

## Myophily in the critically endangered umbelliferous plant *Ostericum palustre* Besser (Apiaceae)

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**Abstract** Globally, many plant species face human-induced habitat loss and an associated reduction in population size and vitality. Their survival is often possible only when appropriate conservation measures are taken that address the biology and ecology of these species, including their reproduction, often the most vulnerable stage in the life history of the organism. Unfortunately, little is known about these aspects of the biology of many listed plant species. For 3 years, we studied the pollination biology of the critically endangered plant species *Ostericum palustre* Besser (Apiaceae), one that is listed in the Bern Convention and Annex II of the EU Flora–Fauna Directive. Flowers of this taxon were visited by over 81 species of anthophilous insects derived from 5 taxonomic orders, indicating the presence of a generalised pollination system. However, detailed analyses of the frequency of insect visits, pollen loads and insect behaviour on inflorescences suggest that the plant is chiefly pollinated by large Diptera, predominantly large Syrphid flies and Muscoid flies, that together are often responsible for over 90 % of total pollinations. Occasionally, wasps (Vespidae) may also be involved in the pollination of this species. With respect to the pollination system of *O. palustre*, our results indicate that this is a classic example of myophily, and generally, this species can be regarded as a functional specialist, but

like many other members of Apiaceae, it is a typical “bet-hedger”. This strategy may probably increase the plant’s reproductive success in a range of habitat conditions, suggesting that the pollination system is unlikely to be the cause of rarity in this species.

**Keywords** *Angelica palustris* · Diptera · Natura 2000 · Pollination · Protandry · Umbelliferae

### Introduction

Globally, many flowering plant species are rare and endangered as a direct result of human pressure on their habitats (Schemske et al. 1994). They usually display a limited geographical distribution and occur in small, isolated populations. Their survival is often possible only with appropriate conservation measures aimed at stabilizing and extending the number and size of these populations (Kwak and Bekker 2006). This goal, however, cannot be successfully achieved without a thorough understanding of the biology of the species and the various ecological interactions that link it to other organisms (Schemske et al. 1994). This is especially true of zoogamous and zoochorous plants which are associated with various animal species that ensure successful pollination of their flowers and dispersal of their seeds. In such cases, growth rate of populations may be directly related to the reproductive success of the plant (Gaudeul and Till-Bottraud 2003), as determined, for instance, by pollination events. Although characterization of the reproductive biology of these threatened plants may provide valuable information, often resulting in their conservation or restoration success (Dixon 2009; Menz et al. 2011), little is known of the biology of many listed plants. For example, the pollination systems of fewer than 20 % of

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the Polish Red List plants have been thoroughly studied (Zych and Jakubiec 2008).

*Ostericum palustre* (Apiaceae) is a good example of the above. This plant occurs in Eastern Europe and Western Asia (Dittbrenner et al. 2005), and it is rare and threatened throughout its range (Schnittler and Günther 1999). Populations of the plant are generally small and reduced in number, mainly due to habitat loss, and exhibit a marked reduction in genetic diversity (Dittbrenner et al. 2005). Owing to its Europe-wide conservation status, this plant has been included in the Bern Convention, and subsequently listed in Annex II of the EU Flora–Fauna Directive—Natura 2000 (Czarna and Załuski 2001). It is generally described as zoogamous (Czarna and Załuski 2001; Załuski 2004), but we failed to find any information relating to its pollination system in the literature. Being a member of the Apiaceae and producing open and unrestricted flowers that are easily accessible to a vast array of potential pollinators, this plant can perhaps, based on its pollination systems, be considered as an ecological and functional generalist (Ollerton et al. 2007). In fact, many umbelliferous plants are reported to be visited by dozens or even hundreds of anthophilous insect species (Knuth 1898; Ellis and Ellis-Adam 1993, 1994; Zych et al. 2007), and according to Corbet (2006), the whole family could be regarded as “morphologically specialized for ecological generalization”. Although generalization of pollination system is suggested to mitigate some factors resulting from population fragmentation and species rarity (Johnson and Steiner 2000; Kwak and Bekker 2006), this may not necessarily hold when tested experimentally (see, e.g. Corbet 2006). However, even in the case of generalist species, their reproductive biology may be threatened by habitat fragmentation, as demonstrated for another endangered member of the family, namely, *Seseli farrenyi* Molero & Pujadas (Rovira et al. 2004). Furthermore, in recent years, the pollination systems of a number of species of Apiaceae have been investigated, and these have proved to be less generalized than anticipated, exhibiting at least ecological and/or functional specialization (Lindsey 1984; Zych 2007; Carvalheiro et al. 2008; Niemirski and Zych 2011). This may also be the case for *O. palustre* with profound effects on preservation of this rare species.

In order to make up the deficit in our knowledge of the reproductive biology of the critically endangered *O. palustre*, we studied, for 3 years, the pollination biology of one of the largest Polish populations of this plant. Our study focussed on: (1) recording those insect species that visited the flowers, (2) their relative importance in pollinating the latter, together with presumed temporal variation, and (3) the nature of the pollination system (degree of generalization) of this species.

## Materials and methods

### *Ostericum palustre* Besser

*O. palustre* [= *Angelica palustris* (Besser) Hoffm.] is a biennial or perennial (hemicryptophyte), with cauline leaves arranged in a rosette producing erect flowering stems up to 1.20 m tall (Cannon 1968; Załuski 2004; Fig. 1). The plant usually grows in wet, traditionally used meadows on peaty soils (Dittbrenner et al. 2005; Nobis and Piwowarczyk 2008; Michalska-Hejduk and Kopeć 2010). It is regarded as an Euroasiatic-continental species, and in Europe, its geographical range includes several Central European countries (Cannon 1968). In Poland, it is found mainly in the central and south-eastern part of the country (Czarna and Załuski 2001; Załuski 2004; Nobis et al. 2008; Krasicka-Korczyńska 2009; Ciosek et al. 2012).

