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An Evaluation of Landscape, Climate, and Management Impacts on Bumble Bees (Hymenoptera: Apidae: *Bombus*) in Agroecosystems

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AN EVALUATION OF LANDSCAPE, CLIMATE, AND MANAGEMENT IMPACTS ON BUMBLE BEES (HYMENOPTERA: APIDAE: *BOMBUS*) IN AGROECOSYSTEMS

by

Morgan Elizabeth Christman

A dissertation submitted in partial fulfillment
of the requirement for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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2022

ABSTRACT

An Evaluation of Landscape, Climate, and Management Impacts on Bumble Bees (Hymenoptera: Apidae: *Bombus*) in Agroecosystems

by

Morgan Elizabeth Christman, Doctor of Philosophy

Utah State University, 2022

Major Professor: Dr. Ricardo A. Ramirez
Department: Biology

Bumble bees (*Bombus*) are integral pollinators of wild and cultivated plant communities, but are undergoing drastic population changes worldwide. Climate change and the alteration of landscape structure are key drivers in pollinator declines; however, little research has evaluated their cumulative effects on *Bombus* assemblages (richness and abundance). Additionally, since insect monitoring traps can attract non-target insects, there are concerns that these captures may further contribute to *Bombus* mortality. Chapter II linked differences in *Bombus* assemblages to landscape composition and climate in Utah agroecosystems. *Bombus* assemblage composition was highest in agricultural sites with more agricultural land cover in the surrounding area, low temperatures, and high humidity during the growing season; and lowest in agricultural sites with more urban land cover, high temperatures, and low humidity. Differences in species among sites highlighted the importance of maintaining diverse habitats to promote resiliency of *Bombus* assemblages in the face of anthropogenic disturbances. Chapter III examined the cumulative effects of climate and landscape structure on *Bombus* assemblages throughout U.S. agroecosystems. Species composition varied widely based on climatic and landscape characteristics, emphasizing that management practices should be implemented based on a continuum of environmental characteristics to increase *Bombus* assemblages throughout the U.S. Chapter IV quantified the impact of pest monitoring trap captures on *Bombus griseocollis* colony growth and development. *Bombus griseocollis* were collected at low rates within traps from field-released colonies, suggesting differences in colony weight change and foraging activity were not a result of trap captures; however, this does not mean that other *Bombus* species were not affected. Chapter V evaluated the commercialization potential of *B. griseocollis* by assessing nest initiation and establishment rates, and identifying lab-reared worker's critical thermal maxima ($\mathrm{CT_{Max}}$). Given their high captive rearing success and $\mathrm{CT_{Max}}$, *B. griseocollis* should continue to be evaluated for commercial purposes. Overall, this research increased knowledge to provide more accurate conservation and management practices of *Bombus* assemblages in agroecosystems throughout Utah and the rest of the U.S., identified that pest monitoring traps are not of concern for *B. griseocollis* at a colony level, and provided a foundation for developing *B. griseocollis* as a commercialized pollinator.

(279 pages)

PUBLIC ABSTRACT

An Evaluation of Landscape, Climate, and Management Impacts on Bumble Bees (Hymenoptera: Apidae: *Bombus*) in Agroecosystems

Morgan Elizabeth Christman

Bumble bees play pivotal roles in pollinating wild and cultivated plant communities. Unfortunately, bumble bee populations are declining due to disturbances such as landscape conversion and climate change. Additionally, traps used to monitor pest insect populations often capture bumble bees, leading to a concern that trap captures increase bumble bee mortality. First, I studied bumble bee communities based on land cover and weather variables in agricultural fields in Utah. Bumble bee communities were more diverse in agricultural fields with more agricultural land in the surrounding area, low temperatures, and high humidity during the growing season, and less diverse in fields with more urban land, high temperatures and low humidity. However, differences in species among sites suggest that all agricultural fields from this study have high conservation value for bumble bees; therefore, management strategies should maintain a variety of habitat types to promote resiliency of bumble bee assemblages. Next, I examined the effects of climate and landscapes on bumble bees in agricultural fields throughout the U.S. Bumble bee assemblages varied based on habitat characteristics, emphasizing that management practices should differ across the U.S. based on the local climate and landscapes in order to conserve bumble bees. I then measured the impact of trap captures on the size and development of field-released brown-belted bumble bee colonies. Only three brown-belted bumble bees were collected from traps, suggesting that these captures had negligible effects on the observed differences in weight and foraging activity. However, this does not mean that all bumble bee species are not affected. Finally, I evaluated the commercial potential of brown-belted bumble bees by determining if they can be successfully raised in a laboratory setting and by identifying the maximum temperature worker bumble bees can withstand before death. Brown-belted bumble bees can successfully be raised in a lab and can tolerate high temperatures, so they should continue to be evaluated for commercial purposes throughout the U.S. Overall, this research increased knowledge to provide more accurate management practices of bumble bee communities in agricultural systems throughout the U.S. and provided a foundation for developing brown-belted bumble bees as a commercialized pollinator.

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CHAPTER I

INTRODUCTION: LANDSCAPE ECOLOGY OF BUMBLE BEES (HYMENOPTERA: APIDAE: *BOMBUS*) IN AGROECOSYSTEMS THROUGHOUT THE UNITED STATES

***Bombus* Biology**

Bumble bees (Hymenoptera: Apidae: *Bombus*) are abundant and diverse native, eusocial pollinators throughout temperate, alpine, and subarctic ecosystems (Kremen et al. 2002; Berenbaum et al. 2007; Klein et al. 2007; Goulson 2010; Strange and Tripodi 2019; Williams and Jepsen 2020). There are more than 265 described *Bombus* species worldwide, 47 of which occur in North America (Colla et al. 2011; Koch et al. 2012; Williams et al. 2014; Williams and Jepsen 2020; Maebe et al. 2021; IUCN 2022). *Bombus* are distributed across the contiguous U.S. and Alaska, filling a wide range of ecological niches (Strange and Tripodi 2019). Species distributions are defined by various geographic and biological constraints, creating regional differences in community composition (Lozier et al. 2011; Williams et al. 2014; Koch et al. 2017; Strange and Tripodi 2019). For example, although some *Bombus* species are widely distributed, distinct assemblages can occur east and west of the Rocky Mountains, and further distinction in community composition can occur west of the Sierra Nevada and Cascade Mountain ranges, with six species restricted along the Pacific Coast (Koch et al. 2012; Koch et al. 2017).

Bombus are primitively eusocial, which is characterized by several overlapping generations within a colony, division of labor (non-reproductive and reproductive), and cooperative care of offspring over the lifetime of the colony. *Bombus* colonies have an annual life cycle that is initiated with the emergence of a mated gyne (i.e., a female that has a potential to become a queen) from winter dormancy. The gyne searches for a suitable nesting site in abandoned rodent burrows, open grass tussocks, hollow logs, or above-ground man-made structures, and then forages for nest provisions (i.e., pollen and nectar) (Williams et al. 2014). The foundress gyne (now queen) constructs a wax honeypot for nectar storage within the nest, oviposits the first brood clutch on a pollen mass moistened with nectar, incubates the first clutch of brood, and continues to forage to provide food for larval workers (Williams et al. 2014). After emergence of the first female workers from brood, the queen restricts activity to oviposition and brooding. The workers then perform tasks for the colony such as foraging, brood care, and colony maintenance. The queen continues to produce more offspring quickly throughout the summer as more floral resources become available, allowing the colony to grow and develop. Towards the end of the growing season, the queen switches to producing sexuals (i.e., gynes and drones (males)). Soon after emergence, gynes and drones leave the colony to feed and mate. The foundress queen, female workers, and drones then die, and the newly mated gynes find an underground hibernaculum to undergo winter diapause before the cycle continues (Alford 1975; Goulson 2010; Strange 2010; Williams et al. 2014; Koch et al. 2021).

Bombus Pollination Services

Bombus are integral pollinators of wild and cultivated plant communities (Klein et al. 2007). *Bombus* are polylectic and have three different proboscis lengths: short, medium, and long, which allow each species to visit a variety of flowers of different shapes and sizes. *Bombus* also have an interesting behavior of sonicating (buzzing) flowers, in which they collect pollen from plants that do not produce nectar by vibrating their wing muscles to shake pollen grains out of the anthers. Buzz pollination is beneficial for several important food crops such as tomato, eggplant, kiwi, and blueberries (Cooley and Vallejo-Marín 2021). As such, a few commercially produced *Bombus* species (i.e., *B. impatiens, B. terrestris, B. vosnesenskii,* and *B. huntii*) are deployed in greenhouse settings for crop pollination in order to increase crop yield and quality. Each year, more than a million *Bombus* colonies are commercially produced and sold around the world, averaging more than $10 billion annually in pollination services (Velthuis and van Doorn 2006; Williams et al. 2014). However, these species are often released in greenhouses well outside their native range; therefore, there is a need to identify regionally appropriate candidates for commercial crop pollination (Goulson 2010; Strange 2010, 2015).

Bombus Population Declines

Despite their importance to agricultural and natural systems, many *Bombus* species are facing population declines, which are attributed to various anthropogenic factors such as habitat loss and fragmentation, climate change, pesticide exposure, pathogens and pests, and competition with non-native bees (Goulson et al. 2005; Potts et al. 2010; Cameron et al. 2011; Colla et al. 2012; Arbetman et al. 2013; Graystock et al. 2013; Morales et al. 2013; Goulson et al. 2015; Kerr et al. 2015; Miller-Struttmann et al. 2015; Cameron and Sadd 2019; Fourcade et al. 2019; Kohler et al. 2020; Soroye et al. 2020; Zattara and Aizen 2021). These factors are also expected to occur in combination and interact, further altering species' responses to these emerging conditions. However, little research has evaluated their cumulative effects, underscoring the need to understand how *Bombus* are affected by a range of environmental changes (Easterling et al. 2000; Kerr et al. 2015; Marshall et al. 2018; Betts et al. 2019; Fourcade et al. 2019; Jamieson et al. 2019; Miljanic et al. 2019; Kohler et al. 2020; Maebe et al. 2021).

Currently, the International Union for the Conservation of Nature (IUCN) lists six *Bombus* species as critically endangered or endangered, and six species as vulnerable (IUCN 2022; Table 1–1). Additionally, *Bombus affinis* and *B. franklini* are listed as endangered by the U.S. Fish and Wildlife Service under the Endangered Species Act (ESA) and the Committee on the Status of Endangered Wildlife in Canada, and *B. occidentalis* is being considered for ESA listing (Hatfield et al. 2015; Graves et al. 2020; Smith et al. 2020). Given that *Bombus* declines have subsequent effects on associated ecosystems, there is a need to create and restore pollinator habitats, improve detection and management of pest and non-native species that threaten native pollinators, monitor *Bombus* populations to increase knowledge of diversity and range shifts, and continually evaluate *Bombus* species and assemblage responses to a wide range of threats.

Threats to *Bombus* Populations: Habitat Loss and Fragmentation

Habitat loss and fragmentation are becoming more prevalent throughout the U.S. as a result of human-mediated alterations to the landscape such as agricultural intensification and urbanization (Ahrné et al. 2009; Glaum et al. 2017; Wenzel et al. 2020). Increases in the extent and intensity of agricultural intensification and urbanization have led to considerable loss and degradation of suitable pollinator habitats, causing changes in *Bombus* diversity and abundance (Meehan et al. 2011; Wagner et al. 2021).

Natural and semi-natural habitats in and surrounding agricultural areas increase bee diversity and abundance by providing nesting sites and diverse floral resources (Ricketts et al. 2008; Garibaldi et al. 2011; Lentini et al. 2012; Andersson et al. 2013; Cusser et al. 2016, 2019; St Clair et al. 2020). However, as a result of agricultural intensification, these patches of diverse plant assemblages are converted to support efficient and cost-effective crop production (Goulson et al. 2015; Koh et al. 2016). This conversion increases the size and connectivity of crop fields, while reducing landscape compositional (i.e., the number of distinct land cover categories) and configurational (i.e., the spatial arrangement of land cover categories) complexity (Kremen et al. 2002; Tscharntke et al. 2005; Le Féon et al. 2010; Meehan et al. 2011; Kennedy et al. 2013; Nelson and Burchfield 2021). Additionally, land management practices in agriculturally intensified landscapes typically consist of increased input of pesticides and fertilizers applications, and frequent soil disturbances (i.e., seeding, tilling, harvesting) (Le Féon et al. 2010; Meehan et al. 2011; Vanbergen et al. 2013; Kohler et al. 2020). The culmination of these factors can subsequently reduce available nesting sites for *Bombus* and result in reduced species abundance and richness (Goulson et al. 2015; Koh et al. 2016). However, depending on the crop type produced, intensified agricultural habitats can provide abundant floral resources for *Bombus* species. For example, mass-flowering crops such as canola, cranberries, and cotton can provide a dense resource pulse, which can promote local bee densities (Westphal et al. 2003; Jha and Kremen 2013; Diekotter et al. 2014; Pfeiffer et al. 2019; Parys et al. 2021). Therefore, habitat quality plays a large role in determining how species respond to agricultural intensification (Kleijn and van Langevelde 2006; Kennedy et al. 2013; Miljanic et al. 2019).

Urbanization involves extensive, persistent modifications to the landscape that increase the number of impervious surfaces (i.e., roadways, buildings, parking lots, and industrial areas), while decreasing the number of natural or semi-natural areas (McKinney 2006; Ahrné et al. 2009; Bennett and Lovell 2019; Wenzel et al. 2020). The proportion of impervious surfaces in the surrounding area determines which and how many species can occur within the landscape (i.e., species richness) (Ahrné et al. 2009; Geslin et al. 2016). However, ubiquitous impervious surfaces have been found to decrease *Bombus* species diversity due to a loss of under-ground and above-ground nesting sites, a loss of foraging sites with stable floral resources and vegetation cover, and increased heavy metal contamination (Ahrné et al. 2009; Geslin et al. 2016; Glaum et al. 2017; Sivakoff et al. 2020). Additionally, dense urban environments lack available and accessible microhabitats that can provide resources and thermal refuge for foraging workers, further making these environments unsuitable for pollinators (Huey et al. 2012; Fortel et al. 2014; Sunday et al. 2014). However, urban green spaces (i.e., city parks, gardens, cemeteries, golf course, and remnant native land) can provide suitable patches of habitats (i.e., stepping stones or corridors) in dense urban environments, which increases landscape compositional and configurational complexity. As such, high quality urban green spaces support abundant *Bombus* populations, emphasizing the importance of allocating space for floral rich patches in urban environments (Ahrné et al. 2009; Hinners et al. 2012; Banaszak-Cibicka et al. 2016; Hall et al. 2016).

Impacts of agricultural intensification and urbanization on *Bombus* assemblages are often species specific, with differences attributed to traits such as tongue length, diet, geographic range, phenology, foraging distance, sex, body size, colony size, and nesting strategy (Goulson and Darvill 2004; Goulson et al. 2005; Williams 2005; Benton 2006; Westphal et al. 2006; Fitzpatrick et al. 2007; Greenleaf et al. 2007; Geslin et al. 2013; Banaszak-Cibicka et al. 2018). For example, urban areas are typically dominated by *Bombus* species that have a broader geographic range and a generalist diet, as these species can better respond to challenges associated with fragmentation and can rely on a wide range of floral resources (Geslin et al. 2013). This underscores the need to document and understand how individual species respond to landscape composition and configuration in order to identify which species may be more at risk to habitat loss and fragmentation (Kohler et al. 2020). Additionally, landscape composition and configuration are expected to interact with climate change, further altering species responses; yet, these cumulative effects have not been studied (Betts et al. 2019; Jamieson et al. 2019; Kohler et al. 2020; Maebe et al. 2021).

Threats to *Bombus* Populations: Climate Change

Anthropogenic climate change is gradually altering key elements of climate (i.e., temperature, humidity, precipitation), intensifying seasonality, and increasing the frequency and intensity of extreme weather events (Easterling et al. 2000; Meehl and Tebali 2004; Martinet et al. 2020; Maebe et al. 2021). These climatic consequences are expected to worsen throughout the 21st century, causing subsequent impacts on ecosystems and local populations (Parmesan 2006; IPCC 2014). *Bombus* populations are undergoing declines and distributional changes as a result of the direct and indirect effects of climate change. Rising ambient temperatures, in particular, directly affect physiology, morphology, behavior, development, and body size (Bale et al. 2002; Oyen et al. 2016; Martinet et al. 2020; Maebe et al. 2021), and indirectly affect *Bombus* via competition between species, spread of non-native plants and insects, and changes in land cover and vegetation composition (Marshall et al. 2018; Gérard et al. 2020).

As a cold adapted genus, *Bombus* have evolved traits that are suited to tolerate the extreme cold, such as being capable of endothermy (shivering to generate heat), the ability to thermoregulate, and having larger bodies covered in long, dense, insulating hairs (Heinrich 1974, 1979; Ploquin et al. 2013; Dehon et al. 2019). Few *Bombus* species are adept at living in environments with long, hot, dry summers and short, moderate winters, which are expected to occur as a result of climate change (Rasmont et al. 2008, 2015). As such, these climatic conditions will have substantial impacts on both worker activity and queen overwintering (Williams 1998; Woodard 2017). *Bombus* workers must remain active in and out of the colony to support colony growth and development.

However, worker foraging activity is reduced in wet conditions and during hot summer days (Peat et al. 2005; Sanderson et al. 2015), since increasing temperatures can induce thermal stress. While thermal tolerance levels are species specific, negative effects of temperature extremes can be observed well before maximum thermal limits are reached, leading to a loss of motor function, an inability to escape conditions, and in extreme cases, death (Heinrich 1974, 1979; Oyen et al. 2016). Therefore, it is necessary to determine the physiological vulnerabilities of each *Bombus* species to rising temperatures. Meanwhile, queens lower their metabolic rate and activity levels, and rely on their energy reserves (i.e., fat storage) during winter diapause. In cold conditions, queens are able to maintain fat reserves, which is necessary for successful hibernation. However, with warmer winter temperatures, overwintering queens burn through fat reserves faster, creating excessive energy demands, and experience increased metabolic rates, which can lead to shorter lifespans (Vesterlund et al. 2014; Kelemen et al. 2019). At the colony level, *Bombus* workers can actively ventilate and thereby cool the nest as internal temperatures increase via wing fanning. However, the thermoregulation abilities of a colony are largely dependent on task allocation, which depends on the probability of response, duration of wing fanning activity, colony experience, and behavioral plasticity (Weidenmüller 2004; Duong and Dornhaus 2012; Westhus et al. 2013; Weidenmüller et al. 2019).

Bombus are also undergoing distributional shifts in response to changing climates. Many species are shifting their distribution towards colder, higher elevation areas where habitat and resource availability are limited (Parmesan 2006; Fourcade et al. 2019; Koch et al. 2019). These shifts are particularly concerning for climate-sensitive species, species living in fragmented habitats or habitats that lack high elevations, or species that are already at their upper elevation limit (Pyke et al. 2016). Additionally, higher elevation environments are associated with delayed and reduced flower bloom as well as a decline in floral density (Williams et al. 2007; Inouye 2008; Miller-Rushing and Inouye 2009; Oyen et al. 2016; Miller-Struttmann et al. 2015; Pyke et al. 2016; Koch et al. 2019). Mismatching functional traits between flower tube depth and *Bombus* proboscis (tongue) length can disrupt mutualism, co-evolution, reproduction, species abundance, and recruitment rates (Miller-Struttmann et al. 2015; Pyke et al. 2016). Therefore, short-tongued bees, which exhibit greater dietary generalization, may have an evolutionary advantage as floral densities decline (Goulson 2010; Miller-Struttmann et al. 2015). This likely explains the observed declines in the proportion of long-tongued *Bombus* populations over the last several decades and the reduced tongue lengths documented in *B. sylvicola* and *B. balteatus* (Bommarco et al. 2012; Miller-Struttmann et al. 2015). Additionally, climate change can shift species phenology, disrupting plant-pollinator synchrony and leading to mismatches in plant-pollinator interactions, which is important for ecosystem function (Williams et al. 2007; Oyen et al. 2016; Pyke et al. 2016; Koch et al. 2019; Vanderplanck et al. 2019). Overall, in order to evaluate *Bombus* diversity, range shifts, and responses to a wide range of threats, it is necessary to continually survey *Bombus* across a wide geographic range.

Bombus **Sampling Methods**

Bees are typically surveyed using a variety of collection methods: bowl traps, netting, and non-lethal field observations. Bowl traps passively collect bees by mimicking natural cues (e.g., color) associated with floral resources (Droege et al. 2010; Portman et al. 2020). Bowl traps are cheap, easy to use, replicable, and reduce capture bias by surveyors. Although bowl traps are effective at detecting changes in bee abundance and richness (Cane et al. 2000; Westphal et al. 2008; Droege et al. 2016; Le Féon et al. 2016; Prado et al. 2017), they are taxonomically biased towards collecting bees in the family Halictidae, making them a poor choice for monitoring *Bombus* and other bee populations (Droege et al. 2010). Meanwhile, netting consists of a collector actively capturing individual bees as they forage over a defined space and time. Active sampling with nets is the most accurate survey method as it allows for a targeted approach, but is labor, time, and cost intensive (Portman et al. 2020). Non-lethal field observations consist of a collector observing or temporarily capturing a bee with a net, identifying the bee, and then releasing the bee back into the environment. Non-lethal field observations reduce the number of pollinators killed during the monitoring process, but similar to netting, are labor, time, and cost intensive. Additionally, *Bombus* identifications can be less accurate or less species specific (may only go to genus level) with non-lethal observations, depending on the experience of the observer and the specific *Bombus* specimen. The timing of sampling also matters with active netting and non-lethal field observations. For example, sampling at different times of the field season would yield different results based on *Bombus* species phenology and distribution (Strange and Tripodi 2019).

Therefore, the timing and location of sampling needs to be based on the research question(s) being asked. Given these drawbacks, multiple survey methods (i.e., active and passive sampling) are often employed, which can cause a backlog of specimens that need to be processed (Portman et al. 2020). Overall, all of these commonly used sampling methods have limitations and flaws that create challenges for monitoring changes in *Bombus* abundance and richness.

More robust and standardized collection of biodiversity and ecological data is needed to better understand global changes in species abundances over space and time (Cardoso and Leather 2019). Currently, there are no standardized protocols in place to survey and monitor *Bombus* species abundance and distribution throughout the U.S. (Strange and Tripodi 2019; Portman et al. 2020). However, analyzing bees captured unintentionally within pest monitoring traps (bycatch) could support national monitoring efforts, especially within agricultural areas and geographic regions that are historically underrepresented in surveys (Carvell et al. 2016; Droege et al. 2017; Jamieson et al. 2019; Woodard et al. 2020).

***Bombus* Bycatch**

Each year, federal, state, and university cooperators conduct annual field surveys to monitor pest insect populations (Spears and Ramirez 2015). Traps use visual (e.g., color) and/or olfactory (e.g., chemical) cues to attract pest insects (Adams et al. 1989; Pair et al. 1989; Weber and Ferro 1991; Spears and Ramirez 2015; Spears et al. 2016, 2021). However, they often also attract and capture a wide range of non-target insects (bycatch), including bees due to an overlap in attraction to visual and chemicals cues (Spears and Ramirez 2015; Sipolski et al. 2019; Whitfield et al. 2019; Grocock et al. 2020; Parys et al. 2021; Spears et al. 2021).

Pest monitoring traps are typically blue, white, yellow, green, or red, which reflect wavelengths that mimic natural cues used by a variety of insects to locate floral resources (Spears et al. 2016; Sipolski et al. 2019; Spears et al. 2021). For example, bees have trichromatic vision, and are most sensitive to ultraviolet, blue-ultraviolet, and green-yellow wavelengths (Chittka and Waser 1997; Briscoe and Chittka 2001; Dyer et al. 2011; Shimoda and Honda 2013; Rao and Ostroverkhove 2015; Chen et al. 2020). Additionally, pheromone lures used to attract specific pest species, have been found to attract congeners and heterospecifics due to an attraction to individual lure components (Spears et al. 2016; Whitfield et al. 2019; Grocock et al. 2020). Wild bees, particularly *Bombus*, are commonly captured within traps baited with moth pheromones that are composed of a mixture of fatty acids, acetates, aldehydes, and alcohols (Meagher and Mitchell 1999; Field et al. 2000; Turnock et al. 2007; Mori and Evenden 2013; Aurelian et al. 2015; Spears et al. 2016). This has raised questions about whether bees can detect and respond to heterospecific signals produced by distantly related insects (Grocock et al. 2020). While the mechanism driving this response is still unclear, it is likely *Bombus* are preadapted to detect these signals due to the structural similarity between pheromone components used to target moth species and signals used by *Bombus* (Grocock et al. 2020). For example, male bumble bees produce species-specific pheromones in the cephalic region of the labial gland for pre-mating recognition (De Meulemeester et al. 2011) that are structurally similar to the pheromone lures used to target different moth species (Appelgren et al. 1991; Bergström et al. 1996; Meagher and Mitchell 1999; Field et al. 2000; Turnock et al. 2007; Mori and Evenden 2013; Aurelian et al. 2015; Spears et al. 2016). Overall, the broad temporal and spatial range of pest monitoring traps leads to a great deal of concern towards the environmental impacts that can occur as a consequence of trap captures (Spears and Ramirez 2015; Spears et al. 2021).

Research on insect and non-insect taxonomic groups, has identified that capture events can lead to population declines, which can have higher order effects on species interactions and ecosystem services (Mondor 1995; Clare et al. 2000; Lewison et al. 2014; Spears and Ramirez 2015; Gibbs et al. 2017; Grocock and Evenden 2020). Therefore, *Bombus* bycatch could have similar impacts at the population, community, and ecosystem level, which is of concern considering current declines in pollinator populations (Spears et al. 2021); however, this relationship has not yet been studied.

Analyzing insect bycatch could also provide insight into biological and ecological patterns and processes to advance knowledge of biodiversity, population fluctuations, and range shifts (Haack et al. 2009; Buchholz et al. 2011; Skvarla and Holland 2011; Taylor and Catling 2011; Looney et al. 2012; Barringer 2015; Hung et al. 2015; Spears and Ramirez 2015; Delphia 2020; Hribar 2020; Grocock and Evenden 2020; Parys et al. 2021; Spears et al. 2021). For example, bycatch from lepidopteran traps were used to determine the effect of landscape composition on bee abundance and richness, which identified that the major land use type that positively related to bee abundance and diversity changed with spatial scales (Parys et al. 2021). Additionally, bycatch examined from funnel traps and purple prism traps used to monitor the spread of emerald ash borer identified four new undescribed species records of native treehoppers in Pennsylvania

(Barringer 2015). Analyzing bycatch from Japanese beetle, *Popillia japonica*, traps identified that the distribution of the non-native wool carder bee, *Anthidium manicatum*, has expanded further than what was originally anticipated, which gives new insights on the species' range and preferred bioclimatic niche space (Strange et al. 2011; Gonzalez and Griswold 2013; Graham and MacLean 2018).

Increasing the amount of insect bycatch analyzed throughout the U.S. could help support national bee monitoring efforts because high numbers of bees are passively collected within standardized traps over broad spatial and temporal scales (Hung et al. 2015; Spears and Ramirez 2015; Grocock and Evenden 2020; Parys et al. 2021; Spears et al. 2021). While further research is needed to evaluate if captures provide a representative sample of the bee community, analyzing bycatch could reduce the time and costs associated with other sampling methods, increase the amount of data obtained from the traps (reduce wasted data), and address concerns associated with over-collecting bees (Barringer 2015; Spears and Ramirez 2015; Looney et al. 2016; Hribar 2020; Spears et al. 2021). Overall, given the composition of species captured while trapping, analyzing bycatch provides a unique opportunity to study *Bombus* assemblages throughout the U.S.

Research Objectives

In order to produce cooperator driven, reproducible ecological research that both informs and enhances positive conservation and management practices of bumble bee populations in agroecosystems we: 1) linked differences in *Bombus* assemblages to shifts in landscape composition and climate in Utah agroecosystems; 2) examined the cumulative effects of climate and landscape structure on *Bombus* assemblages throughout U.S. agroecosystems; 3) quantified the impact of pest monitoring trap captures on *Bombus griseocollis* colony growth and development, and 4) evaluated the commercialization potential of *B. griseocollis* by assessing nest initiation and establishment rates, creating a timeline of colony development, and identifying lab-reared worker's critical thermal maxima (CT_{Max}).

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Tables

Table 1–1. Forty-seven *Bombus* species are found within North America, with considerable variability in species vulnerability. Vulnerability was classified using IUCN status. *IUCN consider *B. californicus* and *B. fervidus* as conspecifics, but are treated as separate species in this work following Koch et al. (2012).

