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Upper and lower treeline biogeographic patterns in semi-arid pinyon-juniper woodlands

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Title

Upper and lower treeline biogeographic patterns in semi-arid pinyon-juniper woodlands

Running title

Upper vs lower pinyon-juniper treelines

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Abstract

Aim: Elevational treelines exhibiting both an upper and a lower ecotone are particularly exposed to a changing climate. It has been hypothesized that upper treelines are constrained by growing season temperature whereas lower treelines are water-limited. We expect different causal mechanisms of upper vs.

lower treeline formation to generate distinct patterns of spatial heterogeneity. Here, we compare dynamics, spatial patterns and shape complexity of upper and lower treelines of semi-arid pinyon-juniper woodlands.

Location: Toiyabe Range of the Nevada Great Basin (western US).

Taxon: The association between *Pinus monophylla* Torr. & Frém. and *Juniperus osteosperma* (Torr.)

Methods: Within 20 sample plots (10 along the upper and 10 along the lower treeline) we mapped tree canopies through photo-interpretation of high resolution imagery. We performed point pattern analyses to compare the spatial arrangement of trees and used LANDSAT 30-year time series and NDVI to understand the vegetation dynamics of these ecotones. We adopted the surface roughness method to measure treeline shape complexity.

Results: Lower treelines were denser and showed a stronger trend of increasing NDVI change over the 1984-2015 period. Trees at the lower treeline were more strongly aggregated than at the upper treeline at spatial scales ranging from 15 to 65 meters. Shape complexity was higher at upper treelines, expressed by a higher mean surface roughness; however, the spatial structures of upper and lower treelines were similar.

Main conclusions: Upper treeline expansion of pinyon-juniper woodlands in the study area has been limited and highly variable, but lower treeline downslope expansion into adjacent shrub steppe vegetation was evident. The expected difference between energy- and water-limited treelines did not manifest in the observed spatial structures. Differences in treeline shape complexity were not significant, although lower treelines exhibited less complex shapes, likely because they have been more strongly influenced by anthropogenic factors.

Keywords

LANDSAT, Pinyon-juniper, PPA, Upper treeline, Treeline shape, Woodland dynamics, Ecotone, Lower treeline

Introduction

Treeline position varies with latitude and elevation following a temperature gradient (Körner, 2012) that is often masked by other limiting factors such as topography, edaphic gradients, natural disturbances and human activities. For these reasons, latitudinal and elevational treelines are commonly classified as climatic, orographic and anthropogenic, depending on the critical limiting factors shaping their structure and response to changing environmental conditions (Holtmeier & Broll, 2005). The critical limiting factors likely differ between upper treelines, at the ecotones with alpine tundra or montane shrublands, and lower treelines that border semiarid or arid scrub vegetation. Therefore, the two types of elevational treelines are likely to respond to global change processes in different ways, with potentially unexpected effects on the large-scale distributions of woodlands and forests.

Climatic treeline ecotones are expected to be vulnerable to climate change that directly acts on plant ecophysiological responses to temperature and precipitation, and indirectly through longer-term influences on disturbance regime. Under the principle of “tree growth-climate relationships”, upper treelines (UT) are known to be energy-limited and hence constrained by growing season temperature (Klinge, Dulamsuren, Erasmí, Karger, & Hauck, 2018; Körner & Paulsen, 2004), whereas lower treelines (LT) are water-limited and constrained by annual precipitation and summer drought (e.g. Fritts, Smith, Cardis, & Budelsky, 1965; Yang, He, Melvin, Zhao, & Briffa, 2013). Following this principle, a warmer climate would cause an upward shift of expanding UT, and a drier climate would cause an upward shift of retreating LT (Romme & Turner, 1991). In regions that are characterized by both upper and lower treelines, the proximity of these treelines allows for comparisons of treeline-structuring processes with minimal influence from confounding factors such as species identity, soil parent material, or precipitation seasonality.

The geographical co-occurrence of both UT and LT ecotones on the same mountain or hillslope is not widespread globally, mainly because LT are confined to close proximity to steppe or desert environments.

The most important examples of LT ecosystems are located in western North America (e.g. Kienast & Schweingruber, 1986), South America (Markgraf & Huber, 2010) and central Asia (e.g. Yang et al., 2013). Treeline shift studies have mostly focused on forest upward expansion at the upper ecotone (e.g. Harsch, Hulme, McGlone, & Duncan, 2009), but lower elevation treeline ecotones, where water availability is considered the limiting factor, are expected to be the most affected by a warming and drying climate (Donato, Harvey, & Turner, 2016). Climate variations during the mid and late Holocene caused different effects on South American upper vs. lower treelines, where precipitation primarily influenced the lowlands and temperature was the most important factor at high elevations (Markgraf & Huber, 2010). Upward shifts of upper treelines under a warming climate are suggested by process modelling experiments (Parmesan & Yohe, 2003) and have been observed in numerous locations globally (e.g. Gehrig-Fasel, Guisan, & Zimmermann, 2007), but with high variability and uncertainty associated with historical land-use legacies and natural disturbances (Ameztegui, Coll, Brotons, & Ninot, 2016; Weisberg, Shandra, & Becker, 2013). The “tree growth-climate relationships” principle is not obvious everywhere, especially in arid ecosystems of the Tibetan Plateau and north western Argentina where similar growth patterns for UT and LT were observed (Esper, Frank, Wilson, Büntgen, & Treydte, 2007; Morales, Villalba, Grau, & Paolini, 2004; Yang et al., 2013).

