# TREE ARCHITECTURE AND SPATIAL DISTRIBUTION ON AN ADVANCING DIFFUSE TREELINE ON PIKES PEAK, CO – YOU CANT TEACH A OLD TREE NEW TRICKS, CLIMAT CHANGE ADDITION

# A THESIS

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# ABSTRACT

Treelines can serve as model ecotones in their response to climate change. However, the role of tree architecture at treelines is poorly understood. This paper examines tree architectures at a fast-migrating diffuse treeline in a bowl on the western slope of Pikes Peak (Colorado). Investigating the spatial distribution of the allometric types, the relationship between the growth rate and height for each architecture type, and the impacts of the changing climate on the architectural spatial distribution. The study site was divided into an Upper Zone (UZ) and Lower Zone (LZ). We found multiple distinct architectures within this diffuse treeline. Unexpectedly, tree architectures did not follow a spatial distribution pattern of clustering or avoiding with like and or different architectures. Krummholz and Cone architectures were found growing in close proximity to one another, signifying that the upper climatic boundary at this site has advanced up in elevation. These multiple architectures are able to represent current and past climatic conditions. Advancement is occurring at such rapid rates that tree established architectures are not able to release from their path dependency. To my knowledge, this is the first study that examines multiple tree architectural types within a treeline and how they are distributed in space.

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#### **INTRODUCTION**

Ecotones, the transitional zone between two distinct habitats, are of special interest to ecologists because of their particular sensitivity to climatic changes (Walther et al., 2002; Risser 1993). Alpine ecotones represent the transition between closed canopy forest and tundra species, where the upper limits of tree species growth is constrained (Elwood, 2012). This zone between closed canopy forest and tundra species can vary greatly in width and character, comprising different treeline typologies (Holtmeier & Broll, 2005). Alpine treeline ecotone are of specific interest in this study because they are valuable indicators of climate change due to their sensitivity to temperature and the pronounced impacts of climate change at higher altitudes (Walther et al., 2002; Fischlin et al., 2007) Worldwide treelines have been advancing to higher elevations altering the ecotone, however the speed and frequency is dependent on tree typology (Harsh & Bader, 2011).

Around the world, researchers are beginning to understand how treeline dynamics are affected by climate change on a population scale. Treeline ecotones can be categorized into four main treeline typologies: Diffuse, Abrupt, Island, and Krummholtz (FIGURE). Diffuse treelines, characterized by a gradual decrease in tree height and density with elevation creates an extended transitional zone between tree habitat and the species limit (Elwood, 2012; Harsch & Bader, 2011). Abrupt treelines must have a distinct rapid change in density and tree height from a continuous forest boarding tundra vegetation (Harsch & Bader, 2011). Tree Islands are characterized by clustered patches and or linear strips of trees called fingers above a continuous forest (Harsch & Bader, 2011). Krummholtz treelines have distinctive severely stunned and deformed trees that can occur in patches, randomly dispersed, and or in a continuous band above the forest, also known as islands (Harsch & Bader, 2011). Each treeline typology has different proposed mechanisms enforcing typology. The main enforcing mechanisms include seedling mortality, growth limitation and dieback of biomass of established trees.

Growth and elevation of an alpine treeline are controlled by the tree specie's upper climatic boundary, the harshest environment possible for successful establishment of tree species (Elwood, 2012). The upper climatic boundary of alpine treelines is likely controlled by temperature, mainly determined by growing season averages (Körner, 1998; Grace et al., 2002). Körner proposes that temperature below a thermal threshold affects tree establishment by limiting cell production and development, this is called the growth limitation hypothesis (Körner, 1998). Shi et. al. research states that carbon supply

does not inhibit treeline growth, rather low temperature inhibits carbon use which supports Körner's growth limitation hypothesis (Shi et al., 2008). The growth limitation hypothesis further explains why warmer growing season temperatures correlate with increased regeneration and faster radial growth above treeline (Bolli et al., 2007; Grace et al., 2002; Feiden, 2010). It is reasonable to expect with increased global temperatures from global climate change that the upper climatic boundary for tree species will rise in elevation causing a migration into a once treeless tundra (Kullman, 2002). Researchers have already reported treeline migration upslope, encroaching on tundra during the last century (e.g., Kullman, 2002; Harsch et al., 2009; Walther et al., 2005; Earnest, 2011; Fieden, 2010). A recent meta-analysis of treeline research found that fifty-two percent of treelines studied were advancing, while only one percent were retreating (Harsh et al., 2009). This is a global trend of treeline migration global climate change (Elwood, 2012). Elevation changes are important to understanding the relationship between treeline and climate change.

To understand this relationship it is essential to understand the mechanisms that control treeline (Elwood, 2012). Treeline typology, correlates strongly with treelines ability to react to climate change. Growth limitation, die back, and seedling mortality are three major mechanisms controlling tree performance (Harsch & Bader, 2011). Growth limitation, die back, and seedling mortality result from various types of physiological stress or damage (Harsch & Bader, 2011). Low temperatures restricting tissue formation and or insufficient carbon balance caused treelines to be growth limited with decreased growth rates (Harsch & Bader, 2011). Pathogenic fungi (snow fungi), wind damage, and summer drought can cause seedling mortality (Harsch & Bader, 2011). Moreover dieback results from freezing damage, snow loading, and wind abrasion (Harsch & Bader, 2011). These mechanisms are neighboring tree relationships that affect the redistribution of wind, snow, shading, or resource competition due to micro and macro climatic conditions (Harsch & Bader, 2011). These major mechanisms play significant roles in maintaining and forming treeline typology, as does climate change in altering the intensity of the mechanisms.

In recent years, according to Harsh et. al. (2009) nearly eighty percent of diffuse treelines are advancing while only 22 percent of abrupt, island and krummholtz treelines are advancing (Harsh et. al. 2009). It is possible that growth limitation is the primary mechanism controlling diffuse treeline advancement. Growth limitation on diffuse treelines, appears to increase on a gradient, as distance from the continuous forest increases (Harsch & Bader, 2011). The dispersed spatial pattern of a diffuse treeline influences wind and temperature dynamics to form a more favorable microenvironment for tree growth and treeline migration upslope through feedbacks (Elwood, 2012). Diffuse treelines are expected to continue to advance as global temperature increase (Harsch et al., 2009).

