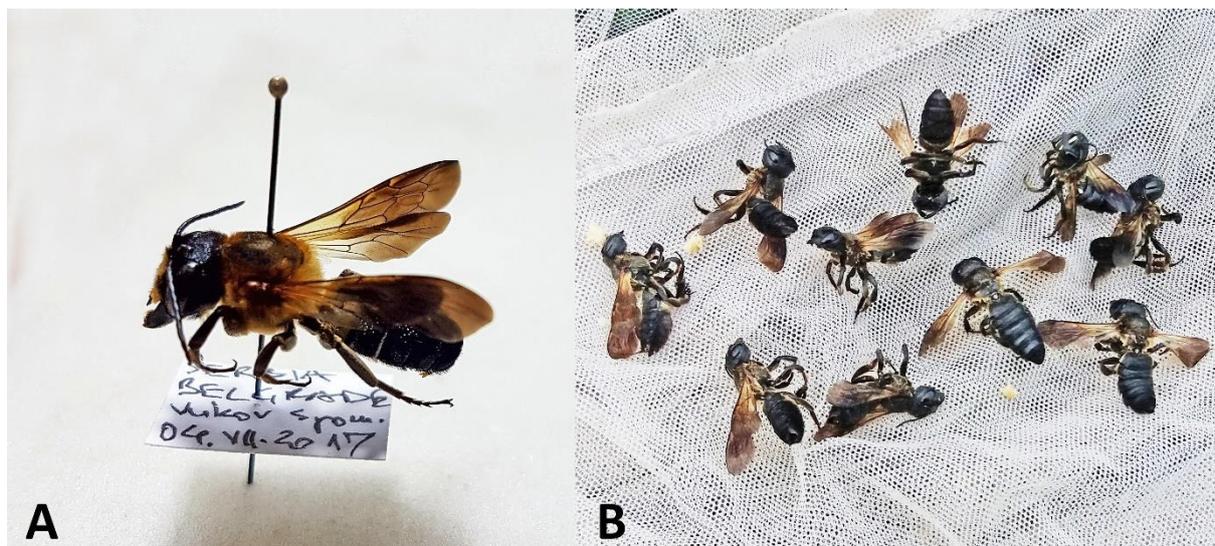
230 *Local scale: survey set up and study design*

231

232 The first record of *M. sculpturalis*, in early July 2017 (a single male), was an unexpected find  
 233 within a routine monitoring of wild bee communities of selected urban habitats in Belgrade  
 234 area (Ćetković and Plećaš 2017; Fig. 2A). However, its establishment in Serbia remained  
 235 unconfirmed during the first two seasons. We extended efforts to explore the state of its  
 236 presence, focusing on locations with Japanese pagoda trees (*Styphnolobium*), as the most  
 237 favorable pollen source for *M. sculpturalis* in Europe. This exotic plant is probably the only  
 238 species with appropriate blooming phenology while also with high density throughout the  
 239 Belgrade area. During the seasons of 2017–2018 our surveys covered 12 locations within 18

240 days (26 “occasions” = unique date/loc combinations), spending about 440 person-minutes  
241 (=7.25 person-hours) in collecting or observing bees on *S. japonicum* throughout the area, and  
242 covering the *M. sculpturalis* main flight period. We parallelly continued with variously focused  
243 wild bee surveys on other abundant summer-blooming plants across Belgrade. This included  
244 extensive survey on *Lavandula* and *Ballota* (Lamiaceae), and sporadically on *Buddleja*  
245 (Scrophulariaceae) – all being listed as attractive or potential food plants for *M. sculpturalis*  
246 (Quaranta et al. 2014; Le Féon et al. 2018; Ivanov and Fateryga 2019). For the observations on  
247 *Lavandula* (8 locations within 18 days, 21 unique occasions, totaling nearly 490 person-  
248 minutes) and *Ballota* (13 locations within 27 days, 32 unique occasions, totaling >1,190  
249 person-minutes) we spent about 28 person-hours during the summer seasons 2017–2019. None  
250 of these efforts yielded any additional point-occurrence or recorded interaction of  
251 *M. sculpturalis* (for *Buddleja* see Results).

252



253 **Figure 2.** (A) the first specimen of *Megachile sculpturalis* (male), caught in Serbia in July  
254 2017; (B) mass-foraging females detected in August 2019.

256

257 The second record of *M. sculpturalis* was also accidental. The summer of 2019 was  
258 characterized with an extreme failure in *S. japonicum* blooming (see details in Results); hence  
259 this plant was excluded from our regular monitoring that year. Then, upon unexpected detection  
260 of numerous sculptured resin bees on August 02, 2019, on a single *S. japonicum* tree (Fig. 2B;  
261 Suppl. material 3: Table S3.2), we undertook an immediate survey across Belgrade, to  
262 document and quantify its eventually confirmed presence. We searched for and checked as  
263 many locations with *S. japonicum* as possible, across all urbanistic zones (Fig. 1; see also:  
264 Suppl. material 2 (iii)). However, the next 7-day period (August 03–09) represented the very  
265 end of *S. japonicum* blooming season in 2019, when many trees had already ceased blooming.

266

267 On all locations with still blooming trees, we conducted counts of bees foraging on flowers,  
268 using binoculars where needed (for high crowns). The priority was to make as many unit-  
269 location checks as possible in a limited available time. We adjusted the procedure accordingly:  
270 (a) at sites with lower activity density, the bees were usually not continually present, so we  
271 recorded the intervals separately for each number of bees observed; (b) when continuous and  
272 more vivid activity was observed (>5 bees visible at any moment), 3–4 snapshot counts were  
273 made over the time spent on site, using two abundance classes: moderate (6–10) or high (11–  
274 20). We adapted the snapshot technique from ornithology (Gaston et al. 1987; Greene & Efford  
275 2012; Barraclough 2020), as suitable for situations when numerous individuals are flying  
276 within the field of view, without possibility to be counted accurately. At a few sites with  
277 variable bee activity on different trees, the combination of both techniques was employed. Due  
278 to differing situations, duration of counting per location varied from 1–50 minutes (usually 10–  
279 20', average ~15.3'). We scaled all recorded values to one minute of continual bee activity on  
280 a defined unit of floral resource within a landscape sector (as elaborated further on), by  
281 averaging all counts against the recorded time (hereafter: Bees per Minute = BpM). Details of  
282 sampling and calculation procedures are available in Suppl. material 3 (explanation of metrics  
283 in Table S3.1; sampling duration and BpM estimates per sectors in Table S3.2). In total, we  
284 spent about 300 person-minutes (5 person-hours) working on 16 sites with at least some  
285 blooming trees (out of 40 surveyed sites), mostly in observation/counting (>260 minutes). At  
286 some sites we also collected bee specimens by hand-net, as vouchers and for future genetic  
287 studies.

