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Elevational Distribution Gradient of *Agapostemon subtilior* in Gunnison County

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Abstract

Climate change is rapidly altering mountain ecosystems by increasing temperatures, reducing snowpack, and extending growing seasons. These changes can result in shifts in species distributions and ecological interactions. While elevational range shifts have been well documented in bumble bees, comparatively little is known about how solitary bees respond to changing climatic conditions. This study investigated whether the ultra-green sweat bee, *Agapostemon subtilior*, has expanded its elevational range in Gunnison County, CO, in response to climate change. Occurrence records of *A. subtilior* collected from 2010-2023 across sites spanning an elevational gradient from approximately 2400 meters to 3400 meters were compiled using data from the Rocky Mountain Biological Laboratory (RMBL) Irwin long-term bee phenology monitoring program. Records of *A. subtilior* were integrated with environmental variables including elevation, temperature, and precipitation obtained from the RMBL Data Hub. Negative binomial generalized linear models were used to test the effects of those environmental variables on *A. subtilior* abundance. Elevation was found to be a strong and significant predictor of abundance, with significantly higher abundance at low-elevation sites. Temperature and precipitation were both significantly associated with abundance, but they also both closely tracked the elevational gradient. However, no significant trend in abundance was detected across sampling years. These results suggest that climate variables are closely tied to current patterns of *A. subtilior* abundance across elevation. This study highlights the need for longer-term monitoring to assess whether solitary bee distributions are beginning to to move with climate change in mountain ecosystems.

Introduction

The Rocky Mountains are trending towards longer, hotter summers with less snowpack due to climate change (Luce, 2018). This leads to shifting biological communities, fluctuating ecosystem functions, and shifting species ranges due to changing water resource availability and temperature gradients. Climate change is especially stressing cold-adapted communities, with negative impacts particularly affecting alpine biomes (Biella et al., 2024). The combination of increasing annual temperature and precipitation changes also disrupts snow-cover and snow-melt patterns, ground insulation, and thus floral availability for pollinators. These changes cascade through communities and alter species composition, competition patterns, trophic interactions, and available resources across elevational gradients (Gray et al., 2018). The net result is a redistribution of species and reshaping of ecosystem function towards higher elevations as more habitat becomes viable for new species (Hollenbeck & Sax, 2024).

Documenting transforming habitats is particularly critical for montane environments because mountainous biomes are excessively sensitive to rising temperatures and altered precipitation (Dolson & Kharouba, 2024). Due to climate change disproportionately affecting elevational gradients, even small shifts in temperature force species to migrate upslope to maintain their thermal niche (Hollenbeck & Sax, 2024), with population decline at lower elevations and population increase at higher elevations. Moreover, alpine environments are experiencing climate change at an accelerated rate compared to lower elevations (Pepin et al., 2025). Temperatures are rising more quickly

at high elevations, making cold-adapted species in these ranges particularly vulnerable to range contractions and local extinctions (Hollenbeck & Sax, 2024). However, several barriers prevent species from shifting their ranges in response to these changing conditions (Wyver et al., 2023). Biological dispersal limitations, elevational summit limits, and phenological or spatial mismatches with resources could affect whether a species can colonize up an elevation gradient (Marshall et al., 2020; Stemkovski et al., 2020). Moreover, bee range limits are also driven by multiple climate factors including temperature thresholds, precipitation patterns, and moisture availability (Gonzalez et al., 2024).

Many plants and insects are moving up in elevation in mountain ecosystems (Shah et al., 2020). For example, bumble bees in the Rocky Mountains of Colorado have shown significant elevational increases from 1974-2007, though this response is not consistent across all species (Pyke et al., 2016). Plants visited by bumble bees have shifted more dramatically in elevation than the bees, creating potential spatial mismatches between pollinators and their floral resources (Marshall et al., 2020). Similarly, bee emergence phenology is heavily influenced by the timing of snowmelt, with sites at higher elevations experiencing later emergence and peak abundance timing. However, those same sites still experienced earlier senescence, resulting in shortened foraging seasons (Stemkovski et al., 2020).

