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RESEARCH ARTICLE

Climatic, landform, microtopographic, and overstory canopy controls of tree invasion in a subalpine meadow landscape, Oregon Cascades, USA

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Abstract Tree invasions have been documented throughout Northern Hemisphere high elevation meadows, as well as globally in many grass and forb-dominated ecosystems. Tree invasions are often associated with large-scale changes in climate or disturbance regimes, but are fundamentally driven by regeneration processes influenced by interactions between climatic, topographic, and biotic factors at multiple spatial scales. The purpose of this research was to quantify spatiotemporal patterns of meadow invasion; and how climate, larger landforms, topography, and overstory trees have interactively influenced tree invasion. We combined airborne Light Detection and Ranging (LiDAR) characterizations of landforms, topography, and overstory vegetation with historical climate, field measurements of snow depth, tree abundance, and tree ages to reconstruct spatial and temporal patterns of tree invasion over five decades in a subalpine meadow complex in the Oregon Cascade Range, USA. Proportion of meadow occupied by trees increased from 8 % in 1950 to 35 % in 2007. Larger landforms, topography, and tree canopies interactively mediated regional climatic controls of tree invasion by modifying depth and persistence of snow pack, while tree canopies also influenced seed source availability. Landscape context played an important role mediating snow depth and tree invasion; on glacial landforms tree invasion was negatively associated with spring snowfall, but on debris flows tree invasion was not associated with snow fall. The importance of snow, uncertain climate change impacts on snow, and mediation of snow by interacting and context dependent factors in complex mountain terrain poses substantial hurdles for understanding how these ecotones may respond to future climate conditions.

Keywords Topography · Oregon Cascades · Snow · Subalpine meadow · Tree invasion · LiDAR

Introduction

Subalpine meadows are transitional areas (ecotones) between forested and meadow ecosystems.

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Contemporary treeline movement and tree invasions of subalpine meadows have been variable, but widespread and often attributed to climate change or altered disturbance regimes (Miller and Halpern 1998; Didier 2001; Harsch et al. 2009). Tree and woody plant invasions are also broadly associated with climate change, altered disturbance regimes, and land use change across a wide range of grass and forb-dominated ecosystems (Scholes and Archer 1997; Bowman et al. 2001; Briggs et al. 2002; Bond et al. 2005; Dovčiak et al. 2005; Gehrig-Fasel et al. 2007). Tree and woody plant invasions of meadows and grasslands may influence surface radiation balance (Foley et al. 1994), carbon balance (Prichard et al. 2000; Knapp et al. 2008), species distributions, and biodiversity (Sala et al. 2000; Dirnböck et al. 2003), so it is important to understand how tree invasion in these systems may respond to future environmental conditions. Potential impacts of tree invasion will largely be determined by the spatial extent and temporal rates of tree invasion, which for many species will be fundamentally determined by seed-based regeneration processes.

Forest-meadow ecotones are often characterized by landscape mosaics containing elements of both forest and non-forest ecosystems. Climate and disturbances such as wildfire are global controls of treeline position and grassland ecosystem distributions (Körner 1998; Bond et al. 2005), yet non-climatic biotic and physical factors become increasingly important at finer spatial scales (Körner 1998), emphasizing the importance of spatial scale in detecting patterns and determining controlling factors. Tree invasion of many meadow and grassland ecosystems has been studied in relation to global and regional factors such as climate, fire, and land use change (Körner 1998; Briggs et al. 2002; Bond et al. 2005; Gehrig-Fasel et al. 2007), as well as finer-scale factors such as seed availability, vegetation interactions, microtopography, and microclimate (Scholes and Archer 1997; Moir et al. 1999; Dovčiak et al. 2008; Halpern et al. 2010). However, how tree and woody plant invasion are influenced by the interactions between large scale and local drivers has received much less attention (although see Wigley et al. 2010; Haugo et al. 2011). Furthermore, attempts to infer multi-scale drivers of tree invasion rarely quantify rates or extent of tree invasion or invasion variability under different landscape contexts, critical for understanding the potential sensitivity of these systems to future climate change (Holtmeier and Broll 2005).

Topographic and biotic influences on tree invasion can be challenging to quantify. Environmental variables and vegetation patterns are often spatially autocorrelated, violating assumptions of many statistical models. Studies of treeline movement and meadow invasion often relate tree invasion to a few dominant variables such as elevation or aspect (Rochefort and Peterson 1996; Lloyd and Graumlich 1997), which may miss important interactions between topographic and biotic factors and landscape context as they relate to tree invasion. Furthermore, sampling along a few dominant environmental gradients may not adequately represent the complex mosaics of forest and non-forest elements in ecotone landscapes, posing problems for scaling-up field data to landscape-level estimates of vegetation change. Recent advances such as Light Detection and Ranging (LiDAR) technology may provide a means of addressing both spatial autocorrelation and scaling problems in quantifying tree invasion. LiDAR can provide unprecedented fine-scale spatial characterizations of vegetation patterns and topography across larger landscapes (Lefsky et al. 2002). LiDAR has been underutilized in treeline and meadow invasion studies, but its spatially explicit characterizations of multiple topographic and biotic factors may facilitate sampling strategies that address spatial autocorrelation, as well as scaling tree invasion from plot to landscape levels.

In this study we used LiDAR-derived characterizations of microtopography, tree canopies, and larger geomorphological landforms to inform sampling of snow depth, tree abundance and invasion of mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) in a 135 ha subalpine meadow complex in the Cascade Range of Oregon, USA. Prior research suggests tree invasion of subalpine meadows in the region is associated with summer temperature and precipitation, as well as spring and summer snowpack depth (Fonda and Bliss 1969; Rochefort and Peterson 1996). Tree invasion may also be associated with longer scale climatic variation, since regional snow water equivalent is associated with Pacific Decadal Oscillation (PDO) (Mote 2003). Furthermore, landscape context (i.e., different landforms, elevations, hydrologic settings, etc.) and biotic interactions with existing trees can influence tree invasion and forest-meadow ecotone vegetation dynamics (Miller and Halpern 1998; Halpern et al. 2010; Haugo et al. 2011).

Based on these prior regional studies, our study objectives were to: (1) characterize spatiotemporal patterns of tree invasion over the past 50 years, and (2) infer how regional climate, dominant landforms, microtopography, microsite radiation, and distance to overstory canopy have interactively shaped spatial patterns of summer snow depth and spatiotemporal patterns of tree invasion. Specifically, we asked five questions:

1. Has the spatial extent of tree invasion increased over the past 50 years?
2. Has tree invasion been associated with seasonal, annual, or semi-decadal climate variability?
3. Has spatial variation of summer snow depth been associated with larger-scale landforms, microtopography, microsite radiation, distance to overstory canopy, and interactions between these factors?
4. Has abundance of tree invasion been associated with the same biotic and topographic factors influencing summer snow depth?
5. How have climate, landforms, and microtopography interactively shaped tree invasion?

