High abundance but low diversity of floral visitors on invasive Heracleum mantegazzianum (Apiaceae)

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Abstract
Currently, plant invasions affect native ecosystems across the Earth. Although much attention has already been paid to their effect on local communities, we still lack basic information on the associations between alien and local species. Here, we present the results of our survey of pollinators of the invasive plant Heracleum mantegazzianum (Apiaceae) in central Europe. At 20 sites within the westernmost part of the Czech Republic, which is strongly affected by the invasion of H. mantegazzianum, pollinators on the flowers of H. mantegazzianum were examined and compared to the species composition of pollinators on native vegetation in the surrounding area. While the flowers of H. mantegazzianum were frequently visited by high abundance of insects, the communities of H. mantegazzianum pollinators were relatively species poor, and the proportion of abundances of H. mantegazzianum pollinators was very uneven, with few species of generalist Diptera and the honey bee (Apis mellifera) dominating over all other flower visitors. Significantly larger species of the family Syrphidae visited flowers of giant hogweed than of other plants. Thus, giant hogweed is not a necessary part of flower communities for flower visiting insects, and it should be eradicated because of its negative effects on other plants, landscape and humans. Our results highlight the need for more detailed studies on direct interactions between alien plant species and native pollinator communities as well as indirect interactions between alien plants and native plants through competition for pollinators.

Keywords
Czech Republic, honeybee, hoverflies, plant invasion, plant-pollinator interactions
Introduction

Invasive or alien plants represent, among the number of non-natives, the most dangerous species, with a certain negative effect on native species, ecosystems, landscapes and often human beings. They usually have a very high ability to overgrow large areas in the landscape of their new area of occurrence and often can destroy or inhibit native communities and species of plants (Randall and Marinelli 1996; Müller-Schärer et al. 2004; Hejda et al. 2009). Therefore, a lot of attention has been paid to this dangerous behaviour of invasive species, and the results of these surveys are used in the elimination of invasive plants. Continental or regional Black, Grey and Watch lists provide information on the most important species and their potential threats (Blackburn et al. 2014; Pergl et al. 2016). Regarding Socio-economic Impact Classification of Alien Taxa (SEICAT), the measuring tool for the potential dangerousness of invasive species of plants and animals, many plant species are marked to bring massive concern for humans (Bacher et al. 2017). Among these plants, the giant hogweed (Heracleum mantegazzianum) is, in most of Europe, one of the best known and most discussed invasive plants (Rijal et al. 2015).

The giant hogweed is a perennial herb of the family Apiaceae, with the original area of occurrence in the western Caucasus. This plant is very conspicuous, 2–5 metres tall, and produces umbelliferous inflorescences with a diameter of approximately 30–50 cm (Pyšek and Pyšek 1995). Most likely, the plant was introduced to Europe in the 19th century as an ornamental plant because of its conspicuous inflorescences (Nielsen et al. 2005). Shortly after its introduction, the plant started to spread in Western and Northern Europe, and in the 20th century, it started to form a very strong population and overgrow large areas of various characteristics (Pyšek and Pyšek 1995; Nielsen et al. 2005). Currently, this species has become highly invasive, especially in cooler and humid regions and causes many problems there. The main negative effect is that this plant reproduces very rapidly, produces hundreds to thousands of diaspores every year, and rapidly overgrows large areas supplanting the native vegetation very fast (Nielsen et al. 2005; Pyšek et al. 2010). Giant hogweed is also dangerous for humans because of its metabolites, which cause strong allergic reactions upon contact with human skin. Thus, policies of countries fund specialized programmes focused on the destruction of this plant species to avoid large invasions in large areas, which were caused several times in the past (Thiele et al. 2007; Pyšek et al. 2010).

