

1 **The fate of bumble bees in the north-central**

2 **United States is linked to historical patterns of**

3 **agricultural intensification**

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8 **Abstract**

9 The decline of North American bumble bees has been tentatively linked to changes in agri-
10 cultural practices over the last century. Researchers posit that a switch from the diverse and
11 less intensive agricultural systems of the early 1900's to the largely monocultural, heavy-input
12 systems of today has impacted both nesting habitat and floral resource availability with neg-
13 ative consequences for bumble bee populations and communities. Despite several long-term
14 analyses highlighting concerning population trends, no studies have yet explicitly linked met-
15 rics of agricultural intensification to bumble bee declines. Using an extensive long term set of
16 both bumble bee and US agricultural census records, we show that metrics of agricultural in-
17 tensity, specifically an increase in proportion of cropland and insecticides as well as a decrease
18 in crop richness and pasture, are clearly associated with the decline of nearly half of bumble bee
19 species in the north-central US. Additionally, we document positive species associations with
20 crop richness and specific metrics such as proportion pasture even under areas of intensive
21 cultivation, suggesting that bumble bee declines are linked to not just the extent of agriculture,
22 but rather the practices implemented on the ground. In addition to spurring future avenues
23 for controlled, manipulative experiments, our results suggest that changes to our agricultural
24 practice and policies are required in order to limit additional declines of Midwestern bumble
25 bees.

26 Significance statement

*27 Authors must submit a statement of no more than 120 words about the significance of their research paper
28 written at a level understandable to an undergraduate-educated scientist outside their field of specialty. The
29 primary goal of the Significance Statement is to explain the relevance of the work in broad context to a broad
30 readership. Significance statements are not required for Brief Reports.*

*31 Recently documented declines of beneficial insects, specifically pollinators, within agricultural
32 landscapes threatens to reduce farmland productivity and suggests that agricultural practices are
33 responsible. Until now, a lack of historical data on important taxa, such as bumble bees, and
34 agricultural practices have limited our ability to test agriculture's role in pollinator declines over
35 time. Here, we use 140 years of bumble bee and agricultural production records to show that
36 metrics of agricultural intensification are strong predictors of bumble bee fate. Declines are not
37 only linked to the extent of agricultural land, but to the manner in which agriculture is practiced on
38 the ground; increasing crop diversity and limiting insecticide use could provide the most benefit
39 to struggling bumble bees. (118 words)*

40 Introduction

*41 Habitat loss via human alteration of terrestrial landscapes is cited as a principle cause of biodiversity
42 declines worldwide (Foley et al. 2005, 2011; Klein et al. 2007; Tilman et al. 2011; Tscharntke
43 et al. 2012). Of human alterations, the intensification of agriculture has been associated with the
44 extensive loss of a number of ecosystem service providing taxa (e.g., birds Benton et al. 2002;
45 Robinson and Sutherland 2002; Meehan, Hurlbert, and Gratton 2010), and there is circumstantial
46 evidence that agricultural practices are driving the recently documented, large-scale decline
47 of insects (Hallmann et al. 2017; Seibold et al. 2019). Pollinating insects, specifically bees, have
48 been particularly hard-hit, sounding an alarm among conservationists across the world (Steffan-
49 Dewenter et al. 2005; Tylianakis 2013).*

*50 Bumble bees (Apidae: Bombus) are among the most well-studied insect taxa with reports of many
51 species declining across Europe and North/South America (Biesmeijer 2006; Colla and Packer
52 2008; Grixti et al. 2009; Cameron et al. 2011; Bartomeus et al. 2013; Morales et al. 2013; Wood*

53 et al. 2019). Studies consistently point to agricultural intensification (defined here as agricultural
54 practices leading to expansive monocultures associated with high inputs of agrichemicals and
55 disturbances) as a key driver of bumble bee population decline [Grixiti et al. (2009); Goulson2015c].
56 Intensification includes both attributes within a farming system (i.e., pesticide use, number and
57 types of crops used), and the effects on agricultural landscapes (i.e., amount of land in cultivation).
58 Despite the suspected threat of agricultural intensification on bumble bees, no studies have yet
59 tied long-term patterns of agriculture and bumble bees owing to a paucity of long-term data of
60 both bumble bee occurrence and historical agricultural patterns at large spatial scales.

61 While contemporary studies examining bumble bee responses to agriculture provide some in-
62 sight, context from historical data, such as museum records, is essential to provide an accurate,
63 data-driven diagnosis of bumble bee decline, as well as provide possible solutions that may elude
64 experimental approaches (Meehan et al. 2011). While unable to draw specific causal connections,
65 several statistical approaches have been developed to account for known biases in the analysis
66 of museum collections (Pearce and Boyce 2006; Bartomeus et al. 2013, 2019). The continued ad-
67 dition of collection records to repositories such as the Global Biodiversity Information Facility
68 (GBIF) combined with modern, extensive surveys of bumble bee fauna (e.g., Bumble Bee Watch,
69 iNaturalist) offer a wealth of species-specific spatial distribution patterns. Moreover, new data
70 describing detailed agricultural production trends in the United States (Crossley et al. in review)
71 permit multi-species exploration of the drivers of change for bumble bee populations, allowing us
72 a unique opportunity to address the question: do patterns in historical agricultural intensification
73 predict the current fate of bumble bee species?

74 To this end, we explore the relationships between long-term bumble bee population trends and
75 historical patterns of agricultural intensification in the north-central US using an extensive data set
76 of historical bumble bee museum records, modern citizen-science surveys and ~~an unprecedented~~
77 dataset of agronomic metrics recently digitized from United States Census of Agriculture over
78 the period 1870-2018. To the above question, we hypothesized that increasing levels agricultural
79 intensification as measured by increasing cropland, number of crops grown, and the proportion
80 pasture and land treated with insecticides are associated with: (1) a decrease in the relative abun-
81 dance of species of conservation concern; and (2) **an increase in the relative abundance of species**

82 thought to be stable. 

83 Methods

84 We focused our study on the North Central US states of Minnesota, Wisconsin, Iowa, Illinois,
85 Michigan, and Indiana as these states share a similar biogeographic contexts and agricultural his-
86 tory. We limited our analysis to bumble bee species whose core ranges overlapped these states and
87  to limit comparisons of species at their range limits, including: *B. affinis* Cresson, 1863; *B. impatiens*
88 Cresson, 1863; *B. griseocollis* DeGeer, 1773; *B. bimaculatus* Cresson, 1863; *B. auricomus* Robertson,
89 1903; *B. ternarius* Say, 1837; *B. vagans* Smith, 1854; *B. borealis* Kirby, 1837; *B. citrinus* Smith, 1854; *B.*
90 *pensylvanicus*  De Geer, 1773; *B. fervidus* Fabricius, 1798; *B. rufocinctus* Cresson, 1863; and *B. terricola*
91 Kirby, 1837. *Bombus fraternus*, *B. perplexus*, *B. ashtoni (bohemicus)*, and *B. variabilis* were removed
92 from our analyses as these species lacked sufficient records to meaningfully interpret changes in
93 relative abundance and county occupancy over time. Of these, three species (*B. affinis*, *B. terri-
94 cola* and *B. pensylvanicus*) are known to be in decline nationally and are of particular conservation
95 concern (Colla and Packer 2008; Jacobson et al. 2018). All data cleanup, analyses, and plots were
96 conducted in R (Version 3.4.6,  ???).

97 Bumble bee record data

98 We obtained bumble bee records using the Global Biodiversity Information Facility (GBIF), query-
99 ing for all records within our study region. These data were combined with records from the North
100 American Bumble Bee Watch program (www.bumblebeewatch.org) provided by the Xerces Soci-
101 ety for Invertebrate Conservation. In total, 25,271 records were compiled from GBIF from 1877 to
102 2017 and 2,611 from Bumble Bee Watch from 2007 to 2018 for a total of 27,882 unique records over
103 358 of 535 total counties in the study region (Fig. S1). The species contained in each dataset were
104 mutually inclusive. We then filtered records to include only those which were appropriately geo-
105 referenced (i.e., having associated longitude and latitude). Each record was assigned to a county
106 based on its collection coordinates so that they could be matched to county-level agricultural cen-
107 sus data. Because 95% of records were from 1890 and beyond, we are confident that county assign-
108 ments are accurate, as changes in county geographic extent in this region were largely complete



¹⁰⁹ by 1890 [Crossley et al. in review].

¹¹⁰ Temporal comparisons of museum and incidental records can be problematic due to non-
¹¹¹ standardized collection techniques as well as collector and spatial biases (Bartomeus et al. 2013,
¹¹² 2019; Richardson et al. 2018). To account for this, we analyzed records using a variety of
¹¹³ techniques to control for potential biases. We filtered the dataset to include only single individual
¹¹⁴ ‘sampling events’ (unique combination of species, date, location, and collector), following
¹¹⁵ Richardson et al. (2018). All analyses presented below were conducted using both the full and
¹¹⁶ reduced datasets. As we found little impact in the analyses between the full and filtered dataset
¹¹⁷ (Appendix 1), we present results from the full dataset.

¹¹⁸ Calculating temporal patterns of diversity

¹¹⁹ We examined temporal trends in species diversity for our study region independent of the agricul-
¹²⁰ tural census (Grixti et al. 2009; Bartomeus et al. 2013; Richardson et al. 2018; Jacobson et al. 2018;
¹²¹ Wood et al. 2019). In this analysis, we used the approach of Bartomeus et al. (2013) and created
¹²² temporal bins of records such that there were approximately the same number of bee observations
¹²³ per temporal bin using quantiles and the rbin package. We created several binning strategies to
¹²⁴ determine if the number of bins affected our results (Bar¹²⁵meus et al. 2013), including a total of
¹²⁶ 5, 8, and 15 temporal bins. Because trends were similar regardless of the number of bins, we
present results from the 15-bin analyses for estimation of species richness over time.

¹²⁷ In order to estimate species richness changes over time, we rarefied records to generate estimates
¹²⁸ of mean species richness for each of 15 temporal bins with 95% confidence intervals using the
¹²⁹ iNEXT package (Hsieh, Ma, and Chao 2016). We then fit a linear model to determine if there
¹³⁰ was a statistically clear change in species richness over time. Because each time bin contained a
¹³¹ different number of years, we used the midpoint of each bin as the value from which to construct
¹³² the model. We also conducted a permutation test to determine a p-value for the relationship, as
¹³³ the assumption of normally distributed data for such a small sample may be violated. Over 1,000
¹³⁴ permutations, we randomly shuffled the temporal bin order, calculating the correlation between
¹³⁵ bin and species richness estimates in each permutation, with the p-value equaling the fraction of
¹³⁶ permuted correlations greater or less than the true chronological correlation value.