Methods

Study area description

The study was conducted in 135 ha of Jefferson Park (44°42′N 121°48′W, 1693–1814 m asl), a subalpine meadow complex in the Mount Jefferson Wilderness, Willamette National Forest, Central Cascades, Oregon, USA (Fig. 1). Climate is intermediate between Mediterranean and maritime temperate, with dry warm summers and substantial winter precipitation. The nearest weather station above 1000 m (Government Camp Station, 45°18′N 121°145′W, 1213 m asl, 1951–2008 time period), reported mean annual maximum and minimum temperatures of 10.2 and 1.1 °C. Annual precipitation averaged 217 cm, the majority falling as snow from December to April. During the twentieth century, both Government Camp and regional temperatures have increased while snowpack has declined (Mote 2003, Supplementary Material 1). At the nearest high elevation SNOTEL station (Mt Hood Test Site, 45°19′N 121°43′W, 1637 m asl, 1981–2011 time period), the average last day of measurable snowpack has been July 4, ranging from May 30 to August 10 (Supplementary Material 1).

Jefferson Park is in the mountain hemlock forest zone. Mountain hemlock and Pacific silver fir occur in Jefferson Park as single and mixed-species "islands" of variable size and shape surrounded by meadows. Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), whitebark pine (*Pinus albicaulis* Engelm.), lodgepole pine (*Pinus contorta* Doug. ex. Loud.), and Alaska yellow-cedar (*Callitropsis nootkatensis* (D. Don) Florin) are sporadically present in very low numbers. Meadow vegetation in Jefferson Park ranges from low statured sedge meadows dominated by *Carex nigricans* C.A. Mey. in poorly drained valleys and depressions, to tall shrublands of *Sorbus sitchensis* M. Roem. and *Vaccinium deliciosum* Piper on well-drained upper slopes and ridgetops (Zald 2010).

Jefferson Park surface geomorphology is dominated by glacial and recent debris flow landforms. Holocene glacial advance and retreat created the Jefferson Park basin and deposited outwash and till (Scott 1977). In 1934, a debris flow covered 20.6 ha of the study area with debris 0.3–2.4 m deep (O'Connor et al. 2001, Fig. 1). A smaller (3.4 ha of the study area) debris flow of older but indeterminate age is located in north Jefferson Park. Besides debris flows, the disturbance history of Jefferson Park is poorly documented. No evidence was found of past avalanches or wildfires within the study area. Sheep grazing occurred in the vicinity during the early twentieth century, but the sheep driveway closest to Jefferson Park was closed to livestock except recreational pack animals in 1937 (Rakestraw and Rakestraw 1991). Prior research suggests grazing suppresses tree establishment at treeline and in subalpine meadows, and a pulse of tree establishment often follows grazing cessation (Miller and Halpern 1998; Didier 2001; Gehrig-Fasel et al. 2007).

LiDAR-derived microtopography, landforms, and overstory canopy variables

We derived gridded landform, microtopography, microsite potential radiation, and overstory canopy variables from LiDAR data; and geospatial analysis of these variables provided the basis of our sampling design measuring snow depth, tree abundance, and tree invasion. Airborne discrete return LiDAR data

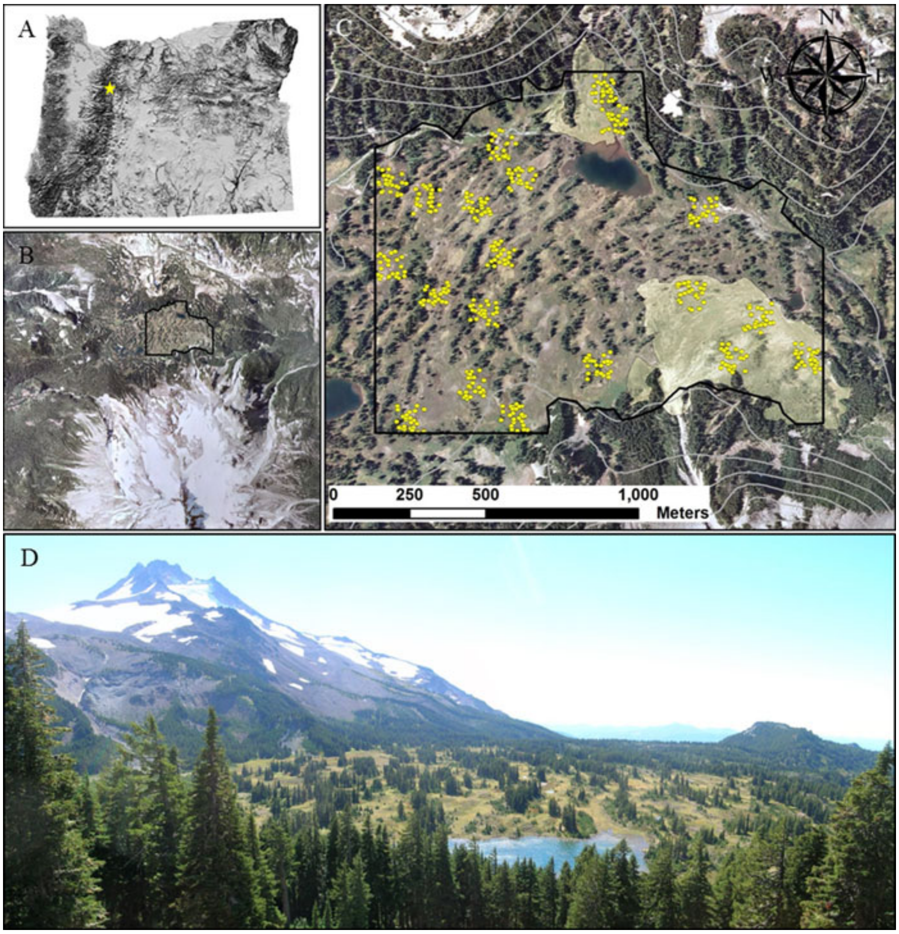

Fig. 1 Jefferson Park study area location maps and imagery. **a** Digital elevation model of the state of Oregon with study area denoted by a *star*. **b** Jefferson Park study area (*black outline*). **c** Aerial photo from 2005 of the study area (*black outline*), showing plots (*light yellow points*) and debris flows (*lighter shaded areas* in northern and southeastern corners of the study area). *Light grey* lines are 25 m contour intervals. **d** Photograph taken in 2007 looking southwest into Jefferson Park, with Mount Jefferson in the *upper left corner*

was collected in September of 2007; covering 4447.5 ha centered on the study area while including major adjacent topographic features. Average LiDAR point density exceeded 10 points/m^2 within the study area. LiDAR point data was used to calculate grids (1 m cell size) of bare ground elevation (ELEV), vegetation elevation (VEG), and vegetation height (VEGHT = VEG − ELEV). See Supplemental Material 2 for LiDAR specifications and methods for generating ELEV and VEG grids.

