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Insects associated with sweet fennel: beneficial visitors attracted by a generalist plant

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Abstract

Insects provide key ecosystem services such as pollination, dung burial, soil enhancement, and pest control. Global insect decline requires restoration of the plant–insect mutualistic interactions. By using magnet plants, it is possible to supply beneficial insects with better resource availability and create more sustainable habitats. Current management practices recommend using Umbellifers (Apiales, Apiaceae) in restoration projects. However, analyses of the structure and dynamics of entomofauna associated with this plant family is needed to facilitate practical actions. Here the attention is focused on species composition and seasonal dynamics of beneficial insects associated with sweet fennel *Foeniculum vulgare* (Apiaceae, Umbelliferae) in Crimea. A 2-year sampling campaign identified 60 insect species from 40 genera across 20 families and four orders: Hymenoptera, Diptera, Coleoptera, and Neuroptera. These insects represented the groups such as social wasps, bees, ants, bumble bees, potter wasps, beetles, lacewings, mud daubers, tachinid flies, and hoverflies. Social wasps and hoverflies dominated in sample collections. Most of insects collected benefit ecosystems and provide essential ecosystem services. During fennel's flowering season, the number of visits by bumble bees, beetles, bees. and wasps decreased. Contrastingly, dipterans visitation increased towards the end of the season. Such trends might be explained with fennel's functional protandry, bias in nectar production between male and female flower stages, and insects' feeding preferences. *F. vulgare* attracts a diverse assemblage of beneficial insects and consequently can be recommended as a magnet species. When aiming to attract specific insect groups, the seasonal dynamics of fennel's associated entomofauna should be considered.

Keywords Ecosystem services · Foeniculum vulgare · Insect attraction · Magnet plants · Pollinators · Predators

Introduction

Insects provide ecosystem services such as food provisioning, recycling organic matter, biological control, and plant pollination (Noriega et al. 2018). The current phenomenon of global insect decline (Sánchez-Bayo and Wyckhuys 2019) and, more specifically, the decline of pollinators is primary caused by intensive agriculture, habitat conversion, and environmental chemicalization (Potts et al. 2010). Modern agriculture is largely dependent on managed pollinators. While causes of the decline in managed pollinators are being

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Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 1627, 70211 Kuopio, Finland elucidated, more investigations underlying the decrease in wild pollinators are needed. Primarily wild pollinators, unlike their managed counterpart, provide ecosystem services (Allsopp et al. 2008). Effective crop diversification schemes are a promising alternative to pesticide-oriented agricultural practice, as they can suppress herbivores, increase the abundance of natural enemies and decrease insect-related crop damage (Scherr and McNeely 2008; Letourneau et al. 2011). Increasing plant biodiversity and creation of wildflower strips is a key tool for the conservation of beneficial insects in commercial ecosystems (Campbell et al. 2012). Flowing plants within these strips, benefit insects providing essential ecosystem services, especially in resource poor ecosystems. Especially attractive plants within these wildflower strips have been coined "magnet" (Laverty 1992) or "framework" plants (Menz et al. 2011). Frequencydependent pollinator visitation increases in species-rich floral mixtures and general pollinator diversity may contribute to pollination service stability (Ghazoul 2006). Plants can



compete for pollinators, and in small or isolated populations, this can result in Allee effects (Courchamp et al. 2008). Alternatively, instead of competition, co-flowering plants may facilitate pollination, especially in species-rich swards (Ghazoul 2006). Pollinators can discriminate between flowers, but if more generalist pollinators are attracted to a specific habitat, then rare or less rewarded plant species receive increased attraction of pollinators to highly rewarding "magnet" species. Furthermore, greater biodiversity of plants favors pest reduction and supports the natural enemy hypothesis (Altieri 1991). However, diverse but arbitrarily composed floral vegetation plots may result in an increase of pest populations or repellence of beneficial insects from the target plant species or specific crop (Wäckers and van Rijn 2012). Therefore, identifying appropriate 'magnet' species and their associated entomofauna when developing eco-agricultural and mixed-agricultural landscapes (Scherr and McNeely 2008) will enhance biodiversity and inform biodiversity management practice.

