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Land-use change reduces habitat suitability for supporting managed honey bee colonies in the Northern Great Plains

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Human reliance on insect pollination services continues to increase even as pollinator populations exhibit global declines. Increased commodity crop prices and federal subsidies for biofuel crops, such as corn and soybeans, have contributed to rapid land-use change in the US Northern Great Plains (NGP), changes that may jeopardize habitat for honey bees in a part of the country that supports >40% of the US colony stock. We investigated changes in biofuel crop production and grassland land covers surrounding ∼18,000 registered commercial apiaries in North and South Dakota from 2006 to 2014. We then developed habitat selection models to identify remotely sensed land-cover and land-use features that influence apiary site selection by Dakota beekeepers. Our study demonstrates a continual increase in biofuel crops, totaling 1.2 Mha, around registered apiary locations in North and South Dakota. Such crops were avoided by commercial beekeepers when selecting apiary sites in this region. Furthermore, our analysis reveals how grasslands that beekeepers target when selecting commercial apiary locations are becoming less common in eastern North and South Dakota, changes that may have lasting impact on pollinator conservation efforts. Our study highlights how land-use change in the NGP is altering the landscape in ways that are seemingly less conducive to beekeeping. Our models can be used to guide future conservation efforts highlighted in the US national pollinator health strategy by identifying areas that support high densities of commercial apiaries and that have exhibited significant land-use changes.

apiary selection models | *Apis mellifera* | land use | land-cover trends | pollinators

Animal pollination service is critical for sustaining ecosystem health and human well-being (1, 2). In many terrestrial systems, plant–pollinator interactions provide the basic framework for all other trophic interactions. Globally, about one-third of crop production depends on animal pollination (3). US agricultural production relies heavily on managed and native insects for pollination services, with an estimated economic value of $15 billion annually (2). Reliance on insects for pollination services is growing even as populations of native and managed pollinators exhibit concurrent declines (4, 5). For example, in 2013–2014, total US honey bee colony losses were 34%, but beekeepers on average lost 51% of their colonies (6). Declines in managed honey bees and native bees put significant pressure on global food supplies, plant–pollinator networks, agricultural producers, and ecosystem function (7, 8).

Proposed reasons for the declines include parasites, diseases, agro-chemical use, forage availability, and land-use change (9, 10). Much of the research investigating anthropogenic disturbance effects on managed and native pollinators focuses on pesticides and less so on habitat fragmentation, land-use, and loss of forage. Although a paucity of data exists for most parts of the world, recent research indicates that land use influences honey bee habitat availability, forage preferences, nutrition, and colony overwintering survival (11–15). In response to reported losses of managed honey bee colonies and declines in native pollinators, a US federal strategy was developed by the Pollinator Health Task Force to promote pollinator health (16). One of the three key objectives of the federal strategy includes the establishment of 7 million acres of pollinator habitat in the United States by 2020. The strategy also calls for additional research on the habitat requirements and foraging needs of honey bees and other pollinators.

From May to October, the Northern Great Plains (NGP) region of the United States hosts ∼1 million honey bee colonies, which represent over 40% of US registered stock (17). Commercial beekeepers transport honey bee colonies to the NGP each summer to produce a honey crop and bolster colony health. During the winter, a majority of the commercial colonies that spend the summer in the NGP are transported throughout the nation to provide pollination services for crops, such as almonds, melons, apples, and cherries, or are moved to southern states for the production of queens and packaged honey bee colonies. In May to June, commercial beekeepers in the NGP select apiary locations based on landscape features that will provide abundant forage for honey bee colonies throughout the growing season. Beekeepers must obtain permission before establishing apiaries on private land. Apiary locations selected by beekeepers likely have a major influence on colony health and honey production because bees are forced to gather resources from the local landscape surrounding the predetermined apiary location.

The NGP has served as an unofficial refuge for commercial beekeepers because of the abundance of uncultivated pasture and rangelands and cultivated agricultural crops, such as alfalfa, sunflower, and canola, that provided forage for bees throughout the growing season. Over the past 100 y, the major agricultural crops in this region have included small grains, flaxseed, hay, sunflower, canola, and dry beans, all with varying forage value to

Significance

Insect pollinators are critically important for maintaining global food production and ecosystem function. Our research investigated how land-use changes occurring in the US Northern Great Plains (NGP) is affecting habitat for managed honey bee colonies in a region supporting >40% of the US commercial colony stock. Our study reveals that land-cover features used by beekeepers when selecting apiary locations are decreasing in the NGP and that corn and soybeans, crops actively avoided by beekeepers, are becoming more common in areas with higher apiary density. These findings suggest that the NGP is rapidly changing to a landscape that is less conducive to commercial beekeeping. Our models identified areas within the NGP that can be targeted for pollinator habitat improvements.

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pollinators. Rising commodity crop prices, increased subsidies for biofuels, such as corn-based ethanol and soy-based biodiesel, and reduction in US Farm Bill conservation programs have facilitated rapid land-use changes in the NGP (18–20). The US Energy and Security Act of 2007 calls for an annual production of 36 billion gallons of liquid biofuels by 2022 (21). Long-term land-cover trends in the region reveal a gradual shift toward increased corn and soybean cultivation and reduction in grasslands and wetlands that have historically dominated much of the NGP (22). For example, in North Dakota, there has been loss of ~647,500 ha (1.6 million acres) of land enrolled in the US Department of Agriculture (USDA) Conservation Reserve Program (CRP) from 2006 to 2014 (23). Additional research is needed to understand how changes in government-managed conservation lands and programs affect ecosystem service delivery and wildlife habitat in the NGP (24, 25). Although renewable biofuels are touted as a mechanism for increasing energy security and potentially reducing greenhouse gas emissions (but see ref. 26), little is known about how rapid expansion of biofuel crops will impact pollinator habitat, health, and pollination services. Farming practices associated with biofuel crops in the NGP often include prophylactic use of pesticides, including neonicotinoids, that may pose health risks to bees via direct and indirect exposure (27, 28) and herbicide use that inhibits growth of noncrop plants that provide a forage base for bees. Recent field studies conducted in the NGP have shown that apiaries surrounded by larger scale agricultural land covers, including biofuels, have lower honey bee colony overwintering survival rates and increased physiological stress (14, 15).

We quantified changes in biofuel crop production and grassland land covers around ~18,000 registered apiary locations in North Dakota (ND) and South Dakota (SD) from 2006 to 2014 (Fig. 1). We then developed habitat selection models to identify remotely sensed land-cover and land-use features that influence apiary site selection by commercial beekeepers residing in areas of significant land-use change within the Dakotas. Specifically, our questions were as follows: (*i*) How has land cover, including biofuel crops and grassland, surrounding registered commercial apiary locations changed in ND and SD from 2006 to 2014? (*ii*) What areas within the Dakotas exhibit substantial rates of land-cover change and also support a large number of commercial apiaries? (*iii*) What land-use and land-cover features do beekeepers target when selecting commercial apiary sites? (*iv*) Do government conservation lands, such as those in the CRP, influence beekeeper apiary selection choices? By identifying land-use trends surrounding commercial apiaries and building beekeeper habitat selection models, we quantified how recent land-use changes, including biofuel crops, are altering habitat for managed pollinators in the NGP.

