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Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palaearctic counterparts

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Andrena is a large genus of bees primarily distributed across the Holarctic. Despite their abundance in temperate regions, the pollen diets of many Nearctic *Andrena* remain incompletely resolved. The pollen diets of 50 species of *Andrena* found in Michigan were characterized using light microscopy. Twenty-four species (48%) were classified as pollen specialists, collecting pollen from one botanical family. The remaining 26 species (52%) were classified as pollen generalists, collecting from many botanical families. *Andrena* species fell into three broad foraging groups: (1) spring-flying species foraging predominantly from woody plants; (2) spring-flying species specializing on herbaceous ephemerals; and (3) summer-flying species specializing on herbaceous prairie plant species. Species of Nearctic *Andrena* specialized on pollens from Asteraceae, Geraniaceae, Hydrophyllaceae and Montiaceae or avoided them almost entirely. Botanical families that hosted specialized bees showed a higher variation in utilization by the *Andrena* community than botanical families without specialists. In contrast, Palaearctic species showed little temporal partitioning and low variation in the utilization of different botanical families. This pattern of pollen use supports previous findings that pollens from certain botanical families cannot be used as a food source without physiological adaptations, but that this phenomenon is more pronounced in the Nearctic *Andrena* fauna.

ADDITIONAL KEYWORDS: Apoidea – Asteraceae – evolution – host plant specialization – oligolecty – pollen mixing – polylecty – solitary bee.

INTRODUCTION

With only a few exceptions amongst the tropical Meliponini (Roubik, 1982; Bänziger *et al.*, 2009), the vast majority of non-parasitic bee species collect pollen from flowers in order to feed their offspring. Through facilitating plant reproduction, the process of pollen collection can increase the fitness of both bee and flowering plant species, an interaction that appears to be different qualitatively from the clearly antagonistic nature of phytophagy (Weisser & Siemann, 2008). However, quantitative studies demonstrate that bees may remove substantial quantities of pollen from flowers whilst providing little in the way of pollination, pollen that is consequently lost from the potential reproductive output of the plant (Schlindwein *et al.*, 2005; Müller *et al.*, 2006; Parker *et al.*, 2016). Small bees can rob pollen from flowers without pollinating them effectively (Minckley & Roulston, 2006), or bees may groom pollen from their body between floral visits, such as bumble bees grooming pollen onto their hindlegs, spatially removing it from any potential interaction with the reproductive parts of the flower (Harder & Wilson, 1998). Flowering plants hence face a trade-off between attracting bees in order to reproduce successfully and, subsequently, preventing them from overharvesting pollen.

Manipulative experiments have shown that bees from the family Megachilidae can have highly variable success rates when developing on different pollen sources (Williams, 2003; Praz *et al.*, 2008; Sedivy *et al.*, 2011; Eckhardt *et al.*, 2014). Transferring eggs from host to non-host pollen provisions demonstrated that pollen specialist bees (oligoleges, bees collecting pollen from one botanical family) showed reduced developmental success on non-host pollens used by other

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specialists (Asteraceae, Ranunculaceae, Boraginaceae and Campanulaceae), despite successfully developing on their own preferred host (Praz *et al.*, 2008). When transferred to mixtures of normal pollen host combined with a novel pollen host used by a generalist *Osmia* (a polylege, bees collecting pollen from many botanical families; in this study Brassicaceae and Boraginaceae), a specialized species of *Osmia* developed normally, in some cases better than on their preferred host alone (Williams, 2003). In contrast, generalist *Osmia* developed more poorly when transferred to mixtures containing the novel host used by the specialist (Asteraceae). In a separate study, two species of pollen generalist *Osmia* were able to develop successfully on Brassicaceae pollen, but both failed on a diet of pure Asteraceae pollen (Sedivy *et al.*, 2011), with *Osmia cornuta* also failing to develop on a diet of pure *Ranunculus* pollen (Sedivy *et al.*, 2011; Eckhardt *et al.*, 2014). This variation in developmental success suggests that pollen of certain botanical families is difficult or impossible to digest by certain bee species, although the exact mechanisms underpinning this phenomenon are unclear and may not be related to inherent toxicity (Sedivy *et al.*, 2012). Owing to this lack of clarity, these are henceforth broadly referred to as 'challenging' pollens rather than 'toxic' pollens (see Roulston & Cane, 2000; Praz *et al.*, 2008).

One botanical family identified as having pollen that appears to be challenging for bees to use is the family Asteraceae. In an assessment of western Palaearctic *Colletes* (Colletidae), Müller & Kuhlmann (2008) found that, although there was a wide variation in pollen specialization within the genus from pollen specialists to pollen generalists, *Colletes* species either specialized on Asteraceae pollen or avoided it almost entirely, with the authors dubbing this phenomenon 'the Asteraceae paradox'. Asteraceae pollen is known to be deficient in several amino acids important to bees (Loper & Cohen, 1987; Praz *et al.*, 2008), and the chemical content of the pollenkitt (the lipid-rich coating found on each pollen grain) may interfere with the nutrient assimilation process, rendering its digestion difficult (Williams, 2003). If an investment in some kind of physiological adaptation is necessary to use a particular resource, we may expect a trade-off with a reduced ability to use alternative host plants (Scriber, 2005; Rasmann & Agrawal, 2011). More broadly, if the differential use of Asteraceae pollen by solitary bees is driven by physiological constraints, the Asteraceae paradox should be observable in any pollen type that requires physiological adaptation in order to be used effectively. Whilst the Asteraceae paradox has been documented in Palaearctic *Colletes*, there is a limited understanding of how widespread this phenomenon is throughout the wider bee phylogeny, and how many other botanical families follow this trend.

The genus *Andrena* is in the subfamily Andreninae in the family Andrenidae, a large family of > 2900 species (Danforth *et al.*, 2013). Andreninae is composed of a few small genera plus the genus *Andrena*, which makes up the overwhelming majority of this subfamily, with 1446 valid species listed in the last global revision (Gusenleitner & Schwarz, 2002). *Andrena* appears to have evolved in North America (Larkin *et al.*, 2008) before expanding out over Beringia to the Palaearctic (but see Dubitzky *et al.*, 2010). *Andrena* contains a mixture of oligolectic and polylectic species in both the Nearctic (Larkin *et al.*, 2008) and the Palaearctic (Westrich, 1989). This variation in pollen preferences makes *Andrena* an excellent genus in which to investigate the Asteraceae paradox in a separate evolutionary lineage from *Colletes*.