The plant is self-compatible (East 1940), and reproduces by seed, and vegetative reproduction is not known to occur (Załuski 2004; Dittbrenner et al. 2005; Krasicka-Korczyńska 2008). Its flowers are white and protandrous, and arranged in compound umbels (Fig. 1) that are visited by various insects for nectar and pollen (M. Zych, pers. obser.). It is andromonoecious, i.e. both bisexual and functionally male flowers are produced on an individual plant. The flowers are protandrous, i.e. the flowering begins with the pollen presentation phase and ends with the stigma receptivity phase, the two being temporally separated in a single flower. As in many Apiaceae (see, e.g. Niemirski and Zych 2011, and lit. cited), this is usually synchronised within the whole inflorescence and the plant, with flowers within a primary (main) umbel entering centripetally male phase (Fig. 1b) and, when all pollen within the inflorescence is shed, the stigmas become receptive (Fig. 1c). Lateral (side or secondary) umbels start to flower not earlier than the main umbel is pollinated. In *O. palustre* protandry within a particular umbel (interfloral) is sometimes incomplete and floral sexual phases may be overlapping for a brief period (Zych, unpublished).

*O. palustre* is a rare and highly threatened plant species. In Poland, it has been protected by law since 2001 (Krasicka-Korczyńska 2008) and is included in the Plant Red Book (EN; Czarna and Załuski 2001) and the national Plant Red List (VU; Zarzycki and Szeląg 2006). It is also red-listed for other Central European countries within its range (Dittbrenner et al. 2005) and is considered to be “critically endangered” (CR) throughout the whole of Central Europe (Schnittler and Günther 1999).

### Study site

The region of the Noteć River Valley and the Bydgoszcz Canal (Kuyavian-Pomeranian Province, NW Poland) are

**Fig. 1** Flowering shoot and inflorescences (compound umbels) of *Ostericum palustre*. **a** Main flowering stem with primary (arrow) and secondary umbels. Scale bar 0.1 m. **b** Primary umbel during the early male phase, note visible anthers (arrow). Scale bar 10 mm. **c** Primary umbel during the female phase, note the lack of anthers and visible elongated styles (arrow). Scale bar 10 mm



rich in *O. palustre* populations (Krasicka-Korczyńska 2009). The survey investigated one of the largest populations of the species in this area, in a large wet meadow complex adjacent to the villages of Minikowo and Ślesin, near Bydgoszcz, N53°08'58", E17°43'03" (Krasicka-Korczyńska 2008).

#### Field observations

Field observations were conducted during 2008–2010, in mid-August, the peak flowering time for *O. palustre* in NW Poland (Krasicka-Korczyńska 2008).

In 2008 we observed only female phase umbels, and in 2009 and 2010 both male and female phase umbels. Only primary umbels, which, in habitats used for agricultural purposes, are mainly responsible for seed production in the species (Krasicka-Korczyńska 2008), were chosen for observations.

We used a slightly modified version of the observation method of Zych (2007) and Niemirski and Zych (2011). Each full study day would comprise a maximum of six rounds of observations. Each round started at alternate hours commencing at 0800 hour, lasted approx. 1 h, and consisted of three phases, namely, random choice of umbel, video recording (15 min), and insect capture (15 min). Once selected, umbels were not excluded from the subsequent round, and therefore it was possible that the same umbel was observed more than once. During inclement weather (strong winds or rain), observations were halted and re-commenced on subsequent days at the appropriate

hour until 12 rounds were completed for a particular umbel sexual phase in any given year (except for 2008, when only 6 rounds for female phase umbels were completed). The analyses were based on a total of 1,620 min of insect recordings and capture.

Once an umbel had been selected, it was staked to prevent wind-induced movements. Insect activities were then recorded for 15 min using a digital video camera (NV-GS75; Panasonic, Matsushita Electric Industrial Co. Ltd or HDRXR106, Sony Corp. Japan). The camera was set on a tripod about 0.5–1 m from the umbel so that the recording field allowed observations to be made over the whole surface of the inflorescence. After recording, for 15 min, all the insects visiting the umbel were collected either with an entomological net (Diptera, Hymenoptera, Lepidoptera) or directly into plastic vials or an entomological exhauster (wingless Hymenoptera, Coleoptera, Hemiptera). Insects were killed with ethyl acetate and pinned and stored for further investigation of their pollen loads. Aphids and other small, sap sucking insects (e.g. Thysanoptera), and those insects smaller than 1 mm, were excluded from the analyses. Despite their well-documented inefficiency as pollinators (Puterbaugh 1998; Beattie and Hughes 2002), we did not exclude ants from our analysis, since recently, they have been reported to pollinate some umbelliferous plants (Carvalho et al. 2008; Cursach and Rita 2012a, b).

The recordings were analysed in the laboratory for the number of visits to individual inflorescences and the number of umbellets visited by a single insect within a particular compound umbel. Similar species were grouped

together on taxonomical and morphological (size) grounds into following visitor guilds: Vespidae (predatory wasps of the family Vespidae), large Syrphids (hoverflies >8 mm in length), small Syrphids (hoverflies <8 mm in length), large Muscoid flies (insects of the families Calliphoridae, Muscidae, Sarcophagidae, Tachinidae >10 mm in length), medium Muscoid flies (insects of the families Calliphoridae, Muscidae, Sarcophagidae, Tachinidae approx. 5–9 mm in length). Rare visitors from other taxonomic groups (e.g. beetles, butterflies, small flies etc.) were pooled as other.

#### Pollen loads analysis

Insects collected in the field were later analysed in the laboratory for their body pollen loads. For the preparation and analysis of insect pollen loads, the gelatine-fuchsine method of Dafni et al. (2005) was used. Using fine forceps, a Nikon SMZ 645 stereomicroscope and a small cube (ca. 3–4 mm<sup>3</sup>) of gelatine-fuchsine jelly, all visible pollen grains adhering to the insect body surface were removed. The jelly was then transferred to a glass microscope slide, a coverslip was applied, and the slide was gently heated over a flame to make a semi-permanent preparation. A Nikon Eclipse 100 light microscope was used to score the total number of pollen grains of both *O. palustre* and ‘other’ taxa. The loads were sub-sampled (all pollen grains were scored for nine areas evenly distributed over the cover slip) and the results, after calculation of the arithmetic mean of the counts, were extrapolated to the area of the coverslip to obtain the pollen load in a given sample.

