

Alpine Plant Spatial Clumping Modifies Leaf Surface Temperature

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Abstract

Alpine plant communities are particularly susceptible to the impacts of climate change, which makes predicting how these communities will respond important for their conservation. This can be better predicted by understanding how the communities assemble, which is highly influenced by species interactions like facilitation. In alpine environments, clustered plants may experience facilitative interactions that can improve vital rates like survival and fecundity. Alpine facilitation is known to occur via increased soil moisture and buffered air temperatures, but this is likely not the full extent of the facilitative interaction. Plant leaf temperature regulation is essential for photosynthesis, respiration, and water retention. Leaf temperature could also be influenced by facilitative interactions in spatially clumped plants. The goal of this study is to address the question: How does leaf surface temperature relate to neighbor density in alpine plant communities? I hypothesized that clumped plants will display smaller Average T_{leaf} measurements compared to spatially isolated plants and that plants will experience temperature buffering, causing leaves in clustered plants to be cooler relative to surrounding soils (larger Soil Plant Delta values). This research occurred in an alpine plant community in the Elk Mountains of Colorado during July and August 2025. Leaf temperature and surrounding soil temperature data were collected using an infrared thermometer for three focal species (*Elymus lanceolatus*, *Eriogonum umbellatum*, and *Ivesia gordonii*) when found alone and when clumped with each of the other focal species. Soil surface temperature, air temperature, plant area and height, and wind speed were also measured. Using linear mixed effects modelling, species were found to respond differently to the effects of clumping. Two species displayed lower Average T_{leaf} and higher Soil Plant Delta values in clumps, whereas the third showed no trend with either. Overall, clumping was determined to be a significant variable impacting both Average T_{leaf} and Soil Plant Delta. This difference in temperature means that plants found in clumps will have different responses to environmental temperature changes because their energy balance is impacted by clumping effects.

Introduction & General Plan of Study

One challenge for ecology is predicting how ecological communities will respond as climate change occurs. Understanding what influences plant community assembly can help indicate how communities will shift (Ehrlén and Morris, 2015; Opedal et al., 2020). The assembly of alpine plant communities is of particular importance because of their vulnerability to climate change. Plants often shift up in elevation as areas with warming temperatures become unsuitable, but, in alpine environments, available habitat decreases as elevation increases (Guisan & Theurillat, 2000). Alpine areas also experience high-elevation amplification, a phenomenon in which warming is more intense at alpine elevations compared to lower elevation areas (Wang et al., 2016). In addition, alpine ecosystems have a high rate of endemism, making the loss of their species more influential in terms of biodiversity (Körner, 2003).

However, there is potential for this climate threat to be smaller than expected for two reasons. Alpine terrains contain large variations in microclimates, which makes local migration an option for alpine plants shifting due to climate change (Anthelme et al., 2014; Scherrer & Körner, 2011; Opedal et al., 2015). Secondly, facilitative interactions between alpine species can

buffer against extreme conditions, allowing greater survival in changing conditions (Choler et al., 2001; Maestre et al., 2009; Molenda et al., 2012). Non-trophic positive interactions, such as facilitation, strongly influence the assembly of communities, but have been poorly considered in modeling (Anthelme et al., 2014). Creating a more robust understanding of facilitative processes can help better predict the future of plant communities in the face of climate change (Soliveres et al., 2015).

Facilitative processes are known to influence functional diversity and community dynamics in alpine communities (Blonder et al., 2018; Choler et al., 2001; Ray et al., 2023; Stark et al., 2017). Facilitation occurs at higher rates in high elevation and high biotic stress areas, which allows plants to persist in harsher conditions (Choler et al. 2001; Maestre et al., 2009). Facilitation can occur via microclimate modification, which can impact resource availability, niche availability, and environmental filtering (Breshears et al., 1998; Ray et al., 2023). Examples of such changes could be insulating effects, buffering temperature, decreasing albedo, enlarging the boundary layer, and wind protection (Choler et al., 2001). Similar to competition, facilitative interactions can occur when species are in close proximity to each other or when common resources are utilized (Brooker et al., 2007). One study found that intraspecific crowding can increase vital rates such as survival, fecundity, and recruitment for alpine species; Interspecific crowding can also increase recruitment (Blonder et al., 2018). However, clustering of the same species or species with similar niches can also lead to increased competition for shared resources (Maestre et al., 2009).

