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Evidence of widespread topoclimatic limitation for lower treelines of the Intermountain West, United States

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Abstract. Many forests in dry mountain regions are characterized by a lower elevational treeline. Understanding the controls on the position of lower treeline is important for predicting future forest distributional shifts in response to global environmental change. Lower treelines currently at their climate limit are expected to be more sensitive to changing climate, whereas lower treelines constrained by non-climatic factors are less likely to respond directly to climate change but may be sensitive to other global change agents. In this study, we used existing vegetation classifications to map lower treelines for our 1.7 million km^2 study region in the U. S. Intermountain West. We modeled topoclimatic drivers of lower treeline position for each of three dominant forest types to identify topoclimatically limited treelines. We then used spatial data of edaphic properties, recent fire, and land use to identify lower treelines potentially constrained above their ecophysiological limits by non-climatic processes. We found that the lower treeline ecotone of pinyon–juniper woodlands is largely limited by topoclimate and is likely to be sensitive to increasing temperatures and associated droughts, though these effects may be heterogeneously distributed across the landscape. In contrast, dry mixed-conifer lower treelines in the northern portion of the study area rarely reached their modeled topoclimatic limit, suggesting that non-climatic processes, including fire and land use, constrain the lower treeline above its ecophysiological limits in this forest type. Our results suggest that much of the lower treeline in the Intermountain West is currently climate limited and will thus be sensitive to ongoing climate changes. Lower treelines in other arid or semi-arid mountainous regions around the globe may also be strongly sensitive to climate, though treeline response to climate change will be mediated at the local scale by soil properties, biotic interactions, and natural or anthropogenic disturbances. Our regional study of lower treeline provides a framework for identifying the drivers of lower treeline formation and allows for more robust projections of future treeline dynamics, which are needed to anticipate shifting global distributions of the forest biome.

Key words: disturbance; ecotone; forest edge; global environmental change; land use; lower treeline; range limits; topoclimate.

Introduction

Lower and upper treelines jointly determine the distribution of forests in many mountainous regions. As climate changes, both treelines are expected to respond by shifting their position (Grace et al. 2002, Clark et al. 2016), directly impacting the distribution of tree cover. In regions where both lower and upper treelines occur, lower treelines typically constitute the lengthier range boundary due to mountain geometry. Therefore, minor shifts in the position of the lower treeline have the potential to disproportionately affect global tree cover and, by extension, carbon stocks and other forest ecosystem services (Anderegg et al. 2012, Ahlström et al. 2015). Forest responses to global change processes depend on the factors controlling range limits (Copenhaver-Parry et al. 2017). Currently, many large-scale changes are occurring simultaneously and in interaction (Barnosky et al. 2012), including warming climate, land use change, exotic species invasions, and shifts in disturbance regimes. In order to anticipate future shifts in the distribution of global forests and woodlands, we must first understand current limitations to lower treelines and how they vary geographically.

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Lower treelines constitute a major forest boundary in dry mountain regions across the globe, including the Intermountain West of the United States, inner Mongolia, interior valleys of the Alps, the Himalaya, and the western edge of the Patagonian Steppe (Peet 2000, Weber et al. 2007, Liu and Cui 2009, Sharma et al. 2014, Mundo et al. 2017). In these regions, aridity is inversely related to elevation, resulting in relatively low water availability, and high levels of abiotic stress, at lower elevations (McDowell et al. 2010, Herrero et al. 2013). At low elevations, unfavorable water balance (precipitation minus evapotranspiration) may impose direct limits to tree demographic processes, creating lower treeline edges defined by the ecophysiological limits of the tree species present (Daubenmire 1943, Rowlands 1993). Lower treelines that are currently limited by water balance are likely to exhibit rapid responses to drought and increased evaporative demand resulting from higher temperatures (Romme and Turner 1991), and drought stress has triggered extensive tree mortality at dry range edges across the globe (Anderegg et al. 2019). However, climatic effects on lower treelines can be difficult to disentangle from other processes. For example, human land uses tend to be concentrated at lower elevation forest boundaries in many mountainous regions, resulting in land cover changes and anthropogenic influences on fire regimes that may determine the position of lower treeline at local scales.

Despite their importance to global tree cover, lower treelines have received little scientific attention. In contrast, a comprehensive framework exists for upper treeline, based on a rich conceptual development that has spanned more than a century (reviewed in Harsch et al. 2009). Ultimate limits to upper treeline position correspond to temperature controls on ecophysiological processes (Körner 1998), though physical barriers, land use, natural disturbance, and biotic interactions can exert secondary constraints, preventing treelines from reaching their climate potential and making them less sensitive to climate changes (Elliott 2011, Weisberg et al. 2013, Liang et al. 2016, Vitali et al. 2018). We expect that the position of lower treeline is similarly controlled by a combination of ultimate ecophysiological limits and secondary constraints, yet the relative importance of climate, land use, fire, and physical barriers for determining the position of lower treeline is largely undescribed.

