

Nesting activity of cavity-nesting bees and wasps is lower in small-scale apple orchards compared to nearby semi-natural habitats

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- Abstract**
- 1 Commercially reared cavity-nesting bees have been studied mainly in large, intensively managed orchards. However, knowledge on wild cavity-nesting bee and wasp communities and their potential limitations in smaller orchards remain insufficient.
 - 2 We compared the colonization rate of trapnests, nesting success, parasitism and response to flower resources of cavity-nesting bees and wasps between apple orchards and nearby semi-natural habitats (SNHs).
 - 3 Trapnests were placed in orchards and neighbouring SNHs. Colonization dynamics were studied and herbaceous flower resources were estimated. Furthermore, nest and brood cell quantity, number of alive offspring and nest parasitism rate were assessed.
 - 4 We found a higher colonization rate in the SNHs than in the orchards. Both bees and wasps made more nests, completed more brood cells and had a higher number of alive offspring in the SNHs. The number of bee nests in the orchards showed a positive correlation with the species richness of the flowering plants. The nest parasitism of wasps was higher in the SNHs.
 - 5 Apple orchards in the studied small-scale system were generally less colonized by cavity-nesting hymenopterans than nearby SNHs that can be important reservoirs of these ecosystem service provider hymenopterans. Our results highlight the importance of diverse flowering herbaceous vegetation in the understory that increased the number of bee nests in orchards and that could have a positive effect on the nesting activity of the bee species active in summer. Therefore, management practices that support flowering plant species in the understory vegetation are highly recommended in such orchards.

Keywords agroecosystems, cavity-nesting hymenopterans, nest parasites, pollinator, semi-natural habitat, trapnest.

Introduction

Cavity-nesting hymenopterans that is bee and wasp species that nest in holes above the ground in plant stems or dead wood are essential to agricultural ecosystems. Cavity-nesting bees in the wild, as well as commercial species (Maeta, 1990; Bosch, 1994; Koh *et al.*, 2018), are excellent pollinators for plants (Vicens & Bosch, 2000; Ladurner *et al.*, 2004) including fruit and nut

crops in the Palearctic and Nearctic regions (Bosch & Blas, 1994; Tepedino *et al.*, 2007; Sedivy & Dorn, 2014). Such wild pollinator species among others can pollinate many crops such as fruit trees more successfully than honey bees due to their morphological and behavioural diversity and complementary environmental tolerance (Bosch & Blas, 1994; Thomson & Goodell, 2001; Winfree *et al.*, 2008; Brittain *et al.*, 2013; Garibaldi *et al.*, 2013) leading to more stable and successful pollination (Garibaldi *et al.*, 2013; Földesi *et al.*, 2016). Cavity-nesting wasps (apoid wasps in the Crabronidae family (Sann *et al.*, 2018) and members of the Vespoidea superfamily in e.g. Pompilidae and Vespidae families) can be effective predators of other insects including

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pest caterpillars (Harris, 1994), aphids and weevils (Tschamtké *et al.*, 1998). On the other hand, some species feed on spiders (Fabian *et al.*, 2013). Natural enemies (predators and nest parasites) of cavity-nesting bees and wasps and the consequent mortality supplement the bioindicator value of the cavity-nesting communities with further information on the ecosystem's health (Tschamtké *et al.*, 1998). Therefore, promoting and preserving the diversity and abundance of cavity-nesting hymenopterans in orchards has high ecological and economic importance (Garratt *et al.*, 2013, 2014).

The distribution and ecology of the cavity-nesting species in orchards have been studied well in intensively managed regions (Sheffield *et al.*, 2008, 2013; Guisse & Miller, 2011; Kraemer *et al.*, 2014; Mallinger *et al.*, 2016). Since the increased need for wild pollinators obviously could not be fulfilled in large industrial orchards by wild bee communities, even the commercial rearing of some mason bee (Megachilidae: *Osmia* spp.) species has become essential (Bosch, 1994; Maccagnani *et al.*, 2003; Artz *et al.*, 2013; Koh *et al.*, 2018). However, knowledge on these bee species, their associated communities and their potential limitations in smaller Central Eastern European orchards are still lacking. It is not known whether these orchards harbour cavity-nesting bee and wasp communities similar to the adjacent semi-natural habitats (SNHs) or whether they need additional help and targeted measures to enhance fruit production from these beneficial insects.

The diversity and abundance of wild bees and wasps in orchards are significantly dependent on the local conditions and the surrounding landscape (Fabian *et al.*, 2013; Sheffield *et al.*, 2013). Intensive agricultural management (i.e. intensive use of pesticides, mineral fertilizers and removal of non-cultivated plants by herbicides) might directly kill native hymenopterans or cause subtle effects by reducing the availability of food and nesting resources (Kovács-Hostyánszki *et al.*, 2011; Gill *et al.*, 2012; Kennedy *et al.*, 2013). Cavity-nesting bees and wasps require standing herbaceous vegetation or dead wood for nesting that is often limited in managed orchards (Sheffield *et al.*, 2013). SNHs provide more suitable foraging and nesting resources for bees and wasps, and a more heterogeneous landscape often enhances their diversity and abundance within the orchards (Brittain *et al.*, 2010; Fabian *et al.*, 2013; Sheffield *et al.*, 2013; Földesi *et al.*, 2016; Mallinger *et al.*, 2016; Kovács-Hostyánszki *et al.*, 2017).

