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Post-Fire Tree Mortality and Regeneration Patterns as Proxies of Conifer Forest Resilience

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Post-Fire Tree Mortality and Regeneration Patterns
as Proxies of Conifer Forest Resilience

by
Sebastian Upton Busby

A dissertation submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy
in
Earth, Environment and Society

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Portland State University
2021

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Abstract

Shifting wildfire patterns and climate conditions, magnified by anthropogenic climate change, are threatening the resilience of conifer forests in North America and more specifically, the western US. If native conifer species are functionally maladapted to novel fire patterns and post-fire climate conditions, large-scale shifts in conifer forest structure, composition, and extent may occur as warming intensifies. Forest resilience in the context of fire and climate can be understood and quantified by the survival of trees through fire events and success of trees to regenerate post-fire and maintain population levels. In this dissertation, I use field observations and remote sensing to examine patterns of fire-induced tree mortality and post-fire tree regeneration as proxies of conifer forest resilience in the western US, across a range of environments and forest types, and particularly within the context of expansive high-severity, stand-replacing wildfires.

In Chapter 1, I evaluate the interactions between climate-environment conditions and the spatial, structural, and temporal characteristics of fire refugia as drivers of subalpine forest recovery in the cool and moist Cascade Range of Oregon and Washington. Seed dispersal pressure, captured at the landscape scale by remotely sensed and spatially explicit fine-grain tree cover post-fire, explained the majority of variance in tree establishment responses across fires. Further, the structure and composition of fire refugia interacted with climate-environment conditions to augment tree establishment responses, creating variable post-fire forest recovery trajectories within the interior of large patches of stand-replacing fire. Toward modelling and predicting tree establishment responses and forest state-transitions after large stand-replacing fire(s), my findings

demonstrate the importance of accurately capturing and accounting for spatially explicit processes and structural seed source characteristics that affect seed dispersal patterns.

In Chapter 2, I quantify large-scale patterns of post-fire delayed conifer tree mortality across three ecoregions and two broad forest types in the western US using high-resolution satellite imagery, and I evaluate whether post-fire delayed conifer tree mortality is a ubiquitous process across broad geographies, and if so, I ask i) what drives it? and ii) can it meaningfully affect seed dispersal and thus forest regeneration processes? I found that between 1-5 years post-fire, delayed conifer tree mortality responses occurred at ecologically significant rates across fire perimeters, varied with scale (i.e., fire perimeter vs. ecoregion levels), and exhibited the potential to critically reduce long-term seed source availability to severely burned forest patches and patches of non-forest, across landscapes. 1-year post-fire burn severity at a 30m resolution was the strongest predictor of delayed tree mortality responses, indicating early patch-scale vegetation change may be a strong proxy for both tree-level fire injuries and subsequent competition with rapidly recovering understory vegetation. Burn severity also strongly interacted with 30-year average and post-fire climatic moisture deficits, illustrating the powerful effects of productivity gradients and compound disturbances (e.g., drought) on delayed tree mortality probability.

Finally, in Chapter 3, I use an aggregated database of post-fire conifer establishment responses, across over 1800 sites and four ecoregions in the western US, to challenge the generalized notion that conifer species' shade-tolerance dictates their regenerative capacity within exposed early seral post-fire environments. Across

ecoregions, I found evidence of strong early seral establishment and dominance (ratio of total conifer establishment) by shade-tolerant conifers. Responses were primarily driven by coarse-scale climatic factors that affect seasonal (i.e., summer) moisture deficits to vegetation, as well as the expression of species' functional traits that contribute to the regeneration niche, or fire resilience. Empirical evidence from this study suggests that conifer species' post-fire recovery responses can be understood across diverse environments via the collective expression of their functional traits, and that individual traits (e.g., shade-tolerance) may be a poor predictor of expected responses when considered in isolation.

Dedication

To my father

Though not a scientist or academic

Instilled deep curiosity and persistence in me

To understand how the world works

One question and inquiry at a time

Acknowledgments

The research conducted in this dissertation is truly a product of the ideas and opportunities lent to me by my advisor through two graduate programs at Portland State University, Andrés Holz. For his mentorship, excitement for ecological research, empathy for his students, and modelling of a balanced relationship with scientific professionalism, I am grateful. Funding for this research and my graduate education was largely provided by the National Science Foundation. Jessica Ibarra and Brian Michie helped collect forest structure and tree regeneration data within severely burned forests of the High Cascades for Chapter 1 and Chapter 3; their perseverance and positive spirits through tough working conditions is greatly appreciated. Meg Krawchuk and Cody Evers provided helpful feedback and edits toward improving Chapter 1 and Cody valuable discussions surrounding the topic of Chapter 2. Chapter 3 was possible due to the gracious sharing of published and unpublished field data by numerous researchers: Kerry Kemp, Camille Stevens-Rumann, Brian Harvey, Alexandra Urza, Garrett Meigs, Robert Andrus, Jonathan Coop, Dan Donato, William Downing, and Christopher Dunn. Finally, it is unlikely that I would have attempted this academic pursuit and/or field of study if Kerry Kemp and Camille Stevens-Rumann had not hired me, many years ago, to help collect field data for their respective dissertations focused on forest and fire ecology in the Northern Rocky Mountains.

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Introduction

In the western temperate and boreal zones of North America, including the western US, substantial concern is mounting around the resilience of present-day conifer forests to rapidly shifting wildfire patterns, compound disturbances, and novel post-fire climate conditions under anthropogenic climate change. Wildfire events are generally increasing in frequency, extent, and severity across most fuel-laden forests, a product of increasingly arid forest fuels and growing human-caused fire ignitions. While shifting climate conditions can influence broad species distribution changes over long time periods (hundreds to thousands of years), wildfire itself is a more immediate catalyst for potentially long-lasting ecosystem change. By repeatedly opening niche space and altering the connectivity of landscape patches over tens to hundreds of years, wildfire can influence species' populations on significantly shorter time scales than changes in climate alone.

Forest ecosystems in western and boreal regions of North America are largely dominated by conifer trees, covering hundreds of millions of hectares of land; in the western US, roughly 80% of forests are coniferous. These forests provide key ecosystem services, natural resources, economic, aesthetic, cultural, and recreational opportunities to communities, and may be a critical strategic asset towards naturally, cost-effectively sequestering atmospheric carbon and reducing the intensity of global warming. Thus, potential widespread changes in conifer forest structure, composition, and extent, due to shifting wildfire regimes and climate conditions, have far reaching consequences for both human and ecological systems.

Despite rising fears surrounding conifer forest resilience, conifer forests and conifer species are no strangers to wildfire or climate change. Their geographic distributions, over time, have been broadly shaped and moved by shifts in pervasive fire-climate patterns. At coarse scales, present day distributions can be largely explained by historical fire regimes and climate conditions, where conifer species' life history and functional traits have synchronized with fire and climate patterns, allowing them to persist at a population level through repeated fire events. As fire patterns and climate conditions change rapidly, however, it is this exact synchronicity that could spell disaster for species' population-level persistence. If conifer species' functional traits are ill-adapted to novel fire patterns and post-fire climate conditions, forests may shift toward persistent alternative forest or non-forest states as established adults are killed and not replaced. It is these two processes that define conifer forest resilience and persistence to fire: (1) the capacity of individuals to survive through one or more fire events to provide seeds and/or propagules necessary for regeneration, and (2) the success of species' post-fire regeneration, i.e., the capacity of newly recruited individuals to reach sexual maturity, disperse seeds and/or propagules, and continue the cycle.

This dissertation uses these two processes as evidence, post-fire conifer tree persistence (survival) and regeneration, to assess the resilience of various conifer forest types in the western US to observed and anticipated changes in fire patterns and climate conditions. Two major components present themselves throughout the chapters below as key mechanisms controlling conifer forest resilience, particularly in the context of large high-severity fires (i.e., most or all trees within a patch are killed by fire effects), which

by themselves or coupled with high fire frequency, have great capacity to initiate persistent post-fire forest state transitions across conifer forest types in North America. These two components are (1) fire refugia and (2) the expression of conifer species' functional traits as they relate to fire resistance, the capacity to survive fire effects, and fire resilience, the capacity to successfully regenerate post-fire to maintain populations through time. Fire refugia, or live tree islands, serve as bastions of seed source within large treeless patches of high-severity fire, and thus based on their spatial, structural, and compositional characteristics, over time, can be the difference between successful forest recovery or persistent state transitions. Species' functional traits that contribute to fire resistance can determine the survival of fire refugia through fire events and traits that contribute to fire resilience control post-fire(s) regeneration responses from fire refugia or contiguous forest edges.

Each chapter was largely inspired by field and remote sensing observations and lessons learned during my master's research, where I assessed mesic mid-to-high elevation conifer forests' resilience to large, severe, and rapidly repeated wildfires in the Cascade Range of the Pacific Northwest. In this system, shade-tolerant conifers dominated pre-fire forest compositions and exhibited compelling recovery responses, the spatial distribution of fire refugia through fire events shaped tree regeneration responses, and post-fire delayed tree mortality was evident from field and remote sensing observations. You will find that these three topics are explored more extensively within individual chapters below.

Chapter overview

In Chapter 1 I explore how the spatial, structural, and temporal (i.e., persistence over time) characteristics of conifer tree fire refugia interact with climate-environment conditions, to determine post-fire forest recovery responses within subalpine forests in the Cascade Range of Oregon and Washington. Mesic and/or cool high-elevation conifer forests, in the Cascade Range and elsewhere, are typically prone to infrequent stand-replacing wildfires, where the size of large high-severity (i.e., tree mortality is near 100%) burn patches can create limitations on post-fire seed dispersal and subsequent seedling establishment for many tree species, even when climate-environment conditions are favorable. Warming conditions and losses in snowpack are progressively drying out high-elevation forests earlier in the summer, increasing the recently observed frequency of large, high-severity fires that can initiate altered or non-forest ecosystem states. As bastions of seed, the spatial and structural arrangement of fire refugia over time may largely determine subalpine forest recovery responses in the present and future. Conceptually and practically, this chapter highlights how post-fire tree establishment responses, and thus forest recovery trajectories, can be understood and predicted via the interactions between seed pressure (i.e., number of seeds that reach a given site based on the spatial and structural qualities of proximate seed sources, i.e., fire refugia) and climate-environment conditions.

In Chapter 2, I quantify large-scale patterns of post-fire delayed conifer tree mortality in montane western US forests, to understand if patterns (1) can be modelled and predicted at large-scales, (2) are of general ecological significance and vary across

broad ecoregions and forest types, and (3) can influence post-fire conifer forest recovery responses and trajectories through meaningful losses in seed source availability (i.e., fire refugia). At present, large-scale patterns of fire effects on forest ecosystems (i.e., burn severity derived from tree mortality) are widely evaluated only one-year post-fire, despite increasing empirical evidence that fire effects can contribute to tree mortality responses over longer temporal periods (e.g., 0 – 15 years post-fire). If delayed tree mortality responses are ecologically significant beyond one-year post-fire, which small-scale field studies have confirmed, scientists and managers may be broadly underestimating the impacts of fire events on forest communities, forest succession, and post-fire forest ecosystem trajectories. At present, little to no work has attempted to quantify large-scale patterns of post-fire delayed tree mortality or contextualize this process within a forest recovery framework.

In Chapter 3, I explore early seral establishment and tree dominance patterns by shade-tolerant conifers after moderate-to-high severity fire, across a broad gradient of climate-environment conditions. Observed establishment patterns are used to challenge the generalized notion that conifer species' shade-tolerance defines their seral role in post-fire forest development and succession after moderate to severe fire effects, and further, test the hypothesis that site environmental moisture availability and species' functional traits control early seral establishment and dominance responses, not necessary shade-tolerance. At present, most of the conceptual and empirical post-fire conifer forest recovery work in the western US comes from relatively arid environments and dry mixed-conifer forests. Within these environments and forests, shade-tolerant conifers are

typically absent or occur as mid-to-late seral species, following the expected forest successional pathway of facilitation. Alternatively, in many mesic and/or cool environments, shade-tolerant conifers have been observed playing multiple seral roles post-fire, including early seral dominance and self-replacement (i.e., passive tolerance). Because of the overrepresentation of successional dynamics in relatively arid environments, conifer species' shade-tolerance has become a shortcut to understanding their post-fire regenerative capacity, or fire resilience. This work attempts to refocus attention on the complete expression of species' functional traits that contribute to fire resilience, as a framework to predict post-fire conifer forest recovery responses across heterogeneous environments, and under altered fire regimes and climate conditions.

Chapter 1:

Spatially explicit fire refugia-climate-environment interactions drive subalpine forest recovery after large and severe wildfires

Abstract

Infrequent stand-replacing wildfires are characteristic of mesic and/or cool subalpine conifer forests in the western US, where forest recovery within high-severity burn patch interiors can be slow, yet successful over long temporal periods (decades to centuries). Increasing fire frequency and high-severity patch size under warming climate conditions, however, may challenge post-fire subalpine forest recovery, potentially leading to persistent alternative forest or non-forest states. After large stand-replacing wildfires, the spatial extent, composition, and structural attributes of landscape-level fire refugia (i.e., seed sources), over time, may determine forest recovery trajectories and potential state-transitions. To examine how the spatial, structural, and temporal attributes of fire refugia interact with climate and environmental factors to determine post-fire forest recovery responses, we developed fine grain maps of fire refugia extent and sampled post-fire conifer tree establishment in the Central Cascade Range of the Pacific Northwest USA. We found that seed dispersal limitations drove the majority of variance in post-fire tree establishment responses within our cool and mesic subalpine study sites, where landscape-level seed pressure associated with fire refugia extent (refugia distance²-weighted-density; D²WD) was the strongest predictor of conifer establishment. Refugia-climate-environment interactions suggested that the structural characteristics of refugia (e.g., tree height) and abiotic/biotic environmental controls (e.g., climate water deficit; canopy cover; coarse woody debris cover) interact with landscape-level seed pressure to

constrain or enhance species-specific establishment responses. Toward modelling and predicting tree establishment responses and forest state-transitions after large stand-replacing fire(s), our findings demonstrate the importance of accurately capturing and accounting for spatially explicit processes and structural seed source characteristics that affect seed dispersal patterns.

1. Introduction

Across montane forests in the western US, observed trends in mountain snowpack loss, earlier spring snowmelt, drier summers, and longer fire seasons are contributing to increasing wildfire frequency, size, and severity (Westerling 2006; Abatzoglou and Williams 2016; Gergel et al. 2017; Parks and Abatzoglou 2020). As fire activity and warming conditions increase across landscapes, many forests may be at risk of climate- and/or fire-induced conversions to altered- or non-forest states (Coop et al. 2020), and especially within lower elevation environments with limited moisture availability (Stevens-Rumman et al. 2018; Davis et al. 2019; Kemp et al. 2019). While increasing moisture deficits under warming conditions may severely limit or prevent post-fire tree establishment within arid low-elevation environments, post-fire establishment may also be limited within mesic and/or cool high-elevation forests due to recently observed and projected increases in fire activity (Reilly et al. 2017; Halofsky et al. 2018; 2020; Turner et al. 2019; Higuera et al. 2021). While large and severe infrequent fires are within the natural range of variation for mesic and/or cool high-elevation forest types, long periods without subsequent fire or other large-scale disturbances may be required for forest recovery (e.g., 50-200+ yr fire return-interval; Agee 1993; Turner and Romme 1994)

when stand-replacing patch sizes exceed species' dispersal abilities. Where large and severe and/or frequent wildfires kill a significant number of live trees within a contiguous area, remnant live tree islands contained within fire perimeter boundaries – known as fire refugia – can be a critical bastion for forest persistence and recovery over time (Blomdahl et al. 2019; Krawchuk et al. 2020). Strong relationships between post-fire conifer forest recovery, post-fire climate conditions, and fine-grain fire refugia extent at the landscape level has been demonstrated in dry mixed conifer forests (Coop et al. 2019; Downing et al. 2019; Rodman et al. 2020). Despite these recent advancements, it is unclear how the fine grain spatial, structural, and temporal legacies of fire refugia interact with climate and environmental factors to determine post-fire forest recovery responses and trajectories, and especially within mesic and/or cool subalpine conifer forest types.

Post-fire conifer forest recovery, across forest types and gradients of moisture availability, is strongly connected to processes that affect seed dispersal over space and time (Clark et al. 1999), and further, how climate and environmental conditions constrain or enhance the establishment of seeds that reach a given site (Kraft et al. 2015). Thus, post-fire conifer forest recovery trajectories can be understood through the interactions between biotic and abiotic controls on tree establishment over time, including seed pressure (i.e., number of dispersed seeds that reach a given location). Seed pressure is dictated by (1) the functional traits of proximate seed sources, (2) their structural attributes (e.g., age, size, height), (3) the distance to them and their density over space, (4) the presence and patterns associated with dispersal vectors (e.g., wind, water, snow, animals), and (5) the arrangement of dispersal barriers (e.g., topography, water,

vegetation) (Clark et al. 1998; 1999). In the western US, conifer species are primarily obligate seeders that reproduce from serotinous and/or non-serotinous wind-dispersed canopy seedbanks (McCaughey et al. 1986; Burns and Honkala 1990). Large and severe fires pose a barrier to naturally occurring post-fire establishment by non-serotinous conifers when the distance to live trees exceeds species-specific dispersal abilities (Harvey et al. 2016; Stevens-Rumann and Morgan 2019; Coop et al. 2020). Alternatively, short-interval fires may kill post-fire reestablishing serotinous and non-serotinous conifers before they can reach reproductive maturity (Buma et al. 2013). As a result, large, severe, and frequent fires may broadly overwhelm obligate seeding conifers reproductive traits and favor resprouting angiosperms instead (Kulakowski et al. 2013; Tepley et al. 2018; Keyser 2020; Andrus et al. 2021). Unlike post-fire drought events that can temporarily inhibit conifer establishment for several years up to a decade (Andrus et al. 2018; Littlefield et al. 2020), dispersal limitations created by large, contiguous patches of high-severity fire can induce long-term changes in forest ecosystems (Johnstone et al. 2016).

Prior work attempting to quantify the influence of complex seed source arrangement and structure in three-dimensional space, as it relates to post-fire tree establishment, is limited in the western U.S., and especially among mesic and/or cool high-elevation forest types. Prior studies have primarily focused on patch edge concepts and metrics for quantifying dispersal limitations (e.g., Agee and Smith 1984; Kemp et al. 2016; Harvey et al. 2016; Urza and Sibold 2017; Busby et al. 2020), which only account for seed source distance as a contributing factor to dispersal and establishment patterns.

Alternatively, other studies have focused on the seed source density (e.g., seed source cover within a specified window surrounding a location; Haire and McGarigal 2010; Rodman et al. 2020), but at the expense of accounting for the distance of those individual seed sources to a location. More recent work has combined seed source distance and density into a single metric with compelling results (i.e., refugia distance-weighted density; Coop et al. 2019; Downing et al. 2019), but that work was limited to relatively dry mixed-conifer forest types and did not consider the structural attributes of seed sources, nor how they interacted with climate and environmental conditions to shape establishment responses. Finally, no known research has attempted to quantify and test whether changes in the extent of fire refugia over time, due to post-fire delayed tree mortality, meaningfully impacts seed pressure and thus observed post-fire establishment responses. Delayed tree mortality may add a critical temporal feature to characterizing seed source availability and understanding forest recovery, given post-fire delayed tree mortality outcomes evolve over relatively short time periods (e.g., ~0-15 years) critical to the early seral ecosystem (Brown et al. 2013; Hood and Varner 2019).

Considering these research gaps, our objective in this study was to evaluate how the spatial, structural, and temporal characteristics of fire refugia interact with climate-environment conditions to influence post-fire forest recovery responses within mesic, subalpine conifer forests. To support our study objectives, we mapped fine grain fire refugia extent (tree cover) at the landscape scale and surveyed forest structure, composition, and conifer juvenile establishment after recent large stand-replacing

wildfires in the Cascade Range of the Pacific Northwest, USA. Field data were collected to support assessment of the following research questions:

- (1) How does post-fire conifer establishment differ among species and study sites at increasing distances from fire refugia patches, and how do varying estimates of seed pressure and forest structure, associated with fire refugia, compare, and interact as predictors of conifer establishment?
- (2) How do leading estimates of forest structure and seed pressure, associated with fire refugia, compare, and interact with climate and environmental conditions as predictors of conifer establishment?

2. Methods

2.1. Study areas

We selected four wildfire perimeters in the Cascade Crest region of Oregon and Washington states for this study, spanning a range of elevation and moisture gradients common to regional subalpine forests, and experiencing a range of time since fires occurred (7-23 years; Fig. 1). These study fires were located on the southwestern face of Mt. Adams, WA (2012 Cascade Creek; ~8,300ha burned); the northeastern face of Mt. Hood, OR (2008 Gnarl Ridge; ~1,400ha burned); west of Big Lake, OR (2011 Shadow Lake; ~2,800 ha); and northeast of Waldo Lake, OR (1996 Charlton; ~3,800ha burned). All study wildfires were lightning ignited, burned between August and September in their respective years, and have no other record of burning in recent history (>75 years since previous fire).

To identify the four field sites for sampling, fire perimeters and burn severity patterns were analyzed from the Monitoring Trends in Burn Severity project (MTBS; Eidenshink et al. 2007) during the period of 1995-2012 in the Central Cascade Range of Oregon and Washington states. This range of fire years was considered to achieve the following criteria: (1) allow enough time since fire to initiate a post-fire conifer recruitment response (≥ 5 yrs) prior to field sampling; (2) high-resolution National Agricultural Imagery Program (NAIP) imagery would be available one and/or 5 years post-fire for each fire perimeter; (3) fire perimeters were targeted which contained subalpine forest compositions (e.g. fir, spruce, mountain hemlock group) using the National Forest Type Dataset (USDA 2008); (4) were accessible via road and trail access; and (5) had experienced contiguous high-severity burn patches at least five hectares or greater in size (following Harvey et al. 2016). High-severity fire effects are commonly defined as causing 75-100% tree mortality one-year post-fire (Miller and Thode 2007); 95-100% tree mortality (at the time of sampling; 2019) was commonly observed in our study areas. For (2) we chose to analyze two post-fire temporal snapshots of live tree extent from NAIP, with the rationale that the 1- and 5-year post-fire images would capture first- and second-order fire effects (i.e., initial and delayed post-fire tree mortality; Key 2006; Hood and Varner 2019), but not post-fire conifer sapling recruitment and/or substantial understory revegetation (Walker et al. 2019).

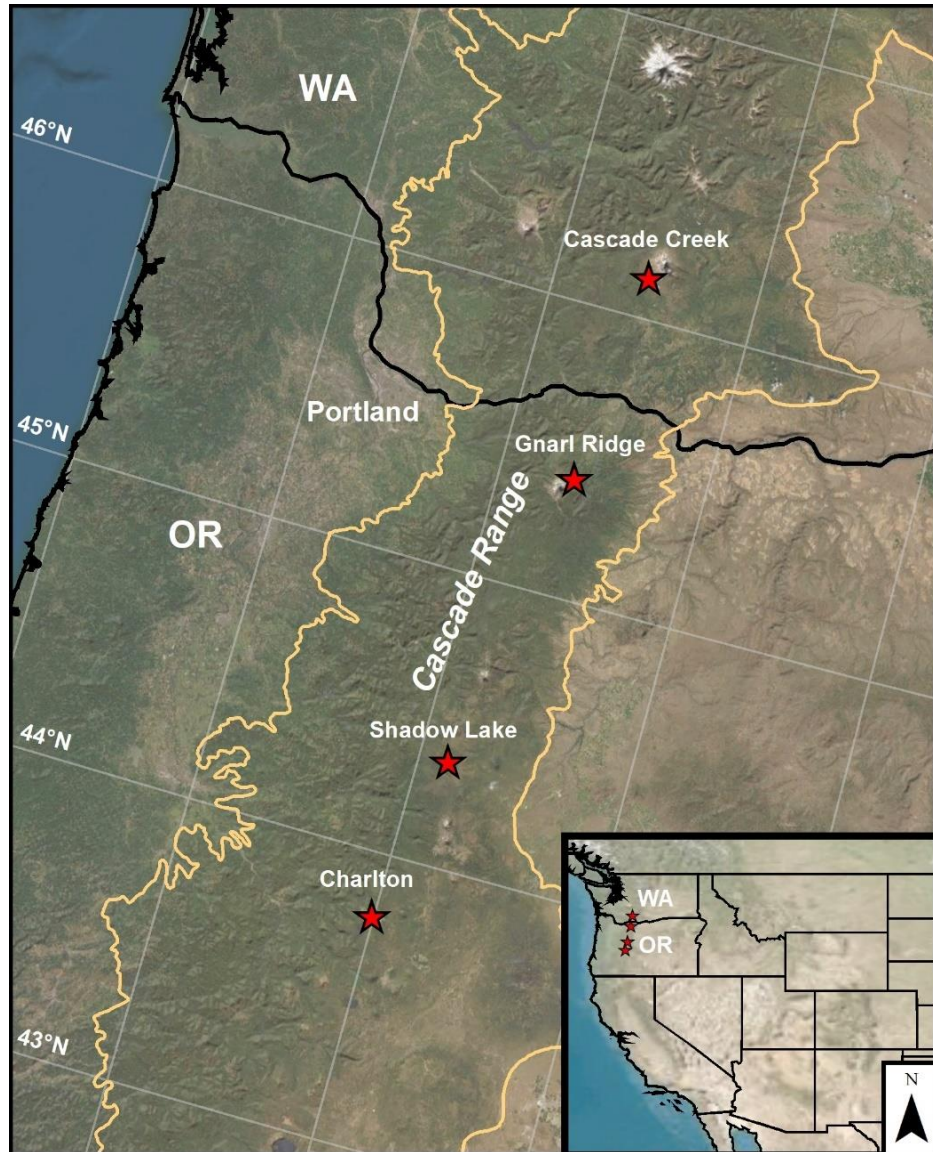


Figure 1. Geographic location of the four wildfires sampled in this study within mesic subalpine forests of the Cascade Crest region of Oregon and Washington states, USA.

Elevation gradients across study fires ranged 1350 - 1800m; at these elevations, substantial snowpack accumulates during winter months. Mean annual precipitation ranges from 1800 - 3200mm across our study fires and mean warmest month temperature ranges from 13.6 - 14.9°C (1981-2010 means; ClimateNA; Wang et al. 2016). Sites in the 2011 Shadow Lake fire were, relatively, the warmest and driest, while forest sampled in

the 2008 Gnarl Ridge fire was the coolest and wettest. Soils in these landscapes are primarily well draining, ashy sandy loam andisols (USDA 2018). Conifer forest composition in the subalpine stands we sampled were generally dominated by mountain hemlock (*Tsuga mertensiana*), true-firs (*Abies lasiocarpa*; *Abies amabilis*), and lodgepole pine (*Pinus contorta* var. *latifolia*) with a low abundance of Engelmann spruce (*Picea engelmannii*) and western white pine (*Pinus monticola*). Western larch (*Larix occidentalis*) was found exclusively in the 2008 Gnarl Ridge fire on Mt. Hood, where it supplemented lodgepole pine as the primary shade-intolerant tree species (Franklin and Dyrness 1973).

2.2. Fire refugia delineation and seed source availability

We delineated post-fire conifer refugia extent (i.e., cover) at a fine grain (i.e., the tree-level) to aid in field plot selection and for the purpose of quantifying conifer seed source availability (i.e., seed pressure) at the landscape-level across each study fire, using high-resolution (1m) NAIP imagery. Since post-fire delayed tree mortality may alter the extent and pattern of fire refugia and thus affect seed dispersal and forest recovery, we delineated fire refugia at two time periods to represent first order (direct; initial) and second order (indirect; extended) fire effects (Key 2006). NAIP imagery was extracted 1- and 5-years post-fire for each fire perimeter, with the exception of the 1996 Charlton fire. NAIP imagery was not available for the Charlton fire until 2005, thus we only delineated post-fire refugia extent after second-order fire effects. Fire perimeter polygons from MTBS were extended (buffered) 200m in distance to ensure contiguous live forest edge was potentially captured in seed source availability/pressure calculations, as described

below. Each buffered fire boundary was then used to clip NAIP imagery scenes to this specified extent. Fire refugia extent was then classified in each clipped NAIP image using a semi-automated, object-based binary classification approach in ArcGIS (ESRI 2020) following Walker et al. (2019). Contrary to Walker et al. (2019)'s work in dry conifer forests, we chose not to close holes in delineated refugia polygons in our mesic forests study areas, as these commonly represent canopy gaps within fire refugia patches.

To assess image classification accuracy, we used equalized stratified random sampling to generate 100 validation points per class (fire refugia and non-forested) across each individual fire perimeter. We then used the source NAIP imagery, in each temporal snapshot (i.e., 1- and 5-years post-fire), to visually assign each validation point to either the fire refugia or non-forest class based on point overlap with canopy cover (Walker et al. 2019). A confusion matrix was generated among 1- and 5-year post-fire snapshots of each fire perimeter to report imagery classification error (Congalton 1991). Classification accuracy varied by fire perimeter but was generally very high; overall accuracy across fire perimeters ranged from 94-98% (Appendix: Supporting information, tables, and figures; Table 4).

To spatially quantify landscape-level seed source availability within each fire perimeter, we considered two metrics of seed pressure originating from fire refugia using the above classified refugia maps and a moving-window neighborhood approach. (1) refugia density (e.g., Haire and McGarigal 2010; Rodman et al. 2020) was calculated by summing all pixel values (refugia cover = 1; non-forest cover = 0) around each focal cell within a user-defined neighborhood radius, and (2) refugia distance²-weighted-density

(D²WD; Coop et al. 2019) was calculated by dividing pixel values by their squared distance to each focal cell (i.e., distance-weighting) then summing all pixels within a neighborhood radius. Functionally, the refugia density metric quantifies the density of seed sources surrounding a location, while the refugia D²WD metric quantifies the density of seed sources, the individual distance of seed sources to a location, and accounts for exponential decay in seed dispersal over distance (i.e., squared term). Considering varied seed dispersal traits reported among conifer species in our study areas and results by prior studies (e.g., Haire and McGarigal 2010; Coop et al. 2019; Rodman et al. 2020), we calculated refugia density and refugia D²WD at three spatial scales using neighborhood radii of 150m, 300m, 500m.

