

1 **Effects of landscape context on different groups of cavity-nesting bees,**  
2 **wasps and the wasps' spider prey**

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33 **Effects of landscape context on different groups of cavity-nesting bees,**  
34 **wasps and the wasps' spider prey**

35 **Running headline:** Landscape effects on cavity-nesting hymenopterans

36 **Abstract**

37 In this study our aim was to assess the diversity and distribution of cavity-nesting solitary  
38 bees, wasps and the spider-hunting wasps' prey with regards to the influence of landscape  
39 context in a study area with relatively low human disturbance. The study took place between  
40 May and August 2018 at eight study sites in the hilly-mountainous central part of Romania,  
41 where the majority of the landscape is used for extensive farming or forestry. During the  
42 processing of the trap nest material, we recorded several parameters regarding the nests of  
43 different hymenopteran groups, the spider prey found inside these nests, and also tested the  
44 influence of the landscape structure surrounding the sites on both hymenopteran groups and  
45 spider prey.

46 The majority of nests was built by the solitary wasp group of *Trypoxylon*, followed by  
47 *Dipogon* and Eumeninae. Solitary bees were much rarer, with *Hylaeus* being most common  
48 group. The groups showed partially differing size preferences concerning the diameter of the  
49 occupied reed stalks. In the nests of *Trypoxylon* we predominantly found spider prey from the  
50 family of Araneidae, followed by representatives from the families of Linyphiidae and  
51 Theridiidae. In contrast to *Trypoxylon*, the wasp group *Dipogon* preferred spider prey from  
52 the family of Thomisidae. Concerning the hymenopteran groups, significant effects of  
53 landscape structure were found on the number of both nests and brood cells of Eumeninae and  
54 on the number of brood cells of *Hylaeus*, *Osmia* and *Trypoxylon*. We also found that the  
55 diversity of *Trypoxylon* spider prey was significantly positively affected by an increasing  
56 proportion of grassland and negatively by an increasing proportion of woodland.

57 Altogether, our study presents several new aspects concerning the diversity and distribution of  
58 solitary bees, wasps and the spider-hunting wasps' prey and also the effects of landscape  
59 context on these groups.

60

61 **Keywords:** Cavity-nesting hymenopterans, landscape effects, solitary bees, spider-hunting  
62 wasps, spider prey

## 63 Introduction

64 Nowadays, an increasing agricultural intensification (Stoate et al., 2009) and urbanization  
65 (McKinney, 2008) can be observed in most countries of the European Union. In the last few  
66 decades, these areas partially experienced a dramatic decline of insect diversity (Batáry et al.,  
67 2010; Fox, 2013; Fox et al., 2014; Hallmann et al., 2017; Maes et al., 2010). Loss of bee  
68 pollinators, including both managed honey bees (*Apis mellifera* L.) and wild bees has already  
69 been demonstrated (Ollerton et al., 2014; Potts et al., 2010). Native solitary bees can be more  
70 efficient pollinators in certain habitats than honeybees (Garibaldi et al., 2013) and their  
71 pollination service in natural habitats without any honeybee effect can be lower and also less  
72 well assessed as several such ecosystems in Europe are highly affected by multiple  
73 agricultural interactions (grazing, beekeeping, deforestation). The effects of landscape context  
74 ‘*sensu lato*’ have already been analysed in numerous studies. Some studies dealing with the  
75 effects of landscape context conducted a simple landscape analysis looking only at the  
76 presence of (Holzschuh et al., 2009; Mayr et al., 2020; Tscharntke et al., 1998) or distance  
77 from certain habitat types like forests (Klein et al., 2006) or ecological compensation area  
78 (ECA) meadows (Albrecht et al., 2007). Other studies, however, looked more specifically at  
79 the landscape structure surrounding their study sites, studying the effects of the proportion of  
80 different habitat types (Coudrain et al., 2016; Kratschmer et al., 2020; Taki et al., 2008) or  
81 even complex landscape analyses (Holzschuh et al., 2010; Steckel et al., 2014) at multiple  
82 spatial scales (Steckel et al., 2014; Taki et al., 2008). With regards to the pollination service  
83 provided by cavity-nesting solitary bees and the biological pest control by some cavity-  
84 nesting wasp species (like *Ancistrocerus gazella*; Harris 1994), additional knowledge about  
85 these species and the influence of landscape context on them may provide help in measures  
86 for their protection. The fact that trap nests provide a good nesting opportunity and thus lead  
87 to an accumulation of cavity-nesting solitary hymenopteran species living in the area  
88 surrounding the nests makes them especially suitable to study landscape effects.

89 It has been demonstrated in several studies that trap nests are ideal tools to examine and  
90 assess the biodiversity of hymenopterans and also their trophic interactions in a certain area  
91 (Albrecht et al., 2007; Klein et al., 2006; Kruess & Tscharntke, 2002; Mayr et al., 2020;  
92 Sabino et al., 2016; Scherber et al., 2010; Staab et al., 2018; Stangler et al., 2015; Steckel et  
93 al., 2014; Tscharntke et al., 1998). Basically, cavity-nesting aculeate hymenopterans can be  
94 divided into two trophic groups of nectar and pollen-feeding solitary bees (representatives of  
95 the families Apidae, Colletidae and Megachilidae), which are pollinators of many wild and

96 crop plant species, and predatory wasps, which either hunt caterpillars (representatives of the  
97 subfamily Eumeninae in the family of Vespidae) or spiders (representatives of the families  
98 Crabronidae, Sphecidae and Pompilidae) (Klein et al., 2006; Mayr et al., 2020; Steckel et al.,  
99 2014). The majority of the studies mentioned above were conducted in agriculturally  
100 dominated areas. However, even in the European Union, there are still a few regions and areas  
101 remaining, which are not under such a strong anthropogenic influence and still harbour a  
102 considerably high insect diversity. An example for such a region is the central part of  
103 Romania, where the population density is relatively low and the majority of the landscape is  
104 used for extensive farming or forestry.

