

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 records and US agricultural census records, we show that metrics of increas-
17 ing agricultural intensity, specifically proportion cropland and a decrease in crop richness, are
18 clearly associated with the decline of nearly half of bumble bee species in the north-central
19 US. Additionally, we document positive species associations with crop richness and specific
20 metrics such as proportion pasture even under areas of intensive cultivation, suggesting that
21 bumble bee declines are linked to not just the extent of agriculture, but rather the practices
22 implemented on the ground. In addition to spurring future avenues for controlled, manipula-
23 tive experiments, our results suggest that changes to our agricultural practice and policies are
24 required in order to limit additional declines of Midwestern bumble bees.

25 **Introduction**

26 Extensive range contractions (Kerr et al. 2015) and possible local extinctions (Rasmont and Iserbyt
27 (2012) of a number of bee species has sounded an alarm among conservationists across the world
28 (Steffan-Dewenter et al. 2005; Tylianakis 2013). Of bee population trends that have been well doc-
29 umented, bumble bees (Apidae: Bombus) are perhaps the most well-studied with reports of many
30 species declining across Europe and North/South America (Biesmeijer 2006; Colla and Packer
31 2008; Grixti et al. 2009; Cameron et al. 2011; Bartomeus et al. 2013; Morales et al. 2013; Wood et al.
32 2019). Owing to their importance as pollinators in both commercial crops (Klein et al. 2007) and
33 natural systems (Ollerton, Winfree, and Tarrant 2011), understanding the factors driving bumble
34 bee decline is essential for their conservation and management.

35 A number of studies have posited mechanisms underpinning bumble bee declines, including cli-
36 mate change (Kerr et al. 2015; Marshall et al. 2017; Sirois-Delisle and Kerr 2018), habitat loss (Grixti
37 et al. 2009; Goulson et al. 2015; Soroye, Newbold, and Kerr 2020), the proliferation of parasites and
38 disease (Cameron et al. 2011; @McArt2017), and competition with managed bees (Torné-Noguera
39 et al. 2016; Cane and Tepedino 2017; Mallinger, Gaines-Day, and Gratton 2017; Ropars et al. 2019).

40 Among potential drivers the expansion and intensification of agriculture is consistently cited as a
41 key factor in long-term declines of once common species in both the US (Grixti et al. 2009; Colla
42 and Packer 2008; Jacobson et al. 2018) and Europe (Goulson et al. 2005; Carvell et al. 2006). In-
43 tensification here refers to a suite of attributes associated with agricultural systems that depend
44 on expansive (large scale) monocultures associated with high inputs of agrichemicals (pesticides,
45 synthetic fertilizers) and disturbances such as annual tillage practices (lots of refs). Intensification
46 of agriculture therefore includes both attributes within a farming system (i.e., pesticide use, crop
47 types used), and the effects on agricultural landscapes (i.e., decreased diversity of crops, amount
48 of land in cultivation). A switch from the more diverse and less intensive agricultural production
49 systems of the early 1900's to intensive production systems practiced in many developed coun-
50 tries may have contributed to bumble bee declines due to the loss of preferred host plant species
51 (Wood et al. 2019) and nesting/overwintering habitat (Liczner and Colla 2019).

52 In the United States, analysis of museum records suggests that bumble bee declines began during

53 periods of agricultural intensification in the mid 20th century (Grixti et al. 2009). Despite sev-
54 eral long-term analyses highlighting concerning population trends as well as studies describing
55 the importance of historical land-use (Cusser, Neff, and Jha 2018), there has been no explicit ex-
56 ploration of whether increased agricultural intensification is related to bumble bee declines. One
57 reason for this is the paucity of long-term data of both bumble bee occurrence and historical agri-
58 cultural patterns at large spatial scales, as well as the difficulty in assessing potential drivers ex-
59 perimentally. Additionally, variable temporal patterns of species declines have been documented
60 (e.g., long-term declines of European species (Williams, Araújo, and Rasmont 2007) vs. the re-
61 cent crash of *Bombus affinis* Cresson in North America (Giles and Ascher 2006), suggesting that
62 the mechanisms driving declines may be species- and/or region-specific. Moreover, some species
63 populations appear stable, or may be increasing in both abundance and range (e.g., *B. impatiens*
64 Cresson: Richardson et al. 2018; Wood et al. 2019). In the US, increases and decreases in bumble
65 bee populations appear to be temporally linked, suggesting that there are shared drivers leading
66 some species to thrive while others struggle.

67 To understand the drivers of bumble bee declines, several approaches have been developed to
68 overcome data limitations, including experiments leveraging space-for-time substitution, as well
69 as curation of historical museum collections to understand species trends (Bartomeus et al. 2019).
70 While unable to draw specific causal connections, the use of historical data provides a unique
71 perspective on large-scale temporal trends that experimental approaches cannot provide. Several
72 statistical approaches have been developed to account for the known biases of museum collection
73 records, allowing new data sources to be implemented and used to explore bumble bee popu-
74 lation trends (Pearce and Boyce 2006; Bartomeus et al. 2013, 2019). The continued addition of
75 museum collection records to repositories such as the Global Biodiversity Information Facility
76 (GBIF) combined with extensive, modern surveys of bumble bee fauna (e.g., Bumble Bee Watch)
77 offer a wealth of species-specific spatial distribution patterns. Moreover, data describing detailed
78 agricultural production trends in the United States (Crossley et al. *in review*) now offer a unique
79 opportunity to assess the relationship between agricultural patterns and bee population trends
80 over time.

81 To this end, we explore the relationships between long-term bumble bee population trends and

82 historical patterns of agricultural intensification in the north-central US using an extensive data
83 set of historical bumble bee museum records, modern citizen-science surveys and agronomic met-
84 rics distilled from United States Census of Agriculture records over the period 1870-2018. Using
85 relating species relative abundance to agricultural intensity at the county level, we expected that
86 increasing levels agricultural intensification at the county level as measured by proportion crop-
87 land, number of crops grown, proportion of pasture, and proportion of land treated with insec-
88 ticides, are associated with: (1) a decrease in the relative abundance of species of conservation
89 concern; and (2) an increase in the relative abundance of species known to be stable.

90 Methods

91 We focused our study on the North Central US states of Minnesota, Wisconsin, Iowa, Illinois,
92 Michigan, and Indiana as these states share a similar biogeographic contexts and agricultural his-
93 tory. We limited our analysis to bumble bee species whose core ranges overlapped these states and
94 to limit comparisons of species at their range limits, including: *B. affinis* Cresson, 1863; *B. impatiens*
95 Cresson, 1863; *B. griseocollis* DeGeer, 1773; *B. bimaculatus* Cresson, 1863; *B. auricomus* Robertson,
96 1903; *B. ternarius* Say, 1837; *B. vagans* Smith, 1854; *B. borealis* Kirby, 1837; *B. citrinus* Smith, 1854;
97 *B. pensylvanicus* De Geer, 1773; *B. fervidus* Fabricius, 1798; *B. rufocinctus* Cresson, 1863; and *B. ter-*
98 *ricola* Kirby, 1837. Additionally, several species of conservation concern known to be in decline
99 nationally (including *B. affinis*, *B. terricola* and *B. pensylvanicus*) have core historic ranges in the
100 north-central US.

101 Bumble bee record data

102 We obtained bumble bee records using the Global Biodiversity Information Facility (GBIF), query-
103 ing for all records within our study region. These data were combined with records from the North
104 American Bumble Bee Watch program (www.bumblebeewatch.org) provided by the Xerces Soci-
105 ety for Invertebrate Conservation. We then filtered records to include only species known to occur
106 within our study region and which were appropriately geo-referenced (i.e., having associated lon-
107 gitude and latitude). Each record was assigned to a county based on its collection coordinates so
108 that they could be matched to county-level agricultural census data. Because 95% of records were

¹⁰⁹ from 1890 and beyond, we are confident that our county assignments are accurate as changes in
¹¹⁰ county geographic extent in this region were largely complete by 1890 [Crossley et al. *in review*].