137 Estimating change in county occupancy

138 Changes in relative abundance may not fully capture declines if species remain stable in occupied
139 counties while the number of occupied counties decreases over time. To account for changes in
140 county-level occupancy (i.e., a proxy for range), we modeled the number of occupied counties
141 per equal-record temporal bin for each study species using a generalized linear model, predicting
142 number of counties as a function of temporal bin.

143 Historical agriculture data

144 To assess the extent, diversity, and intensity of agriculture, we used county-level agricultural cen-
145 sus data projected and geographically corrected by Crossley et al. (in review). Our objective was to
146 estimate county-level (n=535 counties) agricultural metrics, which included aspects of both exten-
147 sive and intensive farming practices. Following Crossley et al., we limited our analysis to the 18
148 most common crops which together represent a majority of cropland area study region (Crossley
149 et al. in review). For each county by census year, we calculated crop richness and the proportion
150 of county area in cropland as two measures of agricultural intensity.

151 We also extracted additional aspects of farm management hypothesized to be drivers of bumble
152 bee declines. These included acreage of specific agricultural land-uses and practices known to
153 affect bumble bees including pasture acreage and acreage treated with insecticides. Because these
154 two variables were not available across the same temporal range as crop richness and proportion
155 of county in cropland, we conducted a separate analysis from 1982 onward where pasture acreage
156 and insecticide-treated acreage were available at the county level. For our analyses, we converted
157 absolute values of pasture and insecticide-treated acreage to proportion of county area.

158 Pairing bumble bee records with historical agriculture dataset

159 Because agricultural census data are collected every decade, not every bumble bee record was
160 collected in a year concurrent with a census. Accordingly, we paired records such that they were
161 within \pm 5 years of the nearest agricultural census date (e.g., bumble bee records from 1926-1935
162 were paired with the 1930 agricultural census). While this pairing may not perfectly reflect the
163 state of agriculture experienced by collected bumble bees, we posit that it is still meaningful given

¹⁶⁴ that large, county-level changes in agricultural practices occurring over several decades are un-
¹⁶⁵ likely to manifest in time spans less than five years. To verify this assumption, we performed
¹⁶⁶ additional analyses with a stricter \pm 3-year pairing rule and found similar results (Appendix 2).
¹⁶⁷ We thus present the analysis with the full dataset and \pm 5-year pairing.

¹⁶⁸ Relating changes in relative abundance to agricultural intensity

¹⁶⁹ We constructed statistical models to examine whether changes in metrics of agricultural intensi-
¹⁷⁰ fication were related to bumble bee relative abundance. For each bumble bee species, we fit a
¹⁷¹ generalized linear model with a binomial error structure to predict county-level relative abun-
¹⁷² dance (for a given agricultural census year, number of records of a given species divided by total
¹⁷³ number of bumble bee records) as a function of number of crops grown within a county, the pro-
¹⁷⁴ portion of county area in agriculture and the year of the agricultural census data associated with
¹⁷⁵ that bumble bee record, allowing us to determine a temporal trend in species relative abundance
¹⁷⁶ while taking into account agricultural intensification. Observations were weighted by the num-
¹⁷⁷ ber of bumble bee records in a county by agricultural census year, effectively giving more weight
¹⁷⁸ to counties that had greater sampling intensity. We assumed that these counties provided more
¹⁷⁹ accurate estimates of species relative abundance at any given time. Additionally, we further lim-
¹⁸⁰ ited our analysis to ~~only~~ include county-by-year combinations with greater than 5 total bumble
¹⁸¹ bee records to eliminate the presence of counties with little sampling effort, and for which low
¹⁸² numbers may artificially inflate the relative abundance of given species.

¹⁸³ Because of the spatial nature of these data, we tested for spatial autocorrelation in the residuals
¹⁸⁴ using a Moran's I test in the `spdep` package (similar to Meehan et al. 2011; and Meehan and
¹⁸⁵ Gratton 2015). We also tested for temporal autocorrelation within the response of  h species.
¹⁸⁶ Because neither spatial nor temporal autocorrelation were ~~found to be problematic~~, we utilized
¹⁸⁷ the generalized linear model framework described above across all species.

¹⁸⁸ To illustrate the estimated change in relative abundance and range, we used our fitted models to
¹⁸⁹ predict occurrence across historical ranges of each species within our study area using county-
¹⁹⁰ level agricultural intensification metrics. These maps describe the predicted probability of occur-
¹⁹¹ rence in each county as  function of crop diversity and proportion of a county in cropland. We



192 selected 6 time points for which to fit models: 1870, 1900, 1930, 1959, 1974, and 2012 to depict how
193 county-level agricultural suitability for bumble bees has changed over time.

194 Another series of models were constructed to test additional hypothesized drivers of bumble bee
195 decline. Generalized linear models with a binomial error structure were fit to predict county-
196 level species relative abundance as a function of the proportion of county in pasture, proportion
197 of county treated with insecticides, and the agricultural census year. Because the agricultural
198 census did not begin capturing insecticide input data until 1982, these models were fit on a subset
199 of data from 1982 to present. By adding additional putative drivers to our original model, we
200 are able to see if the response of the proportion cropland and crop richness remains consistent
201 given additional drivers that may be collinear. If the responses remain consistent, it suggests
202 that the results from the long-term data set using only proportion cropland and crop richness
203 are important for explaining the patterns of bumble bee relative abundance observed even if the
204 additional drivers, pasture and insecticides, are also strong predictors. We examined variance
205 inflation factors (VIF) for each model to determine whether variables were problematically multi-
206 collinear. Finally, while a number of other drivers might be directly or interactively influence
207 bumble bee relative abundance [e.g., climate], other studies have shown independent effects of
208 land-use change and climate (Kerr et al. 2015; Soroye, Newbold, and Kerr 2020), suggesting that
209 it is sufficient to examine agricultural intensification metrics on their own.

210 Results

211 Changes in agricultural intensification

212 The areal extent of cropland peaked in the study region in 1950 ($45\% \pm 22\%$ of county area). Since
213 then, it has decreased almost 10% to an average of $34\% \pm 20\%$ (Fig. 3A,B). Agriculture has re-
214 mained relatively sparse in the north of our study region, while the highest intensity occurs in
215 the “corn belt” that stretches through southern Minnesota, Iowa, southern Wisconsin, central and
216 northern Illinois, and northern Indiana. Throughout the last century, the number of agricultural
217 crops grown has decreased (Fig. 3C,D). Of the 18 crops for which we compiled data, an average of
218 12 ± 1 were grown per county from 1880 - 1950. Since 1950, this number has declined 50%, with

²¹⁹ counties today growing on average 6 ± 1 crops.

²²⁰ The additional agricultural intensification variables we utilized showed diverging patterns, with
²²¹ proportion of pasture declining 90% from 1982 to present from an average of 3% of county area in
²²² 1982 to 0.3% in 2012, while the proportion of total county area treated with insecticides increased
²²³ 54% from an average of 11% of county area in 1982 to 17% in 2012. (Fig. S5). These changes
²²⁴ occurred over similar spatial extents, primarily concentrated in the corn-belt counties throughout
²²⁵ the middle of the study region.

²²⁶ Temporal changes in species richness & county occupancy

²²⁷ Rarefied species richness estimates for each temporal bin show a significant 20% decline in esti-
²²⁸ mated species richness over the study period, from approximately 15 to 12 species from 1824-1925
²²⁹ to present, respectively (Fig. 1, $t_{1,13} = 6.084$, $p = 0.0283$). All fifteen temporal bin species accumula-
²³⁰ tion curves rapidly reached an asymptote, indicating that sample sizes were sufficient to capture
²³¹ bumble bee community diversity within each bin (Fig. S2). A sharp drop in estimated species
²³² richness occurred between 1952 and 1959, followed by a slight rebound in the next 50 years. The
²³³ pattern of decreasing species richness persisted in coarser bin resolutions (Fig. S3).

²³⁴ Overall, species county occupancy patterns varied; roughly one third of species increased, re-
²³⁵ mained stable, and declined, respectfully (Fig. S4). Notably, all species of conservation concern 
²³⁶ showed decreases in county occupancy over time, despite an increase in sampling effort during
²³⁷ the later time periods.

²³⁸ Patterns of bumble bee relative abundance are related to agricultural intensity

²³⁹ Patterns in bumble bee relative abundance showed strong associations with agricultural intensi-
²⁴⁰ fication metrics. Overall, we found that  7 of 13 species decreased in relative abundance, while  3
²⁴¹ remained stable and 3 increased over the study period (Fig. 4, Table S1). These estimates of tem-
²⁴² poral change in relative abundance modeled concurrently with metrics of agricultural intensity
²⁴³ aligned well with changes estimated from generalized linear models fitted with time period as the
²⁴⁴ sole predictor (Appendix 3). Species increasing in relative abundance over time tended to be pos-
²⁴⁵ itively associated with increases in proportion of agriculture as well as crop richness (Fig. 4B,C).

246 Among species estimated to be in decline, the proportion of county in agriculture was negatively
247 associated with relative abundance in all but three species (Fig. 4B). The responses of declining
248 species to crop richness was generally positive, with a majority increasing in relative abundance
249 as crop richness increased (Fig. 4C).

250 When we used county-level agricultural statistics to predict the probability of species occurrence,
251 we saw a marked expansion of common species in space (e.g., *B. impatiens*, *B. bimaculatus*), whereas
252 probability of occupancy decreases across the region for many species, especially those of conserv-
253 ation concern (e.g., *B. terricola*, *B. affinis*, *B. pensylvanicus*, Fig. 3E-H, Fig. S6).

254 Models that included pasture and insecticide metrics, available from 1982 to present, also showed
255 clear patterns with relative abundance (Fig 4,D,E, Table S3). Pasture acreage had a consistently
256 positive association with relative abundance (Fig. 6D), although the acres of pasture per county
257 has markedly decreased over the last century (Fig. S4B). Proportion of county area treated with
258 insecticides had a consistently negative effect on species relative abundance, except for 3 species
259 that exhibited a positive response (Fig. 6E, *B. auricomus*, *B. impatiens*, and *B. pensylvanicus*) and
260 3 species which were positively associated with increased insecticide application (*B. affinis*, *B.*
261 *rufocinctus* and *B. vagans*). One species of conservation concern, *B. terricola*, had the strongest
262 negative relationship with proportion of county treated with insecticides.