Limited biomass gain (growth limitation) and biomass loss (dieback) restrict growth. Both mechanism are form from suboptimal conditions of stress; however growth limitation occurs through long-term mild stress such as low growing season temperatures while dieback occurs from severe short-term stress such as wind, frost, and snow load (Harsch & Bader, 2011). Growth limitation usually creates trees architectures that are small but upright, whereas dieback ultimately forms tree architecture to be smalldeformed trees and Krummholz (Harsch & Bader, 2011). Growth limitation and dieback are controlled by different climatic parameter occurring at different times of the year and day (Harsch & Bader, 2011). Growth is limited by growing season temperatures and by definitions requires sufficient warmth, therefore the summer season, while dieback occurs due to low temperature climate stressor such as wind and frost in the winter (Harsch & Bader, 2011).

Dieback, and seedling mortality control Krummholz, island, and abrupt typology, leading them to be relatively unresponsive to warmer growing season (Harsch & Bader, 2011). Dieback resulting from tissue loss or damage from stressor include wind abrasion, snow loading, freezing damage, and radiation, is strongly evident in Krummholz treelines (Harsch & Bader, 2011). Seedling recruitment is less frequent due to high rates of seedling mortality due to the harsh surrounding environment (Harsh & Bader, 2011). However, increased growth rates and recruitment of seedlings have been correlated with improved winter conditions, such as higher temperatures and more snow at Krummholz treelines. Advancement of Krummholz treelines are observed less than at diffuse treelines (Harsh & Bader, 2011). Advancement of Krummholz treelines in response to warming growing season temperatures is unlikely to facilitate advancement, if climatic factors causing dieback are addressed (Harsch & Bader, 2011).

Spatial distribution of trees at treeline reflects the severity of environmental stressors the treeline is facing (Elwood, 2012; Callaway et. al., 2002; Smith et. al., 2003; Germino et. al, 2002; Maher & Germino, 2006; and Körner, 1998). Harsh environmental conditions usually lead to facilitation among trees through clustering (Callaway et. al., 2002). Tree clustering provides protection and decreased stress through shading from open sky, thermal insulation, moisture retention, and wind protection, as well as improving nutrient availability, soil geology, and other microsite characteristics that improve tree establishment (Smith et al., 2003; Germino et al., 2002; Maher & Germino, 2006; Körner 1998). Although tree clustering is only beneficial when facilitation

compensates for the competition between trees (Callaway et. al., 2002). Trees that can survive as individuals generally grow faster than their clustered counter parts (Robert, 2010).

While diffuse treelines are responding to warming growing season temperatures Krummholz treelines are not. Here we see how treeline typology influenced treeline dynamics on a population scale. Moreover, each typology is formed and maintained through different feedback loops and mechanisms. Treelines are made up of individual tree shaped by feedback loops and mechanisms as well. However, overall little is know about tree architectures and mechanism that control them outside of few specified architecture types – Flag trees and Krummholz.

Given that the treeline typology is connected at least implicitly to tree architecture, it is pertinent to ask what factors shape tree architecture? Krummholz trees are of particular interest to researchers studying individual tree physiology and architecture at treeline. The common shape of Krummholz is formed through low growth and physical damage that has caused the dieback of new growth facing the prevailing winds (Hadley & Smith, 1986). Krummholz are believed to reach establishment through reiterative layers and self-facilitation (Norton & Schöenberger, 1984). The Krummholz tree architecture is a response to stress and not adaptation to stress; however a species' ability to form Krummholz can be adaptive at treeline (Harsch & Bader, 2011). The Krummholz architecture does not have low temperature growing advantages (Pereg & Payette, 1998). Krummholtz are not growth limited, in fact, vertical stem growth occurs in the summer months but is lost in the following winter months by subsequent wind damage (Wardle, 1968). The Krummholz architecture illustrates the stressors the individual tree is facing.

Desiccation by wind, abrasion by wind driven snow particles, and friction from strong winds, can severely damage trees and be key to forming a specific architecture (Scott et. al, 1993). Wind stressor can cause a unique response in tree architecture creating a distinct loss of needles and branches in the zone of abrasion. This abrasion can form a flag shaped tree with the loss of growth on an entire side of the tree or in sections (Scott et. al, 1993). In fact, the age of a tree's needles affected the size and susceptibility zone of abrasion on the tree (Scott et. al, 1993). Needles of the same age have different resistibility to abrasion due to the age of the branch and the history of the formation of the tree (Scott et. al, 1993). There appears to be an eight-year turn over with needles resistance and susceptibility to abrasion. New needles produced on a new branch are initially susceptible, but over an eight-year period each subsequent crop of needles comes from resistance. However, after eight years, again the needles on the branch become

susceptible (Scott et. al, 1993). This gives the tree a time frame of seven to eight years to escape the abrasion zone. Once through the abrasion zone new branches are able to develop with decreased susceptibility to wind abrasion (Scott et. al, 1993). Tree's unique responses to wind stress indicates variations in tree age as well as physical environment in the treeline (Scott et. al, 1993).

With the treeline typologies reviewed above it is implicitly assumed that individuals trees with homogeneous architecture form the treelines. It is implicitly assumed that Krummholz and tree island treelines contain trees with homogenous deformed architectures. While diffuse treelines are implicitly assumed contain trees with homogenous symmetric architectures. This homogeneity of tree architecture has been assumed when studying treeline advancement, simplifying treeline stand. Assuming that treelines have homogeneous architectures stands is an oversimplification of mechanism at treeline. Treeline typologies however contain mixtures of distinguishable tree architectures. Studying the multiple tree architectures within treelines will bring a new perspective in understanding the impacts of climate change on this sensitive alpine ecotone.