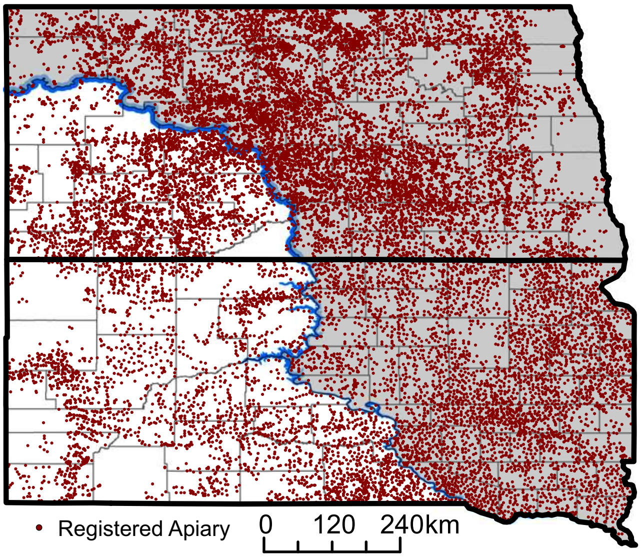

Fig. 1. Location of 18,363 registered apiaries (red dots) in North and South Dakota. Gray counties are in the Prairie Pothole Region, and white counties are in the Badlands and Plains Region. The Missouri River, which separates the two regions, is in blue. An apiary density map can be found in Fig. S1.

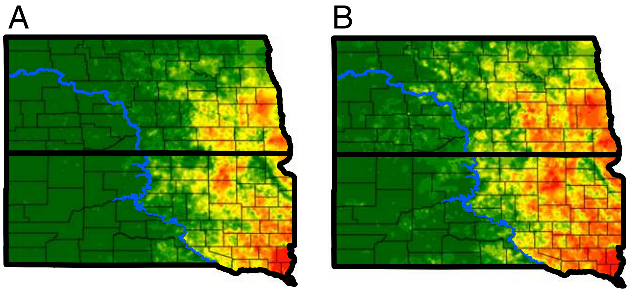

Fig. 2. Heat maps representing the spatial distribution of corn and soybean fields in (*A*) 2006 and (*B*) 2014. Maps were created using interpolation and data from 18,363 registered apiary locations in North and South Dakota. Color ranges from green to yellow to red, with red representing the areas of more corn and soybean production.

Results

Apiary Trends: Land-Use Change and Landscape Stress. In 2006, biofuel crops surrounding commercial apiary locations were generally confined to far eastern portions of ND and SD (Fig. 2*A*). In 2014, biofuel crop area surrounding apiaries generally expanded west and northward across the study region, with continued intensification in eastern ND and SD and southern SD (Fig. 2*B*). Our trend analysis revealed significant annual gains in biofuel crop area around registered apiary locations from 2006 to 2014 [$\hat{\beta}_{YEAR}$ = 9.1 ha annually, 95% credible interval (CI) 8.9–9.3]. Across ND and SD, between 2006 and 2014, there were an additional 1.2 Mha of biofuel crops surrounding registered apiary locations. Much of the increase in biofuel crop area around apiaries was focused in the Prairie Pothole Region (PPR) of the Dakotas, a region extending east and north of the Missouri River in ND and SD (Fig. 3*A*). Average annual gains in biofuel cropping area were four times greater among registered apiaries in the PPR [$\bar{x}$ = 10.3 ha ± 11.3 (1 SD)] than in apiaries west or south of the Missouri River, a region also known as the Badlands and Plains Region (BPR) ($\bar{x}$ = 2.5 ha ± 5.7). There were 13,038 and 5,325 registered apiary locations in the PPR and BPR, respectively. Of the 432 apiary locations exhibiting an annual increase in biofuel crops of >30 ha, 98% were located east or north of the Missouri River, in the PPR. In general, counties with greater gains in biofuel crop area tended to have higher densities of registered apiary locations, suggesting that recent expansion of corn and soybean plantings may be encroaching into the core area of Dakota beekeepers (Fig. 3*A*).

The grassland trend analysis revealed a systematic decrease in grassland land cover surrounding registered apiary locations from 2006 to 2014 ($\hat{\beta}_{YEAR}$ = −0.8 ha annually, 95% CI −0.59 to −0.97). Our interpolation model of grassland change showed that apiaries with larger gains in biofuel cropping area also lost more grassland (Fig. 3*B*). Of the 3,105 apiary locations exhibiting a >10-ha annual decrease in grassland, 81% were located east or north of the Missouri River, in the PPR. Areas that exhibited high levels of grassland loss and high apiary density were generally confined to central and southern ND and the eastern half of SD (Fig. 3*B*).

Apiary Selection Models. Relationships among our land-cover and land-use covariates were highly varied, with *Grassland* and *Biofuels* exhibiting the strongest negative correlation (Fig. S2). All

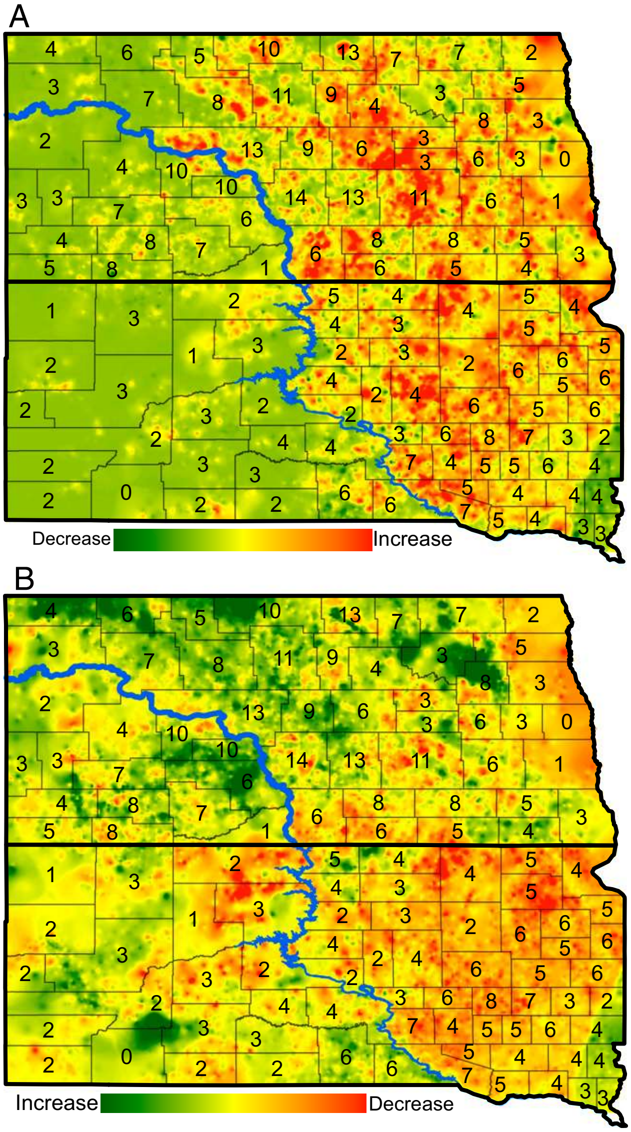

Fig. 3. Heat maps representing the annual rate of change in (*A*) corn and soybean or (*B*) grassland area from 2006 to 2014. Maps were created using interpolation and data from 18,363 registered apiary locations in North and South Dakota. (*A*) Red represents regions with the greatest annual increase of corn and soybean area surrounding commercial apiaries. (*B*) Red represents regions with the greatest annual loss of grassland area surrounding commercial apiaries. Values within county boundaries represent the average number of registered apiaries per 10,000 ha.

