

The Influence of Forest Structure and Composition on Transpiration Rates Among Drought-Stressed Conifer Species in the Upper East River Watershed

Rocky Mountain Biological Laboratory

Ben Golla | Breckheimer Lab

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ABSTRACT

Despite the ecological significance of prominent coniferous forests surrounding RMBL, there are few comprehensive studies on these systems, particularly regarding transpiration dynamics. Their critical role in carbon sequestration, microclimate dynamics, and water resource management in the Upper Colorado River Basin render them subjects of great research interest. With that being said, sustained drought conditions throughout the region are changing energy fluxes within these forests and bringing into question their resilience in increasingly water-limited circumstances. Examining the physiological adaptations and water-use strategies among different conifer species will aid in our understanding of the ways in which forests contribute to a balanced energy budget in the face of changing climatic conditions. The specific focus of this study is on Engelmann Spruce (*Picea engelmannii*), Subalpine Fir (*Abies lasiocarpa*), and Lodgepole Pine (*Pinus contorta*), three dominant conifers within the Upper East River Watershed. This research aims to investigate the variation in transpiration rates among drought stressed conifers in stands with varying species composition and forest structure. The work combines stem-scale trait measurements and high-resolution aerial imagery with unmanned aerial vehicles (drones) to study transpiration dynamics at a landscape level.

INTRODUCTION

The Upper East River Watershed is home to a rich assemblage of coniferous forests that play a crucial role in the greater function of its mountain ecosystems. From regulating the water balance within the watershed to enhancing drought resilience across entire landscapes, these forests are integral to both ecological health and ecosystem services. However, the increasing frequency and intensity of disruptive climatic events (IPCC, 2013) in the region poses significant challenges to the wellbeing of coniferous systems. The future of mixed conifer stands of varying structure and composition is of great interest to forest managers and stakeholders (Franklin et. al., 2002), particularly as it pertains to water quality and quantity in the arid Southwest (Cram et. al., 2017).

One of the greatest consequences to structural and functional changes in coniferous forests due to climate change is the alteration of the surface energy balance, or the exchange and distribution of energy between the land surface and the atmosphere. Conifers contribute to several components of this balance, including radiation interception (reduction of solar radiation beneath the dense canopy [Vitt et al., 2000]), sensible heat flux (decreased convective heat transfer between the surface and atmosphere), microclimate modification (cooler climate patterns in the understory), snowmelt dynamics (delayed release of meltwater), and evapotranspiration (substantial water vapor released to atmosphere [Stuenzi et al., 2021]). A balanced surface energy budget is essential for the regulation of canopy temperature, moisture availability, and microclimatic conditions that directly influence plant physiology and growth.

Transpiration, a key component of the surface energy balance, is the process by which trees release water vapor into the atmosphere through their stomata. Essential for efficient plant functioning, it affects both the water status of the individual and its surrounding ecosystem. The interplay between transpiration and water availability is especially important to conifer forests of the Upper East River Watershed, which experience periodic drought conditions. Drought-induced stress catalyzed by the unavailability of water can result in physiological strain on trees and ultimately increase their susceptibility to mortality. This water stress disturbs the balance of energy exchanges within conifer forests and threatens their greater functionality (Jenkins, 2016).

The effects of physiological differences and varying sensitivities to stand density among conifer species on transpiration at whole-tree levels is not known (Moore et al., 2004). Additionally, although there is good understanding of xylem anatomical changes with tree size among particular species, our knowledge of the functional consequences of these structural changes (K. A. McCulloh et al. 2014) in forests of differing configuration is less well described. Resultantly, this semiarid region's diversity of forest structure and composition makes it an ideal setting to investigate the relationship between species differences in physiology and transpiration rates in conifers under drought conditions. The diverse conifer stands of the Upper East River Watershed exhibit a wide range of hydraulic traits and water-use efficiency, ultimately reflecting the structural heterogeneity and species composition within these forests. This variation in water-use among species will be critical for modeling and predicting the fate of forests under future climatic conditions (Sitch et al. 2008, Jump et al. 2009). By assessing the interplay between different forest configurations on transpiration among different conifer species, we can gain insights into their adaptive water use strategies on a landscape scale.

