

Land cover and climate drive shifts in *Bombus* assemblage composition

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ABSTRACT

Pollinators play pivotal roles in maintaining agricultural and natural plant communities, yet some bee populations are declining. Loss of pollinator habitats as a result of agricultural intensification and urbanization have reduced bee abundance and diversity. Additionally, climate change has affected bee distributions and led to disruption of plant-pollinator synchrony, impacting ecosystem processes. However, how these factors concurrently influence bee assemblages is poorly understood. Therefore, we evaluated bumble bee (*Bombus*) assemblages in relation to the proportion of agricultural, semi-natural, and urban land cover and interannual variation in temperature, precipitation, and relative humidity in Utah agroecosystems using *Bombus* captured as bycatch in pest monitoring traps from 2014 to 2018. *Bombus* assemblage composition was highest in agricultural sites with increased agricultural land cover in the surrounding area, low temperatures, and high relative humidity during the growing season; and lowest in sites with increased urban land cover, high temperatures, and low relative humidity. Functional dispersion did not differ among these groups indicating a range of tongue lengths, body sizes, hair lengths, and hair types were present within all agricultural sites. Further, high beta-diversity, as indicated by unique *Bombus* assemblages among sites, suggests that all agricultural sites in this study have potential conservation value for maintaining *Bombus* communities. Therefore, it is important that diverse habitats for pollinators are maintained through targeted management techniques. Additionally, our collection of *Bombus* from mid-May to mid-September identified phenological overlap within *Bombus* assemblages, which helps ensure pollination services are provided even if a particular species is lost due to environmental disturbances. However, while there is overlap in functional traits and phenology, considerations should be given due to widespread pollinator declines. Overall, evaluating landscape and climate variables together may yield more realistic results and better inform effective management and land-use planning strategies to prevent ecological homogenization and to foster future resiliency of *Bombus* populations.

1. Introduction

Bumble bees (Hymenoptera: Apidae: *Bombus* Latreille) are important pollinators of wild and cultivated plant communities throughout temperate, alpine, and subarctic environments (Klein et al., 2007; Goulson, 2010). *Bombus* are particularly effective at increasing agricultural productivity in cropping systems not typically pollinated by managed bee species because they have the ability to sonicate (buzz) flowers. During sonication, they collect pollen from plants that do not produce nectar (e.g., tomato, eggplant, kiwi, and blueberries) by

vibrating their wing muscles to shake pollen grains out of the anthers (Cooley and Vallejo-Marín, 2021). Despite their environmental and economic importance, *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 species are listed as vulnerable or endangered (e.g., *B. affinis*, *B. franklini*, and *B. suckleyi*) by the International Union for the Conservation of Nature (IUCN, 2022). Additionally, *Bombus* populations are undergoing changes in assemblage composition (calculated as species richness and abundance) due to anthropogenic disturbances (Winfree et al., 2009; Bartomeus et al.,

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2011; Oyen et al., 2016; Strange and Tripodi, 2019).

Habitat loss is becoming more prevalent throughout the U.S. as agricultural intensification and urbanization alter landscape composition (Ahrné et al., 2009; Glaum et al., 2017; Wenzel et al., 2020). Agricultural intensification converts diverse, natural plant assemblages to agricultural land cover to support efficient and cost-effective crop production (Goulson et al., 2015; Koh et al., 2016). As a result, high proportions of large-scale, single-tract farming (i.e., monocultures) are created, which vary in their impact 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, homogenous landscapes with larger extents of agriculturally simplified land, reduced *Bombus* density and diversity (Pfeiffer et al., 2019). Meanwhile, mass-flowering crops (e.g., oilseed rape, red clover, canola, cranberries, and cotton) can provide a dense resource pulse and increase resource continuity, promoting the local densities and persistence of common *Bombus* species, especially during periods of increased floral resources availability (Westphal et al., 2003; Hanley et al., 2011; Jha and Kremen, 2013; Rundlöf et al., 2014; Pfeiffer et al., 2019; Parys et al., 2021). However, this does not necessarily translate to higher reproductive output and is largely dependent on the time of year, space, and the mass-flowering crop (Rundlöf et al., 2014). On the other hand, urbanization increases the prevalence of impervious surfaces (e.g., buildings, roads, parking lots, and industrial areas), while decreasing the proportion of natural or semi-natural land cover. As a result, *Bombus* species richness declines due to a lack of sites with stable floral resources, loss of under-ground and above-ground nesting sites, and increased heavy metal contamination (Ahrné et al., 2009; Geslin et al., 2016; Glaum et al., 2017; Sivakoff et al., 2020). However, urban green spaces (e.g., parks and gardens) can provide suitable habitats for pollinators and enhance their diversity when compared to agriculturally intensified habitats (Martins et al., 2017; Bennett and Lovell, 2019; Wenzel et al., 2020). Further, semi-natural land cover supports increased *Bombus* diversity, abundance, and foraging activity by providing important nesting and floral resources (Potts et al., 2010; Goulson et al., 2015; Senapathi et al., 2017; 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 and more northern latitudes, implying gradual shifts in species' distributions towards colder areas (Parmesan, 2006; Kelly and Goulson, 2008; Grytnes et al., 2014; 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-Struttmann 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-Struttmann 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-López 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 *Bombus* are affected by anthropogenic environmental change in order to inform conservation efforts. In this study, we evaluated *Bombus* assemblages in relation to the proportion of agricultural, semi-natural, and urban land cover and interannual variation in temperature, precipitation, and relative humidity in Utah agroecosystems. Utah landscapes, like many other parts of the U.S., are undergoing changes due to agricultural intensification and urbanization, and this trend will likely continue in the coming decades. 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). We expected that *Bombus* species assemblage composition (richness and abundance) would be highest in agricultural sites with increased semi-natural land cover in the surrounding landscape, decreased temperatures and precipitation, and moderate to high relative humidity. Conversely, we expected *Bombus* assemblage composition to be lowest in sites with increased agricultural land cover, temperatures, and precipitation, and decreased relative humidity. Overall, identifying how landscape and climate variables drive *Bombus* assemblage composition could provide pertinent information for developing more effective management and land-use planning strategies to foster future resiliency of populations in changing environments.