Work in Palaearctic *Andrena* has shown that some of these species do not appear to conform to the Asteraceae paradox, with some polylectic species collecting up to 70% of their pollen from Asteraceae (Wood & Roberts, 2017) and to 30% from Ranunculaceae, another botanical family that has been suggested to possess properties that render its digestion by bees difficult (Praz *et al.*, 2008; Eckhardt *et al.*, 2014; but see Sedivy *et al.*, 2012). Although some researchers have characterized the pollen preferences of Nearctic *Andrena* species (Neff & Simpson, 1997; Tepedino, 2003; Larkin *et al.*, 2008), they did not investigate relative use of these challenging pollen types, particularly within polylectic *Andrena*. Nearctic *Andrena* therefore offer the opportunity to investigate the Asteraceae paradox across a different part of the range of a genus known to deviate from the trend of Asteraceae specialization or avoidance. In the present study, the pollen foraging choices of Michigan *Andrena* species were quantified in order to investigate how patterns of host plant use differ between Nearctic and Palaearctic *Andrena* species.

MATERIAL AND METHODS

Specimen collection

A total of 85 species of *Andrena* have been recorded from Michigan from 23 subgenera (Gibbs *et al.*, 2017). In this study, we selected species with at least five female specimens retaining pollen in the scopa, sufficient to allow for broad characterization of dietary preferences. An effort was made to analyse a greater number of samples from polylectic or poorly characterized species rather than well-established oligoleges. This comprised a total of 616 specimens from 50 species from 21 of the 23 Michigan subgenera, with the exception of *Iomelissa*, a monotypic subgenus containing the single species *Andrena violae* Robertson, a narrow oligolege of *Viola* (LaBerge, 1986) and *Taeniandrena*, because the only North American species, *Andrena* *wilkella* Kirby, is not native to the Nearctic (Cane, 2003).

Although not covering the entire fauna, this analysis captures the broad diversity of this genus in the Great Lakes region of North America. Specimens were taken from the A. J. Cook arthropod research collection and the Isaacs laboratory collection (Michigan State University), and from the private collections of T.J.W. and J. Gibbs (University of Manitoba). Specimens were identified by T.J.W. and J. Gibbs, and material is available for study at these institutions. These results were compared with pollen preferences in Palaearctic *Andrena*, specifically from Britain, using the data from Chambers (1968), Wood & Roberts (2017; 29 species, $N = 1688$) and data for British *Andrena* from the subgenus *Micrandrena* (Wood *et al.*, 2016; plus unpublished data, five species, $N = 266$).

HOST RANGE CHARACTERIZATION

Pollen loads were analysed using the light microscopy method outlined by Westrich & Schmidt (1986) and modified by Wood & Roberts (2017). The size of pollen loads on individual bees was estimated, ranging from a full load to a one-eighth load. Pollen grains were removed from the scopa using an entomological pin and transferred to a drop of water on a microscope slide. Grains were left to absorb water for a few minutes and then the slides were gently heated to allow evaporation. Molten glycerine jelly stained with fuchsin was added, and the slide was sealed with a coverslip. Following Müller & Kuhlmann (2008), the percentage of the load composed of different plant species was estimated along three randomly selected lines across the cover slip at a magnification of ×400. The percentage of the load was estimated by the relative area of the slide occupied by each plant species, rather than the absolute number of grains (Cane & Sipes, 2006). Two-thirds (68%) of pollen loads contained pure pollen from one genus, and the majority of pollen types ranged between 20 and 30 μm in diameter, so consideration of pollen volume would have resulted in only minor changes in the proportions of pollen used by the generalist species. Pollen species representing < 1% of the load were excluded from further analysis because their presence might have arisen from contamination. The percentages of pollen collected were corrected according to the overall size of each load to give a final weighting. Pollen loads were identified to the lowest taxonomic level possible using a reference collection assembled during the project, in most cases to genus (see Supporting Information, Appendix S1 for full list of identified pollens).

Host range was characterized using the criteria of Müller & Kuhlmann (2008; Table 1), who modified the categories proposed by Cane & Sipes (2006). The two empirical methods used to assess these categories can be seen in the Supporting Information (Appendix S2) and are based on either the total volume of pollen collected from one botanical family or the incidence of pure and mixed loads. Following Müller & Kuhlmann (2008), where there was a discrepancy between the two methods, *Andrena* species were assigned to the category with the higher degree of specialization.

The percentage of pollen collected from different botanical families was calculated for each bee species. Evidence suggests that use of challenging pollens (e.g. Ranunculaceae) by polylectic bee species may be mediated by dietary breadth (Eckhardt *et al.*, 2014), and so a dietary breadth score was calculated for each bee species. Owing to different sample sizes, a rarefaction procedure was used to calculate dietary breadth scores (Williams, 2005). Following Wood & Roberts (2017), diets were rarefied to a standardized sample of five pollen loads, chosen at random without replacement 1000 times. As this rarefaction procedure is designed for use on integer data, the pollen load data were first transformed. For example, with a sample size of 14, the percentage of pollen collected from each plant species was multiplied by the sample size to give a whole pollen load equivalent, e.g. 40% becomes 5.6 pollen loads. These values were all multiplied by ten and rounded to the nearest whole number to give an integer equivalent that was used in the rarefaction procedure.

The level of variation in the use of pollens from different botanical families was assessed by calculating coefficient of variation scores. Botanical families were ranked according to their importance to the *Andrena* fauna in each region. The dietary preferences of each *Andrena* species was weighted equally. For example, Hydrophyllaceae (*Hydrophyllum*) pollen was collected only by *Andrena geranii*, representing its entire diet. Hydrophyllaceae therefore comprised an average of 2% of the pollen collected by the characterized Michigan species (1/50 species, 2%). To reduce variation, botanical families composing < 1% of the faunal diet were excluded. Out of the 29 botanical families collected by Michigan *Andrena*, only 15 composed > 1% of the total diet (total importance 97%). For the 48 botanical families collected by British *Andrena*, only 11 composed > 1% of the total diet (total importance 92%). A coefficient of variation score was calculated for each of these families. Botanical families were categorized as hosting at least one specialist (e.g. Asteraceae) or not hosting any specialists (e.g. Sapindaceae) in their respective dataset. In addition, a third category was calculated, i.e. botanical family hosting specialists from which the specialist data have been removed. This was in order to look at variation in use of this family by non-specialized species. If pollen from a particular family is specialized upon or avoided, the coefficient of variation will be small once specialists are removed. Differences in average coefficient of variation

Table 1. Categories of bee host range as applied in this study

Category	Subcategories	Definition
Monolecty	–	Pollen collection on only one plant species even in the presence of one or more sympatric species of the same genus*
Oligolecty	Narrow oligolecty	Pollen collection from two to several species belonging to one plant genus
	Broad oligolecty	Pollen collection from two to several genera belonging to one plant tribe, subfamily or family
	Eclectic oligolecty	Pollen collection from two to four plant genera belonging to two or three plant families
Polylecty *s.l.*	Polylectic with strong preference	Pollen collection from several plant families, but one plant clade (family, subfamiliy, tribe, genus or species) predominates
	Mesolecty	Pollen collection from more than four plant genera belonging to two or three plant families
	Polylecty *s.s.*	Pollen collection from various genera belonging to at least four plant families

Reproduced from Müller & Kuhlmann (2008). *Pollen collection from one plant species in the absence of coflowering congenerics is referred to as a special case of narrow oligolecty.

scores between these three categories were tested using Kruskal–Wallis one-way analysis of variance tests with Dunn's *post hoc* tests for pairwise comparisons.

