

Land-Use and Climate Drive Shifts in Bombus Assemblage Composition

Morgan Elizabeth Christman (✉ morgan.christman@usu.edu)

Utah State University <https://orcid.org/0000-0003-2222-3718>

Lori R Spears

Utah State University

James P Strange

The Ohio State University

William D Pearce

Imperial College London

Emily K Burchfield

Emory University

Ricardo A Ramirez

Utah State University

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Abstract

Context

Pollinators play pivotal roles in maintaining agricultural and natural plant communities, yet some bee populations are declining. The conversion of agricultural and semi-natural lands for urban use has reduced bee abundance and diversity. Meanwhile, climate change has affected bee distributions and led to disruption of plant-pollinator synchrony, impacting ecosystem processes. However, how these factors co-occur to influence bee assemblages is poorly understood.

Objectives

*We linked differences in bumble bee (*Bombus*) diversity to landscape composition and climate in agroecosystems in order to understand their co-occurring effects.*

Methods

*We evaluated *Bombus* assemblages in relation to the proportion of agricultural, semi-natural, and urban landscapes and interannual variation in temperature, precipitation, and relative humidity in Utah agroecosystems from 2014 to 2018.*

Results

**Bombus* species richness and diversity was highest in agricultural landscapes characterized by low temperatures and high relative humidity during the growing season, and lowest in urban areas with high temperatures and low relative humidity. Ongoing and future urbanization and climate change may therefore lead to reduced *Bombus* diversity in Utah. Although some historically uncommon species, such as *B. pensylvanicus*, may thrive under future land-use and climate scenarios, others (e.g., *B. sylvicola*, *B. californicus*, and *B. occidentalis*) are at increased risk of extirpation due to loss of suitable habitat.*

Conclusions

*Continually monitoring *Bombus* populations will help document shifts in assemblages and potential consequential impacts to ecosystem services. These findings emphasize that management strategies moving forward should consider the effect of co-occurring factors as opposed to single factors in order to foster future resiliency of *Bombus* populations.*

Introduction

Native insect pollinators play pivotal roles in maintaining agricultural productivity and wild plant communities (Klein et al. 2007). For example, bumble bees (Hymenoptera: Apidae: *Bombus*) increase agricultural productivity in cropping systems not typically pollinated by managed bee species. As a cold-adapted genus, *Bombus* is largely confined to temperate, alpine, and arctic environments (Goulson 2010).

Consequently, the use of *Bombus* colonies for crop pollination in cooler regions is increasing, particularly in greenhouse production (Williams et al. 2014). Nonetheless, *Bombus* populations and the pollination services they provide are declining (Goulson 2010; Cameron et al. 2011; Dirzo et al. 2014). For example, in North America, several historically common species are now rarely encountered or are listed as endangered (*B. affinis*), and at least one species (*B. franklini*) is thought to be extinct (Williams et al. 2014). Additionally, *Bombus* populations are undergoing changes in abundance and community composition due to anthropogenic disturbances that shift geographic range and phenology, which can disrupt plant-pollinator synchrony (Winfree et al. 2009; Bartomeus et al. 2011; Oyen et al. 2016; Strange and Tripodi 2019).

Urbanization and agricultural intensification are known to impact pollinator diversity by reducing suitable habitat and consequently increasing biotic homogenization (O'Toole 1993; Potts et al. 2010; Groffman et al. 2014; IPBES 2016; Betts et al. 2019). The increased prevalence of impervious surfaces (e.g., buildings, roads, and industrial areas) decreases *Bombus* species richness due to a lack of floral resources, nesting sites, and heavy metal contamination (Ahrné et al. 2009; Sivakoff et al. 2020). High proportions of large-scale, single-tract farming (i.e., monocultures) vary in their impacts on *Bombus* diversity from negative to positive based on the particular crop and the agroecosystem being studied (Westphal et al. 2003; Hanley et al. 2011; Rundlöf et al. 2014; Pfeiffer et al. 2019; Grocock and Evenden 2020). For example, larger extents of homogenous agricultural land reduce *Bombus* density and diversity (Pfeiffer et al. 2019). Meanwhile, mass-flowering crops (e.g., oilseed rape, red clover) typically increase *Bombus* abundance due to increased availability of highly rewarding floral resources (Westphal et al. 2003; Hanley et al. 2011; Rundlöf et al. 2014). Additionally, the presence of semi-natural and diverse habitats increases *Bombus* colony performance (i.e., foraging), while providing important nesting and floral resources to support diverse bee communities (Potts et al. 2010; Goulson et al. 2015; Proesmans et al. 2019).

Climate change also threatens *Bombus* assemblages by impacting species phenology, distribution, and resilience (Bale et al. 2002; Fourcade et al. 2019; Kerr et al. 2021). For instance, *Bombus* species richness declines are correlated with increasing temperature and precipitation (Fourcade et al. 2019). Over time, species richness has shifted to become greatest at higher altitudes, implying gradual shifts in species' distributions towards colder, higher elevation areas (Parmesan 2006; Fourcade et al. 2019; Koch et al. 2019), which is particularly prevalent among southern *Bombus* species in Europe and North America (Kerr et al. 2021). This is problematic given limited habitat suitability and resource availability in high altitude environments, and the potential for shifts to disrupt plant-pollinator synchrony which is important for ecosystem function (Williams et al. 2007; Oyen et al. 2016; Pyke et al. 2016; Koch et al. 2019). In addition to asynchronous phenology between plants and pollinators, flower density is also declining within alpine environments as a result of increasing temperatures and drying soils (Inouye 2008; Miller-Rushing and Inouye 2009; Kopp and Cleland 2014). Short-tongued bees exhibit greater generalization than long-tongued bees, which may be advantageous as flower density decreases, potentially driving the shift in the evolution of shorter-tongued *Bombus* (Miller-Struttman et al. 2015). Mismatching functional traits between flower tube depth and *Bombus* tongue length may also disrupt mutualism, altering co-evolution, reproduction, abundance, and plant species recruitment (Miller-Struttman et al. 2015; Pyke et al. 2016).