2018 Study

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This research focuses on a diffuse treeline advancing dramatically up elevation. From 1953-2009 the treeline gained 18 meters in elevation and 60 meters surface migration (Earnest, 2011; Feiden, 2010). This study sought to merge two perspectives on treeline advancement dynamics research, looking to answer population dynamics and individual tree physiology dynamics operate together to explain the impacts of climate change on this diffuse treeline on Pikes Peak. The combination of the classical ecotone population perspective and individual tree physiology perspective has not been a major point of research with treeline. A detailed analysis of tree architectures and their spatial distribution patterns at a dynamic treeline is critical to understand the movement of treeline in relationship to the rapid impacts and time scale of climate change.

The first research question looks to answer what controls the development of tree architecture. In graphing growth rates to height, this paper hopes to find what other mechanism, if any, influence the relationship's mathematical function. It was anticipated that tree architectures that which relatively not stressed to have a linear function, such as cones. It was also expected that tree architectures, like Krummholz severely deformed trees to follow a logarithmic function due to equivalent dieback and growth.

The second research question is how are different tree architecture distributed across the diffuse treeline. It was anticipated that tree density would decrease linearly as distance from the continuous forest increased. With decreased density, increased environmental stressors would follow, causing an increase in deformed trees as distance from the continuous forest increases. The creation of a distinct and clustering of deformed tree architectures at higher elevations and relatively non-stressed tree at low elevations: these architecture types would be located in different parts of the transect due to varying climatic conditions. It was anticipated, that trees furthest away from the continuous forest, the more damage it would endure. Bulbs and Stilted trees would be at low elevations due to increased snowpack and therefore more snow fungi. Mulit-Tipped trees can be found here and have damaged and multiple tips due to snow fungi and breakage from the weight of snow. Candles would be at low elevations near the continuous forest due to competition for light and little space to grow in width. Curved Trunked trees would be above Candles due to their increased age. Then would come the 'perfect cone' in an environment suitable for tree establishment and growth. Skirted trees would follow. Krummholz release would be found in areas that have become more suitable for trees but that were once harsh. Higher in elevation we will start to see Flagged trees damaged from wind abrasion and ice crystals. Multi-Tipped trees can also be found at this elevation due to wind abrasion and ice crystals. Finally, at the highest

elevation in our transect should be Krummholz, that experience intense dieback, causing a loss of yearly growth.

# METHOD

#### Site Description

The study area is located within a bowl on the western slope of Pikes Peak on the Front Range of the Colorado Rocky Mountains. Within the bowl the transitional ecotone between closed canopy forest and alpine tundra was the area of interested. This transition ecotone's tree boundary was characterized as diffuse beginning in 1977, decreasing tree height and density with increased elevation along the ecotone (Harsh and Bader, 2011). This treeline is known to be experiencing a 2 degree C increase in regional growing season temperatures and rapid upward elevation advancement.

The study site was a polygon transect with the largest width being 51.81 meters and the largest length being 98.93 meters (IMAGE). The elevation of the transect ranged from 3608.08 to 3691.67 m a. s. l. This polygon was located inside a previous study site on the diffuse treeline in 2012 by Kelsey Elwood. This study site was in revisited 2018 to future examine the advancing diffuse treeline relationship with climate change. The only tree species present is Picea engelmannii Parry ex Engelm (Engelmann Spruce). P. engelmannii is native to Pikes Peak Region, considered mainly a high altitude tree growing found roughly between 900 m - 3,650 m. Tundra species, such as grasses and wildflowers during the growing season, are found between and above P. engelmannii's climate and seedling establishment boundary. The steep topography of the transect consists of boulders, divots and mounds from frost and thaw events and or spring runoff. Boulders were found at higher density scattered near the top of the transect, and lower down found in runoff channels. Many tree architectures were found through out the transect.

#### Field Methods

For simplicity, all P. engelmannii trees, saplings, and seedlings in this study are referred to as "trees." Each tree was labeled with a metal coin with an individual ID number. All trees in the transect geographic position were recorded, labeled replicating the ID number, and mapped with Trimble Pathfinder. Additional field measurements for the 206 trees include tree height, leader extension rate growth rate, diameter of tree at ground level, and assignment to an architectural type shape. If tree were below 10 cm in height, they were not recorded. Tree symmetry, percent wind damaged, percent dead needle, proximity to a rock, number of tips, and clonal confidence was accessed and recorded but were not used in this study. Height was measured in center meters (cm) on the downhill slope of the tree's tallest apical bud with a meter stick or for taller trees elongated meter stick read with binoculars; Measure to the closest .5 cm. Leader extension growth rate was measured for 2018 growth in millimeters (mm) with calipers and for the past 10 years growth in center meters (cm) with a meter stick on the tallest apical tip.

To asses architectural type shape ten tree architecture types were established based on field observation: Cone, Flag, Skirt, Stilt, Krummholtz, Krummholtz Release, Candle, Multi-tipped, Curved Trunk, and Bulb. Cones are characterized as symmetric and undamaged similar to a perfect tree. Flags must have a distinct loss of branches in at least one face. Skirts have distinct elongated bottom branches that often cause layering. Stilts are missing lower branches leaving the bottom of the tree's trunk exposed. Krummholtz have no main vertical tip with a trunk creeping along the ground forming a mat or bush shape. Krummholtz Release have the distinct shape of a Krummholtz except with a main vertical tip emerging. Candles are characterized by an elongated cone type with straight vertical growth and branches of all height showing similar diameters. Multi-Tipped have clear multiple vertical leader. Curved Trunk trees have a curved, not straight trunk. Bulbs must have a dead vertical apical bug and lower branches showing upwards growth past

horizontal. Each tree was categorized as a single type, transitioning between types, or multiple types.

#### Analysis Prep

In the field, more than 20 tree architecture types were recorded. For analysis the single types, transitioning types, and multiple types were combined into ten types. Architecture types were simplified into their dominant type. The ten architectures are: Cone, Flag, Skirt, Stilt, Krummholtz, Krummholtz Release, Candle, Multi-tipped, Curved Trunk, and Bulb. Creating the final ten architecture types improve the statically significant of analysis and results in this study.

