SPATIAL STRUCTURE OF TREELINE ON PIKES PEAK

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Abstract

Spatial structure of alpine treeline plays a key role in its response to climate change, yet the processes that are responsible for creating that structure are poorly understood. Here, we describe a treeline on the west side of Pikes Peak with different tools to gain insight of the structure at a local scale and to investigate the potential endogenous mechanisms that appear to influence it. We hypothesized that the trees will be clustered in the system through positive intraspecific interactions and that the treeline is a potential phase transition system with classical criticality. With the classical description of treeline structure, we divided the zone into different sections of increasing elevation range with the assumption that the mechanisms driving the structure of each are the same, and ran Ripley's K function for cluster analyses. Ripley's K function showed significant tree clustering through the sections in the study area, especially between the elevation of 3600m and 3680m. Clustering among large-sized trees were significant across the entire treeline. To examine the potential of the treeline as phase transitions, which allows us to treat the system as continuous rather than in sections, we analyzed presence of fractal structure in the treeline. Analysis of the spatial structure reveals significant fractal geometry in size classes, as well as on the edges of big tree clusters which has the potential to evolve into a percolation cluster. The analyses show evidences that the system could more likely be in robust criticality rather than phase transition. This study provides insights into describing the treeline on a local scale and could contribute to the current study of treeline dynamics and treeline as a complex system.

Introduction

Treeline is an important ecotone where forests border grasslands or tundra. While the response of plant physiology to the externally imposed altitudinal climate gradient plays an important role, it also appears that tree-tree interactions are crucial in shaping the ecotone. The purpose of this study is to examine the description of the spatial structure of treeline on a local scale to draw inferences of the mechanisms driving the forms, and to explore the potential of connecting local-scale treeline description to a generalized method for global treeline structures.

Treeline studies globally focus on the cause of treeline, revealing the similarities of the formation of the ecotone. On a global scale, treelines mostly fall within a seasonal mean ground temperature of 6.7 °C with a moderate regional and taxonomic influence (Körner & Paulson 2004). Daily means of air temperature for treelines are almost the same at 6 - 7.7 °C (Körner & Paulson 2004). The relatively narrow range of temperatures at the high-altitude forest limit across taxa raised the question for a mechanistic explanation, and compelling evidences point towards a direct link between temperature and the structural growth of trees (Körner & Paulson 2004). Trees as a growth form at treeline was found to be different from dwarf shrubs which can survive and reproduce well above the treeline, because shrubs have a considerably higher daytime temperature than air achieved by decoupling from air temperature (Grace et al. 2002). However, as trees grow past their seedling stage to be taller, temperatures of their apical meristems become cooler due to the coupling to the air temperature, and the canopy shadows the soil so that it is colder by day as well (Grace et al. 2002). A microclimatological bottle-neck in the development into mature trees could exist (Grace et al. 2002). Research has suggested that the uniformity in treeline elevation with respect to temperature is likely caused by growth

limitation. As the temperature drops, photosynthetic rate decreases, and the utilization of carbon drops significantly, which limits the growth of the trees at low temperatures (Grace et al. 2002). In the troposphere, temperature generally decreases as altitude increases. The exogenous force of temperature then coincides with the altitudinal limit of tree growth, resulting in the formation of treeline, and deciding their spatial position in the mountains. In turn, the general altitudinal position of the treeline reflects the driving force, temperature, in the area. The existence of the common threshold for forest growth at high elevation thus reflect the essential mechanism of formation of treeline.

Global climate change has received increasing interest in treeline studies due to the close association between temperature and treeline position. As global temperature rises, assumptions can be made that the isotherm of the limiting temperature is higher and that trees have the potential to grow in higher elevation. In fact, change in treeline, especially densification and advancement, have been found in many places (Grace et al. 2002, Harsh et al. 2009). For example, in Khangchendzonga National Park, researchers found that there is significant densification between the treeline and timberline. While not suggesting an upslope advancement of treeline, they are anticipating a further densification due to climate change (Pandey et al. 2018). Petrov and colleagues (2015) found that larch growth is 55% higher than that of 200 years ago and the treeline is advancing about 1m/10 years in Kuznetsk Alatau alpine forest-tundra ecotone. Advancement of treeline can also be found across the Rocky Mountain Range (Elliot & Kipfmueller 2011). These studies focused on the treeline dynamics with the major concern of altitudinal change due to temperature change. Whether densification or treeline advancement, such change in the position and structure of the treeline would result in significant influence on the ecosystems. The transition in the structure of treeline will alter the ecotone itself so studying

such transition would be very beneficial. It is also important to analyze the change in the structure of the treeline with respect to climate change because of the potential loss of tundra ecosystem and further loss of habitat for the animals utilizing the tundra as treeline advances upslope to higher elevation.