Plants within the carrot family (Apiales, Apiaceae, Umbelliferae; hereafter umbellifers) are associated with diverse insect visitors and are often proposed as magnet species in restoration projects (Zych et al. 2007). Experimental removal of umbellifers led to a decline in the specialization of pollinator networks (Goldstein and Zych 2016). Despite much general knowledge regarding entomofauna associated with umbellifers, species-specific information is scarce. As mentioned by Memmott (1999), the proper understanding of the insect community structure requires an assessment of the all possible flower visitors. Umbellifers are often used in restoration projects due to the general knowledge that they attract a diversity of insects. In the current paper the data on the species composition and dynamics of insects, associated with umbellifer plant, *F. vulgare* have been discussed.

Materials and methods

Study species

Originating in the Mediterranean, sweet fennel *Foeniculum vulgare* (Miller, 1768) has been naturalized in many regions of the world. It is currently cultivated in Europe, Asia and North America (Badgujar et al. 2014). In its native range, it occurs in three varieties: as an annual, biennial or perennial herb (Piccaglia and Marotti 2001). *F. vulgare* has an erect hollow stem, up to 2.5 m in high, greenish-yellow flowers and feathery leaves. Its dichogamous flowers are arranged into large inflorescences—compound umbels of different orders. Like many other umbellifers (Stpiczyńska et al. 2015), within individual flower fennel demonstrates functional protandry. At first, flowers pass through a male functional stage with active anthers and then through the

female functional stage with active stigma. In this group of plants, protandry is characterized by centripetal development when earlier anthers occur in outer flowers of the compound umbels and outer umbellets within an umbel (Webb 1981).

Study area

The data collection and field observations were performed in 2009–2010 years in the vicinities of Nikitsky Botanical Garden, Yalta, Crimea (44.50° N, 34.23° E). The study area was previously (approximately 20 years) an experimental field of essential oil plants. Naturally recruited fennel shrubs were growing non-uniformly—denser in some areas and more sparsely in the others. During the *F. vulgare* flowering period, other the plants, including Italian strawflower (*Helichrysum italicum*), oregano (*Origanum vulgare*), thyme (*Thymus vulgaris*), Puget Sound gumweed (*Grindelia integrifolia*), lavender (*Lavandula angustifolia*) were also in bloom. The area of the meadow plot, where the observations were conducted, was approximately 11 200m².

Insect sampling and identification

Insect sampling was conducted in one study site (meadow of essential oil plants) during the summer (June-August) in 2009 and 2010. These data were pooled and analyzed together as the overall insect diversity rather than betweenyear variations was the study target. Four walking transects (100-130 m in length) were selected in both years. The average distance (Mean \pm SD) between transects was 15 ± 3.2 m. In 2009, insects were collected using the hand net within 3-days intervals during the peak flowering stage of F. vulgare in July. In 2010, insects were sampled via the same method but within 3- to 5-day intervals during the entire blooming period of sweet fennel, lasting from the first half of June (10th of June) till the first half of August (16 th of August). Only those insects, visited flowering umbels for pollen and nectar collection were counted during subsequent statistical analyses. Pests, such as sucking bugs, caterpillars and aphids were collected, but not statistically assessed. Hand-net collection was performed via steady pace walking and insect sampling from random flowering fennel umbels on the sides of the transect. That was conducted two times per day (1 h per one-time sampling) in between 10 and 12 AM and in between 2 and 4 PM. While collecting insects, the flowering stage of an umbel (male or female) was recorded. For the analysis, a species was defined as a visitor of both functional stages only if it was collected from both male and female umbels at least one time. Collected insects were stored in a 90% alcohol and further identified to species level with insect identification guides. The insects were assessed to morphotype such as: (a) bee; (b) bumble bee; (c) social wasp; (d) potter wasp; (e) parasitic wasp; (f)



mud dauber; (g) sphecoid wasp; (h) hoverfly; (i) tachinid fly; (j) beetle; (k) net wing. For the further statistical analyses this categorization was simplified and some insect categories (e.g., net wings) were discarded due to low number of registered visitors. As the sampling campaign was performed at a single study site, the further results should be considered at the local level and can't be extrapolated to the whole Crimea.