In our study, we investigated cavity-nesting bees, wasps and their parasitism rate in apple orchards and compared them with that of nearby SNHs to assess differences between the two habitat types and the potential limitations of such communities in the managed ecosystems. Apple (*Malus domestica* Borkh.) is one of the most important orchard crops in Europe, accounting for 16% of the European Union's total economic gains attributed to insect (particularly bee) pollination (Leonhardt *et al.*, 2013). It is significantly dependent on cross-pollination that is mostly assured by honey bees (Garratt *et al.*, 2013, 2014). However, some wild bee species, especially the cavity-nesting mason bees are more effective pollinators of apple (Maeta, 1990; Bosch & Blas, 1994). In fact, a higher diversity of wild pollinators in orchards was found to correlate with a higher fruit set of apple (Földesi *et al.*, 2016). While cavity-nesting wasps have been sampled in previous studies along with bees (Tschamtké

et al., 1998; Steffan-Dewenter, 2003; Fabian *et al.*, 2013), their communities and nesting success in apple orchards seem to be rather unexplored so far. We selected apple orchards of typical size and management in the study region in a rather heterogeneous landscape. We studied the dynamic of nest construction and nesting success in terms of cavity-nesting hymenopterans in trapnests. This also indicates the progression and general amount of available food resources (flowers and preys) within the studied habitats from time to time over the season as well as the phenology of how different hymenopteran species/genera reproduce at different times of the year (Klein *et al.*, 2006; Taki *et al.*, 2008). Similarly, we assumed that the number of nests can indicate cavity-nesting bee and wasp abundance and/or diversity to some extent. Furthermore, the number of brood cells might reflect habitat and food resource conditions at an individual level. We addressed the following questions: (i) To what extent do the dynamics of nest construction by cavity-nesting bee and wasp communities differ in apple orchards compared to adjacent SNHs from spring to early autumn? (ii) To what extent does the number of nests, brood cells built-in artificial nest structures by cavity-nesting bees and wasps and the number of alive offspring differ in apple orchards compared to the SNHs? (iii) How does the parasitism rate of colonized reed stems differ between habitat types? (iv) How does the number of nests, brood cells and alive offspring of cavity-nesting bees correlate with foraging resource characteristics such as species richness of flowering plants and flower abundance?

Materials and methods

Study area

The study was conducted in eight apple orchards in Northern Hungary and their neighbouring SNH pairs (for coordinates see Supporting information, File S1). The landscape structure in the study area is rather heterogeneous, including smaller agricultural fields, orchards, scattered woodlots, treelines and open SNHs (abandoned berry plantations and grasslands). The region has a moderately cool (average annual temperature 8–10 °C) and moderately humid (average annual precipitation 600–750 mm) climate. It is bordered by the Danube and Ipoly rivers with the Börzsöny mountains in the centre and has a primarily deciduous forest cover. Fruit production has substantial economic importance in the region due to which there are numerous orchards, mostly apple. The studied apple orchards were mainly under conventional management (farmers used pesticides following the requirements of Integrated Pest Management (IPM) and artificial fertilizers), while one of them applied organic farming practices (although in terms of the management, we found no significant bias with and without the single organic farm in the dataset; see Supporting information, File S2). There was herbaceous ground vegetation between the rows in all orchards. The average size of orchards was 19 ± 21.31 (SD) ha, and they were planted around 20 years ago (Supporting information, File S1). Based on our GIS (Geographic Information System) analyses using the Corine Land Cover database, the average percentage of SNHs (mostly grasslands and more open, shrubby habitats) was 13.84 ± 11.10 without and 19.16 ± 15.57

including the deciduous forests in a 500 m radius around the orchards.

Close to each orchard, we assigned an SNH as a control site. These were open herbaceous habitats and each of them adjacent to a woody habitat (forest fragments). The average distance (\pm SD) between the edge of the apple orchards and the edge of SNH control sites was 390.12 ± 252.44 m (min. 112 m, max. 789 m) (Supporting information, File S1). These were appropriate distances to sample distinct cavity-nesting bee communities based on average foraging distances (Gathman & Tschamtko, 2002).

Assessment of brood production of cavity-nesting bees and wasps

We sampled cavity-nesting bee and wasp species using trapnests. A pair of nesting blocks were positioned 50–70 m apart in the middle of each apple orchard [average distance from the orchard edge was 142.38 ± 58.39 m (mean \pm SD)] and two in the SNH control sites in herbaceous open vegetation close to a woody habitat [average distance from the SNH edge in direction to the orchard was 193.62 ± 161.81 m (mean \pm SD)]. The average distance (\pm SD) between the trapnests in the apple orchards and in the SNH control sites was 948.38 ± 358.16 m (min. 410 m, max. 1730 m). Each nesting block comprised two trapnests that is. PVC tubes (length: 200 mm, diameter: 100 mm) filled with reed stems (average of 140 reed stems per trapnest, min. 96, max. 219; similar numbers in both habitat types), open from both sides and mounted to a 120 cm high wooden pole. The inner diameter of reed stems varied between 2 and 11 mm, which was suitable for mason bees and other cavity-nesting hymenopteran species to build their nests (Tschamtko *et al.*, 1998; Westphal *et al.*, 2008).

