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LETTER

Historical decrease in agricultural landscape diversity is associated with shifts in bumble bee species occurrence

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Abstract

Agricultural intensification is a key suspect among putative drivers of recent insect declines, but an explicit link between historical change in agricultural land cover and insect occurrence is lacking. Determining whether agriculture impacts beneficial insects (e.g. pollinators), is crucial to enhancing agricultural sustainability. Here, we combine large spatiotemporal sets of historical bumble bee and agricultural records to show that increasing cropland extent and decreasing crop richness were associated with declines in over 50% of bumble bee species in the agriculturally intensive Midwest, USA. Critically, we found that high crop diversity was associated with a higher occurrence of many species pre-1950 even in agriculturally dominated areas, but that current agricultural landscapes are devoid of high crop diversity. Our findings suggest that insect conservation and agricultural production may be compatible, with increasing on-farm and landscape-level crop diversity predicted to have positive effects on bumble bees.

KEYWORDS
Agricultural intensification, *Bombus*, crop diversity, ecoinformatics

INTRODUCTION

Agriculture is a primary way in which humans alter terrestrial landscapes and is cited as a principal cause of biodiversity declines worldwide (Foley et al., 2005, 2011; Klein et al., 2007; Tilman et al., 2011; Tscharntke et al., 2012). In particular, the intensification of agriculture, that is, the widespread planting of crop monocultures, managed for high productivity promoted by fertilisers and pesticides, and high-disturbance agronomic practices such as tillage, has been associated with the extensive loss of a number of ecosystem service providing taxa (Benton et al., 2002; Meehan et al., 2010; Robinson & Sutherland, 2002). There is circumstantial evidence that agricultural practices are important drivers of recently documented large-scale insect declines (Hallmann et al., 2017; Seibold et al., 2019). Pollinating insects, specifically bees, may be particularly impacted, with consequences for both natural and agricultural systems, including a reduction in pollination services of crop and non-crop plants (Burkle et al., 2013; Duchenne et al., 2020; Steffan-Dewenter et al., 2005; Tylianakis, 2013).

Bumble bees (Apidae: *Bombus*) are a well-studied bee taxon that includes many species documented to be declining across Europe and North/South America (Bartomeus et al., 2013; Biesmeijer, 2006; Bommarco et al., 2012; Cameron et al., 2011; Colla & Packer, 2008; Dupont et al., 2011; Grixti et al., 2009; Morales et al., 2013; Wood et al., 2019). Of several putative drivers of bumble bee decline, including climate change (Fourcade et al., 2019; Kerr et al., 2015; Soroye et al., 2020) and pathogens (Cameron et al., 2011; Szabo et al., 2012), several studies also point to agricultural intensification as a key driver of bumble bee population decline (Grixti et al., 2009, Goulson et al., 2015; Vray et al. 2019; Duchenne et al., 2020). Intensification includes both attributes within a local farming system (i.e. pesticide use, number and types of crops planted), and attributes of agricultural landscapes (i.e. amount of land in cultivation compared to natural habitats not used for agriculture). For example a loss of crop diversity and increasing crop extent is likely to reduce landscape-level plant diversity, reducing foraging opportunities for bumble bees. Despite the hypothesised threat of agricultural intensification to bumble bees, no studies have specifically tested the hypothesis that long-term patterns of changes in agriculture are associated with changes in bumble bee occurrence. In general, this is due to a paucity of long-term data of both bumble bee occurrence and historical agricultural patterns at sufficiently large spatial scales.

While contemporary studies examining bumble bee responses to agriculture provide some insights, historical data from archives such as museum records are important tools to explore patterns of bumble bee change over the course of decades and can elucidate drivers at temporal and spatial scales that elude detailed, small-scale experimental approaches (Meehan et al., 2011; Rosenheim & Gratton, 2017). The continued addition of records to repositories such as the Global Biodiversity Information Facility (GBIF) combined with modern, extensive surveys of bumble bee fauna (e.g. Bumble Bee Watch, iNaturalist) offer widespread, species-specific spatial distribution patterns. Moreover, analyses of records from such repositories have benefited from analytical approaches that account for known biases (e.g. spatial sampling bias) in archival data (Bartomeus et al., 2013, 2019; Pearce & Boyce, 2006).

To test the hypothesis that long-term bumble bee occurrence trends are associated with patterns of agricultural intensification, we utilised an extensive data set of historical bumble bee museum records and modern citizen-science surveys for the Midwest USA and combined this with a newly available digital data set of agronomic metrics compiled from the United States Census of Agriculture over the period 1840–2017 (Crossley et al. 2020). We predicted that increasing agricultural intensification, as measured by the amount of cropland in a county, would be negatively associated with bumble bee occurrence (Duchenne et al., 2020; Goulson et al., 2008, 2015; Samuelson et al., 2018; Williams & Osborne, 2009), given that an increase in cropland extent is typically associated with a decrease in a natural or semi-natural habitat. In contrast, we expected that features of agricultural landscapes that increase diversity, as measured by the richness of crops grown, would be positively associated with bumble bee occurrence (Sirami et al., 2019).

MATERIALS AND METHODS

We focused our study in the USA on the Midwest states of Indiana, Illinois, Iowa, Michigan, Minnesota and Wisconsin, as these states share a similar biogeographic context and agricultural history. We limited our analysis to 13 bumble bee species whose core ranges overlapped these states (Williams et al. 2014), including: *B. affinis* Cresson; *B. auricomus* Robertson; *B. bimaculatus* Cresson; *B. borealis* Kirby; *B. citrinus* Smith; *B. fervidus* Fabricius; *B. griseocollis* DeGeer; *B. impatiens* Cresson; *B. pensylvanicus* De Geer; *B. rufocinctus* Cresson; *B. ternarius* Say; *B. terricola* Kirby and *B. vagans* Smith.

Four species, *B. ashtoni* (*bohemicus*), *B. fraternus*, *B. perplexus* and *B. variabilis*, were not included in our analyses as they lacked sufficient records to model adequately. However, we did include them in rarified estimates of species richness change over time (see Appendix 1). Of the study species, three (*B. affinis*, *B. terricola* and *B. pensylvanicus*) are known to be in decline nationally and are of conservation concern (IUCN Red List; Colla & Packer, 2008; Jacobson et al., 2018).