Species	IUCN Status
Bombus affinis	Critically Endangered
B. appositus	Least Concern
B. auricomus	Least Concern
B. bimaculatus	Least Concern
B. bohemicus	Data Deficient
B. borealis	Least Concern
B. californicus	Vulnerable*
B. caliginosus	Vulnerable
B. centralis	Least Concern
B. citrinus	Least Concern
B. crotchii	Endangered
B. cryptarum	Data Deficient
B. distinguendus	Data Deficient
B. fervidus	Vulnerable*
B. flavidus	Data Deficient
B. flavifrons	Least Concern
B. franklini	Critically Endangered
B. fraternus	Endangered
B. frigidus	Least Concern
B. griseocollis	Least Concern
B. huntii	Least Concern
B. impatiens	Least Concern
B. insularis	Least Concern
B. jonellus	Data Deficient
B. kirbiellus	Data Deficient
B. melanopygus	Least Concern
B. mixtus	Least Concern
B. morrisoni	Vulnerable
B. natvigi	Data Deficient
B. neoboreus	Data Deficient
B. nevadensis	Least Concern
B. occidentalis	Vulnerable
B. pensylvanicus	Vulnerable

B. perplexus	Least Concern
B. polaris	Data Deficient
B. rufocinctus	Least Concern
B. sandersoni	Least Concern
B. sitkensis	Least Concern
B. sylvicola	Least Concern
B. ternarius	Least Concern
B. terricola	Vulnerable
B. vagans	Least Concern
B. vancouverensis	Least Concern
B. vandykei	Least Concern
B. variabilis	Critically Endangered
B. vosnesenskii	Least Concern
B. suckleyi	Critically Endangered

CHAPTER II

LAND COVER AND CLIMATE DRIVE SHIFTS IN *BOMBUS* ASSEMBLAGE COMPOSITION

Highlights

- The combined effects of land cover and climate impact *Bombus* in agroecosystems.
- *Bombus* composition was highest with crop land, low temperatures, and high humidity.
- *Bombus* composition was lowest with urban land, high temperatures, and low humidity.
- Phenological overlap among species provides functional redundancy.
- High *Bombus* turnover suggests all surveyed sites have conservation value.

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 and functional diversity 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 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. Unique assemblages comprised of species with a range of tongue lengths, body sizes, and hair types suggests high beta-diversity and functional diversity were present among sites. Further, differences in species among sites suggest that all agricultural sites in this study have potential conservation value for maintaining *Bombus* communities, highlighting the importance of maintaining diverse habitats for pollinators 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 overall 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.

Keywords

Bumble bee; landscape ecology; landscape composition; climate change; agroecosystem

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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). However, *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., 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 (Rundlof 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 Goulden, 2008; Gryntes 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-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 *Bombus* are affected by anthropogenic environmental change in order to inform conservation efforts. In this study, we linked differences in *Bombus* assemblages and functional diversity 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. 2–1) 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 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 -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 *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.

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 A–1). 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 2–1). These land cover types all sum to one, meaning the inclusion of all of them would make the model singular (agricultural + 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 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. A–1). 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 – 23.85°C, mean accumulated precipitation ranging from 0.02 – 106.89 mm, and mean relative humidity ranging from 32.26 – 49.62% (Table 2–1).

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 (βsor) measured total dissimilarity accounting for turnover (species replacements among sites; βsim) and nestedness (species loss/gain among sites; βsne) (Baselga and Orme, 2012). Additionally, information on functional traits: geographic range, tongue length, body size, and hair type (length and evenness) were gathered for each sampled species to determine functional diversity throughout the agricultural sites (Table 2–2; Koch et al., 2012; Williams et al., 2014; IUCN, 2022). Geographic range was indicative of each species known distribution. 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-Uribe et al., 2019). Hair type was 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).

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 2–3), 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. A–2; 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 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).

3. Results

3.1. Collection of *Bombus*

From 2014 to 2018, 3,522 *Bombus* from 15 species were collected in multi-colored bucket traps (Table 2–4), 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 2–2). *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 2–4). 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. 2–2 and Fig. A–3).

Yearly changes in the appearances and disappearances of other species identified that turnover occurred with an average rate of 26.2% per year (Fig. 2–3). 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 2–5). 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. 2–4). When evaluating the geographic range, tongue length, body size, and hair type (length and evenness) of each sampled species within each of these groupings, no clear trends were present (Table 2–2). Moreover, species with a range of tongue lengths, body sizes, 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. 2–5, leaf D-E), and lowest in sites characterized by increased urban land cover and high temperatures (Fig. 2–5, 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. A–4). 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.

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 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 m^2) and in close proximity to other monocultures are more expansive (Plourde et al., 2013). 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 Gouslon 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 2–2; 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 functional redundancy 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 functional redundancy 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 comprised of species with a range of tongue lengths, body sizes, and hair types suggests high beta-diversity and functional diversity were 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.

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Data Availability Statement

Data and code supporting the findings of this study are available on Zenodo at http://doi.org/10.5281/zenodo.6363828.

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Table and Figures

Table 2–1. 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**
Landscape Composition						
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
Climate						
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
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

Table 2–2. *Bombus* collected in pest monitoring traps in Utah from 2014-2019. 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	Body Size
Bombus appositus	Least concern[1]	Cascades, Sierra Nevada, Intermountain West, and Rocky mountains[2,3]	Open meadows, granitic soil slopes, high elevations[2,3]	*Agastache, Cirsium, Delphinium, Gentiana, Geranium, Linaria, Orthocarpus, Oxytropis, Penstemon, Trifolium*[2,3]	Long[3]	Medium and even[3]	Large[3]
B. californicus	Vulnerable[1]	Pacific coast; Intermountain West and Rocky Mountains[2]	Co-occurs with *B. fervidus*[2]	*Abronia, Astragalus, Cirsium, Monardella, Penstemon, Trifolium*[1]	Long[3]	Medium and even[3]	Medium[3]
B. centralis	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]	*Allium, Chrysothamnus, Cirsium, Ericameria, Monarda, Monardella, Penstemon, Phacelia, Symphoricarpos*[2,3]	Long[3]	Short and even[3]	Small[3]
B. fervidus	Vulnerable[1]	Continental U.S.[2]	Open grasslands, farmland, urban parks and gardens, midlatitudes[3]	*Astragulus, Cirsium, Dipsacus, Helianthus, Lonicera, Lythrum, Monarda, Pedicularis, Penstemon, Phacelia, Trifolium, Vicia*[2,3]	Long[3]	Medium and even[3]	Medium[3]
B. flavifrons	Least concern[1]	Pacific coast to Colorado Rocky Mountains[2]	Open grassy prairies, mountain meadows, northern forest areas, high elevations[2,3]	*Cirsium, Epilobium, Geranium, Heliomeris, Lathyrus, Mentha, Penstemon, Trifolium, Vaccinium, Vicia*[2,3]	Long[3]	Medium and uneven[3]	Small[3]
B. griseocollis	Least concern[1]	Across the eastern U.S.; lower elevations in	Open farmland and fields, urban parks and	*Asclepias, Coronilla, Cirsium, Dalea, Dipsacus, Echinacea,*	Short[3]	Short and even[3]	Medium[3]

		Intermountain West and Rocky Mountains to northern California[2,3]	gardens, wetlands[3]	*Helianthus, Lythrum, Medicago, Melilotus, Monarda, Phacelia, Pontederia, Rudbeckia, Solidago, Trifolium, Verbena, Vicia*[2,3]			
B. huntii	Least concern[1]	Sierra-Cascade Crest to Rocky Mountains, northern Great Plains[2,3]	High desert scrub[3]	*Chrysothamnus, Cirsium, Ericameria, Helianthus, Lupinus, Medicago, Melilotus, Penstemon, Phacelia, Ribes, Rudbeckia, Trifolium*[2,3]	Medium[3]	Short and even[3]	Medium[3]
B. insularis	Least concern[1]	Pacific coast to New England in northern states; Intermountain West[2,3]	Overlaps with its host species: *B. appositus, B. fervidus, B. flavifrons, B. rufocinctus, B. nevadensis, B. occidentalis, B. ternarius, B. terricola*[2,3]	*Aster, Erigeron, Eupatorium, Heliomeris, Melilotus, Rubus, Senecio, Solidago, Trifolium, Viccinium, Wyethia*[2,3]	Small[3]	Medium[3]	Medium[3]
B. morrisoni	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]	*Asclepias, Astragalus, Chrysothamnus, Cirsium, Cleome, Ericameria, Helianthus, Lupinus, Melilotus, Senecio*[2,3]	Short[3]	Short and even[3]	Large[3]
B. nevadensis	Least concern[1]	Pacific coast to Great Plains[2]	Occurs across of environmental gradients, open grassy prairies and meadows[2,3]	*Astragalus, Balsamorhiza, Ceanothus, Cirsium, Helianthus, Melilotus, Monarda, Penstemon, Phacelia, Salvia, Stachys, Trifolium, Ribes, Viccinium, Vicia*[2,3]	Long[3]	Very short and even[3]	Large[3]
B. occidentalis	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]	*Ceanothus, Centaurea, Chrysothamnus, Cirsium, Eriogonum, Geranium, Grindellia, Lupinus, Melilotus, Monardella, Rubus, Solidago, Trifolium*[2,3]	Short[3]	Short and even[3]	Medium[3]

B. pensylvanicus sonorus	Vulnerable[1]	Central California to Baja California to west Texas[2]	Open farmland and fields[3]	*Astragulus, Chrysothamnus, Cirsium, Cornus, Dalea, Echinacea, Gossypium, Helianthus, Kallstroemia, Liatris, Linaria, Mentzelia, Silphium, Solanum, Trifolium, Vicia, Viguiera*[2,3]	Long[3]	Short and even[3]	Large[3]
B. rufocinctus	Least concern[1]	Northern half of the U.S., southern Rocky Mountains, Sierra Nevada[2]	Wooded areas, urban parks and gardens[3]	*Arctium, Aster, Chicorium, Cirsium, Eupatorium, Fragaria, Grindelia, Helianthus, Melilotus, Solidago, Tanacetum, Trifolium, Vicia, Viguiera*[2,3]	Short[3]	Short and even[3]	Small[3]
B. sylvicola	Least concern[1]	High mountains in Sierra Nevada, Great Basin, and Rocky Mountains[2]	Open grassy areas and mountain meadows[3]	*Arenaria, Chamerion, Chrysothamnus, Epilobium, Haplopappus, Senecio, Lupinus, Melilotus, Monardella, Petasites, Phyllodoce, Raillardella, Senecio*[2,3]	Medium[3]	Long and uneven[3]	Small[3]
B. vancouverensis	Least concern[1]	Pacific coast to Rocky Mountains[2]	Open grassy prairies, chaparral and shrub areas, mountain meadows, urban parks and gardens[2,3]	*Aster, Centaurea, Chrysothamnus, Cirsium, Epilobium, Ericameria, Haplopappus, Helenium, Lupinus, Melilotus, Monardella, Penstemon, Ribes, Senecio, Solidago, Symphoricarpos*[2,3]	Medium[3]	Short and even[3]	Small[3]

1. IUCN, 2022. The IUCN red list of threatened species. Version 2021-3. http://www.iucnredlist.org
2. Koch, J. B., Strange, J. P., Williams, P., 2012. Bumble bees of the Western United States. Pollinator Partnership.
3. Williams, P., Thorp, R., Richardson, L., Colla, S., 2014. Bumble bees of North America: an identification guide. Princeton University Press, New Jersey.

Table 2–3. 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

Table 2–4. *Bombus* species richness and abundance from 2014 to 2019.

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

Table 2–5. 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

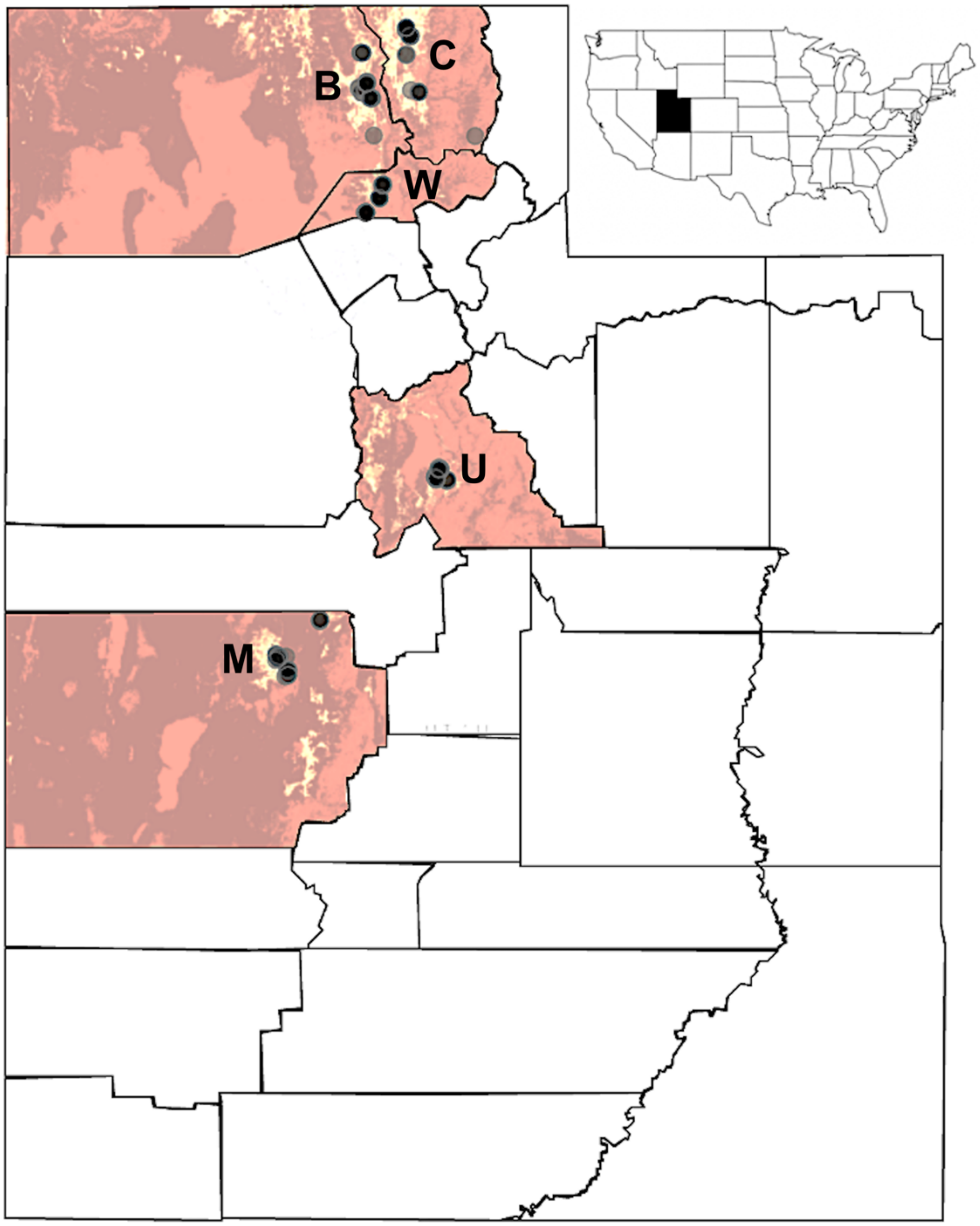

Figure 2–1. Thirty agricultural sites (black points) in Utah were sampled for *Bombus* each year from 2014 to 2019. Six sites were distributed throughout each of the five counties: (C) Cache, (W) Weber, (B) Box Elder, (U) Utah, and (M) Millard.

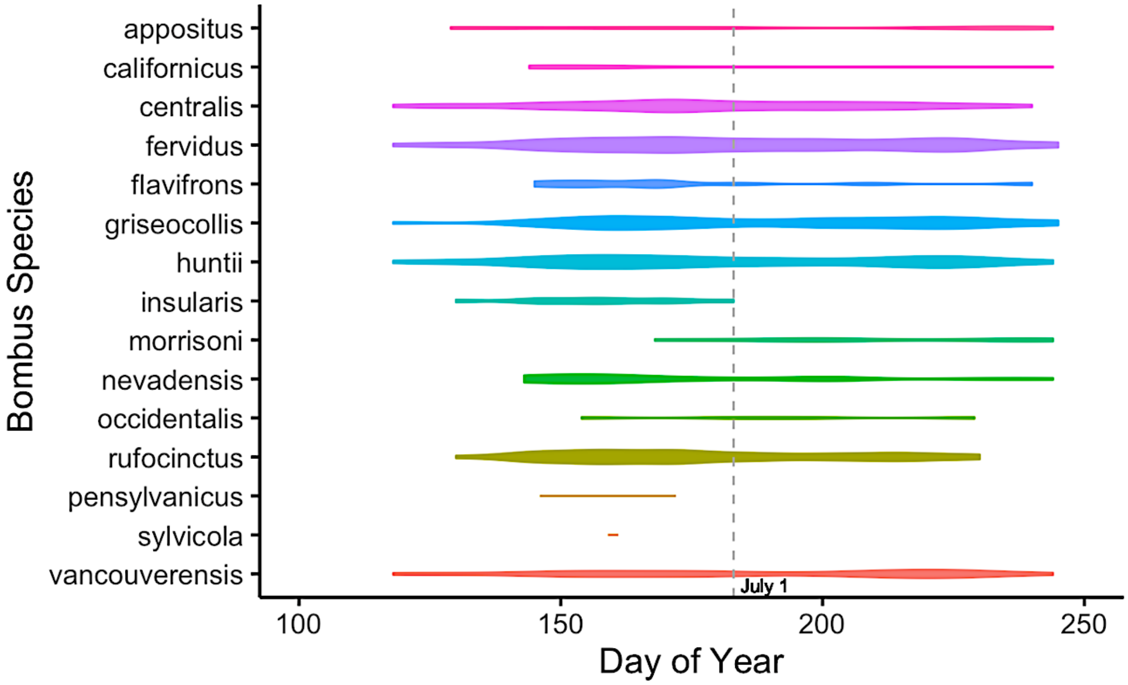

Figure 2–2. Violin plot of *Bombus* species collected from late April to mid-September from 2014 to 2018. Line width indicates the relative number of specimens collected.

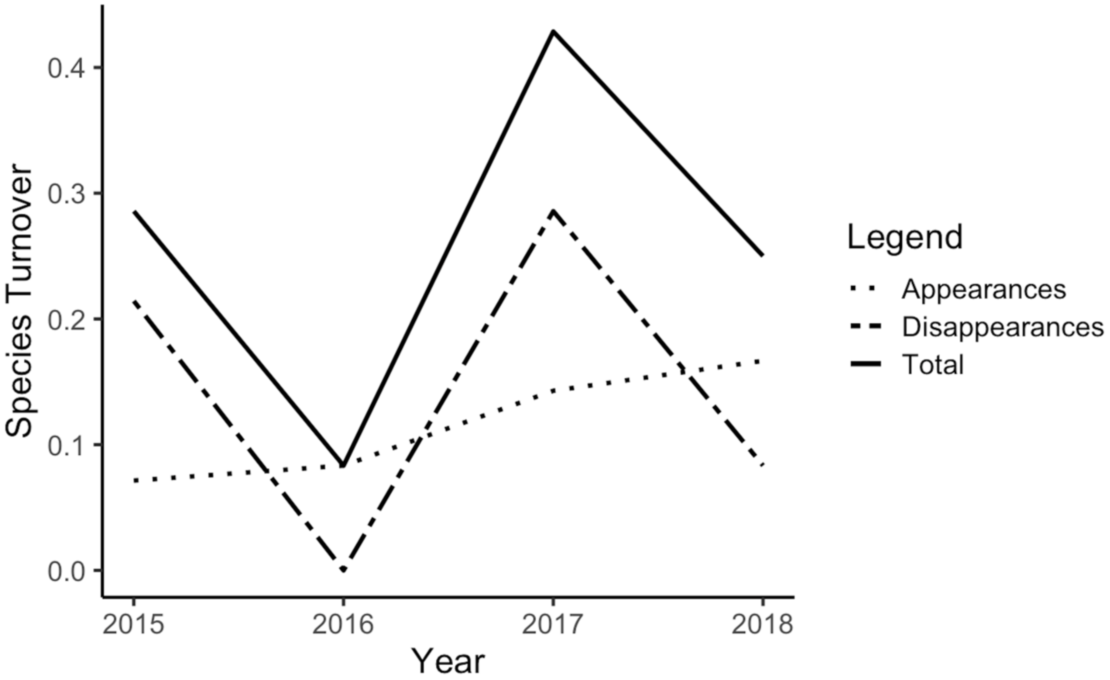

Figure 2–3. Total species turnover with the proportion of species appearances and disappearances from 2014 to 2018. 2014 is not shown since species richness from 2014 was used to calculate species turnover for 2015. Different line styles represent the three species turnover metrics.

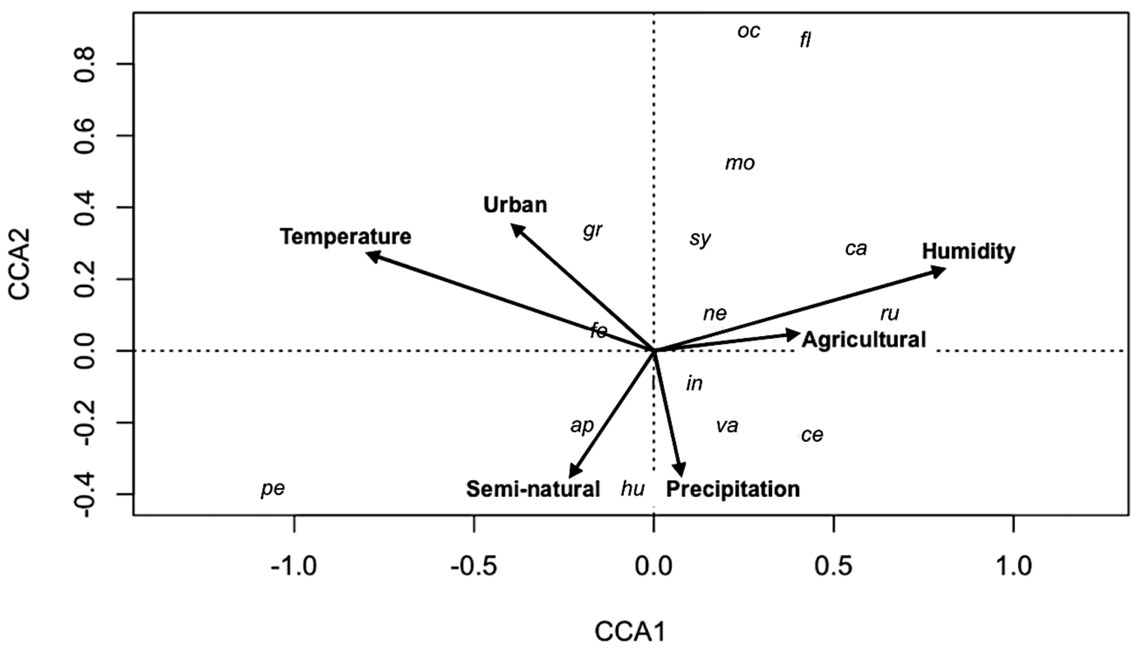

Figure 2–4. Canonical correspondence analyses of the *Bombus* assemblage data in relation to environmental variables (indicated by arrows) from 2014 to 2018. *Bombus* species names are abbreviated as *ap = B. appositus, ca = B. californicus*, *ce = B. centralis, fe = B. fervidus, fl = B. flavifrons, gr = B. griseocollis, hu = B. huntii, in = B. insularis, mo = B. morrisoni, 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).

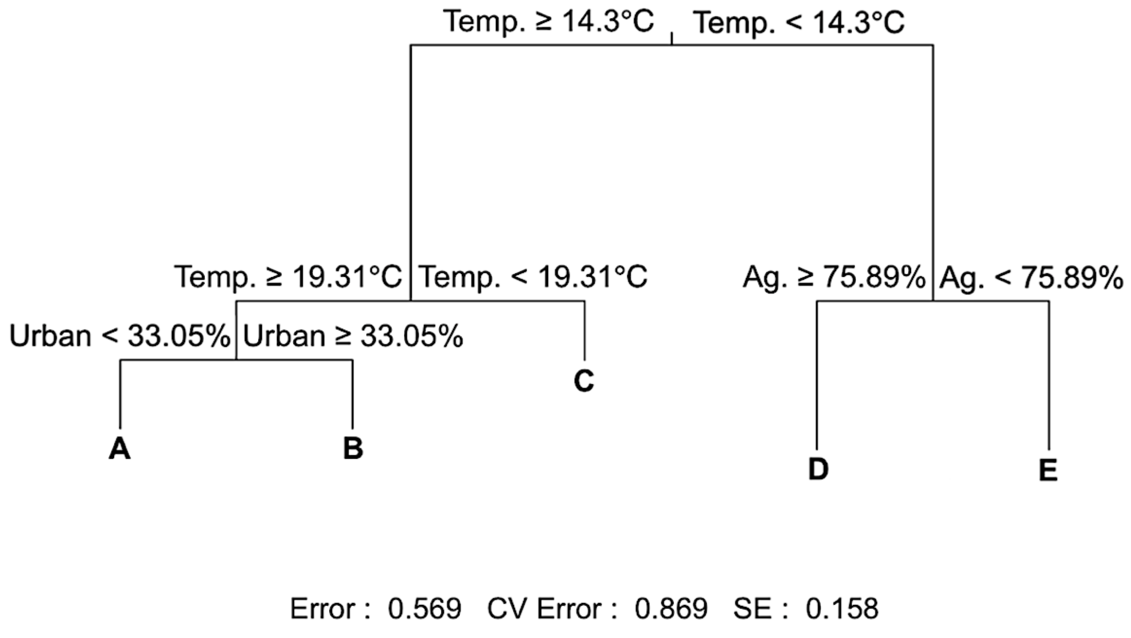

Figure 2–5. Multivariate regression tree (MRT) for the *Bombus* species data in relation to the proportion of urban and agricultural (Ag.) land cover (%) as well as temperature (˚C, Temp). Non-significant variables (semi-natural land cover, precipitation, and relative humidity) were not included in this 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.

CHAPTER III

CUMULATIVE EFFECTS OF CLIMATE AND LANDSCAPE STRUCTURE ON *BOMBUS* ASSEMBLAGES WITHIN AGRICULTURAL FIELDS THROUGHOUT THE U.S.

Abstract

Bumble bees (*Bombus*) are integral pollinators of native and cultivated plant communities, but are undergoing drastic population changes worldwide. Climate change and the alteration of landscape structure are key drivers in pollinator declines; however, little research has evaluated their cumulative effects on *Bombus* assemblages. In this study, we evaluated the cumulative effects of various bioclimatic variables associated with temperature and precipitation, and landscape metrics (Shannon diversity, patch richness density, contiguity, and interspersion and juxtaposition) on *Bombus* assemblages within agricultural fields throughout Florida, Indiana, Kansas, Kentucky, Maryland, South Carolina, Utah, Virginia, and West Virginia from 2018 to 2020. Beta-diversity was dominated by species turnover, indicating unique *Bombus* assemblages are present at each agricultural site. Species abundances were highest at sites with reduced precipitation seasonality and lower temperatures. Therefore, as climate change alters precipitation seasonality and increases mean temperatures, *Bombus* abundances will likely decline due to increased susceptibility to the changing environment. *Bombus* assemblage composition varied based on landscape structure and climate throughout the U.S. Interestingly, Utah *Bombus* assemblages were associated with agricultural landscapes with greater compositional and configurational complexity, increased climate seasonality, and lower annual mean temperatures. Meanwhile, eastern *Bombus* assemblages were associated with agricultural landscapes with less compositional and configurational complexity, decreased climate seasonality, and higher annual mean temperatures. Implementing land management practices based on the continuum of local climatic and landscape conditions throughout the U.S. will help conserve *Bombus* assemblages, while supporting the pollination of crops and wild plants. In simplified agricultural landscapes, we recommend increasing the number and quantity of land cover categories with diverse plant assemblages and diversifying the way in which they are arranged. In complex agricultural habitats, we recommend increasing connectivity between high-quality patches of land. Overall, evaluating climate, landscape composition, and landscape configuration indices together provides more in-depth information on the expected changes to *Bombus* assemblages, leading to more robust interpretations of trends and management practices.

Keywords

Bumble bee, bioclimatic variables, landscape composition, landscape configuration, agroecosystems

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1 INTRODUCTION

Bumble bees (Hymenoptera: Apidae: *Bombus* Latreille) are integral pollinators of native and cultivated plant communities throughout temperate, alpine, and arctic ecosystems (Kremen et al., 2002; Klein et al., 2007; Berenbaum et al., 2007; Goulson, 2010). There are more than 265 *Bombus* species worldwide, 47 of which occur in the U.S. (Colla et al., 2011; Koch et al., 2012; Williams et al., 2014; Williams & Jepsen, 2020; Maebe et al., 2021; IUCN, 2022). Despite their importance to agricultural and natural systems, *Bombus* communities are undergoing drastic changes due to effects such as climate change, agricultural intensification, and urbanization (Kerr et al., 2015; Goulson et al., 2015; Fourcade et al., 2019; Kohler et al., 2020).

Global climate change has led to a rise in average temperatures, changes in precipitation patterns, and an increase in the frequency and intensity of extreme and localized weather events (Easterling et al., 2000; Meehl & Tebaldi, 2004). Changes in climate can have profound impacts on species' abundances, distributions, and dynamics, as well as overall community structure (Easterling et al., 2000; Parmesan & Yohe, 2003; Parmesan, 2006; Kerr et al., 2015; Fourcade et al., 2019). As endoheterothermic bees, *Bombus* display several adaptations to regulating their body temperature in cold climates, but few to high temperatures (Kerr et al., 2015; Pimsler et al., 2020). As a result, frequent and intense heat waves can lead to increased mortality of *Bombus* by inducing hyperthermic stress when foraging (for workers) or during nuptial behavior (for males) (Martinet et al., 2015; Oyen et al., 2016; Fourcade et al., 2019; Martinet et al., 2020). In response to warming climates, some species have shifted their distributions to cooler areas, such as higher altitudes or more northern latitudes (Kelly & Goulden, 2008; Grytnes et al., 2014). This shift can have direct and indirect consequences on species and communities, such as disrupting plant-pollinator synchrony and contributing to changes in vegetation composition, respectively (Gottfried et al., 2012; Pyke et al., 2016; Fourcade et al., 2019). Spatially restricted or climate sensitive species that may not be capable of shifting their distributional range are more likely to experience population declines when exposed to extreme weather events such as heat waves (Pyke et al., 2016; Martinet et al., 2020); whereas widely distributed species that are exposed to more variable climates may be less sensitive to climatic disturbances (Kingsolver et al., 2013). Climate change also interacts with anthropogenic disturbances, such as land cover conversion and intensification, further altering species' responses to these emerging conditions (Easterling et al., 2000; Kerr et al., 2015; Marshall et al., 2018; Fourcade et al., 2019).

