

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

2 **United States parallels 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 likely impacted both nesting habitat and floral resource availability with
13 negative consequences for bumble bee populations and communities. Despite several long-
14 term analyses highlighting concerning population trends, no studies have yet explicitly linked
15 metrics of agricultural intensification to bumble bee declines. Using an extensive long term
16 set of both bumble bee records and US agricultural census records, we show that metrics of
17 increasing agricultural intensity are clearly associated with the decline of a 40% of bumble
18 bee species in the US Midwest. Additionally, we document several species increasing in rela-
19 tive abundance that positively associate with agricultural intensity, suggesting our agricultural
20 practices have inadvertently selected winners and losers in the bumble bee community over
21 the last century. In addition to suggesting future avenues for controlled, manipulative experi-
22 ments, our results suggest that changes to our agricultural practice and policies are required in
23 order to limit additional declines of Midwestern bumble bees.

²⁴ Introduction

²⁵ Extensive range contractions (Kerr et al. 2015) and possible local extinctions (Rasmont and Iser-
²⁶ byt 2012) of a number of bee species has sounded an alarm among entomologists and ecologists
²⁷ across the world (Steffan-Dewenter et al. 2005; ???). Of bee population trends that have been doc-
²⁸ umented, bumble bees (Apidae: *Bombus*) are perhaps the most well-studied with reports of many
²⁹ species declining across Europe and North/South America (Biesmeijer 2006; Colla and Packer
³⁰ 2008; Grixti et al. 2009; Cameron et al. 2011; Bartomeus et al. 2013; Morales et al. 2013; Wood et al.
³¹ 2019). Owing to their importance as pollinators in both commercial crops (Klein et al. 2007) and
³² natural systems (Ollerton, Winfree, and Tarrant 2011), understanding the factors driving bumble
³³ bee decline is critical.

³⁴ A number of studies have posited mechanisms underpinning bumble bee declines, including cli-
³⁵ mate change (Kerr et al. 2015; Marshall et al. 2017; Sirois-Delisle and Kerr 2018), habitat loss
³⁶ (Grixti et al. 2009; Goulson et al. 2015), the proliferation of parasites and disease (Cameron et al.
³⁷ 2011, @McArt2017), and competition with managed bees (Torné-Noguera et al. 2016; Cane and
³⁸ Tepedino 2017; Mallinger, Gaines-Day, and Gratton 2017; Ropars et al. 2019). Among the poten-
³⁹ tial drivers, the expansion and intensification of agriculture is consistently cited as a key factor in
⁴⁰ long-term declines of once common species in both the US (Grixti et al. 2009; Colla and Packer
⁴¹ 2008; Jacobson et al. 2018) and Europe (Goulson et al. 2005; Carvell et al. 2006). A switch from
⁴² the more diverse and less intensive agricultural systems of the early 1900's to the largely mono-
⁴³ cultural, heavy-input systems of today may lead to the loss of preferred host plant species and
⁴⁴ nesting/overwintering habitat - a threat particularly salient to bumble bees unable to adapt to
⁴⁵ these changes (Wood et al. 2019).

⁴⁶ In the United States, analysis of museum records suggests that bumble bee declines began during
⁴⁷ periods of agricultural intensification in the mid 20th century (Grixti et al. 2009). Despite sev-
⁴⁸ eral long-term analyses highlighting concerning population trends as well as studies describing
⁴⁹ the importance of historical land-use (Cusser, Neff, and Jha 2018), no studies have yet explicitly
⁵⁰ linked metrics of agricultural intensification or production to bumble bee declines due to a paucity
⁵¹ of long-term data of both bumble bee occurrence and historical agricultural production, as well

52 as the difficulty in assessing potential drivers experimentally. Additionally, variable temporal
53 patterns of species declines have been documented (e.g., long-term declines of European species
54 (Williams, Araújo, and Rasmont 2007) vs. recent crash of *Bombus affinis* Cresson in North America
55 (Giles and Ascher 2006), suggesting that the mechanisms driving declines may be species- and/or
56 region-specific. Moreover, some species populations appear stable, or may be increasing in both
57 abundance and range (e.g., *Bombus impatiens* Cresson: Richardson et al. 2018; Wood et al. 2019).

58 Several approaches have been developed to overcome data restrictions in order to understand
59 the drivers of bumble bee decline, including experiments leveraging space-for-time substitution,
60 as well as employing historical museum collections to understand species trends (Bartomeus et
61 al. 2019). While unable to draw specific, causal connections, the use of historical data provides
62 a unique perspective on temporal trends that even the most thorough experimental approaches
63 cannot provide. Several statistical approaches have been developed to account for the known
64 biases of museum collection records, allowing new data sources to be implemented and used to
65 explore bumble bee population trends (Pearce and Boyce 2006; Bartomeus et al. 2013, 2019). The
66 continued addition of museum collection records to repositories such as the Global Biodiversity
67 Information Facility (GBIF) combined with extensive, modern surveys of bumble bee fauna (e.g.,
68 Bumble Bee Watch) and data describing detailed agricultural production trends in the United
69 States (Crossley et al. *_in review*) offer a unique opportunity to assess the agricultural factors
70 associated with species population trends over time.

71 Testing specific proposed relationships of agricultural intensification to bumble bee species de-
72 clines is paramount to creating targeted, evidence-based conservation efforts specific to threat-
73 ened species. To this end, we explore the relationships between bumble bee population trends
74 and agricultural intensification in the north-central United States using an extensive data set of
75 historical bumble bee museum records, modern citizen-science surveys, and agronomic metrics
76 distilled from United States Census of Agriculture records. Our results not only confirm existing
77 long-term bumble bee population trends, but also describe clear associations among declines and
78 several measures of agricultural intensification. Together, our results suggest that alterations to
79 our agricultural systems are essential if we hope to stem further loss of bumble bee species in our
80 working landscapes.

81 **Methods**

82 In an effort to strengthen comparisons and analyses, we focused our study on the north-central
83 US states of Minnesota, Wisconsin, Iowa, Illinois, Michigan, and Indiana as these states share a
84 similar agricultural history. We also limited our analysis to species whose core ranges overlapped
85 these states to limit range edge effects, including: *Bombus affinis* Cresson, 1863; *Bombus impatiens*
86 Cresson, 1863; *Bombus griseocollis* DeGeer, 1773; *Bombus bimaculatus* Cresson, 1863; *Bombus aurico-*
87 *mus* Robertson, 1903; *Bombus ternarius* Say, 1837; *Bombus vagans* Smith, 1854; *Bombus borealis* Kirby,
88 1837; *Bombus citrinus* Smith, 1854; *Bombus pensylvanicus* De Geer, 1773; *Bombus fervidus* Fabricius,
89 1798; *Bombus rufocinctus* Cresson, 1863; and *Bombus terricola* Kirby, 1837. Additionally, several
90 bumble bee species known to be in decline nationally (including *B. affinis*, *B. terricola* and *B. pen-*
91 *sylvanicus*) have core historic ranges in the north-central US.

92 **Bumble bee specimen data**

93 We obtained bumble bee records using the Global Biodiversity Information Facility (GBIF), query-
94 ing for all records within our study region. These data were combined with records from the North
95 American Bumble Bee Watch program (www.bumblebeewatch.org) provided by the Xerces Soci-
96 ety for Invertebrate Conservation. We then filtered records to include only species known to occur
97 within our study region and which were appropriately geo-referenced (longitude and latitude).
98 Each record was assigned to a county based on its collection coordinates so that they could be
99 matched to county-level agricultural census data. Because 95% of records were from 1890 and be-
100 yond, we are confident that our county assignments are accurate as changes in county geographic
101 extent in this region were largely complete by 1890.

102 Temporal comparisons of museum and incidental records can be problematic due to collec-
103 tor/spatial bias and non-standardized collection techniques (Bartomeus et al. 2013, 2019;
104 Richardson et al. 2018). To account for this, we analyzed records using a variety of techniques to
105 control for potential biases. First, we filtered the dataset to include only single individual ‘sam-
106 pling events’ (unique combination of species, date, location, and collector), following Richardson
107 et al. (2018). All analyses were conducted using both the full and reduced datasets, but showed
108 no difference in species patterns. We therefore present results from the full dataset. For analyses

109 comparing temporal trends in diversity, we created temporal bins of records such that there were
110 approximately the same number of records per temporal bin, following Bartomeus et al. (2013).
111 Bins were created using quantiles and the `rbin` package. We created several binning strategies to
112 determine if the number of bins affected our results (Bartomeus et al. 2013), including a total of
113 3, 5, 8, and 15 temporal bins. Because trends were similar regardless of the number of bins, we
114 present results from the 8-bin analyses for changes in relative abundance and results from the
115 15-bin analyses for estimation of species richness over time. This binning strategy was used only
116 for analyses only of bumble bee records, not those in tandem with agricultural census data.

117 **Calculating temporal patterns of abundance and diversity**

118 To confirm the reports of decline in a number of bumble bee species in the US (Grixti et al. 2009;
119 Bartomeus et al. 2013; Richardson et al. 2018; Jacobson et al. 2018; Wood et al. 2019), we first
120 examined temporal trends in relative abundance and species diversity for our study region inde-
121 pendent of the agricultural census records. For each species, we calculated relative abundance
122 for each temporal bin as the number of records of a given species divided by the total number of
123 records for all species in that temporal bin. We then tested whether there was a statistically clear
124 change in relative abundance over time by fitting generalized linear models with binomial error
125 distributions for each species using temporal bin as the sole predictor and each point weighted by
126 the number of records (similar to Bartomeus et al. 2013).

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 of the relationship as
133 the assumption of normally distributed data for such a small sample may be violated. Over 1000
134 permutations, we randomly shuffled the temporal bin order, calculating the correlation between
135 bin and species richness estimates each permutation, with the p-value equalling the fraction of
136 permuted correlations greater or less than the true chronological correlation value.

¹³⁷ **Historical agriculture data**

¹³⁸ To assess the extent, diversity, and intensity of agriculture, we used county-level agricultural cen-
¹³⁹ sus data (projected and geographically corrected by Crossley et al. *in review*). These records contain
¹⁴⁰ information about farm number and size, crop extent, yields, inputs, and expenses incurred by
¹⁴¹ farms. Our objective was to estimate county-level agricultural intensity, which includes aspects of
¹⁴² both extensive and intensive farming practices. Following Crossley et al., we limited our analysis
¹⁴³ to the 18 most extensive crops which together represent over 90% of agricultural products across
¹⁴⁴ our study region (Crossley et al. *in review*). For each county by census year, we calculated crop
¹⁴⁵ richness and the proportion of county area in cropland as two measures of agricultural intensity
¹⁴⁶ (Fig. 2).

