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Predicting future patterns, processes, and their interactions: Benchmark calibration and validation procedures for forest landscape models

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ABSTRACT

Process-based Forest Landscape Models (FLMs) rely on first principles to simulate ecological patterns and processes, making them uniquely powerful for forecasting ecological dynamics under unprecedented climatic and disturbance regimes. Persistent challenges with any ecological forecasting model are calibration ("tuning" the model) and validation ("proofing" the model). As no actual future data exist from which to conduct a formal model validation, model credibility is established through numerous tests against empirical datasets and comparisons with other types of models. The purpose of this study was to establish more consistent and generalizable standards for calibrating and validating LANDIS-II, a widely used, open-source FLM. We reviewed methods gleaned from a wide variety of previous FLM studies and advance some new techniques for evaluating the credibility of the model outputs. We used publicly available data with full coverage for the United States (US) so that our methods will be generalizable to other landscapes in the US, and we developed an ecologically meaningful set of validation metrics for evaluating the credibility of new applications.

We found that LANDIS-II could be calibrated to reliably simulate empirical vegetation-disturbance-climate dynamics in diverse, mountainous terrain and fire-prone landscapes of the eastern Cascade Mountains. We performed an inter-model validation between LANDIS-II and the Forest Vegetation Simulator (FVS), demonstrating consistent projections of biomass dynamics for all tree-dominated ecoregions in the study domain. Similarly, simulated fires reliably approximated the empirical fire event size and severity patch size distributions based on observed fire activity from 1984 to 2019. By establishing rigorous, transparent, and repeatable standards for calibrating and validating FLM dynamics, we sought to remove some of the barriers to adapting LANDIS-II to new landscapes and climates, facilitate further validation of existing models, and aid independent assessment of the credibility of forest landscape models.

1. Introduction

Process-based Forest Landscape Models (FLMs) are a uniquely powerful tool for projecting the effects of future climate, management, disturbance, and vegetation succession on forested landscapes (Gustafson, 2013). The spatially explicit nature of FLM simulations enables them to mechanistically represent inherently spatial processes such as wildfire, insect outbreaks, harvesting, seed dispersal, climate effects, and their interactions (Keane et al., 2015; Loehman et al., 2018; Scheller et al., 2018). Maps generated by FLMs reveal how processes interact over space and time, producing plausible visualizations of future landscapes (Mladenoff, 2004).

Process-based models differ from phenomenological models in that they are designed to simulate pattern by modeling ecological processes, rather than by directly modeling the patterns themselves (Connolly et al., 2017). Phenomenological models typically use a mathematical function or statistical algorithm that can be fit to data to describe underlying processes (Hilborn and Mangel, 2013). Although this can make phenomenological models more accurate under historical and contemporary conditions, they generalize to novel futures with greater

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difficulty. In contrast, mechanistic models explicitly track the details of the fundamental components and processes of a biological or ecological system that are thought to give rise to a set of data (Otto and Day, 2011; Connolly et al., 2017). As rapid climatic and ecological changes continue to create novel landscapes and disturbance regimes, process-based FLMs are becoming indispensable for estimating ecological changes over the coming century (Shifley et al., 2017).

A persistent challenge with all FLMs is model calibration (“tuning” the model) and validation (“proofing” the model). As future data do not exist to compare with FLM predictions, it is not possible to empirically validate a future projection (Oreskes et al., 1994; Rastetter, 1996). This point is sometimes wielded as evidence that future FLMs cannot be validated, but this perspective ignores the more practical definition of validation that is well established in the literature (Sargent, 1984, 2013; Rykiel, 1996; Rastetter, 1996; He et al., 2011; Shifley et al., 2009). In the context of ecological simulation models, the term “validation” refers to qualitative and quantitative evaluations of the underlying model structure (i.e., its conceptual validity, *sensu* Sargent, 1984) and comparisons with independent data sources (i.e., its operational validity, *sensu* Sargent, 1984). Open-source, community-developed models (e.g., LANDIS-II) facilitate both types of validation, as users are free to examine model structure and contribute directly to model development. In this sense, validation is the iterative process of model development, implementation, and evaluation that helps process-based models develop into a credible representation of ecological systems (Rykiel, 1996; Rastetter, 1996).

Strategies to validate aspects of ecological simulation models can be grouped in several categories, first outlined by Rastetter (1996): (1) comparing simulation model predictions to existing longitudinal data (e.g., Wang et al., 2014), (2) space-for-time substitutions (e.g., Ma et al., 2017), (3) past-to-present simulations (e.g., Flatley and Fulé, 2016), and (4) model comparisons with other FLMs (e.g., Keane et al., 2004; Petter et al., 2020). Each of these approaches has both merits and limitations.

Longitudinal datasets are scarce and relatively short-term (10–30 years) relative to the temporal scope of many FLM simulation horizons (often 50+ years). Space-for-time substitutions must rely on an assumption that sampled sites or landscapes are biogeoclimatically comparable, only differing in stages of development (or percentage of area in varied stages, Keane et al., 2002), and the unavoidable problem of landscape pseudo-replication can limit inferences of some comparisons (Hargrove and Pickering, 1992). Depending on the nature of simulations, past-to-present simulations may require subjective decisions about the historical landscape and assume that past dynamics are a legitimate future proxy (cf. Keane et al., 2018; Loehman et al., 2018). Comparing the predictions of multiple FLMs offers no comparison against empirical data, and there are limited means of determining which of the models is most reliable. Several other studies have validated LANDIS-II applications using static empirical data (e.g., see Flanagan et al., 2019; Boulanger et al., 2019); this is perhaps more of an “empirical calibration” because there is no direct assessment of model dynamics over time (Table 1).

The focal model of this study is LANDIS-II, a spatially explicit FLM with the capacity to interactively model wildfire, silvicultural management, forest succession, and numerous disturbance processes. LANDIS-II

Table 1
Calibration and validation methods for the succession component of LANDIS-II. The purpose of this table is to characterize and compare methods of calibrating (i.e., tuning) and validating (i.e., proofing) process-based simulation models, and to reference examples from the literature that have applied the following methods with LANDIS-II. This is not meant to be an exhaustive list of all possible validation methods or all relevant studies. We included multiple studies where possible, although examples from the literature became increasingly rare for the more rigorous (and data intensive) validation methods. There is a general trend of increasing credibility throughout the table, but this ranking is approximate; each type of validation test has a unique set of strengths and weaknesses, and the most appropriate type of validation depends on the unique context of each study.

Process	Extensions	Aspect of LANDIS-II under evaluation	Comparison data source	Suggested terminology	Limitations	Examples from the literature
Succession	Net Ecosystem Carbon and Nitrogen (NECN); Photosynthesis and EvapoTranspiration (PnET); Biomass succession	Species parameters, output maps of age & biomass	Expert opinion, previous studies, growth and yield curves	Calibration (parameterization + iterative adjusting)	Not validation (no assessment of the model's capacity to predict future dynamics)	Nearly every LANDIS-II study begins with this step.
		Species parameters, output maps of age & biomass	Static forest inventory or ecophysiological data	Empirical calibration or static validation	Validation of initial vegetation data at Time 0. No validation of the model's capacity to predict dynamics.	Boulanger et al. (2019), Flanagan et al. (2019), Ling et al. (2020), Loudermilk et al. (2013), Suárez-Muñoz et al. (2021)
		Results of past-to-present simulation	Maps of existing vegetation type, static forest inventory data	Intra-model validation (spin-up to present)	Requires subjective decisions about historical landscape, future predictions not validated	Flatley and Fulé (2016)
		Future vegetation dynamicsFuture vegetation dynamicsFuture vegetation dynamicsFuture vegetation dynamics	Other forest landscape models	Inter-model validation (compare predictions of multiple forest landscape models)	No reality check with empirical data. No way to know which model is most reliable.	Petter et al. (2020)
			Space-for-time substitutions based on static forest inventory data	Pseudo-dynamic validation (inferring dynamics based on present-day differences)	Assumes that stands are identical in every way other than age, and that past dynamics are an appropriate proxy for future dynamics.	Ma et al. (2017)
			Forest Vegetation Simulator	Pseudo-empirical inter-model validation (because FVS is an empirical model)	FVS models were parameterized based on decadal time spans. Projection beyond a few decades is questionable.	Syphard et al. (2011)
			Existing longitudinal data	Empirical dynamic validation (comparing to observable trends in longitudinal data)	Limited by availability and the temporal span of longitudinal data (rarely >30 years).	Wang et al. (2014); Jin et el. (2016); Ling et al., (2020)

is one of the most widely used FLMs with over 160 published applications (www.landis-ii.org/publications) and is highly adaptable to new landscapes. As with many FLMs, LANDIS-II is often considered to be a process-based model, but it is actually a hybrid that incorporates phenomenological modeling with process modeling, where processes are not yet fully understood, or where computational limitations deter further complexity (Petter et al., 2020). In this way LANDIS-II harnesses strengths of phenomenological models (e.g., simulating observed patterns) while maintaining a high capacity to project future landscapes through process-based and interactive succession and disturbance algorithms (Gustafson, 2013; Flatley and Fulé, 2016; Liang et al., 2018).

