The hidden diet-examination of crop content reveals distinct patterns of pollen host use by Central European bees of the genus Hylaeus (Hymenoptera, Colletidae)

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The hidden diet – examination of crop content reveals distinct patterns of pollen host use by Central European bees of the genus *Hylaeus* (Hymenoptera, Colletidae)

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Abstract

Masked or yellow-faced bees of the genus *Hylaeus* (Colletidae) differ in their mode of pollen transportation from most other bees in that they ingest the pollen directly on the flowers and carry it back to the nest inside the crop located in the anterior half of the metasoma. Due to this hidden mode of pollen transportation, the examination of pollen collected by *Hylaeus* females requires the dissection of the metasoma. Although this method has never been applied in Europe, the great majority of the Central European *Hylaeus* species were supposed to be pollen generalists based on observations of flower visits. The microscopical analysis of pollen removed from 30 crops each of 36 Central European *Hylaeus* species revealed that the proportion of species exhibiting an exclusive or strong preference for pollen from a single plant taxon is much higher than hitherto assumed and that the current assumption of the genus *Hylaeus* to largely consist of pollen generalists is wrong. Nineteen of the 36 species examined are strictly or largely dependent on a single plant taxon for collecting pollen, such as Apiaceae (n = 11 species), Rosaceae (n = 3), *Reseda* (Resedaceae) (n = 2), *Allium* (Amaryllidaceae) (n = 1), Asteraceae (n = 1) and *Melilotus* (Fabaceae) (n = 1). The 36 *Hylaeus* species examined collected pollen from the flowers of 31 plant families, of which the Apiaceae and Rosaceae (particularly *Potentilla* and *Rubus*) were by far the most important contributing almost 60% to the pollen host spectrum of the entire genus. The comparison between pollen host spectrum and flower visiting records showed that the pollen generalists use the flowers of the Asteraceae as nectar rather than pollen sources, corroborating earlier findings that the digestion of Asteraceae pollen requires physiological adaptations to cope with its unfavourable or protective properties. In summary, the patterns of pollen host use by bees of the genus *Hylaeus* do not substantially differ from those of other Palaearctic bee taxa despite the masked bees' unusual habit to ingest the pollen directly on the flowers and to transport it inside their body back to the nest.

Key Words

Anthophila, Apiformes, Asteraceae paradox, Asteroideae, Carduoideae, oligolecty, polylecty

Introduction

Bees are vegetarian wasps, whose larvae usually develop on a mixture of pollen and nectar within the brood cells of the nests built by the mother bees (Westrich 1989; Michener 2007). In most species, nesting females carry pollen collected on flowers back to the nest on the hind legs and/or on the underside of the metasoma (Westrich 1989; Michener 2007). Due to this external mode of pollen transportation, pollen is easily accessible for examination. In fact, extensive pollen analytical work starting with the seminal publications by Chambers (1968); Raw (1974); Westrich and Schmidt (1986, 1987) and Westrich (1989) and followed by numerous further investigations for example by Müller (1996, 2018); Michez et al. (2008); Müller and Kuhlmann (2008); Sedivy et al. (2008, 2013); Haider et al. (2014); Wood et al. (2016) or Wood and Roberts (2017) led to a fairly good knowledge

of the pollen host preferences of large parts of the Central European bee fauna.

Bees of the genus *Hylaeus* – a cosmopolitan taxon of colletid bees comprising several hundred species worldwide (Ascher and Pickering 2020) – differ in their mode of pollen transportation from most other bees in that they ingest the pollen directly on the flowers and carry it back inside the metasomal crop to the nest, where it is regurgitated into the brood cells (Westrich 1989; Michener 2007). Due to this hidden mode of pollen transportation, pollen is accessible for examination only after dissection of the metasoma, a method that has never been applied for European species of this genus.

Based on field observations, all Central European *Hylaeus* species are currently assumed to be pollen generalists ("polylectic") except for three species, which are most probably pollen specialists ("oligolectic") on *Allium* (Amaryllidaceae), *Reseda* (Reseda) and Asteraceae, respectively (Scheuchl and Willner 2016; Westrich 2018; Wiesbauer 2020). However, reliable identification of *Hylaeus* in the field down to species level is strongly hampered by the small size and the uniform morphology of most Central European species, casting doubt on the field-based assumption that the vast majority of species is polylectic. Furthermore, as the spectrum of flowers exploited for nectar is often much wider than for pollen, observations of flower visits without careful differentiation between pollen and nectar uptake poorly reflect pollen host preferences and often conceal pollen specializations (Westrich and Schmidt 1987). In fact, the analysis of pollen remains in larval faeces of three North American *Hylaeus* species revealed that all three species collected pollen almost exclusively on Rosaceae in spite of long lists of flower visitation records comprising taxa belonging to numerous different plant families (Scott 1996).

In the present study, the pollen host preferences of 36 Central European *Hylaeus* species including four species restricted in their distribution to higher elevations in the Alps were analysed by microscopical analysis of pollen removed from the crops of collected females. Specifically, the following questions were addressed: i) What are the pollen host spectra of the Central European species? ii) Which plant taxa serve as the most important pollen hosts for the genus in Central Europe? iii) Are there differences between the pollen host spectrum of the genus as assessed in the present study and records of flower visits in the field?

Material and methods

Bee species

Masked or yellow-faced bees of the genus *Hylaeus* Fabricius (Colletidae) are distributed on all continents except for Antarctica (Michener 2007). Currently, about 760 species are known, of which 47 occur in Central Europe belonging to ten subgenera (Dathe et al. 2016; Ascher and Pickering 2020). The Central European representatives of *Hylaeus* are small, black, nearly hairless bees usually ranging in length from 3.5 mm to 7 mm. Most species are characterised by the presence of white or yellow markings on the face. The proboscis of all species is very short, limiting nectar uptake to flowers with easily reachable nectar, which is either exposed or – if secreted at the base of the flowers – accessible thanks to the small body size of the bees. The Central European species nest in preexisting cavities such as insect borings in dead wood, hollow stems, soil fissures, abandoned above and below ground nests of aculeate Hymenoptera, abandoned *Lipara* reed galls or between stones; more rarely, they excavate the nests in the pith of plant stems (Westrich 2018). The brood cell walls are constructed with glandular secretions, which solidify after application by the specialised bilobed tongue to a transparent and cellophane-like waterproof membrane (Batra 1980; Almeida 2008).

For the present study, 36 Central European *Hylaeus* species were selected representing about 80% of *Hylaeus* species diversity in Switzerland, Germany and Austria (Dathe et al. 2016). The species identification was based on Amiet et al. (2014) and Dathe et al. (2016). In addition, the publications by Doczkal and Schmid-Egger (1992) and Straka and Bogusch (2011) were used for the proper identification of the two very similar species *Hylaeus pictipes* and *H. taeniolatus* and the three species of the *Hylaeus gibbus* group, respectively.

Pollen host spectrum

To assess the pollen host spectra of the 36 *Hylaeus* species, the crop content of a total of 1027 pinned females from museum and private collections captured between the middle of the 20th century and 2022 was analysed by light microscopy. For each species, 30 pollen-containing crops were dissected originating from females collected at 30 different localities within the study area, which encompassed Switzerland, Baden-Württemberg (Germany) as well as Vorarlberg and Tirol (Austria). Localities were defined as different if the data on the collection labels differed with respect to collection site and/or collection date. For the four rare species *Hylaeus crassanus*, *H. glacialis*, *H. incongruus* and *H. moricei*, the targeted number of 30 different crop contents from 30 different localities was not attained and part of the females originated from outside the study area (see Table 1).

To remove pollen from the crop, which is located in the anterior half of the metasoma, the female was stripped off from the insect pin to a polystyrene underlay and her metasoma was opened in dry state under a stereomicroscope between the second and third tergal segment with a scalpel. This procedure tore open the very thin crop walls, revealing the pollen masses that were located between the base of the metasoma and the proventriculus. The pollen was removed from the crop with a pair of tweezers and its amount was assigned to four classes, ranging from 4/4 (full crop) to 1/4 (crop filled to one fourth), before it was transferred to a microscopical slide and embedded

Table 1. Pollen host spectrum of 36 Central European bee species of the genus *Hylaeus* (Colletidae). Subgeneric classification according to Dathe et al. (2016). n = total number of pollen loads, N = number of pollen loads from different localities. Countries: A = Austria (Vorarlberg, Tirol), CH = Switzerland, D = Germany (Baden-Württemberg), E = Spain, F = France, FL = Liechtenstein, IT = Italy, SK = Slovakia. Plant families: ADO = Adoxaceae, AMA = Amaryllidaceae, API = Apiaceae, ARA = Araliaceae, AST = Asteraceae, BOR = Boraginaceae, BRA = Brassicaceae, CAM = Campanulaceae), CAR = Caryophyllaceae, CIS = Cistaceae, CRA = Crassulaceae, ERI = Ericaceae, EUP = Euphorbiaceae, FAB = Fabaceae, FAG = Fagaceae, GEN = Gentianaceae, HYP = Hypericaceae, LAM = Lamiaceae, LYT = Lythraceae, ORO = Orobanchaceae, PLA = Plantaginaceae, POL = Polygonaceae, RAN = Ranunculaceae, RES = Resedaceae, RHA = Rhamnaceae, ROS = Rosaceae, RUB = Rubiaceae, SAX = Saxifragaceae, SCR = Scrophulariaceae, TIL = Tiliaceae, VIT = Vitaceae; ORO/PLA = indeterminable pollen grains belonging either to *Euphrasia*, *Rhinanthus* (both Orobanchacee) or *Veronica* (Plantaginaceae). Definitions of bee pollen host ranges after Müller and Kuhlmann (2008).