2.3. Field data collection

To connect the structure and composition of fire refugia patches to post-fire conifer establishment responses, we established two types of 30m-diameter (0.07ha) circle plots: one inside the refugia patch and the others along predetermined post-fire regeneration transects extending into patches of severely burned forest. These two plot types followed post-fire forest structure and regeneration surveys developed in Busby et al. (2020). The location of our fire refugia plots and post-fire regeneration plots were predetermined using a distance-buffer ruleset and spatial analysis in ArcGIS to (1) maintain a minimum level of spatial independence between sampled fire refugia patches and post-fire regeneration plots, and (2) reduce the influence of seed source availability originating from live forest edges within our post-fire regeneration plots (Appendix:

Supporting information, tables, and figures; Sample plot selection and distance-buffer ruleset; see Figure 7 for diagram of the distance-buffer ruleset).

A single plot was established inside each refugia patch to quantify patch-level forest structure and composition. Inside refugia plots, we recorded elevation, slope, aspect, and all standing or uprooted trees (defined here as individuals with diameter at breast height, DBH >7.6cm; i.e., trees that contribute to meaningful seed pressure; Stevens-Rumann and Morgan 2016), noting species, status (live/dead), DBH, and vertical heights of live trees using a laser rangefinder (TruPulse 200/Laser Technology). A second plot type assessing post-fire conifer regeneration was established along transects extending into the high-severity fire footprint, where we recorded physical site characteristics (elevation, slope, aspect), post-fire ground and canopy cover, and post-fire conifer regeneration. Post-fire ground cover (shrubs, total understory vegetation, coarse woody debris [CWD], and bare soil/rock) was visually assessed to the nearest 5% within five 1x1m quadrats located at plot center and 7m along the four cardinal direction transects; the five sample locations were then averaged to represent plot-level conditions (Busby et al. 2020). Overstory canopy density (cover) was measured at the same five sample quadrat locations using a densiometer at breast height. Percent canopy cover was recorded facing each cardinal direction, averaged for the sample location, and then averaged among the five sample locations to similarly represent plot-level conditions (Lemmon 1956).

Post-fire conifer juveniles were counted in plots along each transect. We used variable size subplots to increase sampling efficiency depending upon plot-level juvenile

densities, following Busby et al. (2020). For each juvenile, we recorded species, bud-scar count, and stem height. Bud-scar count estimates were used to determine if juveniles had established pre- or post-fire (Urza and Sibold 2013). Finally, if present, the ten nearest live mature conifer trees not contained within the refugia patch were identified at the species level and their individual horizontal distance from plot center was recorded using a laser rangefinder. Utilizing our sample plot selection procedure, we selected and sampled 41 fire refugia patch plots and 213 post-fire regeneration plots distributed across the four study wildfire perimeters in summer of 2019.

2.4. Climate water deficit

To characterize the impact of water stress on post-fire conifer establishment across fire perimeters, we quantified 30-year mean (1981-2010) and post-fire mean and maximum climate water deficit (CWD; the difference between potential and actual evapotranspiration) during the postfire period (until 2019) at the plot level. We used the ClimateNA application (Wang et al. 2016) and plot elevation to downscale gridded monthly climate data (PRISM; Daly et al. 2008; 800m-initial resolution) to the plot level. A modified Thornthwaite-type water balance equation described by Lutz et al. (2010) was then used with (1) 30-year or annual-resolution mean monthly temperature and precipitation data, (2) soil water holding capacity data (POLARIS dataset; Chaney et al. 2016), and (3) a topographic heat load index (HLI; McCune and Keon 2002) to calculate CWD. In this equation, the HLI is used as a terrain modifier to capture the effect of topographic microclimate on evaporative potential, thereby incorporating micro- and macro-scale water balance processes.

2.5. Spatial, structural, and temporal estimates of fire refugia

To explore and compare what spatial, structural, and temporal characteristics associated with fire refugia influenced post-fire conifer establishment, we developed a suite of fire refugia-related patch and neighborhood attributes derived from field data, remote sensing, or both sources combined, that could conceptually influence post-fire conifer establishment (Table 1). For the remote sensing derived refugia density and D²WD variables, we calculated multiple versions these variables using (1) varying neighborhood radii and (2) 1- and 5-year post-fire refugia extent maps, respectively, to capture initial and delayed post-fire tree mortality patterns. Because 1-year post-fire imagery was not available for the Charlton fire, we used the ~5-year post-fire refugia extent map for this fire perimeter to represent 1-year post-fire refugia extent. Other variables were derived directly through field measurements (e.g., refugia distance, live mean tree height), by measuring refugia patch geometry using remote sensing (i.e., patch size, patch width), or by scaling plot-level refugia composition measured in the field to the patch scale using remotely sensed patch size, our fixed refugia plot size, and a multiplicative factor (i.e., total and live patch basal area).

Table 1. Patch- and neighborhood-based predictive variables associated with spatial, structural, and temporal attributes of fire refugia, as derived by field measurements, remote sensing, or both sources.

| Refugia Variable | Derived by | Variable Description | Units | Range |
|---------------------------|---------------------------------|---|----------------------------|-----------------|
| Refugia D ² WD | Remote sensing | The distance ² -weighted density of live tree extent surrounding a post-fire regeneration plot, calculated as multiple versions using 1- and 5-year post-fire fire refugia extent maps, and 150m, 300m, or 500m circular radius neighborhoods. | Unitless | [0 - 11.31] |
| Refugia density | Remote sensing | The sum of live tree extent surrounding a post-fire regeneration plot, calculated as multiple versions using 1- and 5-year post-fire fire refugia extent maps, and 150m, 300m, or 500m circular radius neighborhoods. | Unitless | [0 – 240,622] |
| Refugia distance | Field measured | Horizontal distance from the post-fire regeneration plot center to the exterior edge of the refugia patch -OR- the nearest live tree not contained within the refugia patch | Meters | [15 - 300] |
| Patch total basal area* | Field measured & remote sensing | Total tree basal area of the refugia plot scaled to the extent of the refugia patch | Basal area /m ² | [0.82 - 372.25] |
| Patch live basal area* | Field measured & remote sensing | Total live tree basal area measured in the refugia plot scaled to the extent of the refugia patch | Basal area /m ² | [0.52 - 151.27] |
| Live mean tree height* | Field measured | The mean height of live trees measured within the refugia plot | Meters | [8.5 - 26.8] |
| Patch size | Remote sensing | Spatial extent of the refugia patch | m ² | [700 – 6,470] |
| Patch width | Remote sensing | The width of the refugia patch as perpendicular to the post-fire regeneration transect | Meters | [20 - 300] |

*Each refugia variable was calculated to match the composition of each species assemblage, as described in Data analysis.

2.6. Data analysis

To determine how post-fire conifer establishment and fire refugia composition varied between study wildfires, we summarized observed median post-fire juvenile densities among regeneration sample plots, according to distance from refugia, across all fires combined and within individual wildfire perimeters. For refugia patch plots, we

summarized species-level basal area m² / hectare (i.e., pre-fire species composition) across all fires combined and within individual wildfire perimeters.

To explore how estimates of forest structure and seed source availability associated with fire refugia compare and interact as predictors of post-fire conifer establishment, and further, how they interact with and compare with site environmental conditions as predictors of conifer establishment, we developed boosted regression tree (BRT) models, with a Poisson error distribution, to explore relative variable importance, non-linear relationships, and interactions between sets of predictive variables and post-fire juvenile counts using the gbm package in R (Greenwell et al. 2020; R Core Team 2020). Across modelling analyses described below, five species assemblage models were developed to represent the dominant species in our study areas and potential differences in functional traits between species, and thus post-fire establishment responses, including: (1) all species combined, (2) non-serotinous obligate seeding species (*A. lasiocarpa*; *A. amabilis*; *L. occidentalis*; *P. engelmanni*; *P. monticola*; *T. mertensiana*), (3) the possibly serotinous lodgepole pine (*P. contorta*; PICO), (4) mountain hemlock (*T. mertensiana*; TSME), and (5) *Abies* (*A. lasiocarpa*; *A. amabilis*; *Abies*). Pacific-silver and subalpine fir (*A. amabilis*; *A. lasiocarpa*;) juveniles were difficult to differentiate in the field by species, thus we combined them into a single *Abies* assemblage.

All BRT models were fit with a bag fraction setting of 0.5 to introduce stochasticity and learning rate of 0.01 to ensure at least 1000 trees were fit in each model (Elith et al. 2008). Since BRTs are a stochastic modelling technique, we fit 10 iterations of each model and reported results from the best performing model iteration. Tree

complexity was set to one in the case of additive models (i.e., no interactions) and five in the case of interaction models. We fit additive models when the modeling objective was to determine the best version of a single predictor and interaction models when determining relative importance of and interactions between sets of predictive variables.

To account for the inherent spatial autocorrelation (SAC) in our sampling design between plots set along transects, and more broadly, plots set within the same wildfire perimeters, we computed and included a residual autocovariate (RAC) term in each final fitted BRT model following Crase et al. (2012). We used the `autocov_dist` function in the `dismo` package (Hijmans et al. 2017) to calculate RAC terms for each model, using a 3km search neighborhood, equal weighting, and style “B” following technical critique by Bardos et al. (2015). Model performance, or cross-validated ($k=10$) total residual deviance explained (Leathwick et al. 2006) was reported between each BRT model with and without the RAC term fitted to illustrate model improvement due to accounting for SAC. Because BRTs are a stochastic modelling technique, we fit 10 iterations of each model and reported results from the model with the highest cross-validated total residual deviance explained (i.e., best performing model iteration).

Our first modelling objective was to compare and determine the best performing version among the multiple calculated versions of our climate water deficit, refugia density, and refugia D²WD variables. Additive BRT models were fit on each species assemblage establishment response and all calculated versions of climate water deficit, refugia density, and refugia D²WD separately. Relative variable importance was used to determine the version of each variable that exhibited the strongest relationship with each

species assemblage response. Our second modelling objective was to compare the relative importance of fire refugia-related variables (Table 1), fitting only the strongest versions of refugia density and refugia D²WD as determined from the first analysis, and explore their interactions as predictors of conifer establishment. Interaction BRT models were fit on each species assemblage establishment response and all predictive variables from Table 1. Our third and final modeling objective was to compare the relative importance of and explore the interactions between the top three fire-refugia related variables determined from our second analysis, the top performing version of climate water deficit as determined from our first analysis, and a set of predictive variables describing biotic and abiotic site environmental conditions. These environmental variables included (1) percent remnant overstory canopy cover, as a proxy for shade, (2) percent understory vegetation cover, a proxy for competition or facilitation, (3) percent coarse downed woody debris cover, a proxy for facilitation, (4) topographic slope, (5) the heat load index (HLI), and (6) time since fire (years).

3. Results

Across fire perimeters, post-fire conifer establishment declined exponentially with increasing distance to refugia patches; the largest declines occurred between 15m and 90m from refugia patch edge (Fig. 2a). The rate (i.e., slope) of juvenile establishment decline over increasing distance was largest in the Shadow Lake fire and lowest in the Gnarl Ridge fire (Fig. 2c, d), the warmest, driest, and coolest, wettest sites, respectively. There was a wide range of variability in establishment responses among fires and among distances from refugia. Although total median juvenile establishment was relatively low

300m from refugia patch edges (~250 juveniles/ha) across all fires combined, responses varied by fire perimeter, ranging from ~50 juveniles/ha in the Cascade Creek fire to ~500 juveniles/ha in the Charlton fire. Closer to seed source, at 15m from refugia patch edge specifically, total median juvenile establishment in the Charlton fire was roughly two times higher than our other fires (Fig. 2e). Notably, the Charlton fire was also the oldest fire by a factor of ~2 (23 years since fire occurred).

Post-fire conifer establishment by species generally reflected the composition of refugia patches. The Cascade Creek and Shadow Lake fires were dominated by lodgepole pine (PICO) establishment, while the Gnarl Ridge and Charlton fires experienced a larger proportion of mountain hemlock (TSME) establishment (Fig. 2b, c, d, e). Across fires, subalpine and Pacific silver fir (*Abies*) establishment was very low even when these species were well represented in refugia patches. Additionally, *Abies* species establishment reached zero or near zero at and beyond 45m distance from any refugial patch edge.

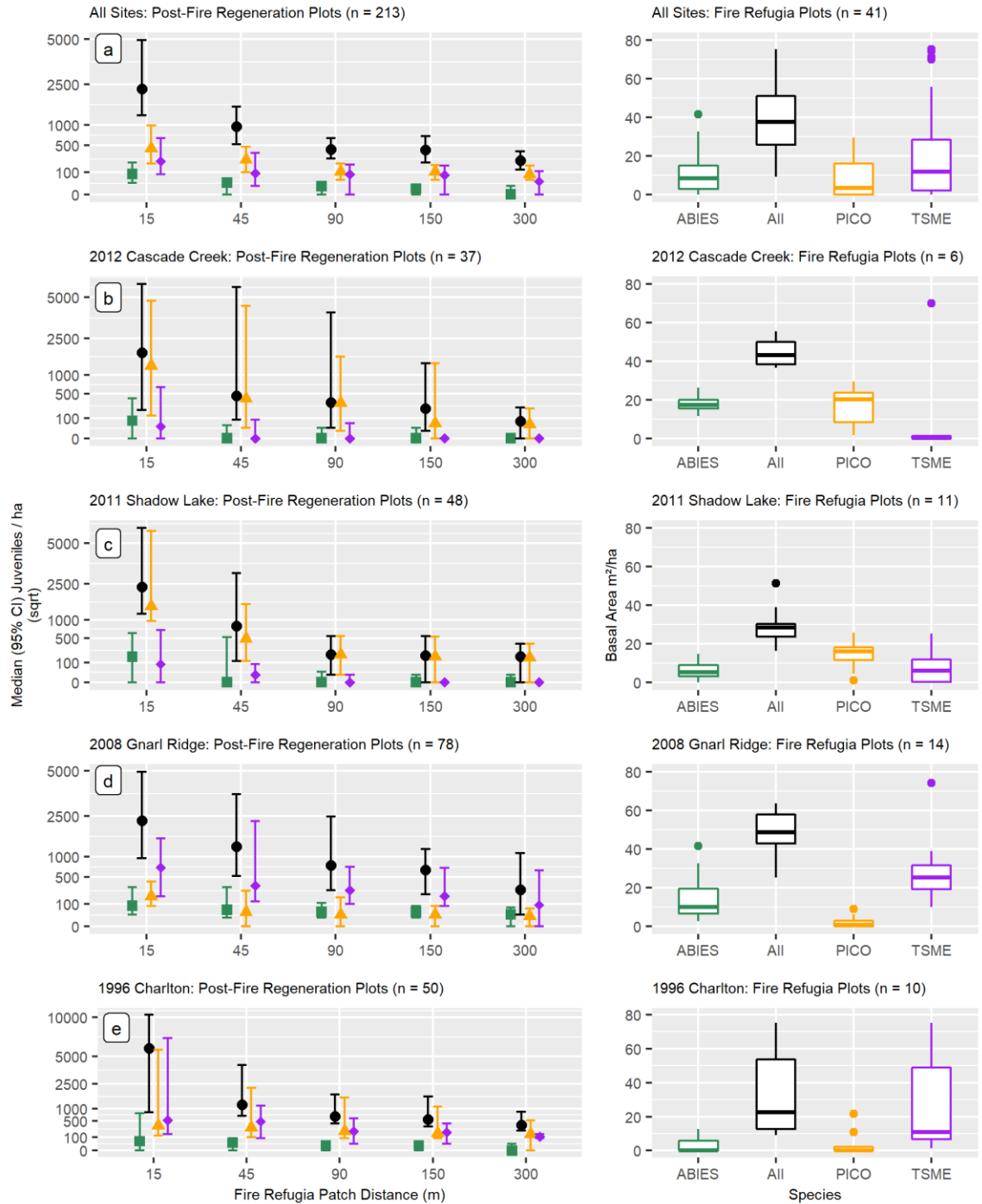


Figure 2. Observed post-fire median (95% confidence intervals) conifer establishment as a function of increasing distance to refugia patch edge and refugia patch composition, represented across all and individual study fire perimeters, by species. The y-axis is scaled using a square-root function. PICO (*Pinus contorta* var. *latifolia*); TSME (*Tsuga mertensiana*); ABIES (*Abies lasiocarpa*; *Abies amabilis*).

Among the three calculated versions of our climate water deficit (CWD) variable, our first modelling analysis determined that 30-yr CWD was more important than post-fire mean or maximum CWD as a predictor of post-fire conifer establishment across species assemblages (Appendix: Supporting information, tables, and figures; Table 5). We also determined the best version (i.e., combination of 150m, 300m, or 500m moving-window neighborhood radius and 1- or 5-year post-fire refugia extent) of our refugia density and refugia D²WD variables, which unlike CWD, varied by species assemblage response (see Table 2 for the top performing versions by species assemblage).

Our second modelling analysis determined the top predictors of conifer juvenile establishment among our refugia metrics. For all species assemblages, refugia D²WD was the best predictor of post-fire conifer juvenile establishment, strongly outperforming other refugia-related variables derived from field measurements, remote sensing, or combined sources (Table 2; Appendix: Supporting information, tables, and figures; Figure 8). Lodgepole pine was the only assemblage where 5-year post-fire refugia extent was a better predictor of juvenile establishment than 1-year post-fire refugia extent. From our field-based metrics, total refugia patch basal area was generally a better predictor of establishment than live basal area (at the time of sampling in 2019, 7-23 years post-fire), and was particularly important for lodgepole pine, in addition to refugia distance (Table 2). Mean live tree height within refugia patches was important for mountain hemlock, to a lesser degree for non-serotinous species combined and lodgepole pine, and was unimportant for *Abies* species.

Table 2. Variable Importance and model performance metrics from BRT models evaluating patch- or neighborhood-based estimates of fire refugia. Metrics are included for each species assemblage.

| Refugia Variables | Species Assemblage Models: Variable Importance (%) | | | | |
|---|--|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| | All Species | Non-Serotinous | PICO | TSME | <i>Abies</i> |
| Residual Autocovariate (RAC) | 8.9 | 3.2 | 14.6 | 2.0 | 14.0 |
| Refugia D ² WD* | 39.8 (1-yr; 150m) | 56.4 (1-yr; 500m) | 24.0 (5-yr; 150m) | 43.7 (1-yr; 500m) | 65.6 (1-yr; 150m) |
| Refugia Density* | 17.6 (1-yr; 150m) | 7.8 (1-yr; 500m) | 3.9 (5-yr; 150m) | 6.2 (1-yr; 500m) | 9.9 (1-yr; 150m) |
| Refugia Distance | 6.1 | 4.6 | 18.8 | 5.3 | 1.8 |
| Patch Total Basal Area | 1.9 | 8.6 | 17.2 | 13.5 | 2.4 |
| Patch Live Basal Area | 2.7 | 2.3 | 8.8 | 4.5 | 1.8 |
| Patch Mean Live Tree Height | 8.9 | 10.3 | 7.1 | 16.9 | 1.3 |
| Patch Width | 7.3 | 5.1 | 3.8 | 5.8 | 2.6 |
| Patch Size | 6.8 | 1.4 | 2.1 | 2.3 | 0.7 |
| CV Total Residual Deviance Explained | 63% | 80% | 51% | 81% | 40% |
| CV Total Residual Deviance Explained (RAC included) | 89% | 90% | 76% | 89% | 70% |

*We pre-determined (see Data analysis) the strongest version of the refugia density and D²WD variables across species assemblages by calculating and comparing post-fire refugia extent at 1- and 5-year timesteps and among varying moving window neighborhood radii.

We observed the strongest pair-wise interactions among refugia variables and across species assemblages for (1) distance to refugia patch and refugia patch live mean tree height, and (2) distance to refugia patch and refugia D²WD (Fig. 3). Taller live trees substantially increased juvenile establishment within roughly 90m from refugia patch edges, but this relationship declined exponentially beyond roughly 90m and was non-linear for lodgepole pine, where tree heights between ca. 14m and 19m maximized establishment over heights that were lower or higher (Fig. 3c). At high values of refugia

D²WD (e.g., ca. threshold of ~2), establishment was high regardless of distance to refugia patch edge for all species assemblages, except lodgepole pine, where distance to refugia patch edge exhibited a stronger influence than refugia D²WD (Fig. 3h). At lower values of refugia D²WD, juvenile establishment declined more strongly as distance to refugia patch edge increased (Fig. 3).

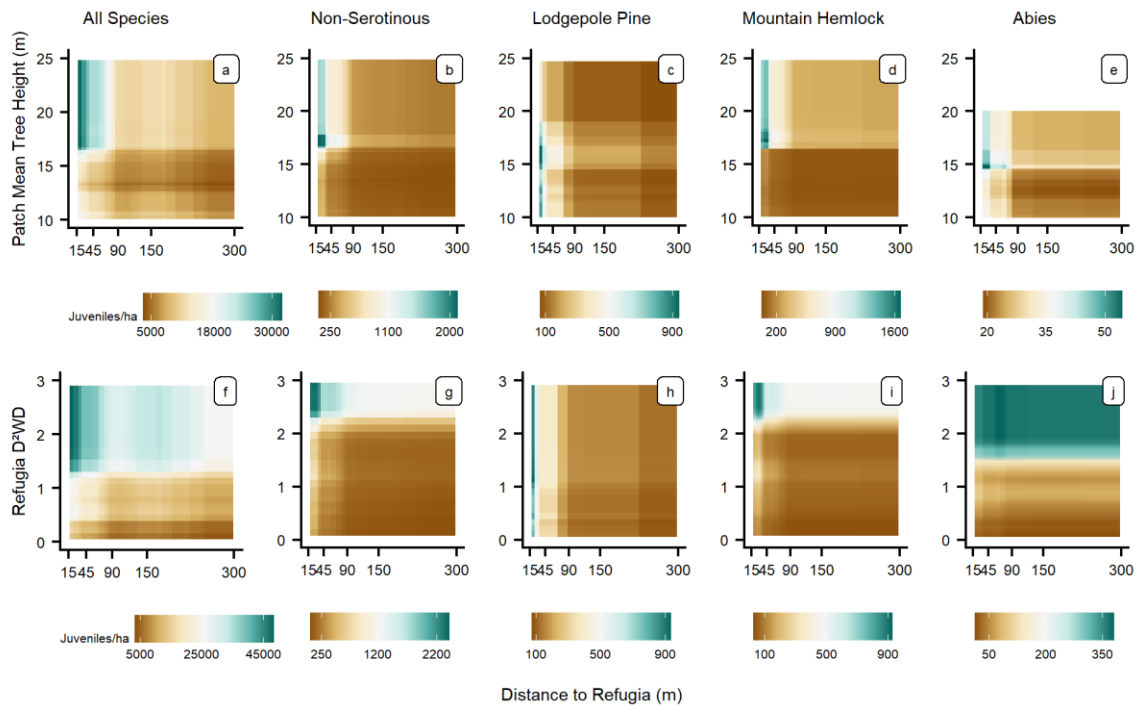


Figure 3. The strongest pair-wise interactions across species assemblage BRT models between three spatial or structural estimates of fire refugia: (1) distance to refugia patch edge, (2) refugia D²WD, and (3) refugia patch mean live tree height. Along the red-yellow-green color spectrum, red shading indicates reduced and green shading increased post-fire establishment due to pair-wise variable interactions.

Our third modelling analysis, comparing the top predictors of conifer juvenile establishment among the best three refugia metrics, best CMD metric, and site environmental variables, determined that across species assemblages, refugia D²WD outweighed the importance of climate water deficit, topographic microclimate (i.e., slope and HLI), and post-fire biotic legacies for conifer juvenile establishment (Table 3). The number of years from when fire occurred to time of field measurements was largely

unimportant across models. Topographic microclimate, climate water deficit, and canopy cover was most important for explaining variability in lodgepole pine establishment. Coarse woody debris cover was important for non-serotinous species combined and mountain hemlock, while climate water deficit was important for the *Abies* species assemblage.

Table 3. Relative variable importance between the best performing estimates associated with fire refugia and environmental predictors across species assemblage BRT models.

| Refugia, Climate, and Environmental Variables | Species Assemblage Models: Variable Importance (%) | | | | |
|---|--|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| | All Species | Non-Serotinous | PICO | TSME | <i>Abies</i> |
| Residual Autocovariate (RAC) | 34.9 | 5.4 | 20.8 | 20.3 | 12.8 |
| Refugia D ² WD | 43.3 (1-yr; 150m) | 56.5 (1-yr; 500m) | 28.2 (5-yr; 150m) | 47.6 (1-yr; 500m) | 68.3 (1-yr; 150m) |
| Coarse Woody Debris Cover (%) | 9.4 | 23.9 | 3.6 | 23.3 | 2.1 |
| Understory Vegetation Cover (%) | 4.2 | 2.0 | 2.7 | 2.6 | 0.5 |
| Canopy Cover (%) | 1.7 | 1.3 | 11.3 | 0.9 | 1.0 |
| Topographic Slope | 2.4 | 3.2 | 7.3 | 1.8 | 1.2 |
| Heat Load Index | 1.2 | 1.8 | 12.9 | 1.0 | 1.3 |
| 30-yr Climate Water Deficit | 2.4 | 5.4 | 12.6 | 2.0 | 10.5 |
| Years Since Fire | 0.5 | 0.5 | 0.5 | 0.6 | 2.3 |
| CV Total Residual Deviance Explained | 50% | 62% | 43% | 64% | 41% |
| CV Total Residual Deviance Explained (RAC included) | 89% | 80% | 73% | 83% | 75% |

Partial dependance plots illustrating relationships between predictive variables and species assemblage responses from our third analysis indicated some threshold-like

relationships and some major differences in the response between lodgepole pine and other species assemblages (Fig. 4). Across species assemblages, increasing refugia D²WD increased juvenile establishment exponentially up to a D²WD value threshold of ~1 for lodgepole pine and ~2-4 for other assemblages, after which increasing D²WD had no effect (Fig.4a). Further, refugia D²WD generally had a much stronger effect on juvenile establishment than other variables, and especially for all species combined, non-serotinous species, and mountain hemlock assemblages. For lodgepole pine only, establishment under low values of refugia D²WD were still notably above zero (~100 juveniles/ha), potentially indicating a serotinous seed dispersal response. Further, juvenile establishment increased under drier topographic settings (HLI), higher values of climate water deficit, and lower coarse woody debris cover for lodgepole pine (Fig. 4b, e, f). Alternatively, for all other assemblages, juvenile established increased with decreasing climate water deficit (but see the bimodal response among the *Abies* assemblage) and increasing coarse woody debris cover (Fig. 4b, e).

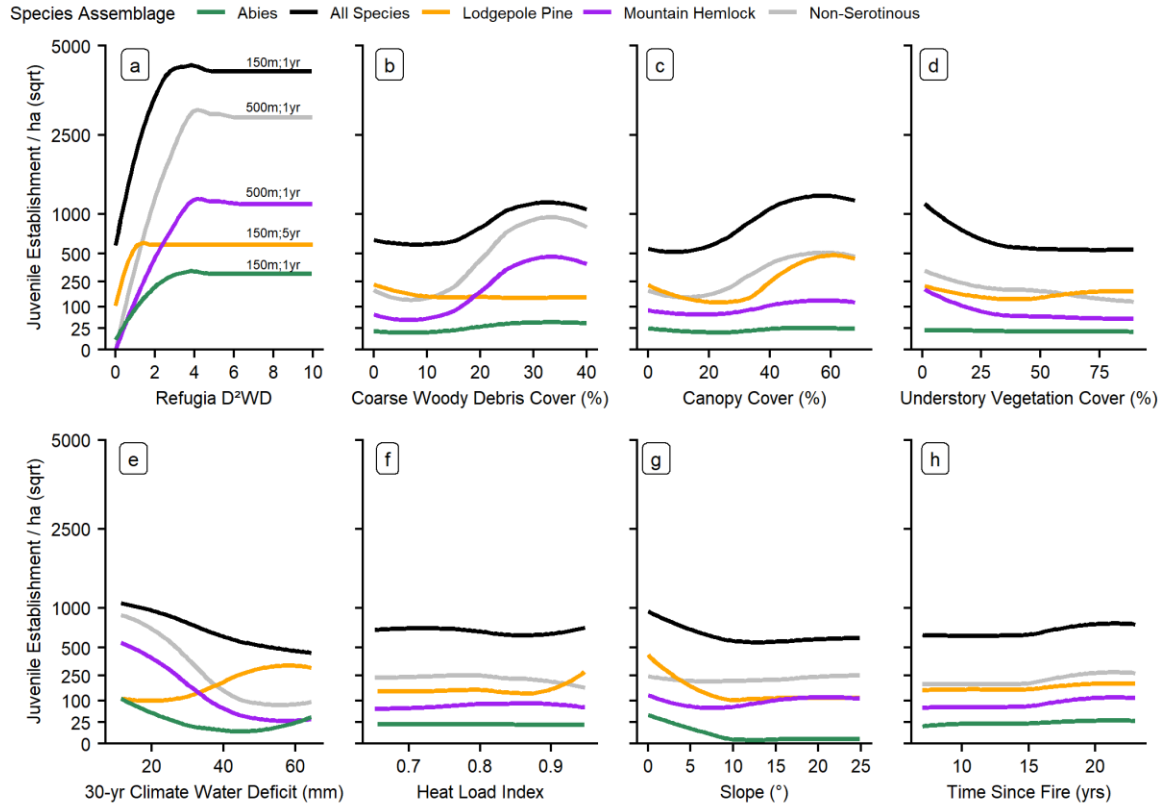


Figure 4. Partial dependence plots illustrating the smoothed flexible relationship between species assemblage establishment responses and refugia, climate, and environmental variables, combined. The y-axis is scaled using a square root function. Each plot represents the fitted values of juvenile establishment response (y) due to the predictor variable (x), while keeping all other predictor variables fitted in models at their average values. For the refugia D²WD variable, the best performing neighborhood radius and post-fire temporal snapshot associated with each species assemblage model is listed above response curves (i.e., #m; #yr). Refugia D²WD was the most important predictor of post-fire juvenile establishment responses across species assemblages (Table 3) and thus exhibited the greatest relative influence on establishment responses (y).

In our models with refugia, climate, and environmental site variables combined, we observed the strongest pair-wise interactions among variables between refugia D²WD and (1) climate water deficit, (2) coarse woody debris cover, (3) canopy cover, and these interactions occurred across species assemblages (Fig. 5). At low levels of refugia D²WD, increasing CWD and decreasing coarse woody debris cover reduced establishment, whereas at high levels of D²WD the influence of these two variables on juvenile establishment was less important. Opposite to the other species assemblage responses,

lodgepole pine establishment increased as CMD increased and coarse woody debris cover decreased (Fig. 5c, h). Performance across species assemblage BRT models in the second and third analyses was high (70-90% cross-validated total residual deviance explained) and generally greatly improved by calculating and including a residual autocovariate (RAC) term to account for spatial autocorrelation (Table 2; Table 3).

