Landscape connectivity and recovery from disturbance: Understanding where and when to implement climate-change adaptation strategies

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Abstract

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As the planet warms, conservation planners and natural resource managers are seeking ways to help species and ecosystems adapt to climatic changes and shifting disturbance regimes. For example, enhancing landscape connectivity may support species' movements to track suitable climatic conditions, and promoting regeneration after disturbance (e.g., wildfire) may ensure robust system recovery. But understanding where and when to implement these climate-change adaptation strategies requires a nuanced understanding of how species and ecosystems respond to climatic variability in time and space. In my dissertation, I address this need through two major projects, complementing each research effort with a conceptual review of the state of the science and future frontiers. First, I mapped key areas likely to facilitate climate-driven species' movements across western North America by linking historic and future climate analogs. My results suggest that *not* including climate projections in connectivity models (i.e., basing connectivity solely on human modification of the landscape) or simplifying the temporal resolution of climatic changes may overestimate species movement and miss critical pathways. Second, I examined how contemporary climatic variability constrains post-fire recovery a decade after stand-replacing wildfire on the eastern slopes of the North Cascades. Juvenile conifer establishment and growth patterns reflected the convergence of ecological, physiographic, and climatic influences operating at multiple spatial and temporal scales, but adequate seed delivery and benign post-fire climatic conditions were key factors in ensuring relatively robust recovery across topographic settings. However, these facilitative factors may diminish as climate change unfolds. Both of these projects—modeling connectivity for climate-driven movements and uncovering the spatio-temporal patterns of post-fire recovery—may help planners and managers to prioritize where and when to implement climate-change adaptation strategies in an uncertain future.

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Chapter 1. CONNECTING TODAY'S CLIMATES TO FUTURE CLIMATE ANALOGS TO FACILITATE MOVEMENT OF SPECIES UNDER CLIMATE CHANGE

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1.1 ABSTRACT

Increasing connectivity is an important strategy for facilitating species range shifts and maintaining biodiversity in the face of climate change. To date, however, few researchers have included future climate projections in efforts to prioritize areas for increasing connectivity. We identified key areas likely to facilitate climate-induced species movement across western North America. Using historical climate data sets and future climate projections, we mapped potential species movement routes that link where current climate conditions are to where those conditions will occur in the future (i.e., future climate analogs) with a novel moving-window analysis based on electrical circuit theory. In addition to tracing shifting climates, the approach accounted for landscape permeability and empirically derived species' dispersal capabilities. We compared connectivity maps generated with our climate-change-informed approach with maps of connectivity based solely on the degree of human modification of the landscape. Including future climate projections in connectivity models substantially shifted and constrained priority areas for movement to a smaller proportion of the landscape than when climate projections were not considered. Potential movement, measured as current flow, decreased in all ecoregions when climate projections were included, particularly when dispersal was limited, which made climate analogs inaccessible. Many areas emerged as important for connectivity only when climate change was modeled in 2 time steps rather than in a single time step. Our results illustrate that movement routes needed to track changing climatic conditions may differ from those that connect present-day landscapes. Incorporating future climate projections into connectivity modeling is an important step toward facilitating successful species movement and population persistence in a changing climate.

1.2 INTRODUCTION

Anthropogenic climate change is driving species range shifts on every continent (Parmesan & Yohe 2003). Paired with paleoecological evidence of species movements during past climate changes (Davis & Shaw 2001), these current trends strongly suggest that range shifts will continue under even the most modest of future climate-change scenarios (Settele et al. 2014). If species are unable to track shifting climatic conditions because of dispersal constraints or anthropogenic barriers to movement, they may experience declines in abundance or even extinction (Thomas et al. 2004; Sinervo et al. 2010). Accordingly, increasing connectivity—the degree to which organisms can move through a landscape (Taylor et al. 1993)—is the strategy most frequently invoked to facilitate species range shifts and, more broadly, conserve species diversity in a warming world (Heller & Zavaleta 2009). However, incorporating future climate projections into efforts to both identify important movement routes and target areas for increasing connectivity remains a significant, unresolved challenge.

1.2.1 *Species movement under climate change*

Climate change challenges the effectiveness of traditional connectivity planning approaches that aim to facilitate movement between protected areas. Species' movements to track suitable climatic conditions may reduce the effectiveness of protected areas that are fixed in space, and species may encounter new anthropogenic barriers as they move (Peters & Darling 1985; Hannah 2011). Thus, maintaining or increasing connectivity under climate change may involve a temporal and directional consideration that strategies focused solely on connecting present-day landscapes do not necessarily require (e.g., movement corridors between existing protected areas) (Groves et al. 2012).

Future species distributions depend on myriad factors such as species-specific habitat requirements, biotic interactions, and species' capacities to adapt to changing climatic conditions in place. However, paleoecological records and observed species movements in response to contemporary climate change indicate that many species will shift their ranges to track suitable climatic conditions (Davis & Shaw 2001; Parmesan & Yohe 2003). Future climate analogs (i.e., climatic conditions that are analogous to those that exist today [Ohlemüller et al. 2006; Carroll et al. 2015]) must therefore be within reach. Enhancing connectivity under climate change (e.g., with landscape corridors, stepping-stone reserves, or increased matrix permeability [Krosby et al. 2010]) would thus ideally accommodate the individualistic responses of multiple species simultaneously. In all cases, species' dispersal capabilities and, relatedly, the accessibility of suitable climate conditions in the future will govern the effectiveness of connectivity-enhancing strategies (Urban et al. 2013).

1.2.2 *Predicting landscape connectivity*

Despite the acknowledged importance of these dynamics associated with connectivity for addressing climate change (e.g., Lister et al. 2015; Robillard et al. 2015), we know of no examples either in the literature or implemented in conservation efforts that specifically include future climate projections and the accessibility of suitable climatic conditions in predicting landscape connectivity. Specifically, three key elements of predicting connectivity under climate change have not been addressed simultaneously: climate analogs and their accessibility as constrained by landscape permeability due to human modification and species dispersal capabilities.

Some studies bypass consideration of dispersal constraints by comparing the spatial overlap of current ranges with either projected future ranges or protected areas as an assessment of connectivity (e.g., Ordonez & Williams 2013; Vieilledent et al. 2013). Others incorporate more biological realism by comparing climate velocities with biotic velocities (e.g., Carroll et al. 2015) or with empirically derived species dispersal rates (e.g., Schloss et al. 2012). Only a few studies that assess whether species will be able to track suitable climates also consider landscape permeability (e.g., Schloss et al. 2012; Lawler et al. 2013), which will largely dictate the success of species movement. These studies, however, do not map specific routes and rely on data-intensive species distribution models. Furthermore, studies that incorporate climate projections, either to compute climate velocities or to generate species distribution models, often represent climate change as a single event (e.g., from a historical period to a point in the future), although climate change is a dynamic process that unfolds continuously.

Some connectivity efforts that consider landscape permeability and protected-area configuration do not rely on future climate projections but instead rely on the first principles that govern the distribution of climatic conditions, for example, the principle that higher latitudes and elevations will tend to remain relatively cooler than lower latitudes and elevations and that species may correspondingly shift uphill and poleward. Other studies have mapped connectivity in a manner that both accounts for human modification and tracks shallow climatic gradients (e.g., delineating routes with the most unidirectional change in present-day temperature [Nuñez et al. 2013; Burrows et al. 2014]). Still others connect basic elements of the landscape (e.g., land facets) as part of a geophysical-based approach that aims to conserve and connect arenas of biological activity under climate change (Anderson & Ferree 2010; Brost & Beier 2012).

Thus, a range of approaches has been used to assess the potential for successful species movement under climate change. However, without simultaneously considering future climate projections, landscape permeability due to human modification, and dispersal capabilities, our understanding of connectivity under climate change is limited. We sought to address some of these limitations through a novel approach based on electrical-circuit theory to map connectivity between historical and future climate analogs across a human-modified landscape. We defined climate analogs based on their multivariate similarity and constrained potential areas of connectivity by dispersal rates that reflect a range of taxa. We use multiple climate-change scenarios and two time steps to assess how varying degrees of climate change and the temporal resolution at which climate change is modeled affects inferences about potential species movement.

1.3 METHODS

1.3.1 *Climate Data*

We used historical climate data sets and future climate projections for western North America and areas therein that were downscaled using the ClimateNA version 5.10 software package (Wang et al. 2016). The software downscales the PRISM 4-km data (Daly et al. 2002) to

1-km gridded data sets and applies a dynamic lapse-rate adjustment that accounts for local spatial and temporal variability in lapse rates (Wang et al. 2016). We used the following 10 variables, with appropriate transformations to normalize their distributions (Supporting Information), mapped at 1-km resolution: mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, difference between the mean temperature of the warmest and coldest months, mean annual precipitation, total summer precipitation, Hargreaves reference evaporation, summer heat-moisture index, number of frost-free days, and number of degree days above 5 °C.

We used the 1961-1990 climate normal period for historical climate conditions. We used future climate projections for 2041-2070 and 2071-2100 (hereafter, the 2050s and the 2080s, respectively) downloaded from the CMIP5 multimodal data set (Taylor et al. 2012) and based on the business-as-usual representative concentration pathway (RCP) 8.5 scenario (IPCC 2013). We used the projections from three global circulation models (GCMs): INM CM4 (Volodin et al. 2010), which projects mild climate change for the study area; MIROC5 (Watanabe et al. 2010), which projects moderate change; and GFDL CM3 (Donner et al. 2011), which projects considerable change.

1.3.2 *Climatic niche breadth and climate analogs*

We identified climate analogs between historical and future climatic conditions based on their multivariate similarity (following Hamann et al. 2014). Using principal component analysis (PCA), we generated a multivariate measure of climate for each 1-km cell in the study area to reduce the dimensionality of the nine-variable data set and minimize the influence of highly correlated climate variables. The first and second principal components explained 87.5% of the variance in the initial data set (Supporting Information), and we applied the scores of these two components to each 1-km cell.

To define climate analogs, we established a similarity threshold below which two cells would be considered analogous. We determined this threshold by calculating climatic niche breadths of species ranges, which were based on digital range maps for 200 birds (Birdlife International 2014), 450 mammals (Patterson et al. 2007), 498 amphibians (IUCN 2014), and 24 tree species in North America (Roberts & Hamann 2012). To calculate niche breadth for each species, we plotted the geographic range in the two-dimensional principal component space, identified the median centroid of this distribution, and calculated the radius of a circle that would capture 75% of the points within the distribution to use as a niche breadth. The median niche breadth was narrowest for amphibians (0.9 PCA units) relative to trees, mammals, and birds (1.5 PCA). We selected the conservative 0.9 PCA unit threshold for identifying climate analogs between historical and future climatic conditions.

1.3.3 *Connecting climate analogs*

We used Circuitscape (McRae et al. 2013) with a novel moving-window algorithm (McRae et al. 2016) to quantify potential species movement—measured as current flow—between historical climates and their future analogs. Circuitscape models connectivity on the basis of electrical circuit theory, treating landscapes as conductive surfaces and replacing cells connected to their neighbors with nodes connected by resistors. Patterns of electrical current (in amperes [amps]) predict the movement patterns of random walkers between source and target cells across a landscape (here between pairs of cells with analogous historical and future climates), where walkers are proportionally more likely to move through intervening low-resistance cells than high-resistance cells. The result of the moving-window analysis is a continuous map of current flow across all possible routes between source and target cells (McRae et al. 2008; Lawler et al. 2013)—here across all possible routes between climate analogs. The more current (amps) flowing through a given cell, the more individuals or more individual movements one might expect to go through that cell.

We used the degree to which the landscape had been altered as a measure of resistance to movement. The values in the human-modification index ranged from 1 to 100 (Theobald 2013, 2016). We squared these values to produce a more effective and meaningful resistance layer. Given that such a transformation is somewhat arbitrary, we compared our results with those produced using an untransformed set of values and those produced using an alternative transformation (Supporting Information). Because we sought to model connectivity between the most natural areas on the landscape, we constrained sources and targets (i.e., climate analogs) to those cells with the lowest human modification index value (1). These included areas represented 84% (9,116,817 km^2) of the overall study area (Supporting Information).

Rather than treating the landscape as a conductive surface with a limited number of fixed source cells and target cells, the moving window iteratively enabled every cell that met our naturalness criteria to act as a target for current flowing from sources (i.e., matching historical climates) within the moving window (McRae et al. 2016). We summed the current within each moving window across the study area, thereby generating a continuous map that summarized movement probabilities between all source and target cells (i.e., between all historical and future climate analogs, respectively) (Figure 1.1). Thus, high densities of current flow indicated important movement pathways between analogous historical and future climates. For comparison purposes, we also modeled connectivity, more conventionally, without matching climate analogs to see how their inclusion would shift patterns of current flow and hence movement pathways. In this case, without matching climate analogs, all cells within areas with the lowest human-modification value (1) could act as sources and targets.

Because species' dispersal capacities will constrain their ability to reach suitable climatic conditions, we limited potential analogs to those within specified sets of search radii. These radii were derived from reviews of maximum known dispersal distances for amphibians, mammals, and birds. Specifically, we used a 0.5-km annual dispersal distance, which represents the majority of amphibian species (Smith & Green 2005). We contrasted this limited dispersal capability with a 5-km annual dispersal distance, which represents most small mammals and dispersal-limited terrestrial birds (Sutherland et al. 2000, Bowman et al. 2002). These values were multiplied by the number of years in each period and then used as moving-window search radii. Dispersal distances of 0.5 km and 5 km corresponded to radii of 40 km and 400 km (historical to 2050s), 55 km and 550 km (historical to 2080s), and 15 km and 150 km (2050s to 2080s). When applied in the connectivity analyses, greater search radii values reflected increasing accessibility of distant climate analogs.

In summary, we modeled connectivity between climate analogs in a manner that reflects species-based climate-niche breadths, landscape resistance due to human modification, and empirically derived dispersal capacities. We summarized the resulting patterns of potential movement across level I and level III ecoregions (U.S. EPA 2010). We conducted model runs in Python version 2.7, used ArcGIS 10.3 for creating maps, and used R 3.2.3 for post hoc calculations and plotting results.

1.4 RESULTS

Western North America's mountainous regions and narrow physiographic features consistently exhibited high current flow, and therefore are likely important pathways for potential future species movements. The importance of these areas increased as degrees of climate change increased. Under the mildest climate scenario, more climate analogs were within reach given that our moving-window search radius was designed to reflect dispersal constraints (0.5 km/year). Accordingly, there was some movement throughout most of western North America (INM CM4) (Figure 1.2a), including within flat ecoregions (level I) such as the interior northern forests and parts of the Great Plains that were not heavily modified by humans. By contrast, potential movement was drastically curtailed and constrained to mountainous ecoregions and narrow features such as isthmuses and peninsulas (e.g., Baja California) under the scenarios that portray moderate and considerable climate change (MIROC5 and GFDL CM3, respectively) (Figure 1.2b, Figure 1.2c). Even under moderate climate change (MIROC5), the flattest ecoregions (e.g., interior northern forests, taiga, and tundra) were predicted to have minimal current flow because climate analogs were not accessible (Figure 1.3).

Potential movement was highest in ecoregions (level III) with intermediate ranges of elevation and slope (e.g., the Columbia Plateau, the astern Cascades foothills) (Figure 1.4). Ecoregions with extreme topographic complexity and therefore localized diversity in climatic conditions (e.g., the Alaska Range, the Sierra Nevada) showed a moderate amount of potential movement. By contrast, our model predicted minimal or no movement in flat ecoregions dominated by agriculture (e.g., entral Great Plains, Willamette Valley).

Maps connecting climate analogs within a human-modified landscape highlighted different areas as being important for potential movement than maps that did not take climate analogs into account (Figure 1.5). Human modification largely determined the underlying permeability of the landscape and thus which parts of the landscape species could traverse, but including climate projections de-emphasized the importance of some pathways. For example, when we did not consider climate analogs, there was connectivity throughout an extensive lattice of narrow natural areas in places that were otherwise extensively cultivated (i.e., channeled scablands of southeastern Washington) (Figure 1.5b). In contrast, connecting climate analogs funneled current through a smaller proportion of the landscape and highlighted mountainous regions (Figure 1.5c). Thus, some areas that appeared important for species movement in the absence of climate change were less important for climate-induced movements, and new pathways became increasingly important under climate change (Figure 1.5d). More broadly, human modification severely restricted potential movement (Figure 1.5a vs. Figure 1.5c).

Modeling climate change in a single time step (i.e., historical to 2080s) obscured pathways that emerged as important for connectivity when we analyzed climate change in two time steps (i.e., historical to 2050s then 2050s to 2080s) (Figure 1.6). For example, some bottlenecks where movement was concentrated in the two shorter time steps were missed in the single time step (e.g., in the western-most foothills of the Cascades). Relative to a dispersal rate of 0.5 km/year, a rate of 5 km/year resulted in greater maximum movement across the landscape. Modeling climate change in a single time step and using this greater dispersal capability did not de-emphasized narrow pinch points that were highlighted in the two shorter time steps.

1.5 DISCUSSION

Incorporating climate projections in connectivity models substantially changed the roadmap for species movement. Connectivity maps that accounted for climate change highlighted a smaller number of specific locations where conservation efforts could be focused. By contrast, connectivity maps based solely on landscape permeability depicted more options for movement. Thus, excluding climate projections from connectivity models may result in an overly optimistic view of landscape connectivity and undervalue specific important connections. Furthermore, representing climate change in one time step obscured some critical pathways for dispersal-limited species that otherwise emerged when climate change was modeled incrementally in two time steps. These results suggest that simplifying the temporal resolution of climate change may miss some important links for climate-induced species movement and that approaches that go beyond a single time step—or even two time steps—to explore climate change as more of a continuous process are likely warranted.

1.5.1 *Drivers of Potential Movement*

Because certain areas of the landscape consistently emerged as key pathways across multiple climate-change scenarios, we can have confidence in their conservation importance, despite inherent uncertainties in climate projections. The consistent importance of mountainous regions in our results reflects lower climate velocities therein (Hamann et al. 2014; but see Dobrowski & Parks 2016) and thus greater accessibility of analogous climates.

Ecoregions (level III) with the most extreme ranges of elevation and slope contain a diversity of climates such that species can make smaller spatial adjustments to track suitable climatic conditions. These areas also tend to have minimal human modification such that there are numerous movement routes. Thus, according to our model, these areas will likely have many small, successful movements but only moderate levels of overall movement. In some cases, however, cold climates in the highest terrain will have no analogs in the future and will likely disappear (Williams & Jackson 2007). Species that need to track such conditions will face climatic cul-de-sacs at the highest elevations and are therefore disproportionately vulnerable to climate change (Ohlemüller et al. 2008; Carroll et al. 2015). Furthermore, the extreme topographic relief of some mountainous regions may hinder movement or introduce intervening climatic conditions in some potential pathways that render them impassable for some species (Dobrowski & Parks 2016).

Ecoregions with intermediate ranges of elevation and slope (e.g., mountain range foothills, high deserts) may harbor accessible climate analogs, but these are separated by greater distances (i.e., source and target cells are farther apart in our models). These greater distances required more overall movement and accordingly resulted in higher mapped current flow in our models. By contrast, minimal to no movement was predicted for the lowest and flattest ecoregions, where climate velocities were too high for climate analogs to be within reach. Humans have the largest effect on landscape permeability in the lowest-lying areas (e.g., due to coastal cities and agriculture [Seto et al. 2011]). As such, these heavily human-dominated areas contained few source and target cells (i.e., climate analogs) that could be connected, given our model parameterization.

1.5.2 *Missed Connections*

Human modification already restricts species movement across landscapes, and the added constraint imposed by climate change highlighted a further reduced set of areas as important movement pathways. Indeed, prioritizing areas for connectivity enhancement based on human modification alone would miss some areas projected to be important for climate-induced movement.

Overlooking the fact that climate change is a dynamic process that unfolds continuously in time may also miss critical pathways. Most studies that model where species may find suitable climate conditions in the future (e.g., species-distribution models) either model climate change as a single event or average projected changes over multiple years. Realistically, climate change will be highly dynamic with fluctuations above and below the dominant directional change that unfolds over long periods (Easterling et al. 2000; Early & Sax 2011). The ability of species to reach suitable climatic conditions in the future will also strongly depend on population dynamics and dispersal processes that play out continuously through time (Keith et al. 2008; Early & Sax 2011).

In our models, mapping connectivity in a single time step obscured pathways that were important for dispersal-limited species when two successive time steps were used and that occurred in areas more susceptible to human modification (e.g., low-elevation coastal zones). In some cases, narrow pinch points, where movement is funneled between climate analogs, in two time steps were downplayed in the single, extended time step. We attribute this difference to the fact that modeling climate change in one longer time step entailed a larger search radius (due to the potential for longer movements over that longer period) and hence more analogs to be connected. There were also more, alternative routes between analogs when a larger search radius was used, so movement may not be restricted to narrow pinch points. Thus, conservation prioritization decisions based on a single, extended time step will likely miss important movement areas, particularly over short periods and for dispersal-limited species for which intermediate stepping stones will be important (Hannah et al. 2014). Instead, using multiple time steps could help identify such stepping stones or siting of movable targets for conservation that could be shifted in space over time. Our models did not represent climate change continuously, but they suggested a broader need in conservation decision-making contexts to consider climate change as a dynamic process that unfolds continuously.

1.5.3 *Model Limitations*

Our framework represents an important advance in incorporating future climate projections, human modification of the landscape, and dispersal capabilities into modeling connectivity under climate change. However, as have others modeling connectivity, we made several simplifying assumptions. First, the pathways between climate analogs may have traversed either intervening climatic conditions that would not be suitable for some species (Nuñez et al. 2013; Dobrowski & Parks 2016) or physiographic barriers (e.g., mountain ranges) that, in reality, may constrain movement. Therefore our models likely overestimated the potential for movement in some places. In the inverse, our approach did not take fine-scaled topoclimate processes into account, which may provide climate microrefugia to dispersing species (Dobrowski 2011; Hannah et al. 2014). We also used a static map of human modification of the landscape even though human population will continue to grow and human land-use patterns will continue to change.

Our approach is biologically informed (i.e., with climatic niche breadths and dispersal abilities), but it is not a species-specific approach. Although one could apply the approach to an individual species, we argue that there are merits to both species-specific and more generalized connectivity modeling approaches. Recent reviews suggest conservation planners use a suite of modeling methods that span a range of complexity, including both species-specific approaches and approaches that are not species-specific (Gillson et al. 2013; Schmitz et al. 2015). Ours is a coarse-filter approach that identifies areas through which a diversity of species may need to move to track suitable climates. This approach may capture the movements of many species for which building individual models would be difficult if not impossible (e.g., due to lack of data necessary to define landscape resistances or dispersal abilities). One could imagine complementing our approach with species-specific models for species with specialized habitat needs, restricted-range species with isolated remnant populations, or other species that might fall through a coarse filter.