¹⁴⁷ We also extracted other crops/aspects of farm management hypothesized to be associated with
¹⁴⁸ bumble bee reductions. These included acreage of specific agricultural crops and practices known
¹⁴⁹ to affect bumble bees including pasture and acreage treated with arthropod-targeting pesticides.
¹⁵⁰ Because these two variables were not available across the same temporal extent as crop richness
¹⁵¹ and proportion of county in cropland, we conducted a separate analysis from 1974 onward where
¹⁵² clover and pasture acreage, as well as pesticide treated acreage were available at the county level.

¹⁵³ **Pairing bumble bee records with historical agriculture dataset**

¹⁵⁴ Because agricultural census data are collected every decade, not every bumble bee record was
¹⁵⁵ collected in a year concurrently with a census. As such, we paired records such that they were
¹⁵⁶ \pm 5 years of the nearest agricultural census date (e.g., bumble bee records from 1926-1935 were
¹⁵⁷ paired with the 1930 agricultural census). While this pairing may not perfectly reflect the state
¹⁵⁸ of agriculture experienced by collected bumble bees, we posit that it is still a meaningful pairing
¹⁵⁹ given that a difference of up to 5 years is not likely to manifest in large, county-level changes in
¹⁶⁰ agricultural practices that we observed occurring over several decades. Additionally, our analyses
¹⁶¹ yielded similar results with a more strict \pm 2 year pairing rule, as such we present the analysis with
¹⁶² the full dataset and \pm 5 year pairing.

163 Relating changes in relative abundance to agricultural intensity

164 We constructed models to determine whether changes in agricultural intensification were related
165 to those in bumble bee relative abundance. For each species, we fitted a generalized linear model
166 with a binomial error structure to predict county-level relative abundance as a function of num-
167 ber of crops grown within a county, the proportion of county area in agriculture and the year of
168 the agricultural census data associated with that bumble bee record, allowing us to determine a
169 temporal trend in species relative abundance taking into account agricultural intensification. In
170 this analysis, relative abundance was calculated for each county by agricultural census year com-
171 bination rather than across equally sized temporal record bins used to determine general species
172 trends. This allowed us to examine more fine-scale changes in relative abundance over time asso-
173 ciated with changes in agricultural practices by more accurately pairing bumble bee records with
174 agricultural census data. Observations were weighted by the number of bumble bee records in a
175 county by agricultural census year - effectively giving more weight to counties that had greater
176 sampling intensity. We felt that these counties provided more accurate estimates of species rela-
177 tive abundance at any given time. Additionally, we further limited our analysis to only include
178 counties with greater than 5 total bumble bee records to eliminate the presence of singleton coun-
179 ties. Allowing singletons might artificially inflate the relative abundance of given species as they
180 would be recorded as 100% of the abundance of each singleton county.

181 Because of the spatial nature of these data, we tested each species model for spatial autocorrela-
182 tion by fitting data to generalized least squares models and then testing model residuals using
183 a Moran's I test using the `spdep` package (???; similar to Meehan et al. 2011; and Meehan and
184 Gratton 2015). We also checked for temporal autocorrelation within the response of each species.
185 Because neither spatial nor temporal autocorrelation were found to be problematic, we utilized
186 the generalized linear model framework described above across all species.

187 To depict the estimated change relative abundance and range, we used our fitted models to predict
188 relative abundance across historical ranges of each species within our study area using county-
189 level agricultural intensification metrics. These maps describe the predicted probability of occur-
190 rence in each county as function of crop diversity and proportion of a county in cropland over
191 time. We selected 6 time points for which to fit models: 1870, 1900, 1930, 1959, 1974, and 2012

192 to depict how county suitability has changed over time. While not a true species distribution
193 model, these maps allow us to highlight the most suitable areas for a given species in terms of
194 their relationship to agricultural intensification.

195 Another series of models were constructed to test more detailed hypothesized drivers of bumble
196 bee decline. Generalized linear models with a binomial error structure were fit to predict county-
197 level species relative abundance as a function of pasture acreage, acreage treated with arthropod-
198 targeting insecticides, and the agricultural census year. Because the agricultural census did not
199 begin capturing pesticide input data until 1982, these models were fit on a subset of data from 1982
200 to present. By adding these more mechanistic drivers to the broad scale intensification metrics,
201 we are able to see if the response of the broad scale metrics remains consistent given additional
202 drivers. If so, we can be confident that the results from the more temporal expansive analysis
203 with broad drivers of agricultural intensification are tenable to explain the patterns of bumble bee
204 relative abundance observed.

205 **Estimating change in county occupancy**

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

211 **Results**

212 A total of 27,882 bumble bee occurrence records were compiled from GBIF and Bumble Bee Watch.
213 The species contained in each dataset were mutually inclusive. We removed *Bombus fraternus*,
214 *Bombus perplexus*, *Bombus ashtoni (bohemicus)*, and *Bombus variabilis* from our analyses as all four
215 species lacked sufficient records to make meaningful temporal interpretations of their change in
216 relative abundance and county occupancy. Of the 535 counties within the study region, 358 con-
217 tained at least 1 bumble bee record.

218 Changes in species richness and relative abundance

219 Rarefied species richness estimates for each temporal bin show estimated species richness declin-
220 ing 20% from 15 species in 1824-1925 to 12 species presently (Fig. 1) - a significant negative trend
221 ($t_{1,13} = 6.084$, $p = 0.0283$). All fifteen temporal bin species accumulation curves rapidly reached
222 an asymptote, indicating that sample sizes were sufficient to capture the diversity of communities
223 within each bin (Fig. S1). A sharp drop in estimated species richness occurred between 1952 and
224 1959 despite standardized sample sizes, followed by a slight rebound in the next 50 years.

225 Of the 13 species included in our simple analysis of change in relative abundance over time, 6
226 saw statistically clear reductions in relative abundance (*B. borealis*, *B. fervidus*, *B. pensylvanicus*, *B.*
227 *rufocinctus*, *B. terricola*, *B. vagans*: Table 1), while 7 increased in relative abundance over time (*B.*
228 *affinis*, *B. auricomus*, *B. bimaculatus*, *B. citrinus*, *B. griseocollis*, *B. impatiens*, and *B. ternarius*). Similar
229 to estimated species richness, reductions in species relative abundance seem to begin in the middle
230 of the 20th century, while those species increasing showing more consistent trends - increasing
231 steadily throughout the study period.

232 Changes in agricultural intensification

233 The areal extent of cropland peaked in our region in 1950 (average of $45\% \pm 22\%$ of county area).
234 Since then, it has decreased almost 10% to an average of $34\% \pm 20\%$ (Fig. 2A,B). Intensive agricul-
235 ture has remained relatively sparse in the north of our study region, while the highest intensity
236 occurs in the “corn belt” that stretches through southern Minnesota, Iowa, southern Wisconsin,
237 central and northern Illinois, and northern Indiana. Throughout the last century, the number of
238 agricultural crops grown has decreased substantially (Fig. 2C,D). Of the 18 crops for which we
239 compiled data, an average of 12 ± 1 were grown from 1880 - 1950. Since 1950, this number has
240 declined, with counties today growing on average 6 ± 1 crops.

241 The more fine-scale agricultural intensification variables we measured showed diverging patterns,
242 with pasture acreage declining rapidly from 1982 to present, while acreage treated with insecti-
243 cides increased (Fig. S2). These changes occurred over similar spatial extents, primarily concen-
244 trated in the corn-belt counties throughout the middle of the study region.

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

246 Patterns in bumble bee relative abundance were clearly associated with trends in agricultural
247 intensification metrics (Fig. 3, Table S1). Species increasing in relative abundance over time tended
248 to be associated with increased county-level proportion of agriculture as well as crop diversity
249 (Fig. 3B,C). Among species estimated to be in decline, county-level proportion of agriculture
250 was negatively associated with relative abundance in all but two species, *B. griseocollis* and *B.*
251 *pensylvanicus* (Fig. 3B). The responses of species in decline to crop richness were generally positive,
252 with a majority increasing in relative abundance in accordance with crop richness (Fig. 3C). When
253 we used county-level agricultural statics to predict the probability of species occurrence, we saw
254 clear patterns of range expansion and reduction associated with the intensification of agriculture
255 over time (Fig. 4).

256 Seven of the thirteen species examined showed declining trends in relative abundance when
257 species trends were modeled with agricultural intensity metrics, while three increased in rela-
258 tive abundance and three were found to not change (Fig. 3A, Fig. 4). These estimates of tem-
259 poral change in relative abundance modeled concurrently with metrics of agricultural intensity
260 aligned well with changes estimated from generalized linear models fitted with time period as the
261 sole predictor (Table 1 and Table S1). One species, *B. griseocollis*, was shown to increase in rela-
262 tive abundance when modeled using time only, while marginally decrease when modeled with
263 agricultural intensity metrics. This difference is likely due to the weighting factors and effective
264 sample size within each model.

265 We also found that more detailed agricultural metrics modeled from 1982 to present were clearly
266 associated with patterns of relative abundance (Fig 4C,D,E, Table S2). Pasture acreage had a con-
267 sistently positive association on relative abundance (Fig. 5D) despite the fact that acres of pasture
268 per county has markedly decreased over the last century (Fig. S2B). Insecticide treated acres had a
269 consistently negative effect on species relative abundance, except for 4 species (Fig. 5E, *B. aurico-*
270 *mus*, *B. bimaculatus*, *B. rufocinctus* and *B. ternarius*) for which there was no effect. *B. auricomus* and
271 *B. bimaculatus* were also found to be positively or neutrally associated with proportion cropland
272 (Fig. 5B - which is correlated with insecticide treated acreage), while *B. rufocinctus* and *B. ternarius*
273 were both negatively associated with proportion cropland. Species of conservation concern were

²⁷⁴ all negatively associated with insecticide treated acreage.

²⁷⁵ **Changes in county occupancy**

²⁷⁶ Overall, most species have increased in county occupancy over time (Fig. 6). Notably, species of
²⁷⁷ concern (*B. affinis*, *B. terricola*, and *B. pensylvanicus*) showed either a decrease in or no growth in
²⁷⁸ county occupancy over time despite the increase in sampling effort that has occurred over the last
²⁷⁹ few decades.