2. Methods

2.1. Collection of *Bombus*

Pest monitoring traps are widely known to attract a large number and wide range of non-target beneficial insects (bycatch), including *Bombus*, due to an overlap in the recognition of olfactory and visual cues (Adams et al., 1989; Pair et al., 1989; Weber and Ferro, 1991; Spears and Ramirez, 2015; Sipolski et al., 2019; Whitfield et al., 2019; Grocock et al., 2020; Parys et al., 2021; Spears et al., 2016, 2021). *Bombus* captures in pest monitoring traps sometimes exceed captures using more common methods of sampling bees, such as pan trapping or net collecting, despite less sampling efforts (Glaum et al., 2017; Grocock and Evenden, 2020; Spears et al., 2016, 2021). Although bycatch is typically discarded, analyzing this data can provide important insight on patterns and processes of broader ecological interest (Buchholz et al., 2011; Spears and Ramirez, 2015; Grocock and Evenden, 2020; Parys et al., 2021; Spears et al., 2016, 2021). Therefore, for this study, we used *Bombus* bycatch from pest monitoring traps to study their assemblages.

Pest monitoring traps were placed along the margin of corn and alfalfa fields 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 2019 (Fig. 1) as part of early-detection surveys for invasive lepidopterans following Spears et al. (2016) and U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Cooperative Agricultural Pest Survey approved methods (CAPS, 2019). Six agricultural sites were surveyed within each county ((3 corn + 3 alfalfa fields) × 5 counties, n = 30). Three multi-colored (green canopy, yellow funnel, and white bucket) bucket traps (International Pheromone Systems, Cheshire, UK) were spaced 20 m apart and hung 1.5 m above the ground along the field margin of each agricultural site (N = 540; 3 traps × 30 sites × 6 years). 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

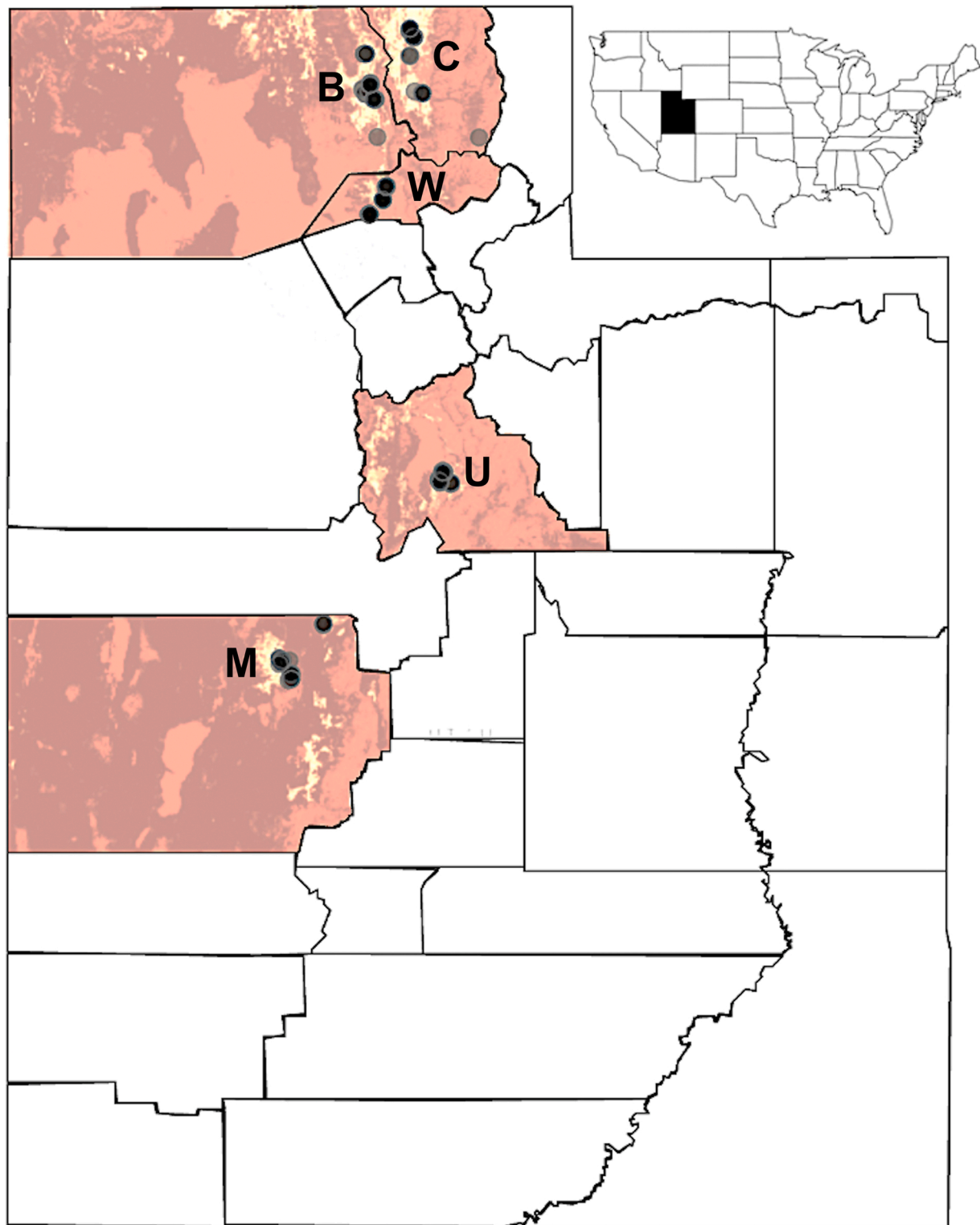


Fig. 1. Thirty agricultural sites (black points) in Utah were sampled for *Bombus* each year from 2014 to 2019. Six sites were distributed throughout each of the five counties: (C) Cache, (W) Weber, (B) Box Elder, (U) Utah, and (M) Millard.

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

USDA APHIS CAPS survey protocols.

