

ENVIRONMENTAL DRIVERS OF BEE COMMUNITY DIVERSITY
IN YELLOWSTONE NATIONAL PARK

by

Kristen Ann Switzer

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2022

©COPYRIGHT

by

Kristen Ann Switzer

2022

All Rights Reserved

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Laura Burkle, and my committee members, Dr. Diane Debinski and Ann Rodman, for their mentorship during this project. Thank you to the Yellowstone National Park scientists who helped me along the way, including Erik Oberg, Shannon Woolfolk, and Jeffrey Mitzelfelt. Thank you to Kathleen Mitchell and Kari LaPierre for assistance in data collection and the energy they brought to tough field days. I would like to thank my lab mates for discussing ideas and always being willing to help: Jessica Eggers, Simone Durney, Will Glenny, Thomas Meinzein, Lauren Gedlinske, and Cayley Faurot-Daniels. Special thanks to all my friends and family, including Sandi Switzer, Scott Switzer, Shannon Switzer, Michael Slattery, Marlene Senecal, and Leeland Senecal, in various time zones for your love and encouragement. I am also grateful for the professors and graduate students at the University of Vermont who helped me pursue graduate school, including Dr. Anthony D'Amato, Dr. Allan Strong, Dr. Jennifer Pontius, Charles Nicholson, Samantha Alger, and Peter Clark. Finally, thank you to the Montana State University Ecology Department staff, faculty, and fellow graduate students who were always willing to provide feedback and support. This work was completed with funding from Montana State University, the Meg and Bert Raynes Wildlife Fund, and the SITKA Ecosystem Grant.

LAND ACKNOWLEDGEMENT

We would like to acknowledge this research was conducted on the lands of Indigenous peoples including, but not limited to, Shoshone, Cheyenne, Apsáalooke/Crow, Blackfeet, Bannock, and Nez Perce tribes, who lived there for thousands of years. We pay respect to individuals and communities who live there now, and those with cultural and spiritual connections to these Homelands.

TABLE OF CONTENTS

ENVIRONMENTAL DRIVERS OF BEE COMMUNITY DIVERSITY
IN YELLOWSTONE NATIONAL PARK

Introduction.....	1
Methods.....	7
Study Area	7
Pan Traps to Assess Bee Community Diversity	8
Quantifying Plant-Bee Interactions.....	8
Environmental Variables	9
Analyses of Bee Abundance and Species Richness.....	10
Analyses of Floral Density and Species Richness	12
Analyses of Bee Community Composition.....	13
Analyses of Plant-Bee Interactions.....	15
Results.....	16
Bee Abundance and Species Richness.....	16
Floral Density and Species Richness	17
Bee Community Composition	19
Plant-Bee Interactions.....	20
Discussion.....	20
Bee Abundance and Species Richness.....	21
Bee Community Composition	25
Plant-Bee Interactions.....	27
Conclusion	28
REFERENCES CITED.....	45
APPENDICES	53
APPENDIX A: Pan Trap Sampling Dates for All Years.....	54
APPENDIX B: Model Selection and AIC Results	59
APPENDIX C: Correlation Plots for Linear Mixed-Effects Models.....	62

LIST OF TABLES

Table	Page
Table 1: Coordinates and Elevations of Sites in Yellowstone National Park	30
Table 2: Linear Mixed-Effects Model Results for Bee Abundance and Species Richness	31
Table 3: Least Squares Means for Bee Species Richness	32
Table 4: Linear Mixed-Effects Model Results for Floral Density and Flower Species Richness	33
Table 5: PERMANOVA Results for Floral Community Composition	34
Table 6: PERMANOVA Results for Bee Community Composition	35
Table 7: Linear Mixed-Effects Model Results for Network Specialization Index Values (H_2') in 2020	36

LIST OF FIGURES

Figure	Page
Figure 1: Scatter Plot of Bee Abundance Over the Growing Season Across All Years at the Three High Elevation Sites	37
Figure 2: Bar Charts of Bee Species Richness Across All Years	38
Figure 3: Scatter Plot of Bee Species Richness Across the Growing Season and an Elevational Gradient	39
Figure 4: Scatter Plot of Bee Abundance in 2012 Across All Sites Over an Elevational Gradient.....	40
Figure 5: Bar Chart of Floral Density and Flower Species Richness in 2020	41
Figure 6: NMDS Ordination of Floral Community	42
Figure 7: NMDS Ordinations of Bee Community Composition Data for Three PERMANOVAs	43
Figure 8: Scatter Plot of the Relationship Between Network Specialization Index Values (H_2') and Bee Species Richness for 2020	44

ABSTRACT

Pollinators are essential to their ecosystems and facing large declines. Studies on environmental drivers of bee community composition are currently lacking in North America, particularly in national parks. Understanding how bee diversity and plant-bee interactions change across environmental gradients gives us insight into the resilience of bee communities in the future. We collected data at seven sites across an elevational gradient in Yellowstone National Park. Pan traps were used to collect bee diversity data from in 2010, 2011, 2012, and 2020, and hand-netting was used to collect plant-bee interaction data from June to August 2020. We hypothesized that elevation would be a major driver of bee abundance, species richness, and community composition and that bee diversity would decrease as elevation increased. We predicted bee diversity would peak in the middle of the growing season in response to floral diversity peaking at that time. Finally, we predicted plant-bee interactions would be more generalized at higher elevations and flower species richness would be a major driver of network specialization (H_2).

Our results revealed that seasonality and elevation were major drivers of bee abundance and species richness, indicating that both spatial and temporal factors are important in driving bee community patterns. Bee species richness was highest in 2010 and declined over years, which may signal that changing environmental conditions are stressing bee communities. Bee abundance and species richness declined as each growing season progressed, which aligns with broader literature on various taxa and mirrors seasonal flower diversity patterns. Despite close alignment between bee and floral diversity patterns, flower species richness was only a significant driver of bee community composition, indicating that other environmental gradients were bigger drivers of bee abundance and species richness patterns.

Bee species richness was a significant driver of plant-bee network specialization and elevation, slope, and flower species richness were marginally significant, suggesting that plant-bee interactions are influenced more by spatial than temporal variables. Additional studies focusing on bee diversity across growing seasons and years could provide insights into how changing environmental conditions in the future may influence bee diversity and community resilience in Yellowstone National Park.

ENVIRONMENTAL DRIVERS OF BEE COMMUNITY DIVERSITY IN YELLOWSTONE NATIONAL PARK

Introduction

Pollinators are essential to their ecosystems, but are declining due to factors like habitat loss, pesticide use, and climate change (Davis et al. 2005, Joshi et al. 2015, Kerr et al. 2015, Wray & Elle 2015). Knowledge of community composition is important for understanding the current state of native bees in the face of multiple threats, yet those data are currently lacking in many areas of North America (Joshi et al. 2015, Kohler et al. 2020). Environmental gradients, such as elevational zones, can serve as proxies for climate zones, so studying community variation and species interactions along such gradients may give us insight into community-level responses to future climate change scenarios (David et al. 2015). In addition to elevational zones, other environmental gradients – including floral diversity, slope, and number of growing degree-days – can influence ecological communities, and investigating the effects of such factors can enhance knowledge on how bee community diversity (i.e. bee abundance, species richness, and community composition) changes across space and time (Hopfenmüller et al. 2014, Bystriakova et al. 2018, Lane et al. 2020).

Declining species richness with increasing elevation is an established and generally accepted pattern of community change for many taxonomic groups, but a unimodal pattern where species richness peaks at mid-elevations may be the dominant trend for some community types (Rahbek 1995, Herzog et al. 2005, McCain & Grytnes 2010, Asase & Adeniyi 2021). The relationship between elevation and species richness depends on the taxa being examined, as

evidenced by the varying results across plant and animal community studies. For example, a unimodal trend in woody plant species richness was found over an elevational gradient in the Indian Himalayas with peak species richness at mid-elevations, while a linear decrease in herbaceous plant species richness was found across the same elevation gradient (Sharma & Kala 2022). Other plant communities, such as tree communities in Costa Rica (Lieberman et al. 1996) and pteridophytes (a group including ferns) in Bolivia, Nepal, and Costa Rica (Kessler 2000, Bhattarai et al. 2004, Kluge et al. 2006), have been found to peak in species richness at mid-elevations. Bird abundance and species richness have been shown to decrease with higher elevations in humid locations such as the Peruvian Andes and New Guinea, likely because of less complex vegetation structures, lower water availability, and colder temperatures (Terborgh 1977, Rahbek 1995, McCain & Grytnes 2010). In arid climates, bird species richness showed a unimodal trend where richness peaked at mid-elevations (McCain & Grytnes 2010). This pattern could be attributed either to more suitable habitat (e.g., higher water availability, tolerable temperatures) at mid-elevations, increased productivity, or the mid-domain effect, in which there can be increased overlap of species ranges towards the center of a habitat compared to its edges due to random distribution of species (Colwell & Lees 2000, Herzog et al. 2005, McCain & Grytnes 2010). Evidence suggests that mammal species richness can decrease with increasing elevations (Bogoni et al. 2021) or peak at mid-elevations (Heaney 2001, McCain 2003, Nor 2008) depending on the taxonomic group and habitat type. These studies reveal that patterns of species richness along an elevational gradient are complex and can vary depending on the location and taxonomic group or vary within a single habitat.

In addition to the taxa above, invertebrate communities have diverse relationships between species richness and elevation depending on the taxonomic group. Researchers have observed increases (Romero-Alcaraz & Ávila 2000), decreases (Richardson et al. 2005, Pryke & Samways 2008, Joaqui et al. 2021), and mid-elevation peaks (Sanders 2002, Adedoja et al. 2020, Joaqui et al. 2021) in species richness as elevation increases. Similar to previous relationships found between invertebrate species richness and elevation, studies of wild bee community diversity have shown mixed relationships with elevation. Bee species richness can decrease (Hoiss et al. 2012, Marini et al. 2012, Sydenham et al. 2014, Classen et al. 2015, McCabe et al. 2019) or increase (Widhiono et al. 2017, Baumann et al. 2021) with elevation, depending on the habitat. The factors driving differences in species' responses across elevation gradients are not thoroughly understood (Adedoja et al. 2020, Baumann et al. 2021), particularly in wild bee species outside of bumble bees (Woodard et al. 2020; Minachilis et al. 2021). Other ecological factors in addition to elevation may be important drivers of invertebrate species richness, given that productivity, abiotic factors (e.g., precipitation, temperature), and food resource availability all can correlate significantly with animal abundance and species richness (Heaney 2001, Sanders 2002). Determining how bee community structure changes along environmental gradients aids in understanding how factors, such as elevation, drive bee abundance, species richness, and community composition (Hoiss et al. 2012). Studies of pollinator community diversity along elevational gradients in North American temperate regions are limited compared to similar studies in temperate regions on other continents, and the results thus far appear to depend on the specific habitat within North America where data are collected (Colla & Dumesh 2010, Rivers et al. 2018; McCabe et al. 2019, Graves et al. 2020).

In addition to elevational gradients, other environmental characteristics of bee habitat influence their species richness and abundance. For example, floral abundance and species richness can act as environmental filters on bee abundance and species richness (Sydenham et al. 2014). Floral density and species richness play important roles in determining the overall structure of a bee community across differing habitat types, where more diverse flower communities generally correlate with higher bee abundance and species richness (Potts et al. 2003; Ebeling et al. 2008, Matteson & Langellotto 2010, Mallinger et al. 2016). Bee species richness and abundance may be higher in areas with more complex habitat characteristics, such as steep average slopes within or near pollinator habitat (Hopfenmüller et al. 2014, Carrié et al. 2018). Spatial environmental gradients play major roles in determining patterns in bee community diversity, but do not account for the effects temporal gradients have on bee community diversity as well.

There is temporal variation between years (Williams et al. 2001, Kremen et al. 2002, Oertli et al. 2005, Bushmann & Drummond 2015, Russo et al. 2015) and across the growing season of a single year (Williams et al. 2001, Rollin et al. 2015, Delgado-Carillo et al. 2018) in bee community diversity. Seasonality is a driving factor in bee species richness, where bee abundance and species richness have been found to peak in the middle of the growing season in response to peak abundance of preferred floral resources (Adedoja et al. 2020). The number of plant-bee interactions may also peak in the middle of the growing season (Pyke et al. 2011). Variation is also seen in bee communities on larger temporal scales, as bee communities have been observed to shift to higher elevations over the course of multiple years in response to warming temperatures (Pyke et al. 2016). Such studies that incorporate consistent monitoring of

pollinators over long periods of time are limited in North America and are often constrained by limitations in time and funding for bee studies (Williams et al. 2001). Due to the high variation in bee community composition over time, data collection across entire growing seasons and multiple years is important for determining trends in bee abundance, richness, and composition (Williams et al. 2001).

In addition to investigating how environmental factors drive bee abundance, richness, and composition over time, we tested how the same factors influence plant-bee interactions. Low bee species turnover at high elevations may lead to higher levels of overlap in the dietary preferences among bee species and subsequently greater levels of generalization at higher elevations (Adedoja 2018). Multiple other studies also found that pollinators may be more generalized at high elevations in their flower selection with accompanying decreases in the degree of network specialization (H_2'), which is the number of links between plants and pollinators in an ecological community (Hoiss et al. 2015, Lara-Romero et al. 2019, Chesshire et al. 2021). Mid-elevation zones appear to have the largest networks of plant-bee interactions (Adedoja 2018), which relates to several aforementioned studies that observed peaks in invertebrate species richness at mid-elevations. Knowledge is limited on how various environmental gradients may influence network specialization.

