

# Modeling the status, trends, and impacts of wild bee abundance in the United States

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Wild bees are highly valuable pollinators. Along with managed honey bees, they provide a critical ecosystem service by ensuring stable pollination to agriculture and wild plant communities. Increasing concern about the welfare of both wild and managed pollinators, however, has prompted recent calls for national evaluation and action. Here, for the first time to our knowledge, we assess the status and trends of wild bees and their potential impacts on pollination services across the coterminous United States. We use a spatial habitat model, national land-cover data, and carefully quantified expert knowledge to estimate wild bee abundance and associated uncertainty. Between 2008 and 2013, modeled bee abundance declined across 23% of US land area. This decline was generally associated with conversion of natural habitats to row crops. We identify 139 counties where low bee abundances correspond to large areas of pollinator-dependent crops. These areas of mismatch between supply (wild bee abundance) and demand (cultivated area) for pollination comprise 39% of the pollinator-dependent crop area in the United States. Further, we find that the crops most highly dependent on pollinators tend to experience more severe mismatches between declining supply and increasing demand. These trends, should they continue, may increase costs for US farmers and may even destabilize crop production over time. National assessments such as this can help focus both scientific and political efforts to understand and sustain wild bees. As new information becomes available, repeated assessments can update findings, revise priorities, and track progress toward sustainable management of our nation's pollinators.

crop pollination | ecosystem services | habitat suitability | land-use change | uncertainty

**B**ees and other flower-visiting animals provide essential pollination services to many US crops (1) and to wild plant species (2). Bees contributed an estimated 11% of the nation's agricultural gross domestic product in 2009 (3), equal to \$14.6 billion per year (4). Of this, at least 20% (\$3.07 billion) is provided by wild pollinators that depend on suitable land for nesting and foraging (5). As the consumption of specialty fruit and vegetable crops has grown (6), the demand for pollination services has increased. However, the supply of managed honey bees (*Apis mellifera* L.) has not kept pace (7), due to management challenges and colony losses over the last decade (8). There is growing evidence that wild, unmanaged bees can provide effective pollination services where sufficient habitat exists to support their populations (9, 10). They can also contribute to the long-term stability of crop pollination, thereby reducing the risk of pollination deficits from variable supply or activity of honey bees (11, 12). As a result, wild pollinators should be integrated into crop pollination management plans as a supplement or alternative to managed bees (13).

Despite the agricultural importance of wild bees, there is increasing evidence that multiple species are declining in range or abundance. Some of the most important crop pollinators, such as bumble bees (*Bombus* spp.), have declined over past decades in the United States (14–16). Among the numerous threats to wild bees, including pesticide use, climate change, and disease (17), habitat loss seems to contribute to most observed declines (18).

Indeed, a National Research Council committee on the status of pollinators in North America reported that conserving and improving habitats for wild bees is important for ensuring continued pollination services and food security (19).

Recognizing both the growing need for pollination services and increasing threats to wild bees, a recent presidential memorandum called for a national assessment of the status of wild pollinators and available habitat in the United States (20). The resulting report sets a goal of 7 million acres of land for pollinators over the next 5 y (21). However, there has been no assessment at the national level of the current status of native pollinator habitat, where and at what rate this habitat is being degraded, and the impact of these changes on bee populations and the pollination services they provide.

A national assessment is challenging because plant–pollinator interactions and dynamics occur at relatively fine spatial scales. Wild bee populations are largely determined by the spatial distribution of habitat resources within their foraging range (22–24), and this varies from ~100–2,000 m (25, 26). Accordingly, most of our understanding of native bee populations is at the scale of landscapes and local sites. Several field-based assessments of habitat resources for native bee species have been developed at landscape scales (23, 27–29). However, the required cost and time to scale this type of field assessment to cover all habitat types and bee species nationwide is logistically challenging and prohibitively expensive.