LANDIS-II is an open-source, community-developed model, and the LANDIS-II developers strive to make the model broadly accessible to new researchers (see www.landis-ii.org). But calibration and validation remain difficult processes, particularly with more sophisticated extensions, and methods employed in some prior published studies are neither sufficiently transparent nor repeatable. The cost and time required to calibrate and validate LANDIS-II applications inhibits development of new models for different landscapes, and the recycling of established models and parameter sets can perpetuate underlying error and uncertainty across multiple studies. Developing rigorous and repeatable methods for systematic calibration and validation will make LANDIS-II a more accessible modeling tool for new research applications, and it will help researchers and end-users evaluate the credibility and ecological validity of LANDIS-II outputs. Although we focused this study on LANDIS-II and two specific extensions, we endeavored to make our methods and findings broadly relevant to other LANDIS-II extensions and other FLM platforms.

In this study, we conducted an empirical evaluation of a newly developed LANDIS-II application (i.e., initialized and calibrated for a specific landscape), with explicit consideration of the wildfire submodel, SCRPPLE (Social-Climate Related Pyrogenic Processes and their Landscape Effects, Scheller et al., 2019). We reviewed prior studies that have validated aspects of LANDIS-II (Tables 1 and 2), and we examined the rigor of various validation methods. We then used several generalizable methods to calibrate and validate a new LANDIS-II application, and we demonstrated the potential for LANDIS-II to reliably model ecological dynamics in mountainous, topo-edaphically and ecologically diverse, fire-prone landscapes of the eastern Cascade Mountain Range.

2. Objectives

The purpose of this paper was to establish benchmark methods for calibrating and validating LANDIS-II and similar FLMs using publicly available data, provide detailed documentation of initialization methods that we employed to adapt a model framework to a new geography, and develop set of ecologically meaningful standards for evaluating the credibility of model outputs. We drew upon previous studies to develop an initial parameter set for our LANDIS-II application to the eastern Cascade region in north-central Washington State. We calibrated forest structural characteristics using Forest Inventory and Analysis data (FIA;

Table 2
Calibration and validation methods for LANDIS-II fire extensions. The purpose of this table is to characterize and compare methods of calibrating (i.e., tuning) and validating (i.e., proofing) the fire sub-modules within LANDIS-II. This is not an exhaustive list of all possible validation methods or all relevant studies. We included multititle studies where possible, although examples from the literature are relatively scarce for SCRPPLE, as it is a recently developed extension (Scheller et al., 2019). The two fire categories reflect extensions characterized by static fire regimes versus those where the fire regime is an emergent property of the spread probability parameters.

Process	Extension	Aspect of LANDIS-II under evaluation	Comparison data source	Suggested terminology	Limitations	Example studies
Fire (static fire regime extensions)	Dynamic Fuels and Fire System and Base Fire	Size and frequency of fires	Size and frequency of fires based on empirical fire activity	Empirical calibration (parameterization + iterative adjusting)	Not validation. User specifies target fire size and frequency. Maximum fire size is pre-determined based on a random draw from the fire size distribution. No emergent behavior to validate.	Cassell et al. (2019), Creutzburg et al. (2017), Flatley and Fulé (2016), Keyser et al. (2020), Krofcheck et al. (2017), Loudermilk et al. (2013), Martin et al. (2015), Syphard et al. (2011)
Fire (dynamic fire regime extensions)	Social-Climate Related Pyrogenic Processes and their Landscape Effects (SCRPPLE)	Number and distribution of ignitions	Empirical fire ignition datasets	Ignition validation	Only considers the pattern and # of ignitions, not fire size or return interval.	Scheller et al. (2019). This study, Fig. 4.
		Size and frequency of fires	Size and frequency of fires based on empirical fire activity	Fire cycle validation (ability to model physical aspects of fire regime)	Does not consider ecological effects of fire (severity).	Scheller et al. (2019). This study, Fig. 4.
		Severity class area based on output maps "site-level severity" ("dNBR" in v3.2) or "fire intensity"	Proportion of area burned by severity class based on satellite-derived severity maps	Severity calibration (tuning the model to approximate realistic proportion of area burned per severity class)	Does not consider spatial pattern of fire effects.	Scheller et al. (2019), Serra-Diaz et al. (2018); This study, Fig. 5
		Spatial pattern of severity based on "site-level severity" or "fire intensity"	Empirical patch size distribution and spatial pattern analysis	Severity pattern validation (ability to model multi-scale ecological effects)	Maps of site-level severity and fire intensity generated by SCRPPLE do not represent actual cohort mortality.	This study, Figs. 7 and 8
		Histogram of percent cohort mortality	Stand-level severity distribution	Non-spatial severity validation (ability to simulate intermediate levels of tree mortality)	Validation is limited to a histogram of percent mortality per site. Does not consider spatial pattern of fire effects.	This study, Fig. 6
		Fire size, frequency, severity, and spatial pattern	Satellite-derived severity maps	Comprehensive empirical validation (ability to produce realistic patterns in fire effects)	Maps of cohort mortality are not output by SCRPPLE (v3.0) so spatial patterns in severity must be evaluated with "site-level severity" maps.	This study, Figs. 4-9

https://www.fia.fs.fed.us), successional dynamics using the Forest Vegetation Simulator (FVS; https://www.fs.fed.us/fvs), and fire regime characteristics using Monitoring Trends in Burn Severity program (MTBS; https://www.mtbs.gov). We then tested the null hypothesis that this LANDIS-II application was a reasonably realistic representation of reality by validating our model against empirical patterns of landscape dynamics based on longitudinal data and independent phenomenological models.