Because of its large white compound inflorescences with open and easily reachable flowers as well as due to its extraordinary height, it is likely that giant hogweed can be attractive for pollinators like other plants of similar size and with large flowers (Ohashi and Yahara 2001). However, only a few studies on this topic have been done to date, and the most comprehensive by Zumkier (2012) remains unpublished. The first study by Grace and Nelson (1981) compared pollinator diversities and the pollen carried by them on H. mantegazzianum and the native H. sphondylium. The authors reported similar number of species and individuals of pollinators on both plants but the species spectra differed. Nielsen et al. (2005) studied marginally pollinators of
*H. mantegazzianum* and Zumkier (2012) examined the competition for pollinators between the native *Heracleum sphondylium* and invasive *H. mantegazzianum* in Germany. Insects, especially honey bees, visited flowers of the larger giant hogweed much more frequently. Diptera were very numerous, while the genus *Lucilia* (Calliphoridae) overwhelmed other groups of this order. Larger pollinators, hover flies (Diptera, Syrphidae), wasps (Hymenoptera, Vespidae) and beetles (Coleoptera), were much more numerous in plots with invasive vegetation led by giant hogweed. However, most of these studies were focused on one group of insects and/or insects were not identified to a species level, so a comprehensive list of species associated with flowers of giant hogweed is still missing. In addition, a comparison with abundances and diversities of insects of the same groups at the same localities is still missing.

We decided to fill the gaps in the knowledge of insects associated with giant hogweed. We studied all insects searching for pollen and/or nectar on flowers of giant hogweed in the region of the Czech Republic where this plant is the most numerous and where it forms homogeneous vegetation. The main aim of our study was to determine whether giant hogweed is attractive for insects and whether specialized pollinators or red-listed species visit the flowers of this invasive plant at higher abundances. The composition of flower visitors on growths of giant hogweed was compared to the composition of flower visitors collected on native plants in nearby vegetation in order to show which part of the flower-visiting insect community could exploit floras’ sources from giant hogweed as well. We also focused on trying to evaluate whether the large compound inflorescences of giant hogweed are visited by larger insects than is the case with flowers of other, smaller plant species (such as the studied example of Syrphidae). Based on the results, we would like to evaluate whether overgrowths of giant hogweed are valuable or dangerous for communities of flower visiting insects.

**Methods**

Insects on flowers of giant hogweed (*Heracleum mantegazzianum*) were studied near the town of Mariánské Lázně in the western part of the Czech Republic (Central Europe) in July 2020. This region suffers from the largest invasion of this plant in the country for decades, and thus, the strongest populations of giant hogweed in the whole country occur there (Pyšek and Pyšek 1995; Dostál et al. 2013). Out of the sites with the highest densities of flowering *H. mantegazzianum*, 20 sites at a distance of at least two kilometres from each other were selected for the survey. Most of the sites were located in relatively humid stream valleys (12 localities), on meadows (8), two locations were field ruderals. The size of the site ranged between 15 935 and 182 137 m² but most of the sites were smaller (mean 59 995 ± SD 9 158 m², median 48 744 m²). The characteristics of the localities are in Suppl. material 1: table S1. The map of the Mariánské Lázně region with all localities is shown in Fig. 1.

At each site, we swept all insects from the flowering parts of all *H. mantegazzianum* plants using an entomological net, and additionally, we swept all insects visiting
other flowering plants at each site. We swept all flowers at each site (one person giant hogweeds, second other flowering plants in nearby native vegetation), while each flower was swept only once. In most localities, we had to sweep all flowers of giant hogweed and other plants; in larger localities we swept a linear transect of the length 150–200 m. Each locality was sampled once, at the time of the year when the giant hogweed was in flower. We did the field work in the warmer part of the day (between 11 a.m. and 4 p.m.) and only on days when the weather was warm (temperature above 20 °C) and sunny with no rain. At each locality, we mapped other flowering plants at a distance not more than 10 m from the nearest giant hogweed methodologically similarly to Braun-Blanquet’s phytosociological relevées (following the methodology of Kaplan (2012)) to illustrate the species spectra of flowering plants. The species spectra of flowering plants quite highly overlapped (see Suppl. material 1: table S2). All captured insects were immediately transferred into 75% ethyl alcohol using a plastic dish. Captured insects were sorted into orders in the laboratory. Although insects of many orders were captured, we studied only those that were associated with flowers, nectar and pollen: Diptera, Hymenoptera, Coleoptera, and Lepidoptera. All captured members of these four orders were identified to the species level if possible; taxonomically problematic groups of Diptera and Coleoptera were sorted to morphospecies only.