While we know that spatial clustering can sometimes increase the positive impacts of facilitative relationships, the mechanisms driving this pattern are diverse (Still et al., 2019). One mechanism that could influence plant performance and species interactions (such as facilitation) in clustered plants is leaf temperature (T_{leaf}). T_{leaf} is important in plant performance because of its impact on energy balance (Monteith & Unsworth, 2007; Salisbury & Spomer, 1964). This can include direct impacts on photosynthetic performance and maintaining homeostasis (Gates, 1968; Jones, 2014). T_{leaf} in alpine environments is partially driven by insolation, which can have high variation in these environments (Salisbury & Spomer, 1964). It is also influenced by leaf morphology, stomatal density, soil moisture, wind speed, and relative humidity (Cavaleri, 2020) and can be regulated by transpiration (Arnold et al., 2025). Plant clumping could have an impact on species interactions, as well as any of the previously mentioned factors, thereby impacting T_{leaf} . Cooling in clumps could come from increased transpiration or protection from reflected ground radiation; Warming could be caused by wind protection or from larger boundary layers.

The goal of this research is to address the question: How does T_{leaf} relate to neighbor density in alpine plant communities? This research took place in an alpine plant community in the Rocky Mountains of Colorado. Three species found alone and found clumped with each other were evaluated for two response variables: Average T_{leaf} , which was the average of 5 leaf surface temperature measurements, and Soil Plant Delta, the difference between soil temperature and leaf surface temperature of the plant. Air temperature, light level, windspeed, plant height, and plant area were measured as well to help account for other environmental impacts of leaf energy balance. I hypothesized that clumped plants will display lower Average T_{leaf} measurements compared to spatially isolated plants of the same species and that clustered plants will experience temperature buffering relative to soil temperature, causing larger Soil Plant Delta values.

Methods

Study Site

The site was located in a set of plots established by Blonder et al., 2018. The plots are found on a southeast-facing ridgeline of Mt. Baldy in the Gunnison National Forest of Colorado at an elevation of 3,540 m. The surface has a ~20% slope and is made of a loose, weathered gravel with shale bedrock occurring at a depth of 5-10 cm. The site has 0-10% vegetative cover with snow cover regularly between October and June or July. The site houses 100 2 m x 2 m plots arranged in a 10x10 grid with 2 m buffer space between each plot.