3. Methods

3.1. Study area

We conducted our study in the adjacent Wenatchee and Entiat

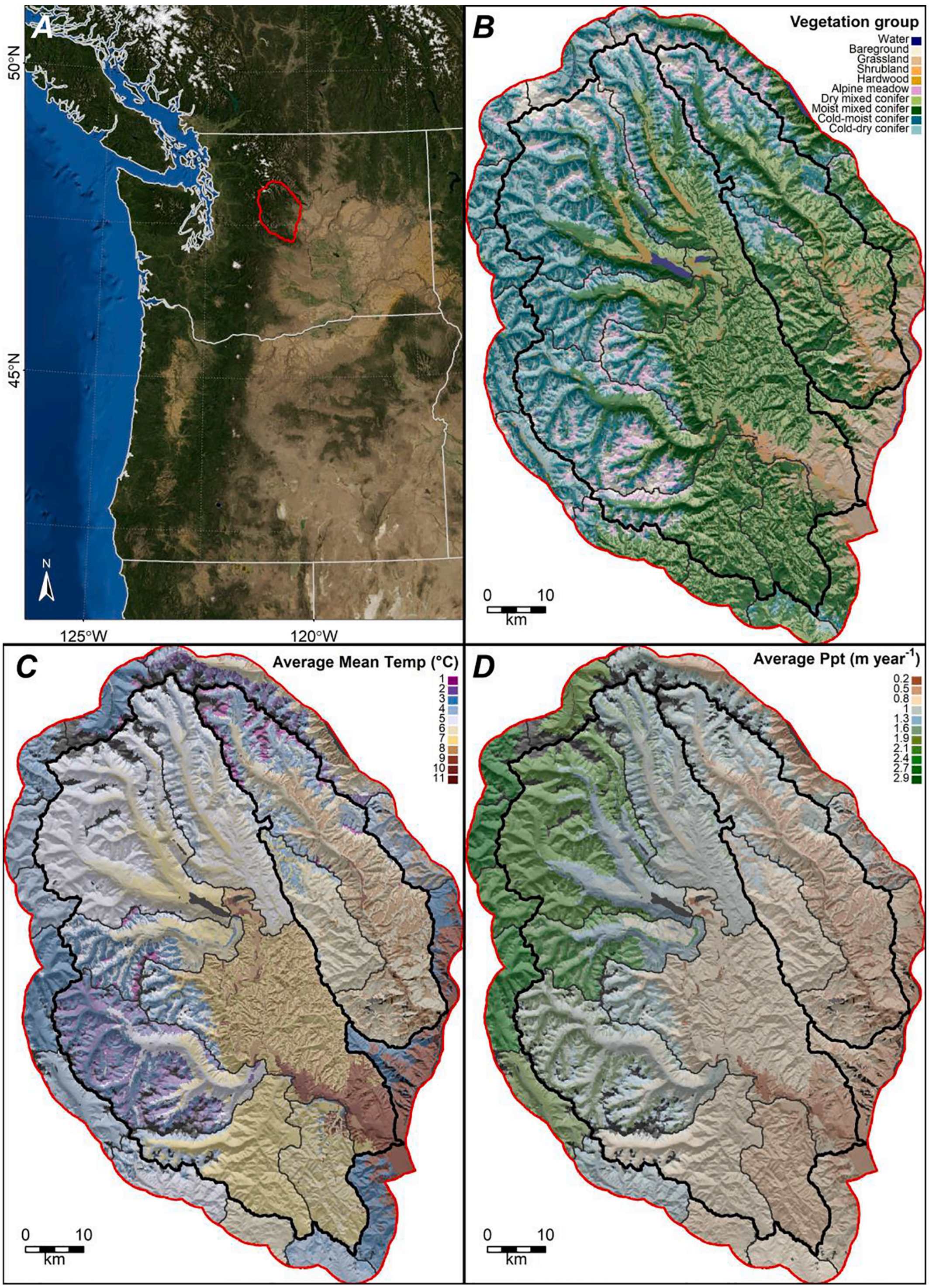

Fig. 1. Location of the Wenatchee-Entiat subbasins on the eastern slopes of the Cascade Mountain Range in central Washington State (A), vegetation groups in the study domain (B; sensu Hessburg et al., 2000), and 30-yr Climate Normals (1980–2010; mean temperature in C and precipitation in D) for the study domain calculated based on the Multivariate Adaptive Constructed Analogs dataset (Abatzoglou and Brown 2012). Imagery in A was derived from Landsat-8 imagery, and the digital elevation model (B-D) was derived from USGS 3DEP data (www.usgs.gov/3d-elevation-program; data accessed with elevatr Hollister et al., 2021).

subbasins on the eastern slope of the Cascade Range in north-central Washington State (Fig. 1A). We applied a 5-km buffer around the watersheds to capture potential edge effects (e.g., seed dispersal and migration of fire) from surrounding areas, resulting in a 6078 km^2 study area (Fig. 1). This area is characterized by steep, highly dissected, mountainous terrain with elevations ranging from 187 to 2870 m, which create highly influential gradients in climate and weather patterns. Mean annual temperature (1980–2010 Climate Normals, Abatzoglou and Brown, 2012) ranges from 11.3 °C at lower elevations to 1.2 °C near the Cascade crest and precipitation ranges from 0.2 m • yr^{-1} to 2.9 m • yr^{-1} along a similar elevation gradient. The climate in both subbasins is humid continental with warm-dry summers, cold-wet winters, and most precipitation occurring as snow.

These broad gradients in precipitation and temperature, along with finer-scale topo-edaphic complexity, produce high beta-diversity in plant community composition and forest structure within the watersheds (Fig. 1, Hessburg et al., 2019). Low-elevation ecosystems are dominated by grasslands, shrublands, and sparse woodlands, with a mix of dry (south aspects) and moist (north aspects) conifer forests at mid-elevations, which transition to subalpine forests, alpine meadows, and rock barrens at the highest elevations (Fig. 1; Hessburg et al., 2000). Douglas-fir (*Pseudotsuga menziesii*) comprises the greatest overall biomass in the moist-mixed conifer zone, while drought-tolerant tree species including ponderosa pine (*Pinus ponderosa*) dominate locally in dry forest sites.

Historical fire regimes in the two subbasins were variable, with low- to moderate-severity, frequent-fire regimes in grassland and mixed-conifer forests at low- to mid-elevations, and a mix of moderate- and high-severity fire regimes in upper montane moist mixed-conifer and cold forests (Agee, 1998; Hessburg et al., 2007, 2016, 2019; Perry et al., 2011). Nearly a century of fire exclusion and intensive timber harvesting led to the accumulation of surface fuels, forest densification, compositional shifts towards less fire-tolerant species, and increased landscape homogeneity (Hessburg et al., 1999, 2005, 2019; Hessburg and Agee, 2003; Hagmann et al., 2021). Fire has returned to the landscape in recent decades, although contemporary fires are larger and more severe (Reilly et al., 2017; Haugo et al., 2019; Hagmann et al., 2021). Despite this recent surge in wildfire activity, annual area burned is likely far below the pre-settlement mean for this landscape (Haugo et al., 2019; Leenhouts, 1998; Parks et al., 2015; Ryan et al., 2013).

Land ownership and management allocation in the study domain is mixed, with actively managed forests at low and middle elevations and wildlands in middle and upper montane settings. Residential development is widespread at low to middle elevations and in valley bottoms. The majority (>80%) of the study area is managed by the USDA Forest Service and over half (56%) of the study area is administratively withdrawn wildland designated as wilderness or roadless areas.

3.2. Model initialization

In the current model application, we used LANDIS-II v7.0 (Mladenoff, 2004; Scheller et al., 2007) with extensions NECN v6.6 (Scheller et al., 2011), and SCRPPLE v3.0 (Scheller et al., 2019). All analyses were performed in R v4.1.1 (R Core Team, 2021) using packages *raster* (Hijmans, 2021), *sf* (Pebesma, 2018), *landscapemetrics* (Hesselbarth et al., 2019), and *ggplot2* (Wickham, 2016).

3.2.1. Vegetation data

We generated maps of initial vegetation for the study domain using TreeMap, a spatially imputed forest inventory dataset developed by Riley et al. (2021). TreeMap uses random forest imputation to develop a continuous map of the best fitting Forest Inventory Analysis (FIA) plot based on LANDFIRE (http://www.landfire.gov) data layers (including biophysical setting, existing vegetation type, vegetation height, percent cover, and disturbance layers) for every 30-m raster cell within the United States. We clipped this raster to the study domain and resampled it to 90-m spatial resolution using nearest neighbor interpolation. Cells that referenced FIA plots outside of the Pacific Northwest (375 out of 4684 unique FIA plot codes present in the imputed raster within our study domain) were replaced with the value of a neighboring cell that referenced a FIA plot from within the region. We performed this replacement because although these foreign plots may have been representative according to the multi-variate random forest imputation performed by Riley et al. (2021), their composition was not representative of the real-world landscape that we were modeling, and species-specific life history traits (i.e., dispersal distance, fire tolerance, life-span) are key parameters within LANDIS-II. If multiple neighboring cells referenced valid FIA plots, the most common cell value was used (methods consistent with Povak et al., 2022). We then converted the FIA tree lists into a LANDIS-II acceptable format (a look-up table of age class and biomass by species present in each raster cell). Biomass was derived from the FIA database, which contains allometrically estimated biomass values for every tree. Tree age was determined based on tree cores taken from a subset of trees in each FIA plot. We used measured ages from 26,346 trees to parameterize a generalized linear regression model that employed tree diameter, species, and ecoregion to predict tree age for trees that were not cored (77,377 remaining trees). The resulting LANDIS-II initialization landscape was a 90-m raster, where each cell value referenced a row in a text file containing biomass values associated with each species–age combination (hereafter, “cohort”) present at each site.