263 Discussion

264 Using bumble bee observations recorded over 140 years across 6 north-central US states and an
265 novel dataset on the historical patterns of agricultural land use and practices (extent of cropland,
266 diversity of crops grown, extent of pasture, pesticide use), we explored the hypothesis that agricul-
267 tural intensification is associated with bumble bee declines. Our results support existing evidence
268 of bumble bee declines throughout the US and suggest that increases in agricultural intensification
269 favor a select few species at the expense of the majority.

270 In contrast to recent studies [e.g., Dornelas 2019], our analyses did not reveal a balance in the
271 number of increasing and decreasing bumble bee species. Of the 13 species analyzed, only 3 were
272 found to increase over the study dataset (1870-2017), while 3 remained at similar levels, and 7

273 were found to have declined in relative abundance. The declining species in our study  274 ~~those found to be in decline elsewhere~~, including in individual state analyses within our study 275 region (Grixti et al. 2009; Wood et al. 2019), the US East coast (Richardson et al. 2018; Jacobs 276 et al. 2018), Canada (Colla and Packer 2008), **and North America, generally** (Cameron et al. 2011; 277 Colla et al. 2012). A few species are of particular concern (e.g., *B. terricola* and *B. pensylvanicus*), 278 both of which we observed decline significantly in relative abundance and range extent over the 279 study period. The patterns of these species of concern match other studies (Jacobson et al. 2018; 280 Wood et al. 2019) and suggest that protection efforts are urgently needed.

281 Our results suggest that the extent of agricultural cultivation is not the sole predictor of the fate 282 of bumble bee species: the manner and pattern in which agriculture is practiced is key. With 283 few exceptions, species whose relative abundance was found to be increasing or stable had either 284 positive or neutral relationships with agricultural intensity metrics, while those in decline were 285 negatively associated with increased agricultural intensity. That is, some species (e.g., *B. impatiens*) 286 thrive in areas and/or times of intense cultivation, while others (e.g., *B. terricola*) struggle. Addi- 287 tionally, the land-use type (e.g., pasture) and an increased diversity of crops generally had positive 288 effects on bumble bee relative abundance, while inputs such as pesticides yielded positive effects 289 for only three species.

290 Given this, landscapes with a high areal extent of agriculture may still support both common and 291 declining bumble bee species provided there is a high diversity of crops, open habitats such as 292 pasture, and limited insecticide use. Sirami et al. (2019) found a similar pattern for farmland 293 biodiversity writ large: increasing the diversity of crops and decreasing field size had a large, 294 positive effect on indices of biodiversity. Our results provide additional evidence that agricultural 295 landscape heterogeneity is key to supporting farmland biodiversity (Benton, Vickery, and Wilson 296 2003; Fahrig et al. 2011).

297 An increase in proportion of agriculture and reduction crop richness may not be the direct causal 298 factors, but rather the consequences of these practices on the ground may indirectly impact bum- 299 ble bees. For example, agricultural intensification reduces diverse, landscape-scale floral habi- 300 tat such as tall-grass prairies [Smith (1998); Brown and Schulte (2011)] and bumble bee forage 301 plants (Carvell et al. 2006; Scheper et al. 2014), as well as increases insecticide use (Meehan et

302 al. 2011; Meehan and Gratton 2015). A shift from the diverse cropping systems of the early to
303 mid 1900's to largely monocultural systems in recent years has also altered the temporal conti-
304 nuity of available floral resources (Schellhorn, Gagic, and Bommarco 2015; ???) and total pollen
305 availability, which has been shown to negatively impact bumble bee colony development (Hass
306 et al. 2018). Some mass-flowering monocultures might benefit bumble bee colony growth (West-
307 phal, Steffan-Dewenter, and Tscharntke 2009), possibly sustaining species that can tolerate highly
308 variable temporal resources [Schmid-Hempel and Schmid-Hempel (1998); Hemberger et al. in re-
309 vision], however they provide little dietary diversity for foraging bees. Such a limit on pollen
310 and nectar diversity may have adverse consequences for bumble bee health (Vaudo et al. 2015),
311 especially those species with a limited diet breadth (Klein and Raemakers 2008; Wood et al. 2019).
312 Lastly, landscapes that restrict floral resource availability during key demographic periods might
313 limit bumble bee colony growth (Williams, Regetz, and Kremen 2012) and subsequent queen pro-
314 duction (Crone, Williams, and Letters 2016), reducing population stability over time.

315 Contrary to other longitudinal studies (Colla et al. 2012; Richardson et al. 2018), we found no ev-
316 idence of decline in the relative abundance of the federally endangered *B. affinis* across our study
317 region, however county occupancy, here a proxy for range, did decline significantly. Additionally,
318 when examining patterns of *B. affinis* decline across its entire range, there is clear evidence for ex-
319 tensive range reductions and local extirpations (Cameron et al. 2011; Colla et al. 2012). Inde the
320 subset of the range observed in our study has the most extensive modern records of *B. affinis*, sug-
321 gesting that our observed regional patterns may differ from range-wide population trends. Given
322 this, it is important to note that examining temporal patterns in relative abundance necessitates
323 that as one species' relative abundance increases, others must decrease. Relative abundance cannot
324 capture declines in absolute abundance, which may also be occurring simultaneously.


325 Care must be taken to account for biases associated with historical collections. For example, mu-
326 seum collection records do not necessarily adhere to standard ecological practices of ensuring ran-
327 dom, equal-effort samples over adequate space and time (Richardson et al. 2018). To account for
328 known issues, we employed a variety of techniques including subsampling and sensitivity anal-
329 yses to determine whether our chosen methods skewed results (for a thorough analysis of tech-
330 niques to leverage historical collections, see Bartomeus et al. 2019). Irrespective of the approaches

331 used, we consistently identified declines in over half of study species with clear associations to
332 metrics of agricultural intensity.

333 While there is much contemporary evidence for the consequences of agricultural intensification
334 on bumble bee communities, other variables may also be driving the observed shifts in abundance
335 and occupancy. For example, climate change has reduced bumble bee ranges in both North Amer-
336 ica and Europe (Kerr et al. 2015). In their analysis, Soroye, Newbold, and Kerr (2020) found that
337 climate impacted bumble bee occupancy, however land-use driven occupancy changes were in-
338 dependent from climate effects. That is to say that while climate may be driving large-scale range
339 shifts, land-use still has strong, negative effects on bumble bee occupancy – an effect that we show
340 strong evidence for here.



341 The scale and intensity of agricultural intensification over the last 60 years is unprecedented and
342 the risks to bumble bees clear, however it is important to place the observed changes in relative
343 abundance and county occupancy into a larger context. Examining changes from 1870 to present
344 day may not accurately capture the pre-European settlement baseline of the study species exam-
345 ined. By 1870, many counties were already extensively altered by both agriculture and deforesta-
346 tion (Rhemtulla, Mladenoff, and Clayton 2007). In some cases (e.g., Michigan), these alterations
347 may have provided more floral resources by creating open habitat, resulting in the increase of
348 some bumble bee species (Wood et al. 2019). In shifting from the agronomic practices of the early
349 20th century to the more industrialized, intensive practices of the later 20th century, the habitat
350 suitability for those previously favored bumble bees decreased paving way for the rise of others.

351 The lack of true historical baselines, however, does not mean that the declines described in this
352 study are normal or unworthy of immediate conservation action.



353 Conclusions

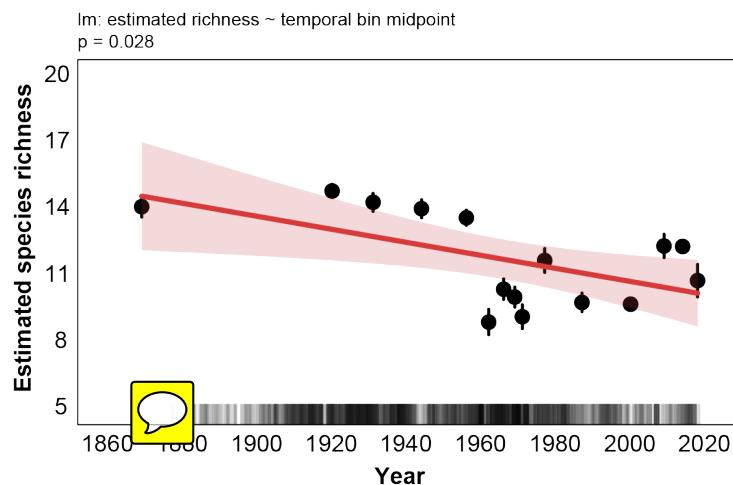
354 We provide the historical context of the extent and duration of bumble bee declines in a criti-
355 cal agricultural region of the US, further solidifying the evidence that agricultural intensification
356 is a key driver of shifts in community composition and abundance over the last century. Over
357 the last 140 years, agricultural intensification has elicited strong, selective pressures inadvertently
358 choosing winners and losers in bumble bee communities. Our work supports an existing body

359 of evidence, including recent, catastrophic declines in insect and arthropod abundance in agri-
360 culturally dominated landscapes (Hallmann et al. 2017; Seibold et al. 2019). The combination
361 of our historical analysis along with a growing body of observational and experimental evidence
362 suggests that changes to agricultural practice and policies are required in order to limit additional
363 declines of bumble bees in agricultural landscapes.

