

Corralling a black swan: natural range of variation in a forest landscape driven by rare, extreme events

DANIEL C. DONATO,^{1,2,4} JOSHUA S. HALOFSKY,¹ AND MATTHEW J. REILLY³

¹Washington State Department of Natural Resources, Box 47014, Olympia, Washington 98506 USA

²School of Environmental & Forest Sciences, University of Washington, Seattle, Washington 98195 USA

³Department of Biological Sciences, Humboldt State University, 1 Harpst Street, Arcata, California 95521 USA

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Abstract. The natural range of variation (NRV) is an important reference for ecosystem management, but has been scarcely quantified for forest landscapes driven by infrequent, severe disturbances. Extreme events such as large, stand-replacing wildfires at multi-century intervals are typical for these regimes; however, data on their characteristics are inherently scarce, and, for land management, these events are commonly considered too large and unpredictable to integrate into planning efforts (the proverbial “Black Swan”). Here, we estimate the NRV of late-seral (mature/old-growth) and early-seral (post-disturbance, pre-canopy-closure) conditions in a forest landscape driven by episodic, large, stand-replacing wildfires: the Western Cascade Range of Washington, USA (2.7 million ha). These two seral stages are focal points for conservation and restoration objectives in many regions. Using a state-and-transition simulation approach incorporating uncertainty, we assess the degree to which NRV estimates differ under a broad range of literature-derived inputs regarding (1) overall fire rotations and (2) how fire area is distributed through time, as relatively frequent smaller events (less episodic), or fewer but larger events (more episodic). All combinations of literature-derived fire rotations and temporal distributions (i.e., “scenarios”) indicate that the largest wildfire events (or episodes) burned up to 10^5 – 10^6 ha. Under most scenarios, wildfire dynamics produced 5th–95th percentile ranges for late-seral forests of ~47–90% of the region (median 70%), with structurally complex early-seral conditions composing ~1–30% (median 6%). Fire rotation was the main determinant of NRV, but temporal distribution was also important, with more episodic (temporally clustered) fire yielding wider NRV. In smaller landscapes (20,000 ha; typical of conservation reserves and management districts), ranges were 0–100% because fires commonly exceeded the landscape size. Current conditions are outside the estimated NRV, with the majority of the region instead covered by dense mid-seral forests (i.e., a regional landscape with no historical analog). Broad consistency in NRV estimates among widely varied fire regime parameters suggests these ranges are likely relevant even under changing climatic conditions, both historical and future. These results indicate management-relevant NRV estimates can be derived for seral stages of interest in extreme-event landscapes, even when incorporating inherent uncertainties in disturbance regimes.

Key words: *Cascade Range; disturbance synchrony; Douglas-fir; early-seral habitat; early-successional forest; historical range of variation; late-successional forest; old-growth forest; stand-replacing fire regime; state-and-transition simulation models; West Cascades; western Washington.*

INTRODUCTION

The natural range of variation (NRV) is well established as an important reference for ecosystem management (Landres et al. 1999, Keane et al. 2009). Although not without limitations (e.g., Moritz et al. 2013), these ranges provide useful context for diverse objectives including ecological restoration, identifying baselines for assessing current and future change, setting habitat goals

for species of concern, and establishing guidelines for promoting resilience to change (Cissel et al. 1999, Landres et al. 1999, Keane et al. 2009, Demeo et al. 2012, Safford et al. 2012, Spies et al. 2018). However, determining a management-relevant NRV is difficult for regions structured by disturbances that are highly infrequent but extreme in size and severity, partly because empirical data are scarce and partly because seemingly singular events can impart strong and lasting influence (Manley et al. 1995, Dale et al. 1998, Romme et al. 1998, Landres et al. 1999).

Prime examples of such regions are wet temperate and cold boreal forests with long-interval (multi-

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⁴E-mail: daniel.donato@dnr.wa.gov

century), stand-replacing fire regimes. Many of these landscapes are characterized by fire rotations (landscape mean fire intervals) several centuries long, and fire events approaching one million hectares in size (Hemstrom and Franklin 1982, Romme 1982, Henderson et al. 1989, Romme and Despain 1989, Agee 1993, Baker 2009). Under these regimes, quasi-equilibrium dynamics may occur only at the broadest spatiotemporal scales, otherwise operating effectively as “nonequilibrium” landscapes (Shugart and West 1981, Turner et al. 1993). Such wide variation challenges efforts to set NRV-informed management targets for seral stages of interest; a common coarse-filter approach to providing critical habitats, enhancing landscape diversity, and fostering adaptive capacity (WADNR 1997, Davis et al. 2015, USFS 2017, DeMeo et al. 2018, Halofsky et al. 2018a). Prior studies have posited extreme events as too unpredictable, variable, and influential to be operationalized in management or reference ranges (e.g., Manley et al. 1995), essentially treating such disturbances as “Black Swans” (rare, unpredictable events with disproportional influence; Taleb 2007) to be ignored in planning. However, recent forest restoration projects on public lands have expressed a need to incorporate the full disturbance regime in setting management targets for seral stages in infrequent-fire landscapes (e.g., USFS 2017).

A major challenge in developing NRV for these landscapes is that empirical data on key fire regime parameters (e.g., fire sizes, intervals) are rare, often lack sufficient temporal depth, and are often erased by subsequent fire events and land management. Estimates of these NRVs therefore must combine available empirical evidence with established statistical tools and modeling (Agee and Flewelling 1983, Agee 1993, Denny et al. 2009, Moritz et al. 2013). Previous work examined static age distributions, including the landscape proportion of old-growth forest, arising from known stand-replacing fire rotations (Van Wagner 1978, Agee 1993, Spies and Turner 1999); but did not quantify dynamic ranges in the abundance of seral stages. More recent studies (Wimberly et al. 2000, Wimberly 2002, Nonaka and Spies 2005, DeMeo et al. 2018) used simulation models to develop ranges for late-seral forests in stand-replacing fire regimes; however, those studies assumed more frequent, regularly occurring (and thus generally smaller) fires, as opposed to a regime of rare, episodic, large fires. Many infrequent fire regimes are best characterized as driven mainly by the extremes: the temporally clustered (regionally synchronous) episodes of large fires that punctuate otherwise relatively quiet periods regionally, rather than semi-regularly occurring fires or fire-free periods (Romme 1982, Henderson et al. 1989, Agee et al. 1990, Morrison and Swanson 1990, Agee 1993, Weisberg and Swanson 2003). The challenge in assessing NRV for these episodic regimes can be overcome by assessing dynamics at sufficiently large spatial and temporal scales.

Here, we estimate reference conditions (NRV) for a large forest region dominated by long-lived conifers and landscapes that were historically structured by a regime of episodic, large, severe fires: the western Cascade Range of Washington, USA. We emphasize the natural range of variation, operationally defined as the range of landscape conditions (seral stage proportions) resulting from known fire regime parameters, instead of historical range of variation (HRV) to indicate we are not attempting to describe a specific era (e.g., the entire Holocene). Rather, we characterize the variability that would occur under different literature-derived inputs on regional fire regimes, to establish likely bounds on landscape behavior (*sensu* Agee 1993).

We estimate ranges in the abundance of both late-seral (mature/old-growth) and early-seral (post-disturbance pre-forest) conditions, two stages of high conservation concern (Franklin and Johnson 2012, Swanson et al. 2014, Spies et al. 2018), as well as the intervening mid-seral stage. We assess the degree to which NRV estimates agree under a broad range of literature-derived inputs regarding (1) overall fire rotations (time required for area equivalent to study extent to burn), and (2) how fire events are distributed through time, as relatively frequent smaller events (less episodic fire) or fewer but larger events (more episodic or temporally clustered fire). We combine empirical evidence with state-and-transition simulation models (STSMs) to develop likely landscape behavior through time, including estimates of maximum area burned in fire events/episodes. Given the dynamic nature of these landscapes, we also take a temporal perspective to ask how often (what fraction of the time) the landscape would reside in a given proportion of seral stages. We further assess how NRV estimates differ at a smaller scale typical of conservation reserves or management units (20,000 ha), as compared to the region as a whole (2.7 million ha). Finally, we estimate differences between current conditions and the modeled NRV based on recent forest inventory data. This analysis is intended to provide a broad framework for developing and applying natural range concepts to this and similar forest regions driven by rare, large disturbances.