3.2.2. Climate data

We used the Multivariate Adaptive Constructed Analogs (MACA; Abatzoglou and Brown, 2012) datasets to provide historical climate data (minimum daily temperature, maximum daily temperature, precipitation, relative humidity, wind speed, wind direction) on a 4-km grid within the study domain. We simulated a “baseline” future climate scenario by randomly resampling from the climate years 1980–2019, where within-year climate was not altered (we drew entire years rather than sampling days within years). We preserved interannual temporal autocorrelation in this baseline climate scenario by sampling every 3 years as a new randomly sampled starting point (a year between 1980 and 2019) and constraining the intermediate two years to be sampled from within ±2 years of the initial starting year. All climate variables (temperature, precipitation, humidity, wind speed, wind direction) were selected from the same sampled climate year.

Climate is input into LANDIS-II via an ecoregion map, where each ecoregion is assigned a unique set of climate data. Unlike most prior LANDIS-II extensions which use the ecoregion map to define ecological characteristics (soil type, fire regime, etc.), the extensions we used for succession and fire (NECN v6.8 and SCRPPLE v3.0, details below) rely on continuous raster surfaces for all input variables, except climate. Thus, the ecoregion map in our model is used only to define distinct climatic regions. We delineated ecoregions within the study domain by intersecting two data layers: a vegetation cover type layer, and a 10-digit Hydrological Units (HUC10) watersheds shapefile (Watershed Boundary Dataset for Washington State, 2019). We generated the vegetation cover type layer by classifying vegetation structure and composition based on biophysical setting, existing vegetation type, and LANDFIRE potential vegetation type. Our classification procedure resulted in eight distinct vegetation cover types: Grassland, Shrubland, Hardwood, Alpine Meadow, Dry Mixed Conifer, Moist Mixed Conifer, Cold-Moist Conifer, and Cold-Dry Conifer forest. Intersecting this vegetation type layer with HUC10 watersheds created 178 unique ecoregions (Fig. 1), within which we calculated area-weighted average climate values using 4-km MACA climate rasters. By classifying ecoregions according to vegetation cover type and terrain features, this method implicitly represented variability in climate due to the prominent elevation gradients in the study domain.

3.3. NECN succession

Forest succession processes (e.g., dispersal, establishment, growth, competition, and mortality) were simulated using the Net Ecosystem Carbon and Nitrogen extension (NECN; Scheller et al., 2011). The NECN extension builds upon the CENTURY soil model (Parton, 1996) and adapts it for LANDIS-II. We opted to use the NECN succession extension because it explicitly tracks carbon dynamics among live, dead, and belowground carbon pools, and allows variability in light, water, and limiting soil resources (e.g., nitrogen) to inform forest growth and successional dynamics. Growth is determined by a combination of species-specific parameters (e.g., optimal growing temperature curves, maximum net primary production [NPP]) and site conditions (leaf area index, water availability, soil resources). Mortality is modeled as a function of species-level parameters (e.g., longevity, NPP, and maximum biomass). Probability of establishment is internally calculated at an annual time step and is dependent upon input weather data. The succession algorithms within LANDIS-II run at the cell-level, meaning that each cell in the raster has the potential to have a unique starting state and successional trajectory. Live cohorts can disperse to surrounding cells (both adjacent and far away) depending on user-defined species-specific dispersal distance parameters.

3.3.1. Soil data

We used gridded SSURGO data (gSSURGO, Soil Survey Staff, 2020) to derive the edaphic variables required for the NECN succession extension. Since the soil maps required for NECN differ from the raw soil variables provided by gSSURGO, we transformed, combined, and scaled the gSSURGO data layers to generate NECN-ready layers (see Appendix B for these methods). Most soil input maps for the NECN extension could be approximated from the gSSURGO database, but initial soil nitrogen was a key exception; soil nitrogen data are not available in the gSSURGO database. Instead, we used a 1-km gridded Total Kjeldahl Soil Nitrogen layer derived from the National Soil Characterization Database (Hargrove and Hoffman, 2004).

3.3.2. Species parameters

We derived an initial set of species parameters based on previous LANDIS-II studies (Tables A1 and A3; https://www.landis-ii.org/projects). For species that were not present in these previous studies, parameters were set based on phylogenetically and functionally similar species. We then adjusted the species parameters as necessary to improve consistency with values found in Silvics of North America (Burns and Honkala, 1990), Fire Effects Information System (https://www.feis-crs.org/feis), empirical FIA data, and trait-based fire tolerance scores (Stevens et al., 2020). Parameters were further calibrated to achieve reasonable model behavior (Tables A2 and A4; details in *Model Calibration*, below).

3.4. SCRPPLE fire extension

We modeled fire behavior and effects with the SCRPPLE fire extension (Scheller et al., 2019), a recently developed extension that does not rely on user-defined parameters to constrain the shape of the fire size distribution, thereby allowing the fire size and frequency distributions to respond dynamically to changing landscape pattern and future climate inputs. SCRPPLE also allows users to explicitly account for various fire management actions such as suppression, wildland fire use (i.e., *prescribed natural wildfire*), and prescribed (Rx) fire. These management actions can be spatially allocated according to ignition type, land ownership, and biogeoclimatic setting. Fires spread from cell-to-cell via both edges and vertices, and probability of spread is modeled as a function of topography, fuels, and weather (wind speed, wind direction, and fire weather index [Canadian Forest Fire Weather Index; FWI]).

Fire severity in SCRPPLE is modeled as a multi-scale process using nested equations. Site-level (i.e., cell) severity is modeled as a function of site characteristics (fuels, climate, soil, and windspeed), and severity values are scaled to approximate a spectral fire severity index (e.g., differenced Normalized Burn Ratio [dNBR]; (Robbins et al., 2022)). Cohort-specific mortality rates are determined by a logistic model that relates site-level severity, species, and age of individual cohorts to probability of mortality.

3.4.1. Ignition probability and suppression effort

Ignitions are generated within SCRPPLE using a zero-inflated Poisson regression model to estimate the number of ignitions on each day of each year as a function of daily Fire Weather Index (FWI) values. Ignitions are then spatially distributed throughout the landscape based on relative ignition frequency given by a gridded probability map. Although the probability map remains constant, the probabilistic regression model produces a unique pattern of ignitions each year. We used empirical data from the Fire Program Analysis Fire-Occurrence Database (FPA-FOD; Short, 2017) to fit the zero-inflated Poisson models and generated maps of relative ignition density. This dataset contains observed ignition date, location, cause, and final fire size for all reported wildfires (both accidental and natural ignitions of any size) between the years 1992–2015, for the entire United States. We calculated FWI using the MACA climate dataset (Abatzoglou and Brown, 2012) using the *cffdrs* R package (Wang et al., 2017). We applied kernel density estimation using the *density.ppp ()* function from the *spatstat* R package (Baddeley et al., 2015) to convert spatial points of ignition locations to raster maps of relative ignition probability.

We zoned likely suppression effectiveness based on land management designation. For lightning ignitions, minimal suppression effectiveness was applied to wilderness and roadless areas but applied light suppression effort within a 1-mile interior buffer to limit wilderness fire escapes. We zoned actively managed public lands with moderate suppression and applied maximal suppression effort to all rural, urban, and private lands. For accidental human ignitions, we applied light and moderate suppression effort in wildlands, and maximal suppression everywhere else.

3.5. Calibration and validation

We use the term calibration to refer to the iterative adjustment of initial parameters, and the term validation to refer to formal comparisons of model outputs to independent data sources (e.g., empirical observations or other simulation models; Tables 1 and 2). These two terms are, however, inter-related. During calibration one adjusts the input parameters to achieve improved correspondence with the ecological patterns and processes that are being simulated, thus requiring some form of validation to occur simultaneously. In this study, we define validation as a more formal process occurring after model calibration that involves comparing model outputs to a new set of independent data, evaluating model behavior over longer time spans, and/or more rigorous goodness-of-fit tests.