#### Pollination importance

Like other umbellifers, *O. palustre* is visited by a wide range of anthophilous insects. Consequently, since direct methods of assessing the performance of floral visitors were impractical (Lindsey 1984; Niemirski and Zych 2011), we used a slightly modified indirect method, as described by Zych (2002, 2007), which is based on counts of insect pollen loads and observations of insect frequency, abundance and behaviour on inflorescences:

$$I_X = V \times U \times PL;$$

where  $I_X$  importance of insect species  $X$ ,  $V$  abundance (number of recorded visits of species  $X$  + number of captured individuals of species  $X$ )/(total number of recorded visits + total number of captured individuals),  $U$  mean number of umbellets visited by species  $X$  within an umbel;  $PL$ , average *O. palustre* pollen load (number of pollen grains) carried by an individual of species  $X$ .

We calculated  $I$  separately for each season and floral sexual phase ( $I_f$  and  $I_m$ , respectively for female and male

umbel sexual phases), and then totalled the results for all the insect groups within a particular study year and sexual phase of the flowers to obtain the maximum possible value. The relative importance coefficient, indicating the insect importance level of guild on male ( $IC_m$ ) and female ( $IC_f$ ) umbels, was expressed as a percentage of the total value. Following Zych (2007), we assumed that efficient pollinators should have  $I_f/I_m > 0$  and  $IC_f > 1\%$ .

#### Statistics

Since the data for visit frequency and number of umbellets visited by various visitor guilds could not be successfully normalized by transformation, we compared them using non-parametric Kruskal–Wallis ANOVAs followed, when necessary, by Kruskal–Wallis tests for multiple comparisons. All calculations were made using Statistica 7.1 (Stat Soft Inc. 2005, Tulsa, OK, USA).

## Results

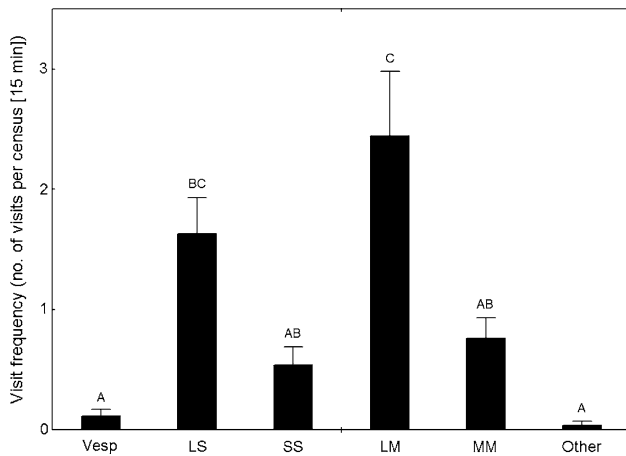
#### Insect visits

During the 3 years of study, we observed 81 insect taxa visiting flowers of *O. palustre* (Appendix). Flower visitors represented 5 taxonomic orders and most belonged to the order Diptera (80 %), with a small proportion of Hymenoptera (11 %, mostly wasps) and other insects (9 %).

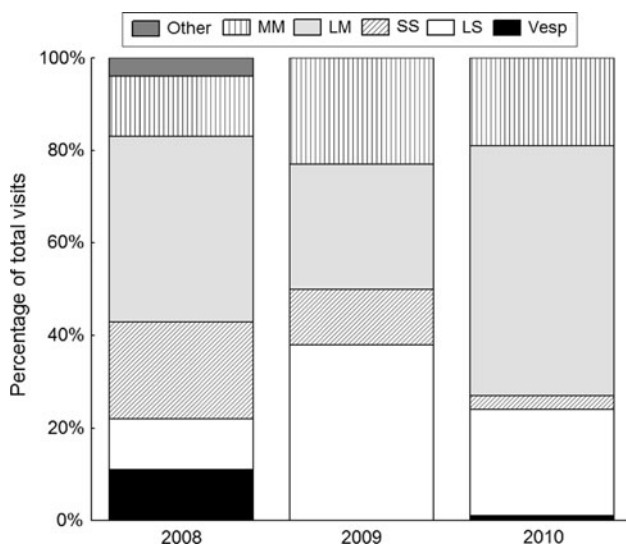
For this same period, we recorded 339 individual visits to umbels of *O. palustre*, and we observed, on average,  $6.2 \pm 6.2$  visits per census (15 min;  $N = 54$ ) per umbel. There were no significant differences in visit frequency between male vs. female phase umbels (Kruskal–Wallis ANOVA for data pooled over 3 years:  $H_{1, N=378} = 0.3220$ ;  $P = 0.57$ ) nor between study years (Kruskal–Wallis ANOVA for data pooled over two umbel sexual phases:  $H_{2, N=378} = 5.6615$ ;  $P = 0.06$ ). Therefore, in subsequent analyses, we decided to pool the visit data derived from both umbel sexual phases and for each of the 3 years of study. We found significant differences between the visit frequency of insects from various guilds (Kruskal–Wallis ANOVA:  $H_{5, N=378} = 72.3772$ ;  $P \ll 0.01$ ). The most frequent visitors were large Muscoid flies and large Syrphids. Visits by the remaining group were relatively rare (Fig. 2).

Regarding the number of visits for a particular year, the largest proportion of visits could be attributed either to large Muscoid flies (40 % in 2008 and 54 % in 2010) or to Large Syrphids (38 % in 2009; in both cases, data based on video recordings were pooled over 2 umbel sexual phases; Fig. 3). Overall, depending on the study year under consideration, visits by Dipterans constituted 85–100 % of all recorded visits.