When field observations are lacking, careful use of expert-derived data has been shown to provide informative estimates that enable habitat assessments (30, 31), including studies on

## Significance

**In 2014, a presidential memorandum called for an assessment of the nation's pollinators, in response to growing awareness of their economic importance and recent declines. We assess, for the first time to our knowledge, the status and trends of wild bee abundance and their potential impacts on pollination services across the United States. We develop national maps of wild bee abundance, report land-use-driven changes over time, and relate them to trends in agricultural demand for pollination. We estimate uncertainty in the findings, so future research can target the least-understood regions and topics. Our findings can also help focus conservation efforts where declines in bee abundance are most certain, especially where agricultural demand for pollination services is growing.**

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Dr. Mogren's unpublished bee observation data has been deposited online at [figshare.com/s/e865f26c9a9e11e5b86e06c4b8d1f61](https://figshare.com/s/e865f26c9a9e11e5b86e06c4b8d1f61).

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are about higher-quality habitats (e.g., shrublands), which can vary in quality over time and space (*Discussion*).

Between 2008 and 2013, wild bee abundance was consistent in 67% of the US land area ( $-0.01 < \text{index change} < 0.01$  in Fig. 1C). However, our model indicates decreases in 23% of the United States (index change  $< -0.01$ ), and these decreases were highly likely in 9% of the United States (likelihood index  $\leq -0.2$  in Fig. 1C; *Methods*). Most of the areas of likely decrease occurred in agricultural regions of Midwestern and Great Plains states and in the Mississippi river valley. Eleven states [Minnesota, Texas (TX), Wisconsin (WI), South Dakota (SD), North Dakota (ND), Illinois, Missouri, Nebraska, Oklahoma, Kansas, and Louisiana] collectively accounted for 60% of the areas of predicted decrease in wild bee abundance. Over the 5-y period in these states, corn and grain cropland increased 200% and 100%, respectively, and mostly replaced grasslands and pasture (Fig. 2A and Fig. S14). Bee abundance increased in 10% of the United States (index change  $> 0.01$ ) and the increase was highly likely in 3% of the country (likelihood index  $\geq 0.2$  in Fig. 1C). Areas of likely increase in bee abundance were found in northern ND, eastern Washington (WA) and Pennsylvania (PA), southern Montana, parts of several states in the Great Plains, and in southeastern coastal areas (Fig. 1C). In these areas, grasslands, pastures, and corn/soy fields were converted to higher-quality habitat, such as shrublands or fallow crop fields (Fig. 2B and Fig. S1B).

**Pollination Supply and Demand.** Bee abundance maps (Fig. 1A) can be interpreted as the potential “supply” of pollination services from wild bees. To compare this measure of supply to potential agricultural demand, we calculated the area of pollinator-dependent crops, weighted by each crop’s degree of pollinator dependence, for each US county in 2013 (*Methods*). By comparing the two maps, we identified counties with relatively high supply of wild bees and relatively low demand (Fig. 1D, light blue) and, conversely, where high demand occurs in counties with relatively low supply (Fig. 1D, purple). We identified 139 counties (which together comprise 39% of pollinator-dependent crop area) where high demand and low supply coincide (Fig. 1D, yellow outline) and 39 counties where this difference was particularly extreme (Fig. 1D, red outline). All of the 139 counties with a pollinator disparity had relatively low uncertainty for 2013 bee abundance (Fig. 1E), which indicates that there is high confidence in this mismatch. These counties tend to contain either a significant percentage of area that consists of highly pollinator-dependent crops [e.g., almonds, blueberries, and apples

in California (CA), Oregon, and WA, respectively] or large amount of less-dependent crops (e.g., soybeans and canola in Midwestern states, cotton in northwest TX and the Mississippi Valley).