364 **Acknowledgements**

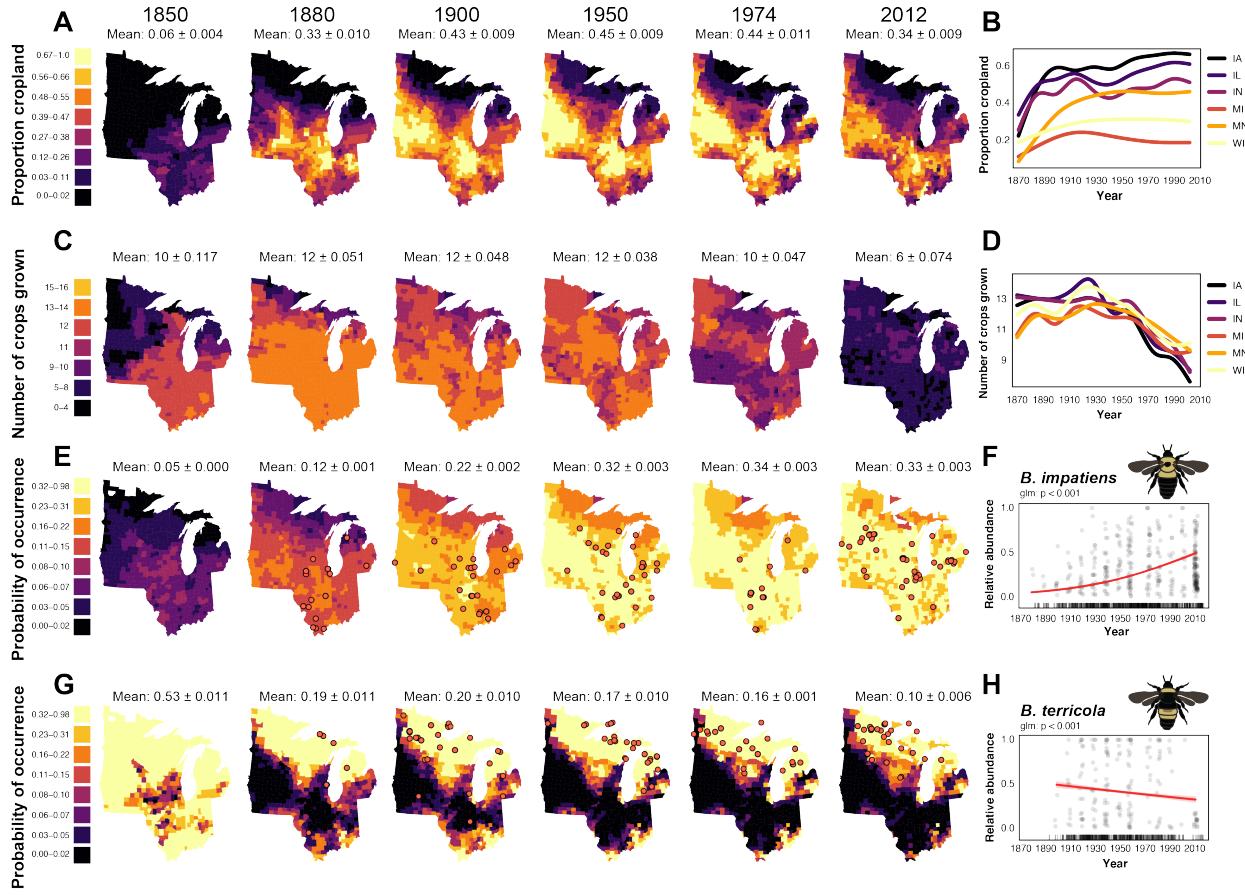
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368 Invertebrate Conservation for providing Bumble Bee Watch data. Data and code for all analyses,
369 figures, and the manuscript will be made publicly available upon publication at <https://github.com/jhemberger>.
370

³⁷¹ **Figures and Tables**



³⁷²

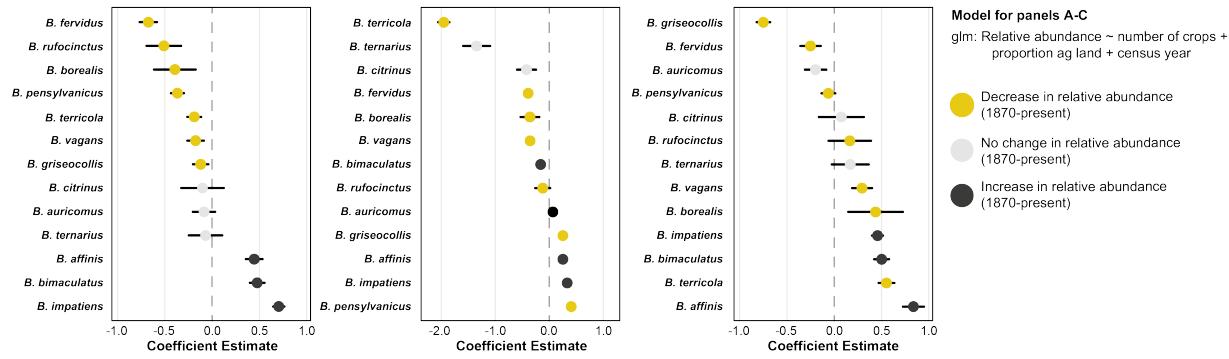
³⁷³ **Figure 1:** Trend in rarified bumble bee species richness from 1877-present. Each point represents a
³⁷⁴ date range that is standardized to contain an approximately equal number of bumble bee records
³⁷⁵ (thus the date range differs for each point), and it is plotted at the midpoint year of the date range.
³⁷⁶ Error bars are 95% confidence intervals. The fitted line is a linear model predicting estimated
³⁷⁷ species richness as a function of temporal bin order using the midpoint of the temporal bin as the
³⁷⁸ predictor. Carpet plot represents temporal collection year for all records from 1877 to present.



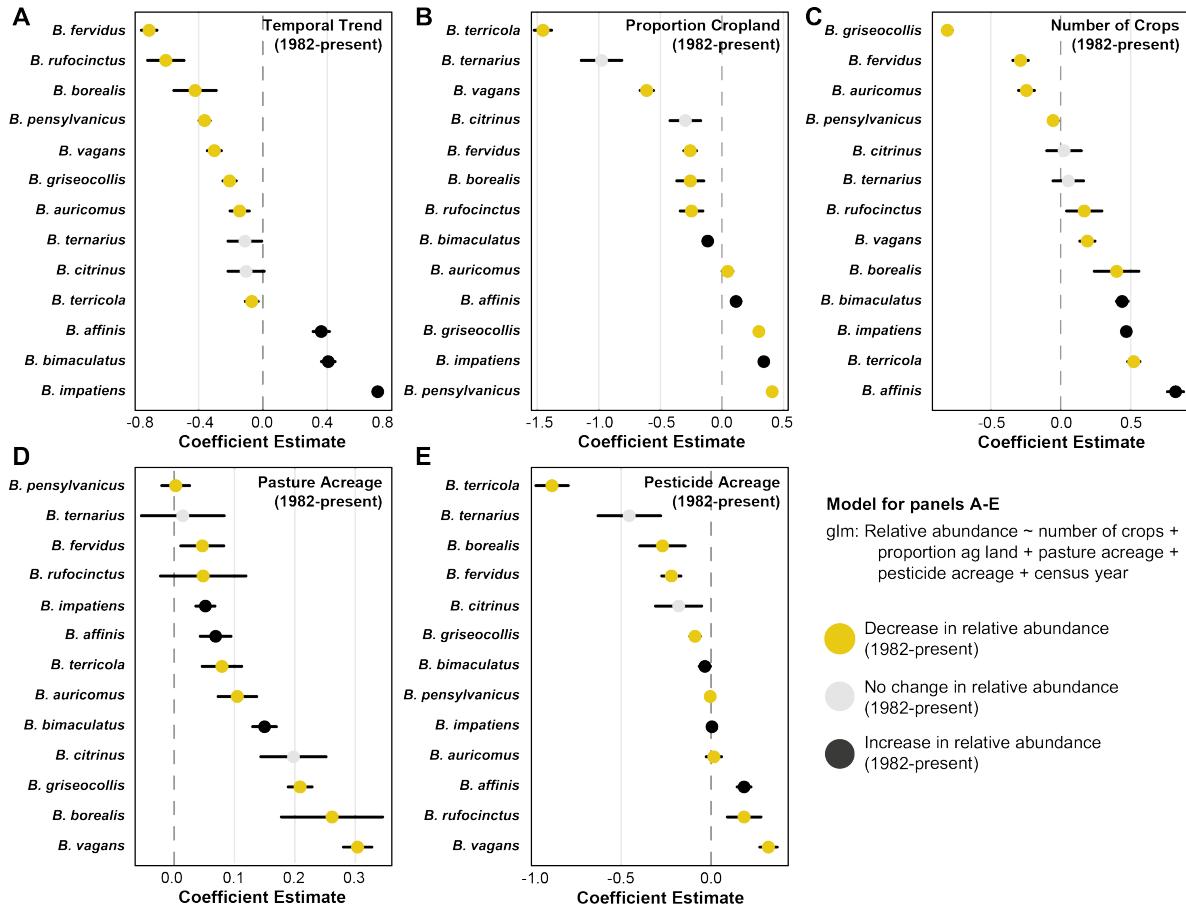
379

380 **Figure 2:** Patterns of agricultural intensification in two metrics: (A) proportion of county under
 381 cultivation and (C) number of crops grown per county. Inset graphs (B,D) depict general trend of
 382 these variables for each state in the study area as modeled by a Loess curve. Predicted probability
 383 of occurrence for two example species, *B. impatiens* (E,F) and *B. terricola* (G,H) in each county given
 384 crop diversity and proportion cropland in each county. Darker colors denote smaller probability of
 385 occurrence, while lighter colors indicate larger probability of occurrence. Red points on each map
 386 are randomly selected occurrence records with a maximum of 50 plotted per year. (F,H) Fitted
 387 temporal trend of relative abundance when modeled with agricultural intensity metrics. Solid
 388 red lines denote statistically clear trend in relative abundance over time ($p < 0.05$), while dashed
 389 lines denote statistically unclear trends ($p > 0.05$). Points on temporal trend are slightly jittered for
 390 visibility. Color palettes derived using quantile binning. Values above maps are mean \pm SEM for
 391 each response.

392



393 **Figure 3:** Fitted model coefficients ($\pm 95\%$ confidence interval) for the relative abundance of each
 394 study species for (A) temporal trend of the species, (B) proportion of county in cropland, and
 395 (C) the number of crops grown in a county. Models were fitted using the entire dataset from
 396 1870-present. The relative abundance trend from 1870-present (a) denotes point colors for b & c:
 397 yellow points are species whose relative abundance declined, gray points are no change in relative
 398 abundance, and black points denote increases in relative abundance.