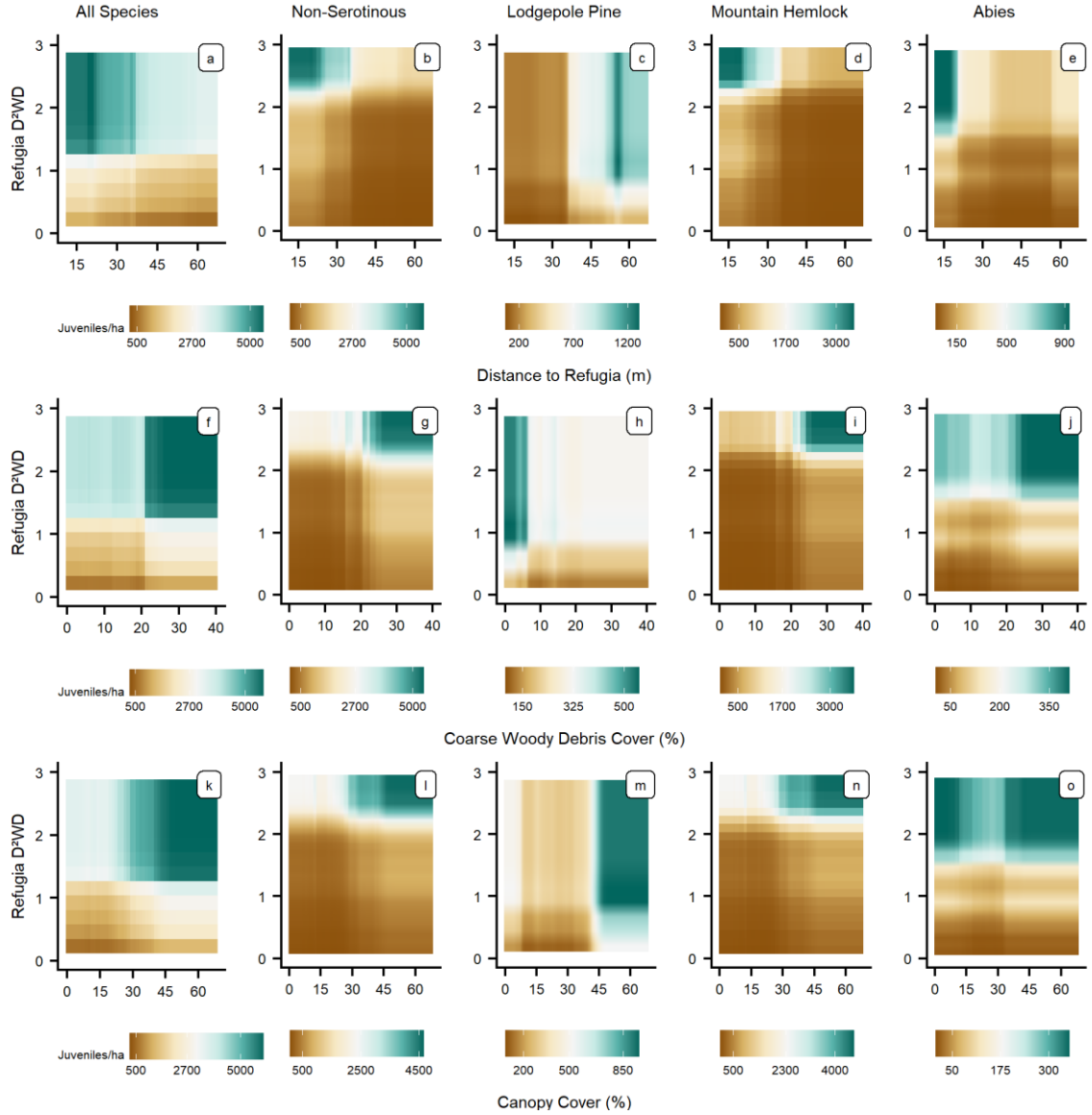


Figure 5. The strongest pair-wise interactions between refugia, climate, and environmental variables across species assemblage BRT models. Post-fire seed pressure (refugia D^2WD) interacted strongly with (1) 30-yr climate water deficit, (2) coarse woody debris cover, and (3) canopy cover. Along the red-yellow-green color spectrum, red shading indicates reduced and green shading increased post-fire establishment due to pair-wise variable interactions. Refugia D^2WD values ranged up to ~10, but interaction responses did not change above a refugia D^2WD value threshold of 3 across species assemblages.

4. Discussion

Our findings suggest that in mesic subalpine conifer forests of the Pacific Northwest (PNW) Cascade Range, post-fire conifer tree establishment after recent large,

stand-replacing fires was primarily limited by landscape-level seed pressure connected to fine grain spatial and structural patterns of fire refugia extent. We found that for serotinous and non-serotinous wind-dispersed obligate seeding conifer tree species, post-fire juvenile density (i.e., a proxy for forest resilience to and recovery from wildfire events) was largely explained by the distance²-weighted density (D^2WD) of remnant live tree extent one-year post-fire, as derived from high-resolution aerial imagery. Species composition, stand structure, and the suite of functional traits expressed by conifer species within field-surveyed fire refugia patches added further nuance to our understanding of post-fire juvenile establishment responses. Although micro- and macro-scale biotic and abiotic environmental controls were overall less important predictors of juvenile establishment in our cool and mesic study areas, they may be critically important toward facilitating post-fire forest recovery within locations where seed pressure is very low and rare dispersal events determine juvenile presence or absence. Toward conceptualizing, quantifying, and predicting post-fire dispersal and tree establishment patterns at varying spatial and temporal scales, our study demonstrates the crucial importance of considering and quantifying dispersal processes associated with the spatial extent and structure of seed source legacies in three-dimensional space.

4.1. Spatial patterns of fire refugia influence seed dispersal and post-fire forest recovery

Seed dispersal patterns that contribute to post-fire conifer forest recovery in the western US are strongly influenced by the arrangement of seed sources surrounding a site (Stevens-Rumann and Morgan 2019), including the density of seed-bearing individuals over space and their individual distances to a site (Clark et al. 1999). Prior studies have

generally focused on quantifying the influence of seed source distance and density separately, as metrics that relate to post-fire conifer forest recovery (e.g., Haire and McGarigal 2010; Kemp et al. 2016; Harvey et al. 2016; Busby et al. 2020; Rodman et al. 2020), while others have attempted to combine seed source distance and density into a single metric (e.g., Downing et al. 2019; Coop et al. 2019). Among the refugia variables we analyzed describing spatial and structural attributes of patch- or neighborhood-level fire refugia, the refugia distance²-weighted density (D^2WD) neighborhood metric strongly outweighed the importance of other refugia-related variables, including metrics that accounted for refugia distance or density individually. In dry to moist mixed-conifer forests of the Blue Mountains of Northeastern Oregon, Downing et al. (2019) also reported that refugia DWD outperformed simple distance to seed source metrics and was strongly correlated with post-fire forest recovery among non-serotinous conifer species.

Empirical seed dispersal kernels (i.e., percent of seeds dispersed along a gradient of distance from source) typically take the form of a negative exponential probability density function, in which seed density declines exponentially over increasing distances (McCaughey et al. 1986; Clark et al. 1999). Thus, it is a commonly observed phenomena that post-fire juvenile densities decline rapidly at increasing distances from live, seed-bearing individual(s) for non-serotinous, obligate seeding tree species (Kemp et al. 2016; Harvey et al. 2016; Stevens-Rumman and Morgan 2019; Busby et al. 2020). In dry mixed-conifer forests of the Southwestern USA, including data aggregated from Downing et al. (2019) in similar dry forest types, Coop et al. (2019) discovered that refugia DWD with a squared distance term (D^2WD) was a stronger predictor of post-fire

forest recovery than without, including this study, presumably due to accounting for exponential decay in seed dispersal over increasing distances from the source tree(s). These results illustrate the importance of accurately capturing and accounting for different spatial factors that affect seed dispersal processes when modelling and predicting post-fire establishment responses.

The strength of neighborhood metrics when modeling dispersal processes is often tied to the expression species-specific functional traits (e.g., seed production, weight, and morphology), thus experimentation with multiple neighborhoods among varying species is standard protocol (Turner and Gardner 2015). For dry-mixed conifer species (e.g., ponderosa pine and Douglas-fir), effective neighborhood radii calculated on dispersal-related neighborhood metrics assessed by previous studies have ranged 60-240m but have generally found that 100-150m effectively captures dispersal processes for these conifer species (e.g., Haire and McGarigal 2010; Coop et al. 2019; Downing et al. 2019; Rodman et al. 2020). We found some variation in the effective dispersal neighborhoods across our species assemblage models, likely tied to the dispersal capabilities of subalpine species in our study areas, which were further supported by observed differences in post-fire establishment at increasing distances to sampled fire refugia patches between our species (Fig. 2). All species combined, lodgepole pine, and *Abies* species' post-fire establishment was best captured by a 150m radius neighborhood, while a 500m radius was best for mountain hemlock and all non-serotinous species combined (i.e., excluding lodgepole pine). This pattern was consistent between both D²WD and refugia density metrics. These observed and modelled differences indicate that some relatively fire sensitive species

(e.g., mountain hemlock) in our subalpine study areas exhibit strong seed dispersal abilities that support juvenile establishment further into the interior of severely burned forest patches than others (e.g., subalpine and Pacific-silver fir; Busby et al. 2020). Thus, fine-scale species composition of fire refugia may initiate broadly different post-fire recovery responses, especially when the size of severely burned forest patches are expansive.

4.2. Post-fire delayed tree mortality and forest recovery

Seed dispersal patterns influencing post-fire forest recovery are linked to the persistence of fire refugia over time, where seed dispersal, and thus tree establishment, may decline over time as sexually mature individuals expire and are not replaced. If climate-environment conditions do not favor seed production and juvenile establishment early post-fire (e.g., Stevens-Rumann et al. 2018; Davis et al. 2019; Kemp et al. 2019), delayed tree mortality and/or compound disturbances may eliminate fire refugia before they can initiate an establishment response that is sufficient for long-term forest recovery (Coop et al. 2020). We modelled the influence of fire refugia extent 1- and 5-years post-fire on conifer establishment responses, and primarily observed that fire refugia extent 1-year post-fire was a superior predictor of establishment over 5-years post-fire. Further, the number of years between when a fire occurred and when we sampled sites (i.e., number of opportunities for establishment; time since fire; 7-23 years) was mostly unimportant as a predictor of post-fire juvenile densities. These results may indicate that climate-environment conditions in our relatively mesic and cool subalpine study areas (i.e., low water deficit to vegetation) generally support early post-fire pulses of juvenile

establishment pending the availability of seeds, likely reducing the influence of post-fire delayed tree mortality patterns on forest recovery trajectories. To improve understanding of how post-fire delayed tree mortality affects seed dispersal processes and forest recovery, future work could test the relationship between post-fire establishment responses and fire refugia extent over time, across a broader range of climate-environment conditions (i.e., drier sites).

4.3. Non-linearity and interactions among fire refugia and climate-environment

Post-fire tree establishment and survival responses can be understood using the concept of environmental filtering, where dispersal limitations, then environmental conditions, then competition control species compositions over time (Kraft et al. 2015). While dispersal limitations appeared to drive the majority of variance in post-fire conifer establish responses in our cool and mesic subalpine study areas, the non-linear relationship observed between establishment responses and refugia D^2WD (e.g., Fig. 4a) indicated that many sites reached a point of seed saturation. This is to say that increasing D^2WD (i.e., greater density of nearer seed sources) did not increase establishment responses beyond a species-specific threshold of D^2WD , which likely varied based on differences in functional traits between species, and thus the variation in responses within those sites were driven by climate and environmental controls, and potentially competition (i.e., understory vegetation cover; Fig. 4d). Although lodgepole pine experienced a weaker relationship with refugia D^2WD than other species assemblages, the relationship was still significant and indicative of a mostly non-serotinous establishment response. In contrast, lodgepole pine establishment has been weakly or

negatively correlated with refugia D²WD within dry to moist mixed-conifer forests elsewhere, (e.g., Coop et al. 2019; Downing et al. 2019). Although broad empirical evidence is limited in the Cascade Range, the post-fire establishment response of lodgepole pine in our high-elevation study areas suggests that the production of serotinous cones among lodgepole pine decreases with elevation in the Cascade Range (Busby et al. 2020), similar to findings in the N. Rockies, where decreasing elevation is related to shorter fire return intervals and greater selection of serotinous cones among lodgepole pine (Lotan 1976; Tinker 1994; Schoennagel et al. 2003). The saturation point of refugia D²WD for lodgepole pine was also lower than other species assemblages, which may speak to its functional traits in our subalpine study areas as a prolific producer of non-serotinous (open cone) wind-dispersed seed crops (OECD 2010).

Species-level dispersal traits are further augmented at the individual and stand scales by forest structure, where older, larger, and taller trees typically produce greater quantities of seeds (Clark et al. 1999; Kroiss and HilleRisLambers 2015; Andrus et al. 2020) until senescence (Qiu et al. 2021) and disperse them further than younger and shorter trees (Gill et al. 2020). Strong pair-wise interactions in our statistical models indicated that mean tree height among fire refugia patches boosted juvenile establishment along a gradient of increasing distance from refugia patch edges when mean height was approx. greater than 15m (Fig. 3). If increasing fire frequency and severity (Abatzoglou and Williams 2016) broadly reduces the age of forests in fire-affected landscapes, increasingly young and short forests may exhibit lower capacity to initiate forest recovery

responses than their older and taller counterparts after large high-severity fires (Hart et al. 2019; Gill et al. 2020).

For landscape-scale processes such as post-fire forest recovery, a keen understanding of how dispersal processes interact with environmental controls is key to understanding and predicting forest resilience to increasingly large, severe, and frequent wildfires. Evidence from this study suggest that climate and biotic environmental legacies (e.g., climate water deficit, canopy cover, coarse woody debris cover; Fig. 5) interact with dispersal processes to enhance or diminish juvenile establishment responses along landscape-level gradients of seed pressure (Fig. 6). Although rare dispersal events (i.e., the thin right-skewed tail-end of a dispersal probability density function) make up a minuscule proportion of total seeds dispersed, they may be disproportionately important for biogeographic processes (Clark et al. 1998) where the difference between zero and marginal establishment leads to either long-term ecosystem state transitions or slow but eventual recovery. In the case of wind-dispersed conifer species, the interactions between rare dispersal events, climate, and environmental controls may determine whether and how forests recover after spatially expansive and contiguous stand-replacing, high-severity wildfires.

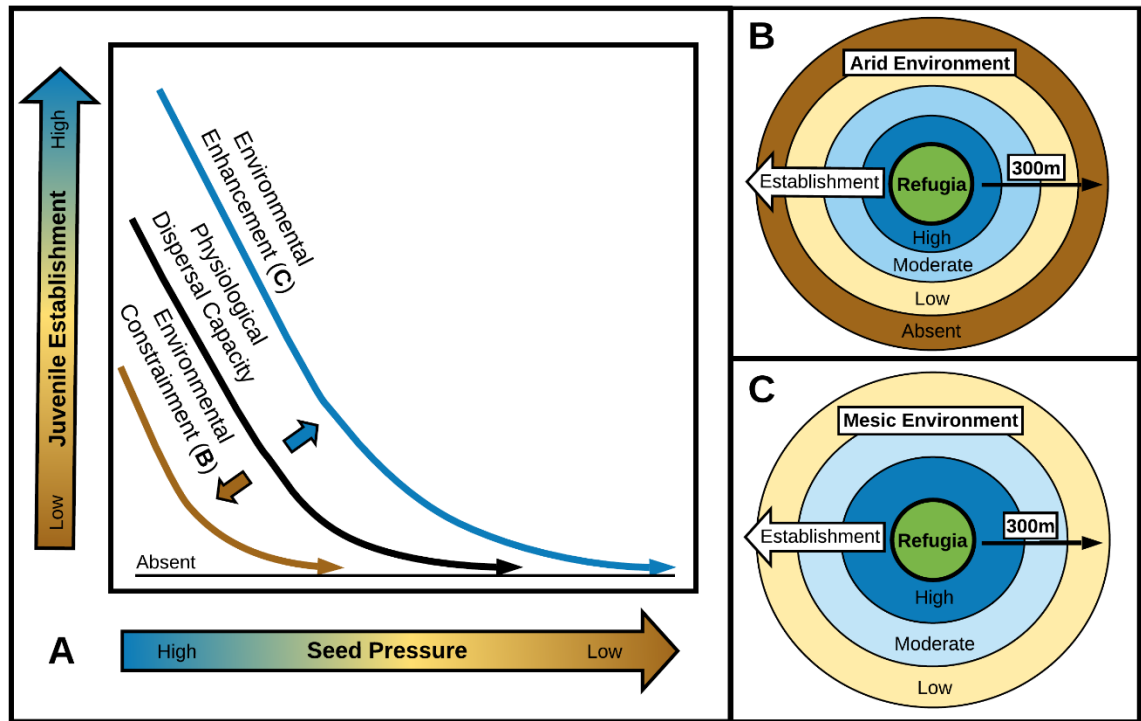


Figure 6. For wind-dispersed tree species along a gradient of seed pressure, post-disturbance juvenile establishment responses are determined by interactions between biotic and abiotic environmental controls and the spatial and structural (i.e., age, size, height) configuration of refugia at the landscape scale (A). Across gradients of water deficit to vegetation explained by micro-scale topographic and macro-scale climatic characteristics, arid environments (B) constrain while mesic environments (C) enhance juvenile establishment at increasing distances from seed sources when refugia extent and associated seed pressure remains constant. Thus, tree establishment into and forest recovery within stand-replacing burn patch interiors is quicker and more successful in mesic environments compared to arid.

4.4. Limitations and opportunities

Quantification of landscape-level seed source availability and pressure via high-resolution remote sensing data and high-accuracy imagery classification, as illustrated by this study, strengthen our ability to test spatial and biotic relationships, and predict post-fire, or more broadly, post-disturbance ecosystem recovery trajectories. These methods are not without their caveats, however. While highly accurate, supervised imagery classification methods used in this and prior studies (e.g., Walker et al. 2019; Downing et al. 2019; Coop et al. 2019) are non-automated, time consuming, rely on user-objectivity, and may

lose accuracy when training samples are drawn from, and assessments conducted over, large spatial extents with topographically and ecologically heterogeneous landscapes (Wulder et al. 2009). Further, high spatial resolution imagery products also entail high data requirements, slowing processing and classification time when the research's aim is to assess large or many landscapes. Thus, while useful for case studies where analysis time and effort are not significantly limited, they are less likely to be used by land managers due to limitations associated with accessibility and efficiency. Greater accessibility and usability of these methods would be enhanced by automated imagery classification workflows and toolsets programmed for statistical and/or geographic information system (GIS) applications.

While moving window neighborhood-based seed pressure metrics used in this study and others are significant improvements over simple distance to edge or patch metrics for modelling dispersal processes and tree establishment responses, they do not account for the biotic structure or composition of seed sources, which strongly influence seed pressure dynamics over space and time (e.g., Gill et al. 2020). Current refugia seed pressure metrics, like refugia D²WD, could be improved by moving from a binary seed source presence or absence classification to a weighted approach. In the context of this study, pixels first classified as refugia presence could be weighted by either structural attributes (e.g., tree height, basal area, or age) or compositional attributes (e.g., percent species composition). This type of approach would rely on secondary fine-to-moderate resolution spatial data of forest structure or composition, which is becoming increasingly available in the continental US (e.g., LANDFIRE; LEMMA GNN).

Finally, in this study, we did not consider topographic complexity, prevailing wind patterns, or snowpack dynamics as they relate to dispersal processes. Topographic complexity can enhance or inhibit dispersal processes and additionally interact with wind patterns (Peeler and Smithwick 2020). Topographic complexity was generally low within our study areas and is more broadly low within high-elevation subalpine forests of the Cascade Range, which may reduce spatial variability in dispersal processes relative to other more topographically heterogeneous landscapes. Although not well empirically studied, winter snowpack in our high-elevation study areas may further enhance the dispersal range of select species, whereby seeds dispersed during winter can “skim” past their initial ground-contact point by gliding on snowpack during surface wind gusts (Matlack 1989; Agee 1993). Theoretically, the low topographic complexity of our study areas would facilitate improved secondary-dispersal of seeds over snowpack vs. more topographically complex landscapes and especially at lower elevations (i.e., less snow), where seeds are more likely to become trapped by topographic variability.

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7. Appendix: Supporting information, tables, and figures

7.1. Sample plot selection and distance-buffer ruleset

To connect post-fire conifer establishment responses to the spatial orientation and structural attributes of individual fire refugia patches, criteria for field sample plot locations were designed with the objective of maintaining a minimum level of spatial independence from other refugia patches and live (unburned) forest edges. Fire refugia patches were considered for sampling if they were (1) spatially contiguous (i.e., tree canopies were spaced less than 5m apart), (2) $\geq 0.09\text{ha}$ in size (i.e., roughly the size of our sample plots and the minimum patch size easily detected by moderate resolution imagery; Landsat), (3) disconnected from live forest edges by $>100\text{m}$ and $>100\text{m}$ from other refugia patches in distance. All distances were calculated using geodesic methods in ArcGIS and live forest edges were excluded from the study for sampling. We also excluded all post-fire management efforts (e.g., salvage logging, replanting) from our potential sampling areas using spatial data (maps) provided by the Gifford Pinchot, Mt. Hood, and Willamette National Forests.

For fire refugia patches that met our initial criteria, additional criteria were then considered for the placement of post-fire regeneration sample transects, to be run outward from individual fire refugia patches into severely burned forest patches, but also away from unburned forest edges to minimize the influence of their seed pressure (see Appendix A: Fig. A.1. for sampling diagram). Sample transects were considered if a 200m minimum distance could be maintained between all sample points on the transect and all other refugia patches, and a 300m minimum distance from live forest edges. To

minimize spatial autocorrelation among transects, all potential transects were buffered a minimum distance of 200m from each other. Transects were run perpendicular to the widest and least wide portion of the refugia patch, so that transects were farthest away from each other. Following an expected negative exponential distribution in tree establishment away from refugia patches (e.g., Stevens-Rumann and Morgan 2019), post-fire regeneration plots were established along transects at 15m, 45m, 90m, 150m, and 300m. In the event any of the abovementioned buffers (rulesets) could not be maintained, sample transects were truncated at the 150m plot. The number of transects established in each study area for sampling was proportional to the availability of refugia patches which fully met the aforementioned distance-buffer ruleset.

Table 4. Confusion matrices of the imagery classification accuracy assessment conducted by fire perimeter and post-fire temporal snapshot.

| Fire | Temporal Snapshot | Producers Accuracy | | User's Accuracy | | Overall Accuracy | Kappa |
|---------------|-------------------|--------------------|------------|-----------------|------------|------------------|-------|
| | | Fire Refugia | Non-Forest | Fire Refugia | Non-Forest | | |
| Cascade Creek | 1-yr post-fire | 1.00 | 0.91 | 0.90 | 1.00 | 0.95 | 0.90 |
| Cascade Creek | 5 yrs post-fire | 0.94 | 0.96 | 0.96 | 0.94 | 0.95 | 0.90 |
| Gnarl Ridge | 1-yr post-fire | 0.92 | 0.99 | 0.99 | 0.91 | 0.95 | 0.90 |
| Gnarl Ridge | 5 yrs post-fire | 0.89 | 1.00 | 1.00 | 0.88 | 0.94 | 0.88 |
| Shadow Lake | 1-yr post-fire | 0.97 | 0.93 | 0.93 | 0.97 | 0.95 | 0.90 |
| Shadow Lake | 5 yrs post-fire | 0.99 | 0.95 | 0.95 | 0.99 | 0.97 | 0.94 |
| Charlton | 1-yr post-fire | NA | NA | NA | NA | NA | NA |
| Charlton | 5 yrs post-fire | 1.00 | 0.95 | 0.95 | 1.00 | 0.98 | 0.95 |
| Mean Accuracy | | 0.96 | 0.96 | 0.95 | 0.96 | 0.96 | 0.91 |

Table 5. Variable importance between three temporal measures of climate water deficit (CWD) across species assemblage BRT models.

| Climate Variables | Variable Importance (%) | | | | |
|--|-------------------------|----------------|-------------|-------------|-------------|
| | All Species | Non-Serotinous | PICO | TSME | Abies |
| Residual Autocovariate (RAC) | 65.7 | 15.4 | 16.2 | 64 | 68.4 |
| 30-Year Mean CWD | 21.8 | 61.2 | 32.7 | 27.6 | 21.9 |
| Post-fire Mean CWD | 6.7 | 14.6 | 31.4 | 4.7 | 6.1 |
| Post-fire Maximum CWD | 5.7 | 8.7 | 19.6 | 3.6 | 3.6 |
| CV Total Residual Deviance Explained | 18% | 32% | 24% | 32% | 26% |
| CV Total Residual Deviance Explained (RAC) | 49% | 42% | 46% | 41% | 48% |

Model performance was evaluated by determining cross-validated (CV) total residual deviance explained by the fitted model. We computed and included a residual autocovariate (RAC) term in each final model to account for spatial autocorellation (SAC) between plot locations.

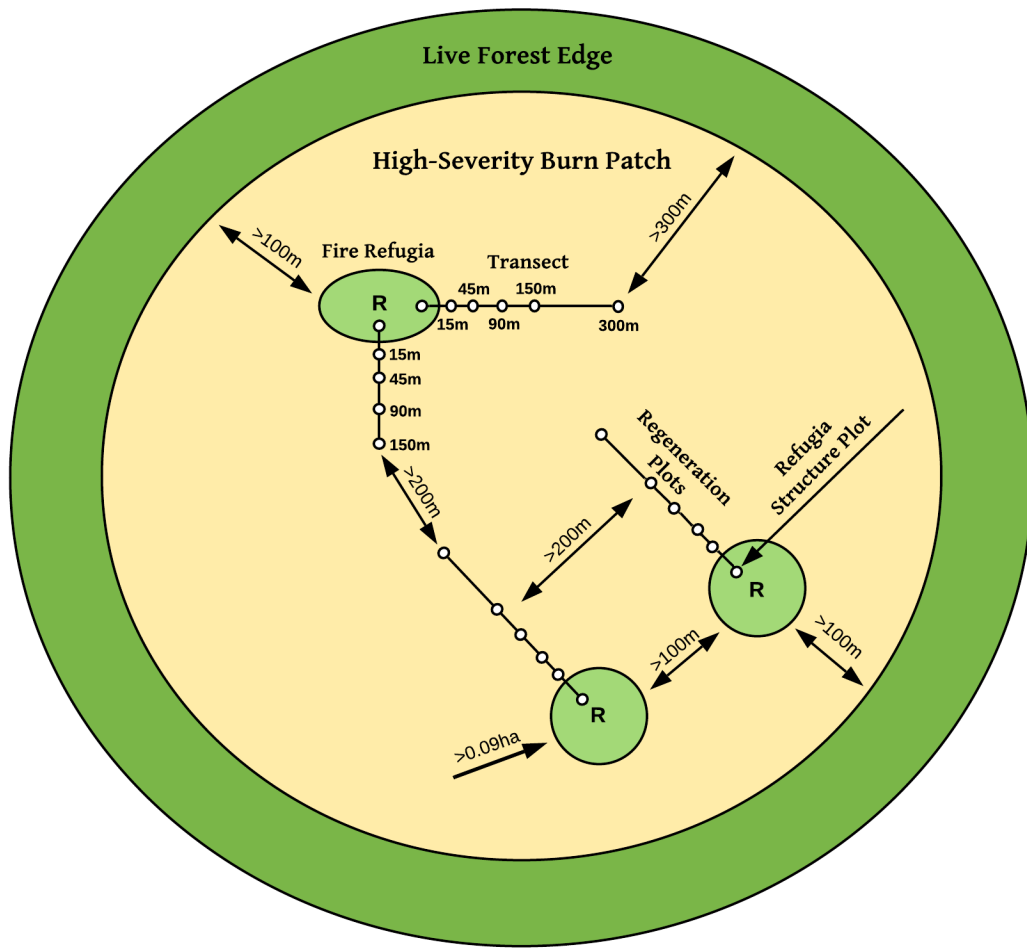


Figure 7. Diagram of the buffer distance ruleset used to maintain a minimum level of spatial independence between sampled fire refugia patches (R) and post-fire regeneration plots, as applied to live forest edges, refugia patches, and sample transects within high-severity wildfire perimeters.