105 Therefore, the goals of our present study were the following: i) to quantify the diversity of the  
106 cavity-nesting hymenopteran assemblage occurring in a study area dominated by natural  
107 habitats; ii) to identify and quantify the spider families preyed by the spider-hunting  
108 representatives of the hymenopteran groups; iii) to analyse the influence of landscape  
109 structure on both the hymenopteran groups and the spider prey. Concerning our first goal, we  
110 assumed that our study area would may harbour a higher diversity or at least a different  
111 taxonomic composition of cavity-nesting hymenopterans compared to other, more intensively  
112 used regions or areas in the European Union. Regarding our last goal, we were curious to find  
113 out, how the different proportion and structure of grassland and woodland, the two main  
114 landscape elements in study areas, would influence the abundance and diversity of both the  
115 cavity-nesting hymenopteran groups and the spider prey at the different study sites.

116

## 117 **Methods**

### 118 *Study area*

119 The study took place in a hilly-mountainous area at the border of the two counties Harghita and  
120 Kovászna (Transylvania, Romania), where the valleys are predominantly used for extensive  
121 farming (Figure S1 supplementary online materials). Due to the extensive use, we can find a  
122 large amount of natural and semi-natural habitat patches in this area, building a mosaic of  
123 flower-rich grasslands, bushy-woody spots and woodlands. The majority of the grassland  
124 patches are used as meadows and pastures. The study sites were located in three valleys  
125 between 530-630 m a.s.l. Two of these valleys were formed by the Vargyas creek (=‘Vargyas  
126 valleys’) and are separated by a canyon (Figure S1 A). The third one is located 5-8 km east to  
127 the Vargyas valleys and was formed by the Körmös creek (=‘Körmös valley’; Figure S1 B).

128 The main flow direction of both creeks in this area is north to south. The northern Vargyas  
129 valley is mostly used for extensive grazing and is dominated by meadows and pastures, while  
130 the southern valley, due to its remoteness, is much less used for grazing and more dominated  
131 by forest patches. Compared to the two Vargyas valleys, the Körmös valley is more  
132 anthropogenically influenced with arable land in its southern part, close to the settlement  
133 Erdőfüle (Filia).

#### 134 ***Study sites and sampling***

135 Each four trap nests were installed at eight sites in the three valleys at the end of May 2018.  
136 There were each three sites in the Körmös valley (K1-K3) and southern Vargyas valley (SV1-  
137 SV3) and two sites in the northern Vargyas valley (NV1-NV2), making it a total of 32 trap  
138 nests, which were placed in the study area. At each site, the trap nests were marked with a  
139 unique code in reference to the sites and placed around a center point. The selection of the  
140 sites happened randomly, only paying attention to that the nests were at a more or less equal  
141 distance from this center point and that the center points of each site should be at least 500 m  
142 away from each other. The trap nests were custom-made, consisting of a PVC tube of 12 cm  
143 diameter and 23 cm length. The tubes were filled with stalks of common reed (*Phragmites*  
144 *australis* Cav.), which were cut off to a length of approx. 22 cm between the nodes, so that the  
145 inner part of the stalks would be freely accessible for any nest-building hymenopteran. The  
146 stalks were placed tightly packed in the tubes to avoid them from falling out. The tubes were  
147 placed in trees or shrubs at 1-2 m above ground. The trap nests were collected at the end of  
148 August 2018 and stored outdoors at a shady place. In January 2019, the nests were put into a  
149 fridge and stored at 4-7 °C. In the same month, we began to collect the data from the reed  
150 stalks. For this, all stalks were cut open and, in case we found a nest within a stalk, it was  
151 recorded with reference to the unique code of the trap nest plus a serial number, giving each  
152 nest a unique code. In case of each occupied stalk (=nest) we recorded the following  
153 parameters: a) diameters of the reed stalks; b) number of occupied brood cells, filled either  
154 with hymenopteran offspring or spider prey (if present) – empty cells were also counted, but  
155 not used in further analyses; c) type of nesting material; d) colour of larvae or cocoons (if  
156 present). Besides these, we also counted the total number of stalks per trap nest. Based on the  
157 parameters c) and d) we were able to identify seven groups of nest types. From each of these  
158 seven groups, we also took a few nest samples (at least two) and reared them at room  
159 temperature. After the emergence of the adults from these samples, several specimen were  
160 collected, killed in 70% ethanol and identified at genus level. We were able to identify the

161 following eight geni: *Ancistrocerus*, *Auplopus*, *Dipogon*, *Hylaeus*, *Megachile*, *Osmia*,  
162 *Symmorphus* and *Trypoxylon*. Except for the two geni *Ancistrocerus* and *Symmorphus* of the  
163 subfamily of Eumeninae (potter wasps), which could be not distinguished based on the nest  
164 type, each genus could be assigned to a specific nest type. Therefore, based on this  
165 information, we distinguished between three groups of solitary bees and four groups of  
166 predatory wasps, giving them the name of the respective genus, with exception for the two  
167 geni of potter wasps, which were named after the subfamily.

168 If present, spider prey was collected from the nests, put into 70% ethanol and marked with the  
169 unique nest-codes. The spider prey was then taxonomically identified at species level, if  
170 possible (but at least at family level), grouped according to the predatory wasp group and the  
171 identified families.

### 172 ***Landscape context***

173 The landscape surrounding the eight study sites was mapped as landscape sectors of 250 m  
174 radius in QGIS 2.18.9 (QGIS Development Team 2009) in the ETRS89/ETRS-LAEA (EPSG:  
175 3035) coordinate reference system. We distinguished between three different landscape  
176 element types: a) ‘grassland’, with less than 30% shrub or tree canopy cover; b) ‘woodland’,  
177 with more than 30% shrub or tree canopy cover and c) ‘other areas’, like the water bodies of  
178 the two creeks and the creek banks without vegetation, dirt roads and arable land, which were  
179 not included in further analyses. In order to quantify landscape structure and diversity, we  
180 decided to calculate the landscape metrics ‘Percentage of Landscape’ and ‘Edge Density’ in  
181 FRAGSTATS v4.2.1 (McGarigal et al., 2002) to quantify the landscape structure around the  
182 eight study sites (Table S1). We chose these two metrics due to their common use in  
183 landscape analysis and their easy interpretability. For calculating the landscape metrics, the  
184 vector layers of the landscape sectors were rasterized with an output raster size of 1 x 1 m. We  
185 used an 8-cell neighbor-hood rule for all calculations carried out with FRAGSTATS v4.2.1.  
186 The calculated values for the proportion and edge density of the landscape elements  
187 ‘grassland’, ‘woodland’ and ‘other areas’ within 250 m around the eight study sites are listed  
188 in the supplementary Table S1.