covariates included in the same model had correlation coefficients <0.3. Grassland was the most common land cover surrounding apiaries in this region, followed by biofuel crops, small grains, and open water (Fig. S3). Our COMMODITY crop model revealed that the probability of a site being used as a commercial apiary was negatively related to our commodity crop covariates (Fig. 4*A*). In general, *Biofuels* (−0.64; 95% CI −0.77 to −0.50) exhibited a stronger negative correlation with site use than *Sm_Grains* (−0.43; CI −0.58 to −0.28), suggesting a slightly stronger avoidance of biofuel crops than small grain fields by commercial beekeepers. Our HABITAT model estimated a strong positive relationship between apiary site use probability and grassland area (*Grassland*, 0.70; CI 0.56 to 0.83), alfalfa (*Alfalfa*, 0.25; CI 0.13 to 0.28), and open water (*Water*, 0.29; CI 0.17 and 0.42) (Fig. 4*B*). The model revealed equivocal results for associations between apiary site use and woodlands (*Forest*, −0.016; CI −0.45 to 0.13) and sunflower fields (*Sunflower*, −0.04; CI −0.18 to 0.11), with both parameters having credible intervals that overlapped zero. Results from our CONSERVATION model show that commercial beekeepers were more likely to use sites with larger areas of CRP land (*CRP*, 0.19; CI 0.08 to 0.31) (Fig. 4*C*). This model also demonstrated a weak positive relationship between other state and federal lands and apiary site selection probability (*Fed_State*, 0.08; CI −0.03 to 0.20); however, the credible intervals overlapped zero.

Model validation showed that all models performed better than random in predicting use of 196 sites (Fig. S4). Our HABITAT and COMMODITY models yielded similar discriminatory results, with both models having comparable area under the curve (AUC) values and correctly discerned a higher number of validation sites than our CONSERVATION model.

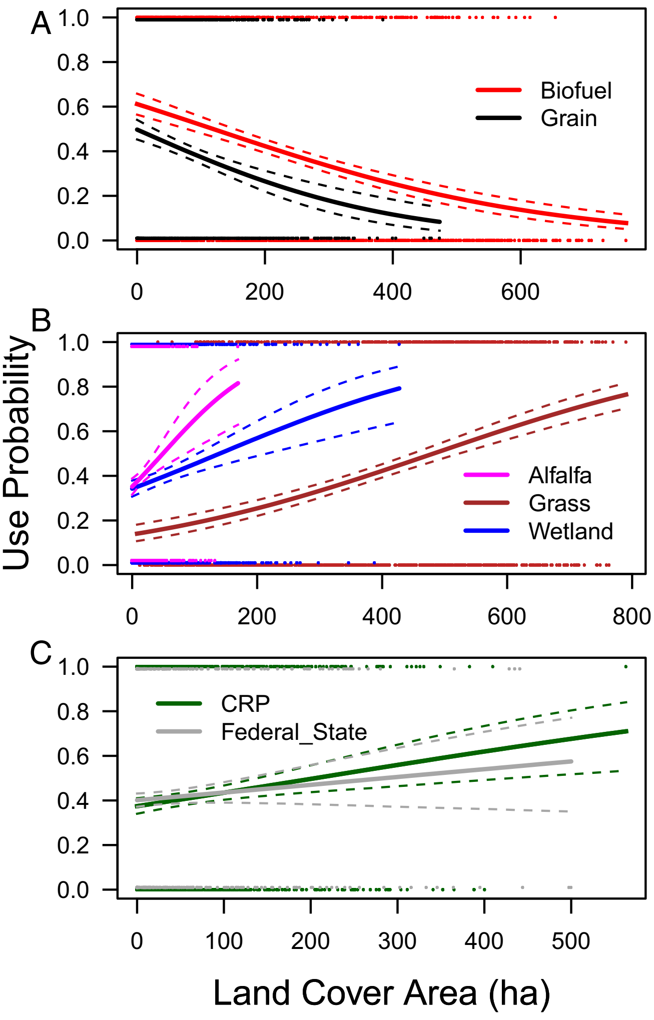

Fig. 4. Apiary site use probability estimates explained as a function of land-cover and land-use covariates for North and South Dakota, 2006. (*A*) COMMODITY crop model including biofuels (red) and small grains (black). (*B*) HABITAT model including alfalfa (magenta), grassland (brown), and open water (blue). (*C*) CONSERVATION model including USDA Conservation Reserve Program land (green) and other federal and state conservation lands (gray). Dashed lines are 95% credible intervals. Colored dots represent raw data used to populate models.

Discussion

Our study provides an empirical investigation of land-use and land-cover change surrounding apiary locations in a region of critical importance to the US honey bee industry. Whereas past researchers found that existing land-cover products lack sufficient local accuracy to monitor actual changes in landscape suitability for honey bees (12), our study demonstrates a continual increase in biofuel crops around registered apiary locations in areas of central and eastern ND and SD, crops avoided by commercial beekeepers when selecting apiary sites in this region. Furthermore, our analysis revealed how grassland land covers that beekeepers target when selecting commercial apiary sites are becoming less common in portions of central and eastern ND and SD, changes that may have lasting impact on pollinator services and conservation efforts. Although past research has shown land-use changes occurring in portions of the Central and Northern Plains (22, 29), our study models large-scale land-use changes from the perspective of the honey bee-keeping industry. Specifically, we used land-use data collected from >18,000 registered apiary locations to derive our spatial models, thereby providing a realistic depiction of how recent land-use changes have affected habitat and foraging area across two states that supported 770,000 colonies in 2014 (17). Our models show that the most substantial rates of land-use change around apiaries are occurring in the PPR, a region currently supporting over 70% of all registered apiaries in the Dakotas.