Treelines in local or landscape scales exhibit great variations in spatial structure across locations, showing complexity of the treeline systems and necessity to address the questions of local scale treeline formation (Malanson et al. 2011). Studies addressing such questions have found variable factors besides temperature driving the treeline forms and treeline responses to changing climatic factors (Malanson et al. 2011), and some have contrasted the general expectation of treeline advancement. For example, although temperature in the Tibetan Plateau has shown an overall warming trend during recent decades reaching the warmest period on record during the past 1000 years, no significant advancement in treeline in response to climate warming were found for the past four decades (Cui et al. 2017). Higher tree recruitment and vertical growth were present in along the treeline ecotone, but a larger proportion of trees established in the lower half of the study area (Cui et al. 2017). Cui and colleagues (2017) suggested the importance to consider non-climatic drivers, such as slope exposure effects, to understand treeline ecotone dynamics. In northern Patagonia, researchers observed spatial and temporal instabilities in vegetation-climate relationships during two distinct periods of shifts in climate from cool-wet to warm-dry in six alpine treelines (Daniels & Veblen 2004). In the sampled treelines, relationship between krummholz radial growth and temperature variation was found to be non-linear, and climate conditions facilitating seedling establishment at high elevations were shown to be often opposite from those that enhanced radial growth. Although temperature-precipitation interactions resulted in variability, moisture availability seemed to be

the dominant climatic factor influencing seedling establishment in the sampled treelines. These findings have demonstrated the complexity of treeline dynamics in the northern Patagonia under the changing climate, and the conclusion was made that the directional increase in temperature will not necessarily result in an upslope movement of the treeline (Daniels and Veblen 2004). Mixed responses to climate warming of treelines have been found globally (Harsch et al. 2009). The variation and complexity of treelines world-wide are very important to understand treeline dynamics further, and addressing the question of treeline in different spatial and temporal scales is essential (Malanson et al. 2011).

Description of treeline forms and structures is critical to the study of the treeline as they imply the underlying mechanisms of treeline formation and dynamics, whether globally or locally. Four basic forms of treeline that have been identified are abrupt, diffuse, island and krummholz, and studies have suggested different forms respond differently to climate change due to the varying underlying mechanisms (Harsch & Bader 2011). Although no consensus has been reached for the mechanisms responsible for structuring each form, growth limitation, seedling mortality, and die back were suggested as primary mechanisms resulting in the structural differences (Harsch & Bader 2011). Many studies focused on how the categorized forms respond to climate change and how the mechanisms that are hypothesized to be responsible for their spatial structure differ between the different treeline forms. Of all the treeline forms, diffuse treelines were mostly suggested to be controlled by growth limitation, and to show most potential for advancing in response to climate change (Harsch et al. 2009). In contrast, abrupt or krummholz treelines may be more strongly influenced by stress factors, controlled by seedling mortality and dieback, and exhibit strong time lags but potential rapid shifts in treeline positions in response to temperature increase (Harsch et al. 2009, Harsch &

Bader 2011). Comparisons among treeline forms have been made on a more local scale controlling large variations in climate. Among three sites in Italian Alps and northern Apennines, two diffuse treelines and one abrupt treeline were studied, where contrasting responses to climate fluctuations were found in the sites, with only one diffuse treeline showing advancing dynamics (Compostella & Caccianiga 2017). Furthermore, although some studies have supported hypothesis for treeline dynamics, contradictory signs have also been found. Treml and Veblen (2017) used tree-ring chronologies and showed that krummholz treelines are potentially limited by temperature-limited tree growth while for diffuse treeline it is more important to consider their population dynamics and not temperature-limited radial growth. These studies demonstrate the advantages of categorizing treeline forms, as different forms usually have different mechanisms and responses to changing factors. However, the studies also show the limitation of such categorization of treeline structures, as the descriptions are qualitative and variations of the mechanisms driving each form and responses of each form are still distinct across locations. It is necessary to further examine the local scale forms with different tools and to further inspect the underlying mechanisms.

Important mechanisms that create different treeline forms are biotic factors including neighboring effect from inter- and intra- specific interactions. Two major neighboring effects are facilitation and competition, where facilitation creates cluster patterns and competition creates over-dispersed patterns. Several recent studies report significant tree clustering at the treeline across different study sites (Lingua et al. 2008, Cui et al. 2017, Harsch & Bader 2011). In central Alps, all tree species and age classes in the study area showed clumped structure, while the clustering tendency was more evident at the treeline in the plots where the environmental conditions are more severe (Lingua et al. 2008). The facilitation of tree seedling establishment in

stressful environment was also found in the Tibetan Plateau, where aggregated spatial patterns provide a positive feedback in ameliorating the harsh environment (Cui et al. 2017). The biotic interactions for treelines not only create patterns and forms, but can also contribute to treeline dynamics on the edge, shifting the rate of change for treeline position. Loranger and colleagues (2017) suggested that alpine grassland plays different roles of facilitator and competitor during different times with a net negative outcome after one year, maintaining treeline position by negatively influencing establishment. Evidences also showed densification of shrubs in Tibetan Plateau slowed the advancement of treeline (Liang et al. 2016). In Montana, contradicting result where intraspecific interactions increasing the speed of treeline advancement in some parts has been found (Bekker 2005). Feedback between existing trees and the establishment and survival of seedlings has shown to allow forest advancement in a linear pattern, with finger-like strips due to the ameliorated environment by existing trees (Bekker 2005). Although complicated, the biotic interactions in the treeline ecosystem play an important role in shaping the structure and position of treeline ecotones, with a possible tendency in facilitative growth pattern of clustering commonly shown in harsh environment.

Besides the many existing methods of describing treeline, recent studies have suggested the application of phase transition theory in ecotones (Naito et al. 2014, Milne et al. 1996), which could be applicable in treeline system to provide us with much potential in understanding the system. Phase transition comes out of classical criticality, which describes sudden changes in the state of the system when underlying processes change slightly (Pascual & Guichard 2005), hence we can use the phase transition theory to understand the shift from forest (state 1) to tundra (state 2), including how abrupt the transition is and the mechanisms that generate patterns at the very edge of that transition. Zeng and Malanson (2006) explored the concept of applying phase transition on alpine treeline by modeling it with cellular automata model, and the treeline exhibited phase transition patterns. Empirical evidences of phase transition have been found in other ecotones, such as patterns of shrub expansion in Alaskan arctic river corridors (Naito et al. 2014) and piñon-juniper woodland to grassland ecotones in south-western USA (Milne 1996). The concepts and studies are encouraging evidences that treeline could be described as a system of phase transition from forest to grassland, driving by factors such as slope, elevation or temperature change from climatic warming.