ELEV and VEGHT were used to generate grids of topographic position, microsite radiation, landform types, and overstory canopy; factors which influence tree invasion, snow persistence, and seed source availability (Moir et al. 1999; Maher and Germino 2006; Dovčiak et al. 2008). Topographic position index (TOPO) was calculated as the difference between ELEV in a given cell and mean ELEV of a 5–10 m annulus around that cell, with positive TOPO values representing ridges and negative values representing depressions. Potential relative radiation (RAD) was calculated from ELEV for the entire LiDAR coverage area as described by Pierce et al. (2005). RAD is an integrative, potential-relative-radiation index which accounts for temporal variability in radiation and topographic shading from surrounding landscape features. RAD was calculated for the growing season (June through September). Landform types (glacial vs.

debris flows) were visually identified from field observations, TOPO, and aerial photographs, and then manually delineated as GIS polygon shapefiles.

Distance to overstory canopy (CANDIST) was calculated as the Euclidean distance to the nearest grid cell in which vegetation height was greater or equal to 8 m (OVERSTORY). Prior field reconnaissance found the 8 m height threshold included all trees influencing light and vegetation conditions underneath them, included the most likely seed sources in the study area, while excluding all non-tree vegetation in the LiDAR data. CANDIST may not be as effective for quantifying seed rain and shade as more sophisticated models (Greene and Johnson 1996; Dovciak et al. 2005). However, secondary dispersal on snow may be underestimated in seed rain models (Greene and Johnson 1997). Additionally, canopy effects on interception, energy balance, and wind redistribution of snow (Storck and Lettenmaier 2002; Winstral et al. 2002; Trujillo et al. 2007) may not be adequately characterized by canopy shade models. These concerns, along with simplicity in stratified sampling and ease of interpretation, led us to use CANDIST to characterize seed source availability and overstory control of snowpack persistence. OVERSTORY also defined the spatial and temporal scope of interest (i.e., meadows) by excluding areas occupied by trees over 8 m tall, which Zald (2010) found to be over 50 years old, thus focusing on tree invasion coinciding with the regional climate record.

Sample design and plot establishment

We used a stratified random design to sample snow depth, tree abundance, and tree invasion across gradients of microtopography and distance to overstory canopy. To reduce the number of sampling strata, RAD and TOPO were combined into a single ecological exposure index (EEI) representing the microtopographic strata. EEI was calculated by normalizing RAD and TOPO by their respective standard deviations and then averaging the normalized variables. CANDIST was the second sampling stratum. EEI and CANDIST were converted from continuous to five-class ordinal grids. Continuous values of EEI were classified into five quantiles, while CANDIST values were classified (0–5, 5–10, 10–20, 20–30, and >30 m) based on seed dispersal rates for the two dominant tree genera *Abies* and *Tsuga* (Franklin and Smith 1974; Carklin et al. 1978). EEI and CANDIST classified grids were then combined into a 25-class grid representing all potential combinations of the two 5-class strata. A 100 × 100 m moving window analysis was applied to the 25-class grid to find small contiguous sampling areas containing all 25 strata. Moving window analysis yielded 23 non-overlapping 100 × 100 m sampling areas containing all 25-class combinations, 20 of which were randomly selected.

In each of the 20 selected sampling areas, 25 circular plots (2 m diameter) were located in a spatially constrained stratified random design. As noted in the introduction, environmental variables and vegetation patterns are often spatially autocorrelated, confounding many statistical analyses. We minimized spatial autocorrelation by quantifying the empirical semivariogram range for each variable of interest, then constrained sampling so as many plots as possible were at least as far apart as the semivariogram ranges. Additionally, plots had to be at least 2 m away from a stratum different from the one occupied and at least 4 m apart from another plot, to ensure that GPS position errors did not result in plots overlapping each other or multiple strata. These spatial constraints avoided strata and plot overlap and largely removed short distance spatial autocorrelation in explanatory variables (Supplemental Material 2). Plots were located in July of 2008 using a GPS receiver with sub-meter precision (mean horizontal positional accuracy = 0.28 m). Three hundred and ninety plots were located on glacial landforms, 110 on debris flow landforms, but one debris flow plot was later discarded because it intersected both landform types.

Species-specific canopy characterization and distance to potential seed sources

The OVERSTORY grid was overlain on a color aerial orthophotograph (0.5 m resolution) taken in 2005 by the National Agricultural Imagery Program to produce overstory canopy maps of the 20 sampling areas (plus 50 m horizontal buffers). Overstory canopy maps were taken into the field; and every overstory tree within each map was visited, identified to species, and its canopy outline delineated. Species-specific canopy outlines were then manually traced as GIS polygons in ArcGIS (Environmental Systems Research Institute, Redlands, California), converted to grids (1 m cell), and the Euclidean distance from each plot to the nearest species-specific overstory canopy calculated (i.e., TSME_DIST for mountain hemlock, and ABAM_DIST for Pacific silver fir). Additionally, the direction to overstory canopy (CANDIRECT) from each plot was calculated.

Plot-level data collection

On each 2 m diameter plot, snow depth was measured between July 29 and August 1, 2008 when snow covered approximately 75 percent of the study area. After snowmelt, all trees on plots that were 5 cm to 8 m tall were tallied by species (5 cm cutoff eliminated first year germinants). Eight hundred and thirty-five mountain hemlock, 758 Pacific silver fir, 12 whitebark pine, 8 Alaska yellow-cedar, and 7 lodgepole pine were recorded. Only mountain hemlock and Pacific silver fir were analyzed. On each plot, the diameter and height of the tallest (assumed oldest) tree of each species was measured, and cored or cross sectioned at the root/trunk boundary. Additionally, if another tree on a plot was of comparable height or was shorter but had characteristics indicating greater age (i.e., greater basal diameter, comparable diameter but growth form indicating prior loss of apical dominance), both trees were cored and/or cross sectioned, and the oldest determined by the number of tree rings. One hundred and nine plots had more than one hemlock cored or cross sectioned due to the criteria described above, and the tallest hemlock was the oldest on 97 % of these plots. Fifty-two plots had more than one Pacific silver fir cored or cross sectioned due to the criteria described above, and the tallest fir was the oldest on 90 % of these plots. From these results, we are confident our sampling procedures consistently aged the oldest trees on plots. Three hundred and seventy-four and 116 cores and cross sections were aged from plots on glacial and debris flow landforms, respectively. Twelve percent of cores and cross sections lacked centers, and their ages were estimated following Applequist (1958). Cores and cross sections were cross dated as described by Yamaguchi (1991) to insure correct assignment of calendar year of establishment.