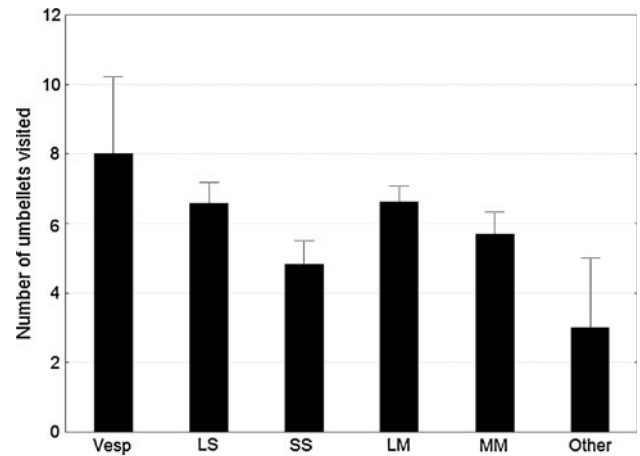


**Fig. 2** Mean visit frequency ( $\pm$ SE) of the key floral visitor guilds to umbels of *Ostericum palustre*. Data were pooled over three study years and both umbel sexual phases. Different letters placed above the mean indicate statistically significant differences at  $P < 0.05$  (Kruskal–Wallis tests for multiple comparisons). *Vesp* Vespidae, *LS* large Syrphids, *SS* small Syrphids, *LM* large Muscoid flies, *MM* medium Muscoid flies



**Fig. 3** Insect visits to umbels of the studied population of *Ostericum palustre* during 2008–2010, expressed as a percentage of total visits for a particular year (47 in 2008, 109 in 2009 and 183 in 2010); data based on video recordings, pooled for both umbel sexual phases. *Vesp* Vespidae, *LS* large Syrphids, *SS* small Syrphids, *LM* large Muscoid flies, *MM* medium Muscoid flies

During bouts on umbels, insects visited, on average,  $6.3 \pm 5.2$  ( $N = 339$ ) umbellets per inflorescence (mean inflorescence size in population was  $17.6 \pm 2.7$  umbellets). Although we observed some differences, especially between visitor guilds (Fig. 4), we found them to be statistically insignificant (Kruskal–Wallis ANOVA:  $H_5, N=339 = 3.8314$ ;  $P = 0.57$ ), together with the effect of study year (Kruskal–Wallis ANOVA:  $H_2, N=339 = 1.7720$ ;  $P = 0.41$ ) and umbel sexual phase (Kruskal–Wallis



**Fig. 4** Mean number of umbellets ( $\pm$ SE) visited during a single bout at an individual umbel of *Ostericum palustre* by representatives of various insect guilds. Data pooled for three study years and umbel sexual phases. *Vesp* Vespidae, *LS* large Syrphids, *SS* small Syrphids, *LM* large Muscoid flies, *MM* medium Muscoid flies

ANOVA:  $H_1, N=339 = 0.5628$ ;  $P = 0.45$ ). Ants (*Myrmica rubra*) were seen on umbels of *O. palustre*. Although we observed them feeding on nectar present on the stylopodium, owing to their small size, they generally did not come into contact with the reproductive organs of the plant, in particular, the anthers and stigmas.

Pollen loads

During the study period, we analysed 261 insect body pollen loads and found large differences between visitor guilds. Some individual insect species, e.g. the ant *M. rubra*, carried no pollen grains on their bodies (these insects were included in “other”), whereas the largest individual *O. palustre* pollen load, comprising 16,197 pollen grains, was found in 2009 on an individual of Vespidae, and the largest “other” pollen load, comprising 4,603 pollen grains, on a representative of the large Syrphids. Generally, *O. palustre* pollen was found on several representatives of each of the insect guilds. The largest average pollen loads were carried by Vespidae (if present) and large Syrphids (Table 1). The latter also usually carried the largest “other” pollen loads.

Pollination importance

On the basis of  $I_f/I_m$  and IC values for male and female umbel sexual phases, the most constant pollinators were generally large flies from the large Syrphids and large Muscoid flies guilds (Table 2). Except for 2008, their summed IC values for each study year constituted the main share in both male and female phase umbels. In 2008, however, the pollination of female phase umbels was

**Table 1** Body pollen loads for six pollinator guilds observed visiting umbels of *Ostericum palustre* during study periods in 2008–2010

	2008			2009			2010								
	F			M			F								
	PL	N	'other'	PL	N	'other'	PL	N	'other'						
Vespidae	1,704 ± 2,381	16 ± 27	8	0	16,197	1,258	1	0	0						
Large syrphids	286 ± 291	25 ± 32	7	2,080 ± 2,162	1,445 ± 1,305	13	2,140 ± 1,774	751 ± 665	14	1,743 ± 1,196	1,039 ± 831	10	755 ± 443	912 ± 944	4
Small syrphids	53 ± 60	6 ± 13	4	205 ± 137	133 ± 133	7	106 ± 52	241 ± 429	5	838 ± 1,078	507 ± 507	12	122 ± 160	830 ± 890	6
Large muscoid flies	176 ± 225	63 ± 89	2	223 ± 121	69 ± 52	8	380 ± 451	143 ± 142	10	366 ± 455	130 ± 133	31	246 ± 331	111 ± 192	17
Medium muscoid flies	214 ± 242	29 ± 44	18	246 ± 267	182 ± 218	9	406 ± 562	144 ± 200	14	469 ± 606	197 ± 337	17	113 ± 138	29 ± 60	6
Other	776	0	1	1,099 ± 1,974	101 ± 120	7	42 ± 73	25 ± 44	3	597 ± 670	31 ± 32	4	12 ± 37	12 ± 37	23

F, female phase umbels; M, male phase umbels; PL, average pollen load of *O. palustre* (no. of pollen grains); PL 'other', average pollen load of other plant species (no. of pollen grains); N indicates sample size; data displayed as mean ± SD

mainly performed by wasps ( $IC_f = 64\%$ ; no  $I_f/I_m$  value available). These insects were, however, almost absent in subsequent years, and hence their IC values were 0.