The primary objectives of this research are as follows:

- 1) Examine the influence of species, size, and neighborhoods (local groupings) on individual conifer transpiration rates
- 2) Analyze the spatial variability of transpiration within forests of differing density and species composition
- 3) Evaluate the implications of the observed transpiration rates for ecosystem health and water resource/forest management in the study area

SPECIFIC METHODOLOGIES

Site Description – The conifers of choice for this comparative study are Engelmann Spruce, Subalpine Fir, and Lodgepole Pine, all of which are dominant and exist at varying proximities to one another within the study area. The site itself is Snodgrass Mountain (Fig. 1a), the slopes of which are rich in structurally heterogeneous coniferous forests and were selected for ease of access, consistent sightlines for safe drone operation, and minimal conflicts with both scientists and recreationalists.

Drone Data – I collected multispectral and thermal imagery at two times during the growing season (late June, late July) on the southeastern slopes of Snodgrass Mountain (as prescribed by Dr. Ian Breckheimer's Forest Dynamics and Evapotranspiration project). To collect the drone imagery, I utilized RMBL's commercial drone platform (DJI Matrice 300 RTK), which has particularly advanced geolocation capabilities, obstacle-avoidance sensors, and a high-resolution stabilized mapping camera (DJI Zenmuse

P1) for mapping. Multispectral and thermal imagery were sourced from a Micasense Altum sensor mounted to the system.

Flights occurred at an altitude of 120m with an average speed of 14 m/s, allowing for the collection of RGB (at ~1.5cm resolution), multispectral (at ~5cm resolution), and thermal imagery (at ~60cm resolution). The drone platform of choice was paired with a grounded RTK system (D-RTK 2) that provided real-time corrections and centimeter-level positioning data for precise mapping of the flight area. Flights occurred near mid-day (within 3 hours of solar noon) in preferable weather conditions (minimal rain probability, wind gusts 75% between images).

UAS Flight Execution - As previously stated, each planned flight adhered to all federal regulations regarding UAS operations under Part 107. Visual line of sight with the aircraft was maintained throughout the entirety of each flight, and operations were ceased when conflicts arose with recreationalists or other wildlife. Flights launched from and landed in USFS non-wilderness lands.

Field Data – Red-phased conifers were identified in the field using two methods:

- 1) Exploratory trips were conducted on the slopes in which trees were marked via Gaia GPS as waypoints and later transferred to QGIS.
- 2) Using an orthomosaic from a round of Dr. Ian Breckheimer's flights in 2022, trees were marked as points in QGIS, transferred to Gaia GPS, and located in the field for proper species ID.

Data Processing – Multispectral and thermal images from the Micasense Altum sensor were imported into Agisoft Metashape, where they were organized and prepared for further processing. The software aligned and matched overlapping features in the images to create tie points, which served as reference points for stitching the images together. A dense point cloud representing the 3D structure of the surveyed area was then created through triangulation of the tie points. Projection of the images onto the point cloud resulted in the generation of an orthomosaic (Fig. 1b), which accurately reflected the true colors and thermal properties of the site following radiometric calibration. To tailor this data to the objectives of the research, additional steps were taken to refine the scale of measurements within the orthomosaic. A canopy segmentation algorithm (Dalponte & Coomes, 2016) was employed in RStudio to yield polygons that represented individual tree crowns (ITC) within the entire scene. Upon layering thermal from the Micasense Altum onto the polygons, indirect measurements of transpiration for each conifer within the segmented sample were made. Red-phased conifers (dead, non-transpiring trees with full sets of coppery needles) of each of the three species were used as-in image standards for the comparison of their living counterparts. These trees, because of their lack of transpiration, represented a baseline temperature for their species. Because of distinct differences in structure and new needle growth, living conifers could be identified using the P1 orthomosaic in QGIS.