Understanding elevational gradients of bees is important because climate change is driving range shifts that could dismantle tightly linked plant-pollinator interactions. This is where interacting species respond differently to a changing climate or differ in dispersal ability. These differences in the direction or speed of range shifts can lead to spatial and phenological mismatches that disrupt pollination networks (Marshall et al., 2020). By documenting how communities are changing along elevational gradients, we can identify which interactions are most vulnerable to disruption and develop conservation strategies that conserve native pollination services.

The genus *Agapostemon* consists of metallic green sweat bees in the insect family Halictidae that are predominantly ground-nesting solitary bees. Some species exhibit communal nesting behaviors where multiple females share a single nest entrance (Eickwort, 1981). *Agapostemon subtilior* is a bivoltine species, producing two generations per year when growing seasons are long enough. Due to *A. subtilior* recently splitting from *A. texanus*, not much is known about its elevational range (Portman et al., 2024). However, recent observations point to this species moving upward in elevation potentially in response to warming temperatures and lengthening growing seasons in the Southern Rocky Mountains (unpublished data, Irwin Lab). As a generalist pollinator, *A. subtilior* visits a wide diversity of flowering plants with documented pollination of *Oppuntia sp.*, various Asteraceae, and many other wildflower species across western North America (Osborn et al., 1988). This generalist foraging strategy may provide *A. subtilior* with greater flexibility to track shifting biotic and abiotic environments along elevational gradients compared to a specialist bee pollinator species. However, whether this potential advantage translates into measurable upslope range expansion for *A. subtilior* or other solitary bees remains largely unknown.

While substantial research has documented bumble bee elevational shifts across multiple mountain systems, significant gaps remain in our understanding of how solitary bees respond to these rapid changes (Marshall et al., 2020). Moreover, *A. subtilior* has been well studied in the Sierra Nevada Mountains and other western regions, yet research on this bee in the Rocky Mountains is largely absent. This knowledge gap is critical because solitary bees, like *A. subtilior*, may differ from bumble bees in their dispersal capacity, thermal tolerance, and phenological responses.

Research Question: Is *A. subtilior* moving up in elevation in response to a changing climate?

Methods of Data Collection & Analysis of Data

Data collection

1. Field Sites: Field sampling was conducted at 16 sites spanning an elevational gradient from Almont (2456 m) to the Mexican Cut Preserve (3438 m) in Gunnison County, Colorado at and around the Rocky Mountain Biological Laboratory. Sites were located in a range of elevations and microclimatic conditions. Site coordinates were recorded using the RMBL Trimble DA2 units (Table 1, Figure 1).

2. Specimen Collection: Bees were collected using standardized aerial netting and colored pan traps following the Phenology of Subalpine Bee and Plant Communities in the Rocky Mountains of Central Colorado Protocol. Sampling occurred throughout the flowering season to maximize detection of *A.* subtilior. For every collection event, data including sampling date, time, coordinates, elevation, habitat type, floral resources, weather conditions, and collection method were recorded.

3. Specimen Preservation: Specimens were pinned, labeled, and curated following standard entomological procedures. Voucher specimens went into the RMBL Natural History Collections to provide permanent records for future taxonomic, ecological, and biodiversity research.

4. Specimen Identification: Collected *A. subtilior* specimens were identified to species using taxonomic keys and verified reference specimens (Portman et al., 2024). Confirmed records were converted into georeferenced occurrence data for species distribution modeling.

Analysis of Data

1. Data Cleaning: Bee occurrence records were combined from previous solitary bee datasets within the Irwin Bee Phenology project and more current bees from 2020-2023 were added to the dataset. The bee occurrences were compiled across multiple sampling sites and merged with site-level climate data using PRISM Weather Data (mean maximum temperature and mean precipitation during the sampling period). Sites were classified into Low, Mid, and High elevation. This was done to bin the higher elevation sites together because the highest sites did not have enough data by themselves.

Due to raw occurrence data consisting of individual bee specimen records, abundance was calculated as the total count of *A. subtilior* individuals collected at each site per-year. All data cleaning and statistical analyses were completed in R.