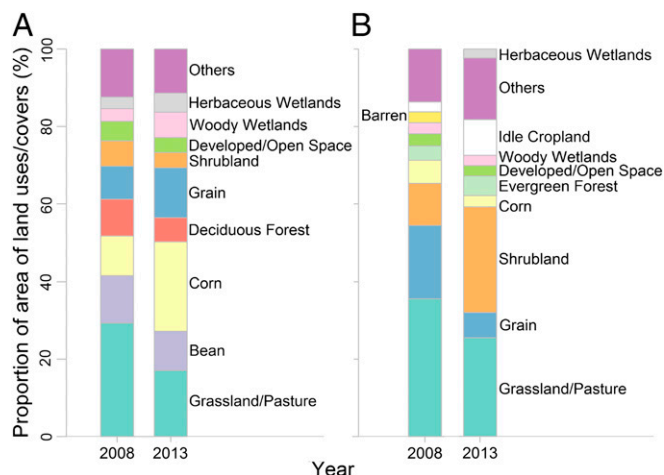
To examine changes in the relationship between wild bee supply and pollination demand, we combined the two trend maps (*Methods*). We found that 106 counties have simultaneously experienced increases in demand for pollination services and decreases in wild bee abundance (Fig. 1F, upper left quadrant). This represents 54% of the 195 counties that have experienced substantial changes in pollination demand ( $>500$  ha of change). In 27 of these counties, declines in supply were highly likely (zone I in Fig. 1F legend), whereas in the remaining 79 counties declines were less certain (zone II in Fig. 1F legend). In counties of West Coast states and Michigan, increases in demand were mostly driven by increases in specialty crops such as almonds, cherries, blueberries, apples, watermelons, and squash. In contrast, demand increases in the Great Plains and Mississippi Valley were driven by increases in crops, such as sunflower, canola, soybeans, and cotton, with moderate to low pollinator dependency.

Trends in our measures of supply and demand vary widely among individual crops (Fig. 3). Most crops that require animal pollination have expanded in area (thus demand) between 2008 and 2013, whereas the predicted supply of wild bees in many of these cropped areas has declined. Specialty crops, such as pumpkins, blueberries, peaches, apples, and watermelons, are among the crops that present the strongest mismatch between changes in supply and demand. Others, such as canola, have experienced increases in both supply and demand. Of particular concern for future abilities to meet pollination demands, crops that are most dependent on pollinators (symbols in Fig. 3) tend to have experienced simultaneous declines in supply and increases in demand.

## Discussion

Our study is the first to our knowledge to map the status and trends of wild bees and their potential impacts on pollination services across the coterminous United States. By combining a spatial model with expert knowledge, we find highly heterogeneous patterns of both predicted abundance of wild bees and our uncertainty regarding those predictions. We also identify counties and crops of potential concern, where declines in wild bee abundance oppose increased need for crop pollination. These analyses form an important step toward a nationwide understanding of the status of wild pollinators. They can also help focus attention and future research toward regions of high uncertainty and to direct management efforts to areas of major concern.

Our mapped index of bee abundance (Fig. 1A) clearly shows that areas of intense agriculture (e.g., the Midwest Corn Belt and California’s Central Valley) are among the lowest in predicted wild bee abundance. Our predictions are also relatively certain in these areas (Fig. 1B). This reflects consensus among experts about the low suitability of intensively managed agricultural land for wild bees and is supported by an abundance of previous research on the negative effects of intensive agriculture on bee populations (37, 38). Recent trends (Fig. 1C) also correspond to increasing agricultural land use over time. Areas of bee abundance where declines are most certain tend to have experienced additional conversion of natural land covers to crops, especially corn (Fig. 2A). These results reinforce recent evidence that increased demand for corn in biofuel production has intensified threats to natural habitats in corn-growing regions (39). For example, a recent land-use simulation found that expansion of annual biofuel crops could reduce pollinator abundance and diversity at the state level (40). In areas where major land-use changes have gone in the opposite direction, however, bee abundance has tended to increase (Fig. 2B). These changes may represent detectable effects from the US Department of Agriculture Conservation Reserve Program, which compensates farmers for retiring marginal lands (41). Given the clear patterns in Fig. 1A–C, supported by other studies at finer spatial scales, this initial assessment can help set management priorities (e.g., habitat restoration or enhancement) to maintain populations of wild bees and other wildlife amid agricultural intensification (42, 43).