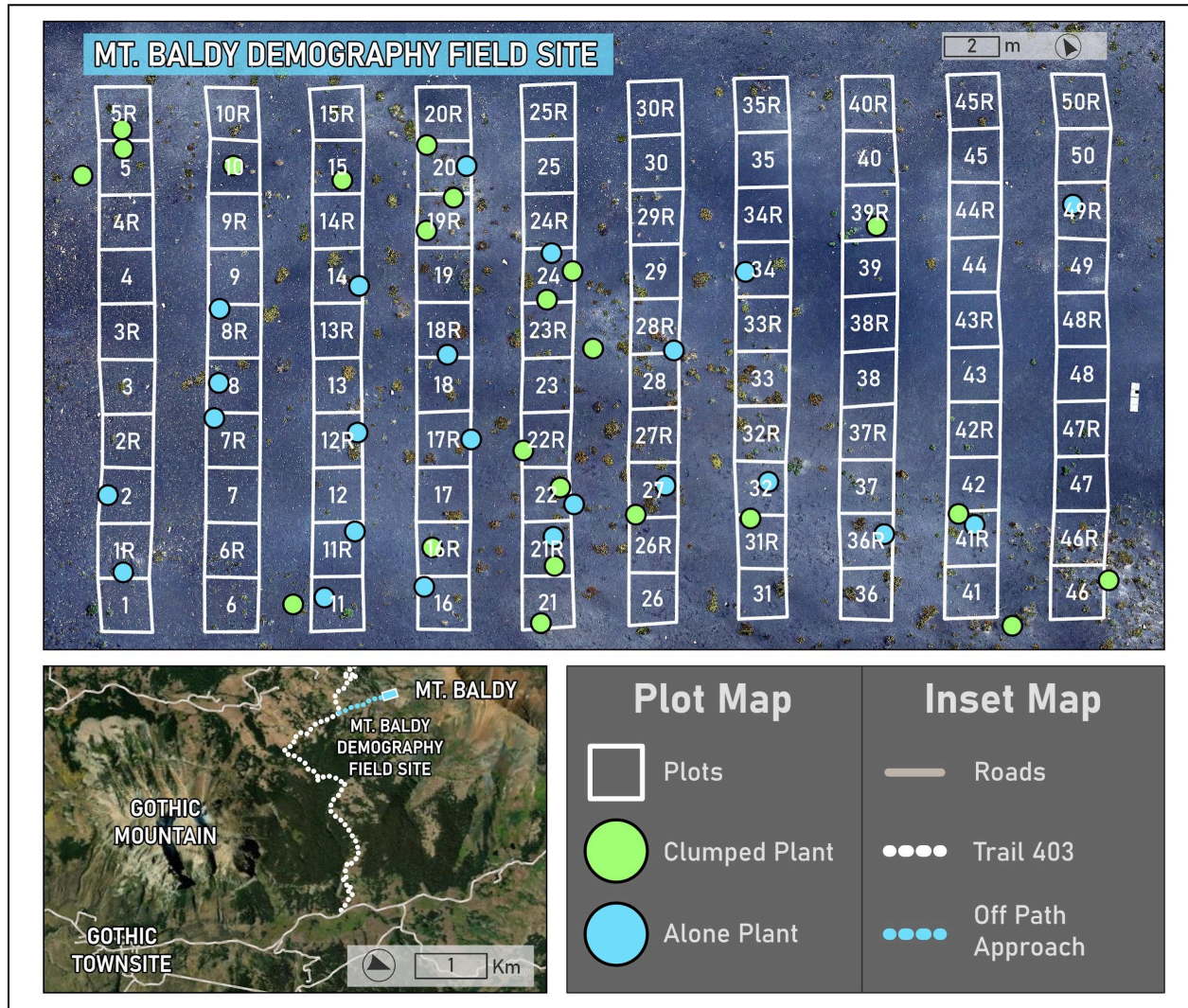


Figure 1. Research Site Plot Schematic and Location Map: Top image displays the Mt. Baldy Demography Field Site, consisting of 100 2x2 m plots arranged in a 10x10 grid. Green and Blue dots represent study plants. Bottom Left map displays the location of the field site in blue in the greater landscape.

Measured Factors

The following species were sampled: *Eriogonum umbellatum* (EU; *Polygonaceae*, Torr.), *Elymus lanceolatus* (EL; *Poaceae*, Gould), and *Ivesia gordonii* (IG; *Rosaceae*, Torr. & A.Gray). These species were selected from the ~20 species present in the site because of their observed clumping frequency, their high occurrence at the site, and the difference in growth forms

between the species. Leaf surface temperature (T_{leaf}) was taken from each species individually and from clusters of each pair of species. The study groups are as follows: EU alone, EL alone, IG alone, EU + EL, EU + IG, and EL + IG. Each study group contains 6-8 plants or clumps. Clumps were two plants found adjacent to one another with less than two finger-widths between them, or when one plant surrounds another. Potential study individuals and clumps were identified using previous imagery collected at the site and during in-person visits. Specific study plants were randomly selected from this pool of potential candidates.

T_{leaf} was taken using an Etekcity Lasergrip 774 infrared thermometer 10 cm above the leaf surface, ensuring that no shadow was cast on the leaf. T_{leaf} was recorded on the perimeter of the plant at each of the 4 cardinal directions and the innermost part of the plant in each cardinal direction (**Figure 2**). Distance from the associated center measurement was recorded for each of the perimeter measurements. Each plant's area was measured using photos taken onsite and the program ImageJ and each plant's height was taken with a measuring tape.

Directly following each T_{leaf} measurement, soil temperature using the infrared thermometer was taken 10 cm from the edge of the sampled plant for each cardinal direction. Wind speed and air temperature were then taken 0.5 m above each plant using a handheld Kestrel 3000 weather meter.



Figure 2. Surface Temperature Measurement Schematic: Shows locations for surface temperature measurements on a focal plant. White circles represent Plant Surface Temperature measurements which occurred on the perimeter of the plant in each cardinal direction. Black triangles represent Soil Surface Temperature measurements which were taken 10 cm away from the plant perimeter at each cardinal direction.

Sampling Schedule

There were a total of 7 sampling dates (**Table 1**), occurring twice a week during July, 2025 between 9:30 AM and 2:30 PM. All study plants or half of the study plants (7/22 & 7/29) were sampled at each occurrence. Weather conditions ranged from lightly cloudy to sunny with air temperatures ranging from 12.5-28.7 °C.

Table 1. Sampling Dates & Time Ranges

Date	Sampling Time Range
7/11/25	10:20 - 12:50

7/14/25	9:30 - 12:20
7/18/25	9:30 - 11:45
7/22/25	9:30 - 10:45
7/25/25	10:50 - 1:10
7/27/25	11:15 - 2:00
7/29/25	9:30 - 10:30

Data Analysis

Data processing and analysis were conducted in R statistical software (R Version 4.5.0) using packages tidyverse (Wickham et al., 2019), lme4 (Bates et al., 2015), effects (Fox and Weisberg, 2018; Fox and Weisberg, 2019), lmerTest (Zeileis and Hothorn, 2002), and broom.mixed (Bolker and Robinson, 2024). **Table 2** provides a summary of analyzed variables and their meanings. Two response variables were evaluated using mixed effects modelling: Soil Plant Delta and Average T_{leaf} . Soil Plant Delta was calculated as follows: $\text{Soil Plant Delta} = ((\text{Soil Temp N} - \text{Plant Temp N}) + (\text{Soil Temp E} - \text{Plant Temp E}) + (\text{Soil Temp S} - \text{Plant Temp S}) + (\text{Soil Temp W} - \text{Plant Temp W})) / 4$. Average T_{leaf} was calculated by averaging the four cardinal direction T_{leaf} values and the center T_{leaf} value together.