We applied our approach over a relatively broad extent to model connectivity across western North America. Such an application relies on general climatic patterns (e.g., latitudinal gradients, elevation-driven gradients, and marine influences), and it likely missed some of the more localized patterns driven by unique or relatively infrequently occurring drivers. One could apply the same approach to a smaller region to highlight more fine-scale, region-specific movement routes. By modeling a large spatial extent, we minimized the relative influence of edge or boundary effects and captured broad-scale potential movements. Nonetheless, our results are less meaningful at the inland edges of the study area, where connections to places outside the study area may be as important or more important than connections within it, and our results are less meaningful in locations with unique climatic gradients.

1.5.4 *Planning for species movements*

Conservation actions in response to climate change are challenged by considerable uncertainty surrounding the rates, magnitudes, and ecological consequences of climate change (Kujala et al. 2013). Despite these uncertainties, conservation planners are necessarily prioritizing areas to protect with the aim of facilitating species movement and persistence under climate change (e.g., Ayebare et al. 2013; Anderson et al. 2014). Although some planners may avoid models that include future climate projections due to their uncertainty, our results suggest that in doing so planners may overlook critical locations for facilitating climate-induced movement.

Some existing networks of protected areas may be sufficiently connected de facto to facilitate species persistence and movement (Mazaris et al. 2013), whereas others may not (Scriven et al. 2015; McGuire et al. 2016). For example, in the United States alone, only 41% of natural land area may be sufficiently connected to ensure that plants and animals can successfully track suitable climatic conditions (McGuire et al. 2016). Similarly, we show that human modification of the landscape and the accessibility of climate analogs severely restricted movement options for species responding to climate change. Thus, prioritizing areas for enhancing connectivity in a climate-informed manner will be critical for facilitating species movement and the protection of biodiversity under a changing climate. This is particularly true because few other viable options (e.g., translocation) exist for many species. Specifically including future climate projections and the accessibility of suitable climatic conditions, given human modification of the landscape and dispersal capacities, will make these prioritization decisions more robust in an uncertain future of inevitable climatic and land-use change.

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FIGURES

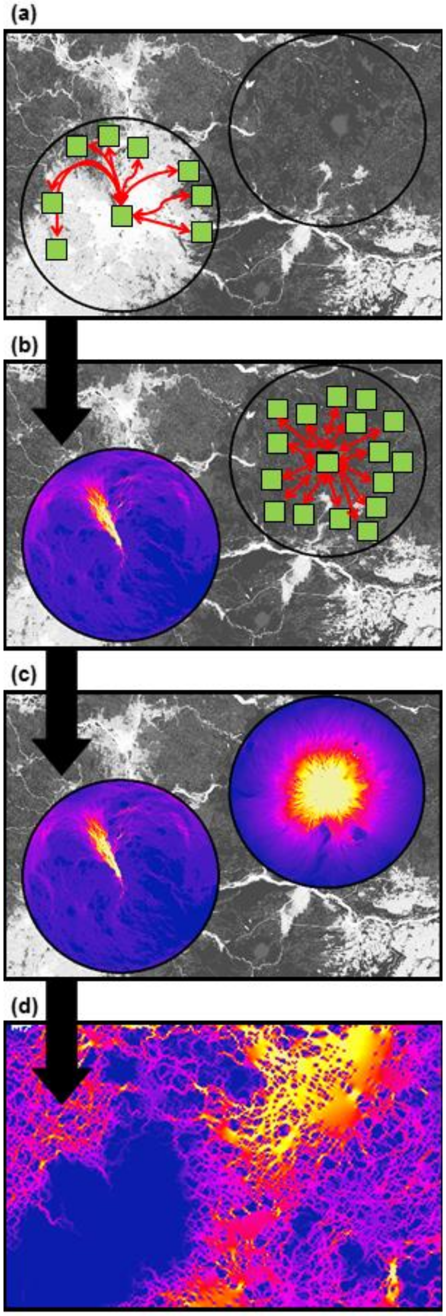

Figure 1.1. Conceptual illustration of the mapping of connectivity between where current climate conditions occur and where those conditions will occur in the future (i.e., climate analogs) in landscapes with varying degrees of human modification (darker grey regions are more natural, lighter regions are more affected by humans) based on electrical circuit theory. (a) Climate analogs in natural areas (green squares [enlarged for illustrative purposes]) within the Portland, Oregon, U.S.A., metropolitan area on the left and the more natural area surrounding Mt. Adams in

Washington State on the right (central green square, future climate conditions [i.e., the target]; other green squares, historical climatic conditions [i.e., sources]). In (a) 1 amp of current is injected into each source, and electrical current then flows between the climate analogs (red arrows) following low-resistance paths in the human-modified landscape (b, c) this procedure is repeated with a circular moving window across the landscape in a spatially continuous manner (windows are separated for illustrative purposes). (d) Continuous map of connectivity between historical and future climate analogs derived from the sum of potential movement within each moving window (low values of potential movement, measured as current flow in amps, in blue and high values in yellow).

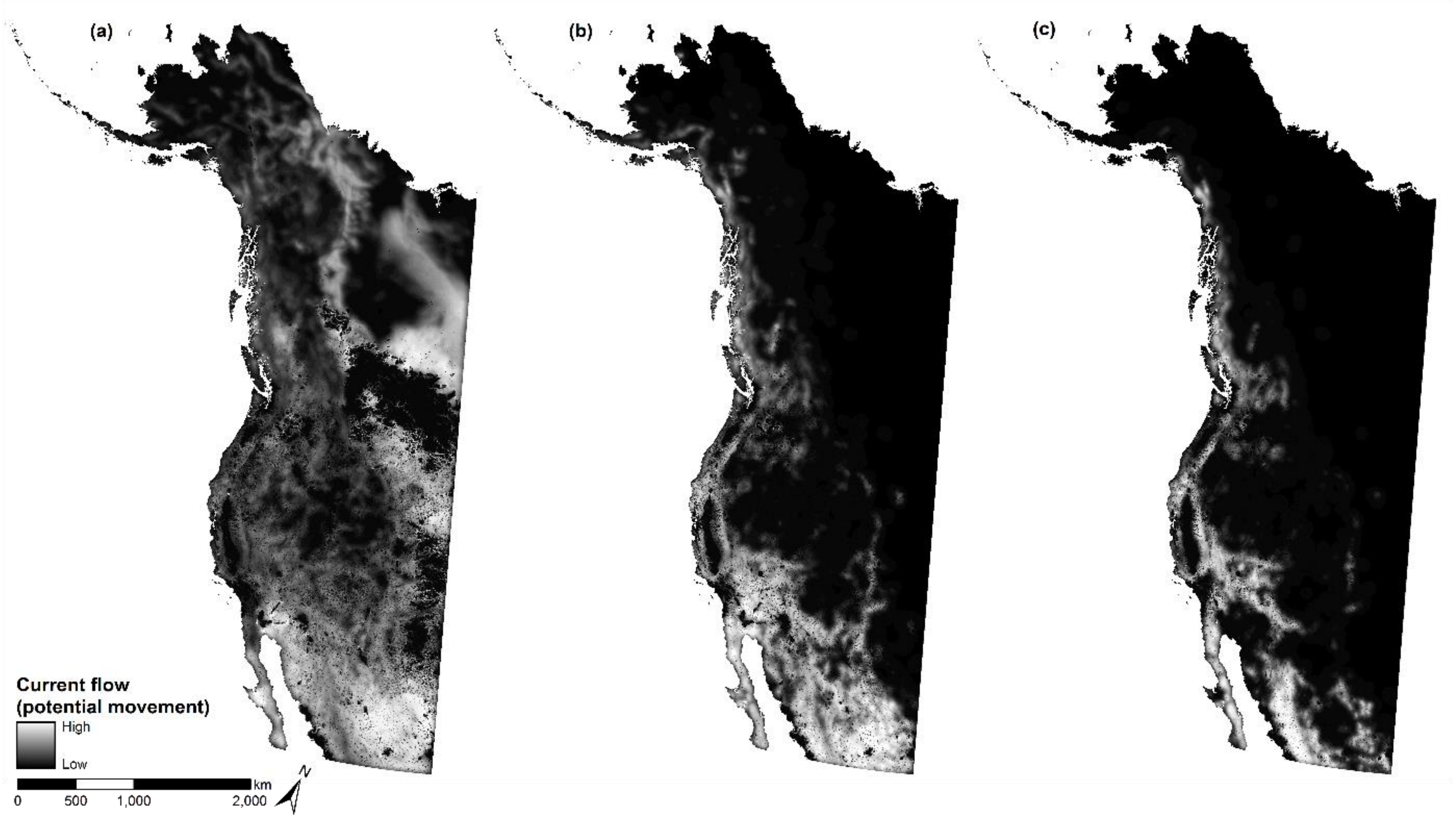

Figure 1.2. Potential species' movements (measured as current flow in amps) between areas of historical climates and their 2080s climate analogs under representative concentration pathway 8.5 as implemented in 3 global circulation models (GCM): (a) INM CM4, (b) MIROC5, and (c) GFDL CM3 (IPCC 2013; Volodin et al. 2010; Watanabe et al. 2010; Donner et al. 2011). Dispersal rate is 0.5 km/year. Shading reflects the values of potential movement for each GCM (maximum values: 2,645,580 amps for INM CM4, 1,250,170 amps for MIROC5, and 830,863 amps for GFDL CM3).

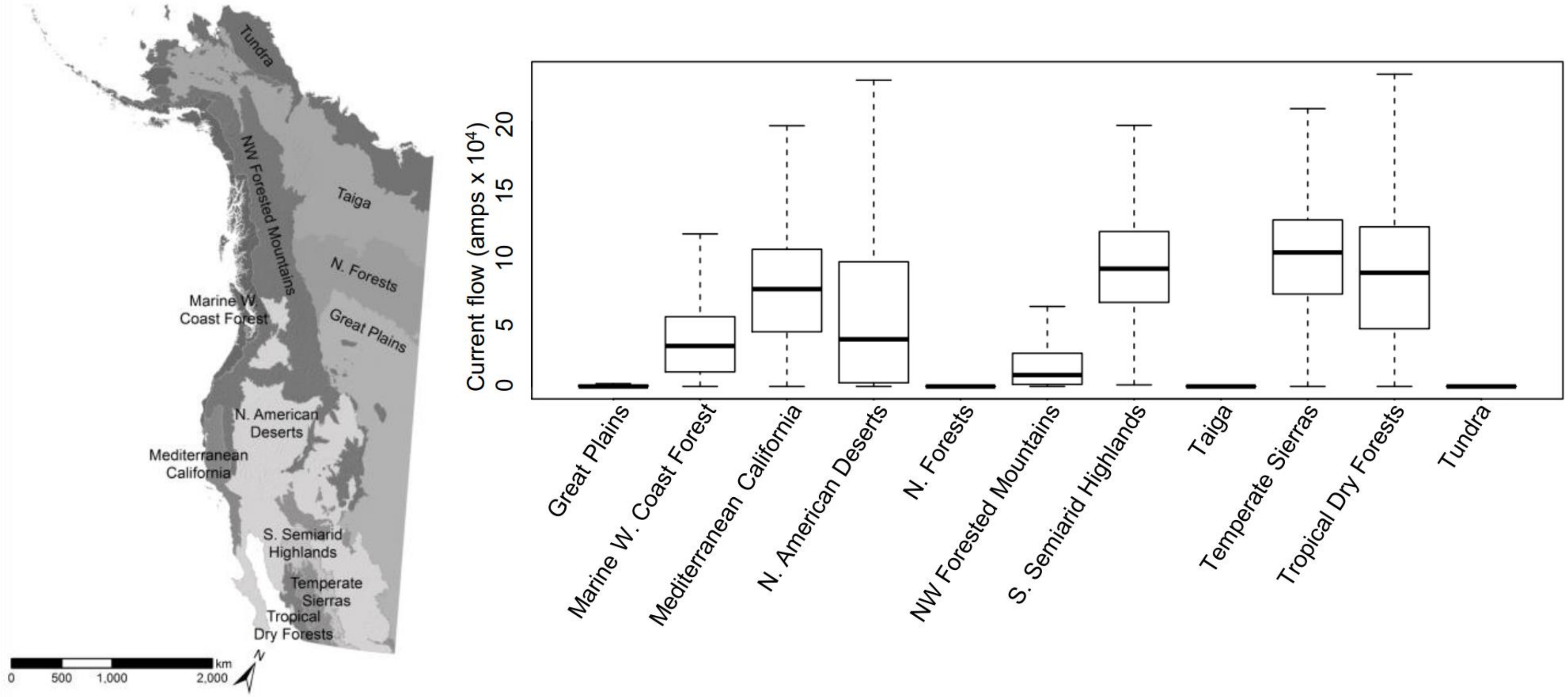

Figure 1.3. Potential species' movements by ecoregion (level I; U.S. EPA 2010) between areas of historical climates and their 2080s climate analogs under representative concentration pathway 8.5 as implemented by MIROC5, which projects moderate climate change for the study area (IPCC 2013; Watanabe et al. 2010). Dispersal rate is 0.5 km/year (boxes, 25th and 75th percentiles of values; horizontal lines, median ; whiskers, most extreme data points [i.e., potential movement value in a pixel within that ecoregion] that are ≤1.5 times the interquartile range from the box). Unplotted outliers do not exceed 10 x 10^4 amps for Northern Forest, Taiga, or Tundra; outliers for Great Plains, Mediterranean California, North American Deserts, Northwestern Forested Mountains, Southern Semiarid Highlands, Temperate Sierras, and Tropical Dry Forests range from 50 x 10^4 amps to 75 x 10^4 amps; and outliers for Marine West Coast Forest are up to 105 x 10^4 amps.

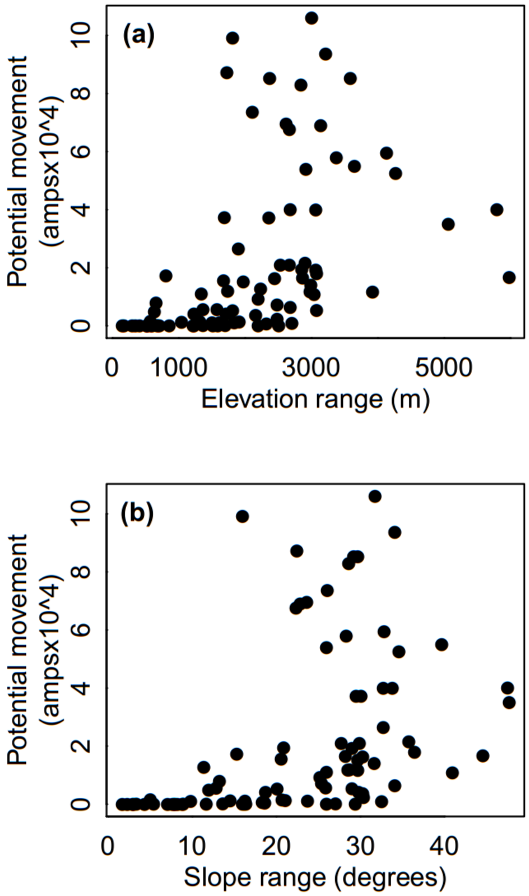

Figure 1.4. Average potential movement between areas of historical climates and their 2080s climate analogs in ecoregions (level III; U.S. EPA 2010) versus the ranges of (a) elevation and (b) slope therein. Potential species' movements are between historical climates and their 2080s climate analogs under representative concentration pathway 8.5, as implemented by MIROC5 (IPCC 2013; Watanabe et al. 2010. Dispersal rate is 0.5 km/year.

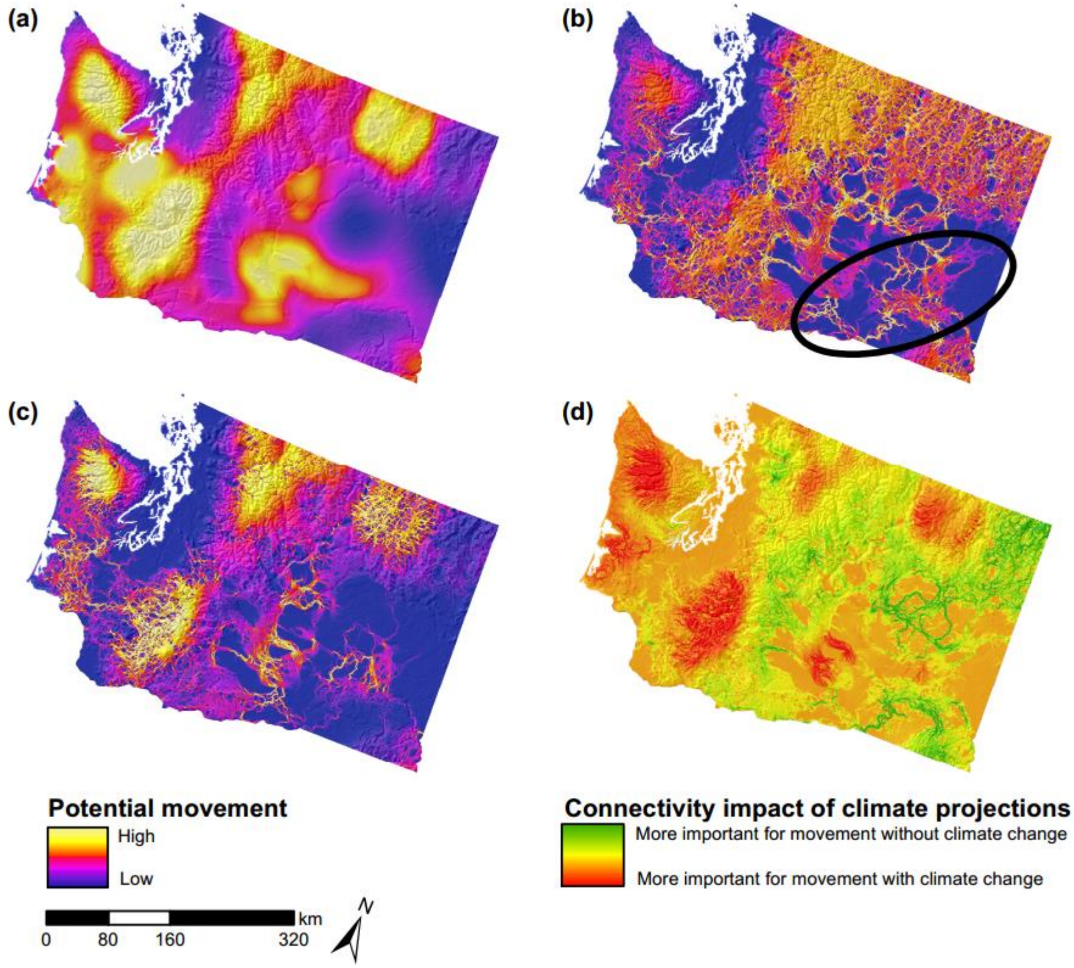

Figure 1.5. Potential species' movement in Washington State based on electrical circuit theory (a) between areas of historical climates and where those conditions will occur in the future (i.e., climate analogs) without considering human modification (i.e., a uniform resistance value of 1 across the study area and no naturalness criteria applied to climate analogs); (b) across a human-modified landscape but not including climate analogs (i.e., within a given moving window, Circuitscape injects current from all natural cells—not only matching climate analogs—that may then flow to the central target cell) (oval, channeled scablands of southeastern Washington); and (c) between climate analogs across a human-modified landscape (as per methods described in the text). The connectivity impact of climate projections (d) was computed by normalizing potential movement values that do (c) and do not (b) link climate analogs and then subtracting the former from the latter. . Sources and targets for connectivity (i.e., climate analogs) were constrained to only the most natural areas, except in (a). The color ramp of (a-c) reflects the low and high values of potential movement for each frame. Thus, colors are not directly comparable across frames and results should be interpreted with regards to relative importance of specific areas for potential movement. Analogous climates are defined for the historical period and the 2080s with MIROC5 projections under representative concentration pathway 8.5 (IPCC 2013; Watanabe et al. 2010). Dispersal rate is 0.5 km/year.