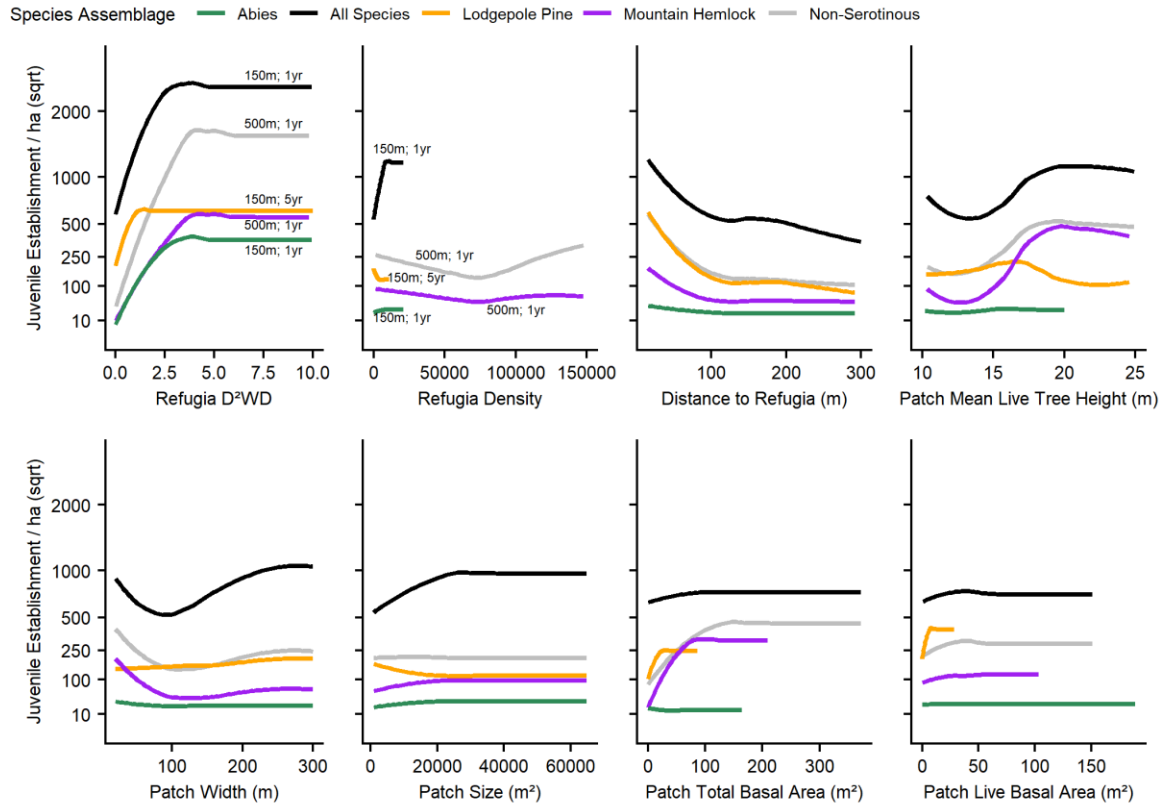


Figure 8. Partial dependance plots illustrating the smoothed flexible relationship between refugia-related predictor variables and post-fire conifer establishment across species assemblage BRT models. Each plot represents the fitted values of juvenile establishment response (y) due to the predictor variable (x), while keeping all other predictor variables fitted in models at their average values. For the refugia D²WD and refugia density variables, the best performing neighborhood radius and post-fire temporal snapshots associated with each species assemblage model are listed above response curves (i.e., #m; #yr).

Chapter 2:

Post-fire death in the slow lane: patterns, drivers, and implications of post-fire delayed conifer tree mortality

Abstract

Increasing wildfire activity and compound disturbance interactions, under climate change, are expected to challenge conifer forest resilience in the western US through high tree mortality and limited post-fire recovery. Post-fire live tree legacies, or fire refugia, can increase forest resilience to fire and compound disturbances, however, by providing critical seed sources necessary for forest recovery. The extent of fire refugia and live forest edges may be shrinking over time due to delayed post-fire tree mortality, however, with large-scale patterns and the ecological implications of such remaining largely unknown. To explore post-fire delayed conifer tree mortality patterns, their drivers, and their effect on seed source availability at large scales, we used high-resolution satellite imagery to quantify conifer tree cover loss between 1- and 5-years post-fire. We conducted delayed tree mortality assessments within thirty fire perimeters distributed across three montane ecoregions and two structurally and functionally dissimilar broad conifer forest types in the Western United States. Percent delayed mortality of live conifer tree extent between 1- and 5-years post-fire ranged from ca. 5-25% at the fire perimeter scale and ca. 12-15% at the ecoregion scale. 1-year post-fire burn severity was the strongest predictor of delayed tree mortality patterns, indicating early patch-scale vegetation change may be a strong proxy for both tree-level fire injuries and subsequent competition with rapidly recovering understory vegetation. Burn severity also strongly interacted with 30-year average and post-fire climatic moisture deficits, illustrating the

powerful effects of productivity gradients and compound disturbances (e.g., drought) on delayed tree mortality probability. Critical increases in seed source distance to severely burned forest patches observed in this study, compounded by increasingly limited temporal opportunities for tree-reestablishment, suggest that post-fire forest recovery may be most negatively impacted by delayed tree mortality patterns in dry conifer forests of the S. Rockies, and potentially dry conifer forests elsewhere. Our work demonstrates that post-fire delayed tree mortality in conifer forests of the Western U.S is a process that can be quantified at a fine grain and coarse scale, has meaningful ecological impacts, and is driven by complex fire-environment interactions.

1. Introduction

As a warming climate drives greater fire activity across Western North American forests (Abatzoglou and Williams 2016; Parks and Abatzoglou 2020), recently observed increases in large, severe, and frequent wildfire events have sparked fears around forest resilience and persistence in many landscapes (Keeley et al. 2019; Turner et al. 2019; Whitman et al. 2019; Busby et al. 2020; Coop et al. 2020; Reilly et al. 2020). Where obligate seeding conifer species dominate forest types, the presence and spatial distribution of fire refugia across severely burned landscapes increase conifer forest resilience and persistence by providing ephemeral or persistent seed sources necessary for forest recovery (Meigs and Krawchuk 2018; Blomdahl et al. 2019; Coop et al. 2019; Downing et al. 2019). Fire refugia and live forest edges may be shrinking over time, however, due to delayed tree mortality patterns linked to initial fire effects (e.g., fire injuries at the tree-level and changes to the biophysical environment at the patch-level)

and compound disturbances (e.g., reburns, drought, insects, and pathogens; Krawchuk et al. 2020). As live seed-bearing tree extent (i.e., seed source availability) shrinks over time (e.g., McDowell et al. 2020), short- and/or long-term reductions in seed source availability may cause major limitations on post-fire forest recovery (Stevens-Rumann and Morgan 2019; Coop et al. 2020), and particularly within fire perimeters affected by high moisture deficits and large patches of high-severity fire (Stevens-Rumann et al. 2018; Davis et al. 2019; Kemp et al. 2019). Evidence from small scale, field-based studies across varying conifer forest types suggest post-fire delayed tree mortality patterns can be highly variable, but also quite significant (e.g., Brown et al. 2013; Whittier and Gray 2016; Rocceforte et al. 2018; Jeronimo et al. 2020). Large-scale patterns of post-fire delayed tree mortality (i.e., at the fire perimeter or ecoregion levels) and their effect on persistent seed source availability and post-fire forest recovery are poorly understood, however.

In the context of conifer forests in Western North America, post-fire delayed tree mortality (i.e., tree mortality that is connected to, but not an immediate response to fire effects; second-order fire effects) is a widely observed phenomenon that is increasingly well-studied mechanistically (Hood et al. 2018; Hood and Varner 2019; Hood 2021) to support modelling and prediction of tree-level mortality patterns for forest and fire managers (e.g., Cansler et al. 2020). Fundamentally, fires influence the probability of tree mortality over time through direct and indirect effects (Hood and Varner 2019). Direct effects include sustained fire injuries at the individual tree level, which may cause immediate mortality or increase the risk of delayed mortality by disrupting a tree's physiological functions and capacity to survive future stress (Hood et al. 2018; Hood

2021). Indirect effects include (1) fire-induced changes to the biophysical environment surrounding a focal tree, thereby altering patch-level resources, exposure, and competition (e.g., van Mantgem et al. 2018; 2020), or (2) another acute or prolonged disturbance event, such as additional fire, drought, windthrow, or insect and pathogen outbreaks, which compound with fire injuries to overwhelm tree vigor over a longer time scale (van Mantgem et al. 2013; 2018; Jeronimo et al. 2020). Depending on a focal tree's individual functional traits (and potentially local adaptations), indirect effects may increase or decrease the probability of delayed mortality. Thus, to comprehensively understand post-fire delayed tree mortality responses and patterns over space and time, it is important to consider both tree- and patch-level responses and feedbacks to direct and indirect effects (Fig. 1).

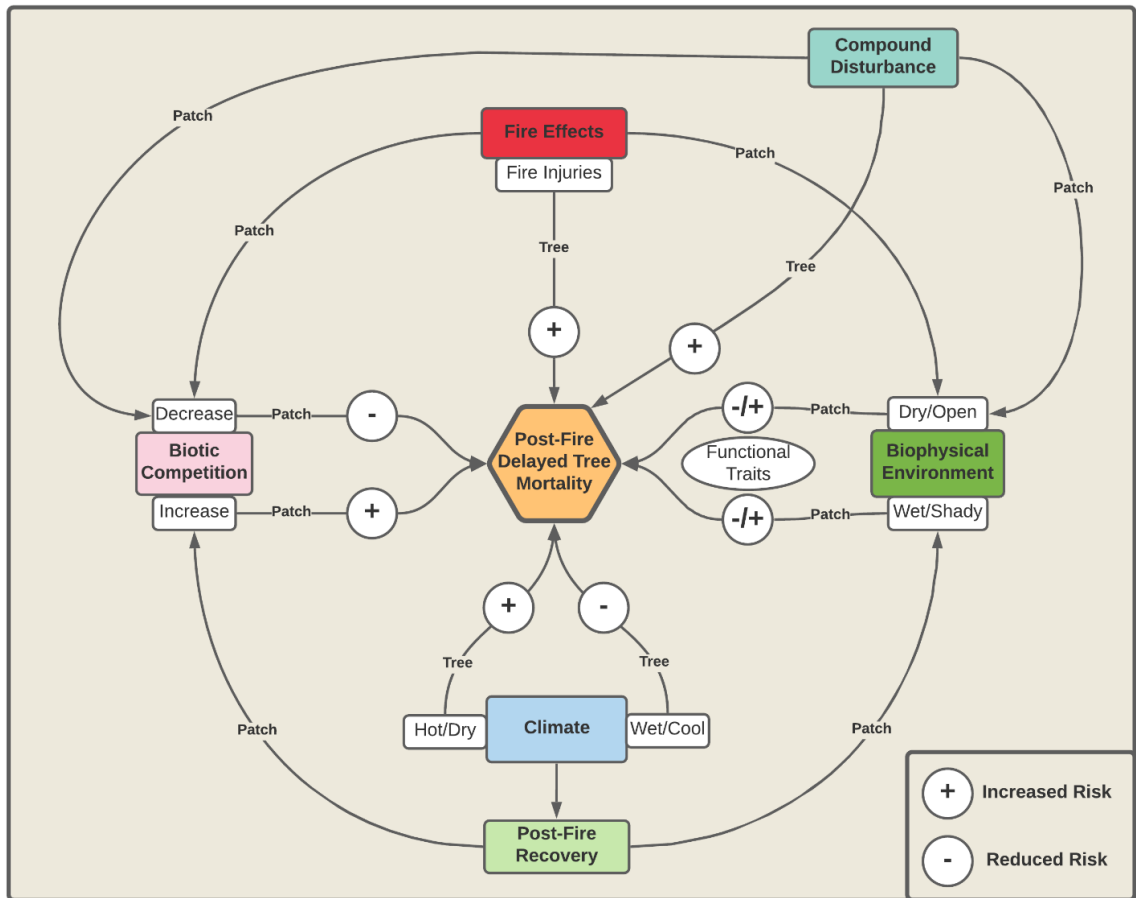


Figure 1. Fundamental factors influencing post-fire delayed tree mortality patterns and their feedbacks; adapted from Hood et al. (2018). Initial fire effects, compound disturbances, and climate (average, pre- and post-fire) can directly cause mortality at the tree-scale by overwhelming physiological function, or indirectly by altering the biophysical environment and biotic competition at the patch-scale. Based on tree species functional traits and local adaptations, changes to the biophysical environment at the patch-scale can increase or reduce an individual tree's probability of delayed mortality.

At large spatial scales, vegetation and tree mortality patterns related to fire effects are commonly referred to as burn severity (Eidenshink et al. 2007; Keeley et al. 2009) and can be used to quantify the magnitude of vegetation change due to fire, and therefore inform interpretations of broader ecological impacts and management caused by fire events (Key and Benson 2006). Burn severity has commonly been derived from two differenced remotely sensed images; one representing pre-fire vegetation cover and one

representing post-fire vegetation cover (Key and Benson 2006; Eidenshink et al. 2007). Early studies developing methodologies for quantifying burn severity over large spatial scales broadly determined that a one-year post-fire temporal snapshot would encompass most fire-related mortality patterns, while minimizing detection misclassification due to vegetation recovery, especially over heterogenous landscapes and ecosystems (Key 2006; Key and Benson 2006). This methodology was subsequently adopted by the monitoring trends in burn severity program (MTBS; Eidenshink et al. 2007), which has systematically produced fire perimeter and severity maps among large (> 200ha) fires in the United States dating back to 1984, with the goal of providing decision making resources to land managers. MTBS' data products have been strongly utilized by the broader U.S. scientific community (Picotte et al. 2020) and their core methodology has become a gold standard for quantifying burn severity globally (e.g., Miller and Thode 2007; Miller et al. 2009).

Criticisms of this core methodology have primarily focused on the subjectivity of methods and classifications (e.g., Kolden et al. 2015), the comparative performance of various burn severity indices across vegetation types (e.g., Parks et al. 2014), and the challenge of connecting ecological change to burn severity index values (e.g., Harvey et al. 2019; Parks et al. 2019). What has gone largely undiscussed beyond early theoretical frameworks (e.g., Key 2006), however, is the temporal component of burn severity and vegetation change assessment, i.e., how the temporal period of post-fire assessment may affect the magnitude of detectable vegetation mortality, and therefore affect interpretations of ecological impacts. If mortality patterns related to fire effects are

substantial beyond one-year post-fire, researchers and managers may be broadly underestimating the impacts of fire events on ecological communities, ecological succession, and post-fire ecosystem trajectories when one-year post-fire imagery is evaluated exclusively. Considering the ecological impacts of increasingly large, severe, and frequent wildfires across montane Western U.S. forests, improving understanding of where, to what degree, and how post-fire delayed tree mortality patterns alter forest extent, resilience, and persistence can aid land managers planning and prediction abilities on multiple fronts (e.g., prescribed fire treatments, post-fire management, landscape dynamics, carbon cycling; Hood and Varner 2019).

To evaluate whether post-fire delayed tree mortality patterns have important ecological implications for conifer forest resilience in the western U.S., we quantified large-scale patterns of post-fire delayed conifer tree mortality within three major ecoregions of the western U.S., between 1- and 5-years post-fire, using high-resolution imagery. To provide ecological context pertinent to recent fire patterns observed within our study ecoregions, we focused on delayed mortality patterns among two broad conifer forest types prone to high-severity fires in recent history (1984 to present), nested within recent (2008-2014) fire perimeters with large proportions and/or patch sizes of high-severity fire. Our specific research questions were:

- (1) What is the spatial extent of post-fire delayed conifer tree mortality between 1- and 5-years post-fire at the fire perimeter and ecoregion scales?

(2) To what degree do post-fire delayed conifer tree mortality patterns reduce long-term seed source availability (i.e., proximate seed-bearing trees) to severely burned and/or non-forested areas?

(3) How do fire and biophysical drivers predict post-fire delayed tree mortality?

We hypothesized that (1) post-fire delayed tree mortality patterns would exhibit greater variance at smaller spatial scales than larger (i.e., fire perimeter vs. ecoregion scales), (2) initial estimates of burn severity would have a strong relationship with the probability of delayed tree mortality as a proxy of tree-level fire injuries and patch-level competition (i.e., vegetation recovery), and (3) topo-climatic factors associated with increasing moisture deficits to vegetation would similarly increase the probability of delayed tree mortality.

2. Methods

2.1. Study areas

To represent and compare large scale post-fire delayed tree mortality patterns in the western U.S. within an ecologically relevant framework, our study focused on three major montane ecoregions and two broad conifer forest types that have experienced a large proportion of high-severity wildfire in modern times: upper-montane and subalpine forests in (1) the Cascades of Oregon and Washington, (2) the N. Rockies of Idaho, Montana, and Wyoming, and (3) dry conifer forests in the S. Rockies of Colorado and New Mexico (Cansler and McKenzie 2014; Reilly et al. 2017; Hessburg et al. 2019; Higuera et al. 2021). Upper-montane and subalpine forests in the Cascade Range and N. Rockies are largely dominated by fire-sensitive and/or shade-tolerant conifers (e.g., *Abies*

grandis, *Abies lasiocarpa*, *Pinus contorta*, *Tsuga mertensiana*, *Picea engelmannii*; Agee 1993; Baker 2009) and exhibit moderate to high tree densities due to historically long (50 – 300+ year) fire-return intervals stimulated by moist and/or cool climate condition (Agee 1998). Alternatively, low- to mid- elevation dry conifer forests in the S. Rockies have been historically dominated by fire-resistant and/or shade-intolerant conifers (e.g., *Pinus ponderosa* and *Pseudotsuga menziesii*) and exhibit low to moderate tree densities due to historically frequent (5 – 50 year) fire-return intervals stimulated by a warm and/or dry climate (Veblen et al. 2000; Sherriff et al. 2014; Johnson and Margolis 2019). While large high-severity wildfires are historically characteristic of upper-montane and subalpine forests in the N. Rockies and Cascades, Euro-American management legacies (i.e., fire suppression and colonial-settler disruption of Indigenous life ways) have been attributed with causing uncharacteristically large and severe fires in low-to-mid elevation dry conifer forests of the S. Rockies (Brown et al. 2015; Battaglia et al. 2018), and elsewhere (Hessburg et al. 2019). Climatically, the Cascades ecoregion experiences the least continentality and greatest annual precipitation, followed by the N. Rockies and lastly, the S. Rockies. Consequently, average annual climate moisture deficit to vegetation is generally the greatest in low- to mid-elevation forests in the S. Rockies and is negatively correlated with elevation across ecoregions (Fig. 2).

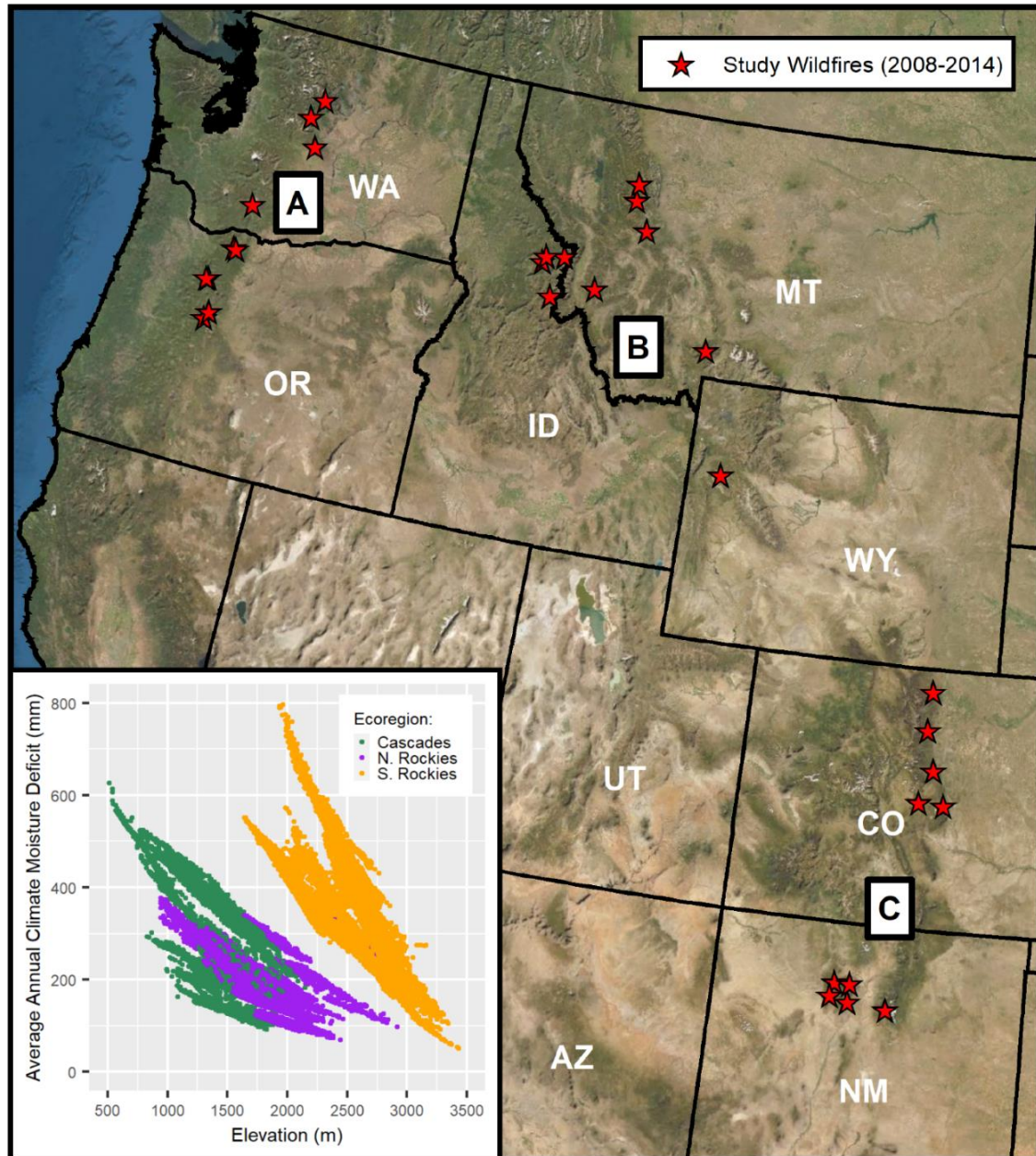


Figure 2. Geographic locations of the thirty wildfire perimeters where delayed tree mortality patterns were quantified in this study between 1- and 5-years post-fire. Fires were distributed equally across three mountain ecoregions in the western U.S., including (A) the Cascade Range, (B) the Northern Rockies, and (C) the Southern Rockies. Inset scatterplot indicates the distribution of and relationship between elevation and climate moisture deficit to vegetation among area nested within the study wildfire perimeters, by ecoregion.

To identify suitable fire perimeters across ecoregions for quantifying post-fire delayed tree mortality patterns, we initially used several sources of spatial data and criteria as filters. First, we used wildfire perimeter delineations and classified burn severity estimates from the Monitoring Trends in Burn Severity (MTBS; Eidenshink et al. 2007) program to select wildfires within each ecoregion that (1) burned between 2008 – 2014 following satellite imagery availability as described below, and (2) experienced relatively large patches of high-severity fire ($>10\text{ha}$; Harvey et al. 2016). Second, we used the LANDFIRE (Rollins 2009) Existing Vegetation Type (EVT) layer to sub-select fire perimeters that were dominated ($> 75\%$ of forested area) by either upper-montane and subalpine forest types (e.g., spruce, true-fir, hemlock, and lodgepole pine) in the Cascades and N. Rockies or dry conifer forests in the S. Rockies (e.g., ponderosa pine and Douglas-fir). From this sub-sample, we chose an equal number of fire perimeters per ecoregion ($n=10$) to quantify delayed tree mortality patterns between 1- and 5-years post-fire (Fig. 2; Appendix: Supporting tables; Table 3). In addition to burn severity, wildfire perimeter delineations as conducted by MTBS generally capture both the extent of contiguous live-forest edges as well as interior “unburned” live-forest islands (i.e., fire refugia) one-year post-fire (Picotte et al. 2020).

2.2. Imagery classification and accuracy assessment

We used paired high-resolution satellite images and an imagery classification scheme to detect and quantify the extent of conifer tree cover loss (mortality) within each wildfire perimeter boundary between 1- and 5-years post-fire. Several freely available, high-resolution imagery products were pre-considered to quantify tree cover change at

roughly the tree level (1-5m crown diameter; Hart and Veblen 2015), including the National Aerial Imagery Program (NAIP; USDA 2020) and Planet RapidEye (Planet Team 2020) satellite products, which are useful for making ecological interpretations about fine-scale processes (e.g., seed dispersal from isolated, undetected trees; Coop et al. 2019). Beginning in 2009, both NAIP and RapidEye imagery include near-infrared (NIR) spectral bands that are advantageous for accurately detecting vegetation cover and change, yet each imagery product exhibits different spatial and temporal resolutions, as well as different systematic geometric distortions. For the purpose of accurately and consistently detecting tree cover change between two images over large spatial extents and across a broad range of geographies, we hypothesized that RapidEye imagery would reduce classification error relative to NAIP due to (1) minimized geometric distortions across paired images (i.e., fewer shadows and terrain-related distortions), (2) substantially higher temporal resolution of the imagery (~7-14 days vs. 1-3 years), and (3) the reduction of spectral and spatial heterogeneity of pixels at the 5m vs. 1m grain, respectively. Based on these technical differences, we quantified post-fire delayed tree mortality patterns using RapidEye imagery at a 5m spatial resolution (i.e., the tree- or several aggregated trees-level) in this study; we acknowledge that the presence of small, isolated trees may go undetected at the chosen 5m spatial resolution (Walker et al. 2019).

RapidEye satellite images were obtained for each wildfire perimeter 1- and 5-years post-fire using several criteria to minimize potential geometric and atmospheric distortions in selected image pairs. We used a < 5% cloud and smoke cover filter to minimize atmospheric distortions and targeted imagery dates near the summer solstice in

the northern hemisphere, as available, to further minimize potential geometric distortions. Specifically for wildfire perimeters in the S. Rockies ecoregion, we considered imagery dates prior to the summer solstice, as necessary, to minimize the greening effect of angiosperms during the mid-late summer monsoon period. For each set of paired images, we chose dates that were within one month of each other to minimize geometric and phenological differences between images. Extracted, pre-processed surface reflectance images were then clipped to the extent of each fire perimeter delineation; any areas within each fire perimeter boundary that were reburned by additional fire(s) between 1- and 5-years post-fire were removed from the study.

Due to high variability of spectral signatures associated with conifer tree cover (i.e., species diversity) and other vegetation across ecoregions, we used an unsupervised classification workflow to classify delayed conifer tree mortality patterns among paired satellite images at the fire perimeter level, following simplified procedures outlined by Rodman et al. (2019; Fig. 3). Prior to classification, (1) paired images were checked for correct geospatial alignment and realigned if necessary. (2) The normalized differenced vegetation index (NDVI) was calculated for the one-year post-fire image and used to separate vegetated areas from non-vegetated, and (3) the red and near-infrared (NIR) bands were used to separate conifer tree cover from angiosperms by visually assessing iso-cluster maximum likelihood classifications of the imagery at each step. (4) Each 5-year post-fire image was then cropped to the extent of conifer tree cover in the 1-year post-fire classified image to minimize classification confusion associated with the regrowth of vegetation over time. Finally, (5) steps 2 and 3 were repeated to classify

remaining conifer tree cover in the clipped 5-year post-fire image. This workflow resulted in classified 5-year post-fire images with three possible categorical values: (1) non-conifer tree cover (i.e., angiosperm cover or non-vegetated), (2) live conifer tree cover (i.e., fire refugia and live forest edges), and (3) delayed mortality of conifer tree cover. We classified post-fire delayed mortality as occurring when individual pixels shifted from live conifer tree cover 1-year post-fire to non-conifer tree cover 5-years post-fire (Fig. 3).

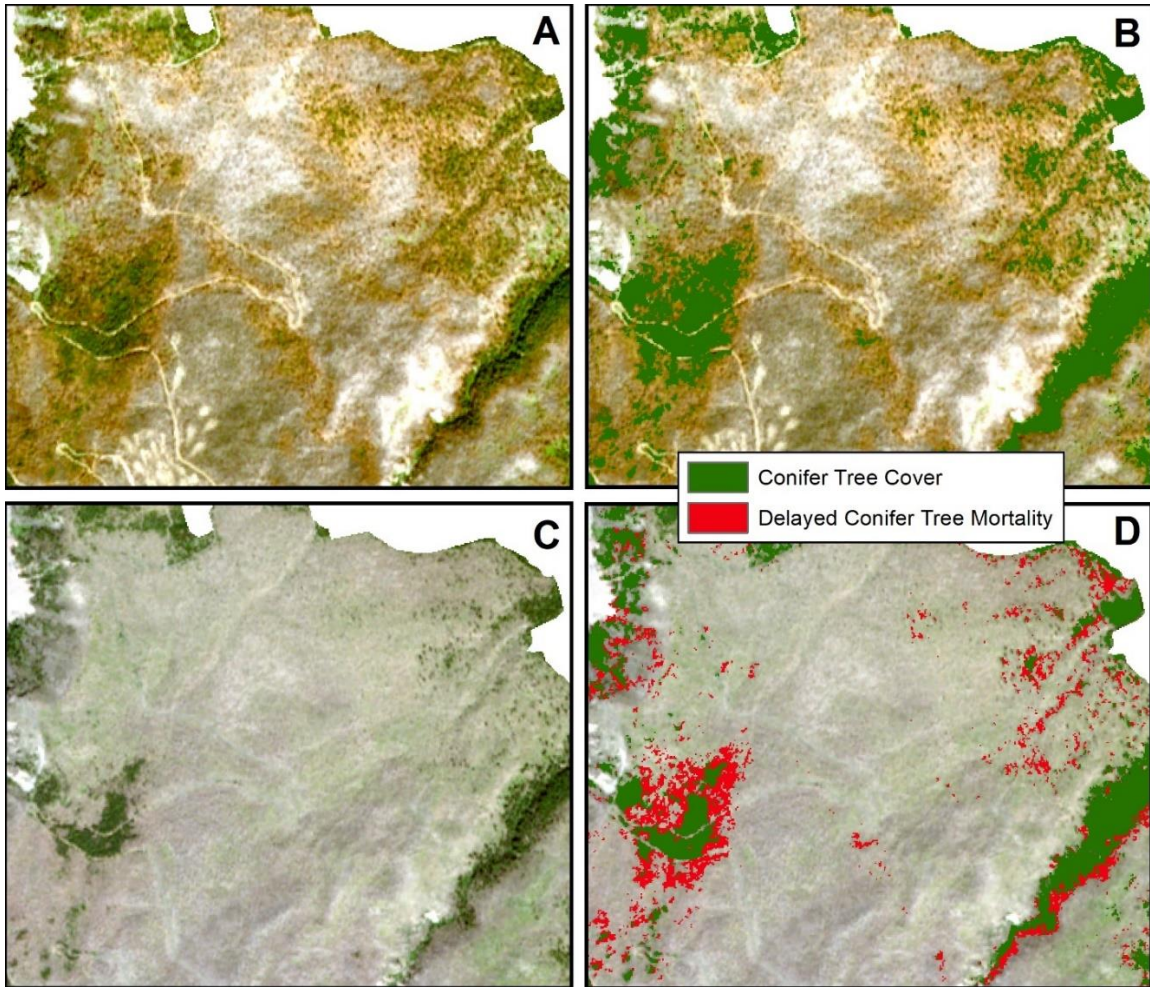


Figure 3. An example of the post-fire delayed tree mortality imagery classification workflow. (A) The 1-year post-fire satellite image cropped to the fire perimeter boundary, (B) the classification of conifer tree cover 1-year post-fire, (C) the 5-year post-fire satellite image clipped to the fire perimeter boundary, and (D) the classification of conifer tree cover and delayed tree mortality (i.e., loss of tree cover) between 1- and 5-years post-fire.