Given that the analysis by Wood & Roberts (2017) focused on polylectic British *Andrena*, few oligoleges are included in the British dataset. Seven of the botanical families (Apiaceae, Brassicaceae, Cucurbitaceae, Dipsacaceae, Ericaceae, Fagaceae and Rosaceae) collected by *Andrena* in the British dataset host specialist *Andrena* when considering the whole fauna (see Supporting Information, Appendix S3). In contrast, the Michigan dataset has a representative sample of specialist *Andrena* for each botanical family composing > 1% of the collected pollen. To ensure that the results from the British dataset are not biased by the low percentage of oligoleges, 11 species native to Britain specializing on Apiaceae (*Andrena nitidiuscula* Schenck, *Andrena proxima* Kirby), Brassicaceae (*Andrena nigrospina* Thompson, *Andrena niveata* Friese), Cucurbitaceae (*Andrena florea* Fabricius), Dipsacaceae (*Andrena hattorfiana* Fabricius, *Andrena marginata* Fabricius), Ericaceae (*Andrena fuscipes* Kirby, *Andrena lapponica* Zetterstedt), Fagaceae (*Andrena ferox* Smith) and Rosaceae (*Andrena tarsata* Nylander) were added (Westrich, 1989), with the assumption they collected 100% of their pollen from their respective botanical family. This brings the percentage of oligoleges into line with the whole British fauna (16/45 species, 36%; see Supporting Information, Appendix S3). Coefficient of variation scores were calculated for this modified dataset as above.

PHENOLOGICAL TRENDS

In addition, phenological trends were investigated across the two faunas. Peak pollen foraging was calculated for each species based on the median pollen foraging day from characterized specimens. For the British fauna, bivoltine species (species with two generations per year) were split into their respective generations and treated as separate entities. All Michigan *Andrena* species are univoltine. Identified pollens were characterized as either woody or herbaceous, depending on the growth pattern of their plant of origin (Supporting Information, Appendix S1). The percentage of pollen collected from woody plants was plotted against the median pollen foraging date to investigate phenological trends in pollen foraging behaviour.

All statistical analyses and figures were produced R version 3.3.2 (R Development Core Team, 2016) using the function *rarefy* in the package *vegan* (Oksanen *et al.*, 2015) to calculate diet rarefaction scores.

RESULTS

HOST RANGE OF MICHIGAN *ANDRENA* SPECIES

A total of 57 pollens from 28 botanical families were identified (Supporting Information, Appendix S1). Almost half of the studied Michigan *Andrena* species were characterized as oligolectic (24/50, 48%; Table 2), with more than a quarter (16/50, 32%) displaying narrow oligolecty on a particular genus, primarily upon *Salix* ($N = 6$) but also on *Claytonia* ($N = 1$), *Cornus* ($N = 2$), *Geranium* ($N = 1$), *Helianthus* ($N = 1$), *Hydrophyllum* ($N = 1$), *Packera* ($N = 1$), *Rhus* ($N = 1$) and *Vaccinium* ($N = 2$). The remaining *Andrena* species (26/50, 52%) were characterized as polylectic to varying degrees (Table 2). Overall, the results presented here are in line with current thought surrounding pollen use in North American *Andrena* (Gibbs *et al.*, 2017), with a few small differences. *Andrena brevipalpis* Cockerell is

Table 2. Host plant use and diet categories for selected Michigan *Andrena* species

Species	*N*	*n*	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Andrena algida Smith, 1853	11	8	SAL 97.5, others 2.5	63.6	100.0	Narrowly oligolectic (*Salix*)
Andrena alleghaniensis Viereck, 1907	11	9	ROS 43.7, ADO 15.0, BRA 13.3, SAL 12.9, API 6.6, RHA 3.9, AST 3.6, others 1.0	27.3	54.5	Polylectic *s.s.*
Andrena andrenoides (Cresson, 1878)	15	5	SAL 100.0	100.0	100.0	Narrowly oligolectic (*Salix*)
Andrena arabis Robertson, 1897	10	5	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
Andrena barbilabris (Kirby, 1802)	23	15	SAL 37.8, ROS 35.9, SAP 16.4, COR 9.6, others 0.3	26.0	43.5	Polylectic *s.s.*
Andrena bradleyi Viereck, 1907	9	8	ERI 100.0	100.0	100.0	Narrowly oligolectic (*Vaccinium*)
Andrena brevipalpis Cockerell 1930	24	10	ANA 100.0	100.0	100.0	Narrowly oligolectic (*Rhus*)
Andrena canadensis Dalla Torre, 1896	6	6	AST 100.0 (*Solidago*/ *Symphyotrichum*)	100.0	100.0	Broadly oligolectic (Asteraceae)
Andrena carlini Cockerell, 1901	20	9	ROS 28.7, SAL 18.5, ERI 15.9, FAG 13.3, BRA 6.8, SAP 6.2, RHA 2.4, OLE 2.2, CAP 2.1, others 3.9	10.0	45.0	Polylectic *s.s.*
Andrena carolina Viereck, 1909	5	5	ERI 100.0	100.0	100.0	Narrowly oligolectic (*Vaccinium*)
Andrena ceanothi Viereck, 1917	13	12	ROS 46.7, RHA 23.4, ANA 11.1, SAL 9.7, COR 6.9, AQI 2.2	38.4	46.1	Polylectic *s.s.*
Andrena chromotricha Cockerell, 1899	6	1	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae)
Andrena commoda Smith, 1879	10	7	ROS 58.0, ANA 20.8, RHA 8.7, RAN 5.8, ADO 3.5, FAB 2.0, others 1.2	20.0	80.0	Polylectic *s.s.*
Andrena crataegi Robertson, 1893	22	13	ROS 47.3, RHA 24.5, ANA 9.3, FAB 6.3, SAL 6.3, unknown 2.1, others 4.1	18.1	63.6	Polylectic *s.s.*
Andrena cressonii Robertson, 1891	18	10	SAL 37.7, ROS 29.4, ANA 17.6, SAP 6.5, ADO 3.7, others 5.1	16.7	44.4	Polylectic *s.s.*