288

289 Simultaneously, we estimated the key floral resource, to assess if its quantity, distribution, and  
290 phenology affect the local differences in activity density and distribution of the bee population.  
291 We recorded the number of *S. japonicum* trees (hereafter: NoT), and visually assessed their  
292 actual blooming status at each visited location: the number of trees that entered blooming in  
293 2019 (hereafter: NoT\_iB), the share of inflorescences developed at each crown in bloom during  
294 2019 (as a fraction of the fully blooming crown; summed value interpreted as: Total Floral  
295 Resource, hereafter: TFR), and finally, the actual share of flowers still in bloom at crown at the  
296 moment we made the observation (summed to: Current Floral Resource, hereafter: CFR). We  
297 continued to survey *S. japonicum* until early September, regardless of the ceased blooming  
298 (and no bee activity), to provide the spatial coverage of resource availability across the study

299 area. For the extended explanations and visual examples of these parameters see in Suppl.  
300 material 3 (Table S3.1).

301

302 All surveyed locations were primarily georeferenced in Google Earth Pro ver. 7.3.3.7786  
303 (Google Inc. 2020), and further prepared as distribution maps in QGIS ver. 3.4 (QGIS  
304 Development Team 2018). To deal with the uneven and patchy distribution of surveyed  
305 *S. japonicum* trees, and the logistic limitations of the sampling approach, we grouped the point-  
306 sampled quantitative data following the rationale similar to landscape ecology studies on wild  
307 bees (e.g. Steffan-Dewenter et al. 2002; Steckel et al. 2014; Cohen et al. 2020). We defined a  
308 primary framework of circular sectors of 250 m radius (hereafter: S250; Suppl. material 2:  
309 Fig. S2.3A), manually fitted to include all surveyed point-locations without overlapping.  
310 Various bees perceive the landscape composition and configuration (particularly distribution  
311 of resources and other habitat features) at different spatial scales, since their foraging ranges  
312 principally depend on size; the radius of 250 m is commonly used to define the smallest  
313 meaningful study scale (Steffan-Dewenter et al. 2002), while larger bodied bees may forage at  
314 much larger distances (Gathmann and Tschardt 2002; Greenleaf et al. 2007). Due to the  
315 spatial limitations of the sampled area, we added just one coarser scale (sectors of 500 m radius;  
316 hereafter: S500; Suppl. material 2: Fig. S2.3B), for testing for different scale effects. As a  
317 result, all recording sites were arranged into two series of standardized circular sectors: 40  
318 locations S250 (ca. 0.2 km<sup>2</sup>), and 23 locations S500 (ca. 0.8 km<sup>2</sup>), and all parameters were  
319 calculated per those spatial units (see more details about the procedure in: Suppl. material  
320 2 (iii)). Therefore, we used some technical concepts and experiences from landscape ecology  
321 studies as a suitable practical approach (and a prospective “working framework”) to quantify  
322 and analyze relationships between bee distribution pattern and resources availability.

323

324 All values from the field assessments were summed per defined sector. To calculate TFR we  
325 summed individual values from each *S. japonicum* tree in bloom, expressed as a fraction of the  
326 whole crown, based on the estimated maximal extent of blooming attained during the summer  
327 of 2019. Similarly, we calculated CFR as a sum of estimated blooming fractions at the moment  
328 of assessment, i.e., representing the actual extent of blooming of each crown within the sector.  
329 We recorded blooming fractions as percentage of the whole crown for each assessed tree, and  
330 then summed the values in decimal form (e.g. blooming of 10% of one crown, 25% of another  
331 and 80% of a third, gives the value of 1.15 “unit crowns” per sector; more details and visual

332 examples for the calculation available in Suppl. material 3: Table S3.1, summed results in  
333 Table S3.2).

334

### 335 *Local scale: statistical analyses*

336

337 We tested if various aspects of floral resource distribution and seasonal dynamics (i.e., change  
338 from TFR to CFR level of blooming) had a measurable effect on local differences in bee  
339 activity. We analyzed the relationship between bee activity density (BpM) and all measured  
340 parameters of key floral resource (NoT, NoT\_iB, TFR, and CFR), calculated in S250 and S500  
341 frameworks, with Generalized Least Square linear regression to account for heteroscedasticity  
342 of errors. We, additionally, used GLS linear regression to analyze the relationship between  
343 BpM and TFR, CFR, percentage of TFR (TFR/NoT), and percentage of CFR (CFR/NoT), all  
344 averaged across each urbanistic zone. Analyses' assumptions were tested by examination of  
345 residuals. Furthermore, we tried to establish was there any local pattern in reduction of  
346 *S. japonicum* blooming (i.e. possible differences caused by environmental effects which  
347 specifically vary with urbanistic gradients, using urbanistic zones as tentative proxies), and if  
348 so, are the bees responding to these differences. Differences in NoT, NoT\_iB, TFR, CFR and  
349 BpM between urbanistic zones were analyzed by Kruskal-Wallis test. All analyses have been  
350 performed in R v3.6.3 (R Core Team 2020) and the R-package nlme v3.1-144 (Pinheiro et al.  
351 2020).

352

### 353 *Regional context: introduction and expansion within the SE-Europe*

354

355 We compiled, from all available sources (Suppl. material 4: Table S4.2), the records from the  
356 region most adjacent to the focal study area (Belgrade) – N-Serbia and E-Hungary, spanning  
357 the period of 2015–2019. Furthermore, we aimed to consider the spatio-temporal relationships  
358 with the nearest records towards the west (i.e., towards the introduction core of Europe), as  
359 well as with rare records in the east (up to the Crimean Peninsula). Therefore, we have covered,  
360 in a very broad sense, the area of SE-Europe, wherein the colonization by this species was  
361 documented only since 2015 (Suppl. material 4: Table S4.1). The compilation and mapping of  
362 records were conducted within a more extensive Europe-wide survey of *M. sculpturalis*  
363 distribution and expansion; preliminary results for the period 2008–2019 were presented as  
364 series of summary phase-maps in Četković et al. (2020; available at:  
365 <https://srbee.bio.bg.ac.rs/english>). We herewith include a slightly modified version of the

366 summary map for 2019 (Suppl. material 1). Records were georeferenced using the combination  
367 of Google Earth Pro ver. 7.3.3.7786 (Google Inc. 2020) and QGIS ver. 3.4 (QGIS Development  
368 Team 2018). Maps were made primarily with QGIS, and the output images further processed  
369 with various picture-editing software. We used the “Ruler” tool in Google Earth Pro to measure  
370 the linear distances between various adjacent occurrences (within and between the years in  
371 relation to the sequence of their detections), in order to quantify the basic spatial elements of  
372 apparent dispersal outcomes.

