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Main pollinators of haskap (*Lonicera caerulea*: Caprifoliaceae) and the effect of different controlled methods of pollination on fruit set

Hlavní opylovatelé zimolezu (*Lonicera caerulea*: Caprifoliaceae) a vliv různých metod opylení na jeho výnos

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ABSTRACT

The fruit set of haskap is dependent on optimal pollination. Thus, the focus of this study was the effect of pollination in haskap (varieties Viola, Gerda, and Sinnaja ptica). The study aimed to verify the impact of different pollination methods on fruit harvest as well as identify the main bee pollinators and compare their significance. The percent fruit set, fruit weight, number of seeds per fruit, and percent fruit set in time order were compared for four treatments: free pollination, self-pollination, cross-pollination, and no manipulation. In general, the observed production parameters were better under the free pollination treatment. As the cross-pollination method was unable to maximise the fruit set and improve other production parameters, it is clear haskap has an entomophilous character. This proves that there is an obscure effect of pollinators on the effectiveness of pollination in haskap. The results regarding haskap bee pollinators suggest a preference by long-tongued bees belonging to *Bombus* spp. and *Apis mellifera*, even though short-tongued species of solitary bees were dominant in the haskaps' vicinity. Based on our results, *Bombus* spp. is the most suitable pollinator in Central European conditions. Other experiments have to be conducted to further clarify the reasons for low haskap productivity under isolation with cross-pollination.

Keywords: honeysuckle, hand pollination, *Apis mellifera*, *Bombus* spp.

ABSTRAKT

Výnos ovoce zimolezu závisí na optimálním opylení. Zaměřením této studie tedy bylo zjistitl vliv opylení zimolezu (odrůdy Viola, Gerda a Sinnaja ptica) na jeho výnos. Cílem studie bylo ověřit vliv různých metod opylování na výnos plodů, identifikovat hlavní včelí opylovatele a porovnat jejich význam. Byl porovnán vliv 4 různých způsobů opylení (volné opylení, umělé samosprášení, umělé cizosprášení a bez opylení). Byl hodnoceno: poměr zralých plodů, hmotnost plodů, počet semen na plod a rovnoměrnost dozrávání. Obecně byly pozorovány lepší výnosové parametry při volném opylení. Protože metoda cizosprášení nedokázala maximalizovat výnos a zlepšit ostatní výnosové parametry, je zřejmé, že zimolez má silně entomofilní charakter. To dokazuje, že existuje nejasný vliv opylovatelů na efektivitu opylení. Výsledky týkající se opylovatelů naznačují, že při opylení se uplatnily včely s dlouhým sosákem (*Bombus* spp. a *A. mellifera*), přestože v blízkosti porostů dominovaly krátkososákaté druhy samotářských včel. V podmínkách střední Evropy jsou nejvhodnějšími opylovateli čmeláci. Je však třeba provést další experimenty, aby se dále objasnily důvody nízkeho výnosu při cizosprášení.

Klíčová slova: zimolez, ruční opylení, včela medonosná, čmeláci

INTRODUCTION

The growing human population is increasing demands on agricultural production (Foley et al., 2011). There is concern regarding meeting the growing demand for food while protecting ecosystems and biodiversity (Brussaard et al., 2010; Perfecto and Vandermeer, 2010). Given the negative impact that agriculture has on biodiversity (Stoate et al., 2001), steps to increase production need to be in line with sustainable development and the environment (Beddington, 2010; Moudrý et al., 2018). One of the ways to increase crop production is to provide cultivated crops with optimal pollination and thus maximise the quality and quantity of a yield (Garratt et al., 2014). The optimal level of pollination can directly increase yields (Köpke and Nemecek, 2010) or the content of nutritionally and economically important substances in the fruit (Bommarco et al., 2012). Another factor that is often directly affected by pollination is the shape of the fruit, as is the case with strawberries (Żebrowska, 1998).

Lonicera caerulea var. *kamtschatica* is a slightly tall fruit shrub characterised by two-flowered inflorescences (Bozek, 2012). The flowers are tubular up to 2.5 cm long with a fused ovary. According to Bozek et al. (2012) and Frier et al. (2016b), a whole fruit is formed by the fusion of two berries and forming a co-formation that looks like one berry. Another specific feature of haskap is its tolerance to very low temperatures. The plant can withstand up to −40 °C, while flowers can endure up to −8 °C (Řezníček and Salaš, 2004). That allows for very early flowering, which usually lasts two to three weeks (Frier et al., 2016a). The ripening of the fruit also occurs very early, in the temperate zone, from the end of May to the beginning of June. The shape of the fruit and the time of its harvest depend on the characteristics of the variety (Bozek, 2012).

Haskap originated in the Northern Hemisphere, namely in Asia, Europe, and America (Frier et al., 2016a). However, it is spreading outside of this area as a result of its popularity, which is mainly due to the tasty blueberry-like fruits and potential health benefits it offers (Svarcova et al., 2007). Haskap fruits are a valuable source of important nutrients (e.g., anthocyanins, polyphenolic substances, vitamins and minerals) (Gazdik et al., 2008). Their consumption can help to prevent many chronic diseases, including cancer, cardiovascular disease, and diabetes mellitus (Svarcova et al., 2007).

Haskap is an attractive source of nectar and pollen for bees (Bozek, 2007; Bożek and Wieniarska, 2006), which suggests its entomophilic demands. This is confirmed by the specific composition of the fruit (double berry), the formation of which needs effective pollination of both flowers in the inflorescence, requiring specific pollinator behaviour (Bozek, 2012; Frier et al., 2016a; Woodcock et al., 2013).

The self-incompatibility of haskap has been confirmed by pollination experiments under open and isolated conditions (Bozek, 2012), as well as cyto-embryologically (Boyarskikh, 2017). For this reason, it is assumed that haskap requires cross-pollination of two compatible varieties (Bors et al., 2012).

However, for a comprehensive experimental investigation of pollination requirements, control pollination under isolation must be included in the experiment (Corbet et al., 1991). In addition to the influence of insect pollinators, this will also reveal the effects of foreign pollination and self-pollination, which have yet to be determined.

