# Bees of Maine, with a State Species Checklist

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# Bees of Maine:
## A State Species Checklist, and Natural History of Native Bees Associated with Lowbush Blueberry

Northeastern Naturalist, Volume 24, Monograph 15, 2017

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**Cover Photograph:** Queen Rusty-patched Bumble Bee, *Bombus affinis*, in her underground nest. Oil painting on panel 11 x 14 inches. © Alison Dibble.

# Bees of Maine: A State Species Checklist, and Natural History of Native Bees Associated with Lowbush Blueberry

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**Northeastern Naturalist, Volume 24, Monograph 15, 2017**

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# Requiem for the Rusty-patched Gals*

Hop, slide, fondle flower upon flower on a morning breeze,
Shaking and collecting while playing your piping tune - A over middle C[A],
On every tenth, delicately sipping nectar with bee bread pollen on your knees,
Now just a memory, I think '09 it was when last enjoyed by me.

Up at dawn - abundant, vibrant, but rarely noticed in times before,
Flashing rusty red medallions on yellow black fleeces - no longer meander here,
Just rows of dull and faded dead, totems in Augusta's museum[B] drawer,
Others[C], black and yellow, take your place, but not without a melancholy tear.

~ Francis A. Drummond

***Bombus affinis* (Rusty-patched Bumble Bee), a once abundant bumble bee in Maine, now has the dubious honor of being listed as endangered. I believe I may have been the last person to see this magnificent animal in Maine during the summer of 2009.

[A] 440 Hz is the buzz pollination cycle of this bumble bee produced by shivering the massive thoracic wing muscles.

[B] Last Maine-collected specimens of the Rusty-patched Bumble Bee are in the Maine State Museum, Augusta, ME.

[C] The black and yellow *Bombus impatiens* (Common Eastern Bumble Bee), a once uncommon bumble bee in Maine has been moving north from southern New England and the Atlantic states. Recently, it has been exploding across the Maine landscape, and is now a consistently common bumble bee.

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# Bees of Maine, with a State Species Checklist

Alison C. Dibble[1,*], Francis A. Drummond[1,2], Constance Stubbs[1,3], Michael Veit[4], and John S. Ascher[5]

**Abstract** - We present a new county checklist developed from bee research in Maine since the 1800s. The list contains 278 bee species in 37 genera and 6 families, of which all but 8 are native, with ≥50 taxa each in *Andrena* and *Lasioglossum*. Data for 16 counties from publications, museum collections, and recent surveys varied in number of species from 8 (Androscoggin) to 197 (Hancock). Research since 1930 on *Vaccinium angustifolium* (Lowbush Blueberry) led to many records. Twenty-one species are considered unusual, including 3 first recorded in 2016: *Epeoloides pilosulus, Melitta melittoides*, and *Holcopasites calliopsidis*. Maine records provide evidence of declines in *Bombus affinis*, decline in *B. terricola* followed by partial recovery, and increase in *B. impatiens*. Crops that should be studied regarding associated bees are *Malus pumila* (Apple), *Vaccinium corymbosum* (Highbush Blueberry), *Vaccinium macrocarpon* (American Cranberry), and Curcurbitaceae (cucurbits). Montane, sandy, and island habitats were identified as priorities for future sampling. We discuss records of bee species from New England relevant to understanding the Maine fauna, bee diversity, changes in abundance, cleptoparasitism, pesticide impacts, habitat requirements, and climate change.

## Introduction

In Maine, native bees have received attention due to their role as pollinators, in particular of native, insect-dependent *Vaccinium angustifolium* Aiton (Lowbush Blueberry). This crop is designated in the industry as "wild blueberry" and also known as Low Sweet Blueberry. It is unusual in that large monocultural stands of a wild shrub are managed commercially (Hall et al. 1979). Extensive studies of Lowbush Blueberry since the 1960s (Boulanger et al. 1967; Bushmann and Drummond 2015; Drummond and Stubbs 1997a, 1997b, 2003; Stubbs et al. 1992) have identified that the most important pollinators for this crop are native bees including *Bombus* (bumble bees), *Andrena* (mining bees), *Halictus* and *Lasioglossum* (sweat bees), *Megachile* (leaf-cutter bees), and *Osmia* (mason or orchard bees). Of particular interest to researchers and growers are the alternate forage plants visited by bees for pollen and nectar before and after the bloom period for the Lowbush Blueberry crop (Bushmann and Drummond 2015, Stubbs et al. 1992). Other research foci within the Lowbush Blueberry pollination system are the effects of pesticides, pests, and diseases on native bees (Bushmann et al. 2012, Drummond 2012a).

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Collecting for purposes other than to understand pollination of Lowbush Blueberry has been less intensive despite the longstanding importance of orchard crops and research on invasive plant pollination since the early 1990s (Stubbs et al. 2007). Procter (1938, 1946) included bees in a general survey of the Mount Desert Region, and in recent decades several bee surveys have been conducted that were not related to Lowbush Blueberry (Dibble et al. 1997; Droege 2010; Stubbs et al. 1996, 2007). Diverse bees also visit other native blueberry species including *Vaccinium corymbosum* L.(Highbush Blueberry), common in Maine wetlands, and also *V. myrtilloides* Michx. (Common Blueberry), which often grows intermixed with Lowbush Blueberry.

In Maine, the study of native bees and their collection has been uneven across time and geographic locale (Table 1). The earliest scientific studies of Maine bees include reports of an entomological collecting trip to northern parts of Penobscot and Piscataquis Counties by Alpheus S. Packard Jr. (1861). There is also a description by Cresson (1863) of 2 currently valid *Nomada* species from unknown localities in Maine: *N. depressa* and the poorly known *N. proxima*; both are from the collection of Edward Norton, and their type specimens are deposited in the Academy of Natural Sciences Philadelphia. Another collector, Frederick Allen Eddy, collected bees in the early 1880s from the vicinity of Orono, Penobscot County, many of which are deposited in the University of Maine Collection.

John H. Lovell made the most important historical contribution to the study of Maine bees by documenting the bee fauna of Waldoboro in Lincoln County where he lived and by making broader studies of regional bees and their floral associations (Covell 1972; Lovell 1900, 1905a, 1905b, 1907, 1908, 1910, 1911, 1913, 1922a, 1922b, 1924, 1925a, 1925b, 1925c; Lovell and Cockerell 1905, 1906, 1907a, 1907b; Lovell and Lovell 1932; Pellett 1939). His collections, which consist of about 16,000 specimens of bees and other flower-visiting insects, were brought to the University of Louisville insect collection (renamed as the Lovell Insect Museum). Most of Lovell's type specimens of New England bees, including those from Maine, are in the National Museum of Natural History, with lectotype designations provided by Covell (1972), and have been databased and imaged. However, the types of 4 additional species described from New England by Lovell (1909) and originally deposited in the Museum of the Boston Society of Natural History, were overlooked by Covell (1972). These types are now in the Museum of Comparative Zoology at Harvard University (Moure and Hurd 1987). In all, Lovell described from New England 15 currently valid bee species (2 of questionable validity; 8 with coauthor T.D.A. Cockerell) and 18 additional names now placed in synonymy, with Waldoboro the type locality of 10 valid species and an additional 14 taxa now considered to be junior synonyms. Lovell made important contributions to what is known about pollination ecology, flower morphology, and the honey plants of North America (see the biography of John Lovell at https://www.encyclopedia.com/doc/1G2-2830902685.html). His work was of particular importance as a foundation for regional investigations of floral specialization (oligolecty), complementing investigations of bees in the Midwestern United States by the pioneering

Table 1. Chronological list of selected collectors of bees in Maine, including those having more than 10 records in available sources, with approximate years of activity, collecting localities, comments and citation if known, and repository if known. det. = determined by. County abbreviations are in Figure 1. Other abbreviations: American Museum of Natural History (AMNH), Maine Department of Agriculture, Conservation and Forestry, Augusta (ME DACF), University of Connecticut Entomological Collection (UCMS). [Table continued on following 2 pages.]

| Collectors | Collection years | Collection localities and/or study focus | Comments and citation if known | Repository, if known |
|---|---|---|---|---|
| Packard, A.S., Jr. | 1861 | Northern PE and PI | Report to Maine Board of Agriculture | Unknown |
| Zabriskie, J.L. | 1898–1900 | Little Deer Isle (HA), Casco Bay (CU) | | AMNH |
| Lovell, J.H. | 1904–1907 | Waldoboro (LI) | Types catalogued by Covell (1972) | Lovell Insect Museum at the University of Louisville; type specimens in the National Museum of Natural History and the Museum of Comparative Zoology at Harvard; some specimens in AMNH |
| Eddy, F.A. | 1881–1884 | Assumed PE | Locale info patchy; “Orono Hill”, “Carre Woods”, “Odlin Road” ; red ink | ME DACF |
| Franklin, H.J. | 1911–1913 | Orono (PE) | *Bombus* | Unknown |
| Woodruff, L.B. | 1915 | Camden (KN) | *Bombus* | AMNH |
| Viereck, H.L. | 1922 | Mount Desert Island (HA) | Viereck 1922 | Unknown |
| Schwarz, H.F. | 1925 | Rangeley (FR) | Schwarz (1926) | AMNH |
| Procter, W. | 1938–1946 | Mount Desert Island (HA) | Part of a general natural history survey; Procter (1938, 1946) | Sawtell Museum Archives, Acadia National Park at McFarland Hill, Bar Harbor, ME |
| Borror, D.J. | 1940 | LI | Academic insect collection | Ohio State University |
| Brower, A.E. | 1933–1960 | Bar Harbor (HA), Augusta (KE), Katahdin (PI) | Maine Forest Service, specialized in Lepidoptera | ME DACF, in part |

Table 1, continued.

| Collectors | Collection years | Collection localities and/or study focus | Comments and citation if known | Repository, if known |
|---|---|---|---|---|
| Unknown | 1927–1929, 1937 | N. Gray (CU) | "Maine Agric Exp Sta"<br>"Entomological Museum" | ME DACF |
| Phipps, C.R. | Late 1920s | CU, HA,WN | With O. Dirks, studied insects associated with blueberry crop | ME DACF |
| Plath, O.E. | 1935 | Caribou (AR) | | University of Connecticut |
| Klots, W.B. | 1954 | Oxford (OX) | | AMNH |
| Wygodzinsky, P. | 1964 | Skowhegan (KE) | | AMNH |
| Osgood, E.A. | 1960s–1980s | Alternate forage for Lowbush Blueberry, including *Rubus, Viburnum* (PE, WN,YO) | Specimens det. by TB. Mitchell, W.E. LaBerge, and, for *Bombus*, H.E. Milliron | ME DACF |
| Boulanger, L. W. | 1961–1965 | Lowbush Blueberry pollinators (WD, WN, YO) | With E.A. Osgood; also sampled New Brunswick, Canada | ME DACF |
| Favreau, M. | 1974 | WD | | AMNH |
| Heinrich, B. | 1970s–1980s | Farmington area (FR) | *Bombus* biology and foraging behavior | Unknown |
| Miliczky, E.R. (student of E.A. Osgood) | 1970s | Blueberry pollinators | Some *Dialictus* det. by S.W. Batra; Masters thesis 1978 | ME DACF |
| Hansen, R. (student of E.A. Osgood) | 1982 | HA, WN | Bees on spruce, T34 (HA) and Washington County, T4 ND, (n. HA) and WN, sent specimens to M. Arduser; *Dialictus* and *Evylaeus* det. by G.C. Eickwort | ME DACF |
| Dibble, A.C. | Early 1990s–present | Conservation of bee diversity on *Amelanchier* (HA, PE); bee/host plant relationships (AR, HA, PE, PI, WN) | Dibble and Drummond 1997, Dibble et al. 1997*; Andrena* det. by W.E. LaBerge, , Halictidae by G.C. Eickwort and J. Gibbs, *Nomada* by S. Droege, *Bombus* by L. Richardson, various by J.S. Ascher and M. Veit | School of Biology and Ecology, University of Maine, Orono, ME |

Table 1, continued.

| Collectors | Collection years | Collection localities and/or study focus | Comments and citation if known | Repository, if known |
|---|---|---|---|---|
| Stubbs, C.S., F.A. Drummond, and H. Ginsberg | 1990s–2010 | Pollinators on Lowbush Blueberry, invasive plants (HA, PE, WD, WN) | *Nomada* det. by S. Droege | Acadia National Park Collection |
| Droege, Sam | 2010 | Schoodic Peninsula, Winter Harbor (HA); Bradley (PE) | Hymenoptera Bioblitz, Acadia National Park; bee diversity study, Penobscot Experimental Forest, Bradley | US Geological Survey |
| Loose, J., F.A. Drummond, and C.S. Stubbs | Late 1990s | WN | Lowbush Blueberry research (Deblois and Cherryfield), det. by S.W. Batra, updates by M. Veit | ME DACF, in part |
| Ascher, J.S. | 2001 | Monhegan Island, Port Clyde (KN) | American Museum of Natural History and University of Singapore | AMNH |
| Maier, C.T. | 2001–2004 | Steuben (WN) | Connecticut Agricultural Experiment Station, New Haven, CT | |
| Bushmann, S. | 2010–present | HA, WD, WN | Blueberry pollinators confirmed or det. by S. Droege, J. Gibbs, R. Jean | School of Biology and Ecology, University of Maine, Orono, ME |
| Veit, M. | 2006–2016 | HA, KE, PE, SO, WD, YO | General bee surveying | Personal collection, Pepperell, MA |

mellitologists Sigmund Graenicher (1905, 1911, 1914, 1927, 1935) and Charles Robertson (1929).

Other earlier scientists who contributed to what is known of Maine bees include Franklin (1911, 1912), who made the first extensive studies of Maine bumble bees (*Bombus* sensu lato, including *Psithyrus*), and cited Orono, ME, among the syntype localities in his description of *Psithyrus fernaldae* Franklin, 1911. This taxon is now cited as *Bombus* (*Psithyrus*) *fernaldae* or treated as a synonym of the Palearctic *B.* (*P.*) *flavidus* Eversmann (see Cameron et al. 2007). Viereck (1922) described from Mount Desert Island 2 *Andrena* species now in synonymy. Herbert F. Schwarz (1926) reported bees collected at Rangeley in Franklin County and deposited voucher specimens in the American Museum of Natural History. William Procter (1938, 1946) included bees in his general biological survey of Mount Desert Island in Hancock County. In Washington, Hancock, Cumberland, Knox, and Lincoln counties and perhaps elsewhere in the late 1920s, Clarence R. Phipps (1930) inventoried insects associated with blueberry species and *Gaylussacia baccata* (Wangenh.) K. Koch (Black Huckleberry). Auburn E. Brower, a well-known microlepidopteran specialist, collected Maine bees among other insects from the early 1930s for almost 50 years, in the Augusta area of Kennebec County and many other Maine locales (Davis and Hevel 1995).

Interest in Lowbush Blueberry prompted many research projects since the work of Phipps (1930). From early times, a high priority was given to documenting bee fauna and obtaining expert identification of specimens, as correct determination to the level of species is a crucial aspect in understanding ecological patterns (see discussion in Cane 2001). In 1961–1965, bees and other insect visitors to Lowbush Blueberry were documented in 3 Maine counties and 4 Canadian provinces (Boulanger et al. 1967). Eben A. Osgood (1972, 1989) examined the nesting biology of *Andrena* and contributed to the identification of 2 *Osmia* species (Rust and Osgood 1993). His students and others extended this research by investigating native plants as floral resources and the response of the bee communities to pesticides applied to control *Choristoneura fumiferana* (Clemens) (Spruce Budworm) outbreaks (Hansen and Osgood 1983; Miliczky and Osgood 1979a, b; Stubbs et al. 1992, 1996).

Bernd Heinrich has been internationally recognized for his research on the ecological physiology of bee and moth thermoregulation, and for his numerous writings in natural history (Heinrich 1971, 1976b, 1979, 1993, 1994, 1995, 2004; Heinrich and Chavarría 2001; Heinrich and Heinrich 1983a, 1983b; Heinrich et al. 1977). Heinrich conducted important research on the behavior and biology of *Bombus* in the Farmington, ME, area. Starting in the 1970s, he elucidated the ecological physiology of bumble bee energy budgets for optimal foraging and thermoregulation (Heinrich 1972a, 1972b, 1972c, 1972d, 1973, 1974a, 1974b, 1975, 1976a, 1976c, 1979, 1995, 2004).

These and additional researchers, natural historians, and collectors who have provided baseline information on Maine's bee fauna and bee biology are listed chronologically and annotated in Table 1. Identification of some Maine bee specimens to species was conducted by resident scientists, especially S. Bushmann and

C.S. Stubbs, and most identifications were by taxonomic specialists on Northeastern bees, including T.B. Mitchell (1960, 1962), G.C. Eickwort, and W.E. LaBerge. More recently the specialists who determined Maine bees have included J. Gibbs, S. Droege, T. Griswold, J.S. Ascher, L. Richardson, and M. Veit.

This report on bee diversity in Maine includes a state checklist of species occurrence by county (Table 2, Fig. 1) based on all available data, including specimens examined by the authors, taxonomic catalogs, revisions, other literature, and digitized specimen records. The latter include specimens from multiple collections in the northeastern United States, including the American Museum of Natural History (AMNH), Cornell University, the University of Connecticut, and other collaborating institutions, compiled using open-source Arthropod Easy Capture (AEC; Seltmann 2013) (see http://biodiversity-informatics-training.org/wp-content/uploads/2014/03/D2_P6_CW_AEC2.pdf) and made publicly accessible through the biodiversity portals Discover Life (http://www.discoverlife.org)

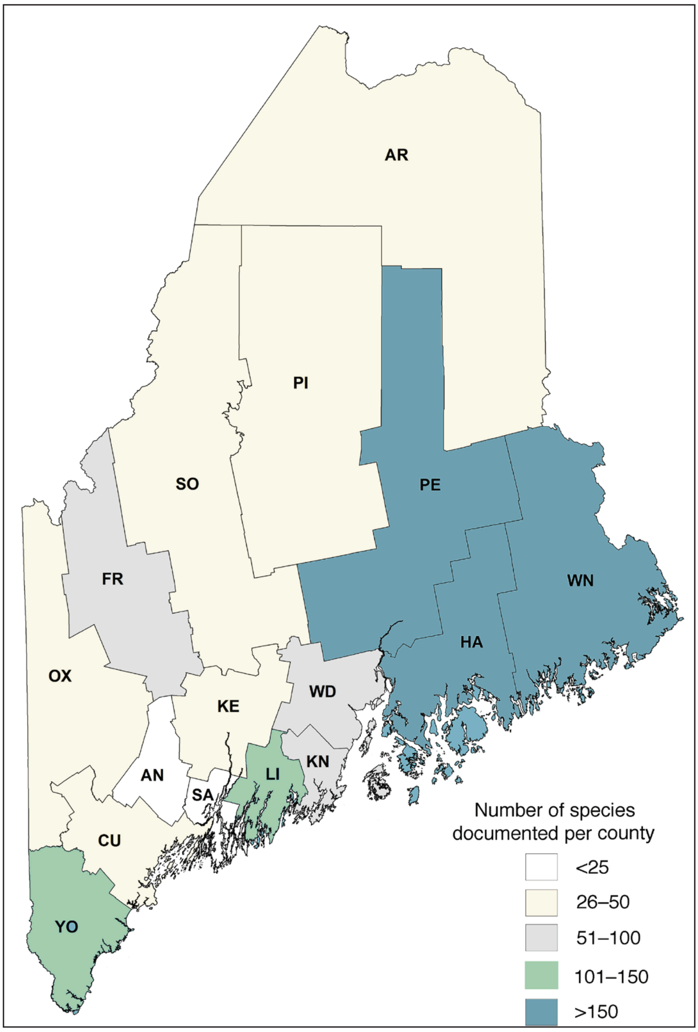

Figure 1. State of Maine, showing approximate boundaries of the 16 counties, and number of bee species known. County names are abbreviated as: AN = Androscoggin, AR = Aroostook, CU = Cumberland, FR = Franklin, HA = Hancock, KE = Kennebec, KN = Knox, LI = Lincoln, OX = Oxford, PE = Penobscot, PI = Piscataquis, SA = Sagadahoc, SO = Somerset, WD = Waldo, WN = Washington, YO = York.

and iDigbio (https://www.idigbio.org/portal/recordsets/8919571f-205a-4aed-b9f2-96ccd0108e4c). The citizen-science website Bugguide (www.bugguide.net) was also consulted as a source for recent records for the subset of species identifiable from digital images. The checklist, while preliminary, provides insight into the state of knowledge of bee species for each of Maine's 16 counties (Fig. 1) and provides a baseline for future assessment of native bee community health and diversity in Maine. For example, a 5-year bumble bee survey initiated in 2015 (http://mainebumblebeeatlas.umf.maine.edu/) will likely expand upon the baseline for bumble bees reported here (Bickerman-Martens et al. 2017).