Statistical analyses

See Supplemental Material 1 for a list of all statistical analyses conducted. Aged trees from plots were used to determine if the proportion of meadow occupied by trees has increased over the past 50 years, with a plot considered occupied from the oldest date of tree establishment on that plot until the present. Proportion of plots occupied was calculated back to the oldest tree establishment dates, but analyzed for the common interval with regional climate data (1950–2008). The proportion of the meadow landscape occupied was estimated by weighting plot occupation over time by the proportional distribution of each sampling strata in the overall study area landscape and each landform to calculate study area and landform-specific average annual invasion rates. Average annual rates of invasion were determined from simple linear regressions of the estimated proportion of the study landscape occupied by trees (both overall study area and separately by landform) over time. Average annual invasion rates between landforms were tested for differences in the slopes of regressions using Partial *F* tests.

Relationships between tree invasion rates and climate were quantified by calculating landscape invasion rates over time, which were then correlated to seasonal and annual climate variables, as well as the PDO (Mantua et al. 1997). PDO is defined as the leading principle component of November through March North Pacific (north of 20°N) sea surface temperature anomalies. Landscape invasion rates (different from the average annual rates described above) were generated by converting the proportion of the landscape occupied by trees into 3 year bins, then calculating the change from bin to bin. Three-year bins were used instead of annual rates because mortality of conifer germinants in subalpine meadows is often high and variable until the second or third year of growth (Rochefort and Peterson 1996). Seasonal, annual, and PDO climate variables were also placed into 3 year bins. Mean, minimum, and maximum values were calculated in each bin for: annual snowfall and temperature, "spring" (April through June) snowfall and temperature, "summer" (July through September) temperature, and PDO (Table 1). Relationships between landscape invasion rates and climate variables were assessed using Pearson product moment correlations.

Differences in snow depth between landforms were assessed using Satterthwaite t tests for samples with unequal variances. Influences of ELEV, TOPO, RAD, CANDIST, and CANDIRECT on snow depth were modeled separately for debris flow and glacial landforms using nonparametric multiplicative regressions (NPMR) in Hyperniche version 1.39 (McCune and

Table 1 Climate variables and their descriptions

Climate variable	Climate variable description
PDO	Mean Pacific Decadal Oscillation (Mantua et al. 1997)
PDO_MAX	Maximum Pacific Decadal Oscillation (Mantua et al. 1997)
PDO_MIN	Minimum Pacific Decadal Oscillation (Mantua et al. 1997)
ANN_T	Mean Annual Temperature
ANN_T_MAX	Maximum Annual Temperature
ANN_T_MIN	Minimum Annual Temperature
ANN_S	Mean Annual Snowfall
ANN_S_MAX	Maximum Annual Snowfall
ANN_S_MIN	Minimum Annual Snowfall
AJ_T	Mean April–June “Spring” Temperature
AJ_T_MAX	Maximum April–June “Spring” Temperature
AJ_T_MIN	Minimum April–June “Spring” Temperature
AJ_S	Mean April–June “Spring” Snowfall
AJ_S_MAX	Maximum April–June “Spring” Snowfall
AJ_S_MIN	Minimum April–June “Spring” Snowfall
JS_T	Mean July–Sept “Summer” Temperature
JS_T_MAX	Maximum July–Sept “Summer” Temperature
JS_T_MIN	Minimum July–Sept “Summer” Temperature

Mefford 2004); which can model and visualize complex response surfaces and is not constrained by additive model terms. NPMR was run using a local mean, Gaussian weighting, and minimum average neighborhood size of five percent of sample units. Explanatory variables were retained if they improved final model fit by at least 5 %, and models were evaluated by a leave-one-out cross-validated statistic (xR^2). Relative importance of individual explanatory variables in the final models were evaluated by sensitivity analysis (SA), defined as the average absolute value of response variable differences induced by nudging the explanatory variable in 5 % increments across its range. An SA value of one indicates nudging a predictor results in a response of equal magnitude, while zero indicates nudging a predictor has no detectable effect on the response.

Plot-level abundance of trees (5 cm–8 m tall) in relation to ELEV, TOPO, RAD, CANDIST, CANDIRECT, ABAM_DIST, and TSME_DIST was assessed using generalized linear mixed models with the GLMMIX procedure in SAS version 9.2 (SAS Institute Inc 2008). Tree abundance was modeled separately by species and landform. Tree abundance was assumed to have a Poisson probability distribution, and sampling areas were treated as random effects. GLMMIX was chosen because it allowed for an information theoretic approach to model selection and inference not possible with NPMR. Multiple models were developed using all explanatory variable combinations, and small sample Akaike’s information criterion (AIC_c) was used to select the “best” models of tree abundance in relation to explanatory variables. The Laplace method was used to approximate marginal likelihood. Following Burnham and Anderson (2002), models were considered to have strong empirical support if delta AIC_c values (Δ_i) were ≤ 2, moderately supported if between 2 and 4, and not empirically supported if >4. Model likelihood given the data ($L(g_i|x)$) and Akaike weights (w_i) were also calculated to aid model evaluation.

Interactive effects of climate, landform, and microtopography on tree invasion were evaluated by testing for differences in TOPO and ELEV values on microsites invaded by trees on different landforms between cool and snowy versus warm and less snowy years. Years were classified as cool and snowy if snowfall was greater than average and annual or summer temperature was below average. Twenty-one years were classified cool/snowy (1953–1956, 1960–1975, and 2007), and 35 years classified warm with low snowfall (1952, 1957–1959, and 1976–2006). Aged trees were assigned to these climate classes, and differences in microsites invaded during the two climate classes were evaluated by Wilcoxon–Mann–Whitney tests. Additionally, contingency tables were developed and Fisher’s exact test used to determine if the relative proportions of observed invasion was different than expected on different microsites (high vs. low topographic position) during different climate types (high vs. low snow years) on different landforms (glacial vs. debris flows). Expected invasion was proportional to the number of years in each climate class.