Our findings are important, considering that habitat loss, lack of forage, and pesticide exposure have been proposed as causative agents of pollinator declines (10). Cropping decisions that lead to the conversion of pasture, conservation grasslands, and bee-friendly cultivated crops to biofuel crops likely have a dual impact on managed and native pollinators because they reduce forage availability and increase the use of pesticides and other agrochemicals that negatively affect pollinators and the ecosystem services they provide (27, 30, 31). For example, conversion of a CRP field to a biofuel crop eliminates native and nonnative forb species that are often targeted by pollinators for forage throughout the growing season. Before planting, corn and soybean seeds are often prophylactically treated with neonicotinoids, systemic pesticides that negatively impact pollinators at the field level and the surrounding landscape (28, 32). Later in the growing season, biofuel crops will often be sprayed with a variety of insecticides, herbicides, and fungicides to control insect pests and undesirable weeds. Thus, converting land from a pollinator-friendly cover to a corn or soybean field likely has impact beyond the scale of the individual field by reducing the forage quality of the landscape and increasing pesticide exposure risk levels in, and adjacent to, the crop field. Given the recent strong focus on pesticide research on pollinators, it is important to recognize that pesticide use is a symptom of cropping decisions made by producers. Although research is needed for developing strategies to ameliorate the negative physiological and behavioral effects of pesticides on pollinators, comparatively little research has been done to investigate how global markets and economic incentives drive land-use changes, the ultimate factor influencing both habitat loss and pesticide applications across landscapes.

Although our study does not link land-use change with pollinator health metrics, it demonstrates how biofuel crop production in the PPR is rapidly creating a landscape that is less conducive to commercial beekeeping. For example, our logistic model revealed that sites supporting more biofuel cropping area were less likely to be used as an apiary. When viewed across the entire study region, apiaries west and south of the Missouri River (i.e., the BPR) saw only modest gains in biofuel cropping area; however, the average apiary within the PPR gained over ∼10 ha annually, from 2006 to 2014. Our trend analysis suggests that the PPR seems to be shifting away from land-use features that are selected by beekeepers when establishing commercial apiaries. Because beekeepers choose where honey bee colonies are deployed on the landscape, it is critically important to understand what landscape features beekeepers select when deploying commercial apiaries (12). In the absence of baseline distribution information for many native pollinators in the NGP, our models may be useful for informing conservation efforts for native pollinators as well.

Shifts in NGP land use are in part driven by renewable fuel standards mandating increased use of biofuels and federal programs subsidizing the production of biofuel crops (18). Although land-use change is generally perceived at the landscape scale, it is important to recognize that cropping decisions are made at the scale of individual farms. In turn, individual cropping decisions are influenced by global commodity crop markets and federal and state policies. The collective cropping decisions made by multiple producers culminate in systemic changes in land use. Our study helps elucidate this process by quantifying regional trends in land use surrounding >18,000 apiaries over a time period where the US Government authorized over $1 billion in mandatory funding (2008–2012) for biofuel crop production (33). In this light, our research shows how economic incentives supporting bioenergy development may have resulted in an unintentional ecosystem disservice by reducing pollinator habitat in a critically important part of the United States. Recent research conducted in North Dakota indicates that honey bee colonies located in apiaries situated in intensive agricultural landscapes had higher overwintering mortality rates and showed increased physiological stress (14, 15). Furthermore, there is growing evidence that current agricultural practices associated with biofuel crops, such as systemic insecticide use, can have lethal and sublethal effects on honey bees (28). These studies suggest that the continued expansion of biofuel crops observed in our study will present additional landscape-related stressors that beekeepers need to consider when selecting locations to support healthy honey bee colonies in the NGP.

Concurrent with expansion of biofuel crops into the NGP, several national efforts have been launched to improve forage availability for pollinators. For example, the USDA has recently unveiled multiple initiatives to improve forage conditions for honey bees and other pollinators residing in the PPR and Upper Midwest. These initiatives are part of the CRP and Environmental Quality Incentives Program (EQIP), voluntary programs that compensate landowners for taking agricultural lands out of production and establishing conservation covers. Additionally, the Pollinator Health Task Force has developed a federal strategy for establishing or enhancing 7 million acres of pollinator habitat over the next 5 y (16). Our models can help guide investment of conservation resources by identifying areas in the NGP that support a large number of commercial apiaries and that have undergone significant land-use shifts in recent years. First, our land-use trend analysis identified a pressing need for pollinator habitat enhancement in areas of high apiary density within eastern ND and SD. Second, our apiary selection model suggests that expansion of federal and state conservation lands, such as those enrolled in the CRP, in the eastern Dakotas is likely to have a positive impact on habitat for pollinators because beekeepers currently select these lands when determining suitable locations for commercial apiaries. Monetary resources appropriated through federally funded pollinator habitat efforts could be used to selectively enhance existing federal- or state-managed lands or establish pollinator habitat in the NGP. A vast majority of the lands beekeepers use when establishing apiary locations are privately owned, thereby demonstrating the importance of including private land management in pollinator conservation efforts and habitat enhancement activities. Land management activities that target pollinators in the NGP will likely have the added benefit of supporting other ecosystem services, such as carbon storage, wildlife habitat, and prevention of soil erosion (34–36).

Future Directions. As global demand for resources and sustainable energy increases, there is a pressing need for a holistic examination of the impact of land-use change on a suite of ecosystem services, environmental tradeoffs, and biodiversity impacts (25, 37, 38). Here, we examined the impact of biofuel crop production on honey bee habitat; however, other impacts could also be evaluated to better understand how socioeconomic factors and global markets drive land-use change and affect multiple ecosystem service outputs. Whereas considerable investments have been directed toward developing commodity crops on private lands, few studies have evaluated how these investments have affected ecosystem services that benefit the public (39, 40). Pollinators serve as effective model organisms for evaluating ecosystem service tradeoffs because their service to humans is directly quantifiable (2, 41) and their health and provided pollination services can be linked with land management activities. Conservation efforts designed to promote habitat for pollinators in the NGP will likely benefit other ecosystem services, including conservation of biodiversity; however, these added benefits need to be quantified so that informed policy decisions can be made that maximize ecosystem service delivery while reducing ecosystem disservices from specific types of agricultural practices.

Future research is needed to understand how land-use change affects honey bee colony health, productivity, and pollination services. Similar to life cycle analyses conducted for naturally migrating species (42), models are needed to guide conservation investment throughout the migratory range of commercial honey bees. To maximize conservation investments, land management activities designed to benefit pollinators should be developed within an adaptive management framework so that management uncertainties can be addressed during the early stages of program development. In addition to quantifying large-scale habitat features that pollinators require, finer scale studies are also needed to investigate floral resources that maximize benefit to pollinators and will grow readily in agricultural landscapes (43–45). This information can be useful for designing and evaluating conservation seed mixes that are cost-effective for implementing across large spatial extents and regional programs. Integrated ecological and economic models are also needed to evaluate how land-use change in one part of the country affects ecosystem service delivery elsewhere in the United States. Development of such models would be useful for identifying stakeholders who may directly benefit from pollinator habitat enhancement in the NGP because healthy honey bee colonies are required for agricultural crop pollination elsewhere in the United States.

