Abundance and diversity of bees visiting flowering pennycress, a new oilseed crop in the midwestern USA

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Abundance and Diversity of Bees Visiting Flowering Pennycress, a New Oilseed Crop in the Midwestern USA

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Abstract

Oilseed pennycress (*Thlaspi arvense*) is a new, autumn-sown, "cash cover crop" for the Midwestern USA and elsewhere. Anthesis occurs in early spring when few other plants bloom, and its flowers attract early-emerging bees. However, the taxonomic composition of these bees was unknown. Consequently, we systematically captured and identified the genera and species of bees (Hymenoptera) visiting pennycress flowers throughout anthesis at five site-years: two in Illinois and three in Minnesota. A cumulative total of 28 bee species were found across site-years. The most common genera were *Andrena* (10 species), *Lasioglossum* (12 species), and *Halictus* (2 species). Rarer genera were *Apis*, *Ceratina*, *Hylaeus*, and *Nomada*. Bee abundance and diversity were related closely and in a negative exponential manner with percent land area devoted to annual cropping. The inclusion of new, early flowering crops, such as pennycress, that provide valuable food resources may enhance bee abundance and diversity, especially if even small areas of uncropped land are nearby.

Keywords: *Andrena*, *Lasioglossum*, *Halictus*, *Thlaspi*, winter cover-crop

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Bees (Hymenoptera) are important pollinators of many horticultural and agronomic crops (Winfree et al. 2011). Unfortunately, agriculture in general, and annual cropping specifically, may reduce population densities and diversity of bees (Goulson et al. 2008, Spivak et al. 2011, Grab et al. 2019). Undisturbed soil is essential for most solitary bees, such as ground-nesting bees (e.g., mining bees, Andrenidae; sweat bees, Halictidae; plasterer bees, Colletidae) (Antoine and Forrest 2021); and over-winter integrity of hollow plant stems is needed for cavity-nesting species (e.g., carpenter bees, Apidae). Thus, the common agronomic practice of tillage can have severe consequences for solitary bees if performed during nesting periods (Ullmann et al. 2016). In contrast, permaculture and no-till farming may facilitate solitary bee survival in agricultural landscapes (Williams et al. 2010).

Bees also need access to abundant pollen and nectar to survive and reproduce. For the vast majority of solitary bees, such forage resources must be near their nests, often within one kilometer (Walther-Hellwig and Frankl 2000, Steffan-Dewenter et al. 2002). Most agronomic crop plants in the Midwestern USA are not valuable forage resources for bees. Exceptions include mass-flowering crops such as spring canola (*Brassica napus* L.) and sunflower (*Helianthus annuus* L.) (O'Brian and Arathi 2018, Mallinger et al. 2019). Although these crops are adapted to the Midwestern USA (i.e., the Corn Belt), neither produces acceptable economic returns for most Midwestern growers (e.g., Fore et al. 2011). Additionally, even though winter canola is highly attractive to pollinators, it typically is not winter-hardy in the Upper Midwest (i.e., Iowa, Minnesota, North Dakota, South Dakota, and Wisconsin) (Eberle et al. 2015). Accordingly, canola and sunflower are not planted extensively in the Corn Belt (Aguilar et al. 2015, Roesch-McNally et al. 2018).

Cropping systems in the Midwest could incorporate novel "cash cover crops" along with traditionally grown corn (*Zea mays* L.), soybean (*Glycine max* [L.] Merr.), and wheat (*Triticum aestivum* L.). Cash cover crops are autumn-sown, winter-hardy, early-flowering, mass-flowering, and revenue-generating winter cover crops. Such cover crops may be advantageous for pollinators generally, and solitary bees in particular (Thom et al. 2016,

Table 1. Characteristics of five experimental site-years, including the location name, year of sowing, latitude, longitude, field size, pennycress genetic line, and the number of weekly samples examined.

Site	Year	Lat.	Long.	Size (ha)	Line	Weekly samples
Morris, MN	2020	45.68	−95.80	0.10	MN106	3
Rosemount, MN	2019	44.71	−93.07	0.15	MN106	4
Rosemount, MN	2020	44.70	−93.07	0.10	MN106	5
Lexington, IL	2020	40.67	−88.78	1.50	B36/73	8
Macomb, IL	2020	40.49	−90.68	0.10	tt8-t/ARV1	6

2018). These new cover crops include the oilseed plants, winter camelina (*Camelina sativa* [L.] Crantz) and pennycress (also known as CoverCress™, *Thlaspi arvense* L.) (Cubins et al. 2019, Ott et al. 2019, Phippen et al. 2019).

