

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

Bees 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/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 ≤ -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. S1A). 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 ≥ 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).

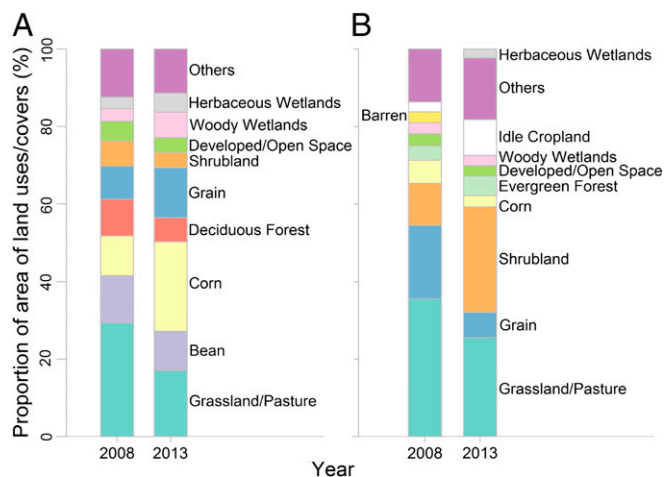


Fig. 2. Changes in land-use/cover corresponding to predicted changes in wild bee abundance. Bars represent land cover in pixels where decreases (A) and increases (B) of wild bee abundance are highly likely between 2008 and 2013 (i.e., bee abundance changes < -0.01 or > 0.01 and the likelihood of changes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

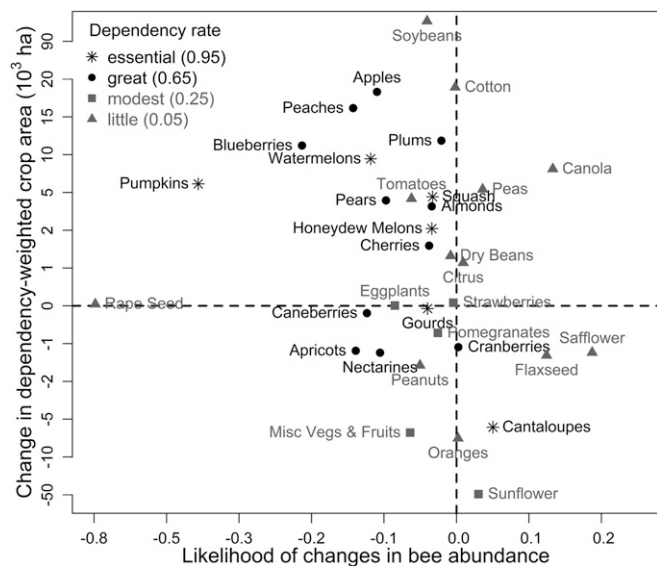


Fig. 3. Nationwide changes in wild bee abundance and cultivated area for pollinator-dependent crops between 2008 and 2013. Symbols represent pollinator dependence for each crop reported by Klein et al. (49).

We put estimates of relative wild bee supply in the context of nationwide demand for pollination services, by comparing predicted bee abundance (Fig. 1A) to county-level information on crops. A total of 139 counties (Fig. 1D) contain almost half of pollinator-dependent crop area but support relatively low wild bee abundance. In these counties, there seems to be a significant mismatch between the supply of wild bees and demand for pollination services. Because our estimates are relative indices, they do not permit absolute comparisons of supply and demand that would determine whether pollinator abundances are adequate to pollinate crops fully. A more robust approach to locate regions of mismatch, therefore, is to identify counties in which supply and demand are changing in opposite directions (Fig. 1F). This comparison of trends pinpoints many of the same counties as Fig. 1D, and adds others. In these counties, regardless of whether demand for pollination services has already overtaken the ability of wild bees to supply them, recent trends indicate that the risk is growing over time (6). Growers of crops dependent on bees for pollination will need to depend more heavily on managed honey bees to supply pollination in the absence of abundant wild bee populations. We predict increasing demand (and rental fees) over time for honey bees in those regions highlighted in Fig. 1F, but a test of that prediction is beyond the scope of this paper. We also suggest that efforts to manage pollinator habitats, monitor bee populations, and evaluate pollen limitation in crops are most important in these regions.