Due to the limited geographic distribution of LT, UT are more frequently studied and usually analysed independently of any LT response. UT and LT have been directly compared only infrequently, to assess climate effects on tree growth and vitality (Klinge et al., 2018; Yang et al., 2013), ecophysiological traits (Sparks & Black, 2000), paleoecological records (Markgraf & Huber, 2010) or ecotone position by means of satellite remote sensing data (Driese, Reiners, Merrill, & Gerow, 1997). Direct comparisons among upper and lower forest ecotones are important for understanding how these treelines are structured in response to different environmental controls, and how they are likely to respond to environmental change. There is a need for the development of unified approaches that inform our understanding of what fundamentally limits tree distribution at its extreme limits across multiple environmental gradients.

The Interior West of US represents an ideal study system for assessing patterns and processes of both LT and UT treelines along the same elevational gradients (Garbarino, Marzano, Shaw & Long, 2015; Long, 2003). In the Rocky Mountains, the LT appears to be controlled by summer droughts (Krebs, 2014) and an upward shift of 460 m in elevation is expected under drier conditions due to climate change (Neilson, King, DeVelice, Lenihan, & Marks, 1989). Treeline dynamics are also constrained by processes of natural disturbance and subsequent forest recovery. Many LT ecotones are frequently disturbed by wildfires and various human activities (Schuster, Mitton, Yamaguchi, & Woodhouse, 1995) and forest regeneration at the lower ecotones can be strongly limited by topo-climatic factors and seed source availability (Rother & Veblen, 2016). LT expansion at Yellowstone National Park was observed to be facilitated by the presence of rocky substrate that limited the competition between deep-rooted trees and grasses (Whitesides & Bekker, 2011). Pinyon juniper (PJ) woodland expansion at the LT was described early on as a process driven by overgrazing, fire suppression, and climatic change (Blackburn & Tueller, 1970; Romme et al., 2009). At a landscape scale, the expansion of PJ woodland was faster on mesic, less moisture limited, sites and appeared as an infilling process (Weisberg, Lingua, & Pillai, 2007).

We consider that insufficient attention has been given to landscape-scale dynamics and recruitment mechanisms at the LT (Whitesides & Bekker, 2011), making them high-priority sites for research and climate change monitoring (Romme & Turner, 1991). Motivated by this information gap, we directly compared treeline spatial pattern, shape and dynamics of pinyon-juniper UT and LT in the Great Basin region of Nevada, USA. Pinyon-juniper woodlands are a highly suitable study system for this research question because the same species (*Pinus monophylla* and *Juniperus ostenosperma*) form both the UT and LT, and so sources of variation that are fundamental to the ecotonal type (UT or LT) are not confounded by differing species composition or interspecific differences in plant traits. Our main hypotheses were: a) recent treeline dynamics are influenced primarily by climate change, showing a general upward shift of woodland both at upper and lower elevations; b) temperature limited UT exhibit a clustered spatial pattern of trees as the outcome of facilitation effects on tree establishment and survival, whereas UT, controlled by competition for limited water resources, are characterized by a uniform spatial distribution of trees; c) treeline shape complexity at the patch level will be greater at upper elevations where natural agents such as wind and snow dominate over anthropogenic disturbances, whereas LT patch shapes will be less complex due to stronger human influences and a higher frequency of wildfire occurrence.

Methods

Study Area

The study was carried out in the Toiyabe Range of the Nevada Great Basin (western US; approx. 39°29'31" N; 117°4'13" W), which is representative of the Central Basin and Range Level III ecoregion (USEPA 2013). The climate is typical of the Great Basin high desert and is characterized by cold winters (average minimum temperature approx. -11°C) and hot summers (average maximum temperature approx. 32°C). Mean annual precipitation ranges from 350 mm at lower elevation to 550 mm at upper elevations and falls primarily as winter snow (PRISM, 2019). The bedrock geology of the Toiyabe range is dominated by sedimentary metamorphosed rocks, but igneous intruded and intrusive granitic rocks are also present (Hill, 1915). The association between *Pinus monophylla* Torr. & Frém. and *Juniperus osteosperma* (Torr.) is dominant on both slope aspects of the range within an elevation belt (1930 – 2630 m a.s.l.) characterized by the minimum moisture needed to allow their establishment. *P. monophylla* is dominant at higher elevations, while a mixture of *P. monophylla* and *J. osteosperma* forms the overstory component at lower elevations (Greenwood & Weisberg, 2008). The semi-arid valleys below the LT are characterized by sagebrush steppe vegetation dominated by several species of shrubs (e.g. *Artemisia tridentata* Nutt. subsp. *wyomingensis*, *Ericameria nauseosa*, *Tetradymia canescens*) and perennial bunchgrasses and forbs (e.g. *Poa secunda*, *Hesperostipa comata*, *Elymus elymoides*, *Phlox hoodii*). Higher elevations above the UT are characterized by dense thickets of mountain mahogany (*Cercocarpus ledifolius* Nutt.) or montane shrub communities composed of a diverse mix of woody and herbaceous species such as *Symphoricarpos oreophilus*, *Chrysothamnus viscidiflorus*, *Lupinus argenteus*, *Eriogonum elatum*, and *Festuca idahoensis* (Urza, Weisberg, Chambers, Dhaemers, & Board, 2017). Groves of quaking aspen (*Populus tremuloides* Michx.) are limited to drainages or micro-topographical depressions where an accumulation of moisture is possible.