In this study, we investigated environmental drivers of bee communities along an elevational gradient in Yellowstone National Park (YNP). National parks are disproportionately impacted by climate change, as evidenced by their annual mean temperatures increasing and annual precipitation decreasing much faster in national parks in the past century when compared to the rest of the United States (Gonzalez et al. 2018). In the Greater Yellowstone Ecosystem

(GYE), temperatures increased 1.28 degrees Celsius from 1950 to 2018 (Hostetler et al. 2021). Additionally, natural areas generally lack consistent, baseline community data (Meiners et al. 2019). YNP supports one of the few remaining intact ecosystems in the lower 48 states (Prato & Fagre 2007), which can be used as a baseline to compare to ecosystems greatly affected by human disturbances. The following questions were considered: 1) How do environmental gradients (i.e., elevation, floral density, flower species richness, growing degree-days, slope) influence bee abundance, richness, and community composition seasonally (sampling periods every two weeks) and across years (i.e., 2010, 2011, 2012, and 2020)? And, 2) within one growing season (2020), how does specialization of plant-pollinator interactions vary across these environmental gradients at the network-level?

Evidence from previous studies suggest that elevation may be a main driver of bee community diversity, with a decrease in bee abundance and species richness as elevation increases (Hoiss et al. 2012, Marini et al. 2012, Sydenham et al. 2014, Classen et al. 2015, McCabe et al. 2019). High elevations are predicted to have harsher conditions, specifically fewer growing degree-days and limited floral resources, thereby supporting fewer bee individuals and species. In addition to elevation as a driving environmental factor, floral density and flower species richness were expected to positively influence bee abundance and richness due to the reliance of bees on flowers for sustenance. For temporal gradients, we expected bee abundance and species richness to peak in the middle of the growing season as evidenced by possible responses to floral abundance peaking at that time (Adedoja et al. 2020). Within a growing season, we also expected elevation to interact with seasonality, with higher elevations (later snowmelt) showing higher levels of bee abundance and species richness later in the growing

season in comparison to lower elevations. Across years, we expected the highest elevation sites to have the lowest species richness compared to lower elevation sites. If any climate change signal could be detected, we expected that bee species richness would be higher in 2020 than in other years at the highest elevation sites because of upward shifts in elevation and warmer temperatures, but we expected overall accumulation of species across all sites would be lowest in 2020. We predicted that plant-bee interactions would be more generalized at higher elevations because evidence from previous studies suggest bee species become less selective in their floral preferences at higher elevations (Hoiss et al. 2015, Lara-Romero et al. 2019). We also predicted that flower species richness would be a major driver of network specialization values and we expected flower species richness to positively correlate with network specialization based on previous findings of this relationship (Ebeling et al. 2011).

Methods

Study Area

Yellowstone National Park (YNP) covers 2.2 million acres of land in Wyoming, Montana, and Idaho. Data were collected at seven sites in northern YNP representing a range of elevations from 1,620 meters to 2,932 meters (Table 1). Plant communities at these sites were open habitats ranging from bluebunch wheatgrass (*Pseudoroegneria spicata*) and big sagebrush (*Artemisia tridentata*) at lower elevations to Idaho fescue (*Festuca idahoensis*) and bearded wheatgrass (*Elymus caninus*) at higher elevations. *Achillea millefolium* and *Potentilla spp.* were common across all sites. *Ericameria nauseosa*, and *Lupinus spp.* were dominant at low elevation, while *Lupinus spp.*, *Geranium viscosissimum*, *Cerastium arvense*, and *Phlox spp.* were common

at mid-elevation, and *Cerastium arvense*, *Phlox spp.*, and *Geum triflorum* were common at high elevation.

Pan Traps to Assess Bee Communities

To investigate bee abundance, richness, and community composition at each site, pan traps (alternating yellow, blue, and white) were deployed every 5 meters along two intersecting transects (100 meters north to south and 50 meters east to west). To maintain spacing among traps, no pan trap was placed where the transects crossed. Pan traps were filled with soapy water and left for 24 hours. Data were collected on sunny days with low wind (<15 mph), which are the optimal conditions for bee foraging. Pan trap data were collected three times in 2010 and seven times in 2011 at three of the sites (Washburn South, Washburn North 2, and Washburn Top; Appendix A). At all seven sites, pan trap data were collected six to nine times in 2012 and six to ten times in 2020 depending on the site, which equated to data collection occurring about every two weeks (Appendix A). Data from 2010, 2011, and 2012 were provided by the National Park Service.

Quantifying Plant-Bee Interactions

To investigate how network specialization of plant-bee interactions varied across environmental gradients, we quantified the identity and frequency of plant-bee interactions by hand-netting native bees contacting the reproductive parts of flowers across one season (2020). At each site, hand-netting was performed in a 100 m x 50 m plot (5000 m²) adjacent to the pan trap transects at the request of YNP to avoid additional impact on the pan trap transects. On each

sampling day, observation periods of two person-hours were conducted by walking throughout the plot. Upon collection, bees were frozen. Queen bumble bees were avoided in sampling to preserve their reproductive capacity. Each site was sampled eight times throughout the growing season (ca. weekly between 10 June and 24 August), except for Washburn North 1 which was sampled seven times. Repeated lethal sampling of native bee communities using pan traps and netting was assumed to have little effect on abundance, species richness, species evenness, or functional group composition in subsequent years (Gezon et al. 2015). All bee specimens collected from pan traps in 2010, 2011, and 2012 were identified to species or lowest taxonomic level possible first at the USGS Patuxent Wildlife Research Center (Prince George's County, MD), then at the USDA Bee Biology and Systematics Laboratory (Logan, UT). All bee specimens collected from pan traps (above) and via hand-netting in 2020 were identified to species or lowest taxonomic level possible at the USDA Bee Biology and Systematics Laboratory (Logan, UT).

Environmental Variables

At each site in 2020, climate stations provided hourly temperature measurements used to calculate the total number of growing degree-days (GDD), a measurement of how many days throughout the year the temperature is above a particular threshold for an organism to function. The Baskerville-Emin calculation method was used, which incorporates trigonometric functions and is more precise than other methods of calculating GDD (Baskerville & Emin 1969). The threshold for calculating growing degree-days was chosen based on an ambient temperature warm enough for bee individuals to begin emerging (10°C) (Hirata & Higashi 2008, Bertrand et

al. 2019). Detection probability for several bee taxa (i.e., Andrenidae, Apidae, Megachilidae, and Nomada), is inversely related to growing degree-days (Landsman et al. 2019). Hourly temperature data were not available for the years 2010, 2011, and 2012 at the seven sites, so growing degree-days were not calculated for those years. Average slope and elevation were determined by YNP biologists for each site, which were all the same size (5000 m²). Each group of sampling dates contained 1-3 days depending on the weather conditions each week. Seasonality is a factor representing these sampling periods across the growing season, ranging from June to October.

To measure floral density and flower species richness at each of the seven sites in 2020 only, we conducted vegetation surveys along a 50 m by 1 m band transect (east-west) across the center of each pollinator transect in which data were collected by pan traps or hand-netting. On every pollinator sampling day, we counted all open flowers of each plant species along the band transect. Inflorescences were counted for plant species with indistinguishable individual flowers (e.g., *Achillea millefolium*, *Eriogonum spp*). At each site on each sampling day, floral density was the sum of the total number of flowers per 50 m² transect, and flower species richness was the sum of the total number of species present per 50 m² transect.

Analyses of Bee Abundance and Species Richness

In order to take advantage of the available data, we created three sets of models: Model Set 1 included all available data from all years; Model Set 2 incorporated data from 2012 only since all seven sites were sampled over a longer portion of the growing season than 2010 or 2011; and Model Set 3 used data from 2020 only in order to take advantage of environmental

data only available for that year. To account for the varying sample efforts in Model Set 1, linear mixed-effects models were used. For Model Set 1 and Model Set 2, bee abundance and bee species richness were log-transformed for normality. Correlation matrices were created to eliminate any highly correlated explanatory variables ('corrplot' function from 'R' package Corrplot) (Appendix C). The only highly correlated variables were elevation and average slope, so average slope was removed from these analyses. Elevation and seasonality showed patterns suggesting that they may have an interactive relationship with each other, and we included this interaction term. The models contained year as a fixed effect and site as a random effect. Model selection was conducted based on the Akaike Information Criterion (AIC) (Appendix B).

Model Set 3 included the same environmental characteristics as those used for Model Sets 1 and 2 as well as floral density, flower species richness, and growing degree-days. Bee abundance and floral density were log-transformed, and flower species richness was square-root transformed for normality. One influential outlier site replicate was also removed from the bee abundance data because many *Halictus tripartitus* (262 of the 378 individuals caught on July 16, 2020) were captured near what appeared to be a nest aggregation of this eusocial species (Packer et al. 2007). A correlation matrix was used to identify and eliminate highly correlated variables ('corrplot' function from 'R' package Corrplot) (Appendix C): average slope, growing degree-days, and floral density. Elevation (correlated with slope and growing degree-days) was retained in the model, as was flower species richness (correlated with floral density). Elevation and seasonality showed patterns suggesting they may have an interactive relationship with each other, and so were considered together as an interaction term. Similarly, flower species richness and seasonality were considered together as an interaction term, since the type and number of

flower species present in bee habitat may depend on the point in time during the growing season. Both models contained flower species richness (square-root transformed), an interaction term between elevation and seasonality, and an interaction term between flower species richness (square-root transformed) and seasonality as the independent variables ('lmer' function in 'R' package Lme4). Site was included as a random effect. Model selection was conducted based on the Akaike Information Criterion (AIC) (Appendix B).

Least squares means were calculated for bee species richness across years and elevations to account for differences in sampling efforts (JMP, Version 16.2.0). In June of 2020 for Tower and Washburn North 1, plant-bee interaction data were insufficient for calculating network specialization index values (H_2).

Analyses of Floral Density and Species Richness

To test how environmental variables influenced floral density and species richness in 2020, linear models were created with these floral factors as response variables. Floral density was log-transformed and flower species richness was square-root transformed for normality. Elevation and seasonality showed patterns suggesting that they may have an interactive relationship with each other, so we included this interaction term. The models contained site as a random effect. To test how environmental variables influenced flower community composition, a PERMANOVA was created using a Bray-Curtis dissimilarity matrix, which had the highest D^2 value (indicating a better fit of the distance matrix to the data) when compared to Manhattan, binary, and Euclidean dissimilarity matrices. Independent variables were ordered in the PERMANOVAs based on how much variance in bee community composition they explained

individually, starting with the highest amount of variance explained (highest R^2 value): elevation and seasonality. The influence of elevation on bee community composition may depend on seasonality, so an interaction term was included between elevation and seasonality. Kruskal's non-metric multidimensional scaling (NMDS) was used to visualize the PERMANOVA results ('ggplot' function from 'R' package GGplot2). Kruskal's NMDS minimizes stress (maximizes the rank correlation between the calculated dissimilarities and the plotted distances). Significant environmental variables from the PERMANOVA were overlaid onto the NMDS ('envfit' function from 'R' package Vegan). Because of the predicted associations between floral community diversity patterns and bee community diversity patterns over elevation and the growing season (Adedoja et al. 2020), testing how these environmental variables separately influenced floral diversity and bee diversity in 2020 was determined to be valuable for the study.

Analyses of Bee Community Composition

Similar to Model Sets 1-3 for bee abundance and species richness, in order to take advantage of the available data to determine environmental drivers of bee community composition, we created three PERMANOVAs ('adonis' function from 'R' package Vegan): PERMANOVA 1 was restricted to data at the three highest elevation sites (Washburn South, Washburn North 2, and Washburn Top) and relative dates during each growing season that were sampled all four years; PERMANOVA 2 incorporated data from 2012 since all seven sites were sampled over a longer portion of the growing season; and PERMANOVA 3 used data from 2020 in order to take advantage of environmental data only available for that year. Unlike Model Set 1, PERMANOVA 1 contained data from similar sampling efforts across years to achieve the

same amount of relative dispersion of data. For all three PERMANOVAs, Bray-Curtis dissimilarity matrices were used because they had the highest D^2 value (indicating a better fit of the distance matrix to the data) when compared to Manhattan, binary, and Euclidean dissimilarity matrices. Independent variables were ordered in PERMANOVAs 1 and 2 based on how much variance in bee community composition they explained individually, starting with the highest amount of variance explained (highest R^2 value): elevation, year, seasonality, and average slope for PERMANOVA 1, and elevation seasonality, and average slope for PERMANOVA 2. The influence of elevation on bee community composition may depend on seasonality or year, so interaction terms were included for both temporal variables. Site was not included as an independent variable since it was determined to provide very similar information as elevation, and therefore would not improve the model. Kruskal's non-metric multidimensional scaling (NMDS) was used to visualize the PERMANOVA results ('ggplot' function from 'R' package GGplot2). Kruskal's NMDS minimizes stress (maximizes the rank correlation between the calculated dissimilarities and the plotted distances). Bee taxa grouped by family were overlaid onto the NMDS ('envfit' function from 'R' package Vegan).

