Warmer Conditions Favor Conifer Tree Establishment at the Muddy River Lahar in Mt. St. Helens, Washington

by

Ignacio D. Falcón-Dvorsky

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Thesis Committee:
Andrés Holz, Chair
Martin Lafrenz
Melissa S. Lucash

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Abstract

Climate variability impacts on Pacific Northwest forests are of great concern, especially on evergreen coniferous ecosystems which dominate a large portion of the landscape. Understanding the effect of climate variability and its potential impacts on forest regeneration is crucial, as this is a foundational process with long-lasting consequences on structure and composition of future ecosystems. The objective of this study was to uncover the possible influences of natural climate variability on conifer tree establishments on the Muddy Rivers Lahar following the 1980 eruption of Mount St. Helens, WA. We hypothesized that tree establishment increased gradually over time, tree establishments was limited by moisture availability and ENSO with temperature mediating tree establishment at higher elevations. Tree-establishment dates at the annual-scale were determined from ca. 744 individual conifer trees that were harvested along the Muddy Rivers Lahar. Tree establishment distribution by species and shade tolerance groups were clustered and plotted to graphically interpret possible spatial patterns across the Lahar. Years of high tree establishment were primarily associated with above average temperature conditions during winter, spring and summer of the year of establishment, but also prior and after the establishment year, suggesting a climatic effect on germination, cone production, and seedling survival, respectively. Our findings also suggest that temperature and tree species traits (i.e. shade tolerance) mediated climate-establishment relationships. Combined, our results suggest that under ongoing warming trends, tree establishments have not been negatively affected at the elevation and maritime conditions of the Muddy River Lahar.

Acknowledgements

I would like to express my deepest gratitude toward my advisor and chair committee member Andrés Holz, for his support and dedication; through the years, he kept me motivated and helped me formalize my graduate studies. During the execution of this research we relied heavily on the effort led by Douglas Thalacker, a former graduate student in the Geography Department and Global Environmental Change Lab directed by Dr. Andrés Holz, who collected, processed and determined the germination dates and cores used in this study. I would like to thank my peers at the Global Environmental Change Lab who offered support and advice that strengthened and broadened my ecological scope. Much gratitude to my committee members Martin Lafrenz and Melissa Lucash for their time and commitment to review my project and offering their insight in helping me finalize my work. Finally, to my mother, friends and family who have listened to all my rants and frustrations and provided unconditional support and constructive criticism. This work would have not been possible without all your support and collective effort, thank you.

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Introduction

Forest regeneration is an integral ecological process that determines future forest structure, function and composition (Veblen 1992; Johnstone et al. 2016). The responses of tree species to large-scale disturbances are likely controlled by long- and short-term legacies (Johnstone et al. 2016). Long-term, evolutionary adaptation and life-history traits may allow specific species to thrive and re-colonize post-disturbed forests (e.g. serotiny, high seed wing/weight ratio; Keeley et al. 2011; Herben et al. 2017). Short-term factors, both biotic (e.g. sufficient seed availability at the site, competition) and abiotic (e.g. suitable micro-site) may additionally mediate post-disturbance recovery (Halpern and Harmond l983; Wood and del Morral 1987). Furthermore, above-normal moisture conditions favors tree regeneration following disturbances, particularly in temperate dry coniferous forests (Davis et al. 2019; Steven-Rumann et al. 2018). Under warming conditions, it is unclear how tree species regeneration will respond to climate, and how such responses will vary by taxa and site conditions.

Tree seedling establishment, in contrast to tree growth and tree mortality, has been understudied, and yet will likely determine the future extent of forest species. The lack of long-term observations on the effect of climate variability on tree establishment following large-scale disturbances might be in part due to longer time lags (i.e.> 10 years) for forest species than for other community types to respond to climate variation, scarcity of opportunities to study climate-tree establishment relationships in protected areas without non-climatic disturbances (e.g. logging). Understanding how forest ecosystems, through the lens of climate-tree establishment dynamics, will respond today and in the future to ongoing warming conditions remains a high priority in ecology (e.g. Kroiss and HilleRisLambers 2015; Andrus et al. 2018).

Climate, specifically interannual climate variability, affects physiological processes in vascular plants, including secondary growth (Pierson 2014; Castagneri 2017), cone and seed production (Woodward et al. 1994; Pierson 2014), and seedling establishment (Andrus et al. 2018), and such effect species' can be mediated by life history traits (e.g. shade tolerance ; Dobrowski 2015; Lienard 2015). Yet, much of our understanding on climate-seedling establishment relationships comes from reconstructive studies (using tree-ring techniques) conducted in dry forests, where wet conditions at the interannual scale favor tree establishment of most tree species either in absent of large-scale disturbances (Villalba and Veblen 1998; League and Veblen 2006; Andrus et al. 2018) or following disturbance (e.g. postfire establishment; Swetnam and Brown 2010; Meinier et al. 2014). Some of these studies also found that above mean conditions were in turn associated with phases of the El Nino Southern Oscillation (ENSO), which is earth's most pervasive large-scale climate driver and operates at the interannual-scale. ENSO occurs in the equatorial Pacific Ocean but affects weather patterns worldwide through atmospheric teleconnections.

Fewer and only short-term climate-tree establishment studies exist for wet forests, where complex relationships have been reported. For instance, in undisturbed mixed conifer forests in the Cascades Mountains in the Pacific Northwest region in the USA, interannual variation in moisture availability (i.e. snowpack duration) favors tree establishment of some tree species but instead hinders that of others (Kroiss and

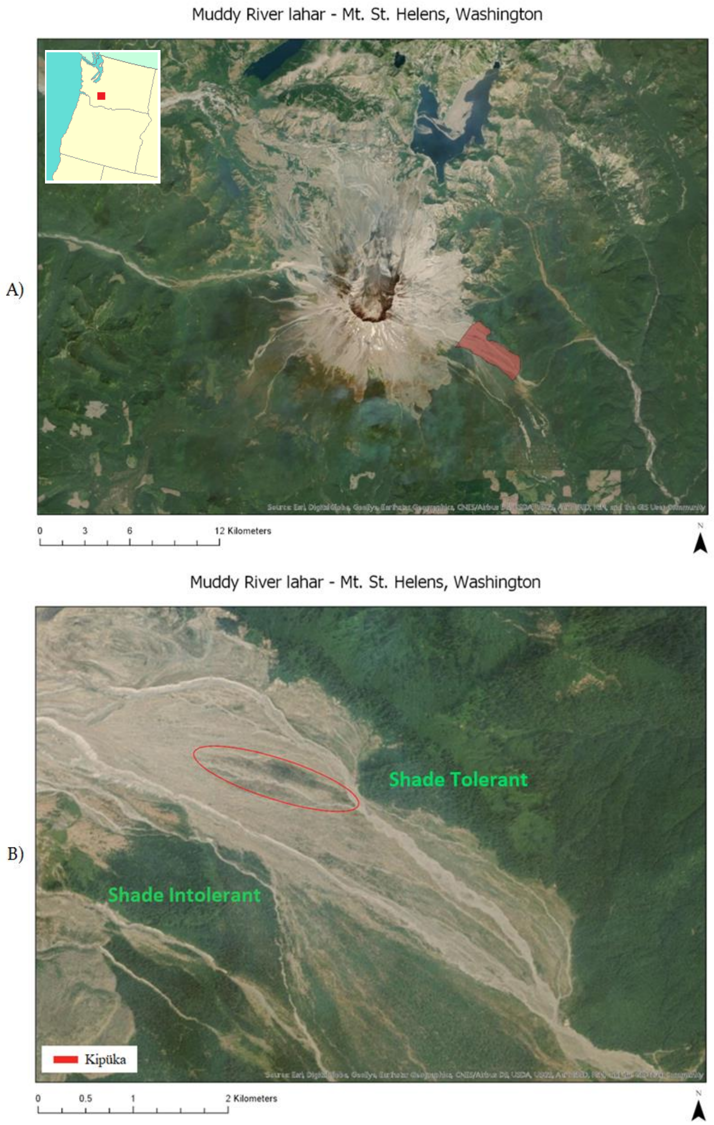
HilleRisLambers 2015). Thus, it is still unclear the effect of climate variability on tree establishment in wet forests in the longer term as well as to how individual tree species respond to such variability. Furthermore, and to the best of our knowledge, there are no studies that have looked at the interannual-scale effect of climate variability on tree establishment (i.e. germination year) in wet forests following a large scale disturbance.