2. Statistical Analyses: *A. subtilior* abundance was found to be overdispersed using DHARMA, so abundance was modeled using negative binomial generalized linear models.

To evaluate the relationship between climate and *A. subtilior* abundance, single-predictor negative binomial models were fitted using mean maximum temperature and mean precipitation during the sampling season independently (April-September). Because these two variables were strongly collinear (Pearson's $r = -0.88$, $p < 0.001$), they were not included together in the same model. Instead, individual model fit was compared using Akaike Information Criterion (AIC) and likelihood ratio tests against a null (intercept-only) model.

The effect of elevation category on abundance was evaluated using a negative binomial GLM with elevation (Low, Mid, High) as a categorical predictor due to elevational data collected being discrete. This was again compared to a null model via likelihood ratio test. Post-hoc pairwise comparisons between elevation categories were conducted using estimated marginal means with Tukey adjustment for multiple comparisons.

One-way ANOVA was used independently to test whether mean maximum temperature and mean precipitation differed significantly across elevation categories, to assess whether elevation could account for the observed climate-abundance relationship.

The effect of sampling year on abundance was tested using negative binomial models with the year included as both a categorical and continuous predictor to account for both smooth trends and irregular year to year patterns. These predictors were compared via AIC and likelihood ratio tests. These results would determine whether the year explained variation in abundance independent of climate. Moreover, climate trends across the 13 years of data were assessed using linear regression of temperature and precipitation against year at individual sites. A linear mixed-effects model with site as a random intercept was also used to test whether trends were consistent across sites.

3. Visualization

Data were visualized using the ggplot2 function in R using the tidyverse package. Boxplots with jittered points displayed abundance and climate variables across elevation categories, with significant pairwise differences indicated from post-hoc tests. Scatterplots with fitted regression lines illustrated relationships between abundance and climate variables.

Results

1. Overview of Sampling and Dataset

A. subtilior was recorded across 16 sites spanning three elevation categories (Low, Mid, High) from 2010-2023 yielding 38 site-year observations. *A. subtilior* was first

detected at both Low and Middle elevation sites in 2010, but was not recorded at High elevation until 2012, a two-year lag. Of the two High elevation sites, *A. subtilior* was recorded 3 times more at North Elko (3230 m; recorded in 6 site-years). As for the other site, the Mexican Cut (3438 m), *A. subtilior* was only recorded once in 2012 and 2015.

2. Elevation is Strongly Associated with Tested Climate Factors

Mean maximum temperature ($F = 94.03$ $df = 2$, $p < 0.001$) and mean precipitation ($F = 114.4$, $df = 2$, $p < 0.001$) both differed significantly across elevation categories. Temperature declined with increasing elevation, while precipitation increased with elevation. High elevation sites showed the lowest mean maximum temperatures and highest precipitation. Low elevation sites showed the opposite pattern. Temperature and precipitation were themselves strongly negatively correlated ($r = -0.88$, $p < 0.001$), indicating both largely track the elevational gradient (Figures 2-4).

3. *A. subtilior* Abundance Differs by Elevation

Elevation significantly predicted bee abundance (negative binomial GLM, $X^2 = 23.83$, $df = 2$, $p < 0.0001$). Post-hoc comparisons showed Low-elevation sites had approximately 14.5 times higher abundance than Middle elevation sites ($p < 0.0001$). Low-elevation sites also had approximately 43.5 times higher abundance than High elevation sites ($p = 0.0002$). Moreover, Middle elevation sites and High elevation sites had almost no differences in abundance and did not significantly differ from each other ($p = 0.517$) (Figure 5).

4. Climate Predicts Abundance, but is Confounded with Elevation

Both mean maximum temperature ($p < 0.001$) and precipitation ($p < 0.001$) individually predicted abundance, each outperforming the null model. Abundance increased with mean maximum temperature ($\beta = 0.348$) and decreased with precipitation ($\beta = -1.48$). This indicates higher abundance at warmer, drier sites. However, the elevation-only model (AIC = 291.28) fit better than either climate-only model (AIC = 298.72 and 297.98), and the collinearity between temperature and precipitation indicated both largely reflect elevation rather than independent climate effects (Figures 6-7).