PERMANOVA 3 included the same environmental characteristics as those used for PERMANOVAs 1 and 2 as well as floral density, flower species richness, and growing degree-days. Independent variables were ordered in PERMANOVA 3 as follows: elevation, seasonality, flower species richness, floral density, and average slope. The influence of elevation, floral density, and flower species richness on bee community composition may depend on seasonality, so interaction terms were included. Site and growing degree-days were not included as independent variables since they were determined to provide very similar information as

elevation, and therefore would not improve the model. Non-metric multidimensional scaling (NMDS) was used to visualize the PERMANOVA results ('ggplot' function from 'R' package GGplot2). Bee taxa grouped by family were overlaid onto the NMDS ('envfit' function from 'R' package Vegan).

Analyses of Plant-Bee Interactions

To test how network specialization of plant-bee interactions varied across sites within one growing season (2020), a linear mixed-effects model was created using network-level specialization index values (H_2') ('H2fun' function in 'R' package Bipartite) for each site in June, July, and August. H_2' is used to examine specialization across the entire network of plant-bee interactions (Blüthgen et al. 2006). Values range from minimum specialization (0) to maximum specialization (1). A correlation matrix was created to eliminate any highly correlated variables ('corrplot' function from 'R' package Corrplot) (Appendix C). Bee abundance and bee species richness were highly positively correlated, as were average floral density and average flower species richness. Average floral density and species richness data per month for each site were used in place of total floral density and species richness per month to account for missing floral data from 6/22/20 – 6/24/20. Bee abundance and average floral density were removed from the model due to less normal distributions than the species richness parameters. For the linear mixed-effects model, we used H_2' values as the independent variable and elevation, month, average slope, bee species richness, and average flower species richness as dependent variables ('lmer' function in 'R' package Lme4). Site was included as a random effect. Only female bees

were included in plant-bee interaction analyses (here and below) since female bees are more likely to be actively pollinating than males.

Results

Bee Abundance and Species Richness

In 2010, 2011, 2012, and 2020, the total numbers of bees collected were 536, 850, 2923, and 3623 respectively, and the total numbers of bee species collected were 158, 285, 947, and 712 respectively.

Across all years (Model Set 1), seasonality was a major driver of bee abundance (Figure 1); no other factors that we measured were significantly related to bee abundance (Table 2). Overall, bee abundance declined as the season progressed (Figure 1). The interaction between elevation and seasonality was a significant driver of bee species richness, and there was a significant main effect of seasonality on bee species richness (Table 2, Fig. 2a-d). Across all years and elevations, bee species richness declined throughout the growing season (Figure 3). The steepest decline in bee species richness from early June to early October across years was at 1,856 meters (Mammoth). At 2,577 meters (Washburn South), there was almost no change in the average bee species richness throughout the growing season of all years (Figure 3). Across all years, earlier in the growing season there were more bee species at lower elevations (Fig. 2a-d). In the middle of the growing season, there were more bee species at higher elevations, and then towards the end of the growing season bee species richness was again higher at lower elevations relative to higher elevations (Figure 2). Year weakly influenced bee species richness (Table 2),

with bee species richness (log-transformed) declining across years from 2.99 in 2010 to 2.35 in 2020 (Table 3).

In 2012 (Model Set 2), elevation was a significant driver of bee abundance (Table 2). Bee abundance decreased with increasing elevation (Figure 4). There were no significant drivers of bee species richness, but elevation and seasonality were marginally significant (Table 2). Bee species richness tended to decrease with elevation and across the growing season for 2012 (Figure 4).

In 2020 (Model Set 3), none of the measured variables were significant drivers of bee abundance (Table 2). Elevation and seasonality were significant drivers of bee species richness, and the interaction between elevation and seasonality was marginally significant (Table 2). As elevation increased, bee species richness decreased (Figure 2d). As the growing season progressed, bee species richness decreased (Figure 2d). When considering the interaction between elevation and seasonality, we found that earlier in the growing season of 2020 there were more bee species at lower elevations (Figure 2d). In the middle of the growing season in late July and early August, bee species richness increased at higher elevations relative to lower elevations. Then towards the end of the growing season, bee species richness once more increased at lower elevations relative to higher elevations (Figure 2d).

Floral Density and Species Richness

Elevation and the interaction between elevation and seasonality were significant drivers of floral density in 2020 (Table 4). Floral density increased as elevation increased (Table 4). Floral density peaked soon after sampling began and then decreased (Figure 5a). This variable

was high at the two highest elevation sites, Washburn North 2 and Washburn Top, in late June through mid-July (Figure 5a). The lower elevation sites had lower floral density relative to the high elevation sites throughout the growing season. Elevation, seasonality, and the interaction between elevation and seasonality were all significant drivers of flower species richness (Table 4). As elevation increased, flower species richness increased (Table 4). Throughout the growing season in 2020, flower species richness decreased (Figure 5b). Flower species richness was higher at the four highest elevation sites (Washburn North 1, Washburn South, Washburn North 2, and Washburn Top) relative to the low elevation sites, from mid-June through the end of July (Figure 5b).

Elevation, seasonality, and the interaction between the two were significant drivers of floral community composition in 2020, collectively explaining 16.5% of variable in floral community composition (Table 5). Of these, elevation explained the most variation (6.5%) in floral community composition. In 2020, the flower species rubber rabbitbrush (*Ericameria nauseosa*), yellow sweetclover (*Melilotus officinalis*), and curlycup gumweed (*Grindelia squarrosa*) were more common at low elevation sites (Figure 6). Spring beauty (*Claytonia lanceolata*), a pea species (*Psoralea spp.*), and the common dandelion (*Taraxacum officinale*) were more common at mid-elevation sites (Figure 6). Forget-me-nots (*Myosotis asiatica*), yellow parsley (*Lomatium triternatum*), slender cinquefoil (*Potentilla gracilis*), thickstem aster (*Eurybia integrifolia*), burnet saxifrage (*Pimpinella saxifraga*), and sticky geranium (*Geranium viscosissimum*) were more common at high elevations.

Bee Community Composition

Across all years (2010, 2011, 2012, 2020; PERMANOVA 1), elevation, year, seasonality, average slope, and the interaction between elevation and year significantly influenced bee community composition, collectively explaining 28% of the compositional variation (Table 6). Of the variables measured, seasonality explained the most variation (6.5%) in bee community composition.

In 2012 (PERMANOVA 2), elevation, seasonality, and the interaction between elevation and seasonality significantly influenced bee community composition, collectively explaining 19.9% of the variation (Table 6). Average slope was marginally significant. Of these factors, elevation explained the most variation (about 9.4%) in bee community composition. *Andrenidae* and *Colletidae* bee families were more common at higher elevations, *Megachilidae* bees were common at mid-elevations, and *Halictidae* bees were common at lower elevations (Figure 7b).

In 2020 (PERMANOVA 3), elevation, seasonality, flower species richness, the interactions between seasonality and flower species richness as well as seasonality and floral species richness significantly influenced bee community composition, collectively explaining 25% of the variation (Table 6). Of these, elevation explained the most variation (10.3%) in bee community composition. Similar to 2012, bees in the *Andrenidae* and *Colletidae* families were more common at higher elevations, while bees in the *Halictidae* family were more common at lower elevations (Figure 7c). Bees in the *Megachilidae* family, however, were common at higher elevations in 2020 than in 2012. *Apidae* bees showed no distinct patterns across elevations and years.

Plant-Bee Interactions

Bee species richness was the only significant driver of network specialization values across sites (Table 7). As bee species richness increased, network specialization decreased (Figure 8). Elevation, average slope, and average flower species richness were all marginally significant as well (Table 7). As elevation increased, network specialization tended to increase. As average slope became steeper, network specialization tended to decrease. As average flower species richness increased, network specialization tended to increase (Table 7).

Discussion

We found that both elevation and seasonality were important for explaining bee abundance and species richness patterns, indicating that there are both major spatial and temporal drivers to consider in conserving these communities. Bee species richness decreased with elevation, which aligns with our hypothesis and previous findings showing that species richness is lower at higher elevations. Bee abundance and species richness also decreased linearly across the growing season, which is not what we expected. Previous findings were mixed on how invertebrate abundance and species richness change throughout the growing season, but the overall declines in bee abundance and species richness do align with some studies of invertebrate taxa. We observed some evidence of a decline in bee species richness across years, which may suggest that changing environmental conditions are putting stress on bee communities over a larger time scale. This could be an important indicator that climate change in coming years will continue to stress bee communities. Overall, temporal gradients and elevation proved to be the most important environmental factors in explaining bee abundance, species richness, and

community composition. As a result of these findings, it is important for Yellowstone National Park to continue monitoring differences in bee communities across the elevational gradient for in future years and across the entire growing season of each year.

Bee Abundance and Species Richness

When considering single years of observation, elevation was a significant driver of bee abundance and marginally related to bee species richness in 2012, and a significant driver of bee species richness in 2020. Bee abundance in 2012 and bee species richness in 2020 declined as elevation increased, indicating that higher elevations may have harsher conditions or fewer resources, therefore supporting smaller bee communities. Elevation as a driver of bee abundance in 2012 but not 2020 may indicate that the number of bee individuals in these communities is decreasing over time, perhaps as a result of changing environmental conditions. Some studies have also found pan traps to be less effective at collecting accurate bee abundance data compared to bee species richness data, where small-bodied bees are overrepresented compared to large-bodied bees (Hudson et al. 2011). These patterns of declining bee abundance and richness align with our hypotheses and other bee and general invertebrate studies (Richardson et al. 2005, Pryke & Samways 2008, Hoiss et al. 2012, Marini et al. 2012, Sydenham et al. 2014, Classen et al. 2015, McCabe et al. 2019, Joaqui et al. 2021). Elevation was not a significant driver of bee abundance or species richness when considering all years, indicating that a larger elevational gradient – spanning 1,620 m to 2,932 m across all seven sites in some years (2012 and 2020) compared to 2,577 m to 2,932 m at the three highest elevation sites in other years (2010 and 2011) – may be needed to detect differences in diversity between bee communities.

Contrary to the relationships between bee abundance and elevation as well as bee species richness and elevation, floral density and flower species richness both increased with elevation. It is possible that floral reproductive strategies that attract pollinators change over elevational gradients. Previous studies have found that with elevation, flower height decreases and the number of flowers per flower head increases (Kieltyk 2021). This indicates that high-elevation flowers are allocating resources more towards flower production and less towards structural elements, such as stalks. This may increase the chance of pollination at high elevations where bee species richness is generally lower (Kieltyk 2021). Another possible explanation for floral density and flower species richness increasing with elevation in YNP is that low elevations had far more big sagebrush (*Artemisia tridentata*) than high elevations. Sagebrush shrubs are large and may be shading out flower species at lower elevations. There was also likely a range of moisture levels and seasonal moisture patterns contributing to variation in floral density and flower species richness across sites. For example, the lowest elevation site, Gardiner, experiences high temperatures and has been observed to dry out earlier than other sites each year. There are also sudden, high-volume rain events at lower elevations in the park. Moisture data would be beneficial to include in future bee and plant community diversity studies in YNP.

Seasonality was a significant driver of bee abundance and species richness when considering all years, a significant driver of bee species richness in 2020, and marginally related to bee species richness in 2012, which has been found in previous studies as well (Williams et al. 2001, Rollin et al. 2015, Delgado-Carillo et al. 2018). As growing seasons progressed, bee abundance and species richness both decreased. This differs from our hypothesis and findings from some previous studies in which bee abundance and species richness peaked in the middle of

the growing season (Sanders 2002, Adedija et al. 2020, Joaqui et al. 2021). Some studies found similar evidence to our results of decreasing abundance and species richness across the growing season for other invertebrate taxa (Richardson et al. 2005, Pryke & Samways 2008, Joaqui et al. 2021). Flower species richness overall was highest towards the beginning of the growing season, which may have supported higher bee abundance and species richness towards the beginning of the growing season given that other studies have found that seasonal patterns of bee community diversity mirror floral community diversity patterns (Carvell et al. 2006, Tucker & Rehan 2016, Seitz et al. 2020). The earliest sampling date across all years of the study was 2 June, so it is possible that small numbers of bees were present earlier in the season before sampling commenced. If that is the case, then bee abundance across the growing season would show more of a unimodal pattern as the aforementioned studies found. Future studies should start sampling earlier in the year to capture earlier emergence of bees in the spring. Employing pan traps before and after the flowering season can provide insights into potential phenological mismatches between the bee foraging season and the flower growing season.

The effect of elevation across the growing season was a major driver of bee species richness, indicating that seasonality may have modified the effect of elevation on bee species richness. Bee species richness was generally high at lower elevation sites earlier in the growing season, likely because flowers had not yet emerged at higher elevations or environmental conditions were too harsh (e.g., low temperatures, high snowpack, strong winds) for bee foraging. In the middle of the growing season (late-July), high elevation sites had higher bee species richness than low elevation sites, suggesting that once environmental conditions became more suitable at higher elevations, bee individuals may have emerged locally at those sites. This

aligns with our hypothesis that bee species richness would increase at higher elevation sites later in the growing season. Other studies have also found evidence of a pattern where bees at higher elevations emerge and peak later in the growing season than bees at lower elevations (Stemkovski et al. 2020). Seasonality allows for diversity in environmental factors throughout the year, like floral density and flower species richness, which promotes diversity in bee communities. At the high elevation sites, bee species richness peaked later in the growing season than flower species richness. There is evidence from other studies that the timing of flower species emergence every year is more aligned with climatic variation than bee emergence (Kehrberger & Holzschuh 2019, Stemkovski et al. 2020). This suggests at high elevation sites in Yellowstone, variation in climate over time may be causing bee species richness to peak later than flower species richness.