Trap contents were collected every other week from late April to mid-September from 2014 to 2019. Since lure comparisons were not the intent of this study (but see [Spears et al., 2016](#)), trap data were combined by agricultural site and collection period. At the lab, trap contents were screened for target pests, and *Bombus* collected as bycatch were separated from all other specimens and then stored in a freezer at -18C until

they could be pin-mounted, labeled, and identified to species using taxonomic keys (Koch et al., 2012; Williams et al., 2014). All *Bombus* were deposited at the United States Department of Agriculture – Agricultural Research Service Pollinating Insect – Biology, Management, and Systematics Research Unit Museum in Logan, Utah. Data collected from 2019 were kept separate from the 2014–2018 data set to be used to evaluate model predictive capabilities. Collection and specimen information can be found at <https://www.gbif.org/dataset/c6fdb7c6-9597-44e2-8b82-32714bb7133c>.

2.2. Landscape composition

Land cover values from 2014 to 2019 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, 2014–2019). The 255 land cover classes listed in CDL were aggregated into four land cover types: agriculture, semi-natural, urban, and forest (Table A1). Agricultural land cover, specifically arable land, included all row/field crops, fruits, and vegetables. Urban land cover included developed land (open space as well as low, medium, and high intensity). Semi-natural land cover included fallow and idle cropland, shrubland, barren land, wetlands, grasslands/pastures (including livestock grazing land), and wildflowers. Forest land cover included deciduous, evergreen, and mixed forests.

A 1, 3, and 5 km buffer was created around each of the 180 agricultural sites to determine the influence of landscape composition at increasing scales on *Bombus* diversity and to account for foraging distances of many *Bombus* species in agricultural landscapes (Rao and Strange, 2012). To determine landscape composition, the number of pixels of each land cover type was extracted from the buffers, and the proportion of agricultural, urban, semi-natural, and forest land cover was quantified surrounding each agricultural site.

Land cover surrounding the agricultural sites varied, creating a landscape gradient across the surveyed sites (Table 1). These land cover types all sum to one, meaning the inclusion of all of them would make the model singular (agriculture + urban + semi-natural + forest = 100%). Therefore, one land cover type had to be excluded from the model to prevent issues with singularities. Forest land cover was rarely observed surrounding the agricultural sites and consistently comprised less than 3% of total land cover, so it was selected for exclusion from further analyses.

A principal component analysis (PCA) was conducted using base

Table 1

Mean proportion and standard deviation of land cover, and mean climate variable measurements and standard deviation from 2014 to 2019.

Explanatory Variables	Year					
	2014	2015	2016	2017	2018	2019
<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	63.7 ± 25.4
Semi-natural (%)	19.2 ± 13.4	16.8 ± 9.9	20.6 ± 18.6	19.2 ± 14.1	21.1 ± 19.0	18.5 ± 19.5
Urban (%)	11.0 ± 12.6	12.5 ± 12.1	11.0 ± 10.8	12.5 ± 11.5	12.4 ± 11.7	15.0 ± 14.5
Forest (%)	1 ± 2	1 ± 2	2 ± 5	1 ± 2	2.8 ± 15.3	2.8 ± 14.9
<i>Climate Variables</i>						
Temperature (°C)	21.1 ± 3.7	21.5 ± 3.6	22.0 ± 3.3	20.3 ± 3.4	21.3 ± 2.1	17.3 ± 3.9
Precipitation (mm)	61.5 ± 50.2	93.0 ± 86.6	90.9 ± 70.4	82.5 ± 79.4	101.2 ± 118	108.4 ± 98.9
Relative Humidity (%)	39.3 ± 6.17	39.1 ± 5.4	30.4 ± 3.9	38.1 ± 5.7	33.5 ± 3.5	42.5 ± 8.2

functions in R version 4.0.3 (R Core Team, 2020) to determine the influence of spatial scale on landscape composition. This classified each agricultural site by the proportion of land cover type at each spatial scale. The spatial scales were clustered by land cover type, suggesting patterns did not differ by spatial scale (Fig. A1). 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.

2.3. Climate variables

Mean daily temperature, accumulated precipitation, and relative humidity were obtained each year from weather stations closest to each agricultural site (MesoWest, 2014–2019). However, since the closest weather station was the same for each agricultural site within a county, climate data were treated as consistent across all sites within a county each year. Climate data were then averaged across each collection period for each agricultural site, with mean temperatures ranging from 13.98° to 23.85C, mean accumulated precipitation ranging from 0.02 to 106.89 mm, and mean relative humidity ranging from 32.26% to 49.62% (Table 1).

2.4. Data analysis

Data were assessed using R version 4.0.3 (R Core Team, 2020). Five aspects of *Bombus* community structure were measured: richness (number of species), abundance per species, assemblage composition (richness and abundance), temporal turnover, and beta-diversity with the *vegan*, *codyn*, and *betapart* libraries. Temporal turnover indicated the temporal change in *Bombus* communities as the proportion of species that appeared or disappeared each year between 2014 and 2018. Beta-diversity determined the extent to which species assemblages present at each agricultural site differed based on turnover or nestedness. A Sørensen index of beta-diversity (β_{sor}) measured total dissimilarity accounting for turnover (species replacements among sites; β_{sim}) and nestedness (species loss/gain among sites; β_{sne}) (Baselga and Orme, 2012).

Spatial autocorrelation was analyzed each year from 2014 to 2019 using a Moran's I test to assess the presence of a spatial pattern in model residuals with the *spdep* library (Bivand and Wong, 2018). The results suggested the residuals were not spatially autocorrelated (Table 2), indicating that unexplained autocorrelation among neighboring samples was not driving the described patterns.

A correlation matrix was generated to examine correlations across all combinations of explanatory variables with the *corrplot* library (Fig. A2; Wei and Simko, 2021). Land cover variables were correlated due to the fact that landscape composition was calculated based on the proportion of agricultural, semi-natural, and urban land cover. Specifically, agricultural land cover was negatively correlated with semi-natural and urban land cover. Further, a canonical correspondence analysis (CCA) was used to assess correlations among explanatory variables (landscape composition and climate) and response variables (*Bombus* species abundances) from 2014 to 2018 with the *vegan* and *picante* libraries. 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

Table 2

Moran's I statistic output of model residuals each year from 2014 to 2019.

Year	Moran's I Index	Expected Index	Variance	p-value
2014	0.337	-0.038	0.097	0.114
2015	0.315	-0.042	0.165	0.189
2016	0.421	-0.040	0.109	0.082
2017	0.360	-0.045	0.202	0.185
2018	-0.215	-0.037	0.143	0.682
2019	-0.054	-0.111	0.129	0.437

significant predictor of *Bombus* species-environment relationships (CCA1: $F_{1, 123} = 7.76$, p -value = 0.029), and was therefore used to evaluate the CCA.