Bumble bee record data

We obtained bumble bee records from the Global Biodiversity Information Facility (GBIF), querying all research-grade records of our selected species group (see above) within the study states (GBIF.org, 2018). To bolster the last decade of data, we combined the GBIF data with expert-verified records from the North American Bumble Bee Watch (BBW) program provided by the Xerces Society for Invertebrate Conservation. This database includes a number of records of rare/declining species. In total, 24,524 records were compiled from GBIF from 1870 to 2017 and 2,606 from Bumble Bee Watch from 2007 to 2018 for a total of 27,130 unique records over 358 of 535 total counties in the study region (Figure S1). The species contained in each data set were mutually inclusive. We filtered records to include only those which were appropriately geo-referenced (i.e. had associated longitude and latitude). Each record was assigned to a county based on its collection coordinates so that they could be matched to county-level agricultural census data. Bee and agricultural census data are therefore compared at the county-level. Because 95% of records were from 1890 and beyond, we are confident that county assignments are accurate, as changes in county geographical extent in this region were largely complete by 1890 (Crossley et al. 2020). As both data sources (GBIF and BBW) are largely comprised of incidental occurrence records, have expert-verified species identifications, and are geo-referenced, we determined that combining them was appropriate.

Bias testing and correcting of bumble bee records

Temporal comparisons of the museum and incidental records can be challenging due to non-standardised collection techniques as well as a collector and spatial biases

(Bartomeus et al., 2013, 2019; Richardson et al., 2018). To account for this, we analysed records using several techniques that attempt to minimise such biases. Following Richardson et al., (2018), we filtered the full data set to include only 'single individual' sampling events (i.e. unique combination of species, date, location and collector) to test whether different sampling methodologies might impact our results. All analyses described below were conducted using both the full and reduced data sets. We found that filtering to 'single individual' sampling events did not impact our conclusions (Figure S2), and thus we present results from the full data set. The inclusion of citizen science data might also introduce potential biases. As such, we excluded all bumble bee watch data from analyses. Doing so did not impact our conclusions (Figure S3).

In order to estimate changes in bumble bee populations over time, we calculated the relative abundance of each species within each county by agricultural census year and paired these county-level data with agricultural records (see below). Additional details, including methods on rarefaction and species diversity trends are included in Appendix 1.

Historical agricultural data

To assess measures of agricultural intensification, we used county-level (*n* = 535) agricultural census data collected every 10 years that were projected and geographically corrected by Crossley et al. (2020). For each county by census year, we used crop richness (range 0–18) and the proportion of county area in cropland (range 0–1) as our metrics of agricultural intensity. These two variables are largely indicative of agricultural intensification, generally, being strongly correlated with other metrics such as insecticide use, farm size and crop yields (Meehan and Gratton, 2011), but are not correlated with one another (all model term VIFs <5). Briefly, Crossley et al. (2020) analysed the spatial patterns of 18 crops at the county-level and computed county cropland proportion and crop richness from 1840 to 2017, correcting for changing county boundaries using area-weighting.

Pairing bumble bee records with historical agriculture data

Because agricultural census data are collected at 10-year intervals, not every bumble bee record was collected in a year coinciding exactly with an agricultural census. Accordingly, we associated bee records with the nearest agricultural census, with 95% of records associating with a census within ±5 years (e.g. bumble bee records from 1925 to 1935 were paired with the 1930 Census of Agriculture data). While this pairing imperfectly reflects the state of agriculture experienced when the bumble bees were collected, we posit that it is still meaningful given that large, county-level changes in agricultural practices occurring over several decades are unlikely to manifest in time spans of less than 5 years. Nevertheless, to verify this assumption we performed additional analyses after filtering data with a stricter ±3-year pairing rule (i.e. dropping bee data from years outside of these narrower windows) and found similar results (Figure S6). We thus present the analysis with the dataset containing all records.

Statistical analyses

Patterns of species richness

We first examined trends in rarefied species richness over time, calculating for occurrence records within each agricultural census bin. We modelled the temporal trend in estimated species richness over time using a generalised additive model (GAM) and conducted sensitivity analyses to test whether the number of bins impacted the estimated trend (Appendix 1).

Relating changes in bumble bee relative abundance to agricultural intensity

We constructed models to examine whether changes in metrics of agricultural intensification were related to bumble bee relative abundance. For each bumble bee species, we fit a generalised linear mixed model (GLMM) with a binomial error structure and logit link function in order to predict county-level relative abundance for that census year as a function of cropland proportion, number of crops, the agricultural census year and all two- and three-way interactions and county as a random grouping factor to account for the repeated observations at the county level. Because binomial models expect binary outcomes (e.g. 0, 1), we modelled measures of species relative abundance (proportion of successes) weighted by the total number of bumble bee records in a county by agricultural census year (essentially the number of binomial trials, Zuur et al., 2009). This approach effectively gives more weight to counties that had a greater sampling intensity as we assumed these counties provided more accurate estimates of species relative abundance at any given time. As binomial GLM predictions can be generated as either log-odds or predicted probabilities, we present our results as predicted probabilities of occurrence for ease of interpretation. While this approach captures changes in an occurrence where species persist, it may not be as sensitive to species range contractions within the data (i.e. the loss of occupied counties over time).

Additionally, we tested for multicollinearity, as well as any spatial and/or temporal autocorrelation present in model residuals. While temporal autocorrelation was not an issue, several species models contained significant spatial autocorrelation for which we accounted using spatial regression models (Appendix 1).

RESULTS

Agricultural extent remains similar while crop richness has declined

From the onset of available land-use records in the 1840 s, cropland cover increased rapidly and began to plateau by the early 1900 s. The areal extent of cropland reached a maximum in the study region in 1950 (45% ±0.9% of county area, mean ±standard error). Since then, it has decreased ~11% to an average of 34% ±0.9% in 2017 (Figure 1a and b). There are within-region differences in cropland cover, with northern areas of the study region remaining relatively low in cropland cover, while the highest intensity of cropland cover occurred in the "corn belt" that stretches through southern Minnesota, Iowa, southern Wisconsin, central and northern Illinois and northern Indiana. Of the 18 crops for which we compiled data, an average of 12 ± 1 was grown per county from 1880 to 1950. Since 1950, this number has declined ~50%, with counties today growing on average 6 ± 1 crops (Figure 1c and d).