Since the family Syrphidae was the most numerous in individuals and species of all families both on giant hogweed and other plants, we compared the overall lengths of species, while the mean and median were determined, and Mann-Whitney test for comparison was performed. We measured the body lengths of 751 specimens from giant hogweed and 701 specimens from flowers of other plants using the measuring tool.
Results

Species recorded

In total, we captured 2,611 individuals of 141 species or morphospecies of insects on flowers of giant hogweed (Suppl. material 1: table S1), of which Diptera was the most numerous group in terms of both species (64) and individuals (1,983). Hymenoptera, with 53 species, was the second most numerous group, but the number of individuals was only 387. We recorded only 236 individuals of 20 species of Coleoptera and five individuals of four species of Lepidoptera. On flowers of other plants, the numbers of species were slightly higher but with a lower number of individuals in Diptera (1,238 individuals of 73 species) and Hymenoptera (296 individuals of 58 species). Coleoptera (588 individuals of 45 species) and Lepidoptera (59 individuals of 18 species) were much more numerous both in individuals and species (Table 1).

Among Diptera, the datasets from giant hogweed showed dominances of several species, while most other species were recorded only in small numbers of individuals. The most numerous flower visitors of Heracleum were Eristalis pertinax (Diptera, Syrphidae) with 371 individuals, Gonia ornata (Diptera, Tachinidae) with 316 individuals,
Sarcophaga sp. with 155, and Phorocera obscura (Diptera, Tachinidae) with 149 individuals. Seven other species were recorded in more than 50 individuals, and an additional 14 species were recorded with more than 10 individuals. On flowers of other plants, Sphaerophoria scripta (Diptera, Syrphidae), with 392 individuals, was the most numerous, followed by Dexia rustica (Diptera, Tachinidae), with 129 individuals, and a small unidentified species of Muscidae (109 individuals). Only one additional species (Melanostoma mellinum, Syrphidae, 77 individuals) was recorded in larger number than 50 and 11 others in larger numbers than 10 individuals.

The honey bee Apis mellifera was the most numerous species among Hymenoptera in both datasets (168 individuals on giant hogweed and 146 on flowers of other plants), while other species were recorded in much lower numbers of individuals. On giant hogweed, Dolichovespula sylvestris (Hymenoptera, Vespidae) was recorded in 31 individuals, and Lasioglossum fulvicorne and Lasioglossum pauxillum (Hymenoptera, Halictidae) were both recorded in 24 individuals; only two other species were recorded in more than 10 individuals. On flowers of other plants, L. pauxillum, with 27 individuals, was the second most numerous species, and only two other species were recorded in more than 10 individuals.

Among Coleoptera, Rhagonycha fulva (Coleoptera, Cantharidae) comprised 127 individuals recorded on flowers of giant hogweed, more than half of all recorded individuals of this order. It was followed by Oedemera femorata (Coleoptera, Oedemeridae) with 32 individuals, Oxythyrea funesta (Scarabaeidae) with 26 individuals and Stenurella melanura (Coleoptera, Cerambycidae) with 17 individuals. Surprisingly, the two most numerous beetles on giant hogweed were also the most numerous on other plants, with 191 and 128 individuals, respectively. S. melanura was the third most numerous, with 63 individuals, and only five other species were recorded in 10 or more individuals.

All species of Lepidoptera represented only small numbers of individuals both on flowers of giant hogweed and other flowering plants, with Aphantopus hyperanthus and Maniola jurtina (both Satyridae) being the most numerous on other plants, both recorded in nine specimens.

Table 1. Diversity indices for all studied groups together and for Diptera, Hymenoptera, Coleoptera and Lepidoptera separately. GH – giant hogweed, other – other plants at the locality.