### 189 ***Statistical analyses***

190 All statistical analyses were conducted in R v3.6.3 (R Core Team, 2020). The relationship  
191 between the number of nests and occupied brood cells for the seven cavity-nesting  
192 hymenopteran groups, was tested fitting a list of linear regression models using the command

193 'lmList' from the R package 'lme4' (Bates et al., 2015). For testing the preferences of the  
194 cavity-nesting hymenopteran groups concerning the reed stalks' diameter, we used an  
195 ANOVA followed by a post hoc Tukey's HSD test (confidence level=0.95).

196 We applied linear regression models to find the strongest effects of the landscape structure on  
197 the cavity-nesting hymenopteran groups and the most frequent families of spider prey. In  
198 these linear models, we used the total number of nests per site and the mean number of  
199 occupied brood cells (=parameter b) per nest and site for the seven cavity-nesting  
200 hymenopteran groups and the mean number of spider prey per nest and site of those spider  
201 families, which were more frequent and occurring at the majority of sites. Before running the  
202 linear models, however, we preliminary checked the distribution of both the data of the  
203 hymenopteran groups (Table S2 A and B) and the most frequent groups of spider prey (Table  
204 S2 C) for the fulfilment of the assumption of normality with Shapiro-Wilk tests (Shapiro &  
205 Wilk, 1965). These tests showed that the number of nests of those hymenopteran groups,  
206 which were not occurring at all study sites (= *Auplopus*, *Megachile* and *Osmia*), strongly  
207 deviated from a normal distribution (Table S2 A). The variance of these data was also very  
208 low so that they were excluded from further analyses. However, these tests also showed that  
209 the mean cell number as well as the mean number of spider prey fulfilled the assumption of  
210 normality for all groups (Tables S2 B and C).

211 We also included the diversities found at the sites for both the hymenopteran groups and the  
212 spider prey of the *Trypoxylon* group, which were assessed by calculating the Shannon's  
213 Diversity Index using the R package 'vegan' version 2.5-6. (Oksanen et al., 2019), in the  
214 linear regression models. The Shannon's Diversity Index was determined using the number of  
215 nests per site for the hymenopteran groups and the total number of spiders per nest and site for  
216 the representatives of the spider families preyed by *Trypoxylon*. In the case of the diversity of  
217 the *Trypoxylon* spider prey representatives of all spider families were included. The  
218 distribution of both indices fulfilled the assumption of normality for both the hymenopteran  
219 groups and the *Trypoxylon* spider prey (Tables S2 A and C). All graphs were created using the  
220 R package 'ggplot2' (Wickham, 2016).

221 Finally, we also checked for spatial autocorrelation (Moran's I) in case of those data, where  
222 we encountered a significant effect of the landscape context, using the R-package 'ape'  
223 (Paradis & Schliep, 2019). The coordinate reference system used for this analysis was WGS  
224 84 (EPSG:4326). We only detected significant autocorrelation in case of the *Trypoxylon*  
225 spider diversity (Table S3). Therefore, besides the normal linear regression models, we also

226 used generalized least squares fits ('gls') by REML from the R package 'nlme' (Pinheiro et  
227 al., 2013) incorporating an exponential correlation structure in order to account for the spatial  
228 autocorrelation of the *Trypoxylon* spider diversity.

## 229 **Results**

### 230 *Nests*

231 In total, we found 990 nests in 4857 reed stalks, with the occupancy per site ranging from  
232 13.162 to 29.590% ( $20.200 \pm 5.934\%$ ). The majority of the nests was built by solitary wasps  
233 (Fig. 1 A), with the *Trypoxylon* group (n=560) being dominant at the most of the sites,  
234 especially at those located in the southern Vargyas valley (SV1-SV3). The second most  
235 abundant group concerning the number of nests was the *Dipogon* group with a total of 158  
236 nests. Their nests occurred at all sites, but never in such a dominant manner as in case of the  
237 *Trypoxylon* group. The third most important group was the group of Eumeninae with 152  
238 nests. Representatives of this group could be found at all sites, but with strongly varying  
239 numbers. Their occurrence ranged from the most dominant group at one site (K1) to nearly  
240 non-existent at another site (K3). The rarest wasp group per site was *Auplopus* with a very  
241 low number of occurrences (n=18), but found at seven of the eight sites. The number of nests  
242 built by solitary bees was relatively low compared to the nest numbers of the solitary wasps  
243 (Fig. 1 B), with *Hylaeus* being the most abundant group (n=61), followed by the *Osmia*  
244 (n=23) and *Megachile* (n=18) groups. From these groups, only *Hylaeus* could be found at all  
245 sites. The total number of nests and cells as well as the mean number of cells per nest and  
246 study site for each hymenopteran group are listed in Table S4. In case of each more common  
247 hymenopteran group, which could be found at all sites, there was a significant, positive  
248 relationship between the number of nests and occupied brood cells (Table 1).

249 Concerning the diameter of the reed stalks with nests inside, we found different size  
250 preferences for the different groups (Fig. 2). The group of the small-sized solitary bee  
251 *Hylaeus* built its nests in stalks with the smallest diameters ( $5.679 \pm 0.747$  mm). The three most  
252 common (wasp) groups found in the trap nests – *Trypoxylon*, *Dipogon* and Eumeninae – all  
253 choose reed stalks of very similar diameters ( $6.572 \pm 1.018$  mm for *Trypoxylon*;  $6.447 \pm 0.815$   
254 mm for *Dipogon*;  $6.616 \pm 1.190$  mm for Eumeninae). The groups of the two medium-sized  
255 solitary bees *Osmia* and *Megachile*, as well as the Pompilid wasp *Auplopus*, which builds  
256 nests with barrel-shaped cells, all favored reed stalks with (more or less) clearly larger  
257 diameters than the three most common groups ( $7.476 \pm 1.398$  mm for *Osmia*;  $8.435 \pm 1.191$  mm  
258 for *Megachile*;  $8.211 \pm 0.893$  mm for *Auplopus*).