Ecological phase transition is based on percolation process and is described by fractal analysis (Naito et al. 2014, Pascual & Guichard 2005). One important part of percolation theory is connectivity, describing how patches are formed starting at a given site and adding neighboring sites, and connected to occupy the space as the same species or state (Pascual & Guichard 2005). Such connectivity is important to capture as it is an integral part of the phase transition. When percolation point is reached where the system is entirely connected, we could potentially predict a critical transition. In the case of treeline, the transition of tundra to forests would start with single trees, forming tree clusters, and the clusters connect with each other as they grow, potentially forming a large cluster across the entire system, resulting in a probable change of state. Evidences for phase transition lie in the structure of patches, which should display fractal geometry. Fractal geometry describes patterns that are self-similar at all scales, and has the potential to provide us with a new way to understand and analyze complex natural spatial structure (Li 2000, Sugihara & May 1990). The self-similarity, or scale invariance, is described by a power law distribution (Pascual & Guichard 2005). In the case of the phase transition, such power law distribution is found in the frequency distribution of patch sizes, as well as the edges of percolation clusters (Li 2000, Pascual & Guichard 2005, Sugihara & May

1990). If such fractal geometry was found in the treeline system, it will provide us with a completely different way of understanding the structure of treeline, and the underlying mechanisms driving the patterns.

Descriptions of treeline structure are essential for understanding the underlying mechanisms and the goal of this study is to describe a local scale treeline. Although there have been efforts describing treeline structures using classical clustered-random-overdispersed trichotomy, none have used fractal geometry/critical transitions tools for such description, and there has not been empirical analysis that asks whether a treeline can be approached as a phase transition. This study aims to fill the gap by exploring the tools to describe treeline structure on a local scale, on the west side of Pikes Peak, and to gain insight of the treeline dynamics. Specifically, we tested the structure of treeline by looking at the classical clustered-randomoverdispersed pattern and fractal structure of phase transitions. Treeline on the west side of Pikes Peak is consisted of single species Engelmann spruce Picea engelmannii, transition into tundra ecosystem. The climatic environment is harsh with low temperatures throughout the year, short growing season and extensive snow and wind. Due to the difficulty of survival at such elevation, we hypothesized that the trees will be clustered through intraspecific facilitation from established trees, by providing ameliorated environment for recruitment and establishment of seedlings. With the patch structure of trees in the treeline, we also hypothesized that the treeline will exhibit fractal geometry for frequency size distribution and the edges of clusters, as it is a potential phase transition system of forest into tundra. The structure of the treeline could be pushed by climate warming.

Methods

Study Area

The study took place on the west slope of Pikes Peak treeline, Teller County, Colorado. The study area is 390 m long along the slope and 215 m wide across the slope with an elevation gain of 170 m from 3580 m – 3750 m. The treeline can be qualitatively described as diffuse treeline with decreasing density along the elevation gradient. It is consisted of single species stand of Engelmann spruce *Picea engelmannii*).

Drone Methodology

DJI Phantom 3 advanced is used for image collection and Map Pilot was used as the control software. The flight path used was lawnmower-like, with individual passes being perpendicular to the slope. The mission was flown at the height of 30m above surface using terrain aware following the slope of the mountain. Four batteries were used with the total of one hour of flight time. The images captured have 88% overlap.

The images were processed with Drone2Map, with ground control points deployed before the flight. The exact GPS location of the ground control points were taken with Trimble GPS, and were later differentially corrected (63% of the readings had accuracy better than 10 cm, and 95% better than 1m). The ground control points were used by the Drone2Map software to correct the errors in the software output. A 3D sparse point cloud and a dense point cloud were generated. The point clouds were then processed into an orthomosaic of the surface, a digital surface model and a digital terrain model.

GIS

All GIS work was done in ArcMap 10.6. The trees were extracted initially by subtracting the digital terrain model by the digital surface model. A classification was conducted only

including trees over 15cm tall as trees being considered to ensure accuracy. The classification polygons were then compared to the orthomosaic and hillshade to correct errors. Individual trees were digitized as points. The tree points were generated automatically through the dissolved polygons generated with the classification of height contour lines, which input a point in the center of each dissolved polygon. The tree points were then checked by hand comparing to the orthomosaic and hillshade, ensuring that they fall onto the tip top of each tree.

Treelines from 1938 and 2017 (Kummel, unpublished analysis) were imported to generally divide the study area into forest, timberline edge and tundra.

Statistical Analysis

Cluster Analysis

Ripley's K function (in ArcMap 10.6.) was used to examine the spatial pattern of the study area. Sections were divided using the two treelines imported. Timberline edge was further divided into two sections and tundra was divided into four sections. For each section, Ripley's K function was run to have 15 distance bands with confidence envelope of 999 simulations, beginning distance of 0.01m, and boundary correction of simulate outer boundary values. Clustering patterns for different height trees, above 3m, above 5m and above 10m, were also examined.