²⁸⁰ **Discussion**

²⁸¹ Entomologists and ecologists have long posited that increases in agricultural intensity are a driv-
²⁸² ing force behind bumble bee population declines (Kremen, Williams, and Thorp 2002; Goulson,
²⁸³ Lye, and Darvill 2008). Several experimental approaches have buttressed this proposed relation-
²⁸⁴ ship, but studies explicitly tying long-term trends in agriculture to trends in bumble bee popu-
²⁸⁵ lations are still lacking. Results from this study provide correlative support to this hypothesized
²⁸⁶ relationship by examining trends in agricultural growing practices and bumble bee records over
²⁸⁷ 140 years across 6 agronomically critical states within the US. Our results confirm the alarming
²⁸⁸ decline of a number of bumble bee species and provide support to the notion that increases in
²⁸⁹ agricultural intensity are a factor driving the decline of insects (Hallmann et al. 2017; Seibold et
²⁹⁰ al. 2019). Our study joins a number of taxa-specific studies that highlight the threat of modern
²⁹¹ agricultural practices to biodiversity (e.g., birds Benton et al. 2002; Meehan, Hurlbert, and Gratton
²⁹² 2010, OTHERS?).

²⁹³ Of the 13 species in this study, 3 were found to increase, 3 remain at similar, and 7 to have declined
²⁹⁴ in relative abundance when modeled with agricultural intensity metrics. The declining species in
²⁹⁵ our study match those found to be in decline elsewhere, including individual state analyses within
²⁹⁶ our study region (Grixti et al. 2009; Wood et al. 2019), the US East coast (Richardson et al. 2018;
²⁹⁷ Jacobson et al. 2018), Canada (Colla and Packer 2008), and North America, generally (Cameron et
²⁹⁸ al. 2011; Colla et al. 2012). Those showing the most concerning trends include *B. terricola* and *B.*
²⁹⁹ *pensylvanicus*, both of which significantly decreased in relative abundance (both when measured
³⁰⁰ by temporal bin analysis and with agricultural intensification metrics) as well as showed distinct

301 decreases in county occupancy over time, having decreasing from peak occupancy between 1930-
302 1950 to present (Fig. 6).

303 We found that the intensification of agriculture through increases in crop land area and reduced
304 diversity of crops was consistently associated with reduction in bumble bee relative abundance.
305 With few exceptions, species whose relative abundance was found to be increasing or stable had
306 either positive or neutral relationships with agricultural intensity metrics, while those in decline
307 were negatively associated with increased agricultural intensity.

308 We suspect that reductions in suitable nesting and foraging habitat associated with agricultural
309 intensification are the likely mechanisms underlying the observed relationships between bumble
310 bees and proportion cropland and crop diversity. Increases in agricultural land have been impli-
311 cated in the loss of diverse floral habitat such as tall-grass prairies (Smith 1998; Brown and Schulte
312 2011), as well as large-scale reductions in bumble bee forage plants (Carvell et al. 2006). A shift
313 from the diverse cropping systems of the early to mid 1900's to largely monocultural systems
314 in recent years has undoubtedly altered total floral resource availability and temporal continuity
315 (Schellhorn, Gagic, and Bommarco 2015) and has been shown to negatively impact bumble bee
316 colony development (Hass et al. 2018). While some mass-flowering crops might benefit bumble
317 bee colony growth (Westphal, Steffan-Dewenter, and Tscharntke 2009), they may also favor species
318 that can tolerate highly variable temporal resources [Schmid-Hempel and Schmid-Hempel (1998);
319 Hemberger et al. in revision] and provide little dietary diversity for foraging bees. Such a limit on
320 pollen and nectar diversity may have adverse consequences for bumble bees (Vaudo et al. 2015).
321 Additionally, landscapes that restrict floral resource availability during key time periods might
322 limit bumble bee colony growth (Williams, Regetz, and Kremen 2012) and subsequent queen pro-
323 duction (Crone, Williams, and Letters 2016), thereby reducing population stability over time.

324 Any changes in floral resource composition brought about by agronomic practices (e.g., changing
325 the number of identity of planted crops, or the control of weedy wildflower species) may favor
326 species with larger diet breadths (Kleijn and Raemakers 2008). For example, species in the Py-
327 robombus subgenus are known to visit a greater diversity of floral resources, including a number
328 of invasive weeds and agricultural crops (Wood et al. 2019). Such traits are likely to allow this
329 group to act as “agricultural utilizers” or “dwellers”, while those declining (e.g., species in Bom-

330 *bus sensu strictu* and *Thoracobombus*) might be considered “agricultural avoiders” (Fischer et al.
331 2015) - unable to adapt to the novel conditions brought about by the rapid changes in plant diver-
332 sity and abundance, as well as the novel abiotic conditions associated with modern agroecosys-
333 tems. Our results align well with this hypothesis: species in *Pyrobombus* are those most increas-
334 ing in relative abundance (e.g., *B. impatiens*, *B. bimaculatus*) with strong, positive associations with
335 agricultural intensity metrics, while species in *Bombus sensu strictu* and *Thoracobombus* (e.g., *B.*
336 *terricola* and *B. pensylvanicus*) are those with the most alarming trends in relative abundance and
337 strong, negative associations with agricultural intensity. Overall, these results fit into a broader
338 framework of species “winners” and “losers” as a result of anthropogenic activity (McKinney and
339 Lockwood 1999; Dornelas et al. 2019).

340 The largely positive response of relative abundance to crop richness suggests that increasing agri-
341 cultural landscape heterogeneity could have benefits for both common and declining bumble bee
342 species. Increasing landscape heterogeneity is known to benefit a number of ecosystem services
343 (Fahrig et al. 2011; Turner, Donato, and Romme 2012) and biodiversity (Benton, Vickery, and
344 Wilson 2003; Sirami et al. 2019), even with relatively simple changes in cropland heterogeneity
345 (e.g., decreasing field size). Such adjustments to agronomic practices could have even larger, pos-
346 itive effects on biodiversity than increasing the amount of semi-natural habitat in the landscape
347 (Sirami et al. 2019) in addition to being easier to implement and easier to incentivize through tra-
348 ditional farm policy frameworks. As natural habitats have become increasingly rare, alterations
349 that we can make to our land use practices (e.g., Landis 2017) will be the key toward building
350 multi-functional agroecosystems that both provide food and fiber for humans, as well as conserve
351 essential ecosystem service providing organisms and biodiversity writ large.

352 Generally, our analysis from 1982-present showed that increases in the acreage of cropland treated
353 with pesticides tended to be associated with decreased relative abundance of all but three species
354 which had no relationship (*B. rufocinctus*, *B. auricomus*, and *B. ternarius*). The relative abundance of
355 *B. rufocinctus* and *B. ternarius*, however, was negatively impacted by proportion cropland, suggest-
356 ing these species still are affected by large-scale agricultural intensification. There is clear evidence
357 that exposure to pesticides, including both insecticides and fungicides, is detrimental to bumble
358 bee foraging (Feltham, Park, and Goulson 2014), colony development (Whitehorn et al. 2012; Crall

359 et al. 2018), and may also facilitate increased pathogen prevalence (McArt et al. 2017).

360 We also found that pasture acreage was positively associated with bumble bee relative abundance
361 for all but three species that showed no relationship. Pastures and grasslands are often a source of
362 floral habitat for foraging bumble bees both in the US and in Europe (Carvell et al. 2006) as these
363 open areas often contain plants in the family Fabaceae, a preferred source of bumble bee forage
364 (Goulson et al. 2005) especially in several Midwestern bumble bees species (Fye and Medler 1954).
365 While pastures and fabaceous cover crops were used heavily in the early 20th century to return
366 nitrogen to soils, technological advancements following the second world war (namely artificial
367 nitrogenous fertilizers) led quickly to the decline in these crops (Williams 1986; Williams and
368 Osborne 2009).

369 Several species showed interesting temporal patterns of relative abundance and/or relationships
370 to agricultural intensity. One species of note is the increasingly common two-spotted bumble
371 bee, *B. bimaculatus*, the only species predicted to be increasing in relative abundance that showed
372 strong, a negative relationship with crop area but a strong, positive relationship with crop diver-
373 sity. *B. bimaculatus* is known nest within woodlands and indeed favor early-emerging woodland
374 plants (Wood et al. 2019). Cropland proportion is known to be negatively correlated to natural
375 habitats such as woodland (Brown, Pijanowski, and Duh 2000; Hemberger and Gratton 2018), and
376 we find that counties that contain increased numbers of crops tend to be correlated with lower
377 proportion cropland - a pattern that has emerged within the last 50 years. Cropland in this region
378 has also decreased slightly in the last 80 years, having been replaced primarily by deciduous forest
379 (Rhemtulla, Mladenoff, and Clayton 2007). This change has potentially increased suitable habitat
380 for *B. bimaculatus*. We conclude that, while not as direct, the rise of *B. bimaculatus* is still likely
381 related to land use changes associated with agricultural intensification in the north central US.

382 Additionally, we found no decline in the relative abundance of the federally endangered *B. affinis*
383 across our study region. This result contradicts findings by almost all other longitudinal studies
384 in which *B. affinis* is considered. In this case, presence-only relative abundance may not offer the
385 best metric by which to judge species declines. For example, if *B. affinis* has been extirpated from a
386 wide swath of its range (as is likely given evidence by Colla and Packer 2008; Cameron et al. 2011;
387 Richardson et al. 2018; Wood et al. 2019), but remained equally abundant in the localities it still oc-

388 copies, presence-only relative abundance would not capture that change. As such, we examined
389 the number of occupied counties over time, and see a distinct unimodal relationship for *B. affinis*,
390 whereby peak county occupancy occurs in the mid 20th century, followed by a sharp decline until
391 recently. This recent increase in occupancy was recorded thanks to the efforts of the citizen sci-
392 ence program Bumble Bee Watch. County level occupancy may simply be a function of sampling
393 effort, however sampling effort (as measured by total bees recorded per time period) remained at
394 or above average following peak county occupancy in 1959. Together, these results suggest that
395 while *B. affinis* has certainly declined in county occupancy within our study region, it may remain
396 at similar or even increased relative abundance in the refuge counties that it still occupies. Impor-
397 tantly, the locations in which *B. affinis* remains include working landscapes with predominately
398 agricultural and urban land-uses. Altogether, this suggests that suspending anthropogenic activi-
399 ties may not be necessary to protect this species. Future studies should examine these landscapes
400 more closely as they may hold important information about the habitat requirements of *B. affinis*.