Landscape structure impacts *Bombus* assemblages via the availability and distribution of floral and nesting resources (Parys et al., 2021). Within agricultural systems, intensification and expansion have led to extensive reductions in landscape compositional (i.e., the number of distinct land cover categories) and configurational (i.e., the spatial arrangement of these land cover categories) complexity, resulting in landscape simplification, which leads to declines in biodiversity worldwide (Meehan et al., 2011; Pfeiffer et al., 2019; Nelson & Burchfield, 2021). As vagile foragers, *Bombus* are known to be relatively resilient to changes in landscape structure; however, they can be inadvertently extirpated in simplified landscapes that lack important and diverse resources (Westphal et al., 2003; Winfree et al., 2007; Hall et al., 2017; Rao & Strange, 2012; Williams et al., 2012). Therefore, increased landscape composition and configuration can positively impact *Bombus* diversity by providing increased availability of feeding, nesting, and breeding resources and greater network connectedness, respectively (Dunning et al., 1992; Benton et al., 2003; Flick et al., 2012; Kaiser-Bunbury et al., 2017; Miljanic et al., 2019).

While the individual effects of climate and landscape structure have been studied, little research has evaluated their cumulative effects, underscoring the need to understand how *Bombus* are affected by a range of environmental changes (Easterling et al., 2000; Kerr et al., 2015; Marshall et al., 2018; Betts et al., 2019; Fourcade et al., 2019; Jamieson et al., 2019; Miljanic et al., 2019; Kohler et al., 2020; Maebe et al., 2021). To begin addressing these effects, Christman et al., (2022) linked differences in *Bombus* assemblages to landscape composition and climate in Utah agroecosystems. *Bombus* assemblage composition was highest in sites with more agricultural land cover in the surrounding area, low temperatures, and high relative humidity; and lowest in sites with more urban land cover, high temperatures, and low relative humidity. However, differences in species assemblages among sites highlighted the importance of maintaining diverse habitats in order to provide a range of resources and microclimates to foster resiliency and conservation of *Bombus* assemblages in the face of anthropogenic disturbances (Christman et al., 2022).

In this study, we further examined these cumulative effects by evaluating various bioclimatic variables associated with precipitation and temperature, and landscape metrics (Shannon diversity, patch richness density, contiguity, and interspersion and juxtaposition) on *Bombus* assemblages within agricultural fields throughout the U.S.

Results from this study contribute to a better understanding of the climate and landscape factors driving *Bombus* biodiversity throughout the U.S., which could lead to improved conservation and management strategies to mitigate the effects of future environmental changes.

2 METHODS

2.1 Collection of *Bombus*

Pest monitoring traps are known to attract and capture a large number and wide range of non-target 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). These captures sometimes exceed those from more common sampling methods, such as pan trapping or net collecting, despite less sampling efforts (Glaum et al., 2017; Grocock and Evenden, 2020; Spears et al., 2016, 2021). Further, many researchers have emphasized the importance of processing and analyzing bee bycatch to advance knowledge of biodiversity, population fluctuations, range shifts, and other ecological objectives instead of discarding these insects (Buchholz et al., 2011; Spears & Ramirez, 2015; Spears et al., 2016; Grocock & Evenden, 2020; Parys et al., 2021; Spears et al., 2021). Therefore, we used *Bombus* bycatch from pest monitoring traps to study their assemblages.

Pest monitoring traps were placed by state cooperators (see Acknowledgements) within agricultural fields across diverse regions in the U.S. 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 for pest surveillance (CAPS, 2022). This study included a total of 434 fields throughout Florida, Indiana, Kansas, Kentucky, Maryland, South Carolina, Utah, Virginia, and West Virginia from 2018 to 2020, where the number of sites varied by state, year, and target pest (Table 3–1). Target pests included Christmas berry webworm (CBW, *Cryptoblabes gnidiella* Milliere, 1867), cotton cutworm (CC, *Spodoptera litura* Fabricius, 1775), Egyptian cottonworm (EC, *Spodoptera littoralis* Boisduval, 1833), golden twin spot moth (GTS, *Chrysodeixis chalcites* Esper, 1789), Old World bollworm (OWB, *Helicoverpa armigera* Hübner, 1808), and silver Y moth (SYM, *Autographa gamma* Linnaeus, 1758). Multi-colored (green canopy, yellow funnel, and white bucket) bucket traps (International Pheromone Systems, Cheshire, UK) were placed 20 m apart and hung 1.5 m above the ground along the edge of vegetable or other commodity crop fields (e.g., alfalfa, corn, small grain). Each trap contained a pheromone lure for a single target pest 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 CBW, GTS, OWB, and SYM were replaced every 28 days, whereas pheromone lures for CC and EC were changed every 84 days. Although the collection period for traps varied by state, most traps were serviced biweekly (monthly in Kentucky) from May to August, but some states extended the trapping season based on the period of expected pest activity (Table 3–1). 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.

Trap contents were screened for target pests by state cooperators, and then all non-target captures (bycatch) were sent to the Utah State University Biology Department. *Bombus* were separated from all other non-target specimens and then stored in a freezer at -18˚C until they could be pin-mounted, labeled, and identified to species using taxonomic keys (Colla et al., 2011; Koch et al., 2012; Williams et al., 2014). All specimens were deposited at the USDA, Agricultural Research Service, Pollinating Insect – Biology, Management, and Systematics Research Unit Museum in Logan, Utah.

2.2 Bioclimatic Variables

Historical weather data over the past 20 years (2000–2020) were extracted from each site at a 1 × 1 km spatial resolution for monthly precipitation, and minimum and maximum temperature from the Daymet Team (Thornton et al., 2020). Bioclimatic variables (BIO) were then derived from the monthly precipitation and temperature values with the *dismo* library in R version 4.0.3 to generate more biologically meaningful variables (Fick & Hijmans, 2017; Hijmans et al., 2020; R Core Team, 2020). These variables represent annual trends, seasonality, and extreme environmental variables, which provide a general sense of the climate within each region over the last two decades (Table 3–2).

2.3 Landscape Structure

The elevation of each site was extracted from the North American elevation 1 km resolution GRID and slope was calculated in ArcGIS Pro 2.8 using the Spatial Analyst slope tool (U.S. Department of the Interior, 2021). Land cover values from 2018 to 2020 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 following landscape composition and configuration indices were then calculated at a 1 km buffer surrounding each site with the *landscapemetric* library: Shannon diversity, Shannon evenness, patch richness, patch richness density, contiguity index, and interspersion and juxtaposition (Hesselbarth et al., 2019; R Core Team, 2020). Shannon diversity takes into account the number of patch types within a landscape and their relative abundance (both evenness and richness). Shannon evenness refers to the relative abundance of each patch type within a landscape. Patch richness represents the number of patch types present within a landscape. Patch richness density is the number of patch types present per hectare, which standardizes richness indices to allow for comparisons among landscapes. Contiguity index refers to the connectedness of cells within a patch. Interspersion and juxtaposition index refers to the arrangement, relationship, and proximity of different patch types (Hesselbarth et al., 2019).

2.4 Data Analysis

Data were analyzed using R version 4.0.3 (R Core 2020). Five aspects of *Bombus* species composition were measured for each state: total count, richness (number of species), Pielou's evenness (abundance per species), Shannon diversity (which accounts for evenness and richness), and beta-diversity with the *vegan, codyn,* and *betapart* libraries. Beta-diversity was calculated to determine the extent to which species assemblages present at each site differed based on turnover or nestedness, using beta diversity partitioning (Dorchin et al., 2018). 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 & Orme, 2012). Additionally, observed species richness was compared to the expected species richness within each state, which was based on published literature (Colla et al., 2011; Koch et al., 2012). The weekly *Bombus* collection rate for each state was also quantified each year to standardize differences between state collection periods. Bubble maps were used to visualize *Bombus* distribution and abundance throughout the surveyed states.

A correlation matrix was generated to examine correlations across all combinations of explanatory variables with the *corrplot* library. One variable was removed from each variable pair with a correlation above ±0.7 to reduce redundancy while still maintaining biological relevance. Variance inflation factor (VIF) was used to test for multicollinearity between the remaining explanatory variables. Variables with a VIF greater than 10 were removed in descending order until all VIFs were lower than 10 to further reduce collinearity between the explanatory variables. Mean annual temperature (BIO1), isothermality (BIO3) (i.e., the ratio of mean diurnal range to annual temperature range), temperature seasonality (standard deviation × 100) (BIO4) (i.e., temperature variation over a year based on the standard deviation of monthly temperature averages), mean temperature of driest quarter (BIO9), precipitation seasonality (coefficient of variation) (BIO15), landscape Shannon diversity (SHDI), interspersion and juxtaposition (IJI), patch richness density (PRD), contiguity index (CI), and slope were included as the bioclimatic variables and landscape indices within the following models.

Spatial autocorrelation was analyzed each year from 2018 to 2020 using a Moran's I statistic to assess the presence of a spatial pattern in model residuals with the *spdep* library. The results suggested the residuals were not spatially autocorrelated (Table 3–3), indicating that unexplained autocorrelation among neighboring samples was not driving the described patterns. Additionally, a generalized additive model (GAM) was used to describe the non-linear pattern of *Bombus* Shannon diversity in relation to the bioclimatic and landscape variables while accounting for spatial covariance among the observed points with the *mcgv* library (Burchfield et al. 2019). Unlike standard multiple regression, GAMs can flexibly estimate non-linear interactions between *Bombus* diversity and the predictor variables (bioclimatic variables and landscape indices) (James et al., 2013). All predictor variables were initially smoothed in the GAM to account for non-linearities. Each individual landscape index and precipitation seasonality (BIO15) had an effective degree of freedom of 1, suggesting that the terms were reduced to a simple linear effect. Therefore, the updated models were specified as:

$$Bombus\ Shannon\ Diversity = s(BIO3) + s(BIO4) + s(BIO9) + BIO1 + BIO5 + SHDI + PRD + IJI + CI + Slope + s(Longitude, Latitude, bs = \text{“re”})$$

where *s*() indicates the function estimated using p-splines (Eilers & Marx, 1996). Space was used as a random effect (*bs = “re”*) in each model. The use of spatial coordinates as a two-dimensional smoothing term reduced model misspecifications by capturing the effects of predictors not included in the model (Legendre & Legendre, 2003; Lautenbach et al., 2012).

A multivariate regression tree (MRT) was used to describe the interactions between *Bombus* species abundance and the environmental variables from 2018 to 2020 with the *mvpart* library. The MRT groups sites based on repeated splits in environmental variable values, minimizing dissimilarity within site groups. Each leaf represents species abundances and the environmental variable values associated with the sites, which are displayed in the form of a tree. A 4-fold cross validation with 100 iterations was generated to validate the model and to evaluate the predictive ability of the MRT.

A canonical correspondence analysis (CCA) was used to assess correlations among explanatory variables (bioclimatic variables and landscape indices) and response variables (*Bombus* species abundances) from 2018 to 2020 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, 2, and 3 were significant predictors of *Bombus* species-environment relationships (CCA1: $F_{1,291} = 95.89$, *p*-value = 0.001; CCA2: $F_{1,291} = 35.44$, *p*-value = 0.001; CCA3: $F_{1,291} = 17.71$, *p*-value = 0.002), and were used to evaluate the CCA.

3 RESULTS

3.1 Collection of *Bombus*

From 2018 to 2020, a total of 5,021 *Bombus* representing 18 species were collected across nine states (Table 3–4). However, collection rates varied by state and year. For example, Florida had extremely low collection rates of one *Bombus* per week in 2019, whereas over forty *Bombus* were collected per week in Utah (2018 and 2020) and West Virginia (2019) (Table 3–5). *Bombus fervidus* (Fabricus, 1798)*,* *B. bimaculatus* (Cresson, 1863), *B. impatiens* (Cresson, 1863), *B. pensylvanicus* (De Geer, 1773), and *B. huntii* (Greene, 1860) were the five most abundant species within traps, comprising 84% of total captures (Fig. 3–1). Additionally, a few of the species (*B. fervidus, B. fraternus,* and *B. pensylvanicus*) that were collected at high frequencies, are listed as vulnerable or endangered throughout their sampled ranges by the International Union for Conservation of Nature (IUCN, 2022). *Bombus* species diversity was consistently highest in Indiana, Kentucky, Utah, and West Virginia (Fig. 3–2, Table 3–5).

The Sørensen index of beta-diversity showed high values of total dissimilarity among sites (βsor = 0.991). Beta-diversity was dominated by species replacement (turnover). Species replacement accounted for a greater portion of total dissimilarity among communities (βsim = 0.981) than nestedness (βsne = 0.009). Species replacement is interpreted as a consequence of environmental sorting or spatial constraints (Baselga, 2010). Therefore, high turnover identified observed differences in *Bombus* species composition, indicating unique bee assemblages were present at each of the sites (Dorchin et al., 2018; Jones et al., 2019).

3.2 Response of *Bombus* to Bioclimatic Variables and Landscape Indices

The GAM described the non-linear and linear patterns of *Bombus* Shannon diversity in relation to each of the bioclimatic variables and landscape composition and configuration indices while accounting for spatial covariance among the observed points (Fig. 3–3, Table 3–6, and Table 3–7). The use of spatial coordinates as a two-dimensional smoothing term further identified that the residuals are independent and thus not spatially autocorrelated (p = 0.704). The GAM indicated that *Bombus* Shannon diversity gradually declined as the isothermal value (BIO3) increased, but insignificantly (Fig. 3–3). *Bombus* Shannon diversity declined as temperature seasonality (standard deviation × 100) increased from a standard deviation of 6ºC (×100) to 8.5ºC (×100), then increased slightly before stabilizing towards higher temperature seasonality values (Fig. 3–3). Shannon diversity was not influenced by mean temperature of driest quarter (BI09) (Fig. 3–3).

In order to describe the interactions between *Bombus* species abundance and the environmental variables, we used an MRT with a 4-fold cross validation with 100 iterations. This resulted in a four-leaf tree where branching was determined by high and low values of precipitation seasonality (BIO15), mean temperature of driest quarter (BIO9), and lower annual mean temperature (BIO1) (Error = 0.67, CV Error = 1.04, SE = 0.23). Species abundances differed across the four leaves. Average species abundance per site was highest in landscapes characterized by reduced precipitation seasonality

(BIO15), lower mean temperature of driest quarter (BIO9), and lower annual mean temperature (BIO1) (Fig. 3–4, Leaf C), while average species abundance per site was lowest in landscapes characterized by increased precipitation seasonality (BIO15) (Fig. 3–4, Leaf A).

The permutation test determined that the overall CCA model was statistically significant ($F_{10, 291} = 16.28$, *p*-value = 0.001). Additionally, the permutation test by term (i.e., explanatory variables) determined that *Bombus* assemblages varied by all environmental variables (Table 3–8). Over the three-year study period, these variables explained 35.9% of variation in *Bombus* assemblages. *Bombus appositus* (Cresson, 1878)*, B. californicus* (Smith, 1854)*, B. centralis* (Cresson, 1864)*, B. fervidus, B. huntii, B. insularis* (Smith, 1861)*, B. morrisoni* (Cresson, 1878)*, B. nevadensis* (Cresson, 1874)*, B. rufocinctus* (Cresson, 1863)*,* and *B. vancouverensis* (Cresson, 1878) were associated with high values of BIO4, BIO9, BIO15, SHDI, IJI, CI, and PRD, and low values of BIO1, BIO3, and slope. Meanwhile, *B. auricomus, B. bimaculatus, B. fraternus, B. impatiens, B. pensylvanicus, B. perplexus* (Cresson, 1863)*,* and *B. vagans* (Smith, 1854) were associated with high values of BIO1, BIO3, and slope, and low values of BIO4, BIO9, BIO15, SHDI, IJI, CI, and PRD (Fig. 3–5). *Bombus griseocollis* (De Geer, 1773) was not associated with either high or low values of BIO1, BIO3, BIO4, BIO9, BIO15, SHDI, IJI, CI, PRD, and slope, meaning they were found ubiquitously throughout the habitats regardless of the bioclimatic variable, landscape composition and configuration indice values.

4 DISCUSSION

Overall, we found differences in *Bombus* assemblages across our study sites in Florida, Indiana, Kansas, Kentucky, Maryland, South Carolina, Utah, Virginia, and West Virginia from 2018 to 2020. These patterns were driven by the cumulative effects of bioclimatic variables, and landscape composition and configuration; therefore, evaluating these factors simultaneously provides more in-depth information on the expected changes to *Bombus* assemblages in agroecosystems.

At the species level, we found that abundances were highest at sites with reduced precipitation seasonality and lower temperatures. As a predominantly temperate-adapted genus, *Bombus* are adept at surviving in cold environments; however, few *Bombus* species are adept at living in environments with long, hot, dry summers and short, moderate winters, which are expected as a result of climate change (Heinrich 1974, 1979; Ploquin et al., 2013; Dehon et al., 2019; Rasmont et al., 2008, 2015). As average annual temperatures increase and precipitation becomes more variable, *Bombus* populations will be negatively impacted. Foraging by *Bombus* workers will be reduced as risk of thermal stress increases, causing a negative impact on colony growth and development (Peat et al., 2005; Sanderson et al., 2015). While *Bombus* are able to regulate their internal temperatures via thermoregulation (Heinrich, 1975), this cannot protect *Bombus* from exposure to extreme high temperatures, which can lead to a loss of motor function, an inability to escape unfavorable conditions, and death (Heinrich, 1974, 1975, 1976; Oyen et al., 2016). Additionally, increases in ambient temperatures and changes in precipitation patterns indirectly impact *Bombus* species by altering plant-pollinator synchrony and changing vegetation composition, resulting in the loss of access to floral resources which are needed to support diverse bee communities and ecosystem function (Gottfried et al., 2012; Pyke et al., 2016; Fourcade et al., 2019). Therefore, as climate change progresses, altering precipitation seasonality and increasing mean temperatures, declines in *Bombus* abundances will likely occur as a response to the changing environment.

Bombus assemblage composition varied based on landscape structure and climate throughout the U.S. Interestingly, Utah *Bombus* assemblages were associated with agricultural landscapes with increased compositional and configurational complexity, increased climate seasonality, and lower annual mean temperatures. Meanwhile, eastern *Bombus* assemblages were associated with agricultural landscapes with less compositional and configurational complexity, decreased climate seasonality, and higher annual mean temperatures. While these contrasting associations may be attributed to each species' geographic range (Williams, 2005), more research is needed, especially in the western U.S., to support this conclusion. Regardless, landscape compositional and configurational complexity tends to be higher in the eastern U.S. than in the western U.S. (Nelson & Burchfield, 2021). Therefore, implementing land management practices based on the continuum of local climatic and landscape conditions throughout the U.S. can help conserve *Bombus* assemblages, while supporting the pollination of crops and wild plants. While differences in species associations to bioclimatic variables are likely a product of differences in elevation and annual temperatures trends among the eastern and western U.S., improving the quality of *Bombus* habitats by modifying land-use and management practices can compensate for the detrimental effect of climate change on *Bombus* assemblages (Wang and Dillon, 2014; Chan et al., 2016; Oyen et al., 2016; Fourcade et al., 2019). In the case of more simplified agricultural landscapes, our data suggests that increasing the number of land cover categories that provide diverse plant assemblages throughout the landscape will support more diverse *Bombus* assemblages by increasing the prevalence of floral and nesting resources (Dunning et al., 1992; Benton et al., 2003; Flick et al., 2012; Goulson et al., 2015; Koh et al., 2016; Kaiser-Bunbury et al., 2017; Miljanic et al., 2019; Christman et al., 2022). Meanwhile, in more complex agricultural habitats, we recommend increasing connectivity between high-quality patches of land to facilitate access to resources (i.e., nectar, pollen, nesting sites) (Miljanic et al., 2019).

Bombus griseocollis was ubiquitous throughout the study areas, which is consistent with its known distribution (Colla et al., 2011; Koch et al., 2012). This species may be more resilient to land cover and climate change as they are able to survive well throughout a range of habitat types (i.e., open farmland and fields, urban parks and gardens, and wetlands) and climates across the U.S. (Koch et al., 2012; Kingsolver et al., 2013; Williams et al., 2014). Continually monitoring *B. griseocollis* populations throughout a range of habitat types in the U.S. may provide more insight on how this species will respond to future environmental changes.

Low levels of nestedness suggest that there is relatively little selective filtering of *Bombus* species as sites become smaller or more isolated (Jones et al., 2019). Meanwhile, the dominance of the turnover component of beta-diversity indicates unique bee assemblages are present at each of the sites, instead of assemblages only representing a fraction of the regional pool of species (Dorchin et al., 2018). This highlights the importance of maintaining ecologically diverse habitat types to retain unique and diverse

Bombus assemblages and pollination services across the U.S. (Si et al., 2015; Dorchin et al., 2018; Christman et al., 2022).

Although this study has some limitation inherent to its design (i.e., state-level differences in sample size, collection dates and period, and target pests), analyzing bycatch reduces cost by allowing more efficient use of time and resources (Spears et al., 2021). Further, this study's substantial spatial coverage and high number of replicates within and across years resulted in a large data set that enriches our knowledge of *Bombus* assemblages across geographic space and time (Kohler et al., 2020). Additionally, the low proportion of singletons in this data set indicates a strong sampling regime (Williams et al., 2001; Kohler et al., 2020). Finally, the inclusion of climatic and landscape composition and configuration indices into one model introduces sources of uncertainty, but may yield more realistic results about their cumulative effects on *Bombus* species assemblages (Conlisk et al., 2013; Evans et al., 2014; Louca et al., 2015).

Overall, this study provides evidence that the cumulative effects of bioclimatic variables, and landscape composition and configuration influences *Bombus* species abundance and assemblage composition across agricultural fields throughout the U.S., which can lead to more robust interpretations of trends and management practices. Differences in landscape characteristics accounted for high levels of species replacement, influencing uniqueness of *Bombus* assemblages across our studied sites. Therefore, land management practices should be based on a continuum of landscape and climatic conditions throughout the U.S. to help increase *Bombus* assemblages, while supporting the pollination of crops and wild plants. If the same management practices are applied everywhere, regardless of environmental characteristics, ecological homogenization will likely occur (Christman et al., 2022), leading to changes in species composition and to the loss of locally/regionally unique species and habitat types (Hobbs et al., 2006). This highlights the importance of creating and restoring diverse pollinator habitats to promote diverse *Bombus* assemblages. Overall, these results contribute to a better understanding of processes driving *Bombus* biodiversity throughout the U.S. in a context of climate and landscape change, which could lead to improved conservation and management strategies to mitigate the effects of future environmental changes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

Conceptualization: MEC, EKB, LRS, WPD, & RAR. Data curation: MEC. Formal analysis: MEC, EKB, & WPD. Funding acquisition: LRS & RAR. Investigation: MEC. Methodology: MEC, EKB, LRS, WPD, & RAR. Project administration: LRS & RAR. Resources: LRS. Supervision: EKB, LRS, WPD, JPS, & RAR. Writing – original draft: MEC. Writing – review & editing: EKB, LRS, WPD, JPS, & RAR. All authors have read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data and code supporting the findings of this study are available on Zenodo at https://doi.org/10.5281/zenodo.6363812.

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TABLES AND FIGURES

Table 3–1. The number of sites, target pests, and collection period by state and year. Target pests included Christmas berry webworm (CBW), cotton cutworm (CC), Egyptian cottonworm (EC), golden twin spot moth (GTS), Old World bollworm (OWB), and silver Y moth (SYM).

State	**Number of Sites**	**Target Pest(s)**	**Collection Period**
2018			
Kansas	86	CC, EC	July-October
Utah	30	CC, EC, OWB	April-September
West Virginia	9	CC, EC, GTS, OWB, SYM	June-September
2019			
Florida	16	OWB	April-September
Indiana	6	CC, EC, GTS, OWB, SYM	May-August
Kentucky	41	CC, EC, GTS, OWB, SYM	May-October
Maryland	26	CC, OWB, SYM	June-July
South Carolina	16	CC, EC, OWB	June-October
Utah	30	CC, EC, OWB	June-August
Virginia	13	OWB	July-September
West Virginia	32	CBW, CC, EC, GTS, OWB, SYM	May-October
2020			
Indiana	6	CC, EC, GTS, OWB, SYM	April-August
Kentucky	63	CC, EC, GTS, OWB, SYM	May-September
Utah	30	CC, EC, OWB	May-August
Virginia	10	OWB	August-September
West Virginia	20	CBW, CC, EC, OWB, SYM	May-September

Table 3–2. Bioclimatic variables used to represent annual trends, seasonality, and extreme environmental factors throughout the sites over the past 20 years (2000–2020).

Variable Number	**Bioclimatic Variable**
BIO1	Mean annual temperature
BIO2	Mean diurnal range (mean monthly (max temperature – min temperature))
BIO3	Isothermality (BIO2/BIO7) × (100)
BIO4	Temperature seasonality (standard deviation × 100)
BIO5	Max temperature of warmest month
BIO6	Min Temperature of coldest month
BIO7	Annual temperature range (BIO5 – BIO6)
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

Table 3–3. Moran’s I statistic output each year from 2018 to 2020.

Year	Moran’s I Index	Expected Index	Variance	*p*-value
2018	-0.407	-0.022	0.137	0.851
2019	0.107	-0.009	0.088	0.346
2020	0.088	-0.020	0.047	0.309

Table 3–4. *Bombus* species richness and abundance in Florida, Indiana, Kansas, Kentucky, Maryland, South Carolina, Utah, Virginia, and West Virginia from 2018 to 2020.

Species	**Abundance by State**								
	FL	**IN**	**KS**	**KY**	**MD**	**SC**	**UT**	**VA**	**WV**
Bombus appositus	0	0	0	0	0	0	9	0	0
B. auricomus	0	16	2	88	0	8	0	2	70
B. bimaculatus	0	171	13	67	148	15	0	5	776
B. californicus	0	0	0	0	0	0	1	0	0
B. centralis	0	0	0	0	0	0	38	0	0
B. fervidus	0	121	0	6	31	0	964	3	99
B. fraternus	3	0	1	0	0	1	0	0	0
B. griseocollis	0	8	29	33	4	1	73	5	76
B. huntii	0	0	0	0	0	0	323	0	0
B. impatiens	5	243	7	235	12	114	0	41	345
B. insularis	0	0	0	0	0	0	36	0	0
B. morrisoni	0	0	0	0	0	0	7	0	0
B. nevadensis	0	0	0	0	0	0	17	0	0
B. pensylvanicus	9	104	155	272	8	52	1	40	11
B. perplexus	0	0	0	0	0	0	0	0	24
B. rufocinctus	0	1	0	0	0	0	107	0	0
B. vagans	0	34	0	2	0	0	0	0	87
B. vancouverensis	0	0	0	0	0	0	15	0	0
Total	17	698	207	703	203	191	1591	96	1488

Table 3–5. Diversity measurements of *Bombus* bycatch collected in Florida, Indiana, Kansas, Kentucky, Maryland, South Carolina, Utah, Virginia, and West Virginia in 2018, 2019, and 2020. "Observed/Expected" is the number of species collected compared to the number of species we expected to collect based on the published literature.

Species	**Abundance by State**								
	FL	**IN**	**KS**	**KY**	**MD**	**SC**	**UT**	**VA**	**WV**
Bombus appositus	0	0	0	0	0	0	9	0	0
B. auricomus	0	16	2	88	0	8	0	2	70
B. bimaculatus	0	171	13	67	148	15	0	5	776
B. californicus	0	0	0	0	0	0	1	0	0
B. centralis	0	0	0	0	0	0	38	0	0
B. fervidus	0	121	0	6	31	0	964	3	99
B. fraternus	3	0	1	0	0	1	0	0	0
B. griseocollis	0	8	29	33	4	1	73	5	76
B. huntii	0	0	0	0	0	0	323	0	0
B. impatiens	5	243	7	235	12	114	0	41	345
B. insularis	0	0	0	0	0	0	36	0	0
B. morrisoni	0	0	0	0	0	0	7	0	0
B. nevadensis	0	0	0	0	0	0	17	0	0
B. pensylvanicus	9	104	155	272	8	52	1	40	11
B. perplexus	0	0	0	0	0	0	0	0	24
B. rufocinctus	0	1	0	0	0	0	107	0	0
B. vagans	0	34	0	2	0	0	0	0	87
B. vancouverensis	0	0	0	0	0	0	15	0	0
Total	17	698	207	703	203	191	1591	96	1488

Table 3–6. GAM model results for p-spline smoothed effects including effective degrees of freedom, *F* values, and *p*-values for the *Bombus* Shannon diversity model.

	edf	*F*	*p*-value
s(BIO3)	3.554	0.909	0.419
s(BIO4)	3.794	2.245	0.043
s(BIO9)	4.821	3.352	0.004
s(Latitude, Longitude)	0.000	0.000	0.704

Table 3–7. GAM model results for linear terms including the coefficient estimate, standard error, and *p*-value for the *Bombus* Shannon diversity model.