373

374

## 375 **Results**

376

### 377 *Local scale: the Belgrade survey*

378

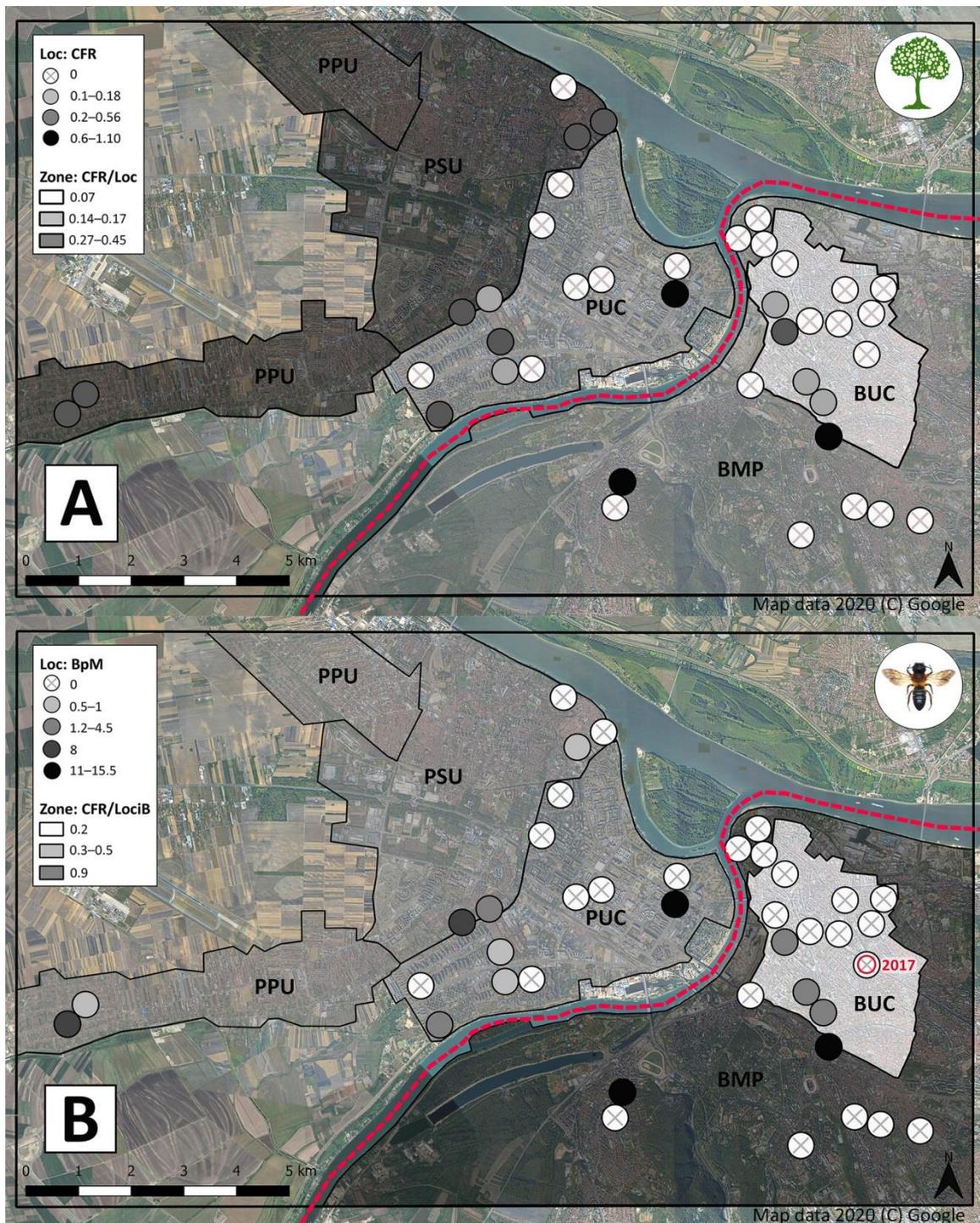
379 Following the first detection of *M. sculpturalis* in Belgrade (and Serbia), in July 2017, we  
380 confirmed the establishment of this species only in August 2019. Our recording was almost  
381 exclusively based on bees foraging on *S. japonicum* trees. Exceptions were the first detected  
382 specimen – a male collected on *Trifolium repens*, and the single female observed around the  
383 *Buddleja* bush; both cases were in downtown parks with nearby presence of *S. japonicum* trees.  
384 We did not detect *M. sculpturalis* neither on *Lavandula* nor *Ballota* during the 2017–2019  
385 period, despite notable efforts.

386

387 Results of statistical testing have shown mostly non-significant values for metrics calculated  
388 within the S500 framework (see in Suppl. material 5); therefore, we herewith present only the  
389 results from the S250 framework. Throughout the Belgrade area, we recorded *M. sculpturalis*  
390 at most locations where the current floral resource (CFR) of *S. japonicum* was sufficient to  
391 attract foraging bees at the moment of survey (Fig. 3A,B). The minimal sufficient value was  
392  $CFR \geq 0.1$ , found in 16 of 40 sectors (40%). Bees were recorded in 14 of 16 suitable sectors  
393 (88%); within 5 locations we also collected specimens (22 females, 3 males). The estimated  
394 activity density of bees per sector ranged 0–15.5 BpM (mean  $4.66 \pm 5.35$  SD). The remaining  
395 sectors were recorded as without any blooming in 2019, or with blooming being already  
396 finished before our survey, hence, without possibility to detect bees (sectors with values for  
397 NoT\_iB, TFR, or CFR less than 0.05; see in Suppl. material 3). Of all tested metrics, only CFR  
398 had a significant effect on BpM (Table 1, Fig. 4A) and when values were averaged across each  
399 urbanistic zone, only CFR and %CFR had a significant effect on BpM (Table 2, Fig. 4B). We

400 did not find significant differences in bee activity density between different urbanistic zones of  
 401 Belgrade ( $H(4)=4.521$ ,  $p\text{-value}=0.341$ ).