Contrary to what we predicted, bee species richness at the three highest elevation sites was lower in 2020 than in previous years. We expected to observe some evidence of bee species moving to higher elevations, consistent with evidence of bee communities shifting to higher elevations over time in the United States (Pyke et al. 2016). Even though there are findings of rapidly rising temperatures in US national parks (Gonzalez et al. 2018), our results suggested upward shifts in bee foraging ranges may not be occurring in Yellowstone National Park, and the reason why is uncertain. There is evidence for some bee species, such as bumble bees, that the upslope movement of plant communities may be outpacing that of bees (Pyke et al. 2016). It is possible that the ability of bees in Yellowstone to shift to higher elevations does not match how quickly the environmental conditions in their current habitats are changing.

Bee Community Composition

Differences in bee community composition among the highest elevation sites (PERMANOVA 1) were due to many different environmental variables: elevation, year, seasonality, average slope, and the interaction between elevation and year. This indicates that bee communities differ significantly across large spatial scales, such as an elevational gradient, as well as small spatial scales, such as the slope gradient across the sites in this study. Additionally, bee communities also differ on smaller and larger temporal scales, which in this study were seasonally and yearly respectively. Seasonality and year each accounted for slightly more variation in bee community composition than the other significant variables, which could indicate that temporal gradients have a slightly stronger influence on patterns in bee community composition than spatial gradients. There has been evidence from other studies that temporal heterogeneity explains more variation in bee community diversity than spatial heterogeneity, but both groups of heterogeneity are deemed important for explaining patterns of bee community diversity across a landscape (Rollin et al. 2015). The highest elevation site in this study is arguably the most vulnerable site for bee communities out of all seven due to harsher conditions (high winds, lower temperatures, etc.) and patterns from our data showing rapid peaks in both bee and floral community diversity during the growing season at this site. Therefore, it is important to continue to monitor for changes in bee communities and possible responses to climate signals at this and other high elevation sites.

Findings from single years of observation reveal that elevation, seasonality, floral density, and flower species richness (when such floral data are available) are major drivers of bee community composition. Elevation, seasonality, and the interaction between the two were

significant in 2012 (PERMANOVA 2), which contains data from a broader elevational range and throughout more of the growing season. Temporal variables play a vital role in determining bee community composition in Yellowstone, as we found with bee abundance and species richness results. Other studies have documented that temporal variation across the growing season of a single year (Williams et al. 2001, Rollin et al. 2015, Delgado-Carillo et al. 2018) is an important factor driving patterns in bee community diversity.

When looking at 2020 (PERMANOVA 3), we found that when adding floral parameters into the model, floral density and flower species richness were significant drivers of bee community composition. Elevation and seasonality were both significant drivers of bee community composition and floral community composition, and both communities showed peaks in abundance and species richness earlier in the growing season. This indicates that these two communities may be reliant on each other, and confirms findings from other studies that patterns in bee community diversity mimics patterns in floral community diversity across a growing season (Adedoja et al. 2020). We observed that there were distinct bee families and flower species that were more common than others depending on elevation. *Halictidae*, *Andrenidae*, and *Colletidae* families were common at their respective elevations in both 2012 and 2020, indicating that bee species within each of these families may show some resilience over time. Bee species in the *Megachilidae* family, however, appeared to move to higher elevations from 2012 to 2020, which is a possible climate signal that warmer temperatures are allowing for upslope movement. Several floral parameters, flower species richness, the interaction between floral density and seasonality, and the interaction between flower species richness and seasonality, were important drivers of bee community composition in 2020 but not

bee abundance or species richness in 2020. One possible reason for these findings could be that bee community composition is influenced by both the number of flowers and which species of flowers are present at a site during a particular point in the growing season. This indicates that flower community composition does play an important role in determining bee community composition, and specifically impacts the areas where bees choose to forage across elevation. Flowers are so heavily relied on by bees for their diets, they are essential to study in order to get a full understanding of how bee communities are influenced by their environments.

Plant-Bee Interactions

Bee species richness, which increased as network specialization decreased, was the only major driver of plant-bee interaction specialization in one growing season (2020). One possible explanation for this pattern is that communities with high bee species richness may be more generalized in their flower choices as a result of dietary overlap between bee species limiting access to their preferred flowers (Rasmussen et al. 2021). As elevation and floral species richness increased, so did network specialization, albeit weakly. This is contrary to our hypothesis and to the results of other studies (Hoiss et al. 2015, Lara-Romero et al. 2019) which found higher levels of generalization at high elevations (Classen et al. 2020, Chesshire et al. 2021).

Network specialization increased weakly as slope of the terrain decreased. Complex habitat characteristics, such as steep slopes that influence local nest density for bees, have been positively correlated with bee abundance and species richness (Hopfenmüller et al. 2014, Carrié et al. 2018). In that case, we would expect that steep slopes with high bee species richness would

harbor specialized bee communities, but we found the opposite to be true in Yellowstone. Instead, shallow slopes had the highest network specialization values, so it is possible the more severe slopes in Yellowstone were too difficult for bee communities to live on, and therefore shallow slopes had higher amounts of bee species in this case.

Conclusion

Understanding how changes in environmental conditions influence bee abundance, species richness, and community composition will be vital for supporting these communities in the future. National parks are experiencing disproportionate rises in temperature compared to the rest of the United States (Gonzalez et al. 2018) so continuing to monitor Yellowstone National Park's bee communities is important. Floral community data, in combination with continued bee monitoring, should be more thoroughly collected in Yellowstone in coming years, as it was not collected from all years of the study and can help explain patterns of bee community diversity. Bee community studies that cover longer periods of time and involve consistent monitoring would be beneficial to address current gaps in the literature (Graves et al. 2020). Given that seasonality was a major driver of bee abundance, species richness, and community composition, and that year was a major driver of bee community composition, temporal gradients strongly influence bee communities. Therefore, extended studies that cover larger temporal gradients would enhance our understanding of bee community resilience into the future. Our data span 10 years, which is a challenging time period to make definitive conclusions beyond identifying possible climate signals within our results about how climate change impacts bee communities. It is our hope that Yellowstone National Park can use these results as baseline data on which they

will expand monitoring bee communities in future years. With limited time and funding, higher elevation sites should be prioritized.

Table 1: Coordinates and elevations of sites, each one 5000 m², in Yellowstone National Park.

Site Name	UTM Values	Elevation (meters)
Gardiner North (COM 6)	522042 E, 4986450 N	1,620
Mammoth (COM 5a/5b)	524266 E, 4979101 N	1,856
Tower (COM 4)	546362 E, 4974376 N	1,910
Washburn North 1 (COM 3)	546549 E, 4968283 N	2,260
Washburn South (COM 1)	541604 E, 4956687 N	2,577
Washburn North 2 (COM 2)	543797 E, 4963695 N	2,645
Washburn Top (VUL)	544703 E, 4961664 N	2,932

Table 2: Linear mixed-effects model results for bee abundance and species richness in YNP for Model Sets 1-3. Bees were collected via pan traps. Significant p-values ($p < 0.05$) are in boldface.

Model Set 1: All Years					
Bee Abundance (Log-Transformed)			Bee Species Richness (Log-Transformed)		
Variable	t value	Pr(> t)	Variable	t value	Pr(> t)
Elevation	-0.483	0.6299	Elevation	-0.878	0.3817
Seasonality	-2.294	0.0234	Seasonality	-3.353	0.0010
Year	-0.717	0.4749	Year	-1.716	0.0884
Elevation* Seasonality	1.581	0.1162	Elevation* Seasonality	2.121	0.0358
Elevation*Year	0.467	0.6414	Elevation*Year	0.859	0.3919
Model Set 2: 2012					
Bee Abundance (Log-Transformed)			Bee Species Richness (Log-Transformed)		
Variable	t value	Pr(> t)	Variable	t value	Pr(> t)
Elevation	-1.255	0.0279	Elevation	-1.106	0.0534
Seasonality	-1.912	0.1492	Seasonality	-2.577	0.0982
Elevation* Seasonality	1.167	0.6161	Elevation* Seasonality	1.248	0.5980
Model Set 3: 2020					
Bee Abundance (Log-Transformed) for 2020			Bee Species Richness for 2020		
Variable	t value	Pr(> t)	Variable	t value	Pr(> t)
Elevation	-0.779	0.4406	Elevation	-2.375	0.0221
Seasonality	-1.095	0.2796	Seasonality	-3.223	0.0021
Flower Species Richness (square-root transformed)	-0.719	0.4753	Flower Species Richness (square- root transformed)	-0.533	0.5962
Elevation* Seasonality	0.546	0.5876	Elevation* Seasonality	1.925	0.0595
Flower Species Richness (square-root transformed)*Seasonality	0.213	0.8318	Flower Species Richness (square- root transformed)* Seasonality	0.658	0.5136

Table 3: Least squares means (LSM) values for bee species richness (log-transformed) in each year across the three highest elevations. Bees were collected via pan traps. Year was marginally significant ($P = 0.0884$) for bee species richness.

Year	LSM Values for Bee Species Richness (Logged)	Standard Error
2010	2.99	0.200
2011	2.77	0.136
2012	2.65	0.081
2020	2.35	0.076

Table 4: Linear mixed-effects model results for floral density (log-transformed) and flower species richness (square-root transformed). Significant p-values ($p < 0.05$) are in boldface.

Linear Model Output					
Floral Density (Log-Transformed)			Flower Species Richness (Square-Root-Transformed)		
Variable	t value	Pr(> t)	Variable	t value	Pr(> t)
Elevation	4.163	0.000128	Elevation	5.164	1.49e-05
Seasonality	1.157	0.252	Seasonality	2.174	0.034
Elevation* Seasonality	-2.978	0.004	Elevation* Seasonality	-3.890	0.000279

Table 5: PERMANOVA results testing for relationships between floral diversity and environmental variables. Significant p-values ($p < 0.05$) are in boldface.

PERMANOVA Output			
Variable	F	R²	Pr(>F)
Elevation	3.69	0.069	0.001
Seasonality	3.02	0.056	0.001
Seasonality*Elevation	2.16	0.040	0.001

Table 6: PERMANOVA results testing for relationships between environmental factors and bee community composition in Yellowstone National Park for model sets incorporating all years, 2012 and 2020 only, and 2020 only. Bees were collected via pan traps. Significant p-values ($p < 0.05$) are in boldface.

PERMANOVA 1: Bee Community Composition for All Years			
Variable	F	R²	Pr(>F)
Elevation	2.11	0.051	0.007
Year	2.40	0.058	0.001
Seasonality	2.67	0.065	0.001
Average Slope	2.12	0.051	0.003
Elevation*Year	2.18	0.052	0.001
Elevation*Seasonality	0.71	0.017	0.874
PERMANOVA 2: Bee Community Composition for 2012			
Variable	F	R²	Pr(>F)
Elevation	5.81	0.094	0.001
Seasonality	4.56	0.074	0.001
Average Slope	1.56	0.025	0.055
Elevation*Seasonality	1.92	0.031	0.025
PERMANOVA 3: Bee Community Composition for 2020 only			
Variable	F	R²	Pr(>F)
Elevation	7.65	0.103	0.001
Seasonality	3.88	0.052	0.001
Flower Species Richness	2.15	0.029	0.007
Floral Density	1.07	0.014	0.349
Average Slope	1.60	0.021	0.056
Seasonality*Elevation	1.56	0.021	0.059
Seasonality*Flower Species Richness	2.50	0.034	0.005
Seasonality*Floral Density	2.01	0.027	0.016

Table 7: Linear mixed-effects model results for plant-bee interaction network specialization index values (H_2') for all sites in YNP in June, July, and August 2020. Average flower species richness was used in place of total flower species richness to account for missing floral data from 6/22/20 – 6/24/20. Bees were collected via hand-netting. Significant p-values ($p < 0.05$) are in boldface.