5. No Clear Abundance Trend Over Time

Abundance did not vary significantly with sampling year, whether modeled as a categorical factor ($p = 0.060$) or a continuous linear trend ($p = 0.165$). Models including year did not outperform climate-only or elevation-only models in an AIC comparison, indicating no detectable temporal trend in abundance over the study period. An Elevation by Year interaction was not formally tested due to insufficient sample size within elevation-year combinations, particularly at High elevation sites.

Discussion

This study asked whether *A. subtilior* is shifting upward in elevation in response to climate change. Elevation strongly predicted abundance, and climate variables tracked the same gradient. However, abundance showed no significant trend over time, providing

no direct evidence of an upward shift in the years tested. Moreover, Abundance was highest at Low-elevation sites and dropped sharply at Mid and High elevations, which did not differ significantly from one another. This threshold-like pattern suggests an ecological transition between Low and Mid elevation sites possibly driven by floral resources, nesting habitat, or thermal tolerance. However, these are not the only factors that could be driving abundance. Temperature and precipitation both predicted abundance individually, and both were strongly associated with elevation as well.

Several factors could explain why an upward shift was not observed even if one is beginning to occur. Range shifts often lag behind climate change (Sirois-Delisle & Kerr, 2018), and our 2010-2023 window may be too short to detect significant upward shifts. Limited sampling at High elevation due to weather or ability to travel to these sites might also reduce statistical power to detect small shifts in abundance.

Sampling effort at higher elevation sites are not the only limitations to this study. Elevation was treated as a three-level categorical variable rather than a continuous measure, which may obscure finer-scale patterns within each category. Similarly, the strong collinearity between temperature and precipitation, small sample sizes at High elevation, and a single-species focus all limit generalization to the broader solitary bee community.

Future work should incorporate a longer time series to increase the statistical power to detect a gradual range shift, and the incorporation of an Elevation by Year interaction could better capture a potential shift. This interaction was not tested due to insufficient sample size per elevation-year combination. Comparing patterns across the full solitary bee community would also clarify whether this response is *A. subtilior* specific.

Elevation is currently the dominant driver of *A. subtilior* abundance patterns at these sites, with climate variables closely tracking this same gradient. While climate is a plausible mechanism, no evidence of an active upward shift with the current data was found. Longer-term data are needed to detect whether *A. subtilior* is beginning to move up in elevation in response to climate change.

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Tables and Figures

Site Name	Elevation (m)	Latitude	Longitude
Davids	2979	38.962124	-106.986896
Tuttle	2877	38.954751	-106.988704
Willey	2884	38.955971	-106.988482
Gothic	3001	38.963088	-106.994866
Seans	2931	38.964099	-106.992616
Beaver	2921	38.961597	-106.993975
Copper	3072	38.96896	-106.96801
Hill	3069	38.96677	-106.97009
Little	3061	38.96732	-106.96885
Almont	2569	38.65622	-106.86203
Mexican Cut	3438	39.02685	-107.06513
Almont Curve	2456	38.66125	-106.85152
CDOT	2588	38.78257	-106.87002
Lypps	2639	38.74812	-106.83269
Rustlers	2977	38.9885	-107.00512
N. Elko	3230	39.01245	-107.05279

Table 1. Sampling site characteristics, including elevation (m) and geographic coordinates (latitude, longitude) for each site included in this study.