## Methods

### Checklist

We compiled records for Maine bees from collections we examined (University of Maine Entomological Museum, American Museum of Natural History, Cornell University, Museum of Comparative Zoology, Maine Forest Service Entomological Collection, Acadia National Park, The Peabody Museum of Natural History at Yale University, and several private collections), published bee research conducted in Maine (Boulanger et al. 1967; Bushmann and Drummond 2015; Dibble and Drummond 1997; Dibble et al. 1997; Miliczky 1978; Procter 1938, 1946; Stubbs et al. 1992, 2007), and additional graduate theses and widely disseminated reports (e.g., Dearborn et al. 1983, Droege 2012). We consulted historical literature for Maine records and ranges of bee taxa, including taxonomic revisions by Bouseman and LaBerge (1978), LaBerge (1956, 1961, 1967, 1971, 1973, 1977, 1980, 1985, 1987, 1989), LaBerge and Bouseman (1970), LaBerge and Ribble (1972, 1975), McGinley (1986), Michener (1947), and Ribble (1968). Species distribution information was also derived from recent taxonomic publications such as Gibbs (2010, 2011), Gibbs et al. (2013), Rightmyer et al. (2010), and Sheffield et al. (2011). Published and unpublished databases were consulted including iDigbio; records from specimens integrated by Discover Life from the United States Geological Survey through efforts of S. Droege and displayed using its global mapper tool; the Maine Forest Service Entomological Museum (see Dearborn et al. 1983) with updates (C. Donohue, Maine Forest Service, Augusta, ME, pers. comm.); and the Maine Bumble Bee Atlas (hosted by the Maine Department of Inland Fisheries and Wildlife with the University of Maine). State records for Maine were also obtained from critical review of Mitchell (1960, 1962), and from taxonomic revisions that also served as a basis for updating all scientific names to current usage, following Ascher and Pickering (2017) and a pending update of the World Bee Checklist in the Integrated Taxonomic Information System (http://www.itis.gov). New records based on specimens collected since 1992 by A.C. Dibble and from 2009 to 2015 by S. Bushmann, F.A. Drummond, B. DuClos, and M. Veit are also reflected in the checklist.

Many vouchers, especially in older collections, have labels with minimal data regarding localities and collecting events. By contrast, collections made for various research projects in Maine may have voucher specimens with detailed ecological and collecting-effort information recorded. Most of these vouchers were obtained in one of the following ways: (1) as an individual bee captured directly on flowers, (2) using sweep nets on flowers of known plants in a repeatable manner, (3) using malaise traps set up at a known plant, (4) using small tent-like nets set up over bee burrows, or (5) using bowl traps with a liquid solution in which insects drown when they arrive to investigate a visual trap mimicking a highly attractive floral resource (Droege 2010). Catch rates for bee groups differ between capture methods (Bushmann and Drummond 2015, Drummond and Stubbs 1997b), but important and complementary data were obtained in Maine by each of the sampling methods. For instance, bowl traps captured large numbers of sweat bees but were ineffective at reliably capturing bumble bees. Hand capture and netting were, by contrast, highly effective for some large and noticeable bees (Bushmann 2013).

The compilation of the checklist by county (Table 2) includes only taxa where historical reports are consistent with species ranges as currently understood and are otherwise considered to be reliable (for some of these, county-level information was unavailable) or for which a specimen is known to us. Additional bee taxa that could be in Maine based on reports that we regard as yet unconfirmed but potentially valid are excluded from the checklist table but are discussed below.

Table 2. Checklist of the bees of Maine by county including selected sources. "Unknown county" means that a locality label or literature source does not include county or town but is from Maine. County abbreviations are explained in Figure 1. Superscripts following county records are representative sources, and are not comprehensive. Numbers refer to sources that are records in the literature or specimens in collections, lower case letters refer mostly to museum specimens (see Source Legend at end of checklist). * = introduced species. [Table continued on the following 10 pages.]

| Scientific name | Counties (selected sources) |
|---|---|
| *Andrena* (*Andrena*) *carolina* Viereck, 1909 | AR[n], CU[13], HA[1,8]PE[1,4,14,53], PI[12], WN[8,9,12,26, 61,n], YO[k] |
| *Andrena* (*Andrena*) *clarkella* (Kirby, 1802) | HA[1,25], PE[1,10,12,19,n], WN[1], YO[±] |
| *Andrena* (*Andrena*) *frigida* Smith, 1853 | AN[a], HA[1,8,25], PE[1,12,14,18,n], WD[8], WN[1,8,10,12,61] |
| *Andrena* (*Andrena*) *mandibularis* Robertson, 1892 | HA[1,8,18], PE[14], WN[c] |
| *Andrena* (*Andrena*) *milwaukeensis* Graenicher, 1903 | HA[25], KE[12], PE[1,12,n], PI, WN[9] |
| *Andrena* (*Andrena*) *rufosignata* Cockerell, 1902 | AR[n], HA[8], KE[12], LI[m], PE[1,14,n], SO[2], WN[8,10,12,26,54,61,c,n], YO[k] |
| *Andrena* (*Andrena*) *thaspii* Graenicher, 1903 | AR[a], FR[a], HA[8,25], PE[1,18], WN[9,24,n], YO[61,c] |
| *Andrena* (*Callandrena* s.l.) *asteris* Robertson, 1891 | HA[25,a,o], KN[p], LI[m], WN[c], YO[c] |
| *Andrena* (*Callandrena* s.l.) *braccata* Viereck, 1907 | YO[29], PE[1] |
| *Andrena* (*Callandrena* s.l.) *placata* Mitchell, 1960 | CU[a,g], HA[g], KN[g], OX[n], PE[1,n], SO[a] |
| *Andrena* (*Cnemidandrena*) *canadensis* Dalla Torre, 1896 | CU[g], FR[a], HA[1,g], LI[1], PE[1], SO[a,i] |
| *Andrena* (*Cnemidandrena*) *hirticincta* Provancher, 1888 | FR[a], HA[1,25,a,c,g], LI[c], OX[q], PE[k,n], PI[a], SO[c], YO[a,k] |
| *Andrena* (*Cnemidandrena*) *nubecula* Smith, 1853 | CU[a,g,]FR[a], HA[1,25,a,g], KE, KN[c], LI[m], PE[1,n], SO[c], WD[2] |
| *Andrena* (*Conandrena*) *bradleyi* Viereck, 1907 | AR[n], HA[8], PE[1,14], WD[8], WN[8,10,12,61] |
| *Andrena* (*Euandrena*) *algida* Smith, 1853 | HA[1], PE[1,14,n], WN[8,12] |
| *Andrena* (*Euandrena*) *nigrihirta* (Ashmead, 1890) | FR[a], HA[25], KN[7], PE[1,2,14,n], WN[9,12], YO[k] |

| Scientific name | Counties (selected sources) |
|---|---|
| *Andrena* (*Gonandrena*) *integra* Smith, 1853 | HA[8], PE[1,12] |
| *Andrena* (*Gonandrena*) *persimulata* Viereck, 1917 | WD[2] |
| *Andrena* (*Holandrena*) *cressonii* Robertson, 1891 | CU[18], HA[1,8], PE[1,14,26,n], WD[a], WN[1,9,10] |
| *Andrena* (*Larandrena*) *miserabilis* Cresson, 1872 | HA[1,25], PE[1,2,12,14,n], WD[8], WN[10], YO[2] |
| *Andrena* (*Leucandrena*) *barbilabris* (Kirby, 1802) | HA[25], PE[12,n] |
| *Andrena* (*Leucandrena*) *erythronii* Robertson, 1891 | PE[19], Unknown county[29] |
| *Andrena* (*Melandrena*) *carlini* Cockerell, 1901 | CU[12,13], HA[1,8,25], KN[12], PE[1,4,10,12,14,19,k,n], WD[a], WN[4,10,12,45,61,n], YO[o] |
| *Andrena* (*Melandrena*) *commoda* Smith, 1879 | HA[1,25] |
| *Andrena* (*Melandrena*) *dunningi* Cockerell, 1898 | HA[1], PE[1,12,14,19,k,n], WN[8,9,61] |
| *Andrena* (*Melandrena*) *nivalis* Smith, 1853 | AR[n], HA[8], KE[c], OX[a,k], PE[1,2,14], PI[k], WN[1,2,9,10,61,] YO[12] |
| *Andrena (Melandrena) pruni* Robertson, 1891 | WN[n] |
| *Andrena* (*Melandrena*) *regularis* Malloch, 1917 | HA[8], KN[12], PE[1,12,14,16,n], WN[4,9,10,12,61] |
| *Andrena* (*Melandrena*) *vicina* Smith, 1853 | CU[i], HA[1,8,20,25], KE[12], KN[12], LI[56,a,p], OX[k,p], PE[1,8,14,19,n], WN[1,8,9,10,12,61], YO[12] |
| *Andrena* (*Micrandrena*) *melanochroa* Cockerell, 1898 | HA[1], KN[n], OX[c], PE[1,12,14,45,n], WD[2], WN[10,12,61], YO[k] |
| *Andrena* (*Micrandrena*) *salictaria* Robertson, 1905 | HA[1,25], LI[45], PE[45], WN[12] |
| *Andrena* (*Plastandrena*) *crataegi* Robertson, 1893 | HA[1,25,a,o], KN[12], LI[m], OX[a], PE[1,4,10,12,14,n], PI[h], WN[10,12,61,c,h], YO[2,12,o] |
| *Andrena* (*Rhacandrena*) *brevipalpis* Cockerell, 1930 | HA[8], PE[2] |
| *Andrena* (*Rhacandrena*) *robertsonii* Dalla Torre, 1896 | KN[m], LI[m], PE[12], WN[12] |
| *Andrena* (*Scrapteropsis*) *alleghaniensis* Viereck, 1907 | HA[1], PE[14,n], WN[8,10,12,61], YO[2] |
| *Andrena* (*Scrapteropsis*) *imitatrix* Cresson, 1872 | HA[1], KE[12], PE[12,n], WN[8,10,61] |
| *Andrena* (*Scrapteropsis*) *kalmiae* Atwood, 1934 | AR[n], CU[13], HA[8], WN[8,c], YO[2] |
| *Andrena* (*Simandrena*) *nasonii* Robertson, 1895 | HA[1], KN[12], PE[1,12,14,n], WN[8,9,10,12] |
| *Andrena* (*Simandrena*) *wheeleri* Graenicher, 1904 | AR[n], HA[1,25], KN[12], PE[1,12,13,14], PI[h], WD[12,a,d], WN[9,10, 12,61], YO[12,o] |
| **Andrena* (*Taeniandrena*) *wilkella* (Kirby, 1802) | AR[n], CU[g], FR[a], HA[1,25,a,o], LI[m], OX[a], PE[1,12,18,n], PI[h,k], SA[i], SO[c], WD[8], WN[1,5,8,12,61], YO[a,c] |
| *Andrena* (*Thysandrena*) *bisalicis* Viereck, 1908 | CU[12], HA[8], PE[1,12], YO[13] |
| *Andrena* (*Thysandrena*) *w-scripta* Viereck, 1904 | HA[25,a as *A. lata*], KE[12], PE[1,12,14], PI[h], WN[9 as *A. lata*,10,12] |
| *Andrena* (*Trachandrena*) *ceanothi* Viereck, 1917 | HA[1], PE[1,12], WN[8], YO[12] |
| *Andrena* (*Trachandrena*) *forbesii* Robertson, 1891 | HA[8], PE[1,12,14,k,n], PI, WD[a], WN[12] |
| *Andrena* (*Trachandrena*) *hippotes* Robertson, 1895 | PE[1,12,16,19,n], PI[h], WD[a] |
| *Andrena* (*Trachandrena*) *miranda* Smith, 1879 | AR[n], FR[a,n], HA[1,25], LI[n], PE[1,2,14,n], PI[h], WN[9,12,61], YO[c] |
| *Andrena* (*Trachandrena*) *nuda* Robertson, 1891 | PE[66], YO[66] |
| *Andrena* (*Trachandrena*) *rugosa* Robertson, 1891 | HA[1,8], LI[m], PE[1,2], WN[8,10], YO[k] |
| *Andrena* (*Trachandrena*) *sigmundi* Cockerell, 1902 | HA[1,20,25], KN[12,n], LI[a], PE[1,12,14,n], WN[1,4,10,12,61,n], YO[12] |
| *Andrena* (*Trachandrena*) *spiraeana* Robertson, 1895 | PE[12,46] |
| *Andrena* (*Trachandrena*) *virginiana* Mitchell, 1960 | CU[c,g], HA[1,8,g], OX[n], PE[1], WD |
| *Andrena* (*Tylandrena*) *erythrogaster* (Ashmead, 1890) | CU[k], PE[f,n] |
| *Andrena* (*Tylandrena*) *perplexa* Smith, 1853 | PE[10] |
| *Calliopsis* (*Calliopsis*) *andreniformis* Smith, 1853 | HA[8,25], KE[56,k], YO[2] |
| *Perdita* (*Perdita*) *octomaculata* (Say, 1824) | CU[c,g], HA[2,g], KN[g], LI[56,a,p], WN[5] |
| *Pseudopanurgus aestivalis* (Provancher, 1882) (= *P. nebraskensis*) | WN[1], Unknown county[43] |

| Scientific name | Counties (selected sources) |
|---|---|
| *Pseudopanurgus andrenoides* (Smith, 1853) | FR[57,a], HA[1,2,c], KN[c], LI[56], PE[1], SO[a] |
| *Anthophora* (*Clisodon*) *terminalis* Cresson, 1869 | HA[25], OX[q], PE[1], SO[2], YO[k] |
| *Anthophora* (*Melea*) *bomboides* Kirby, 1837 | Unknown county[28] |
| **Apis* (*Apis*) *mellifera* L., 1758 | AR[4], AN[4], CU[13], HA[1,4,25,63], KE[4], KN[4,70], LI[4,70], OX[4,n], PE[1,4,12,69,63,70,k], WD[4,8,63,70,q], WN[1,4,5,9,10,61,63,70] |
| *Bombus* (*Bombus*) *affinis* Cresson, 1863 | CU[g,i], FR[27], HA[25], KE[k], LI[h,m], PE[12,n,p], PI[a], WD[4,12], WN[12], YO[a] |
| *Bombus* (*Bombus*) *terricola* Kirby, 1837 | AR[1,4,8,p], CU[4,a,g,o], FR[1,4,27,57,63,a,o], HA[1,4,18,25,63,70,a,f,g,q], KE[4,k], KN[4,70,a,g], LI[o], OX[a], PE[1,4,12,13,14,18,63,69,70,k], PI[a,h,k], SA[4], SO[4,i], WD[4,63,70,p,q], WN[1,4,5,9,12,61,63,70], YO[4,73,a,k,r] |
| *Bombus* (*Cullumanobombus*) *griseocollis* (DeGeer, 1773) | HA[1,63], PE[1,63], PI[a], WN[b] |
| *Bombus* (*Cullumanobombus*) *rufocinctus* Cresson, 1863 | AR[j,n], HA[1], PE[1,63,b] , WN[5] |
| *Bombus* (*Thoracobombus*) *fervidus* (Fabricius, 1798) | HA[1,25,m], KE[k,n], LI[p], PE[1,12], OX[q], PI[a], SO[2], WN[4,61], YO[a,r] |
| *Bombus* (*Thoracobombus*) *pensylvanicus* (DeGeer, 1773) | YO[29,32,66] |
| *Bombus* (*Psithyrus*) *ashtoni* (Cresson, 1864) | CU[a,n], FR[57,a], HA[1,25,k,o,q], KE[k,n], LI[o], OX[a], PE[1,2,n], YO[a,r] |
| *Bombus* (*Psithyrus*) *citrinus* (Smith, 1854) | AR[8], CU[r], HA[25,63,k,p], KE[k], KN[a], LI[p], OX[k], PE[p], WD[p], WN[c], YO[73] |
| *Bombus* (*Psithyrus*) *fernaldae* (Franklin, 1911) | FR[57,a], HA[2,25,p], PE[1], PI[12], WD[63], WN[1,4,5,63] |
| *Bombus* (*Psithyrus*) *insularis* (Smith 1861) | FR[a], HA[n], PE[1] |
| *Bombus* (*Pyrobombus*) *bimaculatus* Cresson, 1863 | AR[8], HA[1,25,63], KE[2], KN[63], LI[6,j], PE[1,2,63,b], WD[5,63], WN[1,4,61,63], YO[2] |
| *Bombus* (*Pyrobombus*) *impatiens* Cresson, 1863 | AR[8], CU[1,13], FR[4,8], HA[1,4,8,63,m], KE[4,k,n], KN[4,63,g], LI[4], OX[n], PE[1,2,4,12,63,b], PI[a,m], SA[i], WD[4,63], WN[1,4,61,63], YO[1,73,a] |
| *Bombus* (*Pyrobombus*) *perplexus* Cresson, 1863 | AR[2,8], HA[1,2,25,63,a,j,q], KE[k], LI[m], KN[63,a], PE[1,2,12,14,63,m], PI[h,k], WD[63,q], WN[1,5,12,63,b], YO[r] |
| *Bombus* (*Pyrobombus*) *sandersoni* Franklin, 1913 | AN[b], AR, FR[a], HA[63,a], KE[b], KN[a], PE[1,63], PI[k,m], WN[1,4,5,63,b], YO[q] |
| *Bombus* (*Pyrobombus*) *ternarius* Say, 1837 | AR[1,2,8], CU[a,g,r], FR[4,57,a,o], HA[1,4,25,63,a,g,k,m,n,p,q], KE[4,m,n], KN[4,63a], LI[j,o,p,q], OX[n], PE[1,4,12,18,63,k], PI[a,h,k], SA[4], SO[a,j], WD[4,63,k,p,q], WN[1,4,5,9,61,63,a,b], YO[a,r] |
| *Bombus* (*Pyrobombus*) *vagans vagans* Smith, 1854 | AR[1,4], CU[13,g,p,r], FR[4,57,a], HA[1,19,25,63,a,k,q], KN[63,a], LI[m], PE[1,2,10,63,m,n], PI[a,h], SO[2], WD[63,k,q], WN[1,4,5,9,10,61,63], YO[a] |
| *Bombus* (*Subterraneobombus*) *borealis* Kirby, 1837 | AR[1,2,4,8], FR[4,57,a], HA[1,2,25], KN[63,e], LI[p], OX[q], PE[1,63,b], WD[5,8,63,q]WN[1,4] |
| *Habropoda laboriosa* (Fabricius, 1804) | LI[m] |
| *Melissodes* (*Apomelissodes*) *apicatus* Lovell & Cockerell, 1906 | LI[48,m,p], WD[48] |
| *Melissodes* (*Eumelissodes*) *agilis* Cresson, 1878 | LI[47,a] |
| *Melissodes* (*Heliomelissodes*) *desponsus* Smith, 1854 | LI[a], PE[1] |
| *Melissodes* (*Eumelissodes*) *druriellus* (Kirby, 1802) | AN[47,o], AR[47], CU[47,c], HA[1,25,a], LI[47], PE[1,47] |
| *Melissodes* (*Eumelissodes*) *illatus* Lovell & Cockerell, 1906 | FR[a,o], HA[1,2,8,25,47,a], KE[47], KN[a], LI[47], PE[1,n], SO[a], WN[1,4,5,7,12,b,c], YO[47,o] |

| Scientific name | Counties (selected sources) |
|---|---|
| *Melissodes* (*Eumelissodes*) *subillatus* LaBerge, 1961 | CU[47], HA[47], LI[47,m] |
| *Melissodes* (*Eumelissodes*) *trinodis* Robertson, 1901 | LI[62,a] |
| *Melissodes* (*Melissodes*) *b. bimaculatus* (Lepeletier, 1825) | Unknown county[66] |
| *Peponapis* (*Peponapis*) *pruinosa* (Say, 1837) | CU[1], HA[1], PE[4] |
| *Holcopasites calliopsidis* (Linsley, 1943) | WA[1] |
| *Holcopasites illinoiensis* (Robertson, 1891) | PE[41] |
| *Epeolus americanus* Cresson, 1878 [= *lanhami* Mitchell, 1962] | WN[40,c] |
| *Epeolus autumnalis* Robertson, 1902 | HA[1] |
| *Epeolus pusillus* Cresson, 1864 | Unknown county[66] |
| *Epeolus scutellaris* Say, 1824 | CU[6,a], HA[1,25,a,g], KN[a,g], WN[1] |
| *Epeoloides pilosulus* (Cresson, 1878) | LI[m], YO[2] |
| *Triepeolus donatus* (Smith, 1854) | HA[25], LI[56,a,m] |
| *Triepeolus pectoralis* (Robertson, 1897) | CU[g], HA[c], KN[a] |
| *Nomada armatella* Cockerell, 1903 | WN[66] |
| *Nomada articulata* Smith, 1854 | CU[n], HA[8], LI[m], PE[14], PI[k] |
| *Nomada bella* Cresson, 1863 | PE[14,16], WD[2] |
| *Nomada bethunei* Cockerell, 1903 | HA[8], WN[8] |
| *Nomada composita* Mitchell, 1962 | HA[a], PE[14], WN[10,45] |
| *Nomada cressonii* Robertson, 1893 | AN[m], HA[1,25], PE[1,14,16], WD[2], WN[9,10,45], YO[2] |
| *Nomada cuneata* (Robertson, 1903) | HA[25] |
| *Nomada denticulata* Robertson, 1902 | PE[18], YO[2] |
| *Nomada depressa* Cresson, 1863 | OX[q], PE[14], WN[8,9] |
| *Nomada dreisbachi* Mitchell, 1962 | Unknown county[29] |
| *Nomada florilega* Lovell and Cockerell, 1905 | AN[m], LI[29,Lovell and Cockerell, 1905,p] |
| *Nomada gracilis* Cresson, 1863 | HA[as *N. inepta*], PE[1], WN[8,10] |
| *Nomada illinoensis* Robertson, 1900 | Unknown county[58] |
| *Nomada imbricata* Smith, 1854 | HA[8], PE[1,14], WN[8,10] |
| *Nomada lepida* Cresson, 1863 | PE[14], WD[2] |
| *Nomada louisianae* Cockerell, 1903 | Unknown county[71] |
| *Nomada luteoloides* Robertson, 1895 | HA[1], PE[14], WD[8], WN[1,10,45] |
| *Nomada maculata* Cresson, 1863 | HA[8], PE[14], WN[8], YO[2] |
| *Nomada ovata* (Robertson, 1903) | PE[14,17,29] |
| *Nomada perplexa* Cresson, 1863 | HA[25], LI[m], PE[14] |
| *Nomada proxima* Cresson, 1863 | Unknown county[28,Cresson 1863] |
| *Nomada pygmaea* Cresson, 1863 | HA[5], PE[1,2,14], WN[9,10] |
| *Nomada sayi* Robertson, 1893 | HA[1], PE[14], WN[9,10] |
| *Nomada subrutila* Lovell & Cockerell, 1905 | LI[Lovell and Cockerell, 1905,p] |
| *Nomada valida* Smith, 1854 | HA[8], WN[10] |
| *Nomada vicina* Cresson, 1863 | HA[g] |
| *Nomada vincta* Say, 1837 | PE[n] |
| *Nomada xanthura* Cockerell, 1908 | Unknown county[29] |
| *Ceratina* (*Zadontomerus*) *calcarata* Robertson, 1900 | HA[1,2,25,o], LI[m], PE[1,2,12,14], SA[i], WD[2], WN[1,8,61], YO[2] |
| *Ceratina* (*Zadontomerus*) *dupla* Say, 1837 | HA[1,25,o], KN[12], LI[m], PE[1,10,12,14,n], SA[i], WN[9] |
| *Ceratina* (*Zadontomerus*) *mikmaqi* Rehan & Sheffield, 2011 | HA[1,8], SO[a], WD[a], WN[8] |
| *Xylocopa* (*Xylocopoides*) *virginica* (L., 1771) | HA[1] |
| *Colletes americanus* Cresson, 1868 | WN[1] |
| *Colletes compactus* Cresson, 1868 | HA[1], PE[18], YO[a] |
| *Colletes consors* Cresson, 1868 [ssp. *mescocopus* Swenk] | HA[8,25,a], LI[a], WN[12,17] |