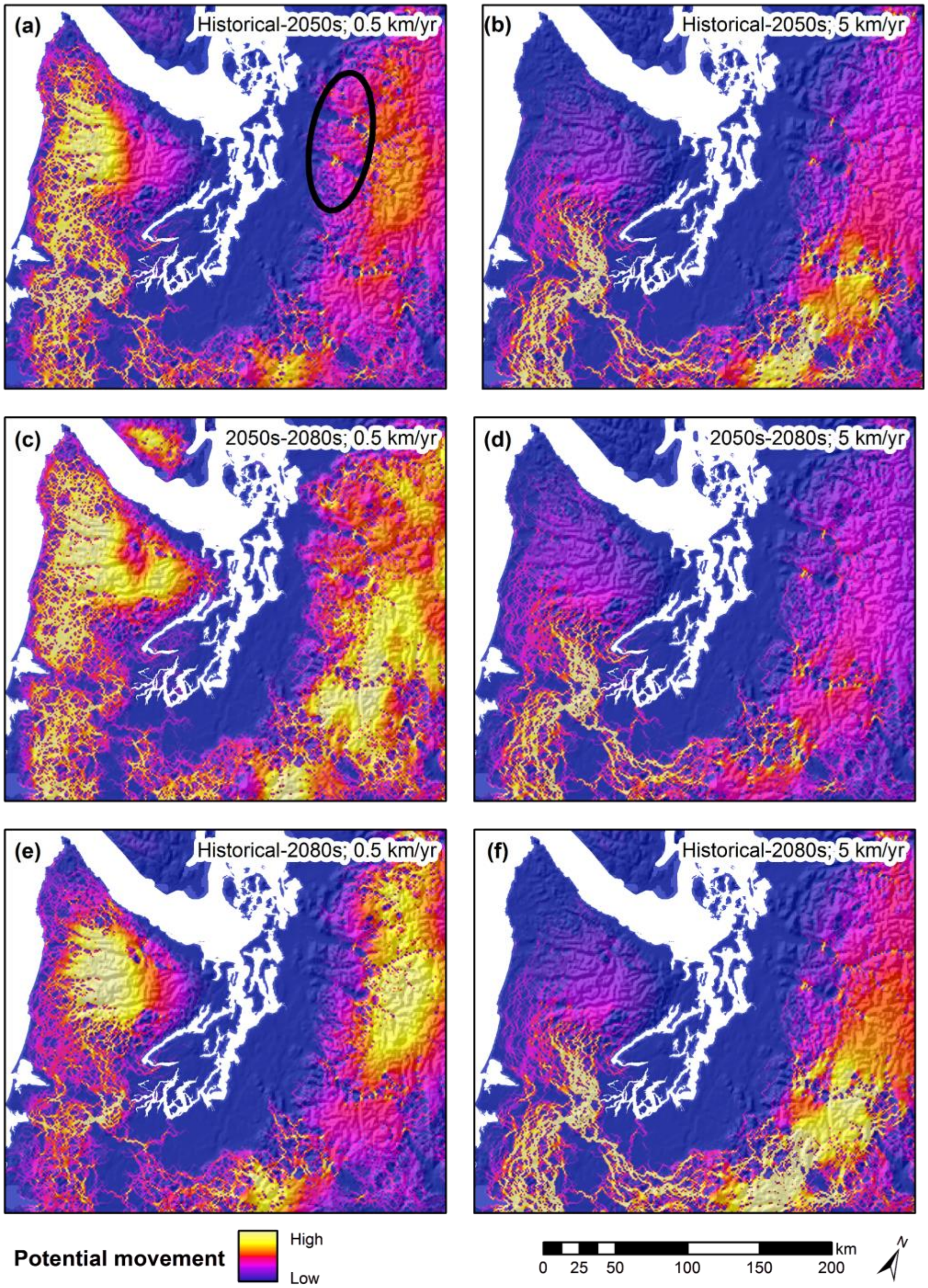

Figure 1.6. Potential species’ movements in 2 time steps for 1 and 2 different dispersal capacities across a human-modified landscape: (a, b) potential movement between areas of historical climates and their 2050s climate analogs (oval, western-most foothills of the Cascade Mountains); (c, d) potential movement between projected climate conditions in the 2050s and their 2080s climate analogs; and (e, f) potential movement between areas of historical climates and their 2080s climate analogs (i.e., 1 extended time step). Analogous climates were defined using MIROC5 projections under representative concentration pathway 8.5 (IPCC 2013; Watanabe et al. 2010). Sources and targets for connectivity (i.e., climate analogs) are constrained to only the most natural areas. The

color ramp reflects values of potential movement for each frame. Thus, colors are not directly comparable across frames and results should be interpreted with regards to relative importance of specific areas for potential movement.

APPENDIX 1.1 SUPPLEMENTARY METHODS AND RESULTS

Table A1.1 Transformations and loadings for each climate variable included in principal component analysis.

	Adjustments	Comp.1	Comp.2	Comp.3	Comp.4
Mean annual temp	none	-0.40	-0.04	-0.01	0.01
Mean temp coldest month	none	-0.39	-0.04	0.01	0.48
Mean temp warmest month	none	-0.37	-0.12	0.00	-0.74
Mean annual precip	log transformed	-0.21	0.50	0.25	0.03
Total summer precip	log transformed	-0.15	0.51	-0.40	-0.25
Total winter precip	log transformed	-0.15	0.38	0.73	0.00
Hargreaves reference evaporation	none	-0.38	-0.13	-0.17	0.22
Summer heat moisture	log-transformed	-0.08	-0.54	0.45	-0.16
Number frost free days	none	-0.39	-0.10	-0.06	0.26
Degree-days above 5°C	sqrt-transformed	-0.40	-0.09	-0.12	-0.14
		Comp.1	Comp.2	Comp.3	Comp.4
Standard deviation		2.47	1.62	0.93	0.45
Proportion of Variance		0.61	0.26	0.09	0.02
Cumulative Proportion		0.61	0.88	0.96	0.98

Table A1.2. Summary statistics and comparisons of component values for historical climate conditions and GCM projections.

Data	Min. component value	Max. component value	Mean component value	SD of component values	Mean difference between GCM and climate normal PC values
PC1: Climate normals (1961-1990)	-5.30	4.55	0.23	2.15	n/a
PC1: INM CM4 (2071-2100, RCP 8.5)	-5.75	3.94	-0.64	2.04	-0.86
PC1: MIROC5 (2071-2100, RCP 8.5)	-5.98	3.76	-1.09	1.85	-1.31
PC1: GFDL CM3 (2071-2100, RCP 8.5)	-6.14	3.48	-1.36	12.79	-1.58
PC2: Climate normals (1961-1990)	-7.83	5.87	0.50	1.67	n/a
PC2: INM CM4 (2071-2100, RCP 8.5)	-8.07	5.95	0.54	1.82	0.04
PC2: MIROC5 (2071-2100, RCP 8.5)	-7.94	6.42	0.72	1.79	0.22
PC2: GFDL CM3 (2071-2100, RCP 8.5)	-7.94	7.13	0.56	1.94	0.06

Table A1.3. Level I ecoregion areas and degrees of human modification

Ecoregion	Total area (square km)	Area of lowest human modification value (hm=1, in square km)	Percentage of ecoregion area with hm=1
Great Plains	1,663,129	909,139	54.66%
Marine W. Coast Forest	568,050	508,532	89.52%
Mediterranean California	217,571	115,824	53.24%
N. American Deserts	2,237,750	1,862,425	83.23%
N. Forests	815,494	698,884	85.70%
NW Forested Mountains	2,007,597	1,810,439	90.18%
S. Semiarid Highlands	195,980	177,345	90.49%
Taiga	1,721,382	1,715,170	99.64%
Temperate Sierras	290,150	264,171	91.05%
Tropical Dry Forests	118,993	91,945	77.27%
Tundra	967,025	962,943	99.58%
Total	10,803,121	9,116,817	n/a

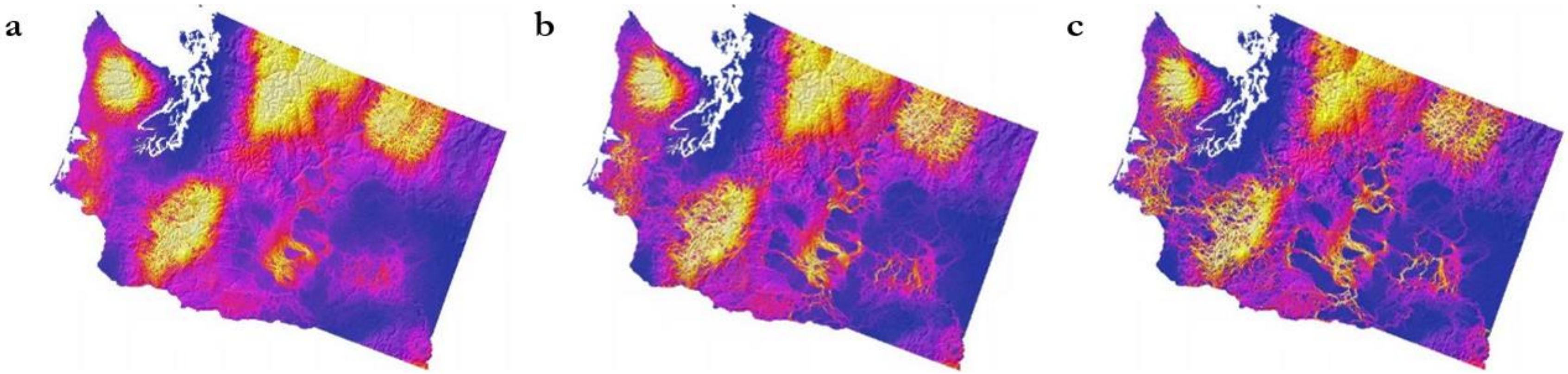

Figure A1.1. Potential movement in Washington State between climate analogs across a human-modified landscape with resistance values expressed differently: a) square root of original resistance values (sqrt[1-100]); b) no modification to original resistance values (1-100); c) squared resistance values ([1-100]2). Yellow areas have more potential movement and blue areas have less potential movement.

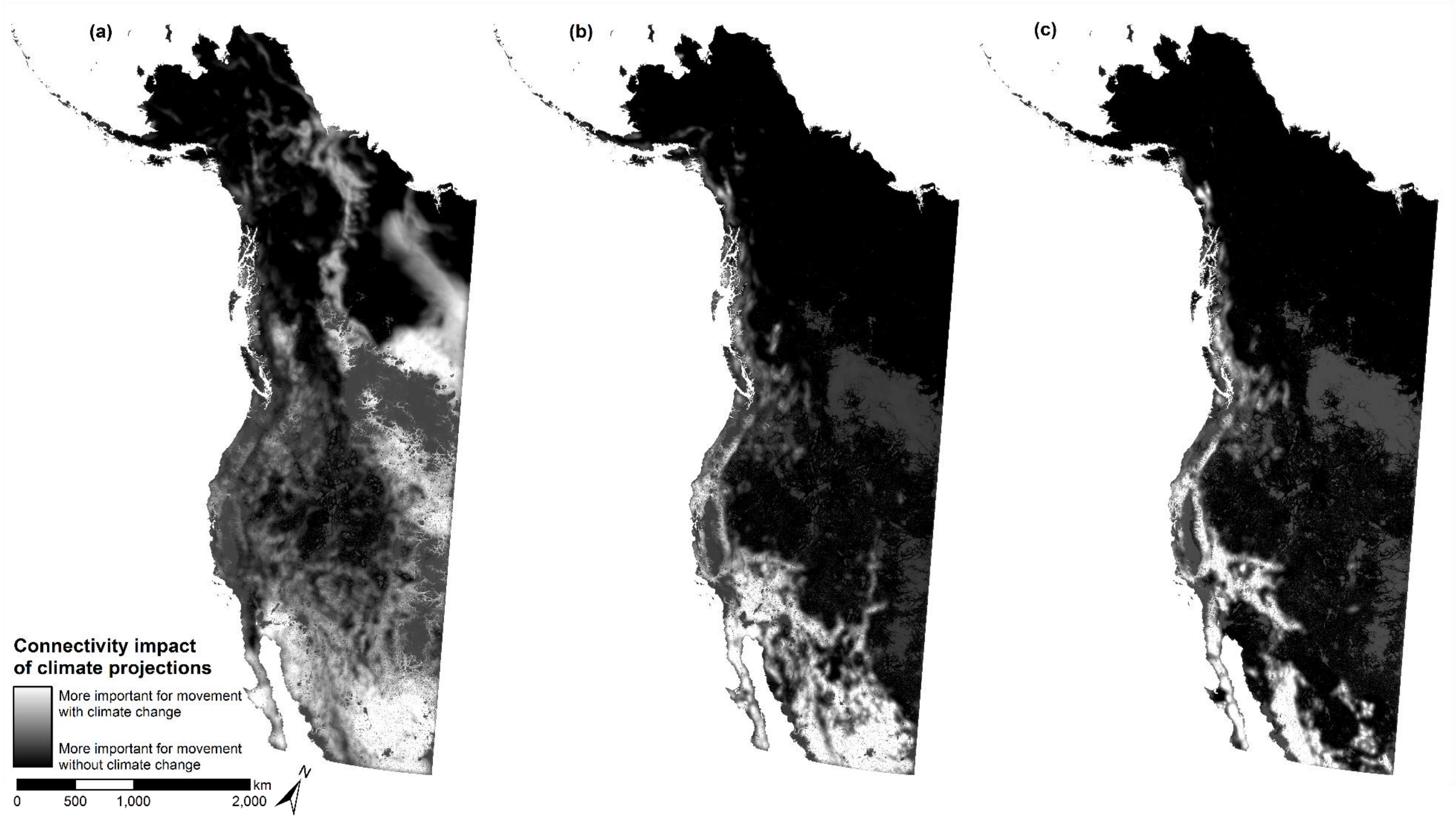

Figure A1.2. The connectivity impact of climate projections for each GCM scenario was computed by normalizing and then taking the difference between potential movement that *does not* and *does* link climate analogs: light areas are important for climate-induced movements whereas dark areas emerge as important for connectivity when climate change is not considered.

Chapter 2. TOPOGRAPHY AND POST-FIRE CLIMATIC CONDITIONS SHAPE SPATIO-TEMPORAL PATTERNS OF CONIFER ESTABLISHMENT AND GROWTH

2.1 ABSTRACT

Concern is mounting that larger, stand-replacing forest fires may accelerate compositional shifts or conversions to non-forested states under a warming climate. Post-fire climatic conditions influence these system trajectories by facilitating or hindering juvenile recruitment. But without an accurate, long-term understanding of where, when, and how climatic variability and other ecological factors affect regeneration, our ability to predict post-fire trajectories is limited. I quantified multiple, interacting facets of post-fire conifer regeneration—including annual establishment rates and growth—on the eastern slopes of the North Cascades a decade since stand-replacing fire. Sites were stratified across topographic settings to specifically capture the potential for topography to moderate seasonal and interannual climatic conditions. Robust recruitment of juvenile conifers occurred every year since fire, with considerable species-specific variability across topographic settings and distance to seed source. Annual establishment rates were strongly correlated with post-fire conditions; rates were highest when growing seasons were relatively cool and moist. A lagged climate signal was apparent in annual growth rates, but standardized climate-growth relationships did not vary across topographic settings, suggesting that topographic setting did not decouple site conditions from broader climatic trends to a degree that affected growth patterns. These results underscore the importance of favorable post-fire climatic conditions in promoting robust establishment and growth while also highlighting the importance of topography and endogenous, stand-level processes (e.g., seed availability and delivery) in shaping recovery

over time. Furthermore, these results suggest that, while the growing concern of post-fire regeneration failure may indeed be warranted under some conditions, failure is not yet the rule in all places and at all times. A more detailed understanding of recovery dynamics through long-term monitoring, and by examining multiple, interacting facets of recovery across spatial scales will improve our predictions of where and when regeneration failure or, conversely, robust recovery may occur under a changing climate.

2.2 INTRODUCTION

Concern is mounting that larger, stand-replacing forest disturbances may cause or accelerate species compositional shifts or conversions to non-forested states, with an accompanying decline in ecosystem services (Millar and Stephenson 2015; Seidl et al. 2016). Evidence from multiple forest systems in the western U.S. suggests that climatic conditions play an important role in determining post-disturbance trajectories. Specifically, research has shown that droughty conditions can constrain regeneration, particularly in moisture-limited settings (Redmond et al. 2015; Harvey et al. 2016; Tepley et al. 2017).

Recovery is predicated on the successful recruitment and survival of juveniles, which may be a more sensitive indicator of long-term system trajectories under climate change than adult trees (Germino et al. 2002; Jackson et al. 2009). Juveniles tend to have different environmental sensitivities than conspecific adults (Grubb 1977), including narrower climatic tolerances (Bell et al. 2014; Dobrowski et al. 2015) and greater susceptibility to drought-induced mortality, frost damage, and photoinhibition, among other stressors (Germino et al. 2002; McDowell et al. 2008; Walck et al. 2011). As such, the juvenile life stage is a particularly important bottleneck to forest recovery.

Given this importance, researchers have sought to document patterns of post-fire regeneration across multiple forest types, with varying spatial and temporal lenses. Most research underscores the importance of adequate seed supply and seed delivery into burned patches (Donato et al. 2009; Kemp et al. 2016; Harvey et al. 2016). Research also documents how recovery varies along environmental gradients: frequently, more robust recovery occurs in cooler and moister topographic settings, whereas arid locations experience less recovery (Dodson and Root 2013; Harvey et al. 2016; Tepley et al. 2017). Some studies find minimal association between post-disturbance regeneration and simple topographic metrics (e.g., elevation) but find strong associations with finer-scaled variability in soil properties related to moisture availability (Donato et al. 2009; Redmond et al. 2015). This research suggests that fine-scaled variability in environmental conditions—even within the same fire or study area—can lead to high degrees of localized spatial variability in recovery.

These varied results highlight the need for considering, simultaneously, how multiple facets of topography at multiple scales shape the climatic conditions experienced by juvenile trees at any given site. These climatic conditions are an integration of broader macroclimate (e.g., atmospheric circulation patterns, on the order of 100+ km), regional mesoclimate (e.g., orographic effects, 1-100 km), topoclimate (0.01-1 km), and microclimate (<10 m; Geiger et al. 2009). Microclimate is influenced by fine-scale surface features and vegetation cover and can strongly affect juvenile establishment (Germino et al. 2002; von Arx et al. 2010). Topoclimate describes the interaction of elevation, aspect, slope, and terrain in mediating how broader-scale climatic conditions are experienced on the ground (e.g., via heat loading or cold-air pooling), with strong implications for fine-scaled variability in moisture balance. Understanding where and when topoclimate plays a role in structuring post-fire regeneration can suggest a natural template for recovery-promoting management interventions (Hessburg et al. 2015).

Much existing research documents species presence and abundance and is often—though not always—conducted within several years of a fire. Research that captures juvenile establishment rates at an annual resolution for multiple years or decades since fire and links establishment rates to climatic variability is not prevalent in the literature (but see Rother and Veblen 2017; Harvey et al. 2016; Urza and Sibold 2017; Stevens-Rumann et al. 2018). Data on annual height growth are even rarer (but see Tepley et al. 2017). Collectively examining these multiple facets of post-fire regeneration and their interactions at longer time-scales offers a more robust picture of system resilience and may foretell disturbance-catalyzed shifts (Reyer et al. 2015; Donato et al. 2016).

In this research, I examined multiple dimensions of post-fire regeneration over 10 years since stand-replacing fire across a broad range of topographic settings. Fire effects on these mixed conifer forests on the eastern slopes of the North Cascades have been documented (e.g., Lyons-Tinsley and Peterson 2012; Prichard and Kennedy 2014), but relatively little work has been done to specifically track post-fire regeneration. Three questions guided this research: first, what are the spatial and temporal patterns of juvenile conifer establishment in this topographically complex landscape? Second, does topographic setting constrain species presence and annual establishment rates or do other limiting factors (e.g., seed source) predominate? Finally, does the relationship between the annual growth of juveniles and broader climatic conditions vary across the landscape? This work builds upon and differs from previous post-fire recovery research by examining multiple facets of juvenile regeneration—including annual growth—by directly linking these recovery dynamics to climatic variability across a range of topographic settings.

2.3 METHODS

2.3.1 *Study area and site selection*

The study area lies within the 2006 Tripod Complex Fire perimeter (hereafter, the "Tripod Fire"). The Tripod Fire burned 70,750 hectares from 700 to 2,400 m in elevation in the Okanogan-Wenatchee National Forest, north of Winthrop, WA[1] (Fig. 1). Mean annual temperature is 7.94°C with -5.05°C as the mean temperature of the coldest month (January) and 20.29°C as the mean temperature of the warmest month (July). Mean annual precipitation is 392 mm, much of which is snow and only 10% of which falls in July, August, and September. Topography within the study area is highly complex, with steep slopes and numerous drainages dissecting the landscape, which contributes to a diversity of localized topoclimatic conditions.

At lower elevations, ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) woodlands historically supported low severity, high frequency fires, but stand densities and surface-fuel accumulation in many locations have increased considerably in the past century due to fire exclusion and the cessation of aboriginal burning (Hessburg et al. 2005). The mixed conifer montane forests (1,000-1,500 m) are largely comprised of ponderosa pine, Douglas-fir, lodgepole pine (*Pinus contorta* var. *latifolia*), and western larch (*Larix occidentalis*), with smaller components of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) that are more prevalent at higher elevations (>1,500 m). The montane forests have historically supported mixed severity fires, whereas higher elevations have a high severity fire regime (Agee 1993). Juvenile conifers that recruit after fire in these mixed conifer forests are the population of inference in this study.

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[1] Winthrop, WA is at 48°28'36.9"N, 120°11'01.3"W.

To capture the breadth of topoclimatic conditions in the study area while avoiding geographic bias, I used a stratified random sampling scheme across topographic settings. I randomly located study sites within strata of elevation, topographic wetness index (TWI), topographic position index (TPI), and heat load index (HLI; Table 1). TWI is a proxy for potential site moisture (Gessler et al. 1995), TPI describes whether a site is on a ridge or in a valley (e.g., where cold-air pooling may occur; Jenness et al. 2013), and HLI reflects insolation, based on slope, aspect and latitude (McCune and Keon 2002).

I sought to isolate the effect of topoclimate by controlling for other factors that were likely to influence regeneration. First, I included only areas that burned at high severity, based on differenced Normalized Burn Ratio (dNBR) classes from the Monitoring Trends in Burn Severity program (MTBS; Eidenshink et al. 2007)[2]. Doing so ensured that all juveniles therein had established since fire and also minimized the effect of intact canopy on localized growing conditions. Second, study sites were located at least 25 m from unburned and low severity patches to further minimize live canopy influence, but no more than 75 m from such patches, to increase the likelihood of adequate seed source. At several sites, on-the-ground conditions were inconsistent with the dNBR classes (Cansler and McKenzie 2012), so these sites were shifted to meet severity criteria. Finally, sites were excluded from areas that were treated prior to the Tripod Fire (e.g., with fuel treatments) or post-fire (e.g., aerial mulching or salvage logging), based on available data (Prichard and Kennedy 2014).

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[2] Data available at https://www.mtbs.gov/direct-download.

2.3.2 *Field data collection*

In a 30-m diameter plot at each of 51 sites, I collected data on post-fire juvenile establishment and growth, post-fire stand structure, and ground cover. I recorded juvenile trees established since fire in five 5-m radius subplots (392.5 m^2 total area) arrayed in cardinal directions from plot center, with one subplot at the center. Following a strict algorithm based on subplot-level densities (*sensu* Kemp et al. 2016; Harvey et al. 2016; Appendix S1), I selected a random subset of juveniles for measuring total height (cm) and interannual growth (distance between terminal bud scars). I recorded any evidence of animal browsing, other damage, and structural features that may have affected germination or establishment (e.g., nurse objects).

In each plot, I tallied snags by size class and noted the presence of extant cones on snags of lodgepole pine, which is serotinous in this region. I estimated the percentage cover of juvenile trees, live shrubs, other vegetation, dead wood, bare ground, and rock in each plot. From the center of the central plot, I used a laser rangefinder to measure the distance to the nearest live, mature tree of all conifer species.

2.3.3 *Climate and growing condition variables*

I analyzed climate-growth relationships using mean monthly temperature, total monthly precipitation, and 1-month standardized precipitation-evapotranspiration index (SPEI) for Washington's Climate Division 6 (East Slope Cascades), obtained from the Westwide Drought Tracker (Abatzoglou et al. 2017)[3]. I specifically used divisional data rather than local station data to capture climatic variations occurring at a spatial extent larger than the study area—and therefore the "average" experience of all study sites—to evaluate if and how the topographic setting of each

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[3] Westwide Drought Tracker data are calibrated to a reference period of 1985-2010 and are available at https://wrcc.dri.edu/wwdt/time.

site modulated broader climatic variations. Using divisional data eliminated the potential bias of applying local station data to sites at variable distances from stations, and dendrochronology studies have shown that growth is more strongly correlated with divisional data than with station data (Peterson and Peterson 2001; Gray et al. 2004).