Methods

Apiary Trends: Land-Use Change and Landscape Stress. We created maps highlighting (*i*) the spatial distribution of biofuel crops (i.e., corn and soybeans) and (*ii*) changes in biofuel crops and grassland area surrounding commercial apiaries in North and South Dakota from 2006 to 2014. We focused on these years because they represent a period of significant land-use change in this region, including loss of CRP and expansion of biofuel crop production (22). We obtained spatial locations of 18,363 registered apiaries from the North Dakota (number of apiaries, 11,629) and South Dakota ($n = 6{,}734$) Departments of Agriculture (Fig. 1) (data accessed January 12, 2015). In a Geographic Information System (R Core Team 2015, packages rgdal, rgeos, raster, sp) (*SI Appendix*), we georeferenced and placed a 1.6-km (~1.0 mile) buffer around each apiary location and quantified annual land covers as classified in the Cropland Data Layer (CDL) (46) within each buffer. We used 1.6 km as buffer distance because commercial beekeepers generally maintain a distance of >3.2 km between apiary locations to minimize colony competition for floral resources. We extracted pixel counts of each CDL land-cover category in Geospatial Modeling Environment, Version 0.7.4.0 (47) and converted these counts to area using annual CDL resolution. We created two new land-cover classes, biofuel and grassland (Table S1), and summed the area values of contributing land-cover categories to calculate area (ha) in biofuel crop and grassland land covers for each registered apiary location and year. We then calculated the annual gains or losses of biofuels and grassland area for each apiary and calculated mean annual change for both land covers for each apiary across the entire study time span. We used inverse distance weighting interpolation in ArcGIS Desktop (48) to create spatial maps of biofuel crop production in 2006 and 2014, the annual rate of change in biofuel cropping area from 2006 to 2014, and the annual rate of change in grassland area from 2006 to 2014. All models used land-cover data from the 18,363 registered apiary locations to create the interpolation surface across the Dakotas. To estimate annual rates of biofuel change from 2006 to 2014, we constructed a linear trend model within a Bayesian framework, with either biofuel cropping area or grassland area at apiary *i* in year *x* as the response and YEAR as the predictor variable. Trend models were fitted using WinBUGS (49) and the R2WinBUGS package (*SI Appendix*) in R (50). For both models, we used normally distributed priors with zero means and large variances (i.e., diffuse priors). We report parameter estimates for the YEAR regression coefficient and associated 95% Bayesian credible intervals. YEAR regression coefficients that do not overlap zero would suggest a systematic trend in biofuel crop or grassland area change surrounding apiaries from 2006 to 2014. To highlight areas of potential landscape stress for managed pollinators, we overlaid a county-level apiary density map with each one of our interpolated land-use change maps. These maps revealed areas within the Dakotas that have a high density of registered apiaries and significant rates of increase or decrease in biofuels and grassland area change from 2006 to 2014. For each county, we report the number of registered apiaries per 10,000 ha (38.6 mi^2). Because of differences in the apiary registration process for each state, apiary density should be interpreted as relative density within each state, rather than as comparisons across states.

Apiary Selection Models. We developed apiary selection models by identifying commercial beekeepers who operate across a broad geographic area, including portions of the Dakotas that have experienced significant gains in biofuel cropping area and grassland loss, as determined from our land-cover trend analysis. We focused our analysis on three large-scale commercial beekeepers who operate in eastern and central portions of the Dakotas. We used the North and South Dakota Departments of Agriculture apiary registration databases to delineate the operating domain of individual beekeepers. Within these domains, we conducted aerial photograph interpretation of all registered apiary locations (~1,500 apiaries) to verify that the apiaries were used from 2005 to 2007. We used 2005 to 2007 as our study period to correspond with the 2006 CRP enrollment data we obtained through a memorandum of understanding with the USDA Farm Service Agency (FSA). This time period represented the height of CRP participation in the Dakotas, when ~1.3 Mha (3.2 million acres) were enrolled. We used a combination of aerial images from Google Earth (2016 Google) and the USDA National Agricultural Imagery Program (USDA Geospatial Data Gateway, https://gdg.sc.egov.usda.gov) to determine whether an apiary was used during a given year. Our aerial interpretation revealed 644 apiaries that were verifiably used from 2005 to 2007. We removed all sites that were within 3.2 km of another known apiary to avoid pseudoreplication. Of these remaining sites ($n = 583$), we set aside one-sixth of the occupied sites ($n = 98$) for model validation and used the remaining 485 sites for model training. Within the operating domain of the commercial beekeepers, we randomly generated 800 points to represent unused apiary locations. Unused sites had the following selection criteria: (*i*) could not be located in a body of water or an urban center or on restricted federal lands, (*ii*) had to be within 50 m of an access road, and (*iii*) could not be within 0.8 km of each other or any known apiary locations. We applied this separation distance to minimize overlap with other used or unused sites. We set aside 98 randomly generated unused sites for model validation and used the remaining points for model training. This selection process yielded 1,183 and 196 sites for model training and validation, respectively. For all used and unused apiary sites, we used the National Agricultural Statistics Service (NASS) 2006 CDL to quantify land-cover and land-use features within 1.6 km of the point location. Similar to the land-cover trend analysis, we combined various land-cover and land-use categories into broader classes to reflect their hypothesized relationship for supporting commercial apiaries (Table S1). We reclassified the CDL by reassigning the original pixel value of each land-cover category to a new value representing one of the broader classes. Land-cover categories that occupied <0.5% of the landscape and were not easily assigned to our broader land-use categories, such as double crop classes, were excluded from quantification (Table S1). We determined the area of each land-cover class by extracting pixel counts within each apiary buffer in Geospatial Modeling Environment, Version 0.7.4.0 (47) and converting counts to area using the 2006 CDL spatial resolution. We also calculated the area of CRP and other private lands enrolled in federal conservation programs and all federal- and state-owned lands (Table S2). Shapefiles of federal and state lands were merged into a single layer, and both this layer and CRP were rasterized and reclassified to binary rasters to reduce processing time. Rasterization can cause loss of polygon edge definition; however, our 900-m^2 pixel resolution minimized potential edge effects. Area of CRP and federal and state land within each apiary buffer were determined by the same method used for the CDL.

We developed three logistic models to quantify how apiary site selection was influenced by land cover and land use. The first model (COMMODITY) was designed to assess how apiary site selection was affected by major commodity crops, which we classified into two broad categories: biofuel crops (covariate *Biofuels*, corn and soybeans) and small grains (*Sm_Grains*) (Table S1).

The second model (HABITAT) included a *Grassland* covariate (Table S1). We also included cultivated crops and other land covers with suspected benefit to honey bees: *Alfalfa, Forest, Water,* and *Sunflower* (12). We did not include canola fields in the model because of a general lack of canola in our study region. The third model we created, CONSERVATION, quantified the role federal and state conservation lands play in influencing apiary site selection. We included *CRP* as a separate covariate because of the sizable amount of private land enrolled in CRP in the Dakotas. All other federal and state lands were combined into a single *Fed_State* covariate. We constructed a Pearson's correlation matrix of all raw covariates before analysis; covariates with a correlation coefficient >0.3 were not included in the same model. All covariates were then scaled to have a mean of zero to allow for comparison of slope parameters generated from the regression models.