In this study, we took advantage of a natural experiment that resulted from a large forest opening suddenly created by the destructive effect of the Muddy River Lahar, a mixture of water, mud, and volcanic rock that flew swiftly downslope on Mt. St. Helens (MSH) in May of 1980, killing almost 100% of trees along its path. Specifically, we ask: what was the pattern of tree establishment over time? How did tree establishment respond to interannual climate variability, including variation in El Niño–Southern Oscillation (ENSO)? Did the effect of climate variability on successful tree establishment vary by tree shade tolerance? Furthermore, was there a mediating effect of elevation (i.e. temperature) on climate-establishment relationships across the Muddy River Lahar? We hypothesized that (H1) tree establishment increased gradually over time, (H2) tree establishment was primarily controlled by moisture availability and ENSO and (H3) temperature controlled tree establishment at highest elevations. To answer these questions, used annually-resolved dates of germination and spatial location of montane and subalpine trees juveniles established following the 1980 MSH's eruption.

Methods

Study Area

Our study was conducted on the Muddy River Lahar, which lies on the southeastern slope of MSH between ca. 880 and 1,270 m.a.s.l. (Fig. 1a). MSH is a stratovolcano that is located on the west margin of the Cascade Range in Washington state, USA. The study area has a mild wet maritime climate characterized by wet/cool winters and warm/dry summers. Total annual precipitation fluctuates at ca. 3000 mm, most of which results from snow at higher elevations (at ca. >1000 m.a.s.l.) during the winter and spring months (Lisle, Major and Hardison 2018). During the winter season, mean annual temperature is ca. 2.1°C and average precipitation is ca. 305mm, and for the spring months average annual temperature is ca. 3.4°C with an average precipitation of ca. 187mm (Climate Mount Saint Helens Viewpoint 2018). In the summer season, mean temperature fluctuates around ca.14°C and average rainfall is at ca. 46mm (Climate Mount Saint Helens Viewpoint 2018). During positive El Niño-Southern Oscillation (ENSO; El Niño) years the study area typically experiences warmer and drier than average winters that transition into warmer than average springs followed by drier anomalies during summer (Morgenstern et al. 2004). The dominant vegetation at MSH prior to the 1980 eruption was characterized by old growth forest intermingled with clear-cut tree plantations (Dale and Crisafulli 2018). Pre-eruption surveys noted the dominance of mature stands of shade-tolerant *Tsuga heterophylla* (western hemlock) and shade-intolerant *Pseudotsuga menziesii* (Douglas-fir) at lower elevations which transitioned into shade-tolerant *Abies amabilis* (Pacific silver fir) at higher elevation (ca. >1,100 m.a.sl.). Scattered shade-intolerant *Pinus monticola* (western white pine) and *Pinus contorta*. var. *latifolia* (lodgepole pine) co-occur with shade-tolerant *Abies lasiocarpa* (subalpine fir) in this region (Franklin and Dyrness 1969; Frenzen et al. 2005).



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

***Figure 1**: (a)* Mount St. Helens, located on the western side of the Cascade Range in the Skamania County of Washington, in the Pacific Northwest region of the USA. The designated study area is found south east of Mt. St. Helen's crater and is known as the Muddy River Lahar (Muddy River Lahar; in red). (b) Undisturbed forest stands of dominant shade-intolerant and tolerant tree species to the SW and NE, respectively, and Kīpuka (or undisturbed green island of tree refugia) in the middle of the upper Lahar.

The explosive 1980 eruption of MSH destroyed a large part (ca. 110 ha) of the northern mature forest, depositing large volumes of erodible fragmental material through a sequence of massive debris avalanches, very hot and explosive pyroclastic density currents, rapid moving lahars, and far reaching tephra fall (Fig. 1a; Lisle, Major and Hardison 2018). Overall, the impact of each of these processes on the landscape declined in severity with distance away from the crater. Perhaps with the exception of lahars, the impact of all these processes were significantly lower south of the crater (Lisle, Major and Hardison 2018). Volcanic lahars are rapid granular flow of a fully saturated mixture of volcanic rock particles and liquid (and sometimes frozen) water, as result of an eruption (Pierson and Major 2014). These flows are among the most destructive and far-reaching ground hazards associated with volcanic eruptions. They can travel many tens of miles down valleys, move tens of miles per hour, and spill far beyond river-channel confines eruption (Pierson and Major 2014).

The 1980's flow engraved new channels and completely removed the vegetation on its path in the upper Muddy River basin (Pierson and Major 2014). Further erosion and bank widening resulted from a rain-on-snow event during the winter of 2006 (del Moral et al. 2009). Between these new channels, only a few raised islands known as kīpukas preserved late ecological successional vegetation that served as seed source within the Lahar (Fig. 1b; del Moral et al 2009; Dale and Crisafulli 2018). Additional seed source were available adjacent to the Lahar from undisturbed forests stands: to the NE mature forest stands are characterized by large-size *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis* trees, with multi-story, shorter *Pinus contorta* stands (with scattered *P. monticola*) to the SW (Fig. 1b). The tall forest stands to the NE are located on relatively steep slopes that increase the seed dispersal potential of these species into the Lahar and provide morning shade to areas immediately adjacent to them in the Lahar. Instead, *P. contorta* stands on the SW of the Lahar, while shorter provided shade from hottest afternoon sunshine, and its SW location increased their chance to successfully colonize the Lahar—as dominant winds at this temperate latitude are westerly winds. These SW stands are thought to have established ca. 200 years ago following a previous lahar event (Yamaguchi 1983). Instead, the older NE forest stands, due to its steeper, more protected slopes, do not show evidence of damage during this older or the 1980 event.

Field Methods

Tree establishment sampling was led in the summer of 2016 by Portland State University MS student Douglas Thalacker, who divided the length of the lahar into eight elevational transects to capture variation in tree establishment along the elevation gradient, as well as along each transect (*unpubl. work*). Each transect was equally spaced every 0.5km, and within each elevational transect, plots ($4m^2$) were set every 50m. Since the width of the Lahar varies with elevation a different number of plots were set along each transect. Roughly ca. 20 plots were set in each elevational transect, with a total of 177 plots in the study area. To estimate ages and frequency of tree species represented in each plot, information on species and location coordinates were recorded, and dendroecological (n= ca. 760) samples from ca. three trees per height-size cohort (class 1: 0-2 cm, class 2: 4-6cm, and class 3: 8-10cm) were collected. In each plot basal cross-section from juveniles were harvested (n= 563) and increment cores (n= 181) were collected from as close to the ground as possible (n= 118 adult trees were cored at height ≤ 5 cm). For each core coring height was recorded. From the total of ca. 760 dendroecological samples, only 744 were used as the rest were established prior to the 1975-2013 period of analysis. We included a period of five years prior to the 1980's eruption to explore the potential survivability of recently established juveniles in the area prior to the disturbance.