In this paper, we present an empirical analysis of lower treelines of the Intermountain West, an extensive dryland region of the United States. The composition of lower elevation forests in the western United States has been broadly described (e.g., Peet 2000), but the extent of lower treeline, its distribution among forest types, and the dominant drivers of lower treeline formation have not been identified. We developed a map of lower treelines and used it to address the following questions: (1) What forest types are most common at the lower treeline? (2) How much of lower treeline is topoclimatically limited and hence most sensitive to climate change? (3) For lower treelines that are not topoclimatically limited, is there evidence of proximate constraints from fire, anthropogenic land uses, or natural barriers? We used existing vegetation cover classifications to produce a map of lower treelines and quantify the distribution of lower treelines by forest type. To identify topoclimatically limited lower treelines, we used boosted regression trees to model the effect of topoclimatic variables on the probability of forest cover near the lower treeline edge, identifying topoclimatic thresholds to forest cover and quantifying the proportion of lower treeline predicted to be climatically unsuitable. Finally, we examined the potential influence of proximate constraints by quantifying the proportion of lower treeline that is adjacent to recently burned patches, agricultural or developed areas, or natural barriers such as wetlands and scree patches. Our study questions were addressed separately for three major forest types, allowing for a comparison of the major drivers of lower treeline position and likely treeline responses to environmental change.

Methods

Study area

This study took place in the Intermountain West of the United States, defined here as the area between the Pacific Crest and the Continental Divide. The study area, which spans more than 15° of latitude, includes portions of 11 U.S. states and covers nearly 1.7 million km^2. The climate of the Intermountain West is strongly influenced by the north-to-south-trending mountain ranges that comprise the Pacific Crest, which cast a rain shadow to the east and result in generally low precipitation across the region. The timing of precipitation ranges from winter-dominated precipitation in the northwest to monsoonal patterns of summer precipitation in the southeast. Mean annual temperature decreases with higher latitudes across the study area. At local scales, temperature and precipitation are strongly related to elevational gradients, a climate pattern that is reflected by dramatic transitions in vegetation types over short distances. One of these vegetation transitions occurs at the lower treeline, where dry forests and woodlands transition into shrub- and grass-dominated communities.

Lower treeline delineation and distribution among forest types

We mapped lower treelines across the entire study area using National Land Cover data from the Gap Analysis Program (U.S. Geological Survey 2011), a 30-m resolution classification of major vegetation types from Landsat imagery. Land cover data were reclassified into a binary forest/non-forest raster. Pixels classified as "forest" included all "Warm or Cool Temperate Forests and Woodlands" in the Formation class from the Gap

Analysis Program National Land Cover data (U.S. Geological Survey 2011). This data set conforms with the National Vegetation Classification Standard, which uses both "forest" and "woodland" to indicate the dominance of the tree growth form, including various combinations of needle-leaved conifer, broad-leaved deciduous, and broad-leaved evergreen tree species of varying height and canopy spacing (Federal Geographic Data Committee 2008). Pixels classified as "non-forest" represented all other land cover types, including vegetation dominated by shrubs and herbaceous species, flooded or swamp forests, and areas used for agriculture or human development. Discrete patches of forest or non-forest smaller than 1,000 pixels were merged with their surrounding cover type, resulting in a minimum cartographic unit of 0.9 km^2. The binary forest/non-forest raster was converted to polygons, and the edges between forest and non-forest polygons were converted to a polyline representing all forest edges. We used the contrast between the elevations for forest and non-forest patches bordering the forest edge to differentiate between upper and lower treelines for each polyline segment. Using Digital Elevation Models (U.S. Geological Survey 2009), mean elevations of forest and non-forest pixels were calculated within a 4-km^2 neighborhood surrounding each polyline vertex. For each polyline segment, the mean non-forest elevation was subtracted from the mean forest elevation. Lower treelines were identified as segments with a positive elevation contrast (where adjacent forested areas were at a higher elevation than adjacent non-forested areas). Lower treeline segments occurring within 100 m of water bodies and segments that were outliers in elevation (mean elevation greater than 2,500 m above sea level) were removed. Finally, we visually inspected the resulting map with high-resolution aerial imagery, excluding segments that were not representative of lower treeline (e.g., sections around interior fires, harvested patches, or meadows), removing <1% of the treelines resulting from the automated process. All spatial processing required for mapping treeline was done in ArcGIS (ArcGIS Version 10.5; Computer Software, ESRI Redlands, California, USA).

We located one sampling point at every 1-km interval along the mapped lower treeline (391,131 sampling points). We intersected the sampled points with the vegetation class for the adjacent forest based on Ecological System categories from the Gap Analysis Program National Land Cover data (U.S. Geological Survey 2011), so that each lower treeline point was attributed with the relevant forest type. We quantified the distribution of lower treelines across forest types and identified the most widespread forest community types to focus on for analyses of lower treeline drivers.

Topoclimatic variables

We used publicly available data sources to generate spatial variables of interest (Table 1). Digital Elevation Models (US Geological Survey 2009) were used to map elevation and to generate a heat-load index (Heatload), which represents topographic effects on solar radiation and potential evapotranspiration (McCune and Keon 2002). We used 30-yr normal gridded PRISM climate data (PRISM Climate Group 2016) to calculate climatic variables that have previously been shown to be strong predictors of tree performance in the Intermountain West (Williams et al. 2013, Redmond et al. 2017): winter precipitation (WinPPT), summer vapor pressure deficit (SumVPD), and the proportion of annual precipitation falling during summer (Monsoon). Soil available water storage (AWS), which represents the amount of water that the soil can store in the top 1 m, was obtained from the USDA soil survey gridded SSURGO database (Natural Resources Conservation Service 2013). A Thornthwaite water balance model (Dingman 2002, Lutz et al. 2010), which incorporates 30-yr normals of monthly temperature and precipitation, elevation, and soil water-holding capacity, was used to calculate annual climatic water deficit (CumlCWD) and annual actual evapotranspiration (CumlAET). Climatic water deficit represents the amount by which potential evapotranspiration exceeds actual evapotranspiration, and is strongly correlated with vegetation distributions (Stephenson 1990, Dilts et al. 2015). Actual evapotranspiration is defined as the evaporative water loss from a site covered by a hypothetical standard crop (Lutz et al. 2010), which represents the simultaneous availability of energy and water and is considered a proxy for site net primary productivity (Stephenson 1990). The water balance model that we used follows Lutz et al. (2010) and incorporates water storage in the form of snowpack, soil water storage, which is controlled by soil AWS, and a topographic modifier based on the McCune and Keon (2002) heat-load index. All data were calculated at monthly intervals using the 30-yr climate normals (1981–2010) and summarized on an average annual basis.