## Discussion

Flowers of *O. palustre* are of the classic, open, dish-shaped type (Faegri and van der Pijl 1966), and, as such, may be easily visited by a wide spectrum of insects, and are thus phenotypically generalized (Ollerton et al. 2007). Indeed, our study showed that they are attractive to over 81 species of anthophilous insects, a result comparable to that found in many other members of the family (Knuth 1898; Corbet 1970; Grace and Nelson 1981; Ellis and Ellis-Adam 1993; Zych 2002, 2007; Zych et al. 2007; Niemirski and Zych 2011). Although the taxonomic spectrum of visitors to our study species extended over 5 systematic orders, most floral visitors to *O. palustre* flowers belonged to a small number of functional groups within a single order, since 99–100 % visits in 2009–2010 and 85 % visits in 2008 were by Diptera. These insects, in particular large Syrphids and large Muscoid flies, were among the most frequent floral visitors, carried the largest pollen loads, and in two out of three study years, seemed to be the key pollinating agents. If, following Niemirski and Zych (2011), the large Muscoid and medium Muscoid flies were clustered into a single functional group, namely, Muscoid flies, then, quantitatively, they would constitute the largest group of floral visitors (over 51 % of visits during both 2008 and 2009, and 73 % in 2010). However, when all parameters of insect performance are considered, they are still inefficient pollinators compared to large Syrphids. Similar results were obtained for *Heracleum sphondylium* L. and *Daucus carota* subsp. *commutatus* (Paol.) Thell. In *H. sphondylium*, and depending on the year and the plant's subspecies, a single species of Syrphid fly, *Eriozona syrphoides*, performed as few as 2.7–5.5 % of visits, but was responsible for a large proportion (up to 80 %) of pollination (Zych 2007). In *D. carota* subsp. *commutatus*, Calliphorid flies (mostly *Lucilia*) accounted for approx. 67 % of visits, whereas syrphids (especially *Eristalis tenax*) were by far the most effective pollinators, but were responsible for only 16 % of visits (Pérez-Bañón et al. 2007). This shows that the hypothesis proposed by some researchers (Gómez and Zamora 1992; Morris 2003; Vázquez et al. 2005), namely, that visit rate is a good surrogate of pollinator performance, should be treated with caution, as it is true only for some plant species (see e.g. Motten et al. 1981; Fishbein and Venable 1996; Olsen 1997; Sahli and Conner 2007; Niemirski and Zych 2011; Zych and Stpiczyńska 2012; Zych et al. 2013), and thus may be misleading in others (e.g. Zych 2002, 2007; Fumero-Cabán and

**Table 2** Pollination importance ( $I$ ) and relative importance coefficient (IC) of all the insect guilds recorded on female (f) and male phase umbels of *Ostericum palustre* in the years 2008–2010

	2008		2009				2010					
	$I_f$	IC <sub>f</sub> (%)	$I_f$	IC <sub>f</sub> (%)	$I_m$	IC <sub>m</sub> (%)	$I_f/I_m$	$I_f$	IC <sub>f</sub> (%)	$I_m$	IC <sub>m</sub> (%)	$I_f/I_m$
Vespidae	2,393	64	0	0	0	0		0	0	0	0	
Large syrphids	410	11	3,043	68	5,380	90	0.57	1,158	60	1,650	43	0.70
Small syrphids	35	1	60	1	162	3	0.37	70	3	271	7	0.26
Large muscoid flies	362	10	800	18	223	4	3.58	656	34	1,148	30	0.57
Medium muscoid flies	456	12	569	13	175	3	3.25	57	3	744	20	0.08
Other	80	2	0	0	0	0		0	0	0	0	

Blank spaces indicate cases where  $I_f/I_m$  could not be calculated. For details on  $I$  and IC calculation, see “Materials and methods”

Meléndez-Ackerman 2007; Sánchez-Lafuente et al. 2012; Watts et al. 2012; and the present study).

Although umbellifers are generally regarded as generalists in terms of their floral visitors (Corbet 2006; Olesen et al. 2007; Ollerton et al. 2007), fly-pollination [myophily, as described in Willmer (2011), p. 308], is probably typical of Apiaceae (Proctor et al. 1996; Zych 2004) and, to date, has been reported for many other European members of this family (Grace and Nelson 1981; Zych 2002, 2007; Niemirski and Zych 2011), including *O. palustre*. Diptera are also important pollinators of umbellifers on remote islands (Pérez-Bañón et al. 2007), and on other continents (e.g. Brookes and Jesson 2007; Danderson and Molano-Flores 2010). However, during 2008, wasps (Vespidae) were the most effective pollinators of our study species. They performed only 11 % of visits but, as a result of their relatively large pollen loads, were responsible for 64 % of pollination. Interestingly, they were almost absent in subsequent years. Visits to flowers by these generally predatory insects are widely reported. Wasps are rather opportunistic floral visitors and may hunt on umbels (Zych 2002), but also, especially during autumn, search for floral rewards (Willmer 2011). Therefore, they are more likely to be encountered on plants flowering late in the season, such as those of *O. palustre*. A drastic reduction in wasp visits during 2009–2010, compared with 2008, may be the result of fluctuations in the natural pattern of populations, caused perhaps by unfavourable climatic conditions (Archer 2001). Such temporal fluctuations in key pollinator groups have also been reported for other members of Apiaceae (e.g. Lamborn and Ollerton 2000), and appear to be natural events resulting in a large assemblage of potential pollinators. They demonstrate, however, that single-season studies are of little value when investigating plant pollination systems.

Despite their general inefficiency in pollination (Puterbaugh 1998; Beattie and Hughes 2002; Willmer 2011), recent reports have shown that ants are important pollinators of three rare and endangered umbelliferous plants,

namely, *Apium bermejoi* L. Llorens (Cursach and Rita 2012b), *Naufraga balearica* Constance & Cannon (Cursach and Rita 2012a) and *Trinia glauca* (L.) Dumort. (Carvalho et al. 2008). We also observed ants, in particular, individuals of *M. rubra*, visiting flowers of *O. palustre*. These visits were relatively rare and, more importantly, pollen was not discovered on the bodies of these insects, indicating their inability to pollinate flowers of this species. Their behaviour also indicated that here, they act as nectar thieves, rather than pollinators.