Sample Processing

Basal cross-sections from harvested juveniles were sliced into 2cm cross-sections until the earliest germination pith date at the shoot-root boundary was found (League and Veblen 2006). Sampled cross-sections and cores were incrementally sanded using standard dendrochronological procedures (Stokes and Smiley 1968) and scanned at high resolution (1200 dpi). The dendrochronology software cDendro was used to electronically examine the imagery and count the rings from all samples and assign them their corresponding establishment years using the list-year (visual marker) method (Yamaguchi 1991).

Climate Data

Monthly climate data for the 1975–2013 period was obtained from Oregon State University's PRISM Climate Group (4km^2 grid resolution) and compiled into seasonal Winter: JFM, Spring: AMJ, Summer: JAS, Fall: OND and growing season April – September indices. Following data exploration (i.e. correlation matrices), we removed redundant datasets (r > 0.8) and kept seasonal parameters hypothesized to be most relevant, including minimum/maximum temperature (°C), total precipitation (mm) and minimum/maximum vapor pressure deficit (hPa). In addition, we obtained and compiled Snow Water Equivalent (SWE) data from the United States Department of Agriculture Natural Resources Conservation Service. Snow telemetry (SNOTEL) sites we included in our analysis were ranged within similar elevations, had continuous data for the designated study years, and were within 15 kilometers from our study area. Finally, we used the Multivariate ENSO Index values (MEI.v2) from the Earth System Research Laboratory's Physical Sciences Division database as an index to pinpoint atmospheric and oceanic anomalies within the tropical pacific basin. All climate data was converted and analyzed as departures from their respective long-term mean in standard deviation units (i.e. z-scores).

Data Analysis

Tree establishment dates included in the analyses included both shoot-root boundary ages (76% of samples) and ages from tree cores (24% of samples), with a total of 182 and 562 samples of shade tolerant and intolerant, respectively. To correct for the unknown number of years due to missing pith in the cores we used the Duncan method (Duncan 1989). To correct for the unknown number of years due to coring height, we developed species-specific age-height growth regression models from cross-sections obtained from complete juveniles that were harvested in the field and processed/analyzed them in the lab. Before conducting any analysis, individual species were aggregated into two groups based on their shade tolerance (Franklin and Dyrness 1969, FEIS 2019; Table 1).

Table 1: Grouping categories based tree species tolerance to shade (Franklin and Dyrness 1969, FEIS 2019).

Shade-intolerant	**Shade-tolerant**
Noble fir *(Abies procera)*	Pacific silver fir *(Abies amabilis)*
Lodgepole pine *(Pinus contorta)*	Subalpine fir *(Abies lasiocarpa)*
Douglas fir *(Pseudotsuga menziesii)*	Western white pine *(Pinus monticola)*
	Western hemlock *(Tsuga heterophylla)*
	Mountain hemlock *(Tsuga mertensiana)*

To test for an association between seasonal climate parameters and successful tree establishment two parallel approaches were conducted. One approach quantify the overall effect of seasonal climate variability on all years of tree establishment, whereas the other on years of disproportionally low vs. high tree establishment. All climate-establishment analyses were conducted in R. First, correlation coefficients between seasonal climate parameters and tree establishment in all 39 years were obtained using the Performance Analytics package in R (Peterson et al. 2020). Years of high and low establishment of shade-tolerant and intolerant tree species across the entire Lahar were then identified using the top 75th percentile as cutoff; i.e. >75th percentile: years of high establishment and years of low establishment <75th percentile. We choose the 75th percentile because it was a sensible compromise between a percentile that might represent anomalous climatic conditions while at the same time have a large-enough sample size for statistical testing of our hypotheses.

To better capture the possible effect of climate on tree establishment at the interannual scale we opted for splitting the tree establishment record into four 10-yr blocks. We chose this strategy because the timeseries of the tree establishment record exhibited a monotically-increasing (first half for the record) and then decreasing (second half of the record) pattern. Thus, we applied the 75th percentile cutoff separately to each individual 10-yr block during the 1975-2013 period (i.e. except for the first block which had a 9 years; 1975-1983 period).

To test for differences in the association between seasonal climate parameters and tree establishment between years of high vs. low tree establishment of shade-tolerant and shade-intolerant trees, we used the non-parametric Mann-Whitney U test functions in R (Hart 2001). To determine whether and how climate parameters was associated with years of high tree establishment on co-occurring (i.e. germination) and/ or subsequent (i.e. seedling survival) years, a Superposed Epoch Analysis (SEA; Grissino-Mayer 1995) was conducted in the dplR package in R. SEA, which allowed us to test for significant interannual-scale departures in climate (from long-term climate conditions) during all years (i.e. composite) of high tree establishment. Significance levels of the departures from the long-term means were determined from bootstrapped 95% confidence intervals estimated from 10,000 Monte Carlo simulations (Mooney et al. 1993). To explore the potential mediating effect of elevation on climate-establishment relationships we split the record into low and high elevation establishment of shade-tolerant and of shade-intolerant tree species. For this, the number of establishments (i.e. in all plots) at each elevational transect was aggregated and natural breaks identified (Appendix Fig. 1).

Results

Establishments across the extent of the Muddy River Lahar

At first glance tree establishment distribution of all species combined (Fig. 2a), and individually by shade tolerance (Fig. 2b,c), followed a normal distributed over time, where gradual establishment began around the mid 1980s, peaked in the mid 1990s, and declined after the early 2000s. Most shade-tolerant tree establishment took place between 1988 and 2000 (i.e. >75 percentile), with local peaks in 1984, 1988-1989, 1993, 1996 (highest peak; n=15; 8.2% of all shade-tolerant establishments), 2000-2001, 2005, 2007, and 2010 (Fig. 2b). The establishment of shade-intolerant was highest between 1986 and 2000 (i.e. >75 percentile), with local peaks in 1986, 1994 (highest peak; n=44; 7.8% of all shade-intolerant establishments), 2000, 2004 and 2012 (Fig. 2c).

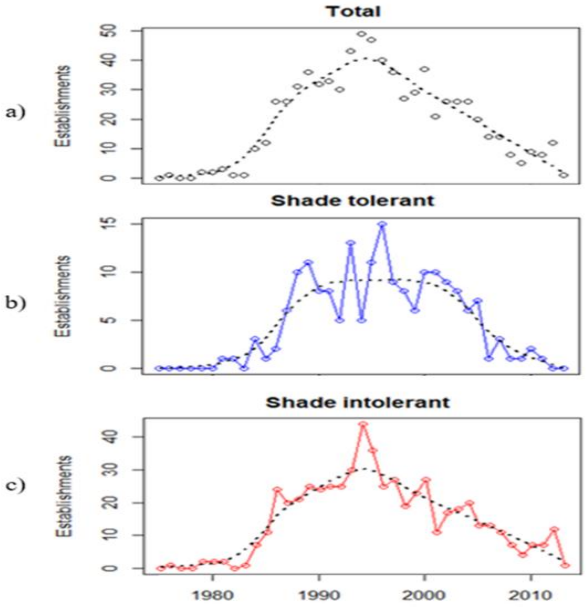


Figure 2. *Tree establishment of all species combined (a), shade-tolerant tree species (b), and shade-intolerant tree species (c) at the Muddy River Lahar over the 1975-2013 period. Notice different scale in the y-axis.*

Most establishments of shade-tolerant tree species occurred along the SW boundary across the Muddy River Lahar, clustered around a small kipüka in the upper middle section of the Lahar, and along the NW boundary in the very upper section of the Lahar (Fig. 3a). Instead, establishment of shade-intolerant tree species spanned across the width of the lahar, with highest density on the edges of both undisturbed stands (SW and NE) at lowest elevation, fairly evenly distributed at mid elevations, and highest density at highest elevation towards the NE edge of the lahar (Fig. 3b).

