Abiotic influences on continuous conifer forest structure across a subalpine watershed

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# Abstract

Understanding the abiotic drivers of high-elevation forest physiognomy is essential for forecasting how these systems will respond to emerging environmental pressures. At broad scales, climate factors often emerge as the strongest constraints on forest structure and composition. However, at finer scales, such as that of a watershed, other locally varying topographic and substrate constraints may mediate the effects of synoptic climate. Here we quantified the relative influence of climate, topographic, edaphic, and geologic factors on conifer forest stand structure and composition, and their functional relationships, at the watershed scale. We used waveform LiDAR data to derive spatially continuous stand structure metrics based on individual tree detection (ITD) within an upper montane–subalpine domain in the Colorado Rocky Mountains. We fused these with a species-level classification map to estimate tree species abundance. We applied generalized additive and generalized boosted models to evaluate the covariability of structural and compositional metrics with abiotic variables. Peak snow water equivalent (SWE), snow disappearance rate and elevation explained the most variation in structural metrics, with nonlinear relationships. The highest stand density, basal area, maximum canopy height, and quadratic mean diameter occurred in sites with low peak SWE (around one standard deviation below mean), but with long snow residence times. Stand density decreased linearly with increasing elevation, while other structural metrics showed non-monotonic relationships, with maxima between 3000 m and 3200 m and asymptotic declines with increasing elevation. Substrate properties were less influential. Our methods contribute important advances in reproducible ITD and quantification of forest structure, and our inferential results add needed detail to the baseline understanding of the dominant controls on forest processes requisite for predicting future forest change.

Keywords: waveform LiDAR; forest structure; conifer; subalpine; environmental gradients; forest ecology

# 1. Introduction

As climate warming accelerates, high-elevation forests face increasing stress exposure, which could induce long-term changes in their structure, composition, and function (Conlisk et al., 2017; Hankin et al., 2024; Kueppers et al., 2017; Macias-Fauria and Johnson, 2013; McDowell and Allen, 2015; Van Mantgem et al., 2013). Because these forests regulate snow accumulation and surface-atmosphere water fluxes, such changes will likely have large effects on the timing and quantity of water released into the major basins of the Western U.S. (Foster et al., 2020). Forecasting how these systems will respond to emerging environmental pressures depends first upon understanding the abiotic drivers of high-elevation forest physiognomy under present conditions. However, several gaps exist in this baseline understanding.

Forest structure and composition emerge from complex interactions between a variable abiotic environment and trait-driven mechanisms of organismal response (Langenheim, 1962; Prentice, 1986; Prentice and Leemans, 1990; Whittaker, 1953). In the large corpus of work that has considered these interactions, climate factors (namely, radiation, moisture, or proxies thereof) frequently emerge as the dominant drivers of community diversity and structure, particularly at global scales (Delcourt et al., 1983; Moles et al., 2009; Shreve, 1915; Stephenson, 1990; Swenson and Enquist, 2007; Urban et al., 2000; Urban et al., 1987; Whittaker, 1953; Zhang et al., 2016). However, several issues complicate interpretation of these dynamics. First, temperature and moisture tend to covary along the same gradients of elevation, aspect, and latitude, and so cannot be easily disentangled (Stephenson, 1990; Urban et al., 2000). Such interdependence may obscure underlying vegetation-environment dynamics: temperature partially drives atmospheric demand and influences stomatal regulation, contributing both positive and negative feedbacks to plant-available moisture (Peters et al., 2019). Prevailing patterns of precipitation input and atmospheric demand in many regions can also lead to seasonal asynchronies in plant-available water and energy (Stephenson, 1990). Further, at least one study has found that soil may explain a greater share of variation in the abundance of trees than climate (Delgado-Baquerizo et al., 2020).

As difficult as it is to isolate the influence of specific abiotic drivers of emergent forest properties at broad scales, the task is perhaps even more daunting at the scale of a mountain watersheds, where microclimate, substrate, and vegetation physiognomy can vary widely with small changes in position (Adams et al., 2014; Barnard et al., 2017; Dobrowski, 2011). Site-species associations are often attributed to functional strategies developed in response to micro-scale radiative (Körner and Paulsen, 2004; Morin et al., 2007; Rehfeldt et al., 2006) and hydrologic (Whittaker and Niering, 1964) regimes. Structural properties such as stem diameter, basal area, and maximum tree height are thought to decline with increasing elevation, with temperature as the key limiting control (King et al., 2013; Monk and Day, 1988). But aspect also modulates radiation input, so the same properties also tend to decline with increasing vapor pressure deficit along a northeast-to-southwest gradient in the Northern Hemisphere (Bolstad et al., 2018; McNab, 1993). Elevation also influences precipitation, with snow input typically increasing upslope. However, local orographic lift, precipitation shadowing, and wind exposure further modulate these processes, with consequent impacts on tree vital rates and attainable stature (Hiemstra et al., 2006; Larjavaara, 2010). At the same time, soil properties such as parent material, texture, pH, and depth vary widely in mountains and directly constrain plant-available water and nutrients (Bruckner et al., 1999; Meyer et al., 2007). All of these factors and their system of interactions impose constraints to which trees must respond.

The preponderance of environmental gradient analyses of forest structure and composition come from Eastern North American deciduous forests and the tropics, with far less information from Western North America, where one might expect more pronounced topoclimatic variability. Among the few studies that have addressed such questions in this region, Kane et al. (2015) found that actual evapotranspiration (AET) and climatic water deficit (CWD) explained the greatest proportion of variance in canopy cover and 95th percentile height in a Sierra Nevada domain, consistent with the theory of radiation-moisture primacy. Fricker et al. (2019) reported that CWD and mean annual precipitation explained the majority of variability in maximum tree heights across four Sierra Nevada forest types. But they also detected a non-linear elevational influence on canopy height, with bimodal maxima at 1200 and 2300 m.a.s.l., potentially pointing to an “ameliorative” effect of radiation on the adiabatic lapse rate. Greenberg et al. (2009) found a unimodal relationship between elevation and stem density in the Sierra Nevada, with peak density around 1900 m.a.s.l. and minima toward the paired extremes of low elevation–high radiation and high elevation–low radiation.

Underlying these findings is an important constraint in high-elevation forests: the ecohydrological limitations that trees face vary with landscape position. Although definitions of ecohydrological limitation differ (Dudney et al., 2023; Hawkins et al., 2003; Whittaker et al., 2007; Roebroek et al., 2020), we adopt the general proposition (Dudney et al., 2023; Roebroek et al., 2020) that in water-limited locations, vegetation productivity is more sensitive to moisture than to radiation, so that a marginal increase in temperature or photosynthetically active radiation (PAR) fails to yield a corresponding productivity increase. In energy-limited locations, a marginal increase in temperature or PAR does yield a productivity increase. Water-limited conditions often arise when potential evapotranspiration (PET) is greater than available moisture. Energy-limited conditions tend to prevail when low temperatures constrain xylogenesis by inhibiting cambial cell division and water-vessel differentiation and expansion (Dudney et al., 2023; Körner, 2008; Cabon et al., 2020). These conditions may vary in time, so that a site may be perennially water- or energy-limited or only intermittently so (Denissen et al., 2022; Faybishenko et al., 2023).