Data analysis

Topoclimatic models of lower treeline position.—To identify topoclimatic thresholds to lower treeline position, we modeled the effects of topoclimatic predictors on the probability of forest cover near the lower treeline. For each of the three major forest types, we randomly generated 7,000 points within a 1-km buffer distance of the lower treeline boundary with a minimum spacing of 1 km and classified each point as either forested (above lower treeline) or non-forested (below lower treeline). Prior to analysis, we removed all non-forested data points that intersected recent fire, agricultural land, developed areas, or wetlands (6.8% of analysis points for CO Plateau pinyon–juniper, 4.2% for Great Basin pinyon–juniper, and 18.7% for N. Rockies dry mixed conifer), since these other factors, rather than their topoclimatic characteristics, are likely to explain the lack of trees in those locations. We used generalized boosted

TABLE 1. Variable descriptions and sources.

Variable					
Number	Name	Definition	Units	Resolution	Date
1	Forest type	classification of forest cover adjacent to (above) treeline†	categorical	30 m	2011
2	Heatload	Topographic heat-load index‡	unitless index	500 m	na
3	WinPPT	winter precipitation (Nov–Mar)§	mm	800 m	1981–2010 (30-yr normal)
4	SumVPD	summer vapor pressure deficit (May–Jul)§	hPa	800 m	1981–2010 (30-yr normal)
5	Monsoon	proportion of annual precipitation falling in summer (Jun–Aug)§	proportion	800 m	1981–2010 (30-yr normal)
6	AWS	soil available water storage for top 1 m of soil¶	mm	100 m	n/a
7	CumlCWD	cumulative annual climatic water deficit#	mm	500 m	1981–2010 (30-yr normal)
8	CumlAET	cumulative annual actual evapotranspiration#	mm	500 m	1981–2010 (30-yr normal)
9	Adjacent land cover	classification of non-forest cover adjacent to (below) treeline†	categorical	30 m	2011
10	Burn	recent burn status||	binary	vector	1984–2010

†Author generated based on U.S. Geological Survey (2011). See Appendix S1: Table S2 for merged categories.
‡Author generated based on U.S. Geological Survey (2009)
§Author generated based on PRISM Climate Group (2016)
¶Natural Resources Conservation Service (2013)
#Author generated based on U.S. Geological Survey (2009, Natural Resources Conservation Service (2013), PRISM Climate Group (2016)
||Monitoring Trends in Burn Severity (2014).

regression trees to model the probability that a point is forested or non-forested (Bernoulli distribution) as a function of topoclimatic variables. Boosted regression trees are a computer-learning approach in which classification and regression trees are iteratively fit to the data and cross-validated on withheld samples (De'ath 2007), allowing for the modeling of interactions, thresholds, and other non-linear relationships. We used the gbm.step function in the R package dismo (Hijmans et al. 2017), which uses 10-fold cross-validation to optimize the number of trees in the final model to minimize variance. Learning rate was adjusted so that the final models included at least 1,000 trees. Models were fit using a random subset of 80% of the data points, and final models were evaluated against the remaining 20%. Seven topoclimatic predictor variables (Variables 2–8 in Table 1) were chosen to represent components of plant water balance, based on a priori hypotheses of the factors limiting tree growth, survival, and establishment below lower treeline (Piedallu et al. 2013, Williams et al. 2013). Models were fit separately for each major forest type identified in the treeline mapping process, in order to account for differences in ecophysiological tolerances and regional climate. For all models, pairwise correlations among predictor variables were <0.7, and variance inflation factors for predictor variables were <2.5 (Appendix S1: Table S1). To compare the rate at which aridity changes in relation to elevation among forest types, we used a linear regression to model cumulative climatic water deficit (CumlCWD) as a function of the interaction between elevation and forest type and used the emtrends function in the R package emmeans (Lenth et al. 2020) to quantify slope differences among forest types.

Lower treeline drivers.—We paired the results of the topoclimatic models with overlays of land cover and fire occurrence to categorize the potential drivers of lower treeline position for each major forest type. The results of the boosted regression tree models were applied to the mapped lower treelines for each major forest type, resulting in a predicted probability of forest cover given the topoclimatic characteristics of lower treeline points spaced at 1-km intervals. Topoclimatic treelines were defined as lower treeline points predicted to be unsuitable for forest cover given their topoclimatic characteristics. We considered a lower treeline point to be topoclimatically limited if the predicted probability of forest cover was <0.5, which was the threshold that optimized model classification accuracy. We intersected the lower treeline points to land cover and fire data, and used these attributes to categorize points that were not classified as topoclimatically limited. To quantify the proportion of lower treeline that is potentially constrained by physical barriers, we identified lower treeline points that were adjacent to either rock, cliff, or scree patches or seasonal or perennial wetlands. Lower treeline points were classified as burned if they intersected a fire (Monitoring Trends in Burn Severity 2014) that occurred after 1984 and before the publication of the National Land Cover Data in 2011. Lower treelines potentially constrained by anthropogenic land uses were adjacent to agricultural or developed land cover types. Adjacent land cover types used for physical barriers and anthropogenic treeline classifications were based on merged land cover categories (Appendix S1: Table S2) derived from Ecological System categories from the Gap Analysis Program National Land Cover data (U.S. Geological Survey 2011).