In total, we placed 32 nesting blocks that is 64 trapnests in the sampling sites in March 2017. Field observations were made seven times during the vegetation period on first, 11th and 22nd April, 16th May, 17th June, 15th July and first September. On each occasion, we counted the number of colonized reeds that are those closed by mud or other nesting material at the end of the reed stem. The difference in the number of nests (i.e. closed reed stems) between the consecutive sampling occasions was calculated to follow the nesting dynamics. It has to be acknowledged that in the field and without disturbance, we could count only those nests, which were closed at the end of the reed stems, while other nests within the stems might have remained undiscovered. Therefore, our estimation about nesting dynamics could be only partial (see the Results section).

We estimated the available herbaceous flower resources around the nesting blocks at each sampling time when the number of finished nests was counted. The flower abundance (percent cover of actually blooming flowers) and the species richness of flowering herbaceous dicotyledonous plants were assessed in five 1 m \times 1 m quadrats 25 m apart along a permanent 100 m long transect adjacent to the nesting blocks (the transect connected the two nesting blocks and run over them in both directions a few metres). The flower community along the transects was generally similar to that of the rest of the orchard or SNH.

We collected all trapnests in the middle of September 2017 and stored them at 4 °C until January (Sheffield *et al.*, 2008;

Steffan-Dewenter & Schiele, 2008). Then we opened all (approximately 8200) reed stems and counted the number of nests and brood cells per trapnest and recorded whether live or dead offspring (adults, larvae or pupae), empty cells or cells with nest parasites could be found in the more than 16 000 internodes. It was also determined whether bees or wasps made them. Bee specimens overwintering as adults were identified at the species level (Móczár, 1958). All other pupae and larvae were identified at the genus/subfamily level as it was not possible to rear them to adulthood. Empty or parasitized nests were categorized based on the remaining larval food (i.e. pollen was categorized as bee cell, while spider or other prey as wasp cell), nesting material and parasitic species.

Statistical analysis

In order to follow the colonization of reed stems over time, we plotted the number of colonized reed stems using loess smoothed (local polynomial regression) trend lines, inbuilt in ggplot2 (Wickham, 2016) package, during the seven observation occasions within the apple orchards and the SNH separately.

We compared the number of nests (number of colonized reed stems after opening), brood cells (any brood cells within the nests) and the number of alive offspring between the apple orchards and the SNHs by Poisson generalized linear mixed models. Nest and brood cell data were pooled at the trapnest level; ‘habitat’ was used as an explanatory variable, ‘study site pair’ that is an investigated orchard and its neighbouring SNH pair, was used as a random factor. First, the data of bees and wasps were separately analysed. Subsequently, the number of nests of the three most abundant bee genera (*Osmia*, *Megachile*, *Hylaeus*), the two most abundant wasp genera (*Trypoxylon*, *Dipogon*) and Eumeninae wasp subfamily were investigated separately with the mixed models; observation-level random effects were introduced when high values of model overdispersion were calculated (Harrison, 2014). Moreover, basic model diagnostic plots were created to confirm the assumptions of residual normality and homoscedasticity (Faraway, 2016).

In the case of bees, we tested the correlation between the available flower resources (average flower abundance along the sampling period, April–September; the cumulative number of flowering herbaceous plant species, hereafter ‘species richness of flowering plants’) and the number of nests, brood cells and alive offspring, respectively. We used Pearson correlation and correlated the data from the apple orchards and SNHs separately. We also compared the average flower abundance and species richness of flowering plants among the orchards and SNHs using Welch’s two-sample *t*-tests.

The parasitism rate was calculated for each trapnest as the number of nests that contained at least one parasitized brood cell divided by the number of all nests in the trapnest, and this was compared between the apple orchards and the SNHs. A binomial generalized linear mixed model was used to analyse the bee data. In the case of wasps, we used the quasibinomial model because of the high number of 0 values. ‘Habitat’ was used as an explanatory variable and ‘study site pair’ was used as a random factor. In addition, model diagnostic plots were checked for model assumptions (Faraway, 2016).