Mapping the mosaic of dominant ecohydrological controls on forest productivity in a landscape has recently become an exciting problem in ecology and geophysics, but it has also proven an elusive quarry (Faybishenko et al., 2023; Greenberg et al., 2009; Pelletier et al., 2018; Roebroek et al., 2020). One major challenge has been the difficulty of acquiring representative measurements of forest properties, particularly in complex, inaccessible terrain (Antonarakis et al., 2014; Antonarakis et al., 2011; Hurtt et al., 2004; Lydersen and North, 2012). Most prior work has relied on plot or transect observations (e.g. Knowles and Grant, 1983; Parker and Peet, 1984; Kueppers and Harte 2005). Even within mature closed-canopy forests, stand density, age-class distribution, allometry, and species dominance can vary widely over space. Additionally, subalpine disturbance and recovery dynamics operate on such long timescales that it can be difficult to distinguish transient post-disturbance characteristics from long-term average site potential. Drawing inferences about such properties from plot observations alone can yield substantial error.

Light Detection and Ranging (LiDAR) helps to overcome some of these limitations by enabling measurement of forest structure on a spatially continuous basis (Mallet and Bretar, 2009). Full-waveform LiDAR data in particular can provide spatially rich information through the vertical forest profile (Mallet and Bretar, 2009; Zhou and Popescu, 2019) and are especially effective for characterizing mid- and sub-canopy structure (Adams et al., 2011; Anderson et al., 2016; Chauve et al., 2009). In addition, imaging spectroscopy has been widely used to quantify species abundance and compositional patterns (Anderson et al., 2008; Falco et al., 2024b; Plourde et al., 2007). Integrating these datastreams can improve the dimensionality and detail of remote-sensing ecosystem representation (Anderson et al., 2008; Chadwick et al., 2020; Falco et al., 2024b; Marrs and Ni-Meister, 2019).

Only a few studies have used LiDAR to evaluate forest structure and/or composition along multiple abiotic gradients in North American forests (Kane et al., 2015; Bolstad et al., 2018; Greenberg et al., 2009; Fricker et al. 2019; Falco et al., 2024b). These projects used lower-density discrete LiDAR returns, which yielded valid canopy structural metrics (height and cover, e.g.) and statistical proxies of maximum density, but not detailed characterizations of the sub-canopy. To our knowledge, no prior study has (a) exploited the higher granularity of waveforms to estimate a suite of ecohydrologically important structural properties through the vertical forest profile, (b) integrated these estimates with species composition, and (c) characterized their associations with underlying environmental gradients on a spatially continuous basis.

To address these gaps, we pursued two objectives:

1. To accurately predict conifer forest stand structure and composition across a Southern Rocky Mountain, USA, watershed.
2. To quantify the relative influence of climate, topographic, edaphic, and geologic factors on conifer stand structure and composition, and their functional relationships.

We expected variables related to moisture availability (CWD, AET, snow-water equivalent (SWE)) and radiation (elevation, heat load) to predominate among multiple interacting factors in explaining stand structural and compositional variation. Further, we expected spruce-fir to dominate north-facing slopes and higher elevation positions, and pine to dominate lower-elevation south-facing slopes.

# 2. Methods

## 2.1. Study area

The study domain comprised upper montane-subalpine conifer forests in Colorado’s East River watershed (38°55’ N, 106°56’ W; Fig. 1). The East River is a headwater tributary of the Colorado River, the principal freshwater source for one in 10 people in the U.S. (U.S. Department of Interior, Bureau of Reclamation, 2012). The 750 km2 catchment includes six major drainages discharging to perennial streams. Mean annual air temperature is 1.9 º C, with a mean monthly maximum and minimum of 11.2 º C and –7.1 º C respectively, measured 1980–2023 at the NOAA Crested Butte weather station (GHCND USC00051959) at 2700 m near the center of the watershed (Berkeley Earth, 2022). Mean annual precipitation is 1400 mm y–1, approximately 85 % snow (Carroll et al., 2022). Beyond these synoptic trends, the domain’s 1420 m of elevational relief and pronounced gradients in slope, aspect, insolation, and hillslope position produce highly variable local climatic conditions (U.S. Geological Survey, 2017). In the domain’s forests, slopes range from 0.5º to 49º, with a median of 17º. Aspects are well distributed around the compass, albeit with a slight southwestern bias. Cretaceous Mancos shale underlies 34 % of the forested domain; Middle-Tertiary granodioritic laccoliths, dykes, and sills underly 24 %; and the coal-bearing sandstone-silt deposits of the cretaceous Mesa Verde Formation another 21 % (Streufert, 1999). Available water capacity (AWC) in the top 100 cm of soil ranges widely, from 0.02 to 0.19 cm H2O cm soil–1 (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2023).

The covariability of vegetation and abiotic factors has been previously studied in this watershed. Langenheim’s (1962) descriptive survey revealed an affinity for north-facing slopes and limestone parent material among conifer species. Wainwright et al. (2022) found conifer stands associated with steep, mid-elevation hillslopes with less fractured bedrock in an analysis integrating airborne hyperspectral and electromagnetic (AEM) surveys with digital elevation and snow data. They also found elevation, aspect, and geologic substrate to be the primary factors associated with plant sensitivity to early snowmelt and growing-season drought. Uhlemann et al. (2022) used AEM surveys and field samples to show that bedrock properties can be reliably estimated as a function of geomorphological features and plant functional types. Further, a recent study mapping the watershed’s dominant plant species through imaging spectroscopy revealed broad heterogeneity in forest species distributions, phenological dynamics, and leaf functional traits, strongly influenced by topographic wetness, solar insolation, and slope (Falco et al., 2024b).

Within the watershed’s forests, the dominant tree species are Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta var. lasiocarpa*), and quaking aspen (*Populus tremuloides*), with occasional Douglas fir (*Pseudotsuga menziesii var. glauca*) and a few known sentinel limber pine (*Pinus flexilis*). Natural histories of subalpine forests elsewhere in Colorado describe species distribution patterns that largely hold in this domain (Peet, 1978a, 1978b). Engelmann spruce and subalpine fir tend to co-occur in high densities throughout the subalpine zone (~2700–3400 m.a.s.l.) and only sparsely in the upper montane zone (~1850–2700 m.a.s.l.) (Alexander, 1987; Falco et al., 2024b). At middle and high elevations up to treeline, the longer-lived spruce often dominate the canopy (up to 75 % of canopy basal area), while fir may occupy up to the same proportion of the understory (Alexander, 1987; Peet, 1978a). Fir tend to be dominant in the lower end of the subalpine zone (Alexander, 1987). Lodgepole pine also occur intermixed with spruce and fir on dry, southerly slopes in the lower subalpine zone (Veblen, 1986). Near the lower spruce-fir range limits, lodgepole often establish as post-disturbance pioneers and mature to even-aged monospecific stands, which are later replaced by the former species (Falco et al., 2024b; Whipple and Dix, 1979). Quaking aspen occur throughout the domain but are not the focus of this study.

Mining-related harvest impacted some parts of the watershed during the 19th and early 20th centuries, with a limited footprint enduring today. But there are extensive swaths of forest where no tree removal occurred, and mature stands of uneven age and size structure are well distributed. All forests in this analysis sit on U.S.D.A. Forest Service land, and 22 % are in management-restricted wilderness. We suggest that because of their low timber value, long fire return intervals, and relative lack of recent management, they offer a valid basis for investigating abiotic influences on subalpine conifer forest structure.