402



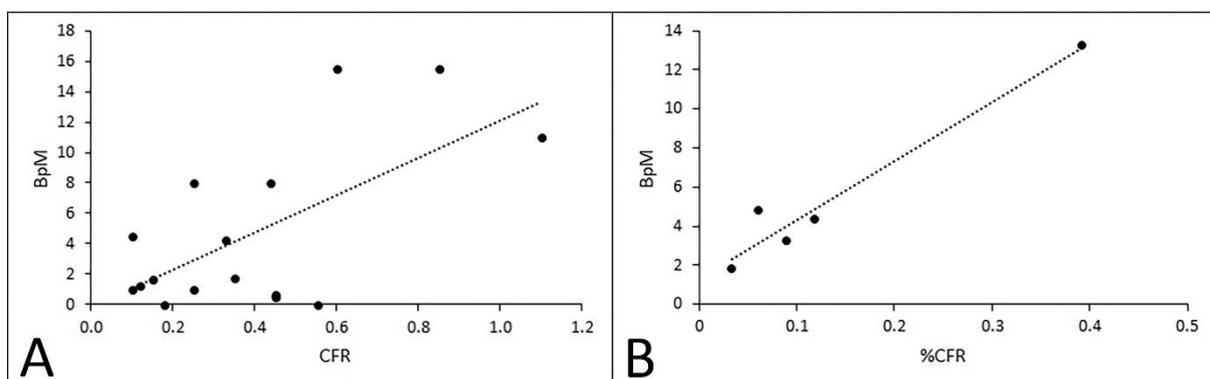
403

404 **Figure 3.** Distribution of (A) effective floral resources of *S. japonicum*, as surveyed in August  
 405 2019 (Current Floral Resource – CFR), and (B) respective metrics of *M. sculpturalis* activity  
 406 density (Bees per Minute – BpM), both presented within the S250 framework (circular sectors  
 407 – “landscapes” of  $r=250$  m; values shown in classes). Urbanistic zones (for acronyms see in  
 408 Fig. 1) are shown as background shades of grey, representing the averaged value of CFR per  
 409 zone calculated either for (A) all 40 sectors, or (B) only for 16 sectors with  $CFR \geq 0.1$ . The

410 location of the first find is marked with “2017”. Numerical data available in Suppl. material 3:  
 411 Tables S3.2–S.3.4; see also maps in Suppl. material 5. for the complete visualization of floral  
 412 resource metrics.

413  
 414 Within the surveyed area (16×9 km was the approximate span of all visited *S. japonicum*  
 415 locations; Fig. 3A), we covered all urbanistic zones, with a varying number of surveyed  
 416 locations between the zones (2–11; see also Suppl. material 2 (iii)). We counted the total of  
 417 490 *S. japonicum* trees (NoT), distributed quite unevenly across the study area (1–64 per  
 418 sector). In 17 sectors (comprising 196 trees) we recorded no sign of blooming during 2019.  
 419 Within the remaining 23 sectors, only on 51 trees we recorded at least some level of blooming  
 420 in 2019 (NoT\_iB; 12.2% of the total NoT). These blooming trees had a variable share of crowns  
 421 effectively in bloom (TFR; 48.4% of the total NoT\_iB); expressed per sector, TFR values  
 422 ranged 0.2–3.0 among these 23 sectors. As a reference high value, we established that the long-  
 423 term average intensity of *S. japonicum* blooming in good seasons is at least  $\geq 85\%$  of the total  
 424 crown volume (based on our observations from several past seasons). Accordingly, the sum of  
 425 detected TFR available to bees during the summer of 2019 represented at most 5.9% of average  
 426 *S. japonicum* resource availability in good seasons. At the time of our survey (August 02–09),  
 427 the extent of available resource (CFR) was further reduced: only about 1.5% of the summed  
 428 crown volume was still in bloom. The effective floral resources in early August (i.e., values of  
 429  $CFR \geq 0.1$ ) were recorded in only 16 sectors (totaling about 30% of the respective TFR summed  
 430 value). Effective CFR values ranged 0.1–1.1 per sector (Fig. 3A). Further details of all metrics  
 431 are available in Suppl. material 3 (Table S3.2 and Table S3.3). For the spatial visualization of  
 432 established raw patterns, we presented distribution of all four aspects of resource availability,  
 433 and respective *M. sculpturalis* activity density metrics, in a sequence of maps (Suppl.  
 434 material 5: Figs. S5.1–S5.2). We found no statistically significant differences in any of the  
 435 floral resource metrics (NoT, NoT\_iB, TFR, CFR) between different urbanistic zones (Suppl.  
 436 material 5: Table S5.1).

437



438

439 **Figure 4.** Relationship between (A) BpM and CFR, and (B) BpM and %CFR averaged across  
 440 each urbanistic zone (BpM – Bees Per Minute; CFR - Current Floral Resource; %CFR –  
 441 percentage of current floral resource).

442  
 443 **Table 1.** Results of the GLS linear regression models of the relationship of bee activity  
 444 density (BpM) and variables NoT, NoT\_iB, TFR, and CFR (N=16).

Model		Estimate	SE	t-value	p-value
NoT	Intercept	6.368	1.638	3.887	<b>0.002*</b>
	Variable	-0.144	0.854	-1.644	0.122
NoT_iB	Intercept	6.092	2.001	3.045	<b>0.008*</b>
	Variable	-0.557	0.579	-0.962	0.352
TFR	Intercept	3.459	2.689	1.286	0.219
	Variable	0.951	1.824	0.521	0.611
CFR	Intercept	-0.154	1.858	-0.089	0.935
	Variable	12.276	3.891	3.154	<b>0.007*</b>

445 Significant p-values in bold (\* p≤0.01).  
 446 NoT- number of trees; NoT\_iB - number of trees in bloom; TFR - total floral resource; CFR - current floral  
 447 resource.

448  
 449 **Table 2.** Results of the GLS linear regression models of the relationship of bee activity  
 450 density (BpM) and variables TFR, CFR, %TFR and %CFR, all averaged across each  
 451 urbanistic zone (N=5).