401 Another interesting pattern we observed was that of *B. pensylvanicus*, which showed a strong,
402 positive relationship with proportion of agriculture. This is likely due to the fact that *B. pensyl-*
403 *vanicus* has historically been associated with agricultural landscapes containing open pasture and
404 hayfields (Franklin 1913), areas likely to be within counties having a larger total proportion of
405 agricultural area. However, we did not find any relationship between *B. pensylvanicus* and pasture
406 acreage in our secondary analysis. This suggests that other agricultural practices, namely insec-
407 ticide use or other aspects of agricultural land management, and/or pathogens (Cameron et al.
408 2011) may be at play. Indeed, we found a strong, negative relationship between *B. pensylvanicus*
409 relative abundance and pesticide treated acreage while controlling for the proportion of agricul-
410 tural land and crop richness. Together, these data suggest that the most suitable landscapes for
411 *B. pensylvanicus* are also highly detrimental to it (i.e., open croplands that are heavily treated with
412 insecticides), resulting in declines in both relative abundance and county occupancy.

413 It is important to place the observed changes in relative abundance and county occupancy into
414 a larger context. Examining changes from 1877 to present day may not accurately capture the
415 pre-European settlement baseline of the study species examined. Many counties were already ex-
416 tensively altered by both agriculture and deforestation (Rhemtulla, Mladenoff, and Clayton 2007).

417 In some cases (e.g., Michigan), these alterations may have provided more floral resources by cre-
418 ating open habitat, resulting in the increase of some bumble bee species (Wood et al. 2019). In
419 shifting from the agronomic practices of the early 20th century to the more industrialized, inten-
420 sive practices of the later 20th century, the suitability for those previously favored bumble bees
421 decreased paving way for the rise of others. The lack of true historical baselines does not mean
422 that the declines described in this study are normal or unworthy of immediate conservation ac-
423 tion. The scale and intensity of agricultural intensification over the last 60 years is unprecedented
424 and the risks to bumble bees clear. The dualism of bumble bee species responses to agricultural
425 intensification both historically and contemporarily suggests that species habitat requirements are
426 variable - something we must explicitly consider in planning bumble bee conservation strategies.

427 Museum records are an invaluable source of data for studies examining changes in species range
428 and long term population trends (Bartomeus et al. 2019), as well as understanding the ecological
429 drivers that underpin changes in species assemblages over time (Wood et al. 2019). A strength of
430 leveraging long-term museum records, including our approach in this study, include the ability to
431 examine spatial and temporal scales that are not amenable to experimental methods (Meehan et
432 al. 2011). However, care must be taken to account for biases associated with historical collections.
433 For example, museum collection records do not necessarily adhere to standard ecological prac-
434 tices of ensuring random, equal-effort samples over adequate space and time (Richardson et al.
435 2018). To account for known issues, we employed a variety of techniques including subsampling
436 and sensitivity analyses to determine whether our chosen methods skewed results (for a thorough
437 analysis of techniques to leverage historical collections, see Bartomeus et al. 2019). Irrespective of
438 the approaches used, we consistently identified declines in over half of study species with clear
439 associations to metrics of agricultural intensity. We also caution against the over-interpretation
440 of the correlative patterns observed in this study. While the observed patterns offer evidence to
441 further test mechanisms of decline, we stress that correlative approaches must be paired with
442 manipulative experiments that can more explicitly test mechanisms over manageable spatial and
443 temporal scales (e.g., understanding how human-mediated factors of bumble bee declines inter-
444 face with bumble bee physiology: Woodard 2017). Our use of public historical records highlights
445 the importance of providing resources and funding to both academic and national natural history

⁴⁴⁶ collections: the inferences available from these data are invaluable.

⁴⁴⁷ **Conclusions**

⁴⁴⁸ By relating changes in county-level agricultural intensity to changes in the relative abundance of
⁴⁴⁹ bumble bee species across the upper Midwest, we provide evidence that agricultural intensifica-
⁴⁵⁰ tion is a key driver of shifts in bumble bee community composition and abundance over the last
⁴⁵¹ century. Over the past century, agricultural intensification has elicited a strong, selective pressure,
⁴⁵² inadvertently selecting winner and loser species in bumble bee communities. Our work supports
⁴⁵³ an existing body of evidence from both manipulative and observational studies, including recent,
⁴⁵⁴ catastrophic declines documented in insect and arthropod abundance in agriculturally dominated
⁴⁵⁵ landscapes. There is still a great need for additional experimentation to understand how land use
⁴⁵⁶ drivers might interact with other known causes of bumble bee decline, namely climate change and
⁴⁵⁷ pathogen and disease prevalence. The combination of our results leveraging museum records and
⁴⁵⁸ historical data along with a growing body of experimental evidence suggests that changes to our
⁴⁵⁹ agricultural practice and policies are required in order to limit additional declines of Midwestern
⁴⁶⁰ bumble bees.

⁴⁶¹ **Acknowledgements**

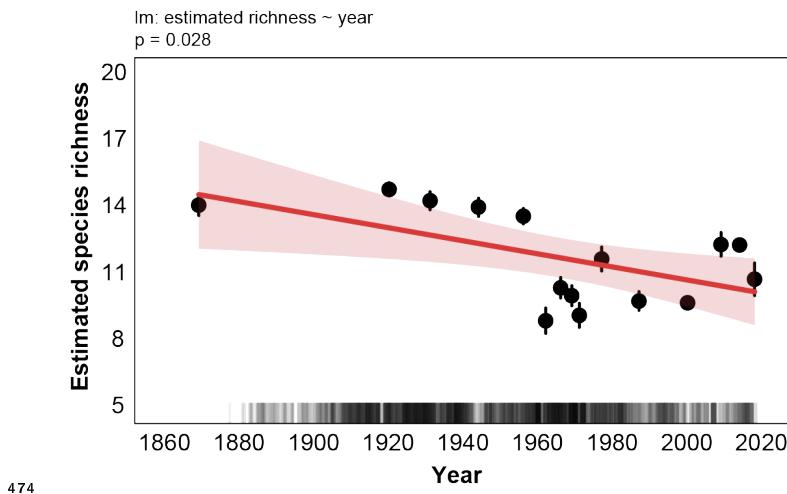
⁴⁶² We would like to thank Christelle Guédot, John Orrock, and Russ Groves for the valuable feed-
⁴⁶³ back that improved this manuscript. We also acknowledge Rich Hatfield at the Xerces Society
⁴⁶⁴ for Invertebrate Conservation for providing the Bumble Bee Watch data. Data and code for
⁴⁶⁵ all analyses, figures, and the manuscript will be made publicly available upon publication at
⁴⁶⁶ <https://github.com/jhemberger>.

467 **Figures and Tables**

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

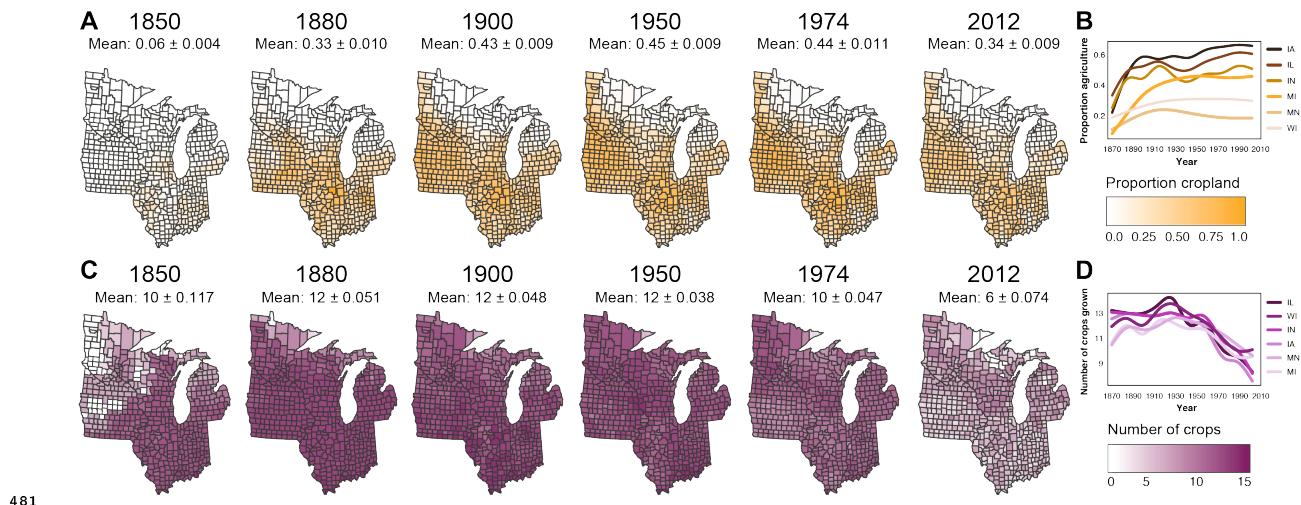
Species	1900-1923	1924-1946	1947-1962	1963-1968	1969-1972	1973-1993	1994-2013	2013-present	N records	Coef. Estimate	P value
<i>B. affinis</i>	0.0118	0.0487	0.1133	0.2896	0.0123	0.0712	0.0637	0.1030	2155	0.049	p < 0.001
<i>B. auricomus</i>	0.0567	0.0191	0.0173	0.0153	0.0360	0.0180	0.0661	0.0432	894	0.069	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

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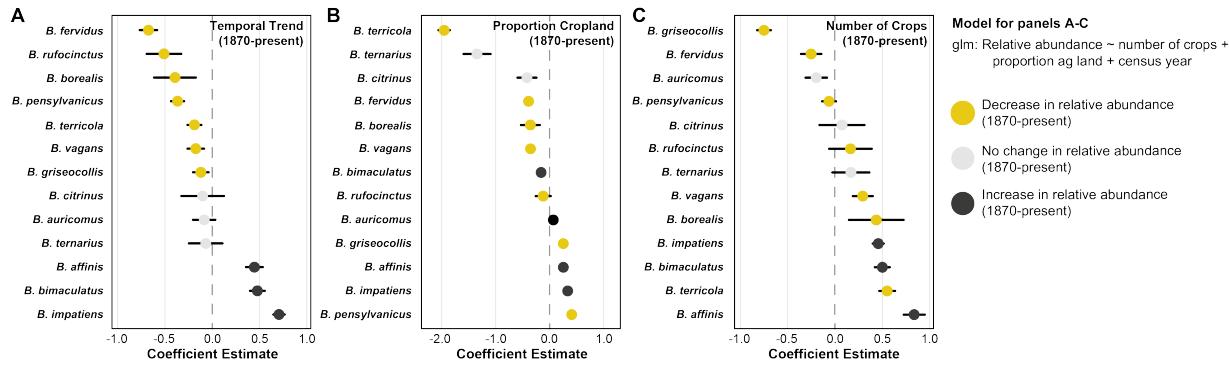
474

475 **Figure 1:** Trend in rarified bumble bee species richness from 1877-present. Each point represents a
 476 date range that is standardized to contain an approximately equal number of bumble bee records.
 477 Each point is plotted at the midpoint of the date range. The fitted line is a linear model predicting
 478 estimated species richness as a function of temporal bin order using the midpoint of the temporal
 479 bin as the predictor. Carpet plot represents temporal collection point for all records from 1877 to
 480 present.