We used manual photointerpretation of reference high-resolution aerial imagery (NAIP; 1m), as available, to conduct an accuracy assessment of the imagery classification workflow. Because NAIP imagery was not available for every study fire perimeter during both 1- and 5-year post-fire periods, we conducted accuracy assessments at the ecoregion level by aggregating classified fire perimeters that had NAIP imagery available during both 1- and 5-year post-fire temporal periods for the Cascades (n=6), N. Rockies (n=7),

and S. Rockies (n=6). To evaluate the classification accuracy of the 1- and 5-year post-fire images within each ecoregion (i.e., six assessments total), we used a stratified random sampling design with equal probability to generate 500 accuracy assessment points per image (Congalton 1991; Rodman et al. 2019). At each accuracy assessment point location, manual photointerpretation of the pixel intersecting the point was used to assign the reference point a value of either non-conifer tree cover, live conifer tree cover, or in the case of the five-year post-fire image, delayed tree mortality by referencing both the 1- and 5-year post-fire NAIP images, respectively (Olofsson et al. 2014). Confusion matrices were generated for each classified image to compare and assess the agreement between RapidEye imagery classifications and conditions observed in the reference NAIP imagery. Imagery classification accuracy varied by post-fire temporal period and ecoregion, with overall classification accuracy ranging 0.86 – 0.94 (Appendix: Supporting tables; Table 2).

2.3. Changes in seed source availability

To evaluate potential losses in seed source availability (i.e., proximate live seed-bearing conifer trees) among non-forested areas (severely burned or otherwise) due to post-fire delayed tree mortality patterns, we calculated and differenced two seed source availability metrics using values derived from the 1- and 5-year post-fire classified images. For all pixels contained within wildfire perimeters classified as non-conifer tree cover 1-year post-fire, (1) Euclidian distance to the nearest seed source (i.e., pixel classified as live conifer tree cover) and (2) seed source density (i.e., percentage of a moving window radius occupied by live conifer tree cover) were calculated using the

Near and Focal Statistics tools in ArcGIS (ESRI 2020), respectively. We excluded all areas from this analysis within fire perimeters that contained ephemeral or persistent waterbodies where conifer seedling establishment could not feasibly occur. When calculating seed source density, we used a 150m radius moving-window size to match the range at which the majority of seeds are wind-dispersed by obligate seeding conifer species within our study areas (McCaughey et al. 1986; Burns and Honkala 1990), and subsequently where the majority of natural post-fire tree establishment may occur (Kemp et al. 2016; Coop et al 2019; Stevens-Rumann and Morgan 2019; Busby et al. 2020). To identify whether delayed tree mortality patterns and subsequent losses in seed source availability were different between ecoregions, we used the Wilcoxon signed-rank test, suitable for non-normal distributions with unequal sample sizes and variance, to test for significant statistical differences ($\alpha = 0.05$) between ecoregions.

2.4. Modelling drivers of post-fire delayed tree mortality

We used logistic boosted regression tree (BRT) models with a Bernoulli distribution to model the importance of, interactions, and flexible (i.e., non-linear) relationships between a suite of predictive variables and post-fire tree mortality, as derived from the classified satellite imagery. Four BRT models were developed to identify potential differences in drivers across individual and combined ecoregions. To increase model convergence and reduce computation time, we used a subsampling scheme of the total raster dataset ($n > 1,000,000$ pixels) spanning all study wildfire perimeters to reduce the sample size of modelling data. First, using ArcGIS, we converted the 5m resolution classified satellite imagery with a binary response (i.e., tree

mortality ~or~ no tree mortality 1- to 5-years post-fire) from raster into a point shapefile. Second, to minimize potential spatial autocorrelation between points, we applied a 50m systematic spatial buffer to all datapoints across fire perimeters. Third, we drew a 10% stratified random sample from all spatially buffered datapoints, stratifying by fire perimeter identity to ensure the modelling data were represented proportionally across all study fire perimeters, in R (R Core Team 2020). We then modelled the response in delayed mortality to nine predictive variables in each ecoregion BRT model, which were associated with four groups of drivers that have been mechanistically linked with hydraulic and physiological tree stress (Hood et al. 2018; Hood and Varner 2019; Fig. 1), and therefore are hypothesized to influence the probability of post-fire tree mortality: (1) burn severity and vegetation change one-year post-fire, (2) average (i.e., 30-yr normal) and post-fire climate moisture deficit, (3) soil water-holding capacity, and (4) topographic microclimate (Table 1). We extracted raster values associated with each predictive variable to the subsampled point data using spatial intersection between pixels and point data.

Table 1. A description of the spatially explicit predictive variables fit into boosted regression tree (BRT) models and the data sources and methods they were derived by.

| Type | Variable | Spatial Resolution | Description & Methodology | Units | Range |
|------------|---|---------------------|---|----------|--------------|
| Fire | RBR | 30m | The relativized burn ratio (RBR), a measure of burn severity calculated as the difference in vegetation cover between one-year pre-fire and one-year post-fire using Landsat imagery; Parks et al. 2014. Negative and positive values respectively indicate increases and decreases in vegetation cover relative to pre-fire imagery. | unitless | [-494 – 800] |
| | Average annual CMD | Downscaled to point | 30-year (1981-2010) average annual climate moisture deficit (CMD), the difference between reference evaporative demand and precipitation. Derived from the ClimateNA application (Wang et al. 2016) using point elevation to downscale values from 800m gridded PRISM data. | mm | [51 - 917] |
| | Post-fire deviation from average annual CMD | Downscaled to point | The percent deviation from the average annual climate moisture deficit (CMD) observed during the one- to five-years post-fire period (i.e., deviation from normal conditions). | % | [-20 - 119] |
| Soils | Soil available water capacity | 30m | The maximum volume of plant available water in the upper 150cm of soils. Extracted from the USDA-NRCS SSURGO database. | mm | [9 - 273] |
| | Elevation | 10m | Elevation above mean sea-level; derived from a 10m digital elevation model (DEM). | m | [510 - 3427] |
| | Slope | 10m | The angle of the dominant hillslope; derived from a 10m digital elevation model (DEM). | ° | [0 - 65] |
| Topography | HLI | 10m | The heat load index (McCune and Keon 2002), a topographic measure of incident solar radiation; derived from a 10m digital elevation model (DEM). | unitless | [35 - 97] |
| | TPI | 10m | The topographic position index (Weiss 2001), a measure of landscape slope position; derived from a 10m digital elevation model (DEM) and calculated using 300m and 750m moving-window radii (i.e., spatial scales). Negative and positives values respectively indicate concave and convex topographic positions. | unitless | [-100 – 100] |

Each stratified subsample of data was then fit into one of four ecoregion-based BRT models using the *gbm* package in R (Greenwell et al. 2020). All models were fit with a bag fraction setting of 0.5 to introduce stochasticity, a learning rate of 0.01 to ensure at least 1000 trees were fit in each model, and a tree complexity of 5 to allow for sufficient variable interactions (Elith et al. 2008). Since BRTs are a stochastic modelling technique, we fit 10 iterations of each model and reported results from the best performing model iteration. We assessed BRT model performance by calculating and reporting the Area Under Curve-Receiver Operator Characteristic (AUC-ROC) for both the training dataset and using 10-fold cross-validation (Elith et al. 2008).

3. Results

3.1. Fire characteristics and post-fire delayed tree mortality

Relativized burn-severity trends (i.e., percent high [RBR > 298], moderate [RBR <298 & >130], and low [RBR <130 & >35]; Parks et al. 2014; Fig. 4A) indicated that on average the Cascades experienced the largest proportion of high-severity fire, followed by the N. Rockies, and S. Rockies, respectively (~50%; ~40%; ~35%); the proportion of moderate severity fire was similar between ecoregions (~30%). Mean fire size and the ratio of live conifer tree cover to non-conifer tree cover 1-year post-fire (Fig. 4B) was similar for the Cascades (~5,700 ha; 31%) and N. Rockies (~6,700 ha; 35%) and distinctly different for the S. Rockies (~27,700 ha; 8%), especially among the three largest fires occurring in that ecoregion: Las Conchas (~140,000 ha; 4%), High Park (~75,000 ha; 4%), and Waldo Canyon (~20,000 ha; 7%). The loss of live conifer tree

cover between 1- and 5-years post-fire, i.e., the rate of post-fire delayed tree mortality, reached up to ca. 25% at the fire perimeter level, ranging widely especially in the N. and S. Rockies, from ca. 5 – 25% (Fig. 4C). At the ecoregion level, however, mean and median percent delayed mortality patterns were similar between ecoregions with no statistical differences detected; ca. 14% and 13% for the Cascades, ca. 12% and 13% for the N. Rockies, and ca. 14% and 16% for the S. Rockies, respectively.

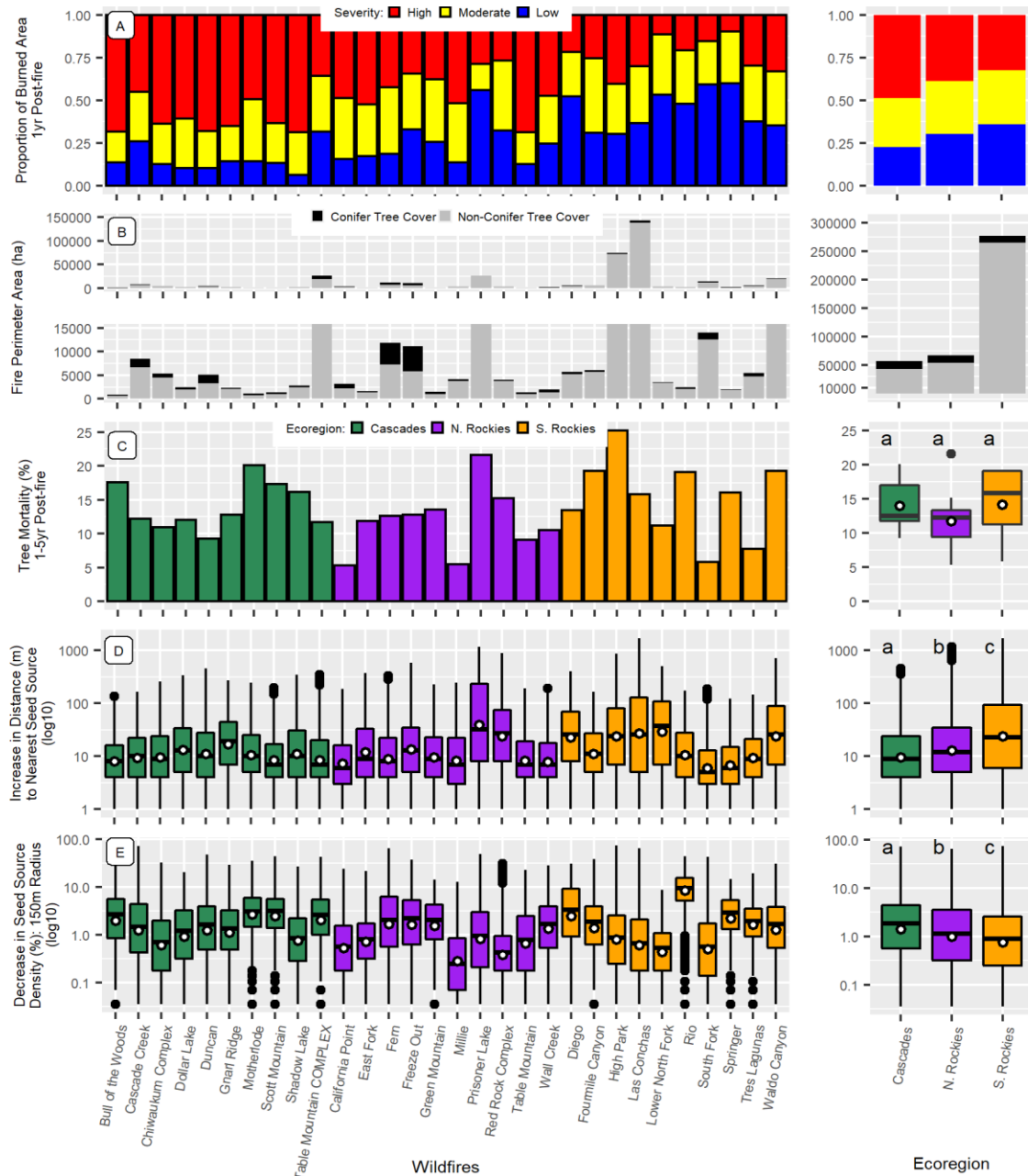


Figure 4. Summary statistics illustrating burn severity, size, post-fire delayed tree mortality, and changes in seed source availability at the fire perimeter and ecoregion levels (Cascades: green, N. Rockies: purple, and S. Rockies: orange). White dots within boxplots indicate mean value. (A) The proportion of burned area represented by high, moderate, and low burn severity (RBR) classes derived from Landsat imagery one-year post-fire, (B) total fire perimeter size and distribution of conifer vs. non-conifer cover one-year post-fire, (C) the percent change in conifer cover between 1- and 5-years post-fire (i.e., delayed tree mortality), (D) the change in distance to the nearest seed source (i.e., conifer cover) for non-forested pixels between 1- and 5-years post-fire, and (E) the percent change in seed source density (i.e., conifer cover within a 150m radius) for non-forested pixels between 1- and 5-years post-fire. Dissimilar letters (a, b, c) in ecoregion panels C, D, E indicate statistical differences in metric distributions between ecoregions.

3.2. Losses in seed source availability

We evaluated changes in the proximity to and nearby density (i.e., percent cover within a 150m radius) of live conifer trees (i.e., seed-bearing trees contributing to post-fire forest recovery) to non-forested areas within fire perimeters, due to delayed tree mortality patterns between 1- and 5-years post-fire (Fig. 4D, E). At the ecoregion level, the S. Rockies (43m; 1685m) experienced the largest mean and maximum increases in distance to the nearest seed source due to delayed tree mortality patterns, followed by the N. Rockies (15m; 1180m) and Cascades (8m; 460m). Contrary, mean decreases in seed source density due to delayed tree mortality followed the opposite trend by ecoregion, with the Cascades (3%) experiencing the largest decreases, followed by the N. Rockies (2%) and S. Rockies (1%); maximum values were 71%, 65%, and 73% for each ecoregion, respectively. Wilcoxon signed-rank tests indicated that increases in distance to seed source and reduction in seed source density due to delayed mortality patterns were statistically different across ecoregions ($p < 0.05$).

3.3. Drivers of post-fire delayed tree mortality

Among the all ecoregions combined BRT model, burn severity (RBR; derived from 30m Landsat imagery one-year post-fire) was the most important variable in predicting post-fire delayed tree mortality, followed by elevation, soil available water capacity, then average and post-fire climate moisture deficit (CMD; Fig. 5A, B, C, D, F). Burn severity, followed by elevation, were also the most important predictors of delayed mortality among individual ecoregion models, except for soil available water capacity in the Cascades (Fig. 5A, D, F). Overall, topographic variables (i.e., slope, topographic

position index, heat load index) were less important predictors of delayed mortality than burn severity and climate. Although the relationships of variables followed similar trends across individual ecoregion models, there were notable differences associated with the strength and non-linearity of responses. For the S. Rockies specifically, burn severity had the strongest effect on delayed tree mortality probability relative to other ecoregion models and exhibited a non-linear, u-shaped response centered near an RBR value of 0 (i.e., no change in vegetation cover; Fig. 5A). We also observed u-shaped responses in most ecoregion models associated with elevation, CMD (post-fire deviation from and average annual), and topographic heat load (HLI) (Fig. 5B, C, D, I). Landscape position (TPI) calculated at finer (300m), and coarser (750m) scales exhibited opposite responses, where at a finer scale convex topography (e.g., ridges) increased delayed tree mortality probability, except in the N. Rockies, and at a coarser scale convex topography (e.g., drainages) increased delayed tree mortality probability (Fig. 5G, H). The predictive accuracy (i.e., cross-validated AUC) among ecoregion BRT models was overall fair, ranging from 0.72 – 0.76; the S. Rockies model exhibited the best predictive accuracy (0.76) and the Cascades the worst (0.72; Appendix: Supporting tables; Table 4).

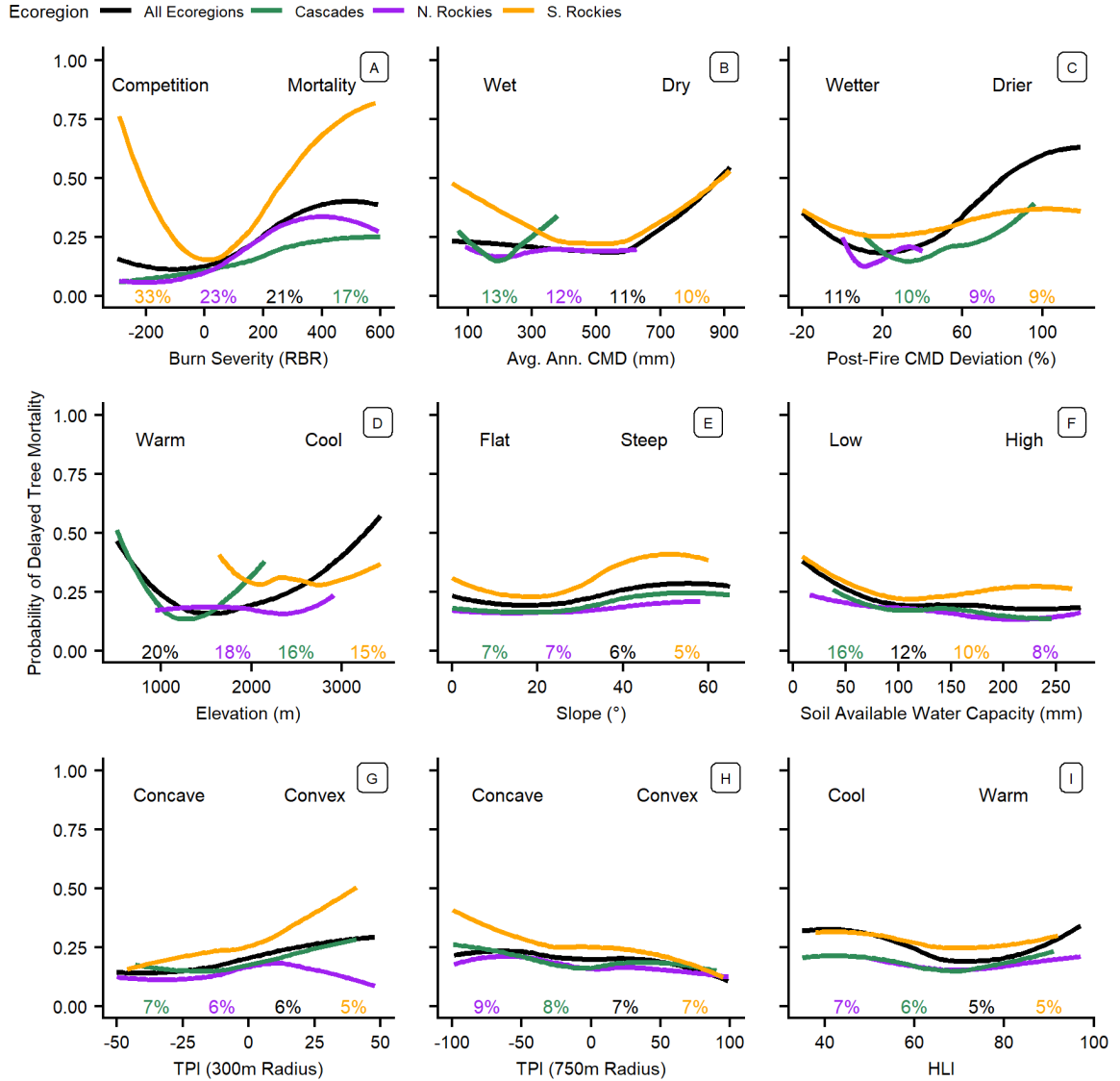


Figure 5. Partial dependence plots showing the importance of and flexible relationships among variables as predictors of delayed tree mortality probability between 1- and 5-years post-fire. Colored response curves and variable importance percentages in each panel are associated with ecoregion BRT model outputs (All Ecoregions [black], Cascades [green], N. Rockies [purple], S. Rockies [orange]). (A) Burn severity (RBR) derived from 30m Landsat imagery one-year post-fire, (B) 30-year (1981-2010) average annual climate moisture deficit (CMD), (C) percent deviation from average annual CMD during the post-fire period, (D) mean elevation above sea level, (E) angle of the dominant hillslope, (F) maximum soil water capacity available to vegetation, (G, H) the topographic position index (TPI) calculated at fine (300m) and coarser (750m) spatial scales, and (I) the heat load index (HLI). See Table 1 for a full description of predictive variables.

3.4. Interactions between burn severity and climate moisture deficit

We observed the strongest interactions among variables between burn severity (RBR) and two measures of climate moisture deficit (CMD) to vegetation, average annual CMD and post-fire deviation from average annual CMD (Fig. 6). These interactions, however, were weak in the Cascades model relative to the other ecoregion models. Interaction values and thresholds varied by ecoregion model, but generally, when RBR values were ca. greater than 200 (i.e., moderate- to high-burn severity), high values in post-fire deviation (ca. > 50%) and average annual (ca. > 750mm) CMD substantially increased delayed tree mortality probability, illustrating a non-linear compound stress effect. For the S. Rockies specifically, delayed tree mortality probability was more complex, as it increased substantially in response to RBR values at both ends of its range, i.e., when greater than ca. 200mm and also when less than ca. -150mm (i.e., increased vegetation cover relative to pre-fire conditions; Fig. 6D).

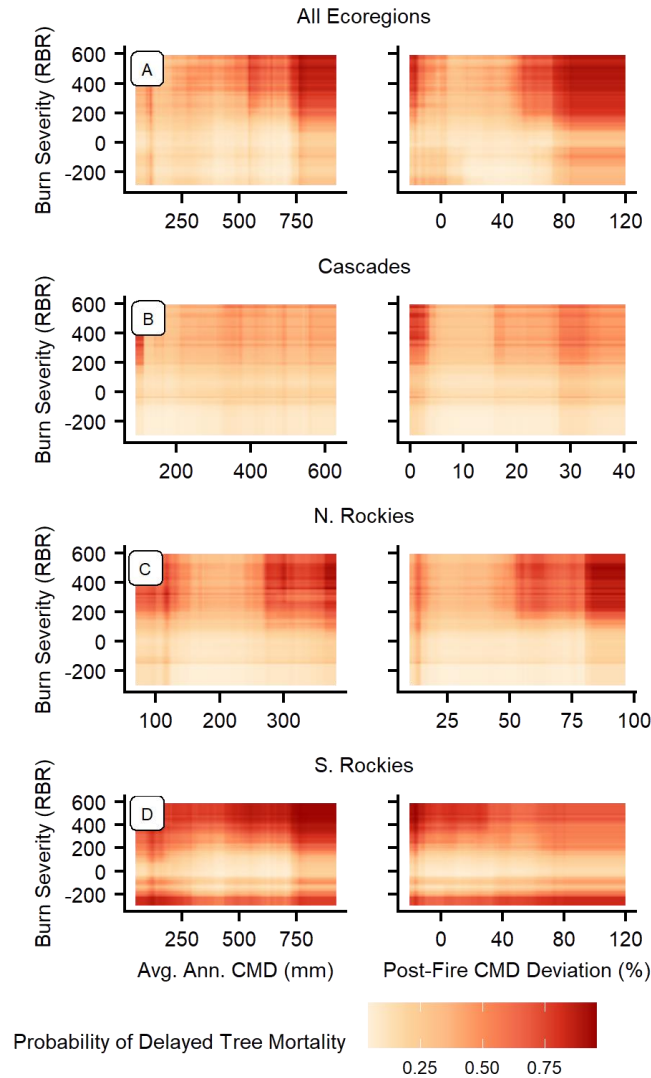


Figure 6. Changes in the probability of post-fire delayed tree mortality at the ecoregion level due to interactions between 1-year post-fire burn severity (RBR) and two measures of climate moisture deficit (CMD), 30-year (1981-2010) average annual CMD and percent deviation from average annual CMD during the post-fire period. Darker red shading indicates increased probability of delayed tree mortality due to variance interactions.

4. Discussion

As sources of seed, fire refugia and live forest edges enhance conifer forest resilience and recovery after large and severe wildfires, but their persistence over time may be limited. Our study suggests that delayed conifer tree mortality between 1- and 5-years post-fire occurs at large scales and ecologically important rates across a range of

conifer forest types in the western US. Further, our results indicate that delayed tree mortality patterns can meaningfully reduce seed source availability necessary for post-fire forest recovery, reducing long-term forest resilience to large high-severity fire(s). This effect may be particularly acute within environments where tree extent and density are already low, and temporal opportunities for tree establishment are infrequent to semi-infrequent, such as within dry conifer forests. Ultimately, our work highlights why extended temporal assessments of burn severity and tree mortality beyond one-year post-fire should be increasingly considered in ecological and management frameworks, especially considering observed and forecasted increases in high severity fire, droughts, and compound disturbances that threaten forest resilience.

4.1. Variability in delayed tree mortality rates at fire and ecoregion scales

We observed that rates of post-fire delayed tree mortality were highly variable at the fire perimeter level and much less so at the ecoregion level, indicating that patterns in this fire-mediated process vary with scale (Agee 1998; Turner and Cardille 2007; Kane et al. 2017). At the fire perimeter level, delayed tree mortality between 1- and 5-years post-fire ranged from 5% to 25%, similar to rates documented by previous field studies focused on post-fire tree mortality patterns among plots nested within a single fire perimeter, across a variety of conifer forest types (ca. 0 – 46% between 1- and 2- to 7-years post-fire; Brown et al. 2013; Whittier and Gray 2016; Rocceforte et al. 2018; Jeronimo et al. 2020). When patterns were analyzed at the ecoregion level, however, mean delayed tree mortality rates were relatively similar between ecoregions (ca. 12-14%) and the forest types included in this study. Particularly with regard to differences in

forest type, this result contradicts prior conceptual understandings that fire-related tree mortality should be comparatively immediate (i.e., 1-year post-fire) within upper-montane and subalpine forests, relative to dry conifer forests, due to substantial differences in the expression of fire-resistance and drought-tolerance among dominant species (Agee 1993; Hood et al. 2018) and post-fire competition (see below). Although we did not quantify mortality rates on an annual basis up to five years post-fire, our results support previous studies' findings that fire-related delayed tree mortality may occur at ecologically meaningful rates beyond 1-year post-fire across a variety of forest types (Whittier and Gray 2016; Rocceforte et al. 2018; Jeronimo et al. 2020), including those dominated by fire-sensitive species (e.g., Pacific-silver fir; Brown et al. 2013).

Variability in the size of fire perimeters and the proportion of forested to non-forested cover within perimeters may cause distinctly different ecological impacts between ecoregions and forest types, even when mean post-fire delayed mortality rates are similar. The S. Rockies exhibited substantially greater mean fire perimeter size compared to the Cascades and N. Rockies, primarily due to the comparatively large Las Conchas (~140,000ha) and High Park (~75,000ha) fires included in our study. Further, the ratio of forested to non-forest cover at 1-year post-fire was much lower in S. Rockies fire perimeters relative to the Cascades and N. Rockies (ca. 8%, relative to 31% and 35%, respectively), possibly due to higher burn severity (but see Fig. 4A), lower pre-fire forest density, and/or pre-fire forest density not captured by the 5m resolution RapidEye imagery (Walker et al. 2019). Functionally, a mean delayed mortality rate of 14% may compound already critically low post-fire forest cover within dry conifer forests of the S.

Rockies (e.g., Las Conchas fire, ~140,000ha perimeter with only ~5,000ha of remaining forest 1-year post-fire), significantly affecting species that rely on, and ecological processes that are connected to, conifer forest density and extent (Nimmo et al. 2019; Andrus et al. 2021; Driscoll et al. 2021), relative to upper-montane and subalpine forests in the Cascades and N. Rockies. Over the last two decades, substantial increases in large high-severity fires have already initiated large scale losses of dry conifer forest cover within the southwestern U.S. (Coop et al. 2020; Stevens et al. 2021) and losses are anticipated to continue increasing, especially in lower-elevation trailing edge forests under a warming climate (Parks et al. 2019).

4.2. Delayed mortality and post-fire forest recovery

Among forests dominated by non-serotinous obligate seeding conifers, the spatial extent, configuration, and structural attributes (e.g., size, age, composition; Agee 1993) of live trees within post-fire landscapes, over time, strongly affect seed dispersal patterns and thus, conifer forest recovery and long-term persistence (Downing et al. 2019; Coop et al. 2020). Continuous reductions in seed rain reaching severely burned patch interiors, due to delayed tree mortality over time, may exacerbate already critically limited seed source availability, preventing or delaying forest recovery. Among non-forested areas (pixels) within our study wildfire perimeters, we assessed two spatial measures of seed source availability change due to post-fire delayed tree mortality that are conceptually understood by and practically relevant to managers: distance to nearest seed source and proximate (i.e., 150m radius) seed source density (Stevens-Rumann and Morgan 2019).

Between 1- and 5-years post-fire, proximate seed source density among non-forested areas changed relatively little; mean percent changes ranged ca. 0.5 – 10% and 1 – 2% at the fire perimeter and ecoregion levels, respectively. Changes in seed source density were greatest in the Cascades, followed by the N. Rockies, and S. Rockies, following expected differences in pre-fire forest density between ecoregions and forest types (Agee 1993; Baker 2009). Mean increases in distance to nearest seed source for non-forested areas ranged ca. 8 – 55m among fire perimeters, with relatively large increases observed at the ecoregion level in dry conifer forests of the S. Rockies (43m) relative to upper-montane and subalpine forests in the Cascades (8m) and N. Rockies (15m). These larger mean increases in distance observed in dry conifer forests of the S. Rockies may speak to inherently lower pre-fire forest densities, larger fire perimeters, and/or larger high-severity patch sizes relative to the other ecoregions and forest types analyzed in this study. Another possible explanation may be that isolated trees and small fire refugia islands experienced delayed mortality at a higher rate in the S. Rockies relative to the Cascades and N. Rockies. Functionally, the death of isolated trees and small refugia islands within large patches of high-severity fire would minimally affect changes in proximate seed source density, but greatly increase distance to nearest seed source. This would occur by shifting the location of the nearest seed source(s) from nearby fire refugia over to potentially distant live forest edges.