Bee species	n	N	Origin (total number/ number of cantons) of pollen loads	% pollen grain volume (number of loads)	Preferred host	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Pollen host range in Central Europe
Subgenus *Abrupta*									
Hylaeus cornutus Curtis, 1831	30	30	CH (26/10), D (4)	API 94.2% (30), AST (Asteroideae) 2.7% (7), BRA 1.8% (1), EUP (*Euphorbia*) 1.3% (1)	Apiaceae	94.2	70.0	100	Polylectic with strong preference for Apiaceae
Subgenus *Dentigera*									
Hylaeus brevicornis Nylander, 1852	30	30	CH (30/12)	API 59.4% (19), ROS (*Rubus*) 15.5% (5), ROS (*Potentilla*) 13.8% (6), ROS (other) 0.4% (1), EUP (*Euphorbia*) 3.5% (1), CRA 3.2% (2), AST (Asteroideae) 0.4% (3), HYP (*Hypericum*) 0.2% (), unknown 3.6% (1)	–	–	–	–	Polylectic (6 plant families)
Hylaeus glacialis Morawitz, 1872	18	17	CH (15/2), F (2), IT (1)	API 68.0% (13), CIS (*Helianthemum*) 8.8% (2), CRA 7.6% (3), SAX (*Saxifraga*) 6.6% (3), ROS (*Rubus*) 3.2% (1), LAM (Nepetoideae) 2.8% (1), BRA 1.5% (2), CAR 1.5% (2)	–	–	–	–	Polylectic (8 plant families)
Hylaeus gredleri Förster, 1871	30	30	CH (29/12), FL (1)	API 91.8% (28), ROS (*Potentilla*) 6.2% (1), EUP (*Euphorbia*) 1.8% (2), AST (Asteroideae) 0.2% (1)	Apiaceae	91.8	86.7	93.3	Polylectic with strong preference for Apiaceae
Hylaeus kahri Förster, 1871	30	30	CH (30/7)	API 93.0% (28), CRA 5.1% (3), FAG (*Castanea*) 1.8% (3), AST (Asteroideae) 0.1% (1),	Apiaceae	93.0	76.7	93.3	Polylectic with strong preference for Apiaceae
Hylaeus pilosulus (Pérez, 1903)	30	12	CH (21/1), E (6), F (3)	RES (*Reseda*) 100% (30)	*Reseda* (Resedaceae)	100	100	100	Narrowly oligolectic on *Reseda* (Resedaceae)
Subgenus *Hylaeus*									
Hylaeus angustatus (Schenck, 1861)	30	30	CH (30/7)	ROS (*Rubus*) 16.8% (6), ROS (*Potentilla*) 15.5% (5), BOR (*Echium*) 13.9% (8), CAM (*Campanula*) 7.8% (3), CAM (*Jasione*) 6.1% (3), LAM (Nepetoideae) 6.9% (5), FAB (*Melilotus*) 6.1% (2), BRA 5.8% (1), RES (*Reseda*) 5.8% (2), AMA (*Allium*) 3.5% (2), CIS (*Helianthemum*) 3.5% (2), CRA 2.8% (1), ORO/ PLA 1.6% (2), PLA (*Linaria*) 1.1% (1), API 1.5% (1), AST (Asteroideae) 0.8% (3), RUB 0.4% (1), unknown 0.1% (1)	–	–	–	–	Polylectic (14 plant families)
Hylaeus annulatus (Linnaeus, 1758)	30	30	CH (26/7), FL (4)	ROS (*Potentilla*) 23.2% (13), ROS (*Rubus*) 10.8% (5), ROS (*Rosa*) 1.2% (1), CAM 13.4% (8), ORO/ PLA 11.7% (10), CIS (*Helianthemum*) 10.3% (6), API 7.5% (5), LAM (Nepetoideae) 6.8% (5), LAM (Lamioideae) 1.6% (2), AMA (*Allium*) 6.8% (4), RAN (*Trollius*) 3.0% (2), RAN (*Ranunculus*) 0.5% (2), ERI 1.5% (3), CRA 0.8% (2), CAR 0.4% (1), AST (Asteroideae) 0.2% (1), BRA 0.2% (1), ORO (*Melampyrum*) 0.1% (1)	–	–	–	–	Polylectic (13 plant families)
Hylaeus communis Nylander, 1852	30	30	CH (30/10)	API 30.6% (14), ROS (*Rubus*) 16.9% (5), CAM 8.6% (4), PLA (*Plantago*) 7.8% (4), PLA (*Linaria*) 1.0% (2), CRA 6.6% (2), RES (*Reseda*) 5.0% (1), FAB (*Melilotus*) 4.6% (4), AST (Asteroideae) 4.3% (7), CAR 3.5% (2), POL (*Fallopia*) 3.3% (1), BOR (*Echium*) 2.6% (1), LAM (Nepetoideae) 2.5% (2), BRA 1.3% (1), RHA (*Frangula*) 0.5% (1), RUB 0.5% (2), HYP (*Hypericum*) 0.4% (1)	–	–	–	–	Polylectic (16 plant families)
Hylaeus leptocephalus (Morawitz, 1871)	30	30	CH (18/5), D (12)	FAB (*Melilotus)* 74.7% (22), BRA 9.4% (4), ROS (*Rubus*) 3.7% (2), ROS (*Potentilla*) 3.2% (1), RES (*Reseda*) 2.7% (1), LAM (Nepetoideae) 1.6% (1), TIL (*Tilia*) 1.6% (1), API 1.3% (1), AST (Asteroideae) 0.8% (3), AST (Cichorioideae) 0.3% (1), EUP (*Euphorbia*) 0.3% (1), HYP (*Hypericum*) 0.1% (1), unknown 0.3% (1)	*Melilotus* (Fabaceae)	74.7	63.3	80.0	Polylectic with strong preference for *Melilotus* (Fabaceae)