Pennycress is a member of the mustard family (Brassicaceae), is of Eurasian origin, and typically is known as a winter annual weed of crop fields, roadsides, and other disturbed areas (Warwick et al. 2002). As a recently bred crop (Phippen et al. 2019), it is sown in autumn, germinates immediately, forms leafy rosettes, enters winter dormancy, bolts and flowers in spring (as early as March in Illinois and April in Minnesota, depending upon weather conditions), and is harvested for its oilseeds in June (Cubins et al. 2022). When bolting in spring, summer crops such as soybean can be drilled into pennycress as relay crops (Cubins et al. 2022). Because pennycress (1) generates economic returns for growers, (2) protects the soil from autumn through spring, and (3) permits overlapping growth and harvesting of soybean (typically in September), it has good potential for increasing economic returns for growers (Trejo-Pech et al. 2019), especially after newer and more productive genetic lines are developed and released (Jez et al. 2021). Moreover, because the soil is largely undisturbed from autumn through summer with relay cropping, ground-nesting insects that emerge in spring may benefit from this system.

With respect to forage availability for insects, pennycress is one of the first plants, and certainly the first agronomic crop plant, to flower in spring and produce pollen and nectar in the Upper Midwest (Thom et al. 2016, 2018). Weedy forms of pennycress attract wild bees (Glenny et al. 2022), and general taxonomic categories of pollinators visiting oilseed pennycress flowers in Iowa and Minnesota were reported by Forcella et al. (2021). However, details of genera and species of bees on pennycress remain unknown. Bee abundance and diversity are ecological attributes strongly and positively affected by the quantity and quality of available floral resources (Goulson et al. 2015). This report specifies the numbers, genera, and species of bees associated with, and likely pollinators of, flowers of pennycress crops in Illinois and Minnesota.

Materials and Methods

Seedbeds with loam soils were prepared with tillage and harrowing in small fields or large plots in September or October in 2019 or 2020 at research farms in Illinois and Minnesota (Table 1). Pennycress was sown in rows separated by 10 to 15 cm with a seeding rate of approximately 10 kg ha⁻¹. Seedlings emerged at most sites within two weeks of sowing and formed rosettes that entered dormancy with the onset of winter. The exception was at Lexington, IL, where many seedlings emerged in spring rather than autumn.

Flowering at each site was monitored at approximately weekly intervals by photographing nine randomly situated 0.1 m² quadrats (three at Lexington), counting the number of open flowers, and calculating flower cover in processed digital images. Monitoring commenced in April in IL and May in MN when flowers first were observed.

Flower-visiting insects were collected with sweep nets on the same dates as flowering was monitored. Nets had circular openings with 40 cm diameters. Sampling consisted of 50 sweeps along three transects at each site; one sweep with each step of the person sampling. Transects were separated from one another by at least 10 m. At the end of each transect, captured insects were placed in coolers and subsequently frozen (within 4 hours) to preserve the samples. Sweep netting was performed only on days with no rain, air temperatures >10 °C, and wind speeds <15 km h⁻¹.

Subsequently, all captured insects from each transect were sorted into broad taxonomic groups. Hymenoptera (i.e., bees and wasps) were of special interest because of their potential importance for pollination,
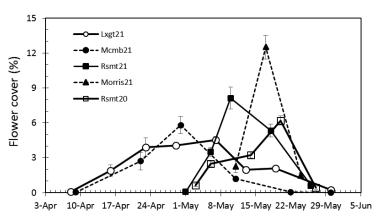
Figure 1. Durations and extents of pennycress anthesis at five site-years. Site-year abbreviations as in Table 3. Vertical bars represent standard errors.

not only for pennycress but many other Midwestern plant species, including crops and native and naturalized plants. All specimens were dried and identified (except wasps) to the species level using taxonomic keys (Mitchell 1960, 1962; LaBerge 1971, 1973, 1986; Roberts 1973; Ribble 1974; McGinley 1986; Gibbs 2011; Rehan and Sheffield 2011; Gibbs et al. 2013) and comparison to previously identified specimens at the University of Minnesota's Bee Research Facility and the University of Minnesota Insect Collection (St. Paul, MN). Although wasps were counted, they were not identified to lower taxonomic levels because, ultimately, they were not considered important pollinators.