Quantitative comparisons between conifers in the scene were sourced from the difference in radiometric surface temperature between the red-phased standard ($T_{R_{Red\ Phase}}$) and the sunlit portion of each segmented living tree crown ($T_{R_{Living}}$) through the following equation:

$$\Delta T_R = T_{R_{Red\ Phase}} - T_{R_{Living}}$$

Observing species differences in transpiration required image-based identification of species present within the orthomosaic. Trees were identified according to species to allow for informed analysis of ΔT_R in the context of varying forest structure and composition.

Statistical Analysis – Once images were processed and species were identified, data from each flight was inputted into a spreadsheet for analysis. Individual trees within particular sample sets were inputted into an Excel spreadsheet and organized into rows. Columns consisted of explanatory variables, which were divided into two categories according to their realm of influence:

Environmental: Elevation, Snow Persistence, Wetness Index, Slope

Structural: Canopy Height, Canopy Volume, Understory Cover, Nearest Neighbor Distance

Linear regressions models were then run in order to compare the strength of the relationships between explanatory variables and the primary response variable: ΔT_R in all conifers within the sample. These regressions were followed by species-specific models for the same covariates. After experiencing difficulties visually differentiating between Engelmann Spruce and Subalpine Fir in the imagery, the decision to group them together in the analysis was made. When compared to Lodgepole Pine, these two species were structurally similar and therefore suitable for statistical synonymy.

RESULTS

Upon the conclusion of the study, a total of 17,384 conifers of varying size, species, and landscape orientation within the orthomosaic were segmented in QGIS and prepared for analysis in the context of transpiration. However, because the thermal imagery for the two 'zones' in the site was collected over the course of two days, each one (and its resident conifers) had to be analyzed separately in the interest of uniformity. In order to account for variability in environmental conditions across the site, a random sample of 600 conifers (300 in each zone) was selected for further investigation. Of the 600, 339 were viable for use in the linear regression models.

Environmental Covariates

Of the 4 predictors tested in this category (Fig. 2a), two exhibited statistically significant effects on ΔT_R ($p < 0.05$). Snow persistence demonstrated a moderate negative correlation ($R^2 = 0.33$) with ΔT_R , indicating an increase in mean canopy temperature (approximately -0.04 °C per day of additional snow persistence) with snow duration. While statistically significant, the negative relationship between landscape slope and ΔT_R sustained a comparatively weaker effect ($R^2 = 0.02$, Coefficient Estimate = -0.04). The remaining environmental covariates (wetness index, elevation) did not appear to have notable bearing on canopy temperatures among conifers of all three species, with respective p-values of 0.4 and 0.15.

Structural Covariates

Much like the environmental covariates, only two predictors within this category (Fig. 2b) proved to be correlated with ΔT_R : Canopy Height and Understory Cover. Canopy Height explained roughly 5% ($R^2 = 0.05$) of the variation in temperature, effecting an average increase of 0.17 °C per additional meter of height. Understory Cover, or the density of growth beneath the upper canopy of the conifer forest, proved to be slightly negatively correlated (Coefficient Estimate = 0.019) with canopy

temperature, accounting for 10% of its variability. ΔT_R , as tested by the linear regressions, was wholly unresponsive to changes in both Canopy Volume ($p = 0.5$) and Nearest Neighbor Distance ($p = 0.6$).

Species

One of the major objectives of this study was to determine if species differences in transpiration rates (as measured from ΔT_R) existed among drought-stressed conifers. In a manner similar to that of the covariates, the effects of Spruce/Fir and Lodgepole Pine were compared to one another in a linear regression model. With a p-value of 6.44e-08 and an R^2 describing nearly 29% of the variance in ΔT_R , this model implies a statistically profound effect of conifer species on canopy temperature (as depicted in Fig. 3). The negative coefficient estimate for Spruce/Fir (-2.0138) signifies that, on average, this species exhibits significantly warmer canopies and lower transpiration rates than Lodgepole Pine within the site.

Combined Analysis

In order to gauge the relative effects of structural and environmental covariates on ΔT_R , predictors from each category were grouped together into a combined analysis (the results of which are found in Fig. 4). The model consisting of strictly environmental predictors exhibited a notably higher R^2 (0.45) than that of the structural covariates ($R^2 = 0.16$), underscoring its greater collective influence over temperature dynamics within the study site. However, when united under a single model, the entire set of covariates (including species) works to explain approximately 63% of the changes in ΔT_R . The statistical power associated with this cumulative model highlights the joint influence of a variety of factors in determining transpiration rates among conifers of several species.