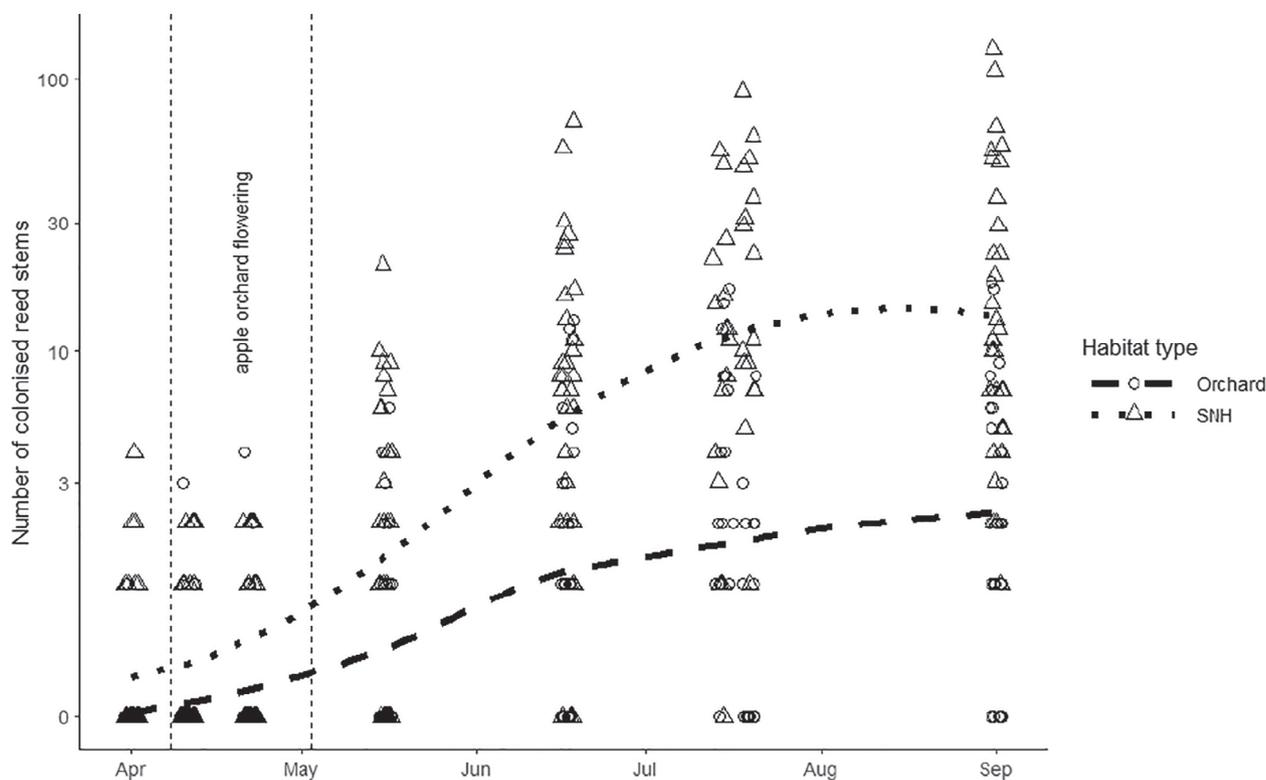


Figure 1 The number of colonized reed stems in apple orchards and semi-natural habitats during the vegetation period according to visual (non-invasive) counting with natural log-transformed y-axis scale; northern Hungary, 2017.

All analyses were conducted with R statistical software (R Core Team, 2018) and the lme4 (Bates *et al.*, 2015), lmerTest (Kuznetsova *et al.*, 2017) and ggplot2 (Wickham, 2016) packages.

Results

Colonization dynamic

We observed 926 colonisations (i.e. closed nests) in total during the seven observation occasions. Opening the nests later revealed that 54.5% of the nests (1698 in total) were visible from the outside and could be used to estimate the dynamic of colonization. During the on-field observations, the colonization of reed stems was continuous but showed different intensities in the different habitat types (Fig. 1). In the apple orchards, the colonization showed a steeper increasing intensity until mid-June and then a more moderate increase until the end of August. In the SNHs, colonization increased until the end of July. We found higher colonization during the entire season in the SNHs than in orchards.

Nesting communities

A total of 1698 nests were recorded; both smaller and larger diameter (from 2 to 11 mm) reeds were occupied. The brood cells' walls and entrance barriers were constructed mostly from mud or plant parts, but nests with membranous cellophane lining (made by *Hylaeus* spp.) or resin walls (made by *Heriades* spp.)

were also found. The 1698 nests contained 6313 brood cells in a total of which we could definitely classify 5641 brood cells in 1494 nests into two groups: made by bees or wasps. We identified 220 bee specimens (which were wintering as adults) at the species level (Supporting information, File S3). Essentially, 1–5 brood cells were made per nest, but some nests contained more than 10 cells (min. 1, max. 19, median: 3). Wasps made a slightly higher number of nests but fewer brood cells than bees. In both groups, the proportion of living offspring was more than half and the parasitism rate was nearly the sixth of the total brood cells (Supporting information, File S4). The rest of the brood cells were destroyed or empty and/or the offspring died without parasitism.

Both bees and wasps made significantly more nests in the SNHs than in the apple orchards (Table 1; Fig. 2(A); see Supporting information, File S4). Twenty percent of all nests (293) were made in orchards – 224 by bees and 69 by wasps. In the orchards, we found on average 4.39 ± 2.84 (mean \pm SD) brood cells per nest built by bees and 3.49 ± 2.05 brood cells per nest built by wasps. In the SNHs, there were on average 3.99 ± 2.29 brood cells per nest built by bees and 3.45 ± 1.98 brood cells per nest built by wasps. Separate analyses of the most abundant bee genera showed significantly more *Osmia* nests in the SNHs. We found no significant difference in the number of nests of the paired orchard–SNH sites in the case of *Megachile* and *Hylaeus* genera (Table 1). We found more nests built by wasps of the *Trypoxylon* and *Dipogon* genera and the Eumeninae subfamily in the SNHs than in the apple orchards. The number of brood

Table 1 Summary table of general linear mixed models testing the effects of habitat type (apple orchards vs. semi-natural habitats) on the number of nests, brood cells and alive offspring of cavity-nesting bees and wasps and parasitized nest rate of cavity-nesting bees