Average daily air temperature data for each site were collected from the PRISM online source (https://prism.oregonstate.edu/explorer/) from the date of pennycress sowing to the end of anthesis. Cumulative growing degree-days (GDD, base 0 °C) from sowing date to the end of May were calculated for each site-year. Method 1 of McMaster & Wilhelm (1997) was used for GDD calculation.

Aerial photographs of each site were accessed from satellite images available online (https://www.google.com/maps/). A circle with a one-km radius was drawn and superimposed on each site, with the experimental area at the circle's center. A grid of 50 points spanning the area of the circle was superimposed upon each circle, and the percentage of points atop annually cropped land was determined (i.e., non-cropland included lawns, grasslands, pastures, woodlands, wetlands, streams, lakes, roads, roadsides, parking lots, and buildings). Regressions were performed to relate relative land use to abundance and diversity of bees

using the "data analysis" package available in Microsoft Excel.

Results and Discussion

Flower Cover. Pennycress flowering in Illinois commenced in early April, peaked in late April and early May, and continued until the end of May (Fig. 1). The very broad peak at the Lexington site likely reflected autumn and spring germinating plants compared to the narrower peak at Macomb from plants that germinated primarily in autumn.

Pennycress flowering in Minnesota started in early to mid-May, about one month later than in Illinois, and its duration was considerably shorter than in Illinois (< 4 weeks vs ≥ 6 weeks). At the Rosemount site, the duration of flowering was almost identical for both years, but flowering peaked earlier in 2021 than in 2020, possibly because more post-sowing GDD were accumulated in 2021 than in 2020 (Table 2). The shortest duration of flowering (2 weeks) was at the Morris site; this site experienced drought during the spring of 2021 (e.g., May received only 43% of normal rainfall [26 mm vs. 60 mm]), which may explain the abbreviated flowering period.

Bee Abundance by Date. The numbers of bees captured per transect (50 sweeps) varied greatly among sampling dates and experimental sites (Fig. 2). Few bees were caught when pennycress flower cover was very low at the beginning and end of anthesis, but high pennycress flower cover did not always correspond with greater numbers of bees (cf. Fig. 1, 2). The greatest bee abundance (mean ± SE) was 16.3 ± 4.70 bees per transect at Rosemount, MN, on 20 May 2020. Abundance levels at all other times and sites

Table 2. Cumulative growing degree-days (GDD, base 0°C) from sowing through specific months across five experimental site-years.

Site	Year	Sowing date	Cumulative GDD from Sowing to			
			February	March	April	May
Morris, MN	2021	16 Sep	513	608	780	1209
Rosemount, MN	2020	17 Sep	508	586	781	1205
Rosemount, MN	2021	19 Sep	525	648	873	1316
Lexington, IL	2021	18 Sep	894	1115	1453	1966
Macomb, IL	2021	18 Oct	381	595	909	1393

were much lower. If averaged across sampling dates, the Rosemount-2020 site-year also had the highest overall bee abundance, with 5.8 ± 1.56 bees per transect. The other site-years averaged 3.7 ± 1.07 (Morris-2021), 1.8 ± 0.23 (Rosemount-2021), 0.5 ± 0.10 (Macomb-2021), and 0 (Lexington-2021) bees per transect. Only a single bee was observed at this latter site, but wasp numbers averaged 1.5 ± 0.13 per transect. Moreover, Lexington was the only site at which wasps were observed consistently.

Cumulative Numbers of Individuals and Species of Bees. Because flowering durations varied greatly across site-years (Fig. 1), so did the number of weekly samples (Table 1). Thus, average bee densities per sample date (described above) provided a consistent basis for comparisons among site-years. However, these averages did not reveal cumulative numbers of bees nor bee diversity among site-years. The total numbers of bees and numbers of bee species captured at each site-year are shown in Fig. 3. Although total numbers of individuals and total numbers of species across site-years were related closely

($R^2 = 0.97$, $P < 0.05$) and linearly (species = 0.25 *individuals + 1.79), large differences in both individuals and species numbers existed among site-years.