3.5.1. Calibration

We calibrated our LANDIS-II application by iteratively adjusting the initial parameters until the model corresponded well with biomass dynamics modeled using the Forest Vegetation Simulator (FVS) and empirical fire activity. We performed exploratory sensitivity analyses to identify the parameters with the greatest influence on model performance; subsequent calibration efforts were aimed at adjusting these key parameters. The primary species-level NECN parameters were temperature sensitivity, annual NPP, maximum biomass, and longevity of each species. For SCRPPLE, the most important parameters for calibration were the fire spread probability coefficients, fire severity coefficients, and the suppression effectiveness input table.

3.5.2. Biomass validation

We used the Eastern Cascades variant of FVS to independently validate LANDIS-II-derived biomass dynamics (e.g., *a pseudo-empirical inter-model validation*, Table 1). FVS is a distance-independent, individual tree growth and yield model that simulates stand-level dynamics over time. Data used to build the height and diameter growth equations in each FVS variant came from geographically relevant forest inventories, silviculture stand examinations, and tree nutrition studies (Keyser and Dixon, 2008). To validate the biomass dynamics produced by NECN, we selected 100 FIA plots (50 of the most abundant FIA plots, plus 50 random plots) per vegetation cover type (Fig. 1B). We simulated 100 years of growth within FVS and compared mean biomass density outputs from FVS to those derived from LANDIS-II with no wildfire disturbance.

3.5.3. Fire validation

We performed an *empirical validation* (Table 2) of the SCRPPLE fire extension by comparing our LANDIS-II simulation outputs with the contemporary (1984–2019) fire regime within the study area. We acquired maps of fire severity from the Monitoring Trends in Burn Severity (MTBS) program, a publicly available dataset containing satellite-derived severity maps for every fire ≥400 ha within the entire US since 1984. We then combined the MTBS fire severity data with the aforementioned FPA-FOD fire atlas (Short, 2017), a spatial point dataset containing ignition date, location, cause, and final fire size for all reported wildfires (including fires <400 ha) between the years 1992–2015. We used the combined fire atlas for metrics that did not require spatially explicit maps of severity (e.g., fire event size distributions), and we used the MTBS dataset alone for severity-based summary metrics (e.g., fire severity patch size distributions). To avoid over-representing the area of actual fires that were only partially contained within the study landscape, we clipped the MTBS maps to the study domain and computed all metrics based on this constrained spatial extent. The combined empirical fire dataset contained a total of 7727 ignitions, 1287 fires >1 ha, and 61 fires >400 ha.

3.5.4. Evaluation metrics

We evaluated the overall validity of our LANDIS-II application by calculating several summary metrics, including biomass density, the slope of the biomass trendline, fire event size distribution, fire severity distribution, and the fire severity patch size distributions. We evaluated goodness-of-fit (GOF) by visually comparing these summary metrics to the empirical fire regime and the results of the FVS simulation. We avoided formal statistical tests of GOF for the fire size and severity patch size distributions because we were interested in whether our model reasonably approximated observed patterns, since a simulation model may be sufficiently accurate without perfectly replicating empirical patterns (Rykiel, 1996). We tested whether there was a temporal trend in the average patch size per severity class by fitting linear models (one per severity class) with year as the predictor variable, and average patch area as the response variable.

4. Results

4.1. Succession

Both LANDIS-II and FVS projected increases in biomass in the absence of fire across all ecoregions, and the models corresponded well in terms of absolute biomass values (Fig. 2). Average biomass density for the initial base landscape (time 0) was 6% higher in LANDIS-II than the average biomass density within the FIA plots selected for the FVS simulation (128 Mg ha^{-1} versus 121 Mg • ha^{-1}, respectively). By the end of the 100-year simulations, average biomass density in LANDIS-II was 8.6% higher compared with the biomass estimate generated through FVS (252 Mg • ha^{-1} versus 231 Mg • ha^{-1}, respectively). Differences between the two models in projected biomass at year 100 were smallest in *Moist Mixed Conifer* and *Cold-Moist Conifer* ecoregions; the two ecoregions with the greatest biomass (Fig. 2).

The slope of the biomass trendline was consistent between the two models for all tree-dominated ecoregions (Fig. 3). In both models, aboveground biomass increased at the greatest rate within the first

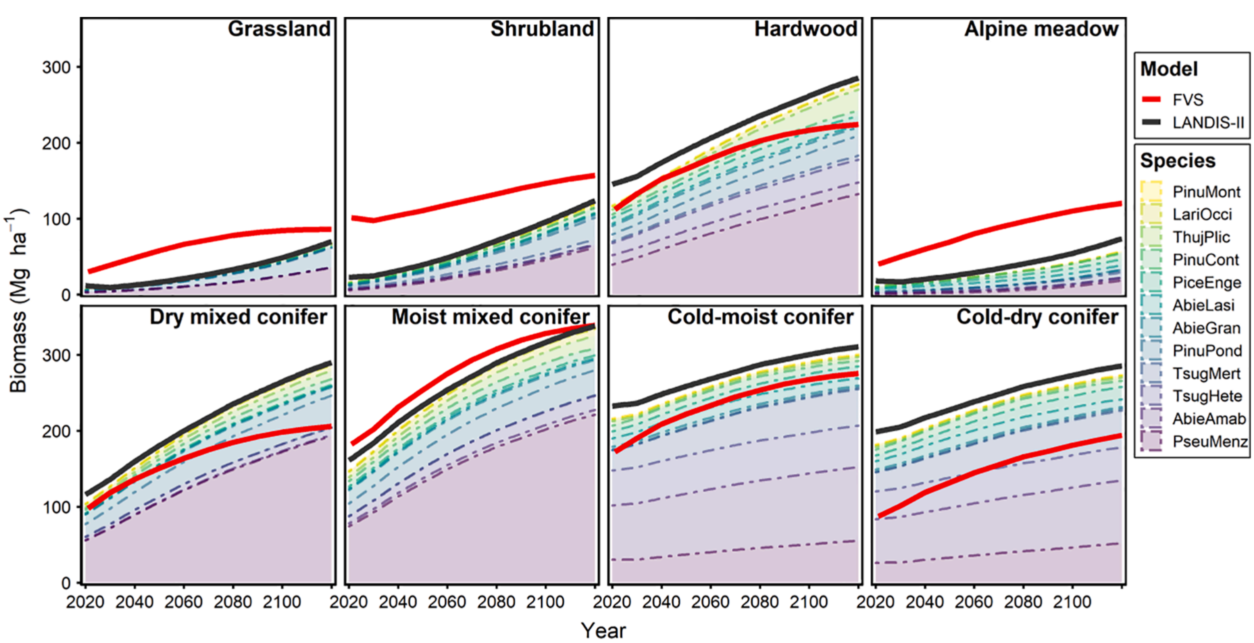

Fig. 2. Comparison of aboveground live biomass trajectories based on 100-yr forest growth simulations using the Net Ecosystem Carbon and Nitrogen (NECN) succession extension within LANDIS-II (black lines), and the Forest Vegetation Simulator (FVS; red lines). Colored areas represent the relative contribution of each species to biomass accumulation within the LANDIS-II model. For the LANDIS-II model, biomass density was averaged among all cells within each group type. For the FVS model, biomass projections were derived by running FVS on 100 Forest Inventory and Analysis plots per ecoregion and averaging the results. Species abbreviations are PinuMont = Pinus monticola; LariOcci = Larix occidentalis; ThujPlic = Thuja plicata; PinuCont = Pinus contorta; PiceEnge = Picea engelmannii; AbieLasi = Abies lasiocarpa; AbieGran = Abies grandis; PinuPond = Pinus ponderosa; TsugMert = Tsuga mertensiana; TsugHete = Tsuga heterophylla; AbieAmab = Abies amabilis; PseuMenz = Pseudotsuga menziesii.