Results

Distribution of lower treeline

Our mapping process resulted in 422,429 km of lower treeline across the 1.7 million km^2 study area (treeline density = 0.25 km/km^2). There were 57 forest types present at lower treeline, but most types were uncommon and spatially discontinuous, and only 16 forest types occurred at 1% or more of the total lower treeline length (Appendix S1: Fig. S1). We combined forest types that shared tree species and co-occurred in a fine-scale mosaic (Appendix S1: Table S2). For subsequent analyses of lower treeline drivers, we focused on three major forest community types, which were spatially continuous and collectively represented 65.2% of lower treeline (Fig. 1): (1) Colorado Plateau Pinyon–juniper Woodlands (30.7%) are dominated by *Pinus edulis* and/or *Juniperus osteosperma* and occur on dry mountains and foothills of the Colorado Plateau region; (2) Great Basin Pinyon–juniper Woodlands (21.5%) are dominated by *Pinus monophylla* and/or *Juniperus osteosperma* and are found on dry mountain ranges of the Great Basin and the eastern foothills of the Sierra Nevada; (3) Northern Rocky Mountain Dry mixed-conifer Forests (13.0%) are dominated by *Pinus ponderosa* with limited presence of *Pseudotsuga menziesii* and are found in foothills of the northern Rocky Mountains, the Columbia and Modoc Plateaus, and the eastern Cascades.

Topoclimatic drivers of lower treeline position

For both Colorado Plateau and Great Basin pinyon–juniper woodland types, topography and climate were strongly related to the position of lower treeline. Soil available water storage (AWS) interacted with cumulative climatic water deficit (CumlCWD) to predict lower treeline position (Fig. 2a, b), such that the probability of forest cover was highest in areas with shallow or coarse-textured soils (low available water storage) and low aridity (low climatic water deficit). Partial dependence functions (Fig. 2a, b; Appendix S1: Section S1) suggest a threshold effect of climatic water deficit at 500–600 mm for Colorado Plateau pinyon–juniper, and at 400–500 mm for Great Basin pinyon–juniper. A steep slope in the relationship between climatic water deficit and elevation in both pinyon–juniper types (Appendix S1: Fig. S2a, $\beta = -0.40$; Appendix S1: Fig. S2b, $\beta = -0.27$) shows that slight differences in lower treeline elevation are associated with large differences in aridity, although this slope was significantly steeper for pinyon–juniper in the Colorado Plateau than in the Great Basin ($P < 0.001$). Considering all topoclimatic characteristics across the current distribution of lower treeline, the topoclimatic models predicted low probability of forest cover (i.e., predicted to be topoclimatically unsuitable for tree cover) for lower treelines across much of the two regions (Fig. 3a, b). In the Colorado Plateau (Fig. 3a), lower treelines predicted to be topoclimatically limited were clustered in northeastern Arizona, while topoclimatically limited treelines were widespread across the southern and central Great Basin (Fig. 3b).

For Northern Rocky Mountain dry mixed-conifer forests, topoclimate was weakly related to lower treeline position. Cumulative climatic water deficit showed a threshold effect on forest cover at 300–350 mm (Appendix S1: Section S1), and there was a non-threshold effect of Heatload, such that the probability of forest cover declined with increasing Heatload or climatic water deficit (combined effect shown in Fig. 2c). The negative relationship between elevation and climatic water deficit was much weaker for the lower treelines of Northern Rocky Mountain dry mixed-conifer forests (Appendix S1: Fig. S2c, $\beta = -0.07$) than for the pinyon–juniper woodland types ($P < 0.001$). This relatively weak relationship between elevation and climatic water deficit is indicative of a shallow elevational gradient of aridity, in which the modeled threshold of cumulative water deficit was rarely (<5%) exceeded at the lower treeline, even at very low elevations. The topoclimatic model predicted relatively high probability of forest cover across the much of the region with the exception of the northern edge of the Columbia Plateau (Fig. 3c), suggesting that this lower treeline is generally not topoclimatically limited.

Lower treeline drivers

The lower treeline categorization process revealed substantial differences among the major forest types (Fig. 4). For Colorado Plateau pinyon–juniper lower treeline, 43.0% was classified as topoclimatically limited (i.e., <0.5 predicted topoclimatic probability of forest cover). A total of 14.4% was adjacent to physical barriers (11.8% adjacent to rock, cliff, or scree and 2.6% adjacent to wetlands). 2.0% intersected recent fire, 2.7% was adjacent to anthropogenic land uses (0.7% developed and 2.0% agricultural), and 38.0% was undefined (i.e., did not fall into any of the other categories).

Approximately one-half (49.7%) of Great Basin pinyon–juniper lower treeline was classified as topoclimatically limited: 7.0% intersected recent fire, while 3.1% was adjacent to physical barriers (2.6% adjacent to rock, cliff, or scree and 0.5% adjacent to wetlands), 0.9% was adjacent to anthropogenic land uses (0.3% developed and 0.6% agricultural), and 39.4% was undefined.