| Scientific name | Counties (selected sources) |
|---|---|
| *Colletes hyalinus* Provancher, 1888 | FR[a] |
| *Colletes impunctatus* Nylander, 1852 [ssp. *lacustris* Swenk] | PI[29,39] |
| *Colletes inaequalis* Say, 1837 | HA[1,8], KE[k], PE[1,12,16,18,19], WN[8,10,12,61,n] |
| *Colletes kincaidii* Cockerell, 1898 | SO[i], WN[1] |
| *Colletes latitarsis* Robertson, 1891 | Unknown county[72] |
| *Colletes simulans* Cresson, 1868 | HA[2,25], KN[c], LI[1,a], PE[1,n], SO[a], WN[1,5,12] |
| *Colletes validus* Cresson, 1868 | YO[12], Unknown county[29] |
| *Hylaeus* (*Hylaeus*) *annulatus* (L., 1758) | AR[4], FR[a,s], HA[2,4,25,s], KN[a], PE[1,4,12], P1[4], WD[4], WN[1,4,5,9] |
| *Hylaeus* (*Cephalylaeus*) *basalis* (Smith, 1853) | FR[a], LI[38], WN[9] |
| *Hylaeus* (*Hylaeus*) *mesillae* (Cockerell, 1896) [ssp. *cressoni* (Cockerell, 1907)] | CU[a], HA[1,25,a], LI[38,m], PE[1], SO[a], WN[1,8], YO[2] |
| *Hylaeus* (*Hylaeus*) *saniculae* (Robertson, 1896) | LI[a] |
| *Hylaeus* (*Hylaeus*) *verticalis* (Cresson, 1869) | HA[8], LI[m], PE[1], PI, WN[9] |
| *Hylaeus* (*Metziella*) *sparsus* (Cresson, 1869) | HA[25] |
| *Hylaeus* (*Paraprosopis*) *floridanus* (Robertson, 1893) | Unknown county[33] |
| *Hylaeus* (*Prosopis*) *affinis* (Smith, 1853) | CU[a], FR[a], HA[1,2,8,25,a], KN, LI[a], PE[1,2,12,o], WN[8] |
| *Hylaeus* (*Prosopis*) *illinoisensis* (Robertson, 1896) | Unknown county[29] |
| *Hylaeus* (*Prosopis*) *modestus modestus* Say, 1837 | FR[57], HA[1,25], PE[1,2,12,14], PI, WN[1,9] |
| *Dufourea novaeangliae* (Robertson, 1897) | HA[25], LI, WN[42] |
| *Augochlora* (*Augochlora*) *pura* (Say, 1837) | FR[c], HA[1,8,25], KN[m], PE[1], WD[k], WN[9,61] |
| *Augochlorella aurata* (Smith, 1853) | CU[a], HA[1,25,a], KE[n], LI[a,m], OX[q], PE[1,12,14,n], SO[a], WD[8,12,a], WN[1,4,5,9,10,12,61], YO[2,f,k] |
| *Augochloropsis* (*Paraugochloropsis*) *metallica* (Fabricius, 1793) | WD[8] |
| *Agapostemon* (*Agapostemon*) *sericeus* (Förster, 1771) | OX[q] |
| *Agapostemon* (*Agapostemon*) *splendens* (Lepeletier de Saint Fargeau, 1841) | PE[n], SA[i] |
| *Agapostemon* (*Agapostemon*) *texanus* Cresson, 1872 | HA[1,8], OX[q], PE[12], WN[58], YO[12] |
| *Agapostemon* (*Agapostemon*) *virescens* (Fabricius, 1775) | HA[1,8,25], LI[m], PE[1,12,19], WN[8], YO[c] |
| *Halictus* (*Odontalictus*) *ligatus* Say, 1837 | HA[1,8], LI[m], PE[1,12,14,16,n], WD[8], WN[1,5,8,12], YO[2] |
| *Halictus* (*Seladonia*) *confusus confusus* Smith, 1853 | AR[i], FR[a,s], HA[1,8,25,a,s], KE[12], KN[a], PE[1,14,s,n], WD[2,a], WN[1,8,9], YO[2] |
| *Halictus* (*Protohalictus*) *rubicundus* (Christ, 1791) | CU[a,±], FR[a,s], HA[1,2,8,25,a,s], LI[a,m], PE[1,12,14,19,s], WD[2,a], WN[1,5,8,10,12,61], |
| *Lasioglossum* (*Dialictus*) *admirandum* (Sandhouse, 1924) | HA[1,8] |
| *Lasioglossum* (*Dialictus*) *albipenne* (Robertson, 1890) | HA[1,8,a], KE[8], WN[1,8], YO[12] |
| *Lasioglossum* (*Dialictus*) *anomalum* (Robertson, 1892) | HA[8], WD[8], WN[8] |
| *Lasioglossum* (*Dialictus*) *atwoodi* Gibbs, 2010 | PE[1,14] |
| *Lasioglossum* (*Dialictus*) *coeruleum* (Robertson, 1893) | WN[61] |
| *Lasioglossum* (*Dialictus*) *cressonii* (Robertson, 1890) | FR[o], HA[1,8,25], LI[a,m], PE[1,12,14,n], PI[a], WN[1,5,8,9,10,12], YO[12,k] |
| *Lasioglossum* (*Dialictus*) *ellisiae* (Sandhouse, 1924) | HA[1], PE[1], WN[5] |
| *Lasioglossum* (*Dialictus*) *ephialtum* Gibbs, 2010 | HA[8], SO[a], WN[8] |
| *Lasioglossum* (*Dialictus*) *heterognathum* (Mitchell, 1960) | HA[8], PE[12,14], SO[a], WD[8], WN[1,8] |
| *Lasioglossum* (*Dialictus*) *hitchensi* Gibbs, 2012 | HA[1,8], PE[1,n (as *L. atlanticum*)], WN[1] |
| *Lasioglossum* (*Dialictus*) *imitatum* (Smith, 1853) | HA[1], LI[a], SO[a], PE[1,n], WD[8], WN[1,8,10] |
| *Lasioglossum* (*Dialictus*) *katherineae* (Gibbs, 2011) | HA[8], WN[66], YO[66] |
| *Lasioglossum* (*Dialictus*) *laevissimum* (Smith, 1853) | FR[a], HA[1,2,8,25], KE[12], PE[1,12], WN[9] |
| *Lasioglossum* (*Dialictus*) *leucocomum* (Lovell, 1908) | HA[1,8], LI[a], PE[1,15], WD[8], WN[8,45], YO[12] |

| Scientific name | Counties (selected sources) |
|---|---|
| _Lasioglossum_ (_Dialictus_) _lineatulum_ (Crawford, 1906) | PE[n], WD, WN[8], YO[q] |
| _Lasioglossum_ (_Dialictus_) _nigroviride_ (Graenicher, 1911) | FR[a], HA[1,8], KN[a], LI[m], PE[1,12,n] |
| _Lasioglossum_ (_Dialictus_) _novascotiae_ (Mitchell, 1960) | KN[a] |
| _Lasioglossum_ (_Dialictus_) _oblongum_ (Lovell, 1905) | HA[1,25,o], LI[m,o], PE[1,14], WN[1] |
| _Lasioglossum_ (_Dialictus_) _oceanicum_ (Cockerell, 1916) | HA[25], WN[8] |
| _Lasioglossum (Dialictus) obscurum_ (Robertson, 1892) | LI[m], PE[m] |
| _Lasioglossum_ (_Dialictus_) _paradmirandum_ (Knerer & Atwood, 1966) | HA[8], WN[8] |
| _Lasioglossum_ (_Dialictus_) _perpunctatum_ (Ellis, 1913) | HA[1,8], PE[1], WN[1,8], YO[12] |
| _Lasioglossum_ (_Dialictus_) _pilosum_ (Smith, 1853) | HA[1,2], YO[12] |
| _Lasioglossum_ (_Dialictus_) _planatum_ (Lovell, 1905) | FR[a], HA[1,2,8], LI[a], PE[1], WD[8], YO[2] |
| _Lasioglossum_ (_Dialictus_) _smilacinae_ (Roberson, 1899) | HA[1,8], SO[c], PE[12,19], WD[8], WN[8], YO[12] |
| _Lasioglossum_ (_Dialictus_) _subversans_ (Mitchell, 1960) | FR[a], HA[2,8], WD[8] |
| _Lasioglossum_ (_Dialictus_) _subviridatum_ (Cockerell, 1938) | HA[8], WN[8] |
| _Lasioglossum_ (_Dialictus_) _taylorae_ (Gibbs, 2010) | HA[8], PE[1] |
| _Lasioglossum_ (_Dialictus_) _tenax_ (Sandhouse, 1924) | FR[a], HA[2], WN[9] |
| _Lasioglossum_ (_Dialictus_) _timothyi_ (Gibbs, 2010) | HA[8], WN[8,10], YO[24] |
| _Lasioglossum_ (_Dialictus_) _versans_ (Lovell, 1905) | HA[1,2,8,a], LI[a], PE[1,n], WD[a], WN[8,9] |
| _Lasioglossum_ (_Dialictus_) _versatum_ (Robertson, 1902) | HA[1,2,8,25], PE[1,n], SO[a], WN[8] |
| _Lasioglossum_ (_Dialictus_) _viridatum_ (Lovell, 1905) | FR[a], HA[1,25,a], KE, LI[m], PE[1,m], WD[8], WN[1,9] |
| _Lasioglossum_ (_Dialictus_) _weemsi_ (Mitchell, 1960) | HA[8], WD[8], WN[8] |
| _Lasioglossum_ (_Dialictus_) _zephyrum_ (Smith, 1853) | HA[25] |
| _Lasioglossum_ (_Evylaeus_) _cinctipes_ (Provancher, 1888) | HA[8,25,c], KE[2,c], LI[a,m], PE[1,n], WD[2], WN[1,8,a], YO[2] |
| _Lasioglossum_ (_Hemihalictus_) _birkmanni_ (Crawford, 1906) (former _L. macoupinense_ sensu auct.) | HA[8,25], WN[1] |
| _Lasioglossum_ (_Hemihalictus_) _foxii_ (Robertson, 1895) | HA[1,25,a,n], PE[1,n], WN[1,9] |
| _Lasioglossum_ (_Hemihalictus_) _inconditum_ (Cockerell, 1916) | FR[a], HA[a,1], PE[1], WD[8], WN[1,9] |
| _Lasioglossum_ (_Hemihalictus_) _macoupinense_ (Robertson, 1895) [non auct.; = _divergens_ (Lovell, 1905)] | HA[8,25], PE[14], WN[9] |
| _Lasioglossum_ (_Hemihalictus_) _nelumbonis_ (Robertson, 1890) | HA[8] |
| _Lasioglossum_ (_Hemihalictus_) _pectorale_ (Smith, 1853) | HA[1,8], PE[1,14], WN[1], YO |
| _Lasioglossum_ (_Lasioglossum_) _acuminatum_ McGinley, 1986 | HA[1,8], LI[a,m], PE[1], WN[1,8,61], YO[10] |
| _Lasioglossum_ (_Lasioglossum_) _athabascense_ (Sandhouse, 1933) | HA[8,25], PE[1], WN[8,9] |
| _Lasioglossum_ (_Lasioglossum_) _coriaceum_ (Smith, 1853) | FR[o], HA[1,2,8,25], LI[m], PE[1,n], WD[2,8], WN[1,8,61] |
| *_Lasioglossum_ (_Lasioglossum_) _zonulum_ (Smith, 1848) | FR[a], HA[a], KN[a], LI[a,c], PE[15,n], WN[8] |
| *_Lasioglossum_ (_Leuchalictus_) _leucozonium_ (Schrank, 1781) | FR[s], HA[1,2,8,25,a,s], SO[a], WD[8], WN[8] |
| _Lasioglossum_ (_Sphecodogastra_) _comagenense_ (Knerer & Atwood, 1964) | SO[2], WN[1,2(Veit det., with “?")] |
| _Lasioglossum_ (_Sphecodogastra_) _quebecense_ (Crawford, 1907) | HA[1,8], KE[c], PE[14], PI[c], WD[8], WN[26,45,c], YO[a,o] |
| _Lasioglossum_ (_Sphecodogastra_) _truncatum_ (Robertson, 1901) | HA[1,2,25], WD[8,a] |
| _Sphecodes atlantis_ Mitchell, 1956 | FR[a] |
| _Sphecodes clematidis_ Robertson, 1897 | CU[a], HA[9,25,a], PE[1] |
| _Sphecodes confertus_ Say, 1837 | PI[c], WN[61] |
| _Sphecodes coronus_ Mitchell, 1956 | HA[2], PI[c], YO[61] |

| Scientific name | Counties (selected sources) |
|---|---|
| *Sphecodes cressonii* (Robertson, 1903) | HA[25], LI[a] |
| *Sphecodes davisii* Robertson, 1897 | HA[1], PE[1,14 (as *S. persimilis*),k], SO[a], WN[1,9,61], YO[2] |
| *Sphecodes dichrous* Smith, 1853 | HA[1,25], KN[c], WN[1] |
| *Sphecodes johnsonii* Lovell, 1909 | HA[25], WN[1] |
| *Sphecodes levis* Lovell and Cockerell, 1907 | FR[a], LI[p], PE[1,14], YO[k] |
| *Sphecodes mandibularis* Cresson, 1872 | PE[14,a], WN[61] |
| *Sphecodes minor* Robertson, 1898 | KE[12] |
| *Sphecodes prosphorus* Lovell and Cockerell, 1907 | HA[10], KN[a], LI[a,p], SO[2] |
| *Sphecodes ranunculi* Robertson, 1897 | FR[a], HA[1,25], PE[14,16], WD[a], WN[12,61], Y O[67] |
| *Sphecodes solonis* Graenicher, 1911 | FR[a], PE[14], SO[2] |
| **Anthidium* (*Anthidium*) *m. manicatum* (L., 1758) | HA[1], LI[1], PE[1] |
| *Dianthidium* (*Dianthidium*) *simile* (Cresson, 1864) | YO[a] |
| *Stelis* (*Dolichostelis*) *louisae* Cockerell, 1911 | Unknown county[30] |
| *Stelis* (*Stelis*) *foederalis* Smith, 1854 | LI[m], WN[9,61] |
| *Stelis* (*Stelis*) *lateralis* Cresson, 1864 | HA[25], LI[29,51,m], PE[1] |
| *Stelis* (*Stelis*) *nitida* Cresson, 1878 | WN[61] |
| *Coelioxys* (*Boreocoelioxys*) *funeraria* Smith, 1854 | Unknown county[31] |
| *Coelioxys* (*Boreocoelioxys*) *moesta* Cresson, 1864 | HA[8], KN[a], PI[4], WN[9,61] |
| *Coelioxys* (*Boreocoelioxys*) *octodentata* Say, 1824 | PE[1], YO[c] |
| *Coelioxys* (*Boreocoelioxys*) *porterae* Cockerell, 1900 | HA[1,2], OX[q], PE[1,4], PI[4], WN[61] |
| *Coelioxys* (*Boreocoelioxys*) *rufitarsis* Smith, 1854 | HA[a], KN[a], PE[1], YO[2] |
| *Coelioxys* (*Coelioxys*) *sodalis* Cresson, 1878 | HA[1,25], PI[1] |
| **Megachile* (*Callomegachile*) *sculpturalis* Smith, 1853 | AR[1], HA[1], PE[1] |
| **Megachile* (*Eutricharaea*) *rotundata* (Fabricius, 1793) | PE[1], WD[4], WN[4,9,61] |
| *Megachile* (*Litomegachile*) *brevis* Say, 1837 | CU[c], HA[25], LI[59] |
| *Megachile* (*Litomegachile*) *mendica* Cresson, 1878 | HA[25], WN[9], YO[b,c] |
| (*?)*Megachile* (*Megachile*) *centuncularis* (L., 1758) | HA[1,25,a], PE[1], WN[c] |
| *Megachile* (*Megachile*) *inermis* Provancher, 1888 | FR[a], HA[4,25], LI[59], PE[1,2,4], SO, WD[4], WN[9,61] |
| *Megachile* (*Megachile*) *montivaga* Cresson, 1878 | PE[17] |
| *Megachile* (*Megachile*) *lapponica* Thomson, 1872 [= *nivalis* Friese, 1903] | Unknown county[35] |
| *Megachile* (*Megachile*) *relativa Cresson*, 1878 | AR[4], CU[c], FR[a], HA[1,2,4,25,a,o], LI[59], PE[1,2,4], PI[4], SO[2], WD[4], WN[1,4,9,61], YO[c] |
| *Megachile* (*Xanthosarus*) *f. frigida* Smith, 1853 | HA[25,a], LI[a], OX[f], PE[1], PI[a], WN[9] |
| *Megachile* (*Xanthosarus*) *gemula* Cresson, 1878 | CU[c], FR[a], HA[1,2,8,a,o], LI[59], PE[1,14,n], WN[1,8], YO[a,c] |
| *Megachile* (*Xanthosarus*) *latimanus* Say, 1823 | HA[1,25], KE[2,n], LI[59], OX[q], PE[1], WN[1], YO[c] |
| *Megachile* (*Xanthosarus*) *m. melanophaea* Smith, 1853 | FR[a,57], HA[1,25], LI[a], PE[1,2,12], SO, WN[1,9], YO[c] |
| *Megachile* (*Xanthosarus*) *mucida* Cresson, 1878 | WA[61, det. Terry Griswold] |
| *Heriades* (*Neotrypetes*) *carinata* Cresson, 1864 | HA[1,25], PE[1,2] |
| *Heriades* (*Neotrypetes*) *leavitti* Crawford, 1913 | SO[2], [29] |
| *Heriades* (*Neotrypetes*) *v. variolosa* (Cresson, 1872) | HA[1], Unknown county[29] |
| *Hoplitis* (*Alcidamea*) *albifrons albifrons* (Kirby, 1837) | HA[9], WN[9] |
| *Hoplitis* (*Alcidamea*) *pilosifrons* (Cresson, 1864) | HA[8], WN[8] |
| *Hoplitis* (*Alcidamea*) *producta producta* (Cresson, 1864) | HA[1,8,25], PE[1,12,14], WN[1,8,9,10], YO[c,n] |
| *Hoplitis* (*Alcidamea*) *spoliata* (Provancher, 1888) [= *H. cylindrica*] | CU[o], HA[25], LI[m], PE[1,12], PI, WN[9,10,12,61], YO[a,c] |
| *Hoplitis* (*Alcidamea*) *truncata truncata* (Cresson, 1878) | HA[25], PE[1], YO[2] |

| Scientific name | Counties (selected sources) |
|---|---|
| **Osmia* (*Helicosmia*) *caerulescens* (L., 1758) | HA[1], PE[4,16,19] |
| *Osmia* (*Melanosmia*) *albiventris* Cresson, 1864 | HA[25], LI[60], PE[2,14,n], WN[9] |
| *Osmia* (*Melanosmia*) *atriventris* Cresson, 1864 | HA[1,25], LI[60], PE[1,2,12,14], WD[2,4], WN[4,5,8,9,10,12,61], YO[k] |
| *Osmia* (*Melanosmia*) *bucephala* Cresson, 1864 | HA[8,25,a], KE[4], LI[60], PE[1,10,n], WD[2], WN[4,9,12,61], YO[2] |
| *Osmia* (*Melanosmia*) *collinsiae* Robertson, 1905 | PE[1,29] |
| *Osmia* (*Melanosmia*) *distincta* Cresson, 1864 | HA[1,25], PE[1,14], YO[o] |
| *Osmia* (*Melanosmia*) *inspergens* Lovell & Cockerell, 1907 | HA[1,8,25], LI[60,p], WN[9] |
| *Osmia* (*Melanosmia*) *laticeps* Thomson, 1872 | KN[36] |
| *Osmia* (*Melanosmia*) *nigriventris* (Zetterstedt, 1838) | WN[61] |
| *Osmia* (*Melanosmia*) *proxima* Cresson, 1864 | HA[25,o], LI[60,o], PE[1,4,14], WN[9,12,61], YO |
| *Osmia* (*Melanosmia*) *pumila* Cresson, 1864 | HA[8,25], PE[1,n], WD[2], WN[8,61], YO[k] |
| *Osmia* (*Melanosmia*) *simillima* Smith, 1853 | CU[g], HA[8,25], YO[c] |
| *Osmia* (*Melanosmia*) *tarsata* Provancher, 1888 [= *O. kenoyeri*] | WN[10,61,66], Unknown county[43] |
| *Osmia* (*Melanosmia*) *tersula* Cockerell, 1912 | HA[1,8,9], PE[1,14], WN[9,10,o] |
| *Osmia* (*Melanosmia*) *virga* Sandhouse, 1939 | HA[8], PE[12], WN[8], YO[2] |
| *Osmia* (*Osmia*) *lignaria lignaria* Say, 1837 | HA[8,25], KE[4], PE[1,2,4,12,16,n], WN[8,61], YO |
| *Macropis* (*Macropis*) *ciliata* Patton, 1880 | LI[29,55] |
| *Macropis* (*Macropis*) *nuda* (Provancher, 1882) | CU[13], HA[25,a], LI[a], PE[1,n], WN[8], YO[2] |
| *Melitta* (*Cilissa*) *americana* (Smith, 1853) | LI[55], WN[37] |
| *Melitta* (*Cilissa*) *melittoides* (Viereck, 1909) | YO[2] |