SPEI is a drought index that expresses deviations from the average water balance at a given site (Vicente-Serrano et al. 2010). It is a biophysically meaningful indicator that incorporates the influence of temperature on evaporative demand and uses the difference between precipitation and potential evapotranspiration to capture moisture balance deficit or surplus (Stephenson et al. 1998). SPEI can be computed to "accumulate" antecedent conditions for a specified number of prior months, but I elected to use 1-month SPEI to examine climate-growth relationships at a monthly resolution.

2.3.4 *Statistical analyses*

To examine the relationship between topographic setting and patterns of establishment and growth, I used a four-step modeling approach. First, I predicted species presence and absence as a function of multiple topographic metrics (Table 2.1) and other ecologically-relevant predictors (e.g., distance to seed source). Second, I modeled juvenile density for all species and individual species as a function of those same independent variables. Third, I compared establishment year patterns within and across species and examined correlations between annual establishment rates and climatic conditions. Finally, I generated time-series of annual growth to examine climate-growth relationships and the topoclimatic influence on these relationships.

I examined pair-wise plots of predictor variables for collinearity to confirm that dropping covariates was not warranted. I centered and scaled all predictor variables prior to analyses to allow for direct comparison of effect sizes across variables. Unless otherwise noted, the unit of analyses was the site (n=51). Because sampling occurred during the 2016 growing season, I excluded any 2016 germinants and growth from analyses. I performed these analyses in R version 3.4.3 (R Core Team 2017) using a suite of data-processing and statistical packages (Appendix 2.1).

Species presence and absence. I modeled the presence of Douglas-fir, Engelmann spruce, ponderosa pine, and western larch using four logistic regression models. All predictor variables were initially included in each model, and I trimmed these saturated models by iteratively removing the least significant terms and evaluating potential model improvement with the Akaike information criterion (AIC). Compared across competing models, AIC reflects model fit with a penalty for increased model complexity. I assessed model calibration—the agreement between observed outcomes and predicted probabilities—using the Hosmer-Lemeshow goodness-of-fit test. Finally, to assess how well the models discriminated between outcomes, I examined the area under the curve (AUC) of a receiver operating characteristic (ROC) curve, which illustrates the trade-off between model sensitivity (ability to correctly classify presences) and model specificity (tendency to incorrectly classify presences). I examined model residuals for spatial autocorrelation using Moran's I and semivariograms.

Species density. I standardized the density of juveniles for each species to stems ha^{-1} by dividing the number of juveniles sampled by the sample area. I then modeled the density of each species and all species using a generalized linear model with a negative binomial distribution, which is appropriate for discrete count data that display significant overdispersion (having a variance greater than the mean). The count data for each species had a high proportion of zeros (Table 2.2), so I constructed zero-inflated negative binomial models for the species-specific models. Zeros in the dataset might reflect absences that could plausibly be presences, or they might reflect absences that could *not* plausibly be presences, for example, because of a complete lack of seed source. Accordingly, I specified distance to live, conspecific seed source as the predictor for the zero-component of the models, which proved significant (α=0.05) in all but one model (lodgepole pine). For the count component of these models, I initially retained all covariates then iteratively trimmed these saturated models based on AIC. The count model for lodgepole pine included the covariate of extant cones on lodgepole pine snags.

I assessed these models for heteroscedasticity (non-constant variance in the error terms) and goodness-of-fit by plotting residuals and observed values against fitted values. I also plotted residuals against leverage to determine if any sites were exerting inordinate influence, then iteratively dropped high-leverage sites to evaluate model sensitivity. These exclusions resulted in little change to parameter estimates, so all sites were retained in the final models. Finally, I examined model residuals for spatial autocorrelation using Moran's I and semivariograms.

Years of establishment. By counting bud scars and measuring distances between them, I determined establishment year and annual height growth for a random subsample of juveniles at each site (Appendix 2.1). Bud-scar counts can underestimate age for some species, but I did not apply a blanket correction factor (e.g., Urza and Sibold 2013) because these factors vary with age and height, and sampled juveniles were highly variable in both. All juveniles were bounded in age by 2006, when the fire occurred, which decreased the likelihood of inaccurate aging.

I used the non-parametric Kruskal-Wallis rank sum test and subsequent Dunn's test to make pairwise comparisons of earliest establishment year between species. I used multiple linear regression to first examine if topographic metrics could explain minimum establishment year patterns within species and, second, if establishment year was a primary predictor of maximum annual growth rates. To investigate the relationship between establishment rates and growing conditions, I calculated Pearson product-moment correlations between annual establishment rates and mean monthly temperature, total monthly precipitation, and SPEI.

Climate-growth relationships. I examined climate growth-relationships for lodgepole pine, focusing on this species because of its prevalence and early establishment after fire, which afforded a longer growth time series than other species. Furthermore, bud-scar identification is reliable for lodgepole pine, especially for the most recent years of growth (Urza and Sibold 2013). I used individuals that had established within the first two years since fire to ensure that every tree was close in age. To ensure adequate sampling depth for all years, I considered only the 14 sites that had at least 10 such trees.

To develop site-level growth chronologies, I adapted standard dendrochonological techniques to the height-growth time series of each tree, using the dplR package in R (Bunn 2010). Each series was detrended with a linear regression model. A standardized growth index series was then created for each tree by dividing the raw growth measurement for each year by the regression value for that year. This removed any age-related growth trend, which I verified with a visual examination of the growth index series. I created site-level chronologies by aggregating the standardized series together by year using a biweight robust mean.

I investigated climate-growth relationships by calculating Pearson product-moment correlations between site-level chronologies with climate variables for years since fire. I used mean monthly temperature, total monthly precipitation, and SPEI from the year prior to the season of growth through the year concurrent with growth. In other words, growth in a given year was related to the growing conditions of that year *and* of the prior year to capture any lagging climatic influences on growth. To test if topographic setting influenced climate-growth relationships, I regressed these correlation coefficients against the topographic metrics. I also regressed the correlations against juvenile density to examine if neighborhood conditions strengthened or diminished any growth response to climate.

2.4 RESULTS

Species presence and density. Conifer juveniles were present at every site sampled, with variability in density and species representation (Figure 2.2; Table 2.2). Of the topographic metrics examined, elevation most consistently accounted for the presence and abundance of species (Table 2.3). Subalpine fir[4], western larch, and Engelmann spruce occurred more frequently and at greater densities at the highest-elevation sites, whereas ponderosa pine was more prevalent at the lowest-elevation sites. Lodgepole pine and Douglas-fir occurred across the range of elevation sampled. Engelmann spruce was more likely to occur in ravines and valleys (per TPI), and densities were highest on north-facing slopes (per slope and HLI). Western larch was more prevalent in valley-like locations (per TPI), whereas ponderosa pine was less likely to occur and less abundant on slopes and in valleys. Few topographic patterns emerged for lodgepole pine or Douglas-fir presence and density, although Douglas-fir density was highest on sloped sites.

Distance to live seed source limited regeneration (Figure 2.3). Juveniles of all species, except lodgepole pine, were rarely observed when live, conspecific seed source was more than 75 m away (only 7 instances). Lodgepole pine was the only species for which greater distance to live seed source was *not* associated with lower densities. A serotinous species, lodgepole pine was more likely to occur at sites where snags had cones (Figure 2.3).

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[4] Because subalpine fir was present at only four sites, I did not generate presence/absence or count models for the species, but all four of these sites were above 1,315 m.

Annual establishment. For the most common species, recruitment consistently occurred every year since fire across sites, although some species recruited significantly earlier than others (Figure 2.4). Based on bud-scar reconstruction of establishment years, some lodgepole pine and ponderosa pine germinated in the late summer or early fall of 2006 immediately following the fire, which passed through the majority of the study sites between late July and late August. No subalpine fir or western larch recruited before 2009, although these species were observed at only 4 and 10 sites, respectively. Sites with the oldest individuals (earliest establishment years) also had maximum annual growth rates for lodgepole pine, ponderosa pine, and Douglas-fir ($t=-8.459$, $df=37$, $p<0.001$; $t=-4.204$, $df=18$, $p<0.001$; $t=-2.567$, $df=22$, $p<0.05$; respectively).

Most juveniles recruited between 2009 and 2012 (Figure 2.5). After 2011, recruitment rates declined for lodgepole pine, ponderosa pine, and Douglas-fir. Annual establishment rates for both lodgepole pine and ponderosa pine were positively correlated ($r>0.6$, $p<0.05$) with April and May SPEI values. Rates for all species except western larch were positively correlated ($r>0.6$, $p<0.05$) with SPEI values of at least one month during the subsequent spring (April, May or June); correlations were particularly strong for lodgepole pine ($r>0.8$, $p<0.01$). In summary, higher establishment rates were associated with cooler, moister conditions (as indicated by positive SPEI values).

Climate-growth relationships. Lodgepole pine growth for a given year was most strongly and consistently correlated with climatic conditions of the previous summer and fall (Figure 2.6; Appendix 2.3). The directions of these relationships were consistent across sites, but the strengths of the relationships were variable and did not follow a consistent pattern across topographic settings. At all sites, growth was negatively correlated with SPEI values of the prior July. In other words, warm, dry Julys tended to precede more growth in the subsequent year and cool, moist

Julys preceded less growth. Conversely, growth was positively correlated with SPEI values of the prior August and September. Growth tended to be negatively correlated with SPEI values of the prior October and November. The few strong correlations between growth and concurrent year SPEI values were scattered across different sites and months (Figure 2.6).

Climate-growth correlations did not map onto the study area in any strong, discernable topographic patterns, but they did vary subtly with juvenile density. The densest sites had the weakest (least negative) correlations with SPEI values for the prior July ($t=2.088$, $df=12$, $p<0.1$), meaning they had less growth than sparser sites when the prior July was droughty. Denser sites also had the weakest (least positive) correlations with SPEI for the prior August ($t=-2.257$, $df=12$, $p<0.05$). Thus, the climate signal in height growth was weaker at denser sites.

2.5 DISCUSSION

2.5.1 *Spatial patterns of juvenile establishment*

A decade after fire, conifer juveniles had established at every site, with considerable variability in time, in space, and across species. As anticipated, distance to seed source was a major control on where and when juveniles established, but topographic setting also determined species presence and juvenile density. These spatial patterns are consistent with the autecology of each species: the infrequent occurrence of subalpine fir and Engelmann spruce is not surprising, given that no study sites were above 1,800 m. With relatively high rates of transpiration, these co-occurring species are more successful in cooler, moister settings like cold-air drainages (Burns and Honkala 1990). Similarly, western larch was most prevalent at higher sites and in topographic concavities. The shade intolerance of this species likely precluded establishment at sites where extensive shrub cover had taken hold.

Shade intolerant ponderosa pine was more prevalent at lower elevations on warmer, drier topographic convexities. Lodgepole pine and Douglas-fir spanned a range of topographic settings with few strong patterns, although Douglas-fir presence was associated with shrub cover, and Douglas-fir density was highest on sloped sites. These two patterns reflect greater Douglas-fir establishment at sites with both adequate moisture and drainage. The patterns may also reflect a potential facilitative effect of nitrogen-fixing *Ceanothus spp.* and *Alnus rubra* on Douglas-fir establishment (Burns and Honkala 1990).

The lack of prominent spatial patterns for lodgepole pine suggests that topoclimatic conditions did not strongly exceed the range of biophysical tolerances for the species. Alternatively, factors that limit the occurrence and abundance of these species may be heterogeneous at scales finer than predictor variable resolution (McKenzie et al. 2003). For example, the proxy for site moisture balance (TWI) emerged as a marginal predictor for only Engelmann spruce density, even though moisture balance can be a limiting factor for other species examined. TWI may simply not reflect finer- or broader-scale hydrologic dynamics that act on juvenile establishment (Wiens 1989).

2.5.2 *Seed source constraints*

Seed availability is a fundamental determinant of successional patterns, especially after intense disturbance (Turner et al. 1999; Johnstone et al. 2016). Post-fire establishment can sharply decline with increasing distance to live seed source (Donato et al. 2009; Dodson and Root 2013; Kemp et al. 2016). That pattern held here, even with an effort to ensure adequate seed source in the sampling design: distance to seed source was a significant constraint on the establishment of all species except lodgepole pine (Table 2.3).

However, many sites had minimal establishment even in the presence of live, mature conspecifics, suggesting that other unmeasured constraints were operating on establishment. Episodic seed production may have contributed to sparse or sporadic recruitment of subalpine fir, Engelmann spruce, western larch, and to a lesser degree ponderosa pine (Burns and Honkala 1990). Age and basal area of mature conspecifics can also dictate seed production, viability, and delivery (Burns and Honkala 1990; Kemp et al. 2016). Spatial orientation of seed source (e.g., upslope vs. downslope of a site) may affect seed delivery as well, though thermal updrafts and dispersal by animals may moderate this effect (Donato et al. 2009). Aboveground and belowground biotic interactions (e.g., facilitation), seed predation, and edaphic characteristics may also account for variability in juvenile density (Teste et al. 2009; Redmond et al. 2015). Finally, mature individuals of a given species may have established under anomalous climatic conditions that enabled them to overcome site-specific limiting factors at the time (e.g., during the Little Ice Age or other cool, moist periods; Gray et al. 2006; Brown 2006). Now, juveniles may no longer be able to recruit at the same sites even in the presence of adequate seed source (Tepley et al. 2017; Stevens-Rumann et al. 2018). However, climatic conditions after the Tripod Fire were generally favorable for regeneration, so other factors (e.g., episodic seed production) were likely more important in constraining juvenile establishment.

Serotiny likely contributed to the robust regeneration of lodgepole pine. Lodgepole pine was the one species for which distance to live, mature individuals did not constrain juvenile density, and sites with cones on lodgepole pine snags had significantly more juveniles than sites where cones were not observed (Figure 2.3). Both of these patterns suggest that serotiny played a more important role in the recovery of this species than seed rain from live individuals. Furthermore, the long interval since prior fire and the high juvenile densities both within study sites and observed elsewhere in large burn patches further suggest that this trait was prevalent in these populations at the time of fire (Tinker et al. 1994). The fact that higher densities coincided with extant cones also suggests an indirect influence of fire effects (Turner et al. 1999; Donato et al. 2016): all sites had complete overstory mortality, but some sites may have experienced severe surface fires that killed the thin-barked lodgepole pine while opening cones and releasing seeds. Crown fires at other sites may have completely consumed the aerial seed bank.

2.5.3 *Temporal patterns of juvenile establishment*

Temporal patterns in climatic variability contributed to the relatively robust and consistent establishment in the years since fire. Favorable climatic conditions likely ensured this establishment success: annual rates of establishment were positively correlated with SPEI values of the current and subsequent years, and the three most common species emerged every year since fire. These cool, moist climatic conditions of 2010-2012, which were associated with a cool phase of the Pacific Decadal Oscillation (PDO), were followed by warmer, drier conditions associated with a warm phase of the PDO and the 2013 emergence of a warm anomaly off the Pacific Coast (Cook et al. 2018). The arrival of these warmer, drier conditions may have contributed to declining establishment rates, but this trend also reflects increasingly constrained growing space, particularly at lodgepole pine-dominated sites.

In contrast to the favorable post-fire conditions here, post-fire drought has impeded establishment elsewhere (Harvey et al. 2016; Tepley et al. 2017; Stevens-Rumann et al. 2018). At broader temporal scales, establishment has been linked to multi-year and decadal modes of climatic variability across forest systems, with more establishment generally corresponding to cooler, moister periods (Woodward et al. 1995; Peterson and Peterson 2001; Gray et al. 2006). These modes of variability may exacerbate or ameliorate stressful conditions anticipated under climate change at some spatial scales (Walther et al. 2002). Here, relatively cool and moist conditions following the Tripod Fire helped to “lock in” robust establishment. Had post-fire conditions instead been droughty, establishment may have been far more protracted.

Finally, the temporal and spatial variability observed in this system is consistent with the well-documented prevalence of localized, divergent successional pathways (Kashian et al. 2005; Harvey and Holzman 2014) and, more broadly, the landscape heterogeneity of mixed-severity fire regimes (Agee 1993; Hessburg et al. 2005). It is important to note, however, that this dataset does not capture juveniles that germinated post-fire but did not survive to the time of sampling. Tracking mortality would provide further insights into how constraints operating on recruitment—climatic or otherwise—may shift in time and space.

2.5.4 *Annual growth response to climatic conditions*

Annual height growth of lodgepole pine juveniles clearly responded to broader climatic patterns, but the strength of these climate-growth relationships did not change across topographic settings. These results do not suggest that annual growth rates *per se* are consistent across all settings. Indeed, maximum annual growth rates (unstandardized, site-level) increased with elevation, suggesting a release from temperature and moisture stresses at lower elevations. The direction and magnitude of the *correlations* between standardized growth and climate did not vary with topography, providing little evidence that topoclimatic influence decoupled site conditions from the prevailing macroclimate.

Annual growth was particularly responsive to prior-year conditions, similar to lagging climatic signatures on radial growth in various forest systems (Brubaker 1980; Restaino et al. 2016; Andrus et al. 2018). The consistently weak response of growth to current-year conditions may be attributable to the fact that lodgepole pine shoots exhibit fixed growth, by which preformed stem units in the terminal buds elongate after winter dormancy (Kozlowski and Pallardy 1997). Therefore, prior-year conditions under which buds form may be more important in determining height growth than current-year conditions.

Growth at most sites was positively correlated with winter precipitation (Appendix 2.2), highlighting the role of snowpack in minimizing the risk of winter injury (Germino et al 2002) and in ensuring adequate moisture for preformed stem units to achieve their height growth potential (Hu et al. 2010). Snowpack contributions to soil moisture may also explain the directional switch in growth correlations with prior summer conditions. In July, soil moisture may have still been sufficiently high such that warmer, drier mid-summer conditions (i.e., more negative SPEI values) did not hinder net carbon assimilation rates and therefore did not hinder investment in preformed stem units and carbohydrate reserves (Kozlowski and Pallardy 2002). By late summer, depleted soil moisture coupled with high vapor pressure deficits would have induced stomatal closure in isohydric species like lodgepole pine. More summer rainfall would have been required to maintain higher rates of net carbon assimilation (Pataki et al. 2000; Hu et al. 2010). Relatively mild conditions in the late fall may have enabled continued carbon investments prior to winter dormancy (Figure 2.6; Appendix 2.2).

Because radial growth occurs secondarily to stem elongation, an examination of radial growth may have revealed a stronger response to current-year climatic conditions than height growth, which is often complete early in the growing season (Kozlowski and Pallardy 1997; Misson et al. 2006). Under less favorable growing conditions, lodgepole pine has been shown to reduce radial growth to a greater degree than height growth (Claveau et al. 2002), and radial growth can be particularly sensitive to fine-scale variability in climate (Case and Peterson 2005). Accordingly, a topographic signal in the strength and direction of a climate-growth relationship, though not observed in height growth, may have been manifest in radial growth. Alternatively, the range of climatic conditions since the fire, and any modulating influence of topographic setting on those conditions, may not have exceeded any thresholds that would differentially affect lodgepole pine height growth across topographic settings.

The relationship between annual height growth and climate varied subtly with stem densities. The climate signal in height growth was weaker at denser sites, suggesting that increased competition may shift resource allocation to root or lateral growth (Litton et al. 2003; D'Amato et al. 2013). Higher density may also dampen individual aboveground growth sensitivity to prevailing climatic conditions. Finally, the juveniles themselves affect microclimate conditions such that higher densities may have moderated broader-scale climatic influences (von Arx et al 2010; Dobrowski et al. 2015).

2.5.5 *Historical and future contingencies*

These post-fire recovery dynamics reflect the convergence of ecological, physiographic, and climatic influences operating at multiple spatial and temporal scales. The convergence here suggests that the narrative of declining forest resilience under climate change may be warranted in some locations, but it is not—or not yet—universal. Indeed, mean annual temperature in the Pacific Northwest increased by "only" 0.6°-0.8°C over the 20th century (1901-2012; Abatzoglou et al. 2014); strong, widespread effects of climate change on fire-prone forests and forest recovery will likely be more apparent under sustained warming and later in this century (Johnstone et al. 2016). The cool and moist post-fire conditions that facilitated robust regeneration observed here, along the eastern slopes of the North Cascades, will become increasingly rare. Washington temperatures are projected to increase 2.5°-8°C above 20th century temperatures by 2100 (USGCRP 2018), and even though winter precipitation is projected to increase, a decreasing snowpack will reduce long-term persistence of soil moisture (Andrus et al. 2018; Harpold and Molotch 2015). Furthermore, even brief fluctuations in growing season temperatures can rapidly deplete available moisture in some settings, and this will be increasingly common under continued warming (D'Odorico et al. 2000). Accordingly, some settings may soon cross limiting thresholds for conifer establishment, thereby amplifying the association between topographic setting and regeneration variability observed here.

Just as the historical contingency of post-fire climatic conditions affected regeneration, unforeseen contingencies in the future will also shape the system trajectory (Jackson et al. 2009). For example, these juveniles may in fact be more vulnerable to future drought because their hydraulic architecture has not been preconditioned via early exposure to non-lethal drought stress to withstand future drought conditions (Kozlowski and Pallardy 2002; McDowell et al. 2008). A high-severity reburn in this recovering system may increase the likelihood of conversion to a persistent, non-forested state for decades (Prichard et al. 2017). On the other hand, areas that burned at lower severity and experienced a reduction in surface fuel loads and small diameter trees may now be more resilient to future fire (Lyons-Tinsley and Peterson 2012; Larson et al. 2013).

In addition to these potential future contingencies, protracted recruitment patterns and divergent successional pathways hinder our ability to project system trajectories from initial post-fire regeneration (Kashian et al. 2005; Gill et al. 2017). The variability observed here a decade after stand-replacing fire underscores the importance of considering multiple facets of recruitment at longer time frames (e.g., both establishment rates and growth) as well as the individualistic dynamics of each species in projecting longer-term responses to climatic changes (Davis and Shaw 2001).