Based on these results, post-fire delayed tree mortality patterns may have particularly negative effects on forest recovery among dry conifer forests in the S. Rockies, and potentially elsewhere, due to ecologically important reductions in seed

source availability and increasingly limited temporal opportunities for successful seedling establishment in these climatically dry environments (Stevens-Rumann et al. 2018; Davis et al. 2020; Kemp et al. 2019; Rodman et al. 2020). If climatic conditions are not favorable for tree establishment within the first several years post-fire, severely burned forest patches may (1) lose critical fire refugia before those seed sources can promote seedling establishment and (2) establish seedlings early enough to successfully compete with recovering understory vegetation (Tepley et al. 2018). Thus, prolonged post-fire conifer establishment failure, exacerbated by long-term losses in seed source availability via delayed tree mortality patterns, may continue to promote post-fire conversion of dry conifer forests in the western US.

4.3. Drivers of delayed tree mortality and interactions

To explore potential drivers of post-fire delayed tree mortality patterns at large scales, we modelled statistical relationships between a suite of spatially explicit predictive variables hypothesized to influence delayed tree mortality probability (i.e., fire injuries, competition, climate, and environment), and our tree mortality classifications derived from high-resolution satellite imagery. Across all ecoregion-specific and combined statistical models, 1-year post-fire burn severity (i.e., vegetation change; RBR) derived from moderate spatial resolution imagery (Landsat; 30m) was the most important predictor of delayed tree mortality probability. Probability of delayed tree mortality increased non-linearly with increasing RBR, but this relationship was uniquely strong in dry conifer forests of the S. Rockies. Further, and unlike other ecoregion models, increased vegetation cover (i.e., recovery) relative to pre-fire conditions (i.e., $RBR < 0$)

dramatically increased tree mortality probability in the S. Rockies. Intuitively, remotely sensed patch-level burn severity may be a strong proxy for fire patterns and thus, the severity of fire injuries sustained by individual surviving trees within a patch (Key and Benson 2006). In mid- to high-elevation forest plots in the Warner Creek fire of the Western Cascades, Brown et al. (2013) observed a similar positive linear relationship between the extent of tree mortality 1-year post-fire (i.e., plot-level burn severity) and the delayed mortality rate of remaining live trees over time. Long-term tree survival is negatively affected by increasing severity of sustained fire injuries, where injuries lower the physiological capacity of affected trees to survive baseline environments stressors (e.g., temperature and precipitation) as well as future disturbances like insect infestation, pathogens, fire, and drought (Hood et al. 2018; Hood 2021). In climatically moisture-limited environments, such as those synonymous with dry conifer forests, competition with recovering vegetation for water resources may compound the effect of fire injuries (e.g., van Mantgem et al. 2018; 2020), substantially increasing mortality probability relative to forests with greater annual moisture availability (e.g., upper-montane and subalpine forests).

Average and post-fire climatic moisture deficits, topography, and soils also play important roles in influencing environmental conditions that facilitate vegetation survival and post-fire recovery (Stevens-Rumann and Morgan 2019). Our statistical models indicated these factors did indeed play important, yet variable roles in influencing post-fire delayed tree mortality patterns. As hypothesized, we generally observed that factors which functionally decreased moisture availability to vegetation increased delayed tree

mortality probability (e.g., van Mantgem 2013), such as 30-year mean and post-fire climate moisture deficit (CMD), which also exhibited the strongest interactions with burn severity. Several factors (e.g., elevation, CMD, heat load index) exhibited non-linear U-shaped responses, however.

U-shaped responses, along a gradient of elevation for example, may speak to leading- and trailing-edge tree species distributions, where tree species and or general populations at the edge of their environmental tolerance may be especially vulnerable to fire effects, moisture limitations, or both, based on local adaptation and their respective functional traits (Agee 1993). Trees in low-elevation environments may exhibit higher fire resistance, but experience greater moisture stress; alternatively, trees in high-elevation environments may exhibit lower moisture stress, but lower fire resistance (Agee 1993; Niinemets and Valladares 2006; Stevens et al. 2020). Meanwhile, environments exhibiting intermediate conditions (e.g., mid-elevation) may include high levels of species diversity (i.e., the mid-elevation bulge; Mutke 2011), conferring greater resilience to both fire effects and moisture stress via increased collective diversity of functional traits among present species. As the climate continues to warm, trailing edge forests - often represented by dry conifer forests in the western U.S., may be especially vulnerable to fire (Parks et al. 2019) and/or climate (Kroiss and HillResLambers 2015) induced ecosystem conversions that may be exacerbated by post-fire delayed tree mortality patterns.

4.4. Future work

Considering the predictive accuracy of our statistical models was only fair (cross-validated AUC = 0.72-0.76), future studies would benefit from modelling relationships with additional conceptually influential factors we did not account for, such as pre- and post-fire compound disturbance effects (e.g., insect and pathogen outbreak) including pre-fire drought (e.g., van Mantgem et al. 2018; 2020), fine-grain tree species composition, and post-fire competition dynamics between trees and other functional vegetation types. Further, analyzing patterns using time-series data (i.e., more than two images) may better capture (1) temporal patterns of post-fire delayed tree mortality, (2) impacts of compound disturbance and vegetation competition dynamics (e.g., Vanderhoof et al. 2018; Bright et al. 2020; Rodman et al. 2021), and (3) help minimize misclassification errors (e.g., Reis et al. 2020). Finally, comparison of delayed tree mortality patterns across multiple imagery products with dissimilar resolution qualities could additionally provide the means for multi-scalar analyses of drivers and patterns (Warner et al. 2009; Wulder et al. 2009). While relatively slow growing, obligate seeding conifer forests are an ideal subject for quantifying post-fire delayed tree mortality patterns (i.e., recovery is slow to detect; Key 2006), ecosystems whose pre- and post-fire dominant species exhibit alternative functional traits, such as fast growing and/or resprouting angiosperms, may be less suited to extended temporal assessments of fire-related tree mortality patterns (Morgan et al. 2015). Thus, intimate knowledge of dominant species' life history traits should first guide the development and feasibility of any extended temporal assessment of post-fire delayed mortality patterns.

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7. Appendix: Supporting tables

Table 2. Confusion matrix of the satellite imagery accuracy assessment.

| Ecoregion | Imagery Period | Producer's Accuracy | | | User's Accuracy | | | Overall Accuracy |
|------------|-------------------|---------------------|------------------------|--------------------------------|--------------------|------------------------|--------------------------------|------------------|
| | | Conifer Tree Cover | Non-Conifer Tree Cover | Delayed Conifer Tree Mortality | Conifer Tree Cover | Non-Conifer Tree Cover | Delayed Conifer Tree Mortality | |
| Cascades | 1-year post-fire | 0.96 | 0.90 | ~ | 0.89 | 0.96 | ~ | 0.93 |
| Cascades | 5-years post-fire | 0.85 | 0.90 | 0.83 | 0.80 | 0.94 | 0.84 | 0.86 |
| N. Rockies | 1-year post-fire | 0.86 | 0.91 | ~ | 0.92 | 0.85 | ~ | 0.89 |
| N. Rockies | 5-years post-fire | 0.86 | 0.91 | 0.84 | 0.81 | 0.90 | 0.90 | 0.87 |
| S. Rockies | 1-year post-fire | 0.93 | 0.95 | ~ | 0.95 | 0.93 | ~ | 0.94 |
| S. Rockies | 5-years post-fire | 0.87 | 0.91 | 0.92 | 0.92 | 0.94 | 0.84 | 0.90 |

Table 3. Fire perimeter attributes, post-fire tree cover extent, and estimated post-fire delayed tree mortality extent.

| ID | Ecoregion | State | Fire Name | Year | Fire Perimeter (ha) | Tree Cover 1yr post-Fire (ha) | Tree Cover 5yr post-Fire (ha) | Delayed Tree Mortality (ha) |
|----|------------|-------|------------------------|------|---------------------|-------------------------------|-------------------------------|-----------------------------|
| 1 | Cascades | WA | Cascade Creek | 2012 | 8501 | 1,780 | 1,563 | 217 |
| 2 | Cascades | WA | Table Mountain Complex | 2012 | 26687 | 7451 | 6,578 | 873 |
| 3 | Cascades | WA | Duncan | 2014 | 5142 | 1841 | 1,670 | 171 |
| 4 | Cascades | WA | Chiwaukum Complex | 2014 | 5295 | 784 | 698 | 86 |
| 5 | Cascades | OR | Bull of the Woods | 2010 | 924 | 296 | 244 | 52 |
| 6 | Cascades | OR | Scott Mountain | 2010 | 1371 | 306 | 253 | 53 |
| 7 | Cascades | OR | Shadow Lake | 2011 | 2812 | 298 | 250 | 48 |
| 8 | Cascades | OR | Dollar Lake | 2011 | 2455 | 517 | 455 | 62 |
| 9 | Cascades | OR | Gnarl Ridge | 2008 | 2336 | 243 | 212 | 31 |
| 10 | Cascades | OR | Motherlode | 2011 | 1178 | 393 | 314 | 79 |
| 11 | N. Rockies | WY | Red Rock Complex | 2011 | 3989 | 204 | 173 | 31 |
| 12 | N. Rockies | ID | Green Mountain | 2012 | 1438 | 370 | 320 | 50 |
| 13 | N. Rockies | ID | Fern | 2012 | 11806 | 4494 | 3,928 | 566 |
| 14 | N. Rockies | ID | California Point | 2013 | 3179 | 960 | 909 | 51 |
| 15 | N. Rockies | ID | Freeze Out | 2012 | 11130 | 5347 | 4,664 | 683 |
| 16 | N. Rockies | MT | Prisoner Lake | 2012 | 26660 | 222 | 174 | 48 |
| 17 | N. Rockies | MT | East Fork | 2012 | 1650 | 269 | 237 | 32 |
| 18 | N. Rockies | MT | Wall Creek | 2012 | 2013 | 687 | 615 | 72 |
| 19 | N. Rockies | MT | Millie | 2012 | 4126 | 312 | 295 | 17 |
| 20 | N. Rockies | MT | Table Mountain | 2009 | 1361 | 309 | 281 | 28 |
| 21 | S. Rockies | CO | Waldo Canyon | 2012 | 20277 | 1265 | 1,021 | 244 |
| 22 | S. Rockies | CO | High Park | 2012 | 74532 | 2684 | 2,007 | 677 |
| 23 | S. Rockies | CO | Fourmile Canyon | 2010 | 6094 | 348 | 281 | 67 |
| 24 | S. Rockies | CO | Springer | 2012 | 1980 | 156 | 131 | 25 |
| 25 | S. Rockies | CO | Lower North Fork | 2012 | 3562 | 98 | 87 | 11 |
| 26 | S. Rockies | NM | South Fork | 2010 | 14011 | 1430 | 1,347 | 83 |
| 27 | S. Rockies | NM | Rio | 2010 | 2450 | 315 | 255 | 60 |
| 28 | S. Rockies | NM | Las Conchas | 2011 | 142934 | 5008 | 4,217 | 791 |
| 29 | S. Rockies | NM | Diego | 2014 | 5702 | 477 | 413 | 64 |
| 30 | S. Rockies | NM | Tres Lagunas | 2013 | 5458 | 752 | 694 | 58 |

Table 4. Sample size (n) and predictive performance (AUC) of the boosted regression tree (BRT) ecoregion models.

| BRT Ecoregion Model | Sample Size (n) | Training AUC | Cross-Validated AUC |
|---------------------|-----------------|--------------|---------------------|
| All Ecoregions | 21,547 | 0.86 | 0.74 |
| Cascades | 6,577 | 0.86 | 0.72 |
| N. Rockies | 5,997 | 0.86 | 0.74 |
| S. Rockies | 8,883 | 0.85 | 0.76 |

Chapter 3:

No facilitation necessary: climate and functional traits support early post-fire establishment and dominance by shade-tolerant conifers

Abstract

In the western US, shade-tolerant conifer species are commonly generalized as playing mid-to-late seral roles in forest recovery and succession after moderate to severe fire effects. This overgeneralization may be disproportionately highlighting the role of conifer species' shade-tolerance in determining early seral post-fire establishment responses, while discounting the role of other functional traits that contribute to those species' fire resilience, or post-fire recovery. To test whether early post-fire shade-tolerant conifer establishment and dominance varies in the western US, and if so, what biophysical variables drive variations in establishment and dominance, we aggregated early seral (< 30 years) post-fire conifer establishment responses after moderate to severe fire effects across multiple field studies, four montane ecoregions, and a wide range of biophysical site conditions. Further, we quantified functional traits conceptually related to fire resilience among species, including shade-tolerance, to investigate the influence of these traits on early seral establishment and dominance by shade-tolerant conifers. We observed evidence of strong early seral tree establishment and dominance patterns by shade-tolerant conifers across the western US, although substantial variability in responses occurred between ecoregions. Across ecoregions at the site-level, except in the S. Rockies, shade-tolerant conifer establishment and dominance was primarily driven by the interaction between summer climate moisture deficits and winter snowfall, where increasing snowfall ameliorated the negative impact of increasing moisture deficits.

Additionally, we found that species' shade-tolerance was an unimportant predictor of their early seral post-fire establishment and dominance. Our study demonstrates that conifer species' post-fire recovery responses can be understood across diverse environments via the collective expression of their functional traits, and that individual traits may be a poor reference of expected responses in isolation, such as shade-tolerance. Quantification of conifer species' functional traits, which contribute to fire resilience and resistance, may provide effective tools for testing and predicting species' persistence in response to present and changing fire patterns and climate conditions.

1. Introduction

In conifer dominated forests of the Western U.S., conifer tree species classified as shade-tolerant are commonly attributed with playing mid-to-late seral roles in post-disturbance recovery dynamics (i.e., secondary succession; Franklin and Dyreness 1973; Connell and Slatyer 1977; Pickett et al. 1987; Veblen 1992) after moderate to high severity disturbances, including wildfire. This general association has been heavily influenced by classical models of plant succession (e.g., relay and initial floristics; Clements 1916; Egler 1954) that argue shade-tolerant species abundance is initially low or absent post-disturbance, yet increases proportionally over time, thanks to environmental facilitation by shade-intolerant pioneer species (Bertness and Callaway 1994). Empirical evidence from modern post-fire forest regeneration studies across the Western U.S., however, provide a compelling narrative of alternative successional pathways (e.g., Tepley et al. 2013; Kemp et al. 2016; Harvey et al. 2016; Urza and Sibold 2017; Downing et al. 2019; Busby et al. 2020), including the pathway in which shade-

tolerant conifer species dominate all stages of a forest sere and self-replace (i.e., the mechanism or pathway of passive tolerance; Connell and Slatyer 1977; Pickett et al. 1987). In certain forest types of the climatically wet and cool Pacific Northwest region, for example, it is a commonly observed phenomena that shade-tolerant conifers can play multiple seral roles post-disturbance (Franklin and Hemstrom 1981; Hemstrom and Franklin 1982; Agee 1993; Tepley et al. 2014). Despite this understanding, shade-tolerance, and seral associations (i.e., early, mid, late), continue to be overgeneralized, simplified, and used interchangeably, as predictors of conifer species' ability to recolonize disturbed areas. These overgeneralizations limit our conceptual and mechanistic understanding of conifer species' recovery response to fire and may lead to ineffective and/or unexpected post-fire forest management outcomes when species' colonizing capacity is misjudged.

While shade-tolerance is a broadly useful and measurable ecological concept that can help explain plant species' distributions over space and time (Valladares and Niinemets 2008), it is often overly simplified and misunderstood. Several common misconceptions in relation to conifer species are that (1) shade-tolerance is a binary classification rather than a spectrum of tolerance, (2) high levels of sunlight and environmental exposure absolutely inhibit the establishment and survival of shade-tolerant species, and (3) individual species' shade-tolerance is fixed across environments and remains static throughout their lifespan. Realistically, shade tolerance is a measure of how well species and individuals can survive, grow, and reproduce in low-light environments, occurs along a spectrum, is not necessarily a preference for or maximum

tolerance to sunlight exposure, and may affect individuals differently over space and their lifespan (Valladares and Niinemets 2008). Pending sufficient moisture availability to meet the evaporative and photochemical stress of high sunlight and environmental exposure (Pallardy and Kozlowski 2008), shade-tolerant conifers can establish and grow unimpeded under exposed conditions, albeit usually more slowly than their shade-intolerant counterparts (Burns and Honkala 1990). Site moisture availability, or its inverse moisture deficit, is specifically influenced by relatively static (e.g., topography, soils) and dynamic (e.g., vegetation) fine-scale and coarse-scale (e.g., climate) processes (Stephenson 1990; Lutz et al. 2010; Krawchuk and Moritz 2011). Thus, in arid environments above a species-specific moisture deficit threshold, shade-tolerant conifers may be inhibited from early seral post-fire establishment and require facilitation by shade-intolerant conifers and pioneer species. Alternatively, in mesic environments at or below species-specific moisture deficit thresholds, the major factors limiting early seral post-fire establishment by shade-tolerant conifers should be biotic in nature, and strongly dictated by surviving species population structure (i.e., size, age, and density), spatial configuration on the landscape, community interactions (i.e., competition), and functional traits (i.e., dispersal, seedling niche requirements, and post-disturbance traits; e.g. Johnstone et al. 2016; Enright et al. 2015).

Increasingly, community and species-specific responses to fire are being generalized, understood, and predicted using frameworks that acknowledge and/or quantify the contribution of functional traits to community- or species-level fire resistance and resilience (e.g., Pausas et al. 2004; Keeley 2012; Urza and Sibold 2017;

Davis et al. 2018; Prior and Bowman 2020; Rodman et al. 2020; Stevens et al. 2020). Fire resistance encompasses functional traits that confer the capacity among individuals to survive and persist through one or more fire events over time (Stevens et al. 2020). Alternatively, fire resilience encompasses functional traits that contribute to successful reproduction, establishment, and population persistence over time (i.e., the regeneration niche; Veblen 1992). Specifically, traits that affect fire resilience may include seed dispersal range and seasonal timing, interannual seed production, seed germination rates, resprouting capability, seed cone serotiny, age of reproductive maturity, growth rate, water and nutrient use-efficiency, and drought-tolerance (Agee 1993; Pausas et al. 2004; Keeley et al. 2011). While functional traits can be defined as contributing to either fire resistance or resilience, some traits can contribute to both (e.g., juvenile growth rate; Enright et al. 2015; Rodman et al. 2020). Shade-tolerant conifers typically exhibit functional traits that confer poor fire resistance (e.g., bark thickness, self-pruning, crown height; Agee 1993; Stevens et al. 2020), making them highly vulnerable to frequent and/or severe wildfire as juvenile and usually adult individuals, which in turn has broadly led to their classification as fire-avoiders (Rowe 1983; Agee 1993). Despite exhibiting poor fire resistance, some shade-tolerant conifers in the Western U.S. exhibit strong fire resilience, manifested through functional traits that confer long seed dispersal range, abundant seed production, high germination rates, sufficient drought tolerance, and preference to establish on post-fire exposed mineral soils (Minore 1986; McCaughey et al. 1986; Burns and Honkala 1990). When species functional traits confer strong fire resilience and synchronize with favorable biophysical conditions and sufficient seed

source availability (i.e., proximate live trees), shade-tolerant, fire avoiding, obligate seeding conifers may even act as effective post-fire invaders, outcompeting remnant shade-intolerant (pioneer) conifer species within early seral environments (Fig. 1; H1).

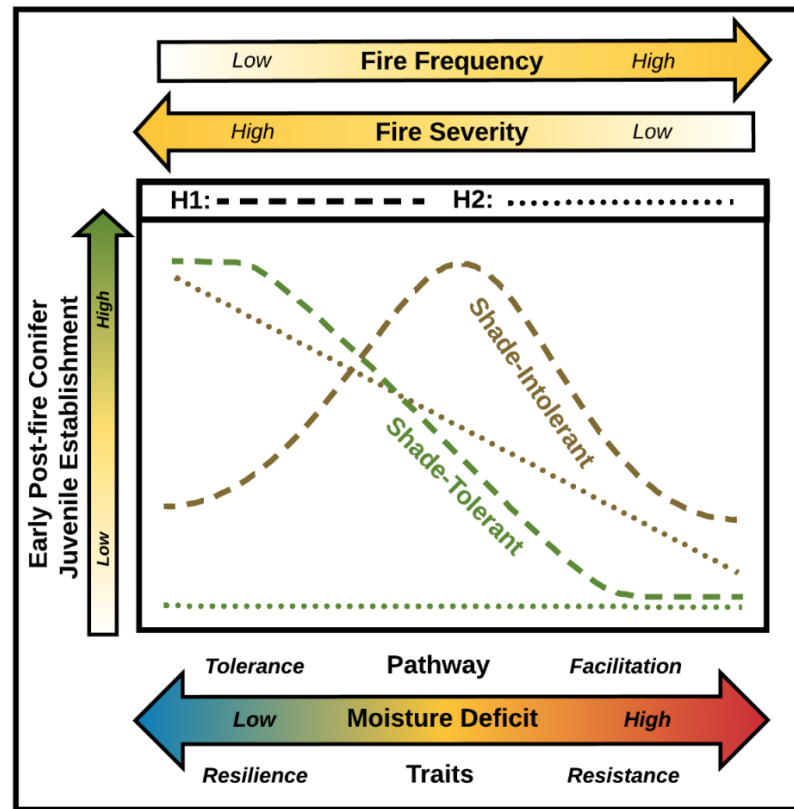


Figure 1. Conceptual diagram hypothesizing the relationship between early post-fire establishment by shade-tolerant and intolerant conifer species, as a function of site moisture deficit (MD), fire regimes, successional pathways, and selection of fire resilience and resistance traits. Site MD controls site productivity and fire regimes, which in turn select for post-fire successional pathways and the expression of functional traits that contribute to fire resilience, resistance, or both among conifer species. Typically, infrequent, high-severity fire regimes facilitated by low MD dominantly select for fire resilience traits and forest succession through the tolerance pathway (i.e., mechanism of passive tolerance; Connell and Slatyer 1977) while frequent, low-severity fire regimes facilitated by high MD dominantly select for fire resistance traits and forest succession through the facilitation pathway. H1 (dashed lines) illustrates the hypothesis that decreasing site MD non-linearly increases early post-fire establishment by shade-tolerant conifers. Meanwhile, shade-intolerant conifer establishment is hump-shaped along a gradient of MD, due to competition and low seed pressure (i.e., low pre-fire dominance) at low site MD and limited moisture availability at high site MD. Alternatively, H2 (dotted lines) illustrates the null hypothesis that early post-fire establishment by shade-tolerant conifers is low regardless of MD, while shade-intolerant conifer establishment increases linearly with decreasing MD, following basic assumptions of the facilitation successional pathway. Figure adapted from Rodman et al. (2020).

As increasing wildfire activity and disturbance interactions under anthropogenic climate change threaten conifer forest resilience and persistence in the western US (Coop et al. 2020) and in North American boreal forests (Whitman et al. 2019; Hayes and Buma 2021), shade-tolerant conifers may play an important role in promoting forest recovery where shade-intolerant conifers are absent, sparsely abundant, or lack effective post-fire dispersal and establishment traits to match fire patterns and other compound disturbances (e.g., serotiny or long-distance dispersal abilities to recolonize large patches of high-severity fire; Hood et al. 2018; Busby et al. 2020). To advance knowledge of where, and why shade-tolerant conifer species exhibit strong early seral post-fire establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment), we aggregated field data from recent published and unpublished studies on post-fire conifer tree establishment responses, nested within four major montane ecoregions in the Western U.S., to ask the following research questions:

- (1) Is there evidence to support the notion that shade-intolerant conifers dominate early post-fire tree establishment after moderate to high severity fire effects across biophysically heterogeneous environments (e.g., Fig.1 H2), or does evidence alternatively support strong establishment and dominance by shade-tolerant conifers within increasingly mesic environments (e.g., Fig.1 H1)?
- (2) What biophysical variables influence shade-tolerant conifer species' early seral post-fire establishment and dominance?

- (3) Does shade-tolerance, and other functional traits conceptually linked to fire resilience, explain early post-fire establishment and dominance by shade-tolerant conifer species?

We hypothesized that post-fire establishment and dominance by shade-tolerant conifers would be (1) greatest in the mesic, least-continental Cascades ecoregion, (2) positively and significantly associated with elevation, as increased moisture becomes available, (3) positively and significantly associated with coarse scale climatic and fine scale topographic factors that reduce moisture deficit to vegetation, and (4) affected by the expression of functional traits linked with fire resilience to a greater degree than shade-tolerance.

2. Methods

2.1. Study domain

We analyzed field data of early seral (1-30 years) post-fire conifer juvenile establishment collected from a total of 1870 plots, nested within 93 fire perimeters where shade-tolerant conifer species were present, that burned at moderate to high severities (tree mortality > 50%) between 1978 – 2015 (Appendix: Supporting tables and figures; Table 4). When compiling our field data, we excluded field sites that experienced short interval reburns (< 25 years between fire events) and/or post-fire management activities (i.e., salvage logging and replanting). Field data were distributed across four western US ecoregions and six states, including: (1) the Cascades of Oregon and Washington, (2) the Blue Mountains of Oregon, (3) the Northern Rockies of Idaho, Montana, and Wyoming,

and (4) the Southern Rockies of Colorado (Fig. 2). Our field data were distributed across broad conifer-dominated forest types (e.g., dry and moist mixed-conifer, subalpine) and a wide range of biophysical settings, including 10 degrees of latitude, 17 degrees of longitude, 704 – 3598m in elevation, 368 – 3303mm in mean annual precipitation, and 0.2 – 10.6 C° mean annual temperature.

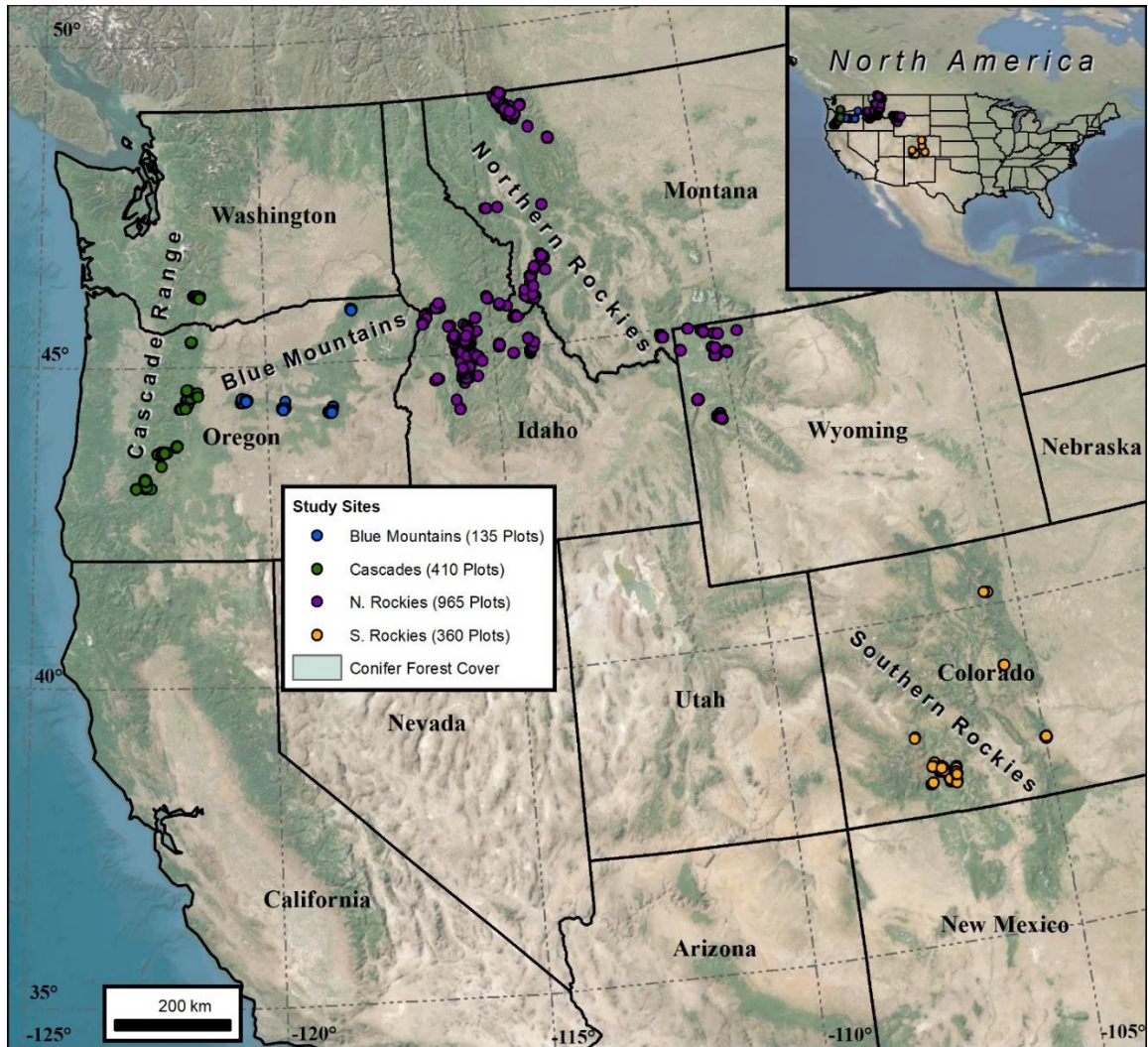


Figure 2. Geographic distribution of the field sites included in this study, distributed across four major ecoregions in the Western U.S. where post-fire conifer establishment (regeneration) was measured.

Among the shade-tolerant conifer species present in our field data, which were classified as such using the USFS Fire Effects Information System (FEIS; Abrahamson

2018) database, species richness was the greatest in the Cascades Range ($n = 9$ species) and similar across the other ecoregions ($n = 2-3$ species), where grand fir (*Abies grandis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmanni*) were the most ubiquitous shade-tolerant conifer species across all ecoregions. Although some of the following species are present in the other study ecoregions, white fir (*Abies concolor*), pacific silver fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), mountain hemlock (*Tsuga mertensiana*), western red cedar (*Thuja plicata*), and incense cedar (*Calocedrus decurrens*) were exclusively present in our field sites within the Cascades.