Fractal Geometry

For cluster size classes, tree cluster polygons were carefully compared to orthomosaic and hillshade to include the entire canopy. Cluster areas were calculated with raster calculator in ArcMap and exported. The sections were re-divided into forests, timberline edge and four sections through the tundra area with the two previous treelines imported. When a tree cluster cuts through the lines, it was classified into the section where the majority of its canopy fell into. Logarithmic bin bands were chosen for the size classes as 0-2 m², 2-4 m², 4-8 m², 8-16 m², 16-32 m², 32-64 m², 64-128 m², 128-512 m², 512-1024 m², as the largest cluster canopy is 790.21 m². The number of clusters in each size class was counted and a graph of frequency to size class were generated. A trendline with power law function was added and R² value was examined. The analysis was conducted for the entire treeline, as well as for each section.

Percolation cluster

Percolation clusters through the study area was searched by looking for clusters that connect through the system, when not found, clusters of the largest areas were examined for fractal geometry. Fractal geometry of the edges were examined by using a compass to measure the approximated length of the perimeter of each cluster with different unit length. The length and the unit length used to measure such length were plotted, adding a trend line with power function, displaying R^2 values.

Results

The study area of Pikes Peak treeline on the west side has an area of 76189 m², a total of 3038 trees and 1433 clusters were identified and used in the analyses.

Ripley's K analyses revealed clustering patterns in several sections in the treeline when including all trees (Table 1). In the tundra sections, trees were generally clustered compared to random, and significant clustering were shown in the lower half of the tundra section (Figure 1). In tundra 2, the second section from the top, there was significant clustering on a smaller scale but not at large scales (Figure 1). Tundra 1 showed fluctuation around random distribution for clustering patterns, with significant clustering in a middle scale (Figure 1). In the timberline edge sections, the upper half exhibited significant clustering, while the lower half showed no statistically significant pattern with close overlap with expected random distribution (Figure 1).

In the forest, the trees presented weakly clustering pattern at smaller scales and over-dispersing pattern at large scales compared to the expected (Figure 1). However, no statistical significance was found (Figure 1).

Cluster analyses of trees within different size class, assuming taller trees are older and more established, revealed clustering patterns in the study area (Table 2). Four sections had enough samples of trees to run cluster analyses for trees over 3 m and taller. In the lowest tundra section, tundra 4, significant clustering could be found in all scales (Figure 2). In the two timberline edge sections, trees over 3 m displayed different spatial patterns (Table 2, Figure 2). Trees were significantly clustered in the higher section of timberline edge (timberline edge 1), while weakly clustering pattern showed statistical significance in small scales but not large scales for the lower section of the timberline edge (timberline edge 2) (Figure 2). Similar to that of all trees in the forest, a weekly clustered to weakly over-dispersed pattern could be found in trees 3 m and taller, but there was not statistical significance (Figure 2). Four sections were analyzed for the group of trees 5 m or taller. Tundra 4 was still the highest section included, showing significant clustering of trees 5 m or more (Figure 3). Both of the timberline edge sections exhibited significant clustering at all scales, different from the results found for all trees and trees 3m or higher (Figure 3). Trees over 5 m appeared to have no statistical significant pattern in the forest section (Figure 3). For analyses on trees that are 10 m and higher, three sections that were the lowest in the study area were included with sufficient number of tree points. For the upper timberline edge, trees 10 m or higher were clustered compared to expected, and significant clustering could be found at small scales (Figure 4). The lower timberline edge presented significant clustering for all scales (Figure 4), and there was weakly clustering pattern in the forest with statistical significance in mid-small scales (Figure 4).

Fractal geometry in size class analyses generated potential existence of such power law relationships. When examining the structure of the entire study area, all clusters identified were classified into the size classes, generating a power function trendline $y = 0.6472x^{-0.938}$ and R² value of 0.986 (Figure 5). Size class structures for individual sections of the study area had different fits to power law functions (Table 5). The highest section of the tundra did not have enough clusters to produce convincing statistical results and was excluded for the individual analysis. Tundra sections in general had high R² values of over 0.93, showing strong fit to power law relationships. However, the proportions of clusters in each size class varied and the powers were different for the three sections (Figure 6). The two timberline edge sections were combined to better incorporate the connected large clusters across both sections. A power law fit of $y = 0.5257x^{-0.798}$ was found with $R^2 = 0.8748$, showing a good fit for a power law function but not as high as those of the tundra sections (Figure 7). Proportion of clusters in the smallest size class was similar to that of the lowest section in tundra, but the powers were different from those found in tundra sections. In the forest section, a power law trendline of y = $0.2449x^{-0.327}$ was generated, and the $R^2 = 0.6263$, showing a very weak fit comparing to the other sections and the entire study area (Figure 8).

No percolation cluster connecting the entire system was found in the study area. However, two largest clusters in the forest and timberline edge were examined closely for the potential of becoming a percolation cluster with edge analyses. The estimated perimeter of the largest cluster in the timberline edge section showed increase in its edge length when the length of the estimator decreased in half each time. The relationship between the perimeter and estimator length for the cluster fitted a power law function $y = 175.59x^{-0.386}$ with an R² value of 0.969 showing very strong fit (Figure 9). The same applied for the largest cluster in the forest section, with $R^2 = 0.996$ for a power law fit $y = 146.93x^{-0.28}$ (Figure 10). The two clusters were close to each other spatially with more than one potential point of connection.

Discussion

In this study, we hypothesized for the spatial structure of treeline on the west side of Pikes Peak that the trees would be clustered through intraspecific facilitation from established trees and that treeline would exhibit fractal geometry for frequency size distribution and the edges of clusters. The first hypothesis is supported as clustering patterns were found in the sections, and the second hypothesis was only partially supported, as the patterns shown do not directly point towards phase transition.