Results

Temporal patterns of tree invasion and correlates with climate

Trees occupied 7.75 % of the total meadow landscape in 1950, increased at an average rate of 0.49 % year^{-1}, with 34.71 % occupied in 2008. In 1950, meadow

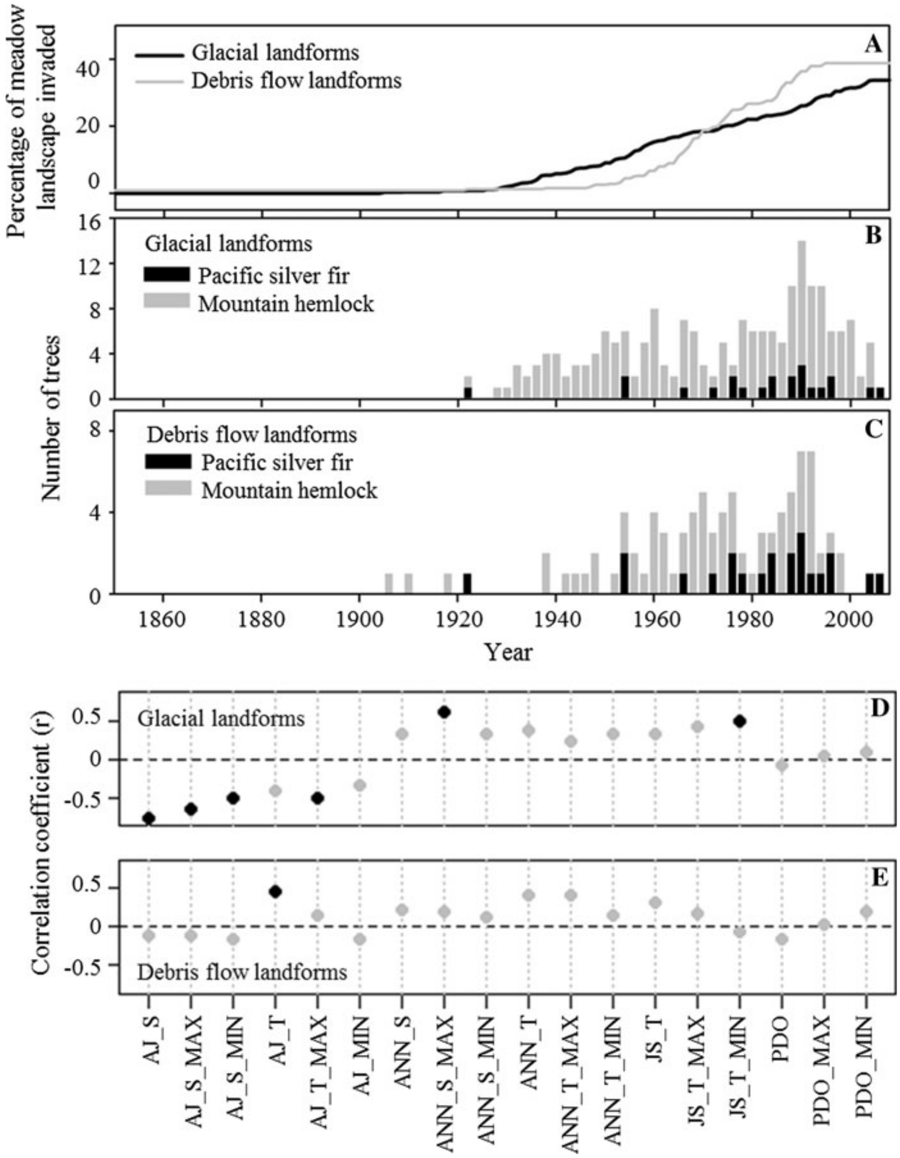

Fig. 2 **a** Percentage of meadow landscape invaded by trees over time by landform type. Counts of trees invading glacial (**b**) and debris flow (**c**) landforms over time. Pearson product-moment correlations (r) between landscape invasion rates and climate variables on glacial (**d**) and debris flow landforms (**e**). Significant correlations ($p < 0.05$) are denoted by *black circles*. See Table 1 for climate variable descriptions

landscape occupancy was greater on glacial versus debris flow landforms (9.06 vs. 2.55 %), but average invasion rates were greater on debris flows (0.76 % year^{-1} ± 0.02 SE vs. 0.42 % year^{-1} ± 0.01 SE, $p < 0.0001$), resulting in greater tree occupation on debris flows by 1974 (Fig. 2a). By 2008, occupancy was 33.68 and 38.82 % on glacial and debris flow landforms, respectively. Tree invasion began on glacial landforms in the 1920s, generally increased until 1984, at which point counts of aged trees increased but invasion rates only slightly increased (Fig. 2b). Tree invasion on debris flows was greatest during the 1963–1968 and 1988–1992 time periods (Fig. 2c). Climatic controls of tree invasion varied by landform type (Fig. 2d–e). On glacial landforms, tree invasion was most strongly associated with reduced AJ_S ($r = -0.77$), and also was positively associated with ANN_S_MAX and JS_T_MIN. In contrast, invasion on debris flows was only associated with AJ_T ($r = 0.47$). Tree invasion was not associated with PDO.

Snow depth in relation to landforms, microtopography, and overstory canopy

Snow was deeper on glacial landforms (mean 0.67 m, 0.59–0.75 m 95 % CI) versus debris flows (0.21 m, 0.14–0.28 m, Satterthwaite t test with unequal variances, $p < 0.0001$). The influence of topographic and biotic variables on snow depth varied between landforms (Fig. 3). Topographic and canopy variables described more variation in snow depth on glacial ($xR^2 = 0.27$) versus debris flow landforms ($xR^2 = 0.12$). Snow depth on glacial landforms was most sensitive to ELEV (SA = 0.60), TOPO (0.43), and CANDIST (0.33), and insensitive to RAD (0.02) and CANDIRECT (0.02). Snow depth on debris flow landforms was most sensitive to RAD (2.24) and CANDIST (0.16), insensitive to ELEV (0.06) and TOPO (0.05), while CANDIRECT was not retained in the final model. On both landforms, snow depth declined with higher ELEV, higher TOPO, and reduced CANDIST. Snow depth on glacial landforms had nonlinear response surfaces in relation to topography and overstory canopy, while snow depth on debris flows had more linear response surfaces and reduced interactions between topography and overstory canopy.