Variable	t value	Pr(> t)
Elevation	2.226	0.056
Month	1.675	0.133
Average Slope	-1.871	0.098
Bee Species Richness	-2.629	0.030
Average Flower Species Richness	1.886	0.096

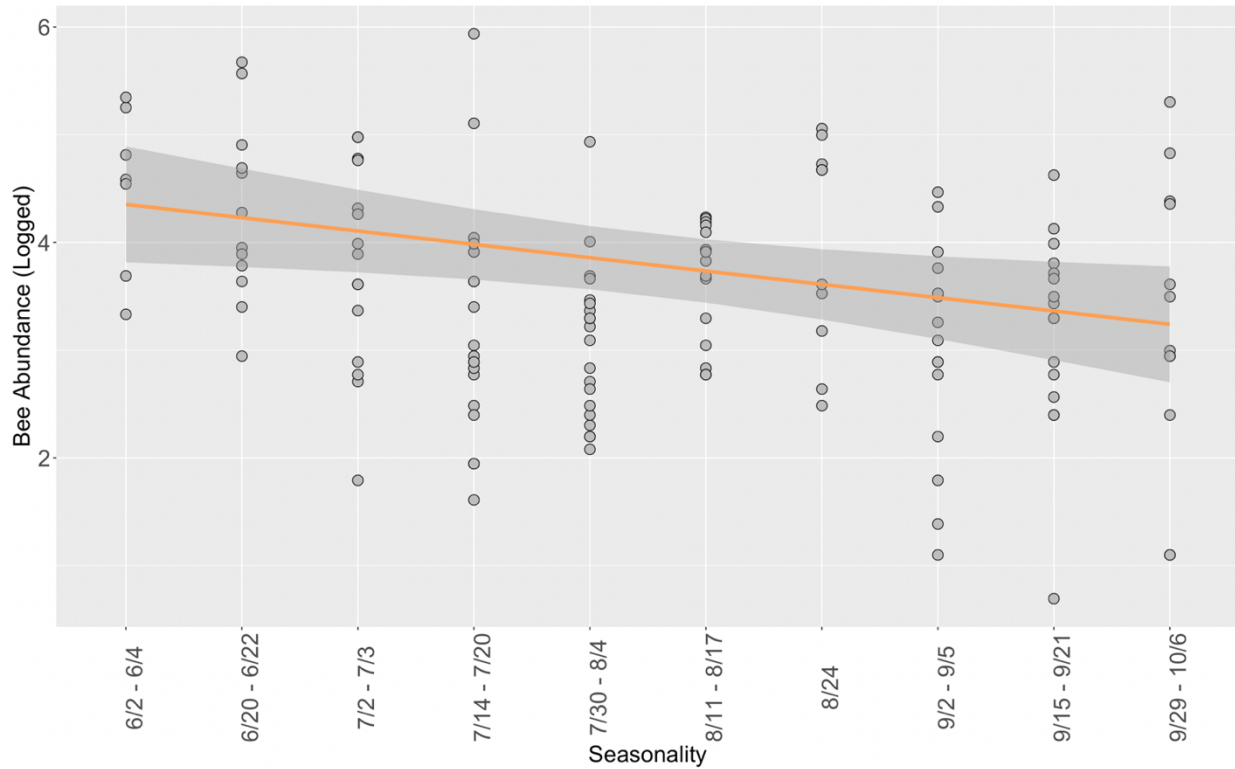


Figure 1: Scatter plot of bee abundance (logged) over all years and sites for dates sampled over the growing season, represented by the variable, “Seasonality”. The trendline (orange) represents least squares means of bee abundance for each sampling period throughout the growing season. Bees were collected via pan traps.

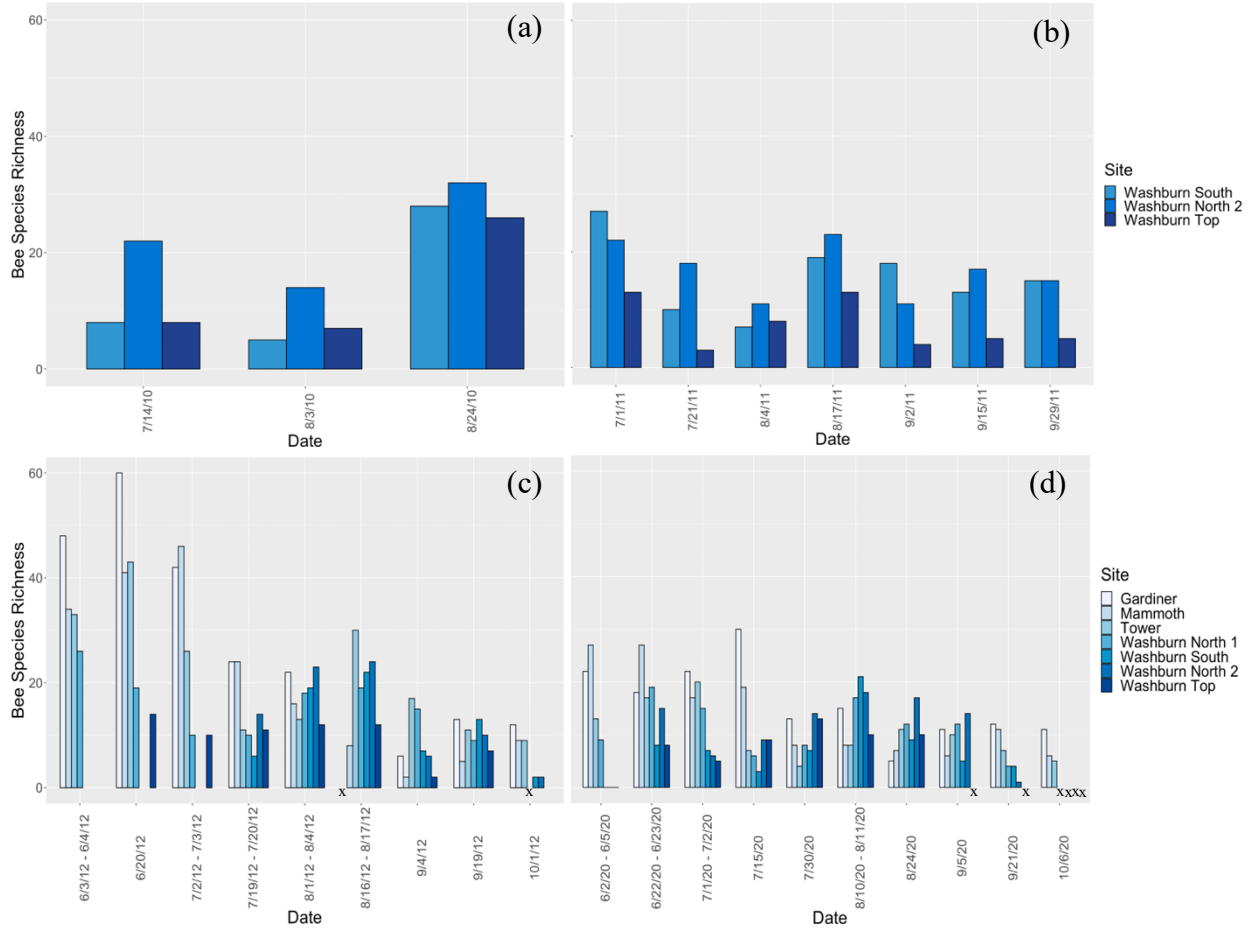


Figure 2: Bar charts of patterns in bee species richness over seasons and sites in YNP in (a) 2010, (b) 2011, (c) 2012 (Model Set 2), and (d) 2020 (Model Set 3). Sites increase in elevation from Gardiner (white) to Washburn Top (dark blue). In 2010 and 2011, data were only collected at the sites and periods displayed. Sites were not able to be sampled on the indicated dates marked with an “x” in the bar charts. All other dates with no data in 2012 and 2020 were sampled and no bees were collected. Model Set 1 is represented in all four panels. Bees were collected via pan traps.

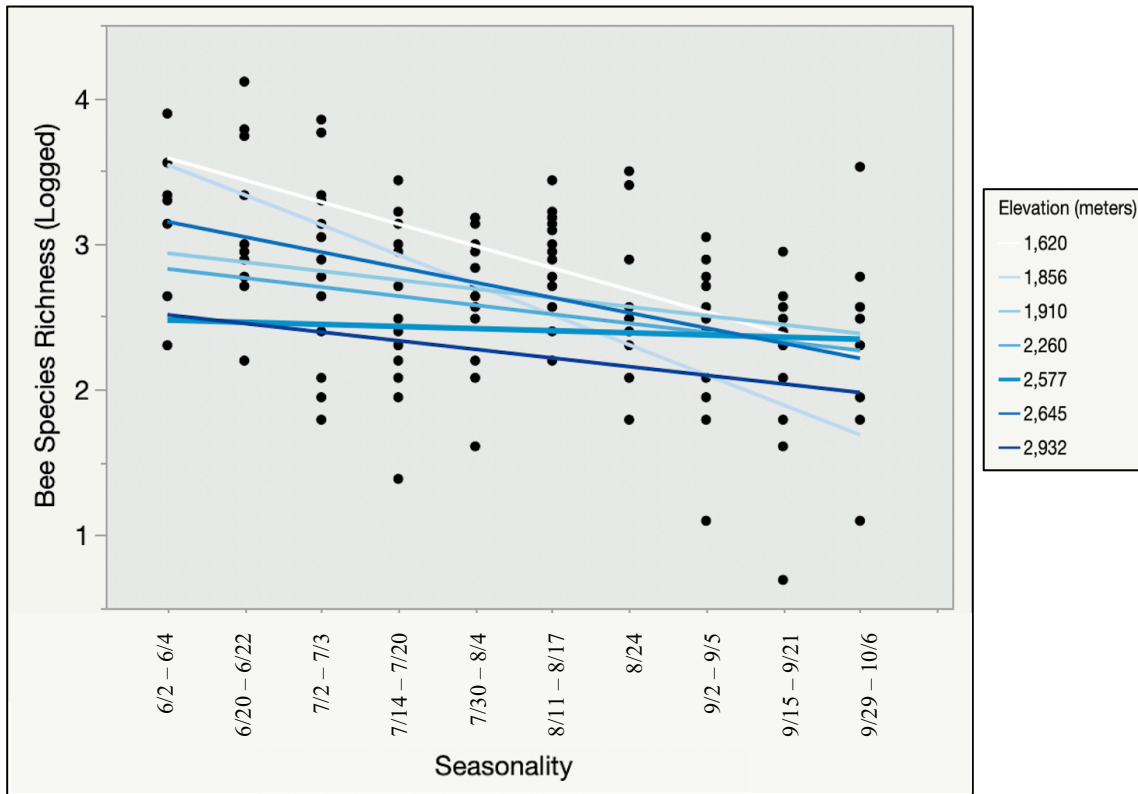


Figure 3: Scatter plot of least squares means of bee species richness (logged) for all years (Model Set 1) throughout dates sampled over the growing season, represented by the variable, “Seasonality”. Elevations are represented by the lines and range from 1,620 meters (white) to 2,932 meters (dark blue). Bees were collected via pan traps.

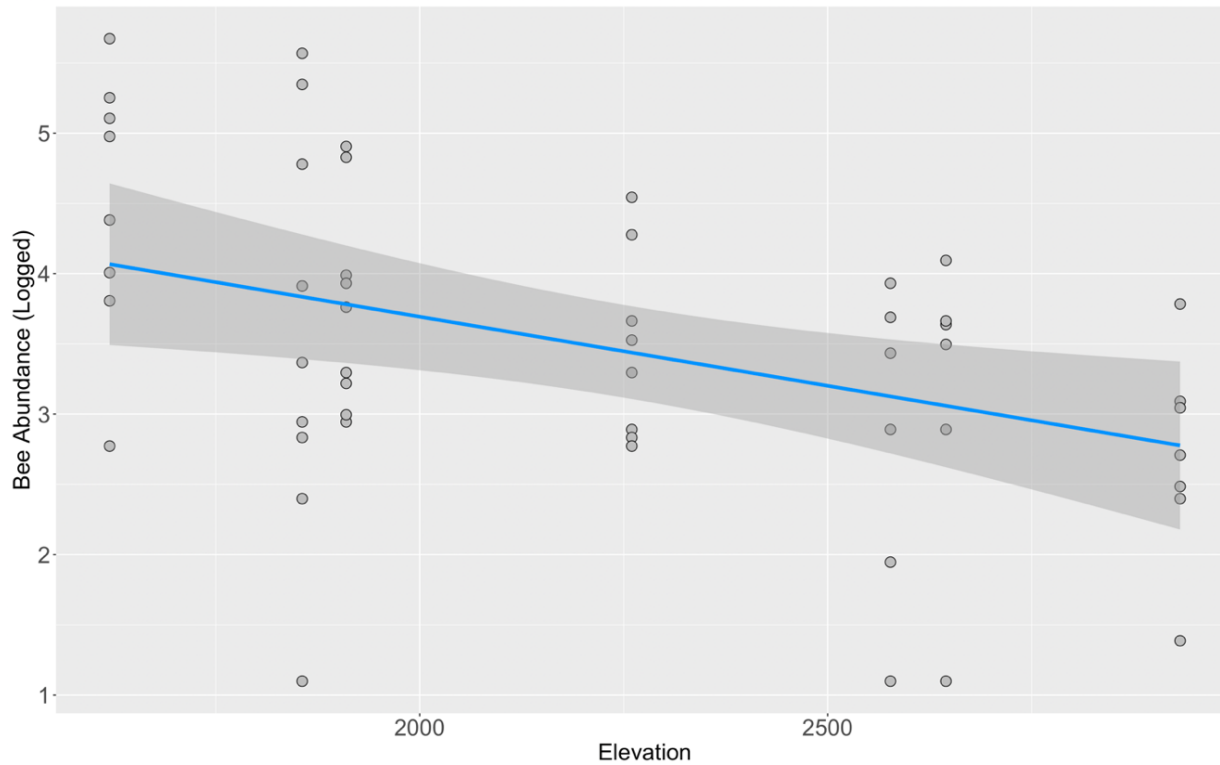


Figure 4: Scatter plot of bee abundance (logged) in 2012 for all sites and sampling dates over an elevational gradient. The trendline (blue) represents least squares means of bee abundance for each elevation ranging from 1,620 to 2,932 meters. Bees were collected via pan traps.