A smaller proportion (10.5%) of Northern Rockies dry mixed-conifer lower treeline was classified as topoclimatically limited: 15.6% was adjacent to anthropogenic land uses (12.7% developed and 2.9% agricultural), 16.3% was adjacent to physical barriers (0.3% adjacent to rock, cliff, or scree and 16.0% adjacent to wetlands), 9.5% intersected recent fire, and 48.0% was undefined.

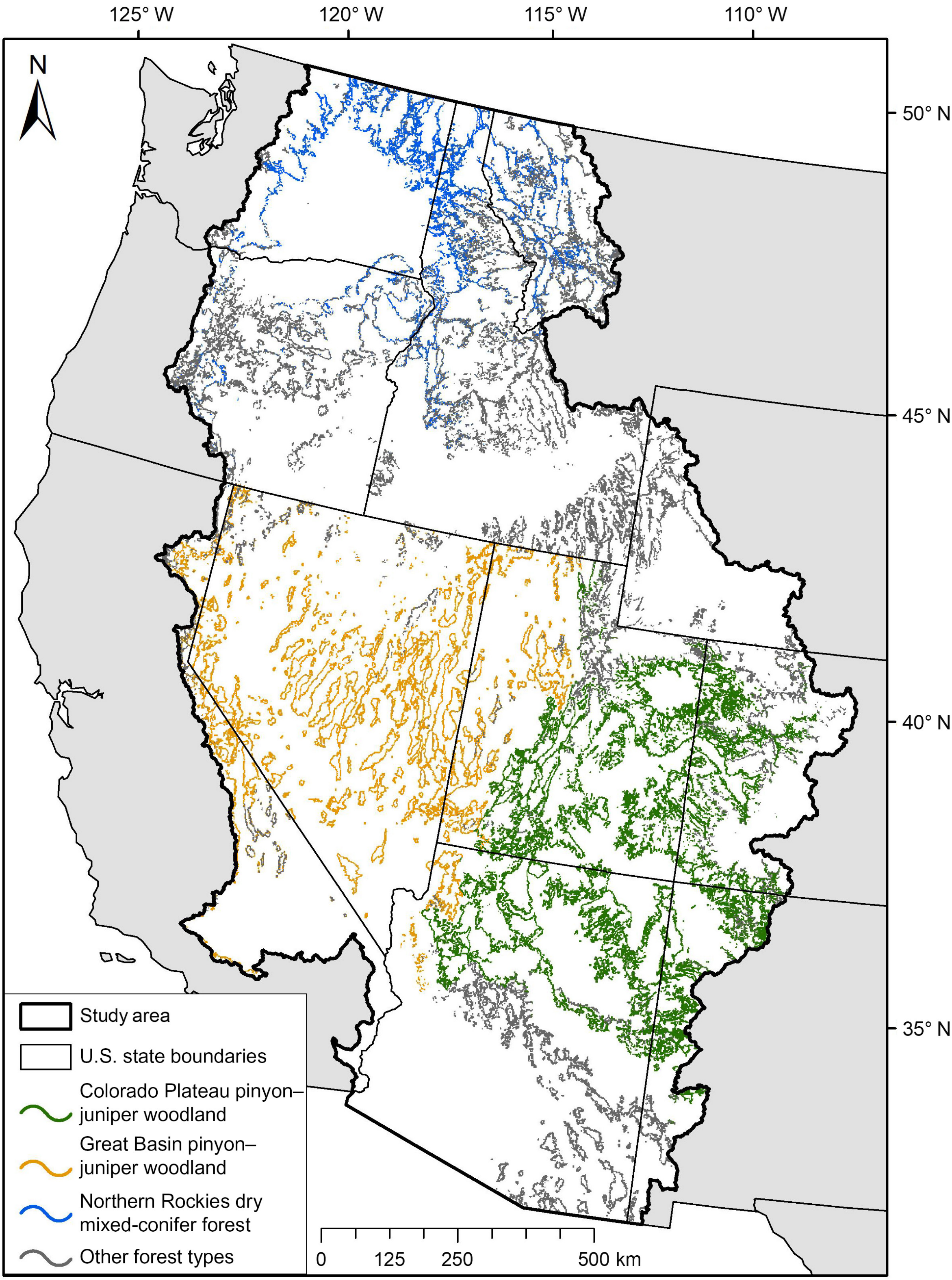

Fig. 1. Mapped lower treelines of the U.S. Intermountain West, colored by major forest type. Projection: Albers Equal-Area Conic, NAD 1983. Lower treeline raster was coarsened to aid visualization.