¹¹¹ Temporal comparisons of museum and incidental records can be problematic due to collector/¹¹² spatial bias and non-standardized collection techniques (Bartomeus et al. 2013, 2019;
¹¹³ Richardson et al. 2018). To account for this, we analyzed records using a variety of techniques to
¹¹⁴ control for potential biases. We filtered the dataset to include only single individual ‘sampling
¹¹⁵ events’ (unique combination of species, date, location, and collector), following Richardson et al.
¹¹⁶ (2018). All analyses presented below were conducted using both the full and reduced datasets.
¹¹⁷ As we found no difference in the analyses between the full and filtered (Appendix 1), we present
¹¹⁸ results from the full dataset.

¹¹⁹ Calculating temporal patterns of abundance and diversity

¹²⁰ We first examined temporal trends species diversity for our study region independent of the agricultural census (Grixti et al. 2009; Bartomeus et al. 2013; Richardson et al. 2018; Jacobson et al.
¹²¹ 2018; Wood et al. 2019). In this analysis, we used the approach of Bartomeus et al. (2013) and
¹²² created temporal bins of records such that there were approximately the same number of bee ob-
¹²³ servations per temporal bin. Bins were created using quantiles and the rbin package in R. We
¹²⁴ created several binning strategies to determine if the number of bins affected our results (Bar-
¹²⁵ tomeus et al. 2013), including a total of 3, 5, 8, and 15 temporal bins. Because trends were similar
¹²⁶ regardless of the number of bins, we present results from the 8-bin analyses for changes in relative
¹²⁷ abundance and results from the 15-bin analyses for estimation of species richness over time.
¹²⁸

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

¹³⁷ bin and species richness estimates each permutation, with the p-value equalling the fraction of
¹³⁸ permuted correlations greater or less than the true chronological correlation value.

¹³⁹ **Estimating change in county occupancy**

¹⁴⁰ Changes in relative abundance may not fully capture declines if species remain stable in occupied
¹⁴¹ counties while the number of occupied counties decreases over time. To account for changes in
¹⁴² county-level occupancy (i.e., a proxy for range), we modeled the number of occupied counties
¹⁴³ per equal-record temporal bin for each study species using a generalized linear model, predicting
¹⁴⁴ number of counties as a function of temporal bin.

¹⁴⁵ **Historical agriculture data**

¹⁴⁶ To assess the extent, diversity, and intensity of agriculture, we used county-level agricultural cen-
¹⁴⁷ sus data projected and geographically corrected by Crossley et al. (in review). Our objective was to
¹⁴⁸ estimate county-level (n=535 counties) agricultural metrics, which included aspects of both exten-
¹⁴⁹ sive and intensive farming practices. Following Crossley et al., we limited our analysis to the 18
¹⁵⁰ most common crops which together represent a majority of cropland area study region (Crossley
¹⁵¹ et al. in review). For each county by census year, we calculated crop richness and the proportion
¹⁵² of county area in cropland as two measures of agricultural intensity.

¹⁵³ We also extracted additional aspects of farm management hypothesized to be putative drivers
¹⁵⁴ of bumble bee declines. These included acreage of specific agricultural land-uses and practices
¹⁵⁵ known to affect bumble bees including pasture acreage and acreage treated with arthropod-
¹⁵⁶ targeting insecticides. Because these two variables were not available across the same temporal
¹⁵⁷ extent as crop richness and proportion of county in cropland, we conducted a separate analysis
¹⁵⁸ from 1982 onward where pasture acreage and insecticide treated acreage were available at the
¹⁵⁹ county level. For our analysis, we converted pasture and insecticide treated acreage to proportion
¹⁶⁰ of county area to match the scale of other model variables, namely proportion of county in
¹⁶¹ agriculture.

162 Pairing bumble bee records with historical agriculture dataset

163 Because agricultural census data are collected every decade, not every bumble bee record was
164 collected in a year concurrently with a census. As such, we paired records such that they were
165 \pm 5 years of the nearest agricultural census date (e.g., bumble bee records from 1926-1935 were
166 paired with the 1930 agricultural census). While this pairing may not perfectly reflect the state
167 of agriculture experienced by collected bumble bees, we posit that it is still a meaningful pairing
168 given that a difference of up to 5 years is not likely to manifest in large, county-level changes in
169 agricultural practices that we observed occurring over several decades. To verify this assump-
170 tion, we performed analyses with a stricter up to \pm 2-year pairing rule and found similar results
171 (Appendix 2), thus we present the analysis with the full dataset and up to \pm 5-year pairing.

172 Relating changes in relative abundance to agricultural intensity

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

187 Because of the spatial nature of these data, we tested for spatial autocorrelation in the residuals
188 using a Moran's I test in the *spdep* package (similar to Meehan et al. 2011; and Meehan and
189 Gratton 2015). We also checked for temporal autocorrelation within the response of each species.

190 Because neither spatial nor temporal autocorrelation were found to be problematic, we utilized
191 the generalized linear model framework described above across all species.

192 To illustrate the estimated change in relative abundance and range, we used our fitted models to
193 predict occurrence across historical ranges of each species within our study area using county-
194 level agricultural intensification metrics. These maps describe the predicted probability of occur-
195 rence in each county as function of crop diversity and proportion of a county in cropland over
196 time. We selected 6 time points for which to fit models: 1870, 1900, 1930, 1959, 1974, and 2012 to
197 depict how county-level agricultural suitability for bumble bees has changed over time.

198 Another series of models were constructed to test more detailed hypothesized drivers of bum-
199 ble bee decline. Generalized linear models with a binomial error structure were fit to predict
200 county-level species relative abundance as a function of pasture acreage, acreage treated with
201 arthropod-targeting insecticides, and the agricultural census year. Because the agricultural census
202 did not begin capturing insecticide input data until 1982, these models were fit on a subset of data
203 from 1982 to present. By adding these more mechanistic drivers to the broad scale intensification
204 metrics, we are able to see if the response of the proportion cropland and crop richness remains
205 consistent given additional drivers that might be correlated to these variables. If the responses re-
206 main consistent, we can be confident that the results from the long-term data set using proportion
207 cropland and crop richness are tenable to explain the patterns of bumble bee relative abundance
208 observed even if the more mechanistic drivers, pasture acreage and insecticide inputs, are also
209 strong predictors of bumble bee relative abundance. In addition, we examined variance inflation
210 factors (VIF) for each model to determine whether variables were problematically multi-collinear.
211 While a number of other drivers might be directly or interactively influencing bumble bee relative
212 abundance [e.g., climate], other studies have shown independent effects of land-use change and
213 climate (Kerr et al. 2015; Soroye, Newbold, and Kerr 2020), suggesting it is sufficient to examine
214 agricultural intensification metrics on their own.

215 **Results**

216 Bumble bee occurrence records were compiled from GBIF (n=25,271 from 1877 to 2017) and Bum-
217 ble Bee Watch (n=2,611, from 2007 to 2018) for a total of 27,882 unique records over 358 of 535
218 counties (Fig. S1). The species contained in each dataset were mutually inclusive. We removed
219 *B. fraternus*, *B. perplexus*, *B. ashtonii (bohemicus)*, and *B. variabilis* from our analyses as these species
220 lacked sufficient records to make meaningful temporal interpretations of changes in relative abun-
221 dance and county occupancy.

222 **Changes in species richness**

223 Rarefied species richness estimates for each temporal bin show estimated species richness declin-
224 ing 20% from 15 species in 1824-1925 to 12 species presently (Fig. 1) - a significant negative trend
225 ($t_{1,13} = 6.084$, $p = 0.0283$). All fifteen temporal bin species accumulation curves rapidly reached an
226 asymptote, indicating that sample sizes with this bin size were sufficient to capture the diversity
227 of communities within each bin (Fig. S2). A sharp drop in estimated species richness occurred be-
228 tween 1952 and 1959, followed by a slight rebound in the next 50 years. The pattern of decreasing
229 species richness was maintained at two other binning levels, 5 and 8 bins (Fig. S3)

230 **Changes in county occupancy**

231 Overall, most species increased in county occupancy over time (Fig. S4). However, some species
232 of conservation concern showed either a decrease (*B. terricola*, and *B. pensylvanicus*), or no change
233 (*B. affinis*) in county occupancy over time despite the increase in sampling effort that has occurred
234 over the last few decades.