Solitary bees, *Bombus* spp. and honey bees are considered suitable pollinators for haskap (Bozek, 2007; Bożek and Wieniarska, 2006), with other pollinators having different efficiencies in pollinating its flowers (Frier et al., 2016a). In the early spring, when haskap blooms, many pollinators are not yet active or able to pollinate at such low temperatures (Frier et al., 2016a). In addition, changes in the composition of bee taxocenoses occur due to different climates (Ottosen, 1987). Given that the relationships between pollinators in connection with the pollination of haskap have not been fully investigated so far (Frier et al., 2016a), it is possible that some synergistic effect in pollination can exist among different taxons of bees (Brittain et al., 2013; Ryba et al., 2024). Thus, it is appropriate to identify pollinators that are essential for pollination (Leung and Forrest, 2019).

The main objectives of this research are to (i) compare fruit yields (i.e. the number of fruit, the average weight of fruit, the number of seeds per one fruit and ripening/harvesting process) after different pollination treatments (i.e. free pollination, self-pollination, cross-pollination and no manipulation), (ii) compare the composition of bee taxocenosis in the haskaps' vicinity with bee taxocenosis on haskap blossoms during the flowering period, (iii) determine the richness and abundance of bee pollinators (Hymenoptera: Apiformes) and (iv) assess their effectiveness and significance in pollination.

MATERIALS AND METHODS

Locations

The experiment was conducted in the spring of 2018 in Žabčice (South Moravian Region, Czech Republic) on the experimental farm of Mendel University. The locality is situated on a flat surface and has, on average, an altitude of 185 m and precipitation of 380–550 mm. The average annual temperature is over 10 °C. In addition to Žabčice, bee collections were also conducted in the foothills of the Bohemian-Moravian Highlands in Příbram in Moravia (South Moravian Region, Czech Republic) on the private haskap orchard. Hilly surfaces with an altitude of 440 m, precipitation of 516–612 mm, and annual temperatures over 7.5 °C on average dominate this area. The last observed locality was Lednice (South Moravian Region, Czech Republic) in a private haskap orchard. Flat surfaces with an altitude of 173 m, precipitation of 328–519 mm, and annual temperatures over 10 °C on average dominate this area.

Experimental design

Three varieties (Viola, Gerda and Sinnaja ptica) were chosen for this experiment. A soft paintbrush was used for hand pollination. Monitored branches were isolated by a textile net (organdy) to prevent insect pollination. The whole shrubs were covered by a plastic net before the fruits ripened. The observed flowers were indicated by a rainproof marker. With respect to their compatibility, Tomichka and variety Průhonický semenáč (wild seedling) were used for the pollination of the tested varieties (Boyarskikh, 2017).

The experiment was performed in accordance with the principles of Corbet et al. (1991). The following treatments were used: a) free pollination (unlimited access to pollinators), b) self-pollination (flowers pollinated with pollen from own shrub, under isolation), c) cross-pollination (hand-pollination by pollen from compatible pollinisers, under isolation) and d) no manipulation (without access to pollinators or hand-pollination, under isolation).

Each treatment (branch) and each variety (shrub) consisted of three replications (n = 3). One hundred flowers on each branch were indicated by a waterproof marker and included in the experiment. The blooming dates were as follows: 9. 4., 11. 4., 13. 4., 15. 4., 17. 4., 19. 4. and 22. 4. (2018). The fruits were harvested on the following dates: 8. 5., 11. 5., 14. 5., 16. 5., 18. 5. and 21. 5. (2018).

Evaluation of fruit yield

The percentage fruit set (%) was evaluated as a proportion of the number of created fruits and monitored inflorescences. For every harvest, the number of fruits (pcs), average fruit weight (g), and average number of seeds (pcs) were assessed. The fruits were weighed on laboratory scales with an accuracy of one thousandth of a gram. After weighing, each fruit was dissected, and the seeds in each individual fruit were counted. From the subtracted values, the average for individual treatments was determined for each variety separately.

Determination of bees present in the haskaps vicinity

In order to explore the spectrum of bee species in the areas (Žabčice, Lednice and Příbram na Moravě), Moericke traps were installed in and around the haskap culture. The traps were always placed between the observed shrubs, maintaining an average distance of 0.5 m from each shrub. For sampling, bees were collected by an entomological hand net in accordance with the Methods of Insect Collection and Preparation (Upton et al., 2010).

Determination of bees at the haskap blossoms

Species that pollinated the haskap were identified using by method of transect sampling (Petersen et al., 2013). Bee visits to haskap blossoms were assessed visually in three transects throughout each field.

The visits were visually observed in three repetitions on each locality once a week for three consecutive weeks, which comprised the majority of the blooming period (Petersen et al., 2013). The sampling of bees was realised between 08:00 and 17:00 (when flowers were open) during appropriate sunny weather. Pollination by bees was observed for a total of 10 minutes each by slowly walking around flowering bushes at 10:00, 12:00, 14:00, and 16:00 for each locality.

Assemblages of bees in the vicinity and at the haskap blossoms were established for all sites together. Following this, the lists of species (including bee species and families, their numbers, and dominance) were established for both communities.

The bee assemblages were divided into guilds (*A. mellifera*, *Bombus* spp., and solitary bees) and by tongue length (short-tongued bees and long-tongued bees).

The assemblages were compared with each other, and their similarities and attachment were determined depending on the affiliation to the guild or the length of the tongue.

The number of flowers visited per minute by bees was determined for *A. mellifera* and *Bombus* spp. An individual bee was observed when visiting the haskap flowers for as long as possible. The number of visited flowers was determined for all sites.

The flower constancy of *A. mellifera* and *Bombus* spp. was measured by determining pollen load composition. Several individuals belonging to *A. mellifera* and *Bombus* spp. were captured directly at the haskap blossoms (n = 30 individuals for both taxons). Pollen loads were removed from the corbiculae and stored dry in micro-centrifuge vials.

The pollen loads were put into 70% ethanol and shaken and mixed to disperse. The mixture of pollen and ethanol was filtered through filter paper (Whatman 1) in a Buchner funnel, subsequently dried and fixed on a microscope slide by a microscope (Nikon Eclipse E200, Prague, Czech Republic) using fuchsine gelatine following Dafni et al. (2005). Pollen grains were recognised and quantified according to Von Der Ohe et al. (2004).

Comparison of a number of flowers visited per day between A. mellifera and Bombus spp.

To calculate the average number of pollinated flowers (f-t), the following were determined: the attendance rate of the monitored guilds, the average number of visits by one bee per hour (a – n – v), øf/1h = average number of pollinated flowers per hour by one bee, the length of the working day (l – w – d).