## 2.2 Full-waveform LiDAR

Between June 12 and 26, 2018, the National Science Foundation National Ecological Observatory Network (NEON) Airborne Observation Platform (AOP) (Kampe, 2010) surveyed approximately 330 km2 of the watershed (Fig. 1) (Chadwick et al., 2020; Goulden and Musinsky, 2020). The AOP collected discrete-range and full-waveform LiDAR returns using an Optech Gemini discrete LiDAR sensor and waveform digitizer with a pulse repetition frequency between 33 and 100 kHz. Discrete-return point density in the post-processed dataset ranged between 1 and 9 returns m–2, which was insufficient for characterizing subcanopy structure. We therefore elected to exploit the higher information content of the full waveforms, with a nominal density between 1 and 4 pulses m–2.

We followed an established preprocessing approach to prepare the waveforms for analysis. First, we deconvolved the target-response signal from its interactions with the outgoing pulse, atmospheric scattering, and system noise. We used the Gold deconvolution algorithm (Zhou and Popescu, 2019), but refactored it for parallel processing in the R statistical computing environment. The output approximates the true distribution of scattering phenomena along the laser pulse’s path. We then applied adaptive decomposition to fit a sum of Gaussian models to the return pulse components:

where is the amplitude of waveform component , is the bin location of (measured as a point in time, ns), is the standard deviation of , and is a penalty that minimizes the model residual over a user-specified number of iterations. Fitting was accomplished using the function *nlsLM* in the R package *minpack.lm*.

We ran the deconvolution and decomposition procedures on the full set of 1.4 109 waveforms on 256 cores on the University of California, Berkeley’s high-performance computing cluster. From the fitted functions, we extracted characteristic metrics, including pulse location, peak amplitude and width, front slope, and time to median intensity. A negligible fraction of returns (~0.5 %) either had no detectable peaks or represented backscatter records that could not be fit to a Gaussian. Where peaks could not be identified, the waveforms were dropped from the set. Where the returns could not be fit, characteristic metrics were estimated from the deconvolved returns directly, without decomposition.

We used the geolocation matrices provided with the NEON data to position the decomposed functions in space and used the R package *rlas* to discretize this information along with the characteristic metrics (Roussel and Boissieu, 2023). We normalized the discretized points to the Earth surface by differencing their z-values against a digital elevation model (DEM) derived from the discretized point cloud. We then decimated the high-density returns to obtain a dataset of 5.72 109 points with a uniform density of 15.3 points m–2 across the domain.

## 2.3 Field census

Between 2018 and 2022, we established twenty-five 1600 m2 conifer forest demography plots in the East River watershed and surrounding drainages, stratified along six topographic gradients (Table A.1; Fig. A.1). Each plot was installed in contiguous forest at least 100 m from edges and major compositional transitions. To mitigate unobserved management and disturbance effects, we selected stands with no evidence of recent harvest or major disturbance based on (a) visual inspection for cutting and (b) stability of the Landsat Normalized Difference Vegetation Index (NDVI) record (1980–2018). We used a survey-grade GNSS receiver (Trimble Geo 7X, Trimble, Inc.) to georeference all plot locations *in situ*. Estimated planimetric accuracy of plot corner locations was 0.3 m.

We conducted a field census in the 25 plots (Table A.2), labeling all trees 1.0 cm diameter at breast height (DBH, measured at 1.3 m above ground) with a permanent aluminum tag and identifying tagged trees to species. We then measured DBH using a standard metric diameter tape (for stems 7.0 cm DBH) or calipers ( 7.0 cm) and stem heights with a LaserPro II (Nikon Corp.) laser hypsometer (for stems 5 m in height) or a rigid metric tape measure ( 5.0 m). To maximize precision, we repeated hypsometer measurements on each stem until measurements converged within 0.5 m. Expected vertical accuracy on hypsometer measurements was 0.75 m. We geolocated stems using the GNSS receiver or by measuring the direction and distance from a previously geolocated reference tree with a digital compass and rigid metric tape. For geotagged trees, mean planimetric accuracy was 1.01 m (s.d = 0.70 m). Seventeen of the 25 plots lay within the overflight footprint of the 2018 NEON AOP acquisition (Chadwick et al., 2020; Goulden et al., 2020; Goulden and Musinsky, 2020). These contained 5828 observed trees, of which 4355 were living at the time of inventory.

## 2.4. Tree crowns, species composition, and stand structure

### 2.4.1 Tree crown detection

We followed the tree-centric schema in Dalponte et al. (2019) to generate an individual tree crown (ITC) map and gridded estimates of conifer forest structure and composition across the watershed. The ITC map comprised point objects describing the position, height, and stem diameter of all trees 1.3 m height in conifer stands. The gridded data comprised continuous estimates of conifer forest structure metrics at the 100m grid scale. To generate these products, we developed an automated procedure to train and test eight individual tree detection (ITD) algorithms. The procedure iterated through many parameter permutations for each algorithm, measuring performance against field inventory data at each iteration. We then selected the best-performing algorithm and parameter set to apply to the watershed’s remaining conifer forest area.

To implement this schema, we first extracted the discretized LiDAR data within a 5 m buffer around the boundaries of each field plot.[[1]](#footnote-1) We then attempted to detect tree crown objects from the discretized data using eight algorithm implementations from the R packages *lidR* and *lidRplugins* (Roussel et al., 2021; Roussel and Auty 2023; Roussel 2023). We forced each algorithm with parameter set , where is a parameter required for the algorithm to proceed, and is a vector of user-specified values on that parameter (Table A.3). For each iteration , we applied the automated matching procedure in Eysn et al. (2015) and Pang et al. (2021) to link detection results to reference observations from field inventory. This provided an objective function against which to evaluate the performance of each algorithm-parameter permutation. We opted for automated matching because (1) our computational scale—up to 2800 runs per algorithm per plot—made manual evaluation infeasible, and (2) it enabled us to enforce clear, objective, reproducible rules for algorithm selection.

The matching procedure began by selecting the tallest detected tree (“target”) and searching for candidate matches among reference trees within specified Euclidean distance limits (Table A.4). The reference candidate with the least ∆XY was chosen as a tentative match to the target. The candidates were then queried a second time. If a candidate with greater ∆XY proved closer in height to the target, and its ∆XY was at most 2.5 m more than the ∆XY of the tentative match, it was selected as the match. However, since an optimal match also depends on other nearby *detected* trees, the target was then compared against other detected neighbors. If another detected tree was closer in horizontal and vertical distance to the matched reference, the pairing was discarded. This process was repeated on all remaining detected trees in descending order of height, until all reference trees had been evaluated. Matches were then removed from the set, and the process was repeated until no further matches could be found under the search criteria.

For each run of on , we tallied the number of detected trees, true positives (TP, or successful matches), false positives (FP, or commission errors), and false negatives (FN, or omission errors). We used these values to compute root mean square (RMS) performance statistics across the 17 plots (Table 1). We then selected the algorithm and parameter permutation with the maximum RMS *F1* score across all . *F1* is a proportion representing the harmonic mean of precision (the proportion of all tree detections that were correctly matched) and recall (the proportion of all possible matches that were correctly matched). Perfect detection and match rates would yield an *F1* of 1.0, while perfect failure would yield 0.0. We chose *F1* as the optimization statistic for its balanced sensitivity to over- and under-detection.

Of the eight algorithms tested, Layer Stacking (Ayrey et al., 2017) yielded the highest *F1* across training and testing sets (Tables 1, A.5, A.6). For the remainder of the LiDAR-surveyed domain, we extracted the discretized waveform data over conifer forests by finding their intersection with conifer-classified pixels from a species map developed through a support vector machine classifier on the 2018 NEON hyperspectral acquisition (Falco et al., 2024a, 2024b). We forced the Layer Stacking algorithm with the optimal parameter permutation and ran it on the conifer-filtered LiDAR data. The result was a set of points describing the locations and heights of all tree crowns 1.3 m height in the watershed’s conifer forests. We then estimated the DBH of each delineated object using an allometric function of stem height with coefficients fit to binned field observations:

where is tree height above ground and the last term is , an approximation of theoretical model error assuming is normally distributed, imposed for unbiased prediction, per Jucker et al. (2017) (Fig. A.2).