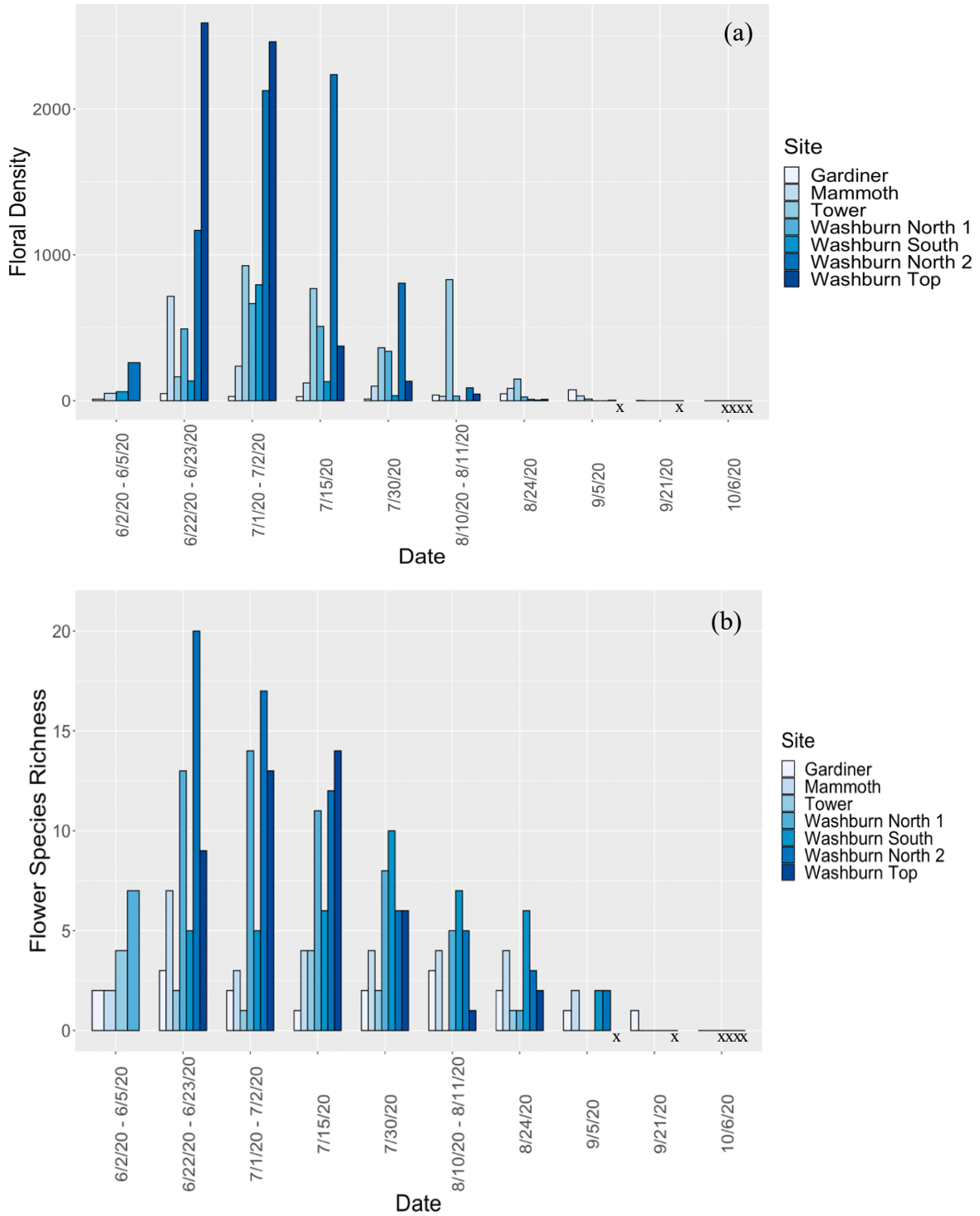


Figure 5: Bar charts showing (a) floral density and (b) flower species richness over the 2020 growing season for all seven sites. Elevation is represented by a color gradient. Sites were not able to be sampled on the indicated dates marked with an “x” in the bar charts. All other dates with no data were sampled and no flowers were observed.

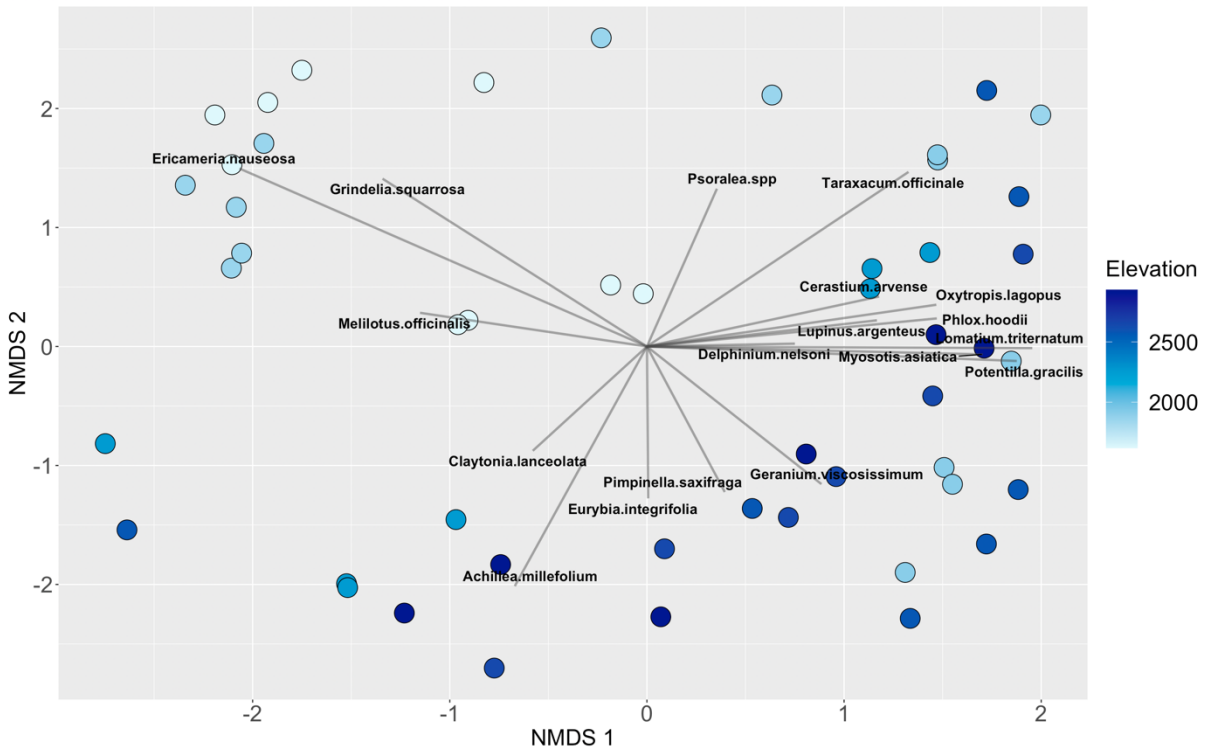


Figure 6: NMDS ordination (Bray-Curtis similarity) of floral community composition across elevation (color gradient) in 2020. Vectors illustrate significant flower species fit to the NMDS. See Table 5 for PERMANOVA results.

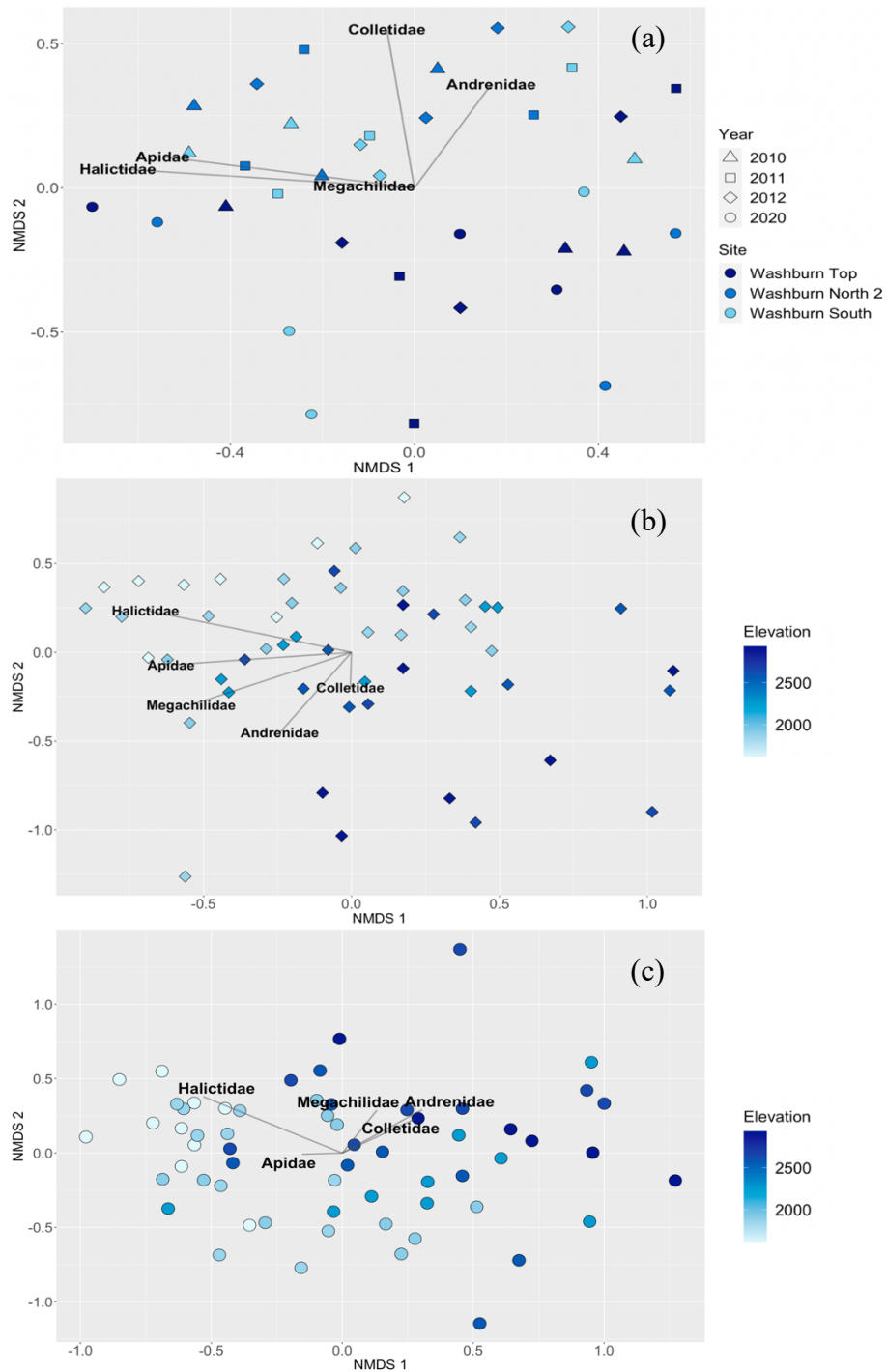


Figure 7: NMDS ordination (Bray-Curtis similarity) of (a) bee community composition across years (shapes) and elevation (color gradient) for the three highest elevation sites (Washburn South, Washburn North 2, Washburn Top), (b) bee community composition data in 2012 across elevation (color gradient) for all sites, and (c) bee community composition data in 2020 across elevation (color gradient) for all sites. Vectors illustrate bee families fit to the NMDS. See Table 6 for PERMANOVA results. Bees were collected via pan traps.

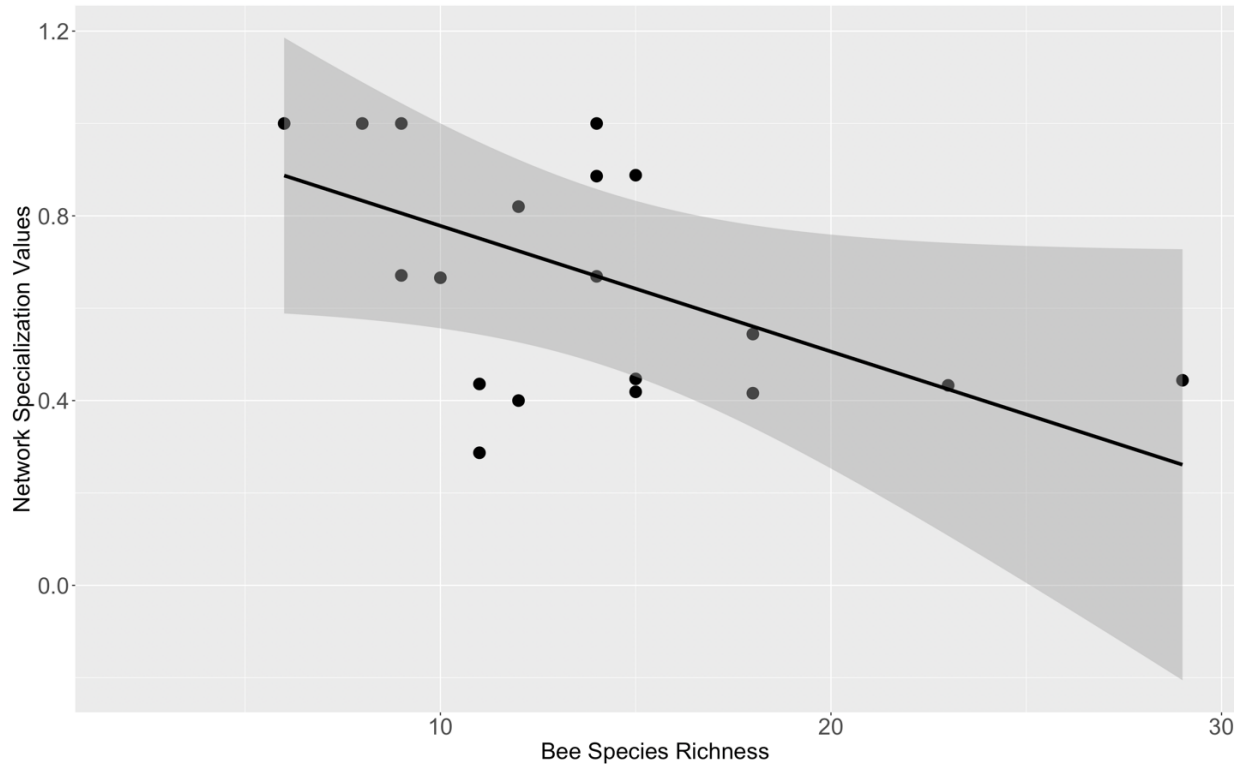


Figure 8: A scatter plot showing the relationship between network specialization index values (H_2') and bee species richness for all sites in YNP in 2020 based on least squares means (trendline). Plant-bee interaction data were collected only in June, July, and August 2020. Bees were collected via hand-netting.