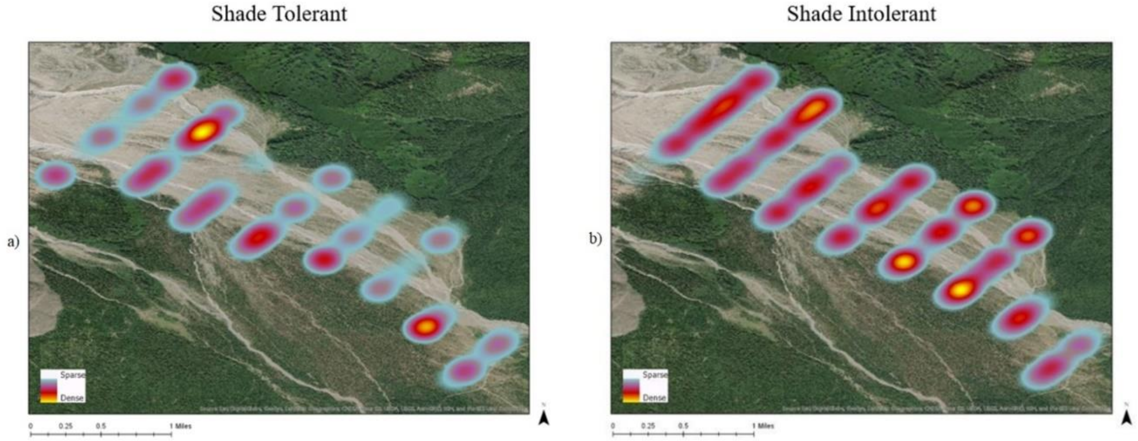


***Figure 3**:* Map of the distribution of tree establishment along the Muddy River Lahar by shade tolerance and the location of seed sources. Density distribution of shade-tolerant (a) and intolerant (b) trees along the Muddy River Lahar conducted using the heat map symbology in ArcGIS Pro v2.2.

Climate-tree establishment relationships across the extent of the Muddy River Lahar

Establishment (i.e. germination) of trees during all years and of both shade tolerance was associated with positive anomalies in maximum temperature (Tmax) during summer and throughout the growing season (Table 2). Positive Spring anomalies in maximum temperature (Tmax) also favored establishment of shade-intolerant tree species during all years (Table 2).

Table 2: Statistically significant association between seasonal climate parameters and tree establishment of shade-tolerant (T) and shade-intolerant (I) tree species during all years over the 1975-2013 period. Tmin, Tmax, VPDmin, VDPmax, MEI and SWE refer to mean min temperature, mean max temperature, mean min vapor pressure deficit, mean maximum vapor pressure deficit, the Multivariate El Niño Index, and Snow Water Equivalent, respectively, and Spring (Apr-Jun), Summer (Jul-Sep), Grow Season (Apr-Sep), Fall (Oct-Dec), and Winter (Jan-Mar) summarize conditions. Associations that resulted from significant (*p<0.05, **p<0.01, ***p<0.001) Spearman correlation coefficients values for the 1975-2013 are reported.

	Precipitation	Tmin	Tmax	VDPmin	VDPmax	MEI	SWE
Spring			I**				
Summer			T**,I**				
Grow Season			T**,I***				
Fall							
Winter							

During years of high establishment, shade-tolerant species were favored by high maximum temperature during spring, summer and grow season. Significant warm conditions took place the year prior to germination during the springs and growing season and two years after the year of germination (summer)(Fig 4a-c). Instead, low establishment years coincided with opposite conditions, with significant cooler springs and growing season one year prior to the year of germination and cooler summer two years after the establishment had occurred (Fig 4d-f). No meaningful and significant association were found for shade-intolerant tree species (Fig. 4g-i).

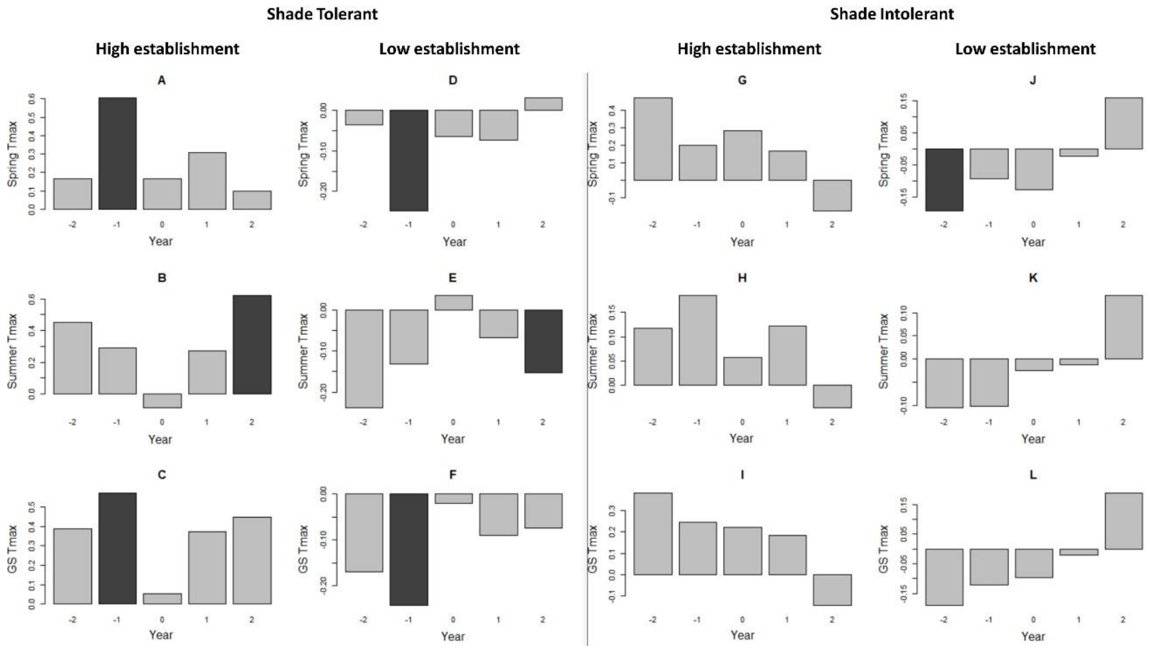


Figure 4: *Departures (SDs) from mean values for seasonal gridded maximum mean temperature (PRISM) for 5-yr windows (t - 2 to t + 2) centered on years of high (>75th percentile) and low (<75th percentile) tree establishment of shade-tolerant and intolerant tree species spanning across the Muddy River Lahar over the 1975-2013 period. Black bars indicate statistically significant departures ($P < 0.05$; derived from 10,000 Monte Carlo simulations).* Seasons are defined as Spring (Apr-Jun), Summer (Jul-Sep), and Grow Season (Apr-Sep).

Establishments across an elevation gradient

When we analyzed the establishments of trees separately by elevation, it was clear that the first peak of tree establishment of shade-tolerant species was slightly earlier at lower (1988) than at higher (1989) elevations, whereas the first establishment peak of shade-intolerant species was simultaneous between high and low elevation (1986) across the Muddy River Lahar (Fig. 5). At lower elevation (842m - 1050m) tree establishment of shade-tolerant species (n=78) was absent up until the mid-1980’s, with successful establishments ranging from 2-6 individuals per year up until 2010, after which no further establishments were reported (Fig. 5a). The year with the highest establishment of shade-tolerant tree species was 1988 with eight establishments followed by 1996/1997 with 6 establishments. Years with establishments above the 75th percentile occurred mostly between 1987 and 1997. At this lower elevation, shade-intolerant species establishment (n=293) spiked during the mid 1990's, with the highest establishment year in 1994 with 22 establishments followed by 1991/1995 with 19 establishments (Fig. 5a).