Cluster analyses (Ripley's K) showed clustering patterns in most sections in the study area. Given that the underlying habitat structure is likely fairly homogenous, the significant clustering is possibly due to endogenous mechanisms, such as facilitation. Clumping patterns are found in the lower tundra and the upper timberline edge, supporting the potential facilitation of growth among spruce trees at treeline in the environment, agreeing with the findings of Cui and colleagues (2017) where tree clustering was found in the Tibetan Plateau through the positive feedback in the stressful environment. The clustering tendency shows strong evidence that established trees could facilitate the recruitment of new seedlings, which has been found in sub-alpine areas (Lingua et al. 2008). Such facilitation could come from the positive feedback of established trees in ameliorating the harsh environment by improving the microsite condition in the treeline ecotone as the established tree clusters can affect snow thickness, soil characteristics and microclimate (Lingua et al. 2008) to create a zone of milder environment (Cui et al. 2017). Engelmann spruce is a shade tolerant species, and requires some shade for the healthy development of seedlings (Markstrom & Alexander 1984). Thus, reduced sky exposure and

relatively cool temperature around established tree clusters could facilitate the recruitment and growth of seedlings, which has also been found in Central Greater Caucasus Mountains, where *Betula litwinowii* has higher seed abundance and healthier seedlings under overstory plantation (Akhalkatsi et al. 2006). Besides, krummholz individuals in tundra sections have been demonstrated to enhance seedling growth and survival by accumulating thicker snowdrifts in their leeward side and effectively minimizing wind speed, which may lead to an increase in seedling survival (Batllori et al. 2009) and create a cluster pattern. The clustering patterns as evidence for facilitation can thus provide us with ideas on future spruce recruitment and establishment patterns.

The clustering patterns are not consistent across all sections of the studied treeline site, showing potentially different degree of biotic interactions at different elevations. Clustering was less evident in the upper edge of tundra, which could be due to the small number of trees that survived in the section and the probability of random seed dispersal into the area. Besides, it is also likely that seeds recruit into proximity of rocks in the upper tundra as rocks could also provide areas of ameliorated conditions. However, the weakly clustered pattern could still serve as evidence that the survival rate might be higher near established trees in severe environments. The lower timberline edge showed random distribution patterns, which could suggest that the endogenous force was not the driving factor shaping the current distribution of trees at timberline edge; at present, the environment at the edge may be mild enough that additional facilitation does not change survivorship strongly enough to create spatial patterns. It could be possible that the clustering patterns used to be in the area when the climate was harsher, but with climate change the spaces between the clusters filled in and the overall patterns disappeared. In addition, trees in the forest section only showed weakly clustering patterns at small scales, suggesting possible

facilitation of survivorship in harsher climatic conditions that existed prior to the anthropogenic climate change while over-dispersed patterns at large scale implies existence of competition among the well-established tree clusters. The inconsistency of the clustering patterns is important in providing more general backgrounds for the formation of clustering patterns, and in showing the importance of taking into account abundance of trees and time scale.

Clustering analyses of trees within different size classes provided more insight into the interaction in the treeline ecotone. The size class can be used as a very imprecise indication of age, and hence some of the patterns found in the spatial distribution of age classes probably also reflect the development of the treeline over time. When only considering trees 3 m and over, spruce saplings and seedlings are eliminated from the analysis. The results showed stronger clustering in most sections, and the trees in the size class of 3 m and taller showed significant clustering in the lower timberline edge. However, this pattern was not detectable when the seedlings and saplings were considered together with the taller trees. Such change in the pattern in the lower timberline area shows evidence that the establishment of trees in the section may have not happened simultaneously; instead, some trees established first and later-establishing trees clustered around the oldest established trees, and through time trees started to cluster around the area, filling the lower timberline section in the end as there were enough large established trees they could benefit from. Such inference was further confirmed with the other two size class analyses with larger spruce trees. Spruce trees over 5 m in the treeline area on Pikes Peak usually reach reproductive maturity, and cluster analyses in the selected tree size class showed significant clustering in the lowest tundra section and the two timberline edge sections, suggesting facilitative interaction among these trees. For spruce over 10 m, there is even more significant clustering in all the sections tested. However, it could also be important to notice that there are fewer trees 10 m tall or higher, and they tend to occupy lower elevation as such height would have required a long time of development and establishment without dieback or mortality in the harsh environment. It is possible that the larger trees are the ones that established first and around each other, but it is also a potential that only certain area with better underlying environments allowed the tree recruitment and establishment in early stages, creating such clustering patterns. The more significant clustering patterns with increasing size classes in the sections generally further confirm the facilitation and positive feedback in the treeline ecotone, and the formation of spatial patterns should be put into context of changing time and environmental harshness as factors.

Fractal analysis was applied in the context of the spatial structure of treeline to determine the potential for a critical transition in the treeline ecotone from tundra to forests. Ecological examples of criticality involve processes of disturbance and recovery, and patchiness develops from local interactions (Pascual & Guichard 2005) which could be used as early warning signs of ecological critical transitions. Near critical points of transition, the size distribution of gaps or clusters of trees exhibits power-law behavior, with patches of all sizes present and no dominant size (Pascual & Guichard 2005). Such pattern would only occur at the critical point if the system is in phase transition as hypothesized. In our study area, the power law behavior was found considering the entire study area as well as divided sections. Cluster size frequency distribution has R square values over 0.93 in the tundra sections, which indicates that the power law presents an extremely good fit to the data. Different power law function fits were found along the gradient of the elevations, where the tundra sections mostly show straight line fit with high R square values, while the timberline section and forest show smaller R square values not fitting the straight line as well. The strong fits of the patterns across the study area suggest that the system is possibly in the process of critical ecological transition, from the tundra to the forests in the study areas, while the different fits could suggest different mechanisms driving the formation of the patterns in each section, or different stages of transition as the change is directional along the elevation gradient.