### 2.4.2. Species composition

We fused the tree crown product with the forest species classification map (Falco et al., 2024a). First, we ran a marker-controlled watershed segmentation on a canopy height model derived from the discretized waveforms at 0.5 m resolution, using the Layer Stacking ITC objects as controls (Plowright, 2024). This produced polygons demarcating the estimated crown perimeters of every detected tree object. Because the NEON passive imaging spectrometer received reflectance signals only from light-exposed portions of tree canopies, we filtered the LiDAR-detected trees to match the hyperspectral targets as nearly as possible by filtering to objects in the 90th percentile of height per 100 m grid cell. We then overlaid the remaining polygons on the classification raster and assigned each object to a single tree species according to a majority vote (Dalponte et al., 2019). If less than 50 % of pixels within a crown polygon belonged to any one species, we labeled the object *NA*.

### 2.4.3. Stand structure

From the fused product, we computed continuous area-based stand structural metrics by summarizing object-level predictions at 100 m grid scale across the watershed. Structural metrics included total density, stand basal area, quadratic mean diameter (QMD), diameter and height percentiles, and skewness of height, all computed at the level of a grid cell. We calculated density (stems ha–1) as the total number of trees per hectare for all trees and by species. We computed basal area (m2 ha–1) as:

and QMD (cm) as:

where is the number of trees in the cell. We specified skewness of height as the third central moment of the distribution of stem heights. Larger positive values signified a larger proportion of trees in smaller height classes than a normal distribution. More negative values signified a larger proportion of trees in larger height classes.

To further restrict the analysis to intact conifer forest stands, we further masked each raster to exclude pixels that had a total density less than 100 stems ha–1 or intersected a 100 m buffer around roads, developed areas, and the outer perimeter of the NEON AOP LiDAR acquisition. A hardware failure during the June 20, 2018, LiDAR flight rendered the waveform data irretrievable (Goulden and Musinsky, 2020). This gap is visible as an empty north-south swath in the forest structure products and was excluded from analysis, along with a 100 m buffer around its perimeter to minimize edge effects.

## 2.5. Abiotic explanatory variables

### 2.5.1. Topography

We generated six topographic variables from the LiDAR-derived DEM (Goulden et al., 2020) at the 100 m grid scale: elevation, slope angle (º), folded aspect, heat load, topographic position index (TPI), and topographic wetness index (TWI) (Table A.1, Fig. A.3). We calculated heat load (unitless index) as a proxy of incident solar radiation using the method in McCune and Keon (2002). We computed the topographic position index (TPI), a morphometric measure of hillslope position, as the difference between a target pixel’s elevation and the mean elevation within 9-pixel (1000 m) neighborhood, normalized to the s.d. of elevation (De Reu et al., 2013). TPI values are more positive when a target point is higher than its neighborhood, and more negative when the target is lower. Topographic Wetness Index (TWI) (log(m2 m–1)) is an estimate of the relative capacity of an area to accumulate water through surface or subsurface flow. We selected this as a proxy for subsurface moisture conditions and computed it as the log ratio between a pixel’s upslope contributing area and its own slope angle (Metcalfe et al. 2018).

### 2.5.2. Climate

To estimate relative spatial patterns of snow accumulation (m), we retrieved snow water equivalent (SWE) data produced by Airborne Snow Observatories, Inc. (formerly NASA/JPL Airborne Snow Observatory; ASO) from snow-on flights on March 31, 2018, April 4, 2019, and April 21, 2022 (Deems et al., 2013; Painter et al., 2016; Painter et al., 2018; see also <https://data.airbornesnowobservatories.com/>). The SWE product was generated from aerial measurements of snow depth, spectral albedo, and radiative forcing, combined with modeled snow density from iSnobal (Painter et al., 2016). We also produced an estimate of the relative velocity of snow disappearance (% day–1). In each flight year, we differenced the snow-on SWE estimates and those from subsequent low-snow flights in late spring of each year (May 24, 2018; June 10, 2019; and May 18, 2022, respectively), and normalized the result to the snow-on values for percent change. We then divided these percentages by the day interval between paired flights. While the ASO data may not have captured peak snow depth or maximum snow-free extent in each season, averaging across three years of flights enabled us to approximate the dominant spatial patterns of depth and disappearance across the domain.

We also retrieved the estimates of mean annual AET and CWD generated by the Basin Characterization Model (BCM) for the Upper Colorado Basin from 1985 to 2012 at 270 m resolution (Buto et al., 2017). The BCM has been widely used in ecological and management applications (Flint et al., 2013). AET is the depth of water (mm) evaporated from the surface or transpired by plants within each pixel. CWD is the difference between PET and AET (mm), where PET is the total depth of water that can be evaporated or transpired given prevailing atmospheric conditions. Under non-limiting moisture conditions, AET equals PET and CWD is 0; positive CWD values indicate a moisture deficit (Buto et al., 2017).

### 2.5.3. Substrate

To evaluate edaphic influences on forest structure and composition, we calculated continuous estimates of soil properties from the U.S. Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) Soil Survey Geographic Database (SSURGO) (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2023). SSURGO contains geospatial information on soil properties predicted via an ensemble of regression, classification, and machine-learning operations on *in situ* soil measurements and environmental predictor variables. The hierarchical data structure contains polygons demarcating map units at 1:12000 scale. Each map unit is made up of one to three major components and potentially several minor components. A component is a field-classified soil type with common characteristics. While the components are not mapped, SSURGO reports their proportional contribution to the makeup of a map unit. Each component is also associated with detailed data from its constituent horizons.

We aggregated horizon-scale data to generate a unique observation per component and aggregated these to map units. We calculated horizon depth–weighted means for available water capacity (AWC, ‘awc\_r’), cation exchange capacity (CEC, ‘cec\_r’), hydraulic conductivity (ksat, ‘k\_sat\_r’), pH (‘ph\_r’), and silt content (‘silt\_r’) in the top 100 cm of soil. We calculated the horizon depth–weighted mean of percent organic matter (OM, ‘om\_r’) in the top 30 cm of soil. We took these variables to be independent estimates of soil constraints on tree growth, and the depths to be those in which the selected variables likely exert the strongest biophysiological effect. We then aggregated the component-scale estimates to the map unit, weighting the mean values by the proportional occupancy of each component. We converted the vector data to raster format using the *rasterize* function in the R package *terra* (Hijmans, 2024).

We characterized the underlying geological substrate using the Colorado Geological Survey vector database “R-37: Geology and Mineral Resources of Gunnison County, Colorado” (Streufert, 1999). We rasterized the vector database, which had been created by digitizing the original U.S. Geological Survey MI-16 Geologic Map of Colorado (Tweto, 1979).

## 2.6. Inferential modeling

To quantify relationships between stand structural and compositional metrics and abiotic variables, we fit generalized additive models (GAM) and generalized boosted models (GBM). All explanatory data were first (dis-)aggregated to the 100 m pixel scale and aligned to a uniform grid using bilinear interpolation (continuous) and nearest-neighbor resampling (categorical). Because of expected spatial autocorrelation in both response and explanatory variables, we also included a tensor product smooth of *x* and *y* pixel coordinates in all models.