Table 2. *Continued*

Species	*N*	*n*	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Andrena distans Provancher, 1888	5	3	GER 100.0	100.0	100.0	Narrowly oligolectic (*Geranium*)
Andrena erigeniae Robertson, 1891	7	3	MON (*Claytonia*) 99.5, AST 0.5	85.7	100.0	Narrowly oligolectic (*Claytonia*)
Andrena erythrogaster (Ashmead, 1890)	14	9	SAL 96.2, ROS 3.8	92.9	92.9	Narrowly oligolectic (*Salix*)
Andrena forbesii Robertson, 1891	24	13	ROS 53.4, SAL 13.4, BRA 8.3, ADO 6.1, FAG 5.1, OLA 4.7, RUT 3.2, others 5.7	41.7	62.5	Polylectic *s.s.*
Andrena frigida Smith, 1853	11	8	SAL 98.2, SAP 1.8	90.9	100.0	Narrowly oligolectic (*Salix*)
Andrena gardineri Cockerell, 1906	5	2	AST (*Packera*) 100.0	100.0	100.0	Narrowly oligolectic (*Packera*)
Andrena geranii Robertson, 1891	5	4	HYD (*Hydrophyllum*) 100.0	100.0	100.0	Narrowly oligolectic (*Hydrophyllum*)
Andrena helianthi Robertson, 1891	6	4	AST 100.0 (*Helianthus*)	100.0	100.0	Narrowly oligolectic (*Helianthus*)
Andrena hippotes Robertson, 1895	20	11	SAL 35.2, ROS 30.0, ANA 27.9, AQI 2.1, others 4.8	30.0	45.0	Polylectic *s.s.*
Andrena hirticincta Provancher, 1888	9	9	AST 100.0 (*Solidago*/*Symphyotrichum*)	100.0	100.0	Broadly oligolectic (Asteraceae)
Andrena illinoiensis Robertson, 1891	8	8	SAL 100.0	100.0	100.0	Narrowly oligolectic (*Salix*)
Andrena imitatrix Cresson, 1872	15	11	ROS 50.2, SAL 29.9, SAP 11.8, BET 5.1, AST 2.2, others 0.8	26.7	66.7	Polylectic *s.s.*
Andrena integra Smith, 1853	8	6	COR 100.0	100.0	100.0	Narrowly oligolectic (*Cornus*)
Andrena mandibularis Robertson, 1892	12	8	ROS 46.3, SAP 37.6, SAL 11.1, AST 2.5, MON 2.2, CAP 0.3	25.0	50.0	Mesolectic (Rosaceae, Sapindaceae, Salicaceae)
Andrena miranda Smith, 1879	17	13	FAB 42.5, ROS 32.9, ANA 14.0, API 10.7	29.4	58.8	Polylectic *s.s.*
Andrena miserabilis Cresson, 1872	23	11	SAP 37.0, ROS 33.5, SAL 26.9, RHA 2.3, others 0.4	34.8	43.5	Polylectic *s.s.*
Andrena nasonii Robertson, 1895	20	15	ROS 60.7, SAL 13.1, API 8.7, ADO 6.8, SAP 2.7, AST 2.7, others 5.2	30.0	80.0	Polylectic *s.s.*
Andrena nigrihirta (Ashmead, 1890)	6	4	FAB 42.5, ROS 32.7, CAP 22.7, others 2.1	16.7	50.0	Mesolectic (Fabaceae, Rosaceae, Caprifoliaceae)

Table 2. *Continued*

Species	*N*	*n*	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Andrena nivalis Smith, 1853	11	9	ROS 69.6, RHA 7.9, ANA 6.7, ADO 6.2, CAP 4.1, COR 4.0, others 1.5	36.4	90.9	Polylectic *s.s.*
Andrena nubecula Smith, 1853	5	4	AST 100.0 (*Solidago*/*Symphyotrichum*)	100.0	100.0	Broadly oligolectic (Asteraceae)
Andrena nuda Robertson, 1891	10	8	ROS 59.4, ANA 17.9, RHA 14.4, ADO 4.6, SAL 2.6, others 1.1	30.0	70.0	Polylectic *s.s.*
Andrena perplexa Smith, 1853	8	7	ROS 25.0, SAL 16.0, IRI 13.4, COR 13.0, ADO 11.1, RHA 6.9, OLA 6.7, AST 4.3, BET 2.6, FAB 1.0	12.5	50.0	Polylectic *s.s.*
Andrena placata Mitchell, 1960	5	3	AST 100.0 (*Solidago*/*Symphyotrichum*)	100.0	100.0	Broadly oligolectic (Asteraceae)
Andrena platyparia Robertson, 1895	7	3	COR 100.0	100.0	100.0	Narrowly oligolectic (*Cornus*)
Andrena robertsonii Dalla Torre, 1896	9	8	ROS 80.8, COR 16.0, RHA 3.2	55.6	88.9	Polylectic with a strong preference (Rosaceae)
Andrena rudbeckiae Robertson, 1891	5	4	AST (*Rudbeckia*/*Ratibida*) 100.0	100.0	100.0	Broadly oligolectic (Asteraceae)
Andrena rufosignata Cockerell, 1902	19	12	ROS 57.8, SAP 20.7, SAL 16.5, ERI 2.4, AST 2.4, BET 0.4	36.8	73.7	Polylectic *s.s.*
Andrena rugosa Cockerell, 1906	17	14	ROS 40.6, SAL 12.9, BRA 11.2, SAP 10.5, ANA 7.4, AQI 5.8, ADO 4.5, COR 2.4, RAN 2.0, others 2.7	23.5	47.1	Polylectic *s.s.*
Andrena spiraeana Robertson, 1895	9	8	ROS 33.6, API 24.0, COR 16.0, RHA 14.9, ANA 8.0, others 3.5	11.1	44.4	Polylectic *s.s.*
Andrena thaspii Graenicher, 1903	9	6	FAB 70.4, API 17.6, ROS 9.0, CAP 2.4, ANA 0.6	55.6	77.8	Polylectic with a strong preference (Fabaceae)
Andrena vicina Smith, 1853	35	20	SAL 24.9, ROS 21.6, ERI 21.0, CAP 8.0, SAP 8.0, BRA 6.5, ADO 3.3, IRI 2.2, others 4.5	14.2	34.3	Polylectic *s.s.*
Andrena virginiana Mitchell, 1960	13	3	ROS 91.3, RHA (*Ceanothus*) 8.4, FAB 0.3	92.3	92.3	Polylectic with a strong preference (Rosaceae)

Table 2. *Continued*

Species	*N*	*n*	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Andrena wellesleyana Robertson, 1897	9	6	SAL 100.0	100.0	100.0	Narrowly oligolectic (*Salix*)
Andrena w-scripta Viereck, 1904	16	14	ROS 67.1, SAP 14.0, FAB 6.8, AST 6.0, API 3.8, SAL 2.3	56.3	81.3	Polylectic with a strong preference (Rosaceae)
Andrena ziziae Robertson, 1891	11	4	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)