Source Legend

| Code | Item |
|---|---|
| 1 | Dibble specimens, or for *Colletes compactus*, photo determined by J.S. Ascher. See Dibble et al. 1997, Dibble and Drummond 1997; Roque Island 2014; Dibble and Drummond field course at Eagle Hill (2012–2016); Bee Module experiment 2012–2015, unpubl. data. |
| 2 | Veit specimens. |
| 3 | Stubbs specimens, or see Stubbs et al., 1992; Stubbs et al. 2007. |
| 4 | Drummond specimens. |
| 5 | Droege bioblitz at Acadia National Park, see Droege 2010. |
| 6 | AMNH database, includes J.S. Ascher specimens. |
| 7 | Ascher specimens and Maine Bee Type Compilation. |
| 8 | Bushmann specimens, 2010–2012 data from her Ph.D. Dissertation, and collections into 2016. |
| 9 | R. Hansen 1981, T30 MD, 1982, T4 ND, both in Washington County, and from Hancock County, see Hansen and Osgood 1983. |
| 10 | L. Guimond 1989, T32 MD, Hancock County; T31, Washington County; Deblois, Washington County; and Orono, Penobscot County. |
| 11 | Droege determinations, *Nomada*. |
| 12 | E.A. Osgood, including Orono, Penobscot County; Deblois, Washington County, 1961–1984; Vienna, Kennebec County, 1961–1990; Kennebunk, York County, 1961–66 (Boulanger et al. 1967), Katahdin, Piscatquis County. |
| 13 | "Me. Agr. Exp. Sta" N. Gray, Cumberland County. 1929 and 1930 (possibly C.R. Phipps). |
| 14 | Miliczky and Osgood 1979a, 1979b, Passadumkeag, Penobscot County. |
| 15 | Frederick Allen Eddy, ca. 1882 (red ink). |
| 16 | s.n., Orono, Penobscot Co., 1929 (C.R. Phipps?), 1941, 1961–1963. |
| 17 | Specimens housed in MCZ Harvard University collections . |

18 Includes specimens collected by A.E. Brower, some mention "Me. Agr. Exp. Sta.", various sites, including Orono (1930, 1936, 1938); Bar Harbor, Hancock County (1937); T19, Washington County (1962); Patten, Penobscot County (1974).

19 s.n. Orono 1936-1938 (C.O. Dirk?).

20 s.n. 17 May 1929, S. Sedgwick, Hancock County.

21 s.n. 1930, Orono, Penobscot County, Maine Agricultural Experiment Station.

22 s.n. 7 June 1961, Twp 19, Washington Co., determined as *Andrena durangoensis*, J.S. Ascher annotated as *A. carolina*.

23 s.n. Machias, Washington County 1929.

24 s.n. Maine Agricultural Experiment Station, 1961.

25 Procter 1938 (amplified and revised in 1946).

26 s.n. Maine Agricultural Experiment Station, 1930.

27 Bernd Heinrich, Wilton, Franklin County, n.d., assumed by Leif Richardson from Bumblebee Economics.

28 "Coll. E. Norton", presumably as "Maine" and no date, locale or county given.

29 Mitchell 1960, 1962, no county given; a few further details by taxon where available:

29a For *Agapostemon sericeus*, mapped as occurring in Maine as A. *radiatus* by Roberts (1972) [revision]

29b For *Anthophora bomboides*, cited by Mitchell 1960, 1962 but not by Brooks 1983.

29c For *Osmia collinsiae*, in Mitchell, but no record information indicated.

30 For *Stelis lousiae*, Parker and Bohart; recorded as extending … north to Maine on p. 147 of Parker and Bohart, JKES 52(1) 1979, but not shown on their map.

31 For *Coelioxys funeraria*, Baker, mapped in Figure 20 of Baker 1975 with no details but shown about half way up Maine coast.

32 For *Bombus pensylvanicus*, cited in Milliron 1973 Vol. II of Monograph. Worker from Saco, York Coounty, 13 Jun 1951, collected by T.B. Mitchell.

33 For *Hylaeus floridanus*, cited by Mitchell but as *H. packardi*. One of the 2 specimens in type series was from Maine (described by Mitchell, 1951). Snelling (1970) proposed the synonymy and cited the Maine occurrence.

34a Gibbs 2011, and Jason Gibbs' determinations of Maine specimens.

34b Gibbs 2010, and Jason Gibbs' determinations of Maine specimens.

34c Gibbs et al. 2013 *Evylaeus* revision.

35 Sheffield et al. 2011, *Megachile nivalis*, now known as *Megachile* (Megachile) *lapponica* Thomson, 1872. Synonymy of N. American *M. nivalis* with European *M. lapponica* at http://cjai.biologicalsurvey.ca/srpg_18/srpg_18.pdf.

36 For *Osmia laticeps*, cited in Rightmyer et al. 2010, i.e., the ZooKeys paper on non-metallic Osmia. Record is from "USA: MAINE, 15 June 1982 (1♀, St. Charles)" (http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3088345/).

37 For *Melitta americana*, collected by Brianne DuClos, 9 July 2013, powerline corridor, Deblois, Washington County, ME, determined by Sam Droege, GPS 44.702139, -67.989309.

38 Lovell, 1910.

39 Stephen (1954), revision of Colletes.

40 For *Epeolus americanus*, cited by Brumley 1965 [as *E. americanus*]; Mitchell, 1962:450; paratype of *E. lanhami* from "Oreno, Me."[sic]. Table 2 refers to a specimen collected by R.A. Morse and C. Zmarlicki, July 19, 1961, "Washington County", no town given.

41 For *Holcopasites illiniosensis*, cited in Hurd and Linsley 1972.

42 For *Dufourea novaeangliae*, collected in Machias (Washington County) by Samantha Gallagher July 2015.

43a For *Pseudopanurgus aestivalis*, listed by Mitchell (1960) as *P. nebrascensis,* see Sheffield and Perron 2014.

43b For *Osmia tarsata*, see discussion on synonymy with *O. kenoyeri* Cockerell, 1915, see Sheffield and Perron 2014.

44 Roque Island 2014, Dibble and Drummond Native Bees field course at Eagle Hill, Steuben, ME.

45 Ribble, D.W. 1967. Revisions of 2 subgenera of *Andrena*: *Micrandrena* Ashmead and *Derandrena*, new subgenus (Hymenoptera: Apoidea). Ph.D. Thesis, published in 1968 as Bulletin of the University of Nebraska State Museum 8(5):237–394 .
46 For *Andrena spiraeana*, recorded from Orono (Penobscot County) by LaBerge 1973:342
47 LaBerge 1961 (*Melissodes druriellus* is former *M. rustica*)
48 LaBerge 1956
49 For *Nomada armatella*, see Mitchell (1960, 1962); J.S. Ascher notes the only record with details at http://www.discoverlife.org/mp/20l?id=BBSL521175; specimen collected 20 May 1967, Deblois (Washington County), sin nom.
50 Mitchell, 1956, descriptions of *Sphecodes*, as "*carolinus*"; collected on Katahdin as "*carolinus*".
51 For *Stelis lateralis*, collected by D.J. Borror on 6 July 1939, no town given, Lincoln County, Ohio State U. record at http://www.discoverlife.org/mp/20l?id=GBIF311451792.
52 Bug Guide photo.
55 Lovell 1922b (Bees of Maine, Part II).
56 Lovell 1925a (Bees of Maine, Part III).
57 Schwarz 1926.
58 Stubbs et al. 1992.
59 Lovell 1925b (Bees of Maine, Part IV).
60 Lovell 1925c (Bees of Maine, PartV).
61 Jennifer (Loose) Ryan, blueberry barrens collections, 1998.
62 Dearborn et al. 1983.
63 Kalyn Bickerman-Martens, Maine collections 2015.
64 Megan Leach, Maine collections 2014.
65 University of Maine Entomological Museum collection, housed in Augusta, ME.
66 Discover Life: within a species, click on global map to see details of voucher specimens.
67 s.n. Kennebunk, York County, 1960s (Boulanger et al. 1967?).
68 For *Andrena cornelli*, cited by LaBerge (1980) as *A. longifacies* LaBerge.
69 University of Maine, Orono collections 1905, 1915, collectors unknown.
70 Brianne DuClos, Maine collections 2014 –2015.
71 Discover Life, http://www.discoverlife.org/mp/20l?id=AMNH_BEES24420
72 Discover Life, http://www.discoverlife.org/mp/20l?id=AMNH_BEES668

| Symbol | Abbreviation | Institution or Collector |
|---|---|---|
| a | AMNH | American Museum of Natural History, New York, NY |
| b | CAES | Connecticut Agriculture Experiment Station, Storrs, CT |
| c | CUIC | Cornell University, Ithaca, NY |
| d | JML | Unknown (cited for *Andrena wheeleri* from Waldo County) |
| e | JSA | John Ascher |
| f | NYSM | New York State Museum, Albany, NY |
| g | RUAC | Rutgers University, Rutgers, NJ |
| h | UCD | University of California, R.M. Bohart Museum of Entomology, Davis, CA |
| i | UCMS | University of Connecticut, Storrs, CT |
| j | UMA | University of Massachusetts, Amherst, MA |
| k | UNHP | University of New Hampshire, Durham, NH |
| l | - | (left blank, could be confused with "l" [one]) |
| m | OSUC | Ohio State University Insect Collection, columbus, OH |
| n | INHS | Illinois Natural History Survey Insect Collection, Champaign, IL |
| o | KU | University of Kansas, Lawrence, KS |
| p | USNM | Smithsonian Institution, Washington, DC |
| q | YPM | Yale Peabody Museum, New Haven, CT |
| r | FMNH | Field Museum of Natural History, Chicago, IL |
| s | BISON | USGS Biodiversity Information Serving Our Nation (https://bison.usgs.gov) |

## Results

Sampling effort was highly uneven, and of Maine's 16 counties, only 8 have more than 50 available county records (see Fig. 1). Of these, only 5 have more than 100 bee species: Hancock County (197 confirmed species), Penobscot County (181), Washington County (162), York County (104), and Lincoln County (102). Androscoggin and Sagadahoc counties have only 11 and 8 species documented, respectively.

Despite these gaps, we list 278 described species of bees in 37 genera and 6 families for Maine (Table 2). For most of these, at least 1 voucher specimen was found or records in the literature are considered reliable. For some species (Table 2), information derived from Mitchell (1960, 1962; for 7 species) or other literature did not specify any county. A few species in Table 2 (i.e., *Colletes latitarsis, Epeolus pusillus, Melissodes bimaculatus*, *Nomada louisianae*) are mapped for Maine in Discover Life, but details about the record, including county, are pending (J.S. Ascher, unpubl. data).

Figure 2. Non-native bee, *Anthidium manicatum* (European Wool-carder Bee); the males are territorial at flowers of *Merostachys lanata* Send (Lamb's Ears), shown here, and other plants in Old Town, Penobscot County. The male chases other bees away while he awaits a visit from a conspecific female. Photograph © A.C. Dibble.

The largest genus is *Andrena* (53 spp.), followed by *Lasioglossum* (50), *Nomada* (28), *Bombus* (includes *Psythirus*) (17), and *Osmia* (16). The total count includes at least 8 non-native species of Old World origin: *Apis mellifera, Lasioglossum leucozonium, L. zonulum, Andrena wilkella*, *Anthidium manicatum* (Fig. 2), *Osmia caerulescens, Megachile rotundata,* and *M. sculpturalis*. *Megachile centuncularis* could be non-native (questionable status due in part to lack of confirmed records for Alaska; see Giles and Ascher 2006).

## Discussion

We consider the Maine bee checklist (Table 2) to be preliminary because none of the state's 16 counties have been exhaustively sampled, despite much effort in recent studies or by some collectors. Counties with few available records may be considered to have less relative documentation, in terms of numbers of bee species (indicated by shading of counties in Fig. 1), so it is not yet possible to say with any confidence that bee diversity in one county is higher than in another. Counties in southern Maine with the warmest climate and expanses of sandy habitat are expected to have the most species, but this is not yet borne out. Penobscot County is particularly well represented because the University of Maine in Orono has been an agricultural research center since the 1860s, with entomologists active on or near campus. Early and continuing research in major Lowbush Blueberry crop areas such as Hancock and Washington counties (Yarborough 2009) have led to better exploration of the bee fauna in those regions (Bushmann and Drummond 2015).

### Species richness

Bee species richness in Maine is relatively low (<300 species), but not unusually so given its latitude and climate (Sheffield et al. 2003, Stubbs et al. 1996). Greater species richness was reported for bees of Wisconsin (Wolf and Ascher 2009), perhaps reflecting in part higher summer temperatures across most of that state, and much greater richness was recorded for western states such as Colorado (Scott et al. 2011). Gibbs et al. (in press) developed a checklist of 465 species in Michigan, with 38 new records. Low species richness in Maine could be due in part to the extent of forest. Maine is the most forested state in the continental US when measured as the proportion of total landscape comprised of forest vegetation landscapes (93% of land area; Wilson and Sader 2002). Much of the Maine landscape is categorized as mixed northern hardwood, coniferous forests, and boreal spruce–fir forests (Davis 1993). Dense, shady forests are not optimal habitats for generalist bees in the region (Dibble et al., in press; Romey et al. 2007) because of insufficient floral resources and lack of open sky for insolation and navigation. Powerline rights-of-way may provide suitable open habitat for many species including regional rarities (Wagner et al. 2014). In Maine, the extent of coniferous forest with a permanently shaded understory may limit the spatial distribution and abundances of native bee communities (Groff et al. 2016), whereas in hardwood forests of southern Maine many specialist bees visit spring ephemerals in the forest understory prior to leafout.

Timber harvest throughout much of Maine creates a changing light environment to which bees are likely to respond.

Native bee species richness in Maine is greatest for genera that are common across the Holarctic region and well adapted to the boreal forest and other habitats characteristic of northern latitudes (Michener 2007). Genera richest in species (*Andrena*, *Lasioglossum*, *Nomada*, *Bombus*, and *Osmia*) all include early emerging species that overwinter as adults. Their ecology has been a subject of the past 45 years in Maine bee research (Bushmann and Drummond 2015; Bushmann et al. 2012; Dibble and Drummond 1997; Dibble et al. 1997; Drummond et al. 2017b; Jones et al. 2014; Osgood 1972, 1989; Stubbs et al. 1992). Of the 30–35 species of *Andrena* that occur regularly in Maine blueberry fields (Bushmann 2013, Bushmann and Drummond 2015), the 5 most common are *Andrena* (*Andrena*) *carolina* and *Andrena* (*A.*) *rufosignata,* both of which have long malar spaces that facilitate their collection of nectar from blueberry flowers, and the generalists *A.* (*Melandrena*) *regularis, A.* (*M.*) *carlini,* and *A.* (*M.*) *nivalis.* These *Andrena* tend to be found in sandy loam soils (Osgood 1972), typified by the vast glacial plains of Washington County (Davis 1993).

Some species in the list (Table 2) are of particular interest because they are seldom collected, have a narrow distribution, were not expected to occur in the area, have been in decline, or have specific habitat requirements. There is a possibility that a taxon is under-recorded due to identification difficulties, so scarcity of records might not reflect rarity in nature. Nonetheless, one might assume that a species represented by a single recent record and 1 historic citation (Lovell 1922b) such as *Melitta* (*Cilissa*) *americana*, found in 2013 by Brianne DuClos, is genuinely less abundant than the many *Andrena* and *Osmia* species each represented by multiple specimens recorded from several counties.

We identified 21 species that could be considered unusual. Among recent state records, *Epeoloides pilosulus* (Macropis Cuckoo Bee) was found in the Kennebunk Plains in York County, June 2016 on *Apocynum* sp., by M. Veit along with its host *Macropis nuda* (known from 6 counties). *Epeoloides pilosulus* is the only member of its tribe in America North of Mexico, was recently rediscovered in New England (Wagner and Ascher 2008), and is now classified as endangered in Canada (COSEWIC 2011). M. Veit also found at this same site a new state record for *Melitta melittoides*, a rarely collected species associated with *Lyonia ligustrina* (L.) DC. (Maleberry; Wagner et al. 2014). In another recent example, Fenja Brodo, entomologist from Ottawa, ON, Canada, collected *Holcopasites calliopsidis* on *Rhus typhina* L. (Staghorn Sumac) on 14 July 2016 along a roadside in Steuben (Washington County).

In addition to the 4 species mentioned above, we consider others notable due to their limited representation in regional bee collections. These include *Colletes consors* (subspecies *mesocopus*), *Colletes hyalinus*, *Colletes impunctatus*, *Macropis* (*Macropis*) *ciliata*, *Hylaeus* (*Hylaeus*) *saniculae*, *Hylaeus* (*Paraprosopis*) *floridanus*, *Hylaeus* (*Metziella*) *sparsus*, *Andrena* (*Scrapteropsis*) *kalmiae* (newly documented for York County by M.Veit in June 2016), *Melitta* (*Cilissa*) *americana*, *Heriades* (*Neotrypetes*) *leavitti*, *Hoplitis* (*Alcidamea*) *albifrons*, *Osmia* (*Melanosmia*) *inermis*, *Osmia* (*Melanosmia*) *laticeps*, *Osmia* (*Melanosmia*) *tarsata*, *Coelioxys* (*Boreocoelioxys*) *funeraria*, *Megachile* (*Megachile*) *lapponica*, *Bombus* (*Psithyrus*) *ashtoni* (collections since 2000 are few and noteworthy), and *Bombus* (*Bombus*) *affinis*, which was listed as Federally Endangered in 2017 and requires careful identification.

No well-known bee species is unique to Maine, but 2 species of *Nomada* of uncertain status are known reliably only from holotypes from the state. *Nomada proxima* has uncertain taxonomic placement and status (Mitchell 1962). *Nomada subrutila*, described from Waldoboro in Lincoln County, has been recorded from 3 other states (Mitchell 1962), but some or all of these records may result from confusion with the widely distributed species *Nomada imbricata* and/or *N. luteoloides*. The taxonomic status of these species was only recently clarified by Schwarz and Gusenleitner (2004). Maine shares most (95%+) of its known bee fauna with New York, Michigan, Massachusetts, and Connecticut. New Brunswick, Canada, has similar climate, soils, and vegetational communities to Maine (Griffin et al. 2009, Smit et al. 2007), and studies of Lowbush Blueberry there (Javorek et al. 2002) record a bee fauna similar to that of comparable sites in Maine (Boulanger et al. 1967, Javorek et al. 2002, Stubbs et al. 1992). Certain species differ, notably *Triepeolus brittaini* Cockerell, which is now well known from all 3 Maritime Provinces of Canada, with numerous recent records (J.S. Ascher, S.K. Javorek [Agriculture and Agri-Food Canada, Kentville, NS, Canada], and J. Klymko, [Nature Serve, Atlantic Canada Conservation Data Centre, Sackville, NB, Canada], unpubl. data), but has not yet been recorded elsewhere. The bee fauna of Nova Scotia is also similar to that of Maine (Sheffield et al. 2003), but includes remarkable disjunct occurrences of "southern" species such as *Colletes willistoni* Robertson, that have not been recorded from Maine (though M. Veit has collected *C. willistoni* in Massachusetts and New Hampshire, and it could be in Maine). The influence of warming by the Gulf Stream and other ocean currents may be more extensive on Nova Scotia (Boughner 1937) than on Maine, and may explain these remarkable distributions.