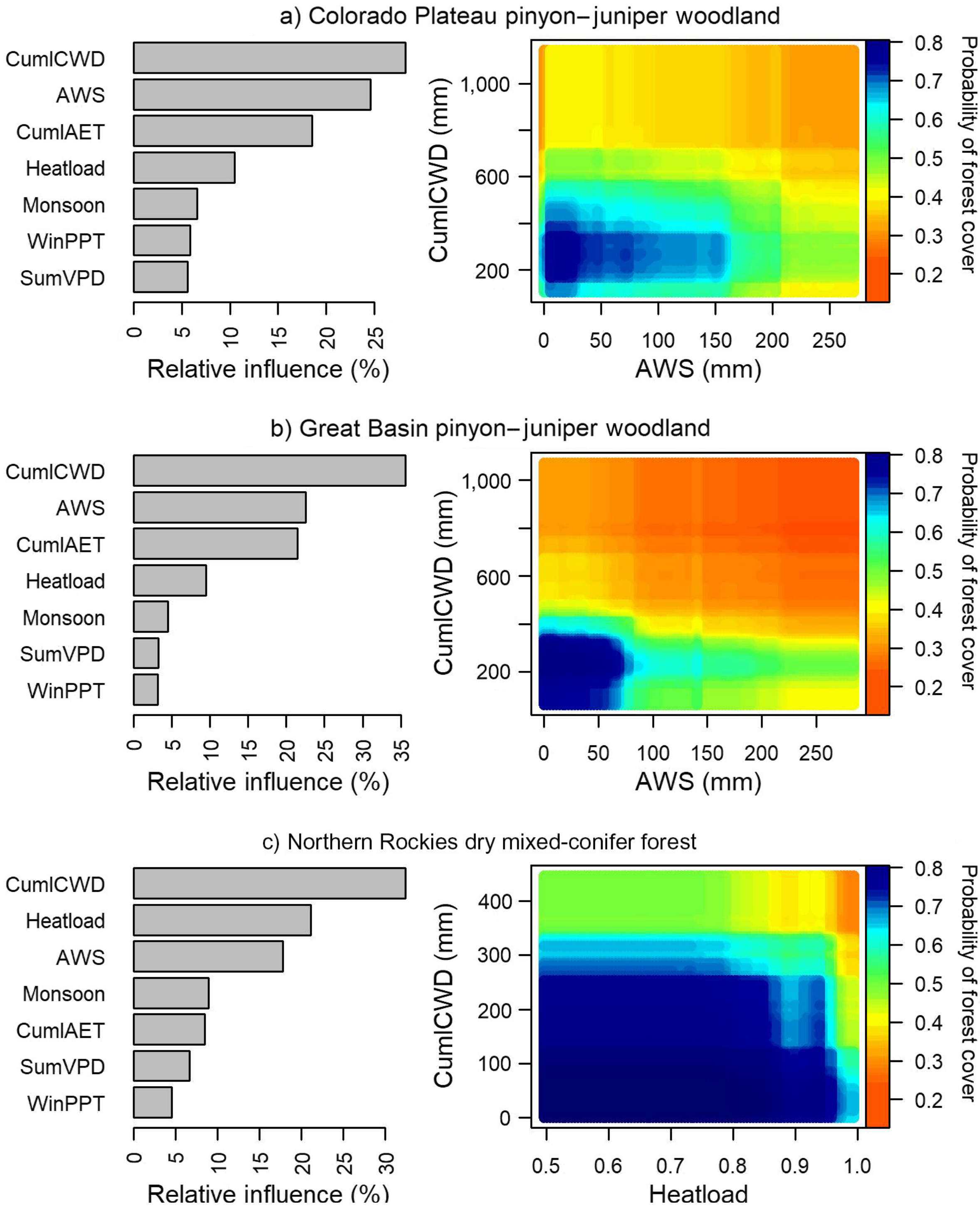

Fig. 2. Topoclimatic predictors of forest cover within 1 km of lower treeline for major forest types of the Intermountain West. Left column shows rank of variable importance. Right column shows probability of forest cover, expressed as a partial dependence function of the two most important predictors. The optimized model was used to estimate the probability of forest cover for all possible combinations of the top two predictors within the range of the training data, providing a visualization of the primary landscape characteristics that are predicted to be topoclimatically suitable (cooler colors) or unsuitable (hotter colors) for tree cover. AWS, soil available water storage; CumlAET, cumulative actual evapotranspiration; CumlCWD, cumulative climatic water deficit; Heatload, heat-load index; Monsoon, summer precipitation/annual precipitation; SumVPD, summer vapor pressure deficit; WinPPT, winter precipitation.

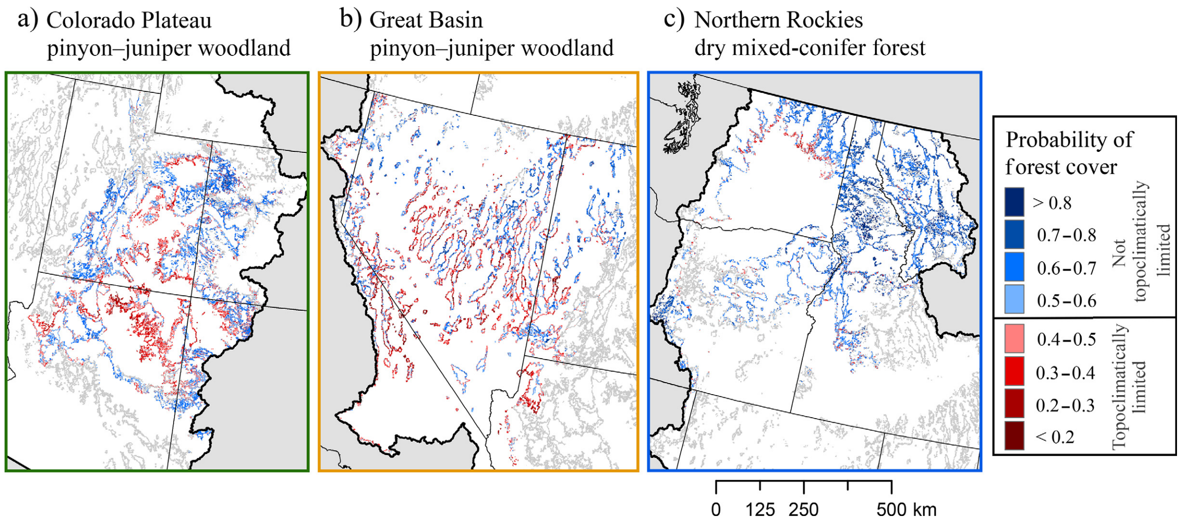

Fig. 3. Predicted topoclimatic probability of forest cover at lower treeline for three major forest types of the Intermountain West. Lower treeline segments are predicted to be topoclimatically limited where the probability of forest cover is <0.5 (shown in red). Predicted probabilities were derived from topoclimatic models of forest cover within 1 km of lower treeline, and separate models were developed for each forest type. Projection: Albers Equal-Area Conic, NAD 1983. Gray lines are lower treelines comprised of other forest types, and gray shaded areas are outside the study area. Lower treeline raster was coarsened using median probability values to aid visualization.