The opposing trends of crop expansion and wild bee abundance may also be causally linked. Crop expansion probably contributed to the declining quality of bee habitats between 2008 and 2013; indeed, we find a negative correlation between changes in crop demand and bee abundance across all US counties ($P < 0.01$, Fig. S2). Studies from northern Europe have shown that mass-flowering crops can enhance wild bee abundance in surrounding landscapes (24, 44), but our analyses indicate the opposite relationship (perhaps because North America has larger-scale mass flowering crops) and emphasize the need for more careful assessment of North American systems.

Analysis of individual crops provides another perspective on potential mismatches between US wild bee supply and demand (Fig. 3). Crops that have decreasing wild bee abundance and increasing cultivated area (upper left quadrant of Fig. 3) tend to be those that are more dependent on bee-mediated pollination (symbols in Fig. 3). Pollination supply and demand are therefore mismatched for precisely the crops that most require pollination.

Variability in US crop yields has been found to increase with greater dependence on pollinators (45), so these trends, if they continue, may destabilize crop production over time. To maintain stability in yields, farmers may need to maintain habitats for wild bees on and around their farms (46) or invest more heavily in managed pollinators.

We consider our estimates of uncertainty to be as informative as the bee abundance predictions themselves. All assessments involve uncertainty, but few report this crucial information with sufficient clarity and rigor (34). We are encouraged to note that our model validation supports the uncertainty estimates; expert-derived parameters improved model fit to a greater degree in areas where experts reported more certainty (Fig. S3). Quantifying uncertainty allows us to make initial predictions about the status and trends of pollinator abundance using uneven and incomplete information. It also helps identify regions where additional studies will most effectively improve our estimates and strengthen the national assessment over time. Highly uncertain regions are also those where the precautionary principle would be appropriate in land management strategies to prevent pollinator loss. In practice, uncertainty in our model can increase for three reasons: First, experts may not be certain about the resource quality of a particular land-cover type (e.g., idle cropland and woody wetland); next, individual experts are certain but disagree about the quality of resources available (e.g., developed open space or evergreen forest); and finally, experts acknowledge that a land-cover type is heterogeneous in its resource quality (e.g., grassland, deciduous and mixed forests, and developed open space). In our case, experts were less certain about the quality of nesting resources than of floral resources; this suggests a need to increase effort to understand the nesting biology of wild bees (29). Experts were also more certain about the quality of crops than of noncrop land covers (Fig. S4); this could reflect relative expertise among experts or greater spatial and temporal heterogeneity of natural land covers.

Although our approach carefully captured expert uncertainty, three other sources of uncertainty arise from the data themselves. First, the Cropland Data Layer (CDL), like all land-cover and land-use data, contains classification errors (47), which contribute to the uncertainty in our estimates. For example, apparent land-use conversion from deciduous forest into woody wetlands contributed to predicted declines in bee abundance between 2008 and 2013, especially in Minnesota (Fig. 1C). Conversely, apparent conversion from grasslands into shrubs was the major driver in areas of increased pollinator abundances (Fig. 1C). Both changes, however, are partly a result of inconsistent classification, which led to apparent changes when none occurred. In addition, urban gardens could support a significant abundance of wild pollinators, but the CDL does not capture these specific features within “developed” categories (Table S1). Despite such inaccuracies, the CDL is the only available national coverage of land-uses/covers in agricultural as well as natural areas (48). Second, for our measures of pollination demand (Fig. 1D), for each crop we rely on Klein et al. (49) for estimates of pollinator dependence (Table S2). These estimates consist of simple percentages of yield and have been widely used in studies of pollination services (50, 51). They also contain some uncertainty, however, because each percentage represents the midpoint of a range reported originally in Klein et al. (49), whereas dependencies vary among crop varieties, climates, field settings, and cultivation practices. Because we focus on analyses of relative demand among crops and counties, our findings are likely robust to this uncertainty. Finally, we elicited expert parameters on nesting resources for different guilds and for floral resources at different seasons. However, we combined these estimates to produce a single probability distribution for each habitat type, which increased the uncertainty of our estimates (i.e., the SD of our probability distributions). In the future, more detailed assessments could integrate information on bee communities, nesting habits, and flight seasons to develop more refined probability distributions for each pixel. Indeed, our model predicted bumble bee abundances more accurately when we used parameters relevant to this genus (i.e., cavity-nesting species and summer floral resources),

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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