Commento [pjw1]: U.S. Environmental Protection Agency [USEPA]. 2013. Level III ecoregions of the continental United States: Corvallis, OR: U.S Environmental Protection Agency, National Health and Environmental Research Laboratory. Map scale 1:750,000. <https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states>.

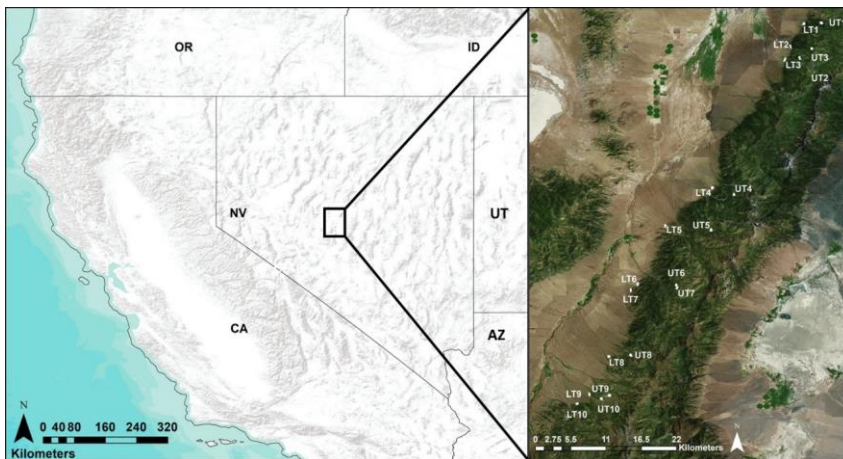


Figure 1. Geographic location of 20 sample plots along the Toiyabe range in the central Nevada. LT indicates lower treelines; UT indicates upper treelines.

Sampling design

Twenty sample plots of irregular shape and a surface area of 11 ha each were established by using a paired-sample design combining 10 pairs of UT and LT on each of the two dominant aspects of the range (Figure 1). Plot locations were generated in a GIS environment by randomly selecting 20 locations along the slope (10 for each dominant aspect), and then creating a line connecting each random point with the limit of all trees up-slope (UT) and down-slope (LT) from the closed forest edge along the gradient of maximum slope. The elevation of sample plots ranges between 1930 and 2611 m a.s.l. and each plot encompasses UT and LT so as to include all living trees detectable in high resolution imagery between the closed forest edge and the limit of all individual trees.

Image Analysis

A remote sensing approach was used to map tree crowns within the 20 sample plots through on-screen photointerpretation of high-resolution (30 cm) aerial photographs (Bing Maps Microsoft Virtual Earth; year 2012) available from the ArcGIS Online service (ESRI, 2012). The approach consists of a manual segmentation of the image at a map scale ranging between 1:400 and 1:600 to identify tree crown polygons, and subsequently the canopy cover and the centroid of each detected tree. The minimum mapping unit (MMU) adopted in the image analysis was 0.78 m² corresponding to a crown radius of at least 0.5 m. The 20 vector maps resulting from this process (Figure 2) were validated through accuracy assessment by ground control plots (GCPs) collected in the field during June and July of 2015. A total of 60 GCPs, having a radius of 15 m each, were placed within 4 lines crossing the UT and LT sample plots. For all GCPs the absolute coordinate of the plot centre was collected with a Trimble GeoXT GPS (estimated precision of 1.3 m) and all living trees with a crown radius > 0.5 m within the plot were mapped and measured (height, species, health status and 2 crown radii). The accuracy of the image classification was obtained by calculating the number of correctly classified trees (matches = M), trees detected in the image but absent on the field (false presence = FP) and trees present on the field but not detected on the image (false absence = FA). The final accuracy, calculated on a total of 104 ground control points (GCPs) was 83% total matches, 10% false absences and 7% false presences.