Model		Estimate	SE	t-value	p-value
TFR	Intercept	1.575	5.663	0.278	0.799
	Variable	3.121	4.184	0.745	0.509
%TFR	Intercept	0.568	2.388	0.238	0.827
	Variable	15.359	6.196	2.479	0.089
CFR	Intercept	-2.492	0.909	-2.741	0.071
	Variable	18.008	1.838	9.798	<b>0.002*</b>
%CFR	Intercept	1.293	0.756	1.711	0.186
	Variable	30.223	3.981	7.592	<b>0.005*</b>

452 Significant p-values in bold (\* p≤0.01).  
 453 TFR - total floral resource; %TFR - percentage of total floral resource; CFR - Current Floral Resource; %CFR  
 454 – percentage of current floral resource.

455  
 456 *Regional context: introduction and expansion within the SE-Europe*

457  
 458 We compiled a total of 14 occurrences of *M. sculpturalis* from the eastern Pannonian region  
 459 north of Belgrade, from the period 2015–2019. All relevant details – data and metadata  
 460 (coordinates, dates, bionomics, sources) used for this regional mini-survey are available in  
 461 Suppl. material 4: Table S4.1; regional records are clearly delimited within the mapped  
 462 European distribution for 2019 (Suppl. material 1). Additional records from Hungary (after  
 463 2015) were mostly discovered through a tailored data-mining within nationally based internet

464 sources (previously being poorly accessible due to a language barrier). Findings from Serbia  
465 also became available with certain delay; in the case of Palić record of 2018 (northernmost  
466 Serbia) it was due to misidentification (at: Insekti Srbije 2018; corrected in 2020 by JBD).  
467 From the more remote areas, we included 11 most adjacent records to the west, which are very  
468 broadly marginal to the wider Pannonian periphery: from E-Austria, Slovenia and SW-Croatia  
469 (2016–2019); there were only three eastern records, from Romania and Crimea (2018–2019).

470

471 The first Serbian record (in Belgrade 2017) was amongst the earliest known so remotely to the  
472 east from the contemporary colonized areas in western Europe. By that time, the closest  
473 previous occurrences were from NE-Hungary in 2015 (Kovács 2015; ca. 330 km linear  
474 distance to the north), and from NW-Slovenia in 2016 (Gogala and Zadavec 2018; ca. 550 km  
475 to the west). The closest contemporary occurrence was the first record in NE-Austria (Westrich  
476 2017; ca. 490 km northwest of Belgrade). With the additional records in 2018, the apparent  
477 distribution gap across the eastern Pannonian Plain was reduced to ca. 160 km (from Belgrade  
478 northwards to Palić and Szeged). Additional adjacent records to the west (Austria, Slovenia,  
479 and Croatia) remained at a fairly large distance throughout 2018–2019 ( $\geq 440$  km). Detections  
480 further east in Europe (2018–2019) were more distant: ca. 1,000–1,150 km between Crimea  
481 (2018) and the closest records in Hungary (2015–2018) or Serbia (2017–2018); ca. 450–  
482 530 km between records in Serbia and Romania (2019); ca. 470–510 km between records in  
483 Hungary and Romania; ca. 640 km between records in Crimea and Romania. Gaps between  
484 the adjacent findings within E-Pannonian Plain were further reduced by the end of the season  
485 2019 (ranging mostly 80–105 km, rarely 115–130 km, but in some areas only ca. 30–40 km),  
486 seemingly approaching the near-continuous distribution. Noteworthy, many records from this  
487 region were from the nesting situations, and none from the proven pollen-source plants.

488

489

## 490 **Discussion**

491

492 We documented and analyzed the widespread local occurrence of *M. sculpturalis* within the  
493 city of Belgrade, highlighting the early phase of its establishment in Serbia (2017–2019). This  
494 initially local case study provided a novel quantitative approach for assessing the bee activity  
495 in relation to floral resource availability, contributing to the framework for early detectability  
496 of the expanding Asian bee. Improved understanding of *M. sculpturalis* dynamic local patterns  
497 triggered an extension of the research scope to the wider, regional-scale context of this

498 introduction – the colonization within the E-Pannonian Plain and SE-Europe (2015–2019). The  
499 combined outcomes of two complementary studies, one of local and another of regional  
500 occurrence patterns during the early colonization, provide important elements for future  
501 monitoring protocols.

502

#### 503 *Local scale: the Belgrade survey*

504

505 Detection and monitoring of a newly established species may be challenging before a  
506 substantial local population build-up is attained (Hui and Richardson 2017), commonly  
507 involving a variously induced time lag after the initial introduction (Crooks 2005). We  
508 confirmed the sculptured resin bee at numerous locations across Belgrade in 2019, only two  
509 years after its first detection in Serbia. We suggest that such an early and widespread detection  
510 was enabled through the effect of “concentration” of bee foraging activities on a limited amount  
511 of the preferred floral resource. Namely, the summer of 2019 was characterized with an  
512 exceptional reduction of bee's key food resource (*S. japonicum*): less than 13% of individual  
513 trees had entered some level of blooming, and only about 6% of the potential “blooming  
514 volume” was actually in bloom (TFR; as compared with good-blooming years); moreover, the  
515 availability of floral resources was further reduced during the short period of our survey (to  
516 1.5%). Therefore, the average bee foraging intensity was concentrated by the factor of nearly  
517 67 (i.e., it was 67 times more likely to observe active bees on inflorescences). Consequently,  
518 recording was highly successful: we detected *M. sculpturalis* in 88% of sectors in which the  
519 blooming of *S. japonicum* was sufficient to support at least minimal bee foraging (the threshold  
520 value  $CFR \geq 0.1$  for this study design). The concentration effect may be particularly emphasized  
521 when a poor-blooming year follows the good year(s). This is based on a more general  
522 mechanism: alternating inter-annual fluctuations of blooming intensity of food plants may  
523 promote phase-delayed good or poor reproduction success of affected bee species (Tepedino  
524 and Stanton 1981; Crone 2013). The phase-delays produce a mismatch between the actual  
525 floral resources and the contemporary bee activity density, and in turn, the alternation of  
526 “concentration” and “dilution” effects. Blooming of *S. japonicum* seemingly follows a sort of  
527 alternating, but basically more irregular bearing pattern, a phenomenon otherwise well known  
528 in numerous tree taxa belonging to widely different plant families (Monselise and Goldschmidt  
529 1982). The good blooming phase of *S. japonicum* in Belgrade during the first two years of  
530 *M. sculpturalis* documented presence (2017–2018) was favorable for the establishment and  
531 initial population build-up, albeit being slow. However, in the same period, its apparent activity

532 has been diluted over this hyper-abundant and widely available floral resource, making it  
533 difficult to detect. We expect that observable activity density of *M. sculpturalis* remains  
534 decisively affected by this interplay of concentration and dilution phases until the substantially  
535 abundant local population is attained. The preliminary outcomes from our 2020 survey  
536 (reduced recording success in conditions of good blooming season), are concordant with this  
537 expectation (Bila Dubaić et al. 2021).