399

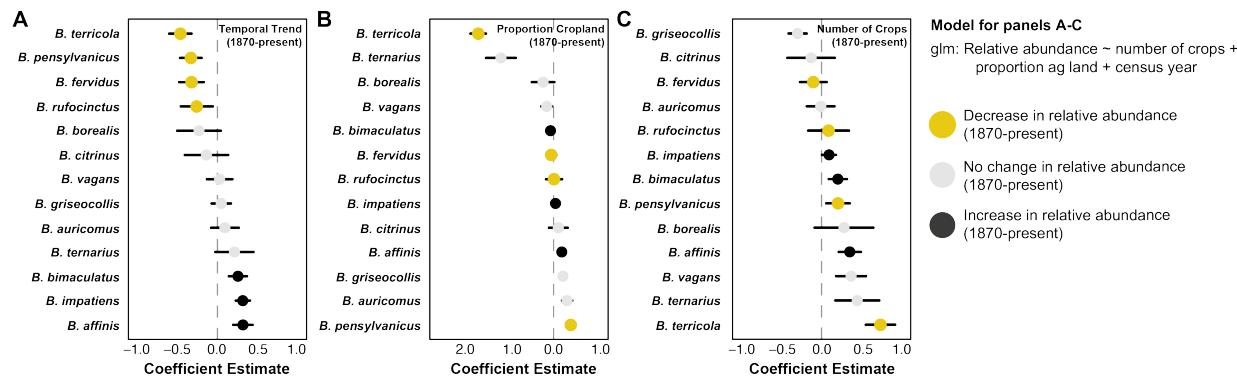
400 **Figure 4:** Fitted model coefficients ($\pm 95\%$ confidence interval) for each study species for (A) temporal trend of the species, (B) proportion of county in cropland, and (C) the number of crops grown in a county, (D) acres of pasture grown in a county, and (E) acres treated with insecticides. Models were fitted using data from 1982-present (only years for which pesticide and pasture acreage are available across all counties). Point colors indicate species relative abundance trend from 1982-present: yellow points denote species whose relative abundance declined, gray points denote no change in relative abundance, and black points denote increases in relative abundance.

407 **Supplementary Material**

408 **Appendix 1**

409 **Analysis filtering data to unique *species x location x collector x date* combinations**

410 To determine whether sampling effort by individuals skewed the results of our analysis, we
 411 fit our primary model ($\text{relative abundance} \sim \text{proportion cropland} + \text{number of crops} +$
 412 agricultural census year; results shown in Fig. 3) to a reduced dataset, filtering records to
 413 include only unique combinations of species, location, collector, and collection date. We found
 414 similar results in terms of the effect magnitude of predictors (proportion of cropland and number
 415 of crops), as well as the direction of the effect across study species (Fig. SA1.1).



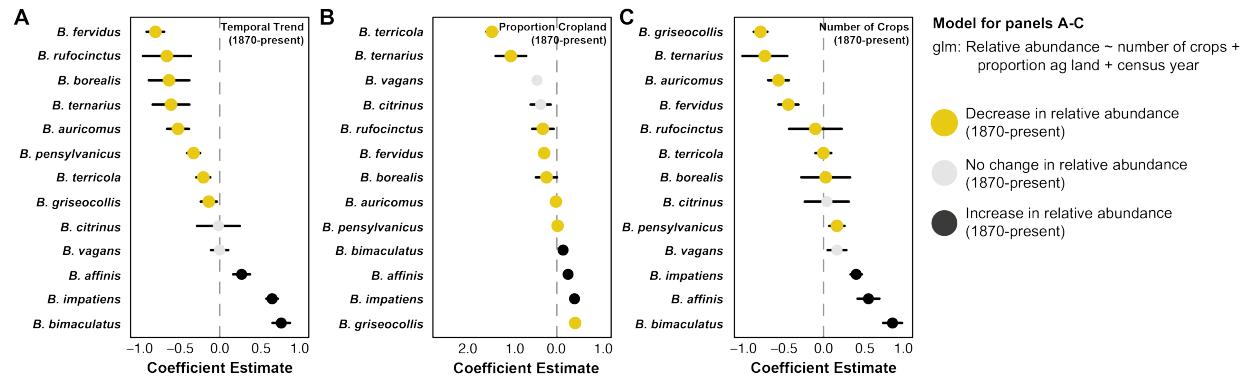
416

417 **Figure SA1.1** Fitted model coefficients ($\pm 95\%$ confidence interval) for each study species for (A)
 418 temporal trend of the species, (B) proportion of county in cropland, and (C) the number of crops
 419 grown in a county. Models were fitted using the entire dataset from 1870-present, but filtered to
 420 unique species x location x collector x date combinations. Point colors indicate species relative
 421 abundance trend from 1870-present: yellow points denote species whose relative abundance
 422 declined, gray points denote no change in relative abundance, and black points denote increases
 423 in relative abundance.

424 **Appendix 2**

425 **Analysis restricting to records within ± 2 years of agricultural census**

426 As agricultural census records are collected every 10 years, we were required to pair bumble bee
 427 records to the nearest agricultural census (a difference of up to ± 5 years). This requirement might
 428 skew results if agricultural metrics display non-linear trends between census years. To determine
 429 if this was the case, we filtered records such that only bumble bee within ± 2 years of an agri-
 430 cultural census data were included. Modeling these data resulted in broadly similar patterns of
 431 species relative abundance trends and response to proportion agriculture. The response of species
 432 to number of crops showed the effect magnitude increase for some species, but the rank order of
 433 species responses was mostly similar (Fig. SA2.1).



434

435 **Figure SA1.1** Fitted model coefficients ($\pm 95\%$ confidence interval) for each study species for (A)
 436 temporal trend of the species, (B) proportion of county in cropland, and (C) the number of crops
 437 grown in a county. Models were fitted using the entire dataset from 1870-present, but filtered to
 438 only include bumble bee records within ± 2 years of an agricultural census. Point colors indicate
 439 species relative abundance trend from 1870-present: yellow points denote species whose relative
 440 abundance declined, gray points denote no change in relative abundance, and black points denote
 441 increases in relative abundance.

442 **Appendix 3**

443 **Raw changes in species relative abundance over time**

444 For each species, we calculated relative abundance for each temporal bin as the number of records
445 of a given species divided by the total number of records for all species in that temporal bin.
446 We then tested whether there was a statistically clear change in relative abundance over time by
447 fitting generalized linear models with binomial error distributions for each species using time (i.e.,
448 temporal bin) as the sole predictor with each point weighted by the number of records (similar to
449 Bartomeus et al. 2013).

450 Of the 13 species included in our simple analysis of change in relative abundance over time, 6
451 saw statistically clear reductions in relative abundance: *B. borealis*, *B. fervidus*, *B. pensylvanicus*, *B.*
452 *rufocinctus*, *B. terricola*, *B. vagans* (Table S1). Similar to the patterns of estimated species richness,
453 reductions in the relative abundance of these declining species seem to begin in the middle of the
454 20th century. There were 7 species which increased in relative abundance over time period covered
455 by this dataset: *B. affinis*, *B. auricomus*, *B. bimaculatus*, *B. citrinus*, *B. griseocollis*, *B. impatiens*, and *B.*
456 *ternarius*.

457 **Table SA3.1:** Relative abundance estimates for each species across 8 time bins, sized in order to
458 contain approximately equal numbers of bumble bee records per bin. Coefficient estimates and p-
459 values derived from models fit to estimate trends in relative abundance over time, where relative
460 abundance of each species is predicted by time bin fit using a generalized linear model, with N
461 records representing the number of records for a given species.

Species	1900-1923	1924-1946	1947-1962	1963-1968	1969-1972	1973-1993	1994-2013	2013-present	N records	Coef. Estimate	P value
<i>B. affinis</i>	0.0118	0.0487	0.1133	0.2896	0.0123	0.0712	0.0637	0.1030	2155	0.049	p < 0.001
<i>B. auricomus</i>	0.0567	0.0191	0.0173	0.0153	0.0360	0.0180	0.0661	0.0432	894	0.069	p < 0.001
<i>B. bimaculatus</i>	0.0436	0.0249	0.1784	0.1499	0.0264	0.1236	0.2028	0.1238	2753	0.155	p < 0.001
<i>B. borealis</i>	0.0256	0.0139	0.0117	0.0019	0.0005	0.0027	0.0057	0.0175	254	-0.152	p < 0.001
<i>B. citrinus</i>	0.0055	0.0063	0.0098	0.0011	0.0057	0.0052	0.0094	0.0199	209	0.167	p < 0.001
<i>B. fervidus</i>	0.1300	0.0284	0.0221	0.0221	0.0104	0.0240	0.0350	0.0387	971	-0.190	p < 0.001
<i>B. griseocollis</i>	0.0764	0.0410	0.0303	0.0221	0.0705	0.0773	0.1862	0.1305	2111	0.224	p < 0.001
<i>B. impatiens</i>	0.0999	0.1514	0.1739	0.1644	0.5408	0.2572	0.1983	0.3519	6669	0.170	p < 0.001
<i>B. pensylvanicus</i>	0.1635	0.1949	0.1123	0.1351	0.2388	0.0560	0.0561	0.0072	3248	-0.213	p < 0.001
<i>B. rufocinctus</i>	0.0235	0.0350	0.0117	0.0046	0.0005	0.0006	0.0078	0.0381	400	-0.065	p = 0.003
<i>B. ternarius</i>	0.0321	0.0293	0.0081	0.0061	0.0017	0.0076	0.0507	0.0837	718	0.219	p < 0.001
<i>B. terricola</i>	0.0968	0.3045	0.2507	0.1599	0.0148	0.2666	0.0389	0.0133	3692	-0.224	p < 0.001
<i>B. vagans</i>	0.1099	0.0383	0.0443	0.0217	0.0357	0.0755	0.0782	0.0278	1395	-0.054	p < 0.001