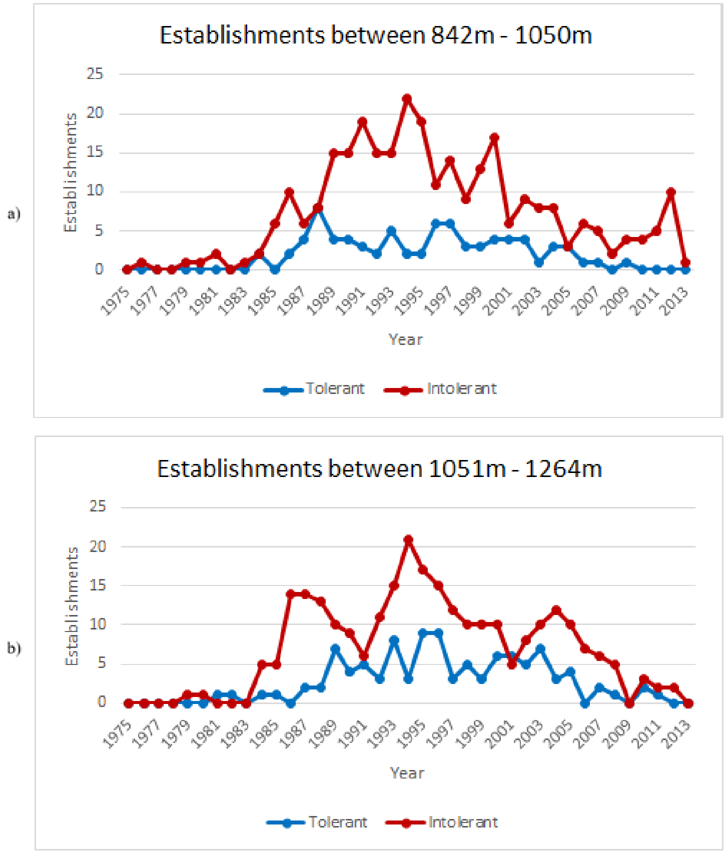


Figure 5: *Tree establishment per year at low (a; 842-1050masl) and high (b; 1051-1264masl) elevation in the Muddy Rivers lahar. The number of establishments vary with elevation, with higher establishment at high elevation for shade-tolerant (blue) species (n=78 vs. n=104) and higher establishments at lower elevation for shade-intolerant (red) species (n=293 vs . 269).*

At higher elevations (1050m – 1264m) the establishment of shade-tolerant species (n=104) averaged two establishments per year with peaks occurring in 1995/1996 and 1993 where nine and seven establishments occurred, respectively (Fig. 5b). Three large peaks were observed for shade-intolerant species (n-269) during the mid 1980s, mid 1990s, and mid 2000s. The year with the highest establishment rate was 1994 with 21 establishments followed by 1995 with 17 establishments. Similar to shade-tolerant establishments, years with establishments above the 75th percentile were spread apart and ranged from 1979-2005.

Climate-tree establishment relationships at low vs. high elevation sections of the Muddy River Lahar

Similar to the observations across the entire lahar, the association between seasonal climate parameters and tree establishment across the elevation gradient indicated that tree establishment of all species was favored by maximum temperatures during the summer months and throughout the growing season (Table 3).

Table 3: Statistically significant association between seasonal climate parameters and tree establishment of shade-tolerant (T) and shade-intolerant (I) tree species at low and high elevation during all years over the 1975-2013 period. Associations that resulted from significant (*p<0.05, **p<0.01, ***p<0.001) Spearman correlation coefficients values for the 1975-2013 are reported.

Under 1050m

	Precipitation	Tmin	Tmax	VDPmin	VDPmax	MEI	SWE
Spring			I*				
Summer			T*,I**				
Grow Season			T**,I**				

Above 1050m

	Precipitation	Tmin	Tmax	VDPmin	VDPmax	MEI	SWE
Spring			I**				
Summer			T*,I**				
Grow Season			T*,I***				
Winter			I*				

At lower elevations, significant warm springs (year prior), summer (two years prior and a year after), and growing seasons (one and two years prior to germination) were associated with high tree establishment of shade-tolerance species during years of high establishment (Fig. 6a-c). The reverse direction in the climate-establishment relationships of shade-tolerant species were found for years of low establishment at this elevation. Years of high or low tree establishment of shade-intolerant trees were not statistically associated with climate parameters at low elevations (Fig. 6g-l). Similarly, maximum temperature yielded no statistically significant values for shade-tolerant or shade-intolerant species at elevations above 1050m.

Additional variables that were highlighted by our SEA included spring minimum temperature, summer/grow season precipitation and winter/grow season MEI. Years of high establishment of shade-tolerant trees were favored by (higher than average) minimum spring temperature (during the year of germination and the previous year) and (lower than average) growing season precipitation (two years following germination) below the 1050m threshold (Fig. 7a,b). Positive winter MEI conditions were influential two years prior to germination date during years of high establishment of shade-intolerant trees at low elevations (Fig. 7g). Above the 1050m threshold years of high establishment for shade-tolerant species were associated with drier summer two years prior to germination (Fig. 7c) while shade-intolerant species responded positively to higher spring temperatures and positive ENSO (MEI) on the year recruitment events occurred (Fig. 7h-i).

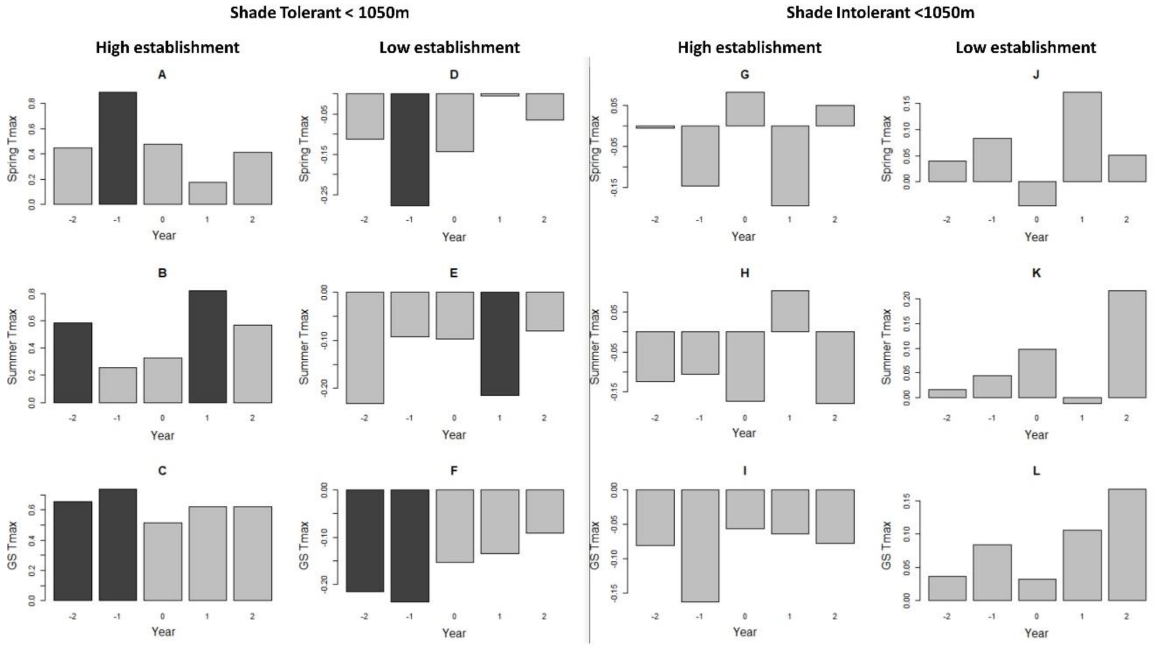


Figure 6: *Departures (SDs) from mean values for seasonal gridded maximum mean temperature (PRISM) for 5-yr windows (t - 2 to t + 2) centered on years of high (>75th percentile) and low (<75th percentile) tree establishment of shade-tolerant and shade-intolerant species under 1050m of elevation within the* Muddy River Lahar *over the 1975-2013 period. Black bars indicate statistically significant departures (P < 0.05; derived from 10,000 Monte Carlo simulations). Seasons are defined as Spring (Apr-Jun), Summer (Jul-Sep), and Grow Season (Apr-Sep).*