In addition to the decline of the number of crop species used in agriculture, especially after the 1940 s, there was also a shift in the crops grown. The proportion of counties that grew corn increased steadily over the last century, and after the 1940 s there was a rapid increase in the proportion of cropland in soybeans (Figure 2a). Coincident with the rise of corn and more recently soy, was the notable decline after the 1940 s of pulses, leguminous hay crops and small grains (Figure 2b).

Bumble bee species richness has declined

Rarefied bumble bee species richness estimates for the study region have declined significantly over the last 130 years. There was a 20% decrease in the average species richness over the study period from ~15 species during the period between 1870 and 1925, to 12 species in 2017 (Figure 3, GAM: $p = 0.01$; permutation test: $p = 0.03$). A sharp drop in estimated species richness occurred in the 1950 s, followed by a slight rebound in the last 15 years. The decrease in estimated species richness in the 1950 s corresponds to the period in which crop richness began to decline significantly across the study region.

Patterns of bumble bee occurrence are related to agricultural intensity

To illustrate the general patterns in this data set, and for brevity, we highlight the results of the six species with the greatest number of county-level relative abundance records within our study region (> 150 county x time

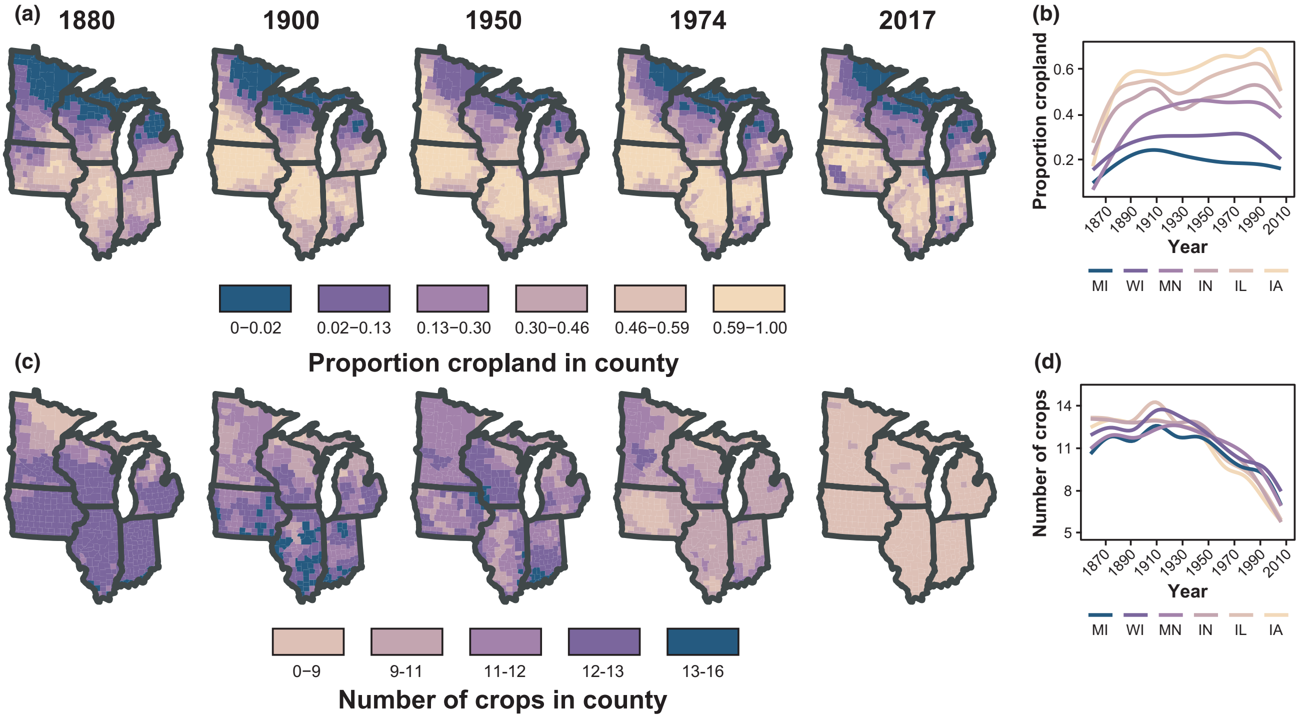

FIGURE 1 Patterns of agricultural intensification from 1880 to 2017 at roughly equal intervals across Illinois, Indiana, Iowa, Michigan, Minnesota and Wisconsin in two metrics: (a and b) proportion of county in cropland and (c and d) number of crops grown per county. Inset graphs (b and d) depict the general trend of these variables for each state in the study area as modelled by a Loess curve

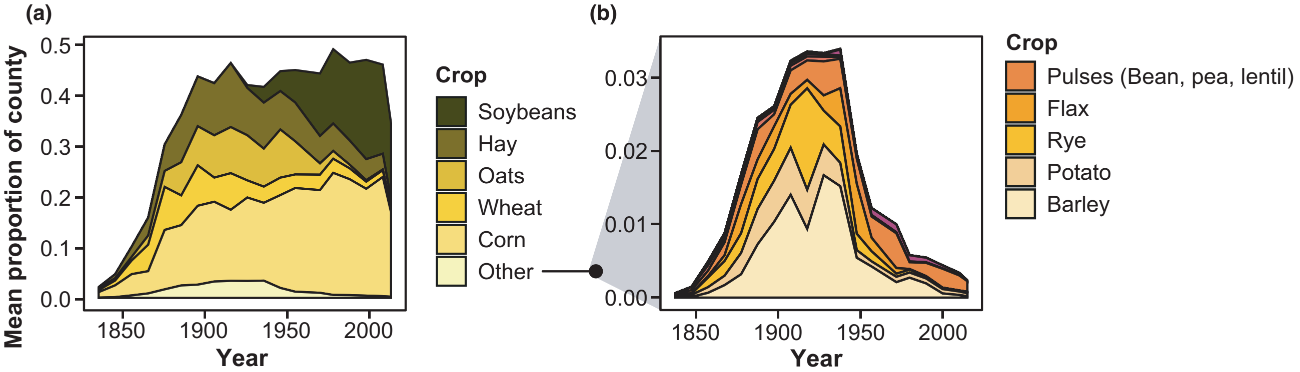

FIGURE 2 (a) The relative proportion of county area of the major crop types included within the study from 1840 to 2017. (b) 'Other' category includes five crops that together comprise less than 5% of county area at any time point. We do not show crops that are rare (occupy less than 0.1% of county area) or that do not occur in the Midwest USA in any given census period (buckwheat, cotton, peanuts, rice, sorghum, sugar cane, sweet potato and tobacco)