METHODS

Study area

We assessed a 2.7-million-ha forest landscape comprising most of the Western Cascade Range of Washington State (i.e., West and North Cascades Level III Ecoregions modified from Omernik [1987]; see Fig. 1). The region has a temperate maritime climate (Mediterranean type), with abundant annual rainfall (~150–250+ cm) falling mostly between October and April, and a pronounced summer dry season. Mean winter snowfall in high-elevation forests (above 1200 m) ranges from 1,000 to 1,500 cm/yr. Forests of the region are highly productive and can carry exceptionally high standing

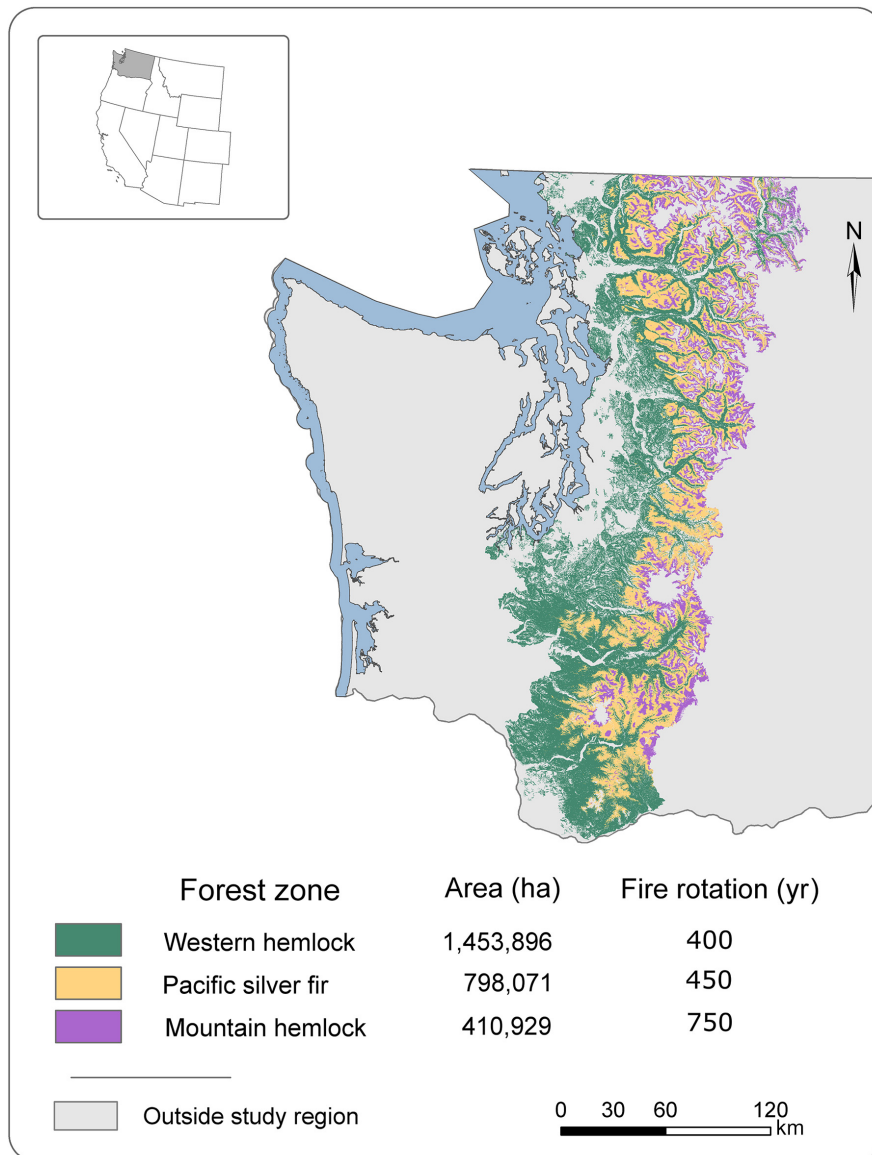


FIG. 1. Map of study area, showing major forest types evaluated within the West Cascade Range of Washington, USA. Fire rotations represent central estimates for each zone.

biomass (Franklin and Waring 1979). Vegetation zones (Fig. 1) include the *Tsuga heterophylla* zone below ~900 m elevation (55% of study area), dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*T. heterophylla*), and western redcedar (*Thuja plicata*); the *Tsuga mertensiana* zone above ~1,300 m elevation (15% of study area), dominated by mountain hemlock (*T. mertensiana*), Pacific silver fir (*Abies amabilis*), sub-alpine fir (*A. lasiocarpa*), and occasionally lodgepole pine (*Pinus contorta*); and a mid-elevation *Abies amabilis* zone (30% of study area) with varying combinations of the above species (Franklin and Dyrness 1973, Agee 1993). Productivity decreases with increasing elevation, from the warm western hemlock zone to the cold

mountain hemlock zone. In this study, we exclude the Douglas-fir zone of the Puget Lowlands (Omernik 1987), which has a distinct mixed-severity fire regime, and high-elevation subalpine parklands with relatively sparse tree cover.

Fire regimes are characterized as infrequent and stand-replacing (Agee 1993), with fire rotations ranging from approximately 200 yr for parts of the western hemlock zone to near 1,000 yr for parts of the mountain hemlock zone (Fig. 1; Agee 1993). The productivity and biomass of these forests mean they are rarely fuel-limited, at any seral stage, and are instead climate- and ignition-limited (Agee 1993). The largest events (the most important in structuring the landscape) tend to occur with the rare

coincidence of severe summer drought, an ignition source, and, generally, a synoptic east wind event that drives high-severity fires over vast areas in a matter of hours or days (Joy 1923, Holbrook 1960, Agee 1993). Fires (or fire episodes) can burn very large extents, readily attaining several hundred thousand hectares (Holbrook 1960, Agee 1993), with some evidence pointing to events exceeding one million hectares (Henderson et al. 1989). Stand re-establishment after fire is generally robust but can take several decades to complete (e.g., Franklin and Hemstrom 1981, Tappeiner et al. 1997, Freund et al. 2014), and mature to old-growth conditions begin to develop after about one to two centuries of succession (Agee 1993, Franklin et al. 2002, Van Pelt 2007).

The West Cascades are a multi-ownership region composed of landscapes managed by the U.S. Forest Service (55%), the State of Washington (9%), other federal entities (e.g., National Park Service, 5%), private entities (30%), and Native American tribes (~1%; not included in this analysis). Management intensity is greatest on private industrial lands, followed by state and tribal lands. Much of the land managed by the Forest Service was harvested from the 1950s to 1980s, but harvests have declined precipitously since the 1990s. Currently, Forest Service and other federal lands are managed the least intensively. Forest Service lands are managed under the Northwest Forest Plan that established, among other things, an extensive regional network of late-successional reserves (LSRs).

Natural range of variation (NRV)

Fire regime parameters.—Because empirical data on fire regime parameters are inherently scarce for these regimes, we used an uncertainty framework to establish likely ranges of landscape behavior. Rather than using a single estimate for a given parameter (e.g., rotation,

temporal distribution), we applied a range of estimates based on the available literature and propagated these factorially through the simulations (Table 1; Fig. 2).

For fire rotations (i.e., overall fire cycles or burn rates, scale independent), central estimates were drawn from average rotations in the Landfire database (Rollins 2009) and cross-referenced with published regional studies (Agee 1993); these were 400, 450, and 750 yr for the *T. heterophylla*, *A. amabilis*, and *T. mertensiana* zones, respectively. These rotations vary by specific area (e.g., plant association within forest zone) and by study, on the order of ± 200 yr (Agee 1993); thus we also assessed shorter (200, 250, and 550 yr for the respective zones) and longer (600, 650, and 950 yr) rotations (Table 1). Note the fire regime studies from which we draw are fire rotations/intervals that effectively incorporate all presettlement ignition sources, including lightning and Native American burning.

Within each set of fire rotations, burn area must also be distributed among discrete events (i.e., as many small events or few large events; see Fig. 2). When events occur within the region more frequently, burn area is scattered among many smaller fires and temporal clustering is low; whereas when events are rarer, burn area is by definition clustered into larger events (or episodes; Fig. 2). We informed these parameters with published sources based on charcoal records (Long et al. 1998, Long and Whitlock 2002, Hallett et al. 2003, Walsh et al. 2010, 2015) and regional age-class and fire-scar data (Henderson et al. 1989, Agee et al. 1990, Morrison and Swanson 1990, Weisberg and Swanson 2003). These studies suggest an episodic regime (Agee 1993) predominated by large events occurring at century-scale intervals, with some degree of regional synchrony (i.e., clustering or peaks in fire area through time; Weisberg and Swanson 2003) at intervals of ~200–300 yr. As with rotations, we incorporated uncertainty to explore how

TABLE 1. Description of fire regime parameters for the nine primary scenarios within the uncertainty framework.