For both *A. mellifera* and *Bombus* spp., the number of flowers visited per day was determined for each site separately. Following this, the average was given. The number of flowers visited per day was calculated as
(f – t) = (a – n – v) x øf/1h x (l – w – d).

Statistical analysis

The comparison of differences in species richness, abundance, and assemblage structure between the haskaps' vicinity and the haskap blossoms was based on a repeated sampling design. Therefore, repeated measures ANOVA with locality as a random variable was used for this analysis. The Wilcoxon test was used to compare the number of pollinated flowers per minute and the proportion of pollen in the pollen loads among bee guilds (*A. mellifera* and *Bombus* spp.). The differences in fruit yield parameters between pollination treatments were statistically analysed with a one-way ANOVA, and a post-hoc Tukey test was used to compare differences between pollination treatments. The percent fruit set was transformed by arcsin (x) to improve normality.

To compare the assemblage composition between the haskaps' vicinity and the haskap blossoms, partial canonical correspondence analysis (pCCA) with locality as a covariable was used. Bees were sampled sequentially along the growing season. Therefore, we maintained the time autocorrelation of individual records using cyclic shifts. The abundances of each species were transformed by a decimal logarithm. Randomisation was restricted by randomising time records within each locality separately using cyclic shifts. The significance of the canonical axis was tested with a restricted Monte Carlo permutation test for the time series with 2,000 permutations. To describe how the ecological traits were distributed between the haskaps' vicinity and the haskap blossoms, community-weighted means (CWMs) were calculated and passively displayed in an ordination diagram. CWMs were calculated as the mean trait value for each sample weighted by the relative abundance of the species sharing a given trait. The arrow direction in the ordination diagram indicates the occurrence of dominant trait values in the assemblages. All ordination analyses were conducted by the statistical software CANOCO, v. 5.

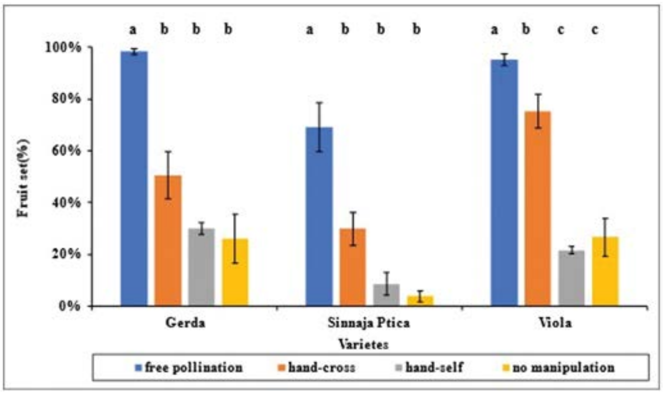
To reveal whether the species composition in the haskaps' vicinity determined the species assemblage at the haskap blossoms, we used co-correspondence analysis. This type of analysis relates two correspondence analyses to maximise covariance among them (ter Braak and Schaffers, 2004). Therefore, we were able to identify and test the patterns that were common to species assemblage in the haskaps' vicinity and at the haskap blossoms, and also whether haskap blossom assemblage was determined by bee assemblages in the haskaps' vicinity.

RESULTS

Yield

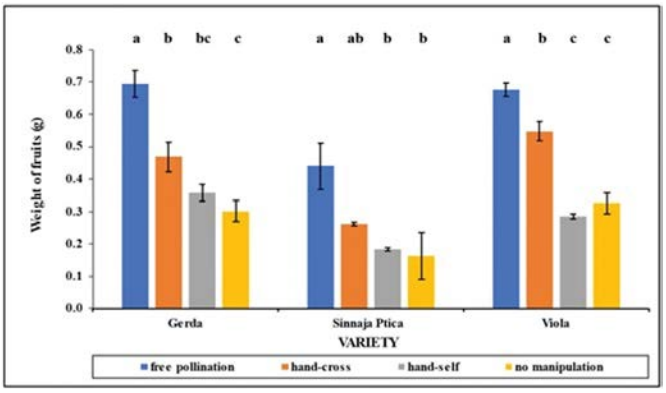
Differences in the percent fruit set are shown in Figure 1. The differences were highly significant in the case of all tested varieties: Gerda ($F_{3,8}$ = 41.99; *P*<0.001), Sinnaja ptica ($F_{3,8}$ = 18.88; *P*<0.001), and Viola ($F_{3,8}$ = 34.53; *P*<0.001). The significantly highest production was found under free pollination for all three varieties (Tukey test, *P*<0.05). Significant change between isolation treatments in fruit production was not observed in the varieties Gerda and Sinnaja ptica. However, a significant difference between treatments in isolation was observed in the case of the variety Viola, which reached the significantly highest yield under the cross-pollination treatment.

The differences in the fruit weight were highly significant in the varieties Gerda ($F_{3,8}$ = 22.12; *P*<0.001) and Viola ($F_{3,8}$ = 56.39; *P*<0.001), and the significantly heaviest fruits were recorded under free pollination treatment for both varieties (Tukey test, *P*<0.05) (Figure 2). The average fruit weight in the case of Viola under isolation was significantly higher only with the cross-pollination treatment. In the case of Gerda, only treatment without manipulation was significantly different from cross-pollination. Regarding Sinnaja ptica ($F_{3,8}$ = 15.64; *P*<0.001), heavier fruit was observed in the case of free pollination compared to other treatments, but only in the cases of no manipulation and self-pollination were the differences significant.



The Tukey test was used to determine differences in the fruit sets between pollination methods for each variety. Error bars represent a 95% confidence interval. Significant differences (*P* < 0.05) among treatments are indicated by different letters. A number of observed flowers per variety was n = 300.

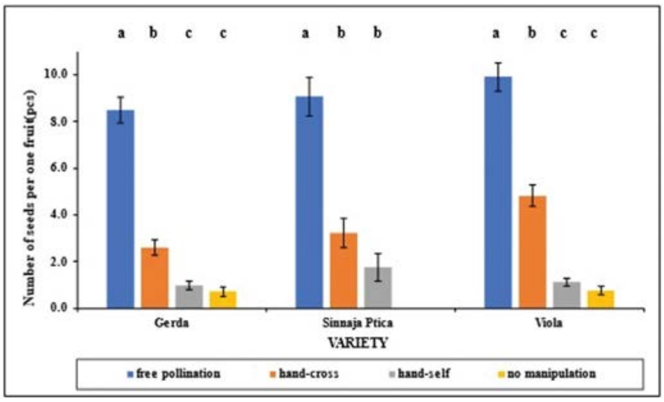
Figure 1. Percent fruit sets according to variety and pollination method



The Tukey test was used to determine differences in fruit weight between pollination methods for each variety. Error bars represent a 95% confidence interval. Significant differences (*P* < 0.05) among treatments are indicated by different letters. The number of weighted fruits per variety was n = 40.