We developed all models within a Bayesian framework to allow for posterior prediction of used and unused sites during model validation. We fitted logistic regression models using WinBUGS (49) and R2WinBUGS (*SI Appendix*) in R (50). Logistic regression was used because our response variable was binary (i.e., 1 = Used apiary, 0 = Unused, randomly generated point) and land-cover predictor variables were continuous (see *SI Appendix* for model code and covariates). For all models, we used normally distributed priors with zero means and large variances (i.e., diffuse priors). We evaluated the 95% credible intervals of the slope coefficients to determine association between site use and habitat covariates.

We used the inverse of the logit-link function to predict apiary use probability for all 196 validation sites based on the slope parameter estimates generated from each model. We used the package pROC (*SI Appendix*) in R to calculate receiver operating characteristic (ROC) curves and integrated the area under the curve (AUC) to assess model performance and predictive capabilities (51). A model with perfect predictive power would yield an AUC of 1.0, and a model with no predictive power would yield an AUC of 0.5.

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Supporting Information

Otto et al. 10.1073/pnas.1603481113

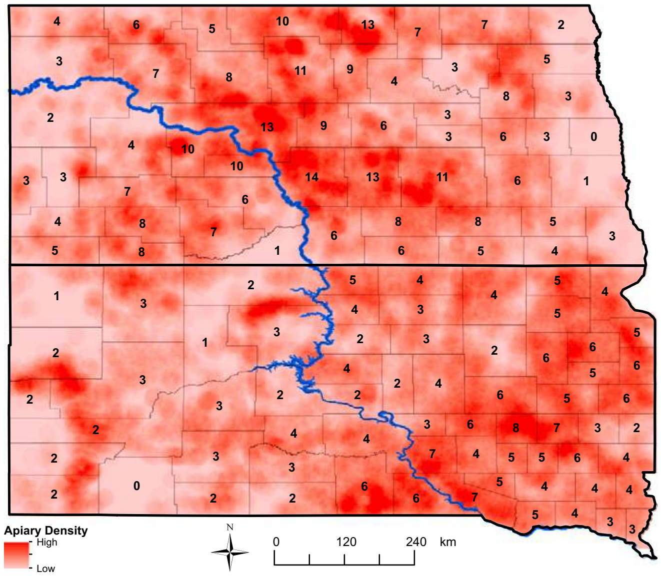

Fig. S1. Map representing the density of registered apiaries in North Dakota and South Dakota. Dark red represents areas with a relatively higher density of registered apiaries, and light red represents lower densities. Density map was created using the Point Density tool in the Spatial Analyst extension of ArcGIS, release 10.3.1 (48). The value for each map pixel was determined by the number of apiary points within a circular neighborhood of a defined radius. The value displayed in each county represents the number of registered apiaries per 10,000 ha.

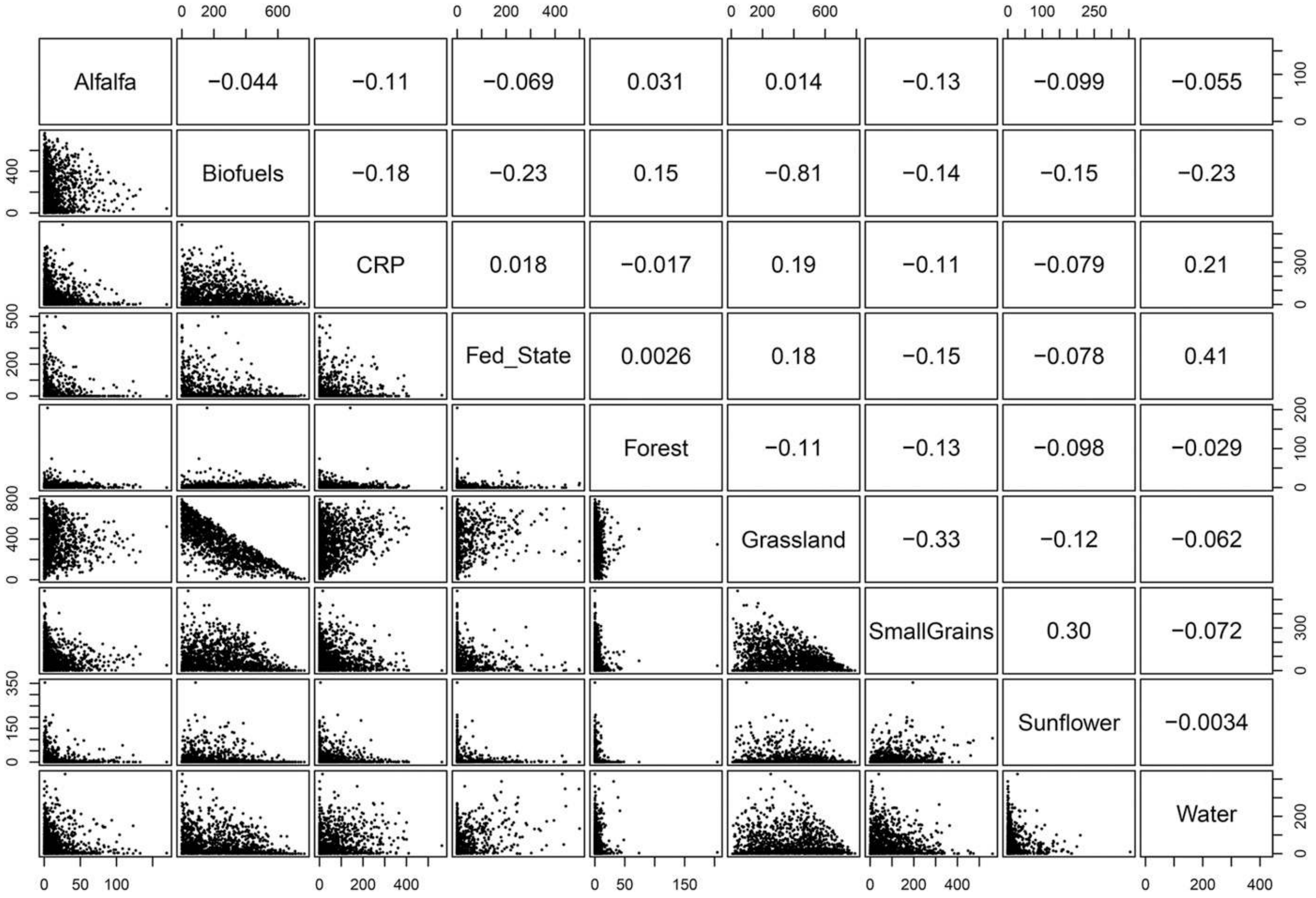

Fig. S2. Pearson correlation coefficients (*Upper Right*) and bivariate plots (*Lower Left*) of land-use and land-cover variables used to create apiary selection models. The name of each variable is shown on the diagonal in alphabetical order. Units for all axes are hectares.