Fire area clustering through time	Distribution of fire events through time†	Combined regional frequency‡	Fire rotations					
			270 yr		470 yr		670 yr	
			Area burned per century	Fire sizes	Area burned per century	Fire sizes	Area burned per century	Fire sizes
Low (less episodic)	12.5-yr, 25-yr, 50-yr, 100-yr	7	high	smaller	moderate	smaller	low	smaller
Moderate	25-yr, 50-yr, 100-yr, 200-yr	13	high	moderate	moderate	moderate	low	moderate
High (more episodic)	50-yr, 100-yr, 200-yr, 300-yr	26	high	larger	moderate	larger	low	larger

Notes: Fire rotation is the time required for an area equivalent to study area to burn. Regional fire rotations are area-weighted averages of the forest zones. The central estimate of 470 is derived from rotations of 400, 450, and 750 yr for the *Tsuga heterophylla*, *Abies amabilis*, and *Tsuga mertensiana* zones, respectively. Longer and shorter rotations were derived by adding or subtracting 200 yr from the rotations of each zone, respectively. See Table 2 for median and maximum fire sizes resulting from these parameters. See Fig. 2 for visual depiction of relationship among fire rotation, temporal clustering, and fire size.

† Event types expressed as intervals in years.

‡ An event somewhere in region every *x* yr on average.

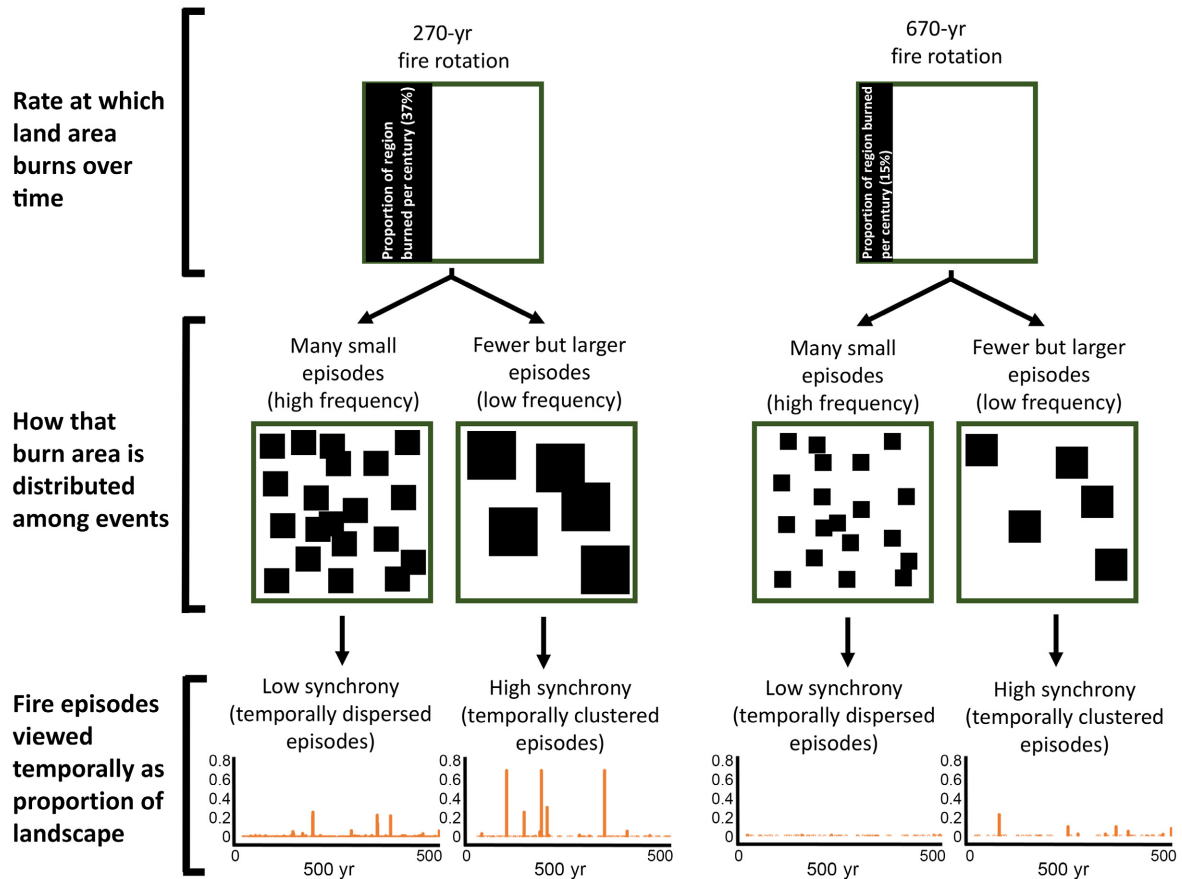


FIG. 2. Conceptual relationship between fire rotation, temporal clustering of fire area, and fire sizes over time. Only the shortest and longest fire rotations, and least and most episodic distributions, that we used are shown for illustration purposes (i.e., four of the most extreme among the nine scenarios). When fire is less episodic (less temporal clustering), fire area is spread out as more numerous, small events; whereas when fire is more episodic (highly clustered temporally), fire area is concentrated in fewer, but larger, events. Area burned under both temporally clustered and dispersed fire events increases as rotations shorten.

different temporal distributions could affect NRV estimates (Table 1; Fig. 2). We distributed area burned among fire events using a discretized version of the widely applied negative exponential distribution, which relates fire intervals and fire sizes (e.g., Malamud et al. 2005, Moritz et al. 2011; see Appendix S1). Within this interval–size relationship, we truncated fire sizes at maximum intervals of 100, 200, or 300 yr to generate distributions emphasizing either more numerous small fires (100-yr maximum), rare large fires (300-yr maximum), or an intermediate distribution (200-yr maximum). See Table 1, Fig. 2, and Appendix S1 for more details on fire regime parameters.

We assessed only the stand-replacement portion of the fire regime. Stand-replacing patches are considered the dominant force shaping landscape structure and age-class distributions in the study region (Agee 1993), even if embedded within coarse-scale burn mosaics. All fire regime parameters in the literature are based on stand-replacing patches only, being derived from stand-origin cohorts (Hemstrom and Franklin 1982, Fahnestock and

Agee 1983, Agee 1993). As such, non-stand-replacing fire patches may occur in addition to, not in lieu of, the stand-replacing patches we assessed. Non-stand-replacing patches largely do not reset succession or stand age (Nonaka and Spies 2005, Tepley et al. 2013) and are not critical to our research question on broad seral-stage abundances. We assumed similar burn probability across seral stages and structural states, as young stands carry sufficient biomass to burn (Spies et al. 2018) and there is ample precedent for early-seral reburning in these forest types (Kemp 1967, Agee 1993, Gray and Franklin 1997). Finally, we note the fire events we modeled likely reflect episodes or complexes of multiple fires, rather than necessarily a single large fire (e.g., Hemstrom and Franklin 1982, Long and Whitlock 2002).

State-and-transition simulation approach.—To develop the NRV for seral stages of interest, we used a state-and-transition approach (Daniel et al. 2016) to simulate wildfire disturbances and forest development through time. The model grows forests through stages (at well-

validated rates; see Appendix S2), and occasionally burns them (stochastically, according to fire regime parameters described above and in Appendix S1). We modified previously developed STSMs that incorporate established patterns and rates of forest succession for each forest zone (Halofsky et al. 2014, 2018a). The STSMs contain numerous states (e.g., seral or successional stages) reflecting distinct combinations of quadratic mean diameter (QMD), canopy closure, and canopy layering (Halofsky et al. 2014). For parsimony in presentation, these states were lumped into three broad classes: early-seral (post-disturbance, pre-canopy closure, abundant legacy dead wood, codominance of non-tree life forms; generally a ~40–70-yr period), mid-seral (closed tree canopy, competitive exclusion), and late-seral (mature to old-growth; large tree dominance, vertically distributed biomass, abundant deadwood; Franklin et al. 2002). We also parsed the late-seral class into mature (~80–200 yr) and old-growth (>200 yr) subclasses using a negative-exponential age distribution (Van Wagner 1978, Agee 1993). See Appendices S2 and S3 for more information on seral stage definitions. STSM states are connected through a series of probabilistic transitions between seral stages as affected by time and disturbances such as insects, disease, and, primarily for this region, fire.