## 259 *Spider prey*

260 The largest number of identifiable spiders was preyed by wasps from the *Trypoxylon* group  
261 (n=1471), followed by the *Dipogon* group (n=99) and the *Auplopus* group with only one  
262 identifiable specimen from the family of Clubionidae. In case of the *Trypoxylon* group (Fig. 3  
263 A) the majority of the preyed spiders were from the family of Araneidae (n=1118), with  
264 *Mangora acalypha* being the most common species found in 14 nests. Other spider families,  
265 which were preyed more commonly by *Trypoxylon*, were the Linyphiidae (n=175), with  
266 *Linyphia triangularis* as the most common species found in 18 nests, and the Theridiidae  
267 (n=131), with *Phylloneta impressa* as the most common species found in 14 nests. The  
268 *Dipogon* group clearly differed in its predatory choice from the *Trypoxylon* (Fig. 3 B), with  
269 mostly preying on spiders from the family of Thomisidae (n=93). The most common species  
270 from this family found in *Dipogon* nests were *Xysticus bifasciatus* (n=4) and *Xysticus*  
271 *cristatus* (n=3). The total number of *Dipogon* and *Trypoxylon* nests with identified spider prey,  
272 the total number of spider prey per nest and the mean number of spider prey per nest and  
273 study site for the identified representatives of predated spider families are listed in Table S5.

## 274 *Landscape context*

275 The linear models testing for the relationship between the landscape structure and the number  
276 of nests revealed that only the number of nests of Eumeninae was significantly, positively  
277 affected by an increasing edge length of woodland around the study sites (Table 2 B). All  
278 other effects were non-significant, even though the number of *Trypoxylon* nests seemed to be  
279 more strongly positively associated with an increasing proportion of woodland around the  
280 study sites (Table 2 B). Regarding the nest numbers of *Hylaeus*, there is also a rather clear  
281 decrease from north to south along the Vargyas valley (sites NV1-SV3; Fig. 1B). For  
282 *Trypoxylon* an opposite, but less clear trend is observable (Fig. 1 A). The diversity of the  
283 cavity-nesting hymenopteran groups seemed to be positively associated with the metrics of  
284 grassland and negatively with those of woodland, but none of these effects was significant.

285 The mean cell number per nest and site of most cavity-nesting hymenopteran groups was  
286 positively affected by an increasing proportion of woodland and negatively by an increasing  
287 proportion and edge density of grassland around the study sites (Table 3 A and B). This  
288 positive effect of a higher proportion of woodland around the sites, however, was only  
289 significant for the groups of Eumeninae and *Hylaeus* (Table 3 B), while the negative effects  
290 of a higher proportion or edge density of grassland were only significant for the groups of  
291 Eumeninae and *Osmia*, respectively (Table 3 A). The groups of *Auplopus* and *Megachile*

292 were the only ones, which were positively, but non-significantly affected by both an  
293 increasing proportion and edge density of grassland (Table 3 A) and negatively associated  
294 with an increasing proportion of woodland around the study sites (Table 3 B). In contrast to  
295 the mostly positive effect of an increasing proportion, the effect of an increasing edge density  
296 of woodland on the hymenopteran groups was predominantly negative. However, only the  
297 group of *Trypoxylon* was significantly affected by an increasing edge density of woodland.

298 The mean number of *Trypoxylon* and *Dipogon* spider prey was largely unaffected by the  
299 landscape structure around the study sites (Table 4 A and B). The strongest relationship was  
300 found in case of the number of Theridiidae, which was positively affected by an increasing  
301 proportion of grassland. The diversity of *Trypoxylon* spider prey, however, was significantly  
302 influenced by the landscape structure around the study sites. While an increasing proportion  
303 of grassland showed a positive effect on the diversity of *Trypoxylon* spider prey, an increasing  
304 proportion of woodland had the opposite effect (Table 4 A and B).

305

306

## 307 **Discussion**

308 Analysing the content of the trap nests revealed that concerning the number of nests, solitary  
309 wasps were dominating the study area. The strongly dominant group of *Trypoxylon*, which  
310 accounted for more than half of all nests, was followed by the groups of *Dipogon* and  
311 Eumeninae, which had similar numbers of nests. The rarest wasp group per site was  
312 *Auplopus*, which was found at nearly all sites, but with very low nest numbers. The nest  
313 numbers of solitary bees were considerably lower than those of solitary wasps. Here, the  
314 group of *Hylaeus* was the most abundant and could be found at all sites, while nests built by  
315 the groups of *Osmia* and *Megachile* were rather rare and not occurring at all sites. The results  
316 of another study using sweep-net methods, conducted parallel to this one during 2018 in the  
317 same area, revealed that the occurrence of *Osmia* species was mainly in spring (April and  
318 May), while their occurrence between June and August, the time when the trap nests were  
319 available for them, was considerably lower (Demeter et al., 2021). In contrast to our findings,  
320 other similar studies from agriculturally dominated areas situated in Southwestern Germany  
321 reported that the majority of nests of cavity-nesting hymenopterans was built by the solitary  
322 bees *Megachile* and *Osmia*, while the genus *Trypoxylon* was only the third most abundant  
323 (Gathmann et al., 1994; Steffan-Dewenter, 2002). Assessments from a heterogeneous

324 landscape dominated by grasslands and forests in Schleswig-Holstein (northern Germany)  
325 reported results, which were more similar to our ones, with the digger wasp *T. figulus* (43% of  
326 all individuals) as the most abundant species, followed by the solitary bee *Osmia rufa* (11%)  
327 and one species parasitizing *T. figulus*, the ruby-tailed cuckoo wasp (*C. cyanea*) (9%) (Kruess  
328 & Tschardtke, 2002). Our results are also more consistent with one study carried out in  
329 central-western Spain (Tormos et al., 2005), where a similar occupation index (19-20%) of the  
330 reed stalks was detected and *Trypoxylon* was the most abundant genus (272 nests, 72.9%), and  
331 with another study, which was conducted in a region with 44% of agricultural management in  
332 central Germany and also found that *Trypoxylon* spp. were the most abundant spider-hunting  
333 geni (Hoffmann et al., 2020).