Figure 2. Average weights of fruit according to variety and pollination method

Regarding the number of seeds per fruit, significant differences were observed between pollination methods. Figure 3 shows that the number of seeds was several times higher under free pollination than under cross-pollination for all observed varieties. Higher seed counts within isolated treatments have always been observed in cross-pollination, but only in the cases of Gerda and Viola were the differences significant (Tukey test, $P<0.05$). When comparing the self-pollination and no manipulation treatments, the average number of seeds in the case of self-pollination was higher for all varieties. In the case of Sinnaja ptica, no seed formation was even observed in the non-manipulation treatment.



The Tukey test was used to determine differences in the number of seeds between pollination methods for each variety. Error bars represent a 95% confidence interval. Significant differences ($P<0.05$) among treatments are indicated by different letters. The number of counted fruits per variety was n = 40.

Figure 3. Average number of seeds per fruit according to variety and pollination method

In free-pollinated plants, an earlier harvest was observed in all varieties (Figure 4). At the same time, the peak of harvest intensity (i.e., the highest set of fruits per harvest day) was observed on the first day of harvest for the varieties Sinnaja ptica and Gerda, and the variety Viola on the second day of harvest. For all varieties in the free pollination treatment, uniform ripening of the fruits was observed at the beginning of the harvest, when most of the fruits were harvested within the first two days. Harvest peaks in the hand-cross and hand-self-pollination treatments occurred later, and substantially less uniform ripening was observed. The most even fruit ripening was observed in the no manipulation treatment when the harvest was spread relatively evenly throughout the harvest period.

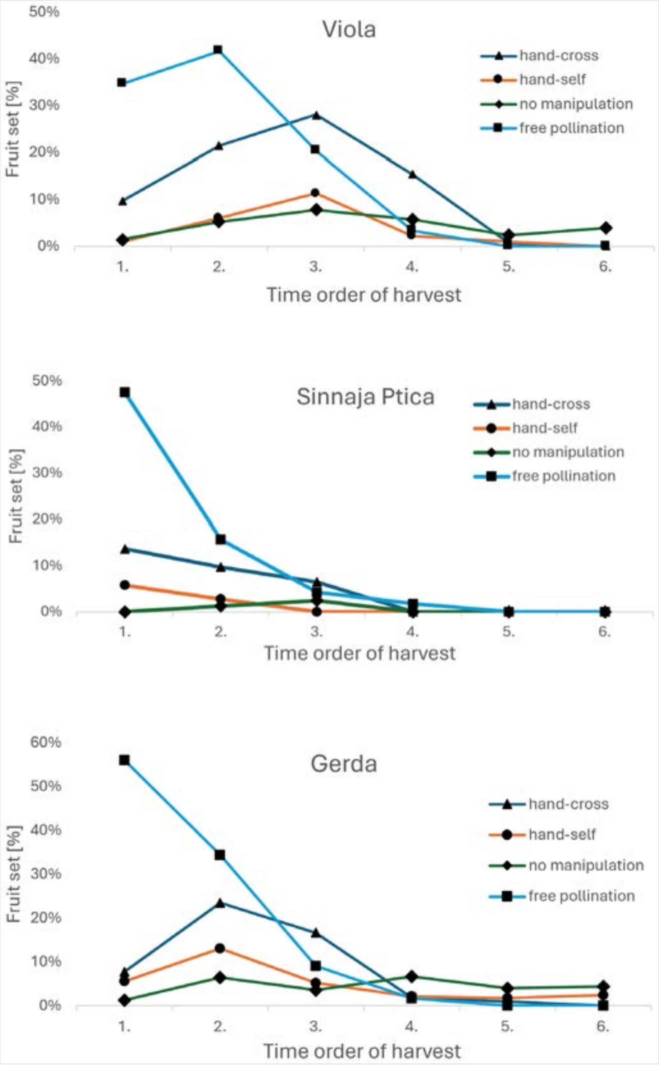


Figure 4. Percentage of fruit set in individual harvests (%) in the time series

Determination of bees present in the haskaps' vicinity

In the haskaps' vicinity, a total of 49 species of bees from five families (Apidae, Andrenidae, Colletidae, Halictidae, and Megachilidae) were registered (Appendix A, supplementary material). Within the taxonomical groups, the majority of the observed individuals were solitary bees (82.14%), represented by *Andrena flavipes* (eudominant), *Andrena gravida* (dominant), and *Evylaeus malachurus* (dominant). There were fewer individuals observed in the case of *A. mellifera* (14.29%, eudominant), and there were even fewer individuals belonging to *Bombus* spp. (3.57%; represented by five species, of which *Bobus terrestris* was the only subdominant species). The remaining four species only occurred subrecessively

(Appendix A, supplementary material). In addition, a significant difference was observed regarding the proportion of long-tongued and short-tongued bees, with most bees belonging to the latter group (75.89%) and less than a quarter belonging to the former group (24.1%; see Figure 5).

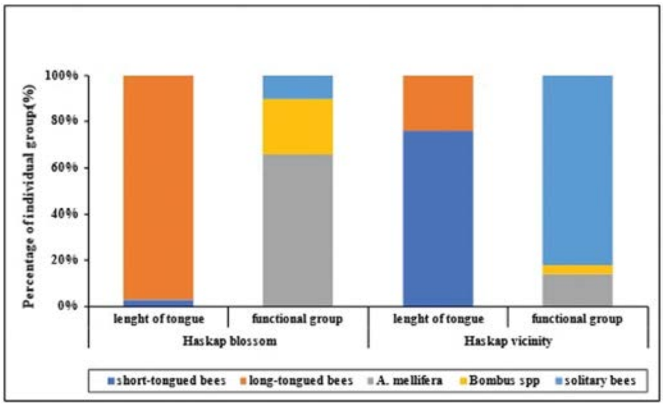


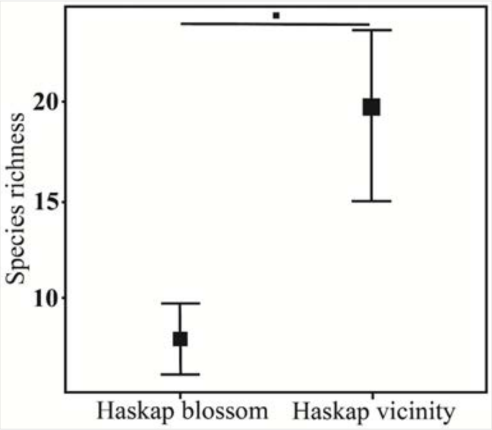
Figure 5. Bar plots showing proportions of pollinator species among taxonomic groups