To effectively capture the episodic regime of the West Cascades, we employed many replicates through space, time, and iterations. First, our study domain was large at 2.7 million hectares, containing 29,500 cells of ~90-ha size (fires under 90 ha are inconsequential for this landscape, based on both empirical records and the distribution of burn area under a relevant power law). Second, we simulated a 10,000-yr time span, meeting the recommendation of 10 times the longest fire rotation (Keane et al. 2002). This span is not intended to represent the entire Holocene specifically, but to derive the range of conditions that would result from known fire regime parameters from the empirical record (i.e., the last millennium; sensu Agee and Flewelling 1983, Agee 1993). Third, we ran 50 model iterations for each of nine fire regime scenarios. We settled on all of these parameters after extensive sensitivity analyses showed no change to outputs beyond this cell resolution, timeframe, or number of iterations.

We initiated the STSM model by distributing the 29,500 cells into grass/forb model states proportionally by area in each forest type, then running the forest growth/succession and fire probabilities for the 10,000-yr period. We found initial conditions to be inconsequential since we later truncated a spin-up period, and any beginning state converged on the same solutions. Models were aspatial, meaning individual cells were tracked through time, but not their location on the landscape. An aspatial approach worked well because (1) our objective was to quantify total land area by seral stage over time, which is driven mathematically by fire rotations and overall fire sizes, not patch structure of fires;

(2) the impact of landscape structure (fuels, topography) is relatively minimal when considered over such a large simulation area, particularly in this productive region in which fuels are virtually never limiting in any seral stage, and fires are largely climate/weather-driven (Joy 1923, Kemp 1967, Agee 1993, Spies et al. 2018); and (3) simulating spatial patch dynamics (sensu Wimberly 2002) is hindered by a paucity of information on patch structure of fires in the West Cascades of Washington. This said, we discuss research needs and roles of spatial pattern in subsequent sections.

We ran nine primary scenarios, a factorial combination of the three rotation sets and three temporal distributions (clustering levels; Table 1). We also repeated the nine scenarios using higher or lower power-law exponent values for distributing fire sizes (i.e., 18 additional scenarios; see Appendix S1). Using the parameters in Table 1, we developed unique temporal sequences of fire years representing the stochastic nature of fire. Each iteration randomly assigned a year to an event size while retaining the assigned fire rotation and temporal distribution across all iterations within a scenario. For each model iteration within each scenario, we calculated the median and 5th and 95th percentiles for the abundance of each seral stage (percent of region), after truncating a 2000-yr spin-up period. We then averaged each summary statistic across all 50 iterations within a scenario to develop NRV estimates. We also drew medians and 5th and 95th percentiles from all 450 iterations across all nine scenarios, which yields a composite range that incorporates the uncertainty and nonlinear distributions associated with the different fire regime assumptions.

Finally, we repeated the simulations for a theoretical 20,000-ha sub-landscape with the same proportions of forest zones and cell resolution, to explore the influence of spatial domain size on resulting NRV ranges (Wimberly et al. 2000). This scale is relevant to landscape forest management strategies that commonly include reserves of that order, e.g., Late-Successional Reserves (LSRs) on federal lands (Davis et al. 2015, Spies et al. 2018), Spotted Owl management units (SOMUs) on state lands (WADNR 1997), or municipal watersheds.

Current conditions

We estimated current forest conditions using 848 1-ha field plots collected by the U.S. Forest Service Pacific Northwest Research Station Annual Forest Inventory and Analysis program (FIA). Plots are spatially balanced across all forested land, with one plot for every ~2,400 ha, providing a statistically unbiased snapshot of forest conditions (Bechtold and Patterson 2005). Reilly and Spies (2015) classified FIA plots into 25 distinct forest structural/developmental types based on nine attributes such as QMD, basal area, canopy cover, snag density, and downed wood abundance. We cross-walked these 25 types into our aggregated classes of early-seral,

mid-seral, and late-seral conditions used in our STSM NRV analysis (see Appendix S3 for groupings and additional method details). Current early-seral stands were further split into simple and complex based on the presence or absence of live remnant trees, snags, and coarse deadwood (Reilly and Spies 2015).

To elucidate whether and how current landscape conditions differ from the NRV, we summarized the FIA data over the entire region, by broad ownership category, and geographically. For the latter, we grouped plots within fourth-field watersheds to estimate the current abundance of seral stages by forest type. Based on the proportional abundance of forest types within each watershed, we calculated the range of complex early-seral, mid-seral, and late-seral conditions under the NRV within each watershed (median and range), then subtracted the nearest end of the range from current amounts to generate a map of estimated differences.

RESULTS

Fire event sizes

Solving for literature-derived fire rotations and temporal distributions yielded maximum event sizes well into the hundreds of thousands of hectares for virtually any plausible set of fire-regime inputs (Table 2, Appendix S1). Under no scenario were estimated maximum fire event sizes less than approximately 200,000 ha, and several scenarios included fire episodes approaching or exceeding one million hectares (i.e., >30% of the region; Table 2).

Natural ranges of variation

Both fire rotation and temporal clustering were important drivers of the NRV, at both region and reserve scales (Figs. 3, 4). Fire rotations were the main determinant of both medians and ranges (Figs. 4, 5), but

greater clustering of fire area (more episodic) also produced substantially larger ranges within each rotation (Fig. 4, Appendix S1). Nevertheless, some common patterns emerged across scenarios in terms of seral stage abundances.

Late-seral forest abundance fluctuated considerably at the region scale, but was the most abundant condition in all scenarios (Figs. 3A–C, 4A–C). Maximum (95th percentiles) late-seral abundance was consistently near 90% of the region (Fig. 4C). Minima (5th percentile) ranged more widely among scenarios, but were ~40–60% of the region for all but the most extreme short-rotation/most-episodic scenarios (Fig. 4C). Median abundance of late-seral conditions was 60–84% of the region for all scenarios (Fig. 4C). The composite estimate was ~47–90% of the landscape in late-seral condition, with a median of 70% (Fig. 4C).

For early-seral conditions, minimum values were consistently 1–3% of the region across scenarios (Fig. 4A), while maxima were 15–35% for most scenarios and up to 50–55% for the two most extreme short-rotation/most-episodic scenarios (Fig. 4A). Median early-seral abundance was between 3% and 12% for all scenarios (Fig. 4A). The composite estimate was 1–30% of the region in the early-seral condition, with a median of 6% (Fig. 4A).

Mid-seral conditions ranged from minima of 4–15% to maxima of 24–43% for all scenarios (53–56% for the two most extreme short-rotation/most-episodic scenarios) (Fig. 4B). Median abundance of mid-seral conditions was 12–29% across all scenarios (Fig. 4B). The composite estimate was ~8–36% of the region in mid-seral condition, with a median of 19% (Fig. 4B).

From a temporal perspective (Fig. 5; Appendix S4), late-seral conditions would occupy more than 60% of the region the vast majority of the time under virtually all scenarios, and only rarely compose <40% of the region. Early-seral conditions would occupy 1–20% of the region virtually all the time, only rarely exceeding

TABLE 2. Estimates of benchmark stand-replacing fire event sizes for forests of the Western Washington Cascades, under different inputs for fire regime parameters.

Fire rotation and event type	Fire event size (ha)		
	Fire area least episodic/clustered (many, smaller events)	Fire area moderately episodic/clustered	Fire area most episodic/clustered (fewer, larger events)
270 yr			
Maximum	700,000	1,400,000	1,900,000
Median	11,000	22,000	50,000
470 yr			
Maximum	350,000	700,000	910,000
Median	6,000	11,000	25,000
670 yr			
Maximum	240,000	470,000	630,000
Median	4,000	7,000	17,000

Notes: Numbers are rounded for clarity. Values are derived from literature estimates of fire rotations and intervals, constrained by a power-law distribution (exponent = -0.5) relating fire interval and fire size. See *Methods*, Table 1, and Appendix S1 for additional details, including fire event sizes using alternative power-law distributions.