N, number of analysed pollen loads; *n*, number of unique sampling localities. Plant taxa: ADO, Adoxaceae; ANA, Anacardiaceae; API, Apiaceae; AQI, Aquifoliaceae; AST, Asteraceae; BET, Betulaceae; BRA, Brassicaceae; CAP, Caprifoliaceae; COR, Cornaceae; ERI, Ericaceae; GER, Geraniaceae; HYD, Hydrophyllaceae; IRI, Iridaceae; LAU, Lauraceae; MON, Montiaceae; OLE, Oleaceae; RAN, Ranunculaceae; RHA, Rhamnaceae; ROS, Rosaceae; RUT, Rutaceae; SAL, Salicaceae; SAP, Sapindaceae.

considered an oligolege of *Rhus*, rather than merely having a preference for this genus (see LaBerge, 1977). Likewise, *Andrena algida* Smith, *Andrena illinoiensis* Robertson and *Andrena wellesleyana* Robertson are also considered oligoleges of *Salix* (see Ribble, 1968; LaBerge & Ribble, 1972; LaBerge, 1977). Goldstein & Ascher (2016) recorded *Andrena ceanothi* Viereck as an oligolege of *Vaccinium*, a result not supported by the present study. The species does visit *Vaccinium* (LaBerge, 1973; Gibbs *et al.*, 2017; T.J.W. pers. obs.), but seemingly only for nectar, as neither it nor any other *Trachandrena* species characterized here collected any ericaceous pollen. The specific epithet '*ceanothi*' is another example of misleading scientific names that can obscure true floral associations (Tepedino, 2003).

USE OF CHALLENGING BOTANICAL FAMILIES

Fifteen botanical families contributed > 1% to the diets of Michigan *Andrena*, with the top ten composing 87% of the overall diet (Table 3). Eleven botanical families contributed > 1% to the diets of British *Andrena*, with the top ten composing 91% of the overall diet. Rosaceae, Salicaceae and Asteraceae were both in the top five botanical families for both faunas. In line with western Palaearctic *Colletes*, Michigan *Andrena* species either specialized on Asteraceae or avoided this family almost entirely (Fig. 1A), with no non-specialist collecting > 10% of their pollen diet from Asteraceae. This trend was also seen in Geraniaceae, Hydrophyllaceae and Montiaceae. Families such as Anacardiaceae, Apiaceae, Brassicaceae, Cornaceae, Ericaceae and Salicaceae that hosted specialists saw intermediate levels of exploitation by generalist bees, with quantities reaching up to 30% of their overall diet.

For the Michigan fauna, botanical families hosting pollen specialists had significantly higher coefficient of variation scores than those that do not (449 ± 62, 232 ± 42, Dunn's test, $z = 1.3$, $P < 0.001$; Fig. 2A). Once pollen specialists were removed, variation in pollen use of these botanical families was significantly lower than for botanical families that do not host specialists (61 ± 16, 232 ± 42, Dunn's test, $z = 2.2$, $P < 0.001$; Fig. 2A). There was no difference between the three categories for British *Andrena* (Kruskal–Wallis $\chi^2 = 4.6$, $P = 0.099$; Fig. 2B). The inclusion of additional oligolectic British *Andrena* ($N = 13$) to bring the percentage of oligoleges into line with the whole fauna (see Supporting Information, Appendix S3) did not change the difference between families hosting pollen specialists and those that do not (340 ± 55 and 285 ± 34, respectively, Dunn's test, $z = 0.0$, $P = 0.982$). Once pollen specialists were removed, variation in pollen use of these botanical families was lower than for botanical families that do not host specialists (220 ± 15 and 285 ± 34, respectively, Dunn's test, $z = 2.2$, $P = 0.081$),

Table 3. The ten most important botanical families for pollen collection by *Andrena* species from Michigan (A) and Britain (B)

A, Michigan *Andrena* (*N* = 50)		B, British *Andrena* (*N* = 34)	
Botanical family	Average percentage of pollen collected (%)	Botanical family	Average percentage of pollen collected (%)
Rosaceae	23.8	Rosaceae	26.3
Salicaceae	18.4	Apiaceae	15.3
Asteraceae	16.6	Salicaceae	10.1
Cornaceae	5.4	Asteraceae	9.3
Anacardiaceae	4.9	Brassicaceae	7.7
Ericaceae	4.8	Sapindaceae	7.5
Sapindaceae	3.5	Fabaceae	5.8
Apiaceae	3.5	Fagaceae	3.9
Fabaceae	3.4	Ranunculaceae	3.3
Brassicaceae	3.0	Ericaceae	1.3
Total	87.3		91.8

Families are sorted by average percentage collected per *Andrena* species.

but this was not significant. Not including the 13 British species included for the coefficient of variation analysis, after rarefaction the Michigan *Andrena* collected an average of 4.8 ± 0.5 pollen genera, significantly fewer than British *Andrena*, which collected an average of 10.7 ± 0.9 (Wilcoxon rank sum test, $W = 1385$, $P < 0.001$).

PHENOLOGY

The pollen collection choices of Michigan *Andrena* species were strongly influenced by phenology (Fig. 3A), with three clear groups forming: (1) spring-flying species foraging predominantly from woody plants; (2) spring-flying species specializing on herbaceous ephemerals; and (3) summer-flying species specializing on herbaceous prairie plant species. Species that break away from this three-group pattern are *Andrena miranda* Smith, *Andrena nigrihirta* Ashmead and *Andrena thaspii* Graenicher, which all collected a substantial percentage of their pollen from European Fabaceae (43, 43 and 70%, respectively). These three species have a northern distribution in Michigan (Gibbs *et al.*, 2017), and their relatively late peaks of 29 June, 10 July and 3 July, respectively, mean that their flight periods coincide with the bloom of many of these introduced plant species, whereas most other spring *Andrena* species have finished collecting pollen by this point, or are specialized on relatively late flowering woody plants, such as *Cornus* or *Rhus*.

British species of *Andrena* showed no such pattern of foraging preferences related to phenology (Fig. 3B), with both early and late peaking bees collecting extensively from woody or herbaceous plant species, or a mixture of both types. The Michigan dataset contained a high proportion of oligoleges (48%), whereas the British dataset primarily comprised polyleges, with only five oligoleges (5/34, 15%). The overall proportion of oligoleges is higher when considering the whole extant British *Andrena* fauna (21/59, 36%; Westrich, 1989; Falk & Lewington, 2015; Supporting Information, Appendix S3), although the addition of these species would not change the overall lack of a relationship between phenology and woody or herbaceous pollen composition. Including more species in the Michigan analysis is also unlikely to change this relationship because, based on current knowledge, the remaining species conform to one of the three outlined groups described above, with probably 42 of the 85 species displaying oligolecty (42/85, 49%; Supporting Information, Appendix S3).