In the GAM approach, we estimated each structural metric as the sum of nonlinear spline functions of the explanatory variables, using the *gam* method in R’s package *mgcv* (Wood, 2017). We examined the main effects of each explanatory variable, along with two-way interactions between a subset of variables (Table A.7). In the GBM approach, we used the stochastic gradient boosting framework in R’s *caret* and *gbm* libraries (Kuhn, 2008; Ridgeway, 2024). We estimated variable influence by multiplying the number of times a variable was selected for splitting by the squared increase in deviance explained at each split, and then averaging this value over the ensemble of decision trees. We pursued both approaches in tandem because of their complementary strengths. The GAM strategy allowed us to interpret partial-effects functions for individual and interacting explanatory variables. While partial-dependence plots can be constructed from the GBM, their interpretability is usually limited, especially when variable interactions exist (Elith et al., 2008; Friedman and Meulman, 2003). On the other hand, the GBM allowed us to quantify feature importance, which can be difficult to achieve with the GAM. We assumed that convergence between inferential strategies would give us greater confidence in the results, while divergence could provide points of departure for further investigation.

We initially explored a large set of potential explanatory variables and interactions and used these to estimate a preliminary run of GAMs for variable screening. We identified pairs of variables with an absolute-value Pearson’s correlation coefficient 0.7 and iteratively dropped highly correlated variables from the models, computing the Akaike Information Criterion (AIC) score at each step. We preserved the feature sets that produced the lowest AIC and fitted final GAMs. We used the restricted maximum likelihood estimator (REML) to select smoothing parameters, because it tends to be less prone to overfitting than generalized cross-validation (GCV) (Wood et al. 2023), and we implemented double-penalty regularization for feature selection by specifying ‘select=TRUE’ in the *mgcv* specification. This applied an additional shrinkage penalty to each smooth, allowing terms flattened into the null space of the original REML penalty to be removed (Marra and Wood 2011).

We then fitted GBMs to each response variable using the same response distributions as in the final GAMs. We did not apply regularization in the GBMs, and we allowed interaction depth to vary rather than specifying two-way interactions. We estimated GBM parameters through a full factorial design with 10-fold cross validation. The design matrix randomized interaction depth (1 to 5 features), number of decision trees (2000 to 10,000 trees in increments of 2000), and shrinkage rate (0.1 to 0.01 in increments of 0.02).

# 3. Results

## 3.1. LiDAR vs. field inventory

The optimal Layer Stacking algorithm extracted 4196 trees across the 17 plots (Table 1). Of these, 55 % were successfully matched to field trees (Fig. 2). The RMS distance between matched trees was 2.45 m in the horizontal dimension and 1.46 m in the vertical dimension. Agreement was strong across all size classes. Underdetection and undermatching were most prevalent in trees below 8 m in height, while some overdetection occurred in canopy-intermediate trees, between 15 m and 20 m in height (Fig. 3).

The median height of all trees detected in training was 8.8 m (IQR: 3.1–15.1 m), versus 6.7 m (IQR: 2.8–13.1 m) in the field inventory. Maximum canopy height, estimated at the 95th percentile, was 24.4 m in detected trees versus 23.8 m in field inventory. Estimated QMD of detected trees was 20.7 cm (s.d. 13.6 cm), versus 18.6 cm (s.d. 12.7 cm) measured in the field. Agreement was strongest in higher-density, uneven-aged sites (i.e., where median height was smaller), and poorer in sites with lower density or a paucity of understory trees (Fig. 3).

For composition, we compared species classifications for top-of-canopy tree objects with their matched field trees. Across species, overall classification accuracy was 0.73 and mean *F1* was 0.62. Per-species performance in this independent sample was similar to but not as strong as the performance that Falco et al. (2024b) achieved in generating the species classification product, where mean *F1* for tree species was 0.87 (Table 2).

## 3.2 Domain-wide structure and composition

Applying the optimal ITD algorithm and parameters to the domain’s conifer forests produced 2.375 107 individual trees. Based on underdetection patterns in training, we assumed that the total was a modest underestimate. We applied a correction to this value by binning plot-level data into 1 m height increments and computing the difference in frequency of occurrence per bin between field-observed and LiDAR-detected trees. We performed the same binning on detected trees for the full domain and scaled the number of trees per bin in this dataset by the plot-level frequency differentials (Fig. 4). The corrected estimate of the total number of conifer trees was 2.392 107. Stand densities ranged from 100 to 2041 stems ha–1 (Fig. 5; Fig. 6). The median height of all LiDAR-detected trees in the watershed was 4.8 m, and 95th percentile height was 21.7 m. Height skewness ranged from –1.8 to 8.8; allometry-estimated QMD was 17.0 cm (s.d. 8.3 cm); and basal area ranged from 0.03 to 248.8 m2 ha–1 (Fig. 6).

The spatial distributions of spruce and fir densities were similar, although their maximum densities differed by a factor of two (Fig. 5). (N.B.: the order of magnitude difference between these values and total density is largely a result of filtering to top-of-canopy tree objects during species assignment). Lodgepole pine density ranged from 2 to 283 stems ha–1, concentrated on low-elevation slopes in the southern portion of the domain.

## 3.3 Abiotic factors associated with stand structure

Climate and topographic factors had the strongest influence on stand structure and composition, at 36.6–51.2 % and 33.4–44.1 % of variable influence, respectively (Fig. 7). Substrate factors were slightly less important, collectively accounting for 13.2–25.2 % of influence. SWE, ∆SWE, and elevation were the dominant single features. Other topoclimatic variables related to the water and energy balance (heat load, AET, CWD, TPI) played a smaller, though still significant role. The five most important variables for any response together accounted for 51.8–71.3 % of relative variable influence, meaning that lower-ranked variables accounted for up to 48.2 %, which suggests that a complex system of controls acts on forest structure and composition (Fig. 7, panel B). The *x-y* smooth was a significant factor in the GAMs, indicating the existence of latent spatial structure in the explanatory features.

GAMs explained a similar percentage of deviance (PDE) across the five full-forest models (Table 3). For models of species-resolved density, PDE was lower, with a nadir at 22.2% for fir. All GAM models were convergent and full rank. Tests for *k* indicated sufficient knots in the basis functions for all parameters (Table A.7), and examination of residual plots indicated low bias in model fits (see optimal tuning parameters in Table A.8).

The effects of explanatory variables were generally coherent between the two modeling strategies. The top five in each GBM also covaried strongly with the response variables in GAMs, based on interpretation of partial-effects plots (Fig. 8). Variables falling below the top five usually had slopes near zero in the GAMs, indicating a null relationship or that the smooths had been selected out of the model. (GAM partial-effects plots for all explanatory variables appear in Fig. A.4). In rare cases, a variable with apparent leverage in a GAM was not highly influential in the corresponding GBM.

### 3.3.1 Climate effects

SWE and ∆SWE were the most influential factors in GBMs of total stand density and basal area and ranked among the top five for every full-forest structure response (Fig. 7). In GAMs, multiple measures of stand structure showed a similar nonlinear relationship with SWE. The highest density, basal area, maximum canopy height, and QMD occurred near 0.3 m SWE (~1 s.d. below mean), and each of these metrics declined as SWE increased. Height skew and species-resolved densities were exceptions to this pattern. Height skew followed an approximately sigmoid increase with SWE, such that stands with more small trees were associated with high snow accumulation, up to a threshold around 2.5 s.d. above the mean. Fir, spruce, and pine densities were highest around average SWE and declined steeply beyond this maximum. In the zone of lower-than-average snow depth, fir and spruce densities varied little, but pine density increased sharply with increasing SWE (Fig. 8).