Model selection was conducted by creating a simple additive model with the measured variables and then adding interaction terms based on a priori theory. Models containing each combination of the possible interaction terms were then compared using Akaike Information Criterion (AIC) values. The model with the lowest AIC values was selected as the preferred model. Compared models with a $\Delta\text{AIC} < 2$ were then compared using a Likelihood Ratio Test; non-significant p-values led to the model with fewer interactions being selected. 95% confidence intervals for the predictor variables were used to determine significance. Intervals passing through zero were considered non-significant, and those not crossing zero were considered significant.

To identify the effect of clumping outside of its interaction with other variables, a Likelihood Ratio Test was run between the selected models containing and not containing the effect of clumping.

Table 2. Analyzed Variables in Study: Definitions and units for variables included in the analysis of this study.

Variable	Unit	Definition
Time	Decimal Hours	Time of data collection for each plant
Date		Day of sampling
UniqueID		Unique identifier assigned to each sampled plant
Treatment		Plant found “Clumped” or “Alone”
Species		<i>Eriogonum umbellatum</i> (EU), <i>Elymus lanceolatus</i> (EL), or <i>Ivesia gordonii</i> (IG)
Soil Plant Delta	°C	Average of (Soil Temperature - Leaf Temperature) from each cardinal direction
Average Leaf Temperature	°C	Average of leaf temperature from each cardinal direction and center leaf temperature
Air Temperature	°C	Air Temperature 0.5 meters above the plant
Average Soil Temperature	°C	Average of soil temperature measurements taken from each cardinal direction surrounding the plant

Windspeed	m/s	Windspeed 0.5 meters above each plant
Light		Light level when taking plant measurements; Partial sun (PS), Cloudy (C), or Full Sun (FS)
Area	cm ²	Area of the base of the plant
Height	cm	Tallest height of the plant

Results

Model Selection: Soil Plant Delta

Model selection for Soil Plant Delta included the following fixed effect predictors, which are defined in **Table 2**: Treatment, Species, Height, Light, Air Temperature, Windspeed, Area, and time. UniqueID and Date were included as random effects. Time was modelled with an additional quadratic term to reflect its relationship with the response variable more accurately. The model selection considered three possible interactions: Treatment*Species, Species*Height, and Light*Air Temperature. The two lowest AIC values for the models were 2153.6 and 2154.9, which were not >2 points apart, so a Likelihood Ratio Test was run, which had a p-value of 0.254. Since this p-value was non-significant, the model with fewer interactions was selected as the chosen model.

The selected model had the formula of: Soil Plant Delta ~ Treatment*Species + Height + Light* Air Temperature + Windspeed + Area + Decimal Hour + Decimal Hour² + (1| UniqueID + Date). Confidence intervals for the model gave significant values for Species EU, Height, Light PS, Air Temperature, Decimal Hour, and Light PS: Air Temperature (**Figure 3**). Height and Time have positive associations with Soil Plant Delta; categorical predictors varied in their associations (**Figure 4**). Predicted model output showed trends for increased Soil Plant Delta for clumps for EL and IG but not EU.