Response	Taxon	Fixed effect (habitat)				AIC	Random effect (study site pair) variance	Model family
		Estimate	SE	z-Value	P-value			
No. nests	Bees	0.823	0.079	10.29	<0.001	560.2	0.244	Poisson
	<i>Osmia</i>	1.543	0.262	5.9	<0.001	348.8	0.321	Poisson+OLRE
	<i>Megachile</i>	-0.37	0.237	-1.56	0.119	184.7	0.525	Poisson
	<i>Hylaeus</i>	-0.656	0.375	-1.75	0.079	224.5	0.099	Poisson+OLRE
	Wasps	2.303	0.126	18.28	<0.001	864.1	0.268	Poisson
	<i>Trypoxylon</i>	3.266	0.561	5.82	<0.001	321.6	1.77e-06	Poisson+OLRE
	<i>Dipogon</i>	2.398	0.39	6.15	<0.001	170.4	0.292	Poisson
	Eumeninae	1.392	0.019	731.3	<0.001	159.6	0.587	Poisson+OLRE
No. brood cells	Bees	0.725	0.039	18.65	<0.001	1616.8	0.266	Poisson
	Wasps	2.287	0.067	33.855	<0.001	2803.1	0.345	Poisson
No. alive offspring	Bees	0.712	0.051	13.88	<0.001	1309.9	0.300	Poisson
	Wasps	2.432	0.097	24.934	<0.001	1527.4	0.480	Poisson
Parasitized nest rate	Bees	0.193	0.623	0.31	0.756	70.5	0	Binomial

cells (Fig. 2(B)) and the number of alive offspring (Fig. 2(C)) were higher in the SNHs in both bees and wasps (Table 1).

Both the species richness of flowering plants ($t = -4.12$, $df = 13.06$, $P = 0.001$) and the average flower abundance ($t = -2.99$, $df = 11.83$, $P = 0.011$) were higher in the SNHs compared to the orchards. In the apple orchards, the species richness of flowering plants showed a significant positive correlation with the number of bee nests ($R = 0.826$, $P = 0.011$) (Fig. 3(A)), a non-significant positive correlation with the number of brood cells ($R = 0.620$, $P = 0.101$) and no correlation with the number of alive offspring of bees ($R = 0.311$, $P = 0.453$). In the SNHs, the species richness of flowering plants showed a non-significant negative correlation with the number of bee nests ($R = -0.677$, $P = 0.065$) (Fig. 3(A)) and the number of brood cells ($R = -0.694$, $P = 0.056$) and a significant negative correlation with the number of living offspring ($R = -0.744$, $P = 0.034$). We found relatively strong but non-significant positive correlation between the flower abundance and the number of nests ($R = 0.686$, $P = 0.060$) and a non-significant relationship with the number of brood cells ($R = 0.589$, $P = 0.124$) and with the alive offspring of bees in the apple orchards ($R = 0.475$, $P = 0.235$). No significant correlation was found between the nesting success variables and the flower abundance in the SNHs (no. nest: $R = 0.311$, $P = 0.454$; no. brood cells: $R = 0.229$, $P = 0.585$; no. living offspring: $R = 0.156$, $P = 0.712$) (Fig. 3(B)).

Nest parasitism

From the 1494 nests, 465 (31%) were parasitized. Nest parasite species showed relatively high diversity and caused damage in different ways. The majority of parasitized nests (87.3%) were damaged by the five most common nest parasite species: *Melittobia acasta* (Walker) (Hymenoptera: Eulophidae), *Sapyga quinquepunctata* (Fabricius) (Hymenoptera: Sapygidae), *Chrysura dichroa* (Dahlbom) (Hymenoptera: Chrysididae), *Trichodes apiarius* (Linnaeus) (Coleoptera: Cleridae) and *Cacoxenus indagator* Loew (Diptera: Drosophilidae) (Supporting information, File S5). In addition, we found dermestids (Coleoptera: Dermestidae), mites (Acarina: Chaetodactylae), *Anthrax anthrax* Schrank

(Diptera: Bombyliidae) bee-flies and other fly species (Diptera) in the nests. The nest parasites were identified as adults, pupae or larvae or were based on the remaining characteristic faces or exuvials using photo documentation, expert guidance (Tibor Bukovinszky) and additional literature (Kronic *et al.*, 2005).

The rate of nest parasitism was higher in the SNHs than in the apple orchards in the case of wasps ($df = 45$, $F = 11.9256$, $P < 0.001$; Fig. 2(D)). We found no difference in parasitism between the two habitat types in the case of wild bees (Table 1, Fig. 2(D)). Among the most common nest parasite species, *C. indagator*, a cleptoparasitic fly occurred mostly in *Osmia* nests in the SNHs. Cleptoparasitic wasps such as *S. quinquepunctata* and *C. dichroa* were found in the nest of Megachilidae and wasp species both in the SNHs and orchards. *M. acasta* parasitized a wide spectrum of bee and wasp nests mostly in the SNHs but also occurred in the orchards. *T. apiarius* occurred almost exclusively in the SNHs and parasitized *Osmia* and other Megachilidae species. *Stelis phaeoptera*, a cleptoparasitic bee species, was found in *Osmia* nests.

Discussion

Wild bees and wasps are essential in agroecosystems due to their pollination and biological control services. Their abundance and diversity as well as their species composition, however, significantly depend on the available nesting and foraging resources. Our results suggest that even in a small-scale system that is in smaller orchards in a heterogeneous landscape, adjacent SNHs show a higher colonization rate and a higher number of cavity-nesting bees and wasp nests and brood cells compared to apple orchards.