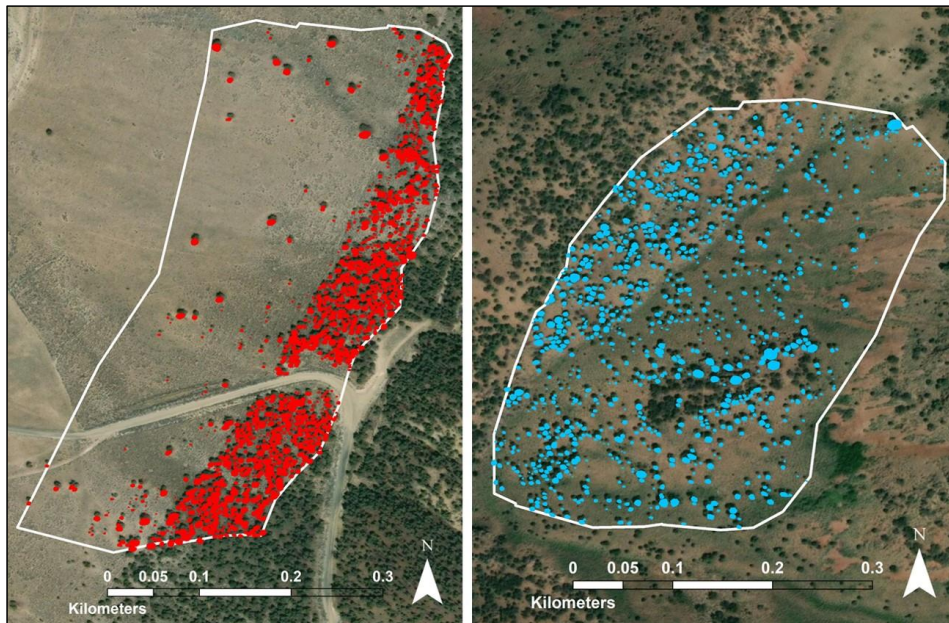


Figure 2. An example of lower (LT3, left panel) and upper (UT7, right panel) treelines as a result of the manual photointerpretation in a GIS environment. The middle part of the right panel includes a cluster of mountain mahogany (*Cercocarpus ledifolius*), an arborescent shrub of generally lower stature that was excluded from the crown digitization.

Treeline structure and dynamics

Treeline structure was assessed using several standard descriptors of stand structure including tree density, stand-level forest canopy cover and frequency distributions of crown surface areas of individual trees. Treeline vegetation dynamics were explored using a series of Landsat annual image composites at one-year

intervals between 1984 and 2015, resulting in a temporal extent of 32 years for each sample plot. Landsat TM (Thematic Mapper) images were used for the 1984-2011 period, ETM+ (Enhanced Thematic Mapper Plus) for the 2012 and OLI (Operational Land Imager) for the 2013-2015 period and all images were corrected to top-of-atmosphere corrections (Chander, Markham, & Helder, 2009). Normalized Difference Vegetation Index (NDVI) was calculated for each year using the median value composite, resulting in a cloud free time series for each pixel within our study area. Image pre-processing and NDVI computation were all made through the cloud computing website Climate Engine (Huntington, Hegewisch, Daudert, Morton, Abatzoglou, McEvoy & Erickson, 2017). A relativized version of NDVI (rNDVI) taking into account the annual influence of climate on vegetation phenology was obtained as the ratio of NDVI to the Palmer Drought Severity index (PDSI). UT and LT vegetation trends over time were calculated and compared using the slope of each NDVI and rNDVI trend line. Wilcoxon paired-sample tests were used to assess statistical differences in median values of UT and LT tree density, canopy cover, and slopes of NDVI and rNDVI trend lines. Mann-Whitney U nonparametric statistical tests were used to evaluate the differences between frequency distributions of tree crown areas.

Treeline point pattern analysis

Univariate point pattern analysis (PPA) techniques were applied to the mapped centroids of tree crowns within the 20 altitudinal plots. We used the pair-correlation function $g(r)$ (Wiegand & Moloney, 2004), a second-order statistic providing information at multiple scales. The univariate pair-correlation function $g(r)$ is defined as clumped, random or regular (hyperdispersed) if the $g(r)$ values are greater than, within, or lower than the confidence envelope defined by two lines, CE+ and CE-, calculated using Monte Carlo simulations (Wiegand & Moloney, 2004). The pair-correlation function is non-cumulative and uses only points separated by a specified distance r , allowing specific scales to be identified where significant point-point interactions occur, particularly over small distances (Wiegand & Moloney, 2004). We analysed patterns across a range of scales from $r = 5$ to 100 m (one third width of the shortest plot border) and verified the robustness of each pattern using the Goodness-of-Fit (GoF) test (Loosmore & Ford, 2006). The results from each of the 20 sample plots were then aggregated within each of the two treeline types (UT and LT), using the 'combine replicates tool' included in the Programita software (Piermattei, Lingua, Urbinati, & Garbarino, 2016). Univariate point patterns were then compared across the two treeline types using a confidence envelope generated assuming the Heterogeneous Poisson null model, which relaxes the assumption of complete spatial randomness and allows the intensity of the point pattern to vary across the study area (Wiegand & Moloney, 2004). In order to compare the spatial pattern of UT and LT, we calculated a measure of relative spatial aggregation, $g(r)/CE$. This index is the ratio between the observed pair-correlation value $g(r)$ and the corresponding upper confidence line (CE+) at a specified distance r (Fajardo, Goodburn, & Graham, 2006). The 95% confidence envelope was computed from 999 Monte Carlo simulations (Stoyan & Stoyan, 1994; Wiegand & Moloney, 2004).

Treeline shape

Treeline shape was assessed on a 2D point cloud dataset where each point represented a tree with its relative (x , y) coordinates within a Cartesian plane with fixed axes (x : 360 m, y : 180 m). For each sample plot two 6th-order polynomial regression curves were fitted to the entire ecotone (treeline) and to the trees having the highest elevation (y -axis) within 5 m intervals along the x -axis (tree species line). We used a 6th-order polynomial regression curve, which well represents the complex nature of the data. This non-linear model that guarantees a reliable fit, low bias and low variance highlighting the physically meaningful differences between the patterns; which may be lost using other polynomial order in the case of complex relationships between variables such as x - and y -coordinates. On the same dataset (tree species line) the surface roughness approach (Vorburger et al., 2014) was applied in order to evaluate shape complexity of each treeline. The approach included the computation of the average line (AL), fitted by the least square method, computed over the primary roughness profile points, and of two roughness indices based on the AL, the average roughness (R_a) and total roughness (R_t). R_a is the most commonly used and recognized parameter to evaluate a surface roughness profile, i.e. the arithmetic average absolute distance of the roughness profile points from the AL:

$$R_a = \frac{1}{l} \sum_{i=1}^N |d_i|$$

where l is the length of the AL, N is the number of points (trees) in the profile, and d_i is the Euclidean distance of each point from the AL. R_i is the mathematical difference between the maximum negative (under AL) and positive (over AL) distance from AL. A Wilcoxon paired-sample test was used to assess statistical differences in median values of UT and LT shape (R_a , R_i).