DISCUSSION

In line with the findings of Müller & Kuhlmann (2008), Nearctic *Andrena* from Michigan exhibit the Asteraceae paradox, with seven of the 50 characterized species specializing on this family. Although it is the second most important family for characterized Michigan *Andrena*, when excluding specialists, Asteraceae represents < 1% of the pollen collected by the remaining species. Specialization on Asteraceae appears to have evolved at least four times in *Andrena* (Larkin *et al.*, 2008), and exclusive use of this botanical family is clearly a successful strategy. A high incidence of Asteraceae specialization

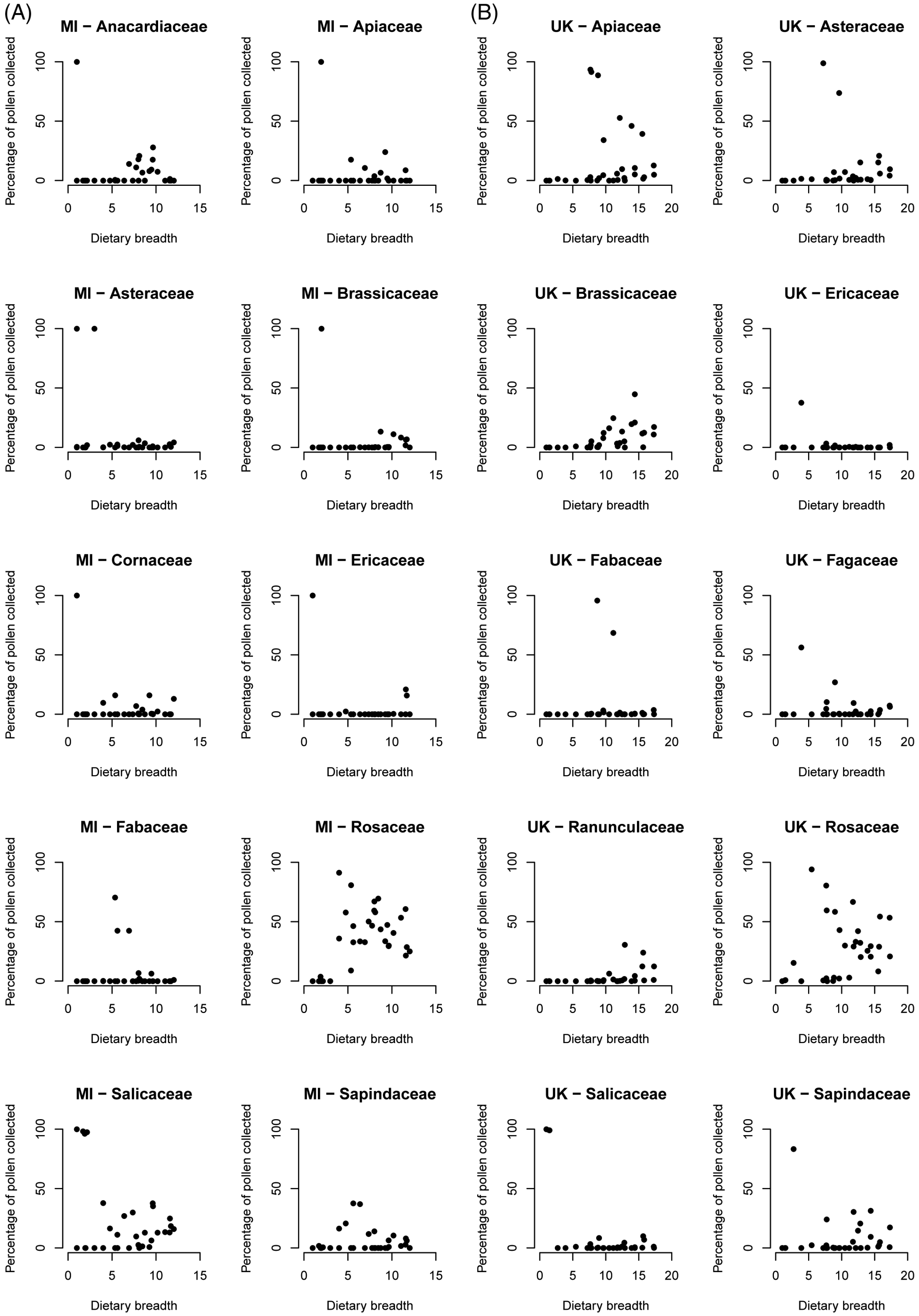

Figure 1. The relationship between dietary breadth and the percentage of pollen collected from the ten most important botanical families for Michigan (A) and British (B) *Andrena* species. 1 January = day 1.