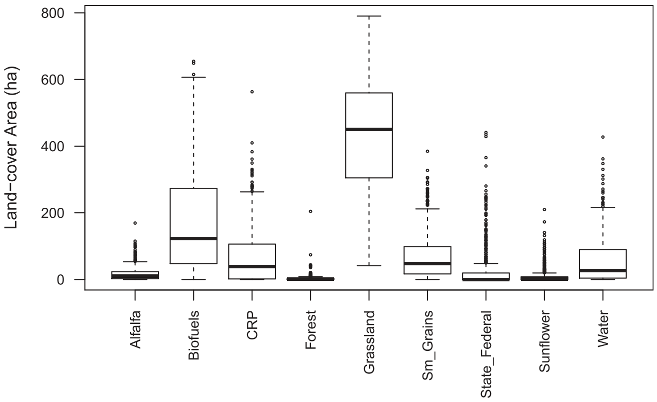

Fig. S3. Land-cover area surrounding 583 apiaries in eastern North and South Dakota used by commercial beekeepers from 2005 to 2007. Area calculations were derived using 2006 remotely sensed land-cover data within 1.6 km of the apiary location.

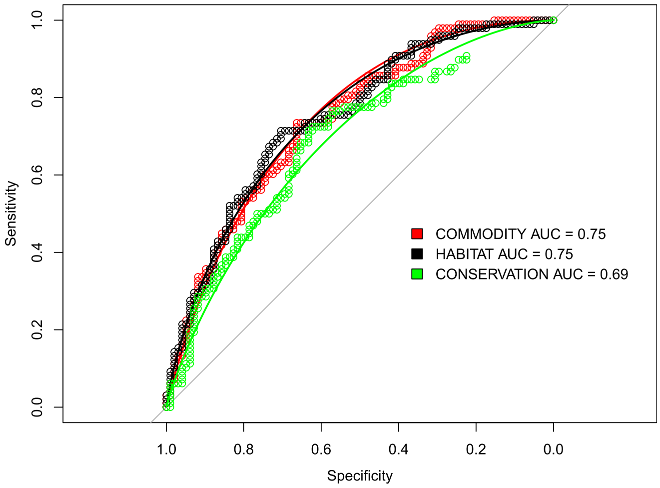

Fig. S4. Model validation results for three resource selection models created for 196 validation apiaries in eastern North Dakota and South Dakota. Smoothed lines and raw values for ROC curves are provided for each model: COMMODITY (red), HABITAT (black), and CONSERVATION (green). Sensitivity is the true positive rate (i.e., site used as an apiary, correctly identified as such), and specificity is the true negative rate (i.e., validation sites not used as an apiary, correctly identified as such). A 1:1 correspondence line (45° line) represents a hypothetical model with no predictive power.

Table S1. Reclassification of USDA National Agricultural Statistics Service Cropland Data Layer (https://nassgeodata.gmu.edu/CropScape/) land covers to (*i*) model land-use trends surrounding 18,363 registered apiaries in North and South Dakota and (*ii*) build apiary selection functions for a subset of apiaries in the eastern Dakotas

CDL land cover	Apiary trends reclassification	Apiary selection model reclassification
Background	NA	NA
Corn	Biofuels	Biofuels
Sorghum	NA	Small grains
Soybeans	Biofuels	Soybeans
Sunflower	NA	Sunflower
Sweet corn	Biofuels	Biofuels
Pop or ordinary corn	Biofuels	Biofuels
Barley	NA	Small grains
Durum wheat	NA	Small grains
Spring wheat	NA	Small grains
Winter wheat	NA	Small grains
Other small grains	NA	Small grains
Double crop winter wheat and soybeans	NA	Small grains
Rye	NA	Small grains
Oats	NA	Small grains
Millet	NA	Small grains
Speltz	NA	Small grains
Canola	NA	Canola
Flaxseed	NA	Cultivated forage
Safflower	NA	Cultivated forage
Rape seed	NA	Cultivated forage
Mustard	NA	Cultivated forage
Alfalfa	NA	Alfalfa
Other hay	Grassland	Grassland
Camelina	NA	Cultivated forage
Buckwheat	NA	Cultivated forage
Sugarbeets	NA	Cultivated nonforage
Dry beans	NA	Cultivated nonforage
Potatoes	NA	Cultivated forage
Other crops	NA	Cultivated nonforage
Miscellaneous fruits and vegetables	NA	Cultivated nonforage
Watermelons	NA	Cultivated forage
Onions	NA	Cultivated nonforage
Lentils	NA	Cultivated forage
Peas	NA	Cultivated forage
Herbs	NA	Cultivated nonforage
Clover or wildflowers	Grassland	Grassland
Sod	Grassland	Grassland
Switchgrass	Grassland	Grassland
Fallow or idle land	Grassland	Grassland
Grassland or pasture	Grassland	Grassland
Forest	NA	Forest
Barren	NA	NA
Apples	NA	Cultivated forage
Developed	NA	Developed
Water	NA	Water
Wetlands	NA	Water
Open water	NA	Water
Developed, open	NA	Developed
Developed, low intensity	NA	Developed
Developed, medium intensity	NA	Developed
Developed, high intensity	NA	Developed
Deciduous forest	NA	Forest
Evergreen forest	NA	Forest
Mixed forest	NA	Forest
Shrubland	Grassland	Grassland
Grassland, herbaceous	Grassland	Grassland

Table S1. Cont.

CDL land cover	Apiary trends reclassification	Apiary selection model reclassification
Hayed pasture	Grassland	Grassland
Woody wetlands	NA	Water
Herbaceous wetlands	Grassland	Grassland
Triticale	NA	Small grains
Vetch	NA	Cultivated forage
Double crop winter wheat and corn	NA	NA
Double crop oats and corn	NA	NA
Pumpkins	NA	Cultivated nonforage
Double crop barley and soybeans	NA	NA
Double crop winter wheat and sorghum	NA	NA
Double crop soybeans	NA	NA
Double crop corn and soybeans	NA	NA
Radishes	NA	Cultivated forage
Turnips	NA	Cultivated forage

NA represents a land-use category that was not quantified in the analysis.

Table S2. Spatial data used to create apiary habitat selection functions, including state and US federally owned lands and private lands enrolled in federally funded conservation programs

Land-use layers	Access	Layer source	Providing organization/agency
US Bureau of Land Management (BLM)	Prohibited	a, b	ND, US Bureau of Land Management; SD, Game, Fish and Parks
Waterfowl Production Areas (WPA)	Prohibited	a, b	ND, US Fish and Wildlife Service; SD, Game, Fish and Parks
Wildlife Management Areas (WMA)/Game Production Areas (GPA)	Prohibited	a, b	ND, Game and Fish; SD, Game, Fish and Parks
National Grassland	Prohibited	a, b	ND, US Fish and Wildlife Service; SD, Game, Fish and Parks
National Wildlife Refuge (NWR)	Prohibited	a, b	ND, US Fish and Wildlife Service; SD, Game, Fish and Parks
Conservation Reserve Program lands (CRP)	Permitted	c	US Department of Agriculture-Farm Service Agency
Grassland and Wetland Reserve Program lands (GRP and WRP)	Permitted	d	US Department of Agriculture-Natural Resources Conservation Service
US Bureau of Reclamation (BOR)	Permitted	a, b	ND, Game and Fish; SD, US Bureau of Land Management
US Army Corps of Engineers (COE)	Permitted	a, b	US Army Corp of Engineers; SD, Game, Fish and Parks
State trust lands	Permitted	a, b	ND State Land Department; SD, Game, Fish and Parks
State parks and recreation areas	Permitted	a, b	ND Game and Fish Department; SD, Game, Fish and Parks
Water surface	Prohibited	e	US Geological Survey
Urban centers	Prohibited	a, b	ND, Department of Transportation; SD, Revenue and Regulation
Roads	Prohibited	a, b	ND, Department of Transportation; SD, Department of Transportation

Access denotes whether randomly generated unused apiary locations were permitted or prohibited for a particular state or federal land-use type. a, https://apps.nd.gov/hubdataportal/srv/en/main.home; b, arcgis.sd.gov/server/sdGIS/data.aspx; c, Memorandum of understanding with FSA; d, https://gdg.sc.egov.usda.gov/; e, viewer.nationalmap.gov/viewer/nhd.html?p=nhd.