235 **Changes in agricultural intensification**

236 The areal extent of cropland peaked in our region in 1950 (average of $45\% \pm 22\%$ of county area).
237 Since then, it has decreased almost 10% to an average of $34\% \pm 20\%$ (Fig. 3A,B). Intensive agricul-
238 ture has remained relatively sparse in the north of our study region, while the highest intensity
239 occurs in the “corn belt” that stretches through southern Minnesota, Iowa, southern Wisconsin,
240 central and northern Illinois, and northern Indiana. Throughout the last century, the number of

²⁴¹ agricultural crops crown has decreased (Fig. 3C,D). Of the 18 crops for which we compiled data,
²⁴² an average of 12 ± 1 were grown from 1880 - 1950. Since 1950, this number has declined 50%, with
²⁴³ counties today growing on average 6 ± 1 crops.

²⁴⁴ The more fine-scale agricultural intensification variables we measured showed diverging patterns,
²⁴⁵ with pasture acreage declining 90% from 1982 to present from an average of 3% of county area in
²⁴⁶ 1982 to 0.3% in 2012, while the total county area treated with insecticides increased 54% from an
²⁴⁷ average of 11% of county area in 1982 to 17% in 2012. (Fig. S5). These changes occurred over
²⁴⁸ similar spatial extents, primarily concentrated in the corn-belt counties throughout the middle of
²⁴⁹ the study region.

²⁵⁰ **Patterns of bumble bee relative abundance are related to agricultural intensity**

²⁵¹ Patterns in bumble bee relative abundance showed strong associations with trends in agricultural
²⁵² intensification metrics. Overall, we found that 7 of 13 species decreased in relative abundance,
²⁵³ while 3 remained stable and 3 increased (Fig. 4, Table S1). These estimates of temporal change in
²⁵⁴ relative abundance modeled concurrently with metrics of agricultural intensity aligned well with
²⁵⁵ changes estimated from generalized linear models fitted with time period as the sole predictor
²⁵⁶ (Appendix 3). Species increasing in relative abundance over time tended to be positively associ-
²⁵⁷ ated with increases in proportion of agriculture as well as crop richness (Fig. 4B,C). Among species
²⁵⁸ estimated to be in decline, county-level proportion of agriculture was negatively associated with
²⁵⁹ relative abundance in all but two species (Fig. 4B). The responses of species in decline to crop
²⁶⁰ richness was generally positive, with a majority increasing in relative abundance in accordance
²⁶¹ with crop richness (Fig. 4C).

²⁶² When we used county-level agricultural statics to predict the probability of species occurrence
²⁶³ within our study region from 1870-2012, we see a marked expansion of common species in space
²⁶⁴ (e.g., *B. impatiens*, *B. bimaculatus*) whereas probability of occupancy decreases across the region for
²⁶⁵ species of conservation concern (e.g., *B. terricola*, *B. affinis*, *B. pensylvanicus*, Fig. 3E-H, Fig. S6).

²⁶⁶ We found that models that included more detailed agricultural metrics, available from 1982 to
²⁶⁷ present, were clearly associated with patterns of relative abundance (Fig 6,D,E, Table S3). Pas-
²⁶⁸ ture acreage had a consistently positive association on relative abundance (Fig. 6D), although

269 the acres of pasture per county has markedly decreased over the last century (Fig. S4B). Propor-
270 tion of county area treated with insecticides had a consistently negative effect on species relative
271 abundance, except for 3 species that exhibited no effect (Fig. 6E, *B. auricomus*, *B. impatiens*, and *B.*
272 *pensylvanicus*) and 3 species which were positively associated with increased insecticide applica-
273 tion (*B. affinis*, *B. rufocinctus* and *B. vagans*). One species of conservation concern, *B. terricola*, had
274 the strongest negative relationship with proportion of county treated with insecticides.

275 Discussion

276 Using bumble bee observations recorded over 140 years across 6 north-central US states and an
277 unprecedented dataset on the historical patterns of agricultural land use and practices (extent of
278 cropland, diversity of crops grown, extent of pasture, pesticide use), we explored the hypothe-
279 sis that agricultural intensification is associated with bumble bee declines. Our results support
280 declines of a number of bumble bee species throughout the region and suggest that increases in
281 agricultural intensification are associated with these declines.

282 Human alteration of terrestrial landscapes via habitat loss is cited as a principle cause of biodiver-
283 sity declines worldwide (Foley et al. 2005, 2011; Klein et al. 2007; Tilman et al. 2011; Tscharntke
284 et al. 2012). Our study joins a number of taxa-specific studies that highlight the threat of mod-
285 ern agricultural practices to biodiversity (e.g., birds Benton et al. 2002; Robinson and Sutherland
286 2002; Meehan, Hurlbert, and Gratton 2010). Recent documented declines in insect populations
287 have speculated that habitat loss and intensification of agriculture are likely key contributors to
288 these patterns (Hallmann et al. 2017; Seibold et al. 2019), though studies explicitly tying long-term
289 trends in widespread agricultural intensification to bumble bee declines have been lacking.

290 Of the 13 species in this study, 3 were found to increase over the study dataset (1870-2017), 3 re-
291 mained at similar levels, and 7 were found to have declined in relative abundance. The declining
292 species in our study match those found to be in decline elsewhere, including individual state anal-
293 yses within our study region (Grixiti et al. 2009; Wood et al. 2019), the US East coast (Richardson
294 et al. 2018; Jacobson et al. 2018), Canada (Colla and Packer 2008), and North America, generally
295 (Cameron et al. 2011; Colla et al. 2012). Those showing the most concerning trends include *B.*

296 *terricola* and *B. pensylvanicus*, both of which significantly decreased in relative abundance as well
297 as showed distinct decreases in the predicted extent of their range over time.

298 With few exceptions, species whose relative abundance was found to be increasing or stable had
299 either positive or neutral relationships with agricultural intensity metrics, while those in decline
300 were negatively associated with increased agricultural intensity. However, agricultural intensifi-
301 cation includes several aspects. While the areal extent of agriculture (proportion of cropland in
302 county) was negatively associated with several species, other species seem to thrive in high pro-
303 portion of agriculture including *B. pensylvanicus*, a species of conservation concern. Moreover,
304 bumble bee species richness was greatest during the period of greatest areal agricultural extent
305 (1900-1930). On the other hand, the land-use type (e.g., pasture) of and increased diversity of
306 crops generally have positive effects on bumble bees relative abundance, while inputs such as
307 pesticides have few positive effects. This suggests that the extent of agriculture is not the sole
308 putative driver of bumble bee decline, but rather the manner in which agriculture is practiced
309 matters greatly. Landscapes with a high areal extent of agriculture may still support a stable and
310 diverse bumble bee community provided there is a high diversity of crops and open habitat such
311 as pasture as well as limited insecticide use.

312 The mechanisms underlying the observed relationships between bumble bees and proportion
313 cropland and crop diversity were not tested in this study. However, we propose that reductions in
314 suitable nesting and foraging habitat associated with agricultural intensification, along with the
315 direct/indirect lethality of insecticides, are likely important underlying factors. Increases in agri-
316 cultural land have been implicated in the loss of diverse floral habitat such as tall-grass prairies
317 (Smith 1998; Brown and Schulte 2011), as well as large-scale reductions in bumble bee forage
318 plants (Carvell et al. 2006; Scheper et al. 2014). A shift from the diverse cropping systems of the
319 early to mid 1900's to largely monocultural systems in recent years has undoubtedly altered total
320 floral resource availability and temporal continuity (Schellhorn, Gagic, and Bommarco 2015) and
321 has been shown to negatively impact bumble bee colony development (Hass et al. 2018). While
322 some mass-flowering crops might benefit bumble bee colony growth (Westphal, Steffan-Dewenter,
323 and Tscharntke 2009), they may also favor species that can tolerate highly variable temporal re-
324 sources [Schmid-Hempel and Schmid-Hempel (1998); Hemberger et al. in revision] and provide

325 little dietary diversity for foraging bees. Such a limit on pollen and nectar diversity may have
326 adverse consequences for bumble bees (Vaudo et al. 2015), especially those with limited diet
327 breadth (Kleijn and Raemakers 2008; Wood et al. 2019). Additionally, landscapes that restrict flo-
328 ral resource availability during key time periods might limit bumble bee colony growth (Williams,
329 Regetz, and Kremen 2012) and subsequent queen production (Crone, Williams, and Letters 2016),
330 thereby reducing population stability over time.