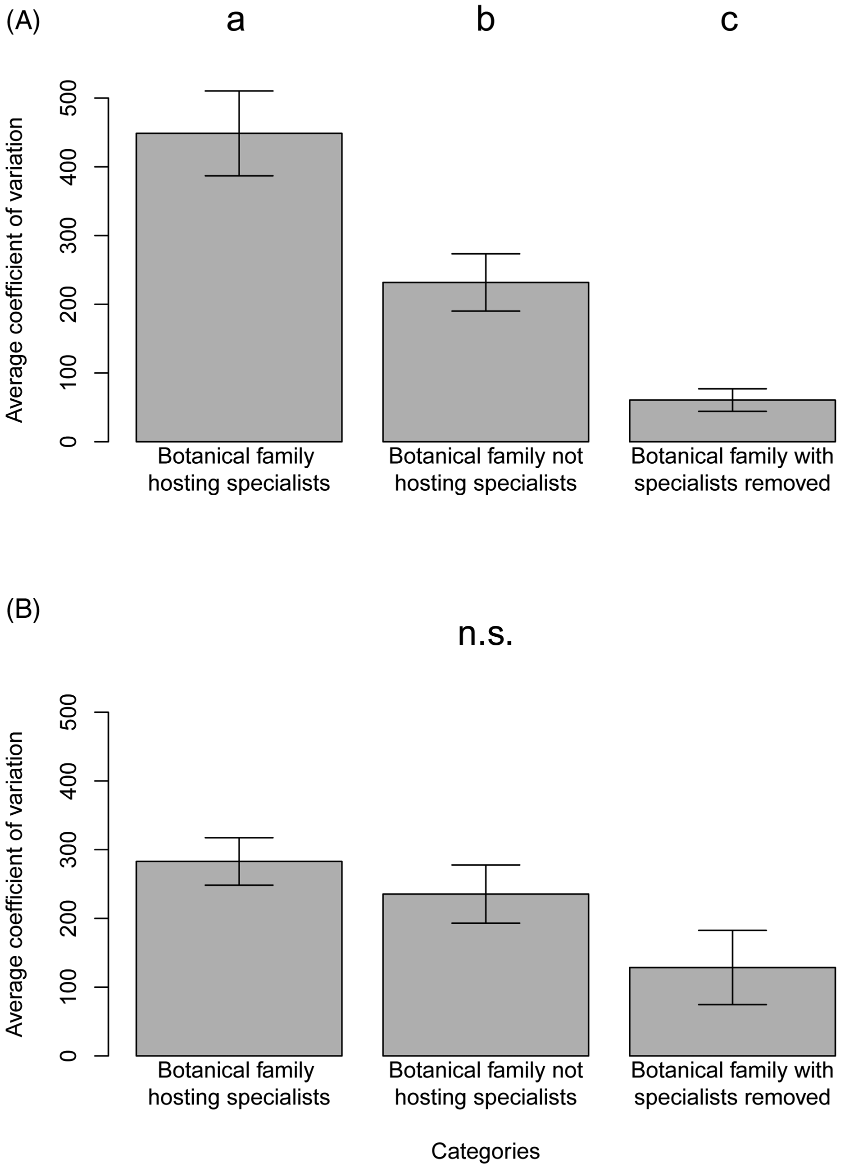

Figure 2. Average coefficient of variation for pollen utilization by botanical family type for Michigan (A) and British (B) *Andrena* species. Categories include botanical families for which a specialist (oligolege) is included in the dataset, botanical families that do not host a specialist in the dataset and botanical families that do host a specialist but the data for the specialist have been removed from the calculation of the coefficient of variation. Bars with different letters are significantly different ($P < 0.05$).

has long been noted in Midwestern bees, with half of all oligolectic species in a region of neighbouring Wisconsin using this family (Graenicher, 1935). However, this trend of specialization or avoidance was not limited to Asteraceae, with *Andrena* displaying this pattern of use on pollens from the families Geraniaceae, Hydrophyllaceae and Montiaceae. These results stand in marked contrast to the Palaearctic *Andrena* considered here. When applying the same criteria of specialization or avoidance to the British fauna, for the 11 most important botanical families in this dataset, none of the families that host specialists also had generalist bees collecting < 10% of their pollen diet from them. It is only when including *A. hattorfiana* (Dipsacaceae) that a specialization or avoidance pattern is seen in the British *Andrena* fauna. It should be noted that the 50 characterized Michigan species represent ~9% of the *Andrena* species diversity found in the Nearctic; therefore, these results are not necessarily representative of North

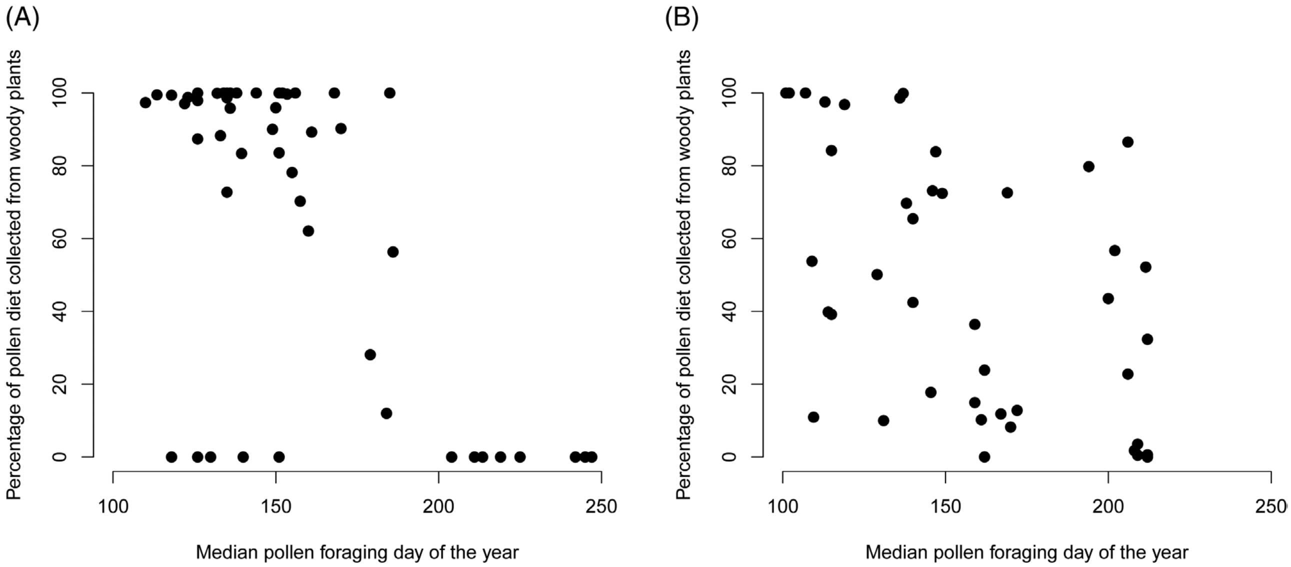

Figure 3. The relationship between phenology (characterized as median pollen foraging day) and the proportion of the pollen diet collected from woody plants for characterized Michigan (A) and British (B) *Andrena* species.

America as a whole, although the 21 studied subgenera account for nearly half the subgeneric diversity in this region.

What can explain the divergent results between these two faunas? The position that unfavourable properties of Asteraceae pollen drive differential use between specialized and non-specialized species (Müller & Kuhlmann, 2008; Praz *et al.*, 2008) would explain only the trend in the Nearctic and not Palaearctic species. Michigan *Andrena* collected 84% of their Asteraceae pollen from the tribes Astereae and Heliantheae, whereas British *Andrena* collected 76% of their pollen from Cichorieae, Anthemideae and Cynareae, reflecting the floral differences between the two regions. It is possible that pollen from Astereae and Heliantheae is inherently harder to digest than pollen from Cichorieae, Anthemideae and Cynareae. However, many European Asteraceae species from these latter tribes, such as *Taraxacum* (Cichoriaceae) and *Centaurea* (Cynareae), have been introduced to Michigan and are now widespread and abundant (Voss & Reznicek, 2012). Despite this, these non-native Asteraceae pollens are little used by Michigan *Andrena*, representing 7% of total Asteraceae collected. Given that the trend towards specialization or avoidance is seen across multiple botanical families in Michigan but not in Britain, the idea that Nearctic pollens within the same botanical family are more difficult to digest than their Palaearctic counterparts is considered unlikely. For Geraniaceae, Hydrophyllaceae and Montiaceae, relatively little is known about their pollen composition or chemistry (Roulston & Cane, 2000), although pollen from members of the Boraginaceae (closely allied to Hydrophyllaceae) contains high levels of pyrrolizidine alkaloids that are toxic to bees (Boppré *et al.*, 2005). The importance of 'toxic' pollen as a direct mechanism affecting bee survival, hence specialization over evolutionary time, is unclear, at least for ranunculin in *Ranunculus* pollen (Sedivy *et al.*, 2012), and may not be sufficient in and of itself to explain the phenomenon of specialization or avoidance.