To conclude, with regard to specialization of the pollination system, *O. palustre*, like other members of Apiaceae and Araliaceae (see e.g. Ollerton et al. 2007; Zych 2007; Jacobs et al. 2010; Niemirski and Zych 2011) is characterized by a high apparent generalization, but by low realized generalization, and is an example of a functional specialist (see Fenster et al. 2004; Ollerton et al. 2007 for discussion), since it is pollinated by a relatively small group of potential pollinators grouped together on morphological grounds into visitor guilds. Thus, *O. palustre* is one more example of Apiaceae being masters of the “bet-hedging” pollination strategy (sensu Willmer 2011) in that, although its flowers are mainly pollinated by large Syrphid and Muscoid flies, they nonetheless remain attractive to many pollinator groups (wasps in this case).

Although our analysis is based on studies of a single population, given the relatively economical way in which *O. palustre* ensures pollination (in theory, two pollen grains are sufficient to produce full seed set in a flower), andromonoecy and prevailing protandry that promotes xenogamy (Gaudeul and Till-Bottraud 2003; Rovira et al. 2004; Zych 2007; Niemirski and Zych 2011; Cursach and Rita 2012a, b), like other members of Apiaceae that are usually pollinated by ubiquitous insect guilds, it is likely to attain considerable reproductive success under various habitat and geographical conditions. This suggests that the pollination biology, and most probably, the breeding system of *O. palustre*, alone cannot adequately explain the rarity of this species.

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## Appendix

Insect visitors to flowers of *Ostericum palustre* in Ślesin (NW Poland). The list contains taxa observed and caught both during and outside study hours during 2008–2010. Some members of families were not identified to the species level, names according to Bogdanowicz et al. (2004, 2007).

Diptera: Anthomyiidae: *Botanophila* Lioy, *Delia* R.-D., Calliphoridae: *Bellardia stricta* (Vill.), *B. viarum* (R.-D.), *B. vulgaris* (R.-D.), *Calliphora stelviana* (Br. et Berg.), *C. vicina* R.-D., *Cynomya mortuorum* (L.), *Lucilia bufonivora* Moniez, *L. illustris* (Meig.), *L. pilosiventris* Kramer, *L. silvarum* (Meig.), *Pollenia amentaria* (Scop.), *P. angustigena* Wainwright, *Pollenia griseotomentosa* (Jacent.), *P. hungarica* Rognes, *P. labialis* R.-D., *P. pediculata* Macq., *P. rudis* (Fabr.), *P. vera* Jacent., *Pollenia* R.-D., Chloropidae, Muscidae: *Coenosia tigrina* (Fabr.), *Drymeia tetra* (Meig.), *Pyrellia rapax* (Harris), Sarcophagidae: *Sarcophaga granulata* Kramer, *S. incisilobata* Pandellé, *S. melanura* Meig., *Sarcophaga* Meig., *S. africa* (Wiedemann), *S. carnaria* (L.), *S. nigriventris* Meig., *S. sinuata* Meig., *S. variegata* (Scop.), *S. villeneuvei* Böttcher, *S.* subgen. *Helicophagella* Ender., *S.* subgen. *Parasarcophaga* Johnston et Tiegs, *S.* subgen. *Sarcophaga* Meig., other Sarcophagidae, Stratiomyidae: *Chloromyia formosa* (Scop.), Syrphidae: *Chrysotoxum festivum* (L.), *Episyrphus balteatus* (Deg.), *Ersitalis anthophorina* (Fall.), *E. arbustorum* (L.), *E. rupium* Fabr., *E. similis* (Fall.), *Helophilus hybridus* Loew, *H. trivittatus* (Fabr.), *Melanostoma mellinum* (L.), *Parasyrphus nigritaris* (Zett.), *Platycheirus holarcticus* Vockeroth, *Syrtrita pipiens* (L.), *Scaeva pyrastris* (L.), *Sphaerophoria scripta* (L.), *S. vitripennis* Meig., *S. latifasciatus* (Macq.), Tabanidae: *Haematopota pluvialis* (L.), Tachinidae: *Eurithia intermedia* (Zett.), *Exorista* Meig., *Fausta nemorum* (Meig.), *Hy-leorus elatus* (Meig.), *Huebneria affinis* (Fall.), *Voria ruralis* (Fall.), other Tachinidae, Tipulidae.

Coleoptera: Cantharidae: *Rhagonycha fulva* (Scop.), Coccinellidae: *Coccinella septempunctata* L., other Coccinellidae, Curculionidae

Homoptera

Hymenoptera: Apidae: *Andrena pilipes* Fabr., Argidae: *Arge Schrank*, *Arge pagana* (Panzer), Formicidae: *Myrmica rubra* (L.), Ichneumonidae, Tenthredinidae: *Tenthredo* L., Vespidae: *Paravespula germanica* (Fabr.), *P. vulgaris* (L.), *Polistes* Latreille,

Lepidoptera: Lycaenidae: *Polyommatus icarus* (Rottemburg), Pieridae: *Pontia daplidice* (L.).