Results

Treeline structure and vegetation dynamics

Within our 20 sample plots we delineated tree density and canopy areas for 25,884 trees (11,831 at the UT and 14,053 at LT). LT were denser but similar to UT in percentages of canopy cover (9.7 and 9.2 % respectively). UT were steeper and approximately 400 m higher in elevation (Table 1). Mean tree crown surface area of UT was greater than for LT (8.8 m² and 7.7 m² respectively). Frequency distributions of tree crown areas at both treelines approximated a negative exponential distribution, but LT exhibited a significantly greater (Mann-Whitney U, $p < 0.0001$) frequency of small tree crown classes (0-15 m²) (Figure 3).

Treeline descriptors		UT		LT	
	Units	Mean	SD	Mean	SD
Elevation	m a.s.l.	2481	115.1	2096	151.4
Slope	°	21.9	5.5	7.2	2.9
Density	Trees/ha	105.7	32.3	124.1	56.5
Canopy Cover	%	9.2	3.9	9.7	4.5
Crown Area	m ²	8.8	10.0	7.7	8.9

Table 1. Topographic and forest structural descriptors of 10 UT and 10 LT sample plots in the Toiyabe Range, Nevada. Mean and standard deviation (SD) values are indicated.

LT showed a strong trend of positive NDVI change over the 1984-2015 period (Figure 4). UT showed more variable trends, of lower magnitude, that were equally likely to be positive or negative. The difference between UT and LT emerged as being statistically significant both when using the NDVI (Wilcoxon test, $W = 50.5$, $p = 0.019$) and the NDVI relativized by the PDSI (Wilcoxon test, $W = 45$, $p = 0.008$). In particular, the mean value of the relativized NDVI slope for the LT was nearly 5 times greater than for UT (0.054 and 0.011 respectively).

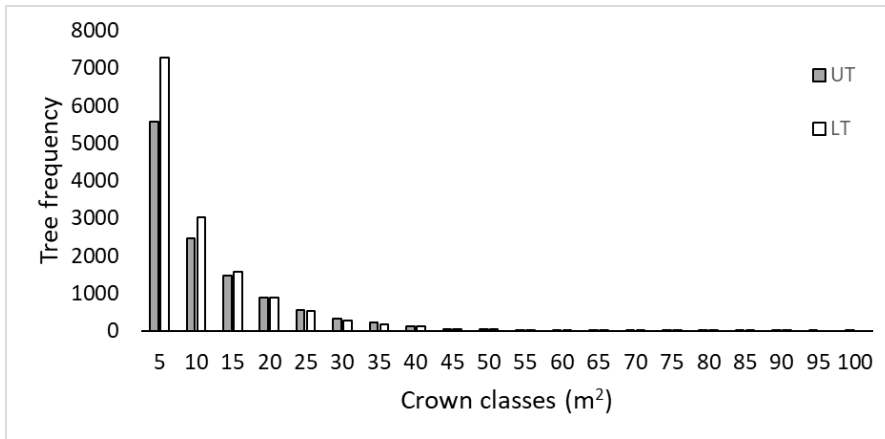


Figure 3. Frequency distributions of 25883 photointerpreted tree crowns at UT and LT sample plots.

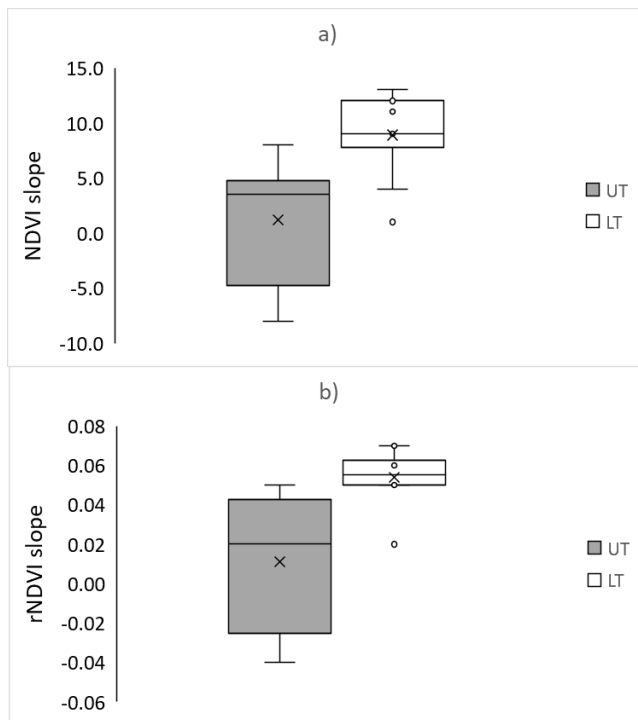


Figure 4. Comparison by box plots between the distribution of the NDVI slopes a) and the relativized NDVI slopes b) derived from linear regression at ten UT and ten LT sample plots within the Toiyabe range, over the 1984 – 2015 period. NDVI values for each year and each treeline were calculated from LANDSAT image composites.