Analyses of seasonal dynamics of insects, associated with fennel

In 2010 ten focal plants were selected along each transect and used to investigate the seasonal dynamics of insect visitors. Five-minute focal observations were made for each control plant through the entire flowering season from the 10th of June till 16th of August in 2–5 days intervals. The flowering stage (male/female) of the umbels was registered for each observation, which allowed the further calculation of the population-level duration differences between stages. Insect visitors were accessed to morphotype (as described further) in 5-min sets of observations on a random umbel of each plant. Only umbels of the first and second orders were selected for observations. Each set of observations (n=40 plants per set) was performed during day peak activity between 10 AM to 4 PM in 1 day. Because the fennel's population in that year was monitored already from the beginning of June, the day when the first umbel started to bloom (10th of June) was selected as a starting point for the beginning of the flowering season. The total time of observations comprised 50 h and 600 observations. One observation was considered as registration of all insect visitors for 5 min at the one umbel (1st or 2nd order) of a fennel plant.

Five merged insect morphotypes were considered when analyzing seasonal dynamics of entomofauna associated with *F. vulgare*: (1) bees, including honey bee and wild bees; (2) bumble bees; (3) wasps, including social, solitary, sphecoid, spider- and parasitic wasps; (4) flies, including hoverflies, flesh and tachinid flies; (5) beetles. Although belonging to the bees' group, bumble bees were not merged with bees. Already during the preliminary data collection stage, they were noticed to visit only umbels of the male functional stage. The other reason for quantifying bumble bees separately was the potential need for such information for practitioners, as bumble bees represent one of the most common groups of managed pollinators.

Statistics

The overall diversity of insects attracted by *F. vulgare* (sample data) was analyzed using Simpson's diversity index. The proportion of each insect group in the collected sample set was estimated in percentages. Further statistical analyses were carried out using statistical software SAS version 9.4

(SAS Institute, Cary, NC, USA). Population-level differences in duration of male and female functional flowering stage (number of days since the start of the fennel's flowering season) of fennel (n = 40 plants) were analyzed using t-Test for independent samples with Satterthwaite approximation of degrees of freedom. The number of days was used as a continuous dependent variable and umbel functional stage was used as a categorical independent variable with two levels (1-male; 2-female). Also, t-Tests were used to assess the difference in insect visitation between functional stages. The seasonal dynamics of fennel-associated entomofauna was analyzed using Generalized Linear Model (GLM procedure Genmod in SAS) using a Poisson error distribution and log link function. This model was selected because all dependent variables (insect morphotypes) did not fit requirements for normally distributed data. Besides, the model was chosen because each insect morphotype was a count-type variable. The duration of the flowering season (number of days from the beginning of the flowering season) was used as an explanatory variable in GLM. Transect id was not included as a random factor into the model as each of four transects was selected randomly in each sampling occasion in the same field, so no generic factor was expected.

Results

Diversity of insect visitors on fennel

A total of 316 insect specimens, representing 4 orders, 40 genera, 20 families and 60 distinct species, were collected from flowering umbels of F. vulgare were over the 2-year study (Table 1). Simpson's index revealed a high diversity of insects, visiting fennel (D = 0.09). The data obtained after species identification demonstrated that in Crimea fennelassociated entomofauna comprised the groups of insects such as social wasps, hoverflies, beetles, bumble bees, potter wasps, mud daubers, tachinid flies, sphecoid and parasitic wasps. Social wasps and hoverflies dominated in sample collections, followed by bees, beetles and bumble bees (Fig. 1). Many groups of insect species attended both male and female functional stages of fennels' umbels. However, some of those, like bumble bees, preferred visiting only male flowers and were not found visiting umbels with the female functional stage.