Species-Specific Findings

In addition to identifying species differences in transpiration rates, this study aimed to explore the sensitivities of individual species (as opposed to all conifers grouped together) to the same environmental and structural variables previously tested. Using the same methods applied to the larger group but with the sample set filtered by species, multiple differences in the relationship between the covariates and ΔT_R were observed (Fig. 5). In accordance with the results from the categorized analyses, the significant effects of understory cover and snow persistence were common to both Spruce/Fir and Lodgepole Pine. With respective coefficient estimates of -0.26 and -0.24, canopy temperatures across the species appear to be similarly positively correlated with snow persistence. Understory Cover once again showed a negative correlation with canopy temperature, this time exhibiting a slightly greater influence in Spruce/Fir than Lodgepole Pine. Interestingly, the influence of elevation on ΔT_R was only (and notably) statistically significant in Spruce/Fir, which had an R^2 of 0.22 and p-value of 0.003 for this negative correlation. With that being said, Lodgepole Pine displayed more sensitivity to a greater range of covariates. Canopy Volume ($R^2 = 0.11$, $p = 0.02$), Canopy Height ($R^2 = 0.23$, $p = 0.0003$), and Slope ($R^2 = 0.09$, $p = 0.03$) were all specifically correlated with ΔT_R in Lodgepole Pine.

DISCUSSION

Covariate Conclusions

As previously mentioned, the environmental covariates proved to contribute more to variability in ΔT_R than their structural counterparts. Snow Persistence, a variable upon which montane forests

have been shown to rely on disproportionately in the Western U.S. (Cooper et al., 2020), had an understandably significant effect on canopy temperature in the study. However, this effect was contrary to the expectation that increased snow duration would result in sustained soil moisture content throughout the growing season and encourage greater transpiration in conifers. It is generally understood that earlier water inputs (due to earlier snowmelt) to the landscape typically result in late-season water stress (Harpold, 2016), so why does this study imply the opposite? One potential consideration lies in the high albedo (or reflectivity) of snow, which can result in the continuous reflection of solar radiation back into the canopy and, in turn, generate higher temperature readings. Additionally, because of the magnitude of 2023's snowpack, pockets of snow remained underneath larger trees late into the season and may not have injected enough moisture into the soil by the flight dates to justify high levels of transpiration (and water loss) in conifers. With that being said, there are a multitude of factors potentially playing into this interesting result, many of which are outside the scope of this particular study due to its temporal limitations. Regardless, snow persistence remains a major environmental predictor of landscape-scale transpiration dynamics and warrants further study in the context of remote sensing.

Unsurprisingly, slope (or the angle at which a tree's base is situated above horizontal) produced a significant response in ΔT_R within the study area. Previous studies have shown that steeper slopes are likely to be drier than flat areas due to lower soil infiltration rates, rapid subsurface drainage, and higher surface runoff (Famiglietti et al., 1998). The negative correlation between slope and transpiration rate (as evidenced by ΔT_R) in this context makes sense, as a lower availability of water on steeper hillsides would constitute less evaporative cooling among conifers.

The structural covariates, while not as perceivably influential in determining transpiration rates as environmental factors, still conjunctively contribute to variability in ΔT_R . Canopy Height, one of the two significant predictors of transpiration within this category, was positively correlated with canopy temperature. Much like slope angle, this result makes objective sense in the context of hydrology. Treetops become increasingly constrained by gravity-induced water stress as they approach maximum height, which results in greater hydraulic friction along longer path lengths (Ambrose et al., 2010). To minimize this energy expenditure and maintain efficient water transport, conifers might modulate their stomatal behavior in a way that decreases transpiration and evaporative water loss. In order to better understand the physiological mechanisms behind these functional differences in transpiration, more tree-specific analyses of hydraulic traits are necessary.