In the study area of the treeline, no percolation cluster was found, showing that the system is not yet entirely connected. However, the largest clusters found in the study area showed significant fractal geometry in the edges, lining with the characteristic of percolation clusters. The large clusters were found quite close to each other, therefore there is a potential to a percolation cluster in the future as the treeline becomes denser. Although percolation point is not directly linked to a drastic change in the actual cover or abundance of individuals, in this case the spruce trees, it is still noteworthy the sudden change in the system-wide connectivity, which could have important functional consequences (Kéfi et al. 2010). The connectivity in the treeline system could shift the functionality of the ecotone, and species expansion of spruce trees could propagate through the system, taking over the tundra. Specifically, the clusters of the vegetation could serve important roles in providing suitable environment of seedling establishment by shading and protecting them from the harsh environment. Close examination of connectivity of the study area should be continued as it could give us a warning sign for the change.

It is important then to further investigate the patterns and the type of criticality associated with the spatial patterns, in order to make predictions of possible threshold for the critical transition. As the power law behavior was found across sections rather than only at the transition point where percolation cluster can be found, the system is unlikely to be in phase transition. The scale invariance across sections in the study area points towards the system being in robust criticality, which signifies a type of criticality where scale invariance, power law in frequency

distribution of patch size without tuning of parameters (Pascual & Guichard 2005). The dynamic spatial patterns are likely to have formed with disturbances in the harsh environment at high elevations at treeline, where cold temperature primarily limit tree growth along with other factors such as strong wind, and with recovery process through seed dispersal and recruitment. The disturbances cannot be described as well-mixed, as the intra-specific interactions among the spruces alter the susceptibility of a particular tree or gap being disturbed or recovered. This kind of non-homogeneous disturbance is also a common characteristic of robust criticality (Pascual & Guichard 2005). Power law distribution in robust criticality does not imply drastic changes and cannot by itself be used as a sign for critical transition (Pascual & Guichard 2005, Schneider & Kéfi 2016). As seen in the studied treeline system, power law behavior was found in the patch size distributions with some variations in different sections, and no percolation cluster was formed, so we could not yet confidently predict whether a shift will happen or not, pointing towards possible robustness of the ecotone dynamics.

Although it seems like the study area is in robust criticality, some part of the story remains unclear. Pascual and Guichard (2005) argued that system of robust criticality usually exhibits three different states, empty, disturbed and occupied, and both empty and occupied can change into the state of disturbed. It is possible that in the treeline ecotone, empty state and occupied state are the tundra state and established tree state, but the third state seems unclear. We suggest that the third state could be tree seedlings, but established trees could not go back to its seedling stage. It is also possible that the third state might be non-upright established trees, for example krummholz, where dieback could result in established trees to become a krummholz and recruitment could result in tundra state into a non-upright tree. The third intermediate state will need more investigation to understand the underlying mechanisms of the robust criticality system, in order to make further predictions on treeline transition.

Systems in robust criticality have been seen frequently with local interactions or associational resistance, which influence the patterns of the system as well as the mechanisms (Kéfi et al. 2010, Schneider & Kéfi 2016), leading to a potential of transitioning. The facilitative recruitment of mussels at local sites, and heterogeneous grazing pressure due to different density of plantation in drylands, have both suggested high pressure for local processes can shift the system from robust criticality to a phase transition with high risks of catastrophic shifts (Kéfi et al. 2010, Schneider & Kéfi 2016). The local feedbacks with the treeline system where the existing spruce clusters alter the intensity of climatic force locally, resulting in variable stress exerted on the system were discussed above. At the same time, local recovery is accelerated as recruitment and establishment is favorable near established tree clusters with the positive feedbacks. The same positive interactions can be further implied with up-bent power law describing size classes where clustering was preferred and more large clusters were found (Schneider & Kéfi 2016), and such relationship was found in the forest section where the power law function has a weaker fit with more large patches than expected power law trendline. In systems with associational resistance, the heterogeneous pressure was suggested to add to the positive interactions and formation of clusters, which could lead to the emergence of a sharp threshold for ecosystem degradation when the pressure changes (Schneider & Kéfi 2016). It is evident that if the assumption stands for the study system, the treeline ecotone in the study area with decreasing pressure of the climate will eventually transition into a system with classical criticality, leading to a drastic change of the landscape.

Although no direct predictions can be made, the power law patterns and fractal geometry in the clusters raise a warning for potential critical shift in the study area of the landscape. Whether the system is transitioning from robust criticality to classical criticality or is in a phase transition, the power law distribution of the patches seems to form by interactions between the outside pressure and endogenous interactions, as a good indicator of the mechanisms and thus can be a predictor of pattern change when the forces strengthen. As the outside pressure of climate or conditions at original elevation change, the pressure exerted on the area changes. The heterogeneous conditions along the elevation gradient could give us an idea of the direction of change in the system, which is shifting from tundra to forest. Upward movement of the treeline in the study area has already been found in the past decades, and the results of this study provide a possible explanation of dynamics under the formation.