For the analysis, the transect was split into two elevation bands: the upper zone (UZ) and lower zone (LZ). ArcGIS was used to outline and split the polygon study area (Figure 1). The transect was split by calculating the mid-point between the high and low elevations sides. The transect was split into two zones to compare spatial patterns over an elevation gradient. With the separation between two zones analysis will be able to find what architectures are found at specific elevations.

#### SPSS Analysis

Using the statistical program SPSS each architecture type and their differing height, growth rates (past ten year growth and 2018 growth), and width to height ratio was explored. Height, growth rates, and ground cover were compared between types through running a one-way anova comparing means, to determine whether there are any statistically significant differences between the architectures. Test of Homogeneity of Variance and Robust Test of Equality of Means were run as well. Tukey's Post Hoc multiple comparisons was chosen and run to confirm which architectures differ. Mean plots were produced comparing architecture types. This procedure was run to compare width and height ratios between architecture types as well.

To further analysis differing height and growth rates between architectures a regression curve estimation procedure was used. Statistics produced from the regression curve estimation procedure include regression coefficients, multiple R,  $R^2$ , adjusted  $R^2$ , standard error of the estimate, analysis-of-variance table, predicted values, residuals, and prediction intervals. Models: linear, logarithmic, inverse, quadratic, cubic, power, compound, S-curve, logistic, growth, and exponential statics for each model (IBM). The produced model summary and parameter estimates are of specific interest for this analysis. The  $R^2$  value is key to understand the model of best fit, either linear function, saturating (logarithmic) function or exponential (power) function. The function that the

relationship between growth rate and height is categorized as indicates if other factors are at play.

#### Pearson's Chi-Squared Analysis

The spatial distribution patterns of tree architecture location was analyzed using Pearson's Chi-Squared Test ( $\chi^2$ ), a statistical test applied to evaluate how likely an observed difference between sets of categorical data arise by chance. A Chi-Squared calculator was used to compare observed and expected frequencies between architecture types and their distribution in the Upper Zone and Lower Zone of the transect with GraphPad, a Chi-Squared calculator. These calculations will access whether architecture type distributions in the Upper Zone and Lower Zone are distributed significantly different or as expected by random in each zone. There is a possibility that the Upper Zone will influence the growth of specific architectures while the Lower Zone has mechanism that inhibit growth of specific architecture types. Pearson's Chi-Squared Test will address the overall distribution of the ten architecture types found at this diffuse site between the Upper and Lower Zone.

### Multi-Distance Spatial Cluster Analysis (Ripley's K Function) in ArcGIS

The spatial distribution of tree architecture location was examined using Ripley's K Function, a point pattern analysis that identifies clustered, random, and or dispersed

distributions at multiple spatial scales for a given study area. ArcGIS, a geographic information system was used to run Ripley's K analysis. ArcGis calculated L(d), a transformation of the K Function, to create a visual representation of the data (ArcGIS Pro, 2018). The L(d) function is as given

$$L(d) = \sqrt{\frac{A\sum\limits_{i=1}^{n}\sum\limits_{j=1,j\neq i}^{n}k(i,j)}{\pi n(n-1)}}$$

Where d is the distance, n is equal to the number of features, A represents the total area of the features, and K<sub>i,j</sub> is a weight (ArcGIS Pro, 2018). The number of distance bands is 10, to compute distance increments. It is important to have appropriate scales of analysis for point pattern analysis, the multiple distances because patterns can change due to the scale. Ripley's K - Function in ArcGIS is able to produce tables expected K and observed K. When the observed K value is larger then the expect K value for a particular distance, the distribution is more clustered than random at that distance band (ArcGIS Pro, 2018). When the observed K value is smaller then the expect K value for a particular distance, the distribution is more dispersed than random at that distance band (ArcGIS Pro, 2018). Confidence intervals were produced when calculating L(d) with 99 permutations, establishing a 99 percent confidence envelope for each architecture. This created low and high confidence envelope. When the observed K is larger then the high

confidence envelope spatial clustering is statistically significant for that distance (ArcGIS Pro, 2018). Inversely when the observed K is smaller than the low confidence envelope spatial dispersion is statistically significant for that distance (ArcGIS Pro, 2019). Ripley's K will examine how clustering or dispersion of individual tree architectures change at different scale.

#### Nearest Neighbor (G-Function) in R

Spatstat is a comprehensive open source package that can be installed in R, a software environment for statistical computing and graphics to run spatial point pattern analysis, modeling fitting, simulations, and tests (CRAN, 2019). Spatstat's exploratory methods, specifically the Nearest Neighbor G-Function with confidence envelopes were used in analysis. Data was imported to R from ArcGIS, turning the data file into point

pattern file. The R code consisted of:

> T <- read\_csv("DateSheets/CorrectFormat/AllTreesCorType.csv",

- + col\_types = cols(TypeC = col\_factor(levels = c("A",
- + "B", "C", "D", "E", "F", "G", "H",
- + "I", "J"))))

> P<-owin(poly = list(x=c(492162.094, 492144.367, 492135.795, 492122.354, 492118.385, 492118.385, 492106.915, 492099.044, 492095.472, 492116.546, 492123.419, 492129.709, 492147.225, 492159.713, 492165.798, 492172.307, 492145.425, 492149.923, 492160.454, 492161.734), y=c(4301246.028, 4301257.458, 4301240.101, 4301248.092, 4301233.592, 4301233.645, 4301257.319, 4301253.449, 4301242.707, 4301217.810, 4301209.970, 4301202.975, 4301183.269, 4301175.384, 4301188.084, 4301192.529, 4301222.586, 4301232.164, 4301235.656, 4301243.749))))</p>

<sup>&</sup>gt; library(spatstat)

> AllT<-ppp(T\$X, T\$Y, window=P, marks=T\$TypeC)