	Coefficient Estimate	Std. Error	*p*-value
BIO1	-0.081	0.022	0.000
BIO15	-0.018	0.005	0.000
SHDI	0.121	0.121	0.319
PRD	-0.077	0.041	0.061
IJI	-0.003	0.005	0.559
CI	-0.125	1.106	0.910
Slope	-0.008	0.050	0.871

Table 3–8. 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
BIO1	1	49.59	0.001
BIO3	1	3.46	0.002
BIO4	1	15.82	0.001
BIO9	1	30.25	0.001
BIO15	1	12.69	0.001
SHDI	1	6.89	0.002
IJI	1	16.96	0.001
PRD	1	17.87	0.001
CI	1	6.09	0.001
Slope	1	3.16	0.015

Figure 3–1. Bubble map showing the distribution and abundance of the five most abundant *Bombus* species: (A) *B. fervidus,* (B) *B. bimaculatus,* (C) *B. impatiens,* (D) *B. pensylvanicus,* and (E) *B. huntii* throughout nine states in the U.S. from 2018 to 2020. Different colors correspond to different levels of species abundance.

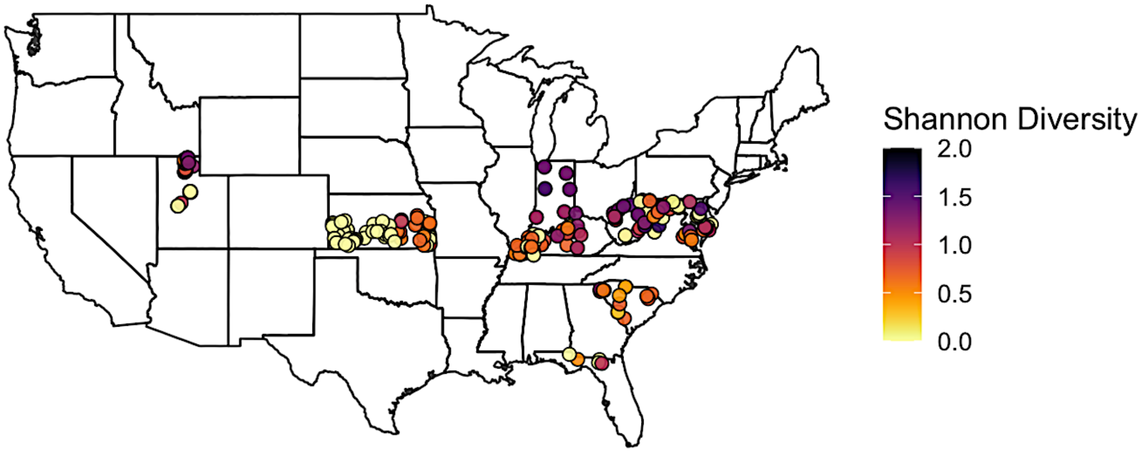

Figure 3–2. Bubble map visualizing *Bombus* Shannon diversity solely by geography throughout nine states in the U.S. from 2018 to 2020. Different colors correspond to different levels of Shannon diversity.

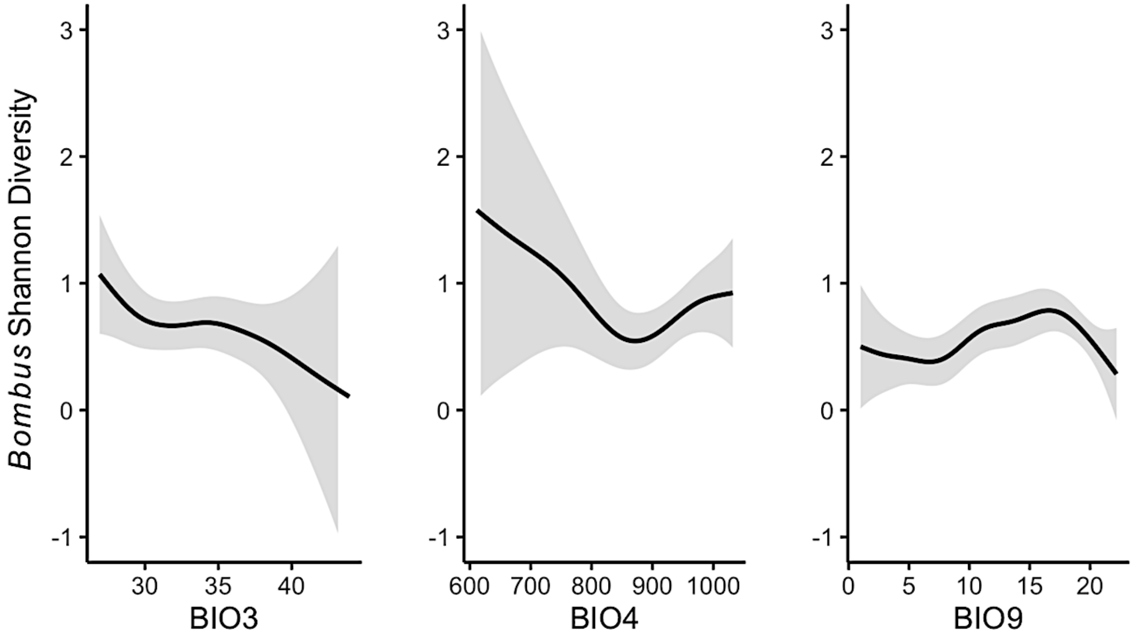

Figure 3–3. *Bombus* Shannon diversity response to three predictors derived from GAM models estimated using p-splines, while holding other variables constant at their mean value. Gray areas represent confidence intervals ± 2 standard errors.

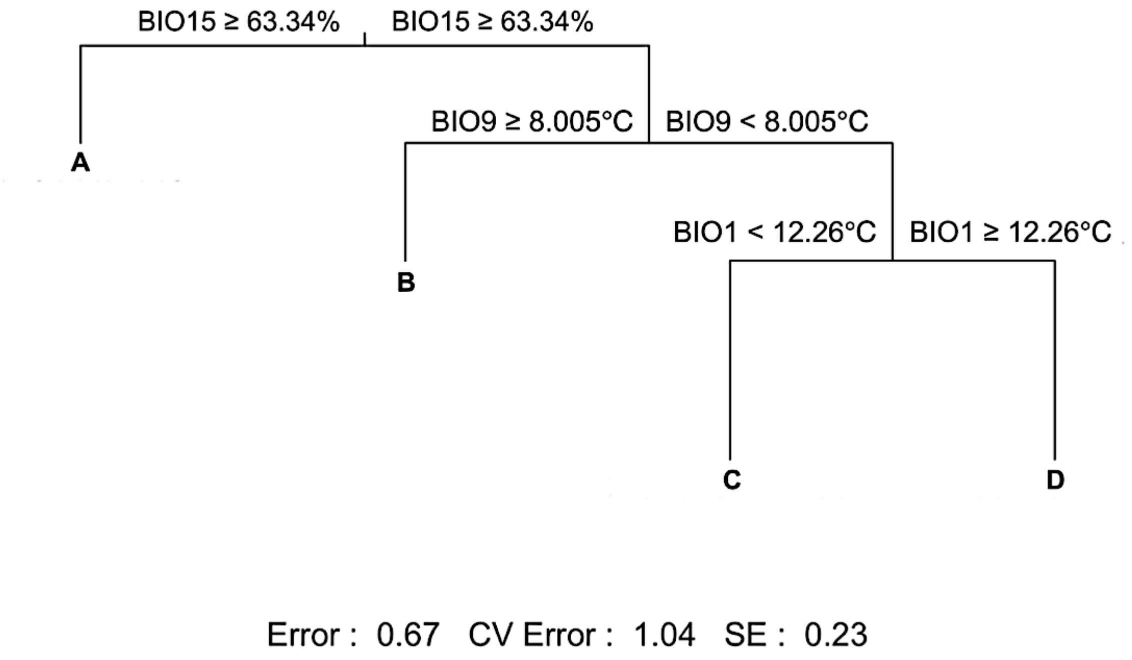

Figure 3–4. Multivariate regression tree (MRT) for the *Bombus* species data in relation to BIO15, BIO9, and BIO1. BIO3, BIO4, SHDI, PRD, IJI, CI, and slope were not selected for inclusion in this model. The four leaves (indicated with letters under each branch) represent species abundances and the environmental variable values associated with the study sites.

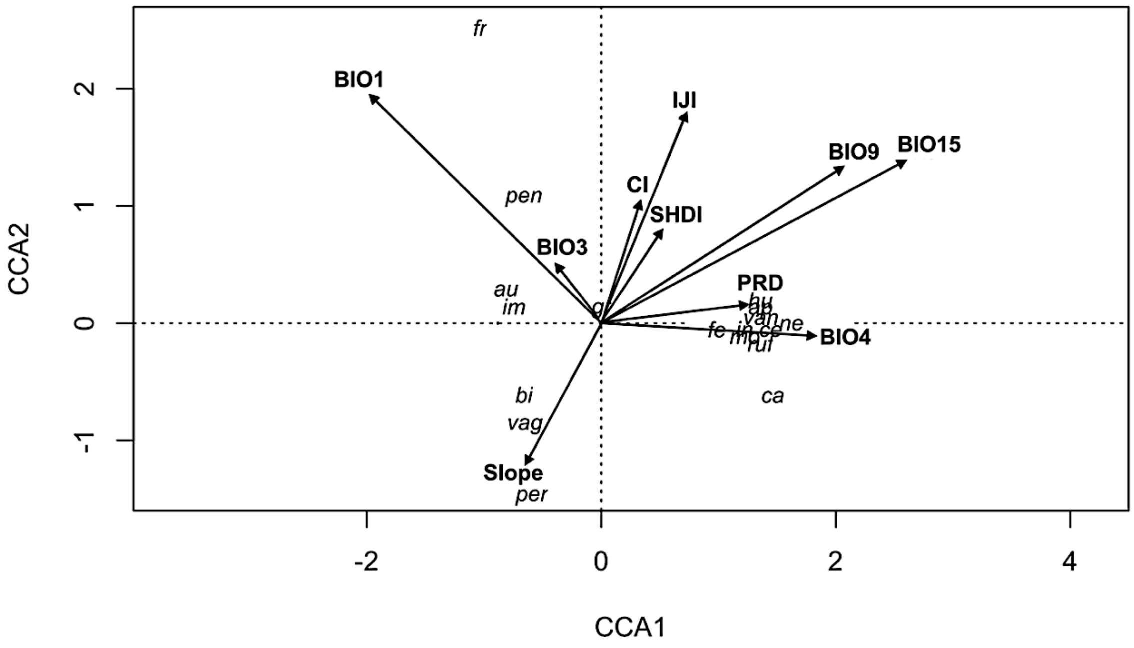

Figure 3–5. Canonical correspondence analyses of the *Bombus* assemblage data in relation to environmental variables (indicated by arrows) from 2018 to 2020. *Bombus* species names are abbreviated as *ap = B. appositus, au = B. auricomus, bi = B. bimaculatus, ca = B. californicus, ce = B. centralis, fe = B. fervidus, fr = B. fraternus, gr = B. griseocollis, hu = B. huntii, im = impatiens, in = B. insularis, mo = B. morrisoni, ne = B. nevadensis, pen = B. pensylvanicus, per = B. perplexus, ru = B. rufocinctus, vag = B. vagans,* and *van = B. vancouverensis.*

CHAPTER IV

ASSESSING THE IMPACT OF PEST MONITORING TRAPS ON *BOMBUS GRISEOCOLLIS (HYMENOPTERA: APIDAE)* COLONY GROWTH AND DEVELOPMENT

Abstract

Insect traps use visual and olfactory cues to attract target pests; however, they vary in their specificity and often unintentionally capture non-target beneficial insects (bycatch), including *Bombus*. Concerns have been expressed that these captures may further contribute to *Bombus* mortality and the consequential loss of pollination services. Here, we quantified the impact of plastic bucket traps on *Bombus griseocollis* captures, colony growth, and development by evaluating the following four treatments: field-released colonies with no trap and no pheromone lure for *Helicoverpa armigera*, colonies paired with traps, colonies paired with traps and lures, and traps and lures (but no colonies). Trap contents were collected biweekly to determine *B. griseocollis* capture rates. Colony growth and development were measured weekly by weighing colonies and recording foraging activity. Based on microsatellite polymerase chain reaction (PCR) amplification, three out of eight *B. griseocollis* that were captured in traps were from field-released colonies, while the remaining were residents within the environment. Given the low number of *B. griseocollis* workers collected, differences in colony weight change and active foraging were likely not a result of pest monitoring trap captures; however, this does not mean that other *Bombus* species are not affected. Future research should evaluate whether trap captures impact other species, functional diversity, colony establishment, and pollination services to provide a more comprehensive view of the impact of pest monitoring traps on *Bombus* populations and to minimize risk to pollination services.

Keywords

Bumble bees, bycatch, pest survey, colony health, microsatellites

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Introduction

Each year, federal, state, and other agencies conduct annual field surveys to monitor pest insect populations throughout the U.S. during periods of expected pest activity (Meagher 2001; Spears and Ramirez 2015; Spears et al. 2016; Sipolski et al. 2019; Grocock and Evenden 2020; Parys et al. 2021; Spears et al. 2021). Traps use visual (e.g., color) and/or olfactory (e.g., chemical) cues to attract pest insects (Clare et al. 2000; Meagher 2001; Spears and Ramirez 2015; Spears et al. 2016; Sipolski et al. 2019; Spears et al. 2021). Despite efforts to improve trapping efficiency and selectivity (Meagher and Mitchell 1999; Martín et al. 2013; Mori and Evenden 2013; Panzavolta et al. 2014), some traps can also attract many non-target insects (bycatch), including beneficial insects such as pollinators (Clare et al. 2000; Spears and Ramirez 2015; Spears et al. 2016; Sipolski et al. 2019; Whitfield et al. 2019; Grocock and Evenden 2020; Grocock et al. 2020; Parys et al. 2021; Spears et al. 2021). For example, pheromone baited multi-colored (green canopy, yellow funnel, and white bucket) bucket traps (International Pheromone Systems, Cheshire, UK) are highly attractive to bees. This could be due to the yellow and white trap components mimicking floral resources and contrasting more strongly with the background environment (Haynes et al. 2007; Rao and Ostroverkhova 2015; Spears et al. 2016; Sipolski et al. 2019; Spears et al. 2021). Multi-colored traps are used over other colors (i.e., all green) because they are more effective at capturing moths (Mitchell et al. 1989; Pair et al. 1989; Meagher 2001). In addition, the compounds that are used in pheromone lures could be detected by and elicit a response from bees (Adams et al. 1989; Asquith and Burny 1998; Meagher and Mitchell 1999; Turnock et al. 2007; Mori and

Evenden 2013; Tewari et al. 2014; Aurelian et al. 2015; Spears et al. 2016; Sipolski et al. 2019; Grocock and Evenden 2020; Grocock et al. 2020; El-Sayed 2021). Pheromone lures are ideally only attractive to the target species, but previous research has identified that both congeners and heterospecifics may be attracted to acetate, alcohol, and aldehyde-based lure components (Spears et al. 2016; Whitfield et al. 2019; Grocock et al. 2020). This attraction may be caused in part by the shared production of pheromone components. For example, male bumble bees produce species-specific pheromones in the cephalic region of the labial gland for pre-mating recognition that contain many chemical compounds related to hexadecenal (De Meulemeester et al. 2011).

The Old World bollworm (*Helicoverpa armigera* Hübner, 1808) is an invasive lepidopteran pest that is continually monitored by the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) using pheromone baited multi-colored bucket traps. Due to the overlap in the recognition of visual and chemical cues, many *Bombus* are captured within traps for *H. armigera* (Hubner, 1808) (Herman et al. 1994; Spears and Ramirez 2015; Spears et al. 2016; Mikulas and Barringer 2018; Spears et al. 2021). Within Utah alone from 2014 to 2019, nearly 2,500 *Bombus* were collected within multi-colored bucket traps containing pheromone lures for *H. armigera* (Christman et al. 2022). Given the wide temporal and spatial range in which these traps are monitored, there is a great deal of concern towards the environmental impacts that occur as a result of trap captures (Spears and Ramirez 2015; Spears et al. 2021).

Previous research in insect and non-insect literature has found that bycatch can lead to population declines and changes in species interactions, which can result in a decline in ecosystem services (Mondor 1995; Clare et al. 2000; Lewison et al. 2014; Spears and Ramirez 2015; Gibbs et al. 2017; Grocock and Evenden 2020). Therefore, pest monitoring trap captures may negatively impact *Bombus* assemblages and pollination services, which is concerning considering the decline in global pollinator populations (Spears et al. 2021). Here, we quantified the impact of pest monitoring traps on *Bombus griseocollis* (De Geer, 1773) captures, colony growth, and development by evaluating colonies paired with various combinations of multi-colored bucket traps and pheromone lures for *H. armigera*. *Bombus griseocollis* was used as our model organism due to its prevalence throughout Utah and the rest of the U.S. (Colla et al. 2011; Koch et al. 2012). We hypothesized that *H. armigera* pheromone baited multi-colored bucket traps capture *B. griseocollis* from released colonies, and that colonies paired with traps and lures experience greater weight loss and declines in the number of active foragers than those without. By studying the effects of pest monitoring traps on *B. griseocollis* colonies, we gain a better understanding of the impact of trap captures on *Bombus,* which is particularly important to producers, pollinator conservationists, and stakeholders that monitor and manage pest insects (Spears et al. 2021).

Materials and Methods

Study Area and Experimental Design

This study was conducted in corn (*Zea mays* Linnaeus) fields in Cache and Box Elder counties in northern Utah in 2020 and 2021 improving on methods developed in 2019

(Appendix B). *Helicoverpa armigera* is surveyed in corn fields throughout the U.S. because they have the potential to cause significant economic damage to corn (CAPS 2022). The following treatments were evaluated: (i) *Bombus griseocollis* colonies with no multi-colored bucket trap and no pheromone lure for *H. armigera* (colony-only), (ii) *B. griseocollis* colonies paired with multi-colored bucket traps (i.e., white bucket, yellow funnel, and green lid and cage), (iii) *B. griseocollis* colonies paired with multi-colored bucket traps and *H. armigera* pheromone lures, (iv) multi-colored bucket traps and *H. armigera* pheromone lures (but no *B. griseocollis* colonies). The four treatments occurred with five randomized replicates in 2020 (n = 20) and four in 2021 (n = 16) (N = 36). For treatments ii-iv, two multi-colored bucket traps (International Pheromone Systems, Cheshire, United Kingdom) were placed in each field 5 m and 100 m from the *Bombus* colony and 1.5 m above the ground. A single pheromone lure for *H. armigera* (comprised of a 2-component blend of Z-11-hexadecenal, Z-9-hexadecenal, and butylated hydroxytoluene) was placed within the lure basket of the trap canopy for treatments iii and iv (NCC 2018). An insecticide strip (Hercon Vaportape II: 10% dimethyl 2,2-dichlorovinyl phosphate, Hercon Environmental Corportation, 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 were changed every 28 days throughout the collection period following U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Cooperative Agricultural Pest Survey approved methods approved methods for pest surveillance (CAPS 2022). Trap contents were collected biweekly (treatments ii–iv), and colony-only fields (treatment i) were net surveyed (36 cm diameter insect net, Bioquip, Compton, CA) over a ten-minute period both 5 and 100 m from the colony to survey the resident *B. griseocollis* community and identify *B. griseocollis* collected from the field-released colonies while foraging.

Bombus Rearing

A total of 134 wild *Bombus griseocolli*s queens emerging from dormancy were net collected in northern Utah from May to June 2020 (n = 82) and June 2021 (n = 52). Captured queens were transferred from the net to 10-dram plastic collection vials (W. W. Grainger Inc., Lake Forest, IL) with ventilation holes and transported in a cooler to the United States Department of Agriculture, Agricultural Research Service, Pollinating Insect – Biology, Management, and Systematics Research Unit in Logan, UT, USA. Individual queens were placed in plastic rearing chambers (178 × 152 × 101 mm; Koppert Biological Systems, Howell, MI) and fed pollen loaves (Fresh Bee Gathered Pollen: Wildflower Varietal, Moon Shine Trading Company, Z Specialty Food, Woodland, CA) and artificial nectar *ad libitum* over the course of colony development (monitored as the number of emerged offspring). Once the queen produced five workers, the chamber was transferred to a larger plastic colony box (292 × 229 × 127 mm; Koppert Biological Systems, Howell, MI). Preparation of pollen loaves and artificial nectar followed Smith et al. (2020).

Prior to deployment, one female offspring was removed from each colony, placed in a labeled vial with 95% ethanol, and subjected to microsatellite polymerase chain reaction (PCR) amplification for colony identification (see section DNA Extraction and

Microsatellite PCR Amplification). Additionally, the number of workers and the weight of each colony was recorded to establish a baseline for each colony.

Field Design

Colonies were deployed on 30 July 2020 and 10 August 2021. Each colony was placed inside a white Rubbermaid bin with large ventilation holes and an entrance/exit hole, and then placed above the ground on a milk crate in a shaded area of the field to allow for foraging and to reduce the risk of overheating. A pollen trap with a plastic excluder measuring 6 mm in diameter (Bees Love Trees S. P., North Logan, UT) was affixed to the entrance/exit hole of each colony to collect pollen loads from returning foragers (Judd et al. 2020, Koch et al. 2021). The plastic excluder was used to prevent *B. insularis* from invading the colonies, while allowing *B. griseocollis* workers to forage for floral resources (Koch et al. 2021). In 2020, many *B. griseocollis* were observed abandoning or dying within the colonies. Given that sunlight can increase the internal temperature of the colony by 5 to 15ºC (Koppert Biological Systems 2021), a 1.2 × 0.6 m piece of plywood covered in double reflective insulation (Reflectix Inc, Markleville, IN) was placed on top of each colony enclosure in 2021 to provide additional shade to reduce the risk of the colonies overheating (Fig. 4–1; Graham et al. 2021). A HOBO temperature/relative humidity 3.5% data logger (Onset Computer Corporation, Bourne, MA) was placed within each colony and on the edge of each field within a solar radiation shield (Onset Computer Corporation, Bourne, MA) to test the effectiveness of the artificial shade structures. Internal colony temperatures were only 0.36ºC higher on average than ambient temperatures, and no colonies were observed abandoning or dying within the colony. Therefore, these shade structures were deemed effective at reducing the risk of colonies overheating.

Monitoring Colony Weight and Foraging Activity

Colonies were monitored weekly from the time of deployment until 9 or 10 September 2020 and 21 September 2021. Each week, the nest was weighed to the nearest gram and the number of workers entering and exiting the nest was recorded over a 10-minute period. Data collections occurred between 9:00 a.m. and 6:00 p.m. to comply with land and homeowner restrictions. This resulted in the concern that colony weights may be underestimated since workers forage during the day. Therefore, colonies were also weighed in the evening (between 7:00 and 9:00 pm) in 2020, and we found no difference in daytime vs. nighttime weights ($t = -0.02$, $df = 27.99$, p-value = 0.98). All collected specimens were stored in a freezer (-18˚C) until they were pin-mounted, labeled, and identified to species. All field-captured female *B. griseocollis* were then subjected to DNA extraction and microsatellite PCR amplification.

DNA Extraction and Microsatellite PCR Amplification

Eluted, double stranded DNA was extracted from the right middle leg of each female worker removed from each colony for colony identification and of every field-captured female *B. griseocollis* using a Zymo quick-DNA miniprep plus kit (Zymo Research

Corporation, Irvine, CA, USA). A subset of the DNA was subjected to a Quibit dsDNA high sensitivity assay (Thermo Fisher Scientific, Waltham, MA) to determine if sufficient concentrations of DNA were extracted. Values ranged from 6.55 to 17.6 ng/μL, identifying sufficient concentrations of DNA were obtained during the extraction process. Extracted DNA was stored at -20ºC until microsatellite PCR amplification.

We performed two 10 μL multiplex reactions on each sampled female *B. griseocollis*, each containing 2 μL of extracted DNA, 2 μL of 5× Promega (Madison, WI) reaction buffer, 0.56 mM of $MgCl_2$ concentration (25 mN), 0.6 mM of dNTP mixture, 0.05–0.228 μM of each primer, 0.2 μL of BSA, 0.08 μL of Taq polymerase (Promega, Madison, WI), and ddH_20 to fill to volume. The two multiplex reactions contained the following primers: (A) B96, B124, BT10, BT28, BT30, BTERN01, and BTMS0081; (B) B126, BTERN02, BTMS0044, BTMS059, BTMS062, BTMS066, BTMS083, BTMS0086, and BL13. Thermocycling conditions for PCR Plex A consisted of an initial denaturation stage at 95ºC for 3 min and 30 s; followed by 31 cycles at 95ºC for 30 s, annealing at 55ºC for 1 min, and extending at 72ºC for 45 s; with a final extension at 72ºC for 15 min. Thermocycling conditions for PCR Plex B consisted of an initial denaturation stage at 95ºC for 3 min and 30 s; followed by 31 cycles at 95ºC for 30 s, annealing at 58ºC for 75 s, and extending at 72ºC for 45 s; with a final extension at 72ºC for 15 min. DNA amplifications were performed with four fluorescent 5’ dye-labeled primers (FAM, NED, PET, and VIC) and separated on an Applied Biosystems 3730xL automated sequencer (Thermo Fisher Scientific, Waltham, MA) at Utah State University’s Center for Integrated Biosystems. Alleles were scored manually using Geneious Prime 2021.01.1 software. Samples with more than 9 loci scored per individual were included in the genetic analysis (Hatfield et al. 2021). Two loci were excluded from further analysis because they either did not amplify (BT30) or were monomorphic (BL13). Of the remaining 14 loci, sibship and colony assignment among the collected *B. griseocollis* was estimated using the maximum likelihood algorithm in Colony v2.0 (Jones and Wang 2010). The mistyping error rate was set to 0.05 based on error rates documented in previous studies (Lozier et al. 2011) and the sex-determination system was set to *haplodiploid* (Koch et al. 2021). This process determined if the *B. griseocollis* captured via bucket traps and net collection were from our field-released colonies or were residents within the environment that were passively collected.

Data Analysis

A one-way random effects analysis of variance (ANOVA) was used to determine the differences among treatment types in relation to cumulative weight change with initial weight and number of initial workers as random effects, and average active *B. griseocollis* with the number of initial workers as a random effect to identify the direct effects of trap and lure presence on *Bombus* colonies. The initial weight and number of initial workers as random effects were used to standardize differences in colony sizes.

Results

In 2020 and 2021, 52 *Bombus* from four species (*B. fervidus, B. griseocollis, B. huntii,* and *B. morrisoni*) were collected in traps. No *Bombus* were collected via aerial netting.

Eight *B. griseocollis* were collected in traps containing lures; four of them were captured 5 m from the colony and four 100 m away. Based on microsatellite PCR amplification, three of the captured *B. griseocollis* were from field-released colonies (2020: n = 2; 2021: n = 1). The two specimens collected in 2020 were captured in traps 5 m from the same colony, and the one collected in 2021 was captured 100 m away. The remaining five captured *B. griseocollis* were residents within the environment (2020: n = 3; 2021: n = 2). Of these resident *B. griseocollis*, one was collected 5 m from the colony and two were collected 100 m away in 2020, whereas one was collected both 5 m and 100 m from the colony in 2021.

In 2020, colony-only (treatment i), colony and trap (treatment ii), and colony, trap, and lure (treatment iii) had cumulative mean weight losses of 18 ± 13.55 g, 17.6 ± 12.56 g, and 43.6 ± 11.46 g, respectively (Fig. 4–2). In 2021, colony-only (treatment i), colony and trap (treatment ii), and colony, trap, and lure (treatment iii) had cumulative mean weight losses of 20.5 ± 15.18 g, 18 ± 4.97 g, and 16.75 ± 16.82 g, respectively (Fig. 4–2). When colony size (initial weight and number of initial workers) was taken into consideration, cumulative colony weight change did not differ among treatments in 2020 (F = 0.202; df = 2, 10; p = 0.82) or 2021 (F = 0.198; df = 2, 7; p = 0.825).

In 2020, colony-only (treatment i), colony and trap (treatment ii), and colony, trap, and lure (treatment iii) had an average activity of 0.28 ± 0.52 bees, 1.28 ± 1.99 bees, and 1.76 ± 1.9 bees, respectively (Fig. 4–3). *Bombus griseocollis* colony activity did not differ among treatments in 2020 (F = 0.616; df = 2, 11; p = 0.558). In 2021, no *Bombus* were reported entering and exiting the colony.

Discussion

Helicoverpa armigera pheromone baited multi-colored bucket traps capture *B. griseocollis* from released colonies, albeit at low densities. Only three of the captured specimens were from field-released colonies. Given these low collection rates, differences in colony weight change and active foraging do not appear to be a result of pest monitoring trap captures. However, this does not mean that *B. griseocollis* or other *Bombus* species will not be affected. Additional trials are needed to better inform the impact of pest monitoring traps on a multitude of *Bombus* species at a colony level.

In 2020 and 2021, all colonies, regardless of treatment, experienced cumulative weight loss; yet, there was not a difference in cumulative weight change among treatments. However, in 2020, prior to taking the initial weight of the colony and the number of offspring into consideration, there was a difference in cumulative weight change between the colony only treatment and the colony paired with trap and lure treatment (18 ± 13.55 g vs. 43.6 ± 11.46, respectively), which was a result of an experimental design error. This difference in weight loss was attributed to the difference in colonies sizes among treatments. Colonies were randomly selected as they were deployed within the corn fields. However, in 2020, all of the colonies that were paired with a trap and lure contained an average of 27.4 offspring at the time of deployment, while colonies without a trap and lure contained an average of 8 offspring. Larger colonies can experience greater loss of weight than smaller colonies, especially as more sexuals (queens and drones) leave the colony to mate. Meanwhile, in 2021, differences in colony sizes were negligible ranging from an average of 11 to 18 offspring. Future studies should exercise caution and take colony size into consideration when randomly assigning colonies to treatments.