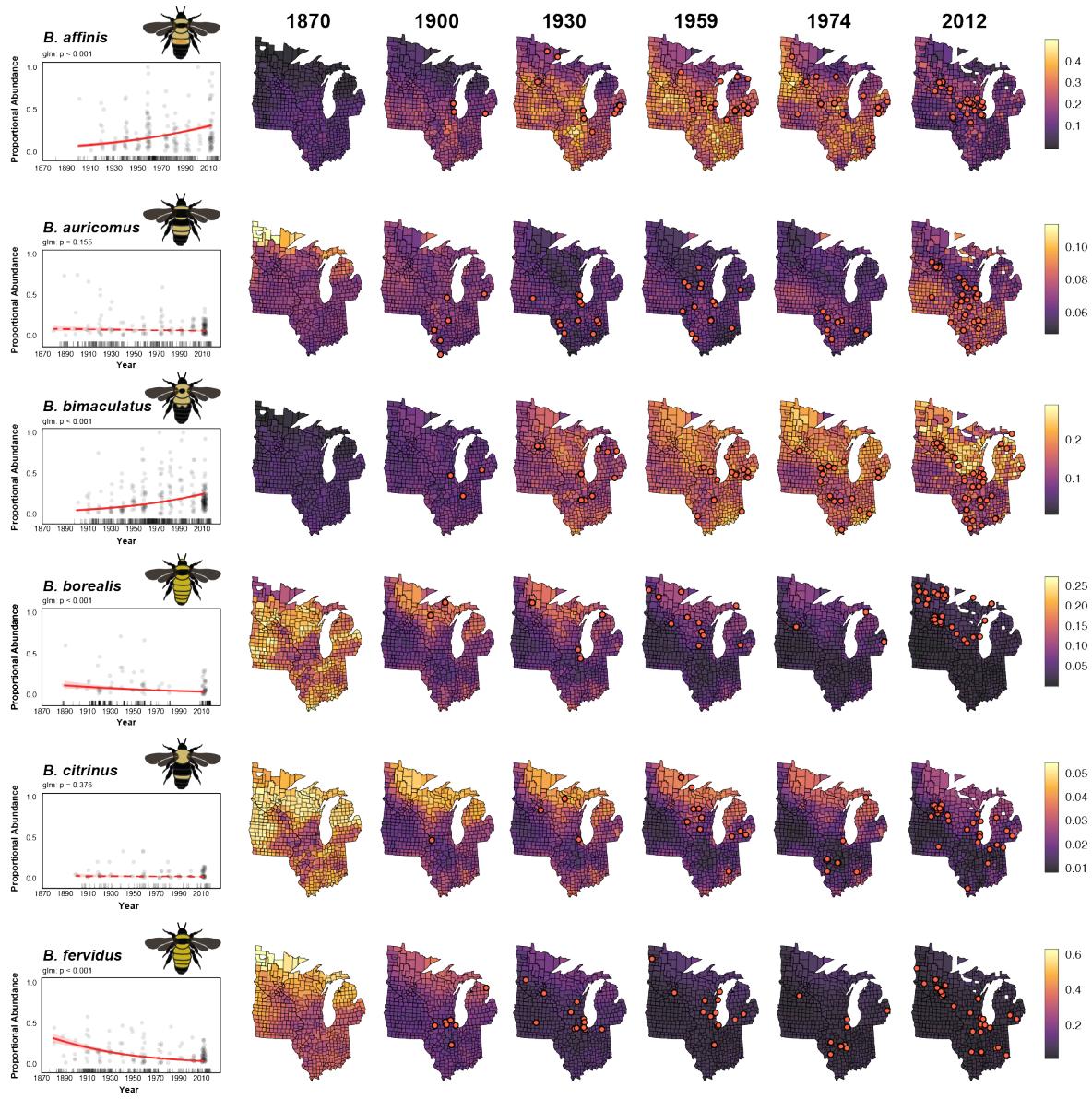


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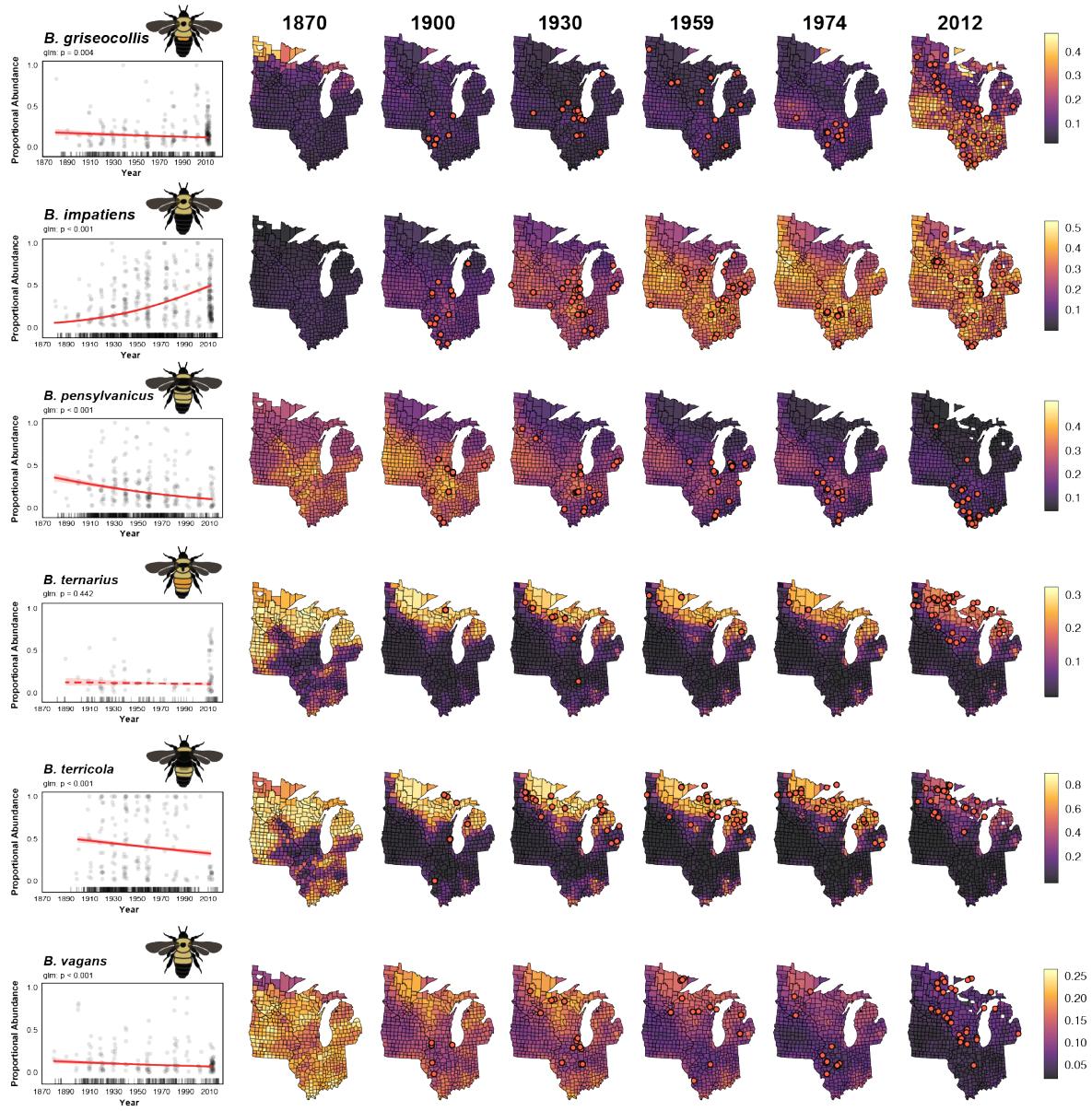
482 **Figure 2:** Patterns of agricultural intensification in two metrics: (a) proportion of county under
 483 cultivation and (c) number of crops grown per county. Inset graphs (b,d) depict general trend of
 484 these variables for each state in the study area as modeled by a Loess fitted curve. Values beneath
 485 years are mean ± SEM.



487 **Figure 3:** 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
488 in a county. Models were fitted using the entire dataset from 1870-present. Point colors indicate
489 species relative abundance trend from 1870-present: yellow points denote species whose relative
490 abundance declined, gray points denote no change in relative abundance, and black points denote
491 increases in relative abundance.