Differences among site-years in numbers of individuals and numbers of species were related in negative exponential manners to the percentage of the landscape devoted to annual cropping (Fig. 3), with R^2 values ≥ 0.94. Sites with the most abundant and diverse bees contained less area devoted to annual crops and more land allocated to pasture, woodland, wetlands, etc. (cf. Grab et al. 2019). These results suggest that with even relatively small increases in non-cropped lands, bee abundance and species richness increased substantially. These latter areas likely provided important nesting and foraging habitats for the many species of native bees that visited the early-flowering pennycress sites.

Bee Species Richness. Seven genera of bees were captured across the five site-years (Table 3). The most common genera captured in our samples were *Andrena* (Andrenidae),
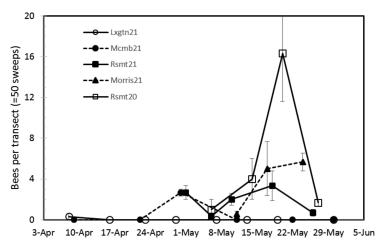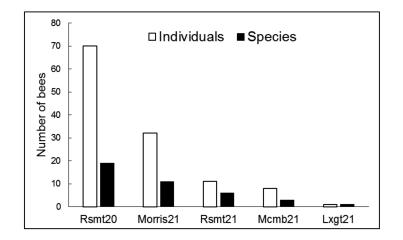

Figure 2. Mean (± SE) densities of bees per transect (50 sweeps of a sweep net) at five site-years. Site-year abbreviations as in Table 3.
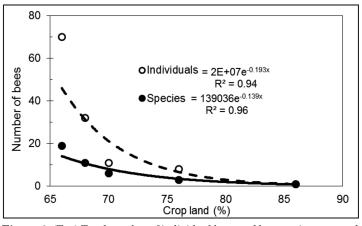
Figure 3. (Top) Total number of individual bees and bee species captured in sweep nets throughout anthesis at five site-years. Site-year abbreviations as in Table 3. (Bottom) Relationships between numbers of individual bees and numbers of bee species with the percentage of land within a 1-km radius circle devoted to annual crops. Relationships were negative exponential, with y = number of bees, and × = crop land percentage. R^2 = adjusted attributable variability, with $P < 0.05$ for both relationships.

and *Halictus* and *Lasioglossum* (both Halictidae), all of which tend to be ground-nesters. *Andrena cressonii* (taxonomic authorities listed in Table 3), *A. hippotes*, and *A. imitatrix* were found in both Illinois and Minnesota sites, whereas *A. arabis* was abundant but found only in Rosemount in 2020. All other species of *Andrena* were rarer and found in only one state (Table 3), and one specimen of *Andrena* could not be identified to species. Species of *Andrena* often are represented amongst early-emerging collections of solitary bees (e.g., *A. carlini*, *A. crataegi*, and *A. miserabilis*; see Bartomeus et al. 2011), and one species (*A. arabis*) is oligolectic and

associated closely with flowers of the Brassicaceae (Wood and Roberts 2018).

Only two species of *Halictus* were found (Table 3); *H. confusus* was relatively abundant, but *H. confusus* was rare. Both species were found only in Minnesota. Foundresses of these sometimes eusocial species are cold-hardy and emerge in early spring in search of food for their offspring (Soucy 2002, Richards et al. 2010).

Although several species of *Lasioglossum* were identified (Table 3), only *L. paradmirandum* was found in both Illinois and Minnesota, but then only rarely, and *L.*

Table 3. Numbers of individuals and species of bees captured in sweep nets throughout anthesis of pennycress at five site-years. Morris21 = Morris, MN, 2021; Rsmt20 = Rosemount, MN, 2020; Rsmt21 = Rosemount, MN, 2021; Lxgt21 = Lexington, IL, 2021; and Mcmb21 = Macomb, IL, 2021.