538

539 Within the sectors with detectable bee activity ( $CFR \geq 0.1$ ), we have found that the activity  
540 density (BpM) was solely affected and significantly related to the levels of currently available  
541 floral resources (CFR); this was shown at both sector/landscape scale and as averaged values  
542 across urbanistic zones defined in this study. We could not detect any effects of other tested  
543 resource parameters (NoT, NoT\_iB, TFR) on bee abundance and distribution patterns, neither  
544 of other possible environmental features that vary between the defined urbanistic zones.  
545 Arguably, the lack of significant effects may be in part ascribed to a high variability of key  
546 floral resources and/or to a small sample size (due to limited surveying period). However, this  
547 may also indicate the ability of *M. sculpturalis* to efficiently trace available key food resources,  
548 owing to its size and expectedly strong flight capacity (Quaranta et al. 2014; Westrich et al.  
549 2015). Accordingly, it might be able to quickly optimize its foraging over sizable distances at  
550 local scale, which is of particular importance when resources become critically restricted.  
551 Probably for the same reasons, our analysis has shown that a coarser-scale framework (S500)  
552 was less meaningful than the finer-scale (S250), which seems counterintuitive for a large bee,  
553 hence worthy of further testing. Upon *M. sculpturalis* reaching higher, more stable abundances,  
554 it will be of interest to examine if other aspects of urban environmental gradients might also  
555 affect its local distribution and activity patterns (in addition to the key food availability). Of  
556 various features of urban environments, commonly emphasized as affecting wild bee diversity  
557 and/or dynamics (Hernandez et al. 2009; Fortel et al. 2014; Fischer et al. 2016; Leong et al.  
558 2016; Baldock 2020), we expect that just a few might be proven as effective predictors of local  
559 differences in dynamic distribution patterns of *M. sculpturalis*. Probably most relevant are  
560 features associated with gradients of urban temperature regimes – including heat island effects,  
561 and associated shifts in local phenology of relevant plants. Bee phenology and the seasonal  
562 availability of food plants (either those foraged for pollen or as nectar sources) might be further  
563 modified by management regimes (watering, pruning, etc.) of different urban settings. The  
564 main purpose of capturing such local differences – if shown significant – is to enable an

565 accurate, while also feasible and rational framework for future monitoring schemes, i.e., for  
566 designing an appropriately stratified sampling (allowing the minimal time investment, etc.).

567

568 Noteworthy, even under dramatically reduced foraging opportunities on *S. japonicum* as the  
569 preferred food-plant, we could not detect the bee's activity on alternative plants within the area.  
570 One such commonly available plant, *Lavandula*, is very frequently visited in bee's European  
571 range, second only to *S. japonicum* (cf. Četković et al. 2020: extracts from ongoing study). In  
572 some country accounts, such as France (Le Féon et al. 2018) and Italy (Ruzzier et al. 2020), it  
573 was even ranked as first (based on all available records); however, more frequent casual  
574 encounters of *M. sculpturalis* in southern France and northern Italy became common only >8  
575 years upon respective first detections. Therefore, a different visitation pattern was likely  
576 affected by a higher population abundance attained due to the *M. sculpturalis* longer local  
577 persistence. Its higher abundances could have promoted a spill-over effects of surplus bees,  
578 which were forced to visit other available plants, at least for nectar (*Lavandula* and *Buddleja*  
579 are probably not suitable as pollen source – cf. Četković et al. 2020). Conversely, the lack of  
580 records on other plants in the Belgrade area may be indicative of the local bee population not  
581 yet reaching the abundance, which could support spill-over effects.

582

583 Apparently, the understanding of genuine plant usage patterns is highly important for  
584 improving the species early detectability, as well as for the further monitoring of its population  
585 trends. The effect of concentration, herewith based specifically on a single key food plant, was  
586 crucial for this early mass recording. Without that, the initially slow population growth would  
587 translate into a prolonged cumulation of rare accidental encounters which commonly lags  
588 behind the actual establishment and expansion. Such detection patterns are documented  
589 elsewhere in Europe (cf. Le Féon et al. 2018; Lanner et al. 2020a; Ruzzier et al. 2020, etc.), but  
590 without any consideration of possible mechanisms (cf. Crooks 2005) behind these time lags.  
591 In turn, our results further emphasize the relevance of *S. japonicum* as the single most important  
592 food plant, both for the establishment/spreading and for efficient recording, at least during the  
593 low population levels. Despite quite numerous plant taxa listed in various treatises of bee-plant  
594 interactions, affiliation of *M. sculpturalis* with selected members of the Fabaceae plant family  
595 seems by far most relevant for pollen provisioning (Četković et al. 2020; see also relevant  
596 references in Introduction). Furthermore, *S. japonicum* is the only widely available, mass-  
597 blooming and phenologically suitable representative of large-flowered Fabaceae in the  
598 Belgrade area, and similar situation exist in many Serbian cities and towns (possibly also in

599 various other parts of Europe). Hence, to enable the early detection and to improve the  
600 efficiency of surveillance efforts in areas of suspected bee presence (or expected arrival),  
601 attention should be focused on locations with easily accessible but not excessively abundant  
602 and too widely dispersed key plant resource. Most suitable test-locations might be small towns  
603 or villages with preferably just a few *S. japonicum* trees, within wider landscapes which are  
604 poor in any proven pollen-source plant. These situations might correspond with effects of  
605 concentration, documented herewith for Belgrade in 2019. However, a suitable approach is yet  
606 to be conceived for assessing the eventual spreading of *M. sculpturalis* through vast semi-  
607 natural or wilderness areas.