A multivariate regression tree (MRT) was used to describe the interactions between *Bombus* species composition and environmental variables from 2014 to 2018 with the *mvpart* library (De'ath, 2014). The MRT groups sites based on repeated splits in environmental variable values, minimizing dissimilarity within site groups. Each leaf represents average species abundance per site and the environmental variable values associated with the agricultural sites, which are displayed in the form of a tree. A 5-fold cross validation with 100 iterations was generated to validate the model. Additionally, independent environmental variables and *Bombus* species data from 2019 were used to assess the ability of our MRT to predict *Bombus* species abundances at future agricultural sites in Utah where only environmental data are available. Environmental data from each independent site were used to place the agricultural sites within one of the leaves formed by the MRT. Since each of these leaves were associated with average species abundance per site, we compared the observed indices to the predicted values using the mean absolute error (MAE) with the *Metrics* library (Hamner and Frasco, 2018). This determined whether the MRT was over- or under-estimating average species abundance per site.

CCA model outputs were evaluated each individual year from 2014 to 2018 to remove temporal autocorrelation as a factor. All explanatory variables were scaled, allowing standard effect sizes to be produced, which allowed the relative importance of the explanatory variables to be determined each year (Gelman and Hill, 2006).

Functional diversity was determined by assessing four traits: tongue length, body size, hair length, and hair type (Table 3; Koch et al., 2012; Williams et al., 2014; IUCN, 2022). Tongue length was selected as an indicator of foraging niche, as it is tied to the flower size that various *Bombus* species are able to pollinate (Williams et al., 2014). Body size was selected as a measure of dispersal and foraging abilities (Atkinson, 1994; Greenleaf et al., 2007; López-Urbe et al., 2019). Hair length and type were selected as a measure of insulation and as a response trait to climatic changes, as differences have been found across different climates and along different elevational gradients (Heinrich, 1993; Peat et al., 2005; Peters et al., 2016; Roquer-Beni et al., 2020). *Bombus* species were classified by three levels of tongue lengths (short, medium, and long), three levels of body sizes (short, medium, and large), three levels of hair length (short, medium, and long), and two levels of hair types (even and uneven). The functional dispersion (FDis) component of functional diversity was measured to quantify the breadth of functional traits across species within the agroecosystems using the *FD* library (Laliberté et al., 2014). Functional distances between species were calculated using a species-by-species Gower distance matrix. Differences in functional dispersion between the habitat groupings produced by the CCA were assessed using a one-sample t -test.

3. Results

3.1. Collection of *Bombus*

From 2014–2018, 3522 *Bombus* from 15 species were collected in multi-colored bucket traps (Table 4), a few of which are listed as vulnerable by the IUCN (e.g., *Bombus fervidus*, *B. pensylvanicus sonorus*, *B. sylvicola*, *B. californicus*, and *B. occidentalis*) (IUCN, 2022; Table 3). *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 4). Some species were collected consistently in varying abundances from late April to mid-September, while others were collected less frequently over the growing season (Fig. 2 and Fig. A3).

Yearly changes in the appearances and disappearances of other species identified that turnover occurred with an average rate of 26.2%

per year (Fig. 3). Temporal turnover was largely characterized by a low, steady increase in the appearance of new species, but also by the loss of species, particularly in 2017. Many of the species appearing or disappearing were captured at lower frequencies, which was expected due to these species being proportionally less common in the environment (Koch et al., 2012).

The Sørensen index of beta-diversity showed high values of total dissimilarity among sites ($\beta_{sor} = 0.968$). Beta-diversity was dominated by species replacement (turnover). Species replacement accounted for a greater portion of total dissimilarity among assemblages ($\beta_{sim} = 0.911$; $\beta_{sne} = 0.057$), indicating unique assemblages were present at each of the agricultural sites (Dorchin et al., 2018; Jones et al., 2019).

3.2. Response of *Bombus* to landscape composition and climate

The permutation test determined that the overall CCA model was significant ($F_{6, 123} = 2.59$, $p = 0.015$). Additionally, the permutation test by term (i.e., explanatory variables) determined that *Bombus* assemblages (richness and abundance) varied by urban and agricultural land cover, temperature, and relative humidity, but not semi-natural land cover or precipitation (Table 5). 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 sonorus* were abundant in agricultural sites with increased urban land cover in the surrounding area, high temperatures, and low relative humidity. Meanwhile, the other ten species were abundant in agricultural sites with increased agricultural land cover in the surrounding area, low temperatures, and high relative humidity (Fig. 4). When evaluating the functional dispersion across species within each of these groupings, no significant differences were identified ($t = 7.2$, $df = 1$, $p = 0.08$). Moreover, species with a range of tongue lengths, body sizes, hair lengths, and hair types were present within all of the agricultural sites, regardless of habitat characteristics.

The MRT with a 5-fold cross validation with 100 iterations resulted in a five-leaf tree where branching was determined by agricultural and urban land cover as well as temperature – all of which were significant predictors from the CCA (Error = 0.57, CV Error = 0.87, SE = 0.16). Average species abundance per site differed across the five leaves (leaf A: 3.12, B: 3.43, C: 5.28, D: 5.25, and E: 7.25). Average species abundance was highest in agricultural sites characterized by increased agricultural land cover in the surrounding area and low temperatures during the growing season (Fig. 5, leaf D–E), and lowest in sites characterized by increased urban land cover and high temperatures (Fig. 5, leaf A–C). The predictive capabilities of our MRT model were assessed using 217 *Bombus* specimens collected in 2019. Agricultural sites in 2019 were split between leaves A and B. Leaf A had an average species abundance per site of 2.39 and leaf B had an average species abundance per site of 1.83. The MRT model over-estimated average abundance per species by 1.2 specimens (predicted = 3.3, observed = 2.1).