2.2. Data responses

Post-fire conifer tree juvenile establishment data used in our analyses were collected from 1870 field sites (i.e., plots), ranging in size from 15 – 707 m², with respective field methods described in recent publications (Meigs et al. 2009; Coop et al. 2010; Harvey et al. 2014; Stevens-Rumann et al. 2014; Kemp et al. 2016; Harvey et al. 2016; Stevens-Rumann and Morgan 2016; Urza and Sibold 2017; Downing et al. 2019; Dunn et al. 2020; Busby et al. 2020; Andrus et al. 2021). All studies recorded post-fire conifer juvenile stem density by species, site coordinates, and an estimate of classified burn severity (i.e., unburned, low, moderate, high) derived from post-fire tree mortality responses observed in the field at the time of sampling. We used site coordinates and a 10m digital elevation model to extract and calculate additional topographic site features, including elevation, slope, aspect, and the heat load index (HLI; McCune and Keon 2002).

To compare the magnitude of juvenile establishment among plots with unequal sample area, we standardized juvenile stem density to the areal measurement of one hectare (10,000m²) across all sites. To connect post-fire conifer juvenile densities with forest recovery outcomes, we defined a minimum threshold of 250 or greater juveniles per hectare, as sufficient to stimulate conifer forest recovery, following general United States Forest Service (USFS) restocking guidelines and thresholds from previous studies (e.g., Stevens-Rumann and Morgan 2016; Busby et al. 2020). While juvenile density can represent the likelihood of the sampled burned forest to recover, juvenile density is sensitive and relative to site productivity that varies over space. Accordingly, we quantified the relative degree of shade-tolerant conifer juvenile establishment in relation to total observed conifer establishment (i.e., including shade-intolerant conifer species) at the site level, by calculating the ratio of shade-tolerant conifer dominance (i.e., total shade-tolerant conifer species' juvenile establishment / total conifer juvenile establishment) and the ratio of shade-tolerant species-specific dominance (i.e., species-specific shade-tolerant juvenile establishment / total [shade-tolerant and intolerant] conifer juvenile establishment). Finally, to determine if time since fire (i.e., number of establishment opportunities) had a significant influence on shade-tolerant conifer juvenile establishment across sites, and thus should be pre-factored into our data analysis, we plotted shade-tolerant conifer establishment against time since fire and conducted a Spearman rank correlation test to test for significance and strength of the relationship. The relationship was non-significant and weak ($p = 0.89$; $\rho = -0.003$; Appendix:

Supporting tables and figures; Figure 8), thus we did not alter our data responses based on time since fire.

2.3. Post-fire seed source availability

To estimate post-fire seed source availability at a coarse scale among sites where fire events occurred as early as the late 20th century (i.e., high-resolution imagery necessary to estimate fine-scale seed source availability was not available until ca. 2009), we used post-fire Landsat satellite imagery and Google Earth Engine to estimate percent conifer forest cover among 30m pixels spatially intersecting and surrounding our sites. First, pre-processed surface reflectance from Landsat missions 5-8, depending on fire dates, were used to calculate the Normalized Burn Ratio (NBR; can estimate forest cover and change; Key and Benson 2006) and extract near-infrared (NIR; can differentiate conifers and angiosperms; Wulder et al. 2009) band reflectance among pixels surrounding our sites at the one-year post-fire timestep. For sites that burned in 1978 (Coop et al. 2010; $n = 150$), we used the earliest functional imagery accessible that was derived from the launch of Landsat 5 (i.e., 1984; six-years post-fire). Second, we used visual interpretation of high-resolution National Aerial Imagery Program (NAIP; 1m) reference imagery and Iterative Self-Organizing Data Analysis Technique (ISODATA) unsupervised classification of NBR to determine NBR value thresholds associated with forest absence and complete cover among the Landsat imagery (NBR = 0 and >500, respectively). Third, in ArcGIS (ESRI 2020), we used the above NBR thresholds and the fuzzy membership function with a linear transformation to derive an estimate of percent post-fire forest cover in each 30m pixel (i.e., 0 – 100%). Fourth, to minimize confusion

between resprouting angiosperms and post-fire conifer forest cover, we used visual interpretation of the NAIP reference imagery and ISODATA unsupervised classification of NIR to determine an NIR value threshold associated with resprouting angiosperms. We then reclassified percent forest cover to zero among pixels identified as dominated by resprouting angiosperms (NIR > 1800). Finally, to estimate conifer seed source availability at each site (i.e., density and proximity of nearby live conifer forest), we used classified percent forest cover and a 150m radius moving window (i.e., the range at which most seeds are dispersed by our study species; McCaughey et al. 1986; Burns and Honkala 1990) to calculate a forest cover distance²-weighted density metric (D²WD; Coop et al. 2019).

2.4. Climate data

To explore long-term average annual and seasonal climate conditions across sites as drivers of shade-tolerant conifer juvenile establishment and dominance post-fire, we calculated a set of climate-related predictive variables to fit into statistical models using the ClimateNA application (Wang et al. 2016; Table 1). ClimateNA uses elevation to downscale 800m resolution PRISM (Daly et al. 2008) gridded monthly climate normal data to scale-free point (site) locations. We calculated predictive variables using PRISM 30-year (1981-2010) monthly normal climate data. Both datasets have been used extensively in other post-fire regeneration studies across the western US (e.g., Stevens-Rumann et al. 2018; Downing et al. 2019; Kemp et al. 2019; Boag et al. 2020).

2.5. Functional traits

To explore if the expression of functional traits related with fire resilience were (1) connected to early post-fire establishment and dominance by shade-tolerance conifer species and (2) more associated with establishment and dominance than shade-tolerance, we identified five functional traits (including shade-tolerance) conceptually relevant to post-fire recovery, with supporting data available across all species, and quantified species-specific average and relativized (normalized departures or z-score) trait values from published studies (Niinemets and Valadares 2006; Abrahamson 2018). The five functional traits we quantified included (1) shade-tolerance, (2) drought-tolerance, (3) mean germination rate, (4) mean juvenile growth rate, and (5) mean seed weight (Appendix: Supporting tables and figures; Table 5). To summarize the combined effect of these five functional traits on individual species' post-fire regenerative capacity (i.e., fire resilience), we also calculated a fire resilience score by averaging all trait z-score values by species, sensu Stevens et al. (2020). Conceptually, we hypothesized that shade tolerance and mean seed weight would have a negative, rather than positive relationship with species' regenerative capacity, and thus averaged the inverse of these two trait's z-score values (e.g., $1 - \text{trait z-score value} [0.75] = \text{inverse z-score value} [0.25]$).

2.6. Statistical analysis

All statistical analyses were conducted in R (R Core Team 2020) using base packages and plots generated using the ggplot2 package (Wickham 2016), unless otherwise noted below. To identify if post-fire shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) varies

across ecoregions and species, we summarized the distribution of species-level and combined shade-tolerant conifer establishment and dominance across ecoregions. To test for statistical differences ($\alpha = 0.05$) in combined shade-tolerant conifer establishment and dominance between ecoregions, and at the species-level, we conducted non-parametric Wilcoxon Rank Sum tests with a Bonferroni correction to account for multiple pairwise comparisons. Plots with absent conifer juvenile establishment (i.e., where seed source availability and/or environmental conditions excluded any conifers from re-establishing; $n = 461$; ca. 25% of sites) were excluded from the analyses below.

To (1) identify statistically significant and potentially non-linear relationships between predictive variables and post-fire shade-tolerant conifer establishment and dominance, and (2) identify if fire resilience functional traits are significantly related to shade-tolerant conifer establishment and dominance, we fit generalized additive mixed models (GAMMs) in the package “mgcv” (Wood 2011) to analyze our count and ratio data responses with negative binomial and beta distributions, respectively. We included fire perimeter identity as a random effect in all models to account for spatial autocorrelation between sites nested within the same fire perimeter. Each model was fit using maximum likelihood (ML) and a penalized regression spline approach to automate smoothing function selection for each fitted variable and to compare models (Leathwick et al. 2006). Predictive variables were fit into GAMMs using forward stepwise selection until only significant variables remained ($\alpha < 0.05$), where model diagnostics (i.e., multicollinearity [concurvity] and residual plots) were assessed at each step (Marra and Wood 2011). For negative binomial count GAMMs, we included an offset variable to

account for differences in sampled plot size across sites. To fit beta GAMMs, we transformed zero and one responses to a ratio format, respectively, by adding or subtracting a small value (0.001). We used the deviance explained statistic (i.e., pseudo- R^2) to assess each GAMM's goodness of fit and reported results from models with the lowest ML (i.e., AIC).

For the first GAMM fitting analysis, we subset our field data by ecoregion (i.e., all sites combined, Blue Mountains, Cascades, N. Rockies, and S. Rockies) and fit five GAMMs per response (i.e., shade-tolerant conifer establishment [counts] and dominance [ratio]) using a suite of biophysical predictive variables, including interactions (Table 1). For the second GAMM fitting analysis, we fit one GAMM per response (i.e., juvenile establishment [counts] and dominance [ratio]) on data from all sites using species' functional trait values as predictors (Appendix: Supporting tables and figures; Table 5). We excluded sites from this second analysis where no post-fire establishment by shade-tolerant conifers occurred ($n = 563$; ca. 30% of sites).

Table 1. Summary list of the predictive variables, and their descriptions, fit into GAMMs to determine statistically significant drivers of post-fire shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment).

| Variable | Abr. | Description | Units | Range |
|----------------------------------|-------------------|---|----------|-------------|
| Elevation* | Elevation | Height above mean sea level. | m | 704 - 3595 |
| Slope* | Slope | Angle of the dominant hillslope. | ° | 0 - 55 |
| Heat Load Index* | HLI | Direct measure of incident solar radiation based on latitude, aspect, and slope (McCune and Keon 2002). A proxy for heat load and evaporative potential. | unitless | 0.25 - 1.07 |
| Time Since Fire | TSF | The year in which a site was sampled minus the year a fire occurred. A proxy for the number of establishment opportunities post-fire. | years | 1 - 30 |
| Forest Cover D ² WD | D ² WD | The distance ² -weighted density (Coop et al. 2019) of remotely sensed percent forest cover among 30m pixels within a 150m radius of each site. A coarse-grain proxy for seed source availability. | unitless | 0 – 1.54 |
| Annual Climate Moisture Deficit§ | Ann. CMD | Hargreaves climate moisture deficit: the monthly difference between precipitation and reference evaporative demand, summed January - December. A proxy for climatic annualized moisture stress on vegetation. | mm | 72 - 678 |
| Summer Climate Moisture Deficit§ | Sum. CMD | Hargreaves climate moisture deficit: the monthly difference between precipitation and reference evaporative demand, summed June - August. A proxy for climatic summer moisture stress on vegetation. | mm | 72 - 421 |
| Annual Precipitation§ | MAP | Cumulative annual precipitation | mm | 368 - 3303 |
| Annual Precipitation as Snow§ | PAS | Cumulative annual precipitation falling as snow. A proxy for winter snowfall and snowpack accumulation. | mm | 32 - 1405 |
| Frost Free Days§ | NFFD | Annual number of frost-free days. A proxy for growing season length. | days | 82 - 280 |
| Annual Temperature Difference§ | TD | Annual difference between the mean warmest month temperature and mean coldest month temperature. A proxy for continentality and isothermality. | C° | 15.4 - 24.7 |

*Topographic variables were derived from a 10m digital elevation model (DEM). §30-yr climate normal variables were derived from the ClimateNA application (Wang et al. 2016) using downscaled 1981-2010 PRISM monthly averages.

3. Results

3.1. Shade-tolerant conifer establishment and dominance

We observed statistical differences in early post-fire shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment), as well as statistical differences in site characteristics like elevation and annual climate moisture deficit between ecoregions (Fig. 3). Sites within the S. Rockies ecoregion were most dissimilar in elevation and annual climate moisture deficit from sites in all other ecoregions. For shade-tolerant conifer establishment, the Cascades, and Blue Mountains, respectively, exhibited higher median densities (ca. 184 and 149/ha) of shade-tolerant juveniles and were significantly different from the N. and S. Rockies, which exhibited very low median densities (ca. 0 per hectare). Similarly, the Cascades and Blue Mountains also exhibited a higher percentage of plots (ca. 45%) above the restocking and forest recovery threshold of 250 shade-tolerant conifer juveniles/ha, compared to the N. and S. Rockies (ca. 26% and 20%), respectively. For shade-tolerant conifer dominance, the Cascades exhibited the highest median proportion (ca. 40%) and was significantly different from the other ecoregions. Observed shade-tolerant conifer species diversity was also substantially higher in the Cascades compared to the other ecoregions

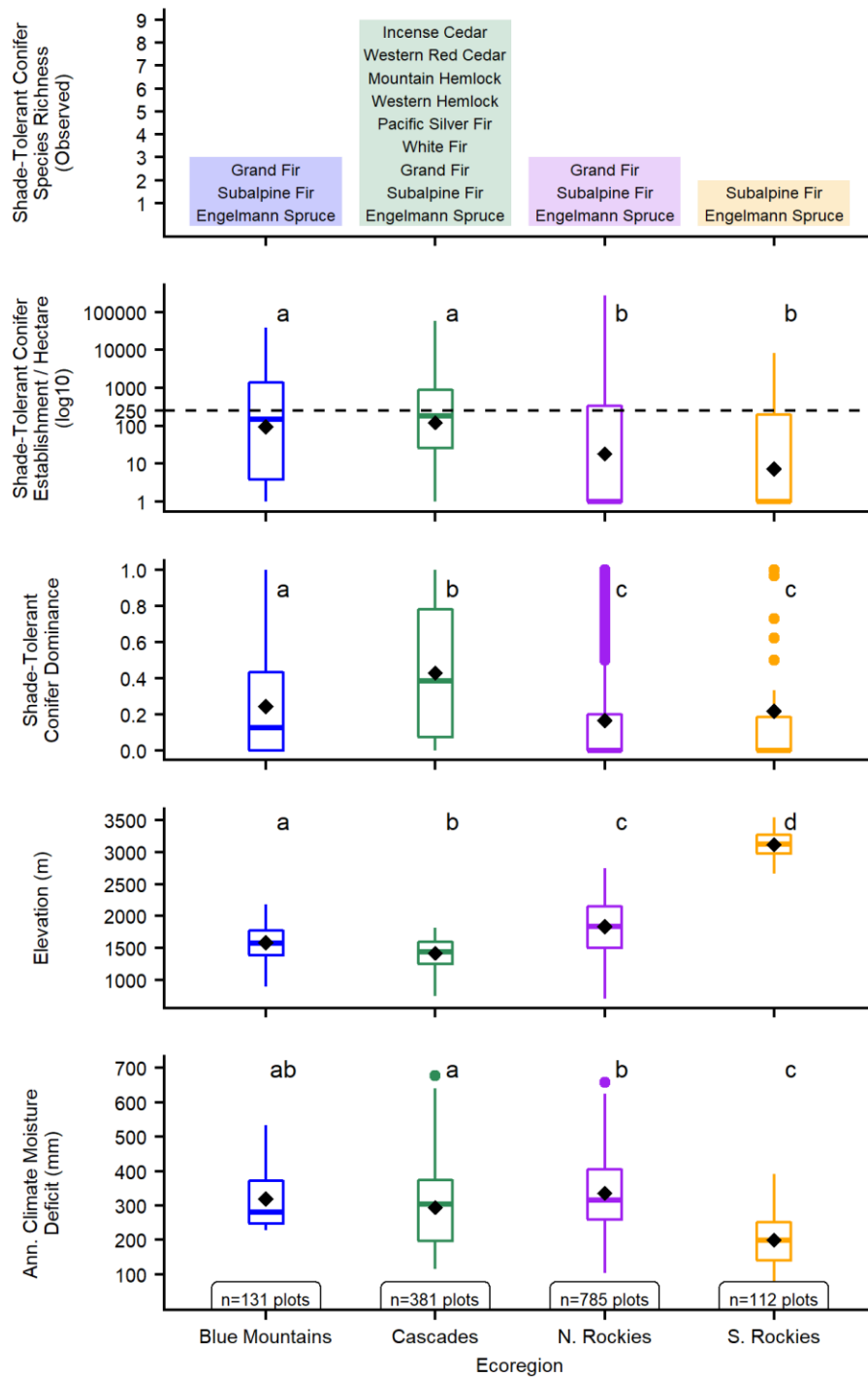


Figure 3. Summary statistics of site characteristics and post-fire shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) across four major western US ecoregions. Black diamonds indicate mean values. Letters (a, b, c) indicate statistical differences ($\alpha = 0.05$) between ecoregions. Black dashed line indicates a conifer juvenile density threshold commonly used for post-fire restocking (i.e., sufficient for forest recovery).

Species-specific establishment and dominance also varied significantly by ecoregion (Fig. 4). Grand fir (*Abies grandis*) establishment was similar in the Cascades, Blue Mountains, and N. Rockies, but its ratio of dominance was significantly different in the Cascades and substantially higher (ca. 80% vs. ca. 25%). Mountain hemlock (*Tsuga mertensiana*) also exhibited a high ratio of dominance specifically in the Cascades (ca. 40%). Engelmann spruce (*Picea engelmannii*) establishment was significantly lower in the Cascades, and its ratio of dominance was significantly higher in the S. Rockies, followed by the N. Rockies. Subalpine fir (*Abies lasiocarpa*) establishment was significantly higher in the S. Rockies, followed by the N. Rockies, and its ratio of dominance was significantly higher specifically in the S. Rockies. Engelmann spruce and subalpine fir exhibited relatively high ratios of dominance specifically in the S. Rockies (ca. 70% and 60%, respectively). Median post-fire juvenile establishment by shade-tolerant species was generally near the 250 juveniles/ha threshold, except for Engelmann spruce and subalpine fir in specific ecoregions, and white fir (*Abies concolor*) and pacific silver fir (*Abies amabilis*). Pacific silver fir exhibited the lowest fire resilience score and lowest post-fire establishment and dominance among shade-tolerant conifer species.

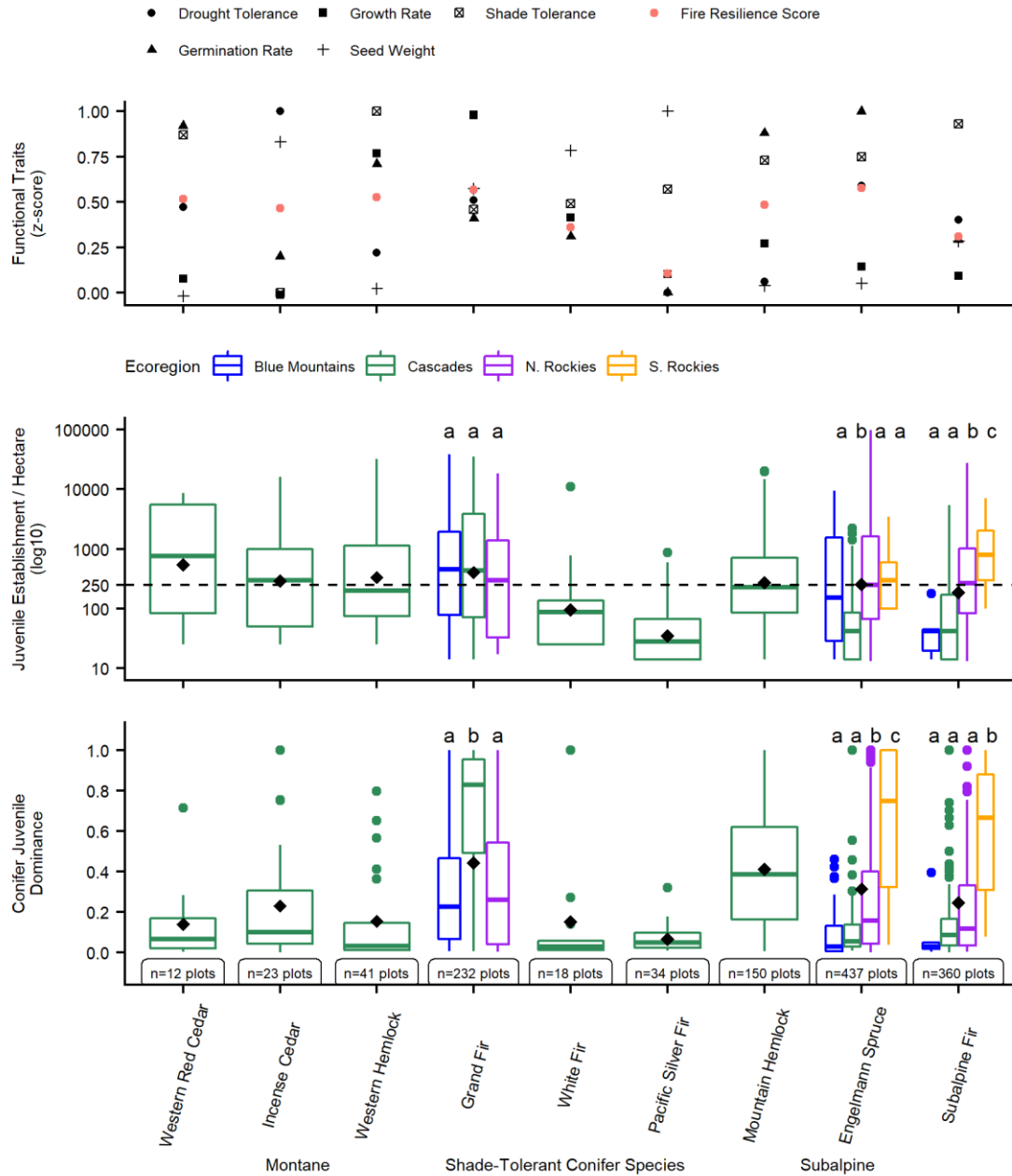


Figure 4. Functional trait values (z-scores) and summary statistics of early post-fire shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment), across four major western U.S. ecoregions, by species. Black diamonds indicate mean values across ecoregions. Letters (a, b, c) indicate species-level statistical differences ($\alpha = 0.05$) between ecoregions. Black dashed line indicates a conifer juvenile density threshold commonly used for post-fire restocking (i.e., sufficient for forest recovery). The fire resilience score was calculated as the species-specific average of drought tolerance, growth rate, germination rate, and inverse of seed weight and shade tolerance z-scores. Only Engelmann spruce and subalpine fir were present in our field data across all ecoregions, and grand fir present in the Blue Mountains, Cascades, and N. Rockies.

3.2. Biophysical predictors of shade-tolerant conifer establishment and dominance

Our ecoregion-based statistical models, fit on post-fire shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) responses, indicated that the interaction between summer climate moisture deficit (sum. CMD) and annual precipitation as snow (PAS) was the strongest predictor of both responses, except in the S. Rockies (Table 2). The interaction between these climate variables suggests that biophysically, shade-tolerant conifer establishment and dominance are linked with high PAS and low sum. CMD, with increasing PAS mitigating the negative effect of increasing sum. CMD on establishment and dominance in most ecoregion models (Fig. 5). Noticeable are shade-tolerant dominance sharp threshold values at ca. 1,200mm PAS and ca. 250 mm sum.CMD for all ecoregions combined (Fig. 5b), that differ from the more gradual threshold and lower values in the Blue Mountains (Fig 5d), the different shape in the overall PAS/sum.CMD relationship in the N. Rockies (e.g. lowest PAS values have positive effects; Fig. 5h), and the optimal conditions at intermediate PAS and mid-low sum.CMD values in the Cascades (Fig. 5f). Other statistically significant predictors among specific ecoregion models included topographic variables: elevation, slope, and the heat load index (HLI) (Table 2; Fig. 6). Elevation exhibited a non-linear relationship with both shade-tolerant establishment and dominance that was ecoregion specific, and a negative relationship with juvenile establishment in all ecoregions combined (Fig. 6a, b). The HLI also exhibited a non-linear, but hump-shaped relationship with shade-tolerant establishment (Fig. 6c), while slope exhibited a negative linear relationship (Fig. 6d). Seed source availability (forest cover D²WD) and time since

fire (years) were statistically unimportant predictors across ecoregion models and responses.

Table 2. Predictive variable estimates (χ^2) and levels of significance (*) among fitted GAMM statistical models describing drivers of shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) by ecoregion. Variables exhibited non-linear relationships with establishment and dominance responses, except for slope, which exhibited a negative linear relationship with both responses (see Fig. 5 and Fig. 6 for the directions of relationships).

| Ecoregion | Response | Sample Size (n) | Deviance Explained | Fixed Effects | | | |
|------------|------------------------|-----------------|--------------------|---------------|------|-------|----------------|
| | | | | Elevation | HLI | Slope | Sum. CMD x PAS |
| All | Establishment | 1409 | 49% | 35*** | 14** | 14*** | 68*** |
| Ecoregions | Dominance | 1409 | 62% | ~ | ~ | ~ | 60*** |
| Blue | Establishment | 131 | 59% | 11*** | ~ | 10*** | 119*** |
| Mountains | Dominance | 131 | 40% | ~ | ~ | ~ | 65*** |
| Cascades | Establishment | 381 | 34% | 24*** | ~ | ~ | 26** |
| | Dominance | 381 | 63% | 25*** | ~ | ~ | 51*** |
| N. Rockies | Establishment | 785 | 49% | ~ | 16** | ~ | 101*** |
| | Dominance | 785 | 40% | 56* | ~ | ~ | 229*** |
| S. Rockies | Establishment | 112 | 37% | ~ | 17* | ~ | ~ |
| | Dominance [^] | 112 | ~ | ~ | ~ | ~ | ~ |

[^] Model convergence and parameter estimates were unreliable due to low sample size and variance in responses.

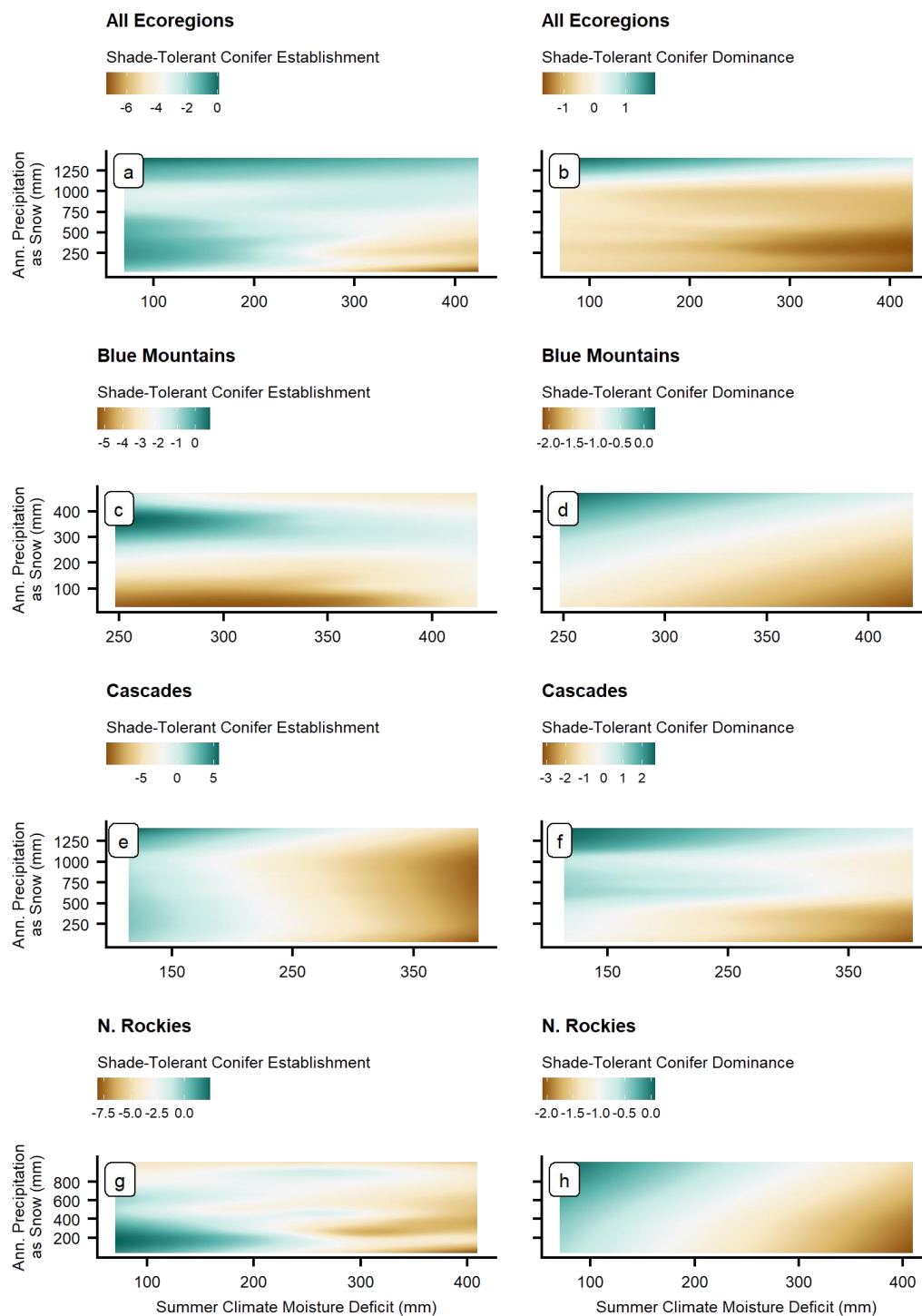


Figure 5. Influence of the significant ($p < 0.001$) non-linear interaction between summer climate moisture deficit and annual precipitation as snow on shade-tolerant conifer establishment (juvenile density; left panels) and dominance (ratio of total conifer juvenile establishment; right panels), by ecoregion model. Across the brown-white-blue color spectrum, brown shading indicates reduced, while blue shading increased establishment and dominance due to variable interactions.