Additionally, climate-sensitive species, species living in fragmented habitats or habitats that lack high elevations, or species that are already at their upper elevation limit have an increased likelihood of extirpation as suitable habitats disappear (Pyke et al. 2016). While the understanding of climate change and its negative impacts on *Bombus* populations have increased (Martínez-Lopez et al. 2021), there is still a great deal of uncertainty regarding the magnitude of future climate impacts on *Bombus* species.

Landscape composition and climate change are key factors influencing pollinator diversity, yet few studies have investigated their co-occurring effects on *Bombus* species (Betts et al. 2019; Fourcade et al. 2019). Given the importance of *Bombus* to agricultural and natural ecosystems, it is necessary to understand how these pollinators are affected by anthropogenic environmental changes in order to inform conservation efforts. In this study, we linked differences in *Bombus* diversity to landscape composition and climate in Utah agroecosystems. Agricultural lands in Utah, like many other parts of the U.S., are continuously being converted into suburban and urban areas, and this trend will likely continue in the coming decades (Farmland Information Center 2016). Additionally, climate change is leading to more high temperature days and more frequent and intense drought conditions in Utah as well as many parts of the U.S. (Lavell et al. 2012). Therefore, identifying land-use and climate variables that influence *Bombus* species could provide pertinent information for developing more effective management and land-use planning resources to foster future resiliency of populations in changing environments.

Methods

Collection of *Bombus*

Insect pheromone traps were placed next to fifteen corn and fifteen alfalfa fields ($n = 30$) across a gradient of agriculturally intensified land in lower elevation areas (874 – 1418 m) throughout five counties in northern and central Utah from 2014 to 2018 (Fig. 1; $N = 150$). These traps were initially placed as part of an early-detection survey for invasive Lepidopterans following Spears et al. (2016) and the approved methods of the United States Department of Agriculture Cooperative Agricultural Pest Survey (CAPS) program. Three multi-colored (green canopy, yellow funnel, and white bucket) unitraps (International Pheromone Systems, Cheshire, UK) were spaced 20 m apart and hung 1.5 m above the ground along the edge of each study site ($n = 90$, $N = 450$). The three traps corresponded to the following target pests: cotton cutworm (CC, *Spodoptera litura* F.), Egyptian cotton leafworm (ECL, *Spodoptera littoralis* Boisduval), and Old World bollworm (OWB, *Helicoverpa armigera* Hübner). A single pheromone lure was placed inside the lure basket of the trap canopy. An insecticide strip (Hercon Vaportape II: 10% dimethyl 2,2-dichlorovinyl phosphate, Hercon Environmental Corporation, Emigsville, PA) and a small cellulose sponge were placed inside each bucket to kill the captured insects and absorb rainwater, respectively. Insecticide strips and pheromone lures for OWB were replaced every 28 days, while the pheromone lures for CC and ECL were changed every 84 days, following survey protocols (CAPS 2014–2018). Trap contents were collected every other week from late April to mid-September from 2014 to 2018. Since lure comparisons were not the intent of this study (but see Spears et al. 2016), trap data were combined by study site and collection period. All specimens were stored in a freezer at -18°C until they could be pin-

mounted, labeled, and identified to species using taxonomic keys (Koch et al. 2012; Williams et al. 2014). All specimens were deposited at the United States Department of Agriculture – Agricultural Research Service Pollinating Insect – Biology, Management, and Systematics Research Unit Museum in Logan, Utah.

Landscape Composition

Land cover values from 2014 to 2018 were obtained from USDA National Agricultural Statistics Service (NASS) CropScape and Cropland Data Layer (CDL), which maps land cover at a 30 m spatial resolution using satellite imagery (USDA-NASS-CDL 2014–2018). The 255 land cover classes listed in CDL were aggregated into four land-use types: agriculture, semi-natural, urban, and forest. Agricultural land included all row/field crops, fruits, and vegetables. Urban land included developed land (open space as well as low, medium, and high intensity). Semi-natural land included fallow and idle cropland, shrubland, barren land, wetlands, grasslands, pastures, and wildflowers. Forest land included deciduous, evergreen, and mixed forests. 1, 3, and 5 km buffers were created around each of the 150 study sites to determine the influence of landscape context at increasing scales on *Bombus* diversity. To determine landscape composition, the number of pixels of each land-use type was extracted from the buffer zones, and the proportion of agricultural, urban, semi-natural, and forest landscapes was quantified for each site. A principal component analysis (PCA) was used to determine the influence of spatial scale on the landscape composition variables. This classified each study site by land-use type for each spatial scale (1, 3, and 5 km). The spatial scales were clustered by land-use type, suggesting there was not a difference in landscape composition by spatial scale. The 1 km buffer accounted for the most variation in landscape composition (75.79% vs. 62.66% for 3 km vs. 60.04% for 5 km), so it was used in all subsequent analyses. Sites varied in proportion of land-use types thus creating a landscape gradient across study sites (Table 1). Forest land cover consistently comprised less than 3% of total land cover, so it was excluded from further analyses.