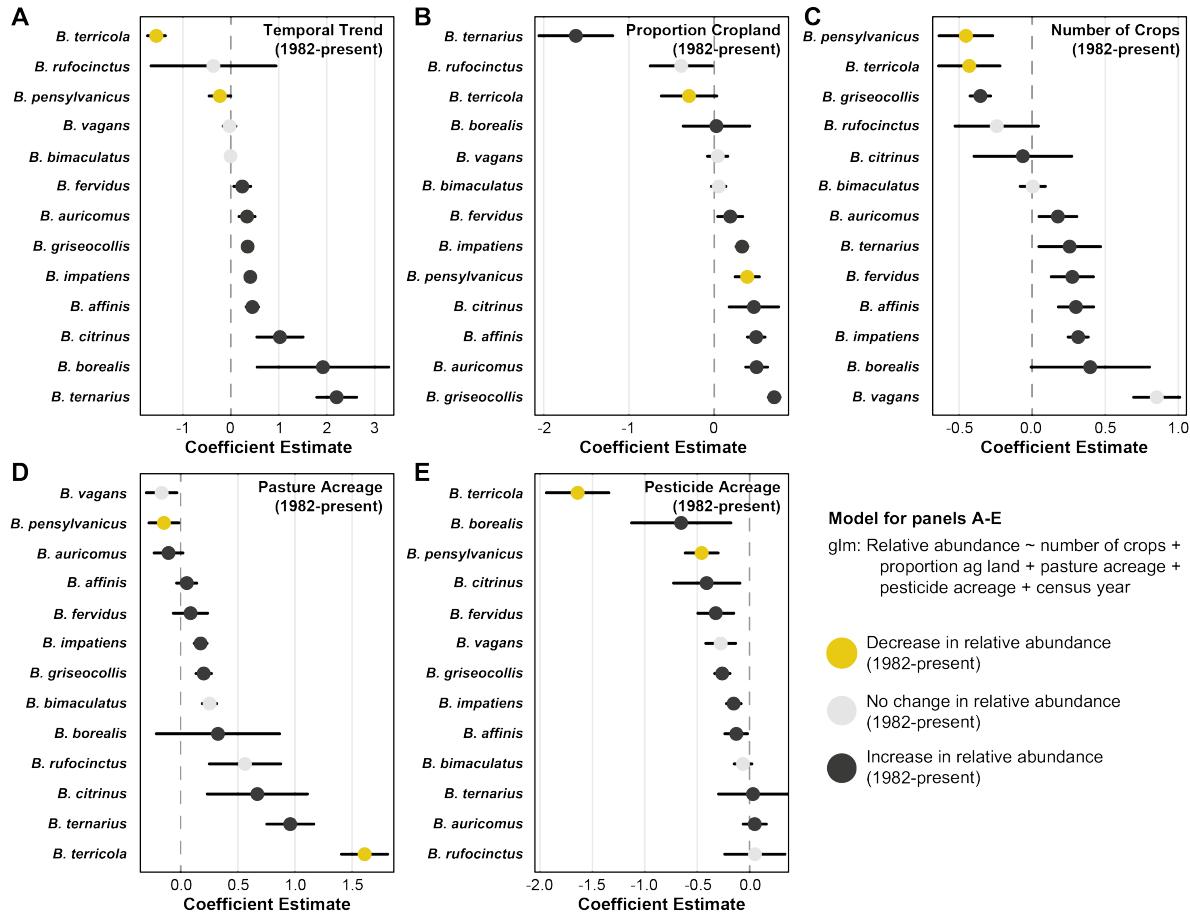


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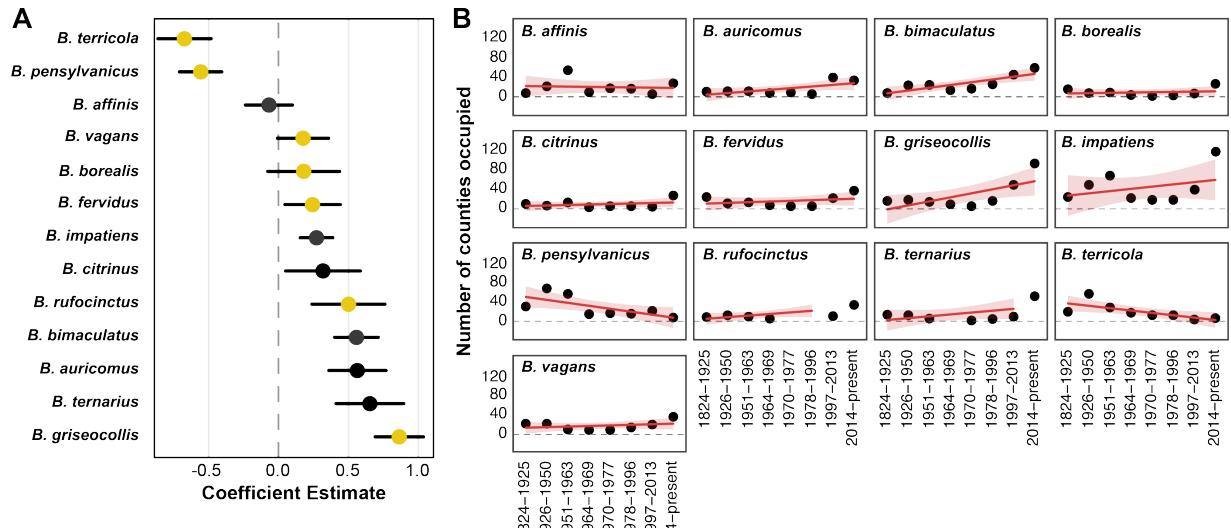
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495 **Figure 4:** Fitted temporal trend of relative abundance when modeled with agricultural intensity
 496 metrics along with the predicted probability of occurrence for each study species in each county.
 497 given crop diversity and proportion cropland in each county. Darker colors denote smaller prob-
 498 ability of occurrence, while lighter colors indicate larger probability of occurrence. Solid red lines
 499 denote statistically clear trend in relative abundance over time ($p < 0.05$), while dashed lines de-
 500 note statistically unclear trends ($p > 0.05$). Points on temporal trend are slightly jittered for visi-
 501 bility. Red points on each map are randomly selected occurrence records with a maximum of 50
 502 plotted per year.



503

504 **Figure 5:** 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.



511

512 **Figure 6:** (A) Fitted model coefficients for each species for change in county occupancy over time.
 513 (B) For each species, plotted temporal trends of county occupancy over time with fitted GLM
 514 models with 95% confidence interval. Point colors indicate species relative abundance trend from
 515 1870-present: red points denote species whose relative abundance declined, black points denote
 516 no change in relative abundance, and blue points denote increases in relative abundance.

517 **Supplementary Material**

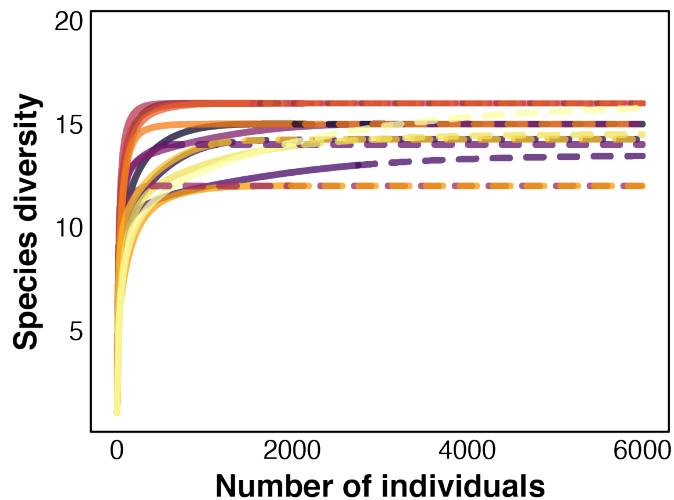
518 **Supplementary Table 1:** Generalized linear model results for each study species including the
 519 sample size (number of counties for which relative abundance is calculated), model term, scaled
 520 coefficient estimate, 95% confidence interval and p-value. Each county is weighted by the total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

Species	Sample size (n counties)	Model term	Coef. 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	-2.5356	< 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

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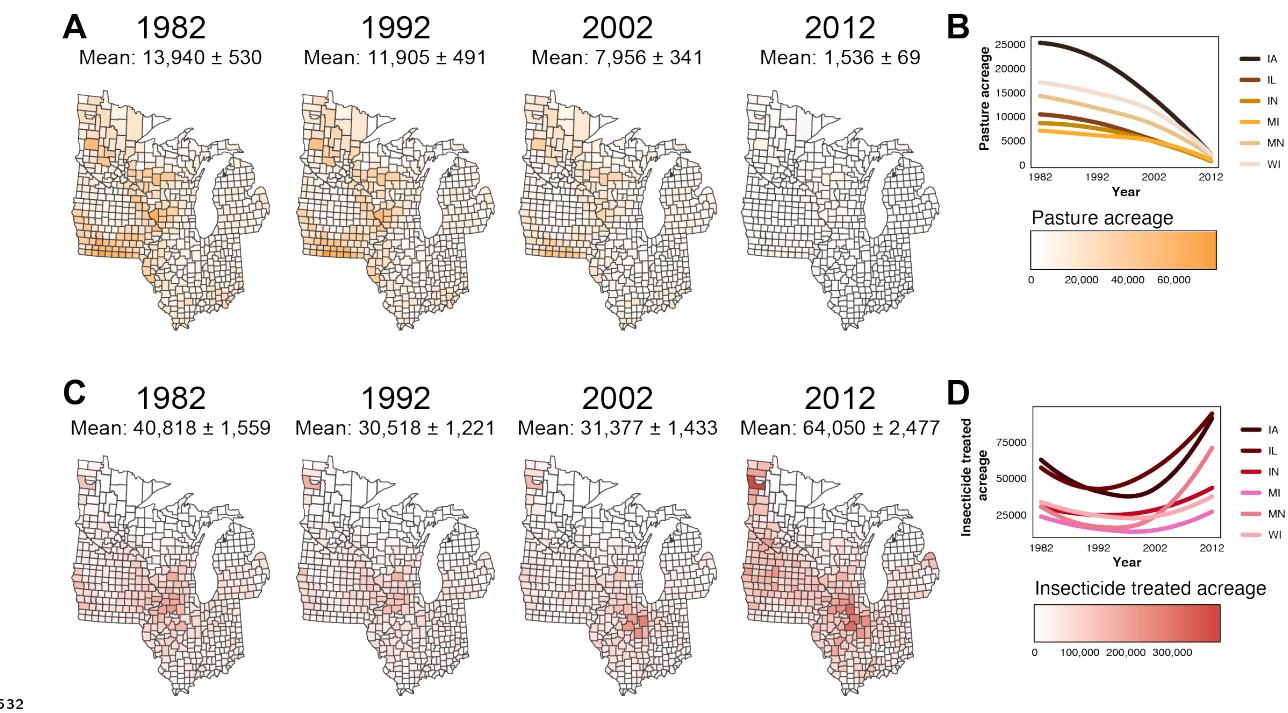
523 **Supplementary Table 2:** Generalized linear model results for each study species including the
 524 sample size (number of counties for which relative abundance is calculated), model term, scaled
 525 coefficient estimate, 95% confidence interval and p-value. Each county is weighted by the total
 526 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



528

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



532

533 **Supplementary Figure 2:** Patterns of agricultural intensification in two metrics additional metrics
 534 from 1982-2012: (a) total acres of pasture per county and (c) total acreage treated with insecticides
 535 per county. Inset graphs (b,d) depict general trend of these two variables for each state in the
 536 study area as modeled by a Loess fitted curve. Values beneath years are mean acres \pm SEM.