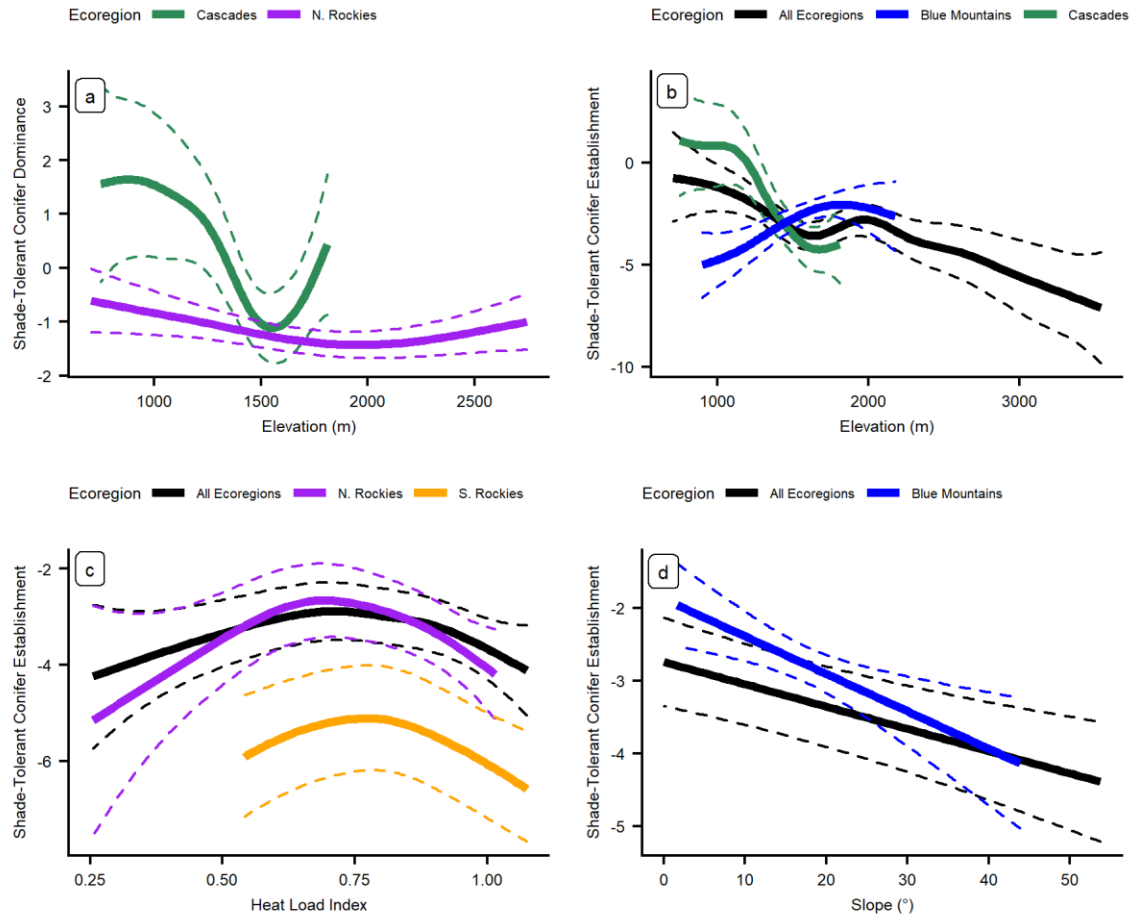


Figure 6. Influence of topographic variables on shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) by ecoregion. Only relationships (i.e., curves) that were statistically significant ($p < 0.05$) in associated ecoregions models are included. Colored dashed lines indicate 95% confidence intervals associated with ecoregion models.

3.3. Functional traits as predictors of shade-tolerant conifer establishment and dominance

Our statistical models highlighted four out of five functional traits as significant predictors ($p < 0.05$) of post-fire shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) responses (Table 3). Trait-response relationships indicated that higher species-level drought tolerance was particularly strong compared to other traits, and positively associated, along with seed

weight (negatively associated), at predicting juvenile establishment (Table 3; Fig. 7).

Generally, traits had greater influence on juvenile establishment than dominance in the statistical models, whose main predictors were juvenile growth rate and drought tolerance. Instead, mean germination rate was less important for either response variables, and the shade tolerance trait was insignificant in both establishment and dominance models (Table 3; Fig. 7).

Table 3. Predictive variables estimates (χ^2) and levels of significance (*) among fitted statistical models describing the relationship between shade-tolerant species' functional trait values and two responses: establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) across all sites (see Fig. 7 for the direction of variable relationships).

| Response | Sample Size (n) | Deviance Explained | Fixed Effects | | | | |
|---------------|-----------------|--------------------|-----------------|-------------------|------------------|----------------------|-------------|
| | | | Shade Tolerance | Drought Tolerance | Germination Rate | Juvenile Growth Rate | Seed Weight |
| Establishment | 1307 | 62% | ~ | 76.8*** | 7.3*** | 6.8*** | 15.8*** |
| Dominance | 1307 | 45% | ~ | 10.1*** | 2.3* | 11.3*** | 1.0* |

Asterisks indicate levels of significance: *P < 0.05, **P < 0.01, ***P < 0.001. Model goodness of fit is described by percent deviance explained (i.e., pseudo-R²).

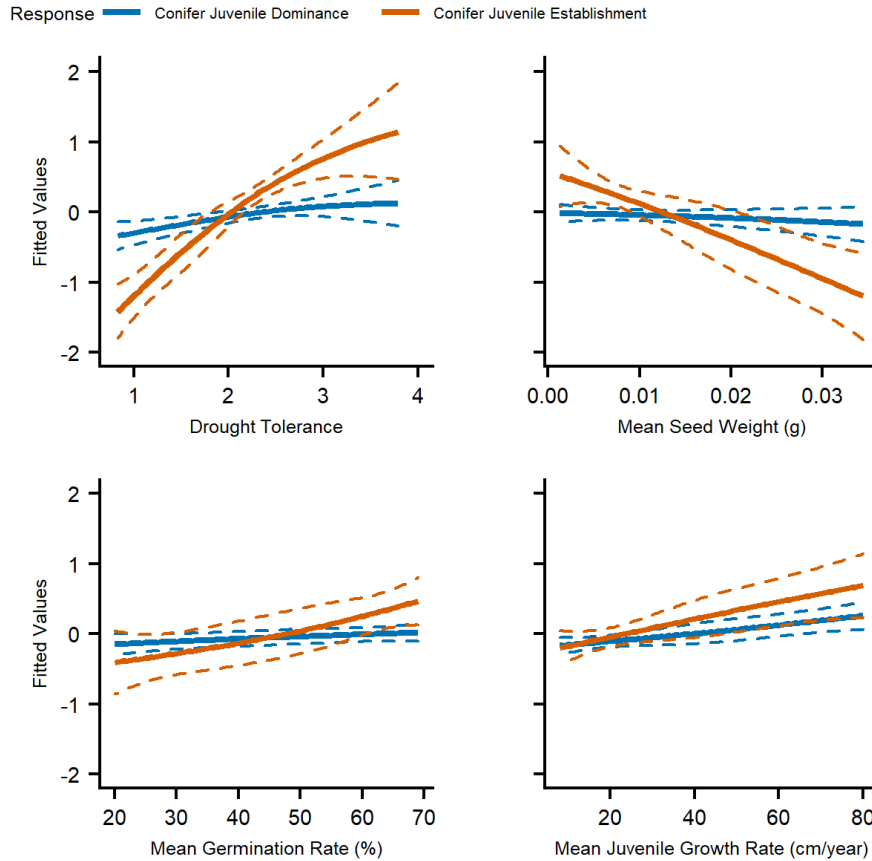


Figure 7. The influence of four functional traits as statistically significant ($\alpha = 0.05$) predictors of shade-tolerant conifer species' early post-fire establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment). Colored dashed lines indicate 95% confidence intervals associated with response models.

4. Discussion

Post-fire conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) following fire events burned at moderate- to high-severity, across 1870 sites, and four major ecoregions in the western US, suggest that shade-tolerant conifer species can play an important early seral role in post-fire conifer forest recovery. Our results challenge the notion that shade-tolerant conifer species requires facilitation by shade-intolerant tree species (e.g., Fig. 1, H2) post-fire, and

alternatively support our hypotheses that shade-tolerant conifer establishment and dominance occurs along a gradient of environmental moisture deficit (e.g., Fig. 1, H1), and at the species-level, is connected to the expression of functional traits that confer fire resilience. Accordingly, we argue that post-fire conifer forest recovery, as an ecological process, is best understood within frameworks that account for species' life history, fire resistance, and fire resilience traits, and their interactions with topo-climatic environmental gradients and the availability of seeds over time. As fire activity in the Western U.S. increases, shade-tolerant conifers are likely to continue playing critical roles in promoting forest recovery and persistence, especially in the mesic Cascade ecoregion, but also elsewhere within finer-scale topo-climatically mesic conditions. It is unclear, however, how changing fire patterns and climate conditions will impact post-fire regeneration by shade-tolerant conifers, and thus the overall resilience of conifer forests in the western US, and elsewhere.

4.1. Seasonal moisture deficit drives shade-tolerant conifer establishment and dominance

The effect of annual or seasonal (i.e., dry, warm summer season) moisture deficit on vegetation strongly influences conifer species distributions in the western US (Minore 1979; Burns and Honkala 1990, Agee 1993) by (1) directly selecting for species whose water-use efficiency and drought tolerance can match deficits and (2) indirectly by influencing vegetation density, fuel aridity, flammability, and therefor fire activity (Agee 1998; Baker 2009). Conifers that exhibit moderate- to high-shade tolerance also typically exhibit poor resistance to fire effects (Stevens et al. 2020), such that they are widely labeled functionally as fire-avoiders (Rowe 1983) and relegated to mesic and/or cool

environments with moderate/infrequent to mixed/high-severity fire regimes (e.g., 50+ year fire-return interval; Agee 1998; Baker 2009). Climate influences broad moisture deficits at coarse scales (e.g., ecoregion level), while topography interacts with climate to influence moisture deficits at fine scales. Our statistical models indicated that the interactions between two climatic variables, 30-year average summer climate moisture deficit (CMD) and annual precipitation as snow (PAS), were the strongest biophysical drivers of shade-tolerant conifer establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) post-fire, except among sites in the S. Rockies ecoregion, which were set at substantially higher elevations than sites in the Cascades, Blue Mountains, and N. Rockies. Further, models suggested that precipitation as snow helped mitigate the negative effect of increasing summer climate moisture deficit on post-fire conifer establishment and dominance, especially for all ecoregions combined (i.e., establishment) and in the Blue Mountain (i.e., establishment and dominance) and Cascades (i.e., dominance) ecoregions.

Functionally, snowfall and snowpack accumulation and duration help mediate drought stress to local and downstream vegetation during the dry and warm summer season (e.g., in the Cascades, Blue Mountains, and N. Rockies) when snow water is released (Harpold et al. 2015; Higuera et al. 2015). While the dependency on moisture availability typically diminishes with elevation, as forests shift to energy-limited conditions, the overall shape of the relationship in the amelioration of drought by snow varies substantially by ecoregion for both juvenile establishment and shade-tolerant dominance. For example, establishment is favored by mid-to-low PAS values in the

colder Northern Rockies and dominance is hindered at low and mid-high PAS values, but not at intermediate nor high values, in the maritime Cascades. Additionally, it was expected to some degree that summer drought (CMD) would be a more crucial predictor than annual PAS (i.e. winter in all study areas) for juveniles, as these have shallow roots and are not able to access moisture from spring snowmelt stored in deeper soil layers (Williams et al. 2009), and overall support previous post-fire regeneration studies in the Northern Rockies (e.g. Stevens-Rumann et al. 2018; Harvey et al. 2016), the Sierras (e.g., Meng et al. 2015), and the Cascades (e.g., Busby et al. 2020).

As declined mountain snowpack continues to increase seasonal fuel aridity that promotes larger, more frequent, and more severe fires (Westerling et al. 2006; Abatzoglou and Williams 2016; Gergel et al. 2017; Parks and Abatzoglou 2020), years with low average summer moisture deficits will be crucial in helping to minimize forest fuel aridity and overall fire activity (Agee 1998; Gergel et al. 2017; Holden et al. 2018). Low summer moisture deficit and overall mesic conditions favor fire regimes aligned with shade-tolerant species' minimal fire resistance (e.g., Steven et al. 2020). Our findings support this general notion (i.e., biophysical settings that are topo-climatically mesic and/ or experience ample winter snowpack accumulation can support shade-tolerant conifer species), but it is novel in that we show shade-tolerant conifers can dominate forest composition as both early- and late-seral dominants after moderate- to - high severity fire effects. This correlation was particularly strong in the Cascades (i.e., 43% of sites were dominated [$> 50\%$] by shade-tolerant conifer juveniles post-fire), where shade-tolerant conifer species richness was also highest, confirming results from

earlier studies (Franklin and Dyrness 1973; Franklin and Hemstrom 1981; Hemstrom and Franklin 1982; Agee 1993), but was also apparent to a lesser degree in the S. Rockies (21% of sites), Blue Mountains (18% of sites), and N. Rockies (14% of sites).

4.2. Fire resilience and shade-tolerance

Species-level fire resilience is affected by the expression of functional traits that promote rapid and widespread post-fire recovery (Pausas et al. 2004; Keeley et al. 2011; Rodman et al. 2020). In the western US, shade-tolerant conifers are primarily obligate-seeders that colonize burned patches via wind-dispersed canopy seedbanks, residing among live individuals within (i.e., fire refugia) and/or nearby to burned perimeters (Meigs and Krawchuk 2018; Krawchuk et al. 2020). Thus conceptually, the expression of functional traits associated with seed (e.g., production, weight, shape, germination success rate) and juvenile (e.g., drought tolerance, growth rate, age of sexual maturity) characteristics are likely strong contributors of fire resilience among shade-tolerant conifers (Enright et al. 2015), assuming fire regime parameters remain within historical range of conditions (e.g., Steel et al. 2015; Johnstone et al. 2016). Our statistical models indicated significant relationships between early seral post-fire shade-tolerant conifer establishment, dominance, and species-specific expression of functional traits, including drought tolerance, germination rate, growth rate, and seed weight, but not shade-tolerance. These relationships provide support for our hypothesis that shade-tolerance is a relatively poor predictor of conifer species' early seral colonizing capacity across a range of biophysical settings. Accordingly, we propose that the use of shade tolerance as a functional trait that explains fire resilience is discontinued, or at least deemphasized, and

its use as an indicator of conifer species' mid- to -late seral capacity for establishment, survival, and reproduction under low light conditions and higher levels of competition is continued (Franklin and Hemstrom 1981; Valladares and Niinemets 2008).

4.3. Species-specific responses

Among the shade-tolerant conifer species observed in our data, the species with the greatest sample sizes (i.e., sites present; seed source was locally available for establishment) and fire resilience scores exhibited evidence of strong post-fire establishment (juvenile density) and dominance (ratio of total conifer juvenile establishment) across individual or multiple ecoregions. In the Cascades, mountain hemlock (*Tsuga mertensiana*) dominated post-fire conifer establishment within subalpine sites, demonstrating strong dispersal and establishment abilities within cool and moist environments (e.g., Fernandez et al. 2021). Grand fir (*Abies grandis*) also dominated post-fire establishment among montane sites in the Cascades and showed lesser, but nonetheless strong establishment and dominance within montane sites in the Blue Mountains and N. Rockies. Within subalpine sites, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) exhibited relatively strong establishment and dominance in the N. Rockies and especially S. Rockies, and poorer establishment in the Blue Mountains and Cascades.

While pre-fire forest structure (size, age, and density) and composition (species) data was not available across all sites for us to analyze in this study, forest structure and composition likely strongly contributed to species-specific establishment and dominance response through seed pressure, as shown elsewhere (e.g., Haire and McGarigal 2010;

Kemp et al. 2016; Downing et al. 2019; Stevens-Rumann and Morgan 2019; Coop et al. 2019; Busby et al. 2020). Our relatively coarse grain seed source availability metric, forest cover D²WD, was unimportant as a predictor of shade-tolerant conifer species establishment and dominance, however. This result may speak to methodological flaws or weaknesses associated with our forest cover D²WD metric, or it may suggest that seed source availability as an effective predictor of post-fire tree establishment and dominance is better quantified using high-resolution data sources that can delineate proximate seed sources at a fine grain (i.e., the tree-level; Downing et al. 2019; Coop et al. 2019; Chapman et al. 2020) and ideally also at the species-level.

4.4. Shade-tolerant conifers in a warming world: future perspectives

As mountain snowfall and winter snowpack accumulation continues to decline (Gergel et al. 2017), growing season length expands, and summer drought intensifies in the mountainous western US under warming conditions (Westerling 2006; Abatzoglou and Williams 2016; Westerling 2016), we expect the protecting role that PAS has on drought amelioration to fade out at mid-elevations and become diminished at high-elevations, shrinking the extent of sites topo-climatically suitable for shade-tolerant conifer establishment post-fire(s). Climate variability may support pulses of establishment by shade-tolerant conifers within increasingly moisture limited sites, yet opportunities for successful and widespread establishment are likely to diminish among sites already near a critical threshold of required moisture availability to species (e.g., Andrus et al. 2018; David et al. 2019; Kemp et al. 2019). Further, as fuel aridity increases and thus fire activity increases (Higuera et al. 2015; Abatzoglou and Williams 2016),

mature shade-tolerant conifer individuals are ill favored to survive and persist through multiple fire events due to their poor expression of functional traits promoting fire resistance (Stevens et al. 2020), except where forest structure and topo-climatic conditions can buffer fire effects from repeated fire events (i.e., persistent fire refugia; Krawchuk et al. 2016; Meigs and Krawchuk 2018; Meigs et al. 2020). Population declines of sexually mature shade-tolerant conifer individuals through mortality by fire(s), over time, may continuously reduce landscape-level seed pressure by those species, further compounding poor establishment responses (Coop et al. 2020) and effectively limiting long-term recovery (Busby et al. 2020).

Considering the implications of climate change on conifer forest persistence and recovery in the western US (Coop et al. 2020), more work is needed, conceptually and empirically, to understand how conifer species in general (shade-tolerant or -intolerant) may respond to warming conditions and altered fire regimes. While we exclusively evaluated the contribution of species' functional traits to fire resilience (i.e., post-fire recovery), future work may benefit from utilizing more complex trait-response frameworks that consider species' life history, fire resistance, and fire resilience traits, and their relative contributions to species' persistence across complex gradients of fire activity and topo-climatic conditions.

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7. Appendix: Supporting tables and figures

Table 4. Post-fire conifer regeneration field studies from which our data was compiled and descriptive attributes.

| Study | Ecoregion | State(s) | Forest Type(s) | Year Sampled - Fire Year | Shade-Tolerant Species Studied |
|--------------------------------|------------------|----------|-------------------------------------|--------------------------|--------------------------------|
| Andrus et al. 2021 | Southern Rockies | CO | Subalpine | 6, 7 | ABLA; PIEN |
| Busby et al. 2020 | Cascades | OR, WA | Moist mixed-conifer; subalpine | 4, 6 | ABLA; ABGR; ABAM; TSME; PIEN |
| Busby Unpublished | Cascades | OR, WA | Moist mixed-conifer; subalpine | 4, 7, 8, 11, 23 | ABLA; ABGR; ABAM; TSME; PIEN |
| Coop et al. 2010 | Southern Rockies | CO | Subalpine | 30 | ABLA; PIEN |
| Coop Unpublished | Southern Rockies | CO | Subalpine | 5 | ABLA; PIEN |
| Donato et al. 2016 | Northern Rockies | WY | Dry/moist mixed-conifer | 24 | ABLA; PIEN |
| Downing et al. 2019 | Blue Mountains | OR | Dry/moist mixed-conifer | 12, 15, 17 | ABGR; ABLA; PIEN |
| Dunn et al. 2020 | Cascades | OR | Moist mixed-conifer | 10, 22 | TSHE; CADE; THPL; ABCO |
| Harvey et al. 2014 | Northern Rockies | WY | Subalpine | 1, 2 | ABLA; PIEN |
| Harvey et al. 2016 | Northern Rockies | MT, WY | Subalpine | 10, 13, 14, 19 | ABLA; PIEN |
| Kemp et al. 2016 | Northern Rockies | ID, MT | Dry/moist mixed-conifer | 6, 13 | ABGR; ABLA; PIEN |
| Meigs et al. 2009 | Cascades | OR | Dry/moist mixed-conifer | 4, 5 | ABGR; CADE; TSHE; PIEN |
| Stevens-Rumann et al. 2014 | Northern Rockies | ID | Dry/moist mixed-conifer | 6 | ABGR |
| Stevens-Rumann and Morgan 2016 | Northern Rockies | ID | Dry/moist mixed-conifer | 7, 8, 14, 20, 25 | ABGR; ABLA; PIEN |
| Urza and Sibold 2017 | Northern Rockies | MT | Dry/moist mixed-conifer & subalpine | 7, 22 | ABLA; PIEN |

ABLA (*Abies lasiocarpa*); ABGR (*Abies grandis*); ABCO (*Abies concolor*); ABAM (*Abies amabilis*); CADE (*Calocedrus decurrens*); PIEN (*Picea engelmannii*); THPL (*Thuja plicata*); TSME (*Tsuga mertensiana*); TSHE (*Tsuga heterophylla*).

Table 5. Functional trait values (relativized z-scores) and fire resilience scores quantified on the interval scale among shade-tolerant conifer species observed in our field data.

| Species | Functional Traits | | | | | Fire Resilience Score |
|--|-------------------------|---------------------------|---------------------------|-----------------------------------|----------------------|-----------------------|
| | Shade Tolerance (0 - 5) | Drought Tolerance (0 - 5) | Mean Germination Rate (%) | Mean Juvenile Growth Rate (cm/yr) | Mean Seed Weight (g) | |
| Grand fir (<i>Abies grandis</i>) | 4.01 (0.46) | 2.33 (0.49) | 40 (0.41) | 80 (1.0) | 0.021 (0.62) | (0.57) |
| Pacific silver fir (<i>Abies amabilis</i>) | 4.21 (0.57) | 0.83 (0) | 20 (0) | 15 (0.07) | 0.034 (1) | (0.11) |
| White fir (<i>Abies concolor</i>) | 4.07 (0.49) | 1.91 (0.36) | 35 (0.31) | 40 (0.35) | 0.029 (0.82) | (0.36) |
| Subalpine fir (<i>Abies lasiocarpa</i>) | 4.83 (0.93) | 2.02 (0.40) | 34 (0.29) | 15 (0.07) | 0.012 (0.32) | (0.31) |
| Engelmann spruce (<i>Picea engelmannii</i>) | 4.53 (0.75) | 2.58 (0.59) | 69 (1.0) | 15 (0.07) | 0.003 (0.06) | (0.58) |
| Western red cedar (<i>Thuja plicata</i>) | 4.73 (0.87) | 2.23 (0.47) | 65 (0.92) | 12 (0.04) | 0.001 (0) | (0.53) |
| Incense Cedar (<i>Calocedrus decurrens</i>) | 3.21 (0) | 3.79 (1) | 30 (0.20) | 8 (0) | 0.030 (0.87) | (0.47) |
| Western hemlock (<i>Tsuga heterophylla</i>) | 4.96 (1) | 1.17 (0.11) | 55 (0.71) | 60 (0.57) | 0.0021 (0.02) | (0.53) |
| Mountain hemlock (<i>Tsuga mertensiana</i>) | 4.48 (0.73) | 1 (0.06) | 63 (0.88) | 25 (0.18) | 0.0023 (0.03) | (0.48) |

Functional traits were quantified using results from prior silvicultural studies and reviews. Mean germination rate, juvenile growth rate, and seed weight estimates were extracted from the Fire Effects Information System (FEIS; Abrahamson 2018). Shade tolerance and drought tolerance estimates were extracted from Niinemets and Valladares (2006). The fire resilience score was calculated as the average of z-score values for drought tolerance, mean germination rate, mean juvenile rate, and the inverse of mean seed weight and shade tolerance.

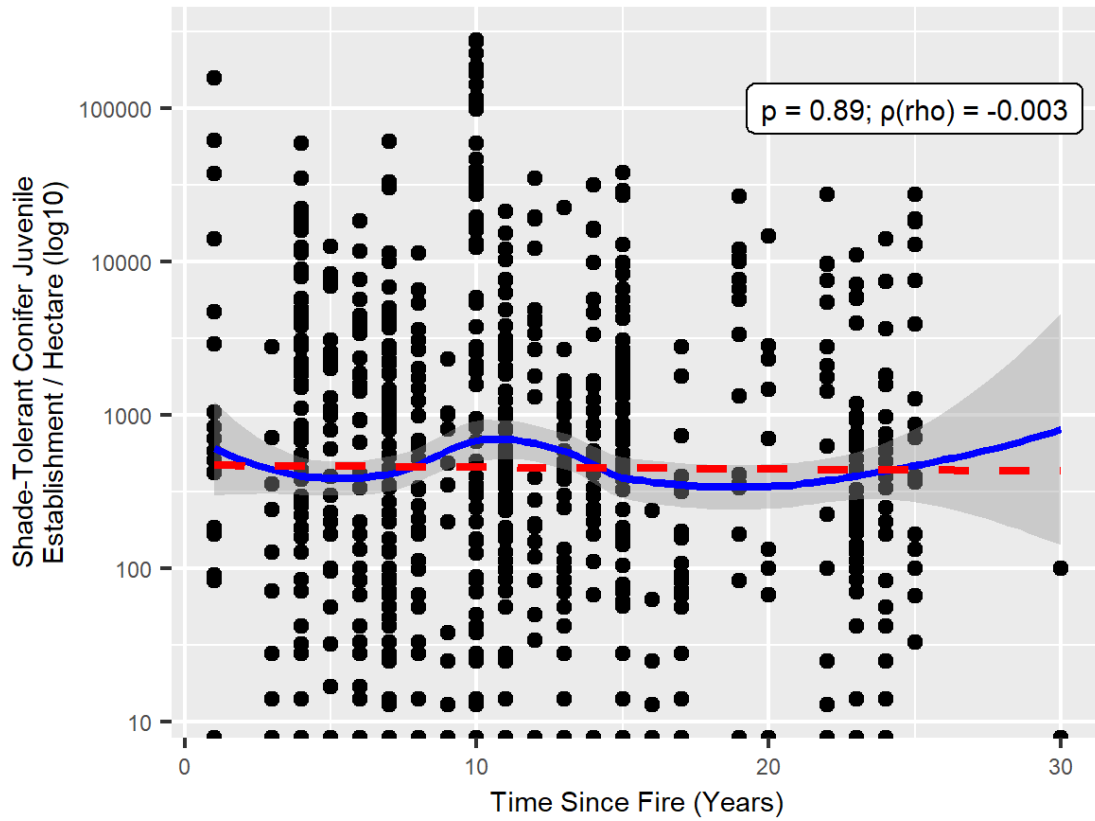


Figure 8. Linear (red dashed line) and smoothed non-linear (solid blue line; loess smooth) relationships between time since fire and shade-tolerant conifer establishment (juvenile density) across all ecoregions and sites where conifer establishment was present ($n = 1409$). Spearman's correlation test indicated no significant ($\alpha = 0.05$) relationship was observed between shade-tolerant conifer establishment and time since fire.

Conclusion

As shifting wildfire patterns and climate conditions continue to challenge the resilience and long-term persistence of conifer species and conifer forest types in North America, and specifically the western US, responses from the past and/or present-day analogs can help inform the fate of conifer forests in the future. Where past data is limited and/or emerging conditions have no analog, however, active study and analysis of conifer species' post-fire mortality and regeneration responses, as conducted in this dissertation, can aid in understanding, predicting, and preparing for inevitable forest ecosystem change. Considering the functionally diverse array of conifer species distributed across North America, quantifying species' functional traits within frameworks of fire resistance and resilience may guide improved understanding of species' responses across heterogeneous environments and a range of fire patterns and climate conditions, including those that are novel. When the expression of species' functional traits is well understood, the spatially explicit characteristics of seed source legacies on landscapes, over time, coupled with climate-environment conditions, can be used to predict post-fire conifer forest recovery responses and trajectories at fine to coarse scales.

Contribution of research and future directions

In Chapter 1, I found that fine-grain seed source availability from fire refugia, derived from remote sensing and a distance²-weighted density (D²WD) approach, can be used to accurately model and predict post-fire seed dispersal patterns and subsequent

mesic subalpine forest recovery responses after expansive high-severity wildfires. Further, I show how the spatial and structural characteristics of fire refugia interact with climate-environment conditions to alter recovery responses. Conceptually, this work demonstrates how the contribution of fire refugia to forest recovery may vary greatly due to forest structure, composition, and environmental moisture gradients. Thus, greater seed pressure is necessary in dry environments relative to wet environments to initiate the same tree establishment response, and seed pressure itself may vary based on (1) the quantity of seed sources surrounding a site, (2) their individual distances to a site, (3) their structural characteristics like height and potentially size or age, and (4) the expression of their fire resilience functional traits (i.e., seed dispersal and seedling establishment and survival abilities). The refugia D²WD metric, used in this study and others to accurately quantify seed source availability, seed pressure, and thus tree establishment responses, could be further improved by weighting seed source attributes. If tree composition or structure can be identified at fine-to-moderate spatial resolutions using remote sensing, attributes like tree height, age, size, or species could be used to weight the refugia D²WD metric further to improve estimates of seed pressure and thus post-fire tree establishment responses.

In Chapter 2, I discovered that delayed conifer tree mortality between one- and - five years post-fire occurs across broad ecoregions in the western US at an ecologically significant rate, that further varies with spatial scale. Additionally, I show that delayed tree mortality responses can substantially reduce post-fire seed source availability necessary for conifer forest recovery at large scales, and especially within forest types

where pre-fire forest density and contiguity are lower, and climatically favorable opportunities for post-fire seedling establishment are less frequent. Considering the predictive accuracy of the statistical models developed in this work, to determine drivers of delayed mortality responses were only fair, future modelling efforts would likely benefit from testing and accounting for the influence of other conceptually important factors. These factors might include presence and severity of pre- and post-fire compound disturbances (e.g., insect outbreak, pre-fire drought), stand competition, and fine-grain forest structure and/or composition. Finally, to improve accurate detection of delayed tree mortality responses via remotely sensed imagery through time, future work should utilize time series data (i.e., more than two images), when possible, over the more traditional image pair methodology used in this study and most others.

In Chapter 3, I show that shade-tolerant conifer species are capable of significant early seral juvenile establishment and dominance, across four major ecoregions in the western US, after moderate- to severe-fire effects. Further, statistical models developed in this work indicated that shade-tolerant conifer establishment and dominance was strongly associated with environmental moisture deficit, primarily manifested through coarse scale climate conditions, and the expression of species' functional traits tied to fire resilience (i.e., seed dispersal and juvenile establishment and survival), but not shade-tolerance. Together, these results provide evidence to challenge the generalized notion that shade-tolerance determines conifer species' regeneration response and successional role after fire events, and instead supports understanding and predicting species' post-fire recovery responses via the expression of their functional traits and local climate-environment

conditions. Future work assessing conifer forest resilience to present and shifting fire and climate patterns may benefit from developing and utilizing more complex trait-response frameworks than this study. More comprehensive quantification of conifer species' functional traits, which contribute to fire resilience and resistance, may provide effective tools for testing and predicting species' persistence in response to present and changing fire patterns and climate conditions