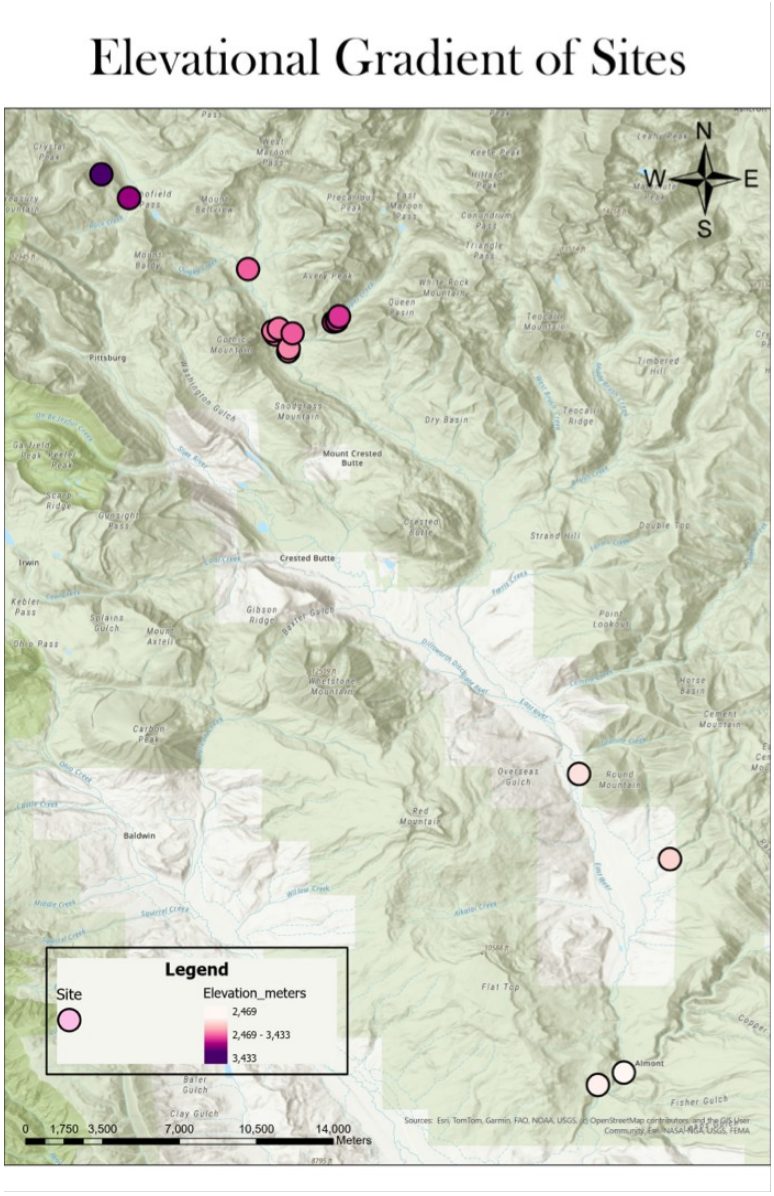

Figure 1. Map of the Elevation Gradient of Field Sampling Sites. This map displays the 16 sites that were used in this study from the lower elevation sites around 2400 meters to the higher elevation sites around 3400 meters. Lower elevation sites are colored more closely to white and higher elevation sites in dark purple. The elevation sites in-between are colored from white to dark purple with pinks in varying saturation.

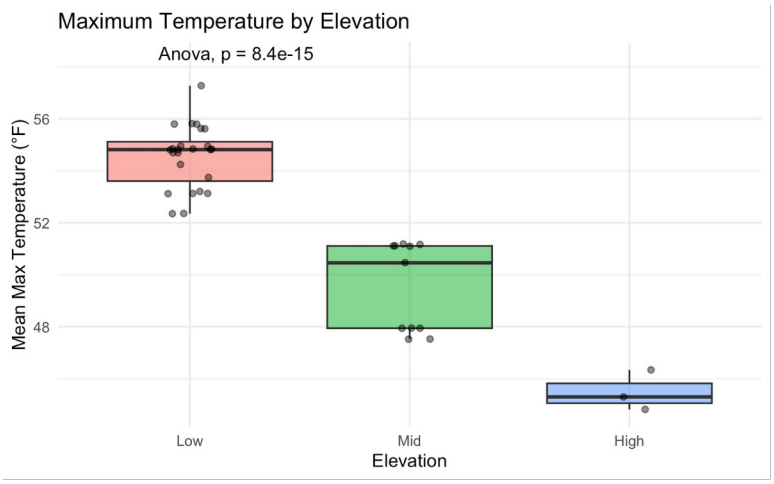

Figure 2. Mean maximum temperature by elevation category (Low, Mid, High). Boxplot shows median and interquartile range; points represent individual site-years (n = 38). Temperature differed significantly across elevation (one-way ANOVA; F(2,35) = 94.03, p < 0.001).