In addition to nearest neighbor distance, understory cover acted as somewhat of a proxy for the crowding of vegetation within this study. As evidenced by its positive correlation with ΔT_R , understory cover ended up playing a significant role in transpiration dynamics among conifers. Studies on California Redwoods (*S. sempervirens*) have shown that understory vegetation can increase moisture availability and therefore aid in water preservation among larger trees (Burgess and Dawson, 2004). This preservation, in conjunction with potential competition for water in the understory, might encourage greater transpiration rates in the midst of drought conditions.

The pronounced species-specific responses to environmental and structural predictors of transpiration rates between Engelmann Spruce/Subalpine Fir and Lodgepole Pine revealed in this study carry potentially significant implications for our understanding of forest hydraulic dynamics and predicting resilience to drought conditions. Lodgepole Pine's particularly heightened transpiration

sensitivity to variables like canopy height, canopy volume, and slope suggest its potential as a drought-adaptive species in the Upper East River Watershed, exhibiting mechanisms that help to minimize water loss in increasingly challenging conditions. Its hydraulic flexibility may contribute to its capacity to withstand prolonged periods of water scarcity in future coniferous forest ecosystems. The collective lack of response in transpiration rates by the covariates tested among Engelmann Spruce and Subalpine Fir may signal vulnerability to warming conditions, but might also indicate sustained hydraulic dynamics in the face of a variety of factors and environmental change. In any case, the nuanced responses of conifers underscore the intricate interplay between species traits, physiological adaptations, and forest structure and composition in determining transpiration dynamics within forested landscapes. By recognizing the diverse set of strategies with which conifers adapt to equally homogeneous environments, we can look to develop more targeted approaches to sustainable forest and water management in the face of ongoing and anticipated climatic challenges.

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FIGURES

Figure 1. Snodgrass Mountain flight “zones”. Red markers signify launch/land locations for each drone flight.

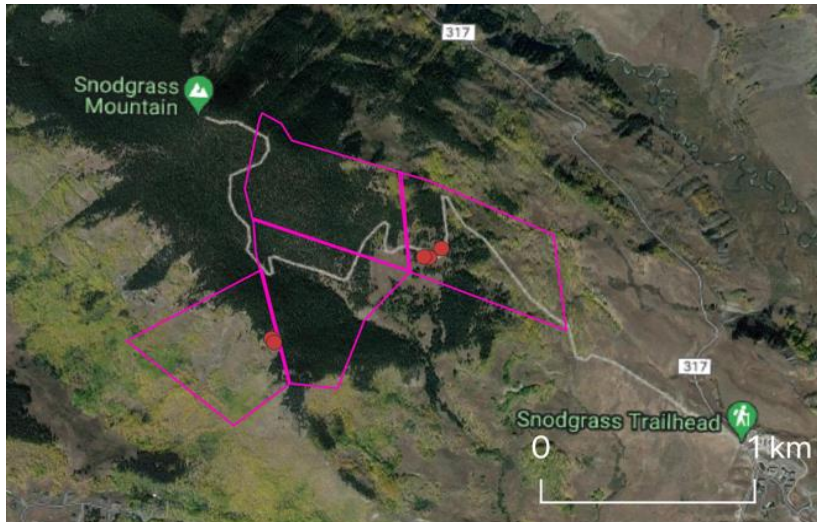


Figure 1b. Processed orthomosaics for use in statistical analysis.