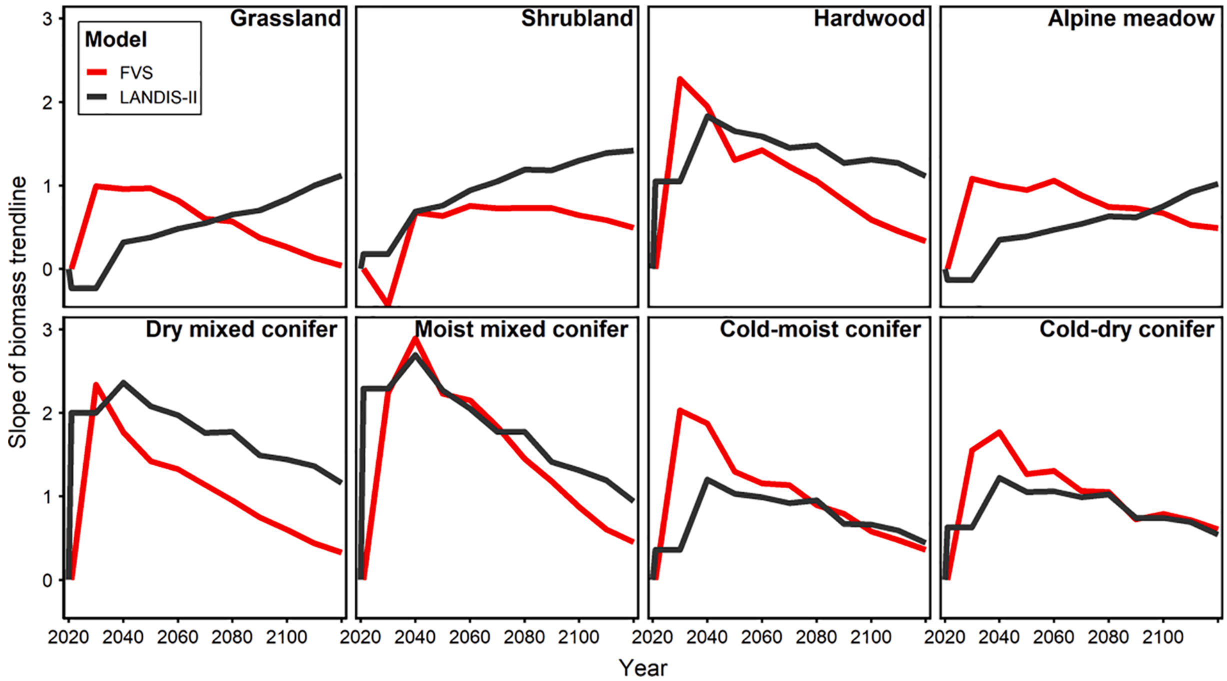

Fig. 3. Slope of aboveground live biomass trajectories (lines in Fig. 1) by group based on 100-yr forest growth simulations using the Net Ecosystem Carbon and Nitrogen succession extension within LANDIS-II (black lines), and the Forest Vegetation Simulator (red lines).

several decades, followed by an inflection point mid-century, and a gradual decline in the rate of biomass accretion (although biomass continued to increase). This pattern was evident across all ecoregions based on the FVS simulations, but it differed for non-forest ecoregions (grassland, shrubland, and alpine meadow) within the LANDIS-II succession model, where the rate of biomass accretion continued to increase over the entire simulation period. The ecoregion with the greatest similarity between the two models was *Moist Mixed Conifer* (Fig. 3) – the

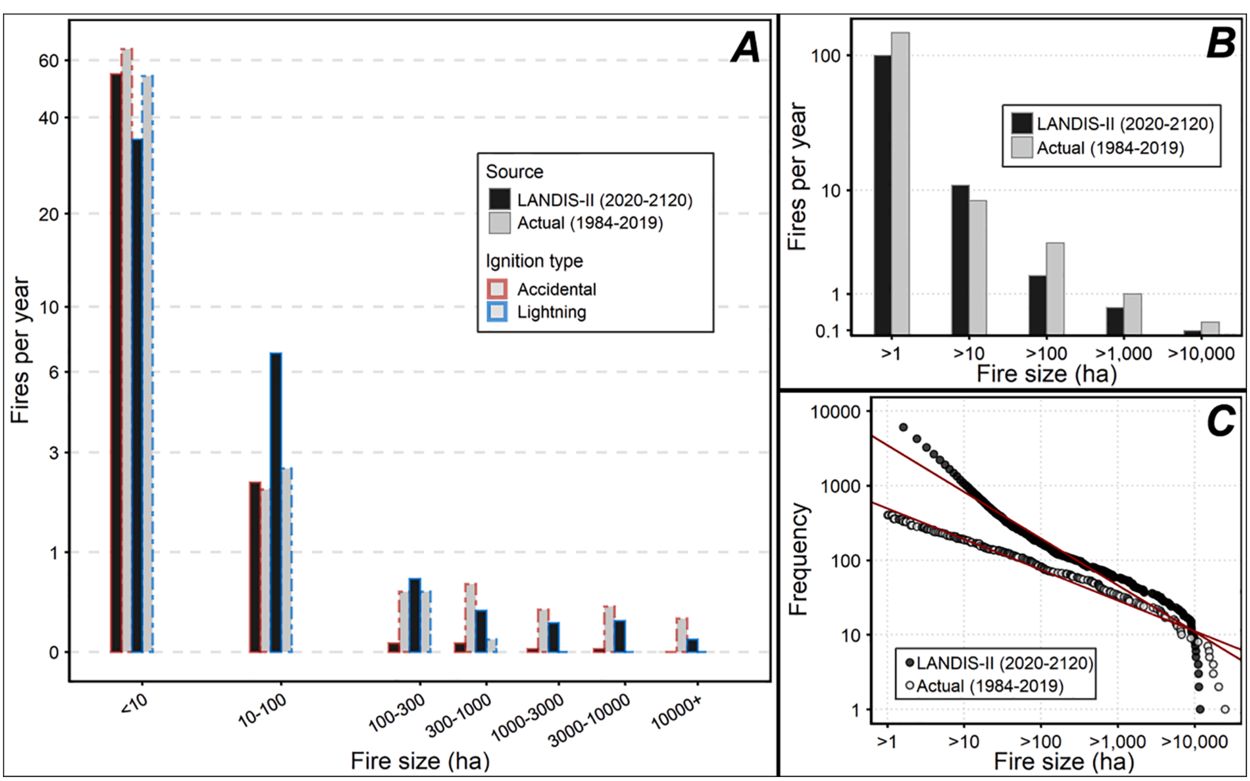

Fig. 4. Comparison of annualized fire size distributions derived from a 100-yr LANDIS-II simulation (black bars) and empirical fire activity (gray bars). The empirical fire dataset is based on the Fire Program Analysis Fire-Occurrence Database (FPA-FOD; Short 2017) and MTBS fire perimeter maps for 1984–2019. Colored borders in A indicate ignition type. In panel B, we lumped all ignition types and re-plotted the histogram on a standard log-log scale (B). Panel C displays power-law fits using un-binned data (dots represent unique fire events, and the y-axis indicates the number of fires equal or greater to that size).

ecoregion with the greatest biomass density (Fig. 2) and the greatest overall area within the study domain (30%).

4.2. Wildfire

With careful tuning of the SCPPLE fire spread parameters, we were able to simulate a fire regime that was a reasonable approximation of the empirical fire size distribution for the study domain (Fig. 4). Both fire size distributions declined logarithmically, with many small fires and relatively few large fires – a pattern typical of frequent-fire landscapes. One notable difference between simulated fires and the empirical data was that accidental human-caused ignitions accounted for the majority of observed fires ≥300-ha, while lightning ignitions accounted for most of the fires ≥300-ha in our simulations (Fig. 4A). We accepted this divergence from the historical record to account for anticipated increases in area burned by naturally ignited fires through wildland fire use over the coming century. For smaller fires (<300-ha), the number of lightning fires was roughly equivalent to the number of fires started by accidental causes in both the LANDIS-II simulation and the empirical fire record (Fig. 4A), suggesting a realistic ignition probability for both ignition types.

As expected, the observed fire size distribution approximated a power-law distribution (linear decline in $\log_{10}$-$\log_{10}$ space; McKenzie and Kennedy, 2012; Moritz et al., 2011) at spatial scales ranging from 1 to 10,000 ha (Fig. 4B,C). Simulated fires also exhibited a logarithmic decline in fire frequency as fire size increased, but the trend was not strictly linear (Fig. 4C). Instead, the simulated fire size distribution was characterized by a steep negative slope for fires <20 ha, a more moderate slope for fires 20–10,000 ha, and a steep decline in frequency for fires >10,000 ha.