608

609 Several studies proposed the establishment of an effective monitoring as urgency action for  
610 this rapidly expanding species (Quaranta et al. 2014; Le Féon et al. 2018; IUCN 2020; Ruzzier  
611 et al. 2020; Ribas Marquès and Díaz Calafat 2021). So far, comprehensive studies in colonized  
612 regions of Europe were more extensively based on opportunistic recordings of nesting activity  
613 (within artificial or natural settings), often with a substantial involvement of citizen scientists  
614 or through casual/scattered public contributions to various internet-based data repositories (Le  
615 Féon et al. 2018; Lanner et al. 2020a; Lanner et al. 2020b; Ruzzier et al. 2020; Westrich 2020).  
616 Nesting-based monitoring may be organized as spatially effective, providing that a sufficiently  
617 wide network of voluntary observers could be organized and motivated to install the tailored  
618 nesting facilities around their homes/workplaces, to regularly observe various bee activities,  
619 and to tediously document and report their recordings. However, this approach may not be  
620 uniformly feasible across Europe, due to regionally variable citizen's attitudes or prior  
621 experiences (Pocock et al. 2018; Requier et al. 2020). Furthermore, it is possibly not best suited  
622 for the early phase of colonization, due to its likely poor effectiveness in recording too sparse  
623 bee activity density (i.e., poor effort-efficiency ratio). Therefore, it should be regarded as  
624 complementary to active and field-intensive surveying of focal plants and bee activities on  
625 flowers. Undoubtedly, the combination of both approaches will be needed for the evaluation  
626 of potential invasiveness of this first widespread alien bee in Europe.

627

628 Currently, we still lack an elaborate and comprehensive monitoring protocol – generally for  
629 any of the alien bee species worldwide. In this study we propose a set of surveying routines  
630 and analytical approaches suitable for a structured assessment of plant resource availability  
631 integrated with the standardized quantification of sculptured resin bee activity density. For  
632 building a functional monitoring approach, this working framework requires further testing and

633 quantitative “calibration” of suggested procedures, under different environmental settings and  
634 varied modalities specific for each local or regional colonization event. This should be based  
635 on extensive comparison of future assessment trials, taking into account the complicated  
636 interplay of resources: the co-occurrence of favorable plants (of different functional status:  
637 pollen or nectar-only sources), their varying phenologies and management regimes at different  
638 scales (from landscape through regional), affected by varying environmental gradients (from  
639 urban to natural), while also considering the particular establishment histories.

640

641 *Regional context: introduction and expansion within the SE-Europe*

642

643 Detection of *M. sculpturalis* in Belgrade (2017) represented the first record of this bee from  
644 the Balkan Peninsula and the second one from the area of eastern and southeastern Europe.  
645 Together with the records from NE-Hungary (Gyöngyös; Kovács 2015) and from NE-Austria  
646 (Vienna; Westrich 2017), these were the only three occurrences east of the Alps, as detected  
647 by 2017. Accordingly, all were considered as likely cases of long-distance jump dispersal  
648 (Kovács 2015; Četković and Plećaš 2017; Lanner et al. 2020a), relative to largely continuous  
649 range expansion within the more western parts of Europe (Suppl. material 1), while most of  
650 the Pannonian Plain represented a wide distribution gap between them. The relative position of  
651 the sole Romanian record, two years later (Bucharest; Hymenopterists Forum 2019), matches  
652 these initial dispersal distances of the first three eastern occurrences; further eastern dispersal  
653 jump, documented in Crimea in 2018, was remarkably more long-distant (Ivanov and Fateryga  
654 2019).

655

656 From this wider perspective, the long-distance jump into Belgrade indeed seems as the most  
657 plausible scenario. Belgrade's status (the capital city), and its position at important traffic  
658 junctions of several major routes from central and western Europe, makes it highly exposed to  
659 a large-scale transportation of diverse goods (Suppl. material 2 (i)). The lack of records from  
660 most of Serbia, and also from most of neighboring countries, might further support the  
661 hypothesis that Belgrade was the genuine introduction point for Serbia (and for the C-Balkans).  
662 The initial dispersal distances of elaborated SE-European cases do not allow for more specific  
663 inferences regarding the origin; hence, the source of this particular colonization is to be  
664 resolved only with molecular genetic approach (Bila Dubaić and Lanner 2021; Lanner et al.,  
665 2021). Generally, human-aided secondary introductions among the recently established but  
666 widely isolated locations within SE-Europe are not likely, since the initial low-abundances

667 reduce the chances for inadvertent passive transportations (Bertelsmeier and Keller 2018).  
668 Therefore, source(s) of these presumed long-distance jumps within SE-Europe could have been  
669 any of the populations from the earlier-established W-European range, even the overseas  
670 origins cannot be excluded (Kovács 2015). The recent estimates of genetic relatedness suggest  
671 that the introduction into NE-Austria represents the independent colonization event in Europe,  
672 i.e., not originating from populations established in France and Switzerland (Lanner et al.  
673 2021).

674

675 However, an in-depth consideration of two contrasting cases (Belgrade vs. E-Pannonian)  
676 suggests that the alternative scenario of the colonization of N-Serbia is even more plausible; it  
677 is based primarily on diffusive mode of spreading (Suarez et al. 2001). The vivid nesting  
678 activity of *M. sculpturalis* in a small Hungarian town of Gyöngyös (Kovács 2015) indicates  
679 that local establishment has happened one or more seasons before the actual detection. Its likely  
680 longer and more extended presence in the NE-Pannonian region is further emphasized with  
681 predominance of nesting-based records over the plant-based ones in reports from 2018. The  
682 seemingly abrupt expansion of its apparent range across the NE-Pannonian Plain in 2018, only  
683 three years after the first detection, cannot be based on further human-assisted jump dispersal  
684 events. More likely, a slow “sneaking” diffusive dispersal was taking place near-continuously  
685 for several years, probably for a much longer period than could be inferred from the available  
686 recordings. Accordingly, before the more substantial abundances could become obvious  
687 (simultaneously throughout the region), the spreading southwards across the Pannonian  
688 lowlands could have already reached the northern Balkans (i.e., Serbia in 2017), without being  
689 detected in the intermediary area before 2018. Therefore, the impression of a genuine, fairly  
690 distant jump into Belgrade, unrelated to the prior introduction in NE-Hungary, is most probably  
691 an artifact, i.e., the “type III” lag phase (Hui and Richardson 2017, after Crooks 2005).  
692 Somewhat contrasting evidence of *M. sculpturalis* spreading patterns at two analyzed spatio-  
693 temporal scales (local vs. regional) indicates that it lacks the true lag phase (i.e., the “type II”  
694 of Hui and Richardson 2017). The usually slow initial population build-up apparently does not  
695 hamper the active and successful spreading of this bee, but coupled with relatively scattered  
696 faunistic research in the area, it resulted in poor detection in the region during at least three  
697 years (since 2015). Noteworthy, the widespread presence (since 2018) was documented merely  
698 through accidental/casual activity of citizen scientists' (Rovarok, pókok 2017–2019; Insekti  
699 Srbije 2018; izeltlabuak.hu 2018), i.e., without any focused research.