There were no differences in average foraging activity among treatments, with average foraging activity below two active workers in 2020 and no active workers in 2021. Overall foraging activity was low compared to other studies which have observed *B. impatiens* entering and exiting the colony once every ten minutes, and *B. bimaculatus* entering and exiting the colony once every two to five minutes (Liczner et al. 2021). Low foraging activity in this study may be due to worker task allocation. Since *B. griseocollis* colonies are small, there may be fewer workers that are responsible for foraging, while others are responsible for brood care and colony maintenance (Williams et al. 2014). Internal factors within the colony, such as heat stress may also require additional efforts to be put towards colony thermoregulation (Westhus et al. 2013). Reduced foraging activity may also be related to the habitats in which the colonies were placed. Corn is a wind pollinated crop and does not provide ample pollen and nectar resources for *Bombus* (Greenleaf and Kremen 2006). As a result, workers may be traveling further distances to forage, so more time may be needed to observe foraging activity. However, further research on *B. griseocollis* foraging behavior is needed to evaluate this relationship. In addition to documenting foraging activity, we also attempted to collect pollen loads from the foraging workers as a proxy for floral availability (Vaidya et al. 2018). However, we were unsuccessful at collecting pollen loads within any of the pollen traps, which may be due to the size of the pollen trap. If the pollen trap is too big, *B. griseocollis* workers can travel through the pollen trap without knocking the pollen load off their corbiculae.

Therefore, additional research is needed to determine the pollen trap size that is most effective at collecting pollen loads from *B. griseocollis* workers.

Future research should continue to evaluate the impact of pest monitoring trap captures on *Bombus* populations and pollination services. Pest monitoring traps capture a wide range of pollinators, but this does not necessarily mean that pollination services will be negatively impacted (Spears et al. 2021). If local species richness and functional diversity are maintained, other ecologically similar species within the environment can provide pollination services even if a particular species is extirpated due to functional redundancy and response diversity (Elmqvist et al. 2003; Laliberté et al. 2010; Blüthgen and Klein 2011; Cadotte et al. 2011). However, if traps attract and capture many individuals from a specialist bee species, this can disrupt ecosystem function and decrease pollination services (Cadotte et al. 2011).

Future research should also expand beyond the colony level to evaluate the impact of trap captures on reproductive queen and male *Bombus*. If queens are collected soon after emergence from dormancy, this could reduce the number of established nests, which serve as a source of future workers, reproductive queens, and drones (males) (Strange 2010). Meanwhile, high capture rates of reproductive queens and males at the end of the season can reduce mating, limiting the establishment of colonies the following spring. Overall, the collection of reproductives within traps is of concern as this may lead to population declines and the subsequent loss of pollination services. Therefore, identifying time periods when queen and male *Bombus* are collected at higher volumes can help inform trap placement dates to minimize bycatch risk (Mondor 1995; Strange et al. 2011; Spears et al. 2021).

Overall, given the low collection rates of *B. griseocollis* from field-released colonies, pest monitoring traps did not appear impact *B. griseocollis* colony growth or development; however, additional trials are needed. Building on this research by evaluating the impact of trap captures on other species, functional diversity, colony establishment, and pollination services will provide a more comprehensive view of the impact of pest monitoring traps on *Bombus* populations and minimize potential risk to pollination services. These factors are important to producers, pollinator conservationists, and stakeholders that monitor and manage pest insects (Spears et al. 2021).

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Author Contributions

MEC: Conceptualization; Methodology; Data curation; Formal analysis; Investigation; Software; Validation; Visualization; Writing – original draft. LRS: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing – review & editing. JBUK: Formal Analysis; Resources; Software; Supervision; Writing – review & editing. TTTL: Investigation; Supervision; Writing – review & editing. JPS: Resources; Supervision; Writing – review & editing. RAR: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing – review & editing.

Data Availability Statement

Data and code supporting the findings of this study are available on Zenodo at https://doi.org/10.5281/zenodo.6364154.

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Figures

Figure 4–1. *Bombus griseocollis* artificial colony on the edge of a corn field with a shade structure to allow for foraging and to reduce the risk of overheating. A HOBO temperature/relative humidity data logger within a solar radiation shield (seen on the right) was placed within each field to test the effectiveness of the artificial shade structure.

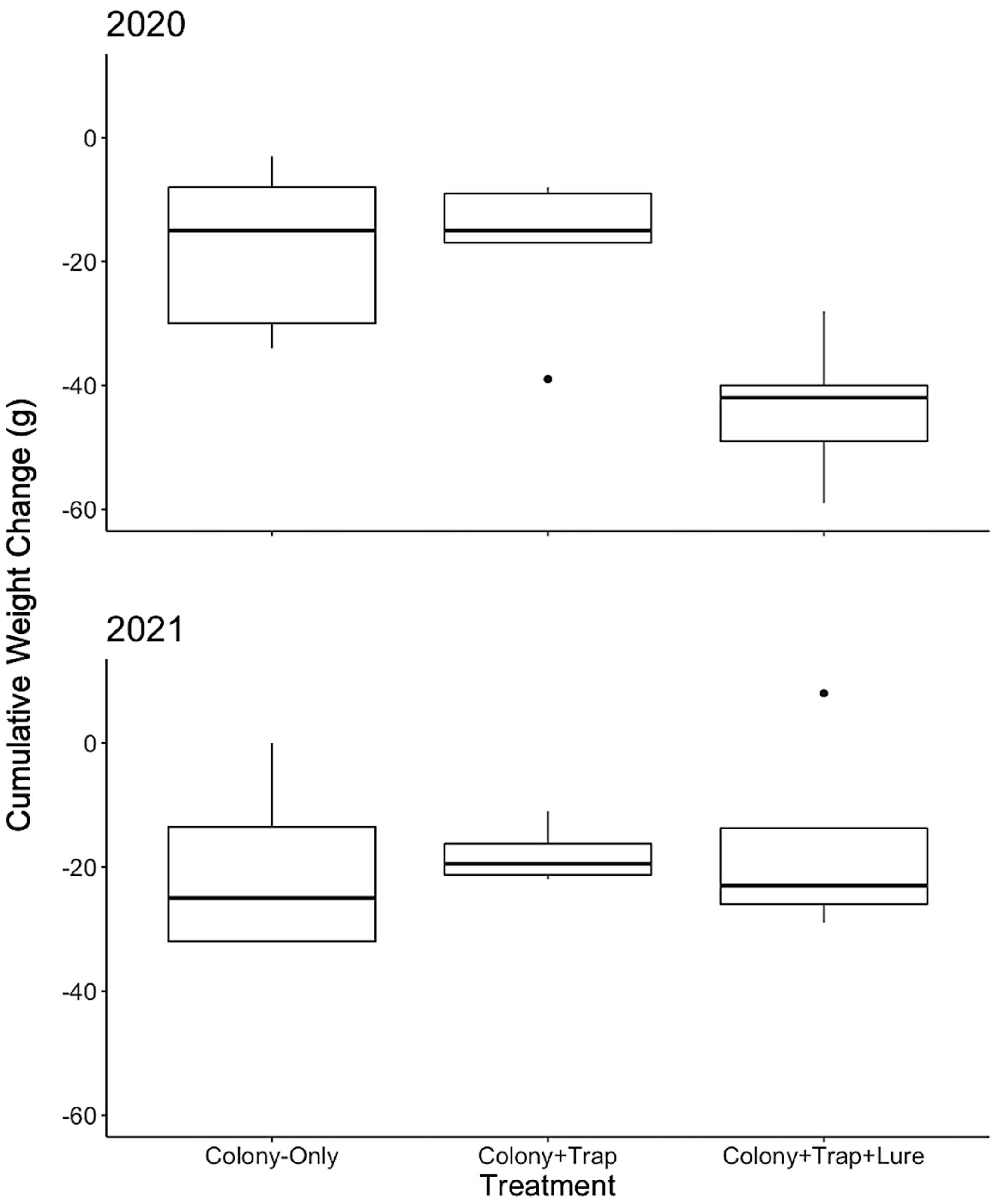

Figure 4–2. Box plot of the cumulative weight change of *B. griseocollis* colonies for each treatment type in 2020 and 2021.

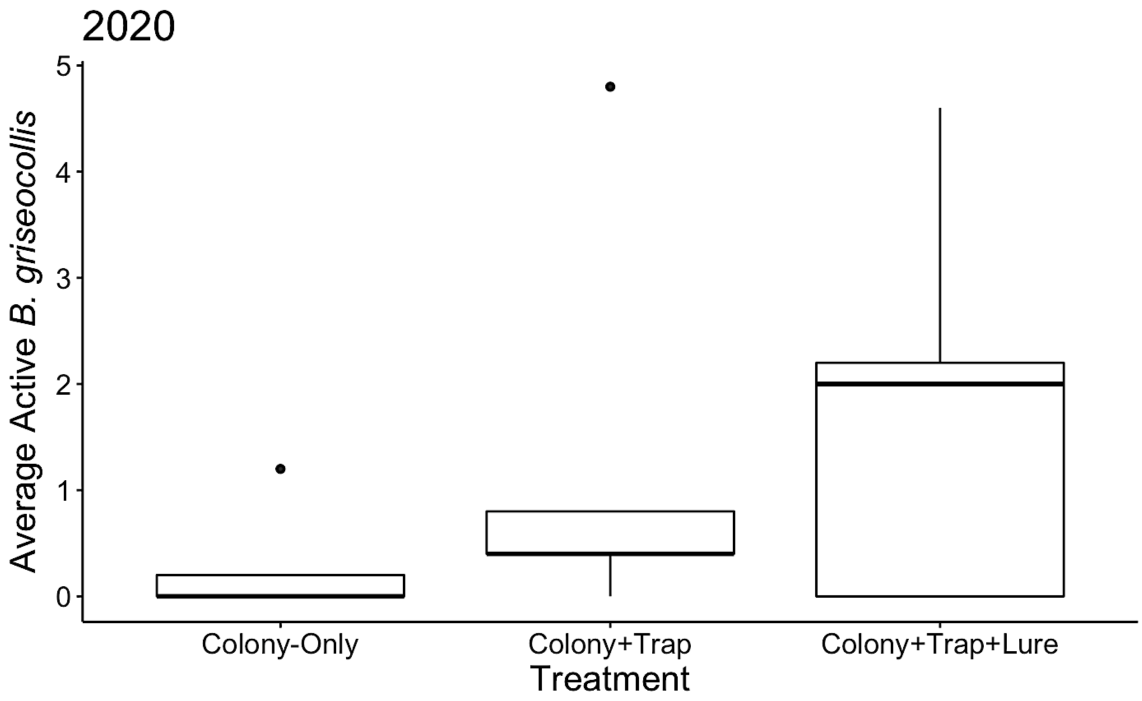

Figure 4–3. Box plot of average *B. griseocollis* colony activity for each treatment type in 2020.

CHAPTER V

COMMERCIALIZATION POTENTIAL OF *BOMBUS GRISEOCOLLIS* (HYMENOPTERA: APIDAE): EVALUATING CAPTIVE REARING SUCCESS AND CRITICAL THERMAL MAXIMA

Abstract

Commercialized bumble bees (*Bombus*) are the primary pollinators of several crops within greenhouse settings. However, *B. impatiens* is the only species widely available for purchase in North America. As an eastern species, concerns have been expressed over their transportation outside of their native range. Therefore, there is a need to identify regionally appropriate candidates for commercial crop pollination services, especially in the western U.S. In this study, we evaluated the commercialization potential of *B. griseocollis,* a broadly distributed species throughout the U.S., by assessing nest initiation and establishment rates of colonies produced from wild-caught queens, creating a timeline of colony development, and identifying lab-reared workers' critical thermal maxima (CT_{Max}) and lethal temperature (ecological death). From 2019 to 2021, 70.6% of the wild-caught *B. griseocollis* queens produced brood in a laboratory setting. Of these successfully initiated nests, 74.8% successfully established a nest (produced offspring), identifying high rearing success rates of *B. griseocollis* in a laboratory setting. Additionally, lab-reared workers produced from wild-caught *B. griseocollis* queens had an average CT_{Max} of 43.5ºC and an average lethal temperature of 46.4ºC, suggesting *B. griseocollis* can withstand high temperatures which may be advantageous considering ongoing and projected climate change. Overall, *B. griseocollis* should continue to be evaluated for commercial purposes throughout the U.S.

Key Words

Bumble bees; nest initiation; nesting success; CT_{MAX}; commercialization

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Introduction

Bumble bees (Hymenoptera: Apidae: *Bombus*) are effective pollinators of cultivated and wild plant communities (Velthuis and van Doorn 2006). The use of *Bombus* in greenhouse production is increasing around the world because commercialized pollinators reduce the need for labor-intensive hand pollination practices and chemical hormones (Velthuis and van Doorn 2006; Williams et al. 2014). However, of the 265 described *Bombus* species worldwide, only a few species have been commercialized to provide pollination services. As a result, the few commercialized species are purchased and intentionally released in greenhouses often well outside of their native ranges (Goulson 2010; Strange 2015). This human-mediated movement has led to the unrestricted release of non-native *Bombus* into novel ecosystems, subsequently causing negative impacts on the local environment (Tsuchida et al. 2010).

Bombus occidentalis (Greene, 1858) was the primary commercialized pollinator in western North America until the late 1990s. While once common throughout the western U.S. (Koch and Strange 2009; Sheffield et al. 2016), *B. occidentalis* has been assessed as Vulnerable by the International Union for the Conservation of Nature (IUCN) and is currently being considered for listing by the U.S. Fish and Wildlife Service (USFWS) under the Endangered Species Act (ESA) (Hatfield et al 2015; Graves et al. 2020; IUCN 2021). Additionally, this species is more susceptible to infection by *Varimorpha bombi* (previously *Nosema bombi*) (Cameron et al. 2011) than other *Bombus* species (Fries et al. 2001; Whittington and Winston 2004; Velthuis and van Doorn 2006; Koch and Strange 2012). These high infection rates harm colony development and increase the potential of pathogen introductions to wild *Bombus* species, which led to the abandonment of *B. occidentalis* as a commercially viable species in the late 1990s (Flanders et al. 2003; Whittington and Winston 2004; Velthuis and van Doorn 2006). As a result, production shifted to *B. impatiens* (Whittington and Winston 2004; Velthuis and van Doorn 2006).

Bombus impatiens (Cresson, 1863) has been the only species widely available for purchase in the U.S. and Canada since the early 2000s (Whittington and Winston 2004; Velthuis and van Doorn 2006; Strange 2010). However, as an eastern species, concerns have been expressed about the potential of this species to expand its range, compete with native species, disrupt plant-pollinator interactions, cause genetic deterioration due to interspecific mating, and introduce new pathogens to wild *Bombus* in habitats surrounding the greenhouses, specifically west of the Rocky Mountains, U.S. (Whittington and Winston 2003, 2004; Colla et al. 2006; Velthuis and van Doorn 2006; Otterstatter and Thompson 2008; Vilsac et al. 2012). These concerns were underscored when *B. impatiens* was imported to British Columbia, Canada for greenhouse pollination in the early 2000s, subsequently became established in the wild, and are now expanding throughout the Pacific Northwest, U.S. (Looney et al. 2019). Now, several states are placing restrictions on importing non-native *Bombus* for pollination. For example, *B. impatiens* is restricted to greenhouse use in California (open field release is prohibited) and a queen-excluder must be used to prevent accidental bumble bee and pathogen introductions (California Food and Agriculture 1973; Velthuis and van Doorn 2006; Strange 2010, 2015). Further, it is illegal to import *B. impatiens* into Oregon for open field or greenhouse pollination (Strange 2010; Oregon Department of Agriculture 2017).

In response to these concerns, *B. vosnesenskii* (Radoszkowski, 1862) and *B. huntii* (Greene, 1860) became available for commercial purposes in North America. *Bombus vosnesenskii* is available for purchase throughout its native range in California, Oregon, and Washington, U.S. (Koppert 2022a), and *Bombus huntii* is being produced and distributed in western Canada (Biobest 2022). Therefore, there is a need to identify regionally appropriate candidates for commercial crop pollination, especially in the western U.S. (Strange 2010).

Several facets must be considered when developing a pollinator species for commercialization, including captive rearing success, mating success, diapause conditions in a controlled laboratory setting, effective pollination of target crop(s) within greenhouse settings, life history traits, and pathogen and pest resistance (Macfarlane et al. 1994; Strange 2010). Despite previous work on captive rearing, nesting initiation and establishment rates can be low when rearing colonies from wild-caught queens (Kwon et al. 2006; Strange 2010). Additionally, given biological differences among species, rearing methods should be tested on individual species to maximize rearing success (Kwon et al. 2006; Yoneda 2008; Strange 2010). Maximizing rearing success and establishing year-round production of offspring is necessary to provide pollination services and to create sources of reproductive males and queens (Velthuis and van Doorn 2006).

One potential candidate for commercialization is *Bombus griseocollis* (De Geer, 1773). *Bombus griseocollis* is a broadly distributed species, occurring in the eastern U.S. as well as in northern California and the Cascade Crest east to the Rocky Mountains (Fig. 5–1; Koch et al. 2012; GBIF 2022). This makes them a good candidate to be released in eastern and western environments for crop pollination, with the exception of some of the southwestern U.S. (i.e., Arizona, Nevada, and Southern California) where they are not distributed. *Bombus griseocollis* survives well throughout a range of habitat types including open farmland and fields, urban parks and gardens, and wetlands (Koch et al. 2012; Williams et al. 2014). Additionally, given their wide spatial distribution, they are exposed to increased climate variability, which may allow them to be less sensitive to climatic disturbances (Kingsolver et al. 2013). In the face of ongoing and projected climate change, species with a wider thermal range may have a competitive advantage over other species (IPCC 2014; Verble-Pearson et al. 2015; Soroye et al. 2020).

In this study, we evaluated the commercialization potential of *B. griseocollis* by assessing nest initiation and establishment rates of colonies produced from wild-caught queens, creating a timeline of colony development in laboratory settings, and identifying lab-reared workers' critical thermal maxima (CT_{Max}) and lethal temperature (ecological death). Results from this study establish systematic nesting biology knowledge on *B. griseocollis* should the species continue to be evaluated for commercial purposes throughout the U.S.

Materials and Methods

Bombus griseocollis Rearing

Bombus griseocollis queens were net collected as they emerged from winter dormancy in northern Utah from May to June 2019–2021. A total of 214 queens were captured across the three years: 80 in 2019, 82 in 2020, and 52 in 2021. The captured queens were removed from the net, transferred into individual 10-dram plastic collection vials (W. W. Grainger Inc., Lake Forest, IL) with ventilation holes, and stored in a cooler until they could be transported to the United States Department of Agriculture, Agricultural Research Service, Pollinating Insect – Biology, Management, and Systematics Research Unit in Logan, UT. Once at the laboratory, the captured queens were placed in individual plastic rearing chambers (178 × 152 × 101 mm; Biobest Canada, Leamington, Ontario) in a rearing room that was maintained between 26-30°C and 60% relative humidity in complete darkness. Each queen was initially provided a pollen loaf (Fresh Bee Gathered Pollen: Wildflower Varietal, Moon Shine Trading Company, Z Specialty Food, Woodland, CA) and a bladder filled with artificial nectar (Koch et al. 2021). As offspring were produced, each colony was fed pollen loaves and additional artificial nectar *ad libitum* (Strange 2010). Once the queen produced five workers, the colony was transferred to a larger plastic colony box (292 × 229 × 127 mm; Biobest Canada, Leamington, Ontario). Preparation of pollen loaves and artificial nectar followed Smith et al. (2020).

Colonies were assessed every other day over the course of their development in the rearing room under red light to avoid disturbing and stressing the colonies (Fig. 5–2). Days to first brood, days to first worker, days to five workers, and total emerged offspring were documented for each colony to provide information on nest initiation and establishment, and to create a timeline of colony development in a controlled laboratory setting. Nest initiation was defined as the ability of a queen to produce brood. Nest establishment was defined as the ability of a queen to rear one adult female offspring (worker) from brood (Strange 2010). An analysis of variance (ANOVA) was used to determine the differences in nest establishment among years.

Bombus griseocollis Thermal Tolerance

In 2020, workers from lab-reared colonies were used in thermal tolerance trials to measure the critical thermal maximum of *B. griseocollis*. Using a modified approach from Barnes et al. (2019) and Verble-Pearson et al. (2015), forty *B. griseocollis* workers from fifteen colonies were placed within individual stoppered glass vials (9.5 × 2.5 cm; Berlin Packaging, Chicago, IL), and submerged approximately nine cm into a water bath with an initial temperature of 25.44 ± 3.65°C for five minutes to allow the worker to acclimate to the chamber. Air holes were provided at the top of the glass vials to allow for respiratory gas exchange. The water bath was established using a hot plate stirrer (Fisher Scientific 1152049SH) and a beaker filled with 800 mL of water. A small stir bar was included at the bottom of the beaker and the hot plate was set to the lowest stir setting to promote even, consistent heating of the water. One empty vial was submerged with each trial as a control to verify that the internal vial temperature was consistent with the water temperature. Temperatures were determined using a Twidec K-type thermocouple and a HOBO 4-channel thermocouple data logger (#UX120-014M, Onset Computer Corporation, Bourne, MA). The temperature of the water bath was increased at a constant rate until the critical thermal maximum (CT_{Max}) and lethal temperature (ecological death) were determined for all workers. The rate of heating for the control vial (0.45 ± 0.04°C per minute) was not significantly different from the rate at which the water was heated (0.45 ± 0.05°C per minute) ($t = -0.35$, $df = 34$, $p = 0.72$), indicating that the internal vial temperature was consistent with the water temperature.

As temperatures increased, bees became more agitated before losing motor function, causing them to fall onto their backs and experience leg spasms (Oyen et al. 2016). The temperature at the initial onset of spasms for each *B. griseocollis* was recorded as the CT_{Max} (Lutterschmidt and Hutchison 1997; Hanna and Cobb 2007; Oyen et al. 2016; Barnes et al. 2019; Burdine and McCluney 2019). Temperatures continued to increase at a constant rate until complete leg curling occurred, indicating the lethal temperature (ecological death) of the individual (Burdine and McCluney 2019). To reduce inconsistencies, the same observer was used to determine the CT_{Max} and lethal temperature of each *B. griseocollis* worker in real time. After death, the distance between wing-attachment points on the thorax (intertegular distance, ITD) of each bee was measured using a Keyence digital microscope VHX-500F (Keyence Corp. Itasca, IL) to determine the body size of each worker. Additionally, each bee was dried at 60°C for 24 hours and weighed to the nearest microgram to determine the dry mass of each worker.

A Pearson's correlation test was used to determine if ITD and dry body mass, proxies for body size, were correlated. ITD and dry body mass were correlated ($r > 0.79$, $n = 40$); therefore, only ITD was used in the following analyses to reduce redundancy. A Pearson's correlation test was also used to determine if correlations existed between the CT_{Max} and lethal temperature. Further, linear regressions were used to determine the effects of ITD on CT_{Max} and lethal temperature for *B. griseocollis* workers. All conditions for the linear regression were met (linearity, normality, independence, and homoscedasticity). Statistics were performed using base functions in R version 4.0.3 (R Core Team 2020).

Results

Bombus griseocollis Rearing

From 2019 to 2021, 70.6% of the wild-caught *Bombus griseocollis* queens produced brood (the criterion for nest initiation) in a laboratory setting 7.6 ± 7 days after the queen collection date. Of the 151 successfully initiated nests, 74.8% produced at least one worker (the minimum criterion of successful nest establishment) 34.8 ± 12.6 days after nest initiation. There was no significant difference in nest establishment among years ($F_{1,11} = 18.07$; $p = 0.147$). Further, 70 of the nests had five workers emerge 46.5 ± 16.6 days after nest initiation (Table 5–1). On average, colonies produced 6.8 ± 6.9 offspring over the course of colony development, with a single queen producing a maximum of 46 workers (Table 5–2).

Bombus griseocollis Thermal Tolerance

We found a positive correlation between the CT_{Max} and lethal temperature for *B. griseocollis* ($r > 0.5$, $n = 40$). The average CT_{Max} was 43.5 ± 0.49ºC, while the average lethal temperature was 46.4 ± 0.27ºC for *B. griseocollis* workers (Fig. 5–3). The mean difference of 2.89 ± 0.4ºC between CT_{Max} and lethal temperatures suggests a short time period (approximately 6 minutes at a heating rate of 0.45ºC) between the loss of critical motor function and death. Further, we found that CT_{Max} and lethal temperatures increased with lower ITD (Fig. 5–4). For every 1 mm gained in ITD, the CT_{Max} decreased by 0.85ºC ($F_{1,38} = 4.77$, $p = 0.035$) and the lethal temperature decreased by 0.61ºC ($F_{1,38} = 8.55$, $p = 0.005$).

Discussion

Bombus griseocollis are broadly distributed throughout the U.S. (Koch et al. 2012). If commercially produced, this broad distribution reduces the risk of *B. griseocollis* being introduced outside their native range and may decrease the likelihood of adverse effects on local ecosystems. Additionally, their ubiquity exposes them to a range of habitat types and climates (Koch et al. 2012; Williams et al. 2014). This may allow them to be less sensitive to habitat and climatic disturbances, and may therefore, be able to tolerate higher temperatures in the face of ongoing and projected climate change.

We found that lab-reared workers produced from wild-caught *B. griseocollis* queens in Utah had an average CT_{Max} of 43.5 ± 0.49ºC and an average lethal temperature of 46.4 ± 0.27ºC. Previous studies have identified that there is little variation in CT_{Max} across geographic thermal gradients (Sunday et al. 2012), which is supported by the similar CT_{Max} (45.31ºC) documented in wild-caught *B. griseocollis* in North Carolina (Hamblin et al. 2017). Additionally, CT_{Max} and lethal temperatures increased with lower ITD, suggesting smaller individuals had a higher CT_{Max} and lethal temperature than their larger counterparts. Smaller organisms may dissipate heat better through more rapid thermoregulation strategies, such as thoracic or evaporative cooling and wing fanning, but may be more prone to desiccation (Heinrich 1976; Willmer and Stone 1997; Gardner et al. 2011; Burdine and McCluney 2019). However, commercialized bees are often larger than their native conspecifics (Ings et al. 2006; Lye et al. 2011), which may increase the likelihood that larger, commercialized *B. griseocollis* reach their CT_{Max} and lethal temperature. However, it is important to note that ambient temperatures rarely reach 40ºC throughout much of the contiguous U.S., reducing the risk of *B. griseocollis* exposure to CT_{Max} and lethal temperatures within well-shaded and well-ventilated colonies. Further, the CT_{Max} of *B. impatiens,* the commercially available *Bombus* species in the U.S., was also tested following the same methodology outlined in this study. *Bombus impatiens* workers from commercially produced colonies had an average CT_{Max} of 44.2 ± 0.46ºC and a lethal temperature of 45.4 ± 0.36ºC (Fig. S1). Given that the CT_{Max} and lethal temperatures for *B. griseocollis* and *B. impatiens* are within 1ºC of each other, this suggests that the upper thermal tolerance of *B. griseocollis* is conducive to commercialization. Next steps should involve evaluating the critical thermal minima (CT_{Min}) of *B. griseocollis,* which is influenced by regional and local temperatures (Pimsler et al. 2020). Determining the CT_{Min} would also allow the thermal tolerance range ($CT_{Min} – CT_{Max}$) to be calculated, which is expected to be broad given the wide thermal tolerance of *B. griseocollis.*

Evaluating the commercialization potential of *B. griseocollis* identified that they were successfully reared within a laboratory setting from wild-caught queens in Logan, UT, with high nest initiation and establishment rates (70.6% and 74.8%, respectively). A timeline of colony development identified an average of 7.6 ± 7 days to nest initiation and 34.8 ± 12.6 days to nest establishment. Using this information, management practices can be optimized to enhance the production of workers and future reproductive males and queens, which are needed to establish year-round production of colonies in laboratory settings (Velthuis and van Doorn 2006; Strange 2015). Next steps should evaluate colony biology (i.e., rearing success, colony development, CT_{Max}) throughout the U.S., as local adaptations may differ across space. Additional research is also needed on other aspects of *B. griseocollis* production in captivity. For example, *B. griseocollis* susceptibility to pathogen infections (e.g., *Varimorpha bombi, Crithidia bombi, Apicystis bombi*) should be monitored, as high infection rates reduce colony development and increase transmission to wild *Bombus* species, causing adverse effects on the local environment.