Colonization dynamic and nesting preferences of cavity-nesting bees and wasps

Both cavity-nesting bees and wasps used the trapnests in large numbers to build their nests. Based on the repeated visual surveys, more nests were built in SNHs and almost continuously

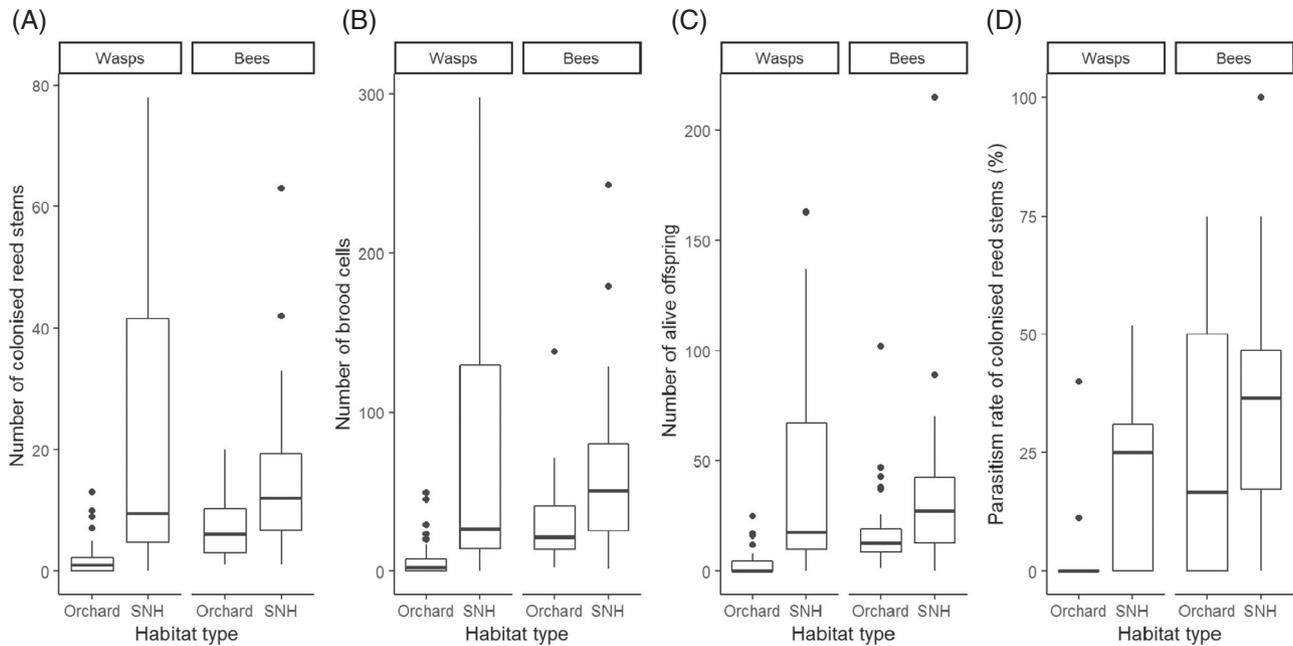


Figure 2 The number of colonized reed stems that is the number of nests (A), the number of brood cells (B), the number of alive offspring within the nests (C) and parasitism rate of nests (D) in apple orchards and semi-natural habitats made by bees and wasps assessed by dissection of the reed stems after the season.