331 The largely positive response of relative abundance to crop richness suggests that increasing agri-
332 cultural landscape heterogeneity could have benefits for both common and declining bumble bee
333 species. Increasing landscape heterogeneity is known to benefit a number of ecosystem services
334 (Fahrig et al. 2011; Turner, Donato, and Romme 2012) and biodiversity (Benton, Vickery, and Wil-
335 son 2003; Sirami et al. 2019), even with relatively simple changes in cropland heterogeneity. In
336 fact, a recent study suggests that adjustments to agronomic practices, specifically decreasing field
337 size, could have larger positive effects on farmland biodiversity than increasing the amount of
338 semi-natural habitat in the landscape (Sirami et al. 2019). Moreover, decreasing field sizes may be
339 easier to implement and incentivize through traditional farm policy frameworks. As natural habi-
340 tats are becoming increasingly rare, alterations that we can make to our land use practices (e.g.,
341 Landis 2017) will be the key toward building multi-functional agroecosystems that both provide
342 food and fiber for humans, as well as conserve essential ecosystem service providing organisms
343 and biodiversity writ large.

344 The proportion of pasture in a county was positively associated with bumble bee relative abun-
345 dance for all but three species (which showed no relationship). Pastures and grasslands are often
346 a source of floral habitat for foraging bumble bees both in the US and in Europe (Carvell et al.
347 2006) as these open areas often contain plants in the family Fabaceae, a preferred source of bum-
348 ble bee forage (Goulson et al. 2005) especially in several Midwestern bumble bees species (Fye
349 and Medler 1954). While pastures and fabaceous cover crops were used heavily in the early 20th
350 century to return nitrogen to soils, technological advancements following the second world war
351 (namely artificial, nitrogenous fertilizers) led quickly to the decline in these crops (Williams 1986;
352 Williams and Osborne 2009).

353 Generally, our analysis of the dataset with insecticide data (1982-present) showed that increases in

354 the acreage of cropland treated with insecticides tended to be associated with decreased relative
355 abundance of all but three species. There is clear evidence that exposure to insecticides is detri-
356 mental to bumble bee foraging (Feltham, Park, and Goulson 2014), colony development (White-
357 horn et al. 2012; Crall et al. 2018), and may also facilitate increased pathogen prevalence (McArt
358 et al. 2017). Our analysis provides additional evidence of the detrimental effect of insecticide use
359 on bumble bees over a large spatial and temporal scale.

360 Interestingly, in this dataset we found no evidence of decline in the relative abundance of the
361 federally endangered *B. affinis* across our study region. This result stands in contrast to other
362 findings by almost all other longitudinal studies in which *B. affinis* is considered (Grixiti et al. 2009;
363 Richardson et al. 2018). However, when examining patterns of *B. affinis* decline across its entire
364 range, there is clear evidence for extensive range reductions and local extirpations [Cameron et al.
365 (2011); Colla2012]. Indeed, the subset of the range observed in our study has the most extensive
366 modern records of *B. affinis*, suggesting that our observed regional patterns may differ from range-
367 wide population trends.

368 Museum records are an invaluable source of data for studies examining changes in species range
369 and long-term population trends (Bartomeus et al. 2019), as well as understanding the ecological
370 drivers that underpin changes in species assemblages over time (Wood et al. 2019). A strength
371 of leveraging long-term museum records, including our approach, includes the ability to examine
372 spatial and temporal scales that are not amenable to experimental methods (Meehan et al. 2011).
373 However, care must be taken to account for biases associated with historical collections. For ex-
374 ample, museum collection records do not necessarily adhere to standard ecological practices of
375 ensuring random, equal-effort samples over adequate space and time (Richardson et al. 2018). To
376 account for known issues, we employed a variety of techniques including subsampling and sensi-
377 tivity analyses to determine whether our chosen methods skewed results (for a thorough analysis
378 of techniques to leverage historical collections, see Bartomeus et al. 2019). Irrespective of the
379 approaches used, we consistently identified declines in over half of study species with clear as-
380 sociations to metrics of agricultural intensity. While there is much evidence for the consequences
381 of agricultural intensification on bumble bee communities, other variables may also be driving
382 shifts. For example, climate change has reduced bumble bee ranges in both North America and

383 Europe (Soroye, Newbold, and Kerr 2020). In their analysis, Soroye, Newbold, and Kerr (2020)
384 found that climate and land-use changes impact bumble bee occupancy independently. That is to
385 say that while climate may be driving large-scale range shifts, land-use still has strong, negative
386 effects on bumble bee occupancy – an effect that we show strong evidence for here.

387 It is important to place the observed changes in relative abundance and county occupancy into a
388 larger context. Examining changes from 1870 to present day may not accurately capture the pre-
389 European settlement baseline of the study species examined. By 1870, many counties were already
390 extensively altered by both agriculture and deforestation (Rhemtulla, Mladenoff, and Clayton
391 2007). In some cases (e.g., Michigan), these alterations may have provided more floral resources
392 by creating open habitat, resulting in the increase of some bumble bee species (Wood et al. 2019).
393 In shifting from the agronomic practices of the early 20th century to the more industrialized, in-
394 tensive practices of the later 20th century, the suitability for those previously favored bumble bees
395 decreased paving way for the rise of others. The lack of true historical baselines does not mean
396 that the declines described in this study are normal or unworthy of immediate conservation ac-
397 tion. The scale and intensity of agricultural intensification over the last 60 years is unprecedented
398 and the risks to bumble bees clear. The dualism of bumble bee species responses to agricultural
399 intensification both historically and contemporarily suggests that species habitat requirements are
400 variable - something we must explicitly consider in planning bumble bee conservation strategies.

401 Conclusions

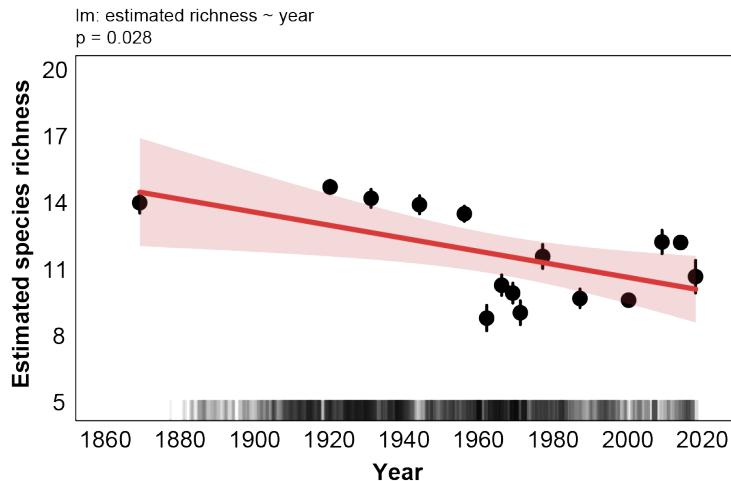
402 Modern experimental evidence has provided evidence of the effect of agricultural intensification
403 on bumble bees. By relating changes in historical, county-level agricultural intensity to changes
404 in the relative abundance of bumble bee species across the upper Midwest, we provide historical
405 context of the extent and duration of declines, further solidifying the evidence that agricultural in-
406 tensification is a key driver of shifts in bumble bee community composition and abundance over
407 the last century. Over the last 140 years, agricultural intensification – specifically how agriculture
408 is practiced rather than simply the amount – has elicited strong, selective pressures inadvertently
409 choosing winner and loser species in bumble bee communities. Our work concurs with an exist-
410 ing body of evidence, including recent, catastrophic declines documented in insect and arthropod

⁴¹¹ abundance in agriculturally dominated landscapes. There is still a great need for additional exper-
⁴¹² imentation to understand how land use drivers might interact with other known causes of bumble
⁴¹³ bee decline, namely climate change and pathogen and disease prevalence. The combination of our
⁴¹⁴ results leveraging museum records and historical data along with a growing body of experimental
⁴¹⁵ evidence suggests that changes to our agricultural practice and policies are required in order to
⁴¹⁶ limit additional declines of bumble bees in our agricultural landscapes.