537 **References**

- 538 Bartomeus, Ignasi, Mia G. Park, Jason Gibbs, Bryan N. Danforth, Alan N. Lakso, and Rachael
539 Winfree. 2013. "Biodiversity ensures plant-pollinator phenological synchrony against climate
540 change." *Ecol. Lett.* 16 (11): 1331–8. <https://doi.org/10.1111/ele.12170>.
- 541 Bartomeus, I., J. R. Stavert, D. Ward, and O. Aguado. 2019. "Historical collections as a tool for
542 assessing the global pollination crisis." *Philos. Trans. R. Soc. B Biol. Sci.* 374 (1763): 1–9. <https://doi.org/10.1098/rstb.2017.0389>.
- 544 Benton, Tim G., David M. Bryant, Lorna Cole, and Humphrey Q.P. Crick. 2002. "Linking agricultural
545 practice to insect and bird populations: A historical study over three decades." *J. Appl. Ecol.*
546 39 (4): 673–87. <https://doi.org/10.1046/j.1365-2664.2002.00745.x>.
- 547 Benton, Tim G., Juliet A. Vickery, and Jeremy D. Wilson. 2003. "Farmland biodiversity: Is habitat
548 heterogeneity the key?" *Trends Ecol. Evol.* 18 (4): 182–88. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9).
- 550 Biesmeijer, J. C. 2006. "Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and
551 the Netherlands." *Science (80-.).* 313 (5785): 351–54. <https://doi.org/10.1126/science.1127863>.
- 552 Brown, D. G., B. C. Pijanowski, and J. D. Duh. 2000. "Modeling the relationships between land use
553 and land cover on private lands in the Upper Midwest, USA." *J. Environ. Manage.* 59 (4): 247–63.
554 <https://doi.org/10.1006/jema.2000.0369>.
- 555 Brown, Paul W., and Lisa A. Schulte. 2011. "Agricultural landscape change (1937-2002) in
556 three townships in Iowa, USA." *Landsc. Urban Plan.* 100 (3): 202–12. <https://doi.org/10.1016/j.landurbplan.2010.12.007>.
- 558 Cameron, Sydney A, Jeffrey D Lozier, James P Strange, Jonathan B Koch, Nils Cordes, Leellen F
559 Solter, Terry L Griswold, and Gene E Robinson. 2011. "Patterns of widespread decline in North
560 American bumble bees." *Proc. Natl. Acad. Sci. U. S. A.* 108 (2): 662–67. <https://doi.org/10.1073/pnas.1014743108>.
- 562 Cane, James H., and Vincent J. Tepedino. 2017. "Gauging the Effect of Honey Bee Pollen Collection
563 on Native Bee Communities." *Conserv. Lett.* 10 (2): 205–10. <https://doi.org/10.1111/conl.12263>.

- 564 Carvell, Claire, David B. Roy, Simon M. Smart, Richard F. Pywell, Chris D. Preston, and Dave
565 Goulson. 2006. "Declines in forage availability for bumblebees at a national scale." *Biol. Conserv.*
566 132 (4): 481–89. <https://doi.org/10.1016/j.biocon.2006.05.008>.
- 567 Colla, Sheila R., Fawzia Gadallah, Leif Richardson, David Wagner, and Lawrence Gall. 2012.
568 "Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens."
569 *Biodivers. Conserv.* 21 (14): 3585–95. <https://doi.org/10.1007/s10531-012-0383-2>.
- 570 Colla, Sheila R., and Laurence Packer. 2008. "Evidence for decline in eastern North American
571 bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson." *Biodivers.*
572 *Conserv.* <https://doi.org/10.1007/s10531-008-9340-5>.
- 573 Crall, James D, Callin M Switzer, Robert L Oppenheimer, Ashlee N. Ford Versypt, Biswadip Dey,
574 Andrea Brown, Mackay Eyster, et al. 2018. "Neonicotinoid exposure disrupts bumblebee nest
575 behavior, social networks, and thermoregulation." *Science* (80-.). 362 (6415): 683–86. <https://doi.org/10.1126/science.aat1598>.
- 577 Crone, Elizabeth E., Neal M. Williams, and Ecology Letters. 2016. "Bumble bee colony dynamics:
578 Quantifying the importance of land use and floral resources for colony growth and queen produc-
579 tion." Edited by Rebecca Irwin. *Ecol. Lett.* 19 (4): 460–68. <https://doi.org/10.1111/ele.12581>.
- 580 Cusser, Sarah, John L. Neff, and Shalene Jha. 2018. "Land-use history drives contemporary
581 pollinator community similarity." *Landsc. Ecol.* 33 (8): 1335–51. <https://doi.org/10.1007/s10980-018-0668-2>.
- 583 Dornelas, Maria, Nicholas J. Gotelli, Hideyasu Shimadzu, Faye Moyes, Anne E. Magurran, and
584 Brian J. McGill. 2019. "A balance of winners and losers in the Anthropocene." *Ecol. Lett.* 22 (5):
585 847–54. <https://doi.org/10.1111/ele.13242>.
- 586 Fahrig, Lenore, Jacques Baudry, Lluís Brotons, Françoise G Burel, Thomas O Crist, Robert J Fuller,
587 Clelia Sirami, Gavin M Siriwardena, and Jean-Louis Martin. 2011. "Functional landscape het-
588 erogeneity and animal biodiversity in agricultural landscapes." *Ecol. Lett.* 14 (2): 101–12. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>.
- 590 Feltham, Hannah, Kirsty Park, and Dave Goulson. 2014. "Field realistic doses of pesticide im-

- 591 idacloprid reduce bumblebee pollen foraging efficiency." *Ecotoxicology* 23 (3): 317–23. <https://doi.org/10.1007/s10646-014-1189-7>.
- 593 Fischer, Jason D., Sarah C. Schneider, Adam A. Ahlers, and James R. Miller. 2015. "Categorizing
594 wildlife responses to urbanization and conservation implications of terminology." *Conserv. Biol.*
595 29 (4): 1246–8. <https://doi.org/10.1111/cobi.12451>.
- 596 Franklin, Henry J. 1913. *The Bombidae of the New World*. Vol. 53. 9. [Philadelphia] : American
597 Entomological Society, <https://doi.org/10.5962/bhl.title.122585>.
- 598 Fye, R E, and J T Medler. 1954. "Spring emergence and floral hosts of Wisconsin bumblebees."
- 599 Giles, Valerie, and JOHN Ascher. 2006. "A survey of the bees of the Black Rock Forest preserve,
600 New York (Hymenoptera: Apoidea)." *J. Hymenopt. Res.* 15 (2): 208–31.
- 601 Goulson, Dave, Elizabeth Nicholls, C. Botias, Ellen L. Rotheray, Cristina Botías, and Ellen L.
602 Rotheray. 2015. "Bee declines driven by combined stress from parasites, pesticides, and lack
603 of flowers." *Science* (80-.), no. February: 1–16. <https://doi.org/10.1126/science.1255957>.
- 604 Goulson, D., M. E. Hanley, B. Darvill, J. S. Ellis, and M. E. Knight. 2005. "Causes of rarity in
605 bumblebees." *Biol. Conserv.* 122 (1): 1–8. <https://doi.org/10.1016/j.biocon.2004.06.017>.
- 606 Goulson, D, G C Lye, and B Darvill. 2008. "Decline and conservation of bumble bees." *Annu. Rev.*
607 *Entomol.* 53 (January): 191–208. <https://doi.org/10.1146/annurev.ento.53.103106.093454>.
- 608 Grixti, Jennifer C., Lisa T. Wong, Sydney a. Cameron, and Colin Favret. 2009. "Decline of bumble
609 bees (*Bombus*) in the North American Midwest." *Biol. Conserv.* 142 (1): 75–84. <https://doi.org/10.1016/j.biocon.2008.09.027>.
- 611 Hallmann, Caspar A., Martin Sorg, Eelke Jongejans, Henk Siepel, Nick Hofland, Heinz Schwan,
612 Werner Stenmans, et al. 2017. "More than 75 percent decline over 27 years in total flying insect
613 biomass in protected areas." *PLoS One* 12 (10): e0185809. <https://doi.org/10.1371/journal.pone.0185809>.
- 615 Hass, Annika Louise, Lara Brachmann, Péter Batáry, Yann Clough, Hermann Behling, and Teja
616 Tscharntke. 2018. "Maize-dominated landscapes reduce bumblebee colony growth through pollen

- 617 diversity loss." *J. Appl. Ecol.*, no. September: 1–11. <https://doi.org/10.1111/1365-2664.13296>.
- 618 Hemberger, Jeremy, and Claudio Gratton. 2018. "Floral resource pulse decreases bumble bee
619 foraging trip duration in central Wisconsin agroecosystem." *Ecol. Entomol.* 43 (4): 447–57. <https://doi.org/10.1111/een.12516>.
- 621 Hsieh, T. C., K. H. Ma, and Anne Chao. 2016. "iNEXT: an R package for rarefaction and ex-
622 trapolation of species diversity (Hill numbers)." *Methods Ecol. Evol.* 7 (12): 1451–6. <https://doi.org/10.1111/2041-210X.12613>.
- 624 Jacobson, Molly M., Erika M. Tucker, Minna E. Mathiasson, and Sandra M. Rehan. 2018. "Decline
625 of bumble bees in northeastern North America, with special focus on *Bombus terricola*." *Biol.*
626 *Conserv.* 217 (August 2017): 437–45. <https://doi.org/10.1016/j.biocon.2017.11.026>.
- 627 Kerr, Jeremy T, Alana Pindar, Paul Galpern, Laurence Packer, Simon G Potts, Stuart M Roberts,
628 Pierre Rasmont, et al. 2015. "Climate change impacts on bumblebees converge across continents."
629 *Science* (80-.). 349 (6244): 177–80. <https://doi.org/10.1126/science.aaa7031>.
- 630 Kleijn, David, and Ivo Raemakers. 2008. "A retrospective analysis of pollen host plant use by sta-
631 ble and declining bumble bee species." *Ecology* 89 (7): 1811–23. <https://doi.org/10.1890/07-1275.1>.
- 633 Klein, Alexandra-Maria, Bernard E Vaissière, James H Cane, Ingolf Steffan-Dewenter, Saul a Cun-
634 ningham, Claire Kremen, and Teja Tscharntke. 2007. "Importance of pollinators in changing land-
635 scapes for world crops." *Proc. Biol. Sci.* 274 (1608): 303–13. <https://doi.org/10.1098/rspb.2006.3721>.
- 637 Kremen, Claire, Neal M Williams, and Robbin W Thorp. 2002. "Crop pollination from native
638 bees at risk from agricultural intensification." *Proc. Natl. Acad. Sci. U. S. A.* 99 (26): 16812–6.
639 <https://doi.org/10.1073/pnas.262413599>.
- 640 Landis, Douglas A. 2017. "Designing agricultural landscapes for biodiversity-based ecosystem
641 services." *Basic Appl. Ecol.* 18: 1–12. <https://doi.org/10.1016/j.baae.2016.07.005>.
- 642 Mallinger, Rachel E, Hannah R. Gaines-Day, and Claudio Gratton. 2017. "Do managed bees have
643 negative effects on wild bees?: A systematic review of the literature." Edited by Nigel E. Raine.