The CCA outputs from each individual year from 2014 to 2018 were consistent with the overall model (Fig. A4). The explanatory variables were again grouped by agricultural sites with increased agricultural land cover associating with low temperatures and high relative humidity, and agricultural sites with increased urban land cover associating with high temperatures and low relative humidity. An exception occurred in 2018, which had agricultural sites with increased agricultural land cover associating with low temperatures and relative humidity, and agricultural sites with increased urban land cover associating with high temperatures and relative humidity. This is to be expected given variation in environmental and *Bombus* data between years. Additionally, species associations by year were fairly consistent with the overall model. The scaling of the explanatory variables identified which variables were important each year: humidity in 2014 and 2015; temperature followed by agricultural and urban land cover in 2016; temperature and agricultural land cover in 2017; and agricultural land cover in 2018.

Table 3

Bombus collected in pest monitoring traps in Utah from 2014 to 2019. Species status within the U.S. is listed as least concern or vulnerable. Geographic range identifies where the species occurs within the U.S. Habitat identifies primary associations within their distribution. Floral associations identify food plants each species commonly uses. Tongue length categorizes the length of their proboscis as short, medium, or long. Hair type categorizes the length (short, medium, or long) and evenness (even or uneven) of their pubescence. Body size categorizes their body size as small, medium, or large.

Species	Status	Geographic Range	Habitat	Floral Associations	Tongue Length	Hair Length and Type	Body Size
<i>Bombus appositus</i>	Least concern ¹	Cascades, Sierra Nevada, Intermountain West, and Rocky mountains ^{2,3}	Open meadows, granitic soil slopes, high elevations ^{2,3}	<i>Agastache</i> , <i>Cirsium</i> , <i>Delphinium</i> , <i>Gentiana</i> , <i>Geranium</i> , <i>Linaria</i> , <i>Orthocarpus</i> , <i>Oxytropis</i> , <i>Penstemon</i> , <i>Trifolium</i> ^{2,3}	Long ³	Medium and even ³	Large ³
<i>B. californicus</i>	Vulnerable ¹	Pacific coast; Intermountain West and Rocky Mountains ²	Co-occurs with <i>B. fervidus</i> ²	<i>Abronia</i> , <i>Astragalus</i> , <i>Cirsium</i> , <i>Monardella</i> , <i>Penstemon</i> , <i>Trifolium</i> ¹	Long ³	Medium and even ³	Medium ³
<i>B. centralis</i>	Least concern ¹	Sierra-Cascade Crest to Rocky Mountains into desert highlands of New Mexico and Arizona ^{2,3}	Open grassy prairies and mountain meadows ³	<i>Allium</i> , <i>Chrysothamnus</i> , <i>Cirsium</i> , <i>Ericameria</i> , <i>Monarda</i> , <i>Monardella</i> , <i>Penstemon</i> , <i>Phacelia</i> , <i>Symphoricarpos</i> ^{2,3}	Long ³	Short and even ³	Small ³
<i>B. fervidus</i>	Vulnerable ¹	Continental U.S. ²	Open grasslands, farmland, urban parks and gardens, midlatitudes ³	<i>Astragalus</i> , <i>Cirsium</i> , <i>Dipsacus</i> , <i>Helianthus</i> , <i>Lonicera</i> , <i>Lythrum</i> , <i>Monarda</i> , <i>Pedicularis</i> , <i>Penstemon</i> , <i>Phacelia</i> , <i>Trifolium</i> , <i>Vicia</i> ^{2,3}	Long ³	Medium and even ³	Medium ³
<i>B. flavifrons</i>	Least concern ¹	Pacific coast to Colorado Rocky Mountains ²	Open grassy prairies, mountain meadows, northern forest areas, high elevations ^{2,3}	<i>Cirsium</i> , <i>Epilobium</i> , <i>Geranium</i> , <i>Heliomeris</i> , <i>Lathyrus</i> , <i>Mentha</i> , <i>Penstemon</i> , <i>Trifolium</i> , <i>Vaccinium</i> , <i>Vicia</i> ^{2,3}	Long ³	Medium and uneven ³	Small ³
<i>B. griseocollis</i>	Least concern ¹	Across the eastern U.S.; lower elevations in Intermountain West and Rocky Mountains to northern California ^{2,3}	Open farmland and fields, urban parks and gardens, wetlands ³	<i>Asclepias</i> , <i>Coronilla</i> , <i>Cirsium</i> , <i>Dalea</i> , <i>Dipsacus</i> , <i>Echinacea</i> , <i>Helianthus</i> , <i>Lythrum</i> , <i>Medicago</i> , <i>Melilotus</i> , <i>Monarda</i> , <i>Phacelia</i> , <i>Pontederia</i> , <i>Rudbeckia</i> , <i>Solidago</i> , <i>Trifolium</i> , <i>Verbena</i> , <i>Vicia</i> ^{2,3}	Short ³	Short and even ³	Medium ³
<i>B. huntii</i>	Least concern ¹	Sierra-Cascade Crest to Rocky Mountains, northern Great Plains ^{2,3}	High desert scrub ³	<i>Chrysothamnus</i> , <i>Cirsium</i> , <i>Ericameria</i> , <i>Helianthus</i> , <i>Lupinus</i> , <i>Medicago</i> , <i>Melilotus</i> , <i>Penstemon</i> , <i>Phacelia</i> , <i>Ribes</i> , <i>Rudbeckia</i> , <i>Trifolium</i> ^{2,3}	Medium ³	Short and even ³	Medium ³
<i>B. insularis</i>	Least concern ¹	Pacific coast to New England in northern states; Intermountain West ^{2,3}	Overlaps with its host species: <i>B. appositus</i> , <i>B. fervidus</i> , <i>B. flavifrons</i> , <i>B. rufocinctus</i> , <i>B. nevadensis</i> , <i>B. occidentalis</i> , <i>B. ternarius</i> , <i>B. terricola</i> ^{2,3}	<i>Aster</i> , <i>Erigeron</i> , <i>Eupatorium</i> , <i>Heliomeris</i> , <i>Melilotus</i> , <i>Rubus</i> , <i>Senecio</i> , <i>Solidago</i> , <i>Trifolium</i> , <i>Vicinium</i> , <i>Wyethia</i> ^{2,3}	Small ³	Medium ³	Medium ³
<i>B. morrisoni</i>	Vulnerable ¹	Sierra-Cascade Crest to Intermountain West to South Dakota to the desert west ^{2,3}	Open dry scrub, highland desert areas, arid environments ^{2,3}	<i>Asclepias</i> , <i>Astragalus</i> , <i>Chrysothamnus</i> , <i>Cirsium</i> , <i>Cleome</i> , <i>Ericameria</i> , <i>Helianthus</i> , <i>Lupinus</i> , <i>Melilotus</i> , <i>Senecio</i> ^{2,3}	Short ³	Short and even ³	Large ³
<i>B. nevadensis</i>	Least concern ¹	Pacific coast to Great Plains ²	Occurs across of environmental gradients, open grassy prairies and meadows ^{2,3}	<i>Astragalus</i> , <i>Balsamorhiza</i> , <i>Ceanothus</i> , <i>Cirsium</i> , <i>Helianthus</i> , <i>Melilotus</i> , <i>Monarda</i> , <i>Penstemon</i> , <i>Phacelia</i> , <i>Salvia</i> , <i>Stachys</i> , <i>Trifolium</i> , <i>Ribes</i> , <i>Vicinium</i> , <i>Vicia</i> ^{2,3}	Long ³	Very short and even ³	Large ³
<i>B. occidentalis</i>	Vulnerable ¹	Historically from Pacific coast to Colorado Rocky Mountains; declining west of the Sierra-Cascade Crest; local populations in the Great Basin, Rocky Mountains, and Alaska ^{2,3}	Open grassy areas, chaparral and shrub areas, mountain meadows, urban parks and gardens ³	<i>Ceanothus</i> , <i>Centaurea</i> , <i>Chrysothamnus</i> , <i>Cirsium</i> , <i>Eriogonum</i> , <i>Geranium</i> , <i>Grindellia</i> , <i>Lupinus</i> , <i>Melilotus</i> , <i>Monardella</i> , <i>Rubus</i> , <i>Solidago</i> , <i>Trifolium</i> ^{2,3}	Short ³	Short and even ³	Medium ³
<i>B. pensylvanicus sonorus</i>	Vulnerable ¹	Central California to Baja California to west Texas ²	Open farmland and fields ³	<i>Astragalus</i> , <i>Chrysothamnus</i> , <i>Cirsium</i> , <i>Cornus</i> , <i>Dalea</i> , <i>Echinacea</i> , <i>Gossypium</i> , <i>Helianthus</i> , <i>Kallstroemia</i> , <i>Liatris</i> , <i>Linaria</i> , <i>Mentzelia</i> , <i>Silphium</i> , <i>Solanum</i> , <i>Trifolium</i> , <i>Vicia</i> , <i>Viguiera</i> ^{2,3}	Long ³	Short and even ³	Large ³
<i>B. rufocinctus</i>	Least concern ¹	Northern half of the U.S., southern Rocky Mountains, Sierra Nevada ²	Wooded areas, urban parks and gardens ³	<i>Arctium</i> , <i>Aster</i> , <i>Chicorium</i> , <i>Cirsium</i> , <i>Eupatorium</i> , <i>Fragaria</i> , <i>Grindellia</i> , <i>Helianthus</i> , <i>Melilotus</i> , <i>Solidago</i> , <i>Tanacetum</i> , <i>Trifolium</i> , <i>Vicia</i> , <i>Viguiera</i> ^{2,3}	Short ³	Short and even ³	Small ³
<i>B. sylvicola</i>	Least concern ¹	High mountains in Sierra Nevada, Great Basin, and Rocky Mountains ²	Open grassy areas and mountain meadows ³	<i>Arenaria</i> , <i>Chamerion</i> , <i>Chrysothamnus</i> , <i>Epilobium</i> , <i>Haplopappus</i> , <i>Senecio</i> , <i>Lupinus</i> , <i>Melilotus</i> , <i>Monardella</i> , <i>Petasites</i> , <i>Phyllodoce</i> , <i>Raillardella</i> , <i>Senecio</i> ^{2,3}	Medium ³	Long and uneven ³	Small ³
<i>B. vancoverensis</i>					Medium ³		Small ³