Family, genus, species, and authority	Morris21	Rsmt20	Rsmt21	Lxgt21	Mcmb21
Andrenidae	3	52	8	0	7
Andrena arabis Robertson		10			
A. barbilabris (Kirby)	1				
A. carlini Cockerell	1	2			
A. crataegi Robertson		1			
A. cressonii Robertson	1	9	5		2
A. forbesii Robertson		2	1		
A. hippotes Robertson		18	1		2
A. imitatrix Cresson		4			3
A. miserabilis Cresson		3			
A. nasonii Robertson		2	1		
A. sp.		1			
Apidae	1	2	0	0	0
Apis mellifera L.		1			
Ceratina mikmaqi Rehan & Sheffield	1				
Nomada denticulata Robertson		1			
Colletidae	0	0	1	0	0
Hylaeus leptocephalus (Morawitz)			1		
Halictidae	28	16	2	1	1
Halictus confusus Smith	8	10			
H. rubicundus (Christ)	1	1			
Lasioglossum admirandum (Sandhouse)	4				
L. cinctipes (Provancher)		1			
L. ephialtum Gibbs	7				
L. lineatulum (Crawford)	2				
L. hitchensi Gibbs		1			
L. leucozonium (Schrank)			1		
L. paradmirandum (Knerer & Atwood)		1		1	
L. perpunctatum (Ellis)	5	1			
L. pruinosum (Robertson)	1				
L. semicaeruleum (Cockerell)			1		
L. versatum (Robertson)					1
L. zephyrus (Smith)		1			

perpunctatum was the sole species found at more than one site within Minnesota. All other species were found only at a single site-year. Many of these species are known from studies on early-blooming canola (Ellis and Barbercheck 2015). Interestingly, species of both *Lasioglossum* and *Halictus* were found on spring-planted and summer-flowering canola in Colorado, but species of *Andrena* were absent (O'Brian and Arathi 2018).

Four genera were represented by a single individual across site-years; these were *Apis*, *Ceratina*, *Nomada* (all Apidae), and *Hylaeus* (Colletidae). Transient colonies of honey bees, *A. mellifera*, typically are not returned to Illinois and Minnesota from the Gulf and West Coasts until after the flowering period of pennycress. Hence, the scarcity of captured honey bees in our samples.

Forty-four species of bees were assessed by Grab et al. (2019) in fruit orchards in the state of New York for their propensities to respond positively or negatively to nearby agricultural land use. Only five species responded positively, five others showed no influence of agriculture, and the remaining 34 species (77%) were affected negatively. Of the total 44 species in the New York orchards, 18 *Andrena*, 2 *Halictus*, and 11 *Lasioglossum* species also were found on pennycress in Minnesota; and 8 *Andrena*, 2 *Halictus*, and 5 *Lasioglossum* species were found on pennycress in Illinois. All twenty-six of the shared *Andrena* species, the two *Halictus* species, and three of the *Lasioglossum* species, responded negatively to agriculture in the New York study, whereas agriculture did not affect two of the shared *Lasioglossum* species.

In our Midwestern study, these same early-emerging species, the majority of which can be impacted negatively by traditional agriculture, were attracted to flowers of oilseed pennycress at a time of year when few other flower resources were available in landscapes dominated by corn, soybean, and wheat. Consequently, these results suggest that inclusion of pennycress as a cash cover crop as part of a relay-cropping system in Midwestern landscapes may help to mitigate the negative influences of agriculture (i.e., reduced floral resources and soil disturbance in spring) on several species of wild bees, if these or analogous species respond similarly to agricultural land use in different regions of the Midwest.

Conclusions

The numbers of individuals and species of bees associated with pennycress flowering suggest that this new crop provides valuable early season forage for an important group of pollinators. This value is context-dependent, however, for native bees. Unlike domesticated honey bees, native ground-nesting bees require relatively undisturbed land for building nests, and these nests must be near forage resources, typically within one kilometer (Steffan-Dewenter et al. 2002). Thus, to maximize the benefits for bees of growing oilseed pennycress as a floral resource, fields of this new crop should be located preferentially near tree lines, fence rows, pastures, etc. (Sirami et al. 2019).