## References

- Archer ME (2001) Changes in abundance of *Vespula germanica* and *V. vulgaris* in England. *Ecol Entomol* 26:1–7
- Beattie A, Hughes L (2002) Ant-plant interactions. In: Herrera CM, Pellmyr O (eds) Plant-animal interactions. An evolutionary approach. Blackwell, Oxford, pp 211–235
- Bogdanowicz W, Chudzicka E, Pilipiuk I, Skibińska E (eds) (2004) Fauna of Poland. Characteristics and checklist of species, vol I. Muzeum i Instytut Zoologii PAN, Warsaw
- Bogdanowicz W, Chudzicka E, Pilipiuk I, Skibińska E (eds) (2007) Fauna of Poland. Characteristics and checklist of species, vol II. Muzeum i Instytut Zoologii PAN, Warsaw
- Brookes RH, Jesson LK (2007) No evidence for simultaneous pollen and resource limitation in *Aciphylla squarrosa*: A long-lived, masting herb. *Austral Ecol* 32:370–377. doi:10.1111/j.1442-9993.2007.01708.x
- Cannon JFM (1968) *Angelica* L. In: Tutin TG et al (eds) Flora Europaea, vol 2. Cambridge University Press, Cambridge, pp 357–358
- Carvalho LG, Barbosa ERM, Memmott J (2008) Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. *J App Ecol* 45:1419–1427. doi:10.1111/j.1365-2664.2008.01518.x
- Ciosek MK, Krechowski J, Piórek K, Szczygielski M (2012) Distribution of *Ostericum palustre* Besser in the central-eastern Poland. *Acta Bot Silesiaca* 8:137–146
- Corbet SA (1970) Insects on hogweed flowers: a suggestion for a student project. *J Biol Edu* 4:133–143
- Corbet SA (2006) A typology of pollination systems: implications for crop management and the conservation of wild plants. In: Waser NM, Ollerton J (eds) Plant-pollinator interactions. From specialization to generalization. The University of Chicago Press, Chicago, pp 315–340
- Cursach J, Rita J (2012a) Implications of the reproductive biology of the narrow endemic *Naufraga balearica* (Apiaceae) for its conservation status. *Plant Syst Evol* 298:581–596. doi:10.1007/s00606-011-0568-2
- Cursach J, Rita J (2012b) Reproductive biology and reproductive output assessment in natural and introduced subpopulations of *Apium bermejoi*, a ‘critically endangered’ endemic plant from Menorca (western Mediterranean). *Nord J Bot* 30:754–768
- Czarna A, Załuski T (2001) *Angelica palustris* (Besser) Hoffm. Starodub łąkowy. In: Kaźmierczakowa R, Zarzycki K (eds) Polska czerwona księga roślin [The Polish plant Red Book]. Instytut Botaniki im. W. Szafera i Instytut Ochrony Przyrody PAN, Kraków, pp 277–279
- Dafni A, Kevan PG, Husband BC (2005) Practical pollination ecology. *Enviroquest*, Cambridge
- Danderson CA, Molano-Flores B (2010) Effects of herbivory and inflorescence size on insect visitation to *Eryngium yuccifolium* (Apiaceae), a prairie plant. *Am Midl Nat* 163:234–246
- Dittbrenner A, Hensen I, Wesche K (2005) Genetic structure and random amplified polymorphic DNA diversity of the rapidly



- declining *Angelica palustris* (Apiaceae) in Eastern Germany in relation to population size and seed production. *Plant Species Biol* 20:191–200. doi:10.1111/j.1442-1984.2005.00138.x
- Dixon KW (2009) Pollination and restoration. *Science* 325:571–573
- East EM (1940) The distribution of self-sterility in the flowering plants. *Proc Am Philos Soc* 82:449–518
- Ellis WN, Ellis-Adam AC (1993) To make a meadow it takes a clover and a bee: the entomophilous flora of NW Europe and its insects. *Bijdrag Dierkd* 63:193–220
- Ellis WN, Ellis-Adam AC (1994) Umbels are not alike. *Entomol Ber* 54:191–199
- Faegri K, van der Pijl L (1966) The principles of pollination ecology. Pergamon Press, Oxford
- Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and floral specialization. *Annu Rev Ecol Evol S* 35:375–403. doi:10.1146/annurev.ecolsys.34.011802.132347
- Fishbein M, Venable DL (1996) Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* 77:1061–1073
- Fumero-Cabán JJ, Meléndez-Ackerman EJ (2007) Relative pollination effectiveness of floral visitors of *Pitcairnia angustifolia* (Bromeliaceae). *Am J Bot* 94:419–424. doi:10.3732/ajb.94.3.419
- Gaudeul M, Till-Bottraud I (2003) Low selfing in a mass-flowering, endangered perennial, *Eryngium alpinum* L. (Apiaceae). *Am J Bot* 90:716–723. doi:10.3732/ajb.90.5.716
- Gómez JM, Zamora R (1992) Pollination by ants: consequences of the quantitative effects on a mutualistic system. *Oecologia* 91:410–418. doi:10.1007/bf00317631
- Grace J, Nelson M (1981) Insects and their pollen loads at a hybrid *Heracleum* site. *New Phytol* 87:413–423
- Jacobs J, Clark S, Denholm I, Goulson D, Stoate C, Osborne J (2010) Pollinator effectiveness and fruit set in common ivy, *Hedera helix* (Araliaceae). *Arthropod Plant Interact* 4:19–28. doi:10.1007/s11829-009-9080-9
- Johnson SD, Steiner KE (2000) Generalization versus specialization in plant pollination systems. *Trends Ecol Evol* 15:140–143
- Knuth P (1898) *Handbuch der Blütenbiologie*, II Band, 1. Teil: Ranunculaceae bis Compositae. Verlag von Wilhelm Engelmann, Leipzig
- Krasicka-Korczyńska E (2008) Effect of the cutting date on blooming and fruit-bearing of *Ostericum palustre* Besser. *Acta Agrobot* 61:129–136
- Krasicka-Korczyńska E (2009) Swamp angelica *Ostericum palustre* Besser in grassland complexes of the Noteć river valley and the Bydgoszcz Canal. In: Sliwińska E, Spychaj-Fabisiak E (eds) Understanding the requirements for development of agricultural production and of rural areas in the Kuyavian-Pomeranian Province as a result of scientific research. University of Technology and Life Sciences Press, Bydgoszcz, pp 199–209
- Kwak MM, Bekker RM (2006) Ecology of plant reproduction: extinction risks and restoration perspectives of rare plant species. In: Waser NM, Ollerton J (eds) Plant-pollinator interactions. From specialization to generalization. University of Chicago Press, Chicago, pp 362–386
- Lamborn E, Ollerton J (2000) Experimental assessment of the functional morphology of inflorescences of *Daucus carota* (Apiaceae): testing the ‘fly catcher effect’. *Funct Ecol* 14:445–454
- Lindsey AH (1984) Reproductive biology of Apiaceae. 1. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. *Am J Bot* 71:375–387
- Menz MHM, Phillips RD, Winfree R, Kremen C, Aizen MA, Johnson SD, Dixon KW (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends Plant Sci* 16:4–12
- Michalska-Hejduk D, Kopeć D (2010) Ecological and sociological spectrum of *Ostericum palustre* at new localities in central Poland. *Biodivers Res Conserv* 17:63–71
- Morris WF (2003) Which mutualists are most essential? Buffering of plant reproduction against the extinction of pollinators. In: Kareiva P, Levin S (eds) The importance of species: perspectives on expendability and triage. Princeton University Press, Princeton, pp 260–280
- Motten AF, Campbell DR, Alexander DE, Miller HL (1981) Pollination effectiveness of specialist and generalist visitors to a North Carolina populations of *Claytonia virginica*. *Ecology* 62:1278–1287
- Niemirski R, Zych M (2011) Fly pollination of dichogamous *Angelica sylvestris* (Apiaceae): how (functionally) specialized can a (morphologically) generalized plant be? *Plant Syst Evol* 294:147–158. doi:10.1007/s00606-011-0454-y
- Nobis M, Piowarczyk R (2008) The distribution, habitat preferences and size of population of *Ostericum palustre* Besser on the south-western limit of its occurrence in Poland. *Nat Conserv* 65:43–49
- Nobis M, Nobis A, Kozak M (2008) The occurrence of *Ostericum palustre* (Apiaceae) in southern Poland. *Fragm Flor Geobot Pol* 15:3–9
- Olesen JN, Dupont YL, Ehlers BK, Hansen DM (2007) The openness of a flower and its number of flower-visitor species. *Taxon* 56:729–736
- Ollerton J, Killick A, Lamborn E, Watts S, Whiston M (2007) Multiple meanings and modes: on the many ways to be a generalist flower. *Taxon* 56:717–728
- Olsen KM (1997) Pollination effectiveness and pollinator importance in a population of *Heterotheca subaxillaris* (Asteraceae). *Oecologia* 109:114–121
- Pérez-Bañón C, Petanidou T, Marcos-García MÁ (2007) Pollination in small islands by occasional visitors: the case of *Daucus carota* subsp. *commutatus* (Apiaceae) in the Columbretes archipelago, Spain. *Plant Ecol* 192:133–151. doi:10.1007/s11258-006-9233-1
- Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Harper Collins, London
- Puterbaugh MN (1998) The roles of ants as flower visitors: experimental analysis in three alpine plant species. *Oikos* 83:36–46
- Rovira AM, Bosch M, Molero J, Blanche C (2004) Pollination ecology and breeding system of the very narrow coastal endemic *Seseli farrenyi* (Apiaceae). Effects of population fragmentation. *Nord J Bot* 22:727–740
- Sahli HF, Conner JK (2007) Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanistrum* (Brassicaceae). *Am J Bot* 94:203–209
- Sánchez-Lafuente A, Rodríguez-Gironés M, Parra R (2012) Interaction frequency and per-interaction effects as predictors of total effects in plant–pollinator mutualisms: a case study with the self-incompatible herb *Linaria lilacina*. *Oecologia* 168:153–165. doi:10.1007/s00442-011-2084-z
- Schemske DW, Husband BC, Ruckelshaus MH, Goodwillie C, Parker IM, Bishop JG (1994) Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75:584–606
- Schnittler M, Günther KF (1999) Central European vascular plants requiring priority conservation measures—an analysis from national Red Lists and distribution maps. *Biodivers Conserv* 8:891–925
- Vázquez DP, Morris WF, Jordano P (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol Lett* 8:1088–1094. doi:10.1111/j.1461-0248.2005.00810.x
- Watts S, Ovalle DH, Herrera MM, Ollerton J (2012) Pollinator effectiveness of native and non-native flower visitors to an apparently generalist Andean shrub, *Duranta mandoni*