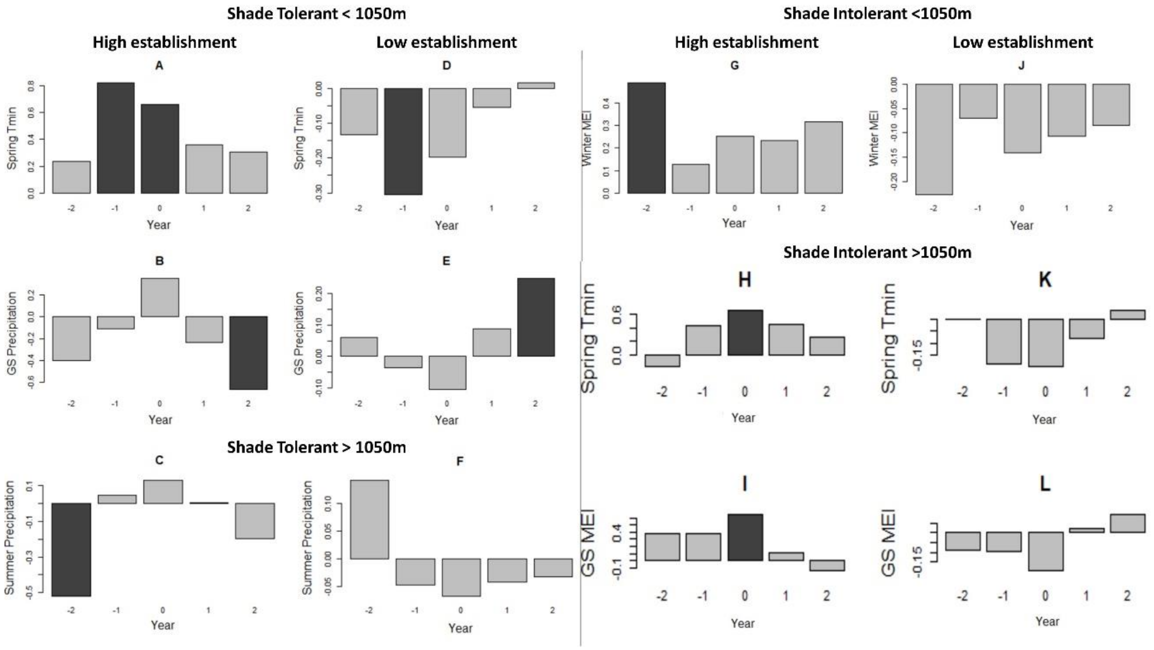


Figure 7: *Departures (SDs) from mean values for seasonal gridded minimum temperature, precipitation and MEI (PRISM) for 5-yr windows (t - 2 to t + 2) centered on years of high (>75^{th} percentile) and low (<75^{th} percentile) tree establishment of shade-tolerant and shade-intolerant species under 1050m of elevation within the* Muddy River Lahar *over the 1975-2013 period. Black bars indicate statistically significant departures (P < 0.05; derived from 10,000 Monte Carlo simulations). Seasons are defined as Spring (Apr-Jun), Summer (Jul-Sep), and Grow Season (Apr-Sep).*

Discussion

The volcanic eruption that occurred on May 1980 in Mount St. Helens and its resulting lahar serve as an example of an infrequent large disturbance that altered more than 20km of river corridor in the region (Frenzen 2005; Turner et al. 1998). Naturally occurring disturbances alter existing forest functions and structures, which rely on ecological legacies for its recovery. In this post disturbance landscape, the surviving marginal legacies played a crucial role in the successional pathway in the Muddy River Lahar by providing a source for seed availability and shaded conditions for new establishments to occur. Throughout the years, the successful establishment of pioneering communities in heavily affected areas such as the Muddy River lahar played a key role in altering the soil and facilitating the establishment of later-stage successional species (Dale & Crisafulli 2018).

Studies at MSH have explored the spatial pattern of these post-lahar communities and descriptively linked their composition with distance to seed source availability at the Muddy River Lahar (del Moral & Ellis 2005). During the 1975-2013, tree establishment of all tree species gradually increased from early 1980, peaked around the mid-1990s, and declined afterwards (Fig 2). Contrary to our initial hypothesis, (H1) tree establishment did not increase gradually, but instead continues to decline since the 1990s. We interpret these temporal patterns as the result of competition. Although there are plenty of areas free of tree competition, the Lahar has been rapidly covered by a *Racomitrium canescens*, a moss that may compete with juvenile trees and inhibit the establishment of seedlings. (Crisafulli. *pers. comm.*). Following our expectations shade tolerance did mediate tree establishment across the Muddy River Lahar with shade-intolerant establishments occurring at a higher frequency than shade-tolerant. As expected, shade-intolerant tree species have been arriving in higher numbers (nearly 2/3 of the complete establishment record) than shade-tolerant tree species resulting in higher recorded establishments. In contrast to our expectations, shade-tolerant species peaked earlier than their counterpart in the lower half of the Muddy River Lahar. On the other hand, at higher elevations shade-intolerant tree species peaked nearly five years earlier than shade-tolerant tree species (Fig 2).

Spatial density patterns of cumulative tree establishment in 2013 indicate high density of tree establishment nearby the adjacent undisturbed boundaries of the Muddy River Lahar, which could be linked to soil conditions, seed source distance and/ or shading preferences (Fig 3). Most shade-tolerant tree species established around the kipuka and mostly on the SW edge of the Lahar, which is the area farthest away from their original seed source. While counterintuitive at first, this SW edge is the only area across the Lahar that juveniles are shaded (by the *Pinus contorta* trees) during the warmest time of the day (afternoon) and where protection was available from predominant and desiccating winds (coming from the west). Instead, shade-intolerant trees established throughout the Lahar. At closer look, highest density of these species occurred at both undisturbed edges at low elevation, at the center at mid elevations, and on the NE edge at highest elevation. This pattern suggest that seeds were able to arrive to all areas, and that juvenile development was favored by shade at low elevation and sunlight and heat at highest elevation.

Our second hypothesis (H2) was based on the literature (Pierson 2014; Andrus et al. 2018) which explored the impact of climate change induced moisture deficit in the establishment and growth of species in mountain ecosystems. Higher summer temperatures increase the rate of evapotranspiration, which reduces soil moisture and deprives young establishments from access to water. In contrast to these studies, we found that in the Muddy River Lahar region high temperature played the most significant role elevations in the success rate of establishment for shade-tolerant and shade-intolerant species at both higher and lower elevations (Fig. 6-7). In addition, low precipitation two years prior during the summer months was highlighted as important in promoting successful tree establishment for shade-tolerant species at elevations >1050m (Fig 7c). The processes associated to the lags found in our SEAs, suggest linkages to the year of the occurrence of the establishment event (germination), in addition to antecedent germination processes (up to 2 years prior), including cone production and seed viability (Woodward et al. 1994).