462

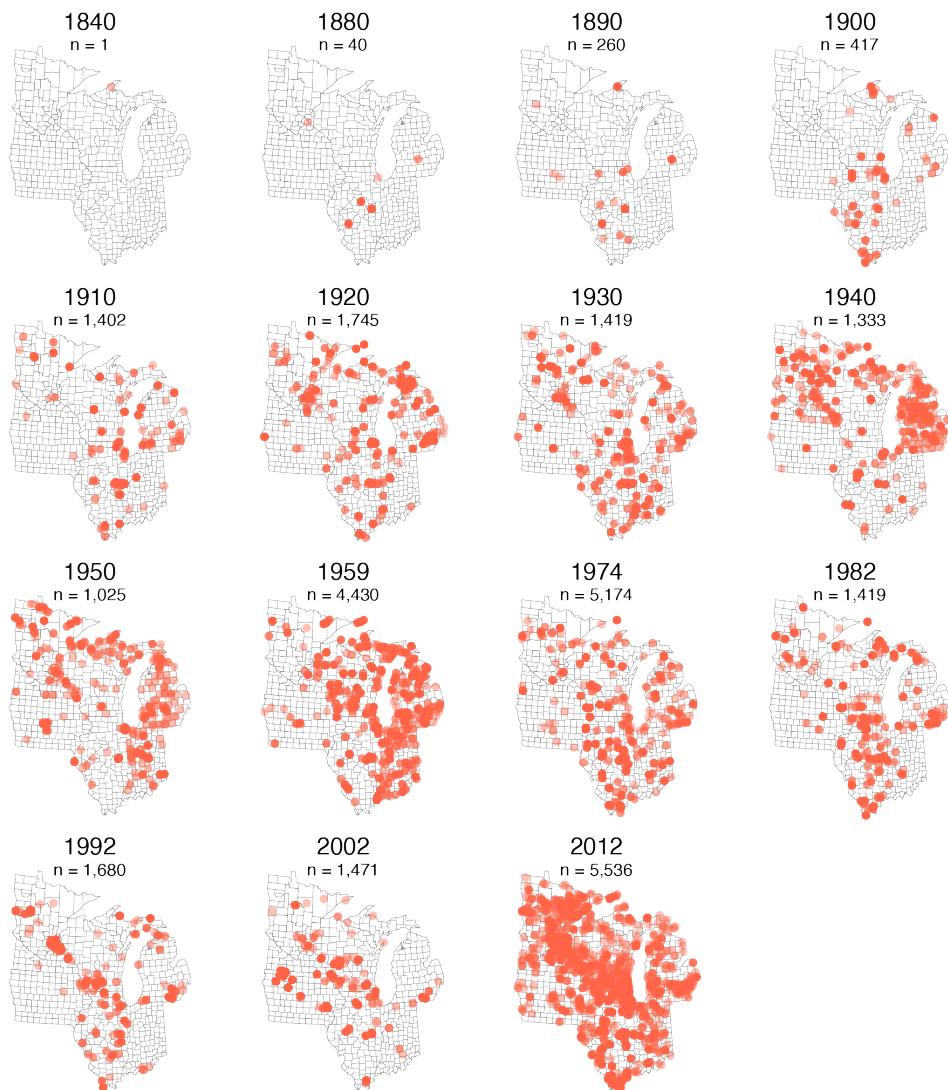
463 **Supplementary Table 1:** Generalized linear model results for each study species including the
 464 sample size (number of counties for which relative abundance is calculated), model term, scaled
 465 coefficient estimate, 95% confidence interval and p-value. Each county is weighted by the total
 466 number of bumble bee records for a given time point (agricultural census year).

Species	Sample size (n counties)	Model term	Coeff. Estimate	Lower 95% CI	Upper 95% CI	P value
<i>B. affinis</i>	181	Intercept	-1.489	-1.5439	-1.4344	< 0.001
		Number of crops	0.838	0.7264	0.9491	< 0.001
		Proportion cropland	0.252	0.1984	0.3058	< 0.001
		Census year	0.445	0.3569	0.5336	< 0.001
<i>B. auricomus</i>	139	Intercept	-2.602	-2.6682	-2.5336	< 0.001
		Number of crops	-0.198	-0.3111	-0.0843	< 0.001
		Proportion cropland	0.066	-0.0054	0.1371	0.07
		Census year	-0.086	-0.2039	0.0325	0.155
<i>B. bimaculatus</i>	252	Intercept	-1.675	-1.7168	-1.6327	< 0.001
		Number of crops	0.501	0.4221	0.5797	< 0.001
		Proportion cropland	-0.16	-0.2052	-0.1141	< 0.001
		Census year	0.477	0.3991	0.555	< 0.001
<i>B. borealis</i>	75	Intercept	-3.064	-3.2255	-2.9034	< 0.001
		Number of crops	0.437	0.1483	0.726	0.003
		Proportion cropland	-0.357	-0.5315	-0.1834	< 0.001
		Census year	-0.395	-0.6152	-0.1739	< 0.001
<i>B. citrinus</i>	71	Intercept	-3.959	-4.1093	-3.8095	< 0.001
		Number of crops	0.074	-0.1639	0.3128	0.54
		Proportion cropland	-0.421	-0.5967	-0.2445	< 0.001
		Census year	-0.102	-0.3265	0.1234	0.376
<i>B. fervidus</i>	139	Intercept	-2.769	-2.8427	-2.6953	< 0.001
		Number of crops	-0.251	-0.3588	-0.1434	< 0.001
		Proportion cropland	-0.391	-0.4661	-0.3152	< 0.001
		Census year	-0.675	-0.7671	-0.5832	< 0.001
<i>B. griseocollis</i>	243	Intercept	-1.878	-1.9252	-1.8313	< 0.001
		Number of crops	-0.75	-0.8218	-0.6782	< 0.001
		Proportion cropland	0.252	0.208	0.2956	< 0.001
		Census year	-0.121	-0.2034	-0.039	0.004
<i>B. impatiens</i>	382	Intercept	-0.814	-0.8449	-0.7823	< 0.001
		Number of crops	0.457	0.399	0.5157	< 0.001
		Proportion cropland	0.332	0.2991	0.3645	< 0.001
		Census year	0.706	0.6462	0.7653	< 0.001
<i>B. pensylvanicus</i>	236	Intercept	-1.468	-1.5102	-1.4266	< 0.001
		Number of crops	-0.062	-0.1352	0.0111	0.096
		Proportion cropland	0.408	0.3643	0.4515	< 0.001
		Census year	-0.367	-0.4362	-0.298	< 0.001
<i>B. rufocinctus</i>	71	Intercept	-2.482	-2.6112	-2.3521	< 0.001
		Number of crops	0.164	-0.061	0.3888	0.153
		Proportion cropland	-0.12	-0.2593	0.019	0.091
		Census year	-0.511	-0.6936	-0.3276	< 0.001
<i>B. ternarius</i>	78	Intercept	-2.309	-2.4522	-2.1656	< 0.001
		Number of crops	0.169	-0.0269	0.3646	0.091
		Proportion cropland	-1.344	-1.5936	-1.0944	< 0.001
		Census year	-0.07	-0.2471	0.1079	0.442
<i>B. terricola</i>	202	Intercept	-0.879	-0.9419	-0.8155	< 0.001
		Number of crops	0.553	0.4693	0.6361	< 0.001
		Proportion cropland	-1.953	-2.0583	-1.8485	< 0.001
		Census year	-0.189	-0.2622	-0.1153	< 0.001
<i>B. vagans</i>	166	Intercept	-2.421	-2.4831	-2.3592	< 0.001
		Number of crops	0.295	0.1889	0.4002	< 0.001
		Proportion cropland	-0.355	-0.4213	-0.2883	< 0.001
		Census year	-0.175	-0.2625	-0.0875	< 0.001

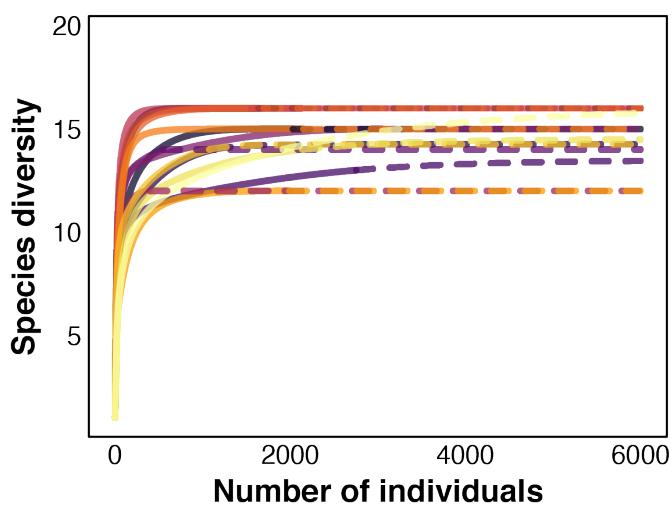
467

468 **Supplementary Table 3:** Generalized linear model results for each study species including the
 469 sample size (number of counties for which relative abundance is calculated), model term, scaled
 470 coefficient estimate, 95% confidence interval and p-value. Each county is weighted by the total
 471 number of bumble bee records for a given time point (agricultural census year).