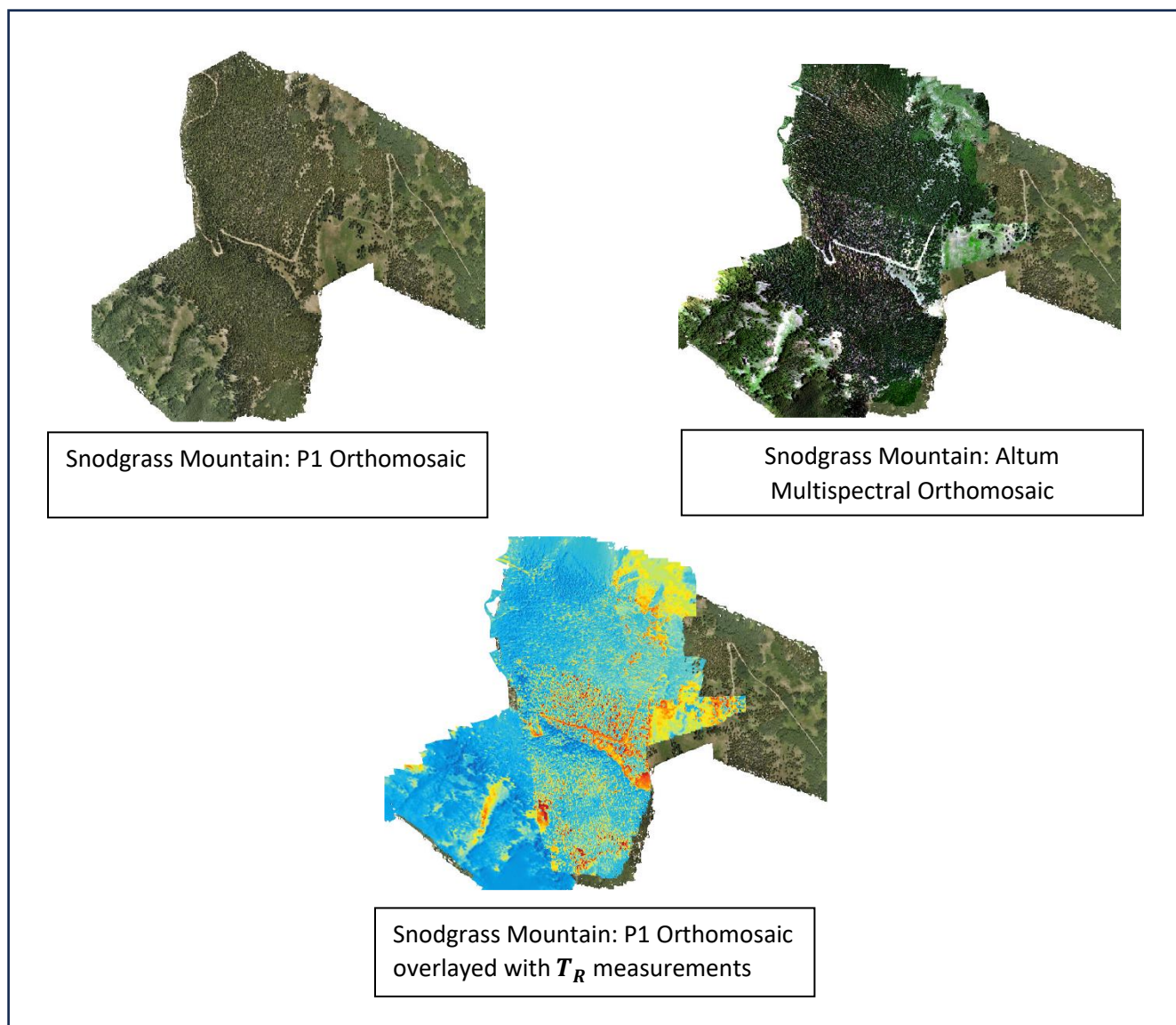


Figure 2a. Linear regressions of the effects of each environmental covariate on ΔT_R across all conifers in the 89-tree sample. Of the 4 covariates tested, only slope and snow persistence proved to be statistically significant predictors.