- 644 PLoS One 12 (12): e0189268. <https://doi.org/10.1371/journal.pone.0189268>.
- 645 Marshall, Leon, Jacobus C. Biesmeijer, Pierre Rasmont, Nicolas J. Vereecken, Libor Dvorak, Una
646 Fitzpatrick, Frédéric Francis, et al. 2017. "The interplay of climate and land use change affects the
647 distribution of EU bumblebees." *Glob. Chang. Biol.*, no. July: 1–16. <https://doi.org/10.1111/gcb.13867>.
- 649 McArt, Scott H., Christine Urbanowicz, Shaun McCoshum, Rebecca E. Irwin, and Lynn S. Adler.
650 2017. "Landscape predictors of pathogen prevalence and range contractions in US bumblebees."
651 *Proc. R. Soc. B Biol. Sci.* 284 (1867): 20172181. <https://doi.org/10.1098/rspb.2017.2181>.
- 652 McKinney, Ml, and Jl Lockwood. 1999. "Biotic homogenization: a few winners replacing many
653 losers in the next mass extinction." *Trends Ecol. Evol.* 14 (11): 450–53. <http://www.ncbi.nlm.nih.gov/pubmed/10511724>.
- 655 Meehan, Timothy D., and Claudio Gratton. 2015. "A consistent positive association between
656 landscape simplification and insecticide use across the Midwestern US from 1997 through 2012."
657 *Environ. Res. Lett.* 10 (11). <https://doi.org/10.1088/1748-9326/10/11/114001>.
- 658 Meehan, Timothy D, Allen H Hurlbert, and Claudio Gratton. 2010. "Bird communities in future
659 bioenergy landscapes of the Upper Midwest." *Proc. Natl. Acad. Sci. U. S. A.* 107 (43): 18533–8.
660 <https://doi.org/10.1073/pnas.1008475107>.
- 661 Meehan, Timothy D, Ben P Werling, Douglas a Landis, and Claudio Gratton. 2011. "Agricultural
662 landscape simplification and insecticide use in the Midwestern United States." *Proc. Natl. Acad.
663 Sci. U. S. A.* 108 (28): 11500–11505. <https://doi.org/10.1073/pnas.1100751108>.
- 664 Morales, Carolina L., Marina P. Arbetman, Sydney A. Cameron, and Marcelo A. Aizen. 2013.
665 "Rapid ecological replacement of a native bumble bee by invasive species." *Front. Ecol. Environ.*
666 11 (10): 529–34. <https://doi.org/10.1890/120321>.
- 667 Ollerton, Jeff, Rachael Winfree, and Sam Tarrant. 2011. "How many flowering plants are pollin-
668 ated by animals?" *Oikos* 120 (3): 321–26. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- 669 Pearce, Jennie L., and Mark S. Boyce. 2006. "Modelling distribution and abundance with presence-
670 only data." *J. Appl. Ecol.* 43 (3): 405–12. <https://doi.org/10.1111/j.1365-2664.2005.01112.x>.

- 671 Rasmont, Pierre, and Stéphanie Iserbyt. 2012. "The bumblebees scarcity syndrome: Are heat
672 waves leading to local extinctions of bumblebees (Hymenoptera: Apidae: Bombus)?" *Ann. La Soc.*
673 *Entomol. Fr.* 48 (3-4): 275–80. <https://doi.org/10.1080/00379271.2012.10697776>.
- 674 Rhemtulla, Jeanine M., David J. Mladenoff, and Murray K. Clayton. 2007. "Regional land-cover
675 conversion in the U.S. upper Midwest: Magnitude of change and limited recovery (1850-1935-
676 1993)." *Landsc. Ecol.* 22 (SUPPL. 1): 57–75. <https://doi.org/10.1007/s10980-007-9117-3>.
- 677 Richardson, L.L, K.P McFarland, S Zahendra, and S Hardy. 2018. "Bumble bee (<i>Bombus</i>)
678 distribution and diversity in Vermont, USA: A century of change." *J. Insect Conserv.* In Review (0):
679 0. <https://doi.org/10.1007/s10841-018-0113-5>.
- 680 Ropars, Lise, Isabelle Dajoz, Colin Fontaine, Audrey Muratet, and Benoît Geslin. 2019. "Wild
681 pollinator activity negatively related to honey bee colony densities in urban context." Edited by
682 Wolfgang Blenau. *PLoS One* 14 (9): e0222316. <https://doi.org/10.1371/journal.pone.0222316>.
- 683 Schellhorn, Nancy A., Vesna Gagic, and Riccardo Bommarco. 2015. "Time will tell: Resource
684 continuity bolsters ecosystem services." *Trends Ecol. Evol.* 30 (9): 524–30. <https://doi.org/10.1016/j.tree.2015.06.007>.
- 686 Schmid-Hempel, Regula, and Paul Schmid-Hempel. 1998. "Colony performance and immuno-
687 competence of a social insect, *Bombus terrestris*, in poor and variable environments." *Funct. Ecol.*
688 12 (1): 22–30. <https://doi.org/10.1046/j.1365-2435.1998.00153.x>.
- 689 Seibold, Sebastian, Martin M Gossner, Nadja K Simons, Nico Blüthgen, Didem Ambarl, Chris-
690 tian Ammer, Jürgen Bauhus, et al. 2019. "Arthropod decline in grasslands and forests is asso-
691 ciated with drivers at landscape level." *Nature* 574 (February): 1–34. <https://doi.org/10.1038/s41586-019-1684-3>.
- 693 Sirami, Clélia, Nicolas Gross, Aliette Bosem Baillod, Colette Bertrand, Romain Carrié, Annika
694 Hass, Laura Henckel, et al. 2019. "Increasing crop heterogeneity enhances multitrophic diversity
695 across agricultural regions." *Proc. Natl. Acad. Sci.*, July, 201906419. <https://doi.org/10.1073/pnas.1906419116>.
- 697 Sirois-Delisle, Catherine, and Jeremy T. Kerr. 2018. "Climate change-driven range losses among

- 698 bumblebee species are poised to accelerate." *Sci. Rep.* 8 (1): 14464. <https://doi.org/10.1038/s41598-018-32665-y>.
- 700 Smith, Daryl D. 1998. "Iowa prairie: Original extent and loss, preservation and recovery at-
701 tempts." *J. Iowa Acad. Sci.* 105 (3): 94–108.
- 702 Steffan-Dewenter, Ingolf, Simon G. Potts, Laurence Packer, and Jaboloury Ghazoul. 2005. "Pollina-
703 tor diversity and crop pollination services are at risk [3] (multiple letters)." *Trends Ecol. Evol.* 20
704 (12): 651–53. <https://doi.org/10.1016/j.tree.2005.09.004>.
- 705 Torné-Noguera, Anna, Anselm Rodrigo, Sergio Osorio, and Jordi Bosch. 2016. "Collateral effects
706 of beekeeping: Impacts on pollen-nectar resources and wild bee communities." *Basic Appl. Ecol.*
707 17 (3): 199–209. <https://doi.org/10.1016/j.baee.2015.11.004>.
- 708 Turner, Monica G., Daniel C. Donato, and William H. Romme. 2012. "Consequences of spatial
709 heterogeneity for ecosystem services in changing forest landscapes: priorities for future research."
710 *Landsc. Ecol.* 28 (6): 1081–97. <https://doi.org/10.1007/s10980-012-9741-4>.
- 711 Vaudo, Anthony D., John F. Tooker, Christina M. Grozinger, and Harland M. Patch. 2015. "Bee
712 nutrition and floral resource restoration." *Curr. Opin. Insect Sci.* 10: 133–41. <https://doi.org/10.1016/j.cois.2015.05.008>.
- 713
- 714 Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2009. "Mass flowering oilseed rape im-
715 proves early colony growth but not sexual reproduction of b1. Westphal, C., Steffan-Dewenter, I.
716 & Tscharntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual
717 reproduction of bumblebees. J." *J. Appl. Ecol.* 46 (1): 187–93. <https://doi.org/10.1111/j.1365-2664.2008.01580.x>.
- 718
- 719 Whitehorn, Penelope R., Stephanie O'Connor, Felix L. Wackers, and Dave Goulson. 2012. "Neon-
720 icotinoid Pesticide Reduces Bumble Bee Colony Growth and Queen Production." *Science* (80-.).
721 336 (6079): 351–52. <https://doi.org/10.1126/science.1215025>.
- 722 Williams, Neal M., James Regetz, and Claire Kremen. 2012. "Landscape-scale resources promote
723 colony growth but not reproductive performance of bumble bees." *Ecology* 93 (5): 1049–58. <https://doi.org/10.1890/11-1006.1>.

- 725 Williams, Paul H. 1986. "Environmental change and the distributions of british bumble bees (bombus latr.)." *Bee World* 67 (2): 50–61. <https://doi.org/10.1080/0005772X.1986.11098871>.
- 726
- 727 Williams, Paul H., Miguel B. Araújo, and Pierre Rasmont. 2007. "Can vulnerability among British
728 bumblebee (Bombus) species be explained by niche position and breadth?" *Biol. Conserv.* 138
729 (3-4): 493–505. <https://doi.org/10.1016/j.biocon.2007.06.001>.
- 730 Williams, Paul, and Juliet L Osborne. 2009. "Bumblebee vulnerability and conservation world-
731 wide." *Apidologie* 40: 367–87.
- 732 Wood, Thomas J., Jason Gibbs, Kelsey K. Graham, and Rufus Isaacs. 2019. "Narrow pollen diets
733 are associated with declining Midwestern bumble bee species." *Ecology* 0 (0). [https://doi.org/10.](https://doi.org/10.1002/ecy.2697)
734 1002/ecy.2697.
- 735 Woodard, S. Hollis. 2017. "Bumble bee ecophysiology: integrating the changing environment and
736 the organism." *Curr. Opin. Insect Sci.* 22: 101–8. <https://doi.org/10.1016/j.cois.2017.06.001>.