<table>
<thead>
<tr>
<th>Species</th>
<th>All groups</th>
<th>Diptera</th>
<th>Hymenoptera</th>
<th>Coleoptera</th>
<th>Lepidoptera</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GH</td>
<td>Other</td>
<td>GH</td>
<td>Other</td>
<td>GH</td>
</tr>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>194</td>
<td>64</td>
<td>73</td>
<td>53</td>
</tr>
<tr>
<td>Individual Species</td>
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<td>2181</td>
<td>1983</td>
<td>1238</td>
<td>387</td>
</tr>
<tr>
<td>Individual Species</td>
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<td>287</td>
<td>77</td>
<td>90</td>
<td>91</td>
</tr>
<tr>
<td>Individual Species</td>
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<td>0.06</td>
<td>0.09</td>
<td>0.13</td>
<td>0.21</td>
</tr>
<tr>
<td>Individual Species</td>
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<td>0.94</td>
<td>0.91</td>
<td>0.87</td>
<td>0.79</td>
</tr>
<tr>
<td>Individual Species</td>
<td>3.53</td>
<td>3.73</td>
<td>3.00</td>
<td>2.90</td>
<td>2.54</td>
</tr>
<tr>
<td>Individual Species</td>
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<td>0.71</td>
<td>0.72</td>
<td>0.68</td>
<td>0.64</td>
</tr>
<tr>
<td>Individual Species</td>
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<td>51.46</td>
<td>12.64</td>
<td>16.96</td>
<td>16.61</td>
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<td>Individual Species</td>
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<td>0.43</td>
</tr>
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<td>–</td>
<td>0.642</td>
<td>–</td>
<td>0.432</td>
</tr>
</tbody>
</table>
Rare and red-listed species

Regarding the Red lists (Hejda et al. 2017 and Farkač et al. 2005), we recorded mostly common and numerous species. Only 16 Red-listed species were recorded, all of them with one or a few individuals (Chrysogaster coemiteriorum, Diptera, Syrphidae, with 14 individuals being the most numerous). Two critically endangered species (CR) were recorded: the crabronid wasp Gorytes quadrifasciatus (Hymenoptera, Crabronidae) and the lepidopteran Zygaena osterodensis (Lepidoptera, Zygaenidae), but both were only on flowers of native plants, not on giant hogweed. The endangered (EN) solitary wasp Symmorphus murarius (Hymenoptera, Vespidae) was recorded on giant hogweed, and the chrysomelid beetle Galeruca dahlia (Coleoptera, Chrysomelidae) was recorded on flowers of native plants. Of seven vulnerable (VU) species, hover flies (Diptera, Syrphidae), Parhelophilus frutetorum, Chrysogaster coemiteriorum, and Xylota tarda, and the crabronid wasp (Hymenoptera, Crabronidae), Gorytes quinquecinctus, occurred both on flowers of giant hogweed and other plants, while the hover fly Parhelophilus versicolor (Diptera, Syrphidae), sweat bee Lasioglossum tricinctum (Hymenoptera, Halictidae) and eusocial wasp Dolichovespula norwegica (Hymenoptera, Vespidae) were recorded only on flowers of giant hogweed. The near threatened (NT) solitary bee Andrena pandellei (Hymenoptera, Andrenidae) and butterfly Melitaea athalia (Lepidoptera, Nymphalidae) were recorded on flowers of native plants, while the butterfly Satyrium w-album (Lepidoptera, Lycaenidae) was recorded on flowers of giant hogweed.

Species diversities

The Chao-1 estimator of species richness was 205 ± 20 species (95% CI) for H. mantegazzianum and 287 ± 26 species (95% CI) for other plants. The value of the Simpson index showing heterogeneity was 0.94 for H. mantegazzianum, which means that several species were numerous and dominant. A similar result was obtained from the Shannon-Wiener index (value 3.529). More surprisingly, the values of both indices were similar for other plants (Simpson index 0.94, Shannon-Wiener index 3.73). Eighty-one species were shared, and the value of the Sørensen similarity index between H. mantegazzianum and other plants was 0.48. The rarefaction curve shows the mean of sorting of repeatedly mixed taxa. We can see that more individuals but fewer taxa were recorded on the flowers of H. mantegazzianum (Fig. 2). The diversity of insects was larger on other plants, while several species dominated in high numbers on the flowers of H. mantegazzianum (Table 1).

Regarding the groups, the estimated diversity on other plants is always slightly higher (Diptera and Hymenoptera) or much higher (Coleoptera) than the estimated diversity on flowers of H. mantegazzianum (Table 1). This is also supported by rarefaction curves for all four insect orders (Fig. 3). Especially in Diptera and Hymenoptera, the diversity is higher on other plants, although numerous individuals of several species over-dominated in numbers on flowers of H. mantegazzianum. For Coleoptera and Lepidoptera, both the abundances and diversities were much higher on other plants than on H. mantegazzianum.
Figure 2. Individual rarefaction for all studied groups A insects of flowers of *Heracleum mantegazzianum* B insects on flowers of other plants at the locality.