To examine spatial distribution patterns of tree architecture location between all architecture types Nearest Neighbor G Function was used. The Nearest Neighbor G Function is a classical distance method technique for investigating inter-point interactions. The distance from each point is measured to its nearest neighbor. The equation is:  $t_i = \min_{j \models i} ||x_i - x_{ij}||(123)$ . Since our point process data is stationary the cumulative distribution function is :  $G(r) = P\{d(u, X \setminus [u] \le r \mid u \in X\}$  (Baddeley, 2010). Where *u* is an arbitrary location,  $(d(u, X \setminus [u])$  is the shortest distance from the point pattern X, excluding *u* (Baddeley, 2010). Clustered, random, and dispersed distributions were examined at multiple spatial scales for all architecture type with one another. The R code consisted of:

> plot(alltypes(AllT, "G"))

To examine the significance of the G-Function plots, confidence envelopes containing the theoretical value of the function, the simulated lower and upper expect G value were produced from the 39 CSR simulations (Baddeley, 2010). If the observed data is above then envelope then the data is clustered, if the observed data is in the envelope then the data is homogenous/uniform, and if the observed data is below the envelope then the data is randomly dispersed (Baddeley, 2010). The R code consisted of: > aE <- alltypes(AllT, Gcross, nsim = 39, envelope = TRUE)> plot(aE)

#### RESULTS

#### SPSS Analysis

Running a one-way anova in SPSS to compare architecture's mean height and mean growth rates proved significant. Figure 2 summaries these results, exemplifying the different heights and growth rates found in the architecture types (Figure 2). Krummholtz and Skirts architectures were on opposite ranges of height, Krummholz having the lowest minimum height of 10.00 cm and Skirts having the largest maximum height of 563.00 cm. While Curved Trunks and Cones were on the opposite ranges of past ten years growth, Curved Trunks having the lowest minimum past ten years growth of 7.00 cm and Cones having the largest maximum growth rate of 193.00 cm. Krummholz and Skirt architecture are also on opposite ranges of 2018 growth rates, with Krummholz having the lowest minimum 2018 growth rate of 7.29 mm and Skirts has the largest maximum 2018 growth rate of 245.00 mm.

Skirts not only have the largest mean height of 153.3 cm but also the largest maximum height of 533 cm, largest maximum 2018 growth rate of 245 mm, and second largest past ten years growth rate of 151.6 cm. While Krummholz almost inversely have the lowest mean height of 41.28 cm but also lowest minimum height of 10 cm and the lowest minimum 2018 growth rate of 7.29 mm. It seems that tree architectures that grew poorly in 2018 constantly grew at slower rates than other architectures over the past ten years, such as Flags, Krummholz, and Bulbs (Figure 2). Flags had a mean 2018 growth rate of 35.51 mm and a mean past ten years growth rate of 23.99cm. Krummholz has a mean 2018 growth rate of 37.45 mm and a mean past ten years growth rate of 30.26 cm. Bulbs had a mean 2018 growth rate of 32.37 mm and a mean past ten years growth of 20.82 cm. While Cones and Skirts grew over 73 mm in 2018 and 66 cm in the past ten years, almost doubling the growth of Flags, Krummholz, and Bulbs. Taller tree 5 cm architectures have faster mean rates of growth, however Stilts is an outlier having the second shortest mean height of 59.9 cm and over the past ten year it has had the largest mean growth rate of 59.701 cm (Figure 2).

To continue to explore architecture's height to growth rate relationships curve estimations were run for the data (Figure 3, Figure 4, Figure 5, and Figure 6). Tree architecture's height to 2018 growth functions found that Cones, Flags, Krummholz Release, Multi-Tipped, and Curved Trunk trees had significant results (Figure 3). Cones, Flags, Silts, Krummholz Release, and Multi-Tipped trees data best fits linear regression relationship function, where height directly affects growth rate (Figure 3 & Figure 4). While Skirts and Curved Trunked tree data best fits a power regression relationship function, where there is another mechanism affecting growth rate beside height (Figure 3 & Figure 3).

Tree architecture's height to past ten years growth ratio functions found that Cones, Flags, Skirts, Krummholz, Krummholz Release, Candles, Multi-Tipped, Curve Trunks, and Bulb trees had significant results (Figure 5). Cones, Stilts, and Krummholz Release best fit a linear regression relationship function (Figure 5 & Figure 6). Flags, Skirts, Krummholz, Candles, Multi-Tipped, and Curved Trunk trees all best fit a power regression relationship function, where there is another mechanism affecting growth rate besides height (Figure 5 & Figure 6). While Bulbs have a logarithmic relationship function, where there is another mechanism controlling growth rate besides height (Figure 5 & Figure 6).

### Pearson's Chi-Squared Analysis

In comparing the architecture type distribution between the Upper Zone and the Lower Zone, several types were distributed significantly differently from random. Means

that Flags, Candles, Cones, Krummholz, Krummholz Release, Multi-Tipped, and Stilt architectures where located in one zone significantly more than the other (Figure 7). Flags with a  $X^2$ =14.4, were overrepresented in the Lower Zone and underrepresented in the Upper Zone (Figure 7). Candles with a  $X^2=12.322$  were Multi-Tipped with a  $X^2=12.322$ 10.497 overrepresented in the Lower Zone and underrepresented in the Upper Zone (Figure 7). Cones with a  $X^2 = 4.733$  were overrepresented in the Upper Zone and underrepresented in the Lower Zone. Krummholz with a  $X^2 = 14.084$  where overrepresented in the Upper Zone and underrepresented in the Lower Zone (Figure 7). Krummholz Release with a  $X^2=7.203$  were overrepresented in the Upper Zone and underrepresented in the Lower Zone (Figure 7). Stilts with a  $X^2$ =4.572 where overrepresented in the Upper Zone and underrepresented in the Lower Zone (Figure 7). Flags, Krummholz, and Candles had the highest  $X^2$  meaning the most significant different distribution in each zone.