2.5.6 *Promoting recovery in an uncertain future*

The spatio-temporal dynamics documented in this study suggest where and when to prioritize management that promotes recovery or reduces vulnerability to future disturbance in mixed conifer forests of the Cascades. For example, the strong influence of distance to seed source on juvenile density highlights the importance of identifying and protecting live tree legacies (Kemp et al. 2016; Johnstone et al. 2016). This also indicates that variability in burn patch size influences spatial heterogeneity in recruitment, so promoting natural regeneration may be a viable management alternative to replanting in some areas (Donato et al. 2009).

However, these results also suggest that natural regeneration and establishment will be most successful under cool, moist conditions and in settings that are not severely moisture limited (Dodson and Root 2013; Harvey et al. 2016). Under droughty conditions and in warm, dry settings (e.g., low-elevation, south-facing slopes), replanting with drought-tolerant ecotypes or reducing moisture stress (e.g., via thinning) may be warranted (Hessburg et al. 2015). Conversely, cool, moist sites with robust recovery of drought-intolerant species may serve as localized climatic refugia that may be considered for protection (e.g., via grazing exclusions; Morelli et al. 2016). For species like lodgepole pine that can establish and grow across a range of topoclimatic conditions, density-dependent processes may be as or more important to consider than topographic setting in guiding management decisions.

Because snapshots in time are insufficient for projecting long-term recovery, a broad spatial and temporal scope that encompasses fine-scaled dynamics both within and across forested systems is needed to refine our understanding how climate change may or may not impede post-fire regeneration. Increasingly, researchers are responding to this need by examining multiple fires across systems, though cross-region comparisons have required simplification of fine-scaled dynamics (e.g., Stevens-Rumann et al. 2018), and efforts to document multiple facets of recovery (e.g., both establishment rates and growth) remain rare (but see Tepley et al. 2017). At a minimum, long-term monitoring of both natural regeneration and the effectiveness of on-the-ground adaptation tactics will be important for continuing to refine our conceptual models and adaptation strategies to promote forest recovery in an uncertain future.

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TABLES

Table 2.1. Topographic variables used in site selection and as candidate predictor variables. All were computed at 100m resolution.

Variable	**Description and units**	**Source**	**Data range for Tripod Complex Fire**	
			range	**mean**
Elevation[1]	Elevation above sea level in meters	National Elevation Dataset (http://nationalmap.usgs.gov)	696.94-2426.25	1721.56
Slope	Slope angle in degrees	Computed from DEM with ArcGIS v10.4 Spatial Analyst (ESRI, Redlands, CA)	0.05-47.69	17.31
Heat Load Index (HLI) [1]	Unitless index that accounts for slope, aspect, latitude, and potential direct incident radiation. Smaller values correspond to less heat loading and larger values correspond to more heat loading.	Computed from DEM using the Geomorphometry and Gradient Metric ArcGIS Toolbox v2.0 (Evans et al. 2014)	0.22-1.03	0.69
Topographic Position Index (TPI)	Unitless index that expresses relative ridge or valley position by comparing the elevation of each cell in a DEM to the mean elevation of a specified neighborhood (here, 1000m) around that cell. More negative values correspond to valleys and more positive values correspond to ridges.	Computed from DEM using the Land Facet Corridor Designer ArcGIS Toolbox (Jenness et al. 2013)	-231.84-277.11	2.81
Topographic Wetness Index (TWI)[1]	Steady-state wetness index that expresses flow-accumulation as a function of both slope and upstream contributing area, thus reflecting potential site moisture balance. Smaller TWI values correspond to less potential moisture, larger TWI values correspond to more potential moisture.	Computed from DEM using the Geomorphometry and Gradient Metric ArcGIS Toolbox v2.0 (Evans et al. 2014)	3.42-16.98	5.89

[1] Values of elevation, HLI, and TWI within the study area were binned into high, medium, and low strata for each metric; sites were randomly geolocated across the resultant nine strata. These strata were used solely for candidate site location; they did not factor into data analysis. Areas above 1800 m were categorically excluded to ensure sites would be within the elevational range where forest management activities in this region are most likely to occur. Furthermore, large swaths of the highest elevations burned at high severity, limiting accessible interfaces with low severity or unburned patches, which was an important criterion in site selection.

Table 2.2. Range and mean of juvenile density (stems ha^{-1}) across all sites (n=51) for each species; percentage of sites at which each species was present; range and mean of annual growth (measured to the nearest cm) for each species from 2006 to 2015 (inclusive) across all sites.

Species	**Min-max density**	**Mean (SE) density**	**Frequency (%)**	**Min-max growth**	**Mean (SE) growth**
Subalpine fir	0 – 127	3.96 (0.36)	7.84	3 – 13	6.60 (0.14)
Western larch	0 – 5,118	164.22 (15.00)	19.60	1 – 67	9.67 (0.05)
Lodgepole pine	0 – 28,928	3,781.64 (114.84)	86.27	1 – 75	15.88 (<0.01)
Engelmann spruce	0 – 806	34.74 (2.50)	19.60	1 – 19	4.60 (0.02)
Ponderosa pine	0 – 3158	386.75 (15.57)	50.98	2 – 45	14.12 (<0.01)
Douglas-fir	0 – 1,401	139.23 (5.10)	64.71	2 – 30	7.42 (0.01)
All species	102 – 29,234	4,510.71 (115.09)	100.00	1 – 75	14.90 (<0.01)

Table 2.3. Results of the logistic regression (presence-absence [p/a]) and zero-inflated negative binomial (count) models of post-fire juvenile establishment. Coefficients and their levels of significance (if p<0.05) are reported for all covariates retained in the final models. Covariates were centered and scaled prior to model construction to facilitate comparison. Area under the curve (AUC) of the receiver operating characteristic (ROC) curve were 0.9415, 0.8707, 0.8908, and 0.8552 for western larch, Engelmann spruce, ponderosa pine, and Douglas-fir, respectively. Plots of fitted values versus observed values for count models are in Appendix S23.

Covariates	**All species**		**Western larch**		**Lodgepole pine**		**Engelmann spruce**		**Ponderosa pine**		**Douglas-fir**	
	p/a[1]	**count[2]**	**p/a**	**count[3]**	**p/a[1]**	**count**	**p/a**	**count[3]**	**p/a**	**count**	**p/a**	**count**
Elevation (m)			0.010 *	5.349 **			0.006 **	0.440	-0.005 *	-1.532 ***		-0.237
Slope (degrees)		-0.211					0.118	1.025 ***	-0.176 *			0.441 *
Heat load index								-2.495 ***				
Topographic position index				-2.562 *		-0.353	-0.026 *		0.020 *	0.669 **		-0.292
Topographic wetness index								0.330				
Shrub cover (percentage)		-0.541 ***	0.052	-2.809 ***		-0.438					0.046 *	
Distance to live seed source (m) [2]		-0.505 ***	-0.999 **	-1.878 ***		0.3284	-0.417		-0.212		-0.566 **	-0.668 *
Extant cones on snags						1.097 *						

Asterisks indicate levels of significance for parameter coefficients: *** p < 0.001, ** p < 0.01, * p < 0.05

[1] Presence/absence models were not constructed for all species combined because juveniles were present on every site sampled. Neither a presence/absence nor a count model for subalpine fir was constructed because subalpine fir juveniles occurred on only four sites, so the models did not converge. Similarly, a presence/absence model for lodgepole pine did not converge, as it occurred on all but seven sites.

[2] For the all species count model, the negative binomial model was not zero-inflated.

[3] Marginal fit for western larch and Engelmann spruce count models suggest these models ought to be interpreted with caution.

[4] For the all species count model, I used minimum distance to live seed source of any species; for the species-specific models, I used bins of minimum distance to live conspecific seed source. Distance to seed source was not captured for every species at every site (e.g., due to true absence or no clear sightline) and so I generated an ordinal variable to account for these unknown distances: I binned known distances by 25m intervals and set unknown distances equal to the largest bin value plus one.

FIGURES

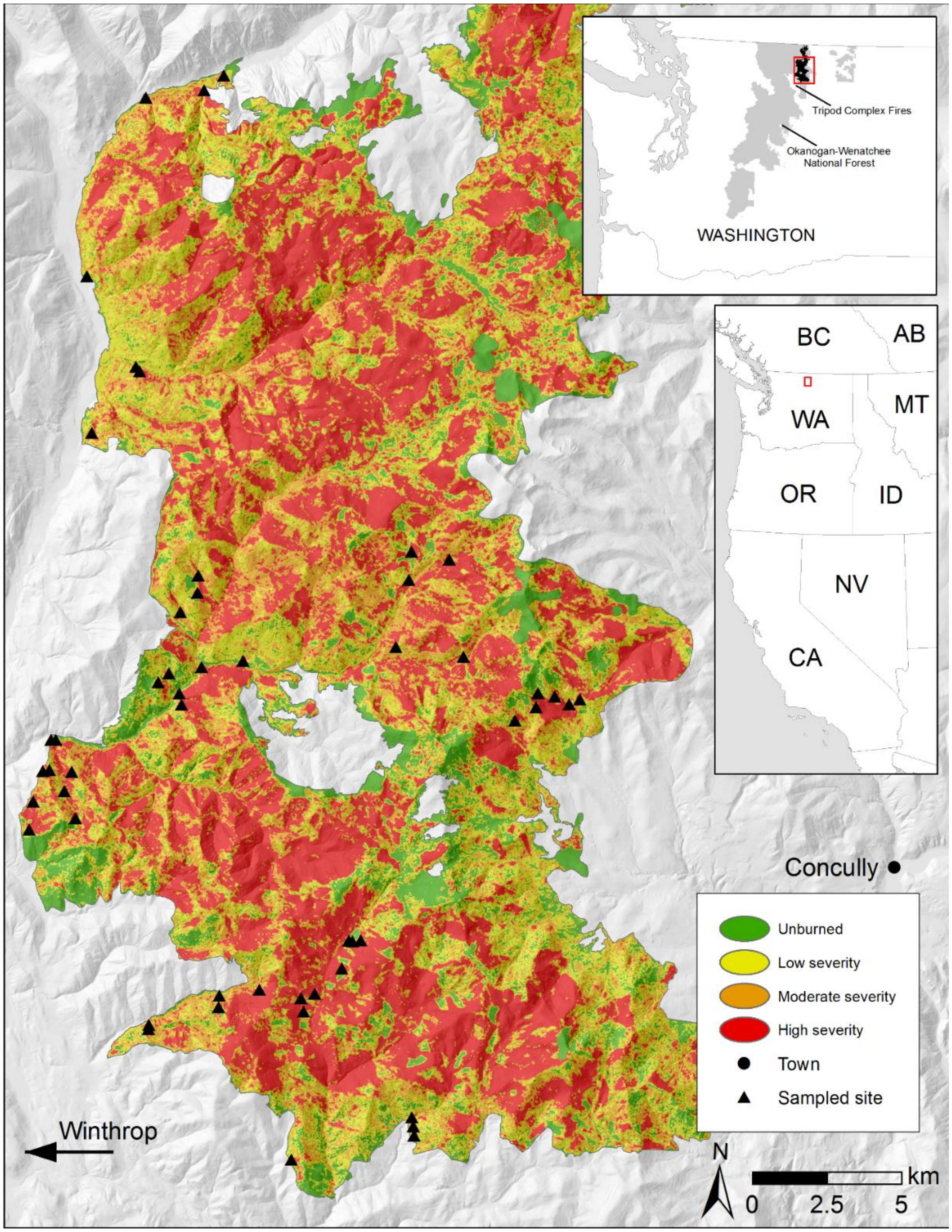

Figure 2.1. Map of the Tripod Fire study area within the Okanogan-Wenatchee National Forest.

Figure 2.2. Variability in regeneration across the study area, from very sparse to very dense conifer regeneration. Site in upper right photo was dominated by *Ceanothus spp.*

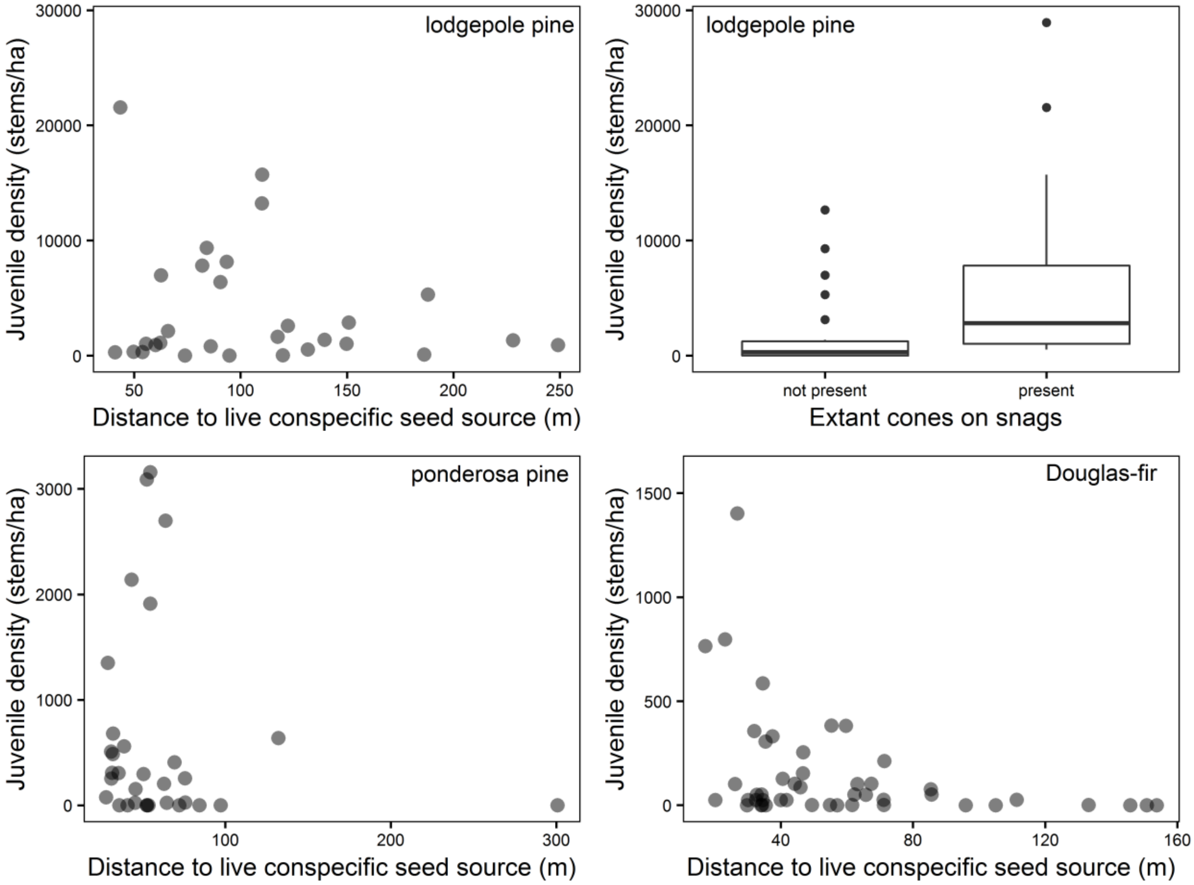

Figure 2.3. Scatterplots of species juvenile density (stems ha^{-1}) by site plotted against distance to live, conspecific seed source for lodgepole pine, ponderosa pine, and Douglas-fir. Boxplot (upper right) compares lodgepole pine juvenile density (stems ha^{-1}) at sites with and without extant cones on snags. Per zero-inflated negative binomial (count) models for each species, distance to live conspecific seed source is a significant predictor of juvenile density for Douglas-fir (z = -2.538, df = 8, p = 0.0112) and presence of extant cones on snags is a significant predictor of juvenile density for lodgepole pine (z = 2.023, df = 8, p = 0.0431).

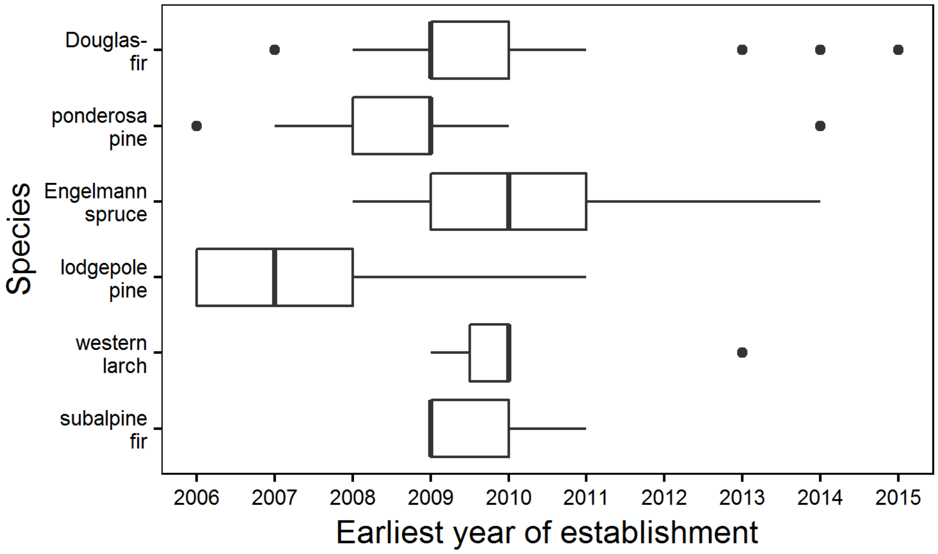

Figure 2.4. The earliest year of establishment for each species across all sites. Per the Kruskal-Wallis rank sum test, there is a significant difference across species (χ^2=43.199, df=5, p<0.001). A subsequent pair-wise comparison using Dunn's test confirms that the earliest year of establishment for lodgepole pine is significantly different than that of all other species; ponderosa pine's earliest year of establishment is significantly different than that of Engelmann spruce.

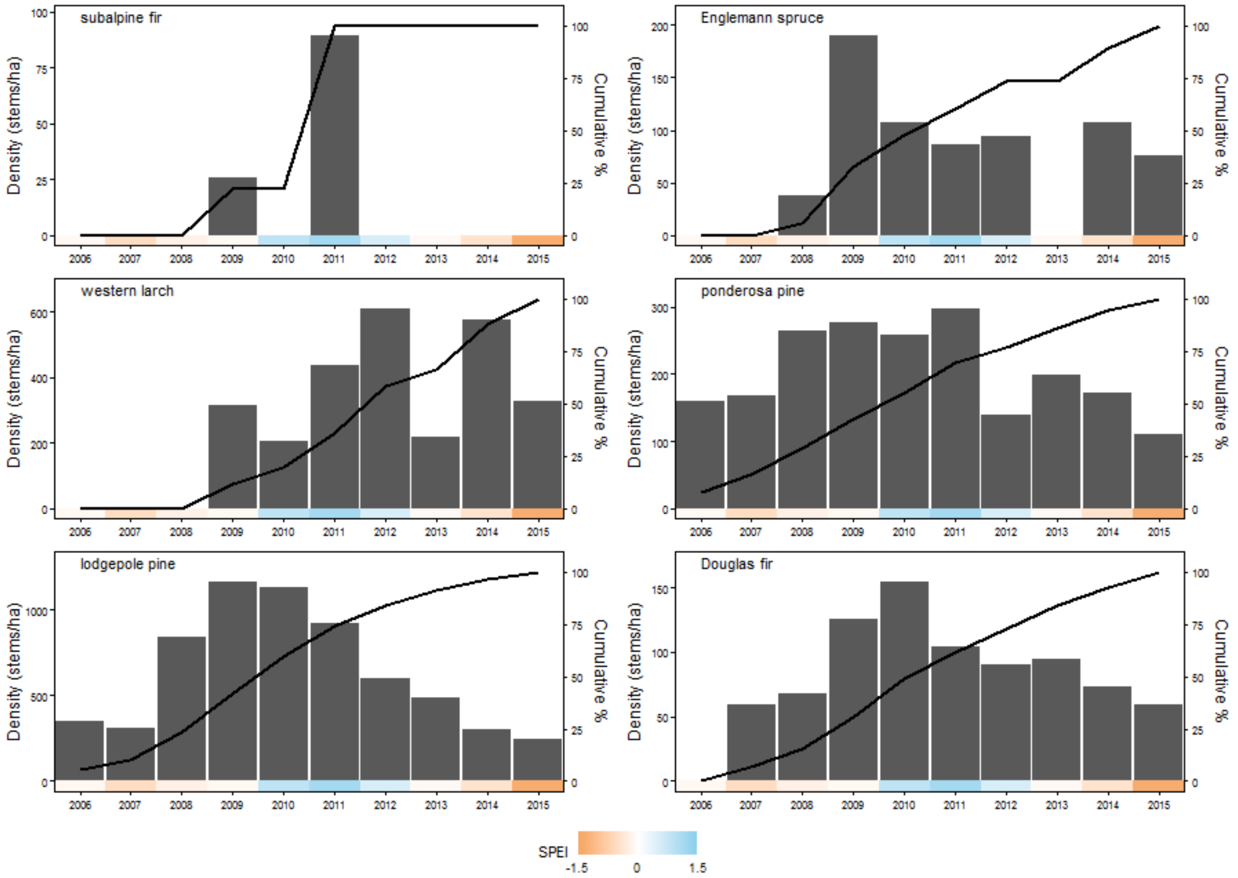

Figure 2.5. Annual establishment (stems ha^{-1}) for each species since the fire. Densities are averages across all sites sampled; note the left-hand y-axis changes for each species. Black lines represent the cumulative percentage of all juveniles established by a given year. Colors below each bar represent the SPEI values averaged for the beginning of the growing season (April, May, June and July) of that year. Orange values indicate doughty conditions and blue values indicate non-droughty conditions. For reference, in the 30 years prior to the Tripod Fire, only 19 months (of 360) had SPEI values less than -1.5 (indicating very droughty conditions), and only 15 months (of 360) had SPEI values greater than 1.5 (indicating very wet conditions).