Seasonal dynamics of fennel-associated entomofauna

Because of fennel's functional protandry, it was important to determine if there was a difference in the duration of male and female flowering stages at the population level. In 2010



 Table 1 Different groups of beneficial insect species attracted by F.vulgare in Crimea

Insect group	Species name	n	Captured on the functional stage		
			Male	Female	Both
Social wasps (Vespidae)	Polistes nimpha	14			×
	Polistes dominula	28			×
	Polistes gallicus	13			×
	Vespula germanica	6			×
	Vespula vulgaris	5			×
	Vespula rufa	3			×
	Dolichovespula sylvestris	1	×		
	Dolichovespula media	2	×		
Ants (Formicidae)	Formica cinerea	2	×		
Potter wasps	Eumenes papillarius	1	×		
(Eumenidae)	Eumenes mediterraneus	5			×
	Eumenes coarctatus	4	×		
	Katamenes dimidiatus	1	×		
	Euodynerus dantici	4	×		
	Syneuodynerus egregius	1	×		
	Ancistrocerus gazella	1	×		
Mud daubers (Sphecidae)	Sceliphron destillatorium	11			×
	Sceliphron caementarium	5			×
	Sceliphron curvatum	1	×		
Sphecoid wasps (Sphecidae)	Philanthus triangulum	5			×
	Larra anathema	1	×		
	Cerceris arenaria	6	×		
Spider wasps (Pompilidae)	Batozonellus lacerticida	1	×		
Parasitic wasps (Leucospidae, Gesteruptiidae, Chrysididae)	Leucospis affinis	5			×
	Gasteruption jaculator	2	×		
	Chrysis sexdentata	2	×		
Honey bees (Apidae)	Apis mellifera	21			×
Bumble bees (Apidae)	Bombus terrestris	8	×		
	Bombus lucorum	7	×		
	Bombus argillaceus	1	×		
	Bombus fragrans	4	×		
Wild bees (Halictidae, Andrenidae)	Halictus quadricinctus	10			×
	Halictus scabiosae	9			×
	Andrena sp.	6			×
Hoverflies (Syrphidae)	Eristalis tenax	12			×
	Eristalis arbustorum	9			×
	Eristalis interruptus	3			×
	Myathropa florea	6			×
	Cheilosia pallipes	6			×
	Volucella zonaria	4		×	
	Eupeodes corollae	9			×
	Merodon tricinctus	5			×
	Sphaerophoria scripta	7			×
	Melanostoma millenium	10			×



Table 1	(Lacreige a.a.)
Table 1	(continued)

Insect group	Species name		Captured on the functional stage		
			Male	Female	Both
Tachinid flies (Tachinidae)	Cylindromyia intermedia	8			×
	Cylindromyia bicolor	2			×
	Tachina sp. 1	1		×	
	Tachina sp. 2	1		×	
	Sarcophaga sp.1	1		×	
	Sarcophaga sp. 2	1		×	
Beetles (Cleridae, Coccinellidae, Cantharidae, Scarabaeidae, Cetoniidae, Cerambycidae)	Trichodes apiarius	6	×		
	Coccinella septempunctata	4	×		
	Coccinella quatuordecimpustulata	4			×
	Adalia bipunctata	4			×
	Rhagonycha fulva	5	×		
	Cetonia aurata	4			×
	Oxythyrea funesta	2	×		
	Chlorophorus varius	5	×		
Net wings (Chrysopidae)	Chrysoperla carnea	1	×		