Climate Variables

Mean daily temperature, precipitation, and relative humidity were obtained each year from weather stations closest to each study site (Mesowest 2019). However, since the closest weather station was the same for each site within a county, climate data were treated as consistent across all sites within a county each year. Climate data were averaged across each collection period for each site, with mean temperatures ranging from 13.98–23.85°C, mean precipitation ranging from 0.02–106.89 mm, and mean relative humidity ranging from 32.26–49.62% (Table 1).

Data Analysis

Data were assessed using R statistical computing software (RStudio Team 2020). Three aspects of *Bombus* species composition were recorded each year from 2014 to 2018: richness (number of species), abundance, and Shannon diversity (which accounts for evenness and richness).

A canonical correspondence analysis (CCA) was used to assess correlations among explanatory variables (landscape composition and climate) and response variables (*Bombus* species abundances). A permutation test was used to determine the significance of each axis, each variable, and the overall model for the CCA. CCA axis 1 was a significant predictor of *Bombus* species-environment relationships (CCA1: $F_1 = 7.76$, $p\text{-value} = 0.029$), and was used in subsequent analyses.

A multivariate regression tree (MRT) was used to describe the interactions between *Bombus* species composition and environmental variables. The MRT groups sites based on repeated splits in environmental variable values, minimizing dissimilarity within site groups. Each leaf represents species composition and the environmental variable values associated with the sites, which are displayed in the form of a tree. We then measured average species richness and Shannon diversity within each of the leaves. To assess the ability of our MRT to predict *Bombus* species composition at future sites in Utah where only environmental data are available, we validated our model using independent environmental variables and *Bombus* species data from 2019. This site-specific data was collected following the same methodology listed above. Environmental data from each site were used to place the sites within one of the leaves formed by the MRT. Since each of these leaves were associated with species richness and Shannon diversity indices, we compared the observed indices to the predicted using the mean absolute error (MAE). This determined whether the model was over- or under-estimating species richness and Shannon diversity. We further validated our MRT model by examining Shannon diversity over time with sites separated by leaf.

Results

Collection of *Bombus*

Across all surveyed years, 3,522 *Bombus* from 15 species were collected in multi-colored bucket traps (Table 2). *Bombus fervidus* was the most abundant species, representing 61% of specimens. Seven species (*B. centralis*, *B. fervidus*, *B. griseocollis*, *B. huntii*, *B. nevadensis*, *B. rufocinctus*, and *B. vancouverensis*) recurred annually from 2014 to 2018 (Table 2). Some species were collected consistently in varying abundances from late April to mid-September, while others were collected less frequently (Fig. 2).

Response of *Bombus* to Landscape Composition and Climate

The permutation test determined that the overall CCA model explained a statistically significant amount of variation in the data ($F_{6, 123} = 2.59$, $p = 0.015$). Additionally, *Bombus* assemblages varied by urban and agricultural habitats, temperature, and relative humidity (Table 3), with urban lands associating with high temperatures and low relative humidity, and agricultural lands associating with low temperatures and high relative humidity (Figs. 3 and 4A). Over the five-year study period, these variables explained 11.2% of variation in *Bombus* assemblages. *Bombus appositus*, *B. fervidus*, *B. griseocollis*, *B. huntii*, and *B.*

pensylvanicus were associated with urban land, high temperatures, and low relative humidity, while the remaining species were associated with agricultural land, low temperatures, and high relative humidity (Fig. 3). It is important to note that there may be increased variability due to the small sample size of specific *Bombus* species, contributing to these findings.

The MRT analysis resulted in a six-leaf tree where branching was determined by agricultural and urban habitats, temperature, and relative humidity – all of which were significant predictors from the CCA. Species composition differed across the six leaves. *Bombus* species richness and diversity were highest in agricultural landscapes characterized by low temperatures during the growing season (Fig. 4, Leaf D-F), and lowest in urban areas with high temperatures and low relative humidity (Fig. 4, Leaf A-C). Model validation using 217 *Bombus* specimens collected in 2019 found that richness estimates differed by 2.4 species on average (mean), while diversity estimates differed by 0.52 on average (mean). Given the small sample size used, this suggests the model fits the data well and has fair predictive capabilities.

Discussion

Bombus species richness, abundance, and overall diversity were highest in agricultural landscapes characterized by low temperatures and high relative humidity during the growing season, and lowest in urban areas with high temperatures and low relative humidity. Ongoing and future urbanization and climate change may therefore lead to reduced *Bombus* diversity in Utah. Although some historically uncommon species, such as *B. pensylvanicus*, may thrive under future landscape and climate scenarios, others (e.g., *B. sylvicola*, *B. californicus*, and *B. occidentalis*) are at increased risk of extirpation due to loss of suitable habitat.