Bee species	n	N	Origin (total number/ number of cantons) of pollen loads	% pollen grain volume (number of loads)	Preferred host	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Pollen host range in Central Europe
Hylaeus moricei (Friese, 1898)	18	16	D (8), A (7), CH (3/2)	BRA 29.1% (5), ROS (*Rubus*) 23.3% (5), ROS (*Potentilla*) 0.4% (1), ROS (*Filipendula*) 0.1% (1), LAM (Lamioideae) 12.8% (4), API 9.0% (4), AMA (*Allium*) 6.7% (1), FAB (*Melilotus*) 6.4% (2), LYT (*Lythrum*) 3.3% (1), SCR 2.7% (1), PLA (*Linaria*) 2.4% (1), BOR (*Echium*) 1.6% (1), BOR (*Phacelia*) 1.3% (1), AST (Asteroideae) 0.5% (3), RHA (*Frangula*) 0.4% (3)	–	–	–	–	Polylectic (12 plant families)
Hylaeus nigritus (Fabricius, 1798)	30	30	CH (30/9)	AST (Carduoideae) 77.4% (27), AST (Asteroideae) 18.9% (28), AMA (*Allium*) 2.1% (2), CAR 0.6% (1), API 0.2% (2), CAM 0.2% (1), CRA 0.1% (1), unknown 0.7% (2)	Carduoideae and Asteroideae (Asteraceae)	96.1	76.7	100	Broadly oligolectic on Carduoideae and Asteroideae (Asteraceae)
Hylaeus nivalis (Morawitz, 1867)	30	30	CH (30/7)	CAM 19.7% (11), CAR 15.6% (14), ORO/PLA 15.5% (7), PLA (Linaria) 1.1% (1), CRA 12.6% (10), ROS (*Potentilla*) 8.9% (7), ROS (*Rubus*) 0.3% (1), CIS (*Helianthemum*) 8.3% (6), LAM (Nepetoideae) 6.6% (8), LAM (Lamioideae) 5.1% (1), AST (Carduoideae) 1.4% (1), AST (Cichorioideae) 0.4% (2), EUP (*Euphorbia*) 1.5% (1), AMA (*Allium*) 0.8% (1), RUB 0.7% (3), API 0.3% (1), unknown 1.2% (3)	–	–	–	–	Polylectic (12 plant families)
Hylaeus paulus Bridwell, 1919	30	30	CH (28/8), D (1), FL (1)	ROS (*Rubus*) 58.3% (20), ROS (*Potentilla*) 25.3% (8), BRA 5.1% (2), AMA (*Allium*) 4.9% (2), API 3.3% (3), PLA (*Veronica*) 1.7% (1), HYP (*Hypericum*) 0.7%, (1), AST (Asteroideae) 0.4% (4), unknown 0.3% (1)	Rosaceae (*Potentilla, Rubus*)	83.6	60.0	83.3	Polylectic with strong preference for Rosaceae (*Potentilla, Rubus*)
Hylaeus tyrolensis Förster, 1871	30	30	CH (27/11), A (2), FL (1)	API 100% (30)	Apiaceae	100	100	100	Broadly oligolectic on Apiaceae
Subgenus *Koptogaster*									
Hylaeus punctulatissimus Smith, 1842	30	30	CH (29/9), D (1)	AMA (*Allium*) 96.0% (29), FAB (*Melilotus*) 2.2% (1), TIL (*Tilia*) 1.7% (1), CRA 0.1% (1)	*Allium* (Amaryllidaceae)	96.0	90	96.7	Narrowly oligolectic on *Allium* (Amaryllidaceae)
Subgenus *Lambdopsis*									
Hylaeus crassanus (Warncke, 1972)	13	10	CH (7/3), IT (4), F (2)	FAB (*Melilotus*) 60.3% (10), CAM (*Jasione*) 12.5% (1), API 11.8% (4), BOR (*Echium*) 11.2% (2), AST (Asteroideae) 4.2% (1)	–	–	–	–	Polylectic (5 plant families)
Hylaeus dilatatus (Kirby, 1802)	30	30	CH (30/8)	API 56.6% (22), AST (Carduoideae) 11.3% (7), AST (Asteroideae) 2.4% (8), ROS (*Rubus*) 5.4% (3), ROS (*Agrimonia*) 1.0% (1), ROS (*Potentilla*) 0.5% (1), CIS (*Helianthemum*) 5.8% (2), CAR 4.0% (4), CRA 3.0% (5), FAB (*Melilotus*) 2.4% (2), HYP (*Hypericum*) 2.4% (1), BOR (*Echium*) 2.0% (2), PLA (*Plantago*) 1.6% (2), RUB 1.2% (2), RAN (*Clematis*) 0.4% (2)	–	–	–	–	Polylectic (12 plant families)
Hylaeus pfankuchi (Alfken, 1919)	30	30	CH (23/9), D (7)	ROS (*Potentilla*) 62.7% (24), ROS (*Rubus*) 11.2% (5), ROS (*Filipendula*) 1.7% (1), API 20.3% (11), ORO/PLA 1.2% (1), BRA 0.8% (1), AST (Asteroideae) 0.3% (2), LAM (Nepetoideae) 0.3% (1), LYT (*Lythrum*) 0.2% (1), unknown 1.3% (2)	Rosaceae (*Potentilla, Rubus, Filipendula*)	75.7	53.3	80.0	Polylectic with strong preference for Rosaceae (*Potentilla, Rubus, Filipendula*)
Hylaeus rinki (Górski, 1852)	30	30	CH (27/10), D (2), FL (1)	ROS (*Potentilla*) 53.5% (21), ROS (*Rubus*) 18.9% (12), API 22.3% (10), EUP (*Euphorbia*) 3.4% (2), AST (Asteroideae) 0.9% (2), AMA (*Allium*) 0.7% (1), unknown 0.3% (1)	Rosaceae (*Potentilla, Rubus*)	72.4	53.3	86.7	Polylectic with strong preference for Rosaceae (*Potentilla, Rubus*)
Subgenus *Nesoprosopis*									
Hylaeus pectoralis Förster, 1871	30	30	CH (24/4), A (3), D (3)	ROS (*Filipendula*) 18.8% (11), ROS (*Rubus*) 16.0% (7), ROS (*Sanguisorba officinalis*) 9.7% (5), ROS (*Potentilla*) 8.8% (5), API 20.2% (17), LYT (*Lythrum*) 7.8% (4), RHA (*Frangula*) 6.6% (10), LAM (Nepetoideae) 3.3% (2), AMA (*Allium*) 3.1% (2), ORO/ PLA 1.7% (1), RAN (*Ranunculus*) 1.7% (2), AST (Asteroideae) 1.5% (2), CAR 0.8% (1)	–	–	–	–	Polylectic (10 plant families)
Subgenus *Paraprosopis*									
Hylaeus clypearis (Schenck, 1853)	30	30	CH (27/13), D (3)	API 97.9% (29), CRA 1.8% (1), RES (*Reseda*) 0.3% (1)	Apiaceae	97.9	93.3	96.7	Broadly oligolectic on Apiaceae

Bee species	n	N	Origin (total number/ number of cantons) of pollen loads	% pollen grain volume (number of loads)	Preferred host	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Pollen host range in Central Europe
Hylaeus pictipes Nylander, 1852	30	30	CH (23/6), D (7)	RES (*Reseda*) 24.7% (9), API 22.2% (6), BRA 22.0% (8), BOR (*Echium*) 11.6% (6), CRA 9.8% (5), ROS (*Rubus*) 4.2% (3), ROS (*Potentilla*) 1.5% (1), ARA (*Hedera*) 1.3% (1), LAM (Nepetoideae) 1.1% (1), AST (Asteroideae) 0.5% (2), EUP (*Euphorbia*) 0.6% (1), LYT (*Lythrum*) 0.5% (1),	–	–	–	–	Polylectic (11 plant families)
Hylaeus sinuatus (Schenck, 1853)	30	30	CH (30/12)	API 98.6% (29), FAG (*Castanea*) 1.4% (1)	Apiaceae	98.6	96.7	96.7	Broadly oligolectic on Apiaceae
Hylaeus styriacus Förster, 1871	30	30	CH (30/10)	API 100% (30)	Apiaceae	100	100	100	Broadly oligolectic on Apiaceae
Hylaeus taeniolatus Förster, 1871	30	30	CH (30/12)	API 92.8% (29), ROS (*Rubus*) 3.9% (1), ARA (*Hedera*) 3.0% (1), AST (Asteroideae) 0.1% (1), unknown 0.2% (1)	Apiaceae	92.8	90.0	96.7	Broadly oligolectic on Apiaceae
Subgenus *Patagiata*									
Hylaeus difformis (Eversmann, 1852)	30	30	CH (30/13)	ROS (*Rubus*) 27.1% (8), FAB (*Melilotus*) 20.4% (7), CAM (*Campanula*) 15.4% (8), SCR (*Scrophularia*) 13.2% (7), BOR (*Echium*) 9.3% (3), LAM (Nepetoideae) 8.3% (4), PLA (*Linaria*) 1.5% (2), ORO/PLA 1.0% (2), HYP (*Hypericum*) 1.3% (2), LYT (*Lythrum*) 1.1% (1), RHA (*Frangula*) 1.1% (2), unknown 0.3% (1)	–	–	–	–	Polylectic (10 plant families)
Subgenus *Prosopis*									
Hylaeus confusus Nylander, 1852	30	30	CH (29/10), D (1)	ROS (*Potentilla*) 28.1% (15), ROS (*Rubus*) 25.2% (15), ROS (*Aruncus*) 0.1% (1), ROS (other) 1.4% (1), CAM 13.2% (6), API 9.2% (6), CIS (*Helianthemum*) 7.8% (5), PLA (*Linaria*) 5.0% (1), ORO/PLA 4.9% (2), PLA (*Plantago*) 1.5% (1), HYP (*Hypericum*) 2.6% (4), AST (Asteroideae) 0.6% (1), ORO (*Melampyrum*) 0.4% (1)	–	–	–	–	Polylectic (8 plant families)
Hylaeus duckei (Alfken, 1905)	30	29	CH (18/7), A (4), D (3), F (3), IT (1), SK (1)	API 97.3% (29), BRA 1.2% (1), ROS (*Rubus*) 0.2% (1), ROS (other) 1.2% (1), unknown 0.1% (1)	Apiaceae	97.3	93.3	96.7	Broadly oligolectic on Apiaceae
Hylaeus gibbus Saunders, 1850	30	30	CH (28/8), D (2)	ROS (*Rubus*) 39.9% (16), ROS (*Potentilla*) 4.1% (4), ROS (other) 0.4% (1), FAB (*Melilotus*) 16.0% (11), API 14.5% (9), CIS (*Helianthemum*) 9.5% (4), CAM (*Campanula*) 3.3% (1), CAM (*Jasione*) 1.1% (1), HYP (*Hypericum*) 3.8% (2), CRA (1.9%) (1), AST (Asteroideae) 1.1% (1), PLA (*Plantago*) 1.0% (2), RES (*Reseda*) 0.8% (1), ADO (*Sambucus*) 0.6% (1), RUB (0.6%) (1), BOR (*Echium*) 0.5% (1), LAM (Nepetoideae) 0.3% (1), RHA (*Frangula*) 0.2% (1), unknown 0.4% (2)	–	–	–	–	Polylectic (15 plant families)
Hylaeus incongruus Förster, 1871	18	18	CH (18/5)	ROS (*Rubus*) 28.3% (7), ROS (*Potentilla*) 2.1% (2), FAB (*Melilotus*) 22.8% (5), CRA 11.2% (4), CAM (*Jasione*) 6.1% (1), CAM (*Campanula*) 4.5% (1), BOR (*Echium*) 7.0% (3), CIS (*Helianthemum*) 5.3% (4), LAM (Nepetoideae) 3.7% (3), Hypericaceae (*Hypericum*) 3.3% (2), API 2.3% (3), RES (*Reseda*) 2.1% (1), BRA 0.4% (1), PLA (*Plantago*) 0.4% (1), VIT (*Vitis*) 0.4% (1), AST (Asteroideae) 0.1% (1),	–	–	–	–	Polylectic (14 plant families)
Hylaeus signatus (Panzer, 1798)	30	30	CH (30/11)	RES (*Reseda*) 100% (30)	*Reseda* (Resedaceae)	100	100	100	Narrowly oligolectic on *Reseda* (Resedaceae)
Hylaeus variegatus (Fabricius, 1798)	30	30	CH (30/5)	API 88.6% (29), EUP (*Euphorbia*) 4.6% (1), ROS (*Potentilla*) 2.3% (1), RES (*Reseda*) 1.4% (1), AST (Asteroideae) 0.8% (2), CRA 0.7% (2), CIS (*Helianthemum*) 0.6% (1), RUB 0.2% (2), unknown 0.8% (2)	Apiaceae	88.6	76.7	96.7	Polylectic with strong preference for Apiaceae
Subgenus *Spatulariella*									
Hylaeus alpinus (Morawitz, 1867)	30	30	CH (28/8), A (2)	CIS (*Helianthemum*) 22.0% (12), ROS (*Potentilla*) 13.6% (10), ROS (*Rubus*) 0.7% (1), ROS (other) 2.8% (2), API 13.2% (7), CRA 11.4% (7), LAM (Nepetoideae) 9.2% (8), LAM (Lamioideae) 0.2% (1), ORO/PLA 9.0% (5), PLA (*Linaria*) 1.1% (2), SAX (*Saxifraga*) 5.4% (6), CAR 3.9% (5), RUB 3.2% (7), FAB (*Trifolium*) 1.0% (2), GEN (*Gentiana*) 0.8% (1), AST (Asteroideae) 0.7% (1), ERI 0.4% (1), unknown 1.4% (3)	–	–	–	–	Polylectic (13 plant families)