Treeline spatial pattern

Pair correlation functions $g(r)$ were used to assess point patterns of stem-mapped pinyon and juniper trees against the heterogeneous Poisson null model. The combined pattern across both LT and UT plots showed a similarly aggregated spatial distribution of trees at spatial scales > 5 m, that significantly differed from the heterogeneous Poisson null model (GoF: $p < 0.001$). The index of relative aggregation [$g(r)/CE+$] revealed that the spatial distribution of trees at the LT was more aggregated than those at the UT, at spatial scales ranging between 15 and 65 m (Figure 5).

Treeline shape

UT showed more complex shapes, indicated by the highly convoluted sixth order polynomial regression curves that resulted from the data fitting process. LT1 and LT2 are good examples of sites that showed a simplified and less complex treeline shape, whereas UT1 and UT6 exemplify the greater shape complexity of upper treelines (Figure 6). LT plots were characterized by a higher average sixth order polynomial regression coefficient (R^2 LT = 0.0131 and R^2 UT = 0.0117), but the difference between UT and LT plots was not significant (Wilcoxon test, $p = 0.79$).

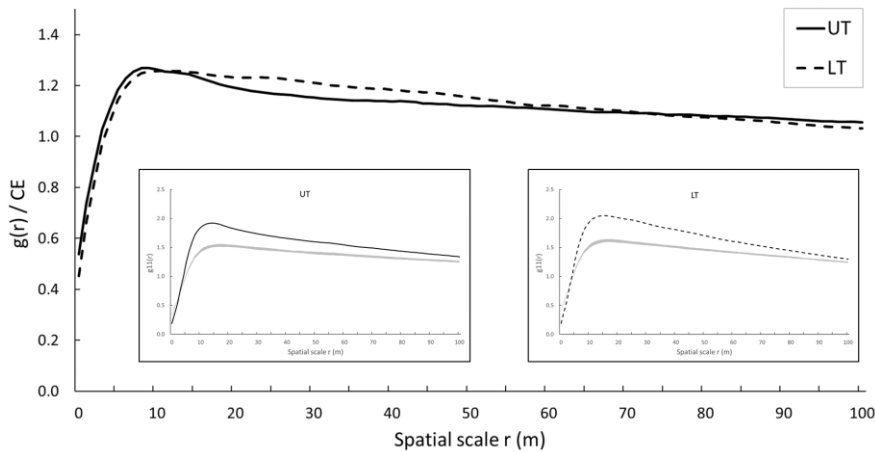


Figure 5. Main figure: ratio between pair correlation value and confidence envelope [$g(r)/CE$] against lag distances (r). Solid line represents UT ($n = 10$), dotted line represents LT ($n = 10$). Insets: univariate spatial pattern analysis of pinyon-juniper woodland in 10 LT plots of the Toiyabe Range adopting combined replicates. Bold line indicates the pair correlation function $g(r)$ and the shaded areas encompass non-significant, i.e. random, distribution, and represent, points within the 2.5th and 97.5th % $g(r)$ values of the 999 Monte Carlo permutations.

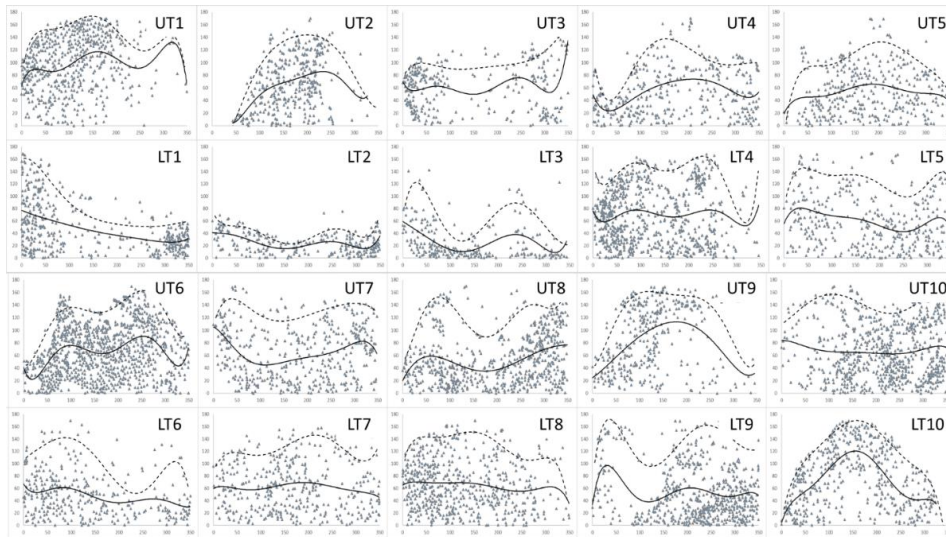


Figure 6. Treelines (solid) and tree species lines (dotted) drawn as sixth order polynomial regression curves (see text for details). Grey dots represent the positions of trees with relative coordinates (X, Y) within plots 350 m wide and 170 m long. The upper part of each panel represents higher elevations for the UT plots, but represents lower elevations for the LT plots.