The majority (58/60) of the Palaearctic *Colletes* species studied by Müller & Kuhlmann (2008) specialized on or avoided Asteraceae pollen, whereas two polylectic species collected > 30% of their pollen from this family, *Colletes dusmeti* Noskiewicz (35%) and *Colletes brevigena* Noskiewicz (55%). In the Palaearctic, both are found in southern Europe and display bivoltine behaviour (Baldock *et al.*, 2018). This use of Asteraceae pollen by at least some species of polylectic Palaearctic *Colletes* is closer to the results seen for the Palaearctic *Andrena* fauna. All Michigan *Colletes* species are univoltine, and the genus contains a mixture of polylectic and oligolectic species (Gibbs *et al.*, 2017), although the use of challenging pollens by polylectic species has not been investigated in detail. It should be noted that bivoltinism in and of itself is not necessarily linked to an increase in dietary breadth, with partial bivoltinism seen in some oligolectic bee species, such as *Diadasia* and *Pseudopanurgus* (Neff & Simpson, 1992; Neff & Rozen, 1995).

Pollen mixing has been proposed as an additional mechanism for utilizing pollens with unfavourable properties, by which challenging pollens are collected and used to provision larvae in small but not insignificant quantities. The Megachilid bee *Osmia cornuta* Latreille collects *Ranunculus* pollen in the wild, and although its larvae cannot develop on pure *Ranunculus* pollen (Sedivy *et al.*, 2011), they have been shown to develop successfully on a mixture of up to 50% *Ranunculus* pollen with seemingly no negative consequences (Eckhardt *et al.*, 2014). Some British *Andrena* appear to exhibit pollen mixing, with a total of six non-specialized Palaearctic *Andrena* species collecting > 10% of their pollen from Asteraceae, and this trend can be seen for each of the British botanical families that host specialized *Andrena* species. Whilst *O. cornuta* appears to rely on pollen mixing to use *Ranunculus* pollen, its relative *Osmia bicornis* L. can develop on a pure diet of this pollen (Sedivy *et al.*, 2011), suggesting that the physiological ability to digest *Ranunculus* pollen has been newly acquired by *O. bicornis* (Haider *et al.*, 2014). Without manipulative experiments, such as those performed on *Osmia*, it is not clear whether the use of challenging pollens by these polylectic Palaearctic *Andrena* is driven by pollen mixing only, as in *O. cornuta*, or by a newly evolved ability to digest certain challenging pollens, as in *O. bicornis*.

However, the question remains as to why this strategy is displayed by British but not by Michigan *Andrena* species, and why the British fauna appears to be more generalized in its pollen foraging patterns. When considering when pollinators should tend towards generalization, Waser *et al.* (1996) argued that this would be more likely when floral rewards are similar across plant species, travel is costly, constraints of behaviour and morphology are minor and pollinator lifespan is long relative to the flowering of individual plant species. Rather than considering bee flight period long relative to the flowering period of individual plant species, the length of the flight period should be considered in relationship to the flowering period of plant genera or families, the level at which the vast majority of bee foraging specialization occurs (Kuhlmann & Timmermann, 2011). Although it may be the case that there is a substantive difference in the reward offered by Nearctic and Palaearctic plants, it is in the seasonal phenology that the greatest differences are seen between these two regions.

Bee diversity peaks in arid or Mediterranean areas, with faunas containing a greater proportion of pollen specialists (Moldenke, 1979; Waser *et al.*, 1996). Although not arid, Michigan has an *Andrena* fauna with a greater proportion of pollen specialists and is more seasonal than Britain, with sharply defined flowering periods for plant groups. For example, the flowering period of *Rubus* species in Michigan is almost entirely restricted to a 6 week period from late May to early July. In contrast, *Rubus* species flower for twice as long in Britain, from May to September, providing pollens from a woody source for second generation *Andrena* species, such as *Andrena bicolor* Fabricius, *Andrena bimaculata* Kirby, *Andrena dorsata* Kirby, *Andrena flavipes* Panzer, *Andrena minutula* Kirby, *Andrena thoracica* Fabricius and *Andrena trimmerana* Kirby (Wood *et al.*, 2016; Wood & Roberts, 2017). Bivoltinism is very rare although not unknown in Nearctic *Andrena* (Linsley, 1937; Youssef & Bohart, 1968), but it is a frequent feature of western Palaearctic *Andrena* (Westrich, 1989), with 22% of extant British species exhibiting obligate bivoltinism (13/59; Falk & Lewington, 2015). This temporal partitioning can be seen in the more restricted foraging choices of Michigan *Andrena* that are tied to flowering trees and shrubs, to woodland understory ephemerals or to late season prairie plants. The presence of the Asteraceae paradox in Michigan *Andrena* cannot be driven simply by availability alone, as native species of spring-flowering Asteraceae can be found throughout Michigan, such as *Packera aurea* (host of *Andrena gardineri* Cockerell), *Krigia* species (hosts of *Andrena krigiana* Robertson, not characterized but present in Michigan' Gibbs *et al.*, 2017) and *Erigeron* species (Voss & Reznicek, 2012). The spring ephemerals in Geraniaceae, Hydropyllaceae and Montiaceae are also available during the flight period of most Michigan *Andrena* species (see Fig. 3), suggesting that it might be a combination of the inherent properties of the pollen and seasonality that drive this trend. The less seasonal environment, at least in parts of the Western Palaearctic, appears to have facilitated a shift towards polylecty, bivoltinism and the utilization of challenging pollens by non-specialist *Andrena* bees.

In conclusion, these results demonstrate that the Nearctic *Andrena* fauna of Michigan show specialization on, or almost total avoidance of, pollens from certain botanical families, in contrast to the Palaearctic British *Andrena* fauna. These findings further support the position that bees require physiological adaptations to use certain plant pollens, but that this phenomenon is more pronounced in more seasonal regions. Intermediate strategies that result in more generalized pollen foraging on challenging plant pollens but fall short of full specialization might be able to evolve only outside highly seasonal environments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Pollens identified from Michigan *Andrena* species and pollen type, from either woody or herbaceous plants.

Appendix S2. Inferring bee host ranges by microscopical analysis of scopal pollen loads of female bees based on two different methods: (1) the number (or volume) of the pollen grains counted; and (2) the individual composition of the pollen loads. From Müller & Kuhlmann (2008).

Appendix S3. Extant *Andrena* species of Michigan and Britain, with subgeneric classification and dietary status. For simplicity, only host range is detailed for oligoleges; all other species are polylectic. Species included in the dietary analysis are highlighted in bold.