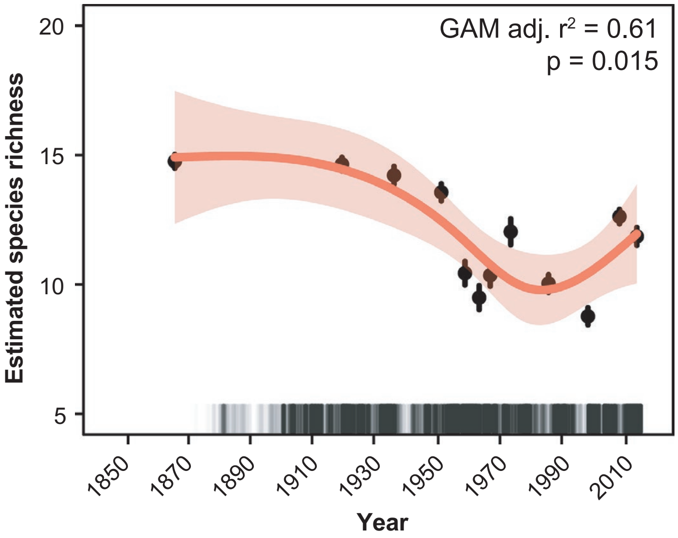

FIGURE 3 Temporal trend of rarified bumble bee species richness from 1877 to 2017. Each point represents a date range that is standardised to contain an approximately equal number of bumble bee records (thus the date range differs for each point), and it is plotted at the midpoint year of the date range. Error bars are 95% confidence intervals. The fitted line is a generalised additive model predicting estimated species richness as a function of temporal bin order using the midpoint of the temporal bin as the predictor value. Carpet plot represents a temporal collection year for all records from 1877 to 2017

records in total), three of which are thought to be increasingly common (*B. bimaculatus*, *B. griseocollis* and *B. impatiens*) and three that are currently of conservation concern (*B. affinis*, *B. pensylvanicus* and *B. terricola*). Where appropriate, we also refer to the model results from the additional seven study species. However, the smaller number of observations (< 150 records) for these additional species warrants caution especially given model complexity (Figure S7, S2). All species models fit without convergence issues and explained 15–69% of the variation in the data (Table S1).

We found significant relationships between the predicted probability of bumble bee occurrence and measures of agricultural intensification over time, but these patterns varied among species (Table S1). Using the fitted models and county-level agricultural metrics over time, we made predictions about the occurrence for each species across the Midwest USA, accounting for trends in occurrence and combinations of the amount of cropland and crop richness across the region (Figure S13). Integrating these patterns over the temporal range of the data yields a predicted occurrence trend for each county, as well as the study region (Figure 4). When these temporal occurrence patterns are depicted spatially, two distinct and contrasting patterns emerge: 7 of 13 species are predicted to be less likely to occur over time across a wide swath of the study region (Figure 4, Figure S9: species maps that are predominately black), whereas six species are predicted to as or more likely to occur throughout the study region (Figure 4, Figure S9; species maps that are predominately dark/bright yellow). Together, these patterns show that even though high crop richness can be beneficial to species in later years (e.g. *B. affinis* and *B. bimaculatus*; Figrue 5b and c), the