Mating success and diapause conditions in a controlled laboratory setting should also be considered when evaluating *B. griseocollis* for commercialization (Macfarlane et al. 1994; Strange 2010). Mating of bumble bees in controlled laboratory settings is both challenging and necessary to establish year-round production of reproductive males and queens. To meet environmental and social conditions, information on optimal age for mating, mating behavior, number of preferred mates, mating duration, inbreeding, and environmental conditions need to be obtained (Tasei et al. 1997; Sauter and Brown 2001; Brown and Baer 2005; Treanore et al. 2021). The duration of queen diapause also needs to be determined along with establishing optimal diapause conditions for captive rearing. Additional research is required to determine the success rates of overwintering *B. griseocollis* queens in cold storage or subjecting queens to CO_2 narcosis, causing them to bypass diapause and begin nest initiation (Roseler 1985; Beekman and Van Stratum 2001; Gosterit and Gurel 2009; Amsalem and Grozinger 2017). Both methodologies can impact the colony life cycle and development, such as the number and timing of producing reproductive males or queens, so determining the best method for establishing year-round *B. griseocollis* production is essential (Treanore et al. 2021). Although we established high rearing success of *B. griseocollis* in the lab, previous research has identified challenges with nest initiation following diapause or CO_2 narcosis. For example, colonies required a social stimulus, pleometrosis, to initiate brood production (Treanore et al. 2021). Without the presence of another *Bombus* queen or a worker honey bee, less than 25% of queens successfully produced offspring (Strange 2015). Therefore, *B. griseocollis* should be evaluated to determine if pleometrosis increases nest initiation and establishment rates, which may help enhance the production of workers and reproductive males and queens.

Future research should also determine the efficacy of *B. griseocollis* pollination efforts within diverse greenhouse settings (Strange 2015). Our lab-reared *B. griseocollis* colonies were small, with colony sizes never exceeding 50 workers. This differs from *B. impatiens*, which are sold with 100–125 workers per colony and can contain between 300–400 workers at maturity (Cnaani et al. 2002; Koppert 2022b). Commercial *B. impatiens* colonies are used for pollinating a wide range of crops grown on surfaces larger than 2 km^2 that produce 25–35 flowers per m^2 every week (Koppert 2022c). Given their small colony size, *B. griseocollis* may not be effective at pollinating crops in large greenhouse settings unless several colonies are used, but could be promising for smaller greenhouse crop production. However, low *B. griseocollis* densities could be beneficial in small greenhouses in order to avoid flower damage from excessive pollination and over-visitation (Strange 2015). Research into the stocking densities of *B. griseocollis* is needed to determine the optimal number of bees for pollinating specific crops in different sized greenhouses (Strange 2015). Crops should also be selected based on phenological overlap between crop pollination and worker emergence periods.

In summary, *B. griseocollis* exhibit traits that are conducive to commercialization. As a broadly distributed species, they present lower risk of causing adverse effects to the ecosystems in which they are placed. Additionally, their high CT_{Max} and lethal temperature indicates potential resilience to ongoing and projected climate change. Further, we demonstrated high success rates when rearing *B. griseocollis* from wild caught queens in Utah and identified a timeline for colony development within a laboratory setting. Overall, *B. griseocollis* should continue to be evaluated for commercial purposes throughout the U.S.

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Data Availability Statement

The data and code supporting the findings of this study are openly available on Zenodo at https://doi.org.10.5281/zenodo.6364010.

Author Contributions

MEC: Conceptualization; Methodology; Data curation; Formal analysis; Investigation; Software; Validation; Visualization; Writing – original draft. LRS: Funding acquisition; Project administration; Resources; Supervision; Writing – review & editing. JBUK: Resources; Supervision; Writing – review & editing. TTTL: Conceptualization; Supervision; Writing – review & editing. JPS: Resources; Supervision; Writing – review & editing. CLB: Conceptualization, Methodology, Validation, Writing – Review & Editing. RAR: Funding acquisition; Project administration; Resources; Supervision; Writing – review & editing.

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Tables and Figures

Table 5–1. Rearing success of *B. griseocollis* as defined by the production of brood (nest initiation) and emergence of one worker (nest establishment) from 2019 to 2021. Colony development of *B. griseocollis* within captivity as defined by days to nest initiation ± SD, days to nest establishment ± SD, and days to five workers from 2019 to 2021.

Year	**Successful Nest Initiation**	**Successful Nest Establishment**	**Days to First Brood**	**Days to First Worker**	**Days to Five Workers**
2019	64/80	53/64	5 ± 5.6	30 ± 10.6	42.9 ± 13.8
2020	50/82	34/50	10 ± 8.9	40 ± 14.6	53 ± 22.7
2021	37/52	26/37	9 ± 4	38.2 ± 9.9	46.9 ± 11.3
Combined	151/214	113/151	7.6 ± 7	34.8 ± 12.6	46.5 ± 16.6

Table 5–2. Average and maximum number of emerged offspring ± SD within *B. griseocollis* colonies from 2019 to 2021.

Year	**Average Offspring Emerged**	**Maximum Offspring Emerged**
2019	4.7 ± 2.1	9
2020	8.4 ± 9.9	46
2021	9 ± 7.5	25
Combined	6.8 ± 6.9	46

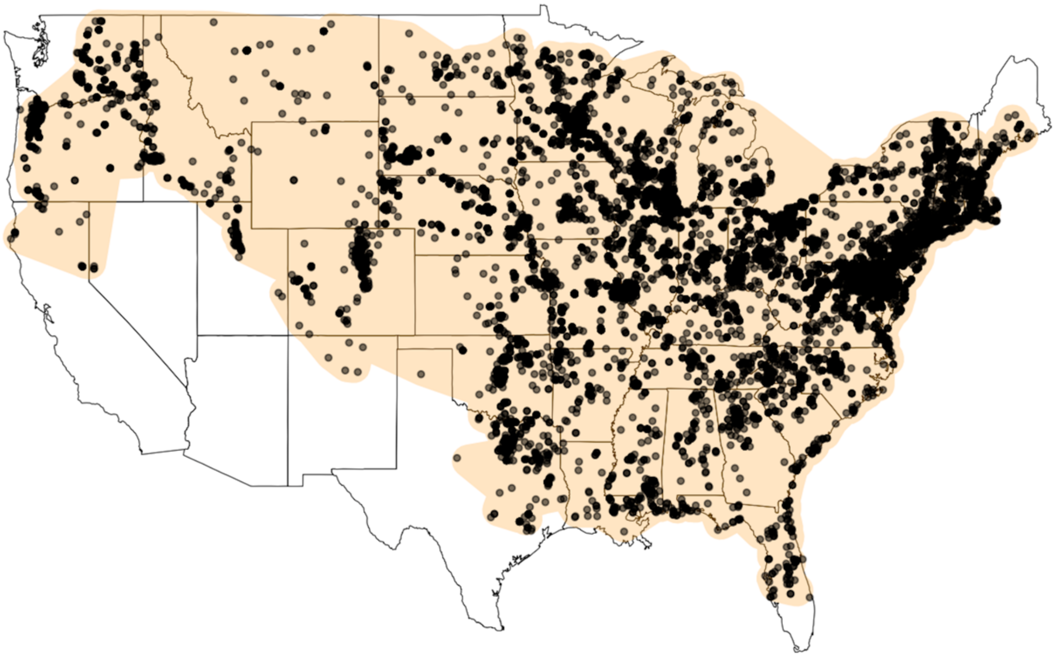


Figure 5–1. *Bombus griseocollis* occurrences (black points) from 2000 to 2022 throughout the contiguous U.S. (GBIF 2022, https://doi.org/10.15468/dl.zfcnd7). The convex hull polygon (shown in orange) informs the geographic extent of *B. griseocollis'* distribution in areas where specimen collection data is lacking.

Figure 5–2. Photograph of a developed lab-reared *B. griseocollis* colony produced from a wild-caught queen.

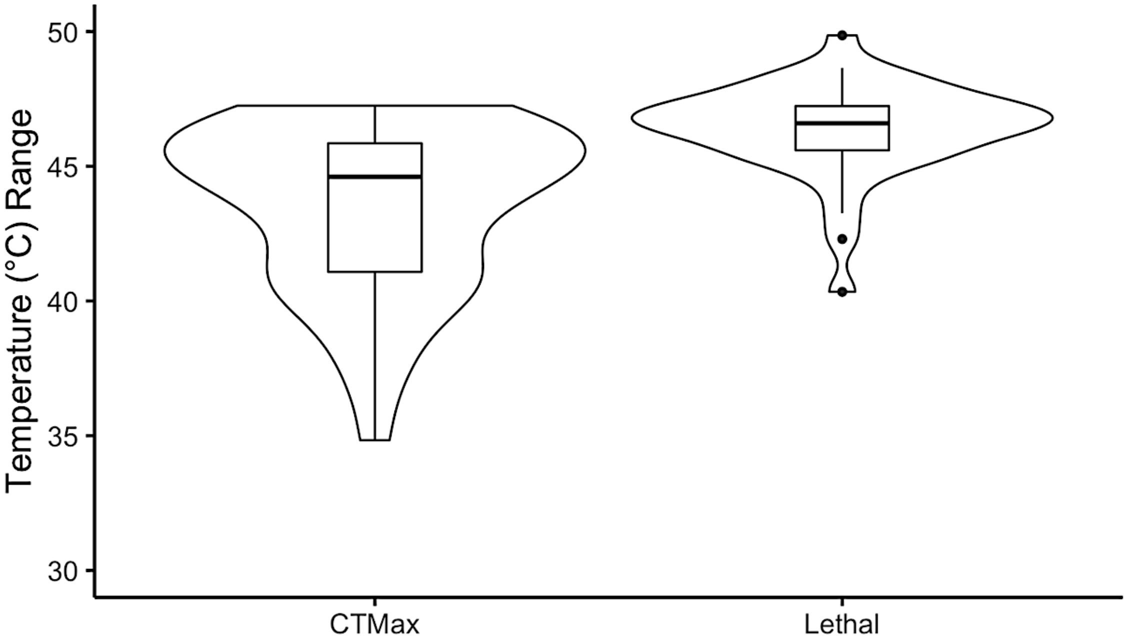


Figure 5–3. Range of CT_{Max} and lethal temperatures (ºC) for *B. griseocollis* workers from 2020.

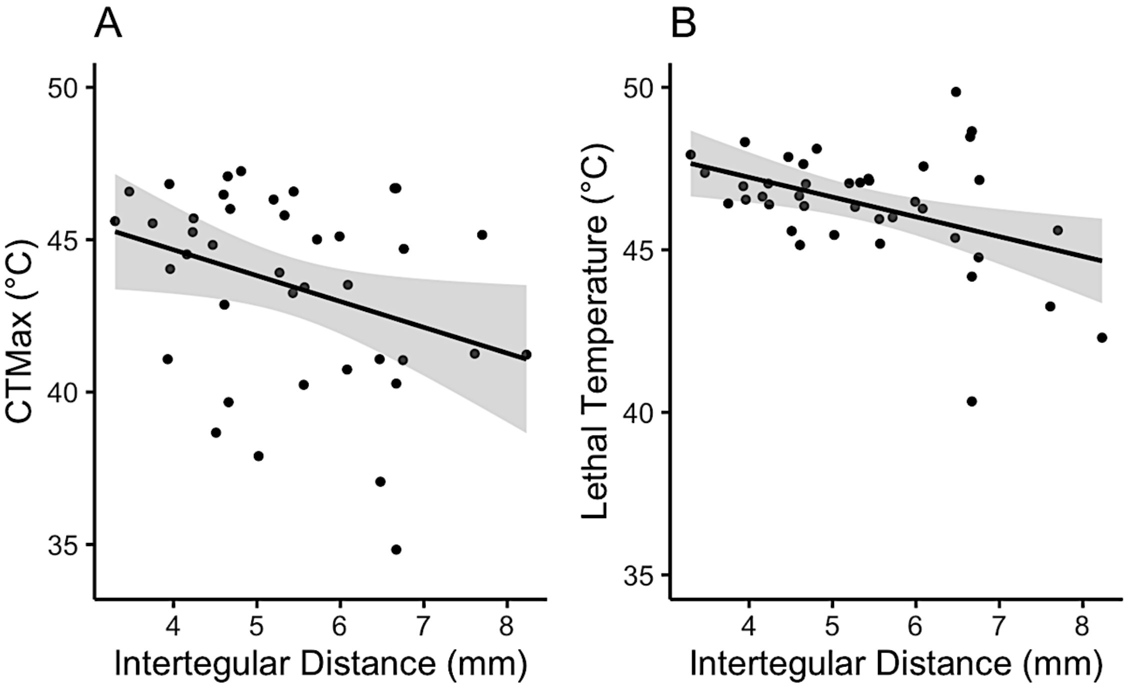


Figure 5–4. Linear regression describing the relationships between intertegular distance (mm) and (A) CT_{Max} and (B) lethal temperatures (°C) for *B. griseocollis* workers from 2020. Shaded regions represent the 95% confidence interval.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Bombus are facing global population declines as a result of factors such as habitat loss, fragmentation, climate change, human mediated introduction of pathogens, and competition with non-native bee species. While the individual impacts of these factors have been well studied, little research has evaluated their cumulative effects on a local or national scale. Additionally, insect monitoring traps unintentionally capture *Bombus* as bycatch, leading to concerns that bycatch may further contribute to *Bombus* declines and the subsequent loss of pollination services for wild and cultivated plant communities. This dissertation underscores the need to assess *Bombus* assemblages under a range of threats and environmental conditions in order to conserve and manage *Bombus* assemblages and pollinator habitats.

I first linked differences in *Bombus* assemblages to landscape composition and climate in Utah agroecosystems. Of the 3,522 *Bombus* from 15 species collected within insect monitoring traps, I found that assemblage composition was highest in sites characterized by more agriculture land cover, low temperatures, and high relative humidity during the growing season; and lowest in sites with more urban land cover, high temperatures, and low relative humidity. However, regardless of species associations, high turnover was observed in *Bombus* species composition, indicating unique assemblages are present at each of the sites. This highlighted the importance of maintaining diverse habitats to promote resiliency of *Bombus* assemblages in the face of anthropogenic disturbance. Additionally, implementing management practices such as minimizing pesticide exposure to foraging bees, planting water-wise native plants, providing suitable nesting sites, reducing the use of weed-barrier fabrics, and avoiding overhead irrigations during daylight hours throughout agricultural sites can help conserve and promote diverse *Bombus* assemblages. Additionally, my collection of *Bombus* from mid-May to mid-September identified phenological overlap within the *Bombus* community, which can help ensure pollination services are provided even if a particular species is lost due to environmental disturbances. Continually monitoring *Bombus* populations will help document shifts in assemblages, loss of species, and potential consequential impacts to ecosystem services. From this study, I took a crucial step towards understanding the cumulative effects of landscape composition and climate on *Bombus* assemblages.

I further examined the cumulative effects of climate and landscape structure on *Bombus* assemblages throughout U.S. agroecosystems. Of the 5,021 *Bombus* representing 18 species collected in insect monitoring traps within Florida, Indiana, Kansas, Kentucky, Maryland, South Carolina, Utah, Virginia, and West Virginia, I found that Utah *Bombus* species were associated with agricultural landscapes with greater compositional and configurational complexity, increased climate seasonality, and lower annual mean temperatures. Meanwhile, eastern *Bombus* species were associated with agricultural landscapes with less compositional and configurational complexity, decreased climate seasonality, and higher annual mean temperatures. Again, I observed high turnover in *Bombus* species composition among sites, indicating that each of the sites in this study have significant conservation value for maintaining unique and diverse *Bombus* communities. In order to support more diverse *Bombus* assemblages, targeted management practices need to be implemented based on the continuum of environmental characteristics throughout the U.S. In simplified agricultural landscapes, I recommend increasing the number and quantity of land cover categories with diverse plant assemblages and diversifying the way in which they are arranged. In complex agricultural habitats, I recommend increasing connectivity between high-quality patches of land. Improving the quality of *Bombus* habitats by increasing access to resources can also help offset the negative effects of climate change on *Bombus* assemblages. Overall, evaluating the cumulative effects of threats on *Bombus* assemblages can yield more realistic results, which can lead to more targeted management and conservation of *Bombus* populations.

These first two studies further verified that insect monitoring traps attract and capture *Bombus* as bycatch throughout the U.S., especially within traps containing pheromone lures for *Helicoverpa armigera.* Given these incidental bee captures, there is a concern that these captures may further contribute to *Bombus* mortality. Therefore, I quantified the impact of traps on *Bombus griseocollis* captures, colony growth, and development by weighing colonies weekly and recording foraging activity. I hypothesized that *H. armigera* pheromone baited multi-colored bucket traps capture *B. griseocollis* from field-released colonies, and that colonies paired with traps and pheromone lures experience greater weight loss and declines in the number of active foragers than those without. I found that pheromone baited traps captured three *B. griseocollis* from field-released colonies. These low capture rates suggest that pest monitoring traps did not alter *B. griseocollis* colony growth or development, though this does not mean that other *Bombus* species are not impacted. Future research should evaluate the effect of trap captures on other *Bombus* species, functional diversity, colony establishment, and pollination services to better understand the impact of pest monitoring traps on *Bombus* assemblages and to minimize risk to pollination services.

In addition to providing pollination services in wild and cultivated plant communities, *Bombus* are also effective pollinators in greenhouse crop production. As a result, several *Bombus* species have been commercialized for use in greenhouse crop production throughout the U.S. However, *B. impatiens,* the eastern bumble bee, is the only widely available species available for purchase, resulting in their release well outside of their native territory. The movement of *Bombus* species to novel environments has led to increased infection rates of pathogens to native *Bombus* species and increased competition for floral and nesting resources. Therefore, I identified a need to develop regionally appropriate candidates for commercialization. In this study, I evaluated the commercialization potential of *B. griseocollis* by assessing nest initiation and establishment rates of colonies produced from wild-caught queens, creating a timeline of colony development, and identifying lab-reared worker's critical thermal maxima (CT_{Max}) and lethal temperature. I successfully reared *B. griseocollis* in a laboratory setting from wild-caught queens, with high nest initiation and establishment rates. This is the first documented case of rearing *B. griseocollis* in a laboratory setting, which adds to the literature on *Bombus* husbandry. Additionally, based on their CT_{Max} and maximum lethal temperature, I identified that *B. griseocollis* can withstand high temperatures before succumbing to spasms and eventually death, which may be advantageous in the face of climate change. Overall, *B. griseocollis* exhibit traits that are conducive to commercialization, and should therefore continue to be evaluated for commercial purposes as an U.S. greenhouse pollinator.

Another important component of this dissertation has been extension outreach to diverse stakeholders. I wrote over 200 fact sheets for non-native bees within Megachilidae, *Anthidium,* and *Osmia,* and illustrated bee morphology diagrams with emphasis on commonly used diagnostic traits for the Exotic Bee ID website (https://idtools.org/id/bees/exotic/). This website was created as a cooperative effort among the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) Identification Technology Program, USDA APHIS Plant Protection and Quarantine, USDA Agricultural Research Service, and Utah State University to develop a screening aid to support the identification of non-native bees. This tool was specifically designed to help non-experts working at ports of entry, state departments of agriculture, and university extension services learn features that are important in the identification of non-native bees. Additionally, I authored newsletter articles on the Exotic Bee ID (Appendix E), and the impacts of land-use and climate variables on *Bombus* in Utah (Appendix F). Disseminating knowledge to diverse stakeholders is vital in conserving and managing *Bombus* assemblages and habitats in the face of pollinator declines. Overall, the cooperator driven, reproducible, ecological research completed in this dissertation informs and enhances management practices of *Bombus* in agroecosystems throughout the U.S.

APPENDICES

APPENDIX A

SUPPLEMENTARY DATA: LAND COVER AND CLIMATE DRIVE SHIFTS IN *BOMBUS* ASSEMBLAGE COMPOSITION

Table A–1. Land cover classes from the USDA National Agricultural Statistics Service Cropscape and Cropland Data Layer aggregated into four land cover types: agriculture, semi-natural, urban, and forest.

Land Cover Types	Land Cover Classes	Attribute Code
Agriculture		
	Corn	1
	Cotton	2
	Rice	3
	Sorghum	4
	Soybeans	5
	Sunflower	6
	Peanuts	10
	Tobacco	11
	Sweet Corn	12
	Pop Corn	13
	Mint	14
	Barley	21
	Durum Wheat	22
	Spring Wheat	23
	Winter Wheat	24
	Other Small Grains	25
	Dbl Crop Winter Wheat/Soybeans	26
	Rye	27
	Oats	28
	Millet	29
	Speltz	30
	Canola	31
	Flaxseed	32
	Safflower	33
	Rape Seed	34
	Mustard	35
	Alfalfa	36
	Other Hay/Non-Alfalfa	37
	Camelina	38
	Buckwheat	39

Sugarbeets	41
Dry Beans	42
Potatoes	43
Other Crops	44
Sugarcane	45
Sweet Potatoes	46
Misc Vegs & Fruits	47
Watermelons	48
Onions	49
Cucumbers	50
Chick Peas	51
Lentils	52
Peas	53
Tomatoes	54
Caneberries	55
Hops	56
Herbs	57
Cherries	66
Peaches	67
Apples	68
Grapes	69
Christmas Trees	70
Other Tree Crops	71
Citrus	72
Pecans	74
Almonds	75
Walnuts	76
Pears	77
Pistachios	204
Triticale	205
Carrots	206
Asparagus	207
Garlic	208
Cantaloupes	209
Prunes	210
Olives	211
Oranges	212
Honeydew Melons	213
Broccoli	214
Avocados	215
Peppers	216
Pomegranates	217
Nectarines	218
Greens	219
Plums	220
Strawberries	221

	Squash	222
	Apricots	223
	Vetch	224
	Dbl Crop Winter Wheat/Corn	225
	Dbl Crop Oats/Corn	226
	Lettuce	227
	Pumpkins	229
	Dbl Crop Lettuce/Durum Wheat	230
	Dbl Crop Lettuce/Cantaloupe	231
	Dbl Crop Lettuce/Cotton	232
	Dbl Crop Lettuce/Barley	233
	Dbl Crop Durum Wheat/Sorghum	234
	Dbl Crop Barley/Sorghum	235
	Dbl Crop Winter Wheat/Sorghum	236
	Dbl Crop Barley/Corn	237
	Dbl Crop Winter Wheat/Cotton	238
	Dbl Crop Soybeans/Cotton	239
	Dbl Crop Soybeans/Oats	240
	Dbl Crop Corn/Soybeans	241
	Blueberries	242
	Cabbage	243
	Cauliflower	244
	Celery	245
	Radishes	246
	Turnips	247
	Eggplants	248
	Gourds	249
	Cranberries	250
	Dbl Crop Barley/Soybeans	251
Semi-Natural		
	Clover/Wildflowers	58
	Sod/Grass Seed	59
	Switchgrass	60
	Fallow/Idle Cropland	61
	Shrubland	64/152
	Barren	65/131
	Clouds/No Data	81
	Water	83
	Wetlands	87
	Nonag/Undefined	88
	Aquaculture	92
	Open Water	111
	Perennial Ice/Snow	112
	Grassland/Pasture	176
	Woody Wetlands	190

	Herbaceous Wetlands	195
Urban		
	Developed	82
	Developed/Open Space	121
	Developed/Low Intensity	122
	Developed/Med Intensity	123
	Developed/High Intensity	124
Forest		
	Forest	63
	Deciduous Forest	141
	Evergreen Forest	142
	Mixed Forest	143

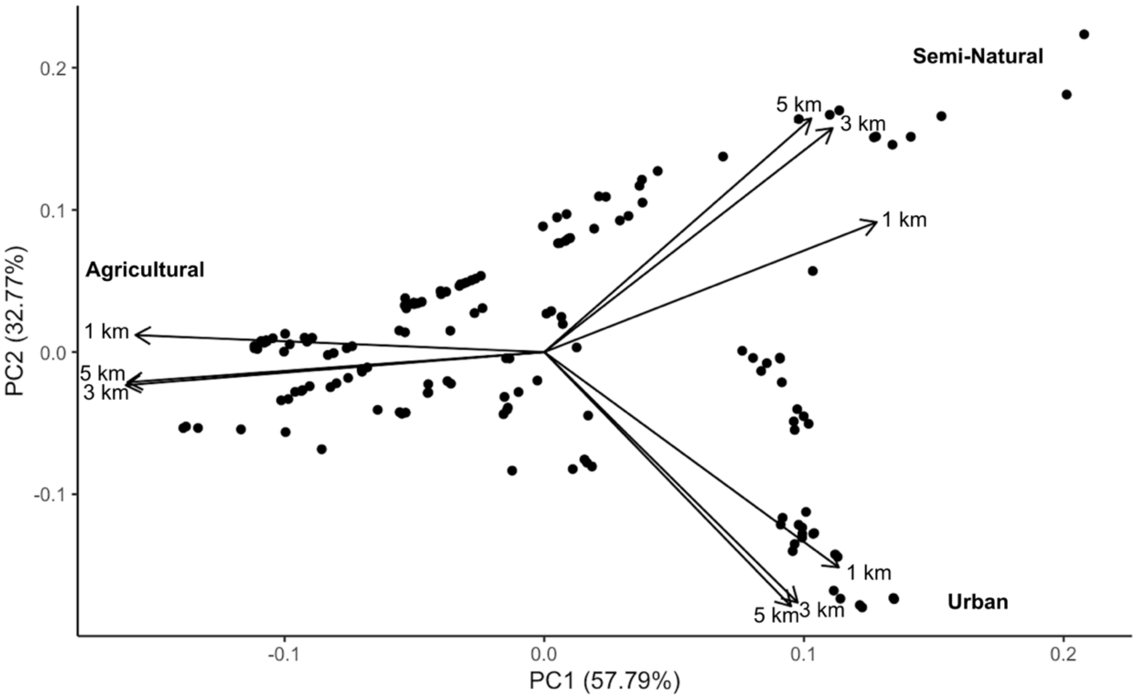


Figure A–1. Principal component analysis of the 180 agricultural sites (black points) surveyed in Utah in relation to the proportion of agricultural, urban, and semi-natural land cover at a 1, 3, and 5 km spatial scale (black arrows). Spatial scales were clustered by land cover type.