Tree abundance in relation to landforms, microtopography, and overstory canopy

Relationships between tree abundance, topography, and overstory canopy varied by species and landform type (Table 2). For mountain hemlock, the best model on glacial landforms had increased abundance with higher TOPO, reduced RAD, higher ELEV, increased CANDIST, and reduced DIST_TSME. The best model of

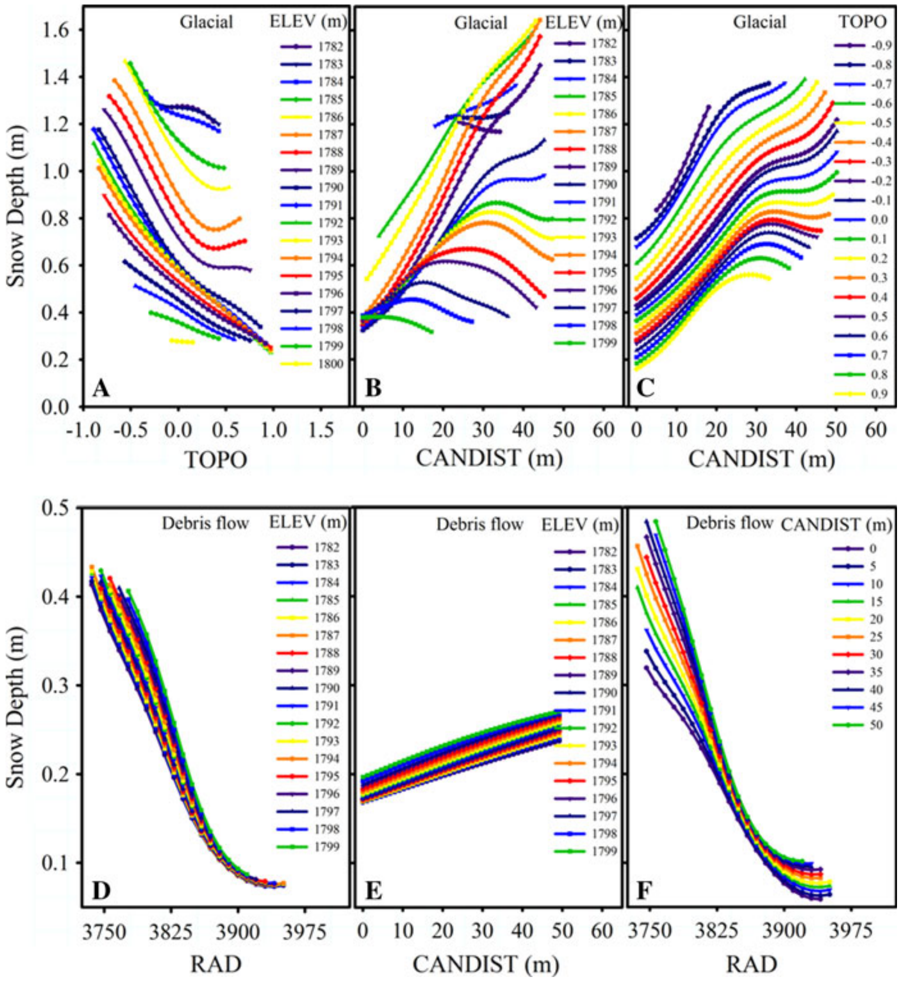

Fig. 3 Response surfaces of snow depth in relation to elevation (*ELEV*), topographic position (*TOPO*), potential relative radiation (*RAD*), and distance to overstory canopy (*CANDIST*) on glacial (**a–c**) and debris flow (**d–e**) landforms

Table 2 Fixed effects in the best empirically supported models ($\Delta_i = 0$) of tree abundance in relation to explanatory variables by species and landform type

Species	Landform	Explanatory variable	Type III fixed effects			
			Estimate ± SE	df	*F* value	*p*
Mountain hemlock	Glacial	RAD	−0.0023 ± 0.0003	1, 368	46.5574	0.0000
		TOPO	1.5975 ± 0.1224	1, 368	170.3093	0.0000
		ELEV	0.0232 ± 0.0132	1, 368	3.0953	0.0794
		CANDIST	0.1318 ± 0.0249	1, 368	27.9603	0.0000
		TSME_DIST	−0.1229 ± 0.025	1, 368	24.0736	0.0000
Mountain hemlock	Debris flow	RAD	−0.0022 ± 0.001	1, 99	5.4005	0.0222
		TOPO	0.8314 ± 0.2564	1, 99	10.5122	0.0016
		CANDIST	−0.0386 ± 0.0194	1, 99	3.9436	0.0498
		TSME_DIST	0.0468 ± 0.0191	1, 99	6.0144	0.0159
Pacific silver fir	Glacial	RAD	−0.0017 ± 0.0003	1, 369	25.4059	0.0000
		TOPO	0.5289 ± 0.1312	1, 369	16.2488	0.0001
		CANDIST	0.0133 ± 0.0082	1, 369	2.5898	0.1084
		ABAM_DIST	−0.0636 ± 0.0073	1, 369	76.8308	0.0000
Pacific silver fir	Debris flow	TOPO	1.5349 ± 0.2817	1, 101	29.6962	0.0000
		ABAM_DIST	−0.0289 ± 0.0068	1, 101	18.1728	0.0000

Explanatory variable as defined in "Methods" section

mountain hemlock abundance on debris flows had increased abundance with higher TOPO, reduced RAD, reduced CANDIST, and increased DIST_TSME. On debris flows, more empirically supported alternative models, smaller differences in $L(g_i|x)$ and w_i, and smaller Δ_i for the null model suggested weaker relationships between hemlock abundance and explanatory variables compared to glacial landforms (Supplemental Material 3). For Pacific silver fir, the best model on glacial landforms had increased abundance with higher TOPO, reduced RAD, increased CANDIST, and reduced DIST_ABAM. The best model of Pacific silver fir on debris flows had increased abundance with higher TOPO and reduced DIST_ABAM. As with mountain hemlock, models of Pacific fir abundance suggest weak relationships between Pacific silver fir abundance and explanatory variables on debris flows (Supplemental Material 3).

Interactive effects of climate and microtopography on tree invasion

Small sample sizes limited the analysis of interactive effects of climate and microtopography to mountain hemlock. On glacial landforms, mountain hemlock invaded sites with higher TOPO during cool and snowy years compared to warmer years with reduced snowfall (Table 3). ELEV of glacial landform sites invaded by mountain hemlock did not differ between the two climate classes. The number of invading mountain hemlocks was greater than expected on low topographic positions during warm and less snowy years on glacial landforms (Table 4). On debris flows, mountain hemlock trees invaded sites with higher ELEV during cool and snowy years versus warm and less snowy years (Table 3). TOPO of sites invaded on debris flows did not differ between climate classes. The number of invading mountain hemlocks was not different than expected on sites with high versus low TOPO or ELEV between cool and snowy versus warmer and less snowy years (Table 4).