Basal area, maximum height, and QMD were highest in positions with longer snow residence times (i.e., lower ∆SWE values), following a linear function. Total density was highest around 0.37 % d–1 (~1 s.d. below mean ∆SWE) and declined toward high and low ∆SWE extremes. As snow melt rate increased across stands, they tended to contain more small trees, but this relationship became asymptotic at 0.96 % d–1 (~1 s.d. above mean) (Fig. 8).

The remaining two climate variables, AET and CWD, were somewhat less influential than snow factors. AET ranked among the five most influential variables for several responses. The relationships were nonlinear but generally declined from lower to higher AET. For basal area, maximum height, and QMD, local maxima existed near 3.3 x 104 mm and 5.9 x 104 mm AET ( 2.5 s.d. from mean). Fir densities declined linearly as CWD increased, while pine densities peaked near 3.4 x 104 mm (2 s.d. above mean CWD) and declined toward the high and low water deficit extremes.

### 3.3.2 Topographic effects

Elevation appeared among the top five covariates for every structural metric and was the most influential factor explaining maximum height and QMD (Fig. 7). Total density decreased linearly with increasing elevation (Fig. 8). Stands with smaller-statured trees tended to occur at higher elevations, while those most strongly skewed toward larger trees occurred near the domain’s mean elevation of 3200 m. All other structural metrics showed non-monotonic relationships, with maxima between 3000 m and 3200 m and asymptotic declines as elevation increased. Heat load was the most influential covariate for fir density and ranked among the most influential for all other responses except basal area. Functional forms varied. Maximum height and QMD increased with heat load, while total density increased exponentially. The TPI–height skew relationship suggested that stands with more small trees occurred on low- and toe-slopes, while stands with more large trees occurred on mid-slopes. Although TPI did not emerge as a top-ranked feature in the other GBMs, it did exert a modest influence on basal area, QMD, and total density in GAMs: all of these structural metrics were highest on mid-slopes (Fig. A.4).

The primary topographic factors (elevation, heat load, TPI) explaining stand structure also interacted with climate factors in important ways (Fig. 9). For example, elevation modified the effects of snow loss rate for all structural metrics. Specifically, basal area and QMD were highest at mid-elevation sites with slow snow disappearance rates. These structural values decreased as the rate of snow loss increased, but the effect was stronger toward higher elevations (Fig. 9). Height skew showed a similar relationship: stands with more large trees occurred at slow-melting, mid-elevation sites. Conversely, the highest densities occurred at the extremes: high elevation—high ∆SWE and low elevation—low ∆SWE positions.

### 3.3.3 Substrate effects

Soil factors accounted for at most 22% of cumulative influence in any GBM. CEC was a top-five feature in the GBM for pine density, although its partial effect in the GAM was weaker than that of other variables. Soil AWC exerted a modest influence on maximum height and QMD, along a bimodal function with minima at 0.06 and 0.15 cm H2O cm–1 soil, approximately –2 s.d. and +1 s.d. from mean. Soil AWC interactions with AET and SWE also had a strong influence on basal area, QMD, and total density (Fig. 9). For example, basal area was greatest in sites with high AET and low soil AWC. Basal area decreased through the midrange of AWC and increased again toward high AWC, but this effect was considerably stronger in sites with high AET (Fig. 9). Total density increased with AWC along a stable ridge between mean and –1 s.d. SWE.

Although geology was among the least influential variables across all models, there were select instances where lithologic parent material had an effect on forest structure and composition. On landslide deposits (Ql), basal area was 10 m2 ha–1 greater, QMD 5 cm greater, and maximum height 4 m greater than average (Fig. 10). Total density was 240 stems ha–1 below average on the Gothic Formation’s Pennsylvanian-Permian sandstone and shale (Pm). Most structural variables tended to be lower than average on granodioritic laccoliths (Tmi).

# 4. Discussion

Our results demonstrate strong direct, interactive, and often nonlinear associations between conifer stand structure and composition and abiotic gradients. Using multiple spatially continuous structural and compositional metrics, we quantified these relationships in the equivalent of more than 19,000 contiguous ha-scale plots. Not only did this sample size exceed what is feasible with ground-based approaches alone; it also included end members of structural and abiotic gradients that are usually poorly represented in field studies.

## 4.1 Continuous estimation of forest structure

We used a fully automated approach to optimize ITD through the vertical profile from discretized full-waveform LiDAR, validating detection with tree inventory data from mixed-age stands. Our rates of detection (0.96), matching (0.55), and commission error (0.51) between field-observed and model-detected trees compared favorably with those from prior studies. In the original paper describing the Layer Stacking ITD algorithm, Ayrey et al. (2017) reported detection rates of 0.66–0.89 and commission errors of 0.22–0.53 in conifer forests. They manually matched trees through visual observation and enforced a minimum DBH threshold of 10 cm, while we automated matching and allowed trees as small as 1 cm DBH to be delineated. In their benchmarking analysis of eight tree-detection algorithms, Eysn et al. (2015) reported a maximum match rate of 0.36 and an extraction rate of 0.55 with 1.6 m ∆Z accuracy and 0.9 m ∆XY accuracy in a mixed-age conifer site, a substantial underdetection rate compared to our results. Pang et al. (2021) reported a match rate of 0.70 on an extraction rate of 1.03 across 10 sites of varying composition. However, their analysis used a minimum height threshold of 4.2 m, while ours was 1.3 m. (Note: neither Eysn et al. (2015) nor Pang et al. (2021) used the Layer Stacking algorithm for ITD). Our performance statistics confirm the viability of predicting individual-scale tree attributes over a large domain while training on only a small proportion of its trees (Objective 1). This viability may have also depended in part on our stratified field sampling design, which yielded training samples well distributed across multiple environmental and structural gradients. That we were able to extract and match a large proportion of true sub-canopy trees with performance comparable to efforts using stricter height thresholds underscores the advantage of full waveform data (Anderson et al., 2016). Our results support Dalponte and Coomes’s (2016) argument in favor of tree-centric approaches to quantifying forest characteristics, in part because they allow for feature estimation on the same epistemological basis as a field inventory.

The Layer Stacking algorithm’s 4% underdetection rate presumably yielded a low density bias, particularly in smaller size classes, which in turn could contribute to high QMD and low basal area biases. However, we would expect this secondary effect to be minor because small trees have a weaker influence on QMD and basal area than they do on density (which weights small and large trees equally). While we corrected the total count of trees (§3.2), we were unable to correct the gridded products because we derived those estimates from individual detections.

Unexpectedly, ITD overestimated median height by 2.1 m across plots and overestimated maximum canopy height (at the 95th percentile) by 0.6 m. LiDAR canopy height estimates are often lower than field measurements because of the small probability of laser pulses striking the topmost point of a crown. Our overestimates were likely the result of three factors: (1) vertical uncertainty in ground returns and in the DEM used to normalize the discretized waveform points, (2) error in hypsometer measurements within the expected vertical accuracy range of ±0.75 m, and (3) underdetection of smaller trees. In the subset of older, even-aged sites with sparse understories, we substantially underestimated median height, likely because overlapping lower branches of large trees were incorrectly differentiated as smaller individuals (Fig. 3, panel A). Allometry-based QMD was negligibly larger (+1.8 cm) than QMD from field data. While QMD is weighted toward larger trees, underestimates of the number of trees in a stand and overestimates of large tree heights likely both explain this difference.