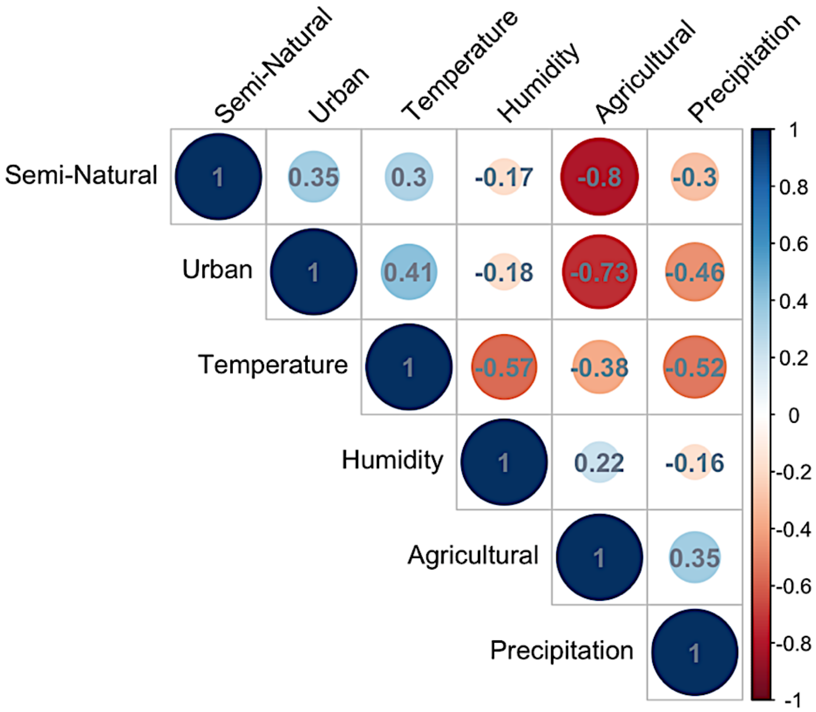
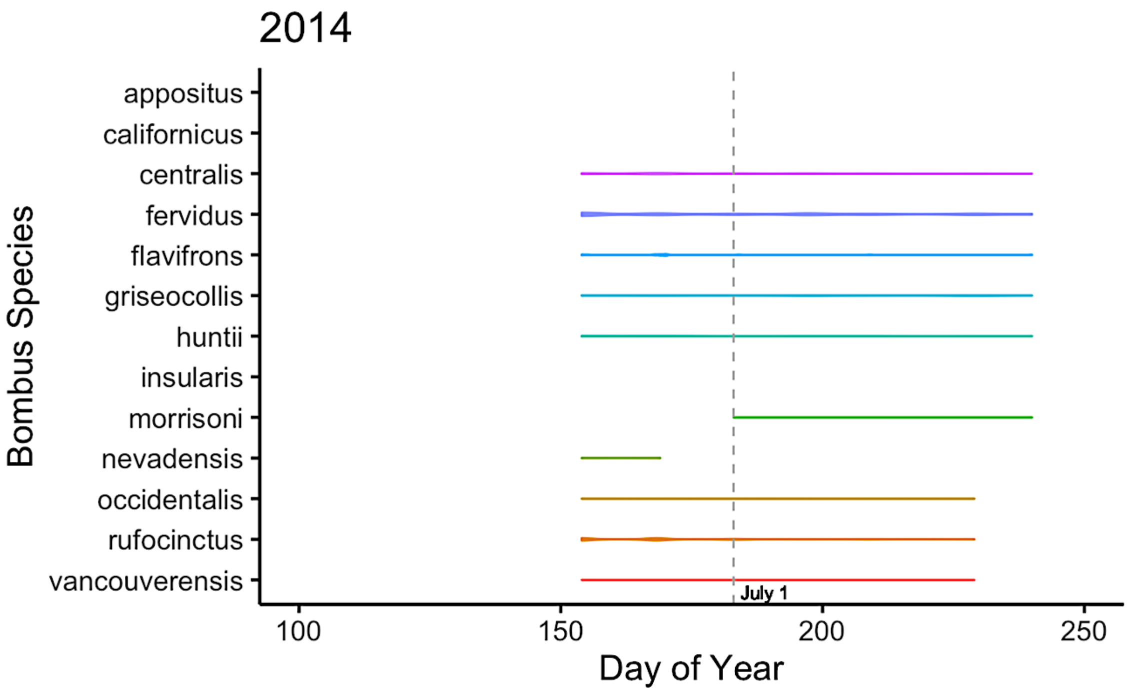
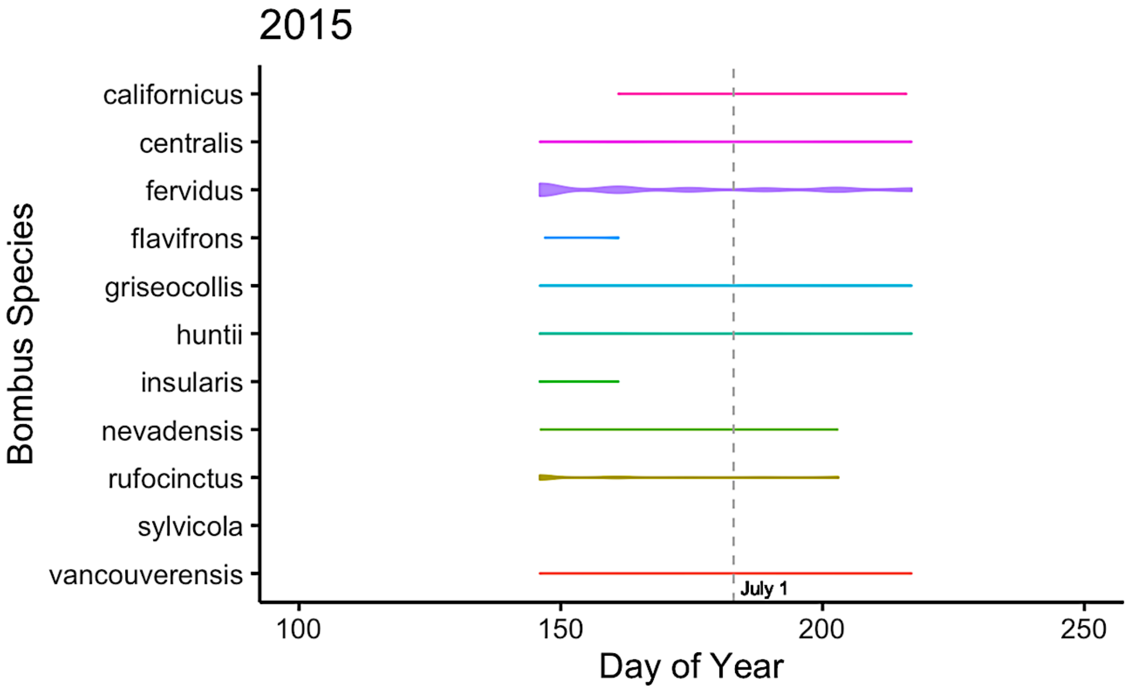
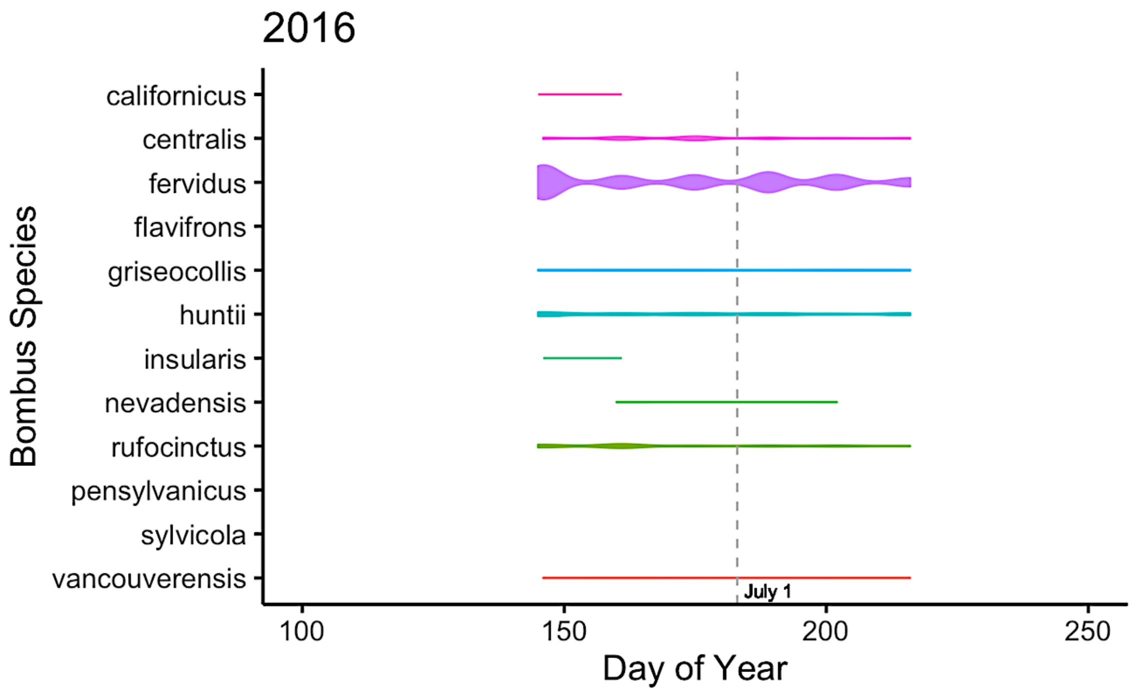
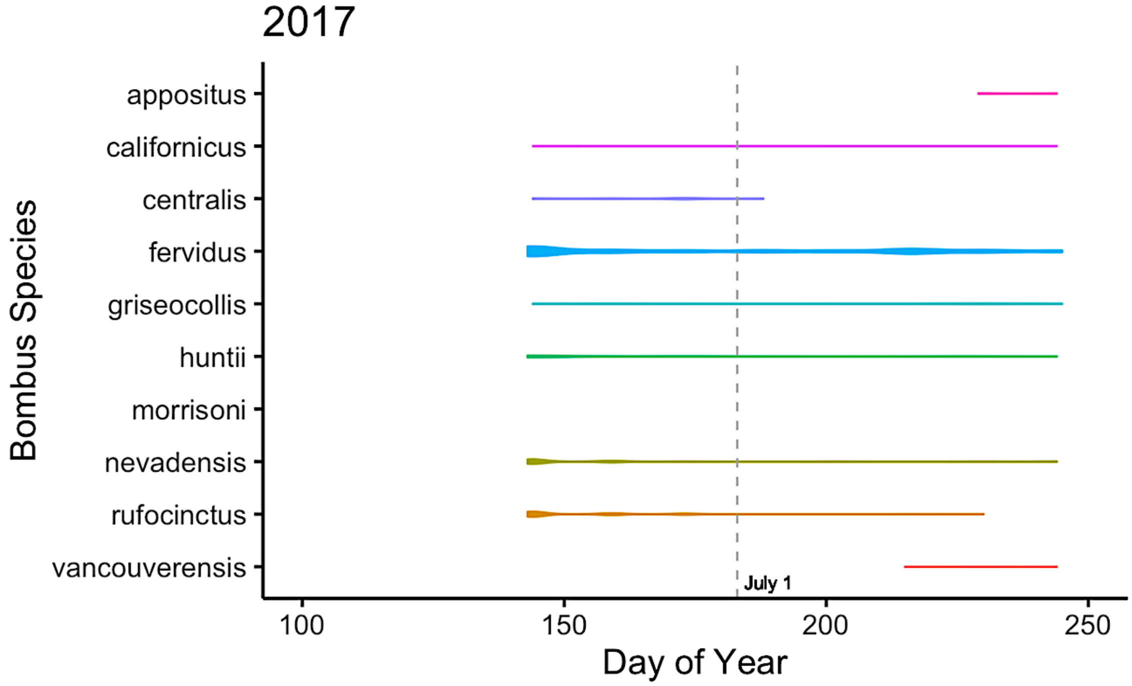


Figure A–2. Correlation matrix across all combinations of explanatory variables. Positive correlations are denoted in blue, while negative correlations are displayed in red. Color intensity and circle size are proportional to the correlation coefficients. Correlation coefficients are denoted in grey.


2014
Bombus Species
appositus
californicus
centralis
fervidus
flavifrons
griseocollis
huntii
insularis
morrisoni
nevadensis
occidentalis
rufocinctus
vancouverensis
July 1
100
150
200
250
Day of Year


2015
Bombus Species
californicus
centralis
fervidus
flavifrons
griseocollis
huntii
insularis
nevadensis
rufocinctus
sylvicola
vancouverensis
July 1
100
150
200
250
Day of Year


2016
Bombus Species
californicus
centralis
fervidus
flavifrons
griseocollis
huntii
insularis
nevadensis
rufocinctus
pensylvanicus
sylvicola
vancouverensis
July 1
100
150
200
250
Day of Year


2017
Bombus Species
appositus
californicus
centralis
fervidus
griseocollis
huntii
morrisoni
nevadensis
rufocinctus
vancouverensis
July 1
100
150
200
250
Day of Year

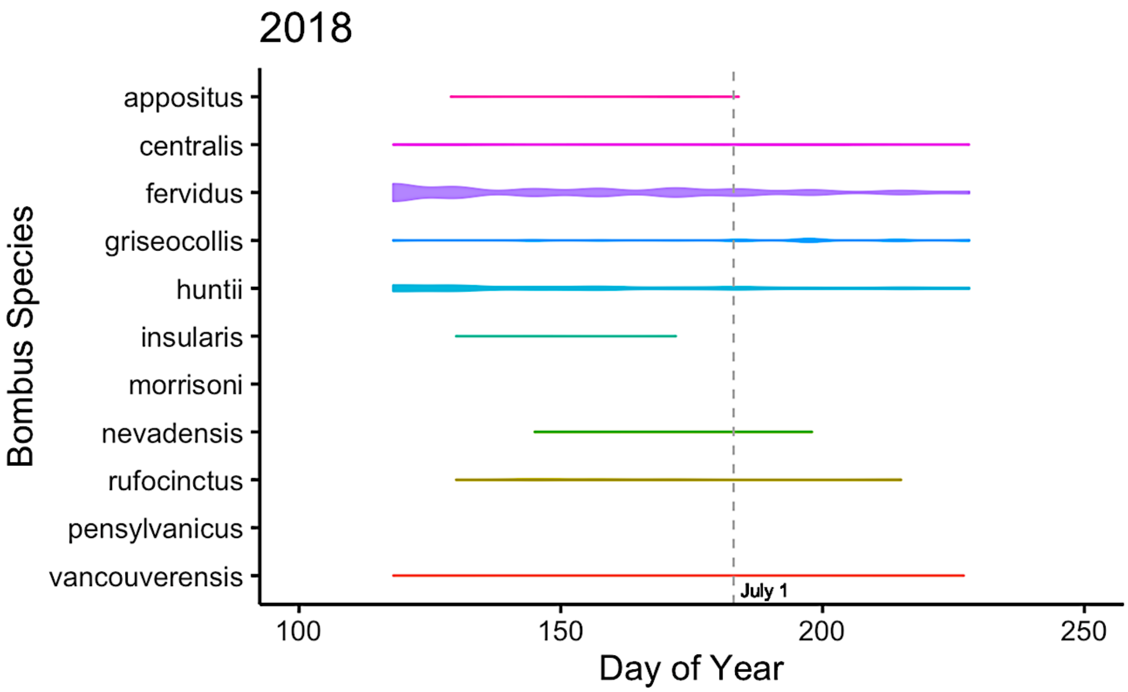
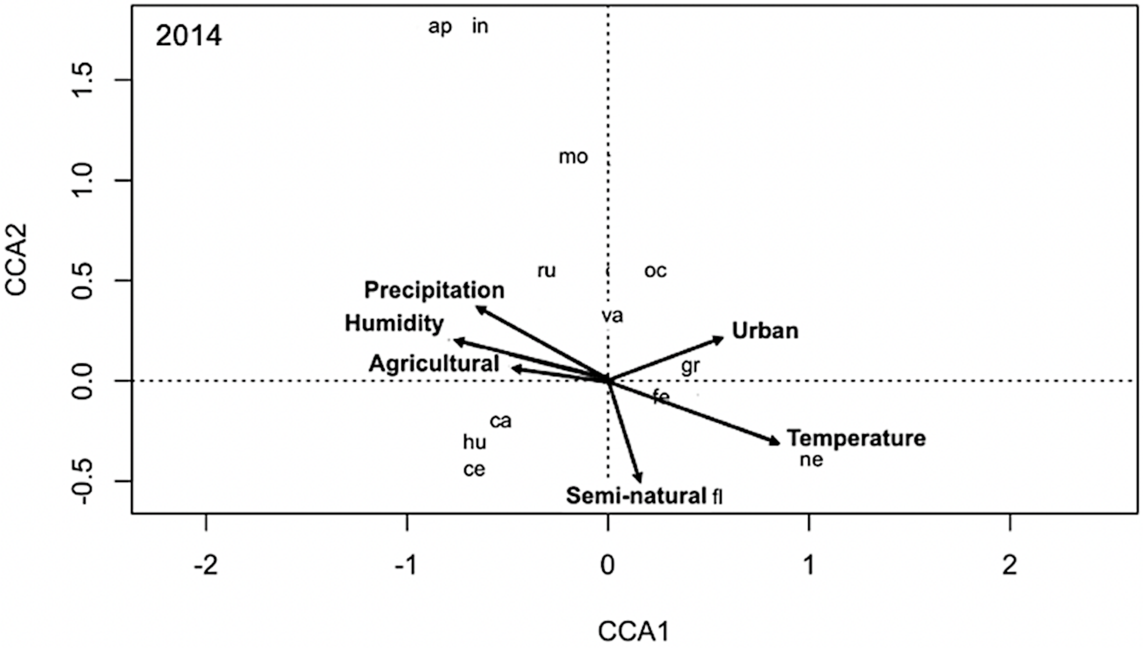
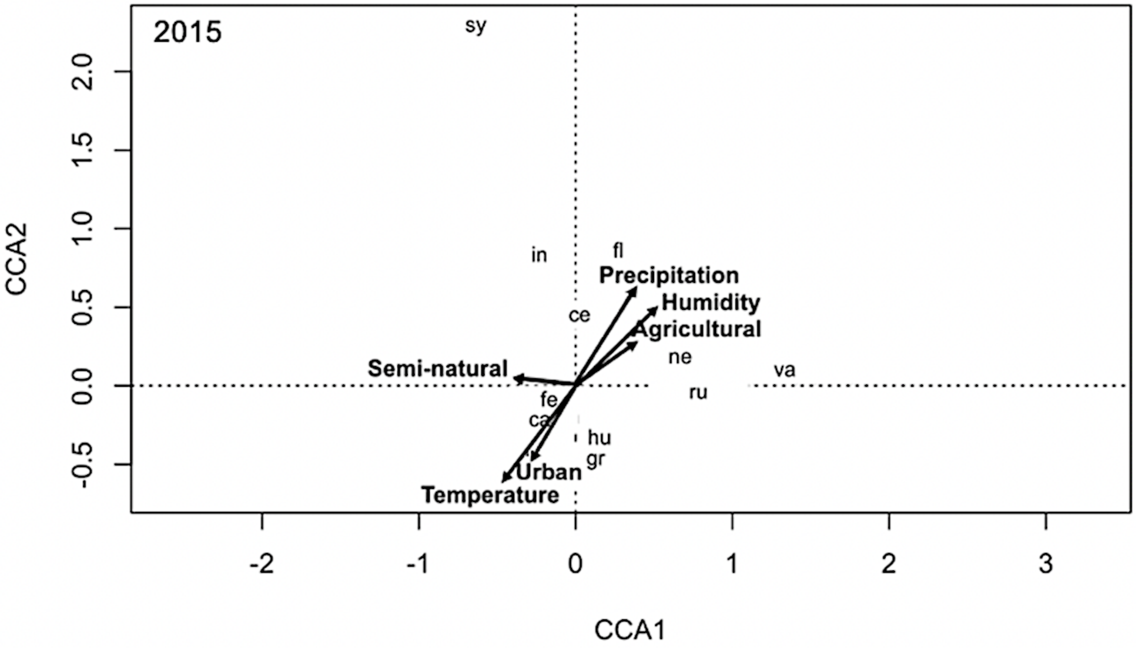
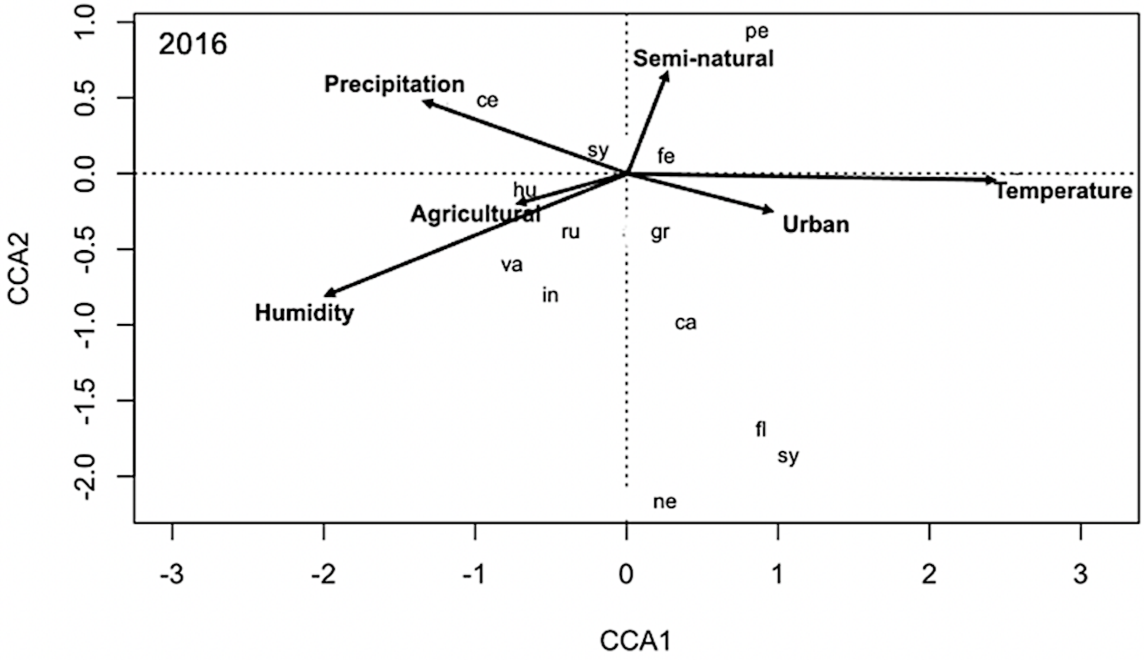
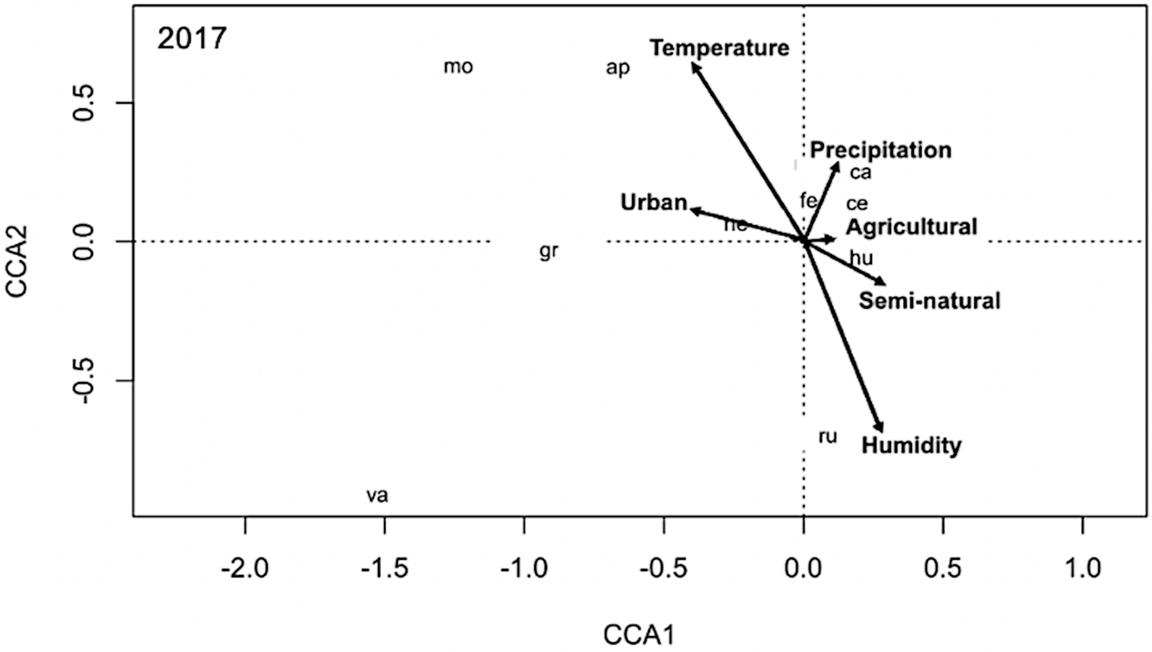


Figure A–3. Violin plot of *Bombus* species collected from late April to mid-September each year from 2014 to 2018. Line width indicates the relative number of specimens collected.


2014
CCA2
CCA1
1.5
1.0
0.5
0.0
-0.5
-2
-1
0
1
2
ap
in
mo
ru
oc
va
gr
fe
ca
hu
ce
ne
fl
Precipitation
Humidity
Agricultural
Urban
Temperature
Semi-natural


2015
CCA2
CCA1
2.0
1.5
1.0
0.5
0.0
-0.5
-2
-1
0
1
2
3
sy
in
fl
ce
ne
va
ru
fe
ca
hu
gr
Precipitation
Humidity
Agricultural
Semi-natural
Urban
Temperature


2016
pe
Semi-natural
Precipitation
ce
sy
fe
hu
Agricultural
Temperature
Urban
ru
gr
va
in
Humidity
ca
fl
sy
ne
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
CCA2
-3
-2
-1
0
1
2
3
CCA1


2017
mo
ap
Temperature
Precipitation
ca
Urban
fe
ce
ne
Agricultural
gr
hu
Semi-natural
ru
Humidity
va
0.5
0.0
-0.5
CCA2
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
CCA1

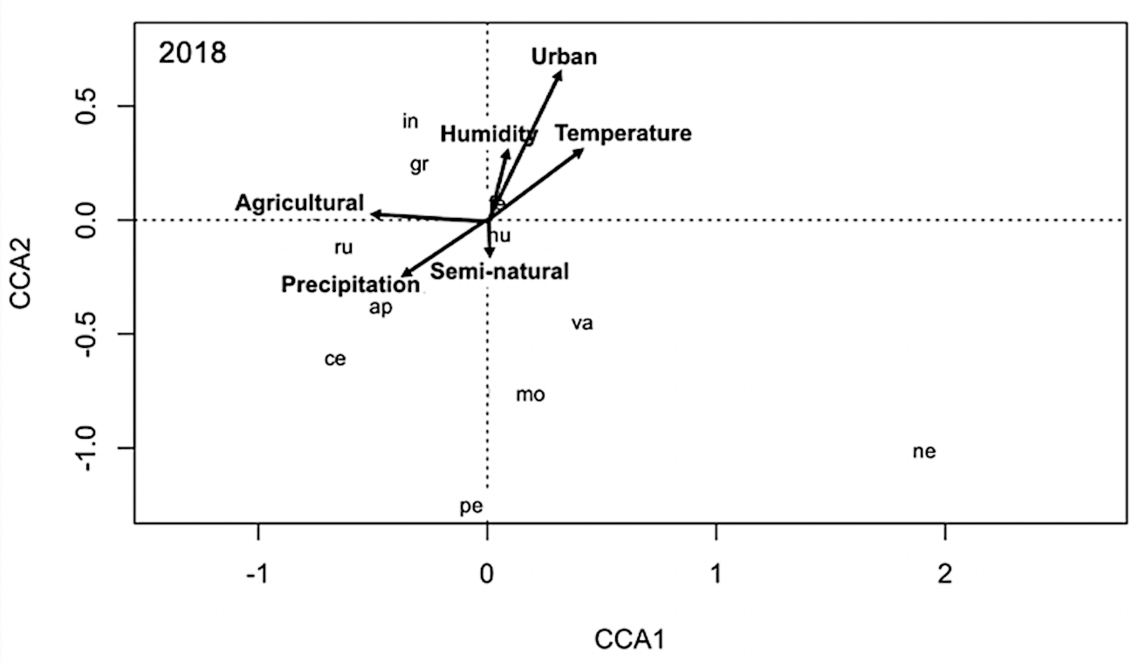


Figure A–4. Canonical correspondence analyses of the *Bombus* assemblage data in relation to environmental variables (indicated by arrows) by year from 2014 to 2018. *Bombus* species names are abbreviated as *ap = B. appositus, ca = B. californicus, ce = B. centralis, fe = B. fervidus, fl = B. flavifrons, 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.*

APPENDIX B

PRELIMINARY DATA: ASSESSING THE IMPACT OF PEST MONITORING TRAPS ON *BOMBUS* GRISEOCOLLIS (HYMENOPTERA: APIDAE) COLONY GROWTH AND DEVELOPMENT

Materials and Methods

Study Area and Experimental Design

In 2019, this study was conducted in corn and vegetable fields in Cache, Box Elder, Davis, and Salt Lake counties. The four treatments occurred with five randomized replicates for each crop type (N = 40; n = 20 for corn, n = 20 for vegetable). Trap, survey, and treatment methods were consistent with those used in 2020 and 2021.

Bombus Rearing

A total of 80 wild *Bombus griseocolli*s queens emerging from dormancy were net collected in northern Utah from May to June in 2019. Rearing methodology was consistent with those used in 2020 and 2021.

Field Design

Colonies were deployed on 22 July, 8 August, and 17 August 2019. Each colony was placed inside a cardboard box with large ventilation holes and an entrance/exit hole, and then placed above the ground on a milk crate in a shaded area of the field to allow for foraging and to reduce the risk of overheating. A cafeteria tray was placed on top of the cardboard box to provide additional shade, and a brick was placed on top to prevent the colony from being blown over (Fig. B–1). The colonies were monitored from July to September in 2019 following the same methodology used in 2020 and 2021. There were major experimental design flaws with this field set up, which negatively impacted data quality. First, inconsistent deployment dates created inconsistencies when comparing cumulative weight change and foraging activity. Second, cardboard boxes with cafeteria trays did not provide the colonies with adequate protection from the elements, causing many colonies to die or flee the colony as a result of heat stress. Significant adjustments were made in 2020 and 2021 to account for these flaws in experimental design. As such, data collected in 2019 was used as preliminary data.

All other methods (monitoring colony weight and foraging activity, DNA extraction and microsatellite PCR amplification, and data analysis) were consistent with 2020 and 2021.

Results

In 2019, 85 *Bombus* from eight species (*B. centralis, B. fervidus, B. flavifrons, B. griseocollis, B. huntii, B. insularis, B. rufocinctus,* and *B. vancouverensis*) were collected in multi-colored bucket traps or via aerial netting. Eight *B. griseocollis* were collected in traps (four 5 m from the colony, four 100 m away) and two were collected via aerial netting (100 m from the colony). Based on microsatellite PCR amplification, one of the *B. griseocollis* captured 5 m from the colony was from a field-released colony.

In corn fields, colony-only (treatment i), colony and trap (treatment ii), and colony, trap, and lure (treatment iii) had cumulative mean weight losses of 10.4 ± 7.6 g, 8.2 ± 7.01 g, and 10 ± 3.4 g, respectively (Fig. B–2). In vegetable fields, colony-only (treatment i), colony and trap (treatment ii), and colony, trap, and lure (treatment iii) had cumulative mean weight losses of 6.8 ± 7.6 g, 8.6 ± 4.7 g, and 9.8 ± 3.4 g, respectively (Fig. B–2). Cumulative colony weight change did not differ among treatments ($F = 0.321$; $df = 2, 25$; $p = 0.728$).

In corn fields, colony-only (treatment i), colony and trap (treatment ii), and colony, trap, and lure (treatment iii) had an average activity of 0.59 ± 0.42 bees, 0.80 ± 0.79 bees, and 0.22 ± 0.36 bees, respectively (Fig. B–3). In vegetable fields, colony-only (treatment i), colony and trap (treatment ii), and colony, trap, and lure (treatment iii) had an average activity of 0.53 ± 0.73 bees, 0.44 ± 0.41 bees, and 0.36 ± 0.29 bees, respectively (Fig. B–3). *Bombus griseocollis* colony activity did not differ among treatments ($F = 0.839$; $df = 2, 26$; $p = 0.444$).

Figures

Figure B–1. *Bombus* colony on the edge of a vegetable field with two bucket traps. Bucket trap placed 100 meters from the colony is not in range in the photo.