Discussion

Integrating LiDAR with field data provided a unique opportunity to examine spatial and temporal patterns of tree invasion across an entire meadow landscape at fine spatial scales. There have been large increases in the proportion of the Jefferson Park meadow landscape invaded by trees over the past 50 years, yet tree invasion varied temporally and spatially as a function

Table 3 Mean topographic position and elevation (with 95 % confidence interval) of micro sites invaded by mountain hemlock during cool and snowy versus warm and less snowy years

Landform	Variable	Cool and snowy years	Warm and less snowy years	*Z* value	*p*
Glacial	N trees	41	99		
Glacial	ELEV	1791.68 (1790.01–1793.35)	1791.07 (1790.04–1792.1)	0.7419	0.4594
Glacial	TOPO	0.24 (0.16–0.33)	0.09 (0.02–0.16)	2.5941	0.0105
Debris flow	N trees	23	28		
Debris flow	ELEV	1782.61 (1781.92–1783.3)	1781.06 (1780.05–1782.07)	2.1209	0.0389
Debris flow	TOPO	0.05 (−0.05 to 0.15)	−0.04(−0.14 to 0.07)	1.0036	0.3204

TOPO and ELEV as described in the "Methods" section. Differences in values of elevation and topographic position invaded between the two climate classes were assessed using Wilcoxon–Mann–Whitney tests

Table 4 Observed versus expected mountain hemlock invasion by landform and establishment type, on micro sites with high and low topographic positions and elevations during cool and snowy and warmer with less snow years

Landform	Variable	Cool and snowy		Warm and less snowy		*p*
		Trees observed	Trees expected	Trees observed	Trees expected	
Glacial	High TOPO	28	26	41	43	0.8616
Glacial	Low TOPO	13	28	61	46	0.0009
Debris	High TOPO	9	6	8	11	0.4905
Debris	Low TOPO	15	13.5	21	22.5	1.0000
Glacial	High ELEV	22	26	47	43	0.5921
Glacial	Low ELEV	18	28	56	46	0.1094
Debris	High ELEV	15	10	11	16	0.2668
Debris	Low ELEV	7	9	17	15	0.7601

TOPO and ELEV as described in the "Methods" section. *p* values are from Fisher's exact test. Expected values are the observed row totals across landforms multiplied by the proportion of years in the climate record within each climate period

of interacting factors at multiple spatial scales. We propose that regional climate in the form of snow strongly influences temporal patterns of tree invasion in this system, while snow depth mediated by microtopography and overstory vegetation within the landscape context of larger landforms shapes the spatial patterns of tree invasion, resulting in complex tree invasion responses to climate over time. Tree invasion is discussed below within a framework of: regional climatic influences; landform, microtopographic, and biotic influences; how interactions between factors at multiple spatial scales generate complex tree invasion responses across landscapes; and implications of these findings for potential climate change impacts on tree invasion in the future.

Influence of regional climate on tree invasion

Snow depth and its seasonal persistence are known to control treeline movement and subalpine meadow tree invasion in the Pacific Northwest (Fonda and Bliss 1969; Rochefort and Peterson 1996; Miller and Halpern 1998). However, these prior studies did not co-measure tree invasion and snow depth across multiple environmental factors or spatial scales. By relating tree invasion to regional climate and co-measuring snow depth and abundance of tree invasion, we found evidence that snowfall and snow depth may shape temporal and spatial patterns of tree invasion. In addition to snowfall, we found invasion was also associated with temperature (spring maximum and summer minimum temperatures on glacial landforms, and spring temperatures on debris flows), although the magnitude these associations was smaller than for snow variables on glacial landforms. Increased tree invasion with higher temperatures is consistent with studies relating global treeline position and tree invasion to air temperatures (Körner 1998; Harsch et al. 2009). However, the maritime climate of the Pacific Northwest results in heavy winter snowfall and deep snowpack that despite mild temperatures can persist until midsummer, conditions which may be regionally more important than air temperatures in controlling growing season length and seedling establishment (Fonda and Bliss 1969; Kuramoto and Bliss 1970). This contrasts with the role of snow in arid and windy climate regimes, where snow can facilitate tree invasion by increasing soil moisture; reducing desiccation, and moderating temperature extremes (Holtmeier and Broll 1992; Geddes et al. 2005), highlighting the importance of regional climatic context on tree invasion.

Curiously, tree invasion was not associated with PDO, which is associated with regional snow water equivalent and high elevation tree growth (Peterson and Peterson 2001; Mote 2003). However, seedling establishment does not necessarily respond to the same climate conditions or at the same temporal scale as tree growth. Tree invasion requires successful seed production, germination, and establishment; a multi-year process more sensitive to both successive years of favorable climate conditions and individual poor years than the physiological responses of mature trees (Holtmeier and Broll 1992; Lescop-Sinclair and Payette 1995).

Landform, microtopographic, and overstory influences on snow persistence and tree invasion

Landforms and microtopography within landforms influenced both temporal and spatial patterns of tree invasion. Compared to glacial landforms, tree invasion on debris flows occurred at a much higher rate, was less constrained to specific topographic conditions or proximity to overstory canopy, and was not associated with annual or spring snowfall. Snow depth was much lower on debris flows, likely resulting in longer snow free periods. LiDAR data allows a synoptic view of landforms not possible with field plots alone, and when combined with analyses of snow depth and tree abundance, suggests landform-dependent microtopography and overstory canopy influence tree invasion by mediating spatial patterns of snow depth and persistence. Debris flows have smoother surfaces and increased distance to overstory canopy (Supplemental Material 3), surface conditions which can increase wind redistribution of snow, and are known to be spatially dependent (Trujillo et al. 2007). Wind redistribution of snow on debris flows likely reduced microtopographic and overstory canopy influences on snow depth and persistence (and therefore tree invasion); as indicated by low variance described and weak interactions of explanatory variables in relation to snow depth, and weak models of explanatory variables in relation to tree abundance. On debris flows there are greater distances to seed sources, which all factors being equal would reduce seed availability and tree invasion, providing indirect support that increased tree invasion on debris flows is a result of reduced snow depth and/or persistence. In contrast to debris flows, microtopography and overstory canopy appear to have influenced snow depth and persistence on glacial landforms, spatially limiting tree invasion to convex topographic positions and higher elevations in close proximity to seed sources.