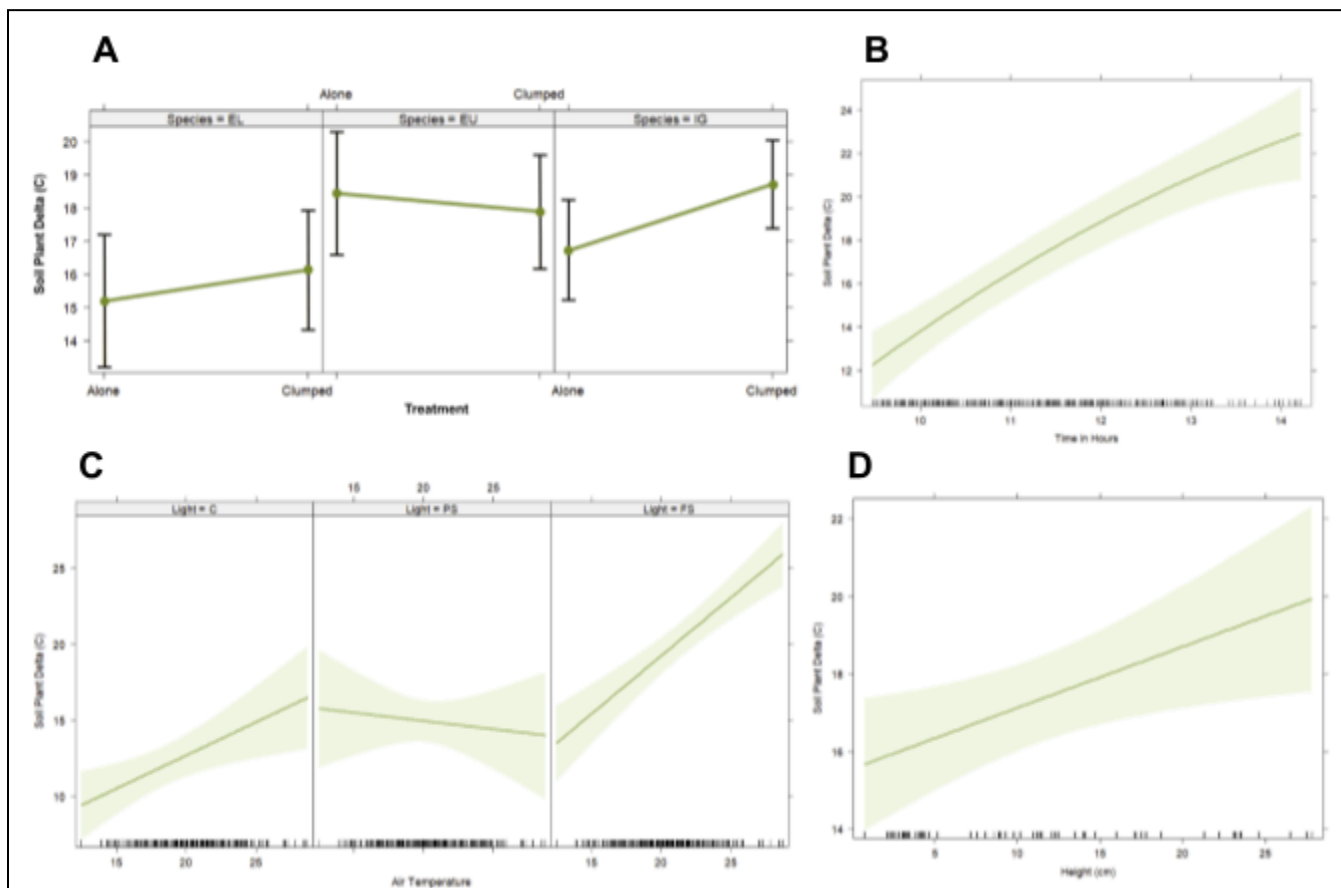
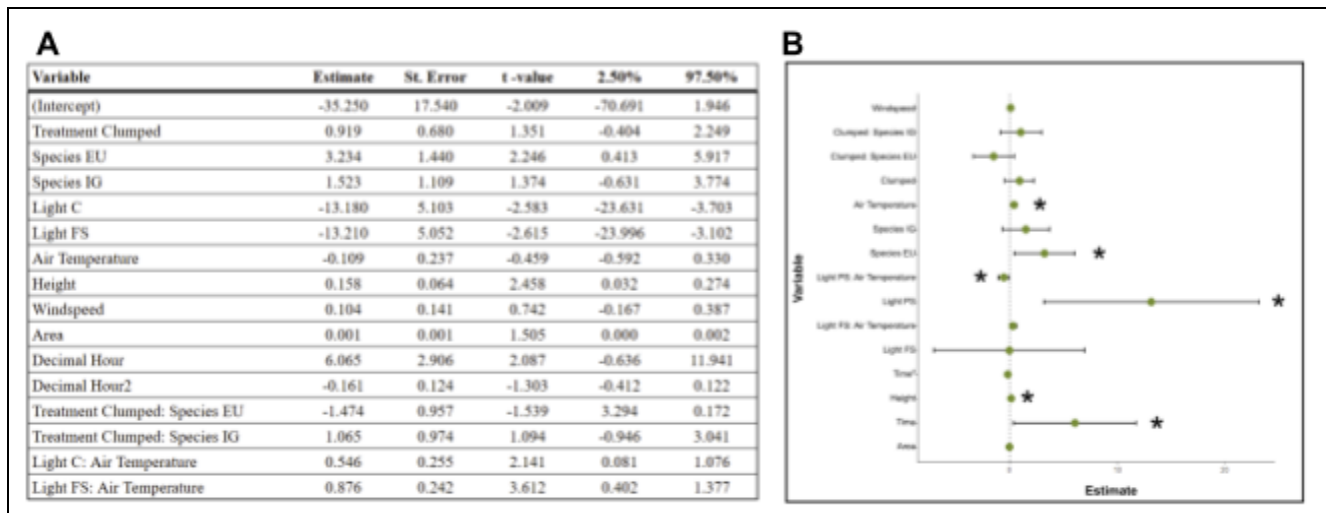


Figure 4. Predictor Effects Plots of Significant Variables and Interaction Terms for Soil Plant Delta: Predictor Effects plots show predicted isolated effect of significant variables in the following model: Soil Plant Delta ~ Treatment*Species + Height + Light* Air Temperature + Windspeed + Area + Decimal Hour + Decimal Hour² + (1| UniqueID + Date). A) Predictor Effects for Treatment and Species, B) Predictor Effects for Time, C) Predictor Effects for Air Temperature and Light, D) Predictor Effects for Height. All give 95% confidence intervals produced from a sample size n=408.