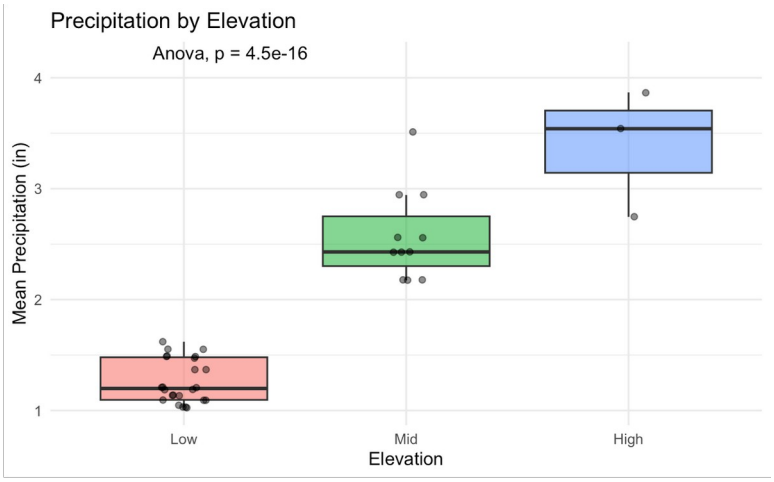

Figure 3. Mean precipitation by elevation category (Low, Mid, High). Boxplot shows median and interquartile range; points represent individual site-years (n = 38). Temperature differed significantly across elevation (one-way ANOVA; F(2,35) = 114.4, p < 0.001).

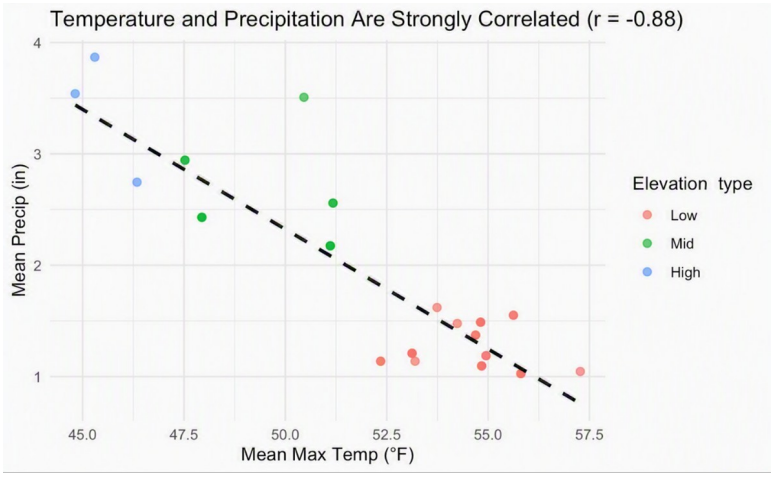

Figure 4. Relationships between mean maximum temperature and mean precipitation across site-years, colored by elevation category. Temperature and precipitation were strongly negatively correlated (Pearson's r = -0.88, p < 0.001), consistent with both variables tracking the same underlying elevational gradient.