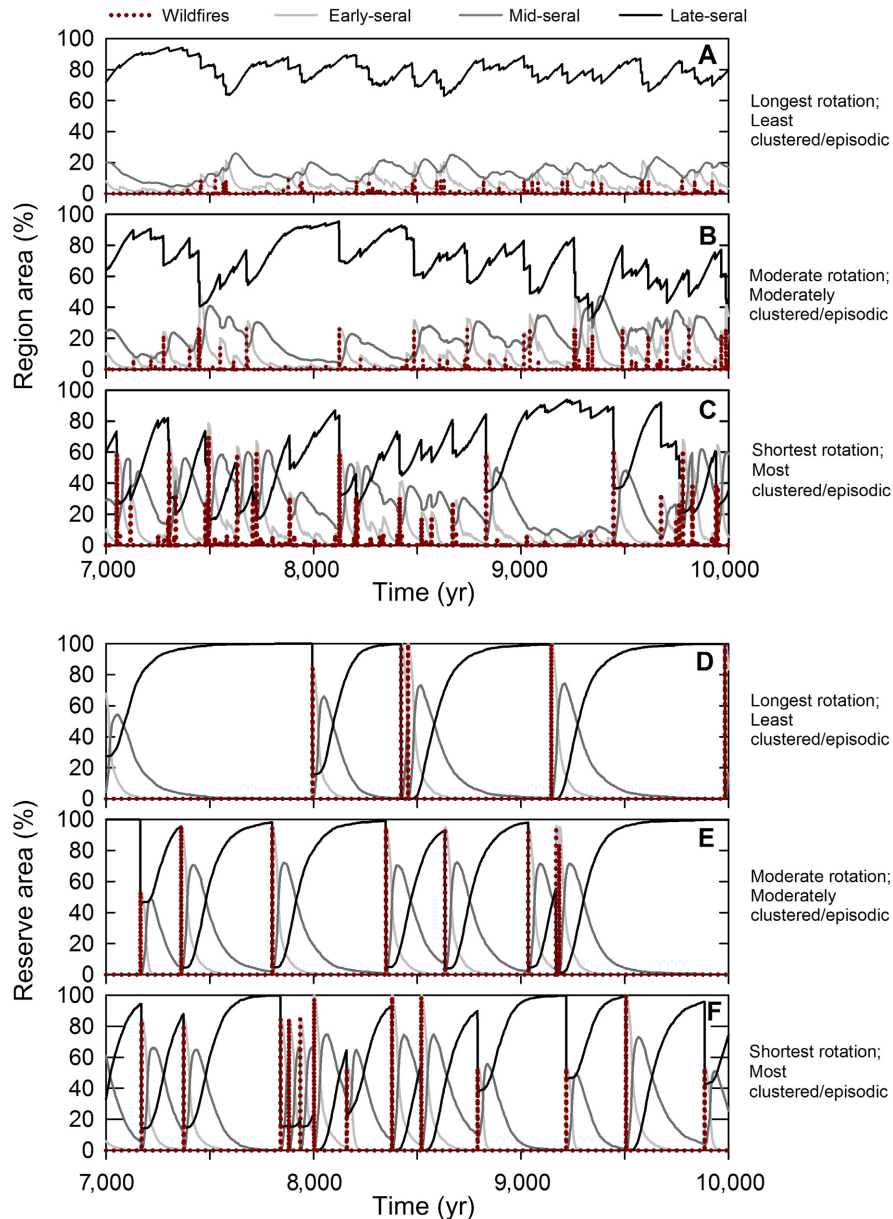


FIG. 3. Example of one randomly selected individual iteration (of 50 for each scenario) at region (A–C; 2.7 million ha) and reserve (D–F; 20,000 ha) scales. The last 3,000 yr are shown of the 10,000-yr simulations. Figures show the percentage of the area in each seral stage and the percentage of the area burned by wildfires at each time point. For brevity, we present the central fire regime scenario (middle row; panels B and E), bracketed by the most extreme scenarios of longest rotation/least episodic (top row; panels A and D) and shortest rotation/most episodic (bottom row; panels C and F). See Fig. 2 and Table 1 for conceptual relationships between fire rotation and temporal distribution of fire.

20% for brief periods. Periods with no complex early-seral conditions anywhere in the region would be exceedingly rare (Fig. 5; Appendix S4).

Reserve scale

At the reserve scale of 20,000 ha, fire intervals were much longer and individual fires regularly approached or exceeded the entire reserve area (Fig. 3D–F). Pulses of

early-seral (and concomitant losses of late-seral) would thus do the same (Fig. 3D–F). We do not display 5th–95th percentile ranges for seral stages at the reserve scale (as in Fig. 4), which all spanned 0–100%. Taking a more illustrative temporal perspective (Appendix S4), by far the most common condition at the reserve scale would be >80% late-seral area, and either 0 or 1–20% early-seral area. Although early-seral can occupy an entire reserve landscape following a fire, because of its ephemeral

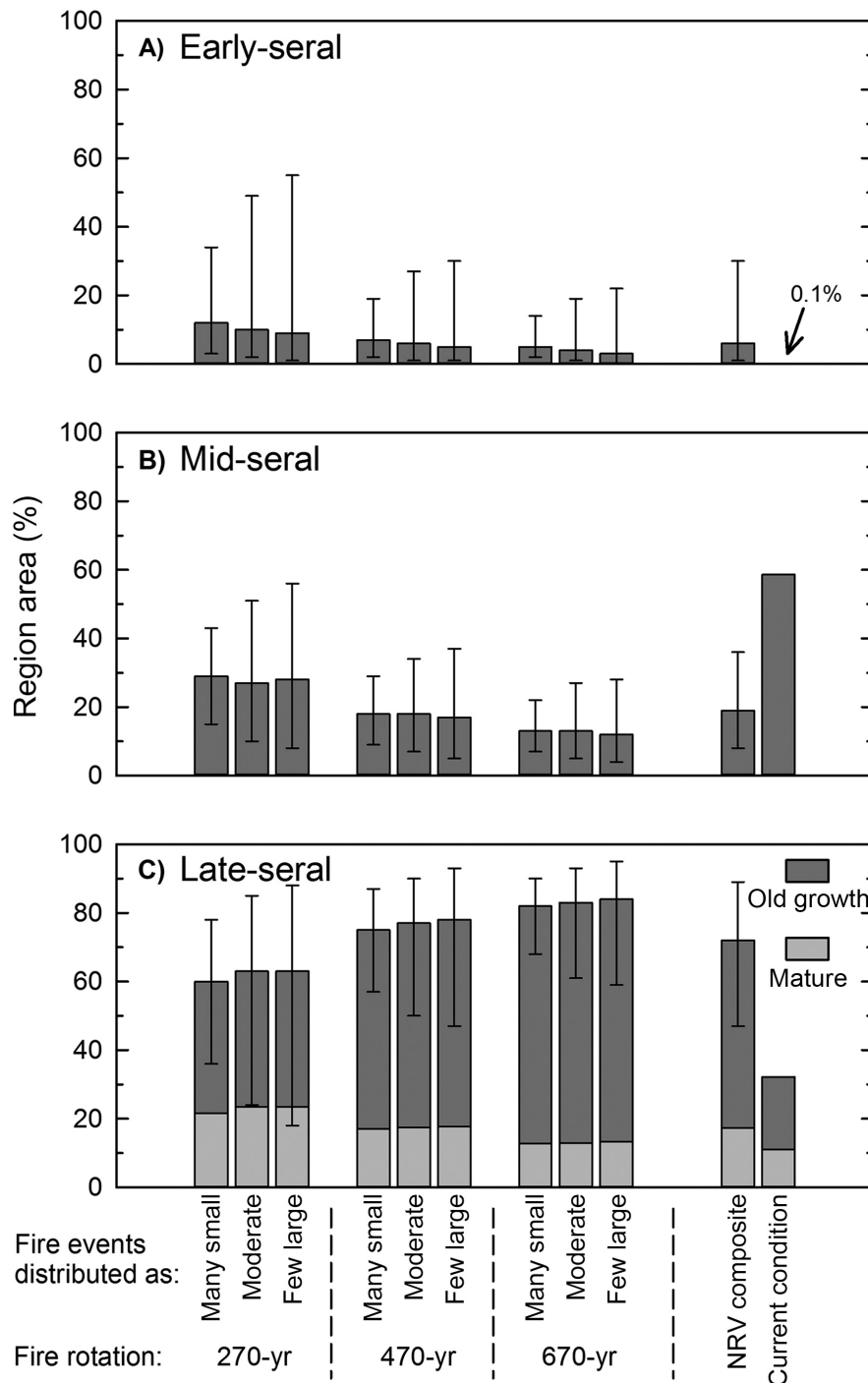


FIG. 4. Natural range of variability (NRV) estimates for major seral stages of the Washington West Cascades, under varying fire regime scenarios. The scenarios span the most and least extreme literature-derived inputs regarding fire rotations and temporal distributions (see Table 1). Data are medians and 5th to 95th percentiles from 50 state and transition simulation model (STSM) iterations for each scenario. (A) Early-seral is defined as post-disturbance but pre-canopy closure (a ~40–70 yr period). (B) Mid-seral is defined as closed canopy, single-layer forests that have not attained late-seral attributes (e.g., large trees). (C) Late-seral is defined as quadratic mean diameter >51.8 cm and a closed, multi-story canopy. Late-seral (C) is parsed into mature (80–200 yr old) and old-growth (>200 yr old) proportions based on a negative exponential age distribution (for the NRV) or an old-growth structural index score (for current conditions). See Appendices S1 and S2 for more details on fire regime parameters and seral stage definitions.