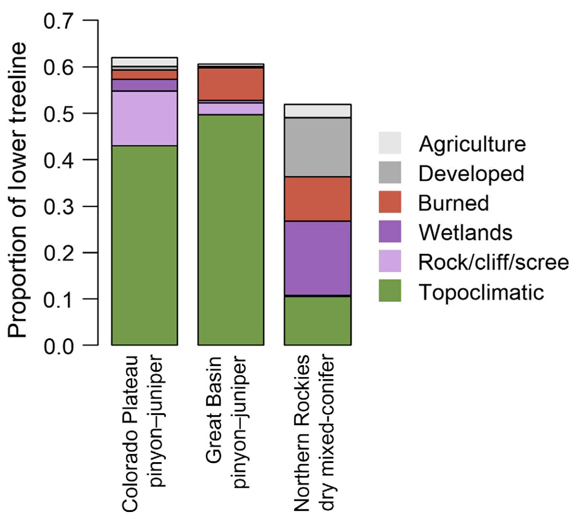

Fig. 4. Lower treeline drivers for three major forest types of the Intermountain West. The height of each bar represents the proportion of lower treeline in each category. Topoclimatic treelines (green) were defined as lower treeline points at which the predicted topoclimatic probability of forest cover was <0.5. Lower treelines constrained by physical barriers (purple) were adjacent to either rock, cliff, or scree patches or seasonal or perennial wetlands. Burned treelines (red) were lower treeline points that have burned since 1984. Anthropogenic treelines (gray) were adjacent to agricultural or developed land cover types.

Discussion

Identifying the drivers of lower treeline can provide important insights into how the forest belt will respond to ongoing climate changes and can identify forests at risk of climate-induced contraction, information that is increasingly important in the current era of rapid global change. Our results suggest that, for an extensive dryland region of the United States, much of the lower treeline is currently climate-limited and will thus be sensitive to ongoing climate changes. However, lower treelines in the northern portion of the study area were found to be largely constrained above their climate potential by physical features, land use, and fire, and will therefore be less responsive to climate change than those at or near their ecophysiological limits (Holtmeier and Broll 2005). By comparing evidence for multiple drivers of forest distribution rather than assuming widespread climatic equilibrium, our approach provides a spatially explicit framework for anticipating future dynamics at the lower treeline ecotone.

We found that three forest types account for 65.2% of lower treeline in the Intermountain West: Colorado Plateau pinyon–juniper woodlands, Great Basin pinyon–juniper woodlands, and Northern Rocky Mountain dry mixed-conifer forests. These lower treeline forest types occur in discrete geographic regions, and thus represent distinct climatic zones, disturbance regimes, and land use histories. Additionally, these forest types are dominated by different tree species with varying tolerances to drought and fire. Although the entire study region occurs in the rain shadow of the Pacific Crest and receives relatively low levels of annual precipitation, there is an overall gradient of increasing aridity toward the south, and a shift from winter-dominated precipitation in the northwest to monsoonal patterns of summer precipitation in the southeast. Pinyon pine and juniper species that dominate the two pinyon–juniper woodland types are highly drought resistant (Niinemets and Valladares 2006), yet intolerant of fire (Romme et al. 2009), and historically this forest type experienced long fire return intervals (Floyd et al. 2004, Bauer and Weisberg 2009). In contrast, ponderosa pine that dominates the Northern Rocky Mountain dry mixed-conifer forest type is moderately drought tolerant yet highly resistant to fire (Fischer and Bradley 1987, Niinemets and Valladares 2006), and likely experienced relatively frequent fires historically (Baker et al. 2007). In the southwestern United States where pinyon–juniper woodlands occur, human land uses are currently concentrated in urban centers, with dispersed agricultural uses occurring primarily in valley bottoms. However, past anthropogenic impacts on lower treeline may have been much more intensive than they are currently, as settlement-era mining and agriculture resulted in extensive wood harvest and land clearing (Ko et al. 2011, Morris and Rowe 2014). In the northern region where dry mixed-conifer forests are at the lower treeline, current population density is higher and intensive agriculture is more widespread.

Topoclimatically limited lower treelines are locations where forest edges reach their ecophysiological limits, beyond which their expansion is limited by unfavorable water balance. By definition, topoclimatically limited treelines are highly sensitive to climate changes, and they are expected to shift uphill in response to increased temperatures and associated increases in atmospheric water demand (Parks et al. 2018). Our results indicate that much of the lower treeline of the Intermountain West currently occurs at or near topoclimatic thresholds of aridity, and are thus likely to respond to future changes in climate that reduce water availability. We found that cumulative climatic water deficit, a proxy of overall aridity, was a strong boundary control for all major forest types within the Intermountain West, resulting in forest-specific thresholds of soil water balance beyond which the probability of forest cover was extremely low. In particular, we found strong evidence that broad-scale gradients of water balance largely control the position of lower treeline in pinyon–juniper woodlands of the Colorado Plateau and the Great Basin, which together represent more than 50% of lower treeline of the Intermountain West. Nearly half of the combined pinyon–juniper lower treeline was predicted to be topoclimatically limited, suggesting that increasing temperature and associated increases in evapotranspiration (Cayan et al. 2010) may result in widespread treeline shifts to higher elevations or more mesic topographic settings (Anderegg et al. 2012).