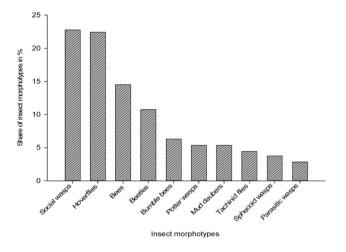


Fig. 1 Frequencies of different insect groups attracted by *F. vulgare*. Data based on sample collections in years 2009-2010 (n=312 specimens)

the duration of days from the start of the flowering period was different between fennels' functional stages (t=-33.11; df=597.94; p<0.0001) (Mean \pm SD: $23.71\pm1.41: n=600$, Fig. 2). Male umbels were mass flowering nearly 25th day from the beginning of the flowering season (model-based mean number of days \pm Cls: male functional stage: $25.04\pm1.18: n=427$). In the studied sample any functionally active female umbel of 1st or 2nd order was recorded before 34th day from the beginning of flowering season (Min=34, Max=56) and the mass flowering peak for that

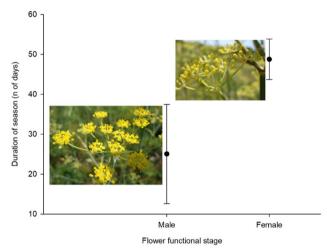


Fig. 2 Mean difference (Mean \pm SD) in the number of days from the beginning of *F. vulgare* flowering season between male and female functional stages. Mean values are obtained from the *t*-test (*T* test procedure in SAS; n = 600)

stage was around 48th day (model-based mean number of days \pm Cls: female functional stage: 48.75 ± 0.76 : n = 173).

When revealing the difference in insects' visitation between male and female functional stages, the significant results were obtained for bees, bumble bees, and beetles, but not for wasps and flies (Table 2).

GLM analyses revealed that the duration of fennel's flowering season significantly affected presence of all five



Table 2 Difference in insects visitation (Mean visits \pm SD) between *F. vulgare* male and female functional stages (*T* test procedure in SAS)

				Male stage		Female stage	
Insect group	t	df	p	n	Mean ± SD	n	Mean ± SD
Wasps	2.5	598	0.012	427	3.1 ± 1.5	173	2.7 ± 1.7
Bees	5.9	598	< 0.005	427	2.1 ± 1.4	173	1.3 ± 1.3
Bumble bees	31	426	< 0.005	427	1.7 ± 1.1	173	_
Beetles	6.2	591	< 0.005	427	0.6 ± 1.1	173	0.2 ± 0.5
Flies	-1.7	598	0.702	427	2.9 ± 1.7	173	3.2 ± 1.6

Significant p values are marked as bold

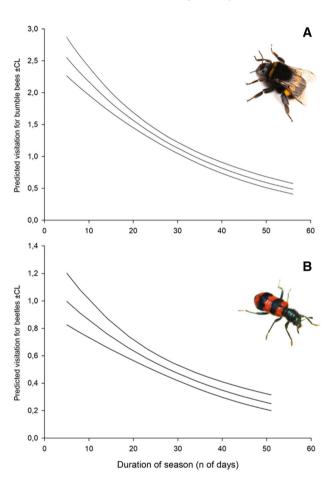


Fig. 3 Predicted visitation \pm CL for bumble bees (a) and beetles (b), affected by the duration of fennel's flowering season (obtained from the GLM model; n=600 observations)

insect groups on umbels, however in different ways. With the continuation of season there was a noticeable decrease in bumble bees ($\chi^2 = 172.78$, df = 1, p < 0.0001, Fig. 3a) and beetles ($\chi^2 = 61.03$, df = 1, p < 0.0001, Fig. 3b). Presence of bees ($\chi^2 = 12.12$, df = 1, p = 0.0005, Fig. 4a) and wasps ($\chi^2 = 8.84$, df = 1, p = 0.003, Fig. 4b) were also decreasing towards the end of the season but to a lesser extent than bumble bees and beetles. Contrastingly, there