**Fig. 2.** Changes in land-use/cover corresponding to predicted changes in wild bee abundance. Bars represent land cover in pixels where decreases (A) and increases (B) of wild bee abundance are highly likely between 2008 and 2013 (i.e., bee abundance changes  $< -0.01$  or  $> 0.01$  and the likelihood of changes  $\leq -0.2$  or  $\geq 0.2$  in Fig. 1C, respectively).





compared with averaged parameters (Fig. S3B). Although we have focused on bees, other taxa can be important crop pollinators (52). For simplicity in this initial nationwide assessment, we have also pooled all bee species into an overall abundance index, but bee taxa clearly vary in their importance as crop pollinators and their response to land use (53). Future work should distinguish pollinator taxa or guilds to model the trends and importance of each separately.

Beyond these uncertainties, three additional caveats deserve mention. First, our assessment is based on a simple landscape model that predicts relative abundance of bees based on nesting resources, floral resources, and foraging distance. Although this model has proved to be informative in a variety of settings (32, 33, 54), it neither captures abundances of individual bee species nor reports visitation rates, pollination efficiency, or other variables important for realized pollination services. Second, although the model validation explained significant amounts of variance in field data, substantial variance remained unexplained. Clearly, other factors influence bee abundance in landscapes, but this study is intended as an initial national assessment of wild pollinators in general. Third, we evaluate trends over only 5 y; analysis of longer-term changes in both wild bee populations and land cover will provide a more robust assessment.

This first national assessment of status and trends of wild bee abundance will be valuable as a response to the recent federal mandates (20, 21) to direct additional research and management attention toward pollinators. A national program to detect future changes in bee populations has been estimated to cost \$2,000,000 (55) and to require 5–10 y. Our national assessment can be used to focus such a costly effort, targeting bee and habitat surveys on regions that show high uncertainty, especially where agricultural demand for pollination services is high. Counties with mismatched levels of relative pollinator “supply” and “demand” warrant priority efforts to conserve and restore habitats for pollinators as well as other actions that can affect bees. As such efforts proceed, national assessments can be repeated with new information to update estimates, revise priorities, and track progress toward sustainable management of our nation’s wild pollinators.

## Methods

**Pollination Model.** The spatially explicit model of wild bee abundance (ref. 32; hereafter, the Lonsdorf model) generates an index of relative bee abundance at each spatial unit (e.g., map pixel). The model assumes that bees forage from a nest site to acquire floral resources in the surrounding landscape and the probability of acquiring resources declines exponentially with increasing distance between the nest site and floral resources. The model also assumes that nesting and floral resources vary among land-cover types in the landscape. To apply these model assumptions to the United States and evaluate their accuracy, we needed to identify a standard land-cover map, estimate the nesting and floral resources of each land cover, and validate the predictions with observations.

**Data Sources.** We used the CDL (30-m resolution) to provide land-use and -cover types. This is the only such dataset produced annually at the national scale by the National Agricultural Statistics Service (NASS) since 2008. We reduced the number of crop cover types from over 100 to 32 representative categories based on shared crop characteristics and we retained 13 noncrop categories that are derived from the National Land Cover Database (Table S1). Based on a synthesis study (26), we applied an average foraging distance (670 m) of temperate wild bees as an input parameter for the forage distance function in the model.

**Expert Opinion of Nesting and Floral Resources.** For each of the reclassified 45 land-use categories, a panel of 14 experts evaluated nesting suitability for four bee nesting guilds (ground, cavity, stem, and wood) and floral resource availability for three foraging seasons (spring, summer, and fall). Experts selected one of five options to represent nesting suitability or floral resource production (0.05, 0.25, 0.5, 0.75, or 0.95). For floral resources they selected the proportion of each 12-wk season in which the cover produced such resources (1–12 wk). For each estimate, panel members also specified one of four levels of certainty (none, low, medium, or high; *SI Methods, Expert Survey and Table S2*). We represented experts’ estimates and uncertainties as a continuous beta probability distribution (hereafter “*pd*”; *SI Methods, Determining Final Probability Distribution of Resource Suitability*). Ultimately we generated a single

nesting suitability *pd* by summarizing across all experts and nesting guilds, and a floral resource *pd* in the same manner using floral seasons (*SI Methods, Determining Final Probability Distribution of Resource Suitability* and Fig. S5).