⁴¹⁷ Acknowledgements

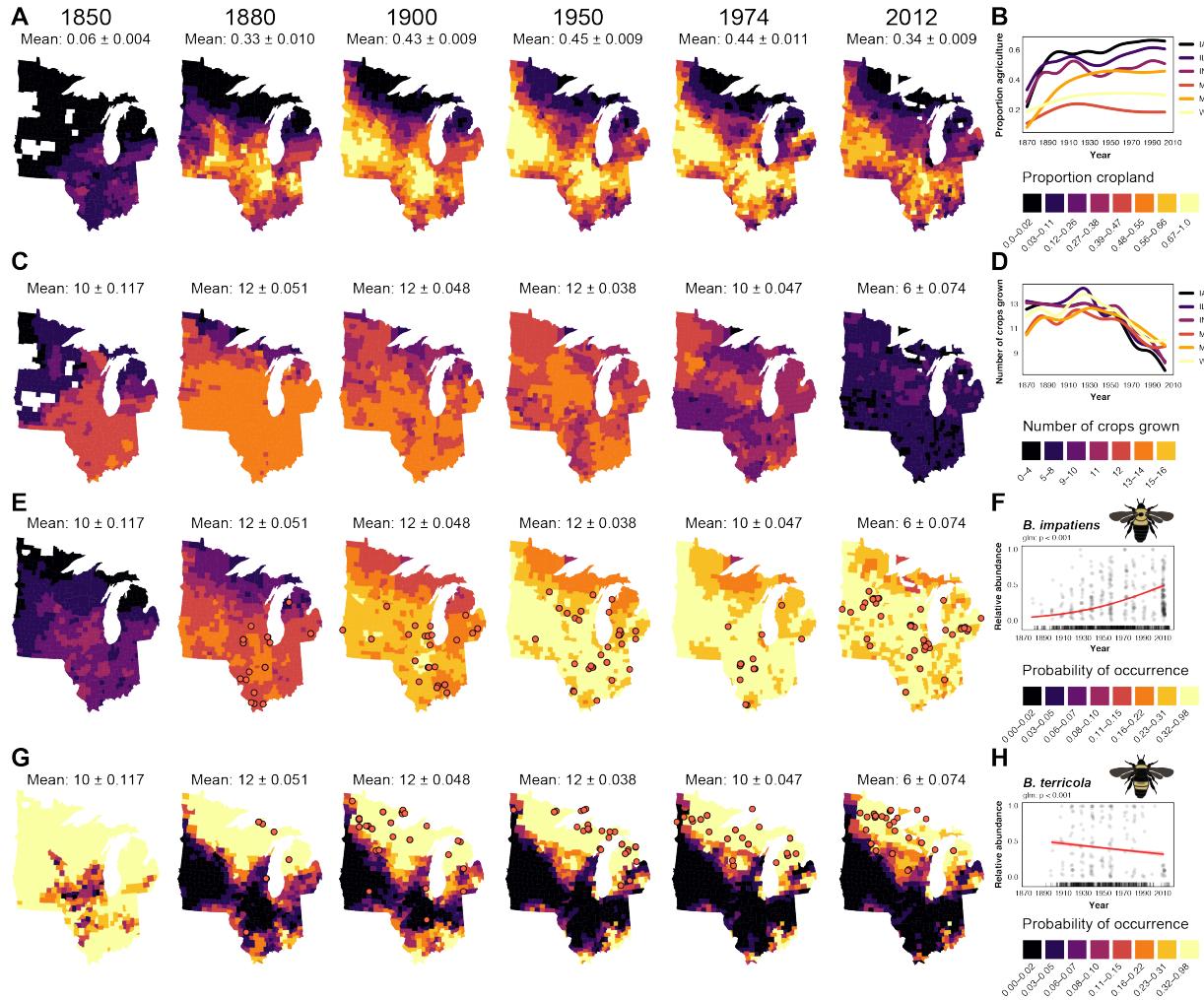
⁴¹⁸ We would like to thank Christelle Guédot, John Orrock, and Russ Groves for the valuable feed-
⁴¹⁹ back that improved this manuscript. Many thanks to Rich Hatfield and the Xerces Society for
⁴²⁰ Invertebrate Conservation for providing Bumble Bee Watch data. Data and code for all analyses,
⁴²¹ figures, and the manuscript will be made publicly available upon publication at <https://github.com/jhemberger>.
⁴²²

423 **Figures and Tables**



424

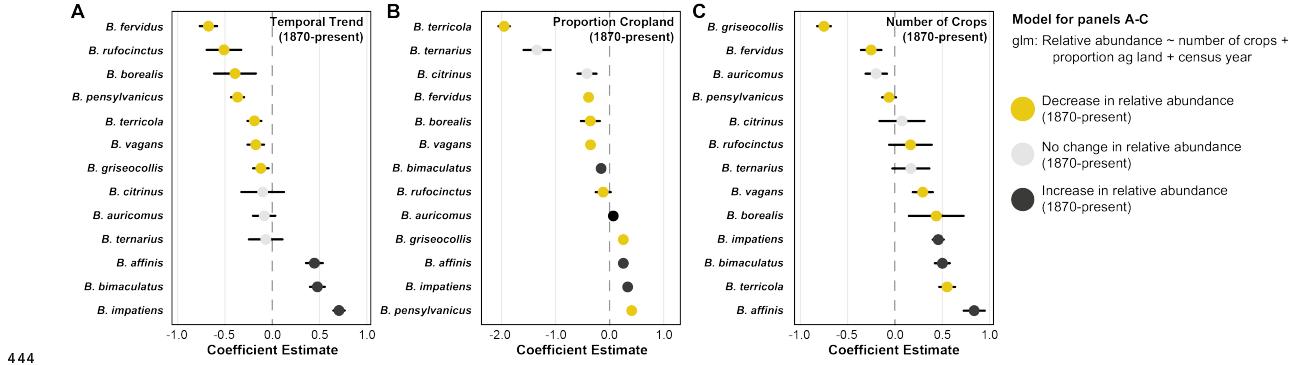
425 **Figure 1:** Trend in rarified bumble bee species richness from 1877-present. Each point represents a
426 date range that is standardized to contain an approximately equal number of bumble bee records,
427 and it is plotted at the midpoint year of the date range. Error bars are 95% confidence intervals.
428 The fitted line is a linear model predicting estimated species richness as a function of temporal
429 bin order using the midpoint of the temporal bin as the predictor. Carpet plot represents temporal
430 collection year for all records from 1877 to present.