As mentioned previously, temperature played a key role in the successful establishment and tree germination where juvenile survival was favored by warmer than average temperature at both higher and lower elevations. We expected warmer temperatures to play a key role in the number of establishments at higher elevation (H3) since precipitation >1000m.a.s.l generally falls as snow leaving a 2-3m thick snowpack which last several months (Lisle, Major and Hardison 2018) but no statistically significant values were yielded from the SEA. At higher elevations the positive relation between shade-intolerant species, spring minimum temperature and GS MEI was highlighted on the year of establishment occurrence (Fig 7h,7i). Positive ENSO years were associated with warmer winters conditions (Morgenstern et al. 2004) which accelerates the rate of snowmelt accumulated during the winter months and opens suitable microsites for germination allowing species to establish earlier than previously observed. (Kroiss, 2015).

At this high elevation and relatively short distance to ocean moisture, we did not find evidence of a negative effect, putatively associated to lack of soil moisture removal, of warm and dry conditions on seedling establishments.

Cooler and wetter summers were expected to play a significant role during years of bellow than average snowpack's due to lesser soil moisture inputs which reduce stress in the recently established root zone (Andrus 2018) It is important to take into consideration that the date of recruitment for establishments is defined as 10cm height pith date opposed to the exact date of germination which usually result in the destruction of the sample (Meinier et al. 2014) this results in the sampling of those juveniles which survived early sensitive development period. Freshly established seedlings have small root system, which make them rely heavily on surface water and nutrient availability (Peterson, 2014). On the other hand low summer temperatures decrease the rate of evapotranspiration, which at this elevation might result in either difficulty for seedings roots to penetrate a cold and/ frozen substrate, and/ or simply high seedling mortality. (Andrus 2018)

As seen in other studies recruitment frequency vary amongst observed species mostly due to individual specific responses to climate change and/or microsite availability (Kroiss 2015). In our study, the direction in the differences (trends) in the seasonal climate parameters between years of high and low tree establishment were consistent with climate-establishment relationships, yet these were not significant and thus not reported (Appendix Fig. 2,3,4).

Higher recorded temperatures and reductions in moisture have been key factors in the increase and frequency of recently witnessed disturbances such as droughts and forest fires in the Western coast of the United States. Frequent repetition of such disturbances can directly influence the structure of forest ecosystems by reshuffling successional processes and allowing the introduction of invasive plants, which can be a catalyst for alterations in future, vegetation composition (Pierson 2014). Successful tree establishment is essential for the survivability of conifer species and their response to climate change allow us to have a better understanding of the potential shift's ecosystems could take.

Conclusion

The expected warming temperatures in cold, high montane subalpine and alpine ecosystem such as the Muddy River Lahar will have a direct impact in accelerating spring snowmelt, which extends the establishment periods in higher elevation ecosystems due to rapid snowmelt. Warmer temperatures and drier conditions in the study area coincided with years of successful seeding recruitment for both shade tolerant and intolerant species, especially at the lower end of the elevational gradient, which is contrary to findings at high elevation in continental, dry forest ecosystems (Andrus et al. 2018). Although ENSO was not an important predictor when tested against most reconstructed establishments, it was important for tree establishment of shade-intolerant at highest elevation. The amplified warming effect that accompanies ENSO and anthropogenic warming might result in more rapid and persistent rising temperatures in the future than in turn might result in rapid tree establishment. Increases in temperature in high montane, subalpine and alpine regions have accelerated the rate of snowmelt during the spring months (Mote et al. 2018) and increased the frequency of droughts, which have already affected the rates of tree mortality due to moisture stress in regions across western North America (e.g. Van Mantgem, 2009). Currently limited by low temperature, emergence of newly available site conditions via warming trends may open the way for new species to colonize further up expanding the forest cover in higher altitude environments.

With this research, we were able to explore the effects of climate variability and its relationship with establishment pulses in colder ecosystems unfrequented by reoccurring disturbance events such as forest fires. With the anticipated increases in CO_2 emissions, future global temperatures are expected to increase resulting in the warming of colder regions. Documented changes in plant establishment have been explored by various scientists and continue to be a subject of concern amongst the ecological community. Further exploration of the effect of warmer temperatures on mesic forest ecosystems where plant communities have adapted to moderate conditions and short growing seasons should inform forecast large-scale on potential future transformation in vegetation composition. We hope that the information generated from this study will be useful to better comprehend the effects of local and global conditions and their effects on future forest structures.

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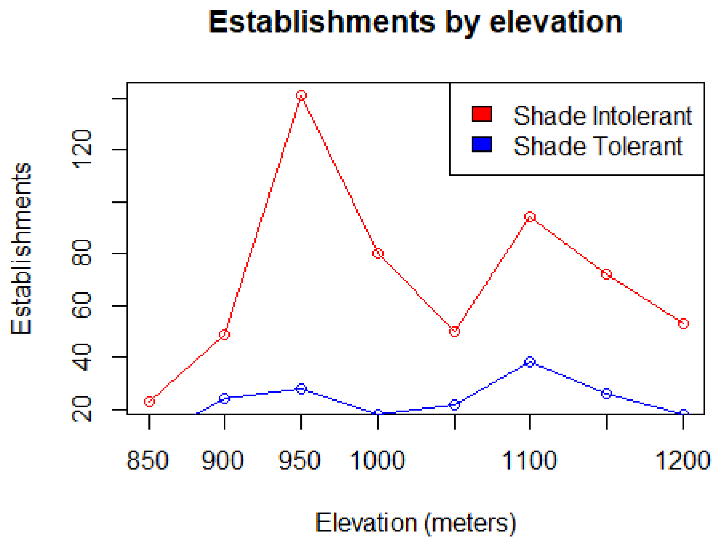
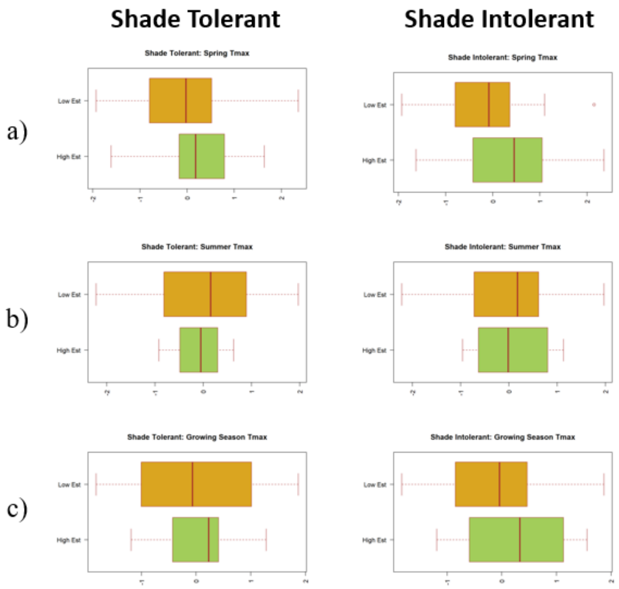
Appendix A – Establishments by elevation



Appendix Figure 1*: Tree establishment of shade-tolerant and intolerant divided by elevation.*

Appendix B – Distribution of maximum temperature throughout the lahar

Above-average maximum temperature in spring was also positively associated with years of high establishment for both shade-tolerant and shade-intolerant species in high establishment years with shade-intolerant species preferring slightly warmer temperatures than shade-tolerant. (Appendix Figure 2) On the other hand, slightly cooler summer temperatures were associated (but not statistically significant) with years of high establishments with values slightly below the temperatures mean. When combined, the growing season yielded similar results to those of the spring maximum temperature where overall above averages were common in years of high establishments. In all cases the range of high establishment temperatures for shade-tolerant individuals was smaller than that of shade-intolerant species. None of the values yielded from the Mann-Whitney U test compare the difference between high establishment years and low establishment years which yielded values under 0.05 and were not normally distributed.