**Modeling and Uncertainty.** The expert-informed probability distributions (*pds*) of nesting and floral resources for all land-use categories of the CDL were used as input parameters of the Lonsdorf model to predict a relative index (0–1) of wild bee abundance at each parcel of land (120 m × 120 m, one pixel). Because these input parameters are probability distributions, we can also express the bee abundance index as a probability distribution. We used Monte Carlo (MC) simulation to estimate the mean and SD for bee abundance at each parcel. These may be interpreted as the best estimate and the uncertainty of the index. Modeling uncertainty with probability distributions, however, bounds the uncertainty (measured as SD) possible for low and high estimates. This tends to result in greater estimates of uncertainty for moderate parameter values (Fig. S4), where bounding effects are not as important (30).

**Model Validation.** We validated the model prediction and its uncertainty with field data of wild bee abundance. We used several data sets (*SI Methods, Validation Data*). All wild bees were observed at 180 sites on crop fields and seminatural and natural areas in six states between 2008 and 2013 (12, 56–60). We also used a separate data set of bumble bees at 343 sites along roadsides in 40 states between 2008 and 2009 (15). We compared the model predictions based on expert-derived parameters and CDL corresponding to the year in which data were collected with the field data. Through the extensive model validation process, we verified that predicted bee abundance and its uncertainty respect current knowledge on wild bees (*SI Methods, Model Validation Process* and Fig. S3).

## Mapping Status and Trends.

**Status.** We used the expert-informed probability distributions (*pds*) and 2013 CDL as inputs to the Lonsdorf model to generate maps of the mean and uncertainty of bee abundance at 120-m resolution across the coterminous United States. For each pixel, we approximated the mean abundance index using the means of expert-informed *pds* and we represented uncertainty by estimating the SD of bee abundance indices again by using the expert-informed *pds* (*SI Methods, Estimation of Mean and SD* and Fig. S6). We recognize that model uncertainty may also have other sources, including the accuracy of classification for land-cover maps, but an examination of these effects on model uncertainty was beyond the scope of this study.

**Trends.** We assessed trends in wild bee abundance as the differences in the mean bee abundance index between 2008 and 2013. To assess the uncertainty of trends, we calculated a pseudo-*t* value of the difference, by dividing the mean difference between the two years by the variation of the difference using the SD estimate for the two years (*SI Methods, Likelihood of Index Change*). High positive or negative values in the likelihood of change indicate a high likelihood of increase or decrease in the mean wild bee abundance index, respectively. Finally, we examined which land-use changes occurred in the counties whose predicted bee abundance changed the most, whether the abundance increased or decreased.

**Supply and Demand Analysis.** We summarized the supply as the relative abundance of wild bees for each US county by averaging the bee abundance index and its uncertainty for all pixels within that county (*SI Methods, Supply Assessment*). We analyzed supply separately for 2008 and 2013. To assess the demand for pollination in each US county in 2008 and 2013, we summed the dependency-weighted area of all pollinator-dependent crops (49) for that county (*SI Methods, Demand Assessment* and Table S1). To assess the current status of supply and demand and to identify those counties with relatively low supply and high demand, we compared the average bee abundance with the dependency-weighted crop area. We also identified counties with relatively high uncertainty in the supply. To assess the trends in supply and demand between 2008 and 2013, we compared the likelihood of changes in bee abundance and the dependency-weighted crop area (*SI Methods, Likelihood of Changes in Supply*). Finally, we analyzed the trend of supply and demand for individual crops by comparing the likelihood of changes from 2008 to 2013 in wild bee abundance and dependency-weighted crop area across the entire coterminous United States.