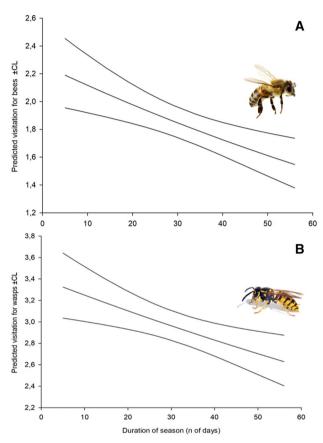


Fig. 4 Predicted visitation \pm CL for bees (a) and wasps (b), affected by the duration of fennel's flowering season (obtained from the GLM model; n = 600 observations)

was an increase in flies' visits towards the end of fennels' flowering season ($\chi^2 = 8.58$, df = 1, p = 0.0034, Fig. 5).

Discussion

Insect diversity and attraction by fennel

Results of the current study demonstrate that fennel attracts taxonomically diverse insect fauna. This is consistent with the previous results obtained for the other umbellifers (Ricciardelli D'albore 1986; Maingay et al. 1991;



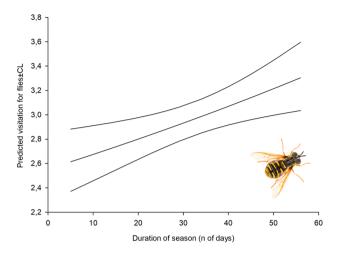


Fig. 5 Predicted visitation \pm CL for flies, affected by the duration of fennel's flowering season (obtained from the GLM model; n=600 observations)

Zych 2007; Zych et al. 2007) and with the study about fennel as an isolation buffer between organic and conventional production areas (Ugrenović et al. 2012). In Crimea major groups of visitors comprised hymenopterans, dipterans and coleopterans. Interestingly, during the 2nd year of observations, it was found that fennel was a feed plant for the old world swallowtail butterfly Papilio machaon, as two larvae of this species were found. Wehling and Thompson (1997) reported that in North America F. vulgare was a very common host plant for anise swallowtail butterfly *Papilio zelicaon*. My data demonstrate that during 2 study years lepidopterans were not registered as visitors in Crimea. Neuropterans were present but rare. However, F. vulgare was shown as a beneficial plant for the fecundity of Chrysoperla carnea (Neuroptera, Chrysopidae), which is an important agent of biological control (Gonzalez et al. 2016). Current data on the insect diversity of F. vulgare allow considering it as a potential magnet species with further comparison between its entomofauna and that of the neighboring plants.

The key attractants of flowers are volatiles, color, architecture and availability of reward (nectar or pollen) (Bronstein et al. 2006; Miller et al. 2011). Key odorants of fennel are *trans*-Anethole, estragole, fenchone, *p*-anisaldehyde and *cis*-anethole (Diäaz-Maroto et al. 2005). Conspicuous greenish-yellow tint of fennel's petal is among the most attractive colors for pollinators (Faegri and Van Der Pijl 2016). Flowers with nectaries that are completely exposed are attractive to taxonomically diverse groups of insects (Bronstein et al. 2006). Due to all these factors, fennel is a highly attractive species to diversity of insects A plant, which is pollinated by a large number of taxonomically

diverse species, follows a generalist plant strategy or simply is called a "generalist" plant (Menz et al. 2011). However, flower visitation does not necessarily lead to pollination (Memmott 1999). Frequently umbellifers, that receive a diversity of visitors can have a limited number of real pollinators (Niemirsky and Zych 2011); and the range of true pollinators of *F. vulgare* has not been yet revealed.