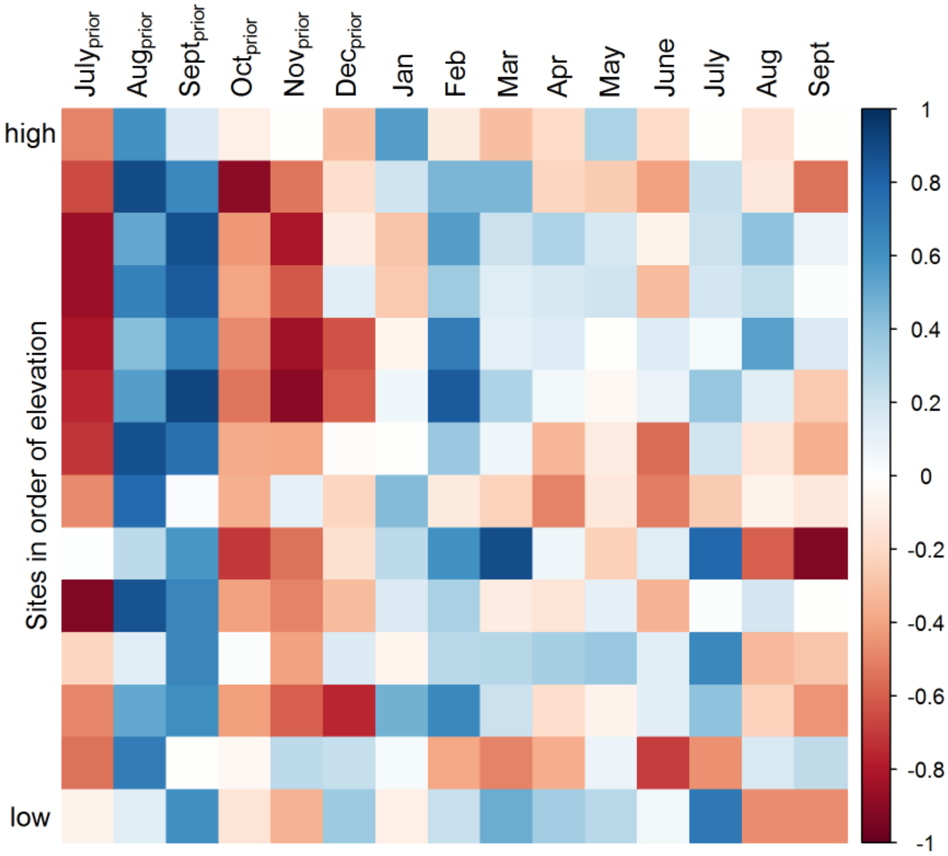

Figure 2.6. Correlation coefficients (Pearson's) between lodgepole pine annual height growth at each site and SPEI values for months prior to the year of growth (July–Dec) and through the growing season. (Only these months are shown to facilitate readability and because very few correlations emerged before the prior July [7] and after the concurrent September [0]. See Appendix S3 for a matrix of 24 months). To ensure adequate sampling depth, only 14 sites were considered in this analysis, and they are ordered with the lowest elevation site on the bottom of the matrix and the highest elevation site at the top. Color intensity indicates the magnitude of the correlation. More negative SPEI values are indicative of droughty conditions while more positive SPEI values are indicative of non-droughty conditions. Thus, a positive correlation between growth and SPEI (blue squares) corresponds to more growth during less droughty conditions while a negative correlation between growth and SPEI (red squares) corresponds to more growth during droughtier conditions. See Appendix S3 for correlation matrices of precipitation and temperature.

APPENDIX 2.1 SUPPLEMENTARY METHODS

Density-based sampling algorithm

If fewer than 40 juveniles were to be captured in the central plot, I measured growth on all juveniles in three plots and tallied (by species) all juveniles in two plots. If greater than 160 juveniles were to be captured in the central subplot, I measured growth on all juveniles in the north-east quadrant of three plots and tallied (by species) all juveniles in the north-east quadrants of two plots.

Subsample of years of establishment

By counting bud-scars and measuring distances between them, I determined establishment year and annual height growth for a random subsample of juveniles at each site. To estimate the total number of juveniles of each species that established each year since fire at each site, I used this subsample to generate the proportion of a given species' establishment for each year since fire at each site and then distributed the remaining tallied, but un-aged, conspecifics to years since fire per those proportions. There were 18 sampled but un-aged juveniles for which there were not aged conspecifics at the site; I excluded these 18 records in computing the total number of juveniles of each species that established each year since fire.

R packages used for statistical analyses

I performed analyses in R version 3.4.3 (R Core Team 2017) using the standard R statistical package for the logistic regression models, the package dunn.test (Dinno 2017) for multiple comparisons, the packages MASS (Ripley et al. 2017) and pscl (Jackman 2017) for the negative binomial models, the packages gstat (Pebesma and Gräler 2018) and ape (Paradis 2018) for assessing spatial autocorrelation, and the package dplR (Bunn et al. 2018) for generating annual growth time-series.

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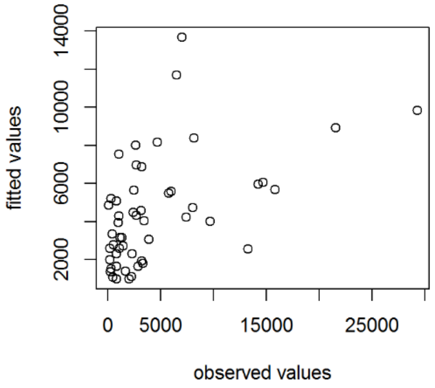
R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

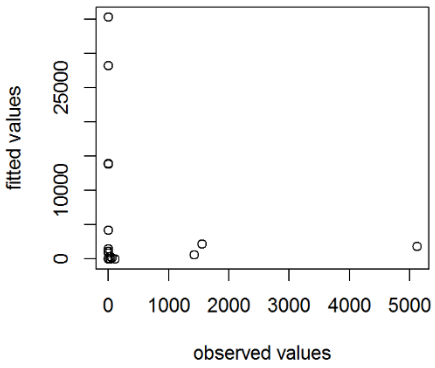
Ripley, B., W. Venables, D. M. Bates, K. Hornik, A. Gebhardt, D. Firth. 2018. Modern Applied Statistics with S. R package version 7.3.5. https://cran.r-project.org/package=MASS

APPENDIX 2.2 FITTED VERSUS OBSERVED VALUES FOR COUNT MODELS

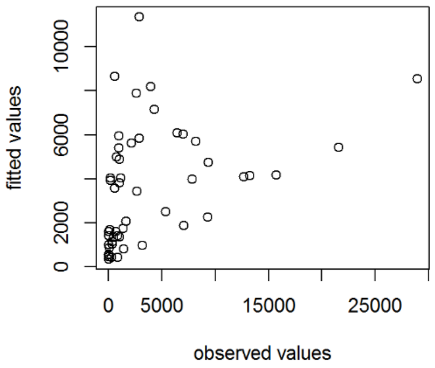
All species



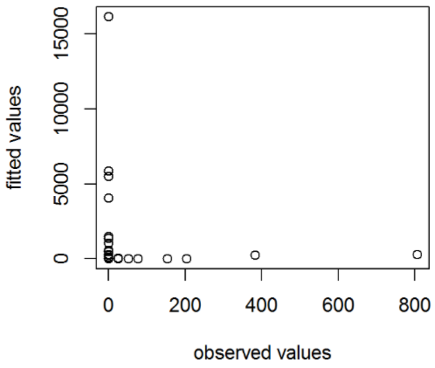
Western larch



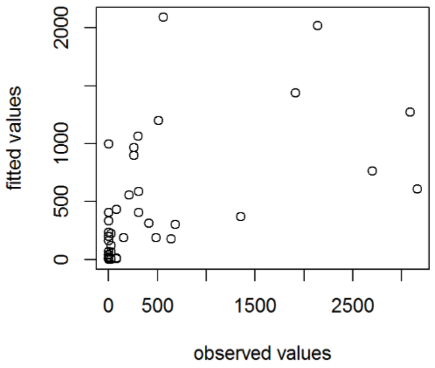
Lodgepole
pine



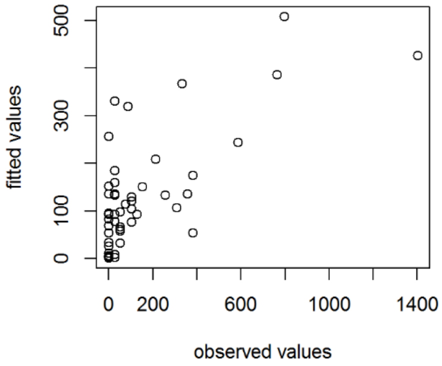
Engelmann spruce



Ponderosa pine



Douglas-fir



APPENDIX 2.3 SUPPLEMENTARY RESULTS

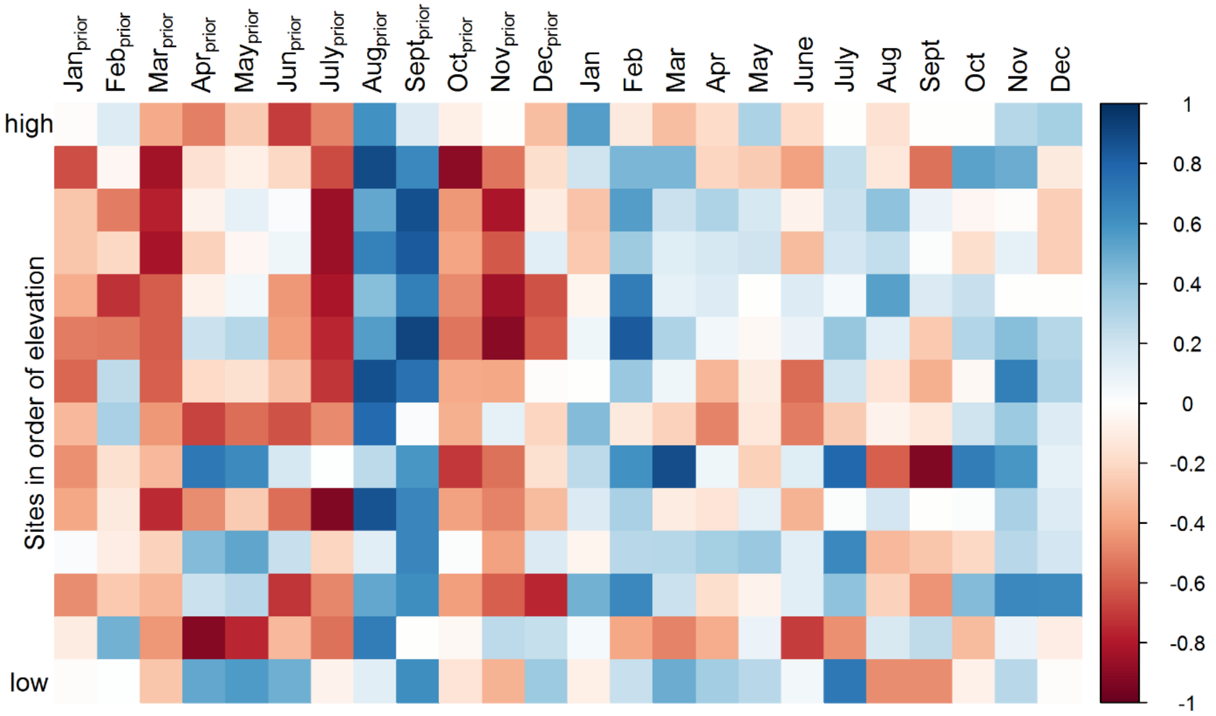


Figure A2.1. Correlation coefficients (Pearson's) between lodgepole annual growth at each site and SPEI values for months prior to the year of growth (July – Dec) and through the growing season (Jan – Sept.). To ensure adequate sampling depth, only 14 sites were considered in this analysis, and they are ordered with the lowest elevation site on the bottom of the matrix and the highest elevation site at the top. Color intensity indicates the magnitude of the correlation. More negative SPEI values are indicative of droughty conditions while more positive SPEI values are indicative of non-droughty conditions. So, a positive correlation between growth and SPEI (blue squares) corresponds to more growth during less droughty conditions while a negative correlation between growth and SPEI (red squares) corresponds to less growth during non-droughty conditions (or more growth during droughty conditions).

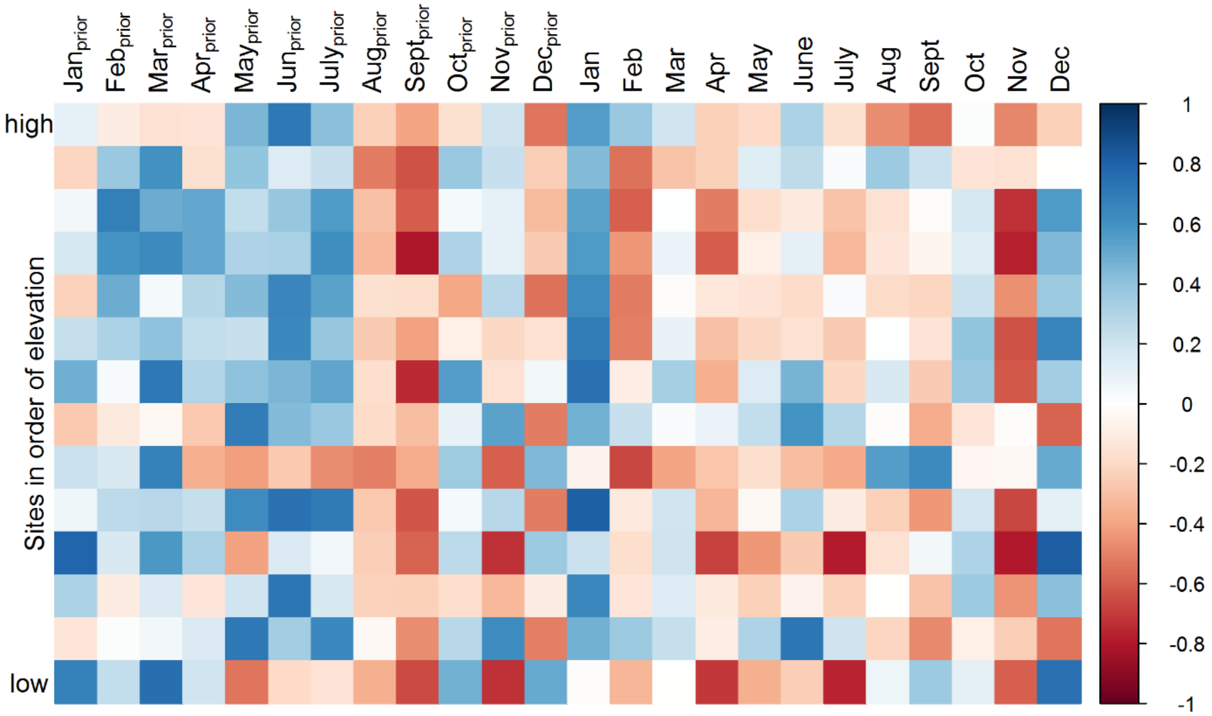


Figure A2.2. Correlation coefficients (Pearson's) between lodgepole annual growth at each site and mean temperature for months prior to the year of growth (July – Dec) and through the growing season (Jan – Sept.). To ensure adequate sampling depth, only 14 sites were considered in this analysis, and they are ordered with the lowest elevation site on the bottom of the matrix and the highest elevation site at the top. Color intensity indicates the magnitude of the correlation. A positive correlation between growth and temperature (blue squares) corresponds to more growth during warmer conditions while a negative correlation between growth and temperature (red squares) corresponds to less growth during warmer conditions (or more growth during cooler conditions).

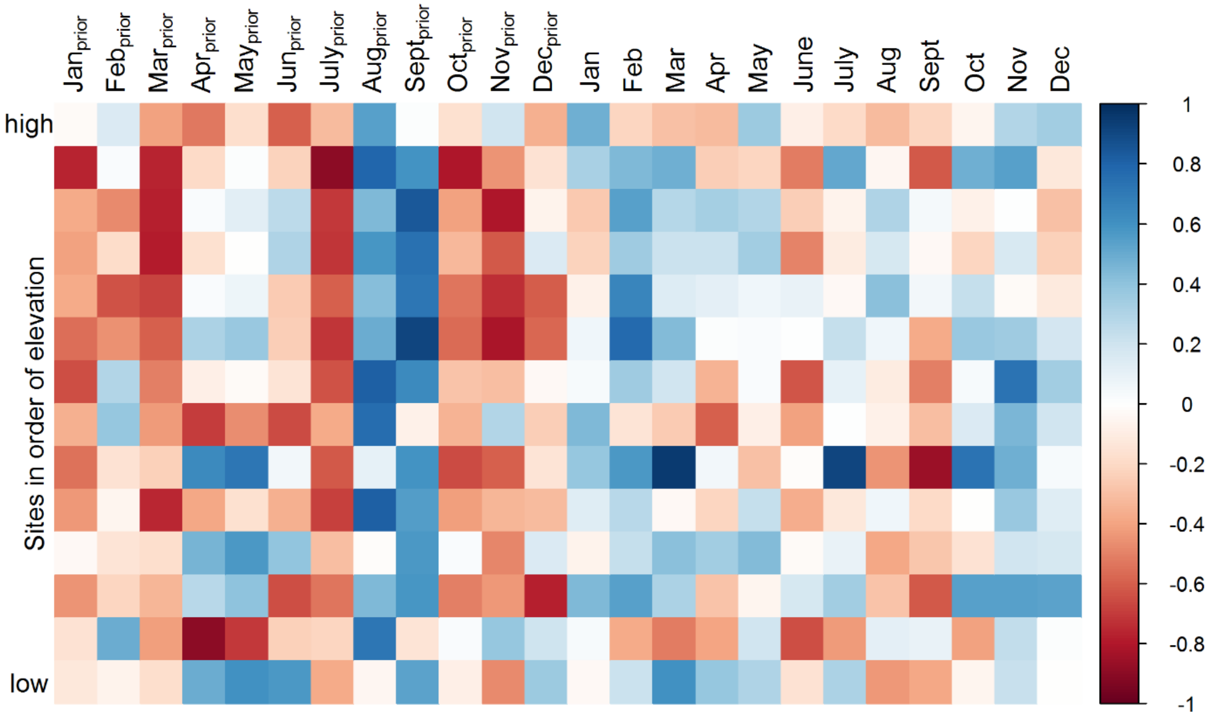


Figure A2.3. Correlation coefficients (Pearson's) between lodgepole annual growth at each site and total precipitation values for months prior to the year of growth (July – Dec) and through the growing season (Jan – Sept.). To ensure adequate sampling depth, only 14 sites were considered in this analysis, and they are ordered with the lowest elevation site on the bottom of the matrix and the highest elevation site at the top. Color intensity indicates the magnitude of the correlation. A positive correlation between growth and precipitation (blue squares) corresponds to more growth during periods with more rain while a negative correlation between growth and precipitation (red squares) corresponds to less growth during periods with more rain (or more growth during periods with less rain).

Chapter 3. WILL A WARMING CLIMATE IMPEDE POST-FIRE FOREST REGENERATION? RESEARCH NEEDS FOR ATTRIBUTING REGENERATION DYNAMICS TO CLIMATE CHANGE

3.1 ABSTRACT

There is growing concern that warming temperatures and shifting precipitation patterns will impede post-fire forest recovery across western North America. Paleoecological evidence, present-day observations, and future projections all suggest that limited seed source (e.g., due to large, stand-replacing fires) and warm, dry post-fire conditions can lead to persistent state changes in forested systems. Therefore, researchers across the globe have been documenting post-fire regeneration to understand how changing climatic conditions may affect regeneration. However, we still lack a preponderance of evidence that directly links limited or failed post-fire regeneration to climate change—in part because of the tremendous spatial and temporal variability in regeneration dynamics as well as the complex interactions of ecological, geophysical, disturbance-related, and climatic factors that affect regeneration. Here, we suggest five interrelated lines of evidence that are necessary for accurately determining if climatic changes impede post-fire regeneration. First, studies must clearly define what comprises regeneration and, ideally, evaluate multiple facets of regeneration. Second, studies must capture the temporal and spatial variability in regeneration dynamics within and across fire-prone forest systems. Third, studies must define and clearly demonstrate a departure from robust regeneration trends. Fourth, studies must rigorously account for non-climatic drivers of regeneration. Finally, studies must directly demonstrate that anthropogenic climatic changes—not natural climatic variability—is

constraining regeneration. We use existing studies of post-fire regeneration in temperate conifer systems of western North America to explore progress towards each line of evidence and, conversely, where research efforts may be improved to advance our understanding of forest recovery in a warming world.

3.2 FEAR OF FAILURE

Concern is mounting that climatic changes and associated shifts in disturbance regimes will hinder forest recovery from fire across western North America. After all, larger, stand-replacing fires may limit seed sources and post-fire climatic conditions may be untenable for conifer regeneration (Walck et al. 2011, Enright et al. 2015). More broadly, we know from multiple lines of evidence that disturbances are key catalysts for enduring ecological changes (Anderson-Teixeira et al. 2013). The paleoecological record (Crausbay et al. 2017, Nolan et al. 2018), present-day observations (Ellison et al. 2005, Allen et al. 2010) and future projections (Westerling et al. 2011, Serra-Diaz et al. 2018) all demonstrate that stand-replacing disturbances coupled with climatic changes can trigger dramatic state transitions in forested systems.

Stand-replacing disturbances are important catalysts for change in forests. Long-lived, sessile trees can have reproductive periods that last for centuries (Brubaker 1986, Petit and Hampe 2006) and exhibit plasticity in traits within generations (Kozlowski and Pallardy 2002, Anderegg 2015). These characteristics and other stabilizing processes—for example, increased adult survival and competitive advantage after low severity disturbance—make forested systems resistant to rapid state changes in the absence of stand-replacing events (Lloret et al. 2012). However, stand-replacing events that open growing space for competitors, reduce seed sources, and are followed by warm, dry conditions may cause forest recovery failures and lead to persistent state changes (Anderson-Teixeira et al. 2013).

Although all life stages and developmental processes (e.g., maturation, seed production; (Figure 3.2. Figure 3.1) are required for robust recovery, juveniles tend to have narrower climatic tolerances (Jackson et al. 2009, Dobrowski et al. 2015) and greater susceptibility to moisture stress, frost damage, photoinhibition, and pathogens (Germino et al. 2002, Walck et al. 2011). Juveniles have shallower root systems, less structural support, less leaf area, and smaller carbohydrate reserves than conspecific adults (Cavender-Bares and Bazzaz 2000, Niinemets 2010). The juvenile stage is therefore a bottleneck to recovery, and changing climatic conditions may tighten this bottleneck via many processes that have been discussed extensively elsewhere (Smith et al. 2009, Classen et al. 2010, Walck et al. 2011, Fisichelli et al. 2014, Kroiss and HilleRisLambers 2015, Petrie et al. 2016). Given these concerns, researchers are increasingly examining post-fire regeneration to understand when, where and how climatic changes may impede recovery.

3.3 SEEKING ATTRIBUTION

Efforts to document post-fire regeneration dynamics and link these dynamics to climatic changes are unfolding across the globe—in the Mediterranean (e.g., van Leeuwen et al. 2010), the Andes (e.g., Gonzáles et al. 2010), Australia (e.g., Denham et al. 2009), and the boreal (e.g., Girard et al. 2008, Johnstone et al. 2010, Pinno et al. 2013). From remote sensing to experimental plantings, researchers are applying a range of methodologies, each with relative strengths and shortcomings (Appendix 3.1). Recent field-based efforts in western North America build upon four decades of post-fire recovery research that emerged after several key events in the 1980s and 1990s (Appendix 3.2).