Microtopography and overstory canopy within the context of larger landforms appeared to influence both temporal and spatial patterns of tree invasion via mediation of snow depth and persistence. However, other factors may contribute to different invasion patterns on landforms. Debris flows had greater exposed mineral soil and reduced vegetation cover compared to glacial landforms (Supplemental Material 3), conditions which generally promote many conifer species, but not necessarily Pacific silver fir (Gray and Spies 1997). Debris flows are also in close proximity to larger topographic features; which may influence snowpack distribution and seed availability by modifying surface radiation, cold air drainage, and prevailing wind patterns. This study did not specifically address spatial scales larger than landforms, yet our findings and prior studies at larger spatial scales (Woodward et al. 1995; Rochefort and Peterson 1996) suggest interactions from microsite to landscape and regional scales are critical in shaping tree invasion responses to climate.

Debris flow landforms are recent disturbance events which buried almost all organic matter and vegetation, initiating primary succession. The Cascade Range has a high concentration of neoglacial lakes and subsequent debris flows (O'Connor et al. 2001), but prior studies of subalpine vegetation recovery after debris flows in the region have largely focused on herbaceous vegetation (del Moral et al. 1995). We found succession on debris flows characterized by rapid development of young mountain hemlock forests, suggesting alternative successional trajectories and high rates of post-disturbance recovery are possible, consistent with disturbances mediating directional ecological change in relation to climate change.

Biotic factors also influenced spatial patterns of tree invasion. Facilitation via autogenic site modification plays an important role in tree invasion of Pacific Northwest meadows (Miller and Halpern 1998; Halpern et al. 2010). Distance to overstory canopy also can influence potential seed availability. Distance from potential seed sources was more important for Pacific silver fir than mountain hemlock, likely resulting from heavier seed and shorter dispersal distances for Pacific silver fir (Franklin and Smith 1974; Carklin et al. 1978). The importance of distance from Pacific silver fir overstory canopy suggests tree invasion into meadows is more spatially restricted near potential parent trees for Pacific silver fir than mountain hemlock, even when suitable micro sites exist.

Interactive influences on tree invasion

In addition to the individual influences on tree invasion discussed above, interactions of climate, landform type, and microtopography resulted in complex patterns of tree invasion in response to climate. Analyses of tree invasion abundance in relation to landform, topographic, and overstory canopy variables indicates tree invasion on glacial landforms was spatially constrained to higher topographic positions in close proximity to overstory canopy. Topographic constraints on tree invasion were even more pronounced during cool and snowy years, while tree invasion on lower topographic positions occurred in greater than expected amounts during warm and less snowy years, findings consistent with topographic mediation of temporal variability in snow depth and persistence. A somewhat similar pattern occurred with elevation on debris flows, although tree invasion was not greater than expected on high or low elevation sites during cool and snowy versus warm and less snowy years. Our findings support previously documented climate-site-tree invasion interactions at larger spatial scales in the Pacific Northwest Region (Rochefort and Peterson 1996; Miller and Halpern 1998), but they also suggest these interactions can occur at finer microsite scales and can be context dependent.

Study limitations and uncertainty

Our study is retrospective, observational, and occurred in one landscape, and therefore has various limitations and associated uncertainty. Snow depth was recorded in a single year, while tree invasion was analyzed over multiple decades. However, topography imposes first order controls on the spatial variability of snow at multiple time scales (Williams et al. 2009); suggesting relative spatial patterns of snow are valid beyond one observation year. Retrospective dendrochronology studies cannot detect tree invasion which may have died and disappeared prior to sampling, which we addressed by restricting inference from 1950 to 2008, excluding trees potentially killed in the 1934 debris flow. Lacking evidence of other past disturbance events or multi-year extreme climatic conditions, we inferred no large mortality events have occurred since 1950. Livestock grazing could have created such mortality events, but it is unlikely grazing or its cessation were associated with rapid tree invasion on the 1934 debris flow, since forage for livestock would have been lacking on debris flows, but readily available on adjacent glacial landforms. Tree invasion on glacial landforms may coincide with the cessation of livestock grazing, but qualitative and regional grazing histories preclude quantification of spatially and temporally explicit grazing effects. Analyses of topographic positions invaded by trees in cool and snowy versus warm and less snowy years needs to be taken in the context that cool and snowy years were more common earlier in the time period of analysis, while seed rain likely increased over time due to tree maturation. Finally, general linear mixed models may not have captured more complex response surfaces of tree abundance with distance from overstory canopy.

Multi-scale and context dependent factors make it difficult to assess how representative tree invasion at Jefferson Park may be of subalpine meadows in the Pacific Northwest. The basic relationships of climate, topography, snow depth, and tree invasion exist in other regional studies (Fonda and Bliss 1969; Rochefort and Peterson 1996), while neoglacial debris flows are common in the Cascades and many North American alpine areas (O'Connor and Costa 1993). However, the importance of landscape context poses difficulties for assigning meadow ecotones into a few representation types based similar environmental variables or vegetation responses (Haugo 2011).

Implications for future subalpine meadow invasion and treeline movement

The association we found between tree invasion and snow may be unique to high elevation systems in maritime climates, emphasizing the importance of regional and local studies, and cautions against extrapolating relationships between climate and tree invasion from more continental or arid climates. Regional models project modest increases in temperature and small changes in annual precipitation, but large future declines in spring snow water equivalent (Salathé et al. 2008; Mote and Salathé 2010), conditions favorable for accelerated tree invasion in the future. However, uncertainty in regional and global climate models is often greatest for precipitation and snowfall, especially in areas with complex mountainous terrain and ocean-land interactions (Good and Lowe 2006; Salathé et al. 2008). Additionally, lower snow depth and rapid tree invasion on debris flows that was not associated with annual and spring snowfall suggests a threshold of snow depth and persistence may exist, below which rapid tree invasion may occur. Threshold snow levels could greatly alter our understanding of potential tree invasion in the future, but observational and experimental evidence regarding threshold snow effects on tree invasion are lacking.

While regional climatic changes are likely to accelerate tree invasion, finer scale topographic and biotic factors influencing tree invasion will persist in the future. In Jefferson Park, tree invasion has been largely absent in wet meadows at low topographic positions over the past 50 years, while seed dispersal limitations may constrain tree invasion and treeline movement for select species. These fine scale spatial constraints on tree invasion may result in high elevation persistence of meadows and meadow obligate species that may be overlooked at larger spatial scales (Randin et al. 2009). Counteracting topographic and seed dispersal constraints are autogenic feedbacks which may increase the favorability of adjacent micro sites for tree invasion (Halpern et al. 2010), but the temporal and spatial extent of autogenic feedbacks are unclear. The importance of multiple spatial scales of factors influencing tree invasion poses considerable challenges for projecting future treeline movement or meadow loss in response to climate change. We believe additional integrated studies such as this one, combining field and remotely sensed data such as LiDAR to assess landscape-level change at multiple spatial scales will be an important component in overcoming these challenges.

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