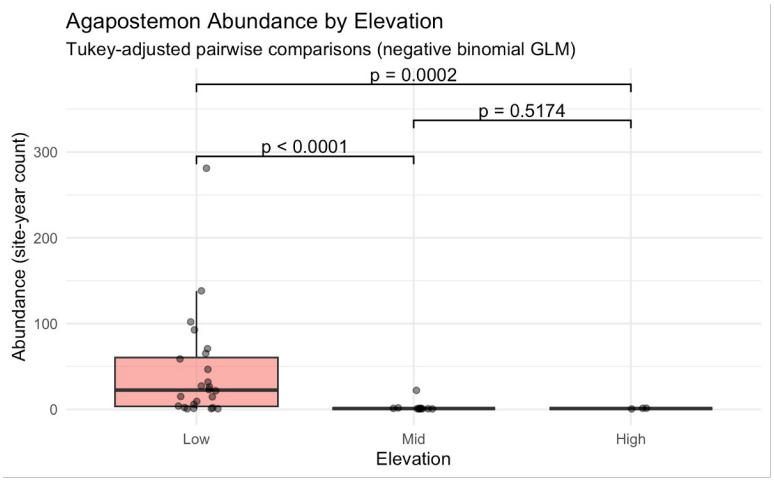

Figure 5. *Agapostemon* abundance by elevation category. Boxplot shows median and interquartile range; points represent individual site-year counts (n = 38). Elevation significantly predicted abundance (negative binomial GLM; $X^2 = 23.83$, p < 0.0001). Brackets show Tukey-adjusted pairwise comparisons; Low differed significantly from Mid (p < 0.0001) and High (p = 0.0002), while Mid and High did not differ significantly.

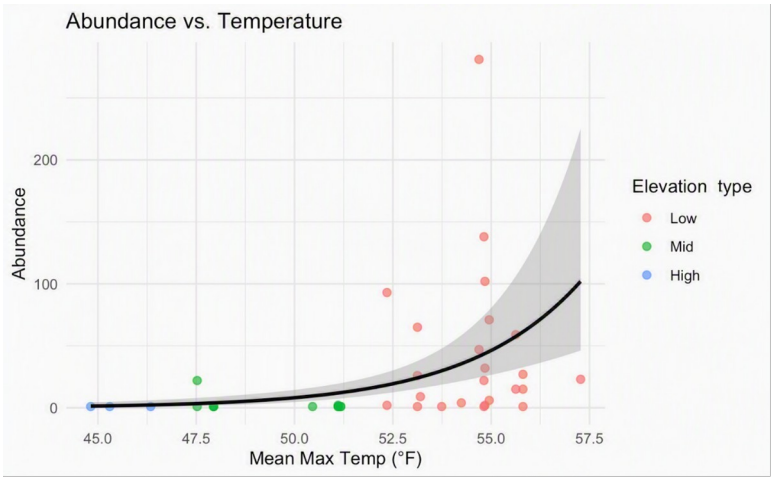

Figure 6. Relationship between *A. subtilior* abundance and mean maximum temperature across site-years, colored by elevation category. The solid line shows fitted regression, with the shaded band representing the standard error. Temperature significantly predicted abundance (negative binomial GLM, p < 0.001).

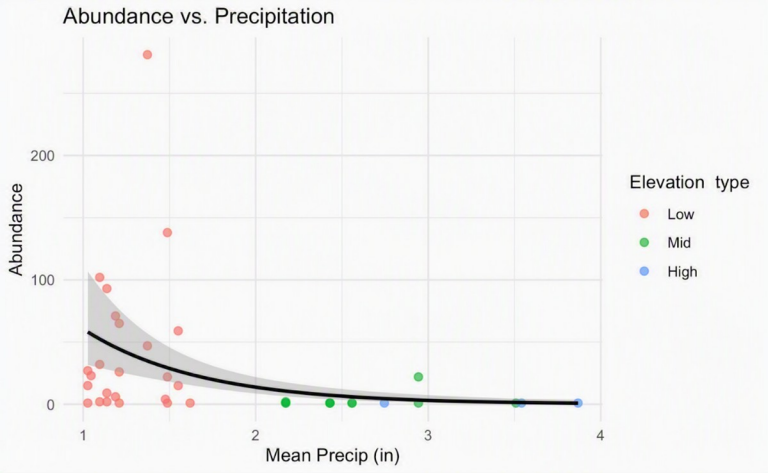

Figure 7. Relationship between *A. subtilior* abundance and mean precipitation across site-years, colored by elevation category. The solid line shows fitted regression, with the shaded band representing the standard error. Precipitation significantly predicted abundance (negative binomial GLM, p < 0.001).