On the other hand, comparing the architecture type distribution between the Upper Zone and the Lower Zone, several types were evenly distributed in each zone as expected by random. Bulbs with a  $X^2=0.816$  was evenly represented in both zones (Figure 7). Curved Trunks with a  $X^2=1.348$  was evenly represented in both zones (Figure 7). Skirts with a  $X^2=0.176$  was evenly represented in both zones (Figure 7). Even

though the p-values for Curved Trunk and Skirts architectures due to the small sample size the raw data shows significant. Twelve Skirts were found in the Lower Zone and eleven Skirts were found in the Upper Zone.

To visualize this data and understand the tree architectures spatial distribution R was used to plot density for each architecture in the polygon study site (Figure 8). The relative proportions (proportions of density intensity), calculated as desnit on a locale scale  $(\#/m^2)$  divided by average density for the whole plot  $(\#/m^2)$ , were plotted as well. Cones, Krummholz, Krummholz Release, and Bulbs had highest relative proportions of intensity at the highest elevation in the transect (Figure 8). However Krummholz density peaked below that of Krummholz Release and Cones(Figure 8). Cones are primarily located and over distributed in the Upper Zone, like the  $X^2$  analysis said (Figure 7 & 8). Flags and Stilts have similar elevation density peaks as well as proportions of intensity on the lower west elevations of the transect, seeming to be primarily located and over distributed in the Lower Zone (Figure 8). Skirts density and proportion of intensity peaks mid elevation in the transect, seeming to primarily be evenly distributed in the transect (Figure 8). The visualization of tree architecture location data in the transect can help explain how microclimates correlate with tree architecture location.

Multi-Distance Spatial Cluster Analysis (Ripley's K Function) in ArcGIS

Ripley's K Function was used to excess whether individual architectural types clustered together or avoiding each other, a major advantage of using Ripley's K is that it uncovers scale dependency of patters (Figure, 9). For example at small scales clustering can occur but at larger scales distribution is uniform. Cones were found to be clustered at small and medium scale while their random at large scales. Flags were clustered at all scales (Figure 9). Skirts were clustered at small scale, random at medium scales, and dispersed at large scales (Figure 9). Multi-Tipped trees were clustered at small scales, random at medium and large scales (Figure 9). Krummholz, Krummholz Release and Candles were dispersed at small scale and distributed randomly at medium and large scales (Figure 9). Bulbs were random at small and medium scales and dispersed at large scales (Figure 9). Stilts were clustered at small scales, lightly clustered at medium scales, and random at large scales (Figure 9). When analysis singly Cones and Flags show the strongest clustering distribution at all scales (Figure 9). While Skirts, Multi-Tipped, and Stilts showed clustering at small scales (Figure 9). Most architectures at large scale were found in the confidence envelopes meaning they were randomly distributed in relationship to their like architectures (Figure 9).

# G-Function Nearest Neighbor

The Nearest Neighbor G-Function allows use to see if two different architecture types co-occur with others or spatially avoided others. Nearest Neighbor G-Function in R was used to run pairwise comparisons between architecture types (Figure 10). Cones once again are cluster with themselves. Cones and Skirts architectures on medium and larges scales were randomly disturbed with each other (Figure 10). While Flags and Skirts were clustered at all scales with one another (Figure 10). Flags and Multi-Tipped architectures are clustered at mediums scales (Figure 10). Flags and Skirts are randomly distributed with each other (Figure 10). Flags and Skirts are randomly distributed with each other (Figure 10). The G Function however found that most architecture types were uniformly distributed in relationship to other architectures in the polygon (Figure 10. Meaning distributions patterns may not be as significant as anticipated.

# DICUSSION

In this analysis, tree architecture forms and their spatial distribution was used to improve the current understanding of the relationship between treeline movement and climate change. The merging of studying treelines as whole populations and as individual trees is a critical part of understanding the relationship between treeline movement and climate change. In the following discussion, this research will first consider how differing tree architectures are formed at treeline, then where these architectures were found and what spatial patterns of tree architecture suggest about past and current climatic conditions.

# Tree Architecture Formation

The ten types of tree architecture under examination are Cone, Flag, Skirt, Stilt, Krummholz, Krummholz Release, Candle, Multi-tipped, Curved Trunk, and Bulb. It was found that the smallest architectures in height: Flags, Stilts, Krummholz, and Bulbs had the lowest growth rates as well (Figure 2). These four architectures are shaped through environmental stressors. Wind abrasion forms flagged shapes trees with a distinct loss of growth on the downslope side of the tree (Scott et. al., 1993). Stilts architecture forms through snowpack melting in the spring at rates that is conducive to producing pathogenic (snow) fungus on the snow covered bottom of the tree. This pathogenic (snow) fungus leads to the loss of branches and needles. Krummholz are formed through equal growth and dieback rates (Hadley & Smith 1986). Flags, Stilts, Krummholz, and Bulbs have environmental mechanisms inhibiting height and growth rate. While Cones and Krummholz Releases can be assumed to be shaped through limited environmental stressors due to a given change in height causing growth rate to produce a corresponding change (Figure 3).

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# Tree Architecture Distribution

If particular architectures are formed through a lack or intensity of environmental stressor, then the spatial distribution of architectures should follow climatic conditions. Before this papers analysis, it was believed that as distance from the continuous forest increases environmental stressors should increase due to a tree's proximity to its upper climatic boundary. It was anticipated that architectures would cluster with architectures with similar growth and dieback mechanisms and architectures would avoid architectures with different growth and dieback mechanisms.

Therefore we should see Cones and Krummholz in different regions and elevations of the transect. However Cones and Krummholz density and proportion of intensity, both peaked at the highest elevations in the transect (Figure 8). Cones and Krummholz were located next to each other maintaining their starkly different architectures. Cones have a height to base ratio of 1.7101 and Krummholz are on the opposite side of the scale have a height to base ratio of 0.7609 (Figure 2). Cones almost double the growth rate of a Krummholz growing 73.398 mm in 2018 compared to 37.4513(Figure 2). How can such extremely different architectures live in such close proximity with each other?