Model Selection: Average T_{leaf}

Model selection for Average T_{leaf} included the following fixed effects, which are defined in **Table 2**: Treatment, Species, Height, Light, Air Temperature, Average Soil Temperature, Windspeed, Area, and Time. UniqueID and Date were included as random effects. Time was modelled as parabolic instead of linear to reflect its relationship with the response variable more accurately. The model selection considered three possible interactions: Treatment*Species, Light*Air Temperature, and Light*Average Soil Temperature. The model with the following formula had the lowest AIC value of 1761.1: Average Plant Temperature ~ Treatment*Species + Air Temperature + Light*Average Soil Temperature + Windspeed + Height + Area + Decimal Hour + Decimal Hour² + (1| UniqueID + Date). This was the selected model because it's AIC was >2 AIC points above all other proposed models. Ninety-five percent confidence intervals for the model gave significant values for Treatment Clumped, Species EU, Species IG, Light FS, Average Soil Temperature, Windspeed, Height, Area, and Treatment Clumped: Species EU (**Figure 4**). Windspeed, Height, and Area had negative associations with Average Plant Temperature; categorical predictors varied in their associations (**Figure 6**). Predicted model output showed trends for decreased Average T_{leaf} for clumps for EL and IG but not EU.

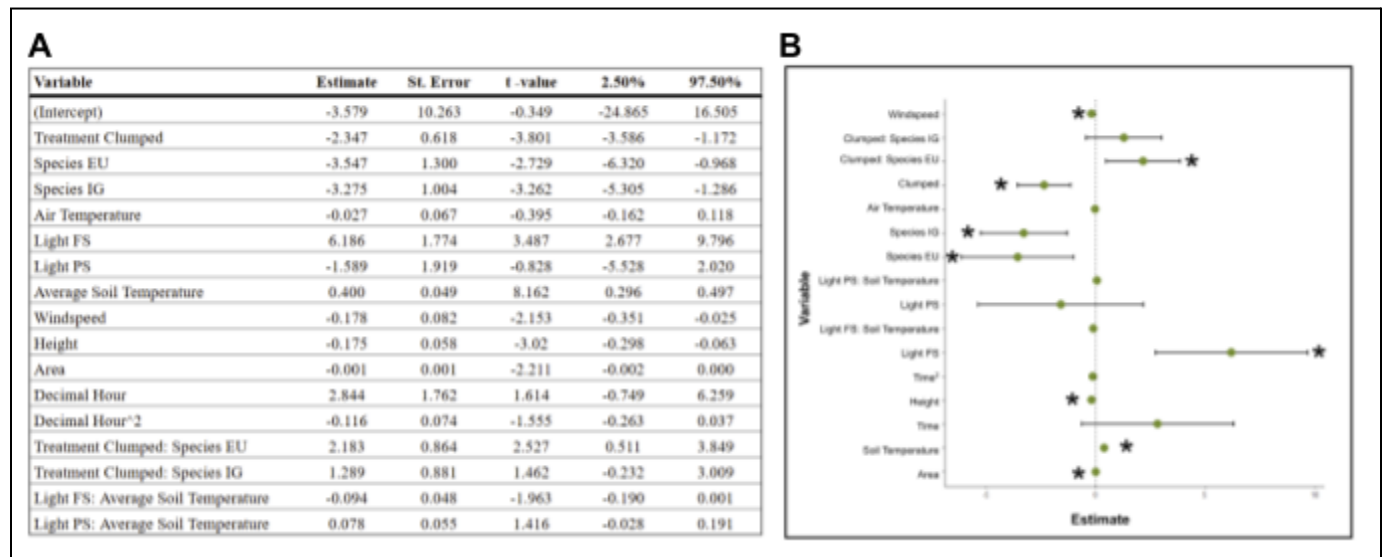


Figure 5. Model Summary for Average T_{leaf} : A) Model diagnostics produced by linear mixed model of the following formula: Average Plant Temperature ~ Treatment*Species + Air Temperature + Light*Average Soil Temperature + Windspeed + Height + Area + Decimal Hour + Decimal Hour² + (1| UniqueID + Date). B) Visualization of 95% confidence interval or the model. Asterisks show coefficients that are statistically significant at $p < 0.05$.