REFERENCES CITED

- Adedoja, O., T. Kehinde, & M.J. Samways. (2020). Asynchrony among insect pollinator groups and flowering plants with elevation. *Scientific Reports*, 10(13268).
- Asase, A. & A. Adeniyi. (2021). Plant diversity and tree community structure along an elevation gradient in Apra Hills Sacred Grove, Ghana. *West African Journal of Applied Ecology*, 29(2).
- Baumann, K., J. Keune, V. Wolters, & F. Jauker. (2021). Distribution and pollination services of wild bees and hoverflies along an altitudinal gradient in mountain hay meadows. *Ecology and Evolution*, 11(16).
- Baskerville, G.L. & P. Emin. (1969). Rapid estimating of heat accumulation from maximum and minimum temperatures. *Ecology*, 50(3): 514-517.
- Bertrand, C., P.W. Eckerter, L. Ammann, M.H. Entling, E. Gobet, F. Herzog, L. Mestre, W. Tinner, & M. Albrecht. (2019). Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. *Journal of Applied Ecology*, 56(11).
- Bhattarai, K.R., O.R. Vetaas, J.A. Grytnes. (2004). Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, 31(3): 389-400.
- Blüthgen, N., F. Menzel, & N. Blüthgen. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, 6(9).
- Bogoni, J.A., V. Carvalho-Rocha, K.M.P.M.B. Ferraz, & C.A. Peres. (2021). Interacting elevational and latitudinal gradients determine bat diversity and distribution across the Neotropics. *Journal of Animal Ecology*, 90(12): 2729-2743.
- Bushmann, S.L., F.A. Drummond. (2015). Abundance and diversity of wild bees (Hymenoptera: Apoidea) found in lowbush blueberry growing regions of downeast Maine. *Environmental Entomology*, 44(4): 975-989.
- Bystriakova, N., T. Griswold, J.S. Ascher, M. Kuhlmann. (2018). Key environmental determinants of global and regional richness and endemism patterns for a wild bee subfamily. *Biodiversity and Conservation*, 27: 287-309.
- Carrié, R., M. Lopes, A. Ouin, & E. Andrieu. (2018). Bee diversity in crop fields is influenced by remotely-sensed nesting resources in surrounding permanent grasslands. *Ecological Indicators*, 90:606-614.

- Carvell, C., W.R. Meek, R.F. Pywell, D. Goulson, & M. Nowakowski. (2006). Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, 44(1):29-40.
- Chesshire, P.R., L.M. McCabe, & N.S. Cobb. (2021). Variation in plant-pollinator network structure along the elevational gradient of the San Francisco Peaks, Arizona. *Insects*, 12(12): 1060.
- Classen, A., C.D. Eardley, A. Hemp, M.K. Peters, R.S. Peters, A. Ssymank, & I. Steffan-Dewenter. (2020). Specialization of plant-pollinator interactions increases with temperature at Mt. Kilimanjaro. *Ecology and Evolution*, 10(4): 2182-2195.
- Classen, A., M.K. Peters, W.J. Kindeketa, T. Appelhans, C.D. Eardley, M.W. Gikungu, A. Hemp, T. Nauss, & I. Steffan-Dewenter. (2015). Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania? *Global Ecology and Biogeography*, 24(6): 642-652.
- Colla, S.R. & S. Dumes. (2010). The bumble bees of Southern Ontario: Notes on natural history and distribution. *The Journal of the Entomological Society of Ontario*, 141: 39-68.
- Colwell, R.K. & D.C. Lees. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, 15: 70-76.
- David, R.S., J. Higgins, & J. Burton. (2015). Bee diversity and abundance along an elevational gradient in Northern Arizona. *The Colorado Plateau VI: Science and Management at the Landscape Scale* (pp. 159-189). University of Arizona Press.
- Davis, J.D., S.D. Hendrix, D.M. Debinski, C.J. Hemsley. (2005). Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *Journal of Insect Conservation*, 12: 69-79.
- Delgado-Carrillo, O., S. Matrn-Rodríguez, L. Ashworth, R. Aguilar, M. Lopezaraiza-Mikel, & M. Quesada. (2018). Temporal variation in pollination services to *Cucurbita moschata* is determined by bee gender and diversity. *Ecosphere*, 9(11).
- Deng, C., T. Daley, & A.D. Smith. (2016). Applications of species accumulation curves in large-scale biological data analysis. *Quantitative Biology*, 3(3):135-144.
- Ebeling, A., A.M. Klein, & T. Tschardt. (2011). Plant-flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. *Basic and Applied Ecology*, 12(4):300-309.

- Ebeling, A., A.M. Klein, J. Schumacher, W.W. Weisser, & T. Tschardtke. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, *117*(12): 1808-1815.
- Graves, T. A., W. M. Janousek, S. M. Gaulke, A. C. Nicholas, D. A. Keinath, C. M. Bell, S. Cannings, R. G. Hatfield, J. M. Heron, J. B. Koch, H. L. Loffland, L. L. Richardson, A. T. Rohde, J. Rykken, J. P. Strange, L. M. Tronstad, and C. S. Sheffield. (2020). Western bumble bee: declines in the continental United States and range-wide information gaps. *Ecosphere*, *11*(6).
- Gonzalez, P., Wang, F., Notaro, M., Vimont, D.J., & Williams, J.W. (2018). Disproportionate magnitude of climate change in United States national parks. *Environmental Research Letters*. *13*(10).
- Hanson, C., M.C. Horner-Devine, J.B.H. Martiny, & J.A. Fuhrman. (2013). Microbial Biogeography. In: Levin S.A. (ed.) *Encyclopedia of Biodiversity*, second edition, Volume 5, pp. 271-279. Waltham, MA: Academic Press.
- Heaney, L.R. (2001). Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, *10*(1): 15-39.
- Herzog, S.K., M. Kessler, & K. Bach. (2005). The elevational gradient in Andean bird species richness at the local scale: A foothill peak and a high-elevation plateau. *Ecography*, *28*(2):209-222.
- Hoiss, B., J. Krauss, & I. Steffan-Dewenter. (2015). Interactive effects of elevation, species richness and extreme climatic events on plant-pollinator networks. *Global Change Biology*, *21*(11): 4086-4097.
- Hoiss, B., J. Krauss, S.G. Potts, S. Roberts, & I. Steffan-Dewenter. (2012). Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceeding of the Royal Society B*, *279*(1746).
- Hopfenmüller, S., I. Steffan-Dewenter, & A. Holzschuh. (2014). Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLOS One*, *9*(8).
- Hostetler, S., C. Whitlock, B. Shuman, D. Liefert, C.W. Drimal, & S. Bischke. (2021). *Greater Yellowstone Climate Assessment: Past, Present, and Future Climate Change in Greater Yellowstone Watersheds*. Bozeman MT: Montana State University, Institute on Ecosystems. <https://doi.org/10.15788/GYCA2021>.

- Hudson, J., S. Horn, & J.L. Hanula. (2011). Assessing the efficiency of pan traps for collecting bees (Hymenoptera: Apoidea).
- Joaqui, T., C.A. Cultid-Medina, W. Dáttilo, F. Escobar. (2021). Different dung beetle diversity patterns emerge from overlapping biotas in a large mountain range of the Mexican Transition Zone. *Journal of Biogeography*, 48(6): 1284-1295.
- Joshi, N.K., T. Leslie, E.G. Rajotte, M.A. Kammerer, M. Otieno, & D.J. Biddinger. (2015). Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. *Annals of the Entomological Society of America*, 108(5): 785-799.
- Kehrberger, S. & A. Holzschuh. (2019). Warmer temperatures advance flowering in a spring plant more strongly than emergence of two solitary spring bee species. *PLoS ONE*, 14(6).
- Kerr, J.T., A. Pindar, P. Galpern, L. Packer, S.G. Potts, S.M. Roberts, P. Rasmont, O. Schweiger, S.R. Colla, L.L. Richardson, D.L. Wagner, L.F. Gall, D.S. Sikes, & A. Pantoja. (2015). Climate change impacts on bumblebees converge across continents. *Science*, 349:177–180.
- Kessler, M. (2000). Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant Ecology*, 149: 181-193.
- Kieltyk, P. (2021). Patterns of floral allocation along an elevation gradient: variation in *Senecio subalpinus* growing in the Tatra Mountains. *Alpine Botany*, 131: 117-124.
- Kluge, J., M. Kessler, & R.R. Dunn. (2006). What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, 15(4): 358-371.
- Kohler, M., A. Sturm, C.S. Sheffield, C.N. Carlyle, & J.S. Manson. (2020). Native bee communities vary across three prairie ecoregions due to land use, climate, sampling method, and bee life history traits. *Insect Conservation and Diversity*, 13(6): 571-584.
- Kremen, C., N.M. Williams, & R.W. Thorp. (2002). Crop pollination from native bees at risk from agricultural intensification. *PNAS*, 99(26).
- Lane, I.G., C.R. Herron-Sweet, Z.M. Portman, & D.P. Cariveau. (2020). Floral resource diversity drives bee community diversity in prairie restorations along an agricultural landscape gradient. *Journal of Applied Ecology*, 57(10):2010-2018.
- Lara-Romero, C., J. Seguí, A. Pérez-Delgado, M. Nogales, A. Traveset. (2019). Beta diversity and specialization in plant-pollinator networks along an elevational gradient. *Journal of Biogeography*, 46(7): 1598-1610.

- Lieberman, D., M. Lieberman, R. Peralta, & G.S. Hartshorn. (1996). Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, 84(2): 137-152.
- Mallinger, R.E., J. Gibbs, & C. Gratton. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, 31: 1523-1535.
- Marini, L., M. Quaranta, P. Fontana, J.C. Biesmeijer, & R. Bommarco. (2012). Landscape context and elevation affect pollinator communities in intensive apple orchards. *Basic and Applied Ecology*, 13(8): 681-689.
- Matteson, K.C. & G.A. Langellotto. (2010). Determinates of inner city cutterfly and bee species richness. *Urban Ecosystem*, 13: 333-347.
- McCabe, L.M., E. Colella, P. Chesshire, D. Smith, N.S. Cobb. (2019). The transition from bee-to-fly dominated communities with increasing elevation and greater forest canopy cover. *PLOS One*, 14(6).
- McCain, C.M. (2003). The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, 31(1): 19-31.
- McCain, C.M. & J.A. Grytnes. (2010). Elevational gradients in species richness. *Encyclopedia of Life Sciences*.
- Meiners, J.M., T.L. Griswold, O.M. Carril. (2019). Decades of native bee biodiversity surveys at Pinnacles National Park highlight the importance of monitoring natural areas over time. *PLOS One*, 14(1).
- Minachilis, K., K. Kougioumoutzis, & T. Petanidou. (2021). Climate change effects on multi-taxa pollinator diversity and distribution along the elevation gradient of Mount Olympus, Greece. *Ecological Indicators*, 132(108335).
- Nor, S.M.D. (2008). Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography*, 10(1): 41-62.
- Oertli, S., A. Müller, & S. Dorn. (2005). Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). *European Journal of Entomology*, 102: 53-63.
- Oleques, S.S., J.N. Radaeski, S. Bauerman, O. Chauveau, & T.T. de Souza-Chies. (2020). The specialization–generalization continuum in oil-bee pollination systems: a case study of six Brazilian species of Tigridae (Iridaceae). *Biological Journal of the Linnean Society*, 129(3):701-716.