Determination of bees at the haskap blossoms

At the haskap blossoms, 21 species of bees from five families (Apidae, Andrenidae, Colletidae, Halictidae, and Megachilidae) were registered (Appendix B, supplementary material). Within the functional groups, the majority of the observed individuals were *A. mellifera* (65.66%, eudominant). A significant proportion of the bees involved in pollination were *Bombus* spp. (23.99%), represented by nine species, of which the most abundant were *Pyrobombus pratorum* (eudominant) and *Bombus terrestris* (dominant). The smallest proportion of individuals consisted of solitary bees (10.35%), represented by 12 species, of which only the most abundant species, *Anthophora plumipes*, was subdominant. The rest of the solitary bees were even less represented (Appendix B, supplementary material). The largest difference was observed in the proportion of long-tongued and short-tongued bees, with the vast majority of bees falling under the former classification (96.97%) and only a fraction falling under the latter (3.03%; see Figure 5).

Comparison of the bee assemblage in the haskaps' vicinity and at the haskap blossoms

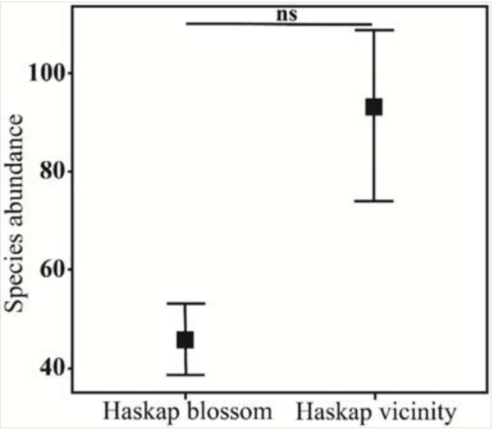
Figure 6 shows the difference in the composition of the pollinator assemblage and species richness in the vicinity and at the haskap blossoms. While the bee assemblage in the vicinity had 49 species, the composition of pollinators of the haskap blossom consisted of 21 species. Moreover, based on the analysis, species diversity ($F_{1,8}$ = 18.06, $P<0.01$) was significantly higher in the haskaps' vicinity compared to at the haskap blossoms (Figure 6).



Repeated measures ANOVA was used as a significance test. Error bars represent 95 % confidence intervals, a black square arithmetic mean, and asterisks significance level.

Figure 6. Comparison of species richness among the haskap blossom and its vicinity

However, we did not find any significant difference regarding species abundance (Figure 7).



Repeated measures ANOVA was used as a significance test. Error bars represent 95 % confidence intervals, a black square arithmetic mean, and asterisks significance level.

Figure 7. Comparison of species abundance between the haskap blossom and the vicinity

While short-tongued bees (largely represented by solitary bees) were tied to the haskaps' vicinity, long-tongued bees (represented primarily by *Bombus* spp. and *A. mellifera*) were tied to the haskap blossom assemblage (Figure 8). The legend of the abbreviations in Figure 8 is in Appendix C.

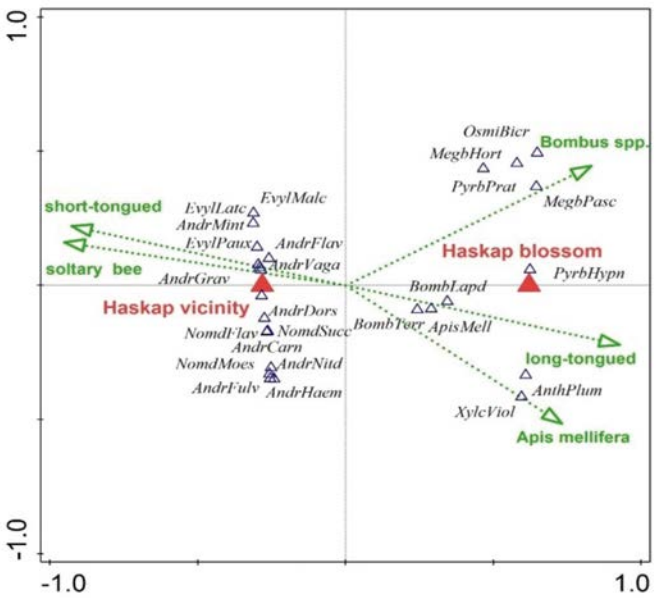
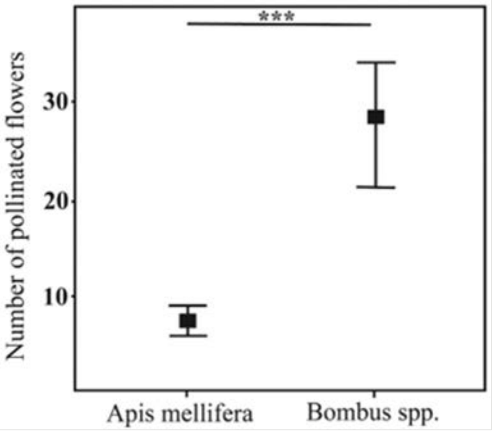


Figure 8. pCCA biplot with the locality as a covariable showing differences within bee assemblages according to the haskap's vicinity and the haskap blossoms. CWMs of species characteristics were passively projected onto the ordination diagram.