Two prevalent groups, which dominated in sample collections, were social wasps (Vespidae) and hoverflies (Syrphidae). Carnivorous larvae of both social wasps and many hoverflies (which can also be saprophagous or phytophagous) require proteins from prey insects, while adults feed on carbohydrates and search for nectar on plants (Gilbert 1981; Hemptinne et al. 1993; Richter 2000). Therefore, they can act as both predators and pollinators. For example, Polistes wasps were effectively used to protect crops from lepidopteran pests (Gould and Jeanne 1984; Southon et al. 2019) and larvae of a hoverfly Episyrphus balteatus were able to suppress aphid colony growth (van Rijn et al. 2013). Hoverflies are among the most important groups of wild pollinators globally (Rader et al. 2016). Polistes and Vespula wasps can make an essential contribution to plant pollination too. In Crimea it was found that the rare and endangered orchids such as broad-leaved helleborinae (Epipactis helleborine), steveniella (Steveniella satyrioides) and bug orchid (Orchis *coriophora*) were pollinated by social wasps (Ivanov et al. 2015). Other Crimean orchids from the genus *Epipactis* were also largely dependent on the pollination service provided by Vespidae wasps (Fateryga and Ivanov 2012).

Besides social wasps and hoverflies fennel attracted honey bees, wild bees and bumble bees, beetles, various groups of wasps and flies. Most of those are beneficial pollinators (Rader et al. 2016) and some are important agents for biological control being predators and parasitoids (Lopez et al. 2013; Wang et al. 2019).

The insect community found in this study differs from that associated with fennel found in other parts of the specie's range. In India honey bees were the predominant group of insects visiting *F. vulgare*, following by wasps and flies (Chaudhary 2006; Shilpa et al. 2014). However, research by Shilpa et al. (2014) recorded only 16 insect species. Studies conducted in Czech Republic suggested that fennel attracts pronominally ladybeetles and hoverflies, and therefore it can be included as a beneficial plant to flower strips (Kopta et al. 2012). Further data about insects associated with *F. vulgare* in different geographic areas will benefit revealing of the community structure at a broader scope.

Insect dynamics

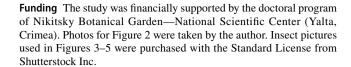
Across a range of fennel's distribution, there might be variation in the duration of its flowering season. In Crimea fennel was in bloom around 9 weeks, while in the USA



flowering period was reported to be 12 weeks (Maingay et al. 1991). Results of the current study revealed that at the population level there was a difference in the duration of male and female functional stages. There was significant bias towards the male functional stage, which lasted for about 23 days longer than the female stage. It has been previously found that in dichogamous species nectar production if often different between sexual stages. For example, in Angelica sylvestris it was three times lower during the stigma receptive period (Stpiczyńska et al. 2015). Therefore, it is more likely that due to functional protandry and different floral nectar production between sexual phases, not all insects visit both types of flowering umbels. Results of the current study confirm that at least visitation by bees, bumble bees and beetles differ between F. vulgare sexual stages. My data also demonstrate that during the flowering season number of bumble bee and beetle visitation decreased after the end of the mass flowering male stage. Wasps and bees were also decreasing towards the season end, however not so rapidly. Contrary to the other groups, the number of fly visitation was increasing towards the season end. Interestingly, medium-size flies were revealed to be the most important pollinators for the Umbeliferrae plant Heracleum sphondylium (Zych 2007). So, it is more likely that hoverflies significantly contribute to pollination of fennel.

The most significant plant-insect mutualistic interactions include pollination, protection and seed dispersal (Bronstein et al. 2006). By attracting diverse insect species, fennel can benefit other plant species and indirectly favor ecosystem services. Current management schemes described as pollinator friendly management techniques appear to benefit the restricted number of aculeate species, mainly honey bees and bumble bees (Wood et al. 2015). Therefore, careful selection of the ways and methods of attracting beneficial insects will contribute to creation better habitat types. High-quality ecosystem services can be provided by insects in habitats with enough resources. Using F. vulgare in creation of wildflower stripes and restoration projects will favor attraction of diverse beneficial insects and will promote the overall conservation of plant-insect mutualistic interactions.

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Compliance with ethical standards

Conflict of interest The author declares that they have no conflict of interest.

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