Our finding that *Bombus* diversity was highest in agricultural landscapes differs from other studies that suggest diversity is negatively impacted by high proportions of agriculture, particularly monocultures, due to a lack of diverse landscapes, reduced availability of floral resources, increased use of agrochemicals, and frequent soil disturbances (e.g., tilling, seeding, and harvest practices) restricting nesting locations (Vanbergen et al. 2013; Pfeiffer et al. 2019; Grocock and Evenden 2020). This may be due to our surveyed corn and alfalfa fields being relatively small (mean of 22 acres) and in close proximity to other crop types (e.g., corn, alfalfa, wheat, and barley) in comparison to other regions of the U.S. where agricultural fields are more expansive (Plourde et al. 2013). This inconsistency may also be driven by differences in agricultural practices, management history, and local environment (Kohler et al. 2020). Additionally, we suspect that increased floral richness within hedge rows surrounding agricultural fields may draw foraging bees away from their nests as these flowering plants provide important nutrients for developing larvae (Tasei and Aupinel 2008; Potts et al. 2009; Roulston and Goodell 2011; Wood et al. 2015; Pfeiffer et al. 2019). This may explain why *Bombus* are captured in relatively high numbers within crop fields (e.g., corn) that do not necessarily provide ideal floral resources. Since *Bombus* are fairly vagile foragers (Rao and Strange 2012; Geib et al. 2015) and are not considered to be area sensitive, they can use these small patches of habitat (as little as 2% of semi-natural habitat within agricultural landscapes) to exploit floral and nesting resources in the surrounding area (Westphal et al. 2003; Pfeiffer et al. 2019). However, not all

species behave similarly, which may influence the degree to which *Bombus* travel for floral and nesting resources (Geib et al. 2015).

Despite *Bombus* diversity being highest in agricultural landscapes, some species were more abundant in agricultural areas with greater urban development (i.e., crop fields in close proximity to suburban housing developments, buildings, roadways, and highways). Urban areas often experience warmer temperatures relative to surrounding rural areas due to the increased prevalence of impervious surfaces (Baldock 2020). Although other studies, including our own, found that *Bombus* diversity decreased with urbanization (Ahrné et al. 2009), urban habitats with higher temperatures appear to favor some *Bombus* species (*B. appositus*, *B. fervidus*, *B. griseocollis*, *B. huntii*, and *B. pensylvanicus*). This indicates that *Bombus* species are differently affected by urban agricultural areas (Ahrné et al. 2009; Baldock 2020). The mechanisms driving this response remain unclear, but are likely due to a multitude of factors, such as increased floral resource availability and nesting opportunities within the surrounding environment, and various life history traits (e.g., emergence periods, colony size, and thermal tolerances) (Goulson and Darvill 2004; Goulson et al. 2005; Williams 2005; Benton 2006; Fitzpatrick et al. 2007; Bennett and Lovell 2019; Burdine and McCluney 2019). For example, *B. griseocollis* is historically known to inhabit open farmlands and fields, urban parks and gardens, and wetlands (Williams et al. 2014). Additionally, they have a relatively small colony size (fewer than 50 workers), which may be advantageous within urban agricultural sites as this reduces their risk of overheating from crowding and insufficient nest ventilation (Weidenmüller et al. 2002). Meanwhile, *B. pensylvanicus*, a species that normally occurs in the southwestern U.S. (Koch et al. 2012; Williams et al. 2014) but is declining in population size (Cameron et al. 2011; Strange and Tripodi 2019), may be expanding its geographic range to include urban agricultural areas of northern Utah characterized by high temperatures.

Ongoing and future climate change may change *Bombus* species' phenology and assemblage composition, which can impact pollination services and ecosystem function. Our collection of *Bombus* from mid-May to mid-September identified phenological overlap within the *Bombus* community. This overlap may aid in fostering future resiliency of pollination services as well as ecosystem function. If a particular species is lost due to loss of habitat, other ecologically similar species present within the environment might be available to fill this gap in pollination services (functional redundancy). Meanwhile, species overlap was lower earlier in the season (late April to mid-May), most likely due to differences in time of emergence from winter diapause. Climate warming has been shown to lead to shifts in *Bombus* emergence periods with bees having earlier springtime activity in the northeastern U.S. (Bartomeus et al. 2011, Pyke et al. 2016). This shift may benefit pollination services earlier in the season when species diversity is low by increasing phenological overlap between pollinator species. However, climate-induced phenological change coupled with shifts in bloom phenology and agricultural cultivation dates can also negatively impact plant-pollinator synchrony, leading to increased competition for floral resources. Adaptive foraging (the ability for pollinators to utilize alternative, less-preferred flowers) may counteract the effects of phenological mismatching between plants and pollinators by preventing the pollinator population from collapsing for long enough to allow for re-synchronization (Valdovinos et al. 2013; Revilla et al. 2015).

In summary, we identified habitat and climatic variables that drive *Bombus* species abundance and diversity in agroecosystems. Further, this study emphasizes that management strategies should consider the effect of co-occurring factors as opposed to single factors in order to effectively foster future resiliency of *Bombus* populations in the face of anthropogenic disturbances. Novel ecosystems will continue to emerge as urbanization, agricultural intensification, and climate change continue. These novel ecosystems may be better at withstanding anthropogenic environmental changes, but also have the potential to be ecologically homogenized (Hobbs et al. 2006; Groffman et al. 2014). If the same drivers are applied everywhere such that spatial, functional, and taxonomic similarity increases, beta diversity can decrease leading to homogenization. Therefore, this response will be largely dependent on management practices, geographic location, and changes in species diversity and distribution. Functional groups and species interactions will change as a result; however, key ecological function will not necessarily be lost (i.e., functional redundancy). Additionally, novel ecosystems may alter species interactions (e.g., mutualism, competition), or lead to the loss of regionally unique species further contributing to homogenized ecosystems (Hobbs et al. 2006). Continually monitoring *Bombus* populations will help document these shifts in assemblages and potential consequential impacts to ecosystem services. Overall, this is a crucial step towards understanding the co-occurring effects of land-use change and climate on pollinator populations.