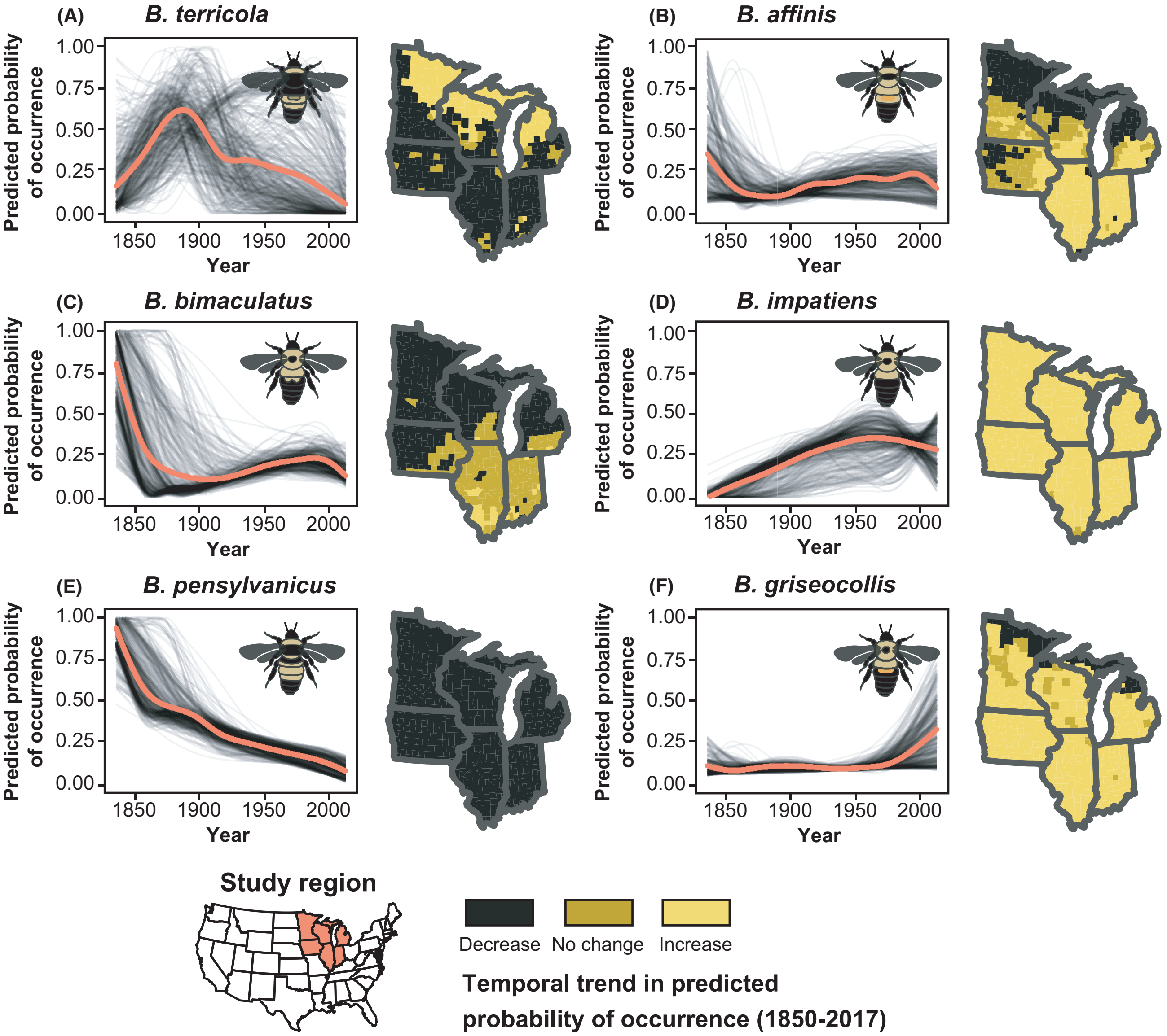

FIGURE 4 Illustration of the temporal trend in predicted bumble bee occurrence across the six focal species (a–f). We use the species-specific models which predict the probability of occurrence given cropland proportion and number of crops (with all interactions) to plot the expected county-level probability for each census year of the model. With this information, for each species, we estimated a county-level time series (GAM-fits, black lines) as well as an overall trend in the predicted probability of occurrence (red lines) for the species. For each county and species, we use the average slope (i.e. temporal change) to create a spatial representation of the trend in predicted species occurrence given local agricultural conditions, where yellow, gold, and black indicate increasing, stable, and decreasing probability of occurrence over time respectively. Together, these panels depict the long-term occurrence trend of each species as predicted by the agricultural intensification metrics (cropland proportion and number of crops), smoothing over short-term fluctuations in predicted occurrence for in any single census year

actual presence of high crop richness in counties is rare (Figure 4, Figure S9).

Several species responses conformed to our predictions regarding the relationship between agricultural intensification and the probability of occurrence. For example patterns of *B. terricola* are consistent with our hypothesis that increasing cropland is associated with a decrease in the probability of occurrence over the duration of the study (Figures 4 and 5a), particularly after the marked increase in agricultural intensification that occurred in the mid-20th century. This general pattern of a negative effect of cropland extent on the likelihood of occurrence was also seen for *B. fervidus*, *B. borealis* and *B. rufocinctus* (Figure S7a, b, c respectively).

On the other hand, and contrary to our expectations, species such as *B. affinis* (Figure 5b), *B. bimaculatus* (Figure 5c) and *B. impatiens* (Figure 5d) were predicted to be more likely to occur in counties with more cropland extent, especially in more recent years (see also *B. auricomus*; Fig S6d). In addition, for these three species, the effect of the higher cropland cover in a county was dependent on the number of crops grown. In areas of high cropland proportion, counties with a higher richness of crops (Figure 5, green-dotted lines) exhibited a higher probability of occurrence of *B.*

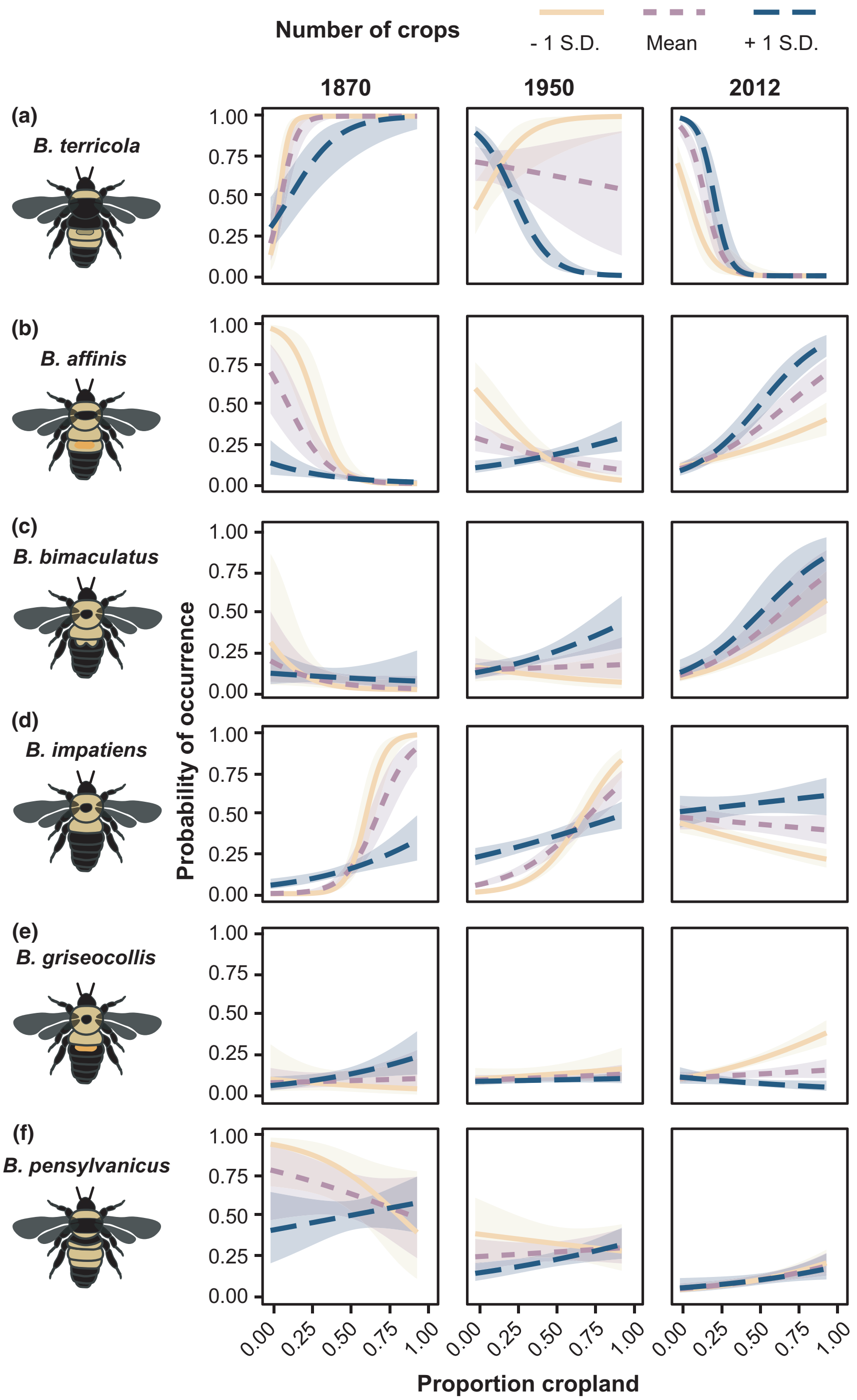

FIGURE 5 Interaction plots for species of conservation concern (first 3 rows) and common species (bottom 3 rows). Each line represents the expected trend (with 95% confidence interval) of the probability of occurrence over time given the cropland proportion (panel columns, mean ±1 standard deviation) and the number of crops (line colour and type, mean ±1 standard deviation)