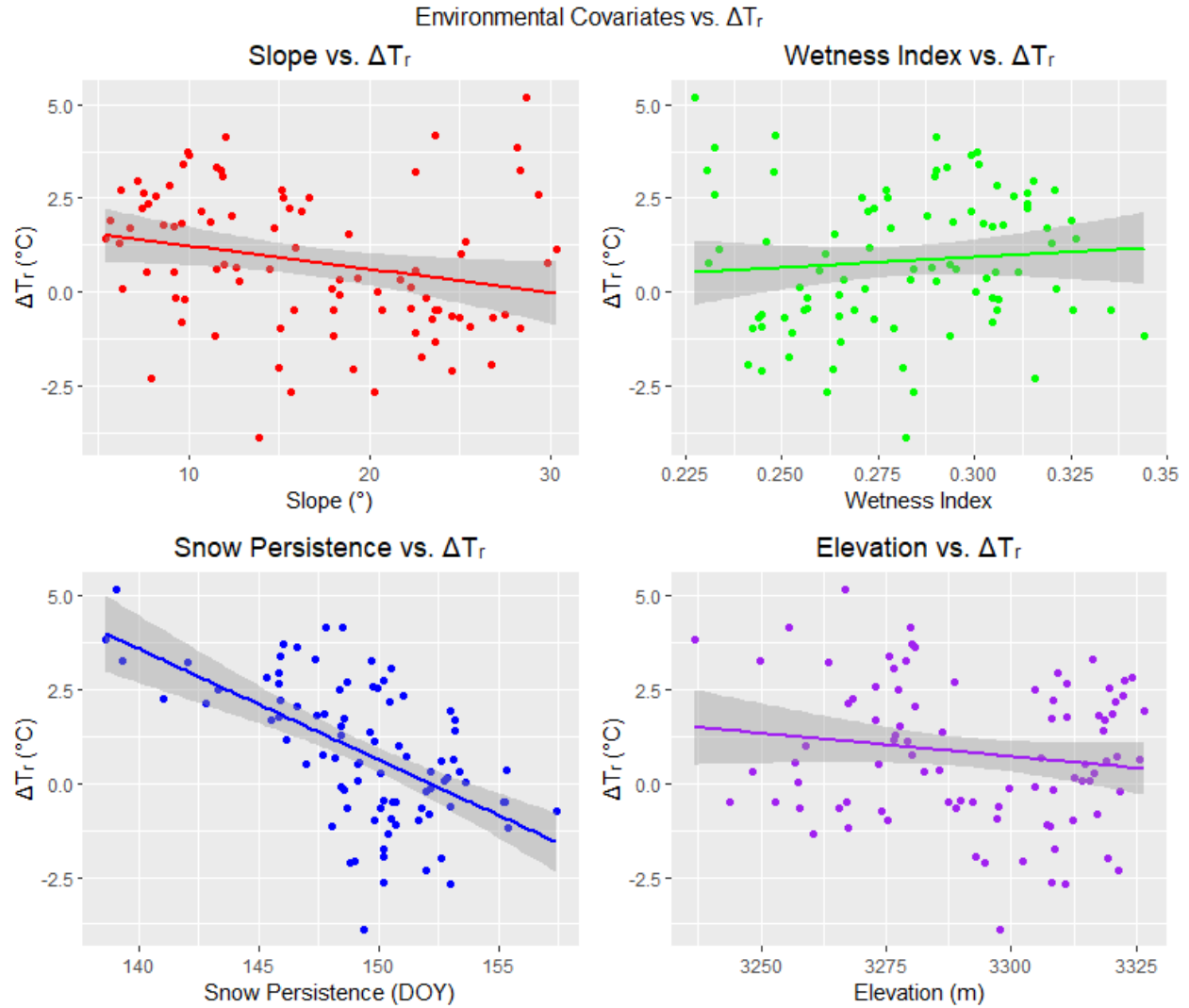


Figure 2b. Linear regressions of the effects of each structural covariate on ΔT_r across all conifers in the 89-tree sample. Of the 4 covariates tested, only canopy height and understory cover proved to be statistically significant predictors.