Bee species other than those included in our checklist have been proposed by various sources to occur in Maine. We excluded the following because of insufficient documentation or problematic identification: *Andrena* (*Andrena*) *cornelli* Viereck, *A.* (*Gonandrena*) *fragilis* Smith, *A.* (*Trachandrena*) *heraclei* Robertson, *A.* (*Tylandrena*) *perplexa* Smith, *A.* (*Gonandrena*) *platyparia* Robertson, *A.* (*Micandrena*) *ziziae* Robertson, *Lasioglossum* (*Dialictus*) *tegulare* Robertson (most if not all records pertain to *L. ellisiae*), *Nomada lehighensis* Cockerell (see Droege 2010), and *N. subnigrocincta* Swenk. All of these species could plausibly occur in the state, but we have not been able to definitively confirm their presence. The taxonomic status of several additional cleptoparasitic *Nomada* "cuckoo bee" species and morphospecies remains uncertain pending completion of ongoing taxonomic revision of the genus (Droege et al. 2010). We have excluded a number of other records of species that cannot plausibly occur as far northeast as Maine, such as *Augochloropsis sumptuosa* (Smith), a species reported for Maine by Mitchell (1960) but recorded reliably no nearer than New Jersey, and *Ceratina metallica* H.S. Smith (syn. *C. strenua*), reported by Procter (1946) but likely to have been misidentified.

## Life history and ecology

Life histories for most of the bees found in Maine are derived from studies conducted elsewhere and assumed to apply in Maine, but some bee species have been studied using Maine populations: *Osmia atriventris* (Drummond and Stubbs 1997a), *Andrena crataegi* (Osgood 1989), and *Bombus impatiens* (Drummond 2012a, Stubbs and Drummond 2001).

Regarding sociality and cleptoparasitism (one bee species lays its eggs in the nest of another bee species), 135 species in the Maine checklist (Table 2) are solitary bees, 39 are eusocial, 55 species are cleptoparasitic (e.g., *Nomada* and other Nomadinae, and *Coelioxys*) or socially parasitic in the case of some halictines (e.g., *Sphecodes*). Four species of *Bombus* (*Psithyrus*) are social parasites of other bumble bees.

Our checklist suggests that 22.7% of the total known bee species in Maine are cleptoparasites or social parasites of pollen-collecting bees. Bushmann and Drummond (2015) reported a similar percentage in a more recent survey of the bee community associated with Lowbush Blueberry in Maine. Their 4-year study involved 44 sites in Hancock, Waldo, and Washington counties. They found that 17.7% of bee species richness and 4.8% of the total bee abundance associated with Lowbush Blueberry in Maine are cleptoparasites. The number of bee cleptoparasites found in Maine is similar in species richness but is about one-fourth the relative abundance compared to that found by Sheffield et al. (2013) in Canada (varied from 1 to 10% cleptoparasite species relative to bee species richness and up to 22% in terms of individual cleptoparasite bee numbers relative to total bee abundance). Actual parasitism rates are not known for the Maine bee fauna. Over North American bee fauna, with respect to species richness, rate of cleptoparasitism might vary between 0 and 91% in individual bee species, and could be as high as 29% at the community level, based on a review of the literature (Wcislo 1996).

About half of the 278 bee species (Table 2) are known or suspected to be soil-nesting bees, including all species of *Andrena* and *Colletes* and most *Lasioglossum*. One *Andrena* species found in Maine, *A. crataegi*, is known to interconnect tunnels between individuals and may form a large communal ground nest in which each solitary sister bee is a queen (Osgood 1989). Of bees listed in Table 2, forty-three species nest in cavities and or stems, including several species of *Lasioglossum* in subgenus *Dialictus* that excavate nests in soft wood (Michener 2007), as do *Auglochlora pura* and *Anthophora terminalis*. Tiny bees in the genus *Ceratina* (small carpenter bee) may exploit an existing hole in a stem to access the hollow or pithy interior in which they lay their eggs. Examples of Maine plant species associated with stem-nesting bees are *Rubus* spp. (blackberry and raspberry), *Sambucus* spp. (elderberry), and *Rhus typhina* L. (Staghorn Sumac). Bees that nest in wood include *Xylocopa virginiana* (Eastern Carpenter Bee), which can excavate galleries in wooden structures and may cause some damage. *Megachile* and *Osmia* can nest in holes in stumps, logs, or standing dead trees, and might use holes made by boring beetles.

Bee species differ in their overwintering condition and time of emergence, with important consequences for pollination of Maine crops (Bushmann 2013). Queen bumble bees overwinter as adults that emerged and mated during the previous autumn, while most other native bees emerge as fully developed adults for their maiden flight in spring or summer, from nests established and provisioned by their mothers during the previous season (or earlier that same season). In most native Maine bee species other than *Bombus*, males typically emerge first, a condition called protandry, and they are ready to mate when the females appear. Emergence is staggered depending on the bee species, with early bees appearing with first flowers of *Salix* spp. (willow) and *Acer rubrum* L. (Red Maple) in spring (Bushmann 2013). The importance of willow to bees active in early spring was studied by Ostaff et al. (2015) and was documented in a common garden study in Maine by A.C. Dibble, F.A. Drummond, and L. Berg Stack (unpubl. data).

Some *Bombus*, especially the currently common species *B. ternarius* (Tricolored Bumble Bee; Fig. 3) and *B. vagans* (Half-black Bumble Bee), are in evidence from early spring (the beginning of April or, recently, in warm years, as early as late March) until late October. The large queens can be seen foraging on flowers

Figure 3. Queen *Bombus ternarius* (Tricolored Bumble Bee) on flowers of *Erica tetralix* L. (Crossleaf Heath) in a garden, on 24 April 2014, Brooklin, Hancock County. Photograph © A.C. Dibble.

into June; new queens are observed as early as late July (Bushmann 2013). Bumble bee workers of various sizes can be found starting in June and then throughout the growing season, with average size of individuals increasing gradually over the summer and fall (Bushmann et al. 2012).

An especially early bee is *Colletes inaequalis*, which often emerges before the snow has fully melted from its nest aggregations. Other bees active early in spring include many species in the genera *Andrena*, *Lasioglossum*, *Nomada*, and *Osmia* (Fig. 4). Adult emergence can begin as early as late March, i.e., in southern Maine in a particularly early spring, but more typically in April (A.C. Dibble, pers. observ.; Bushmann and Drummond 2015; Stubbs et al. 1992).

Bees with long flight seasons (both univoltine and multivoltine) extending from spring until fall include primitively eusocial halictine species, e.g., in the genera *Halictus*, *Lasioglossum* (Fig. 5), and *Augochlorella*, and the subsocial carpenter bees, e.g., genera *Ceratina* and *Xylocopa*. Most *Colletes* (Fig. 6) and their *Epeolus* cleptoparasites, and *Melissodes* and their *Triepeolus* cleptoparasites, fly from summer to fall in association with peak bloom of plants in the family Asteraceae such as asters and goldenrods. Early emerging and late-flying species and most specialists have restricted flight seasons. Data for Maine on flight activity of most species is in the process of being summarized (E. Venturini and F.A.

Figure 4. Female *Osmia* (mason bee) rests briefly on a leaf while foraging on *Vaccinium vitis-idaea* L. (Northern Mountain Cranberry), in Brooklin, Hancock County, 13 June 2015. Photograph © A.C. Dibble.

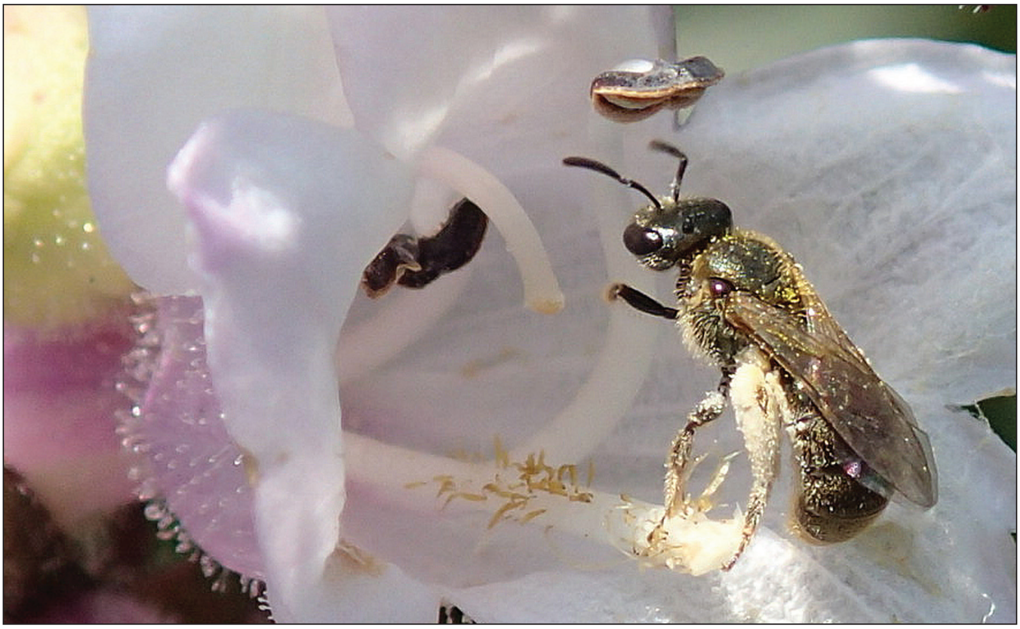

Figure 5. *Lasioglossum* (*Dialictus*) sp. (a metallic sweat bee) female on flowers of *Penstemon digitalis* “Mystica” (Foxglove Beardtongue), 8 July 2014, Blue Hill, Hancock County. Photograph © A.C. Dibble.

Figure 6. *Colletes compactus compactus* (Cellophane Bee) female, late-flying solitary bee species seldom collected in Maine, at her nest entrance, 16 September 2011, Brooklin, Hancock County. Photograph © A.C. Dibble.

Drummond, University of Maine, Orono, ME, unpubl. data). Many species were included in phenological diagrams for offshore islands of New York State (Ascher et al. 2014) and Massachusetts (Goldstein and Ascher 2016). Flight activity varies across sites and years. Likewise, flight activity of most *Osmia* species peaks in May–June, but collections of *O. atriventris* and *O. simillima* have been made in Maine as late as August in Hancock and Washington counties (Droege 2012). Some bee species, including several *Megachile* and their *Coelioxys* cleptoparasites, are aestival, i.e., most active in summer (A.C. Dibble and F.A. Drummond, pers. observ.; Droege 2012). *Colletes* and its *Epeolus* cleptoparasites can be active in mid-September in Hancock and Washington counties (A.C. Dibble, unpubl. data).

Information on host-plant usage includes Stubbs et al.'s (1992) reports of pollen and nectar records for native bee species associated with Lowbush Blueberry. *Osmia atriventris* is considered polylectic, but in a study in Winterport, ME, where 54 species of flowering plants came into bloom during its nesting period, individuals collected pollen from only a few species—90% was ericaceous pollen, most likely of Lowbush Blueberry (Drummond and Stubbs 1997b). Subsequently Bushmann and Drummond (2015) studied flower use and pollen collection by native bees during Lowbush Blueberry bloom, and found that in addition to ericaceous plants, the 3 most common native forage plant species or genera were *Cornus canadensis* L. (Bunchberry), *Rubus* spp. (raspberry and blackberry), and *Houstonia caerulea* L. (Azure Bluet). Fowler (2016) reviewed regional patterns of bee specialization on plants of the northeastern US.

Lowbush Blueberry is one of the native plants on which floral visitors have been studied intensively (Bushmann and Drummond 2015, Drummond et al. 2017b, Stubbs et al. 1992, and numerous other papers). Others include *Amelanchier* (shadbush; Dibble and Drummond 1997, Dibble et al. 1997), *Viburnum nudum* spp. *cassinoides* (L.) Torr. & A. Gray (Withe-rod; Miliczky and Osgood 1979b, Stubbs et al. 2007), and *Spiraea alba* var. *latifolia* (Aiton) H.E. Ahles (White Meadowsweet; Stubbs et al. 2007).

Other than in such pollinator studies, forage-plant information from museum collections of bees is often lacking or may be unreliable. Emphasis on data regarding flowering-plant associations will enhance our ability to protect or manipulate habitat for native bees and can lead to Maine-specific recommendations with potential usefulness in other parts of northeastern North America. The most up-to-date information on Maine forage plants and larger-scale vegetational landscapes can be found in Bushmann and Drummond (2015); Dibble and Drummond (1997); Dibble et al., in press; Droege (2012); Drummond et al. (2017a); Groff et al. (2016); Stubbs et al. (1992); and Venturini et al. (2015). More Maine studies are in the pipeline (A.C. Dibble, F.A. Drummond, and L. Berg Stack, unpubl.data). These kinds of data, when considered with reference to regional reviews of specialist bees (Fowler 2016), will increase the effectiveness of pollinator plant lists (e.g., A.C. Dibble, unpubl. data; Ley et al. 2011; Venturini et al. 2015) so that bee gardens and pollinator strips are more likely to accomplish their intended goals in Maine.

## Changes in abundance

Long-term population dynamics of bee communities have not been well studied in Maine, other than climate-change data reported by Drummond et al. (2017b). In that study, continuous sampling over a 29-year period in a Lowbush Blueberry field in Winterport, Waldo County, resulted in total bee abundance varying 2–3 fold from one year to the next. Bee categories (*Bombus, Andrena, Osmia*, and "Halictids and Other") were not highly correlated with one another and showed independence. *Osmia* declined since 2007, but the total bee community abundance was stable during the 29-year time period. Predictability from models developed by Drummond et al. (2017b) was low to moderate and suggested that abundance fluctuations depend on both density-dependent factors and stochastic density-independent factors such as weather.

The relative abundance of wild native *Bombus* species in Maine has changed dramatically since the early 1960s (Bushmann et al. 2012). Whereas the most common native bees in Maine continue to include bumble bee species such as *Bombus ternarius* (Fig. 3) and *B. vagans*, both in the subgenus *Pyrobombus*, another once-common species, *B. terricola* (Yellow-banded Bumblebee) in subgenus *Bombus,* and its social parasite *B. ashtoni* (treated by Williams et al. 2014, as conspecific with the Old World *Bombus bohemicus*) have declined in Maine (Bushmann et al. 2012; Heinrich and Heinrich 1983a, b) and across the region (Bartomeus et al. 2013, Cameron et al. 2011, Kerr et al. 2015). *Bombus affinis* (Rusty-patched Bumble Bee), also parasitized by *B. ashtoni*, appears to have been relatively common at one time in Maine and is recorded for 10 counties, but today it is seldom found. It was noted by Procter (1946) as scarce for Mount Desert Island. Boulanger et al. (1967) listed *B. affinis* from New Brunswick but did not specify any Maine counties. On the other hand, several species of subgenus *Pyrobombus* such as *B. ternarius* and especially *B. impatiens* (Eastern Bumble Bee) have increased (Bushmann and Drummond 2015). Surveys of *B. terricola* distribution in Maine in 2014–2015 indicate a resurgence of that species at many sites (Drummond 2015), but not of its social parasite *B. ashtoni*.

## Habitat and landscapes

Using literature and specimen-label data to assess relative sampling effort by habitat, we found studies in blueberry fields to be well represented, and edge habitats associated with mixed conifers were also relatively well studied. Many habitats in Maine require more attention, including coastal islands, well-drained sandy soils on islands and elsewhere, hardwood forests, swamps, bogs, open mountain summits, roadsides, and urban and suburban plantings. Bees on coastal islands in New England are of particular interest because they potentially include relictual or disjunct species (see Goldstein and Ascher 2016) or those that have potentially declined on the mainland due to infection by a microsporidian pathogen, *Nosema bombii* Fantham and Porter (Bushmann et al. 2012). On a 1-day visit in late July 2014 to Roque Island, ME, 6 *Bombus* species were documented including *B. fervidus* (Yellow Bubmblee), which is relatively scarce in Washington County, but not *B. impatiens* (A.C. Dibble, unpubl. data). In visits to Monhegan Island, ME, and when studying samples in the Cornell University Insect Collections from Appledore

Island, ME, we found no strikingly unusual species. Counties in southern Maine with sandy soils, such as York and Cumberland, could be under-represented in the checklist, and harbor bees such as *Nomada tiftonensis* that have a restricted distribution in the state. Additional bee species characteristic of northern climates have been found on Mount Washington in New Hampshire and may also extend their ranges southward into mountainous habitats in Maine, but surveys of the most promising high-elevation sites in Maine, such as Katahdin, are lacking. Bees may be genuinely scarce there. No bees other than a single *Bombus terricola* were seen on a 4-day hiking trip to a lowland forest area near Katahdin in August 2014 (A.C. Dibble, pers. observ.). In a scenario of upward-shifting treeline with climate change, open habitats that support unusual montane bee faunas in the state could change greatly in coming decades due to upslope advance of coniferous trees (Dibble et al. 2009), putting some as yet unstudied cold-adapted bee species at risk (Kerr et al. 2015) before they have been inventoried.

### Conservation concerns

Native bees of Maine could encounter competition with non-native bees for floral resources or nest sites. They could be impacted by pesticides, natural enemies, diseases, habitat degradation (through invasive plant encroachment), habitat fragmentation, and climate change (Brown and Paxton 2009, Goulson et al. 2015, Kerr et al. 2015).

Non-native bee species can be adventive, or they could arrive in Maine as purposeful introductions. Non-native bees can alter ecosystems in subtle but significant ways (Goulson 2003, Goulson et al. 2015). They may compete for floral resources and nest sites, spread pests and pathogens to native bee populations, and effect diminishing plant repoduction in native plant species that depend on native bee pollinators but are not visited much by introduced bees.

The best-known and most economically important managed non-native bee in Maine is *Apis mellifera* (European Honey Bee), which has been in North America since 1622 (Kingsbury 1906). Since 1630, when Maine was a part of Massachusetts, *Apis mellifera* has been established in the state (Martin et al. 1980). It has been used in Lowbush Blueberry pollination since the 1950s (Lee 1958), with managed colonies supplemented by feral honey bees, but since the 1990s persistent overwintering feral hives are seldom found in Maine (F.A. Drummond, unpubl. data). The disappearance of feral colonies is a phenomenon that has been observed across the entire US and is attributed to the accidental introduction of the parasitic mite *Varroa destructor* (Delaplane 2001). Colony Collapse Disorder in managed *Apis mellifera* demonstrates the collective impact of multiple simultaneous threats (Drummond 2012c, Ellis et al. 2010, Neumann and Carreck 2010, Ratnieks and Carreck 2010). This syndrome, which became evident in 2006, prompted new research on pollinator habitat quality as a means of enhancing existing native bee populations in Maine, with the idea that native bees might be required to play an increasing role as pollinators of Lowbush Blueberry and other Maine crops (Asare 2013, Venturini et al. 2015). High rates of honey bee colony losses (averaging greater than 30%; Lee et al. 2015, vanEngelsdorp and Meixner 2010) across the US since 2006 have resulted in severe economic hardship for commercial beekeepers. Honey bee colonies continue to be reared in Maine and brought from out of state (more than 75,000 commercial colonies per year; Drummond 2012c). Many of these colonies swarm and produce initial feral colonies that last only 2–3 years in the absence of management (Drummond et al. 2012). *Apis mellifera* is present in all Maine counties, though voucher specimens could not be found for some counties. A recent survey among Maine beekeepers (most are assumed to be hobbyists) to obtain pollen for analysis of pesticide residue from honey bee colonies will be reported separately. Any counties not vouchered were filled into Table 2 based on beekeeper responses to that survey (E. Ballmann, University of Maine, Orono, ME, unpubl.data).

*Bombus impatiens* is both a native bumble bee (categorized as such in Table 2) and the species that is purchased from commercial suppliers and brought into Maine in colonies (quads) annually for blueberry, *Malus pumila* Miller (Apple), *Solanum lycopersicum* L. (Tomato), and Curcurbitaceae (curcurbits) pollination in both the greenhouse and in the field (Drummond 2012a). Several thousand colonies are set out each year in Maine Lowbush Blueberry fields (Drummond 2012a, Stubbs et al. 2001). *Bombus impatiens* abundance and collecting frequency was lower in Maine prior to the 1990s compared to more recent times (Bushmann et al. 2012). Current populations of *B. impatiens* found in Maine could have multiple sources including both managed commercial colonies brought from Michigan (Drummond 2012a, Stubbs and Drummond 2001, Stubbs et al. 2001), and wild native genotypes with populations that appear to be expanding their range northward in possible association with climate change (Bushmann et al. 2012). Recent collections in more than 200 locations from 2011–2015 have shown that *B. impatiens* individuals make up ~10–20% of bumble bee individuals in Maine (F.A. Drummond, unpubl. data). Bushmann et al. (2012) showed that relative abundance of *B. impatiens* in the 1960s was much lower than current estimates in Maine (1961–1963: not detected, 1997–1998: 1–4%, 2010–2015: 10–20%). Procter (1946) did not record *B. impatiens* in coastal Hancock County.