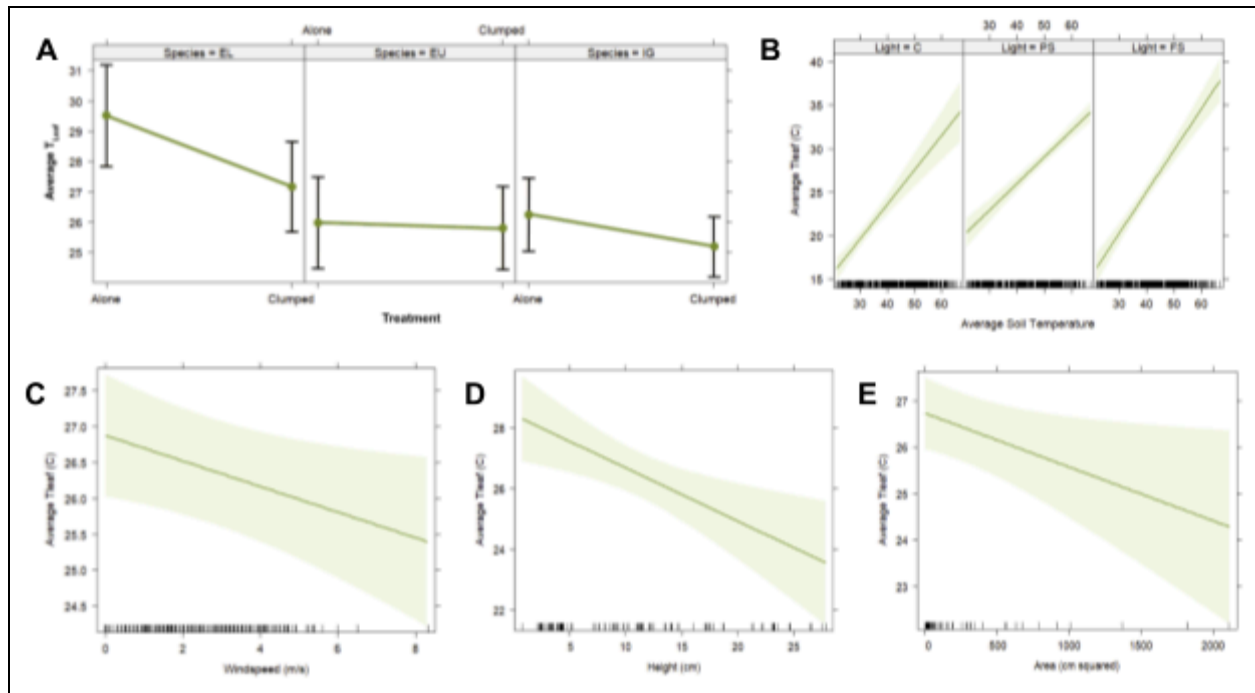


Figure 6. Predictor Effects Graphs of Significant Variables and Interaction Terms for Average T_{leaf} : Predictor Effects graphs show predicted isolated effect of significant variables in the following model: Average Plant Temperature $\sim$ Treatment*Species + Air Temperature + Light*Average Soil Temperature + Windspeed + Height + Area + Decimal Hour + Decimal Hour² + (1| UniqueID + Date). A) Predictor Effects for Treatment and Species, B) Predictor Effects for Soil Temperature and Light, C) Predictor Effects for Windspeed, D) Predictor Effects for Height, E) Predictor Effects for Area. All give 95% confidence intervals produced from a sample size $n=408$.

Model Comparison: Impact of Clumping

Likelihood Ratio Tests were utilized to compare the two selected models containing and not containing the Treatment (Clumped or Alone) variable. The test for the Soil Plant Delta models had a p-value of 0.01976. The test for the Average T_{leaf} models had a p-value of 0.001277. These significant values ($p < 0.05$) show that clumping is a significant predictor for Soil Plant Delta and Average T_{leaf} . This gave strong statistical support for clumping impacted both Average T_{leaf} and Soil Plant Delta.

Discussion

Two response variables were assessed to determine the relationship between spatial clustering and leaf surface temperature: Soil Plant Delta and Average Leaf Surface Temperature. These variables were analyzed using mixed effects modelling with the following variables: treatment type (clumped or alone), species identity, light level, air temperature, soil temperature, windspeed, time of day, plant area, and plant height. The hypothesis was supported by trends of increased Soil Plant Delta and decreased Average T_{leaf} for some species of clumped plants. Two species experienced cooling of Average T_{leaf} in clumps, as well as increased Soil Plant Delta. Clumping was found to be a significant factor in models of the two response variables, supporting the idea that leaf temperature regulation is impacted by clumping.

The measurement of Soil Plant Delta was intended to identify if temperature buffering was occurring for the leaf surface temperature, since this is a phenomenon known to occur with

air temperature surrounding facilitated plants (Anthelme et al., 2014). If buffering was occurring, Soil Plant Delta values would be larger for facilitated plants. Observed Soil Plant Delta ranged from 2.9 °C to 34.6°C, indicating that there is strong thermoregulation happening in alpine plants. Alpine plant temperature is largely influenced by solar insolation, which can explain the correlation found between soil plant delta and light level during temperature measurements. Soil Plant Delta had a positive correlation with air temperature and time of day, which is likely because plants respond more slowly to temperature change than the soil, so the Soil Plant Delta increases as air temperature increases and the day progresses towards the afternoon. Alternatively, Soil Plant Delta increasing over time could be driven by changes in transpiration rates throughout the day. Windspeed had no significant impact, potentially because cooling by the wind would lower plant and soil temperature equally, resulting in no net effect on soil plant delta. Plant Area also had no impact, which could be driven by the soil plant delta measurement being calculated from perimeter temperature measurements as opposed to center temperature measurements that would be more impacted by area effects.