(continued on next page)

Table 3 (continued)

Species	Status	Geographic Range	Habitat	Floral Associations	Tongue Length	Hair Length and Type	Body Size
	Least concern ¹	Pacific coast to Rocky Mountains ²	Open grassy prairies, chaparral and shrub areas, mountain meadows, urban parks and gardens ^{2,3}	<i>Aster</i> , <i>Centaurea</i> , <i>Chrysothamnus</i> , <i>Cirsium</i> , <i>Epilobium</i> , <i>Ericameria</i> , <i>Haplopappus</i> , <i>Helenium</i> , <i>Lupinus</i> , <i>Melilotus</i> , <i>Monardella</i> , <i>Penstemon</i> , <i>Ribes</i> , <i>Senecio</i> , <i>Solidago</i> , <i>Symphoricarpos</i> ^{2,3}		Short and even ³	

¹IUCN, 2022. The IUCN red list of threatened species. Version 2021–3. <http://www.iucnredlist.org>

²Koch, J. B., Strange, J. P., Williams, P., 2012. Bumble bees of the Western United States. Pollinator Partnership.

³Williams, P., Thorp, R., Richardson, L., Colla, S., 2014. Bumble bees of North America: an identification guide. Princeton University Press, New Jersey.

Table 4

Bombus species richness and abundance from 2014 to 2019.

Species				Abundance by Year			
	2014	2015	2016	2017	2018	2019	All Surveyed Years
<i>Bombus appositus</i>	1	0	0	3	8	0	12
<i>B. californicus</i>	2	3	2	4	0	0	11
<i>B. centralis</i>	115	16	47	14	26	4	222
<i>B. fervidus</i>	512	308	446	441	452	163	2322
<i>B. flavifrons</i>	19	5	1	0	0	0	25
<i>B. griseocollis</i>	63	9	24	49	33	7	185
<i>B. huntii</i>	79	18	80	79	189	11	456
<i>B. insularis</i>	2	3	2	0	3	6	16
<i>B. morrisoni</i>	9	0	0	1	1	1	12
<i>B. nevadensis</i>	10	2	3	38	5	1	59
<i>B. occidentalis</i>	4	0	0	0	0	0	4
<i>B. pensylvanicus</i>	0	0	1	0	1	0	2
<i>B. rufocinctus</i>	162	44	52	79	20	21	378
<i>B. sylvicola</i>	0	1	1	0	0	0	2
<i>B. vancouverensis</i>	6	5	6	4	9	3	33
Total	984	414	665	712	747	217	3739