*Megachile rotundata* (Alfalfa Leaf-cutter Bee) was used commercially as a managed pollinator for Lowbush Blueberry in Maine for more than a decade in the 1990s through to the early 2000s (Stubbs et al. 1997b) but not subsequently (F.A. Drummond, pers. observ.). Many hundreds of thousands of prepupae in individual leaf cells were imported from the western US and Canada and released by Maine growers for pollination of the Lowbush Blueberry crop (Stubbs and Drummond 1997a, b, c; Stubbs et al. 1997a, b). The bee was commonly trap nested and observed in blueberry fields in the 1990s when releases were made in Maine. Intensive bee surveys conducted from 2010 to 2012 using diverse sampling methods (Bushmann and Drummond 2015) in the same regions as these earlier releases have not recorded a single individual of *M. rotundata*, suggesting that it may be poorly adapted to long-term establishment at these sites (Stubbs and Drummond 1997a, b, c).

Several other non-native megachilids are adventive in the New World and may be a detriment to native species (Roulston and Malfi 2012, Strange et al. 2011). *Megachile sculpturalis* (Giant Asian Resin Bee) was detected in the southeastern

US in 1994 and has been dispersing rapidly across the US (Hinojosa-Díaz 2008, Mazurkiewicz 2010). It was collected in Portland, ME, by M. Mazurkiewicz in 2008, and by A.C. Dibble and S. Bushmann in Aroostook County in 2013, with additional documentation since. *Anthidium manicatum* (European Wool-carder Bee) males defend flowers of *Merostachys lanata* Send (Lamb's Ears; Fig. 2), *Agastache foeniculum* (Anise Hyssop), and horticultural bedding plants in the genus *Salvia* (Mealy Sage) against other floral visitors in Maine, and they attack bumble bees that attempt to visit such flowers (Gibbs and Sheffield 2009). *Anthidium manicatum* appears to be increasing in numbers and locales in Maine (A.C. Dibble, pers. observ.). *Osmia caerulescens* (Blue Mason Bee) may be associated with urban habitats, and has been found in Maine as early as the 1930s (see sources cited in Table 2). *Osmia lignaria* (Blue Orchard Bee), indicated in Table 2 as non-native, has been recommended as a managed bee for orchards (Torchio 1976); in Maine it is relatively scarce. *Osmia (Osmia) cornifrons* (Radoszkowski) (The Horned faced Bee) was deliberately introduced from East Asia by USDA scientists (Yamada et al. 1971) and is abundant farther south in eastern North America, but has not yet been documented in Maine. Changes in abundance over time for some species of Megachilids were studied by Drummond et al. (2017b).

Additional small-bodied non-native bees could have negligible influence on native bees, but this relationship has not been measured. A mining bee, *Andrena wilkella*, and 2 sweat bees, *Lasioglossum leucozonium* and *L. zonulum*, are examples of ground-nesting bees native to Europe that are found in the Northeast and are documented for Maine. In general, with the exception of *Apis mellifera*, non-native bees appear to be increasing in richness and abundance in Maine, but they still comprise a far lower proportion than in states to the south, such as New York (see Matteson et al. 2008). Some possible explanations for this difference include Maine's colder climate, more limited international trade, and limited extent of cities and suburbs (Simberloff 2013).

Pesticide exposure may not be as important a threat to native bee health in Maine as in other states where crops are routinely treated, e.g., with imidacloprid, a widely used, systemic neonicotinoid (one class of persistent insecticides thought to harm beneficial insects even at sublethal doses; Blacquiere et al. 2012). Coating of crop seed with neonicotinoids is not much in use in the state compared to levels applied to *Brassica napus* L. (Oilseed Rape) crops in the United Kingdom, Hungary, and Germany (Woodcock et al. 2017) and *Zea mays* subsp. *mays* L. (Corn) in Ontario and Quebec, Canada (Tsvetkov et al. 2017). Even so, exposure in Maine crops can be at levels that impact local bee populations as demonstrated in a study on honey bees by Drummond (2012c). Exposure of native bees to pesticides and the resulting effects are complicated and not well studied. As an example, a recent study by Ciarlo et al. (2012) showed that the "inert ingredients" in pesticide formulations have negative effects on honey bee learning. Studies of managed pollinators such as *Apis mellifera*, *Bombus*, *Osmia*, and *Megachile* suggest either significant negative effects (Drummond 2012b, Ladurner et al. 2008, Laycock et al. 2012) or no measurable impact (Drummond

2012b, c). No true consensus has emerged with all of the conflicting data that currently exist, especially for the neonicotinoids, though recent studies suggest that site differences affect exposure rates to bees and subsequent impacts (Tsvetkov et al. 2017, Woodcock et al. 2017). In Maine, the effects of pesticides on native bees have not been extensively researched. Drummond and Stubbs (1997a) showed a negative relationship between the amount of insecticide active ingredient applied during the Lowbush Blueberry growing season and the relative abundance of *Osmia* spp. in blueberry fields. Ten percent of the variation in *Osmia* density was attributed to pesticide exposure. Bushmann (2013) in a 3-year study of native bee communities in more than 40 blueberry fields did not find evidence to suggest increased pesticide use affected native bee abundance or richness. Natural population fluctuations of bee communities between years and locations make it difficult to assess the impacts of pesticide exposure, and pesticides continue to be a serious potential concern.

Natural enemies of native bee pollinators in Maine include cleptoparasitic bees such as *Nomada* cuckoos of *Andrena* species (Bushmann and Drummond 2015), parasitoid wasps in the genus *Monodontomerus* (Torymidae), and the bee flies (Bombyliidae). *Myopa* spp. (white-faced flies) (Conopidae) attack *Bombus* in flight and lay their eggs in the abdomen of the living host. Velvet ants (Hymenoptera: Mutillidae) are found in Maine blueberry fields (Jones et al. 2014) where they parasitize soil-nesting bees and wasps. Crab spiders in the genus *Thomisus* (Thomisidae) camouflage on flowers and attack bees when they arrive to forage. Although such pests can thwart efforts to enhance populatons of native species as pollinators (Cane et al. 1996), these species and their interactions might also be considered indicators of a healthy or naturally functioning ecosystem and bee community (Sheffield et al. 2013). Perspective might shift according to management goals. Drummond and Stubbs (1997a) found that *Osmia* spp. (mostly *O. atriventris*) populations nesting in artificial nest blocks had ~20% parasitization by aculeate wasps after 4 years of nest block utilization in a blueberry field in Winterport. Presence of these pest wasps might not be considered an index of a commercially healthy bee community, at least from a blueberry farmer's perspective. On the other hand, lack of *Stelis* bee cleptoparasites may indicate a disturbed system or unhealthy host-bee populations (see Sheffield et al. 2013).

A question remains regarding whether some exotic or cosmopolitan pathogens might be contracted by native bees from managed bees brought in to pollinate Lowbush Blueberry or other crops. Bushmann et al. (2012) found that *Nosema bombi*, a microsporidian pathogen of *Bombus* associated with blueberry fields, varied in its infection rate according to the bumble bee species, with a much higher rate in *B. terricola*—a species that had been in documented decline throughout its range—than in other common bumble bees. There was no correlation between farms employing the use of commercial bumble bees (*B. impatiens*) for pollination of Lowbush Blueberry and localized infection rates. Nonetheless, this is an example in which a threat can be more lethal to some species of native bees than to their congeners.

Another potential threat to native bees is encroachment into native habitats by non-native invasive plants (Pimentel et al. 2005, Stubbs et al. 2007, Weber 2017). Although many invasive plants in Maine do attract native bees (A.C. Dibble, unpubl. data; Stubbs et al. 2007), their presence can be considered a detriment because they displace native plants with which native bees evolved. We think it is possible that habitats dominated by invasive plants have lower diversity of pollen and nectar resources and subsequently a narrower range of overlapping flowering phenologies that support native bees. Stubbs et al. (2007) tested the supposition that invasive plants can become sinks for pollinators that would otherwise pollinate flowers of native plant species, leading to lower fruit set in the native flora. They found that pollination and bee abundance were not much affected by presence of 2 invasive plants, *Lythrum salicaria* L. (Purple Loosestrife) and *Rhamnus frangula* L. (Glossy Buckthorn), in Acadia National Park, but flowering period for *Berberis thunbergii* DC. (Japanese Barberry) overlapped that of Lowbush Blueberry and attracted floral visitors, mostly native bees, to such an extent that significantly lower floral visitation rates were observed on Lowbush Blueberry in the vicinity of barberry patches. In another example, Purple Loosestrife, a perennial of wet soils, attracts generalist bees (in Eurasia, where native, it also attracts specialists) but displaces native vegetation (Stubbs et al. 2007). Among the numerous bee-visited native plants that could be affected by Purple Loosestrife is *Lysimachia*, the oil and pollen source for *Macropis* (in turn, the only host of the associated cleptoparasitic genus *Epeoloides*). When meadows and roadsides become dominated by invasive *Lupinus polyphyllus* Lindl. (Bigleaf Lupine), then *Asclepias syriaca* L. (Common Milkweed) has less habitat. The latter is much more attractive to diverse native bees, including numerous *Bombus* species, and other insects such as *Danaus plexippus* (L.) (Monarch Butterfly), for which milkweed is a host for the larval stage. Bigleaf Lupine emerges earlier in spring than does Common Milkweed, and quickly shades and outcompetes any Common Milkweed that is already present.

Other examples of invasive plants that could impact Maine bees by reducing floral resources are: (1) herbs such as *Impatiens glandulifera* Royle (Ornamental Jewelweed or Himalayan Balsam), *Hypericum perforatum* L. (St. John's-wort), and *Fallopia japonica* (Houtt.) Ronse Decr. (Japanese Knotweed); (2) grasses such as *Phragmites australis* (Cav.) Trin. ex Steud. (Common Reed) and *Phalaris arundinacea* L. (Reed Canary Grass) (but pollen of nonnative *Phleum pratense* L. [Common Timothy] is gathered by bees; Rivernider et al., in press); (3) tender and woody vines such as *Solanum dulcamara* L. (Bittersweet Nightshade) and *Celastrus orbiculatus* Thunb. (Oriental Bittersweet); (4) shrubs including Japanese Barberry, *Elaeagnus umbellata* Thunb. (Autumn Olive), and *Lonicera morrowii* A. Gray (Morrow's Honeysuckle); and (5) trees including *Acer platanoides* L. (Norway Maple) and *Robinia pseudoacacia* L. (Black Locust). Most of these examples, but not all, are on the Maine Department of Agriculture, Conservation, and Forestry Invasive Plant List (http://www.maine.gov/dacf/mnap/features/invasive_plants/invsheets.htm).

Habitat changes apart from invasive plant encroachment, that could impact bee populations, include agricultural practices, urbanization, and forest succession. Bee responses to most of these are not fully quantified in Maine. Venturini et al. (2017) found that pollinator plantings for native bees in association with Lowbush Blueberry agroecosystems increased abundance of native bees. This finding suggests that diverse gardens in cities and towns are also beneficial to bee diversity and abundance in Maine (Dibble et al., in press), but data are lacking. Regarding forest succession, Miliczky (1978) found 65 bee species at edges and small openings in a *Picea* (spruce)–*Abies* (fir) forest, suggesting that areas adjacent to or gaps within closed-canopy conifer stands are not necessarily devoid of bee communities. It appears likely that in additon to anthropogenic alterations to the landscape, fire, floods, and catastrophic wind-throw can be associated with early successional openings in which bees find suitable habitats. Native Americans in Maine burned small openings for centuries (Cronon 1983); presumably they altered habitats near waterways and maintained blueberry-dominated openings in conifer and mixed hardwood stands. Beginning ca. 1605, European colonists conducted what we might consider a vast deforestation (Cronon 1983), and brought in *Apis mellifera* and nonnative plants, some of which became important bee forage (e.g., *Taraxacum officinale* F.H. Wigg. [Common Dandelion]). Populations of many native bee species had potential to expand in response to increased open sky and additional forage and ground-nesting opportunities. Beginning in the the mid-1800s, large areas of agricultural fields were abandoned in Maine and many other parts of New England, and overall the trend in vegetation composition in uplands continues today toward forest-dominated ecosystems (Dibble et al. 2008, Wessels 1997). The Penobscot Experimental Forest of the University of Maine in Bradley, Penobscot County, is an example of such a forested landscape. It is dominated by *Picea rubens* Sarg. (Red Spruce) and other conifers, and some stands within this forest are periodically harvested in patches under various cutting regimes. The landscape features 343 plant species (Dibble 2013) of which about 59% offer pollen and nectar resources that might be taken by bees. Timber harvest in Maine continues, leading to large openings that favor bees in the short term; this is a landscape shift that, along with habitat fragmentation and urbanization, alters bee habitat resources, and not necessarily for the worse (Romey et al. 2007). In patches, ongoing transition through succession of edge habitats to closed-canopy forest may reduce bee diversity and abundance temporarily. Would bee communities then resemble those that were present prior to intense anthropogenic habitat alteration? This cannot be measured, and we do not know precisely what bee diversity may have been lost, but we can compare to historic collections and reasonably interpret Maine's current bee fauna as an artifact of human disturbance and its current diversity as indicative of the capacity of these animals to adapt and exploit opportunity, demonstrating resilience in a changing landscape.

Climate change and in particular hotter summer temperatures may already be resulting in changes to *Bombus* ranges in Maine and elsewhere (Kerr et al. 2015). Campbell et al. (2009) speculated that climate change will result in wetter conditions in Northeastern North America. Rainy springs, as documented by Drummond et al. (2017b), and summers could detrimentally affect bees of Maine and other regions of northern New England in several ways: (1) upset a synchrony between bloom period for host plants and active period for native bees (but see Bartomeus et al. 2011), (2) limit good weather conditions for foraging with the result that insects are unable to provision sufficient brood for subsequent generations, and (3) lead to prolonged conditions that enhance fungal infections in soil-nesting bees (Batra et al. 1973).

Data from Drummond et al. (2017b) indicate that climate change that might affect bee activity and foraging during the spring bloom period of Lowbush Blueberry is already in effect in Maine. Their estimate of pollination days for Blue Hill in Hancock County between 1960 and 2015 showed a significant increase in the average number of pollination days as of 1990 but then a decline through to 2015. They ascribed this trend to an increase in rainy weather during bloom since 1990. There are potential impacts on crop pollination and on long-term bee population dynamics. Lack of synchrony between bees and their host plants could lead to an inadequacy of pollen and nectar sources (Miller-Rushing and Primack 2008) that might impact bee populations. A recent study (Bartomeus et al. 2011) showed that bee responses were comparable to and less extreme than the response of relevant plant species.

## Conclusions

Maine has a diversity of native bees typical for northeastern North America but with fewer species than states with warmer climates such as those to the south and west. Native bee species richness is rather high for typically Holarctic genera that overwinter as adults and are otherwise well adapted to a cold temperate climate (Michener 2007). While *Apis mellifera* feral colonies are in decline, other non-native bees could be increasing in species richness and abundance.

The preliminary county checklist focuses attention on gaps in available data, with the goal of informing future inventories. Additional sampling is needed in western, northern, and southern Maine, with particular attention to Androscoggin, Somerset, and Sagadahoc counties, along with other counties from which few species have been recorded.

Many vouchers we examined are from studies of pollinators for Lowbush Blueberry. Similarly intensive surveys of other crops (Apple, *Vaccinium macrocarpon* Aiton [American Cranberry], Highbush Blueberry, curcurbits) are needed in Maine. Crops that are pollinator-independent might also be surveyed for associated bees, as for *Solanum tuberosum* L. (Potato) in Michigan (Buchanan et al. 2017). Natural habitats that could be targeted for more intensive sampling include well-drained sandy openings, coastal islands, and higher elevations with features such as tablelands and balds, among other Maine plant communities (Gawler and Cutko 2010). Our assumption that York and Cumberland County sandy areas could have high diversity compared to other counties may be confounded by the extent to which habitats are being developed in that part of the state, where changed land use, intensive lawn management, or forest succession occupy areas that were formerly openings with abundant flowers. Bee associations with vegetation dominated by heaths (Ericaceae, e.g., *Vaccinium*) such as bogs, and other types of wetlands (Anderson and Davis 1998, Davis 1993) need further survey.

New collections should be subjected to identification by expert taxonomists. We urge that if regional bee faunas are to be fully useful assessments then they must be based on careful consideration of taxonomy and behavior (e.g., host plants and habitat associations), with attention to known biogeographic patterns (Goldstein and Scott 2015). Cane (2001) cautioned that ecological studies require correct bee identifications for their validity. Bee label data should include floral records so that host-plant associations and phenology can be summarized, and specimens should ideally include preservation of associated pollen loads for morphological and metagenomic studies. We hope that this first checklist of the bees of Maine can serve as a baseline for measuring the effects of anticipated climate and habitat changes on native and exotic bee populations in coming decades.

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# A Natural History of Change in Native Bees Associated with Lowbush Blueberry in Maine

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**Abstract** - More than 120 native bee species have been documented in Maine since 1930 in association with the native plant *Vaccinium angustifolium* (Lowbush Blueberry). We report 3 studies in commercial Lowbush Blueberry fields: (1) a survey of diversity in *Osmia* (mason bees) and closely related *Megachile* (leaf-cutter bees) using trap nests in 93 fields from 1990 to 2012, (2) a 29-year study of a native bee community, and (3) an examination of climate-change effects on bee-foraging periods during blueberry bloom. *Osmia* appeared to be more stable over a 22- year period in their species richness and relative abundances in Lowbush Blueberry fields when compared to *Megachile* over a similar 17-year period. The native bee community in a single location in Winterport was observed to fluctuate in abundance 2 to 3 times annually. Modeling of the total bee community and taxa-specific group abundances (*Bombus*, Megachilid*s*, Andrenids, and Halictids and other bees) suggest that while stochastic density-independent processes such as weather can play a role in determining their annual oscillations, density-dependent lags of 1 and 2 years appear to be the main driving forces. Estimation of fruit set over the same 29-year period, based upon native bee abundance, suggests that pollination is more buffered than community bee abundance, resulting in a lesser degree of fluctuation over time. We speculate that this finding is due to redundancy in floral preferences, multiple floral visitations, and differing pollination efficiencies by the highly diverse native bee community associated with Lowbush Blueberry. Effects of climate change in Maine Lowbush Blueberry fields during May bloom was investigated using a historic weather database. Since the early 1990s, precipitation has, to a large degree, reduced the number of optimal bee foraging days during bloom, with implications for pollination and bee species abundances. This new information reinforces the need for provision of pollinator gardens to support native pollinators of Lowbush Blueberry.

## Introduction

In Maine, native bees have received attention due to their role as pollinators, in particular of native, insect-dependent *Vaccinium angustifolium* Aiton (Lowbush Blueberry; Bell et al. 2009, Jones et al. 2014). No other plant species that grows in Maine has received the extent of research on pollinators that was directed to Lowbush Blueberry. From this body of research on the natural history of native bees and this particular host plant, there has emerged an understanding of the associations

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between as many as 120 bee species (Bushmann and Drummond 2015). None of these are known to specialize on Lowbush Blueberry, but they may rely on its flowers for pollen and nectar in spring before many other plants are flowering. We lack an understanding of the temporal dynamics of bee abundance over decadal time intervals, and ways in which climate change might affect future bee abundance.

Lowbush Blueberry is a wild shrub that is found throughout Maine, including in closed-canopy forest (Dibble et al. 1999). The nutritious fruits are consumed by many species of birds and mammals in Maine and throughout its range. Pre-contact fields managed by Native Americans using slash and burn culture (Moore 1994) were later burned and harvested by European colonists. At the time of the Civil War, more than 80,000 ha were managed and harvested, and the fruit was shipped to Boston and New York by train (Phipps 1930). Today this native, perennial plant, designated in the industry as Wild Blueberry and also known as Low Sweet Blueberry, is unusual in that large monocultural stands are managed commercially in Maine and eastern Canada (Hall et al. 1979). Management has become more intensive over time. Since the 1940s, pest management of weeds and insects was incorporated (Drummond and Collins 1999). Current production can comprise some or all of the following practices: fertilization, pest management, soil acidification, rock removal, mowing or burning for pruning, mechanical harvesting, and importation of *Apis mellifera* L. (Honey Bee) or *Bombus impatiens* Cresson (Common Eastern Bumble Bee) for pollination (Yarborough 2009, Yarborough et al. 2017). Current management typically involves a 2-year cycle with crop flowering in May of the first year, when the number of flowers in a field may exceed millions (~$8 \times 10^7$ flowers/ha; Bajcz et al. 2017), followed by harvest of the berries in July–August, then pruning in the fall followed by a year of vegetative growth with no blueberry flowers at all in the second year (Yarborough 2009).

Extensive studies of Lowbush Blueberry since the 1960s (Boulanger et al. 1967; Bushmann and Drummond 2015; Drummond 2016, Drummond and Stubbs 1997a, 1997b, 2003; Stubbs et al. 1992) have identified native bees as important pollinators including *Bombus* (bumble bees), *Andrena* (mining bees), *Halictus* and *Lasioglossum* (sweat bees), *Megachile* (leaf-cutter bees), and *Osmia* (mason or orchard bees). Of particular interest to researchers and blueberry farmers are the alternate forage plants visited by bees for pollen and nectar before and after the bloom period for the Lowbush Blueberry crop (Bushmann and Drummond 2015, Drummond et al. 2017, Stubbs et al. 1992, Venturini et al. 2017a). Other research foci within the Lowbush Blueberry pollination system are the effects of pesticides, pests, and diseases on native bees (Bushmann et al. 2012, Drummond 2012, Yarborough et al. 2017).