One novel contribution of this analysis was our workflow optimizing ITD from massive waveform LiDAR data (see Data Availability Statement). A critical challenge in large-scale tree mapping is justifying algorithm and parameter selection for a given site and vegetation type (Eysn et al., 2015). We addressed this challenge by leveraging a statistical learning approach, systematically iterating through multiple algorithms and parameter sets and testing against an objective loss function. While we acknowledge that other ITD algorithms exist, and that others among those we did test may have proven optimal in other domains, we suggest that our workflow offers an example of reproducible ITD for the discipline.

## 4.2 Species composition

Species classification accuracy was highest for spruce and lowest for fir. The largest source of error was the misclassification of fir as spruce. As these species co-occur in high-density, closed-canopy stands, spectral mixing at the interfaces of intersecting crowns likely accounted for much of this confusion. Further uncertainty derived from positional error in geolocating tree crowns in the field, detecting crowns from LiDAR, and delineating crown polygons. While positional matching fidelity was high for top-of-canopy trees, any error from misalignment between field-observed and LiDAR-derived objects would have propagated into the species assignment. Similarly, to the extent that crown polygons were over- or undersegmented, pixels associated with adjacent trees of another species could have been improperly included in the majority vote. Nevertheless, the spatial pattern of single-species density distributions cohered with expectations: spruce and fir co-occurred throughout the watershed up to treeline; spruce density exceeded fir density in the canopy top; and pine were largely restricted to lower-elevation southerly slopes and areas where disturbance had occurred within the last 100 years (Alexander, 1987; Falco et al., 2024b; Whipple and Dix, 1979).

## 4.3 Abiotic constraints on stand structure and composition

At the scale of this analysis—hectare units across a 700 km2 watershed—SWE, ∆SWE, and elevation predominated among the multiple interacting influences on conifer stand structure and composition. These variables integrate key aspects of the energy and water balance, but in different ways.

### 4.3.1 Snow

The dominance of snow in explaining structural and compositional variation in a subalpine forest system was a novel finding. SWE quantified peak snow water just before the onset of the growing season—the net of wintertime snow input, ablation, and intermittent melt fluxes. ∆SWE, the relative rate of snow disappearance, primarily indexed spring and early summer radiation load. (These metrics partially interact: high SWE can be associated with low ∆SWE, as deeper masses of snow self-insulate and melt more slowly). For basal area, maximum height, QMD, and total density, the rising limb of the SWE curves in low-snow areas (Fig. 8) coheres with other findings that marginal additional SWE can enhance annual tree growth in water-limited locations by providing a reservoir that delays soil drydown (Coulthard et al., 2021; Hu et al., 2010). This subsidy may have a multiplying effect, as greater snowpack magnitude has been shown to enhance conifers’ capacity to use summer monsoon rain (Berkelhammer et al., 2020). However, in the falling limb of the SWE curves (Fig. 8), deeper snow may impose temperature constraints that contract the growing season, inhibiting xylogenesis and diminishing seedling survival (Coulthard et al., 2021; Littell et al., 2008). The shape of these relationships points to the existence of a water-energy limitation threshold in the domain, likely driven by asynchronous and spatially heterogeneous patterns of snow and radiation input (Pelletier et al., 2018; Wainwright et al., 2022; Dudney et al. 2023).

The linear relationships between ∆SWE and basal area, maximum height, and QMD suggest that longer snowpack persistence (independent of peak depth) may enable the development of larger-statured trees. Longer snowpack duration was also associated with higher stand density in sites with ∆SWE above 0.37% d–1, consistent with the water-subsidy hypothesis. Below the 0.37% d–1 threshold, longer snowpack persistence may have imposed an energy constraint on density. The interactive effect of elevation and ∆SWE on stand density lends support to this interpretation (Fig. 9): the lowest stand densities appeared along a high elevation–long snow persistence frontier (where temperature was likely the dominant constraint on tree productivity) and along a low-elevation–short persistence frontier (where low water was likely the dominant constraint). At the same time, the highest densities occurred along the high elevation–short persistence frontier (where higher radiation driving faster snowmelt likely ameliorated the temperature constraint) and along the low elevation–long persistence frontier (where a durable water subsidy likely ameliorated the moisture constraint).

While the interpretation above focuses on the effects of snow dynamics upon stand structure, the mechanistic relationships between these factors run in both directions, with potential feedbacks. For example, by shading snow from incoming shortwave radiation, trees can slow snowmelt, but as longwave radiating bodies they can hasten it (Lawler and Link, 2011). The net effects depend in part on stand density and scale (Bonner et al., 2022; Lundquist et al., 2013; Veatch et al., 2009). In our results, stand density in sites with short snow persistence (i.e., ∆SWE greater than 0.37% d–1) likely had a direct positive effect on snowpack duration, such that snow disappeared more slowly in areas of higher density due to shading and wind sheltering. Over time, a persistent water subsidy may have further enhanced stand density development, producing a positive feedback.

Species composition appeared to mediate snow-density relationships. Spruce and fir densities were similarly unimodal functions on SWE and negative linear functions on ∆SWE, but the effects were stronger for spruce than for fir (Fig. 8). The departure of the pine density–SWE relationship from these patterns was consistent with our expectations that pine would dominate xeric positions, while spruce-fir would dominate higher-elevation positions with greater snow input and longer residence times. *P. contorta* is a relatively drought-tolerant species and competes well on high-radiation, low-moisture sites, but it is shade-intolerant and competes poorly where spruce and fir are abundant (Veblen, 1986).

### 4.3.2 Topography

Along the elevation gradient, the maxima of the partial-effects curves for maximum height, QMD, basal area, and density all occurred between 3000 and 3200 m.a.s.l. This result matches findings from prior process-based modeling studies in this watershed, which reported maximum conifer density at the same elevation (Carroll et al., 2024, 2022). It also broadly coheres with findings of a non-linear elevational influence on maximum canopy height (Fricker et al., 2019) and maximum density (Greenberg et al., 2009) in the Sierra Nevada, although our maximum occurred roughly 1000 m higher than in those studies, squarely within the Rocky Mountain subalpine zone. Whether energy or moisture contributes more to this band of high site potential is uncertain. The adiabatic process tends to produce both warmer and drier conditions at lower elevations and colder, wetter conditions at higher elevations, although these trends can be mediated by other topoclimatic factors. The prior modeling work in this watershed has identified a water-energy limitation threshold in low-precipitation years within this elevational range (Carroll et al., 2024, 2022). Moreover, the domain’s highest summer groundwater losses (Carroll et al., 2024) and maximum annual AET occur around 3100 m, suggesting that stands sustain a larger evapotranspirative flux during the growing season at this elevation than elsewhere. This elevation range may therefore support the domain’s most ecohydrologically optimal conditions, i.e., the best balance of water availability and evaporative demand for tree productivity (Roebroek et al. 2020). This said, the greatest canopy height and QMD also occurred where high heat load coincided with high SWE, while the greatest basal area occurred in low- to mid-slope topographic positions with slow snow disappearance rates (Fig. 9), suggesting that other topographic factors can interact to produce high-potential conditions.