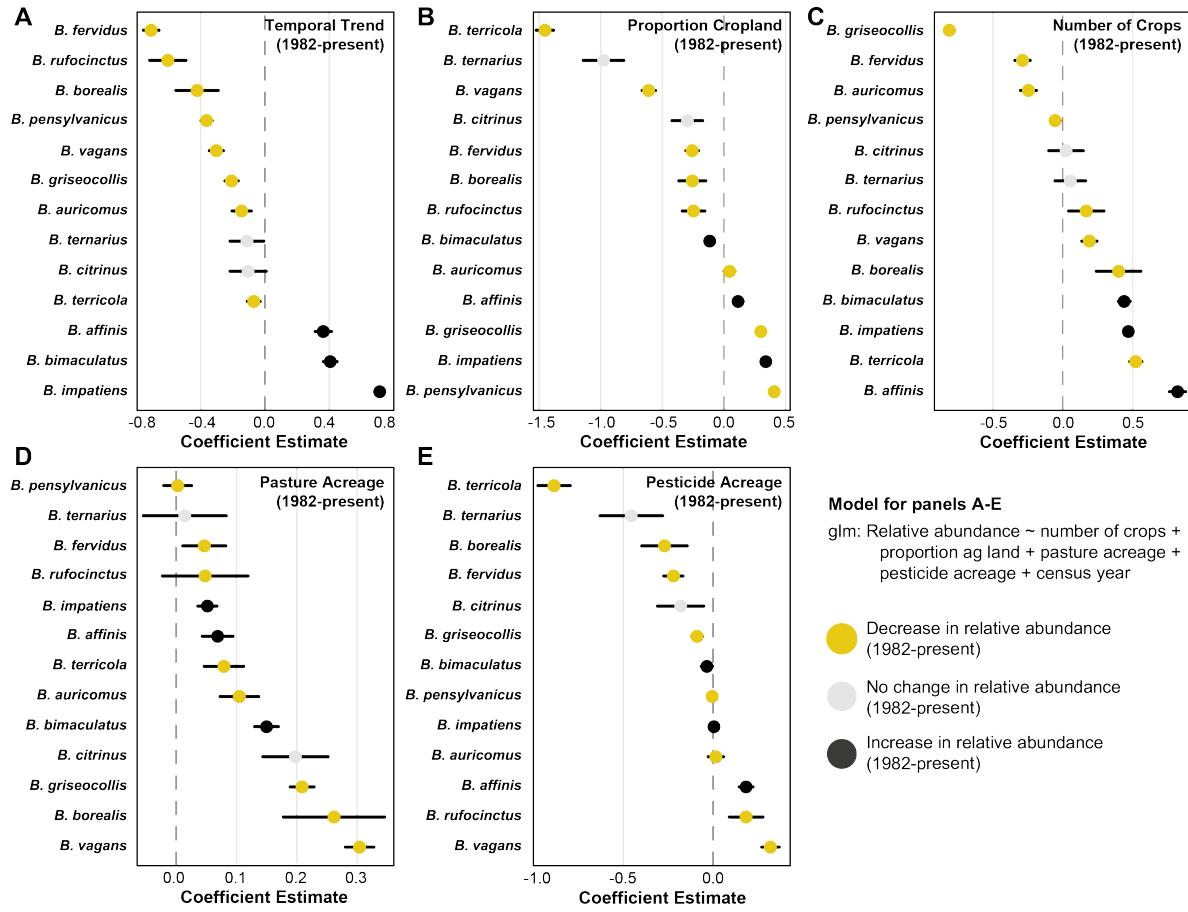
431

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

443 each response.



445 **Figure 3:** Fitted model coefficients ($\pm 95\%$ confidence interval) for each study species for (A) tem-
 446 poral trend of the species, (B) proportion of county in cropland, and (C) the number of crops grown
 447 in a county. Models were fitted using the entire dataset from 1870-present. Point colors indicate
 448 species relative abundance trend from 1870-present: yellow points denote species whose relative
 449 abundance declined, gray points denote no change in relative abundance, and black points denote
 450 increases in relative abundance.



451

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

⁴⁵⁹ **Supplementary Material**

⁴⁶⁰ **Appendix 1**

⁴⁶¹ **Analysis filtering data to unique *species x location x collector x date* combinations**

⁴⁶² Appendix 2

⁴⁶³ Analysis restricting to records within ± 2 years of agricultural census

464 **Appendix 3**

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

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

472 Of the 13 species included in our simple analysis of change in relative abundance over time, 6
473 saw statistically clear reductions in relative abundance: *B. borealis*, *B. fervidus*, *B. pensylvanicus*, *B.*
474 *rufocinctus*, *B. terricola*, *B. vagans* (Table S1). Similar to the patterns of estimated species richness,
475 reductions in the relative abundance of these declining species seem to begin in the middle of the
476 20th century. There were 7 species which increased in relative abundance over time period covered
477 by this dataset: *B. affinis*, *B. auricomus*, *B. bimaculatus*, *B. citrinus*, *B. griseocollis*, *B. impatiens*, and *B.*
478 *ternarius*.

479 **Table SA3.1:** Relative abundance estimates for each species across 8 time bins, sized in order to
480 contain approximately equal numbers of bumble bee records per bin. Coefficient estimates and p-
481 values derived from models fit to estimate trends in relative abundance over time, where relative
482 abundance of each species is predicted by time bin fit using a generalized linear model, with N
483 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

484

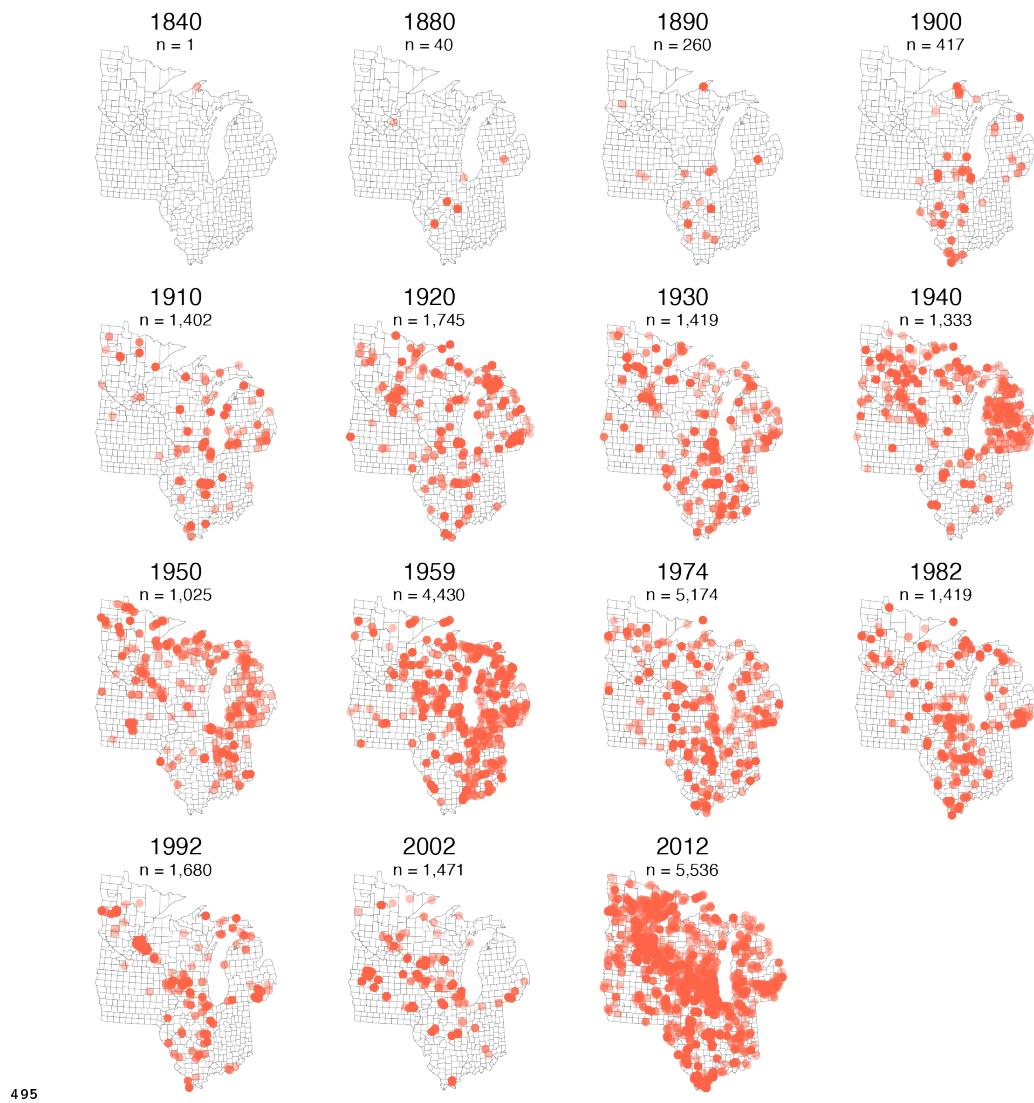
485 **Supplementary Table 1:** Generalized linear model results for each study species including the
 486 sample size (number of counties for which relative abundance is calculated), model term, scaled
 487 coefficient estimate, 95% confidence interval and p-value. Each county is weighted by the total
 488 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

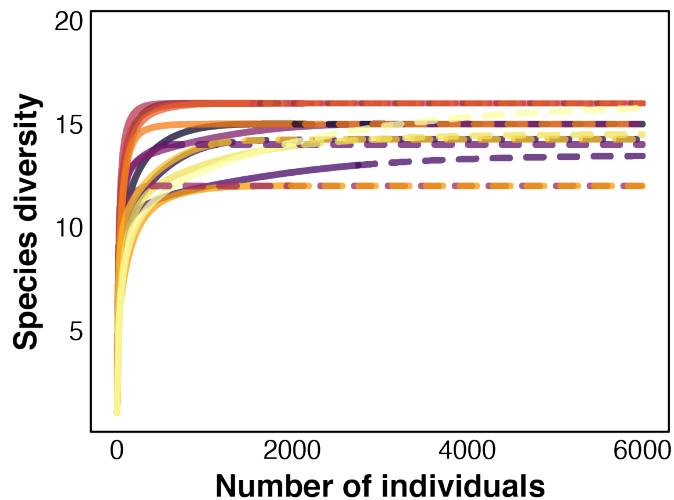
489

490 **Supplementary Table 3:** Generalized linear model results for each study species including the
 491 sample size (number of counties for which relative abundance is calculated), model term, scaled
 492 coefficient estimate, 95% confidence interval and p-value. Each county is weighted by the total
 493 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