Species	Sample size (n counties)	Model term	Coeff. Estimate	Lower 95% CI	Upper 95% CI	P value
<i>B. affinis</i>	80	Intercept	-1.833	-1.9203	-1.7451	< 0.001
		Number of crops	0.3	0.1794	0.4204	< 0.001
		Proportion cropland	0.493	0.3898	0.5967	< 0.001
		Pasture acres	0.052	-0.0355	0.1402	0.243
		Pesticide acres	-0.128	-0.2364	-0.0202	0.02
		Census year	0.447	0.3174	0.5768	< 0.001
<i>B. auricomus</i>	78	Intercept	-2.478	-2.5791	-2.3765	< 0.001
		Number of crops	0.176	0.0464	0.3052	0.008
		Proportion cropland	0.498	0.3703	0.626	< 0.001
		Pasture acres	-0.106	-0.2327	0.0199	0.099
		Pesticide acres	0.049	-0.061	0.1589	0.383
		Census year	0.337	0.1691	0.5045	< 0.001
<i>B. bimaculatus</i>	139	Intercept	-1.441	-1.5022	-1.3802	< 0.001
		Number of crops	0.004	-0.082	0.0901	0.926
		Proportion cropland	0.053	-0.0318	0.1379	0.22
		Pasture acres	0.252	0.1898	0.3147	< 0.001
		Pesticide acres	-0.063	-0.1473	0.0209	0.141
		Census year	-0.006	-0.1051	0.0923	0.899
<i>B. borealis</i>	33	Intercept	-5.188	-6.3871	-3.9899	< 0.001
		Number of crops	0.397	-0.0076	0.8024	0.054
		Proportion cropland	0.027	-0.364	0.4175	0.893
		Pasture acres	0.326	-0.2127	0.8654	0.235
		Pesticide acres	-0.653	-1.1265	-0.1791	0.007
		Census year	1.919	0.5472	3.2903	0.006
<i>B. citrinus</i>	39	Intercept	-3.735	-3.962	-3.5075	< 0.001
		Number of crops	-0.064	-0.3984	0.2709	0.709
		Proportion cropland	0.466	0.1761	0.7563	0.002
		Pasture acres	0.671	0.2321	1.1092	0.003
		Pesticide acres	-0.409	-0.7258	-0.0931	0.011
		Census year	1.024	0.5418	1.5056	< 0.001
<i>B. fervidus</i>	62	Intercept	-2.666	-2.7807	-2.5508	< 0.001
		Number of crops	0.275	0.1306	0.419	< 0.001
		Proportion cropland	0.188	0.0424	0.334	0.011
		Pasture acres	0.086	-0.064	0.2359	0.261
		Pesticide acres	-0.323	-0.4942	-0.1516	< 0.001
		Census year	0.237	0.0607	0.413	0.008
<i>B. griseocollis</i>	141	Intercept	-1.36	-1.4218	-1.2984	< 0.001
		Number of crops	-0.355	-0.4254	-0.284	< 0.001
		Proportion cropland	0.704	0.6345	0.7736	< 0.001
		Pasture acres	0.202	0.1348	0.2692	< 0.001
		Pesticide acres	-0.26	-0.3333	-0.1876	< 0.001
		Census year	0.351	0.2523	0.4497	< 0.001
<i>B. impatiens</i>	170	Intercept	-0.951	-1.0024	-0.8997	< 0.001
		Number of crops	0.315	0.2456	0.3835	< 0.001
		Proportion cropland	0.326	0.2567	0.3958	< 0.001
		Pasture acres	0.175	0.1182	0.2311	< 0.001
		Pesticide acres	-0.152	-0.2214	-0.0817	< 0.001
		Census year	0.403	0.3256	0.4806	< 0.001
<i>B. pensylvanicus</i>	60	Intercept	-2.434	-2.5546	-2.3126	< 0.001
		Number of crops	-0.454	-0.6375	-0.2702	< 0.001
		Proportion cropland	0.388	0.2457	0.5297	< 0.001
		Pasture acres	-0.147	-0.2778	-0.0166	0.027
		Pesticide acres	-0.458	-0.6145	-0.3008	< 0.001
		Census year	-0.228	-0.4534	-0.0024	0.048
<i>B. rufocinctus</i>	32	Intercept	-2.536	-3.777	-1.2947	< 0.001
		Number of crops	-0.243	-0.5282	0.043	0.096
		Proportion cropland	-0.386	-0.7505	-0.0224	0.037
		Pasture acres	0.563	0.2511	0.8758	< 0.001
		Pesticide acres	0.05	-0.2375	0.3369	0.734
		Census year	-0.362	-1.6648	0.9398	0.585
<i>B. ternarius</i>	41	Intercept	-2.71	-2.9336	-2.4871	< 0.001
		Number of crops	0.257	0.0461	0.4674	0.017
		Proportion cropland	-1.624	-2.0569	-1.1906	< 0.001
		Pasture acres	0.959	0.7542	1.1642	< 0.001
		Pesticide acres	0.033	-0.2966	0.3625	0.844
		Census year	2.206	1.7917	2.6211	< 0.001
<i>B. terricola</i>	40	Intercept	-1.252	-1.4001	-1.1043	< 0.001
		Number of crops	-0.431	-0.641	-0.22	< 0.001
		Proportion cropland	-0.295	-0.6203	0.0304	0.076
		Pasture acres	1.609	1.4077	1.811	< 0.001
		Pesticide acres	-1.642	-1.9395	-1.3436	< 0.001
		Census year	-1.352	-1.7384	-1.3657	< 0.001
<i>B. vagans</i>	75	Intercept	-2.416	-2.5271	-2.3041	< 0.001
		Number of crops	0.852	0.6945	1.0099	< 0.001
		Proportion cropland	0.041	-0.0785	0.16	0.503
		Pasture acres	-0.167	-0.3003	-0.0334	0.014
		Pesticide acres	-0.276	-0.4188	-0.1339	< 0.001
		Census year	-0.028	-0.1612	0.1049	0.678

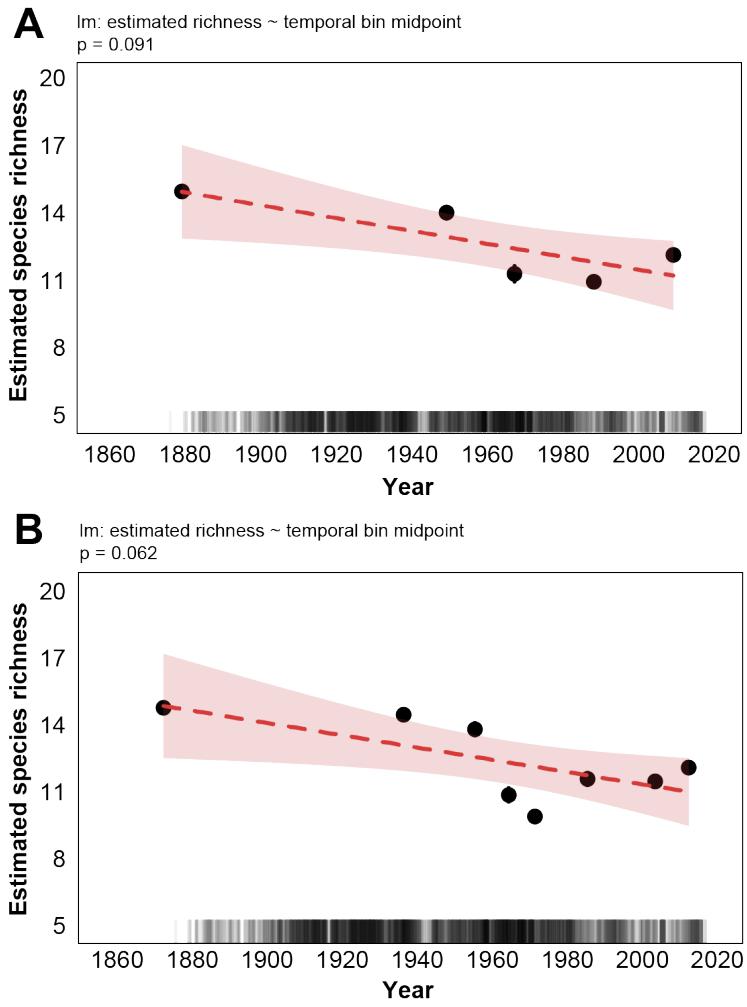


474 **Supplementary Figure 1:** The location of bumble bee records for each US Census of Agriculture
 475 year considered in our analysis. The number of records is noted below the year. Points are partially
 476 transparent and jittered slightly for visibility.



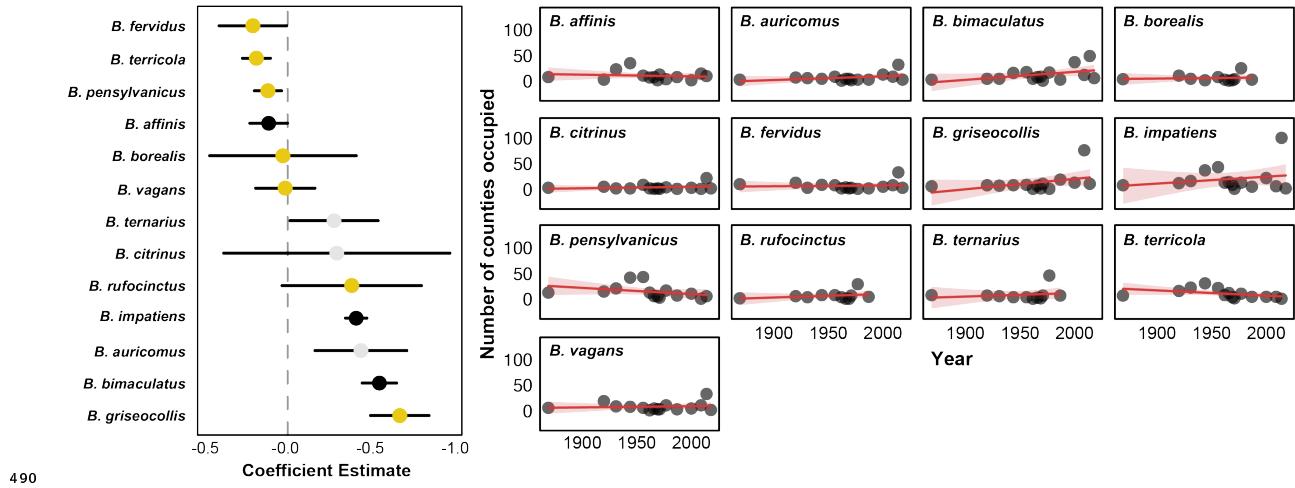
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478 **Supplementary Figure 2:** Sample-based species accumulation curves for each of 15 temporal bins
 479 (different colors) from which estimated species richness was calculated (Fig. 1). Each accumula-
 480 tion curve is constructed for temporal bins with a roughly equal number of records. Solid lines
 481 are interpolated from data, while dashed lines are extrapolated to a 6,000 record limit.

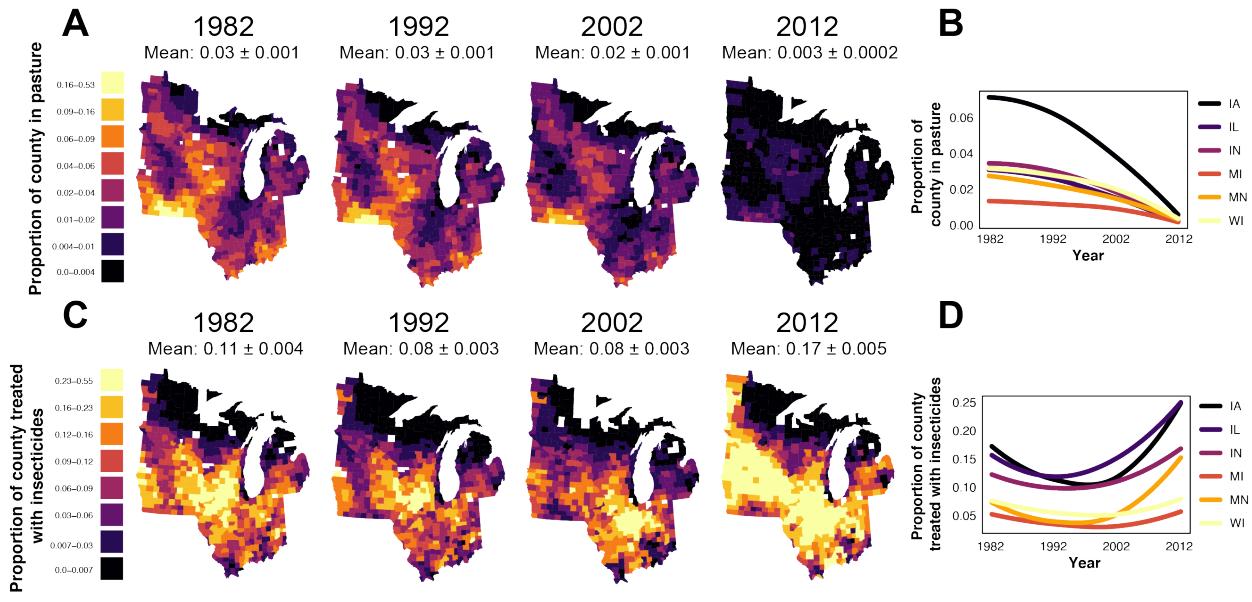


482

483 **Supplementary Figure 3:** Trend in rarified bumble bee species richness from 1877-present for al-
 484 ternative numbers of temporal bins, each representing approximately equal numbers of bumble
 485 bee records: (A) 5 temporal bins and (B) 8 temporal bins. Each point is plotted at the midpoint
 486 of the temporal bin date range. Error bars are 95% confidence intervals. The fitted line is a linear
 487 model predicting estimated species richness as a function of temporal bin order using the mid-
 488 point year of the temporal bin as the predictor. Carpet plot represents temporal collection year for
 489 all records from 1877 to present.