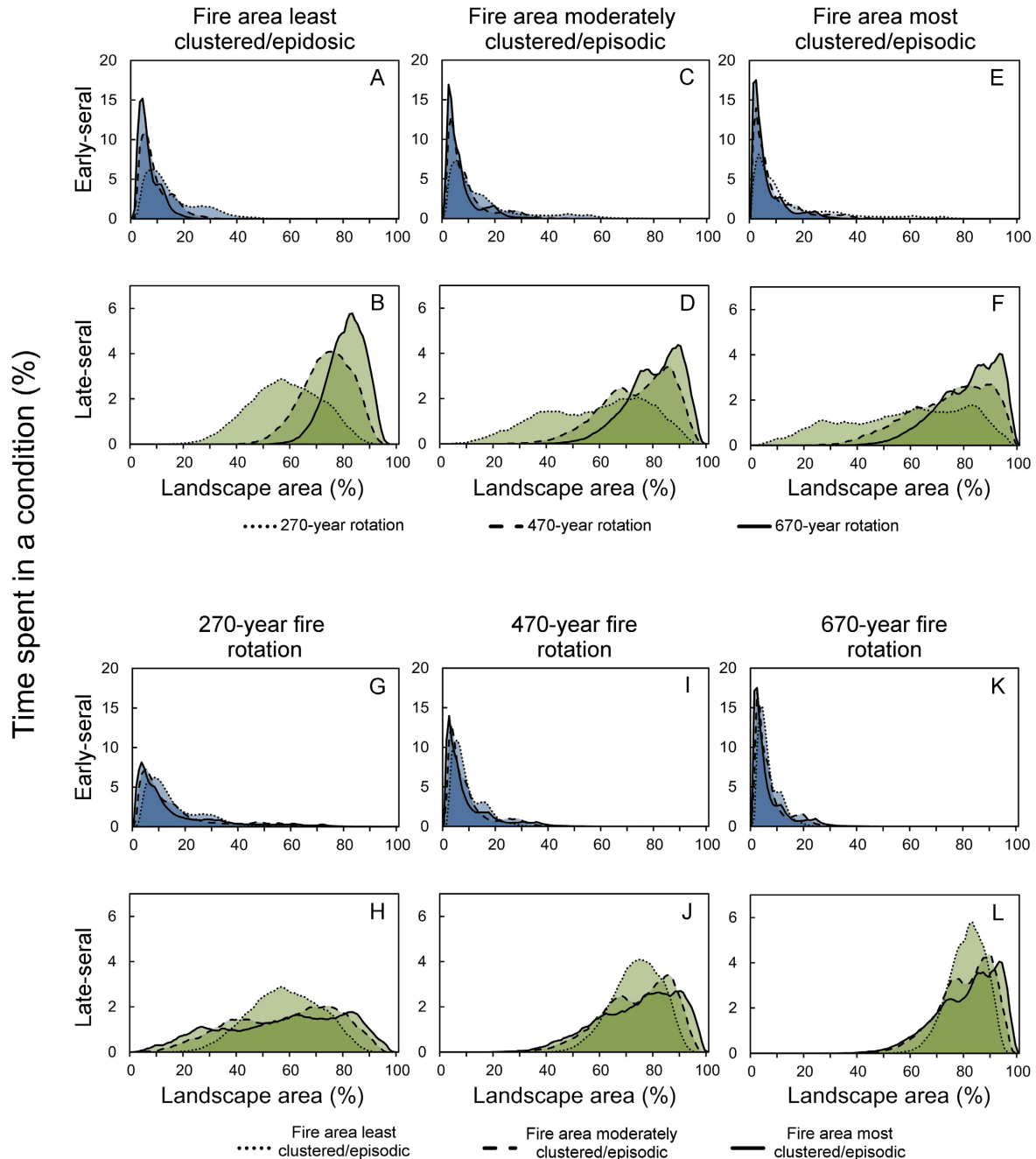


FIG. 5. Percentage of time spent in a given condition for key seral stages of the Washington West Cascades. Top panels (A–F) show the effect of different fire rotations within each temporal distribution of fire events; bottom panels (G–L) show effect of different temporal distributions within each fire rotation. Fire rotations are weighted averages of forest zones.

nature the proportion of time spent near 100% early-seral area is overall rare when integrated over time.

Current conditions

Regionally, current conditions based on FIA data differ substantially from the NRV estimates, for all three seral stages (Fig. 4). Structurally complex early-seral

conditions are nearly absent from the entire region (0.1% of area; Fig. 4A). Similarly, late-seral forests currently constitute 32% of the region, which is lower than nearly all the NRV ranges (Fig. 4C). Most of this difference is in the old-growth class (>200 yr old), while the mature class is closer to estimated natural ranges (Fig. 4C). In contrast, mid-seral stands constitute 59% of the current landscape, well above the NRV for all

scenarios (Fig. 4B). Another 9% is occupied by structurally simple early-seral stands (young tree plantations).

The regional trends are common across all major landowners, but to varying degrees (Table 3). State and especially private lands contain the lowest proportions of late-seral conditions and the highest proportions of mid-seral and structurally simple early-seral stands (Table 3). Federal lands are the closest to the NRV estimates, as a higher proportion of those lands are in late-seral condition compared to other ownerships (as well as the only complex early-seral forests); however, federal lands still differ substantially from the NRV proportions (Table 3).

Viewed geographically (Fig. 6), late-seral proportions are currently most departed from the composite range in lower-elevation watersheds; however, they are lower than the estimated NRV to some degree nearly everywhere. Mid-seral conditions are above the NRV range to varying degrees everywhere (Fig. 6). Complex early-seral conditions, being absent almost everywhere, only attain something <100% difference from the NRV estimates in one watershed (Fig. 6).

DISCUSSION

Three prevailing themes emerged regarding the NRV in this extreme-event region: (1) very large fire events/episodes (10^5 – 10^6 ha) are part of the disturbance regime under any plausible set of fire regime parameters; (2) while fire rotation is the principal driver of NRV estimates, the degree to which fire is episodic (clustered through time) also plays an important role; and (3) there is general agreement among scenarios that, under the NRV, the region would most often be composed of primarily (at least ~50%) late-seral forests, followed by mid-seral forests, with some structurally complex early-seral conditions present at virtually all times (commonly 1–30%), all of which differ substantially from the current landscape condition.

Fire event sizes

The event/episode sizes we derived are consistent with the historical occurrence of extremely large fires (100,000–1.2 million ha) in the study region and greater

Pacific Northwest (Plummer et al. 1902, Holbrook 1960, Kemp 1967; Henderson et al. 1989, Spies et al. 2018). These include the 1902 Yacolt Burn in the southwest Washington Cascades (~400,000 ha) and the 1933 Tillamook Burn in the Oregon Coast Range (>100,000 ha; Holbrook 1960, Kemp 1967). Combining available evidence on fire regime parameters and solving for fire sizes creates a mathematical necessity that at least some fires are extremely large (10^5 – 10^6 ha). In essence, area burns at a certain rate over time (fire rotations ranging from ~200 to 1000 yr), but fire events are relatively rare (most years with no significant fire), meaning that when fires do occur, they must affect large areas at a time. This is the case whether the region experiences multi-centennial episodes (Henderson et al. 1989, Weisberg and Swanson 2003), or operates as a series of quasi-independent subregions with more frequent and smaller fire events (Tables 1, 2). Notably, our event size estimates arose from available evidence on stand-replacing fire patches only (stand origin dates; e.g., Hemstrom and Franklin 1982, Agee 1993). Thus, these patches were likely embedded within larger coarse-scale burn mosaics, making our fire size estimates conservative in that sense.