### 4.3.3 Substrate

Other researchers have reported moderate effects of soil horizon thickness, pH, moisture, and parent material on conifer stand characteristics (Bruckner et al., 1999; Fricker et al., 2019; Meyer et al., 2007). The substrate factors we expected to be influential—AWC and geologic parent material—were tertiary to climate and topographic factors. Our geological categories captured broad differences in geochemistry, fracturing potential, and substrate age, but they did not differentiate all the important lithologic constraints on tree growth. For instance, there was no dataset available quantifying fine-scale groundwater storage or flow in this domain. Although evidence suggests that the shallow-rooting conifer species in this study typically do not access bedrock water (Langs et al. 2020), and that subalpine conifers in general exhibit limited source plasticity between soil and rock water (Goodwin et al. 2023), developing such a dataset through ecohydrological modeling or gravimetric remote sensing (e.g. GRACE-FO) could improve our understanding of the variation in stand structure not explained by climate or surface components of the water balance.

# 5. Conclusions

To our knowledge, this paper is the first to evaluate abiotic influences on a complement of conifer forest structural and compositional characteristics on a spatially continuous basis at watershed scale. We have made original methodological contributions in developing a workflow for systematically training and validating a large suite of ITD algorithms and parameter permutations against an objective loss function. This approach could be applied to benchmark new ITD algorithms and to validate spaceborne LiDAR acquisitions, including NASA GEDI products. Our inferential analyses demonstrated that stand structure and composition are associated with a complex system of interactions dominated by snow and elevation. The primacy of snow dynamics is an important finding not well documented in the literature. In some cases, our inferences were limited. For instance, with instantaneous stand structural metrics, we did not account for disturbance or stand development processes. Nor did we infer the causal direction of snow-structure relationships. Further measurements of site soil moisture, interannual tree growth, subsurface water storage, and snowpack dynamics could help to clarify these processes.

Over the past two decades, Southern Rocky Mountain forests have experienced warmer and drier conditions than in any prior period in the last millennium (Williams et al., 2022). Given the evident importance of snow to the structure and composition of these forests, a low-to-no snow future could yield widespread changes in their physiognomy and function (Siirila-Woodburn et al., 2021). The results we have presented provide an important foundation for predicting how these systems may respond to synoptic environmental change in the future.

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# CRediT authorship contribution statement

**H. Marshall Worsham:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – Original draft, Writing – review and editing. **Haruko M. Wainwright:** Funding acquisition, Data curation, Writing – Review and editing. **Thomas Powell**: Conceptualization, Investigation, Methodology, Writing – Review and editing. **Nicola Falco**: Data curation, Methodology, Validation, Writing – Review and editing. **Lara M. Kueppers**: Conceptualization, Funding acquisition, Project administration, Methodology, Supervision, Writing – Review and editing.

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# Data availability statement

Code for the analytical workflow and reproducible tables and figures is available at [https://zenodo.org/doi/[10.5281/zenodo.12775449](https://zenodo.org/doi/10.5281/zenodo.12775449)](https://zenodo.org/doi/10.5281/zenodo.12775449). Waveform LiDAR source data are available on ESS-DIVE at <https://data.ess-dive.lbl.gov/datasets/doi:10.15485/2403350>, and other source, intermediate, and final data at <https://data.ess-dive.lbl.gov/datasets/doi:10.15485/2404585>.

# Appendix A. Supplementary material

Supplementary material includes variable definitions, ITD algorithms and parameters, details on allometric diameter estimation methods, raster images of explanatory variables, and GAM partial-effects plots.

# Tables

**Table 1.** Summary statistics for the best-performing runs of eight individual tree delineation (ITD) algorithms. Parameters and tested values for each algorithm appear in Table A.3. Reported values are root mean squares (RMS) computed across the 17 training plots. Results for the best performing algorithm, Layer Stacking, appear in bold.

| Model | Reference trees | Detected trees | Extraction rate | Match rate | Overall accuracy | OR | CR | RMS ∆XY | RMS ∆Z | RMS ∆XYZ | Precision | Recall | F1 |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **LayerStacking** | **4,355** | **4,196** | **0.96** | **0.55** | **0.55** | **0.49** | **0.51** | **2.45** | **1.46** | **2.85** | **0.53** | **0.55** | **0.51** |
| Li (2012) | 4,355 | 3,247 | 0.75 | 0.34 | 0.34 | 0.67 | 0.59 | 2.73 | 1.67 | 3.21 | 0.43 | 0.34 | 0.37 |
| LMF-auto | 4,355 | 3,071 | 0.71 | 0.31 | 0.31 | 0.72 | 0.57 | 2.83 | 1.64 | 3.27 | 0.45 | 0.31 | 0.34 |
| LMF fixed window | 4,355 | 3,738 | 0.86 | 0.37 | 0.37 | 0.65 | 0.61 | 2.69 | 1.62 | 3.14 | 0.41 | 0.37 | 0.37 |
| LMF variable window | 4,355 | 9,861 | 2.26 | 0.54 | 0.54 | 0.47 | 0.75 | 2.38 | 1.32 | 2.72 | 0.27 | 0.54 | 0.35 |
| MultiCHM | 4,355 | 3,254 | 0.75 | 0.42 | 0.42 | 0.60 | 0.52 | 2.79 | 1.52 | 3.17 | 0.51 | 0.42 | 0.43 |
| PTrees | 4,355 | 8,305 | 1.91 | 0.53 | 0.53 | 0.49 | 0.74 | 2.58 | 1.44 | 2.96 | 0.28 | 0.53 | 0.34 |
| Watershed | 4,355 | 1,047 | 0.24 | 0.16 | 0.16 | 0.85 | 0.47 | 2.99 | 1.93 | 3.56 | 0.56 | 0.16 | 0.23 |

LMF = local maximum filter; OR = omission rate; CR = commission rate

**Table 2.** Classification performance metrics by species. *F1* is a proportion representing the harmonic mean of precision (the proportion of true positives among all predicted species assignments) and recall (the proportion of predicted assignments to a species out of all trees that truly belong to that species).

| Class | Sensitivity | Specificity | Precision | Recall | F1 | Detection rate | Balanced accuracy |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Fir | 0.42 | 0.81 | 0.14 | 0.42 | 0.20 | 0.03 | 0.61 |
| Pine | 0.65 | 0.98 | 0.87 | 0.65 | 0.74 | 0.11 | 0.81 |
| Spruce | 0.77 | 0.67 | 0.88 | 0.77 | 0.82 | 0.59 | 0.72 |

**Table 3.** Training error and cross-validation (CV) error from generalized boosted models (GBM) and percent deviance explained (PDE) from generalized additive models (GAM) estimated on conifer forest metrics and abiotic data across the full domain. GBM error values are reported in the units of the response variable. GAM PDE is reported as a percentage (%).

|  | GBM | | GAM |
| --- | --- | --- | --- |
| Response | Training error | CV error | PDE |
| Basal area (m2 ha–1) | 7.46 | 17.60 | 64.2 |
| Height 95P (m) | 2.18 | 4.02 | 61.0 |
| Height skew (unitless) | 0.52 | 0.68 | 50.4 |
| QMD (cm) | 2.10 | 3.89 | 62.4 |
| Total density (stems ha –1) | 182.43 | 347.14 | 63.4 |
| Fir density (stems ha–1) | 11.59 | 13.13 | 22.2 |
| Spruce density (stems ha–1) | 30.56 | 41.45 | 47.4 |
| Pine density (stems ha–1) | 13.78 | 30.14 | 49.4 |

QMD = quadratic mean diameter; 95P = 95th percentile

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1. The buffer ensured that LiDAR points associated with trees along plot boundaries were included in the operation; however, any tree objects detected in the buffer zone beyond the plot boundaries were removed. [↑](#footnote-ref-1)