Declarations

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Conflicts of interest/competing interests: Not applicable.

Ethics approval: Not applicable.

Consent to participate: Verbal approval was granted by all producers to allow us to complete research on their corn and alfalfa fields.

Consent for publication: This work has been approved by all authors.

Availability of data and material: The data supporting the findings of this study are available on Zenodo at doi: 10.5281/zenodo.4701633. Geographic coordinates of the study sites are not publicly available to protect information that could compromise the privacy of the producers involved in this research project.

Code availability: The code supporting the findings of this study are openly available on Zenodo at doi: 10.5281/zenodo.4701633.

Authors' contributions: Morgan Christman: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data Curation, Writing – Original Draft; Lori Spears: Conceptualization, Methodology, Resources, Writing – Review & Editing, Funding Acquisition, Supervision, Project Administration; James

Strange: Validation, Writing – Review & Editing, Supervision; William Pearse: Software, Formal Analysis, Writing – Review & Editing, Supervision; Emily Burchfield: Software, Writing – Review & Editing, Supervision; Ricardo Ramirez: Conceptualization, Methodology, Writing – Review & Editing, Funding Acquisition, Supervision, Project Administration.

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Tables

Table 1

Mean proportion and standard deviation of land-use type, and mean climate variable measurements and standard deviation from 2014 to 2018

Explanatory Variables	Year				
	2014	2015	2016	2017	2018
<i>Landscape Composition</i>					
Agriculture (%)	69.7±19.4	70.6 ± 18.4	68.3±24.1	68.2±20.6	63.7 ± 25.0
Semi-natural (%)	19.2± 13.4	16.8 ± 9.9	20.6 ± 18.6	19.2 ± 14.1	21.1 ± 19.0
Urban (%)	11.0±12.6	12.5 ± 12.1	11.0 ± 10.8	12.5 ± 11.5	12.4 ± 11.7
Forest (%)	1±2	1± 2	2 ± 5	1 ± 2	2.8 ± 15.3
<i>Climate Variables</i>					
Temperature (°C)	21.1 ± 5.5	21.5 ± 5.04	22.0 ± 5.1	22.1± 5.0	21.6 ± 5.4
Precipitation (mm)	57.1 ± 54.9	89.1 ± 86.97	90.9 ± 69.7	82.9 ± 79.2	80.6 ± 98.9
Relative Humidity (%)	39.3 ± 18.5	39.1 ± 15.8	30.4 ± 13.0	34.7 ± 12.8	33.5 ± 14.2

Table 2

Bombus species richness and abundance from 2014 to 2018

Species	Abundance by Year					
	2014	2015	2016	2017	2018	All Surveyed Years
<i>Bombus appositus</i>	1	0	0	3	8	12
<i>B. californicus</i>	2	3	2	4	0	11
<i>B. centralis</i>	115	16	47	14	26	218
<i>B. fervidus</i>	512	308	446	441	452	2159
<i>B. flavifrons</i>	19	5	1	0	0	25
<i>B. griseocollis</i>	63	9	24	49	33	178
<i>B. huntii</i>	79	18	80	79	189	445
<i>B. insularis</i>	2	3	2	0	3	10
<i>B. morrisoni</i>	9	0	0	1	1	11
<i>B. nevadensis</i>	10	2	3	38	5	58
<i>B. occidentalis</i>	4	0	0	0	0	4
<i>B. pennsylvanicus</i>	0	0	1	0	1	2
<i>B. rufocinctus</i>	162	44	52	79	20	357
<i>B. sylvicola</i>	0	1	1	0	0	2
<i>B. vancouverensis</i>	6	5	6	4	9	30
Total	984	414	665	712	747	3522

Table 3

Significance of each explanatory variable from 2014 to 2018 based on a permutation test for the Canonical Correspondence Analysis model

Variable	df	F	<i>p</i> -value
Agricultural	1	1.71	0.039
Urban	1	2.78	0.030
Semi-natural	1	0.71	0.467
Mean Temperature	1	4.31	0.001
Mean Precipitation	1	1.33	0.114
Mean Relative Humidity	1	2.11	0.021