Bee species	n	N	Origin (total number/ number of cantons) of pollen loads	% pollen grain volume (number of loads)	Preferred host	% pollen grain volume of preferred host	% pure loads of preferred host	% loads with preferred host	Pollen host range in Central Europe
Hylaeus hyalinatus Smith, 1842	30	30	CH (30/10)	ROS (*Potentilla*) 13.8% (8), ROS (*Rubus*) 10.5% (6), API 21.6% (12), CAM (*Jasione*) 8.9% (3), HYP (*Hypericum*) 8.8% (3), LAM (Nepetoideae) 7.1% (5), CIS (*Helianthemum*) 6.4% (2), CRA 4.3% (4), RUB 3.4% (4), FAB (*Melilotus*) 3.3% (3), BRA 2.8% (1), RES (*Reseda*) 2.5% (1), BOR (*Echium*) 1.1% (2), PLA (*Plantago*) 1.1% (1), EUP (*Euphorbia*) 0.9% (1), CAR 0.2% (1), unknown 3.3% (3)	–	–	–	–	Polylectic (15 plant families)
Hylaeus punctatus (Brullé, 1832)	30	30	CH (30/11)	API 74.2% (26), RES (*Reseda*) 7.8% (2), HYP (*Hypericum*) 6.5% (3), ROS (*Rubus*) 5.5% (4), CRA 5.1% (1), LAM (Nepetoideae) 0.3% (1), BRA 0.2% (1), unknown 0.4% (2)	Apiaceae	74.2	56.7	86.7	Polylectic with strong preference for Apiaceae

in glycerol gelatine. When a crop contained more than one pollen type, the percentages of the different pollen types were estimated either by counting the grains along two entire transects chosen randomly across the cover slip (12 × 12 mm) at a magnification of 400× or, if the sample contained large numbers of pollen, by counting at least 500 grains on two partial transects. Pollen types represented by less than 5% of the counted grains were excluded to prevent a potential bias due to foreign pollen grains transported to the host flowers by other flower visitors or to pollen grains accidentally swallowed during mere nectar uptake. For crop contents consisting of two or more different pollen types, the proportion of the different types was corrected by their volume. For that purpose, the relative volume of all pollen types within the sample was estimated by eye and the counted numbers of each type multiplied by a factor that corresponded to its volume. After assigning different weights to crops according to their degree of filling (full crops were weighted four times more strongly than crops filled to only one fourth), the estimated percentages were summed up over all crop samples for each species.

The pollen grains were identified down to family or, if possible, to subfamily, tribal or genus level at a magnification of 400× or 1000× with the aid of the literature cited in Westrich and Schmidt (1986), Beug (2004) and a pollen reference collection. Difficult pollen types were identified by the palynologist Katharina Bieri (Biological Institute for Pollen Analysis, Kehrsatz, Switzerland). Pollen of the two closely related genera *Fragaria* and *Potentilla* (Rosaceae) could not be reliably separated by the method applied in the present study, both being subsumed under the "*Potentilla* type" in palynology (Beug 2004). Since Central European species of *Hylaeus* start to fly in early and mid-summer, when the spring flowering *Fragaria* is no longer in bloom, all pollen grains of the *Potentilla* type were assigned to the genus *Potentilla*, which is supported by observations in the field, where no visits to *Fragaria* flowers were recorded for *Hylaeus* bees (A. Müller unpublished data). The pollen grains of *Euphrasia*, *Rhinanthus* (both Orobanchacea) and *Veronica* (Plantaginaceae) are similar and morphologically merge into each other, so that it proved to be impossible to unambiguously separate the pollen of these three taxa; this undeterminable pollen is referred to as ORO/PLA in Table 1 and Figures 2–5. All pollen slides were deposited in the Entomological Collection of ETH Zurich. Information on nectar content and nectar availability of the pollen host flowers of *Hylaeus* was inferred from Kugler (1970) and Proctor and Yeo (1973).

Categories of pollen host range

To characterise the degree of host plant association, such as "narrow oligolecty", "broad oligolecty", "polylecty with strong preference" or "polylecty", definitions proposed by Müller and Kuhlmann (2008) were followed. Two contrasting approaches were applied to infer oligolecty for a given species. The first approach averaged pollen host use across all individuals: a species was classified as oligolectic if 95% or more of the pollen grain volume belonged to the same plant family or genus. The second approach relied on the incidence of pure and mixed pollen loads: a species was classified as oligolectic if 90% or more of the females collected pure loads of one plant family or genus. In the present study, the two approaches differed only for one species, i.e. *Hylaeus taeniolatus*, which was classified as polylectic with strong preference for Apiaceae by the first approach and broadly oligolectic on Apiaceae by the second approach. As all crops except for one contained pollen of Apiaceae and most related species of the subgenus *Paraprosopis* proved to be Apiaceae specialists, *H. taeniolatus* was categorised as broadly oligolectic on Apiaceae.

Comparison between pollen host spectrum and flower visiting records

To clarify possible differences between pollen and nectar host use in the Central European *Hylaeus* species, the pollen host spectrum as assessed in the present study was compared with the flower records of females contained in the database of the Wildbienen-Kataster Baden-Württemberg. At the time of data retrieval in September 2021, the database comprised 3175 female flower records from 29 Central European *Hylaeus* species without differentiation between pollen and/or nectar uptake. These

flower visiting observations were distributed all over Baden-Württemberg, recorded from 1916 to 2021 and provided mainly by H.R. Schwenninger, A. Schanowski, R. Prosi, M. Klemm, S. Krausch, M. Haider, H. Burger, R. Burger and V. von Königslöw. The pollen host spectra of the seven species not represented by flower visiting records in the Wildbienen-Kataster database, i.e. *Hylaeus alpinus*, *H. annulatus*, *H. crassanus*, *H. glacialis*, *H. nivalis*, *H. pilosulus* and *H. tyrolensis*, were removed and the comparison was limited to those 29 species, for which both pollen and flower visiting data were available.

