

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

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Running headline: Landscape effects on cavity-nesting hymenopterans

Abstract

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

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

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

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

Introduction

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

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

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

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

Methods

Study area

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

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

Study sites and sampling

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

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

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

Landscape context

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

Statistical analyses

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

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

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

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

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

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

Results

Nests

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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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.

Group	Estimate	Std. Error	t value	Pr(> t)
<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

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

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

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	0.046
	<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

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

A) Grassland

Metric	Group	Estimate	Std. Error	t value	Pr(> t)
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	0.005
	<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	0.022
	<i>Trypoxylon</i>	-0.009	0.005	-1.99	0.094

B) Woodland

Metric	Group	Estimate	Std. Error	t value	Pr(> t)
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	0.013
	<i>Hylaeus</i>	0.107	0.029	3.674	0.01
	<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

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

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

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	0.009
	Diversity (Try) - gls	0.021	0.004	5.765	0.001
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

B) Woodland

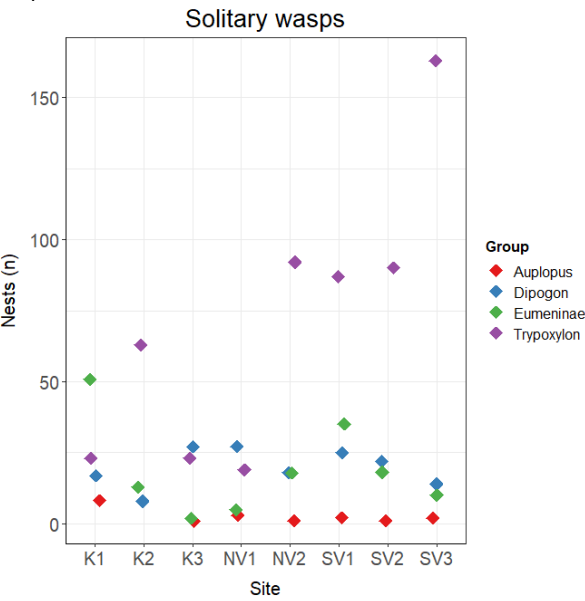
Metric	Family	Estimate	Std. Error	t value	Pr(> t)
Proportion	Araneidae (Try)	0.080	0.070	1.137	0.299
	Linyphiidae (Try)	-0.007	0.040	-0.182	0.863
	Theridiidae (Try)	-0.045	0.029	-1.529	0.187
	Thomisidae (Dip)	0.013	0.016	0.775	0.473
	Diversity (Try)	-0.027	0.004	-7.005	0.000

	Diversity (Try) - gls	-0.026	0.004	-5.767	0.001
	Araneidae (Try)	-0.010	0.016	-0.646	0.542
	Linyphiidae (Try)	-0.005	0.013	-0.419	0.693
Edge	Theridiidae (Try)	0.002	0.007	0.233	0.825
density	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

589

Figures

A)



B)

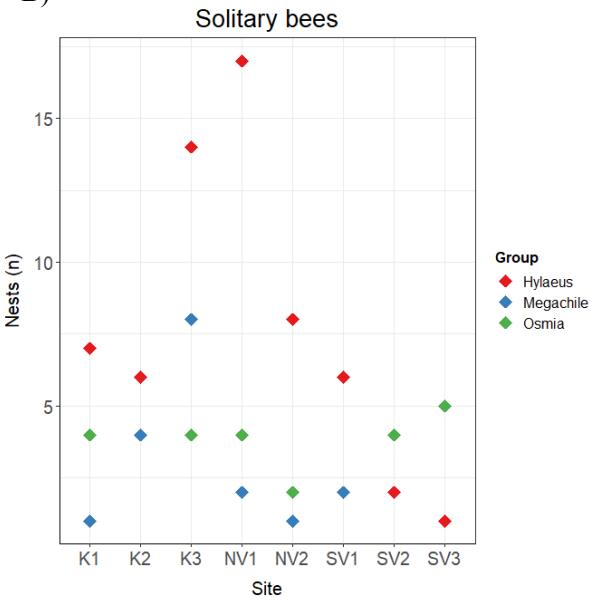


Fig. 1.