334 Regarding the diameter of the reed stalks with nests inside, the hymenopteran groups showed  
335 partially differing size preferences. The group of *Hylaeus*, which represents a genus of small-  
336 sized solitary bees (ca. 6-8 mm body length), built its nests in stalks with the smallest  
337 diameters (mostly below 6 mm). The representatives of *Trypoxylon*, *Dipogon* and Eumeninae  
338 choose reed stalks of very similar diameters (around 6.5 mm), while the bee groups *Osmia*  
339 and *Megachile*, as well as wasp *Auplopus* favoured reed stalks with rather larger diameters  
340 (above 7 mm). Our findings are consistent with other studies, which reported partially similar  
341 mean diameters for these groups: *Ancistrocerus* with diameters of 5-6.5 mm, *Symmorphus*  
342 mostly 4-6 mm, *Trypoxylon* 3-5 mm, *Hylaeus* 3-4 mm, *Osmia rufa* 6 mm in Budrienè et al.  
343 (2004) and average diameters of 6 mm for *Trypoxylon* and 9 mm for *Megachile* in Campbell  
344 et al. (2017).

345 In case of the *Trypoxylon* group the majority of the preyed spiders were from the family of  
346 Araneidae with *Mangora acalypha* as most common species. Other spider families, which  
347 were preyed more commonly by *Trypoxylon*, were Linyphiidae with *Linyphia triangularis*,  
348 and Theridiidae with *Phylloneta impressa*. *Dipogon* preyed almost exclusively on  
349 Thomisidae, with *Xysticus bifasciatus* and *Xysticus cristatus* as the two most common  
350 identified species. A study conducted in Southwest Germany also found that *Phylloneta*  
351 *impressa* and *Mangora acalypha* were the main prey of *Trypoxylon figulus* (Pfister et al.  
352 2015). In contrast to this, however, two other studies reported that Theridiidae, especially the  
353 species *Phylloneta impressa*, which accounted for about 80 % of all spiders collected in  
354 Coudrain et al. (2013) and about 82% in the study of Hoffmann et al. (2020) were the  
355 dominant prey of *Trypoxylon figulus*. A possible explanation for the different findings of  
356 these two studies is that they were carried out in agriculturally dominated landscapes in

357 contrast to our study, which was conducted in a study area predominantly used for extensive  
358 farming or forestry.

359 Concerning the influence of landscape structure, the clearest effects were found for the group  
360 of Eumeninae or potter wasps, where the number of brood cells per site was positively  
361 affected by an increasing proportion of woodland and negatively by an increasing proportion  
362 of grassland. The number of Eumeninae nests was also positively associated with an  
363 increasing edge density of woodland. These findings are very similar to those reported by  
364 Holzschuh et al. (2009), who found the abundance of wasps (Sphecidae, Eumenidae,  
365 Pompilidae) were highest at forest edges, which provide natural nesting sites, and lowest in  
366 grass strips, with few natural nesting sites. They reported that wasp abundance in grass strips  
367 connected to forest edges was clearly higher than in slightly isolated grass strips and much  
368 higher than in highly isolated grass strips. In contrast to these positive effects of woodland,  
369 however, Schüepp et al. (2011) reported that abundances of wasps tended to decrease with an  
370 increasing percentage of woody habitat, while the abundances of solitary bees were not  
371 significantly influenced by the percentage of woody habitats at the landscape scale. These  
372 results are consistent with our findings for the brood cell number of the *Trypoxylon* group,  
373 which was negatively affected by an increasing edge density of woodland. Such negative  
374 effects are quite possible, as Fabian et al. (2013) reported that plant biomass, measured as leaf  
375 area index, negatively affected the species richness of herbivore-predating wasps like  
376 Eumenidae and also the abundance of spider-predating wasps like *Trypoxylon*. They also  
377 found that forest cover had a positive effect on the total abundance of wasp brood cells, which  
378 is in accordance with our observations, too.

379 In case of the solitary wild bee groups we only encountered significant effects of landscape  
380 structure on the number of brood cells per site for the groups of *Hylaeus*, which was  
381 positively affected by an increasing proportion of woodland, and *Osmia*, which was  
382 negatively affected by an increasing edge density of grassland. This latter finding may come a  
383 bit unexpected, since most *Osmia* species feed on wild flowers, but many species are closely  
384 associated with forest habitats due to their nesting habits as they create small burrows for their  
385 nests in tree barks (Müller et al., 2019).

386 We did not find any significant effects of landscape structure on the diversity of the cavity-  
387 nesting hymenopteran groups in our study. Similarly, Taki et al. (2008) reported that in  
388 relation to forest loss, the species richness of the cavity-nesting wasps was not significantly  
389 related to forest coverage. Two previous other studies, however, made different observations:

390 Schüepp et al. (2011) found that species richness of wasps was more than doubled and  
391 diversity three-times higher in sites with high percentages of woody habitats, compared with  
392 sites including lower percentages of woody habitats and Fabian et al. (2013) also reported that  
393 forest cover had a positive effect on the species richness of wasps. Again, these contrasting  
394 findings can be possibly traced back to the stronger agricultural influence in their study areas.

395 Concerning the spider prey of *Dipogon* and *Trypoxylon*, the strongest, but non-significant  
396 relationship was found in case of the number of Theridiidae, which was positively affected by  
397 an increasing proportion of grassland and negatively by an increasing proportion of woodland.  
398 Similar observations were made by Pfister et al. (2015) in a study conducted in Southwest  
399 Germany, where they found reduced densities of *Phylloneta impressa* along woody field  
400 margins, possibly due to predation by *Trypoxylon* wasps. In contrast to the hymenopteran  
401 groups, landscape structure had a clearly significant effect on the diversity of *Trypoxylon*  
402 spiders prey. An increasing proportion of grassland showed a positive effect on the diversity  
403 of *Trypoxylon* spider prey, while an increasing proportion of woodland had the opposite  
404 effect. Hoffmann et al. (2020), however, reported exactly the opposite, with an increasing area  
405 of grassland having a negative effect on spider species diversity in *Trypoxylon* nests. Also  
406 here, this contrasting finding may be explained by the different landscape composition and  
407 structure in their agriculturally dominated study area, where they found that *Trypoxylon*  
408 mostly preyed in grassland patches. Therefore, they also assumed that a higher proportion of  
409 grassland may caused *Trypoxylon* specifically hunting for its preferred prey species, resulting  
410 in a lower prey diversity found in their nests.