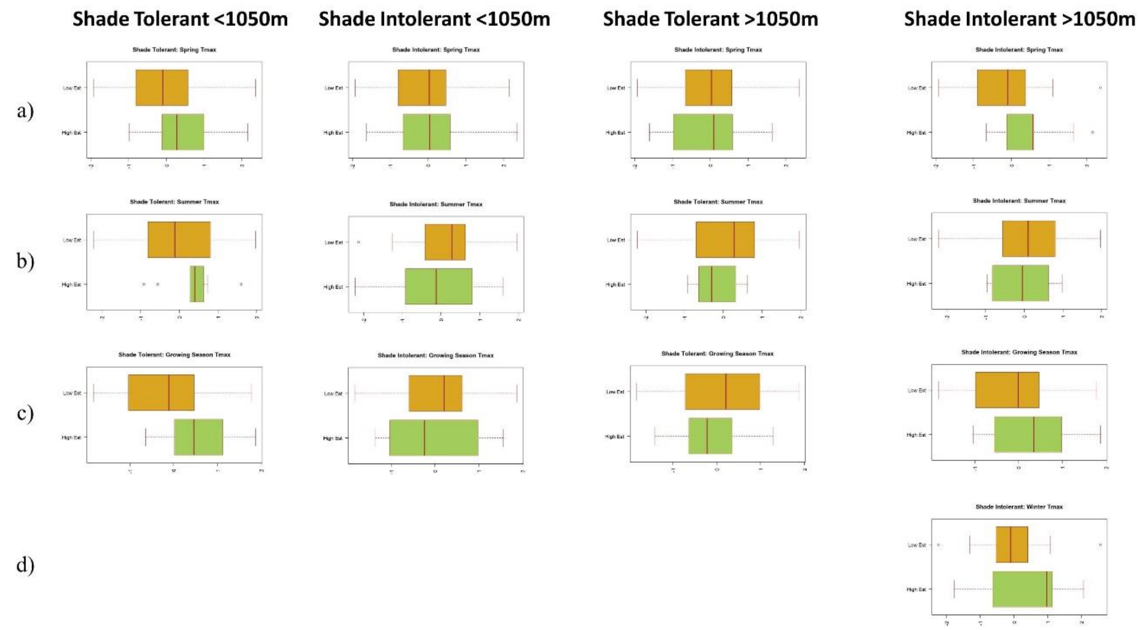


Appendix Figure 2: *Comparison in maximum temperature departures (in SD units) between years of high vs. low tree establishment of shade-tolerant and intolerant tree species for a) Spring, b) Summer, and c) Growing Season, at the Muddy River Lahar over the 1975-2013 period. Seasons are defined as Spring (Apr-Jun), Summer (Jul-Sep), Grow Season (Apr-Sep), Fall (Oct-Dec), and Winter (Jan-Mar).*

Appendix C – Distribution of maximum temperature by elevation

Winter maximum temperature was highlighted as positively affecting the number of successful establishments for shade-intolerant species at higher elevations. On establishment years at elevations under 1050m shade-tolerant species prefer overall warmer temperatures during the spring, summer and grow season months which positively influences the successful rate of establishments (Appendix Figure 3). Shade-intolerant species on the other hand showed little variance between high establishment and low establishment temperatures during the spring months. Contrary to shade-tolerant establishments, summer and grow season months favored successful establishments with slight cooler conditions and a wider range in values.

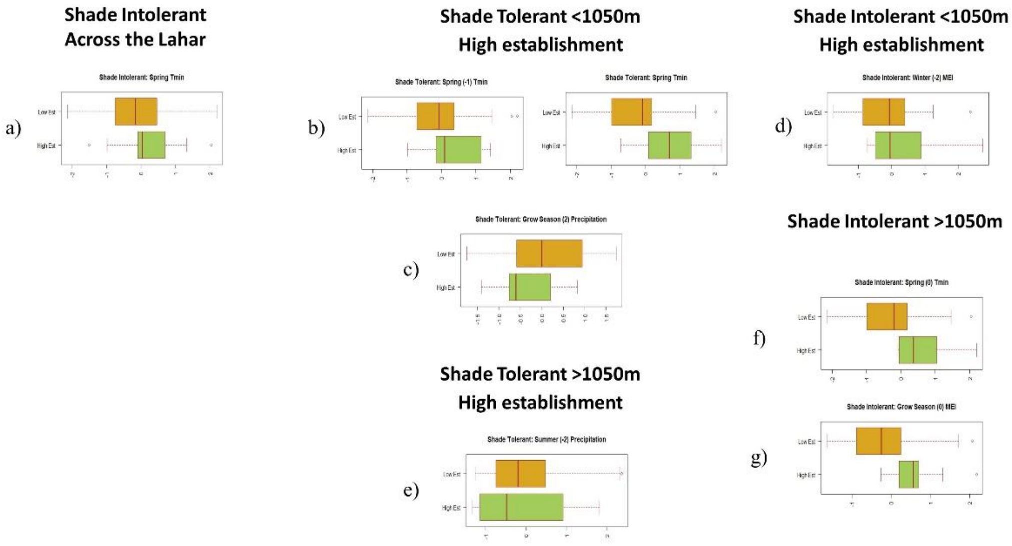
The outputs yielded for elevations above 1050m contrast those found at lower elevations, with shade-tolerant establishments having similar means in both high and low establishment years during the spring months. (Appendix Figure 3) During the summer and grow season months shade-tolerant species have a higher establishment success rate when cooler temperatures are present in the region. Shade-intolerant high establishment years were characterized by cooler conditions during the summer months and warmer temperatures during the spring, grow season and a new statistically significant variable winter maximum temperature. Similar to the distribution across the entire Muddy River Lahar, none of the values yielded from the Mann-Whitney U test yielded values under 0.05.



Appendix Figure 3: *Comparison in maximum temperature departures (in SD units) between years of high vs. low tree establishment of shade-tolerant and intolerant tree species for a) Spring, b) Summer, and c) Growing Season, at the Muddy River Lahar over the 1975-2013 period. Seasons are defined as Spring (Apr-Jun), Summer (Jul-Sep), Grow Season (Apr-Sep), Fall (Oct-Dec), and Winter (Jan-Mar).*

Appendix D – Distribution of minimum temperature, precipitation and MEI

Climate conditions during years of low establishment strongly supported the results described above, as most relationships were inversed; i.e. low establishment of shade-tolerant and intolerant at low and high elevations were commonly associated with weak-to-significantly cooler and/or wetter conditions than average. Additional variables which did not yield statistically significant variables on the year of the event but were highlighted in lagged years were reported (Appendix Figure 4).



Appendix Figure 4: *Comparison in maximum temperature departures (in SD units) between years of high vs. low tree establishment of shade-tolerant and intolerant tree species for a) Spring, b) Summer, and c) Growing Season, at the Muddy River Lahar over the 1975-2013 period. Seasons are defined as Spring (Apr-Jun), Summer (Jul-Sep), Grow Season (Apr-Sep), Fall (Oct-Dec), and Winter (Jan-Mar).*