Indeed, extensive drought-induced tree mortality has been observed at dry forest range edges across the globe (Anderegg et al. 2019). Past drought events have triggered high levels of tree mortality in pinyon–juniper woodlands of the Colorado Plateau (Breshears et al. 2005) and the Great Basin (Flake and Weisberg 2019), and in both regions, the mortality has been greatest in hotter, drier sites within the woodland belt. An abnormally severe recent drought resulted in widespread tree mortality in mixed conifer forests of the western slope of the Sierra Nevada Mountains, and the highest levels of mortality again occurred in lower-elevation forest stands (Fettig et al. 2019). Lower treeline shifts in response to climate change can occur even where adult trees are capable of persisting in or adapting to novel climate conditions. For example, where regeneration or reproduction is limited by current climate conditions (e.g., Will et al. 2013, Simeone et al. 2019), the longevity of trees can create inertia in treeline responses to climate change, and stand-replacing disturbance can catalyze rapid shifts of forest edges (Donato et al. 2016, Davis et al. 2019, Parks et al. 2019).

Soil properties can mediate the effect of climate on plant-available resources, and in some cases, substrate can be a stronger predictor of drought-induced mortality than precipitation inputs (Looney et al. 2012). In our study, soil properties appeared to mediate the effects of climate-driven aridity on lower treeline position. Our results suggest that topoclimatic limits to lower treeline are characterized by a broad ecotone that is marginally suitable for trees. Within these marginal locations, soil properties that ameliorate water stress may increase the probability of tree establishment and survival. In pinyon–juniper woodlands, we found that treeline extended to climatically drier locations in coarse soils where near-surface soil available water storage was low. Coarse soils allow for rapid infiltration of water, limiting losses to surface evaporation and runoff (Noy-Meir 1973, Sala et al. 1988), increasing water storage in deep soil pools and rock fissures to which trees and other deep-rooted plants have access (Schwinning 2010), and facilitating tree expansion into adjacent plant communities (Whitesides and Bekker 2011). Consistent with our findings, higher levels of tree mortality occurred in sites with finer textured soils after a recent drought in the Great Basin (Flake and Weisberg 2019).

Based on studies of upper treeline, we expected to find widespread evidence that physical barriers, land use, and fire constrain the distribution of trees, preventing lower treelines from reaching their climate potential (Motta and Nola 2001, Weisberg et al. 2013). For example, in some regions of the world, upper treelines are found in mountain ranges where trees are not expected to be limited based on climate alone (Vitali et al. 2018). For extensive areas within dry mixed-conifer forests in the northern portion of the Intermountain West, our results suggest that non-climatic processes functionally constrain lower treeline above its ecophysiological limits. Our analysis detected a threshold of aridity for northern dry mixed-conifer forests, yet only one-tenth of lower treeline in this forest type was classified as topoclimatically limited. The fact that overall aridity was low even at very low elevations suggests that landscapes in this region may not be dry enough to create extensive topoclimatic lower treelines. Instead, these forests were frequently located adjacent to perennial and seasonal wetlands, recently burned areas, and human land uses, indicating that lower treelines are primarily formed by physical barriers, fire, and anthropogenic effects. In contrast, for the more southern portions of our study region, we found that little of the pinyon–juniper lower treeline bordered or intersected recent fire or anthropogenic disturbance, suggesting that these factors do not exert strong constraints in these woodlands.

Broad-scale drivers likely interact with historical legacies to determine the current position of lower treeline. Because dry woodlands have slow rates of post-disturbance recovery (Bristow et al. 2014), the current position of lower treeline may be impacted by the legacy of past disturbances (Lanner and Frazier 2011). Extensive wood harvest to support settlement-era mining and construction resulted in widespread deforestation in many areas of the western United States, particularly in easy-to-access areas near transportation corridors that often coincided with the lower treeline boundary (Ko et al. 2011). The short record of fire occurrences and poor available records of historic land uses limited our ability to account for historical legacies in our analysis, and may partially explain why 38–48% of lower treeline within our study area could not be classified. In other cases, the undetermined treelines may be influenced by local biotic interactions that could not be modeled at the scale of our study. Given the coarse scale of our analysis, these results are not intended to directly support management decisions at specific locations, which would require site-specific information on species interactions, legacies of land use and disturbance, and other factors.

Lower treeline often constitutes the dry edge of the forest belt and as such can be expected to be responsive to global climate changes that result in increased aridity. Lower treelines in other arid or semi-arid mountainous regions around the globe may also be strongly linked to climate, though treeline response to climate change will be mediated at the local scale by soil properties, biotic interactions, and natural or anthropogenic disturbances. Our study of lower treelines for an extensive dryland region provides a model for identifying the broad-scale drivers of lower treeline formation, and the results can be applied to future climate scenarios to produce more robust projections of future treeline dynamics and global distributions of the forest biome. Given the pressing need to anticipate forest responses to future climate change, we recommend a much more intense focus on lower treeline than heretofore, paralleling the development of the extensive body of research concerning upper treeline dynamics.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2158/full

Data Availability

A line shapefile of lower treelines and a polygon shapefile of the study area are available from Dryad Digital Repository: https://doi.org/10.5061/dryad.g4f4qrfmw