Figures

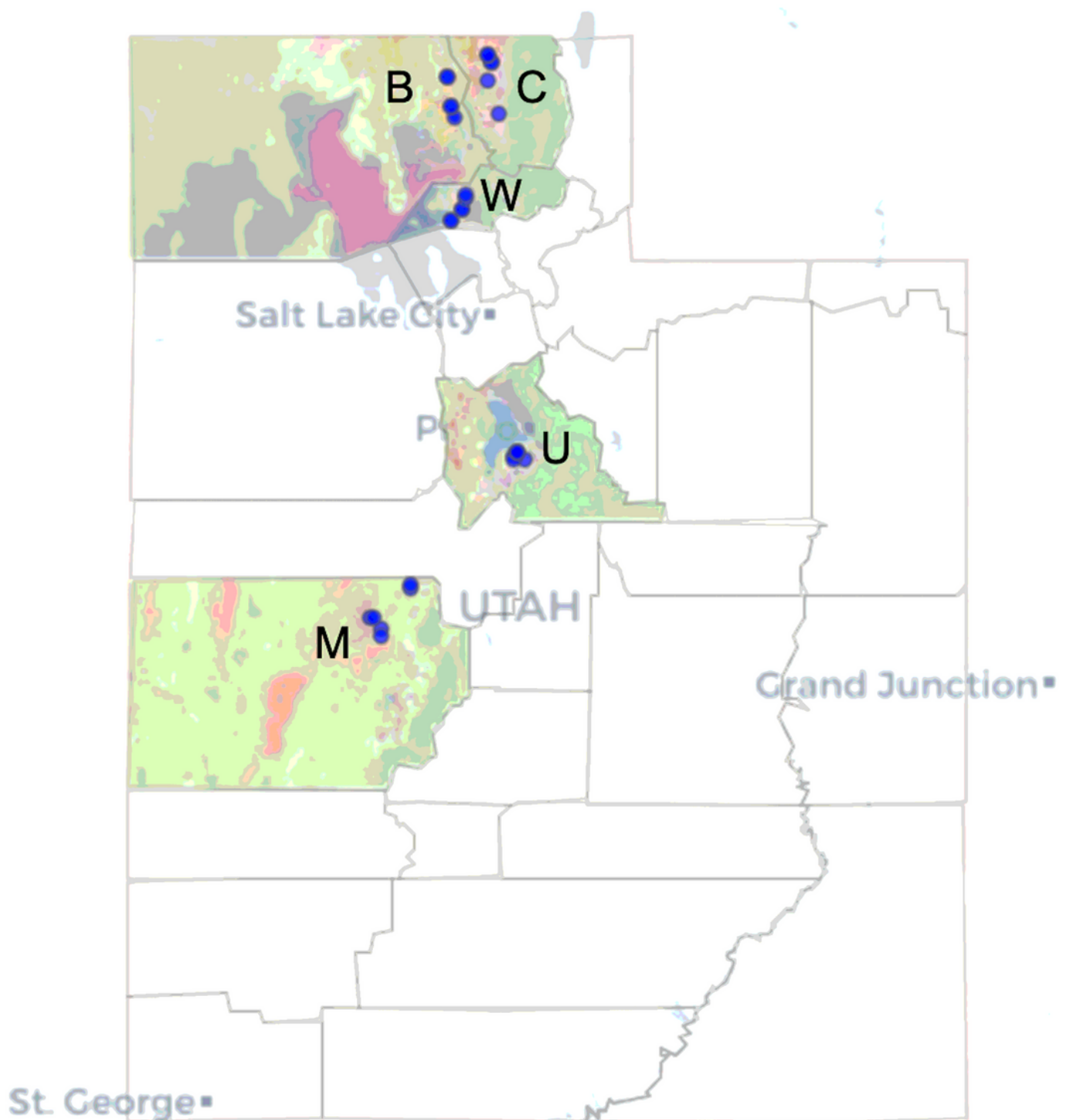


Figure 1

Distribution of survey locations (blue points) in Utah. Letters represent the five sampled counties: (C) Cache, (W) Weber, (B) Box Elder, (U) Utah, and (M) Millard. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the

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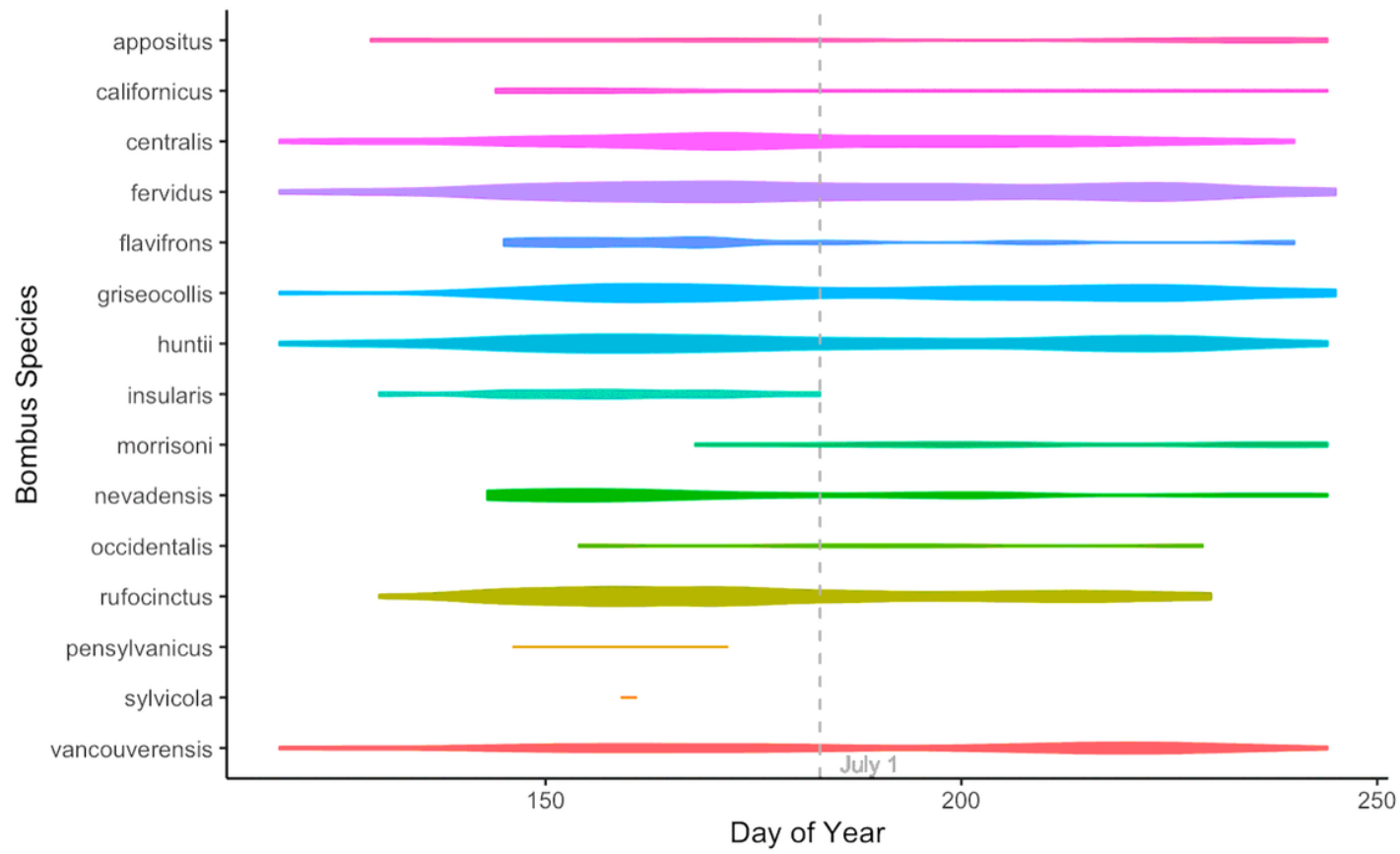