Treeline shape complexity evaluated through roughness indices showed that in six of ten paired-samples, UT plots had a higher roughness (R_a). Average roughness indices of UT were also higher ($R_a = 34.51$ and $R_t = 153.54$) than those calculated for the LT ($R_a = 31.00$ and $R_t = 149.51$), but the differences between them (Figure 7) were not significant (Wilcoxon test on R_a , $W = 33$, $p = 0.575$ and on R_t , $W = 32$, $p = 0.646$).

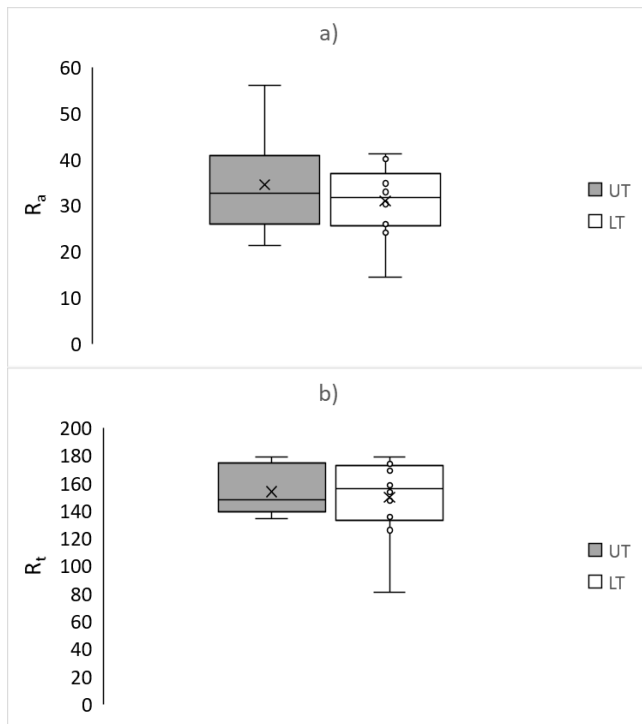


Figure 7. Box plots of roughness parameters distributions evaluated over 20 treelines plots comparing upper and lower types. a) R_a = the arithmetic average absolute distance of the roughness profile points from the average line; b) R_t = the mathematical difference between the maximum negative and positive distance from the average line (see text for further description).

Discussion

Multidecadal dynamics of upper and lower treelines

Pinyon-juniper woodlands of the Great Basin have experienced dramatic changes in distribution and structure over the past 150 years, which have been attributed to multiple, interacting influences including climate variability, increased atmospheric CO_2 , over-grazing by cattle and sheep, and reforestation following historical tree harvest (reviewed in Romme et al., 2009). Thus, we expected this dynamic vegetation type to be sensitive to environmental change agents at its elevational limits. Specifically, we expected to find upward shifts in both UT and LT reflecting expansion to warming microclimates (UT) and contraction in response to drying conditions (LT). Instead we found limited and highly variable evidence for UT expansion, indicating lack of a consistent UT response to warming over the approximately 30-year period. **This pattern could be explained by the time lag between climate warming and the slow population processes associated with woody species of high longevity, previously described by Kullman (1989) as leading to treeline inertia.** Also contrary to our predictions, we observed LT that were relatively dense, dominated by smaller size classes of trees, and that showed a strongly increasing NDVI trend, suggesting a downslope expansion of conifer-dominated woodland into adjacent shrub steppe vegetation.

This downward expansion has occurred despite the prevalence of intense regional drought during much of the 1999-2015 period (McEvoy, Huntington, Abatzoglou, & Edwards, 2012; Strachan, 2016). Drought

conditions have been associated with extensive canopy dieback and tree mortality within pinyon-juniper woodlands of nearby mountain ranges in the Great Basin (Flake & Weisberg, 2019). Elsewhere in the western United States, there has been regional dieback of pinyon-juniper woodlands that are dominated by *Pinus edulis*, a closely related species of pinyon pine that does not occur in our Great Basin study area (Breshears et al., 2005).

Expansion of Great Basin pinyon-juniper woodlands to lower elevations has been documented in mountain ranges adjacent to the Toiyabe Mts. study area (e.g. Tausch, West, & Nabi, 1981; Weisberg et al., 2007) and attributed to greater competitive ability of upper-elevation shrub-steppe communities, or a more intense history of anthropogenic disturbance, such as tree harvesting to produce charcoal for the mining industry (Ko, Sparrow, & Weisberg, 2011; Lanner & Frazier, 2011), at the lower elevations. Regionally widespread land uses such as the removal of native vegetation to plant exotic forage grasses such as crested wheatgrass (*Agropyron cristatum*) also would have been more prevalent at lower elevations at the edges of valley bottoms and along the slopes (Morris & Rowe, 2014). Thus, although precise disturbance histories are not available for our study area, the observed downslope expansion of LT may have arisen from the cessation of historical land uses that had earlier resulted in an anthropogenic elevation of the woodland's lower limit. LT dynamics must therefore be understood as the outcome of potentially interacting processes of climate change and changing historical land uses, just as has been emphasized for UT globally (Vitali et al., 2019; Vitali, Urbinati, Weisberg, Urza, & Garbarino, 2018), further complicating our ability to predict future response of either elevational tree limit.