affinis, *B. bimaculatus* and *B. impatiens* than did counties with lower crop richness (red dotted lines). This trend was consistent for other study species as well (see *B. fervidus*, *B. borealis*, *B. rufocinctus*, *B. auricomus* and *B. citrinus*, Figure S7), and overall, eight of the 13 species examined had a greater probability of occurrence in areas with higher crop richness (Figure 5, Figure S7).

It is important to note that for some species the influence of crop richness on species occurrence patterns changed over time. For example while increasing crop richness in the early part of the last century tended to result in a higher probability of occurrence for the majority of species (e.g. *B. grisiocollis*, Figure 5e), in more recent periods this effect reversed or was lost altogether (e.g. *B. fervidus*, *B. citrinus* and *B. borealis*, Figure S7d, c, b). This temporal interaction is coincident with the rise of soybean cultivation and the decline in overall crop richness in the last few decades (Figure 2). Thus, not only is crop richness important in influencing the response of bumble bees to agriculture, but the composition of crops may also be a relevant factor influencing bumble bee patterns. Notably, croplands in 1950 and earlier included a greater amount of bumble bee forage crops (e.g. pulses and leguminous hay crops) in addition to higher crop richness (Figure 1, Figure 2).

Other species, such as *B. pensylvanicus* (Figure 5f) and *B. vagans* (Figure S7e), showed increasing sensitivity to cropland extent over time. For example while increasing cropland cover was associated with an increase in the probability of occurrence prior to 1950, these species are now predicted to be rare (~10% probability of occurrence) across all landscapes with agriculture. Additionally, the number of crops had little impact on the patterns of predicted occurrence of each species; model predictions suggested a decrease in predicted occurrence across the range of crop richness in our data.

The predicted occurrence of the remaining species, specifically *B. auricomus* (Figure S7d), *B. citrinus* (Figure S7f), and *B. griseocollis* (Figure 6e), remained relatively rare until the last 40 years, when predicted occurrence increased significantly in accordance with increasing cropland proportion and decreasing crop richness. The rise of *B. citrinus*, a brood parasite, is coincident with the increase in its primary hosts *B. bimaculatus* and *B. impatiens*.

DISCUSSION

Using bumble bee observations recorded over 130 years across six agriculturally important US states and a novel data set on the historical patterns of agricultural land cover, we explored the hypothesis that agricultural intensification is associated with changes in bumble bee species occurrence. Agricultural intensification patterns can be categorised by both the extent of land under crop cultivation and the kinds of management decisions made, such as the number of crops grown. Our analysis shows how these different facets of agricultural intensification have changed at different rates. Although the amount of land in cultivation rapidly increased in the early 1900 s, the average number of crops grown during that time also increased. After the 1940 s, despite the relative stability of cropland extent in the Midwest USA, there was a rapid decline in the number of crops grown, with contemporary crop richness falling to 50% of what it was in the early 1900 s. These shifts in agricultural production patterns after the mid-century were coincident with a 20% decline in bumble bee species richness and showed strong associations with bumble bee species occurrence trends at a county level.

Contrary to our initial predictions, the directionality of bumble bee responses to cropland extent was mixed, with predicted occurrence for some species increasing while others decreased. Moreover, the effect of cropland proportion was also mediated by the richness of crops grown. In fact, high crop diversity had a broadly positive influence on bumble bee species occurrence, regardless of the amount of cropland in the landscape. However, this effect was apparent only at times when the regional average crop richness was high. This means that the positive impact of crop richness only occurred in time periods before the mid-20th century. While an increasing amount of cropland was detrimental to some species, this effect could be tempered by increasing crop diversity in the landscape. However, most species do not profit from the benefits of higher crop richness in more simplified, modern agricultural landscapes. For example even a species such as the common *B. impatiens* that had increased in occurrence from 1850 onward instead was predicted to decline slightly in recent years as crop richness has continued to decrease (Figure 4).

Of the crops included in our analyses, we observed a large decrease in the extent of hay crops, which include bumble bee food plants in the family Fabaceae, as well as other bumble bee attractive crops including buckwheat and pulses. Together, these changes suggest that the post-war era of intensification of agriculture, with its loss of crop diversity, bumble bee attractive crops, and pasture, as well as increasing insecticide use (Meehan et al., 2011, Fernandez-Cornejo et al. 2014, Meehan & Gratton, 2015), rather than the areal expansion of agriculture *per se*, has been a driver of bumble bee community change. It is worth noting that changes in crop diversity were likely associated with suite of other agricultural practices, such as increases in agrochemical use, field size, as well as farm mechanisation (similar to patterns in Europe, Benton et al., 2002). While such changes may also have impacted bumble bee occurrence, the potential correlation of these factors with our chosen agricultural metrics makes it is difficult to parse which has most affected bumble bees. Multicollinearity among these variables (e.g. pesticide use, average farm size) made using additional variables in our models problematic. As such, we used two variables that had a low correlation and that we felt best-encapsulated changes in both agricultural landscape composition (proportion of land in crops) and on-farm practices (as indexed by crop diversity).