Summer annual crops dominate landscapes in the Upper Midwest of the USA, and crop diversity in this region has trended downward in recent decades (Aguilar et al. 2015). Decreasing crop diversity in North America and Europe has lessened multi-trophic diversity, including bee diversity (Sirami et al. 2019). Inclusion of an autumn-sown, winter-hardy, oilseed crop, like pennycress, that blooms with attractive pollen- and nectar-rich flowers (Thom et al. 2016, 2018) in early spring represents an appreciable change in agroecosystem management for this region. Agricultural intensification often is thought to impinge upon the diversity of pollinators, especially bees (Potts et al. 2010, Winfree et al. 2011, Grab et al. 2019), but the introduction of pennycress and other novel mass-flowering oilseed crops into cropping sequences of the Midwestern USA (Eberle et al. 2015) could lessen the negative effects of agriculture on bees and other pollinators depending, of course, on other important factors such as field size and configuration (Sirami et al. 2019) and pesticide use (Goulson et al. 2015). Anthesis for these diverse crops ranges from early spring (as with penny-cress) to late summer (e.g., cuphea, *Cuphea viscosissima* Jacq. × *lanceolata* W.T. Aiton; and calendula, *Calendula officinalis* L.), and post-harvest volunteers of some species even flower through late autumn (e.g., canola). Accordingly, diversification of Midwestern cropping systems could provide season-long forage resources and appreciably change the effects of agriculture on bee populations from negative to neutral or even to positive while simultaneously generating positive economic returns for growers (Trejo-Pech et al. 2019). Oilseed pennycress could be an integral part of new and diversified Midwestern cropping systems.

Acknowledgments

Literature Cited

Aguilar J., G.G. Gramig, J.R. Henrickson, D.W. Archer, F. Forcella, M.A. Liebig. 2015. Crop species diversity changes in the United States: 1978–2012. PLoS ONE 10(8): e0136580. Available from https://doi.org/10.1371/journal.pone.0136580.

Antoine C.M., J.R.K. Forrest. 2021. Nesting habitat of ground-nesting bees: a review. Ecological Entomology 46: 143–159.

Bartomeus I., J.S. Ascher, D. Wagner, B.N. Danforth, S. Colla, S. Kornbluth, R. Winfree. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proceedings of the National Academy of Sciences 108: 20645–20649.

Cubins J.A., M.S. Wells, K. Frels, M.A. Ott, F. Forcella, G.A. Johnson, M.K. Walia, R.L. Becker, R.W. Gesch. 2019. Management of pennycress as a winter annual cash cover crop. A review. Agronomy for Sustainable Development 39: 46. Available from https://doi.org/10.1007/s13593-019-0592-0

Cubins J.A., S.S. Wells, M.K. Walia, D.L. Wyse, R. Becker, F. Forcella, R.D. Gardner, G.A. Johnson, R.W. Gesch. 2022. Harvest attributes and seed quality predict physiological maturity of pennycress. Industrial Crops and Products 176: 114355. Available from https://doi.org/10.1016/j.indcrop.2021.114355

Eberle C.A., M.D Thom, K.T. Nemec, F. Forcella, J.G. Lundgren, R.W. Gesch, W.E. Riedell, S.K. Papiernik, A. Wagner, D.H. Peterson, J.J. Eklund. 2015. Using pennycress, camelina, and canola cash cover crops to provision pollinators. Industrial Crops and Products 75: 20–25.

Ellis K.E., M.E. Barbercheck. 2015. Management of overwintering cover crops influences floral resources and visitation by native bees. Environmental Entomology 44: 999–1010.

Forcella F, S. Patel, A.W. Lenssen, C. Hoerning, M.S. Wells, R.W. Gesch, M.T. Berti. 2021. Weather and landscape influences on pollinator visitation of flowering winter oilseeds (field pennycress and winter camelina). Journal of Applied Entomology 145: 286–294.

Fore S.R., W. Lazarus, P. Porter, N. Jordan. 2011. Economics of small-scale on-farm use of canola and soybean for biodiesel and straight vegetable oil biofuels. Biomass Bioenergy 35: 193–202.

Gibbs J. 2011. Revision of the metallic *Lasioglossum* (*Dialictus*) of eastern North America (Hymenoptera: Halictidae: Halictini). Zootaxa 3073: 1–216.