Our failure to observe UT expansion despite documented increases in temperature over the recent multidecadal period could reflect any number of limitations reported in the literature that serve to curb the climate-driven upward expansion of UT. Seed availability could be limiting because of low seed production at upper range edges (Kroiss & HilleRisLambers, 2015). Multidecadal declines in seed cone production associated with drought, which were greatest for cooler, high-elevation sites, have been observed for *Pinus edulis* in pinyon-juniper woodlands of the Colorado Plateau (Redmond, Forcella, & Barger, 2012). Suitable microsites for germination may also be limiting to UT expansion (Harsch & Bader, 2011; Kroiss & HilleRisLambers, 2015), as can interspecific interactions with both shrub and herbaceous components of the plant community (Liang et al., 2016). In the case of pinyon-juniper woodland tree lines, pinyon pine establishment depends strongly on the availability of nurse shrubs (usually *Artemisia* species) to provide suitable microsites (Chambers, 2001) and to allow *Pinus monophylla* to overcome a critical population bottleneck associated with first-year seedling survival, thus permitting establishment in areas without pre-existing tree cover (Urza et al., 2019). An important role of different species of jays and other birds as vectors for seed dispersal in pinyon-juniper woodlands has been well documented (Gabrielson & Jewett, 1970; Miller & Wigand, 1994).

Differences in pattern and structure among upper and lower treelines

Few studies have compared dynamics of UT and LT ecotones simultaneously along the same altitudinal gradient. Those that have done so have generally found that temperature is a limiting factor exclusively at UT, but that precipitation becomes a constraint mostly at LT ecotones (Driese et al., 1997; Klinge et al., 2018; Markgraf & Huber, 2010). Exceptions occur in very dry environments where the differences between UT and LT are negligible (Yang et al., 2013). Our underlying conceptual model reflected hypothesized differences in the causal mechanisms driving the formation of UT, which are believed to be energy limited, from LT, which are believed to be water limited. We expected these differences to be manifested in the spatial structures of UT and LT within our study region. Surprisingly, we found little difference in treeline shape and pattern. The few meaningful differences in stand structure that were observed (e.g. greater density of smaller trees at LT) indicate different stages of stand development associated with trajectories of treeline change, as discussed previously. Another important difference that we observed was a more aggregated pattern of trees at LT indicating an earlier stage of woodland development, associated with the observed recent downslope expansion, where self-thinning processes have not yet resulted in more uniform tree distributions (Larson et al., 2015). Differences in treeline shape complexity were not statistically significant, although they followed the hypothesized relationship where LT sites are expected to exhibit less complex shapes because they are more influenced by anthropogenic factors (Harsch & Bader, 2011).

Commento [MG2]: Miller, R. F., & Wigand, P. E. (1994). Holocene changes in semiarid pinyon-juniper woodlands: response to climate, fire, and human activities in the US Great Basin. *BioScience*, 44(7), 465-474.

Further comparisons of UT and LT structural differences are needed to advance our understanding of the fundamental mechanisms that limit tree distribution, as well as to forecast major vegetation shifts in response to global environmental change. Although we captured detailed information on numerous individual tree crowns, our study was limited in its geographical scope. Future comparative studies of UT and LT should incorporate a more representative array of environmental conditions across broad ecoregions, and thereby encompass a broader range of regional, climatic and taxonomic diversity. This may prove challenging because of the difficulty in identifying a suitable representation of replicate study units at the landscape level, where “every landscape is different” and it can be problematic to control experimentally for confounding sources of environmental variation (Hargrove & Pickering, 1992). However, mapping of tree crowns within replicate treeline landscapes could be made more efficient using automated approaches to tree crown detection and delineation (Freeman, Stow, & Roberts, 2016; Greenberg, Dobrowski, & Ustin, 2005).

Another possible limit to our study is related to species composition differences between UT and LT. Juniper is generally more drought tolerant and can extend to lower elevations, whereas the pinyon pine is more cold tolerant (West, 1999). This species-specific pattern may have influenced our results, unfortunately was not possible to differentiate these two tree species in the aerial imagery that we used.

In the paper, we should acknowledge the potential for tree species composition differences between UT and LT, pointing to the literature indicating that the juniper can extend to lower elevations, and the pinyon to higher elevations (likely the case in the Toiyabes).

Similarities in treeline structure across the elevational bands, combined with a general lack of support for hypothesized directions of treeline change, suggest that our conceptualization of UT and LT as being “energy limited” vs. “water limited” was an overly simplistic model. A more sophisticated approach might look at energy and water limitation at a finer temporal resolution (monthly or even weekly) to predict the amount of growth that can occur during the growing season. Local-scale drivers may dominate treeline change, and land-use history can be of overriding importance (Ameztegui et al., 2016; Vitali et al., 2018). Dynamics of Great Basin pinyon-juniper woodlands in particular have been influenced by land-use change and historical tree harvesting (Lanner & Frazier, 2011; Young & Budy, 1979) and slow successional response to episodic, high-severity wildfire (Bauer & Weisberg, 2009; Romme et al., 2009). Treeline ecotones are likely shaped by the complex interactions of multiple drivers, challenging the development of general predictions for how LT vs UT vary in their spatial structure or will differ in their response to environmental change.

Data availability statement

The authors of this manuscript declare that the data supporting the results of our work will be archived in a public repository, such as Dryad.

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