Results

Pollen host spectrum at bee species level

Among the 36 Central European *Hylaeus* species, 19 (53%) exhibited an exclusive or strong preference for pollen from a single plant taxon (Table 1, Figs 1–3). Three species turned out to be narrowly oligolectic, i.e. *Hylaeus pilosulus* and *H. signatus* on *Reseda* (Resedaceae) and *H. punctulatissimus* on *Allium* (Amaryllidaceae). Seven species were found to be broadly oligolectic, i.e. *H. clypearis*, *H. duckei*, *H. sinuatus*, *H. styriacus*, *H. taeniolatus* and *H. tyrolensis* on Apiaceae and *H. nigritus* on Asteroideae and Carduoideae (Asteraceae). Nine species were classified as polylectic with strong preference, i.e. *H. cornutus*, *H. gredleri*, *H. kahri*, *H. punctatus* and *H. variegatus* with preference for Apiaceae, *H. paulus*, *H. pfankuchi* and *H. rinki* with preference for *Potentilla* and *Rubus* (Rosaceae) and *H. leptocephalus* with preference for *Melilotus* (Fabaceae). The remaining 17 species proved to be polylectic harvesting pollen on up to 16 plant families (Table 1, Fig. 4), i.e. *H. angustatus*, *H. brevicornis*, *H. communis*, *H. confusus*, *H. crassanus*, *H. difformis*, *H. dilatatus*, *H. gibbus*, *H. hyalinatus*, *H. incongruus*, *H. moricei*, *H. pectoralis*, *H. pictipes* as well as *H. alpinus*, *H. annulatus*, *H. glacialis* and *H. nivalis*, which are restricted in their distribution to the Alps.

Pollen host spectrum at bee genus level

The 36 Central European *Hylaeus* species collected pollen from the flowers of 31 plant families (Table 1, Fig. 5). However, only a few families were represented in high percentages in the pollen host spectrum of the genus as a whole. When summing the percentages of the plant families found in the host plant spectrum of each species across all species, the Apiaceae contributed 39.6% to the pollen host spectrum, followed by the Rosaceae with 18.7%, the Resedaceae with 7.0%, the Fabaceae with 6.1%, the Asteraceae with 3.7%, the Amaryllidaceae with 3.5% and the Campanulaceae with 3.4% (Figs 1, 5). These seven plant families accounted for more than 80% of the plants that the Central European *Hylaeus* species exploited for pollen, whereas the other 24 families were all represented by less than 3.0% in the genus' pollen host spectrum.

Pollen of Apiaceae was collected by all Central European *Hylaeus* species except for *Hylaeus difformis* and three oligolectic species specialised on Asteraceae or Resedaceae (Table 1, Figs 2–4). Based on field observations and the strongly differing morphology and size of the Apiaceae pollen grains recorded in the crop contents, all species including the oligolectic ones exploited several different genera among the Apiaceae. In contrast, almost 95% of all pollen of Rosaceae originated from the two genera *Potentilla* and *Rubus* (Fig. 5), pollen of Resedaceae and Amaryllidaceae exclusively came from the genera *Reseda* and *Allium*, respectively, over 99% of all pollen of Fabaceae was from the genus *Melilotus*, among the Asteraceae solely the two subfamilies Asteroideae and Carduoideae served as hosts and among the Campanulaceae only the two genera *Campanula* and *Jasione* were exploited.

About 89% of the pollen collected by the 36 *Hylaeus* species originated from herbs. Pollen of shrubs, such as *Clematis*, *Frangula*, *Hedera*, *Rosa*, *Rubus*, *Sambucus* and *Vitis*, was represented by slightly more than 10% with *Rubus* alone accounting for 9.6%. Pollen of trees, such as *Castanea* and *Tilia*, contributed only 0.2% to the host plant spectrum of the genus, while 0.4% of the pollen could not be attributed to one of the three vegetation layers.

About 93% of the pollen collected by the 36 *Hylaeus* species originated from flowers with easily accessible nectar, which is either exposed or secreted at the base of flowers that can be reached by the short-tongued *Hylaeus* bees thanks to their small body size. The remaining pollen came from flowers that either do not produce nectar or whose nectaries are not accessible due to their position at the base of narrow flower tubes. Pollen of nectarless flowers, such as *Agrimonia*, *Aruncus*, *Filipendula*, *Hypericum*, *Plantago*, *Sambucus*, *Sanguisorba* and *Rosa*, accounted for 2.3% of the flowers exploited for pollen. Pollen of flowers with inaccessible nectar, such as Carduoideae (Asteraceae) and *Trifolium*, was represented by 2.5% in the host plant spectrum of the genus, while 1.7% of the pollen could not be attributed to one of the three classes of nectar availability.

Comparison between pollen host spectrum and flower visiting records

The high importance of Apiaceae as host plants for the Central European *Hylaeus* species was also evident from the flower visiting records of 29 species from Baden-Württemberg. Out of 3175 flower visiting females observed, 1258 (39.6%) were recorded on Apiaceae, which is similar to the percentage of Apiaceae pollen in the crop contents of the same 29 species amounting to 42.4%. In striking contrast, with 838 (26.4%) flower visiting records the Asteraceae were the second most important plant family after the Apiaceae, whereas the percentage of Asteraceae pollen in the crop contents was only 4.3% across all 29 species. By excluding the Asteraceae specialist *Hylaeus nigritus*, this discrepancy