Gibbs J., L. Packer, S. Dumesh, B.N. Danforth. 2013. Revision and reclassification of *Lasioglossum* (*Evylaeus*), *L.* (*Hemihalictus*) and *L.* (*Sphecodogastra*) in eastern North America (Hymenoptera: Apoidea: Halictidae). Zootaxa 3672: 1–116. Available from https://doi.org/10.11646/zootaxa.3672.1.1

Glenny W., J. Runyon, L. Burkle. 2022. Assessing pollinator friendliness of plants and designing mixes to restore habitat for bees. US Forest Service RMRS-GTR-429. 60 p.

Goulson D., G.C. Lye, B. Darvill. 2008. Decline and conservation of bumble bees. Annual Review of Entomology 53: 191–208.

Goulson D., E. Nicholls, C. Botias, E.L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347: 1255957. doi: 10.1126/science.1255957

Grab H., M.G. Branstetter, N. Amon, K.R. Urban-Mead, M.G. Park, J. Gibb, E.J. Blitzer, K. Poveda, G. Loeb, B.N. Danforth. 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. Science 363: 282–284.

Jez J.M., C.N. Topp, M.D. Marks, R. Chopra, J.C. Sedbrook. 2021. Technologies enabling rapid crop improvements for sustainable agriculture: example pennycress (Thlaspi arvense L.). Emerging Topics in Life Science 5: 325–335.

LaBerge W.E. 1971. A revision of the bees of the genus Andrena of the Western Hemisphere. Part IV. Scrapteropsis, Xiphandrena and Rhaphandrena. Transactions of the American Entomological Society 97: 441–520.

LaBerge W.E. 1973. A revision of the bees of the genus Andrena of the Western Hemisphere. Part VI. Subgenus Trachandrena. Transactions of the American Entomological Society 99: 235–371.

LaBerge W.E. 1986. A revision of the bees of the genus Andrena of the Western Hemisphere. Part XII. Subgenera Leucandrena, Ptilandrena, Scoliandrena and Melandrena. Transactions of the American Entomological Society 112: 191–248.

Mallinger R.E., J. Bradshaw, A.J. Varenhorst, J.R. Prasifka. 2019. Native solitary bees provide significant pollination services to confection sunflowers (*Helianthus annuus* L.) (Asterales: Asteraceae) grown across the northern Great Plains. Journal of Economic Entomology 112: 40–48.

McGinley R.J. 1986. Studies of Halictinae (Apoidea: Halictidae), I: Revision of new world *Lasioglossum* Curtis. Smithsonian Contributions to Zoology 429: 1–294.

McMaster G.S., W.W. Wilhelm. 1997. Growing-degree days: One equation, two interpretations. Agricultural and Forest Meteorology 87: 291–300.

Mitchell T.B. 1960. Bees of the Eastern United States. Volume 1. North Carolina Experiment Station Technical Bulletin, 538 pp.

Mitchell T.B. 1962. Bees of the Eastern United States. Volume 2. North Carolina Experiment Station Technical Bulletin, 557 pp.

O'Brian C., H.S. Arathi. 2018. Bee genera, diversity and abundance in genetically modified canola fields. GM Crops and Food 9: 31–38.

Ott M.A., C.A. Eberle, M.D. Thom, D.W. Archer, F. Forcella, R.W. Gesch, D.L. Wyse. 2019. Economics and agronomics of relay-cropping pennycress and camelina with soybean in Minnesota. Agronomy Journal 111: 1281–1292.

Phippen W.B., R. Chopra, S. Bansal, B.A. Jarvis, M.E. Phippen, K.M. Dorn, M. Esfahanian, T.J. Nazarenus, E.B. Cahoon, T.P. Durrett, M.D. Marks, J.C. Sedbrook. 2019. Molecular tools enabling pennycress (*Thlaspi arvense*) as a model plant and oilseed cash cover crop. Plant Biotechnology Journal 17: 776–788.

Potts S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, W.E. Kunin. 2010. Global pollinator declines: Trends, impacts, and drivers. Trends in Ecology and Evolution 25: 345–353.

Rehan S.M., C.S. Sheffield. 2011. Morphological and molecular delineation of a new species in the *Ceratina dupla* species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. Zootaxa 50: 35–50.

Ribble D.W. 1974. A revision of the bees of the genus *Andrena* of the Western Hemisphere subgenus *Scaphandrena*. Transactions of the American Entomological Society 100: 101–189.