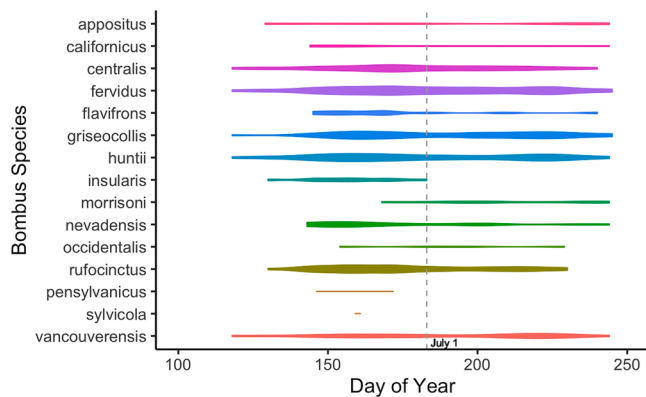


Fig. 2. Violin plot of *Bombus* species collected from late April to mid-September from 2014 to 2018. Line width indicates the relative number of specimens collected.

4. Discussion

We found that the co-occurring effects of landscape composition and climate drive *Bombus* assemblage composition in Utah agroecosystems. Specifically, *Bombus* assemblage composition was highest in agricultural sites with increased agricultural land cover, low temperatures, and high relative humidity during the growing season; and lowest in agricultural sites with increased urban land cover, high temperatures, and low relative humidity. Our finding that *Bombus* assemblages were highest with increased agricultural land cover differs from other studies that suggest diversity is negatively impacted by high proportions of agriculture due to a lack of diverse landscapes, reduced availability of floral

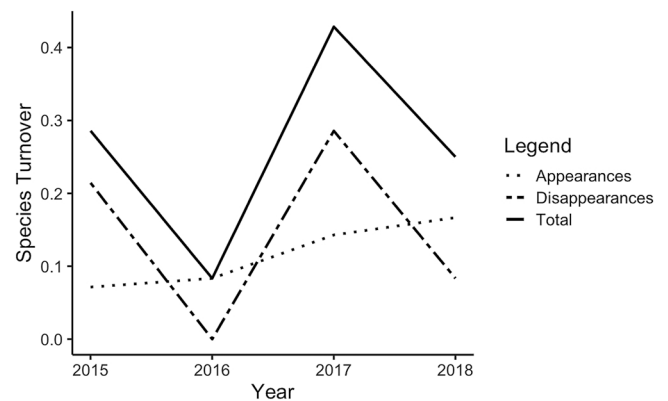


Fig. 3. Total species turnover with the proportion of species appearances and disappearances from 2014 to 2018. 2014 is not shown since species richness from 2014 was used to calculate species turnover for 2015. Different line styles represent the three species turnover metrics.

Table 5

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

Variable	df	F	p-value
Agricultural	1	2.50	0.029
Urban	1	3.35	0.023
Semi-natural	1	0.70	0.454
Mean Temperature	1	6.27	0.001
Mean Precipitation	1	1.72	0.130
Mean Relative Humidity	1	3.12	0.016

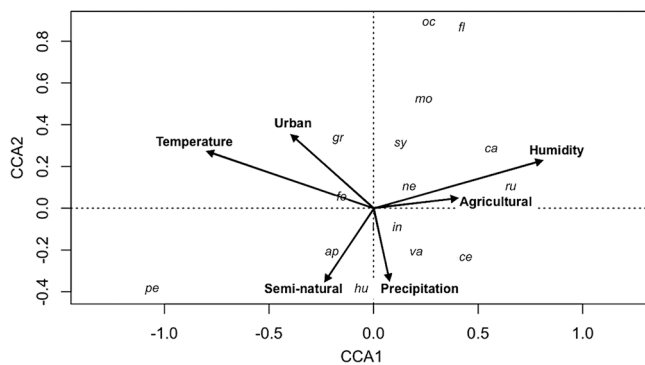


Fig. 4. Canonical correspondence analyses of the *Bombus* assemblage data in relation to environmental variables (indicated by arrows) from 2014 to 2018. *Bombus* species names are abbreviated as ap = *B. appositus*, ca = *B. californicus*, ce = *B. centralis*, fe = *B. fervidus*, fl = *B. flavifrons*, gr = *B. griseocollis*, hu = *B. huntii*, in = *B. insularis*, mo = *B. morrisi*, ne = *B. nevadensis*, oc = *B. occidentalis*, pe = *B. pensylvanicus sonorus*, ru = *B. rufocinctus*, sy = *B. sylvicola*, and va = *B. vancouverensis*. Agricultural sites with more urban land cover in the surrounding area were correlated with high temperatures and low humidity during the growing season (left side), while agricultural sites with more agriculture land cover were correlated with low temperatures and high humidity (right side).

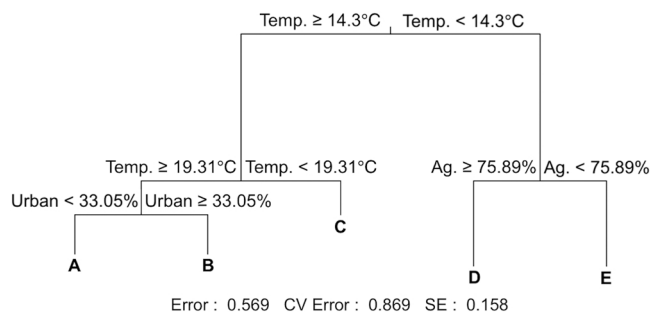


Fig. 5. Multivariate regression tree (MRT) for the *Bombus* species data in relation to the proportion of urban and agricultural (Ag.) land cover (%) as well as temperature (C, Temp). Non-significant variables (semi-natural land cover, precipitation, and relative humidity) were not included in this model. The five leaves (indicated with letters under each branch) identify clusters of environmental variable values associated with the agricultural sites. Average species abundance per site for each leaf was calculated – Leaf A: 3.11, B: 3.42, C: 5.27, D: 5.25, and E: 7.25.