- (Verbenaceae). *Plant Species Biol* 27:147–158. doi:[10.1111/j.1442-1984.2011.00337.x](https://doi.org/10.1111/j.1442-1984.2011.00337.x)
- Willmer P (2011) *Pollination and floral ecology*. Princeton University Press, Princeton
- Załuski T (2004) *Ostericum palustre* Besser. Starodub łakowy. In: Werblan-Jakubiec H, Sudnik-Wójcikowska B (eds) *Poradnik ochrony siedlisk i gatunków Natura 2000—podręcznik metodyczny. Gatunki roślin, vol 9*. Ministerstwo Środowiska, Warszawa, pp 160–163
- Zarzycki K, Szelaż Z (2006) Red list of the vascular plants in Poland. In: Mirek Z (eds) *Red list of plants and fungi in Poland*. Instytut Botaniki im. W. Szafera i Instytut Ochrony Przyrody PAN, Kraków, pp 10–20
- Zych M (2002) Pollination biology of *Heracleum sphondylium* L. (Apiaceae). The advantages of being white and compact. *Acta Soc Bot Pol* 71:163–170
- Zych M (2004) Biologia zapylania baldaszkowatych (Apiaceae)—stare mity i nowe perspektywy. *Wiad Bot* 48:7–15
- Zych M (2007) On flower visitors and true pollinators: The case of protandrous *Heracleum sphondylium* L. (Apiaceae). *Plant Syst Evol* 263:159–179. doi:[10.1007/s00606-006-0493-y](https://doi.org/10.1007/s00606-006-0493-y)
- Zych M, Jakubiec A (2008) Pollination of the Polish red list plants: a preliminary statistical survey. *Acta Agrobot* 61:85–90
- Zych M, Stpicyńska M (2012) Neither protogynous nor obligatory out-crossed: pollination biology and breeding system of the European red-list *Fritillaria meleagris* L. (Liliaceae). *Plant Biol* 14:285–294. doi:[10.1111/j.1438-8677.2011.00510.x](https://doi.org/10.1111/j.1438-8677.2011.00510.x)
- Zych M, Niemczyk P, Niemirski R (2007) Umbellifers as potential keystone species in restoration projects. *Acta Agrobot* 60:45–49
- Zych M, Goldstein J, Roguz K, Stpicyńska M (2013) The most effective pollinator revisited: pollen dynamics in a spring-flowering herb. *Arthropod Plant Interact* 7:315–322. doi:[10.1007/s11829-013-9246-3](https://doi.org/10.1007/s11829-013-9246-3)