### Climatic Conditions

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If Krummholz are formed and controlled by dieback and Cones through height in perspective to growth rate, then climatic conditions at treeline may not be as anticipated. It was anticipated that if the distance from the continuous forest increased, environmental stressors would increase linearly. After analysis it was clear that climatic conditions and environmental stressors did not increase as distance from the continuous forest increased. Cone architectures are formed through little to no environmental stress was found at the highest elevations in the transect (Figure 7 & Figure 8). If Cones are able to keep their form at higher elevations, it can be assumed that outside climatic conditions are no longer inhibiting growth rates of trees at that elevation. This change in climatic conditions can be explained through the advancing upper climatic boundary at the study site (Elwood, 2012).

The upper climatic boundary is defined as the harshest environment possible for successful establishment of tree species. Harsh environmental conditions usually lead to facilitation among tree populations (Callaway et. al., 2002). Facilitation is seen through tree clustering near the upper climatic boundary, providing protection through shading from open sky, thermal insulation, moisture retention, and wind protection, as well as improving nutrient availability, soil geology, and other microsite characteristics that improve tree establishment (Smith et al., 2003; Germino et al., 2002; Maher & Germino, 2006; Körner 1998). However, tree clustering is only beneficial when facilitation compensates for the competition between trees (Callaway et. al., 2002). Trees in clusters generally grow slower than their separated counter parts (Robert, 2010). If clustering no longer occurs at an elevation it once did, it is believed that the climatic boundary has moved and the climate at that elevation has become milder.

To monitor the advancement of the upper climatic boundary researchers have studied treeline's edge typology. The treeline at this study site has transitioned from a cluster edge prior to 1940, to a mix of clusters at lower elevations and a randomly distributed edge at higher elevations from 1941-1977, to a randomly distributed edge in 1977 (Elwood, 2012). Here we see that facilitation through clustering is no longer beneficial due to changing climatic conditions. This advancing climatic boundary at our study site can explain why Cones are able to grow at high elevations next to Krummholz. The environment is suitable to establish and maintain Cone architecture. Why are Krummholz maintaining their architecture with a milder climate?

#### Physiological Feedbacks

It was found that most architecture types were randomly distributed in relation to other architecture types (Figure 9 and Figure 11). If these architecture types are randomly distributed, it can be interpreted that climatic conditions are not controlling distribution at this time. If climatic conditions were controlling distribution, for example, we would find stressed architecture types to cluster with one another and avoid non-stressed architecture types. Climatic condition across elevations in the transect seem to be suitable for most architecture types.

If the climate is suitable for Krummholz to live next to Cones, some mechanisms must be enforcing the Krummholz architecture. The Krummholz are still maintaining their shape due to internal feedback loops, causing a lag in response to the moving upper climatic boundary. The ability for trees to adapt to the advancing climatic boundary depends on the architectures formation.

The lack of reaction from Krummholz architectures to an advancing upper climatic boundary can be an example of path dependency, a concept that emphasizes selfreinforcing mechanisms that lead to a narrowing scope of capable actions (Schreyogg & Sydow, 2011), in this case tree architecture release. There are two phases: the Preformation Phase and the Formation Phase. The Preformation Phase is defined when actions and choices cannot be predicted but are influenced by prior events of initial conditions (Schreyogg & Sydow, 2011). The Formation Phase where a dominant action pattern begins and starts a dynamic self-reinforcement process, slowly renders the process more difficult to reverse (Schreyogg & Sydow, 2011). This process can be equated with the phenomenon of imprinting which states that organizations formed at a particular time must contrast themselves with the present resources and systems in place (Stinchcombe, 1965). This process of path dependency can be explained through an architectures stable state.

The path dependency hypothesis also suggest that there are multiple and alternative stable states (Tekwa et. al., 2018). For example, why are some Krummholz releasing and others are not. This can be analyzed by looking at the best-fit regression curve for each architecture's growth rate and height (Figure 4 & 6). Every tree is controlled by its growth rate (biomass gain) and attrition (biomass loss). When examining the best-fit regression graphs, attrition is takes place. When the equation for attrition and growth crosses a stable state is formed. If the equation for growth is curved this allows attrition and growth to cross multiple times creating multiple equilibriums. Forming a first a repeller than an attractor. For example, Krummholz architectures may be stuck at a repeller causing the inability for architecture to change. Some Krummholz are able to release due to specific needs being meet allowing them to surpass the repeller towards an attracter. Age may be a factor in transitioning to another stable state. For example,

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younger Krummholz found at higher elevations than older are able to release due, to their plasticity from a shortened Formation Phase.

Research has tested, that the age of branches and needles have different resistance to wind abrasion. Needles of the same age also have different resistance to removal, which reflects the history of the tree, including crown formation and branch age (Scott et. al., 1993). New needles on a new branch are initially susceptible to abrasion, but over the course of eight years resilience builds (Scott et. al., 1993). However, after those eight years, branches become more susceptible to needle loss (Scott et. al., 1993). This causes a window of seven to eight years where a tree/shoot must grow 80cm to escape the abrasion snow (Scott et. al., 1993). Escaping this abrasion zone, new branches that develop have a lower change of needle abrasion (Scott et. al., 1993). Here we see the age of the tree affecting the ability of Flag trees to transition to another stable state.

#### CONCLUSION

Tree typology is important in understanding the function of the ecotone. However, typology perspective research commonly assumes all ecotones are made up of uniform tree architectures. Although tree architectures have been studied, they are typically only studied at an individual tree level. This individual level does not to acknowledge that multiple tree architectures with in a treeline and how they are distributed in space. This paper merges treeline population research with individual tree physiology level research to form a unique understanding on climate change is controlling treeline advancement.

Our study site did not contain individual trees with homogenous architectures throughout the treeline transect. The implicit assumption that treeline typologies contain single architecture is proven false at this diffuse treeline due to ten architecture types categorized after consolidation. Treelines contain a mixture of tree architectures. The distinct architectures found along the treeline can depict current and past climatic condition due their spatial distributions and mechanisms that control their form.