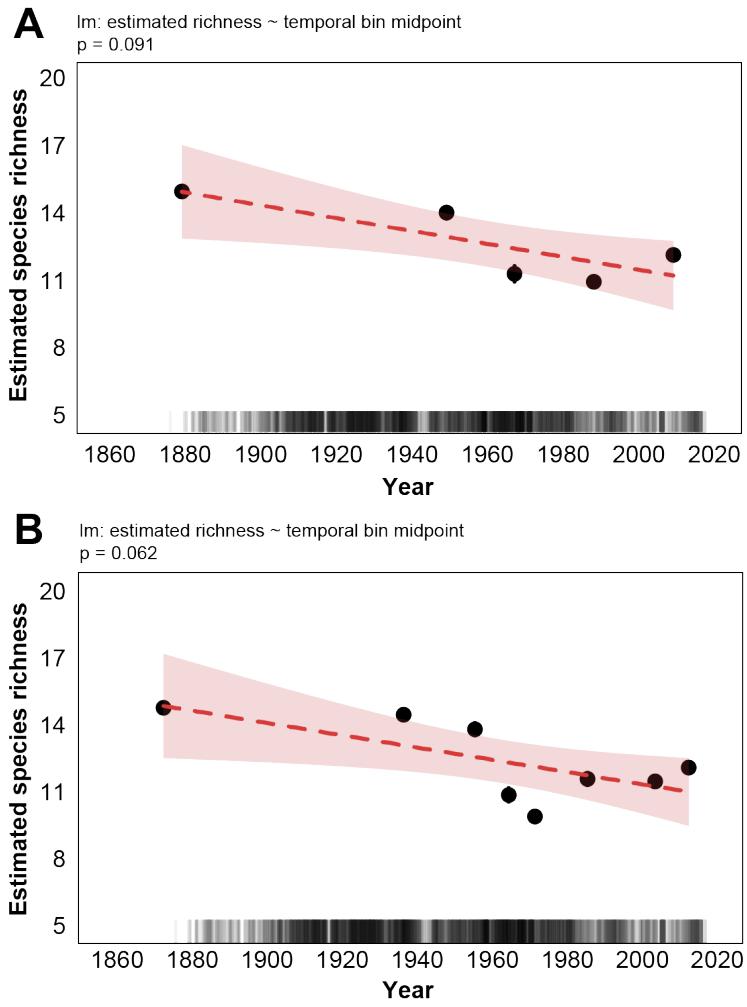


496 **Supplementary Figure 1:** The location of bumble bee records for each US Census of Agriculture
 497 year considered in our analysis. The number of records is noted below the year. Points are partially
 498 transparent and jittered slightly for visibility.



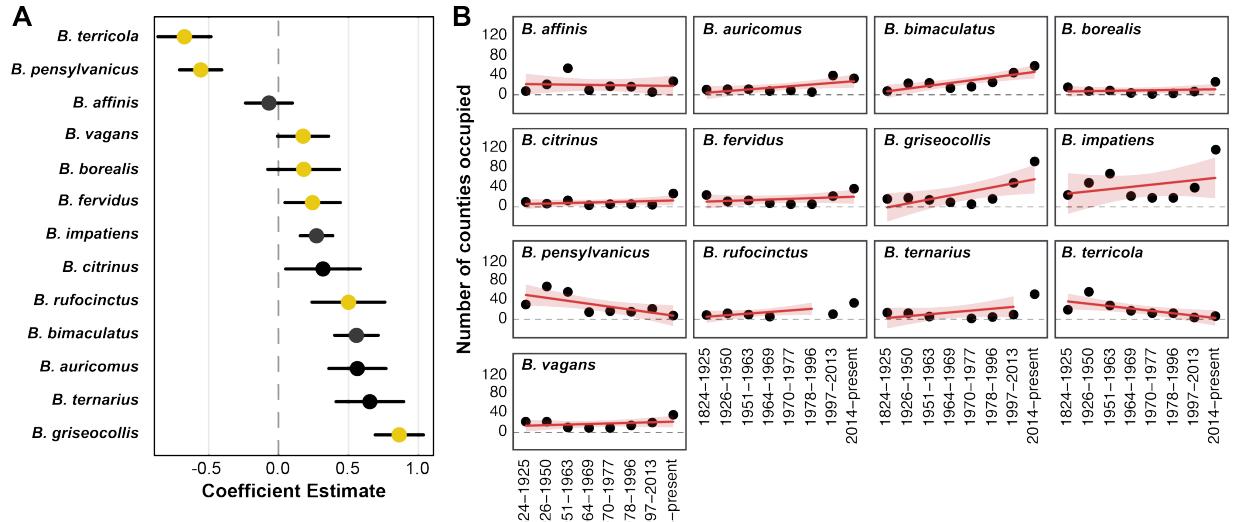
499

500 **Supplementary Figure 2:** Sample-based species accumulation curves for each of 15 temporal bins
501 (different colors) from which estimated species richness was calculated (Fig. 1). Each accumula-
502 tion curve is constructed for temporal bins with a roughly equal number of records.