Studies in alpine treeline ecotones will help us understand treeline formation and treeline dynamics, which is essential in predicting the behavior of such ecosystems. Especially with the current trend in the changing climate, the shift in alpine treeline could change the functionality of the ecotone as well as taking over tundra ecosystem which supports a different group of organisms. Long term study in the treeline on the west side of Pikes Peak should continue to monitor the change in patterns of the clusters and patches, and it could be used as an example to predict behaviors of other treelines and provide input for land management in the area. Models and empirical studies of other local scale treelines across locations should be implemented in order to check for the potential of generalization of the changes in the patterns of treeline, and to look for more accurate signs in critical changes in the ecosystem.

Conclusion

Although the structure of the treeline on the west side of Pikes Peak is complex, the spatial patterns suggest that there is significant facilitation in the environment, and the study area is potentially in robust criticality. With global climate change, the treeline on Pikes Peak will likely continue to advance and close attention and monitoring should be implemented.

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References

- Akhalkatsi, M., Abdaladze, O, Nakhutsrishvili, G. & Smith, W. K. (2006). Facilitation of seedling microsites by *Rhododendron caucasicum* extends the *Betula litwinowii* alpine treeline, Caucasus mountains, Republic of Georgia. *Arctic, Antarctic, and Alpine Research, 38*(4), 481-488. doi:FOSMBR 2.0.CO;2
- Batllori, E. J. Camarero, J., Ninot, J. M, Gutiérrez, E. & Marin Sykes. (2009). Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones.
 implications and potential responses to climate warming. *Global Ecology and Biogeography*, *18*(4), 460-472. doi:10.1111/j.1466-8238.2009.00464.x
- Bekker, M. F. (2005). Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. Arctic, Antarctic, and Alpine Research, 37(1), 97-107. doi:PFBTEA 2.0.CO;2
- Compostella, C., & Caccianiga, M. (2017). A comparison between different treeline types shows contrasting responses to climate fluctuations. *Plant Biosystems an International Journal Dealing with all Aspects of Plant Biology*, *151*(3), 436-449.
 doi:10.1080/11263504.2016.1179695
- Cui, J., Qin, J. & Sun, H. (2017). Population spatial dynamics of *Larix potaninii* in alpine treeline ecotone in the eastern margin of the Tibetan Plateau, China. *Forests*, 8(10), 356. doi:10.3390/f8100356
- Daniels, L. D. & Veblen, T. T. (2004). Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, *85*(5), 1284-1296. doi:10.1890/03-0092
- Elliott, G. P., & Kipfmueller, K. F. (2011). Multiscale influences of climate on upper treeline dynamics in the southern Rocky Mountains, USA: Evidence of intraregional variability and

bioclimatic thresholds in response to twentieth-century warming. *Annals of the Association* of American Geographers, 101(6), 1181-1203. doi:10.1080/00045608.2011.584288

- Grace, J. Berninger, F., & Nagy, L. (2002). Impacts of climate change on the tree line. *Annals of Botany*, *90*(4), 537-544. doi:10.1093/aob/mcf222
- Harsch, M. A., Hulme, P., McGlone, M. & Duncan, R. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12(10), pp.1040-1049.
- Harsch, M. A., & Bader, M. Y. (2011). Treeline form a potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, 20(4), 582-596. doi:10.1111/j.1466-8238.2010.00622.x
- Kefi, S., Rietkerk, M. G., Roy, M., Franc, A., Ruiter, P. C. d., & Pascual, M. (2011). Robust scaling in ecosystems and the meltdown of patch size distributions before extinction. *Ecology Letters*, 14(1), 29-35. doi:10.1111/j.1461-0248.2010.01553.x
- Körner, C. & Paulsen J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31(5), 713-732. doi:10.1111/j.1365-2699.2003.01043.x
- Kummel, M. Unpublished analysis.
- Li, B. (2000). Fractal geometry applications in description and analysis of patch patterns and patch dynamics. *Ecological Modelling*, *132*(1), 33-50. doi:10.1016/S0304-3800(00)00303-3
- Liang, E., Wang, Y., Piao, S., Lu, X., Camarero, J. J., Zhu, H., . . . Peñuelas, J. (2016). Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. *National Academy of Sciences*. doi:10.1073/pnas.1520582113.

- Lingua, E., Cherubini, P., Motta R. & Nola P. (2008). Spatial structure along an altitudinal gradient in the Italian central alps suggests competition and facilitation among coniferous species. *Journal of Vegetation Science, 19*(3), 425-436. doi:10.3170/2008-8-18391
- Loranger, H., Zotz, G., & Bader, M. Y. (2017). Competitor or facilitator? the ambiguous role of alpine grassland for the early establishment of tree seedlings at treeline. *Oikos, 126*(11), 1625-1636. doi:10.1111/oik.04377
- Malanson, G. P, Resler, L. M., Bader, M. Y., Holtmeier, F., Butler, D. R., Weiss, D.J.... Fagre.
 D. B. (2011). Mountain treelines: A roadmap for research orientation. *Arctic, Antarctic, and Alpine Research*, 43(2), 167-177. doi:10.1657/1938-4246-43.2.167
- Markstrom, D. C. & Alexander R. R. (1984). Engelmann Spruce. An American Wood.
- Milne, B. T., Johnson, A. R., Keitt, T. H., Hatfield, C. A., David, J. & Hraber, P.T. (1996).
 Detection of critical densities associated with piñon-juniper woodland
 ecotones. *Ecology*, 77(3), 805-821. doi:10.2307/2265503
- Naito, A. T., & Cairns, D. M. (2015). Patterns of shrub expansion in Alaskan arctic river corridors suggest phase transition. *Ecology and Evolution*, 5(1), 87-101. doi:10.1002/ece3.1341
- Pandey, A., Hemant K. B., Sandhya R., & Surendra P Singh. (2018). Timberline structure and woody taxa regeneration towards treeline along latitudinal gradients in Khangchendzonga national park, eastern Himalaya. *PLoS One, 13*(11), e0207762. doi:10.1371/journal.pone.0207762
- Pascual, M. & Guichard, F. (2005). Criticality and disturbance in spatial ecological systems. *Trends in Ecology & Evolution*, 20(2), 88-95. doi:10.1016/j.tree.2004.11.012