The regulation of leaf surface temperature is essential for plant processes like photosynthesis, respiration, and water retention (Gates, 1968; Jones, 2014). Facilitative processes are known to alter the climate surrounding plants (Breshears et al., 1998; Choler et al., 2001; Ray et al., 2023), so clustering has the potential to alter leaf surface temperature by altering the environmental factors that drive leaf energy balance.

Our model supported this idea, showing that leaf surface temperature was associated with certain environmental drivers, and by clustering. The model showed a negative impact of area, which could be driven by larger plants experiencing more transpiration, though this was not measured in this study. Interestingly, Average T_{leaf} did not have a significant relationship with the air temperature predictor like Soil Plant Delta did. However, this relationship could have been obscured by the significant correlation of Average T_{leaf} with soil temperature. Soil temperature and air temperature had a Pearson's Correlation Coefficient of 0.7233; both variables were included in the model to capture the differences in their impact.

Both Soil Plant Delta and Average T_{leaf} showed strong species-level differences as seen in **Figure 4** and **Figure 6**. *Elymus lanceolatus* (EL) and *Ivesia gordonii* (IG) both showed a trend of increased Soil Plant Delta and decreased Average T_{leaf} for clumped plants. However, *Eriogonum umbellatum* (EU) showed no trend for either metric. It is likely that these species differences are driven by the different growth forms of the study species. EU typically grows in flattened mats close to the substrate, whereas the other two species have smaller bases and grow taller. Therefore, EU likely receives much more heating from the soil, and would not feel the cooling effects of increased transpiration adjacent to them. On the other hand, if the other two species are adjacent or surrounded by another smaller species, they might get protection from ground radiation and receive cooling from the transpiration of their neighboring plant.

Models with clumping were statistically preferred over models without clumping, which shows that clumping has a significant impact on Soil Plant Delta and Average T_{leaf} . This conclusion, alongside the trends described above, supports the idea that there is a temperature difference between clumped and unclumped plants, which could be associated with facilitation. However, since the ideal temperature is not known for these species, an assertion cannot be made as to whether this temperature difference is beneficial to the plant or not. The ideal air temperature for photosynthesis is said to be between 30-35 °C, however, this varies by species and environment (Nobel, 2009; Pan et al., 2024). One study based in an alpine meadow ecosystem found that the optimal air temperature for photosynthesis in that environment was

11.92°C, though the difference between air temperature and leaf temperature could be significant (Zhang et al., 2023). The majority of air temperature and T_{leaf} measurements taken for this study occurred between these two temperature claims, so no conclusion about whether a cooler temperature is closer to optimal can be made.

While the study had a large sample size of 408 observations, the bounds of which these observations were taken could have impacted the results of this study. Due to time, weather safety, and site access constraints, all measurements were taken during a constrained time period (9:30 AM-2:30 PM) and mostly on clear-weather days. With the high variability of alpine weather, the range temperature variation of the alpine plants was certainly not captured. This data could be skewed by data collection occurring during hotter afternoon hours, which likely impacted transpiration rates of observed plants (Morrow et al., 2025). This study also only evaluated 3 of the ~20 species found in the plots, and of the many more species found in the vicinity. Species with taller canopies or wider leaves would likely display varied responses to clumping and facilitative effects.

Some future directions of this research could be accounting for some of this variation by using equipment that continuously logs leaf and soil temperature, including the full diurnal cycle. Research could also be done to identify the ideal leaf surface temperatures for the metabolic processes of alpine plants. This study could also be expanded to look at more than three focal species to help identify what plant traits are associated with certain thermodynamics in alpine ecosystems. Including seedlings in the study could also provide insight into the factors impacting successful establishment.

Conclusion

This study has demonstrated that leaf surface temperature and surface temperature buffering effects are partially driven by clumping of plants in the alpine. Clumping is also associated with lower average leaf surface temperatures and larger effects of buffering. This difference in thermoregulation means that plants found in clumps will have different responses to environmental temperature changes because they are able to regulate their own temperatures more strongly. If plants are threatened by higher temperatures, this also might mean that plants that cluster will have better survival rates since their microclimate is less impacted.

Data Availability

Paper and data will be uploaded to the Rocky Mountain Biological Laboratory's publications database (<https://www.rmbll.org/scientists/resources/publications/>).

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