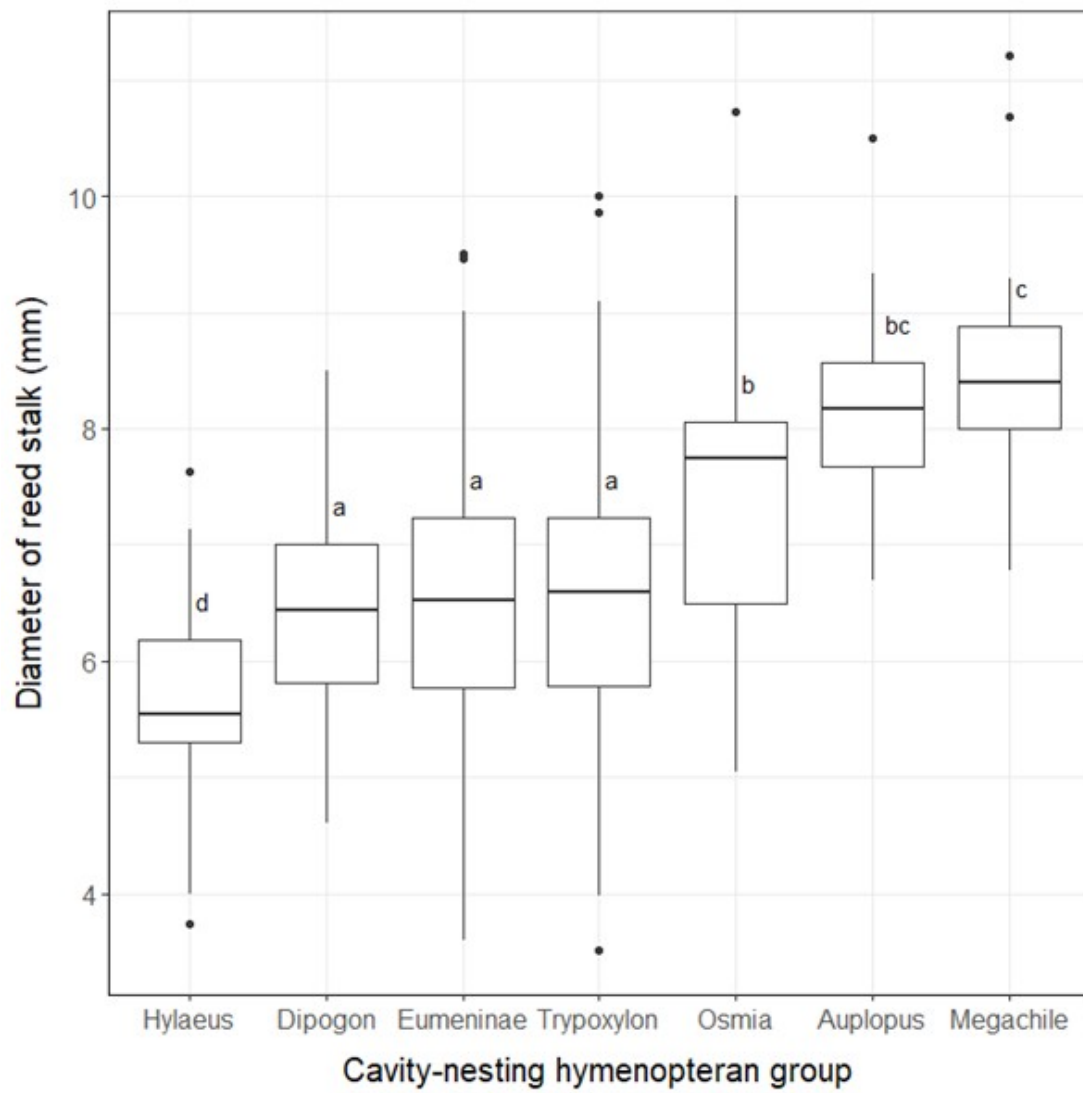


Fig. 2.

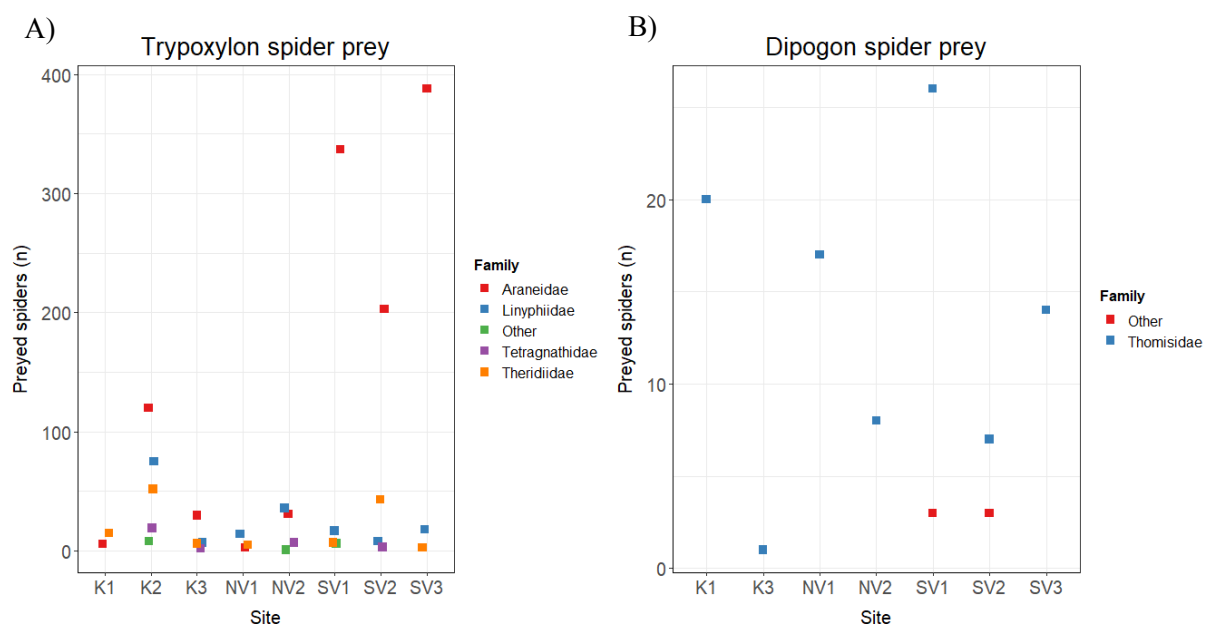


Fig. 3.

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*.