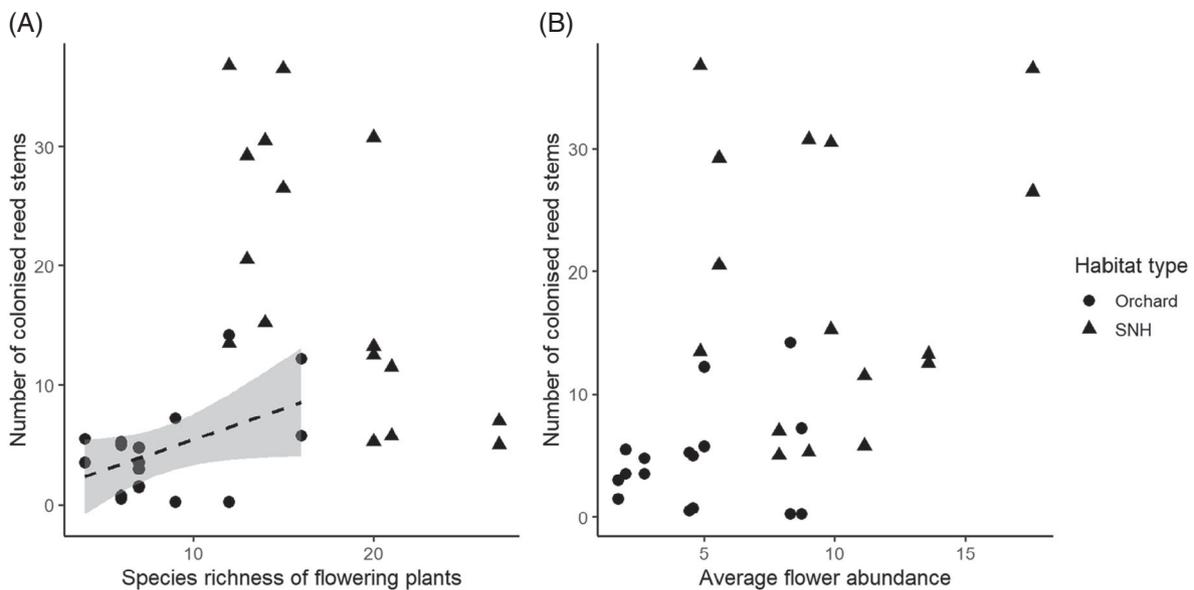


Figure 3 The correlation between the cumulative number of flowering plant species (A), the average flower abundance (B) during the sampling period and the number of reed stems colonized by bees in apple orchards and semi-natural habitats. Colonization was assessed by dissection of the reed stems. The linear trend line was also fitted for the significantly correlated orchard data points.

during the growing season. On the other hand, in apple orchards, a lower number of finished nests was observed, and from mid-summer, their number showed only a slight increase. The dissection of the reed stems underlined that both the bees and the wasps, in general, built significantly lower numbers of nests in the apple orchards compared to the SNHs. Moreover, there were fewer brood cells and fewer living offspring in the orchards than in the SNHs both in the case of bees and wasps.

The amount and availability of key resources such as food (nectar, pollen, arthropod preys), nesting place, nesting material and/or the agricultural management treatments can easily restrict the cavity-nesting bee and wasp communities within orchards (Westrich, 1996; Sheffield *et al.*, 2008). Regarding bees, during the apple flowering period, orchards offer mass amounts of pollen and nectar that could boost the nesting activity of bees to some extent. However, this period lasts only one to two

weeks, and alternative food resources are needed before and after within the orchards or nearby SNHs to maintain wild pollinator diversity and abundances (Williams & Kremen, 2007; Kraemer *et al.*, 2014; Mallinger *et al.*, 2016). Our results underlined this hypothesis as we found a strong positive correlation between the species richness of flowering plants and the number of bee nests in the orchards, suggesting a higher abundance and/or diversity of cavity-nesting bee species in the orchards in the case of diverse understory vegetation. However, the relatively species-poor and mown understory vegetation in and between the rows of apple trees, often treated by herbicides, often does not provide permanent and sufficiently diverse nectar and pollen resources during the vegetation period (Williams & Kremen, 2007; Földesi *et al.*, 2016). This could lead to lower species richness and diversity of bees and therefore a lower nesting activity, but it can also result in lower nesting success showing a lower number of brood cells and fewer alive offspring (Potts *et al.*, 2003, 2004; Müller *et al.*, 2006). In contrast, the higher availability of flower resources found in the SNHs could sustain more diverse, abundant and stable wild bee communities (Potts *et al.*, 2003; Ebeling *et al.*, 2008), and therefore, higher and more consistent nesting activity (Müller *et al.*, 2006). Interestingly, the species richness of flowering plants correlated negatively with the number of living bee offspring in the SNHs, which could suggest other confounding limiting factors.

The higher observed colonization dynamics in the SNHs during the entire season could also be explained by the higher colonization of wasps, which built 10 times more nests in the SNHs than in the orchards based on the data of the dissected reed stems. Cavity-nesting wasps are important biological control agents of many crop pests and can be an indicator of predator-prey interactions (Tscharntke *et al.*, 1998). Their low nesting activity in orchards suggests that wasps probably suffer from the lack of diverse arthropod communities in the orchards where the application of insecticides reduces pest, predator and natural enemy arthropod abundances (Markó *et al.*, 2017). This scarcity in food resources seems to be an even stronger limiting factor for the wasps than for the bees based on their lower nest and brood cell number in orchards compared to bees. Moreover, as these wasps also forage on nectar as adults (while feeding their larvae with other arthropods), the lower nectar resources might be a limiting factor for the wasp communities similar to the bees (Kevan & Baker, 1983; Taki *et al.*, 2008). Therefore, wasps might face a double and probably synergistic forage limitation within the apple orchards.

The availability of nesting materials could also be a limiting factor for both taxa. The special nesting requirements of cavity-nesting species such as plant species providing pithy stems and the occurrence of pre-existing burrows probably played a key role in their generally lower colonization success in the studied orchards compared to SNHs (Potts *et al.*, 2005; Sheffield *et al.*, 2013). Conventional orchard management and the use of insecticides can negatively impact non-target organisms as well, including hymenopterans, thereby reducing their overall number, diversity and fecundity compared to the SNHs (Williams & Kremen, 2007; Sheffield *et al.*, 2013).