411 Altogether, our study presents several new aspects of the diversity and distribution of solitary  
412 bees, wasps and spider-hunting wasps' spider prey and effects of landscape context in an area  
413 with relatively low human influence. As only few such habitats still remain in Europe and as  
414 the maintenance of insect biodiversity is crucial for well-functioning ecosystems, our results  
415 can be important for future researches in areas, which are both less or more strongly  
416 influenced by humans.

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548

549 **Tables**

550 **Table 1:** Results taken from a fitted list of linear models using the command ‘lmList’ from  
 551 the R package ‘lme4’ (Bates et al., 2015), testing for the relationships between the number of  
 552 nests and the total number of occupied brood cells for the seven cavity-nesting hymenopteran  
 553 groups.

<b>Group</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<i>Auplopus</i>	3.208	2.992	1.072	0.291
<i>Dipogon</i>	2.502	1.028	2.434	0.020
Eumeninae	3.056	0.423	7.219	0.000
<i>Hylaeus</i>	3.761	1.268	2.965	0.005
<i>Megachile</i>	3.139	3.062	1.025	0.312
<i>Osmia</i>	10.862	8.358	1.300	0.202
<i>Trypoxylon</i>	3.859	0.141	27.297	0.000

554

555

556 **Table 2:** Results of linear regression models testing for the relationship between the  
 557 proportion and edge density of A) grassland and B) woodland within 250 m around the eight  
 558 study sites and the number of nests built by different cavity-nesting hymenopteran groups.  
 559 The Shannon's Diversity Index at each site, which was calculated based on the number of  
 560 nests, was also included in this analysis. Significant relationships are marked bold.

561 A) Grassland

Metric	Group	Estimate	Std. Error	t value	Pr(> t )
Proportion	<i>Dipogon</i>	-0.195	0.231	-0.846	0.430
	Eumeninae	0.164	0.589	0.278	0.791
	<i>Hylaeus</i>	0.111	0.192	0.576	0.586
	<i>Trypoxylon</i>	-1.673	1.637	-1.022	0.346
	Diversity	0.002	0.003	0.584	0.580
Edge density	<i>Dipogon</i>	-0.012	0.052	-0.225	0.830
	Eumeninae	0.106	0.119	0.893	0.406
	<i>Hylaeus</i>	0.037	0.039	0.951	0.378
	<i>Trypoxylon</i>	-0.419	0.337	-1.243	0.260
	Diversity	0.000	0.001	0.909	0.398

562

563 B) Woodland

Metric	Group	Estimate	Std. Error	t value	Pr(> t )
Proportion	<i>Dipogon</i>	0.130	0.211	0.617	0.560
	Eumeninae	0.059	0.527	0.112	0.914
	<i>Hylaeus</i>	-0.170	0.162	-1.054	0.332
	<i>Trypoxylon</i>	2.162	1.309	1.651	0.150
	Diversity	-0.002	0.002	-1.094	0.316
Edge density	<i>Dipogon</i>	-0.026	0.044	-0.587	0.579
	Eumeninae	0.192	0.076	2.513	<b>0.046</b>
	<i>Hylaeus</i>	-0.013	0.036	-0.352	0.737
	<i>Trypoxylon</i>	-0.095	0.326	-0.291	0.781
	Diversity	0.000	0.001	-0.035	0.973

564

565

566 **Table 3:** Results of linear regression models testing for the relationship between the  
 567 proportion and edge density of A) grassland and B) woodland within 250 m around the eight  
 568 study sites and the mean number of occupied brood cells per nest, which were built by  
 569 different cavity-nesting hymenopteran groups. Significant relationships are marked bold.

570 A) Grassland

<b>Metric</b>	<b>Group</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
Proportion	<i>Auplopus</i>	0.032	0.12	0.27	0.798
	<i>Dipogon</i>	-0.028	0.018	-1.606	0.159
	Eumeninae	-0.056	0.013	-4.341	<b>0.005</b>
	<i>Hylaeus</i>	-0.09	0.046	-1.955	0.098
	<i>Megachile</i>	0.107	0.055	1.933	0.125
	<i>Osmia</i>	-0.175	0.08	-2.189	0.094
	<i>Trypoxylon</i>	-0.025	0.027	-0.923	0.391
Edge density	<i>Auplopus</i>	0.03	0.02	1.523	0.188
	<i>Dipogon</i>	-0.002	0.004	-0.51	0.628
	Eumeninae	-0.008	0.005	-1.668	0.146
	<i>Hylaeus</i>	-0.015	0.011	-1.341	0.228
	<i>Megachile</i>	0.03	0.013	2.227	0.09
	<i>Osmia</i>	-0.038	0.01	-3.659	<b>0.022</b>
	<i>Trypoxylon</i>	-0.009	0.005	-1.99	0.094

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572 B) Woodland

<b>Metric</b>	<b>Group</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
Proportion	<i>Auplopus</i>	-0.076	0.106	-0.717	0.505
	<i>Dipogon</i>	0.028	0.015	1.908	0.105
	Eumeninae	0.047	0.013	3.465	<b>0.013</b>
	<i>Hylaeus</i>	0.107	0.029	3.674	<b>0.01</b>
	<i>Megachile</i>	-0.104	0.053	-1.947	0.123
	<i>Osmia</i>	0.169	0.074	2.275	0.085
	<i>Trypoxylon</i>	0.018	0.024	0.721	0.498
Edge density	<i>Auplopus</i>	-0.005	0.022	-0.224	0.832
	<i>Dipogon</i>	0	0.004	-0.013	0.99
	Eumeninae	-0.005	0.004	-1.03	0.343
	<i>Hylaeus</i>	0.003	0.011	0.255	0.807
	<i>Megachile</i>	0.013	0.01	1.341	0.251

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<i>Osmia</i>	-0.028	0.014	-2.045	0.11
<i>Trypoxylon</i>	-0.011	0.003	-3.504	<b>0.013</b>

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575 **Table 4:** Results of linear regression models testing for the relationship between the  
576 proportion and edge density of A) grassland and B) woodland within 250 m around the eight  
577 study sites and the mean number of *Dipogon* (Dip) and *Trypoxylon* (Try) spider prey per nest.  
578 Only representatives of those spider families were included in the analyses, which were more  
579 frequent and occurring at the majority of sites. The Shannon's Diversity Index of *Trypoxylon*  
580 (Try) spider prey at each site, which was calculated based on the total number of preyed  
581 spiders, was also included in this analysis. In this case, representatives of all spider families  
582 were included. Since the diversity of *Trypoxylon* spider prey was significantly autocorrelated,  
583 we also used generalized least squares fits ('gls') by REML from the R package 'nmle'  
584 (Pinheiro et al. 2020) incorporating an exponential correlation structure in their case.  
585 Significant relationships are marked bold.