700

701 The recognition of one vs. another mode of dispersal and identification of likely introduction  
702 and expansion pathway(s) may be severely difficult, and often speculative, but nevertheless  
703 highly important for understanding the spatio-temporal patterns of each non-native  
704 colonization (Suarez et al. 2001; Trakhtenbrot et al. 2005; Hui and Richardson 2017). Herewith  
705 we contrasted the evidence from methodologically different approaches (focused/systematic  
706 surveillance based on focal plant resources and casual/opportunistic recording through  
707 unfocused citizen observations) at two similar temporal scales (3 vs. 5+ years), but over largely  
708 different spatial scales (<20 km vs. >300 km). The study revealed somewhat contrasting, but  
709 complementary expansion and detection patterns, as important aspects of usually hidden early  
710 colonization dynamics, which are of great methodological relevance for future monitoring. We  
711 suggest that, in case of the bee with relatively narrow and well-established trophic  
712 requirements, focusing on key floral resources and concentration-dilution effects is a highly  
713 profitable approach. Nevertheless, the evidence which lacks this component may also be highly  
714 useful in reconstruction of expansion modes and pathways, if interpreted within the suitable  
715 spatio-temporal framework and well-understood recording context. Finally, we have shown  
716 that, contrary to common expectations (Quaranta et al. 2014; Lanner et al. 2020a), the striking  
717 appearance and easy to observe behavior of *M. sculpturalis* is not sufficient to ensure the very  
718 early detection and real-time tracking, without a specifically tailored surveillance approach.  
719 However, it is a highly suitable and prospective model organism for comprehensive studies of  
720 non-native bee colonizations.

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730

### 731 **Authors contribution**

732 AĆ conceived the survey concept, JBD and MP contributed to survey methodology. All  
733 authors except JL contributed equally to collection of field data. MP performed statistical

734 analysis and JBD provided geospatial visualization. JBD and AĆ wrote the initial draft of the  
735 manuscript, JR and MP assisted with editing the draft and finalizing the manuscript. After  
736 receiving revision of the manuscript, JL critically contributed during the rewriting process.  
737 All authors gave final approval for the publication.

738 **Disclosure**

739

740 The authors declare that they have no conflict of interest or disputes over the ownership of the  
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1051

1052 **Figure legends**

1053

1054 **Figure 1.** Landscape/urbanistic zonation of the study area in Serbia (18×11 km), within  
 1055 Belgrade proper (light blue outline; sections separated by the red dotted-line): BUC – Balkan  
 1056 Urban Core; BMP – Balkan Mixed Periphery; PUC – Pannonian Urban Core; PSU – Pannonian  
 1057 Semi-Urban; PPU – Pannonian Peri-Urban.

1058

1059 **Figure 2.** (A) the first specimen of *Megachile sculpturalis* (male), caught in Serbia in July  
 1060 2017; (B) mass-foraging females detected in August 2019.

1061

1062 **Figure 3.** Distribution of (A) effective floral resources of *S. japonicum*, as surveyed in  
 1063 August 2019 (Current Floral Resource – CFR), and (B) respective metrics of *M. sculpturalis*  
 1064 activity density (Bees per Minute – BpM), both presented within the S250 framework  
 1065 (circular sectors – “landscapes” of r=250 m; values shown in classes). Urbanistic zones  
 1066 (acronyms as in Fig. 1) are shown as background shades of grey, representing the averaged  
 1067 value of CFR per zone calculated either for (A) all 40 sectors, or (B) only for 16 sectors with  
 1068 CFR ≥0.1. The location of the first find is marked with “2017”. Numerical data available in  
 1069 Suppl. material 3: Tables S3.2–S.3.4; see also maps in Suppl. material 5. for the complete  
 1070 visualization of floral resource metrics.

1071

1072 **Figure 4.** Relationship between (A) BpM and CFR, and (B) BpM and %CFR averaged across  
 1073 each urbanistic zone (BpM – Bees Per Minute; CFR - Current Floral Resource; %CFR –  
 1074 percentage of current floral resource).

1075

1076

1077 **Supplementary materials**

1078

1079 **Supplementary material 1**

1080 **Summary visualization of the *Megachile sculpturalis* distribution and spreading through**  
 1081 **Europe for the period 2011–2019, shown as series of tentative expansion phases.**

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1084 Data type: text & figure (map); \*.pdf

1085

1086 **Supplementary material 2**

1087 **Study area – Belgrade (Serbia): basic topography, biogeography, ecological patterns**  
 1088 **(habitats, land-use, landscapes) and urbanistic zonation:**

1089 **(i) City of Belgrade: general features (Figure S2.1);**

1090 **(ii) Zonation of Belgrade (version\_01: survey in 2019; Figure S2.2);**

1091 **(iii) Survey design and processing of geospatial framework (Figure S2.3).**

1092 (This is the PDF version of selected pages from the thematic project website (Ćetković et al.

1093 2020), by: Centre for Bee Research of the Faculty of Biology, University of Belgrade

1094 (available also at: <https://srbee.bio.bg.ac.rs/english/belgrade-general-features;>

1095 <https://srbee.bio.bg.ac.rs/english/m-sculpturalis-2019-survey;> with occasional updates.)

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1098 Data type: text & figures (maps); \*.pdf

1099

1100 **Supplementary material 3**

1101 **Quantitative survey of distribution and abundance parameters of *M. sculpturalis* (BpM)**  
 1102 **and *S. japonicum* (NoT, NoT\_iB, TFR, CFR) in the Belgrade area in August 2019: Tables**  
 1103 **S3.1–S3.4.**

1104 Authors: Jovana Bila Dubaić, Milan Plećaš, Jovana Raičević, Julia Lanner, Aleksandar  
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1106 Data type: spreadsheet database (data & metadata); \*.xlsx

1107

1108 **Supplementary material 4**

1109 **Table S4.1. Records of *M. sculpturalis* from the broader SE-European region and the**  
1110 **adjacent areas (compiled for: 2015–2019). Table S4.2. Published data sources used.**

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1113 Data type: spreadsheet database (records and sources); \*.xlsx

1114

1115 **Supplementary material 5**

1116 **Belgrade area: results of statistical testing (Tables S5.1–S5.3) and distribution maps of**  
1117 **estimated metrics (Figures S5.1–S5.2).**

1118 Authors: Jovana Bila Dubaić, Milan Plećaš, Jovana Raičević, Julia Lanner, Aleksandar  
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1120 Data type: text, tables & figures (maps); \*.pdf