While our results showed heterogeneity in occurrence trends across species, we generally saw a negative effect of extensive cropland, in line with other studies that found agricultural intensification to be a primary correlate of the decline of insect pollinators (Duchenne et al., 2020; Fox, 2013; Ollerton et al., 2014) and biodiversity (Robinson & Sutherland, 2002) in the UK, of bumble bees in Illinois (Grixti et al., 2009), and of butterflies and waterfowl within the same geographic range of our study (Lark et al., 2020). Of the 13 species analysed, five showed an increase in predicted occurrence given agricultural conditions in the landscape (1870–2017), whereas eight species declined, indicating that some species benefit from current conditions while others struggle. Those species in decline are also found to be in decline elsewhere, including in individual state analyses within our study region (Grixti et al., 2009; Wood et al., 2019), the US East coast (Jacobson et al., 2018; Richardson et al., 2018), Canada (Colla & Packer, 2008) and North America (Cameron et al., 2011; Colla et al., 2012), generally. For the federally endangered *B. affinis*, most counties showed no net change in predicted occurrence along with some increases in northerly areas of the study region. It is possible that interest and participation in the Bumble Bee Watch programme has resulted in higher reporting of rare species, but this is unlikely given that model predictions were nearly identical when the Bumble Bee Watch data were excluded (Figure S3). Moreover, our analysis was not designed to explore changes in range, but rather focused on changes where species were present. As such, the range contractions noted elsewhere for *B. affinis* still warrant concern and additional research. For the remaining species of conservation concern (e.g. *B. pensylvanicus* and *B. terricola*), we observed declines in predicted occurrence over the study period, following patterns seen in other studies (Jacobson et al., 2018; Wood et al., 2019), indicating that these species warrant protection efforts to prevent further losses.

In addition to potentially direct effects of agricultural intensification on bees (e.g. increased insecticide exposure, Meehan & Gratton, 2015; Meehan et al., 2011), these changes in land cover are also associated with decreases in the amount of other natural habitats that support diverse floral resources (Brown & Schulte, 2011; Carvell et al., 2006; Scheper et al., 2014; Smith, 1998). A shift from the diverse cropping systems of the early- to mid-1900 s to largely monocultural systems in recent years has altered the temporal continuity of available floral resources and total pollen availability (Schellhorn et al., 2015, Timberlake et al. 2019), which negatively affects bumble bee health (Cameron & Sadd, 2020; Vaudo et al., 2015) and colony growth and development (Hass et al., 2018; Williams et al., 2012), and may be of particular concern for species with restricted diet breadths (Kleijn & Raemakers, 2008; Wood et al., 2019). Indeed, declines associated with agricultural intensification tended to be greater among species that are more specialised (e.g. *B. terricola*, *B. pensylvanicus*), while generalist species were often increasing (e.g. *B. impatiens*, *B. griseocollis*; Wood et al., 2019). This suggests that the loss of food plants (including both crops and wild plants) accompanying agricultural expansion may be an important driver of bumble bee declines. Future experimental investigations could be designed to explore, for example contemporary relationships between bumble bee abundance and gradients of agricultural intensity such as crop diversity and areal amount of agriculture, specifically in relation to food plant abundance and diversity, to reveal a more mechanistic understanding of how specific agricultural factors are impacting bumble bee populations (but also see Bartomeus et al. 2018, Martin et al. 2019). Additionally, population changes in other pollinating taxa, especially wild bees, may also be related to the increases in agricultural intensity described here (Bartomeus et al., 2013; Kennedy et al., 2013). For example phylogenic analyses have revealed how intensive agricultural landscapes shape the community structure of wild bees (Grab et al., 2019). Compiling occurrence records for other wild bee species with sufficient spatiotemporal data coverage would allow a more thorough assessment of the impacts of agricultural intensification on pollinators writ large.

The contrasting patterns revealed in this study suggest opportunities for bumble bee conservation even within predominately agricultural landscapes. Such landscapes may still be supportive of both common and declining bumble bee species provided there is a high diversity of crops. Sirami et al., (2019) found a similar pattern for farmland biodiversity: increasing the diversity of crops and decreasing field size had a large, positive effect on multi-trophic indices of biodiversity. Our results provide additional evidence that agricultural landscape heterogeneity is key to supporting farmland biodiversity (Benton et al., 2003; Fahrig et al., 2011). It is important to note, however, that the ideal agricultural conditions for the occurrence of many of the bumble bee species we examined may have long since disappeared. As of 2017, the mean number of crops grown across all study counties was 6, half that of the early 1900 s. Combatting bumble bee population declines might involve programmes that incentivise diversifying agricultural landscapes, especially including those crops that may support bees (e.g. cover crops, Mallinger et al., 2019; Schulte et al., 2017; Wilson et al., 2017). Such efforts would not only benefit bumble bees and biodiversity generally but may also provide economic relief to growers experiencing plummeting profits from corn and soybean (USDA 2018) without negatively impacting major crop yields (Tamburini et al. 2020).

Other factors that have changed in the last century, such as climate change (Kerr et al., 2015; Soroye et al., 2020) and pathogen spillover from greenhouse operations (Colla et al., 2006; Szabo et al., 2012), have also been associated with bumble bee declines. However, the contribution of increasing agricultural intensity to changes in bumble bee occurrence appears distinct. Rising global temperatures over the last century have been linked to the widespread, gradual decline in bumble bee species richness (Kerr et al., 2015; Soroye et al., 2020), while the declines in occurrence reported here seem to be more abrupt, occurring largely after the 1950 s. Additionally, pathogen spillover from commercial bumble bees in managed greenhouse operations is cited as another key factor driving bumble bee declines (Cameron et al., 2011; Colla et al., 2006; Szabo et al., 2012), but the timing of observed declines linked to agricultural intensification predate the commercialisation of bumble bee pollination in the late 1980 s (Velthuis & Doorn, 2006) as well as the expansion of greenhouse pollination of crops such as tomato in the USA (Szabo et al., 2012). Given that there is still unexplained variance (our models accounted for

15–69%), additional factors influencing insect populations could be explored in future studies (Duchenne et al., 2020). Ultimately, the loss of suitable habitat via agricultural intensification, changing climatic norms, and the recent expansion of pathogens from commercial operations likely act synergistically in contributing to the decline of bumble bees in the USA and elsewhere (Goulson et al., 2015).

CONCLUSIONS

Over the last 130 years, agricultural intensification has negatively impacted natural animal populations. Our study found support for the hypothesis that agricultural intensification has contributed to changes in bumble bee occurrence and community composition over the last century in the Midwest USA, in line with reports of broad arthropod declines in other agriculturally dominated landscapes (Hallmann et al., 2017; Seibold et al., 2019). However, we also show that this effect appears to be mediated by the richness of crop types, or other factors associated with them, in the landscape. The combination of our historical analysis along with a growing body of observational and experimental evidence suggests that changes to agricultural practices and policies that promote agricultural diversification at the landscape scale are a potential avenue for limiting additional declines of bumble bees in agricultural landscapes.