Estimated natural ranges of variation

In addition to fire rotation, the degree to which fire area is clustered/episodic through time (see Fig. 2) also plays an important role in determining the NRV (Figs. 3, 4). Although empirical studies document regionally synchronous fire events or episodes (Henderson et al. 1989, Weisberg and Swanson 2003, Walsh et al. 2015), such temporal clustering has received comparatively little study in the NRV/HRV or fire ecology literature, in which fire frequency is most commonly conceptualized as semi-regular or random over time. Our finding suggests that, in episodic fire regimes, studies of large-scale periodicity in fire activity and fire sizes (not just fire rotations) are important in establishing NRV estimates to fully inform ecological assessments and land management.

The uncertainty approach we used yielded a surprisingly consistent set of natural ranges, despite wide variations in fire regime inputs (most scenarios qualitatively similar to ~45–90% late-seral, 8–40% mid-seral, 1–30% early-seral; Table 1; Fig. 4). Substantively wider ranges only arose from the most extreme scenarios, in which very large or clustered fire events generated the largest pulses of early-seral conditions (Fig. 3). The NRV estimates were responsive to the fire regime inputs we used (Fig. 4), but it may be that the long time scales, long fire intervals, and high productivity of the regime serve to produce generally consistent ranges overall.

Even though our analysis incorporated extreme (low-probability/high-impact) events, the ranges that emerged were surprisingly similar to previous estimates of NRV for moist forests of the Pacific Northwest. Wimberly et al. (2000) and Wimberly (2002) used an age-based landscape simulation and estimated historical late-seral

TABLE 3. Current seral stage abundance on major ownerships of the Washington West Cascades.

Landowner (percentage of total land area)	Early-seral (%)	Mid-seral (%)	Late-seral (%)
Private (30%)	0	73	11
State (9%)	0	66	25
U.S. Forest Service (55%)	0.2	50	44
National Park Service (5%)	0	54	44
NRV composite estimate	1–30	8–36	47–90

Note: Rows do not necessarily add to 100%, as structurally simple early-seral conditions (i.e., young plantations with closed tree canopy and scarce deadwood) are not included. Such conditions range from 2% of National Park Service lands to 17% of private lands. NRV, natural range of variation.

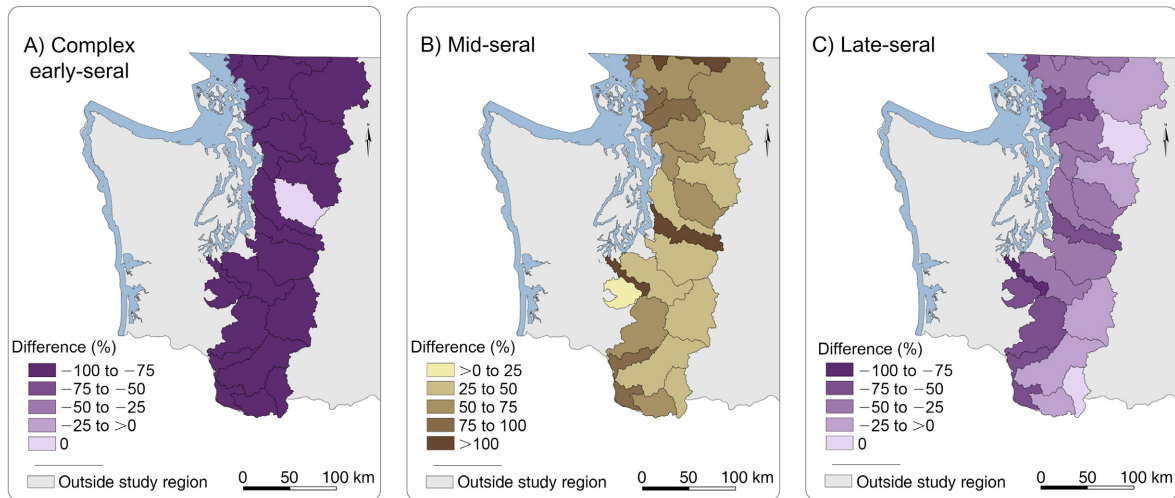


FIG. 6. Map of current differences in seral stage abundance from the estimated NRV, by fourth-field watershed. For visual parity among the seral stages, differences are quantified in relative, not absolute, terms; for example, if all 47% of the NRV low-end late-seral is currently absent, the difference is shown as -100% . Differences are evaluated using the composite NRV estimates (see Fig. 4). Early-seral (A) is defined as post-disturbance but pre-canopy closure (a $\sim 40\text{--}70$ yr period). Mid-seral (B) is defined as closed canopy, single-layer forests that have not attained late-seral attributes (e.g., large trees). Late-seral (C) is defined as quadratic mean diameter >51.8 cm and a closed, multi-story canopy.

conditions ranging from $\sim 50\text{--}85\%$ of the Oregon Coast Range, with early-seral conditions ranging from $\sim 12\text{--}29\%$. The early-seral estimate has a similar maximum but higher minimum than ours, likely because they assumed a more frequent stand-replacing fire regime in which several fires per decade maintained higher minimum levels of early-seral conditions. Other analyses covering portions of western Washington and/or western Oregon also found similar, but somewhat narrower, ranges than ours via either settlement-era land records (Teensma et al. 1991), a restoration needs assessment (DeMeo et al. 2018) using fire regime parameters from the Landfire database (Rollins 2009), and stand age maps and fire rotations (Ripple 1994). Some of these analyses include portions of the western Oregon Cascades in which mixed-severity fires were an important influence on successional pathways historically (Agee 1993, Tepley et al. 2013, Spies et al. 2018). Such fire effects would have diversified old-growth structure and increased landscape diversity, but not reset successional trajectories. Overall, the general consistency of our estimates with prior work suggests that, while extreme events are important in shaping the temporal distribution of seral conditions over time, the ultimate outcomes for management-relevant ranges (e.g., restoration targets) may be similar (see Fig. 4).

The temporal patterns of seral conditions (Fig. 5; Appendix S4) show that despite wide ranges associated with extreme events, the region would rarely spend extended periods with low levels ($<40\%$) of late-seral and high levels ($>20\%$) of early-seral conditions. This pattern emerged even within the most extreme fire regime scenarios assuming very large and temporally clustered fire episodes, and in spite of the multi-decade early-seral phase we incorporated in the simulations (Appendix S2).

Notable is that there would virtually never be a time when early-seral conditions are completely absent from the entire region. This temporal continuity at large scales may help maintain certain species associated with early-seral habitats (Swanson et al. 2014) over time despite widely fluctuating landscape conditions.

At the management-relevant scale of 20,000 ha, most fire sizes would approach or exceed the entire landscape area, meaning that anything between 0% and 100% of the landscape in any seral stage could be considered within a natural range (Fig. 3D–F). This phenomenon of increasing landscape variability as mean disturbance size increases relative to the area of interest is well described in both theoretical and empirical studies (Turner et al. 1993, Wimberly et al. 2000). While the effects of large fires can be dampened at regional scales, individual landscapes or reserves may experience large changes in seral stages over short time scales (Reilly et al. 2018). In this sense, smaller sub-landscapes within this region can be considered highly nonequilibrium (Turner et al. 1993). Nevertheless, under the NRV such landscapes would spend most of their time dominated by late-seral conditions, occasionally punctuated by predominantly early-seral conditions at multi-century intervals.

Current conditions

Currently, nearly 70% of the West Cascades region is dominated by closed-canopy mid-seral forests or young tree plantations (i.e., simple early seral). Such a condition is well outside the natural ranges we quantified, even for the upper bounds of the most extreme fire regime scenarios (Fig. 4B). The relative lack of late-seral forests we found is consistent with prior assessments (Wimberly

et al. 2000, Davis et al. 2015, DeMeo et al. 2018), all of which suggest successional restoration needs where late-seral forests are a management objective. Our estimate of 32% of the landscape currently in late-seral condition (Fig. 4C) is similar to other recent estimates (e.g., Davis et al. 2015, Spies et al. 2018), with small differences likely arising from varying classifications of inventory plots into successional stages (Appendix S3).