Other Supporting Information Files

SI Appendix (PDF)
Dataset S1 (XLSX)

Supporting text for Methods. R statistics packages used for spatial modeling and statistical analysis.

R statistics packages used for quantifying land covers surrounding registered apiary locations.

rgdal: Bivand, R, T Keitt, and B Rowlingson (2015). rgdal: Bindings for the Geospatial Data http://CRAN.R-project.org/package=rgdal.

rgeos: Bivand, R and C Rundel (2015) rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-15. Accessed 12/03/15. http://CRAN.R-project.org/package=rgeos

raster: Hijmans, R. J. (2015) raster: Geographic Data Analysis and Modeling. R package version 2.4-30. Accessed 12/03/15. http://CRAN.R-project.org/package=raster

sp: Bivand, R. S. E. Pebesma, and V. Gomez-Rubio (2013) Applied spatial data analysis with R, Second edition. Springer, NY. Accessed 12/03/15. http://www.asdar-book.org/

R statistics package used for running WinBUGS from R

R2WinBUGS: Sturtz, S, U Ligges, and Gelman A (2005) R2WinBUGS: A Package for Running WinBUGS from R. Journal of Statistical Software 12(3):1-16.

R statistics package use for calculating Receiver Operating Characteristic curves

pROC: Xavier Robin, N. T., A. Hainard, N. Tiberti, F. Lisacek, J.-C. Sanchez, and M. Müller (2011) pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 12:77.

Citation for R

R Core Team (2014) R: A language and environment for statistical computing. Vienna, Austria http://www.R-project.org/).

Supporting text for Methods: Apiary Selection Models section. Code used to construct apiary use models for analysis in WinBUGS with the R2WinBUGS package in R.

```
####
#COMMODITY CROP MODEL
####
```

Fixed effect covariates used in the COMMODITY crop model
bio_area[i]: area (ha) of corn or soybeans within 1.6 km of site *i*
grain_area[i]: area (ha) of small grains within 1.6 km of site *i*

```
library(R2WinBUGS)  #loads R2WinBUGS package

sink("ApiaryBiofuelSmallGrains_Dec2015.txt")
cat("
   model {
   # Priors
   α ~ dnorm(0,0.01)
   β_{biofuel} ~ dnorm(0,0.01)
   β_{sm_grains} ~ dnorm(0,0.01)


   # Model for apiary use
   for (i in 1:nsite) {      # Loop over n sites
         C[i] ~ dbern(p[i])
         logit(p[i]) <- α + β_{biofuel} * bio_area[i] + β_{sm_grains} * grain_area[i]

   }
   # Predict use probability for validation sites
   for (i in npred:nsite){    # Loop over just the validation sites
         pred[i] <- exp(α + β_{biofuel} * bio_area [i] + β_{sm_grains}* grain_area [i]) /
          (1+exp(α + β_{biofuel} * bio_area [i] + β_{sm_grains} * grain_area [i]))
   }
   }
   ",fill=TRUE)
sink()
```

```
#####
#HABITAT MODEL
#####
```

Fixed effect covariates used in the HABITAT model
grass_area[i]: area (ha) of grassland within 1.6 km of site *i*
forest_area[i]: area (ha) of forest within 1.6 km of site *i*
water_area[i]: area (ha) of open water within 1.6 km of site i

alfalfa_area[i]: area (ha) of alfalfa within 1.6 km of site *i*
sunflower_area[i]: area (ha) of sunflower within 1.6 km of site i

```
  # Priors
  α ~ dnorm(0,0.01)
  βgrass ~ dnorm(0,0.01)
  βforest ~ dnorm(0,0.01)
  βwater ~ dnorm(0,0.01)
  βalfalfa ~ dnorm(0,0.01)
  βsunflower ~ dnorm(0,0.01)

  # Model for apiary use
  for (i in 1:nsite) {      # Loop over n sites
        C[i] ~ dbern(p[i])
        logit(p[i]) <- α + βgrass * grass_area[i] + βforest * forest_area[i] + βwater * water_area[i] +
                βalfalfa * alfalfa_area[i] + βsunflower * sunflower_area[i]
  }
  # Predict use probability for validation sites
  for (i in npred:nsite){    # Loop over just the validation sites
         pred[i] <- exp(α +βgrass * grass_area[i] + βforest * forest_area[i] + βwater * water_area[i] +
                βalfalfa * alfalfa_area[i] + βsunflower * sunflower_area[i]) / (1+exp(α + βgrass *
                grass_area[i] + βforest * forest_area[i] + βwater * water_area[i] + βalfalfa *
                alfalfa_area[i] + βsunflower * sunflower_area[i]))
  }
  }

####
#CONSERVATION MODEL
####
```

Fixed effect covariates used in the CONSERVATION model
crp_area[i]: area (ha) of Conservation Reserve Program enrolled land within 1.6 km of site *i*
fed_state_area[i]: area (ha) of U.S. federal or state owned land within 1.6 km of site *i*

```
model {

  # Priors
  α ~ dnorm(0,0.01)
  βcrp ~ dnorm(0,0.01)
  βfed_state ~ dnorm(0,0.01)


  # Model for apiary use
  for (i in 1:nsite) {      # Loop over n sites
        C[i] ~ dbern(p[i])
```

```
        logit(p[i]) <- $\alpha + \beta_{crp}$ * crp_area[i] + $\beta_{fed\_state}$ * fed_state_area[i]
    }
    # Predict use probability for validation sites
    for (i in npred:nsite){     # Loop over just the validation sites
        pred[i] <- exp($\alpha + \beta_{crp}$ * crp_area[i] + $\beta_{fed\_state}$ * fed_state_area[i])/
                (1+exp($\alpha + \beta_{crp}$ * crp_area[i] + $\beta_{fed\_state}$ * fed_state_area[i]))
     }
    }
####END CODE
```

<u>Citations for R and R2WinBUGS</u>

Sturtz, S, U Ligges, and Gelman A (2005) R2WinBUGS: A Package for Running WinBUGS from R. Journal of Statistical Software 12(3):1-16.

R_Core_Team (2014) R: A language and environment for statistical computing. Vienna, Austria http://www.R-project.org/).