DATA AND AVAILABILITY STATEMENT

All data and R code used to curate data and conduct analyses are available on FigShare at 10.6084/m9.figshare.14461828.

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AUTHORS' CONTRIBUTIONS

JH and CG conceived of the study. MC provided geocorrected agricultural census data, JH performed the analysis, JH wrote the initial manuscript, JH, CG and MC contributed to subsequent drafts.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13786.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at: https://doi.org/10.6084/m9.figshare.14461828.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1.

Calculating bumble bee relative abundance

In order to estimate changes in bumble bee occurrence over time, we calculated the relative abundance of each species within each county by agricultural census year. Bumble bee records were associated with the closest agricultural census year (see section below 'Pairing bumble bee records with historical agriculture data set'), and we divided the total number of records of a given species by the total number of records for all species within each county-census year combination. We only calculated relative abundance where species were observed (i.e. no pseudo-absences were used). Additionally, we limited our analysis to only include county-year combinations with greater than five total bumble bee records to eliminate counties with limited sampling effort and where low numbers may artificially inflate the relative abundance of given species.

CALCULATING TEMPORAL PATTERNS OF DIVERSITY

To estimate how bumble bee species richness changed over time, we rarefied bee records to generate estimates of mean species richness for several temporal bins. Records were split into a set number of bins ($n = 5, 8, 12$) such that each bin had approximately an equal number of observations. As such, bins varied in the number of years that were included for each bin. To determine if the number of bins used in analyses affected estimated species richness patterns, we split records into 5, 8 or 12 equal-record bins and calculated the estimated species richness for each bin with 95% confidence intervals using the *iNEXT* package (Hsieh et al., 2016). All temporal bin species accumulation rapidly reached an asymptote, indicating that sample sizes were sufficient to capture bumble bee community diversity within each bin (Figure S4). It is worth noting that in determining patterns of species richness over time, species richness and evenness are confounded by dominant species. That is as dominance increases, the chances of including rare species in a sample decrease. As such, an increase in dominance might signal that some species are in decline (see Figure S10).

We fit a generalised additive model (GAM) to examine the change in species richness as a function of time for each of the data sets binned to different temporal bin sizes. Because each time bin contained a different number of years, we used the midpoint of each bin as the value from which to construct the model. We also conducted a permutation test to determine if the correlation between species richness and time could have been observed by chance alone, given the small number of points with which to fit a GAM. Using the maximum number of permutations (given the number of bin time points), we randomly shuffled the temporal bin order, calculating the correlation between bin and species richness estimates in each permutation, with the p-value equalling the fraction of permuted correlation coefficients greater or less than the true chronological correlation coefficient.

Estimated species diversity trends were consistent regardless of the number of bins used (Figure S5), however, p-values varied with the number of bins (significant and marginally significant trend for 12 and 8 bins, respectively, but not for 5 temporal bins). We present results from the 12-bin analyses for estimation of species richness over time in order to portray the highest resolution of the estimated species richness pattern.

SPATIAL AND TEMPORAL AUTOCORRELATION

Because of the spatial nature of these data, we tested for spatial autocorrelation in model residuals. As the structure of each species GLM above contains the same counties from multiple agricultural census years, testing for spatial autocorrelation on the entire model is misleading as only spatial autocorrelation within a given agricultural census year may be problematic. As such, we used the agricultural census time period with the greatest number of records for a given species to test for spatial autocorrelation. For each species, we constructed a generalised linear model fitting relative abundance as a function of cropland proportion and number of crops as described above. We then tested model residuals for spatial autocorrelation using a Moran's I test in the *spdep* R package (Bivand et al., 2013, similar to Meehan et al., 2011, and Meehan & Gratton, 2015) using a p-value of 0.05 at the critical threshold. Of the 13 study species analysed, *B. affinis*, *B. impatiens*, *B. ternarius* and *B. vagans* showed significant spatial autocorrelation. To account for this, we fit spatial error models for these three species using the *spdep* package and used the GLM framework for the remaining species. We chose spatial error models given the results of Legrange multiplier tests, similar to Meehan et al., (2011). As the spatial models constructed are unable to be used with the *interactions* package, we compared prediction results from the GLM and spatial models and determined, as most values were nearly identical (95% ±0.05 of one another), to use GLM models for visualisation of predictor interactions.

We also tested for temporal autocorrelation within the residual response of each species in models from the entire span of the data set from 1870 to 2017. For each species model, we visually examined residuals plots and residual lag correlation values using the *acf* function in base R. As no species showed temporal autocorrelation across the range of the data set, we did not incorporate any temporal autocorrelation structure into our models.

VISUALISING MODEL RESULTS

Because significant interactions were the primary driver of our models, we present each model for each species as a series of interaction plots using the *interactions* and *jtools* R packages (Long, 2019, 2020). Briefly, the *interactions* package generates model predictions and confidence intervals across the temporal span of our data using the mean and ±1 standard deviation for values of cropland proportion and crop richness.

While model analyses suggest interactions between agricultural intensification variables and time, and these effects vary among species, we **also** examined how the actual variables were distributed across time and space to make spatiotemporal predictions of species occurrence. That is while some variables may be deemed to be statistically important in predicting species occurrence, these variables, or their combinations may be relatively rare, making them biologically less relevant across the landscape. We used our fitted models from 1870–2017 to predict species occurrence across our study area using county-level agricultural intensification metrics at each agricultural census year (19 total). County-level predictions were then visualised spatially to depict how bumble bee occurrence changed over time as a function of agricultural variables in each county (Figure S13). This allows us to examine how actual agricultural intensification variables present in this landscape at a particular time influence the occurrence probabilities of different bumble bee species.

We also plotted the change in predicted occurrence across all counties as a time series fitted by a simple generalised additive model (GAM) to show the temporal trend in species occurrence (Figure S9). To summarise the change in species occurrence for each county across all agricultural census time points in a single map, we took the predicted occurrence values for each species by county and fit a GAM with agricultural census year as a predictor and three-dimensional basis function to avoid over smoothing. For each species separately, if the model showed the effect of census year was not significant (p>0.05), then the species was deemed not showing any consistent temporal trend over time as a function of the agricultural intensification variables (i.e. no change). If the coefficient was significant (p<0.05), we then calculated the average of the first derivative across the temporal range of the smoothed GAM to determine the mean temporal trend of the GAM model. If this value was >0, predicted occurrence had increased whereas counties with a value <0 had decreased.