Most of the area burned within the LANDIS-II simulation burned at moderate-severity, while observed fires burned with roughly equal proportions of moderate and high severity (Fig. 5). We note, however, that the "site-level severity" value (that which is analyzed in Figs. 5, 7 and 8; Note: this has been re-named "dNBR" in output maps generated by SCRPPLE v3.2) produced by SCRPPLE does not necessarily reflect the amount of mortality that each fire causes. Accordingly, we summarized percent of cohorts killed for each fire event (Fig. 6). We were not able to validate this with empirical data because tree mortality data are not available in the MTBS dataset, but the mortality distribution produced by our LANDIS-II simulation fit matched the ecological definition of a mixed-severity fire regime (*sensu* Hessburg et al., 2016) with a mix of low (0–25% mortality), moderate (25–75% mortality), and high (>75% mortality) severity fire effects (Figs. 6 and 9).

Fire severity patch size distributions derived from simulated fires were a reasonable approximation of the empirical fire severity patch size distributions (Fig. 7). Most patches were ≤10 ha, with 96% of all patches falling under 10-ha for both simulated fires and the MTBS record. The average high-severity patch sizes were slightly smaller in the LANDIS-II simulated outputs compared with the MTBS data, with mean patch sizes of 3.4-ha and 3.9-ha, respectively. Neither dataset displayed a statistically significant trend in patch sizes over time (i.e., the slope of the regression lines was not distinguishable from 0), although seven out of eight patches ≥10-ha occurred during the latter half of the MTBS fire

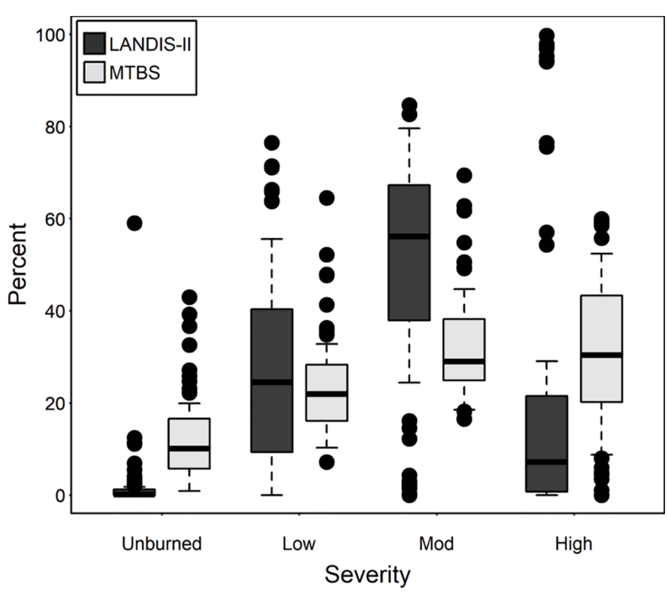

Fig. 5. Area burned by fire severity class comparing fires simulated within LANDIS-II and an empirical fire record based on Monitoring Trends in Burn Severity (MTBS) data from 1984 to 2019 for the Wenatchee-Entiat subbasins. The y-axis indicates the percentage of total area burned by severity class. Fires smaller than 400-ha are not included in the MTBS dataset.

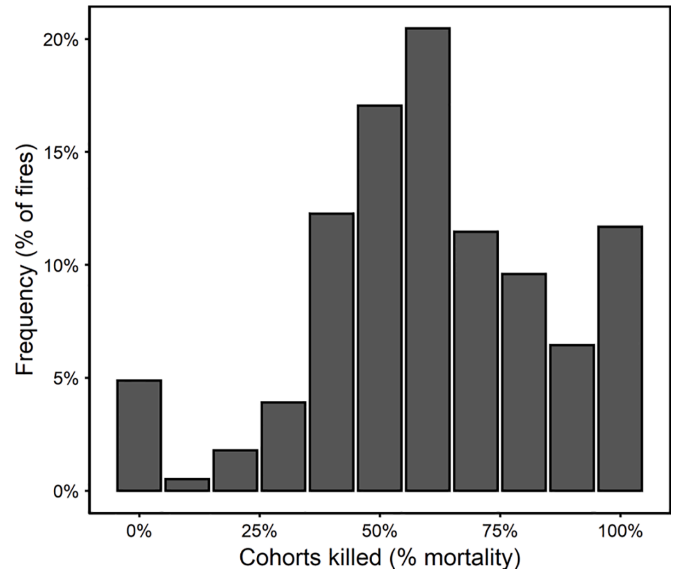

Fig. 6. Fire mortality distribution shown as the percentage of cohorts killed per fire within the LANDIS-II simulation. Although the fire extension SCRPPLE generates maps of "site-level severity", these maps do not necessarily reflect the actual amount of mortality that the model imposes on each site. Percent of cohorts killed reflects the proportion of trees within each cell that are killed following fire; in other words, this is the actual severity (within the model) associated with each fire event.

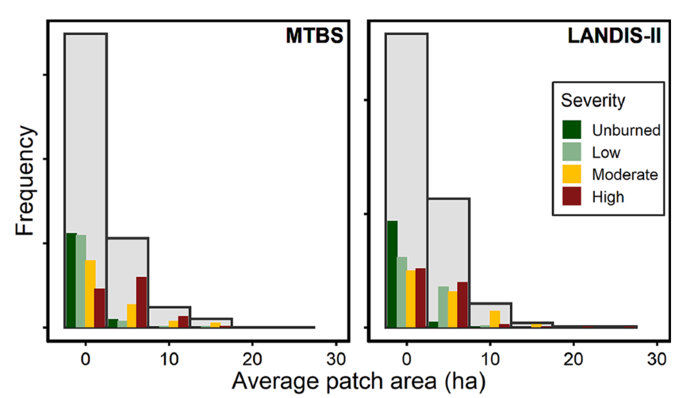

Fig. 7. Fire severity patch size distribution based on empirical fire activity (left) and our LANDIS-II simulation (right). Empirical fire severity patch size distributions were generated based on Monitoring Trends in Burn Severity (MTBS) data from 1984 to 2019 for the Wenatchee-Entiat subbasins. The large gray bars represent total frequency per size class, while the colored bars indicate frequency per severity class.

record (Fig. 8). Low-severity and unburned patches were restricted to smaller patch sizes, while moderate- and high-severity patches occurred in small and large sizes. For both the empirical and simulated fire records, nearly all patches ≥10-ha burned at moderate- or high-severity (Figs. 7 and 8).

5. Discussion

Previous studies have used a variety of methods to validate aspects of LANDIS-II (Table 1), and these efforts have established credibility for LANDIS-II applications in many contexts. This study provides further evidence for the potential credibility of LANDIS-II as we failed to reject the null hypothesis that a well-tuned FLM model can reliably simulate several key landscape-scale ecological processes. As forest landscape models (FLMs) gain attention as a credible means of projecting system-level dynamics, however, there is a growing need to develop a more transparent and consistent framework for initializing, calibrating, and validating new model applications (Petter et al., 2020; Suárez-Muñoz et al., 2021). Building on previous efforts, the methods we demonstrate in this study provide such a framework for validating FLMs that can be broadly applied to any landscape where full-coverage calibration datasets are available (e.g., Eidenshink et al., 2007; Riley et al., 2021).

5.1. Succession

Overall, LANDIS-II biomass dynamics corresponded well with FVS-modeled projections (Fig. 2). The two models were particularly well aligned in *Moist Mixed Conifer* and *Cold-Moist Conifer* ecoregions, which together comprised 62% of the biomass and 47% of the area within the study domain. The phenomenological forest growth models contained within FVS were parameterized using longitudinal forest inventory data, providing an empirical basis for projecting biomass dynamics over time. We found that the process-based algorithms contained within the NECN extension matched trends in forest biomass accumulation over time (Fig. 3), demonstrating the ability for NECN to capture relevant tree growth, competition, mortality, and forest succession processes.