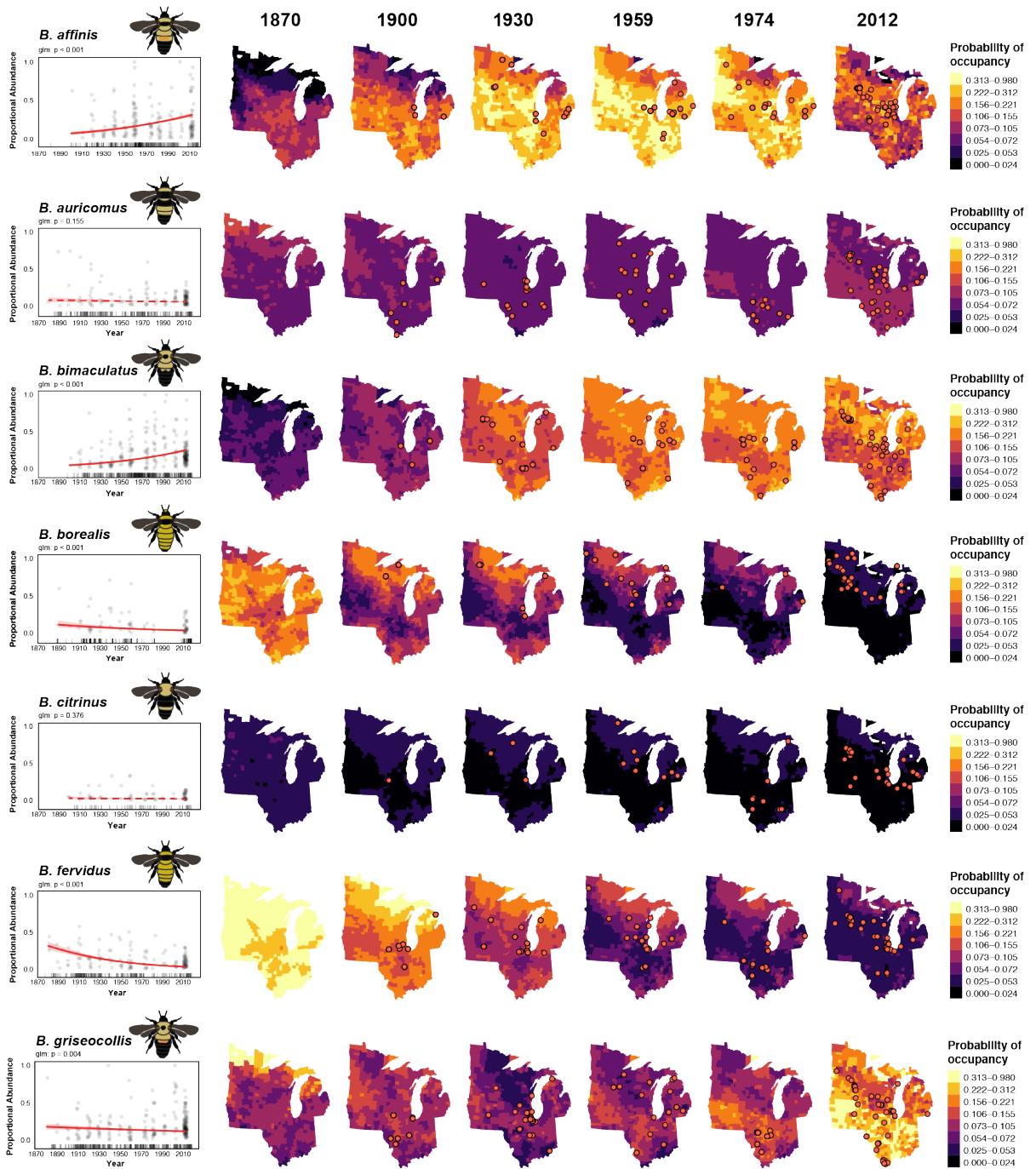


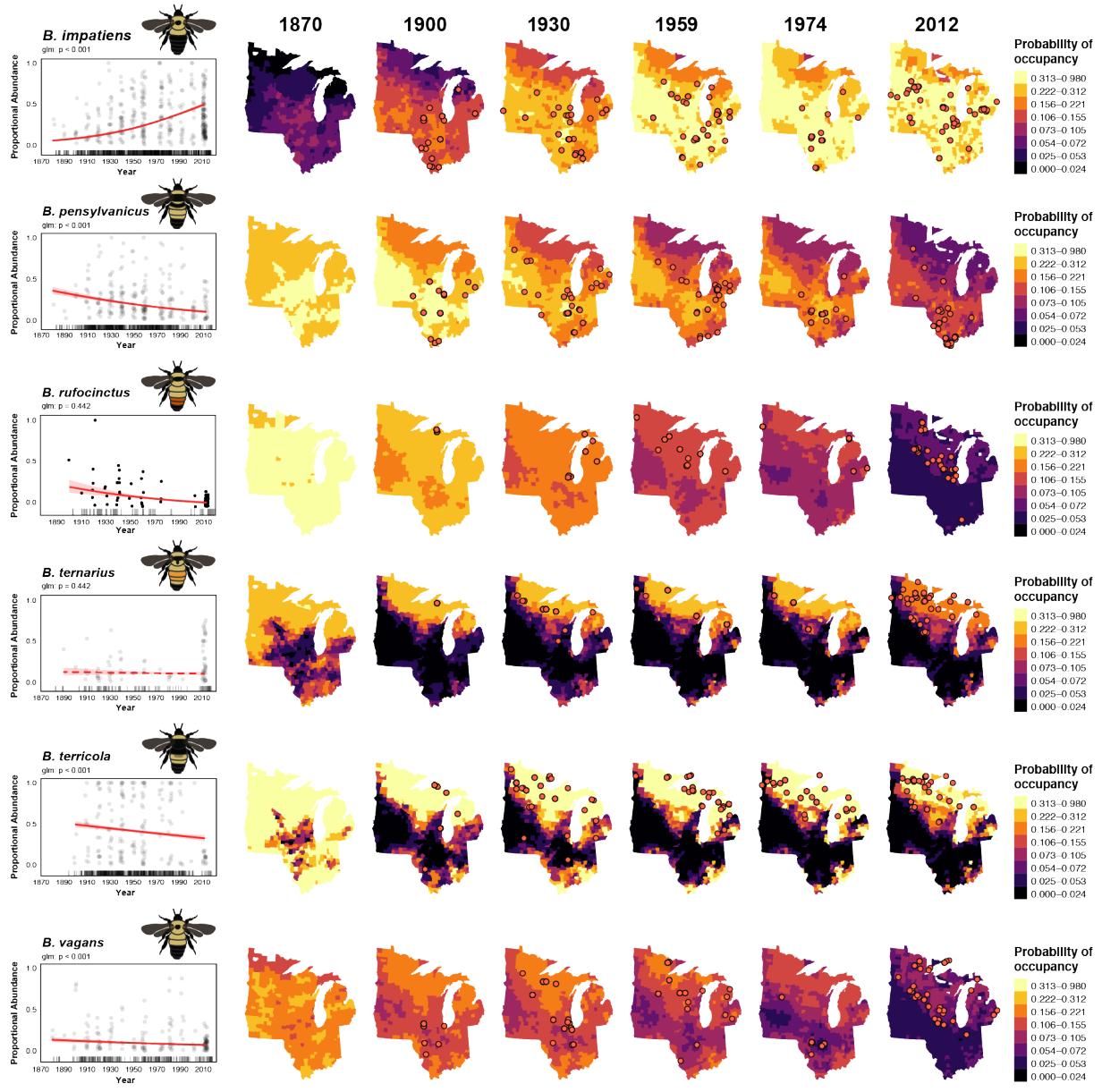
491 **Supplementary Figure 4:** (A) Fitted model coefficients for each species for change in county occu-
 492 pancy over time. (B) For each species, plotted temporal trends of county occupancy over time with
 493 fitted GLM models with 95% confidence interval. Point colors indicate species relative abundance
 494 trend from 1870-present (see Fig. 3a): yellow points denote species whose relative abundance de-
 495 clined, gray points denote no change in relative abundance, and black points denote increases in
 496 relative abundance.



497

498 **Supplementary Figure 5:** Patterns of agricultural intensification in two additional metrics from
 499 1982-2012: (a) proportion of county area in pasture and (c) proportion of county area treated with
 500 insecticides. Color palettes derived using quantile binning. Inset graphs (b,d) depict general trend
 501 of these two variables for each state in the study area as modeled by a Loess curve. Values beneath
 502 years are mean proportion \pm SEM.





504

505 **Supplementary Figure 6:** Fitted temporal trend of relative abundance when modeled with agri-
 506 cultural intensity metrics along with the predicted probability of occurrence for each study species
 507 in each county given crop diversity and proportion cropland in each county. Darker colors denote
 508 smaller probability of occurrence, while lighter colors indicate larger probability of occurrence.
 509 Solid red lines denote statistically clear trend in relative abundance over time ($p < 0.05$), while
 510 dashed lines denote statistically unclear trends ($p > 0.05$). Points on temporal trend are slightly
 511 jittered for visibility. Red points on each map are randomly selected occurrence records with a
 512 maximum of 50 plotted per year.

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