- Packer, L., A.I.D. Gravel, & G. LeBuhn. (2007). Phenology and social organization of *Halictus* (*Seladonia*) *Tripartitus* (Hymenoptera: Halictidae). *Journal of Hymenoptera Research*, 16(2).
- Potts, S.G., B. Vulliamy, A. Dafni, G. Ne'eman, & P. Willmer (2003). Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology*, 84: 2628-2642.
- Prato, T. & D. Fagre. (2007). Sustaining Rocky Mountain landscapes: Science, policy, and management for the Crown of the Continent Ecosystem. Rff Press.
- Pryke, J.S. & M.J. Samways. (2008). Conservation of invertebrate biodiversity on a mountain in a global biodiversity hotspot, Cape Floral Region. *Biodiversity and Conservation*, 3027:3027-3043.
- Pyke, G.H., J.D. Thomson, D.W. Inouye, & T.J. Miller. (2016). Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. *Ecosphere*, 7(3).
- Pyke, G.H., D.W. Inouye, & J.D. Thomson. (2011). Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects. *Ecological Entomology*, 36(4):511-521.
- Rahbek, C. (1995). The elevational gradient of species richness: a uniform pattern? *Ecography*, 18(2): 200-205.
- Rasmussen, C., Y.L. Dupont, H.B. Madsen, P. Bogusch, D. Goulson, L. Herbertsson, K.P. Maia, A. Nielson, J.M. Olesen, S.G. Potts, S.P.M. Roberts, M.A.K. Sydenham, P. Kryger. (2021). Evaluating competition for forage plants between honey bees and wild bees in Denmark. *PLOS One*, 16(4).
- Richardson, B.A., M.J. Richardson, & F.N. Soto-Adames. (2005). Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. *Ecology*, 74(5): 926-936.
- Rivers, J.W., S.M. Galbraith, J.H. Cane, C.B. Schultz, M.D. Ulyshen, U.G. Kormann. (2018). A review of research needs for pollinators in managed conifer forests. *Journal of Forestry*, 116(6):563-572.
- Rollin, O., V. Bretagnolle, L. Fortel, L. Guilbaud, & M. Henry. (2015). Habitat, spatial and temporal drivers of diversity patterns in a wild bee assemblage. *Biodiversity and Conservation*, 24: 1195-1214.
- Romero-Alcaraz, E. & J.M. Ávila. (2000). Effect of elevation and type of habitat on the abundance and diversity of scarabaeoid dung beetle (*Scarabaeoidea*) assemblages in a Mediterranean area from Southern Iberian Peninsula. *Zoological Studies*, 39(4): 351-359.

- Russo, L., M. Park, J. Gibbs, B. Danforth. (2015). The challenge of accurately documenting bee species richness in agroecosystems: bee diversity in eastern apple orchards. *Ecology and Evolution*, 5(17): 3531-3540.
- Sanders, N.J. (2002). Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography*, 25(1): 25-32.
- Seitz, N., D. van Engelsdorp, & S.D. Leonhardt. (2020). Are native and non-native pollinator friendly plants equally valuable for native wild bee communities? *Ecology and Evolution*, 10(23): 12838-12850.
- Sharma, N. & C.P. Kala. (2022). Patterns in plant species diversity along the altitudinal gradient in Dhauladhar mountain range of the North-West Himalaya in India. *Trees, Forests, and People*, 7(100196).
- Stemkovski, M., W.D. Pearse, S.R. Griffin, G.L. Pardee, J. Gibbs, T., Griswold, J.L. Neff, R. Oram, M.G. Rightmyer, C.S. Sheffield, K. Wright, B.D. Inouye, D.W. Inouye, & R.E. Irwin. (2020). Bee phenology is predicted by climatic variation and functional traits. *Ecology Letters*, 23(11):1589-1598.
- Sydenham, M.A.K., S.R. Moe, Ø. Totland, & K. Eldegard. (2014). Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? *Ecography*, 38(2): 140-153.
- Terborgh, J. (1977). Bird species diversity on an Andean elevational gradient. *Ecology*, 58(5):1007-1019.
- Tucker, E.M. & S.M. Rehan. (2016). Wild bee pollination networks in northern New England. *Journal of Insect Conservation*, 20: 325-337.
- Widhiono, I., E. Sudiana, & D. Darsono. (2017). Diversity of wild bees along elevational gradient in an agricultural area in Central Java, Indonesia. *Psyche: A Journal of Entomology*, 2017
- Williams, N.M., R.L. Minckley, & F.A. Silveira. (2001). Variation in native bee faunas and its implications for detecting community changes. *Ecology and Society*, 5(1): 7.
- Woodard, S. H., S. Federman, R.R. James, B.N. Danforth, T.L. Griswold, D. Inouye, et al. (2020). Towards a U.S. national program for monitoring native bees. *Biol. Conserv.* 252, 108821.
- Wray, J.C. & E. Elle. (2015). Flowering phenology and nesting resources influence pollinator community composition in a fragmented ecosystem. *Landscape Ecology*, 30: 261-272.

APPENDICES

APPENDIX A

PAN TRAP SAMPLING DATES FOR ALL YEARS

Table 1: Sampling dates for bees collected via pan traps in Yellowstone National Park in 2010, 2011, 2012, and 2020.

Sampling Date(s)	Sampling Period	Sites
7/14/2010	4	Washburn South Washburn North 2 Washburn Top
8/3/2010	5	Washburn South Washburn North 2 Washburn Top
8/24/2010	7	Washburn South Washburn North 2 Washburn Top
7/1/2011	3	Washburn South Washburn North 2 Washburn Top
7/21/2011	4	Washburn South Washburn North 2 Washburn Top
8/3/2011-8/4/2011	5	Washburn South Washburn North 2 Washburn Top
8/17/2011	6	Washburn South Washburn North 2 Washburn Top
9/2/2011	8	Washburn South Washburn North 2 Washburn Top
9/15/2011	9	Washburn South Washburn North 2 Washburn Top
9/29/2011	10	Washburn South Washburn North 2 Washburn Top
6/3/2012-6/4/2012	1	Gardiner Mammoth Tower Washburn North 1
6/20/2012	2	Gardiner Mammoth Tower Washburn North 1 Washburn Top

Table 1 Continued

7/2/2012-7/3/2012	3	Gardiner Mammoth Tower Washburn North 1 Washburn Top
7/19/2012-7/20/2012	4	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
8/1/2012-8/4/2012	5	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
8/16/2012-8/17/2012	6	Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
9/4/2012	8	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
9/19/2012	9	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top

Table 1 Continued

10/1/2012	10	Gardiner Mammoth Tower Washburn South Washburn North 2
6/3/2020-6/6/2020	1	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
6/23/2020-6/24/2020	2	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
7/2/2020-7/3/2020	3	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
7/16/2020	4	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
7/31/2020	5	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top

Table 1 Continued

8/11/20-8/12/2020	6	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
8/25/2020	7	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2 Washburn Top
9/6/2020	8	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2
9/22/2020	9	Gardiner Mammoth Tower Washburn North 1 Washburn South Washburn North 2
10/6/2020	10	Gardiner Mammoth Tower

APPENDIX B

MODEL SELECTION AND AIC RESULTS

Table 1: Initial and final models for Model Sets 1-3. Initial explanatory variables included all possible explanatory variables prior to transformations and correlation analysis. Final explanatory variables include variables transformed for normality and don't include highly correlated variables. Site was included as a random effect for all models.

	Response Variable	Initial Explanatory Variables	Final Explanatory Variables
Model Set 1	Bee abundance (log-transformed)	Elevation Average slope Seasonality Year Elevation*Seasonality Elevation*Year	Elevation Seasonality Year Elevation*Seasonality Elevation*Year
Model Set 1	Bee species richness (log-transformed)	Elevation Average Slope Seasonality Year Elevation*Seasonality Elevation*Year	Elevation Seasonality Year Elevation*Seasonality Elevation*Year
Model Set 2	Bee abundance (log-transformed)	Elevation Average slope Seasonality Elevation*Seasonality	Elevation Seasonality Elevation*Seasonality
Model Set 2	Bee species richness (log-transformed)	Elevation Average slope Seasonality Elevation*Seasonality	Elevation Seasonality Elevation*Seasonality
Model Set 3	Bee abundance (log-transformed)	Elevation Average slope Seasonality Growing degree-days Elevation*Seasonality Elevation*Year Floral density Flower species richness	Elevation Average slope Seasonality Growing degree-days Elevation*Seasonality Elevation*Year Floral density (log-transformed) Flower species richness (square-root transformed)
Model Set 3	Bee species richness	Elevation Average slope Seasonality Growing degree-days Elevation*Seasonality Elevation*Year Floral density Flower species richness	Elevation Average slope Seasonality Growing degree-days Elevation*Seasonality Elevation*Year Floral density (log-transformed) Flower species richness (square-root transformed)

Table 2: AIC values for initial and final models for Model Sets 1-3. Final models were chosen based on lower AIC values.

	Response Variable	Initial Model AIC Score	Final Model AIC Score
Model Set 1	Bee abundance (log-transformed)	459.3434	452.6611
Model Set 1	Bee species richness (log-transformed)	303.3718	295.0345
Model Set 2	Bee abundance (log-transformed)	181.4404	174.7023
Model Set 2	Bee species richness (log-transformed)	139.333	131.6884
Model Set 3	Bee abundance (log-transformed)	334.8305	212.3437
Model Set 3	Bee species richness	495.7692	406.2403

APPENDIX C

CORRELATION PLOTS FOR LINEAR MIXED-EFFECTS MODELS

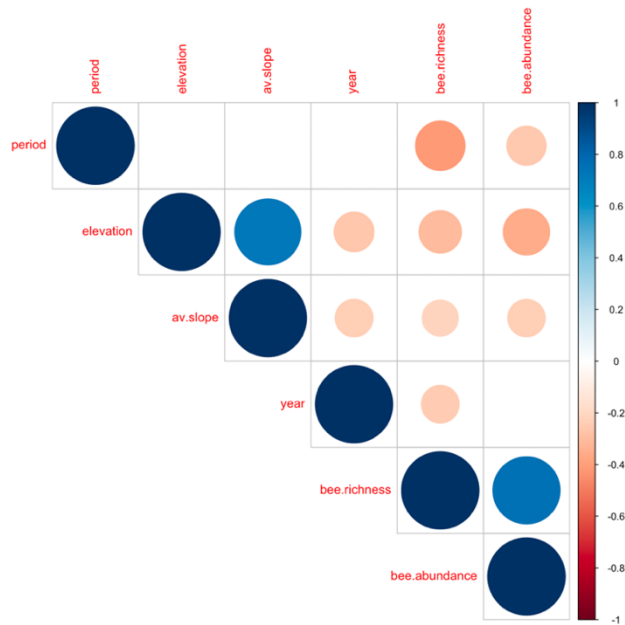


Figure 1: Correlation plot ('corrplot' function in R package Corrplot) for independent variables in the linear mixed-effects models for bee abundance and species richness in all years (Model Set 1).



Figure 2: Correlation plot ('corrplot' function in R package Corrplot) for independent variables in the linear mixed-effects models for bee abundance and species richness in 2012 and 2020 (Model Set 2).

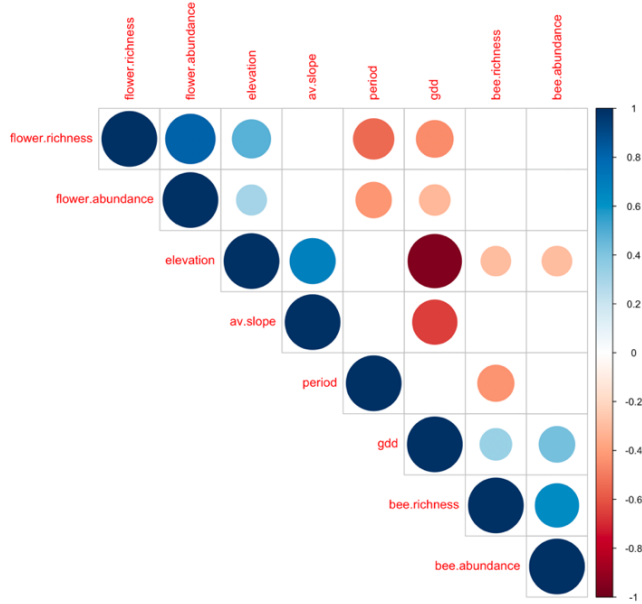


Figure 3: Correlation plot ('corrplot' function in R package Corrplot) for independent variables in the linear mixed-effects models for bee abundance and species richness in 2020 only (Model Set 3).

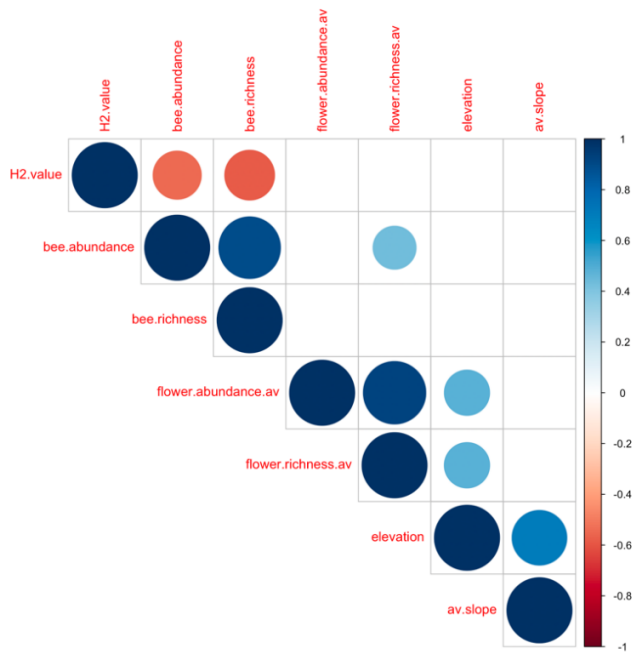


Figure 4: Correlation plot ('corrplot' function in R package Corrplot) for independent variables in the linear mixed-effects models for the degree of network specialization (H_2) in 2020 only (Model Set 3).