Despite these growing efforts, we still lack a preponderance of evidence that directly links limited or failed post-fire regeneration to climate change. The burden of proof for attributing these post-fire regeneration dynamics to climate change remains high because of the tremendous natural variability in regeneration as well as the complex interactions of ecological, geophysical, disturbance-related, and climatic factors that affect regeneration. Attribution to climate change first requires disentangling the effects of these factors and then assessing how anthropogenic climatic changes, versus natural climate variability, is driving regeneration dynamics (Parmesan et al. 2011, Cramer et al. 2015). This is challenging because each driving factor—including climatic factors—operate at multiple spatial and temporal scales, and field-based assessments that are limited in time and space may not achieve a strong signal-to-noise ratio (Stott et al. 2010). Furthermore, most studies to date do not explicitly incorporate climatic data into their analyses, though that is changing. Growing efforts to uncover the fingerprint of climate change in post-fire regeneration dynamics and predict future dynamics (e.g., Tepley et al. 2017, Stevens-Rumann et al. 2018, Serra-Diaz et al. 2018) help move us closer to the burden of proof—while also highlighting the methodological challenges of attributing highly variable ecological dynamics to climate change.

3.4 BURDEN OF PROOF

Here, we suggest five interrelated lines of evidence that are important for accurately determining if climatic changes impede post-fire regeneration in the coniferous forests of western North America. First, studies must clearly define what comprises regeneration and, ideally, evaluate multiple facets of regeneration. Second, studies must capture the temporal and spatial variability in regeneration dynamics within and across fire-prone forest systems. Third, studies must define and clearly demonstrate a departure from robust regeneration trends. Fourth, studies must rigorously account for non-climatic drivers of regeneration. Finally, studies must directly demonstrate that anthropogenic climatic changes—not natural climatic variability—is constraining regeneration.

We use existing studies of post-fire regeneration in temperate conifer systems of western North America to explore progress towards each line of evidence and, conversely, where research efforts may be improved. To identify these studies, we searched Web of Science (see Table 3.4 for search terms), which uncovered 1950 papers. Because our focus is on natural juvenile conifer regeneration in conifer-dominated systems, we primarily considered papers that 1) address regeneration from discrete, known wildfire events versus papers that described general stand development patterns or are based upon reconstructions (e.g., from centuries-old fire scars); 2) are not specifically framed as evaluating pre- and post-fire management effects (e.g., from prescribed fire, salvage logging, planting); and 3) focus on conifer dynamics, although we considered non-conifer dynamics (e.g., understory recovery, oak sprouting) when reported in light of conifer regeneration. Because we did not search the grey literature or technical reports, this is not a full census of all work regarding post-fire dynamics. Nonetheless, the 70 studies that met our criteria represent a comprehensive survey of the questions researchers are asking and the methodologies they are using to examine post-fire conifer regeneration.

3.4.1 *Defining and evaluating the multiple facets of regeneration.*

Defining regeneration. Post-fire regeneration requires the establishment, survival, and growth of juvenile trees. And yet, many studies do not explicitly define what constitutes a juvenile nor specify what is included in sampling. Some studies specify a particular size (e.g., 5 cm in height) or age (e.g., 1 year old) above which juveniles were sampled, acknowledging that many juveniles below those thresholds were unlikely to survive (Cocking et al. 2014). In many studies, however, sampling criteria are ambiguous and leave open questions—for example, were current-year germinants included in field tallies? The inclusion of current-year germinants, which may emerge in dense clusters as from a seed cache (Figure 3.2), can exert inordinate influence on density estimates even though germinant presence may be fleeting, as shown by several studies that specifically documented survivorship of post-fire germinants during the initial growing season (Chappell and Agee 1996, Bonnet et al. 2005). Therefore, abundance estimates that do include current-year germinants are highly sensitive to the timing of sampling within a given growing season. Some studies that did sample germinants—and are explicit about having done so—are cautious to draw inferences about annual establishment rates (Harvey et al. 2014a, Dodson and Root 2015, Klutsch et al. 2015). Explicitly stating criteria for what constitutes a juvenile will improve our ability to identify the most relevant constraints at different stages of conifer regeneration.

Juvenile densities. Nearly all post-fire regeneration studies quantify abundance or density estimates of juveniles by species. Species specificity is critical, given the tremendous range in densities across species. For example, lodgepole pine (Pinus contorta) densities can range from 0 to 100,000s stems/ha within the same study system (Turner et al. 2004, Harvey et al. 2014b). That upper bound is an order of magnitude greater than densities reported for other conifer species across western North America. Densities are almost universally reported on a per hectare or per acre basis, which is consistent with planting guidelines and stocking standards. However, sampling units are often orders of magnitude smaller than a hectare or an acre. Expressing densities on this basis may therefore give a false impression of either no or prolific regeneration blanketing the landscape. Instead, expressing densities per square meter (e.g., Tomback et al. 1995, Turner et al. 1997, 1999) may more accurately convey the spatial variability of recruitment, even though doing so is nothing more than a simple arithmetic transformation. At the very least, density ranges—and not simply central tendencies—would provide a more useful picture of regeneration (Ratajczak et al. 2018).

Exceptions to using juvenile densities include efforts to document transitions between community compositional and structural states (e.g., DeSiervo et al. 2015, Coop et al. 2016, Cansler et al. 2018). Instead of juvenile densities, these studies primarily report percent cover or structural classes. These metrics can integrate the entire condition of a given sampling unit, whereas juvenile densities alone express one aspect of plant community composition and structure. Considering juvenile densities jointly with percent cover or structural classes may help illustrate the capacity a given site to support juvenile recruitment.

Annual establishment rates. Increasingly, researcher have used repeated sampling and multiple aging approaches to estimate annual establishment rates (Figure 3.3). Some have identified annual cohorts through successive years of sampling (e.g., Turner et al. 1999, Tomback et al. 2001, Gill et al. 2017). Others aged juveniles by cross-dating rings at the root-shoot boundary (Kashian et al. 2005, Klutsch et al. 2015, Tepley et al. 2017) or by counting branch whorls or bud-scars, formed annually when protective scales covering terminal leader buds are shucked off (e.g., Donato et al. 2009b, Haire and McGarigal 2010, Pierce and Taylor 2011, Harvey et al. 2016, Donato et al. 2016). The accuracy of these approaches varies across species and declines with both age and height, which typically leads to an underestimation of age (Urza and Sibold 2013, Hankin et al. 2018). Therefore, age estimates—and hence annual establishment rate estimates—can benefit from correction factors that account for these age- and size-related challenges (Pierce and Taylor 2011, Urza and Sibold 2013, Hankin et al. 2018). Alternatively, expressing ages in multi-year bins may avoid the false representation of aging precision (e.g., Donato et al. 2016), though this precludes examining potential limiting factors (e.g., climatic conditions) at annual resolutions.

Survival. Ideally, studies would consider annual establishment rates in parallel with annual survival rates. After all, seemingly high rates of annual establishment will not ensure robust recovery if juveniles do not survive, and tallying or aging only live individuals does not capture juveniles that have died. Successive sampling over multiple years at the same plots may give an indication of survivorship and mortality. Even so, precise interannual survival and mortality rates can only be captured by tracking individual juveniles within and across years. As noted above, several studies did so for current-year germinants (Chappell and Agee 1996, Bonnet et al. 2005). However, how juvenile mortality may counter-balance survival in post-fire settings remains largely undocumented—a shortcoming of using snapshots in time to document ongoing processes like stand recovery (Johnson et al. 1994).

Growth. Few post-fire regeneration studies examined juvenile growth, even though growth is an indicator of progress towards reproductive maturity, particularly for species that can remain suppressed and not bear cones indefinitely (e.g., whitebark pine (*Pinus albicaulis*); Perkins 2015). Several studies did, however, specifically examine growth or productivity. For example, Turner et al. (2004) developed allometric equations for lodgepole pine juveniles from one year's stem, branch, twig, and foliage growth to compute stand-level annual net primary productivity and leaf-are index in Yellowstone. Tepley et al. (2017) measured distances between bud-scars on recruiting juveniles in the Kalmath Region and found that height growth decreased with later years of establishment. For whitebark pine in western Montana, Perkins (2015) measured both the terminal internode stem diameter to represent the prior year's radial growth as well as new needle bundles in the top whorl of all branches to represent the concurrent year's growth. Higher growth rates corresponded with greater site availability of soil nitrogen and phosphorous. Such efforts to evaluate annual juvenile growth—and associated limiting factors—can augment more simplistic recovery metrics (e.g., density) because growth metrics better indicate the likelihood of juveniles achieving reproductive maturity.

3.4.2 *Capturing temporal and spatial variability in regeneration dynamics within and across fire-prone forest systems.*

To date, post-fire regeneration research highlights the tremendous variability of regeneration—within and across burn patches, study sites, fires, and regions (Turner et al. 2004, Donato et al. 2009a, Coop et al. 2010, Chambers et al. 2016, Owen et al. 2017). This underscores the need for clearly defining a sample, a population of inference, and the associated spatial and temporal contexts. When studies are tightly limited in their temporal and spatial scope, one's ability to draw broad generalizations about post-fire recovery—and what constrains recovery—is limited because of potential unseen constraints (O'Neill et al. 1989, Bradshaw 1998). Furthermore, a sampling design that does not capture the full range of variability in regeneration can lead to biased estimates of demographic parameters (Lesser and Brewer 2012). However, a constrained temporal and spatial scope does not necessarily limit the robustness of results or the confidence of inferences as long as the relevant domain of the study is clearly defined.

Some researchers specifically targeted areas where limited recovery was expected (e.g., large, high-severity patches; Haire and McGarigal 2008, 2010, Owen et al. 2017). This approach inherently precludes capturing the spatial heterogeneity in regeneration and drawing inferences about dominant constraints across a single burn area. Again, this limited scope does not invalidate such studies. However, focusing a priori on places where limited or no regeneration is expected can represent a departure from classic null-hypothesis testing (Stout 1989). Bypassing null-hypothesis testing and specifically examining areas where limited or failed regeneration is expected may be appropriate from a resource risk management perspective (Nichols and Williams 2006, Trenberth et al. 2015). However, attributing limited or failed regeneration to climate change requires an explicit rejection of the null hypothesis—that climate change is not hindering post-fire regeneration—and therefore requires that all spatial variability in post-fire regeneration is accounted for.

Within a given fire, the known spatial variability of fire dynamics and effects can be used to inform sampling design to ensure that the spatial variability in regeneration is captured. For example, many researchers stratified sampling across severity classes (e.g., Doyle et al. 1998, Pierce and Taylor 2011, Chambers et al. 2016, Acker et al. 2017), patch sizes (e.g., Turner et al. 1997, Collins and Roller 2013) and abiotic gradients (e.g., Dodson and Root 2013, Kemp et al. 2016, Tepley et al. 2017). Alternatively, prior investigations of spatial heterogeneity in regeneration or remote sensing observations of initial post-fire vegetation dynamics (e.g., Meng et al. 2015) can inform subsequent sampling schemes. However, few studies report that known spatial variability in regeneration was used to inform sampling unit area or total area sampled (but see Romme et al. 2016 following results from Turner et al. 2004). Across studies, the total area sampled within a given study ranges across two order magnitudes—from hundreds of square meters to tens of thousands of square meters. Expanding sampling unit area or total area sampled per se does not automatically equate to a more rigorous sampling design, but it does decrease the likelihood that variability in regeneration is overlooked. In addition, examining regeneration variability within a given fire at multiple spatial scales (e.g., plot- or site-level versus patch-level; Kashian et al. 2004, Donato et al. 2009a, Collins and Roller 2013) can reveal dominant constraints that may be relevant at one scale but not another. Of course, drawing broad generalizations about widespread limitations on post-fire regeneration will require looking beyond individual fire events. Researchers are increasingly doing so by examining multiple fires across forest systems (Fig. 4), for example, within and across Colorado’s subalpine systems (e.g., Coop et al. 2010), the northern

Rockies and Cascades (e.g., Kemp et al. 2016, Harvey et al. 2016, Cansler et al. 2018, Stevens-Rumann et al. 2018), and the Klamath (e.g., Tepley et al. 2017).

In addition to capturing the spatial variability in regeneration, the temporal variability must also be considered before regeneration dynamics can be attributed to climatic changes. To date, many studies report single sampling efforts that occurred within the first two years of a fire. Increasingly, however, researchers are revisiting fires to track regeneration dynamics through time (Fig. 3). For example, there is now a large body of literature documenting recovery since the 1988 Yellowstone fires (Turner et al. 2016b, Donato et al. 2016, e.g., Romme et al. 2016). Successive sampling efforts are important because immediate post-fire vegetation dynamics can be inappropriate for predicting longer-term trajectories (Kashian et al. 2005, Cocking et al. 2014, Nelson et al. 2016, Gill et al. 2017). Rather, protracted recruitment and divergence in successional trajectories can take years or decades to unfold (Tomback et al. 2001, Coop and Schoettle 2009, Turner et al. 2016b). This is true even within highly localized areas—for example, Tomback et al. (1993) observed an eight-year difference in germination dates of whitebark pine from the same seed cache. Furthermore, constraints operating on regeneration may be relevant one year but not in subsequent years (Harvey and Holzman 2014, Hansen et al. 2016). Therefore, drawing conclusions about dominant limiting factors immediately post-fire or from a single year may be premature and inaccurate.

3.4.3 *Defining and demonstrating a departure from robust regeneration trends.*

Defining what robust recovery looks like within a given spatial and temporal domain is a necessary but often overlooked aspect of determining that regeneration is limited or failing. For example, such terms as understocked, unnaturally dense, or hyperdense (e.g., Savage and Mast 2005, Roccaforte et al. 2012, Pinno et al. 2013) imply that natural regeneration is proceeding in an atypical manner, but a rigorous comparison to a quantitative baseline is necessary to demonstrate a departure from expected regeneration. Some studies compare observed densities to planting guidelines or stocking standards to gauge the relative robustness of recovery (e.g., Crotteau et al. 2013, Chambers et al. 2016). These guidelines may be reasonable estimates, but because they are typically generated with specific objectives in mind (e.g., maximizing yield), their application to natural regeneration can be limited (Franklin et al. 2002, Donato 2006). Comparing natural regeneration to minimum stocking standards can be a conservative approach to using these as baselines for comparison (Tepley et al. 2017). Other baselines have their own challenges. For example, comparing juvenile densities to pre-fire conditions can confound recovery and temporal variation, and assumes a steady-state equilibrium within the system(Parker and Wiens 2005). On the other hand, comparing juvenile densities to non-affected conditions within the same system can confound recovery with systematic spatial differences within systems (Parker and Wiens 2005). Even BACI designs (e.g., Fulé and Laughlin 2006) do not avoid these challenges.

Life history traits and natural stand development patterns further challenge the use of unburned or pre-fire conditions as a baseline. For example, substantially lower juvenile densities of shade-tolerant species such as mountain hemlock (Tsuga mertensiana) and Pacific silver fir (Abies amabalis) can be expected in burned areas than in unburned areas (Acker et al. 2017). On the other hand, shade-interolant species such as lodgepole pine can be prolific after stand-replacing disturbance (Harvey et al. 2014b, Turner et al. 2016b). These life history traits mean that reconciling post-fire juvenile densities with unburned or pre-fire densities requires accurate models of juvenile survivorship (Clark et al. 1999, Rother and Veblen 2016). Using very conservative benchmarks in comparisons between post-fire densities and unburned or pre-fire densities can help address these challenges. In Yellowstone's montane forests, for example, Donato et al. (2016), defined ineffective regeneration densities as those that were less than 10% of pre-fire densities. By contrast, Stevens-Rumann et al. (2018) assigned each of 1485 sites a binary score of “1” if post-fire densities were 100% or greater than pre-fire densities and “0” if densities were lower. They state that their results—suggesting declines in post-fire tree regeneration over time—are insensitive to this recruitment threshold, and that this simplification was necessary to use a diverse, multi-regional dataset.

Historical contingencies that have led to on-the-ground conditions today also compromise comparisons of post-fire densities to unburned or pre-fire conditions. For example, mature individuals of a given species may have established during episodes of cooler, moister climatic conditions (e.g., the Little Ice Age) that enabled them to overcome site-specific limiting factors at the time (Woodward et al. 1995, Gray et al. 2006, Brown 2006). Comparing post-fire regeneration dynamics to trees that established under these anomalous establishment contexts may be inappropriate, particularly under directional warming. Finally, present-day conditions across much of western North America reflect widespread fire exclusion, which further challenges one’s ability to determine an appropriate baseline for recovery. This is particularly true in dry, frequent-fire systems in which exclusion has led to major deviations in stand structure from historical variability (Hessburg et al. 2005). Even when the past century of management has not exceeded natural fire return intervals (e.g., in moist forests with infrequent fire), fire exclusion has effectively homogenized landscapes that may otherwise have more spatial variability (Chappell and Agee 1996, Halofsky et al. 2018b). Therefore, the best contemporary references for defining robust recovery may be landscapes that have long-established fire restoration programs or protected areas (e.g., National Parks) that have had minimal human interference in natural disturbance regimes (Turner et al. 2016a, Collins et al. 2016).

3.4.4 *Accounting for non-climatic drivers of regeneration*

Once a departure from a relevant, scale-appropriate baseline is demonstrated, attributing limited or failed regeneration to climatic changes requires accounting for all non-climatic drivers. Most post-fire regeneration studies identify a range of non-climatic predictors of regeneration—including ecological, geophysical, and disturbance-related factors. It is important to note that many predictor variables that are evaluated are just that—predictors—and do not necessarily indicate the precise mechanisms or limiting factors that may constrain regeneration (Wiens et al. 1993, Li and Wu 2004). For example, many studies find that pre-fire stand structure and composition predict post-fire regeneration patterns (e.g., Halofsky and Hibbs 2009, Roccaforte et al. 2012, Harvey et al. 2016, Gill et al. 2017). A logical explanation is that seed delivery from trees that survived the fire is the primary limiting factor of regeneration, but without evaluating the process of seed delivery *per se*, one cannot conclude that it is a limiting factor. Nevertheless, predictive patterns can strongly suggest mechanisms and limiting factors operating on regeneration, and strong predictors can clarify the environmental and ecological contexts where regeneration may be limited.

Ecological factors. Most post-fire regeneration studies highlight the role of autecological and synecological dynamics in shaping post-fire recovery. In particular, seed source and availability, which are contingent upon trees that survive the fire, consistently emerge as important predictors of juvenile density (Donato et al. 2009a, Kemp et al. 2016, Urza and Sibold 2017). Most studies evaluated a site’s potential seed source and availability using distance to the nearest live, cone-bearing individuals (e.g., Kemp et al. 2016, Urza and Sibold 2017) or distance to the nearest unburned or low severity edge (e.g., Donato et al. 2009a, Collins and Roller 2013). These distance measures can serve as coarse proxies for seed availability, although a simple Euclidean distance may overestimate seed availability and delivery. Instead, including a measure of live basal area may better indicate the likelihood of seed reaching a given site (Haire and McGarigal 2010, Tepley et al. 2017).

Distance to live, cone-bearing trees is not a consistently strong predictor of lodgepole pine regeneration. Rather, this species tends to rely on seed release from serotinous cones opened during fire. This direct seed rain can result in prolific densities of juveniles within the first few years of fire, even in large patches that experienced complete overstory mortality (Turner et al. 1997, Kashian et al. 2004). In these systems, prevalence of serotiny, which varies in space and with stand age (Tinker et al. 1994), can be an important predictor of lodgepole pine densities (Schoennagel et al. 2003). These differences in regeneration patterns between species with different reproductive strategies highlight the importance of considering autecology when drawing inferences about constraints on post-fire regeneration (Halpern 1989, Chase and Myers 2011, Romme et al. 2016).

Biotic interactions also shape juvenile conifer establishment, and many studies have indirectly evaluated the role of competition through the prevalence of other non-conifer species. In particular, species with long-lasting soil seed banks that survive fire (e.g., *Ceanothus spp.*) species that resprout (e.g., *Ceanothus spp.*, quaking aspen [*Populus tremuloidies*], many oaks [*Quercus spp*.]) may outcompete conifer juveniles (e.g., Kobziar and McBride 2006, McKenzie and Tinker 2012, Crotteau et al. 2013, Buma and Wessman 2013). This has been widely demonstrated with oaks in the mixed-species systems of southern Oregon and northern California—though conifers can maintain a competitive edge in areas that burn at lower severity (Cocking et al. 2014, Tepley et al. 2017, Nemens et al. 2018). On the other hand, lodgepole pine establishment can be so immediately prolific that inter-specific competition does little to impede recruitment (Anderson and Romme 1991). In other cases, biotic interactions may facilitate conifer establishment—for example, through ameliorating harsh conditions or affording nutrients (Baumeister et al. 2006, Oakley et al. 2006, Teste et al. 2009). The diversity of community dynamics that act on regeneration underscores the importance of considering synecological dynamics in determining constraints on post-fire recovery.

Geophysical factors. Nearly all studies considered some aspects of the geophysical setting where post-fire regeneration plays out. Researchers have examined patterns based on singular metrics like elevation, slope and aspect, or on integrative metrics such as topographic wetness index (Beven and Kirkby 1979), heat-load index (McCune and Keon 2002), or cold-air pooling index (Lundquist et al. 2008) that serve as proxies for localized climatic and edaphic processes. Because geophysical factors are very slow to change, one may conceive of a geophysical setting as a relatively "permanent" arena upon which ecological dynamics play out (Hunter et al. 1988, Lawler et al. 2015). Accordingly, the relative strength of geophysical factors as predictors of post-fire regeneration may shift in time, but *how* geophysical setting affects regeneration at a given site may remain fairly constant. Exceptions to this relative permanence include riparian systems in which geomorphological processes can occur at shorter time-scale, resulting in ephemeral environmental conditions that shape post-fire regeneration heterogeneity at some scales (Kobziar and McBride 2006, Halofsky and Hibbs 2009, Jackson and Sullivan 2009).