- Petrov, I., Kharuk, V., Dvinskaya, M., & Im, S. (2015). Reaction of coniferous trees in the Kuznetsk Alatau alpine forest-tundra ecotone to climate change. *Contemporary Problems of Ecology*, 8(4), 423-430. doi:10.1134/S1995425515040137
- Schneider, F., & Kéfi, S. (2016). Spatially heterogeneous pressure raises risk of catastrophic shifts. *Theoretical Ecology*, *9*(2), 207-217. doi:10.1007/s12080-015-0289-1
- Sugihara, G., & M. May, R. (1990). Applications of fractals in ecology. *England: Elsevier Ltd.* doi:10.1016/0169-5347(90)90235-6
- Treml, V., & Veblen, T. T. (2017). Does tree growth sensitivity to warming trends vary according to treeline form? *Journal of Biogeography*, 44(7), 1469-1480. doi:10.1111/jbi.12996
- Zeng, Y., & Malanson, G. P. (2006). Endogenous fractal dynamics at alpine treeline ecotones. *Geographical Analysis*, *38*(3), 271-287. doi:10.1111/j.1538-4632.2006.00686.x

Section	Elevation Range	Patterns (Compare to expected)	Statistical Significance
Tundra 1	3580m - 3593m	Weakly clustered	No \rightarrow Yes \rightarrow No
Tundra 2	3593m - 3602m	Clustered at small scale	Yes → No
Tundra 3	3602m - 3620m	Clustered	Yes
Tundra 4	3620m - 3645m	Clustered	Yes
Timberline Edge 1	3645m - 3677m	Clustered	Yes
Timberline Edge 2	3677m - 3707m	Random	No
Forest	3707m - 3750m	Weakly clustered → weakly over-dispersed	No

Table 1. Summary of cluster analyses for all trees in each section.

Section	Elevation Range	Patterns (Compare to expected)	Statistical Significance
Tundra 4	3620m - 3645m	Clustered	Yes
Timberline Edge 1	3645m - 3677m	Clustered	Yes
Timberline Edge 2	3677m - 3707m	Weakly clustered	Yes → No
Forest	3707m - 3750m	Weakly clustered → weakly over-dispersed	Yes → No

Table 2. Summary of cluster analyses for trees over 3 m in each section.

Section	Elevation Range	Patterns (Compare to expected)	Statistical Significance
Tundra 4	3620m - 3645m	Clustered	Yes
Timberline Edge 1	3645m - 3677m	Clustered	Yes
Timberline Edge 2	3677m - 3707m	Clustered	Yes
Forest	3707m - 3750m	Random	No

Table 3. Summary of cluster analyses for trees over 5 m in each section.

Section	Elevation Range	Patterns (Compare to expected)	Statistical Significance
Timberline Edge 1	3645m – 3677m	Clustered → Weakly clustered	Yes
Timberline Edge 2	3677m – 3707m	Clustered	Yes
Forest	3707m – 3750m	Clustered \rightarrow weakly clustered	Yes

Table 4. Summary of cluster analyses for trees over 10 m in each section.

Section	Power law equation	R ²
Tundra 1	Too few data	
Tundra 2	$y = 171.46x^{-1.739}$	0.93809
Tundra 3	$y = 598.48x^{-1.693}$	0.96808
Tundra 4	$y = 513.51x^{-1.179}$	0.93834
Timberline Edge	$y = 285.97 x^{-0.798}$	0.8748
Forest	$y = 10.286x^{-0.327}$	0.62628

Table 5. Summary of fractal geometry analyses of size classes for clusters.



Figure 1. Ripley's K graph for distribution of all trees in the six sections.



Figure 2. Ripley's K graphs for distribution of trees 3 m and higher in the four sections.



Figure 3. Ripley's K graphs for distribution of trees 5 m and higher in the four sections.



Figure 4. Ripley's K graphs for distribution of trees 10 m and higher in the three sections.



Figure 5. Frequency of different size clusters in the entire study area represented proportionally and by count with respect to the size classes. Power trendline, the equations and R^2 values are displayed.



Figure 6. Frequency of different size clusters in the tundra sections represented proportionally and by count with respect to the size classes. Power trendline, the equations and R² values are displayed.



Figure 7. Frequency of different size clusters in timberline edge represented proportionally and by count with respect to the size classes. Power trendline, the equations and R² values are displayed.



Figure 8. Frequency of different size clusters in the tundra sections represented proportionally and by count with respect to the size classes. Power trendline, the equations and R² values are displayed.



Figure 9. Largest cluster in the timberline section and the analysis of the cluster edge.



Figure 10. Largest cluster in the forest section and the analysis of the cluster edge.