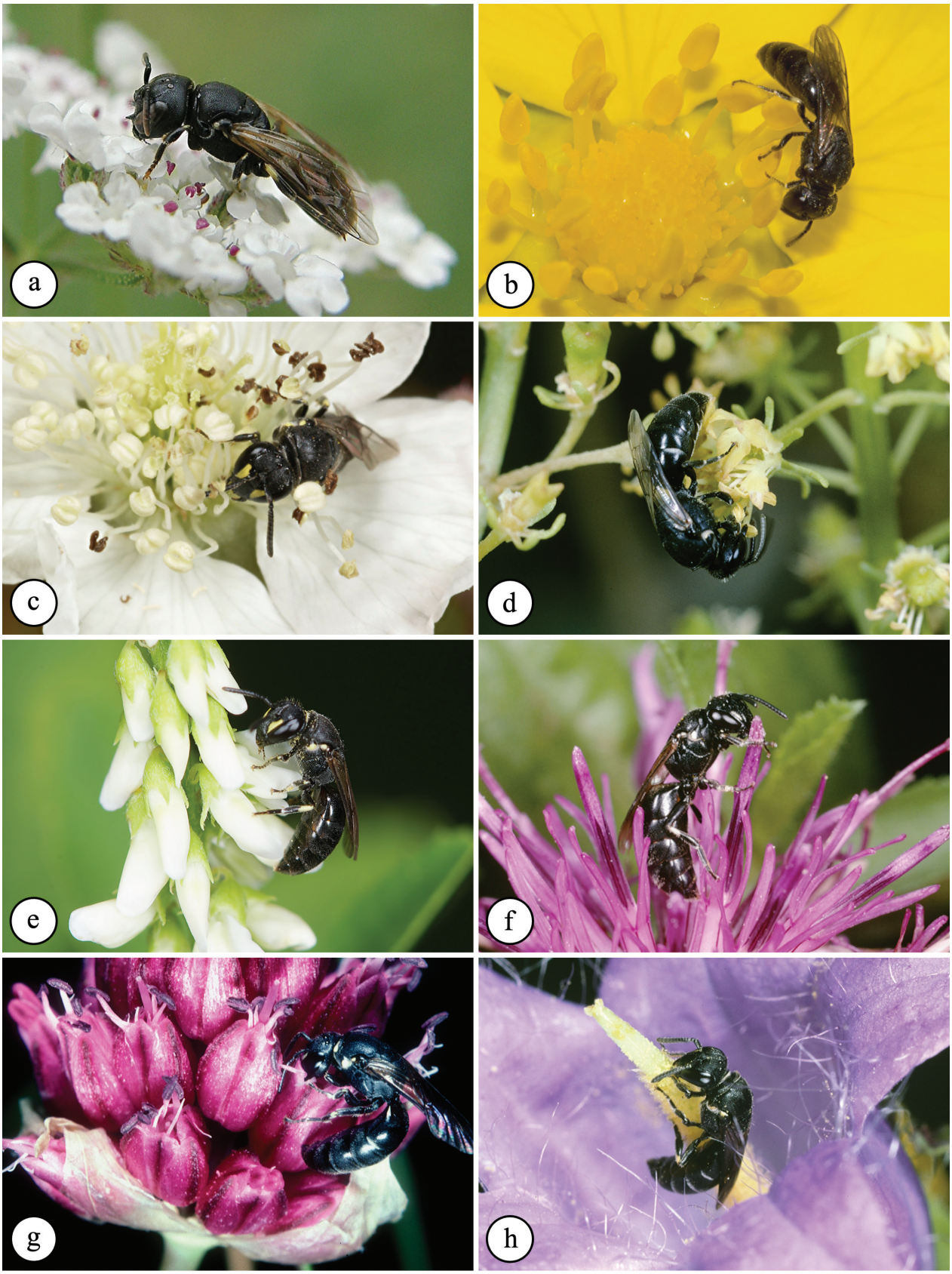

Figure 1. Important pollen hosts of Central European *Hylaeus* species. (**a**) *Daucus carota* (Apiaceae) and *Hylaeus cornutus* (photo S. Falk). (**b**) *Potentilla recta* (Rosaceae) and *Hylaeus brevicornis* (photo A. Haselböck). (**c**) *Rubus* spec. (Rosaceae) and *Hylaeus* spec. (photo B. Jacobi). (**d**) *Reseda lutea* (Resedaceae) and *Hylaeus signatus* (photo A. Krebs). (**e**) *Melilotus albus* (Fabaceae) and *Hylaeus* spec. (photo N. Vereecken). (**f**) *Centaurea scabiosae* (Asteraceae, Carduoideae) and *Hylaeus nigritus* (photo A. Krebs). (**g**) *Allium sphaerocephalon* (Amaryllidaceae) and *Hylaeus punctulatissimus* (photo A. Müller). (**h**) *Campanula trachelium* and *Hylaeus* spec. (photo A. Krebs).

Figure 2. Pollen host spectra of the ten Central European *Hylaeus* species classified as oligolectic. x-axis: Plant families: ADO = Adoxaceae, AMA = Amaryllidaceae, API = Apiaceae, ARA = Araliaceae, AST = Asteraceae, BOR = Boraginaceae, BRA = Brassicaceae, CAM = Campanulaceae), CAR = Caryophyllaceae, CIS = Cistaceae, CRA = Crassulaceae, ERI = Ericaceae, EUP = Euphorbiaceae, FAB = Fabaceae, FAG = Fagaceae, GEN = Gentianaceae, HYP = Hypericaceae, LAM = Lamiaceae, LYT = Lythraceae, ORO = Orobanchaceae, ORO/PLA = *Euphrasia*, *Rhinanthus* or *Veronica*, PLA = Plantaginaceae, POL = Polygonaceae, RAN = Ranunculaceae, RES = Resedaceae, RHA = Rhamnaceae, ROS = Rosaceae, RUB = Rubiaceae, SAX = Saxifragaceae, SCR = Scrophulariaceae, TIL = Tiliaceae, VIT = Vitaceae, ? = unknown pollen types. y-axis: Percentage of pollen volume contained in the female crops.

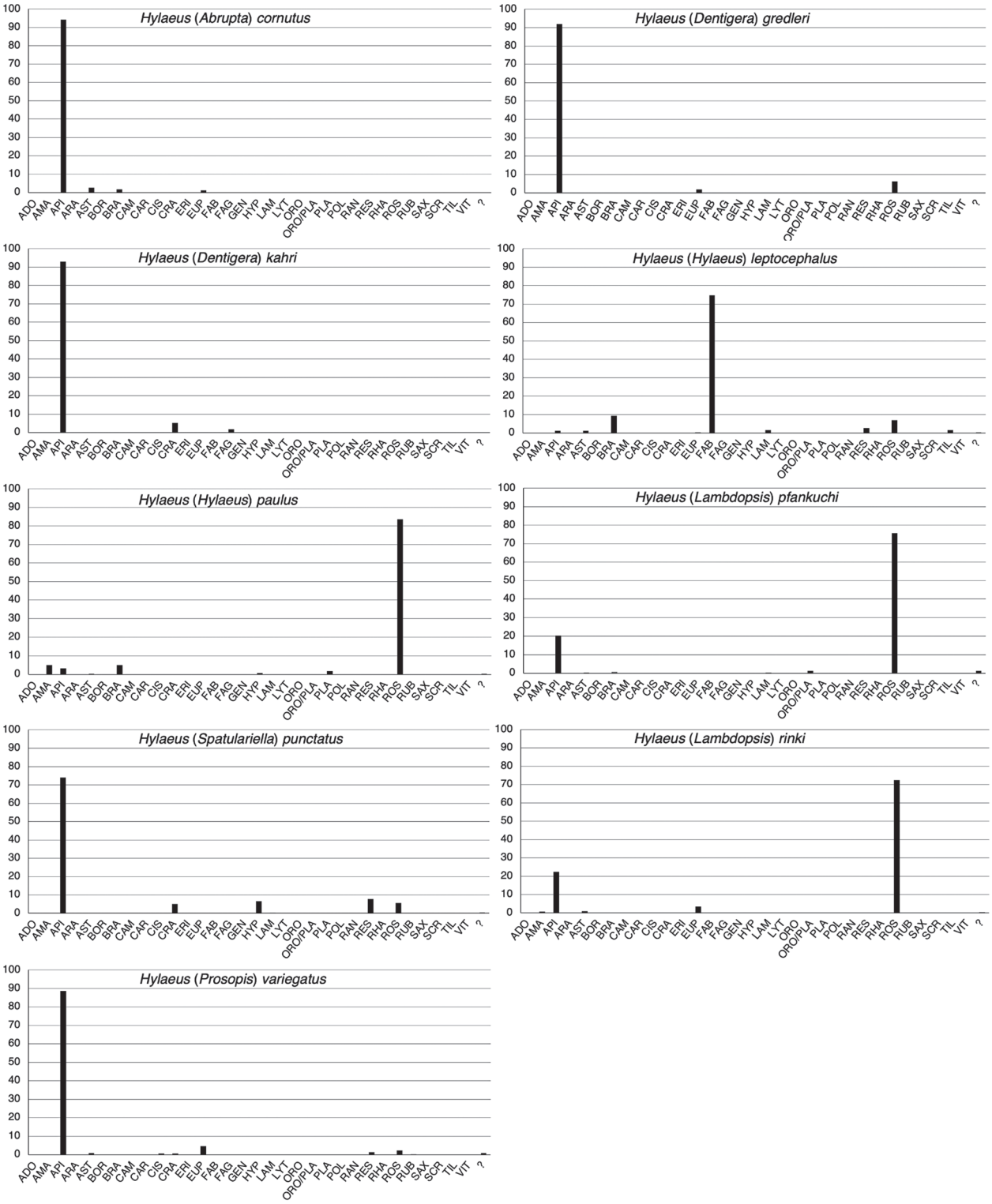

Figure 3. Pollen host spectra of the nine Central European *Hylaeus* species classified as polylectic with strong preference. Abbreviations as in Figure 2.

was even more pronounced with the percentage of female flower visits to the Asteraceae being 20.5% and the percentage of Asteraceae pollen in the crops being 1.1%. Although Asteraceae pollen was found in the crops of 22 out of the 26 polylectic *Hylaeus* species, its proportion was usually very small and ranged from 0.1–4.3% (mean 1.2%); the only exception was *H. dilatatus*, whose host plant spectrum included 13.7% Asteraceae pollen.

Discussion

The results of the present study show that the proportion of Central European *Hylaeus* species exhibiting an exclusive or strong preference for pollen from a single plant taxon is much higher than hitherto assumed and that the current assumption of the genus *Hylaeus* to largely consist of pollen generalists is wrong. Nineteen of the 36