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- Winfree R, Williams NM, Gaines H, Ascher JS, Kremen C (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J Appl Ecol* 45(3):793–802.
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120(3):321–326.
- Lautenbach S, Seppelt R, Liebscher J, Dormann CF (2012) Spatial and temporal trends of global pollination benefit. *PLoS One* 7(4):e35954.
- Morse RA, Calderone NW (2000) The value of honey bees as pollinators of U.S. crops in 2000. *Bee Culture* 128:1–15.
- Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. *Bioscience* 56(4):311–323.
- Calderone NW (2012) Insect pollinated crops, insect pollinators and US agriculture: Trend analysis of aggregate data for the period 1992–2009. *PLoS One* 7(5):e37235.
- Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr Biol* 19(11):915–918.
- Steinhauer NA, et al. (2014) A national survey of managed honey bee 2012–2013 annual colony losses in the USA: Results from the Bee Informed Partnership. *J Apic Res* 53(1):1–18.
- Winfree R, Williams NM, Dushoff J, Kremen C (2007) Native bees provide insurance against ongoing honey bee losses. *Ecol Lett* 10(11):1105–1113.
- Garibaldi LA, et al. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339(6127):1608–1611.
- Brittain C, Kremen C, Klein AM (2013) Biodiversity buffers pollination from changes in environmental conditions. *Glob Change Biol* 19(2):540–547.
- Rader R, Reilly J, Bartomeus I, Winfree R (2013) Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Glob Change Biol* 19(10):3103–3110.
- Kremen C (2005) Managing ecosystem services: What do we need to know about their ecology? *Ecol Lett* 8(5):468–479.
- Grixti JC, Wong LT, Cameron SA, Favret C (2009) Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol Conserv* 142(1):75–84.
- Cameron SA, et al. (2011) Patterns of widespread decline in North American bumble bees. *Proc Natl Acad Sci USA* 108(2):662–667.
- Bartomeus I, et al. (2013) Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc Natl Acad Sci USA* 110(12):4656–4660.
- Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347(6229):1255957.
- Potts SG, et al. (2010) Global pollinator declines: Trends, impacts and drivers. *Trends Ecol Evol* 25(6):345–353.
- Committee on the Status of Pollinators in North America, National Research Council (2007) *Status of Pollinators in North America* (National Academy, Washington, DC).
- The White House (2014) Presidential memorandum – Creating a federal strategy to promote the health of honey bees and other pollinators (The White House, Washington, DC).
- Pollinator Health Task Force (2014) *National strategy to promote the health of honey bees and other pollinators* (The White House, Washington, DC).
- Roulston TH, Goodell K (2011) The role of resources and risks in regulating wild bee populations. *Annu Rev Entomol* 56:293–312.
- Williams NM, Regetz J, Kremen C (2012) Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology* 93(5):1049–1058.
- Rundlof M, Persson AS, Smith HG, Bommarco R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biol Conserv* 172:138–145.
- Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia* 153(3):589–596.
- Ricketts TH, et al. (2008) Landscape effects on crop pollination services: Are there general patterns? *Ecol Lett* 11(5):499–515.
- Hines HM, Hendrix SD (2005) Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: Effects of local and landscape floral resources. *Environ Entomol* 34(6):1477–1484.
- Carvell C, et al. (2011) Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecol Appl* 21(5):1760–1771.
- Sardiñas HS, Kremen C (2014) Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic Appl Ecol* 15(2):161–168.
- Lee GM, Molen D, Boogaard HP, Klis H (2006) Uncertainty analysis of a spatial habitat suitability model and implications for ecological management of water bodies. *Landscape Ecol* 21(7):1019–1032.
- O'Neill SJ, Osborn TJ, Hulme M, Lorenzoni I, Watkinson AR (2008) Using expert knowledge to assess uncertainties in future polar bear populations under climate change. *J Appl Ecol* 45(6):1649–1659.
- Lonsdorf E, et al. (2009) Modelling pollination services across agricultural landscapes. *Ann Bot (Lond)* 103(9):1589–1600.
- Kennedy CM, et al. (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol Lett* 16(5):584–599.
- Johnson CJ, Gillingham MP (2004) Mapping uncertainty: Sensitivity of wildlife habitat ratings to expert opinion. *J Appl Ecol* 41(6):1032–1041.