For early-seral conditions, despite a large volcanic event in 1980 (Mount St. Helens; Crisafulli and Dale 2017) and recent increases in wildfire activity (Reilly et al. 2017), the region is below the NRV estimate (Fig. 4). This finding is partly because recent wildfires and even the Mount St. Helens blast zone are likely small compared to historical fires. For example, the ~15,000 ha of secondary succession in the volcanic blast zone constitute only ~0.5% of our West Cascades study area. Most of the blast zone is not classified as complex early-seral, due either to complete loss of structural legacies (areas of primary succession), lack of pre-disturbance structural complexity, succession to canopy closure, or post-eruption timber harvest and plantation establishment. This finding underscores the ephemeral nature of early-seral conditions and the importance of occasional disturbances to maintain them through time.

Management objectives for much of the publicly owned lands in the West Cascades include habitat for late-seral species, such as the Northern Spotted Owl (*Strix occidentalis caurina*; e.g., Davis et al. 2015, Spies et al. 2018). Some of these ownerships, such as state forest lands, have target thresholds of around 50% of landscapes in late-seral condition (WADNR 1997), while others target higher levels (e.g., U.S. Forest Service lands under the Northwest Forest Plan; Davis et al. 2015). Our analysis suggests that a 50% goal is at least consistent with likely natural ranges under which biota have persisted in the past, albeit at or near the lower end. While this absolute amount may be sufficient to be within the NRV, uncertainties remain, such as (1) whether managing near the NRV low end continually will ultimately achieve conservation objectives, (2) how much buffer above NRV minima may be needed to account for large natural disturbances, (3) whether current habitat is well represented across biophysical settings (e.g., most reserves are located at mid- to high elevations), and (4) the degree to which current spatial patterns of habitat (generally highly fragmented; Davis et al. 2015) may differ from the NRV (likely in coarser mosaics created by large disturbances).

For landscape management plans that include mesoscale reserves (e.g., LSRs, special habitat areas, or municipal watersheds), our results suggest that individual reserves at these smaller spatial domains (e.g., 20,000 ha) should be expected to fluctuate widely in seral stage abundance due to natural disturbances (Fig. 3D–F). In this region, it may be impossible for reserves to meet the “minimum dynamic area” criterion (i.e., many times larger than the largest disturbance

patches; Pickett and Thompson 1978, Baker 1992). However, the key is that reserves are as large as possible and well distributed to buffer against losses from large wildfires, and that reserve targets and adequacy are assessed at the scale of the entire network as well as in any single reserve (Reilly et al. 2018).

Relating NRV to historical and future dynamics

In relating our findings to the historical era, our ranges likely reflect dynamics of the most recent several centuries to millennium, from which the available fire regime parameters were derived, based on extant forest cohorts (Hemstrom and Franklin 1982, Agee et al. 1990, Agee 1993). Over longer time periods (i.e., multi-millennial scales relevant to long fire rotations), climate, fire regimes, successional patterns, and even vegetation assemblages are known to change substantially (Whitlock et al. 2008, Walsh et al. 2015). Even compared to the presettlement period documented in dendrochronological studies, relatively little is known about how specific quantitative parameters such as fire rotations, fire sizes, and resulting seral stage abundances behaved over the entire Holocene. The uncertainty framework we used is instructive in demonstrating that, even if fire regimes varied substantially through the Holocene (e.g., much shorter or longer fire rotations), ranges of seral stages were likely generally similar to those we quantified (Fig. 4). That is, assumptions of climatic stationarity are not strictly necessary to infer that seral stage abundances have likely been broadly similar over time (to a point, short of wholesale changes in vegetation assemblages).

For future dynamics, climate projections suggest an intensifying of the region’s summer drought pattern (Mauger et al. 2015) and, with it, increases in wildfire activity (Littell et al. 2010) and potential changes in landscape structure (Halofsky et al. 2018a). However, no future projections include the drivers associated with the most influential (largest) fires that drive our study region, specifically synoptic east wind events. The uncertainty approach we used is again illustrative in demonstrating how these changes may affect seral stage abundances. For example, a near doubling of fire area (shorter rotations) may increase temporal variability, while more frequent fires (less clustering) would conversely dampen variability (Fig. 4). Overall, the general pattern of seral stage abundances may remain qualitatively similar despite some degree of climatic and fire-regime change (Fig. 4). However, if productivity decreases and growth and recruitment are sufficiently reduced, the landscape may become less resilient, with longer lags until late-seral conditions again predominate. Our analysis framework could again be useful for assessing the potential future range of variability where novel climatic conditions indirectly alter landscape dynamics through controls of fire activity, and directly through demographic processes (e.g., growth, recruitment, and mortality).

Spatial dynamics

This analysis focused on absolute abundances of seral stages over time, which did not require a spatial modeling approach (see *Methods*). Although most studies indicate the amount of habitat area is more important than its spatial pattern (e.g., Hodgson et al. 2011), patch distribution can be important for connectivity and core area functions of focal habitats. The main drivers of fires in this and similar regions (extreme weather events like synoptic east winds) suggest landscapes would typically be structured as coarse-scale mosaics, dominated by very large stand-replacing patches ($\sim 10^4$ – 10^5 ha) and thus large contiguous patches of both early- and late-seral conditions (Hemstrom and Franklin 1982, Henderson et al. 1989, Agee 1993). In contrast, modern land management has emphasized finer-scale patterns (e.g., regeneration harvests of $\sim 10^1$ – 10^2 ha), leading to a more fragmented patchwork of seral stages (Davis et al. 2015, Spies et al. 2018). Future work should build on our analysis by incorporating spatial dynamics, including patch sizes, shapes, and arrangements, to best inform landscape restoration plans, for which an operational scale must be selected (e.g., USFS 2017).

Relevance across forest regions

The wide range of fire regime inputs we used (fire rotation, temporal clustering) suggests that the ranges we quantified are not necessarily unique to the West Cascades. At the core, our findings emerge from a straightforward numerical exercise relating rates of disturbance and succession, many of which are qualitatively similar among many infrequent stand-replacing fire regimes. However, differences in productivity could affect the abundance and persistence of seral stages in other regions. Dynamics in drier or colder regions (e.g., northern Rockies, boreal forests) may be characterized by longer, protracted early-seral stages and greater lags in late-seral development; while warmer, wetter regions (e.g., Coast Range of the Pacific Northwest) may experience shorter early-seral periods and longer periods with abundant late-seral conditions. Our analysis framework provides a means of testing such hypotheses in other regions where similarly long-interval or episodic fire regimes operated historically, but may require different conservation and management approaches.

CONCLUSION

Although extreme disturbance events are commonly considered a challenge to, or even outside the scope of, landscape planning targets, this analysis shows that management-relevant NRV estimates can be derived in the presence of such regimes. Our findings provide ecologically based targets for landscape restoration projects in this and similar infrequent/stand-replacing fire regimes. In many such landscapes, current conditions suggest

treating over-abundant mid-seral stands to either accelerate late-seral development (e.g., variable-density thinning) or create structurally complex early-seral conditions (e.g., variable-retention harvest; Franklin and Johnson 2012, USFS 2017). Under climate change, these ranges will remain useful as both management targets (as ranges remain qualitatively similar even with some degree of fire-regime change; Fig. 4), and as a baseline for assessing whether major thresholds are crossed in wildfire or seral stage proportions. The large fires that operated in the region historically likely will also occur in the future, with or without climate change. Management of these landscapes will benefit by preparing for the extreme events that will inevitably occur (e.g., having post-disturbance management plans in place; Dale et al. 1998, Halofsky et al. 2018b). Indeed, our fire-size estimates suggest recent West Cascade fires (under $\sim 30,000$ ha), despite their large socioeconomic impacts, should be considered small by regional ecological standards. Finally, given modern realities of populated regions, resource needs, and infrastructure, all overlain by accelerating climatic change, the NRV provides a starting framework, upon which bounded ranges of variability (Moritz et al. 2013) can be established incorporating socioecological thresholds and anticipated tipping points.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2013/full>

DATA AVAILABILITY

State-and-transition simulation models (STSMs) and raw output for all 27 landscape scenarios and nine 20,000-ha scenarios are available on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h01d6sq>.