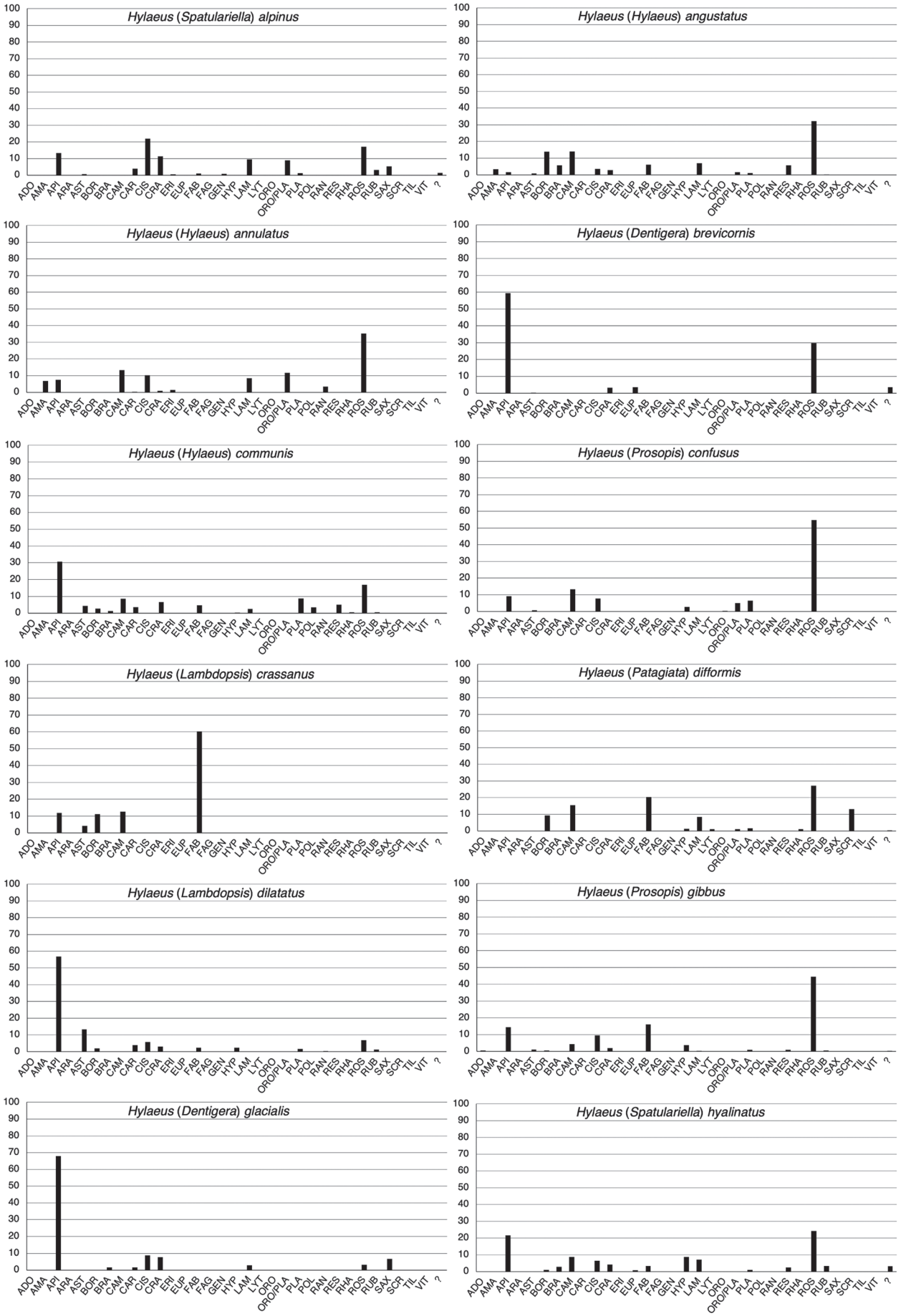

Figure 4. Pollen host spectra of the 17 Central European *Hylaeus* species classified as polylectic. Abbreviations as in Figure 2.

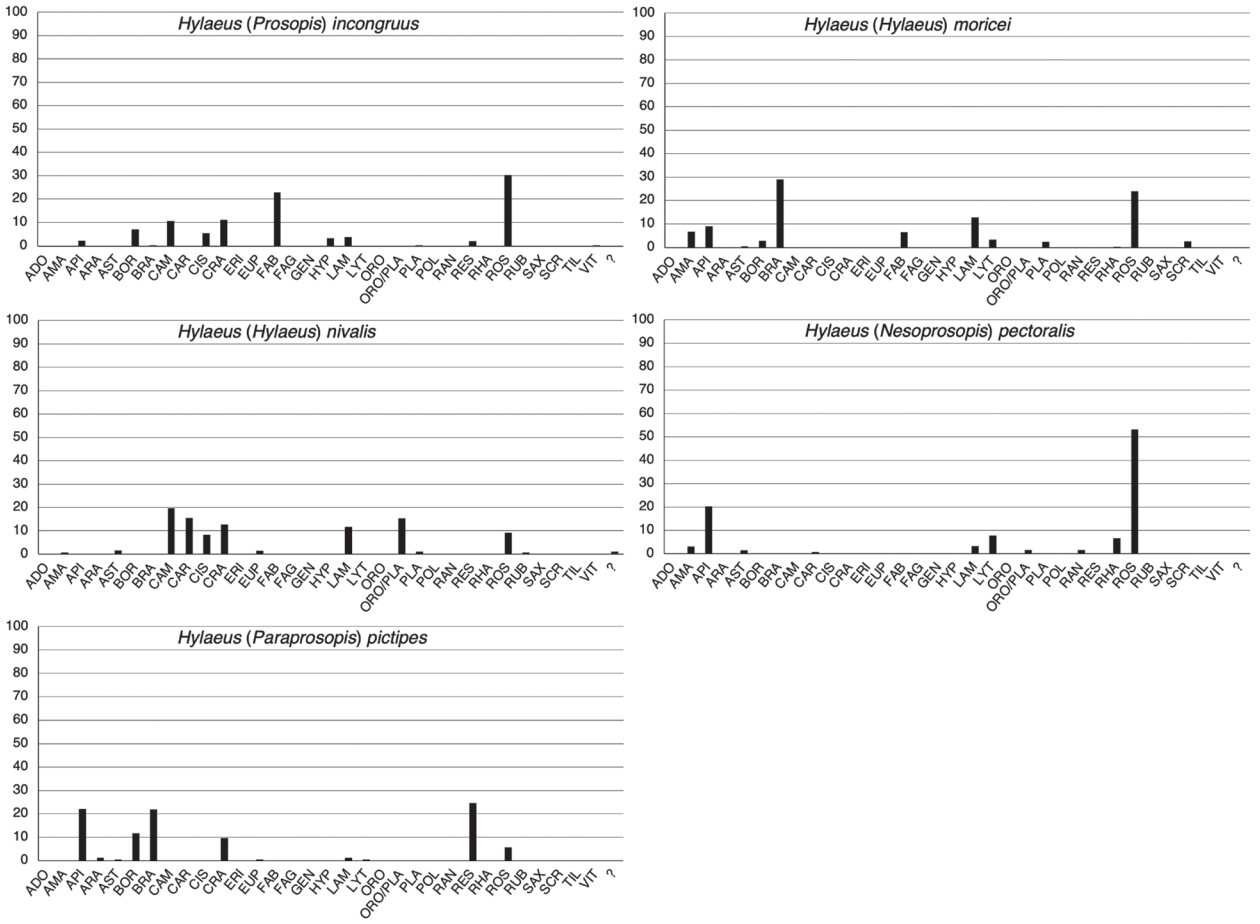

Figure 4. Continued.

Central European species examined are strictly or largely dependent on a single plant taxon for collecting pollen. For eleven of these species, flowers of the Apiaceae are the exclusive or strongly preferred hosts. The high significance of this plant family is also substantiated by the finding that the Apiaceae serve as pollen hosts for all Central European *Hylaeus* species with the exception of one polylectic species and three oligolectic species specialised on plant taxa other than the Apiaceae.

Phylogenetic inference is a powerful tool to reconstruct the evolution of pollen host preferences in bees (Müller 1996; Larkin et al. 2008; Sedivy et al. 2008, 2013; Haider et al. 2014). To date, no phylogeny of the genus *Hylaeus* including its Central European representatives is available, rendering any hypotheses on the evolution of pollen host use in this group of bees premature. Nevertheless, the results of the present study allow for some preliminary insights. First, species that show an exclusive or strong preference for Apiaceae occur in six out of the ten Central European subgenera; this finding suggests that the preference for Apiaceae might be an ancestral trait in the Palaearctic *Hylaeus* fauna or, alternatively, has independently evolved several times in the evolutionary history of the genus. Second, most species of the subgenus *Paraprosopis* are Apiaceae oligoleges, which suggests that the ancestor of the subgenus was specialised on Apiaceae. Third, the two morphologically similar and probably very closely related species *Hylaeus pfankuchi* and *H. rinki* (both belong to the subgenus *Lamdopsis*) have an almost identical pollen host spectrum with roughly 95% of the collected pollen originating from *Potentilla*, *Rosa* (both Rosaceae) and Apiaceae. Considering that these two *Hylaeus* species distinctly differ in their habitat choice with the former mainly occurring in wetlands with reed beds and the latter in forest clearings and along forest edges (Westrich 2018), the largely concordant pollen host choice likely has a genetic basis. The same might apply to two closely related species of the subgenus *Dentigera*, i.e. *H. gredleri* and *H. kahri*, which exhibit a strong preference for Apiaceae, as well as to the three species of the *Hylaeus gibbus* group, i.e. *H. confusus*, *H. gibbus*, *H. incongruus*, whose pollen host spectra are all dominated by Rosaceae and additionally include Apiaceae, Campanulaceae, Cistaceae, Hypericaceae and partly Fabaceae.