In general, species autecology explains patterns of post-fire species presence and abundance across geophysical settings. For example, subalpine species like Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are more abundant in cooler and moister settings (e.g., north-facing slopes, areas with high topographic wetness index values; Doyle et al. 1998, Harvey et al. 2016). Across forest systems, the most arid sites (e.g., at lower elevations, on warmer aspects) frequently have lower densities or slower establishment rates than more mesic sites (Dodson and Root 2013, Donato et al. 2016, Tepley et al. 2017). Microtopographic features and physical objects (e.g., logs, rocks) can also ameliorate localized conditions and affect regeneration at fine spatial scales. For example, Acker et al. (2017) found significantly greater densities of mountain hemlock juveniles on the north-side of downed logs than on the south side in a high severity burn. Few post-fire regeneration studies, however, have specifically examined microtopography or nurse objects (but see Coop and Schoettle 2009, Cocking et al. 2014, Acker et al. 2017).

Soil is another key abiotic variable that is rarely examined in post-fire regeneration research, despite the known importance of edaphic properties and processes in shaping forest dynamics at multiple spatial scales (Binkley and Fisher 2013). Studies that did directly measure soil properties report variable to strong positive influences of soil moisture on recruitment rates (Bonnet et al. 2005, Buma and Wessman 2012) and positive effects of soil-available nutrients (Perkins 2015). Even studies that used coarser, mapped indicators of soil type or productivity report strong patterns—for example, generally lower establishment rates in coarse-grained, igneous soils and serpentine soils than elsewhere (Donato et al. 2009a, Leonard et al. 2015, DeSiervo et al. 2015, Stine and Butler 2015). However, the coarseness of mapped indicators and the limited scope (including depth) of actual soil sampling can hinder broader inferences about how edaphic properties and processes may constrain regeneration.

Relatedly, the predictive power of geophysical variables may strongly depend on the spatial resolution of the data. Results in which geophysical factors have nominal predictive power on regeneration metrics may truly reflect a lack of influence in that given context. Alternatively, the scale at which geophysical setting is analyzed may not correspond to the scale at which regeneration dynamics are affected. Therefore, examining geophysical metrics at multiple spatial scales, using high resolution data, and computing integrative metrics using multiple neighborhood sizes may improve predictions of how geophysical setting influences post-fire regeneration (Theobald et al. 2015).

Disturbance-related factors. By definition, fire dynamics and fire effects shape the post-fire landscape. Regeneration patterns vary across severity classes, largely because fire severity affects post-fire seed source and availability as well as seed bed conditions. In lower severity, the persistence of some organic matter on the seedbed (e.g., scorched versus fully consumed needles) may ameliorate moisture stress on juveniles (Bonnet et al. 2005). On the other hand, exposed mineral soil in more severely burned areas can be conducive to germination and establishment of some species (Turner et al. 1999, Coop and Schoettle 2009). In other cases, a weak or diminishing signal of burn severity in regeneration metrics may reflect the convergence of abiotic conditions across severity classes within several years (e.g., in locations with minor organic horizons; Romme et al. 2016). Otherwise, if class-based representations of severity are used (i.e., unburned, low, moderate, and high), a weak predictive signal may mean that classes are obscuring nuanced fire effects and that continuous measures of severity are preferable (Coppoletta et al. 2016, Harvey et al. 2016). For example, severe surface fires may kill thin-barked lodgepole pine while opening cones and releasing seeds, whereas severe crown fires may completely consume canopy seed banks (Turner et al. 1999, Donato et al. 2016). And yet both contexts would be classified as high severity.

Regeneration from a fire event may also be shaped by successive, compounding disturbances and synergizing stressors (Turner 2010, Peterson and McKenzie 2011). In particular, researchers are increasingly examining short-interval fires (i.e., reburns), including how initial post-fire vegetation dynamics play-out and affect subsequent burns. For example, Stevens-Rumann and Morgan (2016) found that repeatedly burned forests in central Idaho had lower juvenile densities than areas that burned only once. Elsewhere, research suggests that reburns may reinforce limited conifer regeneration and shift systems towards non-conifer dominance—as Nemens et al. (2018) found with sprouting oak species in the northern Sierras and Coop et al.

(2016) showed in the high plateaus of New Mexico. In Colorado's subalpine forests, multiple studies have shown that compounding disturbances (e.g., blowdown and wildfire) tend to reduce conifer densities but that this effect depends on regeneration strategies (Buma and Wessman 2012, Kulakowski et al. 2013, Gill et al. 2017). Finally, there is little evidence suggesting that pre-fire insect outbreak severity consistently affects post-fire regeneration in montane systems. Rather, regeneration is largely contingent upon the interaction of seed availability and fire severity (Harvey et al. 2013, 2014b). Still, potential interactions between successive disturbances highlights the importance of considering the historical context in which post-fire regeneration plays out (Carlson et al. 2017, Gill et al. 2017).

3.4.5 *Directly demonstrating that anthropogenic climate change—not natural climatic variability—is constraining regeneration.*

After accounting for non-climatic limiting factors operating on regeneration, researchers must demonstrate a clear link between climatic changes and post-fire regeneration dynamics to conclude that climate change is hindering post-fire recovery. Importantly, this requires disentangling the effects of anthropogenic forcing on the atmosphere from the effects of inherent climatic variability. And yet, only a few studies (described below) explicitly examine long-term climatic or meteorological data as potential constraints on regeneration. Many studies surmise that directional warming and shifting precipitation patterns played a role in observed patterns, or they note that observed patterns are consistent with projections under warming temperatures. Until recently, however, most studies have relied on proxies for climatic variability (e.g., across elevation strata) to examine regeneration patterns rather than use actual climatic data.

Increasingly researchers are directly using climatic data to study how post-fire climatic conditions may constrain establishment rates and growth. In the Klamath region, for example, Tepley et al. (2017) demonstrated that a higher propagule pressure (expressed as smaller high-severity patch size) is required to counteract increasing moisture deficits to achieve a given juvenile conifer density. In Colorado's front range, Rother and Veblen (Rother and Veblen 2017) observed that establishment of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga* *menziesii*) was concentrated in years of above-average moisture availability. In the northern Rockies, Harvey et al. (2016) found densities of subalpine fir and Englemann spruce to decline sharply with both post-fire drought severity and increasing distance to seed source, though this effect was not apparent for other species examined (e.g., lodgepole pine, Douglas-fir, western larch [*Larix occidentalis*]). Urza and Sibold (2017) examined the same suite of species and found consistently positive relationships between establishment rates and both growing degree days and growing season precipitation. Examining 1485 sites across the northern Rockies, Stevens-Rumann et al. (2018) compared attainment of a recruitment threshold to post-fire climatic water deficit in two time periods (pre-2000 and post-2000). Prior to 2000, water deficit was negatively related to attainment of recruitment thresholds, but this relationship was not significant after 2000. The researchers suggest this is evidence of declining forest resilience because water deficit increased after 2000 and there were fewer cool and moist periods, which would have boosted recruitment rates and therefore resulted in a significant relationship.

Although such research represents progress towards understanding how climate change may affect post-fire regeneration, limiting or simplifying the temporal domain (e.g., binning time periods) is problematic because climatic conditions vary at multiple temporal scales. Directional warming is definitively underway, but multi-year and decadal modes of natural climatic variability have shaped, and will likely continue to shape, juvenile establishment and growth across forest systems (Woodward et al. 1995, Brown and Wu 2005, Gray et al. 2006). Therefore, one must demonstrate that the post-fire climatic variability at a given site exceeds the envelope of historical conditions under which robust recovery has proceeded. This requires examining regeneration dynamics and climatic variability as it unfolds annually for years—if not decades—after fire.

Studies must also account for the spatial variability in climatic conditions, which can be achieved through stratified sampling across known climatic gradients both within and across study areas (e.g., Donato et al. 2016, Tepley et al. 2017). The spatial resolution of climatic data may also substantially affect results, because climatic conditions vary at multiple spatial scales. For example, ground-surface temperatures—as experienced by juveniles—can depart significantly from coarse-resolution values interpolated between 2 m-high weather stations distributed across the landscape (Dingman et al. 2013). Ideally, the temporal and spatial scales at which climatic conditions are examined will match the scales of influence on juvenile establishment and growth (Connell and Sousa 1983, Walker and Wardle 2014). At the very least, researchers ought to directly acknowledge unresolved spatio-temporal variability in climatic conditions, which can shed light on unexpected patterns—for example, an apparent lack of relationship between coarsely resolved, simplistic metrics (e.g., annual precipitation) and recruitment rates (Donato et al. 2009a, Turner et al. 2016b).

Furthermore, simplistic climatic metrics (e.g., annual precipitation) can obscure the interaction of energy and water on regeneration. Moisture balance metrics that integrate both energy and water (e.g., actual evapotranspiration and deficit) are more biophysically meaningful correlates of vegetation dynamics than metrics that implicitly assume independent effects of energy and water on vegetation (Stephenson 1998). Relying only on precipitation or temperature metrics may obscure trade-offs associated with site conditions. For example, a high value of snow-water equivalent may suggest adequate moisture supply and a snowpack that protects juvenile roots (Germino et al. 2002), but a deep, persistent snowpack may also inhibit germination or encourage pathogens (Drescher and Thomas 2013).

Finally, climatic changes are likely to affect regeneration dynamics both directly and indirectly. One could imagine placing the effects on regeneration along a continuum: from direct heat-induced mortality (Allen et al. 2010), to moderately direct drought-induced declines in seed production (Pérez-Ramos et al. 2010), to indirect effects of potential increases in area burned (McKenzie and Littell 2017), to indirect effects on forest health due to the release of forest pests from cold-induced mortality (Bentz et al. 2010). The challenge of disentangling these indirect effects of climate change from non-climate drivers—especially human interference in disturbance regimes—hinders one’s ability to draw strong lines of attribution to climate change (e.g., Abatzoglou and Williams 2016). Furthermore, the role that climate plays in shaping ecological dynamics may not remain stationary in the future (Littell et al. 2018), which challenges one’s ability to make confident predictions about regeneration. On the other hand, because climate change will likely affect regeneration in myriad indirect and direct ways, the expectation that climate change will impede post-fire regeneration is a compelling one. The burden of proof for directly attributing limited or no regeneration to climate change remains high, but it will be easier to achieve as temperatures continue to warm in this coming century.

3.5 CONCLUSIONS

Given these challenges of explicitly attributing post-fire regeneration dynamics to climatic changes, one may question the utility of attempting to do so. Indeed, some have questioned whether we need more climate change attribution research in ecological contexts because of these impediments (Parmesan et al. 2013). Furthermore, myriad climate-change adaptation options are well established (e.g., Millar et al. 2007, Halofsky et al. 2018a), and focusing on implementation of these strategies rather than on precise, quantitative attribution to climate change may be more fruitful (Parmesan et al. 2013).

However, without understanding how climatic changes may tighten existing constraints on regeneration if not directly hinder regeneration, we run the risk of missing or misplacing opportunities for promoting forest recovery. For example, many studies highlight the importance of seed availability in constraining post-fire regeneration (e.g., Kemp et al. 2016, Harvey et al. 2016, Tepley et al. 2017). Understanding how burn patterns—and therefore post-fire seed availability—are affected by climatic changes versus fuel build-up can suggest the most appropriate adaptation strategies in a given context. For example, early post-fire interventions to alleviate drought stress may be most appropriate in some contexts (Millar et al. 2007, Hessburg et al. 2015) whereas broader restoration efforts to reduce fire severity may ensure more robust, long-term recovery in other contexts (Prichard and Kennedy 2014).

The growing body of research documenting post-fire regeneration is helping to clarify where, when, and how numerous factors come into play and interact—whether ecological, geophysical, disturbance-related or climatic. Collectively, these studies demonstrate the tremendous variability in regeneration dynamics at multiple spatial and temporal scales. This underscores the importance of long-term monitoring of post-fire regeneration as well as the need for sampling designs that expressly address spatially-structured drivers (e.g., via stratified random sampling). Such variability in regeneration as well as the variability in methodological approaches to date also challenge synthetic research efforts (e.g., Stevens-Rumann et al. 2018). However, synthetic analyses and coupling field-based efforts with other approaches (e.g., remote sensing, experimental plantings; Table 1) will continue to improve our understanding of how climatic changes may affect regeneration. Although we cannot yet definitively conclude that climate change is impeding post-fire regeneration across western North America, the growing body of research will continue to inform how management can best promote robust forest recovery in an uncertain future.

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TABLES

Table 3.4. Search term used in the Web of Science databases. The operator * was applied to multiple terms to capture various tenses and conjugations (e.g., “wildfire*” returns “wildfire” and “wildfires”; “germinat*” returns “germinate”, “germination”, etc.). The initial search (completed in early 2018) returned 1950 articles, but the full number of articles evaluated exceeded 2000 because an automated alert with the same search terms was maintained until July 15, 2018 when new articles that fit the search criteria were added to the Web of Science database. Each of these new articles was considered for inclusion.

CRITERION	**KEYWORDS**
Forest fire	forest, forestry, tree, fire, wildfire, post-fire, postfire, burn
Recovery	recovery, recruitment, regeneration, germination, establishment, seedling, juvenile, seed source
Geography	Washington, Oregon, California, Nevada, Idaho, Montana, Wyoming, Utah, New Mexico, Arizona, Colorado, Alaska, British Columbia, Alberta, western North America, western Canada, western U.S., Pacific Northwest, Rocky Mountains, Rockies, intermountain

FIGURES

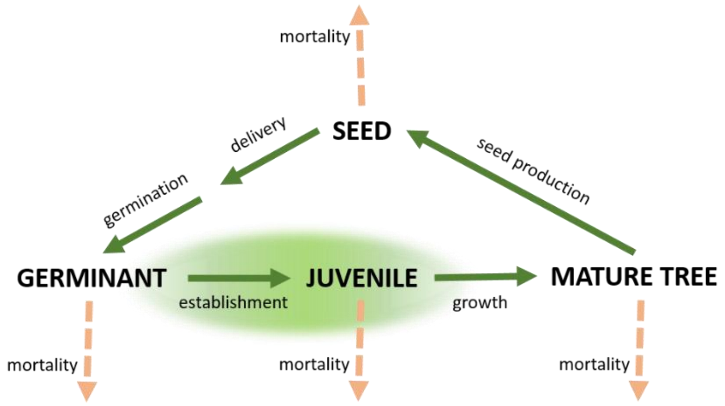

Figure 3.1. Simplified schematic of key processes associated with successful forest recovery. Post-fire recovery research addressed herein primarily focuses on the establishment of juveniles, shaded in green. Adapted from Clark et al. (1999).

Figure 3.2. Current-year germinants face steep mortality rates such that their inclusion in estimates of annual establishment rates may misrepresent likely density trajectories. Photo taken in 2016 within the 2006 Tripod Complex Fire area in Washington's Okanogan-Wenatchee National Forest.

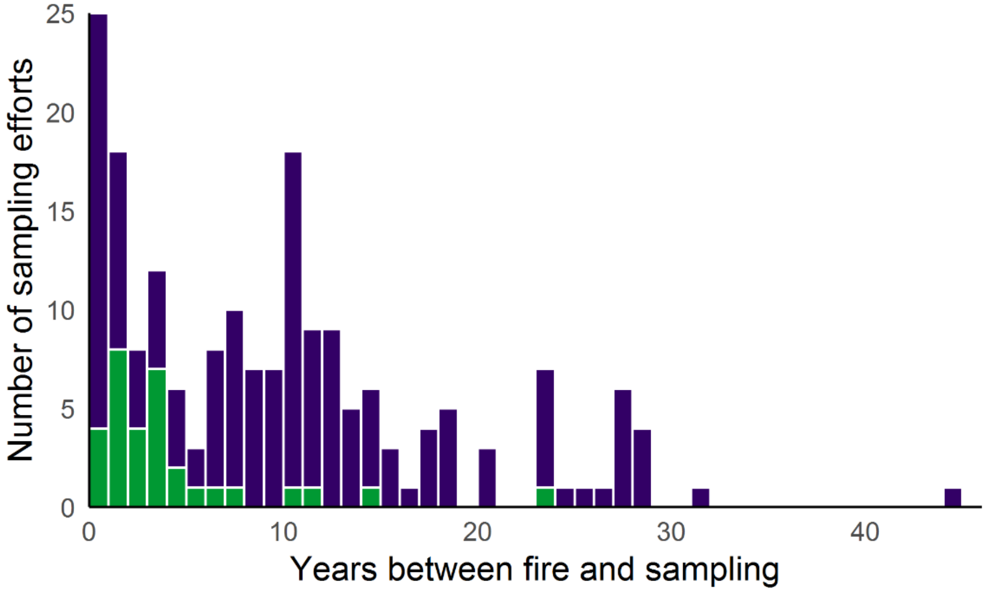

Figure 3.3. The number of field-sampling efforts of natural recovery carried out by interval since fire, as reported in 59 studies that met our review criteria (see text) and fell within the following ecoregions (Omernik and Griffith 2014): Northwestern Forested Mountains: Western Cordillera, Marine West Coast Forest, and Temperate Sierras: Upper Gila Mountains. These ecoregions were used as a coarse filter to capture conifer-dominated systems. Green areas represent efforts that are reported in conjunction with multiple, successive sampling efforts (i.e., re-measurements) within the same study.

Figure 3.4. Increasingly, studies examine multiple fires across forest systems. Clockwise from top left: the 2002 Biscuit fire in the Klamath region of southern Oregon (Forest Service photo); the 2016 Fawn Fire in Yellowstone National Park (National Park Service [NPS] photo); the 2013 Big Meadows fire in Rocky Mountain National Park (NPS photo); the 2018 Obi fire on the north rim of the Grand Canyon (NPS photo). All photos are in the public domain.

APPENDIX 3.1 ALTERNATIVE APPROACHES TO EVALUATING POST-FIRE FOREST REGENERATION

A range of approaches has been used to examine post-fire forest regeneration, each with their own strengths and challenges, as briefly describe here.

Class of approaches	**Description**	**Major strengths**	**Primary shortcomings**	**Examples**
Paleoecology	Using charcoal, pollen, spore, and macrofossil record to reconstruct forest composition and change on geological time scales.	Longest temporal record, tracking plant dynamics and climatic changes throughout the late Quaternary.	Cannot resolve dynamics of discrete events or patterns at fine resolution in time or space; gaps in the record may exist; does not capture ecological dynamics that may contribute to shifts in vegetation patterns (e.g., rapid competitive replacement)	(e.g., Fletcher et al. 2014, Crausbay et al. 2017, Alt et al. 2018)
Stand reconstructions	Leveraging extant aspects of stand structure and records therein (e.g., tree rings and fire scars) to reconstruct stand dynamics.	Decades and centuries of spatially-explicit stand dynamics are integrated into a single record that reflects a strong signal of climate variability.	May not be able to resolve precise dynamics of discrete events; may not be detecting individuals that have died.	(Romme and Knight 1981, Brown and Wu 2005, Tepley et al. 2013)
Remote sensing	Leveraging satellite observations or aerial imagery to track forest dynamics.	Repeatedly captures broad spatial extents; multi-decadal archives of comparable, fine- and moderate-resolution imagery now exist (e.g., Landsat); site access is unconstrained	Unable to detect fine-scaled ecological dynamics; vegetation indices derived from spectral bands are imperfect (e.g., due to band saturation)	(Stueve et al. 2009, Frazier et al. 2015, Meng et al. 2015)
Simulations	Using stand- to landscape-level forest simulation models to predict recovery (spatially-explicit or not)	Can illustrate a range of plausible futures in a spatially-explicit manner, typically annually; high repeatability and low-cost	Requires field data for accurate parameterization; future projections cannot be validated immediately; trade-offs between representing processes that occur at fine spatial and temporal scales (e.g., photosynthesis) over longer scales (e.g., years of recruitment) statistically or mechanistically; present-day models of stochastic dynamics (e.g., area that burns at a given severity) may not hold forth into the future	(Schoennagel et al. 2006, Feddema et al. 2013, Serra-Diaz et al. 2018, Braziunas et al. 2018)

Experimental manipulations	Manipulating plausible limiting factors to evaluate influence on juvenile recruitment	Can clarify physiological mechanisms constraining recovery and represent likely future conditions—including possible management options—under which recovery will unfold	Inherently artificial; controlled settings may exclude other significant factors that shape recovery; time-scale often constrained	(Rother et al. 2015, Sparks et al. 2018)

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APPENDIX 3.2 HISTORICAL CONTEXT OF POST-FIRE RECOVERY RESEARCH IN WESTERN NORTH AMERICA

Although forest regeneration has undoubtedly been a topic of interest since humans began managing forests, several key events in the late 20th century focused attention on post-disturbance recovery. Large natural disturbances in the 1980s and 1990s—particularly the 1980 eruption of Mt. St. Helens and the 1988 fires in Yellowstone National Park—sparked questions about the causes and consequences of disturbances in ecological systems (Turner 2010). These events coincided with growing intellectual interest in disturbances and patch dynamics as fundamental drivers of landscape heterogeneity (Pickett and White 1985) and, more formally, the emergence of the field of landscape ecology (Turner 1989).

Evaluating post-disturbance dynamics has provided the opportunity to revisit more traditional models of stand development (e.g., Anderson and Romme 1991, Romme et al. 2016). Those models may have reflected the perceptions that some forest systems consistently experience rapid and dense establishment following stand-replacing disturbance (Show and Kotok 1924, Munger 1940) or follow a fairly consistent trajectory of community succession (e.g., initial or relay floristics; Egler 1954) and stand development (Oliver 1980). Some models were likely based on patterns observed after managed disturbances (e.g., clear-cut timber harvest) such that the complexity and variability in trajectories of natural recovery dynamics were not well represented. Only as post-disturbance management objectives have broadened beyond accelerating tree growth has attention been focused on the complexity and variability in early stand trajectories (Donato et al. 2012).

The impetus for understanding post-fire regeneration goes far beyond revisiting ecological models, of course: there is the critical question of how management interventions can affect recovery outcomes (Noss et al. 2006, Hessburg et al. 2016). The implications of post-fire management on regeneration and subsequent fire risk has been widely explored—for example, the implications of salvage logging (e.g., Donato et al. 2006a, Keyser et al. 2009), erosion control efforts (Dodson and Peterson 2010), and replanting (Ouzts et al. 2015). Given the vast fire-prone areas in need of restoration (Haugo et al. 2015, Hessburg et al. 2015), questions of how pre-fire management affects subsequent stand dynamics has also spurred research: for example, related to how treatments affect fire severity (Prichard and Kennedy 2014), survival of juveniles (Lyons-Tinsley and Peterson 2012); recovery (Bormann et al. 2015), and carbon storage (James et al. 2018). Increasingly, the threat of climate change is shaping the questions researchers ask about post-fire regeneration. After all, understanding regeneration dynamics can help inform where, when, and how to leverage natural regeneration or otherwise actively intervene to adapt forest systems to climate change.

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