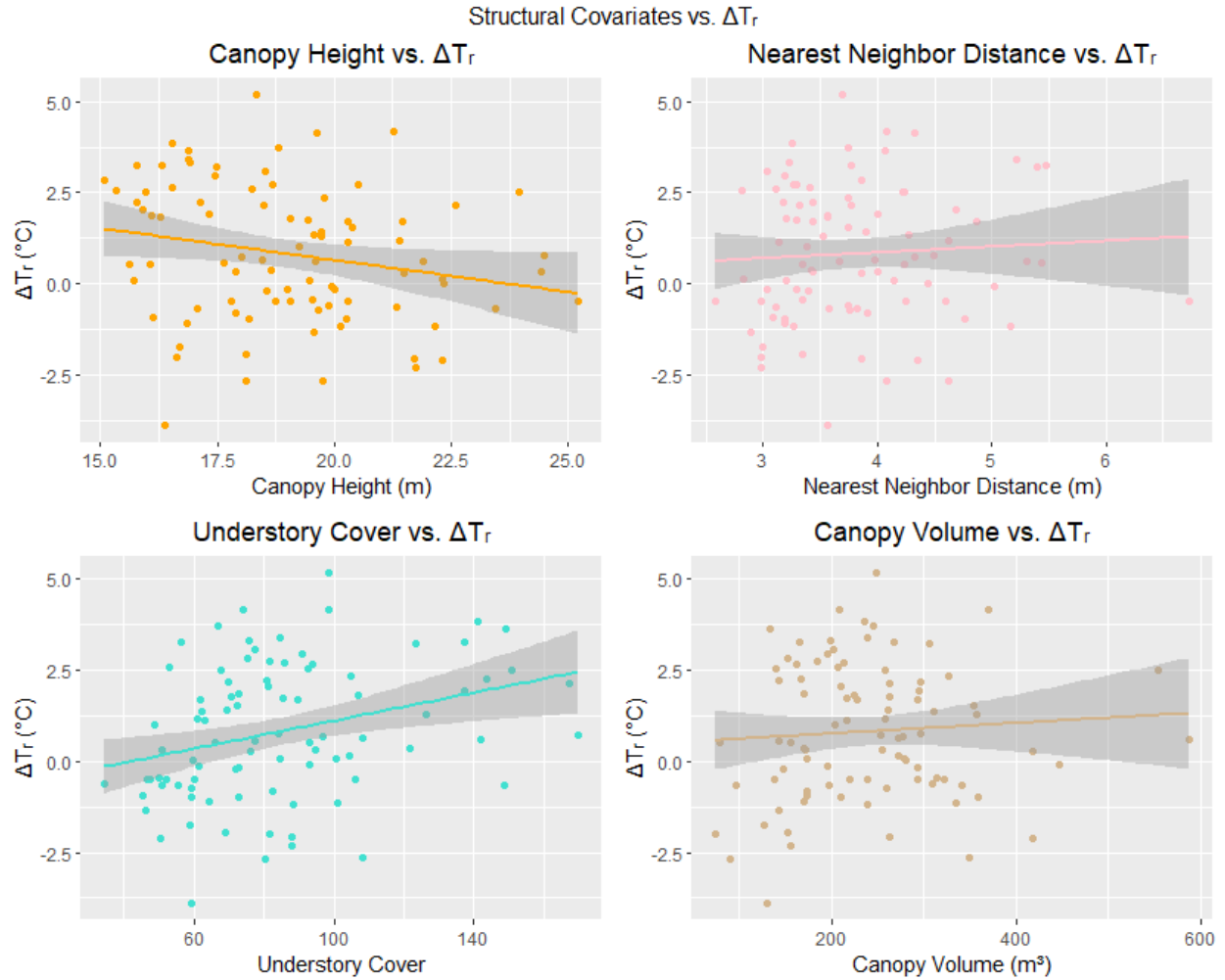


Figure 3. Box plot depicting mean ΔT_R between Spruce/Fir and Lodgepole Pine. The linear regression model testing the relationship between conifer species and ΔT_R yielded a statistically significant correlation.



Figure 4. Table for both covariate category-specific and combined (environmental + structural) multiple linear regression models testing the predictors' collective relationships with ΔT_R . The environmental covariates accounted for more variability in ΔT_R than their structural counterparts, while the combined model exhibited the greatest statistical power of the three models.

Covariate Category	R^2 value	p-value	F-statistic
Environmental	0.54	1.57e-07	13.87
Structural	0.16	0.004	4.01
Combined	0.63	4.477e-14	15.27

Figure 5. Linear regressions of the effects of each structural covariate on ΔT_R between conifer species in the 89-tree sample. Snow persistence and understory cover were statistically significant predictors of ΔT_R in both Spruce/Fir and Lodgepole Pine, whereas elevation was only significant for Spruce/Fir. Conversely, canopy height, canopy volume, and slope proved to be only significant for Lodgepole Pine within the sample.