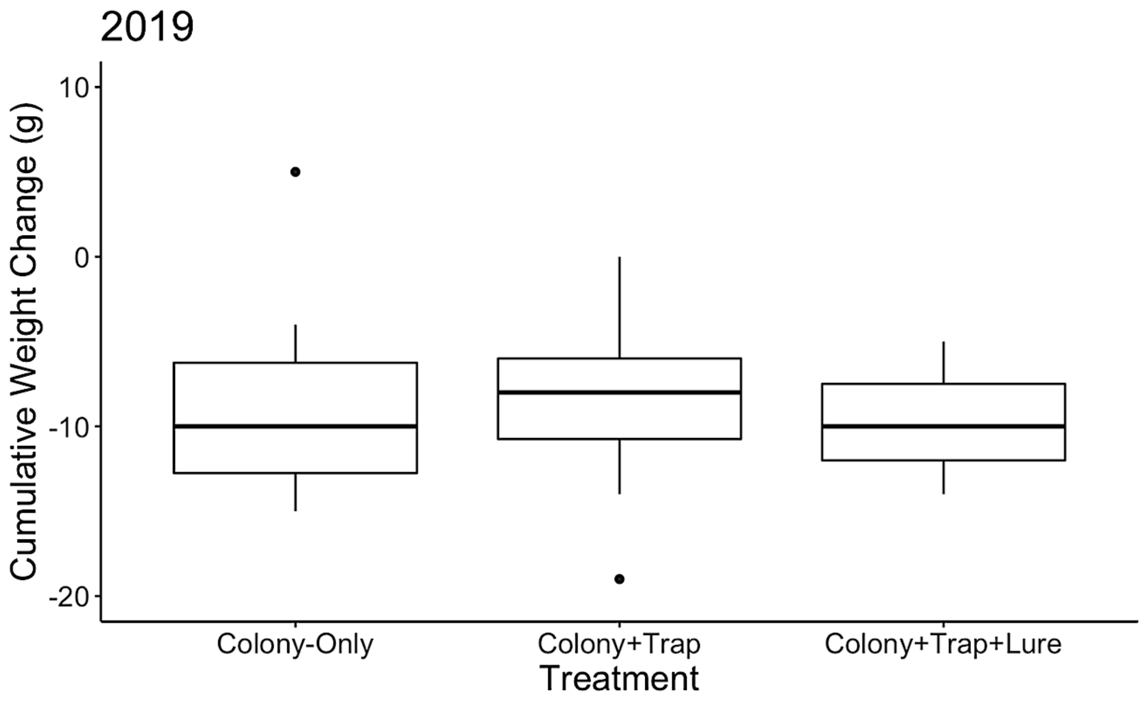


Figure B–2. Box plot of the cumulative weight change of *B. griseocollis* colonies for each treatment type in 2019.

Figure B–3. Box plot of average *B. griseocollis* colony activity for each treatment type in 2019.

APPENDIX C

SUPPLEMENTARY DATA: COMMERCIALIZATION POTENTIAL OF *BOMBUS GRISEOCOLLIS* (HYMENOPTERA: APIDAE): EVALUATING CAPTIVE REARING SUCCESS AND CRITICAL THERMAL MAXIMA

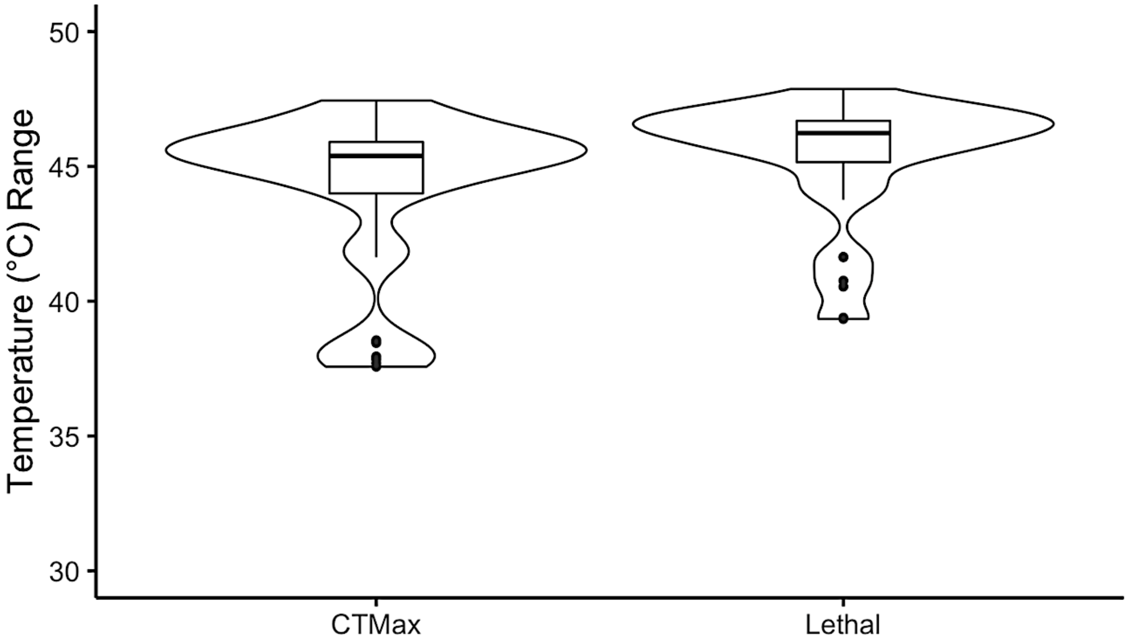


Figure C–1. Range of CT_{Max} and lethal temperatures (ºC) for *B. impatiens* workers from 2020.

APPENDIX D

LETTERS OF PERMISSION

1 March 2022

To whom it may concern:

I, Jonathan B. Koch, grant Morgan Christman permission to use “Assessing the impact of pest monitoring traps on *Bombus griseocollis* (Hymenoptera: Apidae) colony growth and development” and “Commercialization potential of *Bombus griseocollis* (Hymenoptera: Apidae): evaluating captive rearing success and critical thermal maxima”, of which I am a coauthor, in her dissertation.

Sincerely,

Jonathan B. Koch

1 March 2022

To whom it may concern:

I, Thuy Tien Lindsay, grant Morgan Christman permission to use “Assessing the impact of pest monitoring traps on *Bombus griseocollis* (Hymenoptera: Apidae) colony growth and development” and “Commercialization potential of *Bombus griseocollis* (Hymenoptera: Apidae): evaluating captive rearing success and critical thermal maxima”, of which I am a coauthor, in her dissertation.

Sincerely,

1 March 2022

To whom it may concern:

I, Cody Barnes, grant Morgan Christman permission to use “Commercialization potential of *Bombus griseocollis* (Hymenoptera: Apidae): evaluating captive rearing success and critical thermal maxima”, of which I am a coauthor, in her dissertation.

Sincerely,

Cody L. Barnes

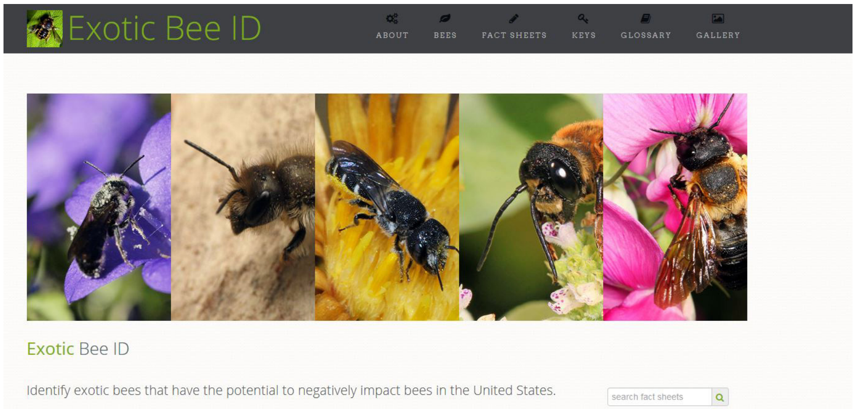
APPENDIX E

A NEW TOOL FOR IDENTIFYING EXOTIC BEES (UTAH PESTS QUARTERLY NEWSLETTER PUBLISHED VERSION)

ENTOMOLOGY NEWS AND INFORMATION

A New Tool for Identifying Exotic Bees

Exotic Bee ID is a new web tool to help reduce risks of non-native bee introductions. The site can be accessed at idtools.org/id/bees/exotic



Exotic Bee ID

Identify exotic bees that have the potential to negatively impact bees in the United States.

Bees play an essential role in ecosystem function as the dominant insect pollinators in both agricultural and natural landscapes. Unfortunately, the number of native bee species and bee populations in the U.S. are declining due to habitat loss, pesticides, parasites and pathogens, and the introduction of non-native bees and other insects.

Currently, there are 46 known non-native bee species established within the U.S. that were either intentionally or accidentally introduced. For example, a few non-native species, such as the horn-faced bee (*Osmia cornifrons*) and the European orchard bee (*Osmia cornuta*), have been intentionally introduced in the U.S. for commercial crop pollination. Many accidental introductions are due to the nesting behavior of the bee (such as in rock crevices, plant stems, or man-made structures), allowing them to be easily carried with cargo or baggage into the U.S. A well-known example is the crevice-nesting European wool carder bee (*Anthidium manicatum*) which was introduced in eastern North America in the early 1960s. This bee has a strong ability to colonize urban environments, which has allowed it to spread across the U.S. and into other countries. Whether intentional or accidental, these introductions are problematic because non-native bee species compete with native bees for flower resources and nesting sites, introduce and transmit pathogens and parasites, modify the local plant-pollinator community, and enhance the spread of non-native plants.

The European wool carder bee is an exotic bee that has successfully spread throughout the U.S.

Proper identification is crucial to preventing new introductions. *Exotic Bee ID* is a comprehensive and sophisticated new web tool to help identify both native and non-native bees. The website is a multi-year collaborative project with USDA APHIS Identification Technology Program (ITP), Utah State University, USDA APHIS PPQ, and USDA ARS.

Exotic Bee ID contains interactive identification keys, fact sheets, an image gallery, and supporting information for easy bee identification of 9 species, 3 subgenera, and 77 genera. Currently, the primary focus is bee genera within the family Megachilidae (leaf cutting bees, mason bees, carder bees), and bees in the genus *Apis* (honey bees, family Apidae). Interactive keys allow users to select characteristics that apply to their target specimens. Fact sheets can be used to find images and information on a particular bee genus or species, including their distribution, diagnostic characteristics, host associations,

continued on next page

and nesting behaviors. The image gallery allows the user to compare images from differing groups of bees. Additionally, this resource can be used to learn about bee biology, behavior, and the relevant terminology used for identification.

The project team is continuing to add content and keys to identify many other native and non-native bees including additional species from *Pseudoanthidium* (Megachilidae), *Osmia* (Megachilidae), *Anthidium* (Megachilidae), *Megachile* (Megachilidae), *Xylocopa* (Apidae), and *Ceratina* (Apidae). The team is focusing on these groups because they include the majority of bees that have already been introduced into or have the high potential to invade the U.S.

Exotic Bee ID is aimed primarily at individuals working at ports of entry, state departments of agriculture, and university extension services, as well as citizen scientists with an interest in bees. Overall, the goal of this tool is to help reduce the loss of valuable native bee pollinators through early detection of non-native species.

—— Morgan Christman, USU Biology Graduate Student,
Lori Spears, USU CAPS Coordinator, and
Ricardo Ramirez, Extension Entomologist

The ***Exotic Bee ID*** website includes hundreds of vivid bee images, including this one, showing the scutellum (portion of the thorax) of a female *Osmia calla*.

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APPENDIX F

WHERE THE WILD BEES ARE: IDENTIFYING LAND-USE AND CLIMATE VARIABLES IMPACTING BUMBLE BEES IN UTAH (UTAH PESTS QUARTERLY NEWSLETTER PUBLISHED VERSION)

UTAH PESTS QUARTERLY
NEWSLETTER
Fall 2021
Vol. XV
Utah Plant Pest Diagnostic Laboratory
USU Extension

IN THIS ISSUE

NEW MEDIA

- Beginner's Guide to Common Native Bees
- Invasive Species Handbook
- Recordings of Vegetable IPM Twilight Meetings (beneficials, drones, gophers, and more)
- Sycamore Scale
- Video: How to Scout
- What is Biochar and How is it Used?

WHERE THE WILD BEES ARE:

Identifying Land-Use and Climate Variables Impacting Bumble Bees in Utah

Wild and managed bees play pivotal roles in maintaining agricultural productivity and wild plant communities by pollinating flowering plants. Bumble bees, for example, increase agricultural productivity of crops grown in greenhouses, which are not typically pollinated by managed bee species such as honey bees. Bumble bees benefit producers by reducing production costs and increasing crop quality and yield, particularly for crops that are predominantly hand-pollinated. Bumble bee communities thrive in semi-natural and diverse habitats which provide a variety of nesting and floral resources.

Unfortunately, bumble bee populations are negatively impacted by human-caused disturbances, such as urbanization, agricultural intensification, and climate change. Specifically, impervious surfaces such as roads and buildings reduce nesting sites and monoculture farming reduces floral resources. Weather patterns impact bumble bee phenology (timing of life history events), distribution, and resilience. As the climate changes, more bumble bee species are being found at higher elevations. This is problematic given the limited resources in these environments and the possibility that bee activity and flowering will not overlap. Bumble bee species that are climate-sensitive, living in fragmented or low-elevation habitats, or are already at their upper elevation limit, have an increased likelihood of local extinction as suitable habitats disappear.

In a study investigating bee captures in pest-insect bucket traps, the golden northern bumble bee, *Bombus fervidus*, was the most commonly collected species.

In Utah, bumble bees are impacted by urbanization around agricultural lands, loss of agricultural lands to development, and a hotter and drier climate, trends that will likely continue in the coming decades. Identifying land-use and climate conditions that influence bumble bee species in Utah could help land managers, researchers, and other interested parties develop more effective and targeted strategies to increase resiliency of bumble bee populations in changing environments.

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extension.usu.edu/pests

Land-Use and Climate Impacting Bumble Bees, continued

Multi-colored bucket traps have been placed throughout Utah for insect pest monitoring for many years. Sometimes, bumble bees were captured in these traps, and that bee catch data were used for this study.

Morgan Christman and team (USU Biology) researched bumble bee abundance and diversity based on land use and weather variables in Utah agroecosystems. The research team utilized data from bucket traps that were set at the edge of corn and alfalfa fields located in either rural or urbanized areas in Cache, Box Elder, Weber, Utah, and Millard counties. From 2014 to 2018, the team recorded a total of 3,522 bumble bees representing 15 species. The most common species were:

- Golden northern bumble bee, *Bombus fervidus*
- Hunt's bumble bee, *Bombus huntii*
- Red-belted bumble bee, *Bombus rufocinctus*
- Central bumble bee, *Bombus centralis*
- Brown-belted bumble bee, *Bombus griseocollis*

The research team found bumble bee species abundance and diversity was highest in the rural agricultural fields with low temperatures and high relative humidity during the growing season, and lowest in the urbanized agricultural fields with high temperatures and low relative humidity. However, differences in bumble bee species among sites suggest that all corn and alfalfa fields from this study have high conservation value for bumble bee communities. Therefore, management practices to promote bees should be focused in both rural and urbanized agricultural areas to foster future resiliency of bumble bee populations in the face of human-caused disturbances.

Land managers interested in promoting bee abundance and diversity are encouraged to integrate practices that reduce pesticide poisoning of bees, diversify agricultural areas, and increase floral resources and nesting sites. Specifically, pesticides that are non-toxic to bees should be selected and applied following the "Bee Advisory Box" on the label, which provides steps to minimize exposure of pesticides to bees while they are foraging. Planting water-wise native plants such as western prairie clover, Russian sage, and yarrow within gardens and yards diversifies the landscape while providing bees with nectar and pollen, which is needed to feed themselves and their offspring. To provide suitable nesting sites, consider keeping some small patches of well-drained, bare soil surfaces. Additionally, avoiding overhead irrigation during the daylight hours, reducing the use of weed-barrier fabric, and using mulch sparingly can provide more suitable habitats for bees.

——— Morgan Christman, graduate student, Biology (PhD),
Lori Spears, USU CAPS Coordinator, and Ricardo Ramirez, Entomologist

For more information

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Cane J.H. & Kervin, L. (2013). Gardening for native bees in Utah and beyond. [Fact Sheet] Utah State University Extension.

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Environmental Protection Agency. (2013). The new EPA bee advisory box: On EPA's new and strengthened pesticide label. Environmental Protection Agency.

APPENDIX G

CURRICULUM VITAE

Morgan Christman

Utah State University | Department of Biology
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EDUCATION

Ph.D., Ecology. Utah State University. Logan, UT 2017–2022
Climate Adaptation Science, National Science Foundation Traineeship Program
Geographic Information Systems Certificate
Advisors: Drs. Ricardo Ramirez and Lori Spears
Dissertation: *An evaluation of landscape, climate, and management impacts on bumble bees (Hymenoptera: Apidae: Bombus) in agroecosystems*

B.S., Biology; B.A., Environmental Studies. Denison University. Granville, OH 2013–2017
Advisor: Dr. Thomas Schultz
Senior Thesis: *Comparative study of insect diversity at three successional landscapes*

PROFESSIONAL EXPERIENCE

Graduate Research Assistant. Utah State University. Logan, UT 2017–2022
Advisors: Drs. Ricardo Ramirez and Lori Spears, Department of Biology & Ecology Center

- Integrated field research and advanced quantitative procedures to evaluate the impact of anthropogenic disturbances on bumble bee assemblages on multiple spatial and temporal scales in agroecosystems to provide the scientific basis for management decisions and conservation practices
- Collected and identified 7,796 specimens representing 21 bumble bee species
- Conducted cooperator driven, applied ecological research on the impact of bycatch on bumble bee colony growth and development
- Reared 216 *Bombus griseocollis* colonies in a controlled lab setting, assessed nest initiation and establishment rates, and created a timeline of colony development
- Performed thermal tolerance trials, lipid extractions, DNA extractions, and microsatellite PCR amplification on *Bombus*
- Wrote 211 fact sheets and illustrated bee morphology diagrams for Exotic Bee ID, a screening aid to support identification of non-native bees
- 1 invited research presentation; 8 contributed research presentations; 2 research publications; 3 extension publications; 1 open-source website
- Supervised 12 undergraduate research technicians in a field and laboratory setting while providing professional, educational, and personal support

Climate Adaptation Science Trainee. Utah State University. Logan, UT 2018–2020
Advisor: Dr. Nancy Huntly, Ecology Center Director

- Designed and implemented a collaborative and interdisciplinary research project to develop a climate risk assessment of northern goshawks in Utah national forests
- Predicted mountain pine beetle risk susceptibility in Utah national forests from 2020 to 2100 using U.S. Forest Service Forest Vegetation Simulator software
- 5 contributed research presentations

Utah Statewide Wellbeing Survey Programmer. Utah State University. Logan, UT 2020
Advisor: Dr. Courtney Flint, Department of Environment and Society

- Produced relevant data visualizations using qualitative survey data on personal and community wellbeing in Utah
- 2 extension publications

Utah Wildlife Migration Initiative Intern. Department of Natural Resources 2019
Division of Wildlife Resources. Salt Lake City, UT
Advisor: Dr. Daniel Olson, Utah Department of Natural Resources

- Developed a database in RShiny to allow wildlife migration and covariate data to be visualized, mined, and analyzed by internal Wildlife Migration Initiative stakeholders

Undergraduate Researcher. Denison University. Granville, OH 2017
Advisor: Dr. Andrew McCall, Department of Biology

- Assisted in the collection and identification of spicebush pollinators

Undergraduate Researcher. Denison University. Granville, OH 2016–2017
Advisor: Dr. Thomas Schultz, Department of Biology

- Conducted a comparative study of insect diversity at three successional landscapes
- Identified 4,233 insect specimens representing 76 families, and 12 orders
- 3 contributed research presentations

Undergraduate Researcher. Denison University. Granville, OH 2015
Advisor: Dr. Geoff Smith, Department of Biology and Dr. John Iverson, Earlham College

- Captured, weighed, measured, and PIT tagged 455 Allen's Cay rock iguanas on three islands to determine the effects of tourism on the size and growth of the iguanas
- 2 contributed research presentations

RESEARCH PUBLICATIONS

Spears, L. R., **M. E. Christman**, J. B. Koch, C. Looney, and R. A. Ramirez. 2021. A review of bee captures in pest monitoring traps and future directions for research and collaboration. Journal of Integrated Pest Management 12: 1–12. https://doi.org/10.1093/jipm/pmab041

Christman, M. E., L. R. Spears, J. P. Strange, W. D. Pearse, E. K. Burchfield, and R. A. Ramirez. 2022. Land cover and climate drive shifts in *Bombus* assemblage composition. (*Under Review*) http://dx.doi.org/10.2139/ssrn.4000300

EXTENSION PUBLICATIONS

Burrows, S., C. Ritner, **M. Christman**, L. R. Spears, A. Smith-Pardo, S. Price, R. A. Ramirez, T. Griswold, and A. J. Redford. 2021. Exotic Bee ID – Edition 3. USDA APHIS Identification Technology Program (ITP), Fort Collins, CO. http://idtools.org/id/bees/exotic

Christman, M., L. R. Spears, and R. A. Ramirez. 2021. Where the wild bees are: identifying land-use and climate variables impacting bumble bees in Utah. Utah Pests News, Utah Plant Pest Diagnostic Laboratory and USU Extension. Vol. 15: Fall edition. https://extension.usu.edu/pests/files/up-newsletter/2021/UtahPestsNews-fall21.pdf

Flint, C., C. Trout, **M. Christman**, and R. Sagers. 2020. Utah Statewide Wellbeing Survey Report. Utah State University Extension. https://extension.usu.edu/business-and-community/utah-wellbeing-project/files/Statewide-Wellbeing-Survey-Report-2020.pdf

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Burrows, S., **M. Christman**, L. R. Spears, A. Smith-Pardo, S. Price, R. A. Ramirez, T. Griswold, and A. J. Redford. 2018. Exotic Bee ID – Edition 1. USDA APHIS Identification Technology Program (ITP), Fort Collins, CO. http://idtools.org/id/bees/exotic

Christman, M. E., L. R. Spears, and R. A. Ramirez. 2018. A new tool for identifying exotic bees. Utah Pests News, Utah Plant Pest Diagnostic Laboratory and USU Extension. Vol. 12: Fall edition. https://extension.usu.edu/pests/files/up-newsletter/2018/UtahPests-Newsletter-fall18.pdf

RESEARCH PRESENTATIONS

Invited

Christman, M. E., L. Spears, and R. Ramirez. 2019. Exploring the landscape ecology of bumble bees in agroecosystems using bycatch. Entomological Society of America. St. Louis, MO. 19 November. *Invited oral presentation*

Contributed

Christman, M., L. Spears, and R. Ramirez. 2021. Incidental captures of *Bombus* species in pest traps: a national survey to evaluate the cumulative effects of climate and land-use on *Bombus* assemblages. Entomological Society of America. Denver, CO. 1 November. *Oral presentation*

Christman, M., L. Spears, and R. Ramirez. 2020. Assessing the impact of bycatch on *Bombus griseocollis* colony growth and development. Entomological Society of America. Virtual Meeting. 11–30 November. *Oral presentation*

Christman, M., L. Spears, and R. Ramirez. 2020. Incidental captures of *Bombus* species in traps: a national survey. Entomological Society of America. Virtual Meeting. 30 November. *Poster presentation*

Christman, M., L. Spears, and R. Ramirez. 2020. Interactive effects of landscape composition and abiotic factors on bumble bees in agroecosystems. Ecological Society of America. Virtual Meeting. 3–6 August. *Poster presentation*

Brunson, M. W., N. J. Huntly, S. Bogen, L. Capito, **M. Christman**, S. Koutzoukis, B. Morgan, C. Morrisett, W. Munger, and K. A. Spangler. 2020. Integrating ecological and social system models and data: An application of the 4DEE approach for graduate education. Ecological Society of America. Virtual Meeting. 3–6 August. *Oral presentation*

Pinto, D., C. Morrisett, S. Koutzoukis, and **M. Christman**. 2020. Graduate researchers collaborating on interdisciplinary climate adaptation science. Ecological Society of America. Virtual Meeting. 3–6 August. *Poster presentation*

Bogen, S., **M. Christman**, H. Panosyan, B. Shield, and M. Wright. 2020. Climate risk assessment of Utah National Forests: A case study of northern goshawks. Science, Management, and Policy Exchange. Moab, UT. 28 February. *Oral presentation*

Bogen, S., **M. Christman**, H. Panosyan, B. Shield, and M. Wright. 2019. Climate risk assessment of Utah National Forests: A case study of northern goshawks. Science, Management, and Policy Exchange. Logan, UT. 4 October. *Oral presentation*

Christman, M. E., L. Spears, E. Burchfield, and R. Ramirez. 2018. Effects of land use and climate variability on beneficial insects in agronomic crops of Utah. Entomological Society of America, Entomological Society of Canada, and Entomological Society of British Columbia Joint Annual Meeting. Vancouver, British Columbia, Canada. 11 November. *Oral presentation*

Christman, M. E., L. Spears, and R. Ramirez. 2018. Landscape ecology of beneficial insects in agronomic crops of Utah. Society for Advancement of Chicanos/Hispanics & Native Americans in Science. San Antonio, TX. October. 12 October. *Poster presentation*

Christman, M. E., L. Spears, E. Burchfield, and R. Ramirez. 2018. Landscape ecology of beneficial insects in agronomic crops of Utah. Pacific Branch Entomological Society of America. Reno, NV. 11 June. *Poster presentation*

Christman, M. E., L. Spears, T. Griswold, and R. Ramirez. 2017. Landscape and seasonal effects on beneficial insects in agricultural crops of Utah. Entomological Society of America. Denver, CO. 6 November. *Poster presentation*

COMMUNITY ENGAGEMENT

Christman, M. 2021. Utah State University College of Science Fall Convocation graduate representative. Utah State University Virtual Ceremony. 30 September. *Invited speaker*

Christman, M. 2021. Denison University alumni panel: graduate school. Denison University Virtual Panel. 28 September. *Invited panelist*

EXTENSION–OUTREACH

Entomology Club Insect Tours. Utah State University. Logan, UT. 2018–2020 17 hours

- Presented about insect biology, physiology, and behavior in an accessible manner
- Audience: 456 people from the general public, particularly K–12 students and teachers

Gaining Early Awareness and Readiness for Undergraduate Programs. Utah State University. Logan, UT. 2018 2 hours

- Presented on careers in entomology to foster the success of students in higher education
- Audience: 103 high school students and teachers

Science Unwrapped. Utah State University. Logan, UT. 2017–2020 14 hours

- Communicated scientific information and lead hands-on learning activities with the Biology Graduate Student Association and Entomology Club
- Increased representation of women in science to the general public
- Audience: 2,100 people from the general public, particularly K–12 students and teachers

SCHOLARSHIPS, ASSISTANTSHIPS, AND GRANTS

Biology Graduate Student Association Travel Award. $500. Utah State University. 2021–2022
Claude E. Zobell Scholarship. $1,000. Utah State University. 2021–2022
USUSA Graduate Enhancement Award. $8,000. Utah State University. 2020–2022
USUSA Graduate Enhancement Award. $4,000. Utah State University. 2020–2021
Ecology Center Research Award. $2,000. Utah State University. 2018–2019
Ecology Center Travel Award. $400. Utah State University. 2018
Graduate Student Travel Award. $400. Utah State University. 2018
Dr. Leslie Paxton Barker Travel Award. $200. Utah State University. 2018

PROFESSIONAL DEVELOPMENT, CERTIFICATIONS, AND TRAININGS

USDA–ARS–Pollinating Insect Research Unit Volunteer. USDA. Logan, UT 2017–2022
Laboratory Safety Training. Utah State University. Logan, UT 2017–2022
Power Dynamics Training. Utah State University. Logan, UT 2022
Boundaries and Effective Relationships Training. Utah State University. Logan, UT 2022
Discrimination Training. Utah State University. Logan, UT 2021
Faculty Member Title IX Training. Utah State University. Logan, UT 2021
Sexual Violence Prevention Training. Utah State University. Logan, UT 2021
Rethinking Relationships Training. Utah State University. Logan, UT 2021
Wilderness First Aid. Desert Mountain Medicine. Logan, UT 2021
Wilderness Anaphylaxis Training. Desert Mountain Medicine. Logan, UT 2021
Urban and Wilderness CPR Training. Desert Mountain Medicine. Logan, UT 2021
Environmental Careers Seminar Micromentor. Denison University. Granville, OH 2021
Upstander Training. Utah State University. Logan, UT 2019
Implicit Bias Training. Utah State University. Logan, UT 2019

LEADERSHIP ROLES

Secretary. Society for Advancement of Chicanos/Hispanics and Native Americans in Science. Utah State University. Logan, UT 2019–2021
President. Entomology Club. Utah State University. Logan, UT 2019–2020
Outreach Coordinator. Entomology Club. Utah State University. Logan, UT 2018–2019
Vice President. Society for Advancement of Chicanos/Hispanics and Native Americans in Science. Utah State University. Logan, UT 2018–2019
Ecology Center Seminar Selection Committee. Utah State University. Logan, UT 2018–2019
Social Chair. Biology Grad Student Association. Utah State University. Logan, UT 2017–2018

TECHNICAL SKILLS

Programming in R/RMarkdown (expert), ESRI ArcGIS (expert), Forest Vegetation Simulator (proficient), Python (familiar)
Apply industry standard GIS tools to natural resource issues using R and ArcGIS
Dashboard development in Rshiny
Data acquisition, management, and manipulation
Maintain repositories for code and open-source projects in Github
Perform thermal tolerance trials, lipid extractions, DNA extractions, and microsatellite PCR amplification on *Bombus*
Operate a motor vehicle as an incidental driver and possess a valid driver’s license

PROFESSIONAL AFFILIATIONS AND STUDENT ORGANIZATIONS

Entomological Society of America
Ecological Society of America
Utah State University Ecology Center
Society for Advancement of Chicanos/Hispanics & Native Americans in Science (SACNAS)
Utah State University Entomology Club
Utah State University Bio Nerd Herd (Programming Club)