Richards M.H., J.L. Vickruck, S.M. Rehan. 2010. Colony social organization of *Halictus confusus* in southern Ontario, with comments of sociality in the subgenus *H.* (*Seladonia*). Journal of Hymenopteran Research 19: 1444–158.

Roberts R.B. 1973. Bees of northwestern America: *Halictus* (Hymenoptera: Halictidae). Agricultural Experimental Station: Oregon State Technical Bulletin 126: 1–23.

Roesch-McNally G.E., J.G. Arbuckle, J.C. Tyndall. 2018. Barriers to implementing climate resilient agricultural strategies: The case of crop diversification in the U.S. Corn Belt. Global Environmental Change 48: 206–215.

Sirami C., N. Gross, A.B. Baillod, C. Bertrand, R. Carrie, A. Hass, L. Henckel, P. Miguet, C. Vuillot, A. Alignier, J. Jirard, P. Betary, Y. Clough, C. Violle, D. Giralt, G. Bota, I. Badenhausser, G. Lefebvre, B. Gauffre, A. Vialatte, F. Calatayud, A. Gil-Tena, L. Tischendorf, S. Mitchell, K. Lindsay, R. Georges, S. Hilaire, J. Recasen, X.O. Sole-Senan, I. Robleno, J. Bosch, J.A. Barrientos, A. Ricarte, M.A. Marcos-Garcia, J. Minano, R. Mathevet, A. Gibon, J. Baudry, G. Balent, B. Poulin, F. Burel, T. Tscharntke, V. Bretagnolle, G. Siriwardena, A. Ouin, L. Brotons, J-L. Martin, L. Fahrig. 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proceedings of the National Academy of Science 116: 16442–16447.

Soucy S.L. 2002. Nesting biology and socially polymorphic behavior of the sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). Annals Entomological Society of America 95: 57–65.

Spivak M., E. Mader, M. Vaughan, N.H. Euliss. 2011. The plight of bees. Environmental Science and Technology 45: 34–38.

Steffan-Dewenter I., U. Munzenburg, C. Burger, C. Thies, T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421–1432.

Thom M.D., C.A. Eberle, F. Forcella, R. Gesch, S. Weyers, J.G. Lundgren. 2016. Nectar production in oilseeds: Food for pollinators in an agricultural landscape. Crop Science 56: 727–739.

Thom M., C.A. Eberle, F. Forcella, R. Gesch, S. Weyers. 2018. Specialty oilseed crops provide an abundant source of pollen for pollinators and beneficial insects. Journal of Applied Entomology 142: 211–222.

Trejo-Pech C.O., J.A. Larson, B.C. English, T.E. Yu. 2019. Cost and profitability analysis of a prospective pennycress to sustainable aviation fuel supply chain in the southern USA. Energies 12: 3055 (doi:10.3390/en12163055).

Ullmann K.S., M.H. Meisner, N.M. Williams. 2016. Impact of tillage on the crop pollinating, ground-nesting bee, *Peponapis pruinosa*, in California. Agricultural Ecosystems and Environment 232: 240–246.

Walther-Hellwig K., R. Frankl. 2000. Foraging habitats and foraging distances of bumble bees, *Bombus* spp. (Hymenoptera; Apidae), in an agricultural landscape. Journal of Applied Entomology 124: 299–306.

Warwick S.I., A. Francis, D.J. Susko. 2002. The biology of Canadian weeds. 9. *Thlaspi arvense* L. (updated). Canadian Journal of Plant Science 82: 803–823. Available from https://doi.org/10.4141/P01-159

Williams N.M., E.E. Crone, T.H. Roulston, R.L. Minckley, L. Packer, S.G. Potts. 2010. Ecological and life history traits predict bee species responses to environmental disturbances. Biological Conservation 143: 2280–2291.

Winfree R., I. Bartomeus, D.P. Cariveau. 2011. Native pollinators in anthropogenic habitats. Annual Review of Ecology, Evololution, and Systematics 42: 1–22.

Wood T.J., S.P.M. Roberts. 2018. Constrained patterns of pollen use in Nearctic *Andrena* (Hymenoptera: Andrenidae) compared with their Palearctic counterparts. Biological Journal of the Linnean Society 124: 732–746.