Comparison of pollination effectiveness between the main haskap pollinators

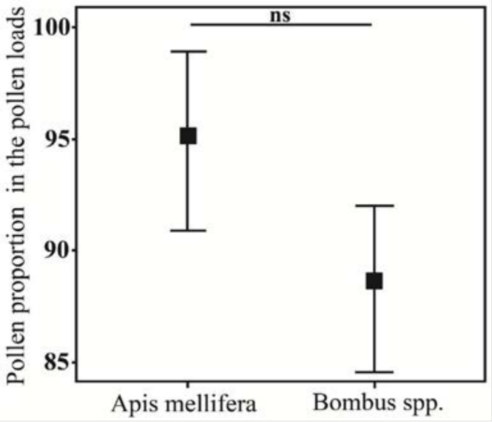
The rate of pollination varied considerably between *A. mellifera* and *Bombus* spp. While individual *A. mellifera* visited an average of 7.53 flowers per minute, *Bombus* spp. visited an average of 28.27 flowers per minute. The speed of work, therefore, significantly differed in both groups ($P<0.001$) (Figure 9).

Another factor that influenced the efficiency and significance of pollinators was the proportion of pollen transmitted by the pollinator. In the case of *A. mellifera* (95.5%), a significantly higher transmission of haskap pollen grains was not observed in comparison to *Bombus* spp. (75.5%) ($P=0.7438$) (Figure 10).



One-way ANOVA was used as a significance test. Error bars represent 95 % confidence intervals, a black square arithmetic mean, and asterisks significance level.

Figure 9. Number of pollinated flowers per minute by *Apis mellifera* and *Bombus* spp.



The Wilcoxon test was used as a significance test. Error bars represent 95 % confidence intervals, a black square arithmetic mean, and asterisks significance level.

Figure 10. Proportion of lonicera pollen in the pollen loads of *Apis mellifera* and *Bombus* spp.

Individuals of *A. mellifera* were observed from about 09:00 to 16:00, so the length of their working day was set at an average of seven hours. *Bombus* spp. were observed from 08:00 to 17:00, so the length of their working day was set at nine hours. From all recorded flower visits at all habitats, the average number of individuals visiting haskap flowers per unit of time was calculated for *A. mellifera* and *Bombus* spp. The average number of visits was higher in the case of *A. mellifera* compared to *Bombus* spp. Nevertheless, the average number of flowers visited per hour per bee was many times higher in the case of

Bombus spp. Furthermore, the working day length was longer for *Bombus* spp. (nine hours) than for *A. mellifera* (seven hours). Considering these results, *Bombus* spp. could participate in more flower visits, even in smaller numbers (Table 1).

Table 1. Comparison of the average number of visited flowers per day between *A. mellifera* and *Bombus* spp.

A. mellifera	a – n – v	109.5
	øf/1m	7.53
	l – w – d	7
	f – v – d	346,305
Bombus spp.	a – n – v	28
	øf/1m	28.27
	l – w – d	9
	f – v – d	427,442

Legend: a – n – v = average number of visitors (one hour), øf/1m = average number of visited flowers per minute per bee, l – w – d = length of working day, f – v – d = number of flowers visited per day.

DISCUSSION

The significantly highest percent fruit set was observed in all varieties of haskap under free pollination. In contrast, the percent fruit set under isolation conditions without manipulation was three times lower for Viola and Gerda and even lower in the case of Sinnaja ptica. The same trend was detected regarding the weights of fruit. This is consistent with the results obtained by Bozek (2012). Free pollination had the greatest effect on the number of seeds per fruit. Regarding the varieties Gerda and Viola, the numbers of seeds per fruit were found to be more than ten times higher under free pollination compared to under isolation conditions without manipulation. In the case of Sinnaja ptica under isolation and without manipulation, seed formation did not occur at all. This suggests a higher possible susceptibility of different varieties to seed formation depending on insect pollination. This finding is in line with Bozek (2012) and applies to other fruit species (Garratt et al., 2014). The positive effect of insect pollinators is also undeniable concerning uneven ripening, which leads to harvest complications in the case of treatments under isolation. This pattern of optimal pollination causing shorter harvest periods is known to also be the case for other crops (Williams, 1985).

We observed that cross-pollination did not maximise the fruit set. This indicates that there can be a 'pollinator' factor or factors that increase the efficiency of pollination. This is reflected in all monitored yield parameters (fruit set, weight, and number of seeds). There are possible explanations: haskap flowers require a) greater amounts of pollen grains transported on the stigma, which is ensured by a higher number of flower visits (Frier et al., 2016a; Rader et al., 2009) and/or b) higher demands on the specificity of polliniser necessary to achieve compatibility (Bors et al., 2012; Boyarskikh, 2017). These factors seem to be the main cause of the differences in fruit and seed productivity between the cross-pollination and self-pollination treatments. The differences in the fruit set, weight of fruit, and number of seeds per fruit were dependent on the variety.

We did not find any significant difference between the self-pollination and without manipulation treatments regarding the fruit set and the weight of fruit. The same pattern was observed concerning the number of seeds per fruit, except for the case of Sinnaja ptica, in which no seeds were created under treatment without manipulation. This suggests a limited level of self-compatibility, which is in line with Bors et al. (2012). Flowers without manipulation were pollinated by an expected internal process of self-transfer of their own pollen grains from anther to stigma (Frier et al., 2016b). This self-fertilisation process likely maximised fruit productivity by itself; therefore, the hand-transferred pollen grains inside the same flower by paintbrush were surplus. However, there was a difference in the case of cross-pollination compared with self-pollination in that the transfer of foreign pollen increased fruit productivity, as previously discussed. To explain the low productivity of the haskap in the case of the cross-pollination treatment, it would be appropriate to perform further experiments.

A relatively high number of bee species was observed in the localities in the haskaps' vicinity. Short-tongued species, represented mainly by individuals from the

Andrenidae family, comprised the majority of these bees. In contrast, the assemblage of bees observed at the haskap blossoms was dominated by long-tongued bees that belonged mainly to the Apidae family. Short-tongued bee species barely participated in pollination (Figure 8). Despite the species richness of the bees pollinating haskap being significantly lower compared to the number of species occurring in the haskaps' vicinity, their abundance was not significantly reduced (Figures 6 and 7). These results indicate a high competitive potential of long-tongued bees due to the deep flowering corolla of haskap flowers (Hummer et al., 2012). This is supported by the fact that haskap was originally a circumpolar species, meaning *Bombus* spp., the classical representatives of long-tongued bees, are by far the best adapted pollinators (Kevan et al., 1993). However, in conditions outside the Arctic and subarctic zones, *A. mellifera* also seems to be another important pollinator of haskap, perhaps even the most abundant pollinator in warmer conditions. This is in line with the findings of Frier et al. (2016a) and Olmstead (2019).