Figure 2

Violin plot of *Bombus* species collected from late April to mid-September throughout 2014 to 2018. Line width indicates the relative number of specimens collected

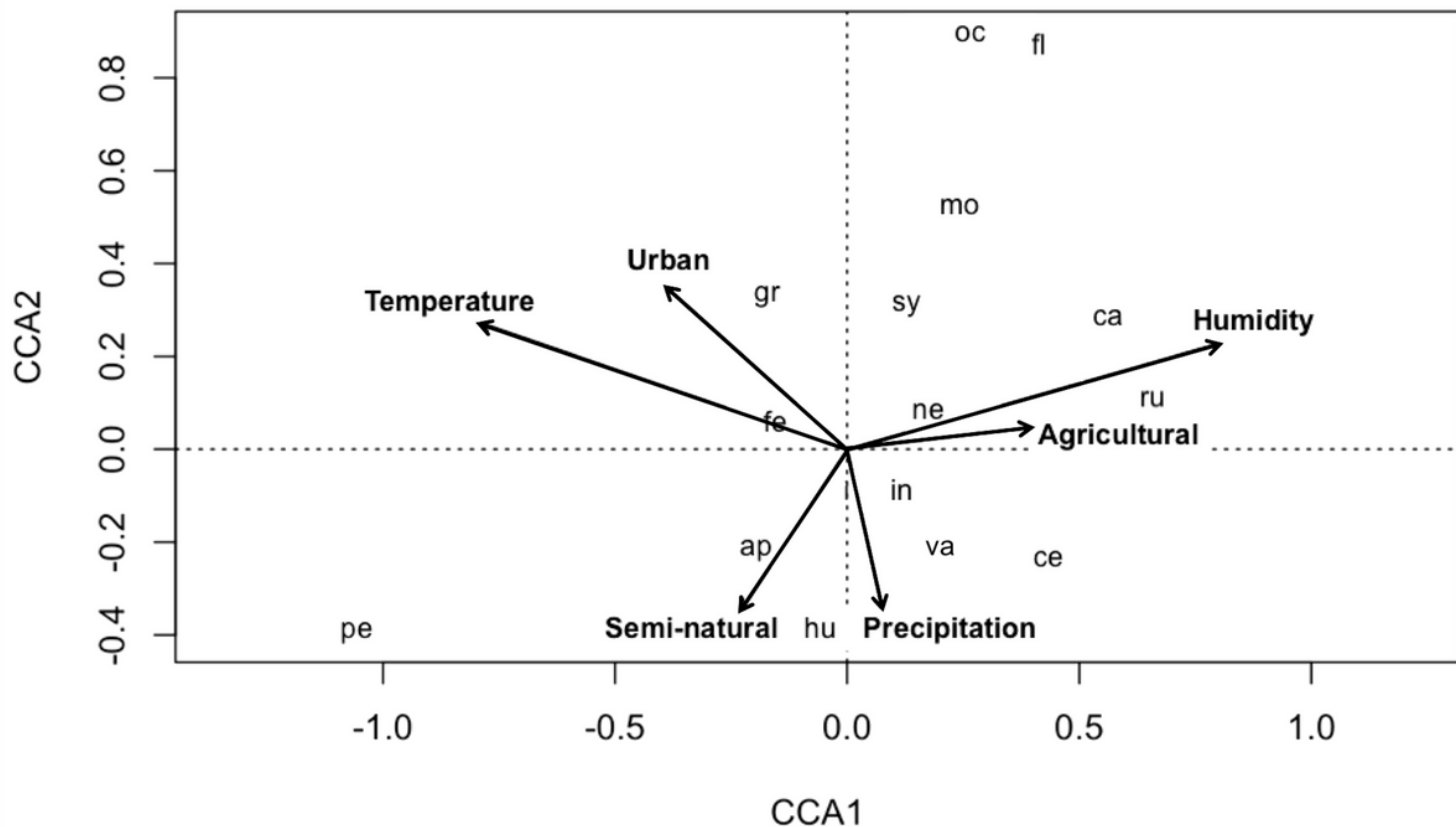


Figure 3

Canonical correspondence analyses of the *Bombus* assemblage data in relation to environmental variables (indicated by arrows) from 2014 to 2018. *Bombus* species names are abbreviated as ap = *B. appositus*, ca = *B. californicus*, ce = *B. centralis*, fe = *B. fervidus*, fl = *B. flavifrons*, gr = *B. griseocollis*, hu = *B. huntii*, in = *B. insularis*, mo = *B. morrisoni*, ne = *B. nevadensis*, oc = *B. occidentalis*, pe = *B. pensylvanicus*, ru = *B. rufocinctus*, sy = *B. sylvicola*, and va = *B. vancouverensis*. Urbanized habitats are correlated with high temperatures and low humidity during the growing season (left side), while agricultural habitats are correlated with low temperatures and high humidity (right side)