Figure 3. Individual rarefaction for the studied groups separately A insects of flowers of *Heracleum mantegazzianum* B insects on flowers of other plants at the locality.
Regarding the diversity indices, both the Simpson index and Shannon-Wiener index showed that the distribution of species of Diptera was very similar both on *H. mantegazzianum* and on other plants, several species were very numerous, and the distribution of individuals was different among the species, with several species dominating. In Hymenoptera, the situation is similar; only the species distribution shows lower differences than in Diptera. In Coleoptera, the distribution of individuals was equal on *H. mantegazzianum* but unequal on other flowers, with slight dominance of several species. For Lepidoptera, the number of species and individuals recorded was very small, and thus, we cannot make any conclusions.

The Sørensen similarity index is the highest in Diptera, where more than half of the species are shared between *H. mantegazzianum* and other plants. In Hymenoptera, the value is lower than 0.5; in Coleoptera, the value is less than 0.33, and the lowest is in Lepidoptera, which may be due to the low number of recorded species and individuals on the flowers of *H. mantegazzianum*.

The median total length of hover flies found on *H. mantegazzianum* was 12.35 mm, the same for hover flies found on other plants was 9.60 mm (Fig. 4). When compared, we found that flowers of *H. mantegazzianum* were visited by significantly larger species ($p < 0.001$).

**Figure 4.** Box plot with the comparison of total lengths of 751 individuals of hover flies recorded on *Heracleum mantegazzianum* (**A**) and 705 individuals on other plants (**B**).

**Discussion**

The numbers of species recorded in our study are much higher than in all previous surveys, partly because a very large portion of species were identified to a species level, contrary to previous studies (Nielsen et al. 2005; Zumkier 2012). Thus, our study can
serve as the first comprehensive information on insect species associated with flowers of giant hogweed compared to flower visitor communities on nearby native vegetation, and as a starting point for further studies on related topics. Despite the high numbers of individuals recorded, the total number of species recorded on composite flowers of giant hogweed was not very high; the high densities of flower visitors on this plant are driven mostly by a few very numerous species. Thus, the honey bee represented 46% of all individuals of Hymenoptera and common larger hover flies (i.e., *Eristalis pertinax*) represented 48% of all individuals of Diptera. Except for the Apiaceae specialist *Rhagonycha fulva*, only a few species of beetles and butterflies were recorded on flowers of giant hogweed, contrary to many more species and specimens recorded on flowers of native plants at the studied sites. Our results thus correspond with those of Zumkier (2012), who recorded that composite flowers of giant hogweed hosted high numbers of individuals of common and usually unspecialized species. The fact that we have not recorded any specialists bound on this plant also supports the results of both abovementioned studies. Interestingly, during the field work, we did not record any bee species collecting pollen from giant hogweed, which is in contrast with the study of Grace and Nelson (1981).

In contrast with previous authors (Grace and Nelson 1981; Nielsen et al. 2005; Zumkier 2012), we didn’t compare the flower visitors’ spectra between native *Heracleum sphondylium* and the invasive *H. mantegazzianum*. The native *H. sphondylium* flowers about a month later than giant hogweed and the differences of insects visiting the flowers of both species can thus result from the phenology, not only from the preferences of insect species visiting the inflorescences of each plant (see Pyšek and Pyšek 1995). Further, *H. sphondylium* is not very numerous in the studied region and forms usually weak populations. Significantly, *H. sphondylium* is one of the favourite nectar sources for the Gasteruptiidae family (Parslow et al. 2020; Bogusch 2021) but Grace and Nelson (1981) did not record any species of this family and neither did we.