Overall, the distribution of architecture types were random, even with significant differences in height and growth rates between architectures. This random distribution of architecture implies that climatic conditions are not longer inhibiting specific architecture growth. The climate at this study site is transitioning from a harsh to mild causing architectures formed mild climate to establish next to older architectures formed from a harsher climate. Past climatic conditions at this site were harsher causing the development of Krummholz and a clustered treeline edge. Present climatic conditions are suitable for a randomly distributed treeline edge and for Cone architecture to live at higher elevation. These transitions signify the upward migration of the upper climatic boundary. Both the transition from a clustered and Krummholz edge to a randomly dispersed and Cone edge, expresses that the climatic boundary is moving too fast for seedling establishment and architecture release. Tree architectures spatial distributes are transitioning to a more random patterns due to decrease climatic constrains on younger trees.

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# APPENDIX



**Figure 1**. Aerial orthomosaic of the diffuse polygon transect site constructed with Drone2Map through photogrammetric analysis of drone-captured images. The mutli-tipped end of the transect is downslope of the higher elevations tail end of the transect.



**Figure 2.** Each graph visualizes the average mean of height, 2018 growth, past ten years growth, and the height to base ratio in each tree architecture. Architecture types are found on the x-axis: 1= Cones, 2= Flags, 3= Skirts, 4= Stilts, 5=Krummholz, 6= Krummholz Release, 7= Candles, 8= Multi-Tipped, 9= Curved Trunk, and 10= Bulbs.

Architecture	Cone	Flag	Skirt	Stilt	Krum.	Krum Candle		Multi.	Curved.	Bulb
						Rel.				
Equation	Linear	Linear	Power	Linear	Power	Linear	Logarithmic	Linear	Power	Power
R <sup>2</sup>	.555	.689	.438	.373	.176	.724	.731	.400	.447	.444
Sig.	.000	.000	.001	.145	.120	.015	.065	.000	.012	.071

**Figure 3:** Results from SPSS 2018 growth rate to height functions. The most accurate equation, either Linear, Power, or Logarithmic for each architecture types, has an  $R^2$  value closest to 1 measures how close the data is to the fitted regression line. The  $R^2$  values for equations are only significant if its significant figure is below 0.05.





**Figure 4.** Results from SPSS curve estimation regressions for architecture types 2018 growth rate. There is no curve estimation regression for the Candle architecture type because the results were not significant.

Architecture	Cone	Flag	Skirt	Stilt	Krum.	Krum	Candle	Multi.	Curved.	Bulb
						Rel.				
Equation	Power	Power	Power	Linear	Power	Linear	Power	Power	Power	Logarithmic
R <sup>2</sup>	.752	.373	.366	.001	.580	.817	.953	.694	.445	.752
Sig.	.000	.00	.003	.943	.001	.005	.004	.000	.009	.002

**Figure 5.** Results from SPSS past ten years growth rate to height functions. The most accurate equation, either Linear, Power, or Logarithmic for each architecture types, has an  $R^2$  value closest to 1 measures how close the data is to the fitted regression line. The  $R^2$  values for equations are only significant if its significant figure is below 0.05.





Figure 6. Results from SPSS 2018 growth rate to height functions. The most accurate equation, either Linear, Power, or Logarithmic for each architecture types, has an  $R^2$  value closest to 1 measures how close the data is to the fitted regression line. The  $R^2$  values for equations are only significant figure is below 0.05.

Architecture	Cone	Flag	Skirt	Stilt	Krum	Krum	Candle	Multi	Curved	Bulb
						Rel.		Tipped	Trunk	
Chi- X <sup>2</sup>	4.7330	14.400	0.1760	4.5720	14.084	7.2030	12.322	10.497	1.3480	0.8160
P- Value	0.0296	0.0001	0.6752	0.0325	0.0002	0.0073	0.0004	0.0012	0.2456	0.0004
Degrees of	1	1	1	1	1	1	1	1	1	1
Freedom										





**Figure 8.** Results from R Density and Proportions of Intensity plots. The Y shaped polygon is oriented with the tail being higher in elevation and the arms reaching down slope to lower elevations in the bowl. Yellow, warm tones represent high density and high proportions of intensity, while the cooler tones mark a decreased in density as well as proportion of intensity. Architecture types are found above each individual plot: A= Cones, B= Flags, C= Skirts, D= Stilts, E=Krummholz, F= Krummholz Release, G= Candles, H= Multi-Tipped, I= Curved Trunk, and J= Bulbs.







**Figure 9.** Result from Ripley's K Function in ArcGIS. If K observed is above the envelopes the data is cluster at that distance band. If K observed is in the envelopes the data is randomly distributed at that distance band. If K observed is below the envelopes the data is dispersed uniformly at that distance band.



**Figure 10.** Results from running the Nearest Neighbor G-Function for multiple comparisons between architectures. Architecture types are labeled as: A= Cones, B= Flags, C= Skirts, D= Stilts, E=Krummholz, F= Krummholz Release, G= Candles, H= Multi-Tipped, I= Curved Trunk, and J= Bulbs. The solid black line represents the isotropic correction estimation of the G function.

The red dotted line represents the translation-correction estimation of the G function. The green dotted line represent the border-correction estimation of the G function. The blue dotted line represents the theoretical Poisson of the G function.



**Figure 11.** Results from running the Nearest Neighbor G-Function for multiple comparisons between architectures with confidence envelopes. Architecture types are labeled as: A= Cones,

B= Flags, C= Skirts, D= Stilts, E=Krummholz, F= Krummholz Release, G= Candles, H= Multi-Tipped, I= Curved Trunk, and J= Bulbs. The solid black line represents the isotropic correction estimation of the G function. The red dotted line represents the theoretical Poisson of the G function. The shaded regions of the graphs represent their confidence envelopes. If the isotropic correction estimation is above the envelopes the data is cluster at that distance band. If isotropic correction estimation is in the envelopes the data is randomly distributed at that distance band. If isotropic correction estimation is below the envelopes the data is dispersed uniformly at that distance band.