Nesting communities of cavity-nesting bees and wasps and their nest parasites

We found a significantly lower number of *Osmia* nests, brood cells and alive offspring in the orchards compared to the nearby SNHs. *Osmia* species are mostly active in spring and early summer (Móczár, 1958), and therefore, some of them can play a crucial role in apple pollination, proving to be even more effective than honey bees (Bosch & Blas, 1994; Vicens & Bosch, 2000; Ladurner *et al.*, 2004; Gruber *et al.*, 2011). From the six *Osmia* species found, *Osmia caerulescens* (Linnaeus) and *Osmia bicornis* (Linnaeus) seemed to be more abundant; both are polylectic and visit Fabaceae as well as other flowers. While the abundance of *O. bicornis* along with the also present *Osmia cornuta* (Latreille), the European orchard bee, is increased artificially by targeted measurements in several countries for efficient pollination in orchards (Kronic & Stanislavljevic, 2006; Gruber *et al.*, 2011; Sedivy & Dorn, 2014), they are abundant and widespread in Hungary (Józán, 2011). We suppose that these species here might easily and frequently colonize and/or visit the orchards from the nearby SNHs if suitable nesting and feeding resources are available. Therefore, provisioning early flower resources in the season can be critical for the *Osmia* species that emerge the earliest in spring. Former studies have found a higher number of *Osmia* nests and a higher reproduction success at the orchard edges compared to the interior (Sheffield *et al.*, 2008; Gruber *et al.*, 2011) and increased profit potential with the use of artificial nest boxes (Koh *et al.*, 2018). While it is usually easy to find mud as nesting material used also by the *Osmia* species even in orchards in eligible rainy conditions, nesting material could be limited for the species of more specific needs such as *Anthidium* spp. (plant hairs) and *Heriades* spp. (resin), which can explain their lower number of nests in our trapnests.

Leafcutter bees (*Megachile* spp.) and yellow-face bees (*Hylaeus* spp.) built a similar number of nests in the orchards and in SNHs. The primary activity period of the found *Megachile* species (*Megachile centuncularis* (Linnaeus) and *Megachile pilidens* Alfken) is from May to early autumn (Móczár, 1958), meaning that they cannot benefit from apple flowers. They might be rather a generalist, visiting a wide spectrum of wild and cultivar plant species, and perhaps more tolerant of modified environments (Móczár, 1958). The similar nesting activity of these bee genera between habitats suggests that apple orchards might offer flower resources during summer.

The cavity-nesting wasps *Trypoxylon*, *Dipogon* and *Eumeninae* species all had more nests, brood cells and living offspring in the SNHs and only a few in the orchards. *Trypoxylon* and *Dipogon* species are active hunters of spiders, therefore, their low nesting number within the orchards might indicate the low spider prey availability. As spiders are important predators of pests, they can provide important biological control services in the orchards (Markó *et al.*, 2009). However, as insecticide treatments eliminate pests, spider communities also decline, which shifts the balance of arthropod assemblages (Markó *et al.*, 2009) including predatory wasps. Adult *Eumeninae* wasps typically collect beetle larvae, spiders or caterpillars as food for their larvae. Therefore, their rare presence in the orchards has indicator values similar to the other cavity-nester wasps found in our study.

The nest parasitism rate was higher in the SNHs than in the apple orchards in the case of wasps, while no difference was

found in parasitism between the two habitat types in the case of bees. The parasitism rate can be enhanced by host density (Farzan, 2018) that can explain the higher parasitism rate of wasps in the SNHs where the number of wasp nests and brood cells was higher as well. Similar to our results, Tscharntke *et al.* (1998) found a higher parasitism rate of cavity-nesting hymenopterans in more natural environments where brood cells of cavity-nesting bees and wasps might be more exposed to some nest parasites than brood cells of bees in the managed orchard.

Conclusions

We can conclude that the apple orchards in the studied, relatively small-scale system are generally less colonized by cavity-nesting bees and wasps than nearby SNHs. The lower nesting activity of early active *Osmia* species might suggest that mass flowering of apple trees in a short period provides an insufficient foraging resource for cavity-nesting bees to increase their nesting activity in the orchards. In contrast, flowering herbaceous vegetation in the understory of fruit trees might be sufficient as we found a positive correlation between flower species richness and the number of bee nests in the orchards, and this might be responsible for the similar nesting activity of summer active *Megachile* and *Hylaeus* bee species than in the SNHs. Therefore, management practices that support flowering plant species in the understory vegetation are highly recommended in orchards. They have promising potential benefits in crop production according to previous studies (Taki *et al.*, 2008; Földesi *et al.*, 2016). The studied SNHs were found to be important reservoirs of these important ecosystem provider hymenopterans, especially cavity-nesting wasps that reached multiple nest/brood cell numbers there. These SNHs can be potential sources of distribution into/colonization of apple orchards by the cavity-nester species. Such spillover of cavity-nesting bees and wasps into apple orchards in the case of enhanced flower and nesting resources and low intensive management would be interesting for further research in the study system.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1. Geographic locations, area and year of the plantation of the studied apple orchards and the distance from their control semi-natural habitat pairs; closest settlements to the study site locations: 1–4: Berkenye, 5: Szob, 6: Ipolydamásd, 7: Vámosmikola, 8: Perőcsény. (Table)

File S2. Comparing the key findings of analyses with or without the data of the single organic orchard-SNH site pair.

File S3. Identified bee species from trapnets in the studied apple orchards, semi-natural habitats and their total number in 2017. The numbers of specimens indicate only the number of identified samples but do not represent the total number of nests. (Table)

File S4. The number of nests, brood cells, living offspring and parasitized brood cells made by cavity-nesting bees or wasps in the trapnets in 2017. The data shown are summarized for apple orchards and in semi-natural habitats separately. In the case of bees and wasps, the most abundant genera and subfamily are shown. (Table)

File S5. The number of different nest parasites in the nests of cavity-nesting bees and wasps in the orchards and semi-natural habitats and their summed number in 2017. (Table)

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