In addition, we cannot compare our results with other studies in detail because most previous studies did not identify the collected material to species level, but only to higher taxonomic levels; (Zumkier 2012) recorded a much lower number of species or dealt with phytophagous species, not pollinators. Zumkier (2012) reported that honeybees were also the most numerous species of Hymenoptera in his studies, as well as larger species of hover flies. The results are contrary to our unpublished records from studies of Canadian goldenrod (*Solidago canadensis*) and hartleaf oxeye (*Telekia speciosa*), which both hosted rich communities of Hymenoptera and many species of bees. Furthermore, females of both polylectic and Asteraceae oligolectic bees were recorded in high numbers collecting pollen, while no bee female collecting pollen was recorded on flowers of giant hogweed. Interestingly, there are ten bee species specialised to pollen from the family Apiaceae recorded in the Czech Republic and several of these species are quite common and widespread and certainly occur in the studied region (Bogusch et al. 2020). However, none of them has been recorded on giant hogweed. In contrast with some other invasive plants, giant hogweed does
not seem to be that important for insects as a source of pollen, and the results copy those of studies in which invasive and native plant species were compared (Seitz et al. 2020; Abdallah et al. 2021; Parra-Tabla and Arceo-Gómez 2021). Most species use large composite flowers of this plant only or predominantly as a source of nectar, and larger and numerous species can be found on composite flowers of this plant in very high numbers. However, we think that the negative effects of giant hogweed on other plants, landscapes and people (for details, see Pyšek et al. 2010; Nentwig et al. 2014) outweigh its potential benefit as a nectar source.

Klečka et al. (2018) showed that while representatives of Hymenoptera visit mainly flowers with the same height as surrounding vegetation, many representatives of Diptera prefer highly placed flowers to less laid flowers. We suppose that this difference between both taxa could have affected the composition of flower visitors of Heracleum compared to other plants as Heracleum is usually much higher than the surrounding herbal vegetation, attracting several representatives of Diptera very effectively. For other taxa, however, such as Hymenoptera, giant hogweed is not as attractive in comparison with other plant species. This effect could thus lead to the observed flower visitation pattern. Consequently, due to the extraordinary height of H. mantegazzianum, this invasive species could negatively affect the native plants that are pollinated by Diptera by competition for pollinators, while its effect on plants pollinated by Hymenoptera could be lower. However, further research will be needed to test this hypothesis.

Among hover flies, the majority of rare and endangered species recorded on Heracleum as well as other plants were those with saprophagous semiaquatic larvae, associated predominantly with wetlands and oligotrophic fens (Speight 2020). The presence of these rare species is thus driven by the conditions of the surrounding habitats rather than the species composition of flowering plants. It is also necessary to study the interactions among species, bringing more comprehensive information on the ecology, diversity and landscape, than to study only one species (Jordano 2016).

Despite its high population densities and distinctive inflorescences, the giant hogweed hosts only limited spectrum of flower visitors compared to the local species pool of flower visitors recorded on native vegetation. Giant hogweed may represent a good and rich source of nectar for some larger insects (honey bee, social wasps, golden beetles and larger syrphids) but is probably not useful for the majority of insects. We think that its role as a nectar supplier is not as important as its negative and harmful effects on native vegetation, landscape, and humans. It is good to eradicate this plant in areas where it behaves invasively (Dodd et al. 1994; Pyšek and Pyšek 1995; Nielsen et al. 2005; Pyšek et al. 2010; Dostál et al. 2013). The management of habitats connected with the destruction of giant hogweed is thus necessary (Pyšek et al. 2010). We can also support this fact with our observations – giant hogweed was completely absent or present in 1–3 plants in many localities, which local botanists recommended, but it was very simple to find new unmanaged sites with many plants of this species, where nearly nothing else grew under and around giant hogweeds (Fig. 5).
Acknowledgements

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References


Floral visitors of giant hogweed


Supplementary material 1

List of localities
Authors: Petr Bogusch, Terezie Vojtová, Jiří Hadrava
Data type: Occurences (Excel spreadsheet)
Explanation note: table S1: List of localities - of total 39 localities, several were not sampled because no giant hogweeds were present there or the localities were too near to another locality and composed one locality together.
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Link: https://doi.org/10.3897/neobiota.86.100625.suppl1

Supplementary material 2

List of all species
Authors: Petr Bogusch, Terezie Vojtová, Jiří Hadrava
Data type: Occurences (Excel spreadsheet)
Explanation note: table S2: Lists of all species in all localities - occurrences of all four studied groups.
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Link: https://doi.org/10.3897/neobiota.86.100625.suppl2

Supplementary material 3

Other flowering plants in the localities
Authors: Petr Bogusch, Terezie Vojtová, Jiří Hadrava
Data type: Occurences (Excel spreadsheet)
Explanation note: table S3: Other flowering plant species at all localities with dominances measured in Braun-Blanquet scale.
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Link: https://doi.org/10.3897/neobiota.86.100625.suppl3