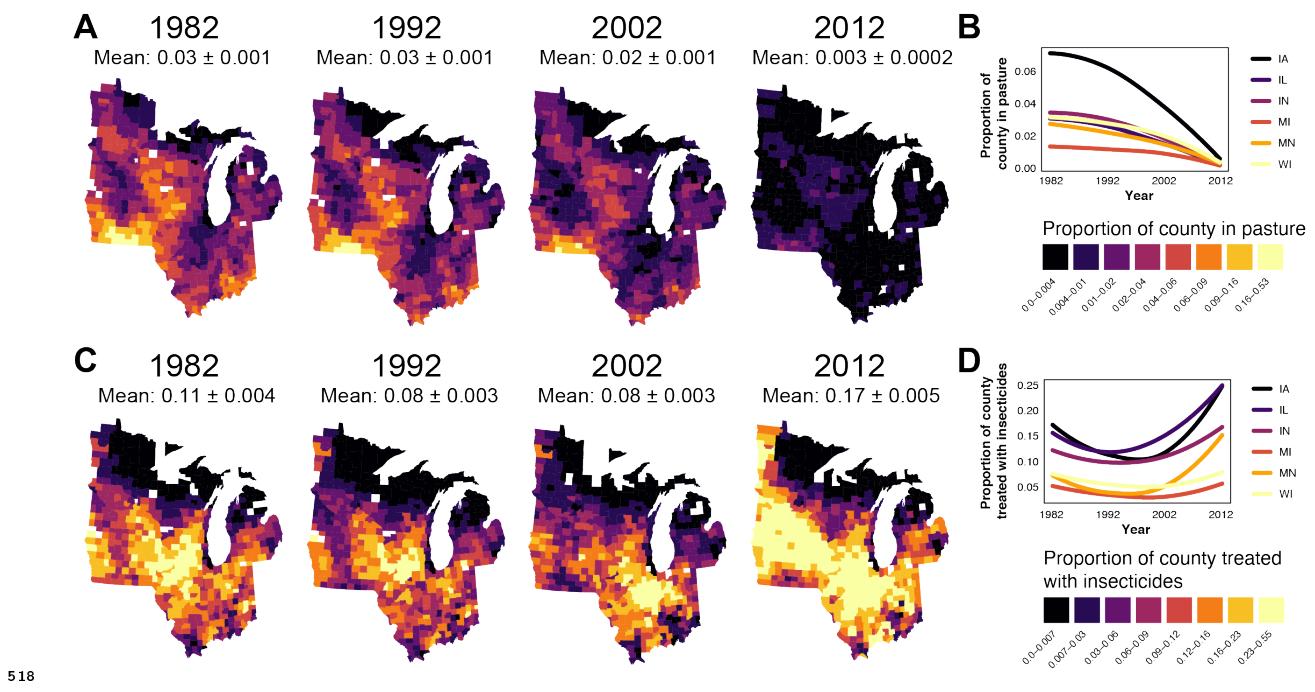
503

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

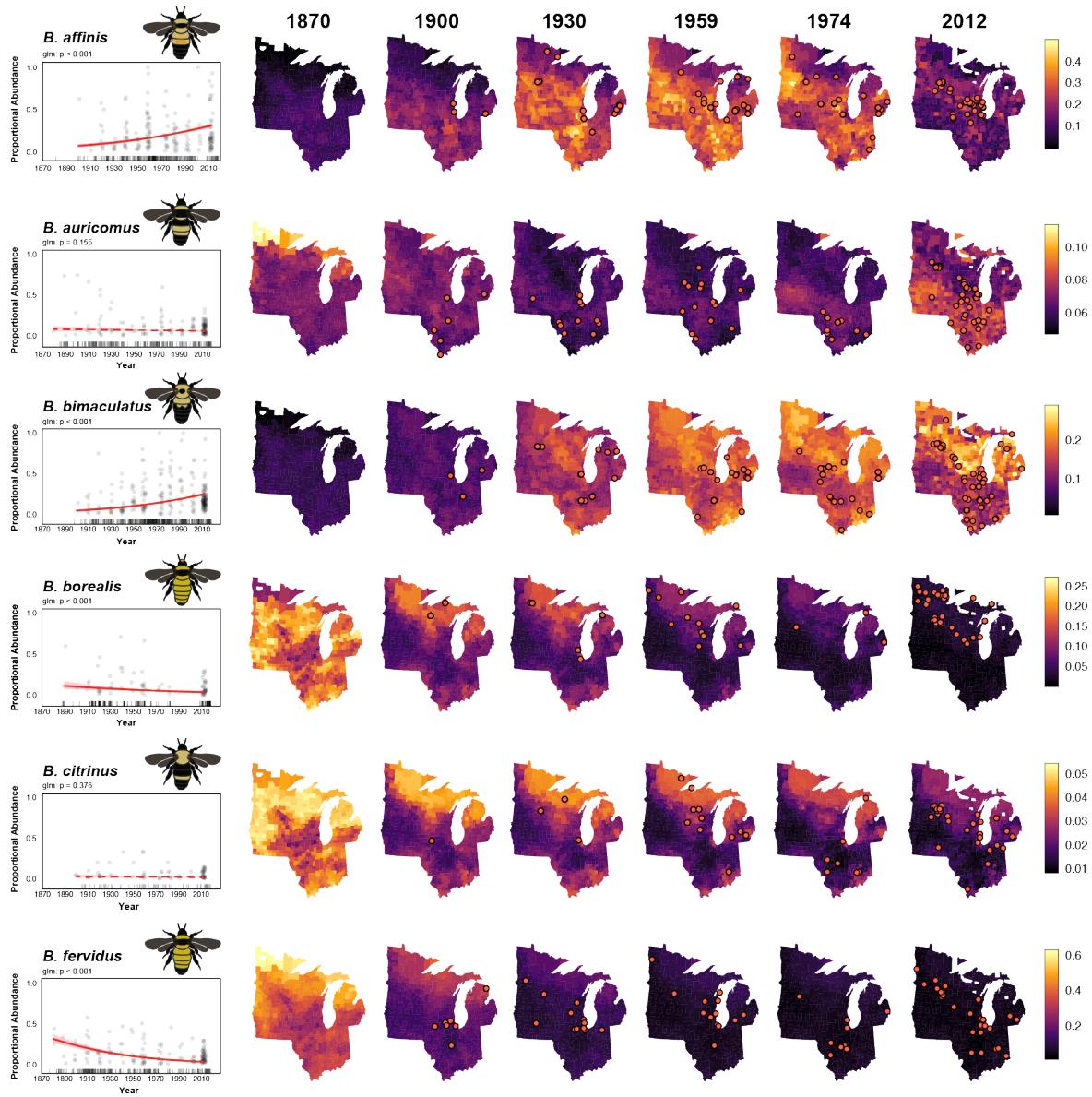


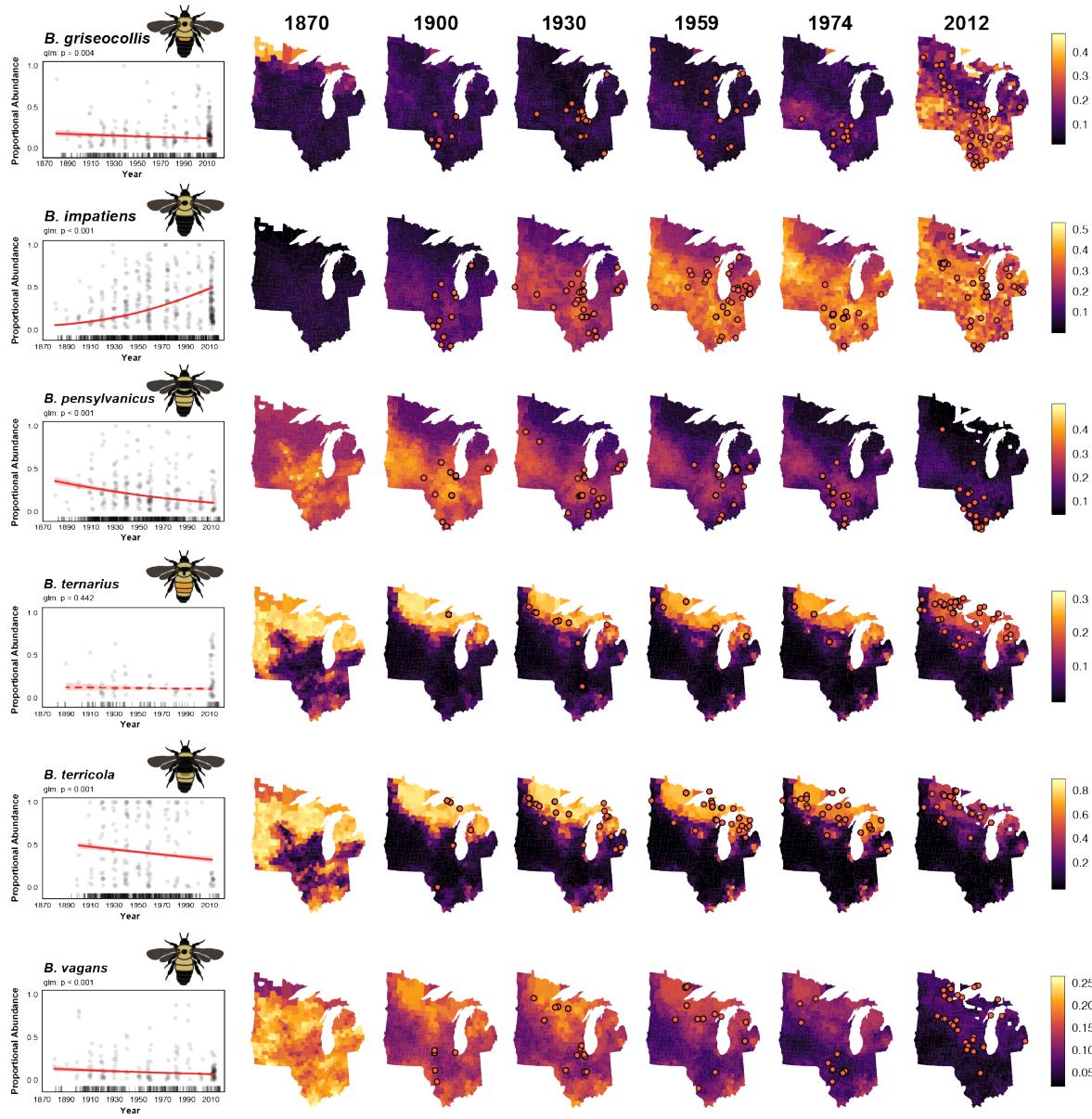
511

512 **Supplementary Figure 4:** (A) Fitted model coefficients for each species for change in county oc-
 513 cupancy over time. (B) For each species, plotted temporal trends of county occupancy over time
 514 with fitted GLM models with 95% confidence interval. Point colors indicate species relative abun-
 515 dance trend from 1870-present: red points denote species whose relative abundance declined,
 516 black points denote no change in relative abundance, and blue points denote increases in relative
 517 abundance.



519 **Supplementary Figure 5:** Patterns of agricultural intensification in two additional metrics from
 520 1982-2012: (a) proportion of county area in pasture and (c) proportion of county area treated with
 521 insecticides. Color palettes derived using quantile binning. Inset graphs (b,d) depict general trend
 522 of these two variables for each state in the study area as modeled by a Loess curve. Values beneath
 523 years are mean proportion \pm SEM.





525

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

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