Although the haskap-pollinating bee assemblage differed significantly from the bee assemblage in the haskaps' vicinity, the species composition of the haskap-pollinating assemblage was logically directly influenced by the bee assemblage in the haskaps' vicinity. Therefore, there were many species observed on haskap flowers that were also present in the bee assemblages observed in the haskaps' vicinity (Appendix A and B). However, the species common to both assemblages differed significantly in abundance (Figure 8). A different trend was observed in each assemblage: while short-tongued bee species represented by the solitary bee guild were associated with the bee assemblages in the haskaps' vicinity, long-tongued bee species were linked with the bee assemblages at the haskap blossoms, particularly *A. mellifera* and *Bombus* spp. (Figure 8). A similar trend was observed by Leung and Forrest (2019). The nesting of various native species of solitary bees was observed in the haskap orchard, of which only a few long-tongued species participated in pollination, with the vast majority of the solitary bees preferring other food sources.

We also determined a difference among the main guilds of haskap pollinators (*A. mellifera* and *Bombus* spp.) regarding the number of flowers visited by an individual per unit of time, pollen load composition (indicating the flower constancy of the guilds and working day length (which is closely related to the number of potentially visited/pollinated flowers per day). Based on this, we compared the effectiveness and importance of both guilds for haskap pollination. While one *A. mellifera* worker visited an average of 7.5 flowers per minute, the average *Bombus* spp. was able to visit almost four times more flowers in the same time (Figure 9). Although *A. mellifera* was expected to have a higher degree of floroconstancy compared to *Bombus* spp. and thus a significantly higher proportion of transported haskap pollen (i.e. a lower probability of contamination of stigma with pollen from different plant species), this was not confirmed, and a high proportion of haskap pollen was observed in both guilds (Figure 10). Both guilds seemed to be extremely effective compared to the Osmia lignaria (long-tongued solitary bees considered a natural pollinator of haskap) mentioned in the study of Frier et al. (2016a), where the average pollen load was only 5% of haskap pollen. After observing the activity of individuals belonging to the guilds of *A. mellifera* and *Bombus* spp., the working day was set at two hours longer for *Bombus* spp. This is due to the ability of bumblebees to function even at significantly lower temperatures than *A. mellifera* can (Frier et al., 2016a; Lundberg, 1980).

The most numerous bee guild that participated in haskap pollination was *A. mellifera*, which is consistent with Frier et al. (2016a) and Olmstead (2019). When calculating the potentially visited/pollinated flowers per day, using the data obtained, however, it turned out that despite the significantly higher involvement of *A. mellifera*, bumblebees were still able to visit more flowers. This result reflects their ability to visit many flowers per unit of time and the longer length of their working day. Frier et al. (2016a) further stated that bumblebees can transfer more pollen to the stigma per visit to the haskap flower and thus ensure complete fertilisation in a single visit, unlike *A. mellifera*, which have to visit the flower several times for complete fertilisation. However, the sexual parts of the flowers are active for several days, even in the case of pollination (Frier et al., 2016b), meaning there is a relatively high probability that many flowers will be visited/pollinated more than once.

Some studies have assessed the suitability of pollinators by body size, which has a crucial impact on circadian rhythms (Hoehn et al., 2008). In the present study, however, due to the flower biology (length of the corolla and the long-term activity of the sex parts of the flower), we focused on the suitability of pollinators according to the length of the tongue, following the pattern of Fontaine et al. (2006). Frier et al. (2016a) assumed that haskap uses a generalist pollination strategy. This assumption was based on the characteristics of the flower and aimed to explain how the plant maximizes the use of the limited number of pollinators available in the spring. However, we found that in the relationship between plants and pollinators, haskap primarily relies on long-tongued generalist bees.

To ensure optimal pollination, a supply of social bee species such as bumblebees and *A. mellifera*, which are the most effective pollinators of haskap, is recommended. The benefits of these species are their easy displaceability, numerous colonies, and affordability. A supply of commercially bred pollinators is particularly recommended when the community of native pollinators is disturbed and there is a risk of reducing the fruit set (Hoehn et al., 2008; Klein et al., 2007; Ryba et al., 2012). Furthermore, these bee species are relatively more resistant to anthropogenic changes in the landscape (Hybl et al., 2020).

CONCLUSIONS

The harvest parameters of haskap (percent fruit set, fruit weight, number of seeds per fruit, and term and duration of harvest) were found to be most optimised under free pollination compared to under other treatments, including cross-pollination. This proves that some obscure effect of pollinators on the effectiveness of the pollination process in haskap must exist.

Despite the dominant occurrence of short-tongued bee species belonging to solitary bees, the pollination of haskap was almost exclusively due to long-tongued bee species, mainly represented by *Bombus* spp. and *A. mellifera*. Thus, it can be assumed that the most important bees for pollination and yield generation are social species of bees that are traded, great in number, and easily movable.

The most abundant bee species observed during the pollination of haskap was *A. mellifera*. Although significantly fewer *Bombus* spp. were observed on the flowers, it is assumed that they did more work in total than *A. mellifera*, mainly due to their higher work efficiency and longer working day.

In warmer areas with sufficient density, *A. mellifera* can likely become the most important pollinator of haskap. During a high flight, they can pollinate more flowers per day than *Bombus* spp. (Frier et al., 2016a). This could be particularly valid in areas with strongly reduced occurrences of wild pollinators (Hoehn et al., 2008).