586 A) Grassland

Metric	Family	Estimate	Std. Error	t value	Pr(> t )
Proportion	Araneidae (Try)	-0.128	0.069	-1.840	0.115
	Linyphiidae (Try)	0.012	0.046	0.270	0.798
	Theridiidae (Try)	0.075	0.032	2.329	0.067
	Thomisidae (Dip)	-0.004	0.019	-0.198	0.851
	Diversity (Try)	0.027	0.007	3.783	<b>0.009</b>
	Diversity (Try) - gls	0.021	0.004	5.765	<b>0.001</b>
Edge density	Araneidae (Try)	-0.010	0.018	-0.570	0.589
	Linyphiidae (Try)	-0.002	0.011	-0.150	0.887
	Theridiidae (Try)	0.001	0.009	0.152	0.885
	Thomisidae (Dip)	0.000	0.004	0.091	0.931
	Diversity (Try)	0.005	0.002	2.221	0.068
	Diversity (Try) - gls	0.004	0.002	2.004	0.091

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588 B) Woodland

Metric	Family	Estimate	Std. Error	t value	Pr(> t )
Proportion	Araneidae (Try)	0.080	0.070	1.137	0.299
	Linyphiidae (Try)	-0.007	0.040	-0.182	0.863
	Theridiidae (Try)	-0.045	0.029	-1.529	0.187
	Thomisidae (Dip)	0.013	0.016	0.775	0.473
	Diversity (Try)	-0.027	0.004	-7.005	<b>0.000</b>

	Diversity (Try) - gls	-0.026	0.004	-5.767	<b>0.001</b>
Edge density	Araneidae (Try)	-0.010	0.016	-0.646	0.542
	Linyphiidae (Try)	-0.005	0.013	-0.419	0.693
	Theridiidae (Try)	0.002	0.007	0.233	0.825
	Thomisidae (Dip)	0.002	0.003	0.644	0.548
	Diversity (Try)	0.002	0.002	0.829	0.439
	Diversity (Try) - gls	0.001	0.002	0.794	0.457

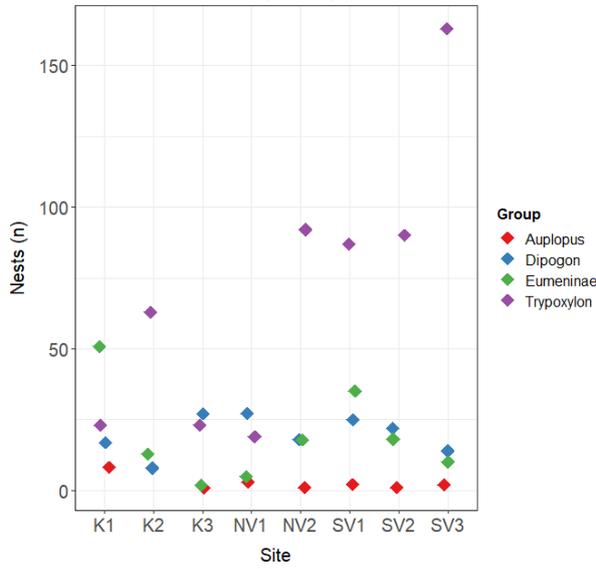
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590 **Figures**

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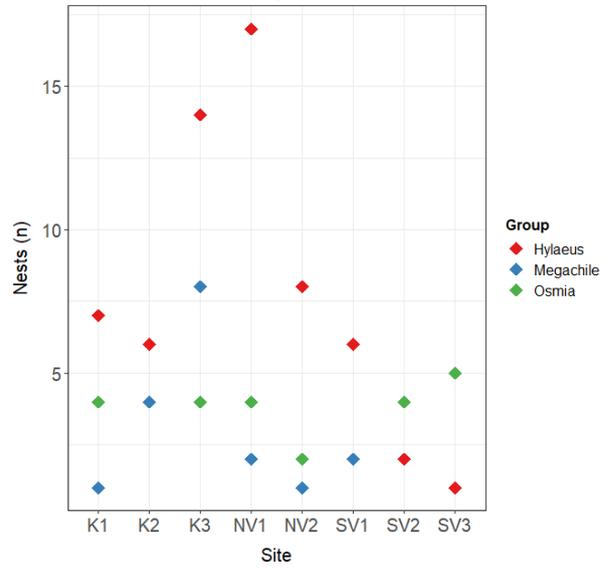
A)

Solitary wasps



B)