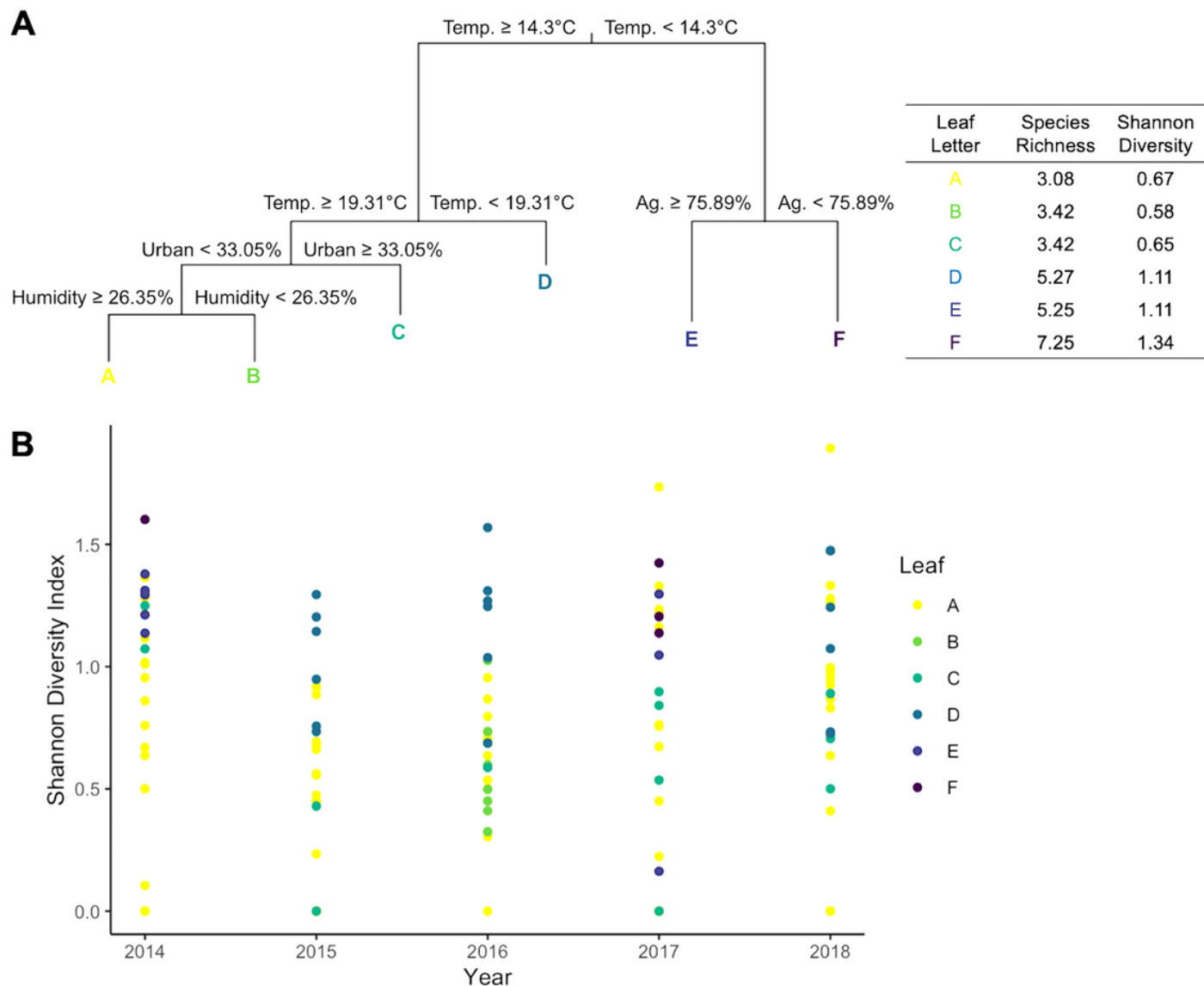


Figure 4

a) Multivariate regression tree (MRT) for the *Bombus* species data in relation to urban and agricultural (Ag.) habitats (%) as well as temperature (°C, Temp) and relative humidity (% Humidity). Non-significant variables (semi-natural habitats and precipitation) were not included in this model. The six leaves (indicated with letters under each branch) identify clusters of environmental variable values associated with the study sites. The table shows the species richness and Shannon diversity associated with each leaf. Sites with cooler temperatures during the growing season and more agricultural habitats had higher *Bombus* diversity and richness. b) Shannon diversity of *Bombus* assemblages by field site from 2014 to 2018. Different colors correspond to different leaf letters from the MRT model

Supplementary Files

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