- Murray JV, et al. (2009) How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. *J Appl Ecol* 46(4):842–851.
- Czembor CA, Morris WK, Wintle BA, Vesk PA (2011) Quantifying variance components in ecological models based on expert opinion. *J Appl Ecol* 48(3):736–745.
- Hendrickx F, et al. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J Appl Ecol* 44(2):340–351.
- Le Feon V, et al. (2010) Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agric Ecosyst Environ* 137(1–2):143–150.
- Wright CK, Wimberly MC (2013) Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proc Natl Acad Sci USA* 110(10):4134–4139.
- Bennett AB, Meehan TD, Gratton C, Isaacs R (2014) Modeling pollinator community response to contrasting bioenergy scenarios. *PLoS One* 9(11):e110676.
- USDA Economic Research Service (2013) The Conservation Reserve Program is regionally concentrated. Available at [www.ers.usda.gov/data-products/chart-gallery/detail.aspx?chartId=40030&ref=collection&embed=True](http://www.ers.usda.gov/data-products/chart-gallery/detail.aspx?chartId=40030&ref=collection&embed=True). Accessed August 1, 2015.
- Hopwood JL (2008) The contribution of roadside grassland restorations to native bee conservation. *Biol Conserv* 141(10):2632–2640.
- Blaauw BR, Isaacs R (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J Appl Ecol* 51(4):890–898.
- Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol Lett* 6(11):961–965.
- Sinnathamby S, et al. (2013) Pollinator decline: US agro-socio-economic impacts and responses. *J Nat Environ Sci* 4(1):1–13.
- Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. *Proc Natl Acad Sci USA* 99(26):16812–16816.
- Foody GM (2002) Status of land cover classification accuracy assessment. *Remote Sens Environ* 80(1):185–201.
- Wright CK, Wimberly MC (2013) Reply to Kline et al.: Cropland data layer provides a valid assessment of recent grassland conversion in the Western Corn Belt. *Proc Natl Acad Sci USA* 110(31):E2864.
- Klein AM, et al. (2007) Importance of pollinators in changing landscapes for world crops. *Proc Biol Sci* 274(1608):303–313.
- Gallai N, Salles JM, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol Econ* 68(3):810–821.
- Giannini TC, Cordeiro GD, Freitas BM, Saraiva AM, Imperatriz-Fonseca VL (2015) The dependence of crops for pollinators and the economic value of pollination in Brazil. *J Econ Entomol* 108(3):849–857.
- Orford KA, Vaughan IP, Memmott J (2015) The forgotten flies: The importance of non-syrphid Diptera as pollinators. *Proc Biol Sci* 282(1805):20142934.
- Cane JH, Minkley RL, Kervin LJ, Roulston TH, Williams NM (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol Appl* 16(2):632–644.
- Ricketts TH, Lonsdorf E (2013) Mapping the margin: Comparing marginal values of tropical forest remnants for pollination services. *Ecol Appl* 23(5):1113–1123.
- Lebuhn G, et al. (2013) Detecting insect pollinator declines on regional and global scales. *Conserv Biol* 27(1):113–120.
- Kremen C, McGonigle LK (2015) Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. *J Appl Ecol* 52(3):602–610.
- Morandin LA, Kremen C (2013) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol Appl* 23(4):829–839.
- Hendrix SD, Kwaizer KS, Heard SB (2010) Bee communities (Hymenoptera: Apoidea) of small Iowa hill prairies are as diverse and rich as those of large prairie preserves. *Biodivers Conserv* 19(6):1699–1709.
- Harmon-Threatt AN, Hendrix SD (2015) Prairie restorations and bees: The potential ability of seed mixes to foster native bee communities. *Basic Appl Ecol* 16(1):64–72.
- Gaines-Day H (2013) Do bees matter to cranberry? The effect of bees, landscape, and local management on cranberry yield. PhD dissertation (Univ of Wisconsin, Madison, WI).
- Michener CD (2007) *The Bees of the World* (Johns Hopkins Univ Press, Baltimore).
- R Development Core Team (2012) R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna), Version 2.15.0.
- Steffan-Dewenter I, et al. (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proc Natl Acad Sci USA* 104(12):4973–4978.
- Winfree R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conserv Biol* 21(1):213–223.
- Cane JH (1991) Soils of ground-nesting bees (Hymenoptera, Apoidea) - texture, moisture, cell depth and climate. *J Kans Entomol Soc* 64(4):406–413.
- Shuler RE, Roulston TH, Farris GE (2005) Farming practices influence wild pollinator populations on squash and pumpkin. *J Econ Entomol* 98(3):790–795.