Flowers of 31 plant families serve as pollen hosts for the Central European *Hylaeus* species. With 33 families, the number of plant taxa exploited for pollen is similar in the western Palaearctic species of the related genus *Colletes* (Colletidae), and nearly 70% of the plant families used by the *Hylaeus* bees as pollen sources are also exploited by the *Colletes* bees (Müller and Kuhlmann 2008). Furthermore, there is no plant family in the pollen

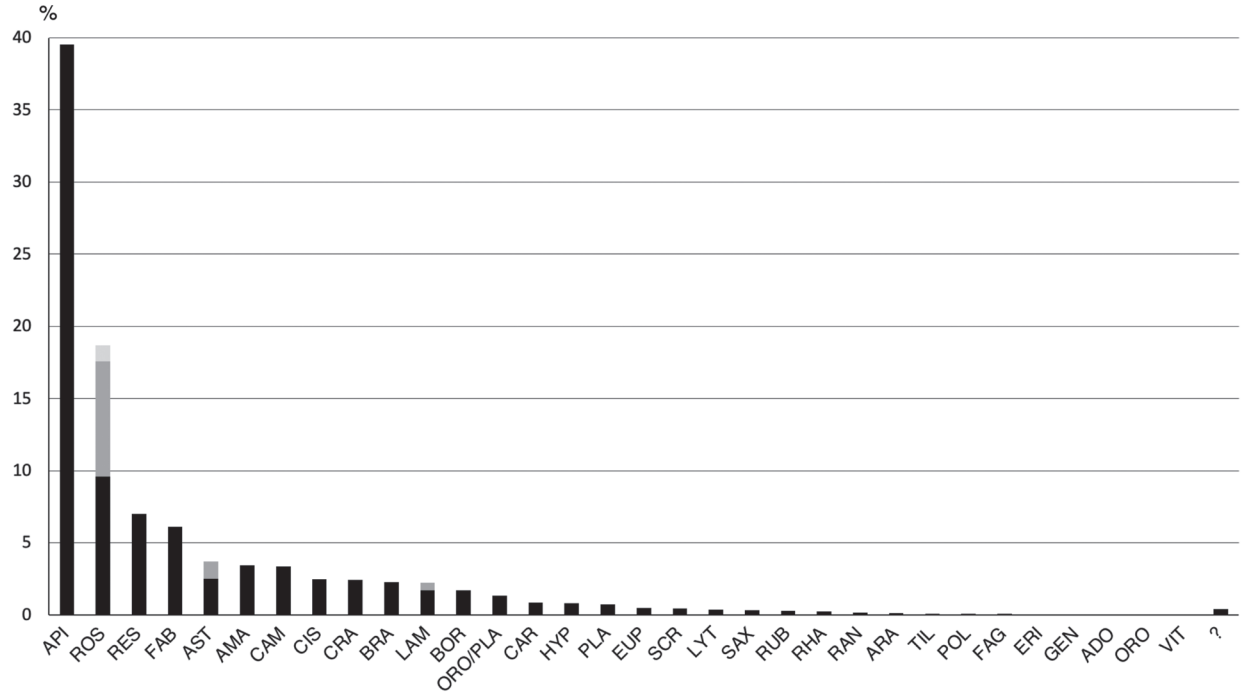

Figure 5. Pollen host spectrum of the genus *Hylaeus* in Central Europe (n = 36 species). Abbreviations as in Figure 2. ROS: black = *Rubus*, dark grey = *Potentilla*, light gray = other; AST: black = Carduoideae, dark grey = Asteroideae; LAM: black = Nepetoideae, dark grey = Lamioideae.

host spectrum of the genus *Hylaeus*, whose pollen is not collected by other short-tongued Central European bees, such as species of *Andrena* or *Lasioglossum* (Westrich 2018). Thus, the peculiar habit of *Hylaeus* bees to ingest the pollen directly on the flowers and to transport it back to the nest inside the crop does not translate into a pollen host spectrum different from other bee taxa.

The finding that 89% of the pollen collected by the Central European *Hylaeus* species originated from herbs and a further 9.6% from *Rubus*, which usually grows as a prostrate shrub, suggests that *Hylaeus* females restrict pollen harvesting mainly to the herbal layer. However, this finding might be biased since the females dissected for the present study were all netted by hand, which possibly resulted in an underrepresentation of specimens harvesting pollen in the shrub or tree layer. In fact, part of the pollen diet of *Hylaeus communis* in five European cities originated from trees (Casanelles-Abella et al. 2022).

About 93% of the plant taxa used by the Central European *Hylaeus* species as pollen hosts can also be exploited for nectar due to the easy access to the nectaries. In contrast, approximately 5% of the pollen hosts lack nectar or secrete nectar that is inaccessible to the *Hylaeus* bees. To compensate for this lack or inaccessibility of nectar, the females must visit other flowers to gain enough nectar for provisioning their brood cells, as is probably exemplified by the Asteraceae specialist *Hylaeus nigritus* and the pollen generalist *H. dilatatus*, for which flowers of Carduoideae (Asteraceae) are important pollen hosts. Although neither species is able to reach the nectaries at the base of the long-tubed Carduoideae flowers with their short proboscis, pollen of Carduoideae contributed 77.4% and 11.3% to the host plant spectra of *H. nigritus* and *H. dilatatus*, respectively. Interestingly, 25 out of 30 crop contents of *H. nigritus* contained a mixture of pollen from Carduoideae and Asteroideae, whereas only two contained solely Carduoideae pollen. Similarly, pollen of Carduoideae was recorded in 7 out of 30 crops in *H. dilatatus* but never constituted the only pollen type. This finding is likely explained by the necessity to combine mere pollen visits to the Carduoideae with visits to the Asteroideae or other plant taxa to obtain nectar.

The comparison between pollen host spectrum and flower visiting records revealed a striking discrepancy in the use of Asteraceae as host plants by the Central European *Hylaeus* species. After exclusion of the Asteraceae specialist *Hylaeus nigritus*, the percentage of Asteraceae pollen in the crop contents averaged only 1.1%, whereas more than 20% of all flower visiting females were observed on this plant family. The most likely explanation for this discrepancy is that the flowers of Asteraceae serve as nectar sources, but not or only marginally as pollen sources. This pattern of use of Asteraceae pollen by the *Hylaeus* bees supports recent findings that the pollen of this plant family possesses unfavourable or protective properties, which render its digestion difficult and necessitate physiological adaptations to successfully utilize it, resulting in a reduced ability to use alternative hosts (Müller and Kuhlmann 2008; Praz et al. 2008; Wood and Roberts 2018; Vanderplanck et al. 2020). This scenario –

known as the Asteraceae paradox – neatly applies to the polylectic *Hylaeus* species, which hardly exploit Asteraceae for pollen, and to *Hylaeus nigritus*, which is specialised on Asteraceae. However, it does not apply to *H. dilatatus*, which is the only polylectic *Hylaeus* species in Central Europe that collects pollen to a considerable degree on Asteraceae. This species might have inherited the ability to successfully utilise Asteraceae pollen from an ancestor specialised on this plant family, as is possibly the case in the *Colletes succinctus* group, which comprises both Asteraceae oligoleges and polyleges that partly exploit Asteraceae for pollen (Müller and Kuhlmann 2008).

Bee diversity and abundance have considerably declined in large parts of Europe during the last decades (Nieto et al. 2014; Powney et al. 2019). Species of the genus *Hylaeus* are no exception: thirteen of the 40 *Hylaeus* species recorded for Switzerland and six of the 31 species occurring in Baden-Württemberg are red-listed (Westrich et al. 2000; Müller and Praz in prep.). The results of the present study enable the targeted improvement of the food supply for these species at risk. Moreover, given the high importance of Apiaceae, Rosaceae, Resedaceae and Fabaceae as pollen hosts, the promotion of summer flowering Apiaceae (particularly *Daucus*), of *Potentilla* and *Rubus* (both Rosaceae), of *Reseda* (Resedaceae) and of *Melilotus* (Fabaceae), for example by including them into wildflower seed mixtures for pollinators, benefits a large part of the Central European *Hylaeus* species.

Conclusions

Although species of the genus *Hylaeus* differ from most other bees by their unusual habit to ingest the pollen directly on the flowers and to transport it internally back to the nest, their patterns of pollen host use are comparable to those of numerous other Palaearctic bee taxa in that i) the genus comprises species that cover the whole spectrum of host plant associations ranging from narrow oligolecty to broad polylecty, ii) a similar set of pollen hosts is used as in many other short-tongued bees, such as *Andrena*, *Colletes* or *Lasioglossum*, and iii) Asteraceae are hardly exploited for pollen by the polylectic species.

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