Some species of native bees, especially bumble bees, are known to be effective pollinators of the Lowbush Blueberry crop (Asare et al. 2017; Drummond 2012, 2016; Javorek et al. 2002). Despite this, Honey Bees are moved by truck from distant earlier-blooming crops, especially California almonds, and set out in Maine blueberry fields that are in the crop year as opposed to the alternate, or prune year for any given field (Asare et al. 2017, Drummond 2002). Approximately 75,000 colonies are brought to Maine for the pollination of Lowbush Blueberry, the second largest number of migratory Honey Bee hives annually of any crop; only almond pollination in California uses more hives (Drummond 2012). After crop bloom, the Honey Bees are removed to other parts of North America to pollinate other crops. Managed non-native bees such as Honey Bees and *Megachile rotundata* (Fabricius) (Alfalfa Leaf-cutter Bee), while economical, have been shown to be less effective pollinators of Lowbush Blueberry on a per-individual-bee basis than some of the more common native bees (Drummond 2016; Javorek et al. 2002; Stubbs and Drummond 1997a, 1997b, 1997c). For the sake of risk management, growers rely on Honey Bees, given the super-abundance of flowers during the bloom period (~8000 flowers/m$^2$; Bajcz et al. 2017). Hive rental costs for Honey Bees continue to escalate across the US (Rucker et al. 2012, Sumner and Boriss 2006) because of severe losses due to Colony Collapse Disorder and other causes of Honey Bee colony losses (Drummond et al. 2012, Lee et al. 2015, Ratnieks and Carreck 2010). Therefore, pollination strategies are shifting toward providing more habitat and floral resources for native bees adjacent to the blueberry crop (Drummond et al. 2017; Venturini et al. 2015, 2017a, 2017b).

Due to experimental evidence confirming the importance of insect pollination for fruit production, Phipps (1930) began to document wild bee species associated with Lowbush Blueberry flowers. From these early times, a high priority was given to documenting bee fauna and obtaining expert identification of specimens, as correct determination to the level of species is a crucial aspect in understanding ecological patterns (see discussion in Cane 2001). In 1961–1965, bees and other insect floral visitors to Lowbush Blueberry were documented in 3 Maine counties and 4 Canadian provinces (Boulanger et al. 1967). Eben A. Osgood (1972, 1989) examined the nesting biology of *Andrena* and contributed to the identification of 2 *Osmia* species (Rust and Osgood 1993). His students and others extended this research by investigating native plants as floral resources and the response of the bee communities to pesticides applied to control *Choristoneura fumiferana* (Clemens) (Spruce Budworm) outbreaks (Hansen and Osgood 1983; Miliczky and Osgood 1979a, 1979b; Stubbs et al. 1992, 1996).

Building on this historical perspective of research on native bees in Lowbush Blueberry, we report here on 3 previously unpublished studies, each involving native bees associated with Lowbush Blueberry and their temporal dynamics. These studies were conducted in Maine between 1989 and 2017 and focused on native bees, not Honey Bees, because the prospects of Lowbush Blueberry pollination in the absence of Honey Bees was our interest. We sought to take what is known of the natural history of a native pollination system, but under commercial management, and search for patterns indicative of change in bee abundance over time, and to identify weather factors that could influence such change. The first study was designed to assess the diversity of *Osmia* and *Megachile* species associated with Lowbush Blueberry fields in Maine in 1990, 1997 and 1998, and 2010–2012. In the second, we examined the long-term annual fluctuations in the bee community associated with a Lowbush Blueberry field in Winterport, ME, and consequences for fruit set. The purpose of the third study was to estimate current climate-change effects on the number of days available for bee foraging during the 3-4-week bloom period for the Lowbush Blueberry crop in Maine.

## Field-Site Description

A total of 103 commercial Lowbush Blueberry fields were sampled for bee abundance and species diversity between 1989 and 2017 in Maine. Lowbush Blueberry fields were located in Knox, Lincoln, Waldo, and Washington counties over the course of the 3 studies reported here. Lowbush Blueberry fields are embedded within a range of different landscapes across Maine, from upland deciduous forest to glacial outwash plains along the Downeast coast (Drummond et al. 2009). Most fields are a result of forest clearing and management through burning or herbicide use to minimize continuous colonization of competitive vegetation (Yarborough 2009). Plant species diversity typically found within Lowbush Blueberry fields is listed in Bushmann and Drummond (2015) and Drummond et al. (2017). Invertebrate species diversity in these managed habitats is discussed by Jones et al. (2014).

## Methods

### *Osmia* and *Megachile* diversity in Lowbush Blueberry fields

We estimated the species richness and relative abundances of *Osmia* and *Megachile* species in Maine in 3 time periods and varous sites. We surveyed bees in Knox, Lincoln, Waldo, and Washington counties in 1990; Washington County in 1997 and 1998; and Hancock, Waldo, and Washington counties in 2010–2012. In the first 2 samples (1990 and then 1997–1998), we used wooden trap-nest blocks with holes measuring 6.4 mm and 8.5 mm in diameter (16 holes, 8 per diam size, per 51 x 102 x 254 mm kiln-dried pine block). We deployed 20 blocks along forested edges in each of 30 wild blueberry fields in 1990 and 20 blocks along forested edges in each of 18 and 15 Lowbush Blueberry fields, respectively, in 1997 and 1998. We placed the blocks 1.5–2 m above ground oriented south–southeast. The trap nests were deployed in March well before *Osmia* and *Megachile* species emergences and collected in August and September after adult activity ceased. Trap nests were overwintered in a non-heated utility shed in Winterport and moved in March to the laboratory at the University of Maine Orono, individually enclosed in metal screen cages and incubated at room temperature. Emerged bees were collected, pinned and sent to T. Griswold and W.E. LaBerge for identification. Due to the focus of the 1990 survey, only *Osmia*, not *Megachile* specimens, were identified to species. We calculated relative abundance for each species by genus and by year and compared these data to that of richness and relative abundance of species from the same genera captured by hand on Lowbush Blueberry flowers or bowl traps in 40 fields in Hancock, Waldo, and Washington counties during 2010–2012 (detailed methods described in Bushmann and Drummond 2015).

### A long-term temporal study of a native bee community in Lowbush Blueberry

Starting in 1989, we sampled the bee community annually in a Lowbush Blueberry field in Winterport, ME, over a 29-year period, although 7 years were missed. This crop flowers in mid-May for as long as 3–4 weeks. We did not sample the bee community in 1998, 2001, 2005, 2010, 2012, 2014, and 2016. Each year at peak bloom (50–80% open flowers), 20 1-m$^2$ quadrats placed in flowering Lowbush Blueberry were observed for 1 minute. The quadrats were approached slowly, and the observer (F.A. Drummond) waited 1 minute without moving and then proceeded to count the number of bees within and entering the quadrats for 1 minute. This sampling was conducted 2–3 times during peak bloom and performed on only sunny days between the times of 1000 and 1400 hrs when air temperatures were >15.6 ºC and winds were <24 kph. These conditions are conducive to native bee foraging activity (Drummond 2016). We recorded bees as belonging to the following groups: *Bombus* spp. (bumble bees), Megachilids (mostly *Osmia* spp. with a few *Megachile* spp.), Andrenids (*Andrena* spp., [mining bees]), and Halictids (sweat bees) and Other Native Bees (Colletidae and non-social Apidae). Honey Bees were recorded, but not included in our analysis of native bee densities. Bushmann and Drummond (2015) and Drummond et al. (2017) list representative species identifications of bees that were captured and identified during the time period of this study. We converted bee density per minute of each taxa group to a per-hectare basis for graphical analysis. We estimated the fruit set contribution by the bee community using the formula we had derived for estimating fruit set in Lowbush Blueberry based upon native wild bees per m$^2$ per minute (Asare et al. 2017). We used time-series analysis (autoregressive moving average regression [ARIMA]) to assess periodicity in abundance fluctuations from 1989 to 2015 and serial cross-correlation to test temporal synchrony among pairs of taxa groups (Shumway 1988). We utilized linear interpolation to estimate the bee community densities in the non-sampled years (Wei 2006) and sample data from 2017 to assess or validate future predictions of the models. Pollination level was not measured annually in the Winterport field where bee densities were measured. Using a predictive formula of fruit set based upon native bee densities per m$^2$ per minute (Asare et al. 2017), we estimated percent fruit set over the 29-year time period. Statistical analysis was performed by using JMP statistical software (SAS Institute, Inc. 2015).

### Estimated current climate-change effects on bee foraging periods during Lowbush Blueberry bloom

For a single site in Blue Hill, Hancock County, where an automated weather station records hourly conditions, we used a degree-day model developed and validated in Nova Scotia by White et al. (2012) to estimate the bloom "window", or the period between the beginning and end of bloom from 1960 to 2015. We generated estimates of the number of cumulative degree-days from the historical maximum and minimum air temperatures. Historical weather data for the site (1960–2015) were downloaded from archived weather reports (NOAA 2017). Most bees are not actively foraging in weather conditions such as cold, precipitation including mist or rain, or brisk winds. To predict the number of potential pollination days during the bloom window, we subtracted days that were below a high of 4.4 ºC, had 2.54 cm or more of rain in a day, or had winds greater than 32.2 kph. These conditions have been reported as thresholds for some native and exotic bee species in Maine that visit wild blueberry during bloom (Drummond 2016). This subtraction yields the number of days during bloom that bees pollinated flowers or "pollination days". Use of daily weather parameters did not allow us to develop a high-resolution, hourly prediction of foraging activity. We assume that our predictions based upon the use of 3 weather metrics (air temperature, precipitation, and wind velocity) aggregated over a 24-hr period will underestimate foraging activity, but should be consistently biased over the ~1 month-long period of bloom in Maine and should also average out annually. We employed piecewise linear regression (Oosterbaan et al. 1990) to fit the number of bee foraging days during the bloom window over time (years), and multiple linear regression with mean daily air temperature, mean daily precipitation, and mean daily wind velocity to determine explantory power of weather factors during the segment exhibiting a negative slope (SAS Institute, Inc. 2015). We collected actual bloom data in 2016 and 2017 and calculated the number of pollination days based upon the bee flight-activity parameters described above.

## Results

### *Osmia* and *Megachile* diversity in wild blueberry fields

The relative abundances of *Osmia* and *Megachile* species associated with Maine Lowbush Blueberry (collected in 1990, 1997–1998, and 2010–2012) are shown in Figure 1. *Osmia atriventris* Cresson and *O. inspergens* Lovell & Cockerell, were the 2 most abundant species in all 3 collection periods (Fig. 1A).

In 1997–1998 and more than 20 years later in the same geographic areas, 8 *Megachile* species were observed (Fig. 1B), of which *Megachile brevis* Say*, M. centuncularis* L.*,* and *M. latimanus* Say were each found in only 1997–1998, or 2010–2012. The *Megachile* species with greater relative abundance appear to fluctuate more dramatically among sampling periods (Fig. 1B) than did the more common *Osmia* species (Fig. 1A).

### A long-term temporal study of a native bee community in Lowbush Blueberry.

Continuous sampling over a 29-year period in a Lowbush Blueberry field in Winterport, Waldo County, shows that total community bee abundance varies 2–3 fold from one year to the next (Fig. 2). Bee taxa groups (*Bombus,* Andrenids*,* Megachilids, and Halictids and Others) were correlated, showing some degree of dependence. Halictids and Others are highly correlated with Andrenids ($r = 0.704$, $P = 0.0004$), *Bombus* were correlated with both Halictids and Others ($r = 0.489$, $P = 0.024$) and Andrenids ($r = 0.588$, $P = 0.005$). However, Megachilids are not correlated with any of the other taxa ($P > 0.05$). For instance, Megachilids exhibited a continuing decline in numbers since 2007, although in 2017 a slight increase in Megachilid density did occur, while *Bombus* abundance increased during the same time period, except for 2011 where Bombus density decreased. (Fig. 2).

The fluctuations in the entire bee community (all inidivduals in all taxa groups pooled), modeled using time-series methods, resulted in a significant fit ($P < 0.05$), but poor overall predictability (Table 1). The time-series second-order model explains only 7.3% of the variation (adjusted $r^2 = 0.019$) in bee numbers over the 29-year period (Table 1). The significant factors are the numbers of bees the previous year ($P = 0.049$) and a stochastic random-walk factor ($P = 0.029$). The statistical model suggests that the dynamics of the entire native bee community is driven

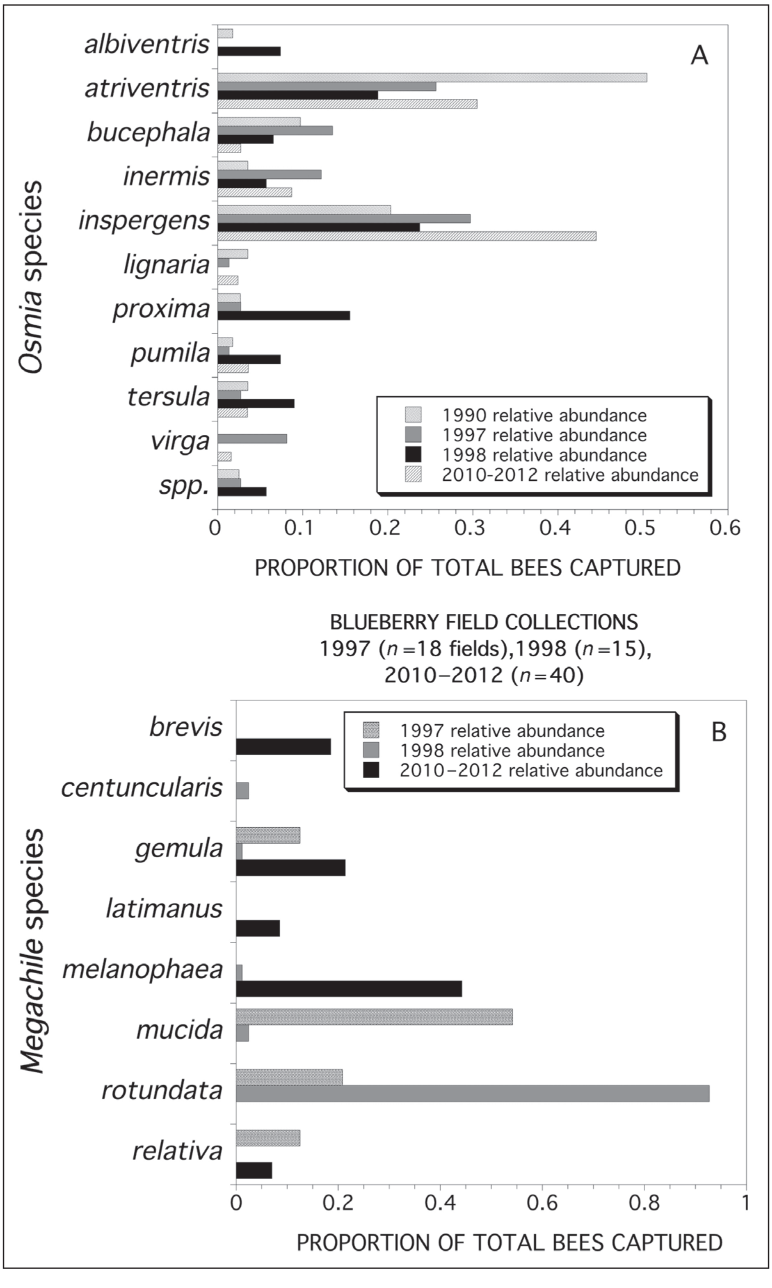

Figure 1. Relative abundance of (A) *Osmia* species and (B) *Megachile* species collected in Maine Lowbush Blueberry fields in 1990 ($n$ = 30 fields), 1997 ($n$ = 18), 1998 ($n$ = 15), and 2010–2012 ($n$ = 40) (data from Bushmann and Drummond 2015).

by density-dependenct factors, possibly disease, competition for nesting sites, or flowers, but fluctuations in density from year to year could also be due to weather and other stochastic events as suggested by the significant random-walk parameter (Table 1). Modeling individual taxa did not result in a significant predictive model for *Bombus* ($P > 0.05$), but significant time-series predictive models were developed for Andrenids, Megachilids, and the Halictids and Others (Table 1). The

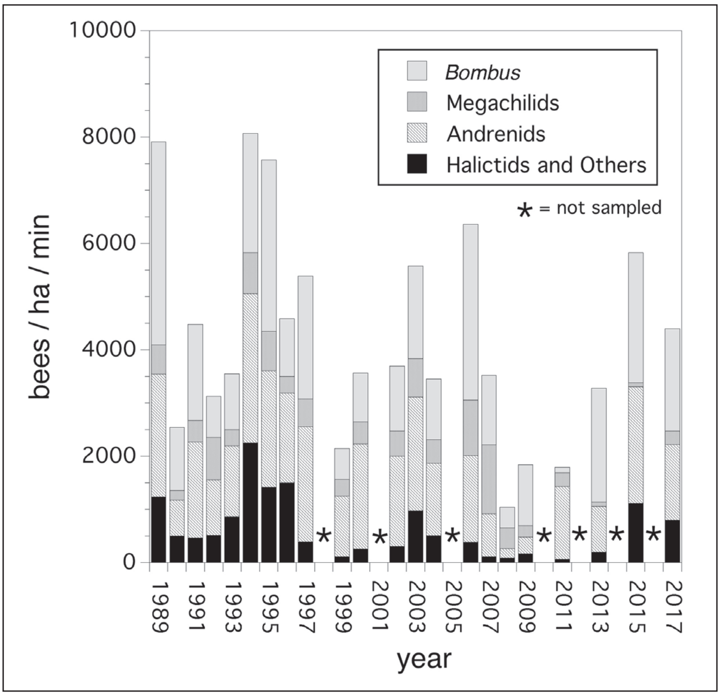

Figure 2. Data from a 29-year bee community survey in a Lowbush Blueberry field at Winterport, Waldo County, with bee abundance by group in timed quadrat surveys. The symbol "*" denotes years when sampling was not conducted. The taxa group "others" refers to observed individuals assigned to the families Colletidae, Apidae (other than *Bombus*), or unidentified individuals.

Table 1. Time-series predictive models (ARIMA) used to predict taxon density at time = *t* + 1.

| Taxa | Coefficient | Coefficent value ± s.e. | *P*-value | $r^2$ (adjusted $r^2$) |
|---|---|---|---|---|
| Andrenids | | | | 0.208 (0.059) |
| | Intercept | -46.795 ± 50.13 | 0.373 | |
| | Andrenid density (*t*) | -1.026 ± 0.148 | <0.0001 | |
| | Andrenid density (*t* - 1) | -0.786 ± 0.166 | 0.001 | |
| | Random walk (*t*) | -0.999 ± 0.247 | 0.002 | |
| Megachilids | | | | 0.339 (0.215) |
| | Intercept | -21.109 ± 21.202 | 0.343 | |
| | Megachilid density (*t*) | -0.727 ± 0.292 | 0.032 | |
| | Megachilid density (*t* - 1) | -0.736 ± 0.202 | 0.005 | |
| Halictids and others | | | | 0.237 (0.196) |
| | Intercept | 241.52 6± 77.120 | 0.006 | |
| | Halictid and others density (*t*) | 0.549 ± 0.193 | 0.010 | |
| Total native bee community | | | | 0.073 (0.019) |
| | Intercept | -126.607 ± 151.429 | 0.421 | |
| | Total native bee density (*t*) | 0.624 ± 0.283 | 0.049 | |
| | Random walk (*t*) | 1.002 ± 0.401 | 0.029 | |

model for the Andrenids provided evidence that both 1- and 2-yr time lags (Andrenid bee densities at time *t* and time *t* - 1 for prediction of Andrenid densities at time *t* + 1) and a stochastic random-walk (possibly an abiotic effect) were significant in the community temporal dynamics. The Megachilid community dynamics were also described by 1- and 2-yr time lags, but not a random-walk component, whereas the temporal variance in the Halictid and Others community was only explained by the densities in the previous year (year [*t*]). The 2017 samples from the same field in Winterport suggest that the time-series models for Halictids and Others, Megachilids, and the total bee community described the future predictions for 2017 quite well. The Andrenid time-series model over-predicted density substantially (~27%). We also found that fruit set predicted by the abundances of the wild bee community varies by nearly a 2-fold amount over the study time period (Fig. 3). The coefficient of variation for the total bee community compared to fruit set was 47.9% versus 15.3%, respectively.