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APPENDIX

Appendix A. Bee assemblages observed in the haskaps' vicinity

Number	Family	Specie	Abundance	Level of dominance	Dominance
1	andrenidae	*Andrena bifasciata*	1	subr	0,18
2	andrenidae	*Andrena carantonica*	5	subr	0,89
3	andrenidae	*Andrena cineraria*	14	subd	2,50
4	andrenidae	*Andrena congruens*	1	subr	0,18
5	andrenidae	*Andrena dorsata*	5	subr	0,89
6	andrenidae	*Andrena flavipes*	154	eud	27,50
7	andrenidae	*Andrena fulva*	5	subr	0,89
8	andrenidae	*Andrena gravida*	37	dom	6,61
9	andrenidae	*Andrena haemorhoa*	4	subr	0,71
10	andrenidae	*Andrena humilis*	1	subr	0,18
11	andrenidae	*Andrena lagopus*	24	subd	4,29
12	andrenidae	*Andrena minutula*	21	subd	3,75
13	andrenidae	*Andrena nigroaenea*	23	subd	4,11
14	andrenidae	*Andrena nitida*	4	subr	0,71
15	andrenidae	*Andrena sericata*	1	subr	0,18
16	andrenidae	*Andrena simontornyella*	1	subr	0,18
17	andrenidae	*Andrena susterai*	1	subr	0,18
18	andrenidae	*Andrena taraxaci*	4	subr	0,71
19	andrenidae	*Andrena tibialis*	1	subr	0,18
20	andrenidae	*Andrena vaga*	4	subr	0,71
21	andrenidae	*Andrena varians*	1	subr	0,18
22	apidae	*Apis mellifera*	80	eud	14,29
23	apidae	*Bombus lapidarius*	3	subr	0,54
24	apidae	*Bombus terrestris*	13	subd	2,32
25	colletidae	*Colletes cunicularius*	19	subd	3,39
26	halictidae	*Evylaeus calceatus*	10	rec	1,79
27	halictidae	*Evylaeus laticeps*	6	rec	1,07
28	halictidae	*Evylaeus malachurus*	40	dom	7,14
29	halictidae	*Evylaeus marginatus*	4	subr	0,71
30	halictidae	*Evylaeus parvulum*	1	subr	0,18

Continued. Appendix A

Number	Family	Specie	Abundance	Level of dominance	Dominance
31	halictidae	*Evylaeus pauxillus*	19	subd	3,39
32	halictidae	*Lasioglossum pallens*	1	subr	0,18
33	halictidae	*Lasioglossum xanthopus*	2	subr	0,36
34	apidae	*Megabombus hortorum*	2	subr	0,36
35	apidae	*Nomada bifasciata*	9	rec	1,61
36	apidae	*Nomada flava*	3	subr	0,54
37	apidae	*Nomada fucata*	2	subr	0,36
38	apidae	*Nomada fulvicornis*	3	subr	0,54
39	apidae	*Nomada moeschleri*	3	subr	0,54
40	apidae	*Nomada ruficornis*	2	subr	0,36
41	apidae	*Nomada signata*	4	subr	0,71
42	apidae	*Nomada succincta*	8	rec	1,43
43	apidae	*Nomada trispinosa*	1	subr	0,18
44	megachilidae	*Osmia bicornis*	1	subr	0,18
45	megachilidae	*Osmia caeruelscens*	1	subr	0,18
46	megachilidae	*Osmia cornuta*	7	rec	1,25
47	megachilidae	*Osmia rufa*	2	subr	0,36
48	apidae	*Pyrobombus lapidarius*	1	subr	0,18
49	apidae	*Pyrobombus pratorum*	1	subr	0,18

Appendix B. Bee assemblages observed in the haskaps blossoms

Number	Family	Specie	Abundance	Level of dominance	Dominance
1	andrenidae	*Andrena flavipes*	1	subr	0,25
2	andrenidae	*Andrena nigroaenea*	2	subr	0,51
3	andrenidae	*Andrena varians*	1	subr	0,25
4	apidae	*Anthophora plumipes*	9	subd	2,27
5	apidae	*Apis mellifera*	260	eud	65,66
6	apidae	*Bombus hortorum*	5	rec	1,26
7	apidae	*Bombus sylvarum*	2	subr	0,51
8	apidae	*Bombus terrestris*	27	dom	6,82
9	colletidae	*Colletes cunicularius*	6	rec	1,52
10	halictidae	*Evylaeus calceatus*	1	subr	0,25
11	halictidae	*Evylaeus marginatus*	1	subr	0,25
12	apidae	*Megabombus hortorum*	7	rec	1,77
13	apidae	*Megabombus pascuorum*	4	rec	1,01
14	apidae	*Nomada bifasciata*	1	subr	0,25
15	apidae	*Nomada signata*	1	subr	0,25
16	megachilidae	*Osmia bicornis*	7	rec	1,77
17	megachilidae	*Osmia cornuta*	4	rec	1,01
18	apidae	*Pyrobombus hypnorum*	4	rec	1,01
19	apidae	*Pyrobombus lapidarius*	5	rec	1,26
20	apidae	*Pyrobombus pratorum*	41	eud	10,35
21	apidae	*Xylocopa violacea*	7	rec	1,77

Appendix C. List of abbreviations

AndrBifs	*Andrena bifasciata*	CollCunc	*Colletes cunicularius*
AndrCarn	*Andrena carantonica*	EvylCalc	*Evylaeus calceatus*
AndrCinr	*Andrena cineraria*	EvylLatc	*Evylaeus laticeps*
AndrCong	*Andrena congruens*	EvylMalc	*Evylaeus malachurum*
AndrDors	*Andrena dorsata*	EvylMarg	*Evylaeus marginatus*
AndrFlav	*Andrena flavipes*	EvylPaux	*Evylaeus pauxillus*
AndrFulv	*Andrena fulva*	LasiPall	*Lasioglossum pallens*
AndrGRav	*Andrena gravida*	LasiXant	*Lasioglossum xanthopus*
AndrHaem	*Andrena haemorhoa*	MegbHort	*Megabombus hortorum*
AndrLagp	*Andrena lagopus*	MegbPasc	*Megabombus pascuorum*
AndrMint	*Andrena minutula*	NomdBifs	*Nomada bifasciata*
AndrNigr	*Andrena nigroaenea*	NomdFlav	*Nomada flava*
AndrNitd	*Andrena nitida*	NomdFuct	*Nomada fulvicornis*
AndrSimn	*Andrena simontornyella*	NomdMoes	*Nomada moeschleri*
AndrSust	*Andrena susterai*	NomdRufc	*Nomada ruficornis*
AndrTarx	*Andrena taraxaci*	NomdSucc	*Nomada succincta*
AndrVaga	*Andrena vaga*	OsmiBicr	*Osmia bicornis*
AndrVari	*Andrena varians*	OsmiCaer	*Osmia cornuta*
AnthPlum	*Anthophora plumipes*	OsmiRufa	*Osmia rufa*
ApisMell	*Apis mellifera*	PyrbHypn	*Pyrobombus hypnorum*
BombLapd	*Bombus lapidarius*	PyrbLapd	*Pyrobombus lapidarius*
BombSylv	*Bombus sylvarum*	PyrbPrat	*Pyrobombus pratorum*
BombTerr	*Bombus terrestris*	XilcViol	*Xylocopa violancea*