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 finding may be due to differences in agricultural practices, management history, and the local environment (Kohler et al., 2020). The agricultural sites surveyed in this study are relatively small (mean of 89,030 m²) and in close proximity to other monocultures. This increases heterogeneity in landscape composition, which can increase the availability of floral, nesting, and breeding resources. Additionally, the low temperatures associated with agricultural land cover may provide favorable microhabitats, which can act as areas of thermal refuge for *Bombus* species (Maebe et al., 2021). High humidity has also been found to positively influence *Bombus* foraging rates of nectar, particularly on cooler days, due to increased nectar secretion rates (Peat and Goulson, 2005). These factors may explain why *Bombus* are captured in relatively high numbers within crop fields (e.g., corn and alfalfa hay) that do not necessarily provide ideal floral resources. Additionally, since *Bombus* are fairly vagile foragers (Rao and Strange, 2012; Geib et al., 2015) and are not considered to be area sensitive, they can exploit floral resources within hedge rows and weedy areas surrounding agricultural

fields to 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). However, the degree to which *Bombus* travel for floral and nesting resources is species specific (Geib et al., 2015) and dependent on landscape configuration (the spatial arrangement of land cover categories), which emphasizes the importance of future research evaluating the impact of landscape configuration in conjunction with landscape composition and climate.

Although other studies, including our own, found that *Bombus* richness decreased with more urbanization (Ahrné et al., 2009), several species (*B. appositus*, *B. fervidus*, *B. griseocollis*, *B. huntii*, and *B. pensylvanicus sonorus*) were more abundant in agricultural sites with increased urban land cover in the surrounding area (e.g., crop fields in close proximity to suburban housing developments, buildings, roadways, and highways), increased temperatures, and low humidity. This indicates that *Bombus* species respond differently to urban land cover surrounding 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, environmental characteristics, 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). Drier (warmer and less humid) environments facilitate the release of pollen grains (anther dehiscence) and reduce challenges associated with grooming wet pollen into the corbiculae, leading to an overall increase in pollen collection (Peat and Goulson, 2005). These factors may help explain the increased abundance of certain *Bombus* species at agricultural sites with increased urban land cover. 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 reduce their risk of overheating from crowding and insufficient nest ventilation (Weidenmüller et al., 2002), especially within urban land cover that is known to have warmer temperatures relative to surrounding agricultural habitats due to the increased prevalence of impervious surfaces (Baldock, 2020). Meanwhile, *B. pensylvanicus sonorus*, a species that normally occurs in open farmland and fields in the southwestern U.S. (Table 3; Koch et al., 2012; Williams et al., 2014) but is declining in population size (Cameron et al., 2011; Strange and Tripodi, 2019), was detected in Northern Utah within high temperature agricultural sites surrounded by urban land cover. Rising temperatures within the southwest may be causing this species to expand northward towards a relatively cooler climate within agricultural settings. Continually monitoring their population with respect to climate will help provide more information on changes in demographics (e.g., distribution and population size).

Ongoing and future climate change may alter *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, both on an individual and multi-year level. Overlap in phenology may aid in fostering future resiliency of pollination services. If a particular species is lost due to loss of habitat, other ecologically similar species within the environment might be available to fill this gap in pollination services due to similar functional diversity and response diversity (Elmqvist et al., 2003; Laliberté et al., 2010; Blüthgen and Klein, 2011). However, species overlap was lower earlier in the season (late April to mid-May) potentially due to differences in time of emergence from winter diapause. Climate warming has been shown to lead to shifts in *Bombus* emergence with bees having earlier springtime activity in the northeastern U.S. (Bartomeus et al., 2011; Pyke et al., 2016). This shift may benefit Utah 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 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); however, more in-depth research on shifts in plant-pollinator synchrony are needed to better understand the potential for adaptive foraging.

Novel ecosystems will emerge as a result of urbanization, agricultural intensification, and climate change. 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). Additionally, novel ecosystems may alter species interactions (e.g., mutualism or competition), or lead to the loss of regionally unique species further contributing to homogenized ecosystems (Hobbs et al., 2006). For example, some vulnerable species, such as *B. pensylvanicus sonorus*, may thrive under future landscape and climate scenarios, while others (e.g., *B. californicus* and *B. occidentalis*) are at increased risk of extirpation due to loss of suitable habitats. Overall, functional groups and species interactions will change; but key ecological function will not necessarily be lost as high functional diversity and response diversity are retained (Elmqvist et al., 2003; Laliberté et al., 2010; Blüthgen and Klein, 2011). *Bombus* assemblage responses will be largely dependent on land management practices, geographic location, and changes in species diversity and distribution.

5. Conclusion

In summary, we identified land cover and climatic variables that drive *Bombus* species assemblage composition in agroecosystems. *Bombus* assemblage composition was highest in agricultural sites with increased agricultural land cover, low temperatures, and high relative humidity during the growing season; and lowest in agricultural sites with increased urban land cover, high temperatures, and low relative humidity. If the same drivers are applied everywhere such that spatial, functional, and taxonomic similarity increase, beta-diversity can decrease leading to homogenization. However, unique assemblages with a breadth of functional traits suggests high beta-diversity and functional diversity is present among sites. Regardless, considerations should be given due to overall pollinator declines. Further, these differences in species among sites suggest that all agricultural sites in this study have potential conservation value for maintaining *Bombus* communities, which highlights the importance of maintaining diverse habitats for pollinators through targeted land management techniques (Si et al., 2015). Minimizing pesticide exposure to foraging bees, diversifying agricultural areas by planting water-wise native plants, providing suitable nesting sites, and avoiding overhead irrigation during daylight hours can help conserve and promote diverse *Bombus* assemblages to effectively foster future resiliency of *Bombus* populations in the face of anthropogenic disturbances. Continually monitoring *Bombus* populations will help document these shifts in assemblages and potential consequential impacts to ecosystem services. Overall, this study takes a crucial step towards understanding the co-occurring effects of landscape composition and climate on *Bombus* assemblages.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data and code supporting the findings of this study are available on

Zenodo at <http://doi.org/10.5281/zenodo.6363828> and the Global Biodiversity Information Facility at <https://www.gbif.org/dataset/c6fdb7c6-9597-44e2-8b82-32714bb7133c>.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2022.108113](https://doi.org/10.1016/j.agee.2022.108113).

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