## Estimated current climate change effects on bee foraging periods during Lowbush Blueberry bloom

Historical weather data from Maine indicate that bee activity and foraging during the spring bloom period of Lowbush Blueberry is already affected by climate change (Fig. 4). Our estimates of the average number of pollination days, or days in which weather conditions are conducive for bees to visit Lowbush Blueberry

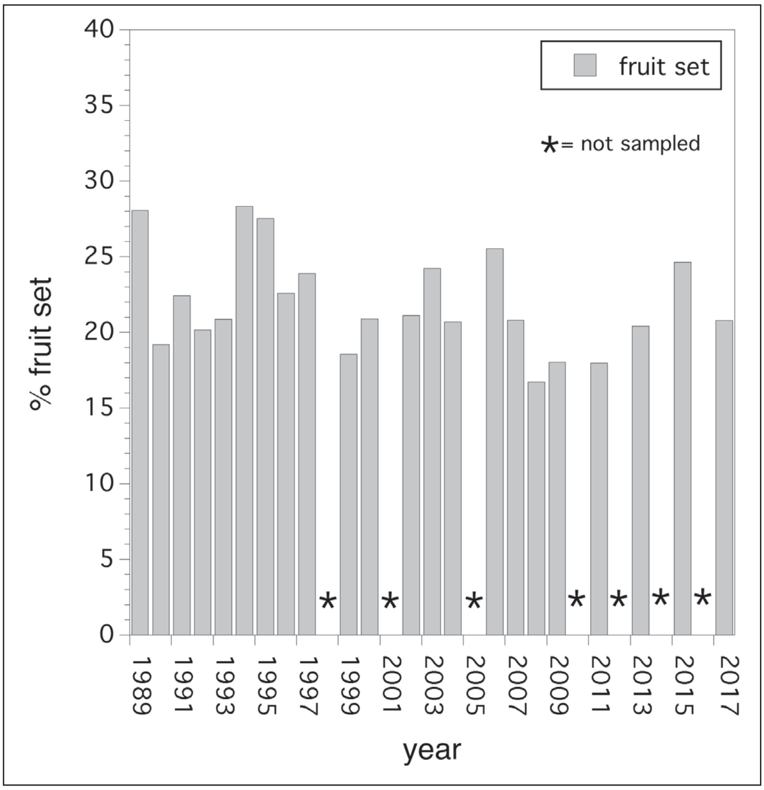

Figure 3. Predicted percent fruit set in Winterport, ME, from 1989 to 2017. The symbol "*" denotes years when sampling was not conducted. The taxa group "others" refers to observed individuals assigned to the families: Colletidae, Apidae (other than *Bombus*), or unidentified individuals.

flowers, for Blue Hill in Hancock County between 1960 and 2015 had no significant change (*P* = 0.993) from 1960 until 1990 (30 years). On any given year, the number of pollination days was estimated from the models to vary from 7 to 25 days. Starting in the early 1990s, average number of pollination days declined at a linear rate (*P* = 0.047) through 2015. The major cause of this trend is the increased spring rainfall during bloom. Validation data (2016 and 2017) were used to assess the mean regression-model prediction for the future years in 2016 and 2017. It can be seen in Figure 4 that the regression model based upon the 1960 to 2015 data, underestimates the 2016 bee foraging days by 12 days, but the 2017 prediction is within 2 days. This result is not unexpected since year-to-year variation in climate change has been demonstrated to be high with only a mean trend being representative of field observations.

## Discussion

### *Osmia* and *Megachile* diversity in Lowbush Blueberry fields

In Maine, deployment of nest blocks has been shown to be both an effective sampling method and a good conservation technique for enhancing *Osmia* abundance (Stubbs et al. 1997a) when combined with a reduction in pesticide exposure (Drummond and Stubbs 1997b). *Osmia* are mostly vernal cavity nesters (Michener 2007), and many Maine species occur in blueberry field habitats, including those documented to pollinate *Vaccinium* (Drummond and Stubbs 1997a). These species nest in pre-existing cavities such as old borer holes or galleries in trees, and use either mud or disks of leaf material that they have cut with their large mandibles

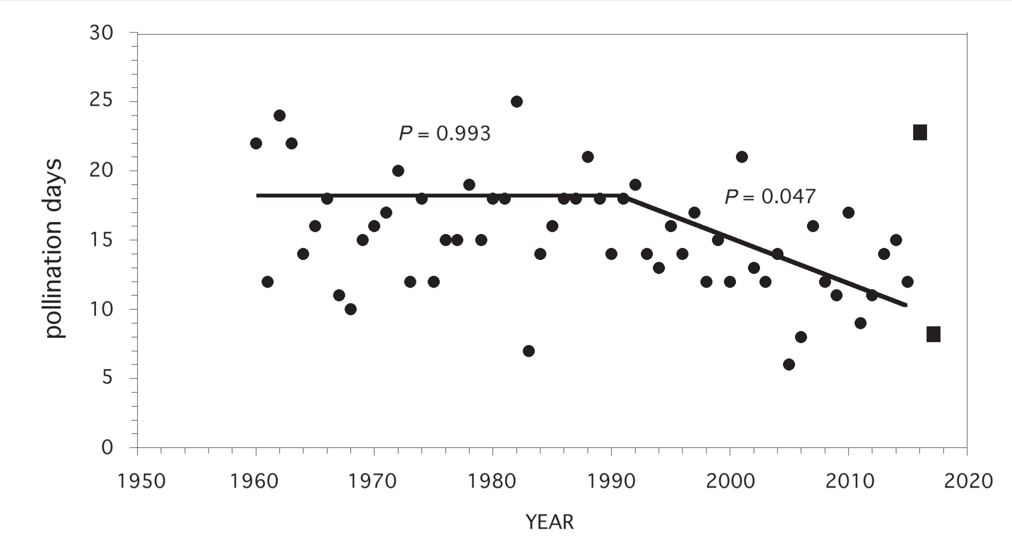

Figure 4. Estimation of the number of bee foraging days during Lowbush Blueberry bloom in Blue Hill, Hancock County, from 1960 to 2015 (piecewise regression used to estimate decline in bee foraging-days over time). Square symbols represent observed validation data from 2016 and 2017.

to construct cell partitions and closures. A total of 16 *Osmia* species have been recorded in Maine (Dibble et al. 2017).

Bushmann and Drummond (2015) found that the 4 most common *Osmia* in blueberry fields sampled are: *O. atriventris*, *O. pumila* Cresson*, O. tersula* Cockerell*,* and *O. inermis* (Zetterstedt) sensu Mitchell (1962), although see Rightmeyer et al. (2010). Currently, *Osmia* specimens collected that have suspect identifications or are in poor condition have been categorized in Figure 2 as "*Osmia* spp.". Some, or possibly all, Maine specimens housed in the Maine State Museum should be checked regarding *O. laticeps* Thomson, a species overlooked by regional workers prior to Rightmyer et al. (2010). Inspection of Figure 1A suggests that overall there is little evidence of significant decline in the relative abundances of the most common species of *Osmia* over the past 25 years, with the exception of the less abundant *O. albiventris* Cresson and *O. virga* Sandhouse. This finding bodes well for Maine blueberry growers because *Osmia atriventris* and other *Osmia* spp. are effective pollinators of Lowbush Blueberry (Drummond 2016, Javorek et al. 2002) and any major decline in their numbers might have implications for the Lowbush Blueberry farming community. However, if the absolute abundance of native *Osmia* spp. is in decline (see Fig. 2), we have evidence from only a single Lowbush Blueberry field, and so at this point assessment of mason bee health would need to be conducted over a broader geographic range. Non-native *Osmia* species were not found in Maine during the sampling years, although *Osmia cornifrons* (Radoszkowski) is now abundant farther south in New England and was recently reported from New Hampshire (Tucker and Rehan 2016). *Osmia cornifrons* was introduced into the Northeast from East Asia for pollination (Yamada et al. 1971).

Information on the diversity and abundance of *Megachile* is not as available for Maine as for *Osmia* in the region. In large part this lack of data might be due to phenology. The most intensive sampling for Megachilidae in Maine has been in Lowbush Blueberry fields (Dibble et al. 2017). It is our experience that *Megachile* species occur toward the end of Lowbush Blueberry bloom and increase during the summer (Bushmann and Drummond 2015, Chandler et al. 2012). Thirteen *Megachile* species have been reported from Maine (Dibble et al. 2017), including 2 species, *Megachile brevis* Say and *M. latimanus* Say*,* that were absent from our collection in the 1990s, possibly reflecting population abundance oscillations over time. *Megachile mucida* Cresson was found abundantly in the 1990s, but was not found in 2010–2012 (Fig. 1B). This finding might suggest that this species is in decline in Maine. We are not aware of any recent reports on its occurrence, although it has been reported in southern New England recently (Ascher and Pickering 2016). Therefore, *M. mucida* may not be in decline throughout New England. The non-native *M. rotundata* was not found in 2010–2012, even though it was introduced in the early 1990s (Stubbs and Drummond 1997a, 1997b). This finding suggests that this species might not have become established in Maine or if it was, has since disappeared. This is understandable as *M. rotundata* is not a cold-tolerant bee species, based upon studies conducted in Orono, ME, during the early 1990s (Stubbs and Drummond 1997b).

If we were to speculate a cause for a potential decline in the Megachilidae as a whole or for select species, 2 factors other than climate change come to mind. The increase in the importation of migratory Honey Bee colonies for blueberry pollination in Maine could have resulted in increased competition for floral resources or spillover of pathogens that might have been virulent to Megachildae. Another factor might have been the brief period of time in the early 1990s when the Alfalfa Leafcutting Bee was introduced for blueberry pollination. This might have resulted in undetected introduction of pathogens adapted to native Megachilidae or resulted in competition for forage or nest sites in the wild. None of these speculative causes, however, can be supported by evidence derived from data.

## A long-term temporal study of a native bee community in Lowbush Blueberry

Annual fluctuations in bee communities have not been well studied in Maine (Bushmann and Drummond 2015, Venturini et al. 2017b). It is not surprising that the individual taxa groups result in better model fits considering the diverse mixture of life-history patterns (e.g., bumble bees are eusocial, living in colonies, whereas all others are solitary or might have connecting tunnels, as is the case for *Andrena* spp.; Dibble et al., in press). The dynamics of the individual taxa groups show strong evidence of density dependence, especially in both Andrenids and Megachilids with a second-order model ($t$ [1-year] and $t$ - 1 [2-year] lags; Table 1). Royama (1992) has shown that these dynamics are typical in insect populations that are regulated by parasitoids and pathogens. This finding, therefore, in the Maine bee community is not surprising as disease and parasites are common in the bee taxa we observed (Batra et al. 1973, Brown and Paxton 2009, Hedtke et al. 2015) and kleptoparasites can make up 10–20% of the bee fauna in Maine (Dibble et al. 2017). Floral abundance, represented both as managed pollinator reservoirs (Venturini et al. 2017b) and natural wildflower communities along Lowbush Blueberry field edges (Drummond et al. 2017, Stubbs et al. 1992), has been shown to increase native bee abundance. Venturini and Drummond (in press) have provided evidence of farm-management effects: biennial fluctuations in *Andrena* spp. in blueberry fields that are geographically isolated and managed on a single cycle (i.e., the entire field is either fruit bearing or vegetative in a given year) have been demonstrated to result in lower *Andrena* spp. abundances. Figure 5 shows the model predictions for the taxa groups and forward predictions up to and including the year 2020. In general, the model predictions represent the fluctuations in the observed abundances well for the specific taxa groups, except for the total native bee community model predictions (Fig. 5D). The model predictions suggest that long-term and future abundances are stable for Andrenids as well as Halictid and Others. The Megachilids show a decline without recovery since 2006. This decline over time of an entire taxon group is supported by the findings of Bartomeus et al. (2013), who suggest that species with shared ecological traits, as many sepcies of the Megachilids do, may decline together. Three of the 4 models showed high similarity for the future prediction of 2017 with sample data collected for the purpose of validation, suggesting that the mechanisms of density dependence and independent stochastic factors, such as weather events, driving community abundance fluctuations might be a reasonable hypothesis. The decline in Megachilid abundance is addressed below in the section on potential climate change.

The rate of fruit set estimated for the 29-year period by use of the formula developed by Asare et al. (2017) is typical for what is expected from background pollination by native bees in the absence of Honey Bees in Lowbush Blueberry fields (Stubbs and Drummond 1997c). Estimated fruit set appears to be highly buffered from major changes in the native bee community. This is an important dynamic because it suggests that the redundancy in the native bee pollination network due to bee species composition (Bushmann and Drummond 2015) and varying foraging behavior and pollination efficiency (Drummond 2016) provides resiliency in pollination level to changes in bee abundance over time. We speculate that this result is due to redundant floral visitation by bees during bloom. Most bee species probably do not recognize previously visited flowers, such has been documented for some species of bumble bees (Goulson et al. 1998), and so

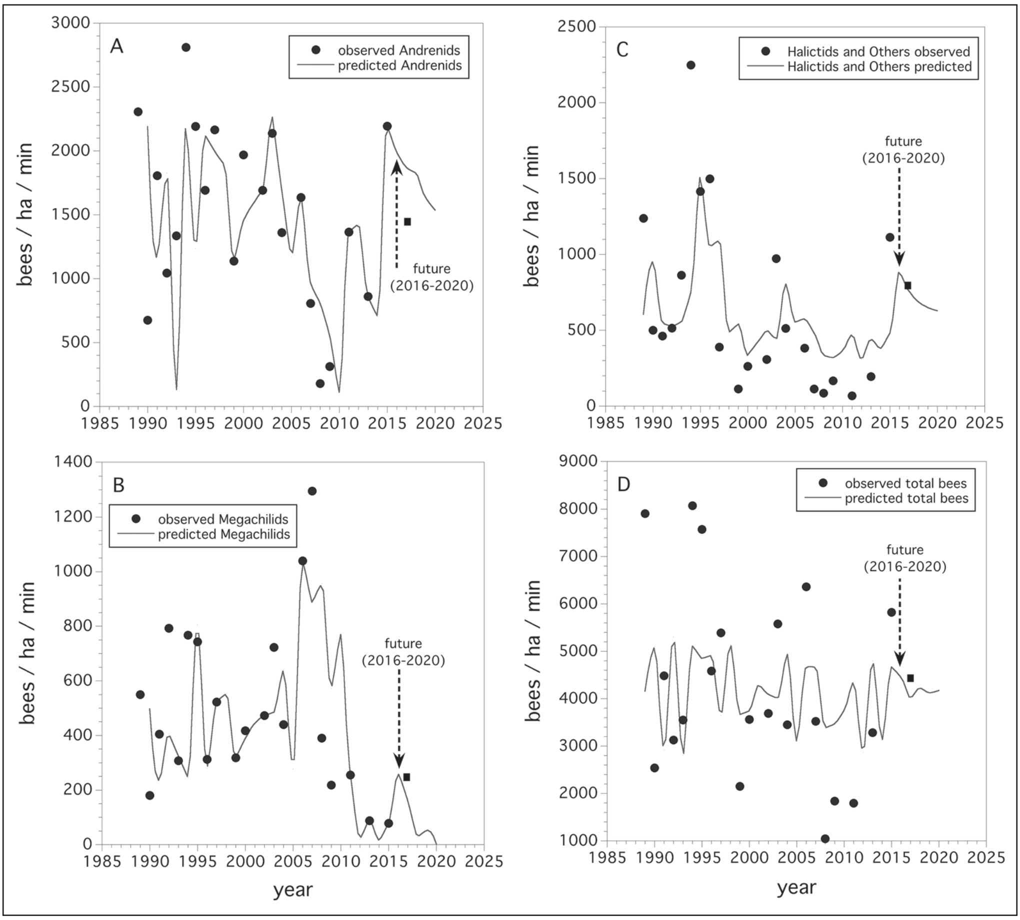

Figure 5. Model predictions of taxa group and total native bee community over a 27-year time period in Winterport, ME. (A) andrenids, (B) megachilids, (C) halictids and others, (D) total bee community density observed. Dashed arrow denotes forward prediction of bee abundance from 2017 to 2020, square symbols denote 2017 validation samples.

multiple visits in excess of what is necessary for fruit set is probably characteristic of the Lowbush Blueberry system. The same may not be true of yield, as higher rates of pollen deposition result in more fertilized ova per flower and higher numbers of seeds per fruit, and larger fruit is a consequence of higher numbers of seeds per fruit (Bell et al. 2010).

### Estimated current climate-change effects on bee foraging periods during Lowbush Blueberry bloom

Climate change and in particular hotter summer temperatures may already be resulting in significant changes to bumble bee distributional ranges in Maine and elsewhere (Kerr et al. 2015). Climate change appears to affect not only bee species shifts, but also the flowering phenology for plant communities that they depend upon (Bartomeus et al. 2011). It has been speculated that climate change will result in wetter conditions in northeastern North America (Campbell et al. 2009). Rainy springs and summers could detrimentally affect bees of Maine and other regions of northern New England in several ways: (1) upset a synchrony between bloom period for host plants and active period for native bees (but see Bartomeus et al. 2011), (2) limit good weather conditions for foraging with the result that insects are unable to provision brood for subsequent generations, and (3) increase conditions that enhance fungal infections in soil-nesting bees (Batra et al. 1973).

With climate change, our results suggest that in the future Lowbush Blueberry growers will experience fewer days in which pollinators visit flowers in their fields compared to 30 years ago (Fig. 4). This has potential implications for food-resource acquisition by female bees during this time and possibly long-term bee population dynamics because the females are provisioning their brood for the next generation. Even during the decline period, there have been years with good pollination windows, such as 2016 (Fig. 4). It remains to be seen whether a limit to the number of bee-foraging days in the spring will affect bee survival and reproduction. Among Maine bees, we know of relatively few that demonstrate host-plant specificity, although ~15% of northeastern US bee species have been classified as pollen specialists (Fowler 2016, but compare pollen forage with same species in Stubbs et al. 1992). However, most bee species of temperate zones forage on a wide number of plant species depending on what may be in flower. This fact does not diminish the severity of a proposed lack of synchrony between bee emergence and flowering of host plants. In such a scenario, bees emerge from their nests according to influences such as soil temperature that differ from those that trigger phenology in their host plants (e.g., day length, weather and climate cues, depth of frost in winter, rainfall in the previous growing season). Thus, there is potential for bees to have inadequate or suboptimal nectar and pollen resources (Miller-Rushing and Primack 2008). However, it appears that bees respond less variably than do their plant forage species (Bartomeus et al. 2011).

In conclusion, the results of our 3 long-term studies in Maine provided evidence for changes in native bee community dynamics as well as the potential influence of climate change on those shifting dynamics. Our first study suggests that *Osmia* bees might be more stable and resistant to change than *Megachile* bees. Bartomeus et al.

(2013) showed through a survey of museum specimens that bee species are in flux, with some species increasing in abundance, some in decline, and most maintaining their long-term abundances. Maine has more species of *Osmia* than *Megachile* (Dibble et al. 2017), and our data suggest that richness has been more variable in *Megachile* until recently, but if *Osmia* abundance is in decline, as seen in Figure 5B, then an intensive survey is required in Maine to determine if *Osmia* are suffering from climate change.

In our second study, our 29-year data from Winterport, ME, indicate that the taxa we measured, except *Osmia,* appear to be characterized at a single location by stable abundance over time, but can fluctuate dramatically from year to year. Our data suggest that the drivers might be density-dependent factors such as pathogens or parasites in concert with a potential suite of stochastic density-independent factors. However, one density-dependent factor also playing a role in bee community dynamics could be floral resources, which have been shown to be directly and indirectly related to native bee abundance in Maine (Bushmann and Drummond 2015, Drummond et al. 2017, Groff et al. 2016, Venturini et al. 2017b). When bees congregate at a patch of flowers, they might contract pests or diseases from other floral visitors, and this is another factor. Parasites and pathogens are certainly common in native bee communities (Bushman et al. 2012, Cameron et al. 2011, Goulson et al. 2015). Management of parasites and pathogens is not practical in most cases, whereas floral resources can be managed both locally and regionally (Groff et al. 2016; Venturini et al. 2015, 2017a). Response to density of floral resources and to parasites/pathogens is one of the main hypotheses regarding bumble bee species range shifts and decline in abundance in North America and Europe (Kerr et al. 2015).

Abiotic factors such as climate should also not be ruled out, as suggested by our time-series modeling and pollinator-day “window” modeling. Is the decline in *Osmia* abundance since 2005 a result of climate change and wetter springs? This is unknown, but should be put forth as a viable hypothesis. Wet springs might differentially affect *Osmia* in 2 ways. First, we have observed that *Osmia* cease foraging on overcast days (Drummond and Stubbs 1997a). This finding suggests that *Osmia* might not use polarized light for navigation back to the nest as many bees do (Rossel 1993). Second, a significant disease of *Osmia* bees in Maine can be due to fungi of the genus *Ascosphera* (Batra et al. 1973, Drummond and Stubbs 1997a). Fungal diseases of insects are often enhanced by cool, wet weather (Tanada and Kaya 2012).

Our third study adds evidence that climate change is already occuring in Maine. The number of days for spring bees to forage on Lowbush Blueberry flowers has been declining since the early 1990s. Lowbush Blueberry farmers are already aware of this (F.A. Drummond, unpubl. data). They have continued to import an increasing number of Honey Bees (from about 25,000 colonies in 1990 to more than 74,000 in 2013 and to more than 80,000 in 2015; Drummond 2012, Yarborough 2009). The reason for the increase in Honey Bee importation has been due to Lowbush Blueberry growers attempting to reduce risk of crop loss if a wet spring occurs, resulting in fewer days for bees to visit flowers, but the same number of flowers to set into fruit (F.A. Drummond, unpubl. data). Therefore, increasing rain during bloom is costing farmers financially, but is it affecting native bees? One might expect that it would because the provisioning of immatures by female bees might be reduced due to less time available for food-resource foraging or potentially a more complex interaction involving competition with Honey Bees.

Some of these changes in bee abundances might be addressed through emphasis on habitat improvement. For growers of Lowbush Blueberry, that will include adding floral resources to sustain bees near the crop even in the prune year (when no crop flowers are available) and minimizing pesticide exposure (Goulson et al. 2015, Grixti et al. 2009, Venturin et al. 2017a).

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