Solitary bees



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602 **Fig. 1.**

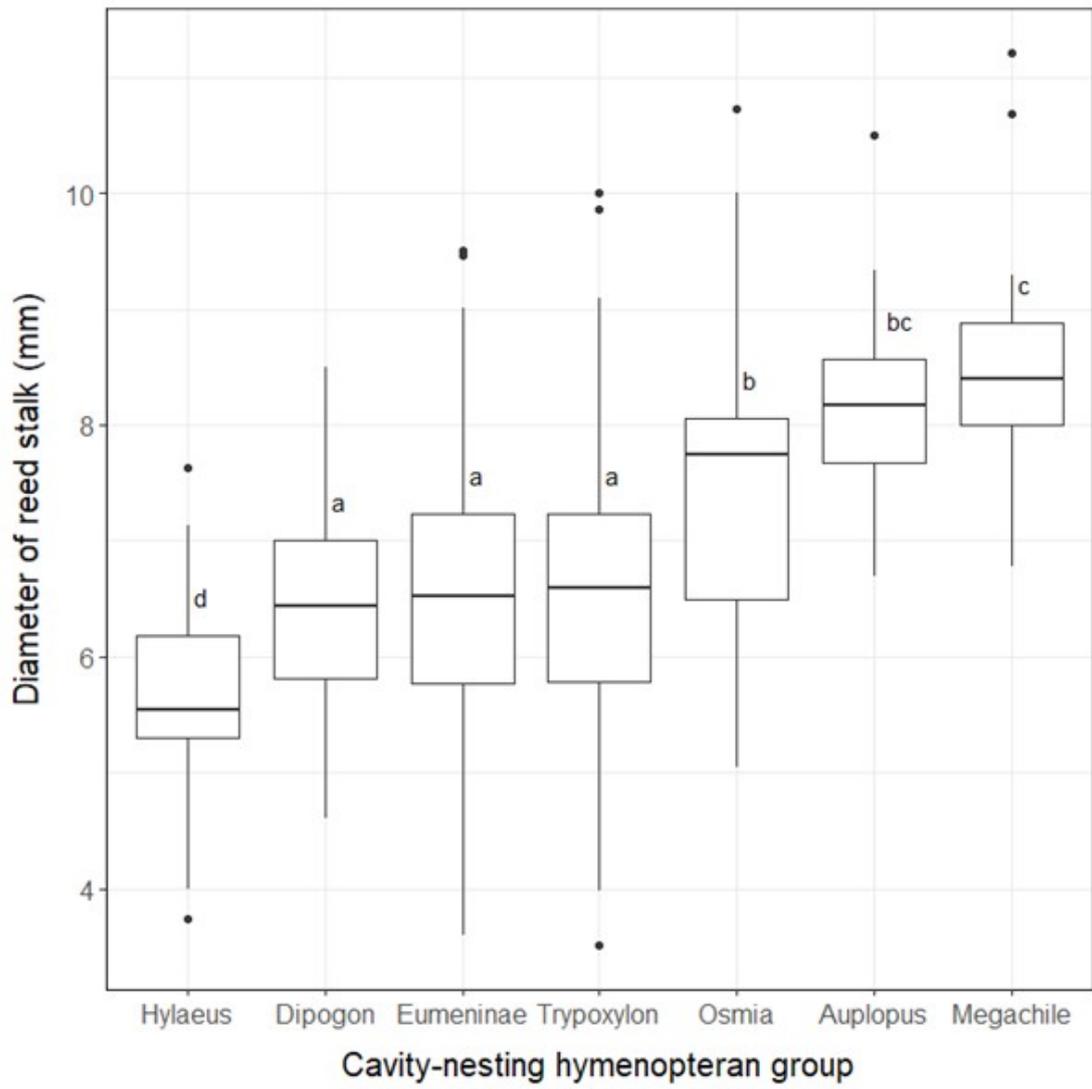
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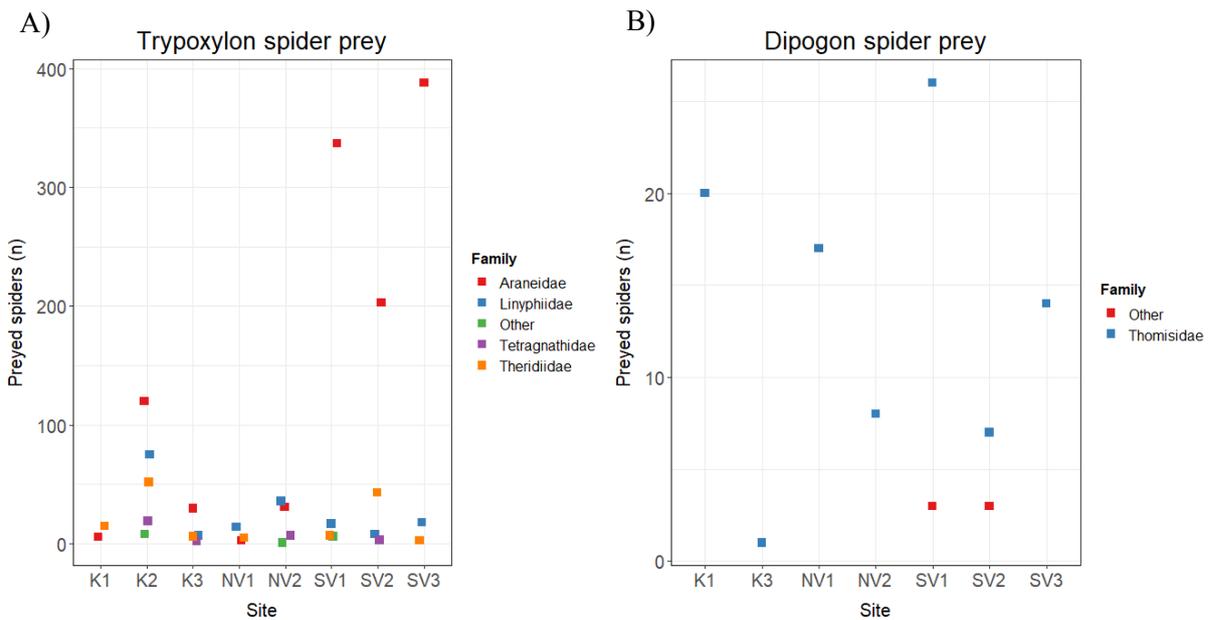


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609 **Fig. 2.**

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**Fig. 3.**

**Figure legends**

**Fig. 1:** Total number of nests per site in case of the hymenopteran groups of A) solitary wasps and B) solitary bees.

**Fig. 2:** Diameter of the reed stalks with nests for the seven cavity-nesting hymenopteran groups. The horizontal lines indicate the median value. The lower and upper whiskers represent the maximum values of the data that are within 1.5 times the interquartile range under the 25th and over the 75th percentile, respectively. Outlier values, indicated by black dots, are any values under or over this range. Same letters indicate no statistical differences between groups (Tukey’s HSD test,  $p < 0.05$ ).

**Fig. 3:** Total number of preyed spiders from different families per site, preyed by the two predatory wasp groups of A) *Trypoxylon* and B) *Dipogon*.