Previous studies have used longitudinal FIA plot data to validate LANDIS-II biomass dynamics (Wang et al., 2014; Jin et al., 2016; Ling et al., 2020), but empirical validations are limited by the relatively short time span of longitudinal plot data (rarely more than several decades) compared with longer desired simulation lengths (often >50 years). By leveraging the tree growth and mortality models contained within FVS, which were parameterized using repeat measurements and space-for-time substitutions of forest inventory data, we were able to validate LANDIS-II biomass dynamics over the entire 100-yr simulation period using a widely respected phenomenological forest growth model.

We do note that the phenomenological models contained within FVS are not necessarily more valid than the biomass algorithms in NECN, since neither NECN nor FVS have been validated with empirical stand development data that span more than several decades. The correspondence between these models bolsters confidence in their predictive capabilities, but validations of long-term (>50 years) biomass dynamics continue to be limited by a core lack of long-term, longitudinal data. Remotely derived datasets can help fill this need for longitudinal data of forest disturbances that can be detected by satellites, but more elusive ecological processes such as tree growth, competition, and background mortality require precise, field-based forest inventory data to discern. This underscores the importance of creating and maintaining longitudinal forest demography datasets (e.g., Lutz, 2015) to support our capacity to project landscape dynamics over the coming decades.

The rate of biomass accretion in non-forest ecoregions peaked within the first 20 years of the FVS simulation, while LANDIS-II projected that the rate of biomass accumulation would continue to increase throughout the 100-yr simulation period (Fig. 3). A plausible reason for this difference is that in LANDIS-II, sites that begin as non-forest can be colonized by tree species from nearby cells if site conditions are permissive (Mladenoff, 2004), and we observed forest encroachment in our simulations. This is in contrast to FVS, which is aspatial and simulates natural regeneration without consideration of neighborhood influences (e.g., dispersal from surrounding stands; Dixon, 2002). The explicit consideration of multi-scale neighborhood processes (e.g., seed dispersal) is a key advantage of landscape simulation models, and it enables them to capture ecological dynamics that elude non-spatial models, such as FVS. The accuracy of this result will require further examination, however, as LANDIS-II may be projecting forest establishment in non-forest sites that are, in fact, maintained as non-forest by biogeoclimatic mechanisms (edaphic limitations, harsh microclimate, herbivory, etc.) that may not be well captured by our model.

5.2. Wildfire

The simulated fire regime that we produced with SCRPPLE was

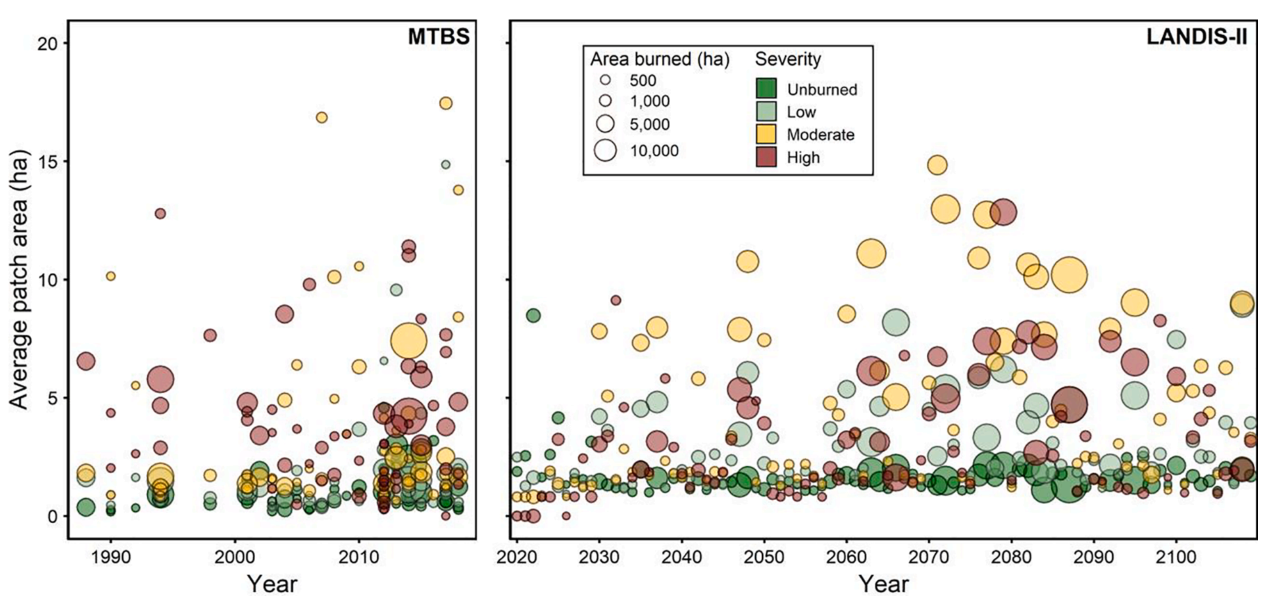

Fig. 8. Fire patch size trend based on empirical fire activity (left) and our LANDIS-II simulation (right). Empirical fire severity patch size distributions were generated based on Monitoring Trends in Burn Severity (MTBS) data from 1984 to 2019 for the Wenatchee-Entiat watersheds.

consistent with recent fire history in the Wenatchee and Entiat sub-basins. Empirical fire regimes in this landscape are temporally and spatially variable, and we were able to produce a mosaic of low-, moderate- and high-severity fire characteristic of mixed-severity fire regimes in the area (Figs. 5–7). Maps of fires produced by SCRPPLE were visually realistic with respect to topography and fuels breaks. Simulated fires mirrored natural wildfire behavior (see Povak et al., 2018) in that they burned with complex shapes and patchy severity, and topographic influences on fire spread and severity were intuitively patterned and readily apparent (Fig. 9).

The fire regimes produced by SCRPPLE are an emergent property of interactions among weather, fuels, and topography. As the fire regime created by SCRPPLE is not based on an *a priori* fire size distribution (as with some other fire models), the model can simulate shifting fire regime dynamics, feedback mechanisms, and unforeseen system-level behavior as we model fire activity under novel future climates. This has created more potential for the model to produce surprising results, and hence more opportunities for providing ecological insights regarding future climate-fire-vegetation dynamics (Table 2).

The simulated fire size distribution was well aligned with the empirical fire size distribution, but fire size and frequency alone are insufficient to characterizing the complex ecological impacts of fires (Agee, 1998; Collins et al., 2017). To evaluate the full ecological impact of simulated fire events within the model, we examined fire severity, cohort mortality, and the severity patch size distribution. Explicitly validating the severity and spatial pattern of the simulated fire regime helped us evaluate the ecological impact of simulated fire, which is required to simulate landscape-level dynamics such as ecological stability, feedbacks, and resilience. Future studies should consider fire severity and patch metrics (e.g., Figs. 5–8) when calibrating and validating SCRPPLE, since the physical characteristics of a fire regime (e.g., fire size and frequency) do not reflect the actual impact of fire on fuels, carbon, and forest structure.

5.2.1. Fire size

Fire is a complex, multi-scale, biophysical process (Scholl and Taylor, 2010; Larson and Churchill, 2012; Jeronimo et al., 2019; Furniss et al., 2020b, 2022), and realistically simulating fire behavior, spread, and severity is a long-standing challenge (Keane et al., 2004). The SCRPPLE extension has greatly advanced the capacity of LANDIS-II to simulate a dynamic wildfire regime, but some aspects of realistic wildfire simulation remain elusive. The fire spread algorithm in SCRPPLE represents fine-scale energy transfer from each cell to its adjacent cells, thereby simulating the contagious nature of fire and producing spatially aggregated fire effects (Fig. 9). However, there are no mechanisms within SCRPPLE (or any LANDIS-II fire extension) to modify fire behavior as a function of fire size. Wildfire behavior changes as a function of fire size (e.g., Cansler and McKenzie, 2014; Povak et al., 2020a), creating positive feedbacks that drive large fires through fire-altered wind dynamics, broad-scale preheating, plume-dominated events, and long-distance spotting. These factors drive rare, yet exceptionally large, “right-tail” fire events that have come to dominate total area burned in the western US (Coop et al., 2022), and they are likely to continue to increase in their importance as climate drives increasing frequency and severity of large wildfires (Cansler and McKenzie, 2014). Although incorporating multi-scale fire behaviors would increase model complexity and slow model runtime, it would improve fidelity to the physical process of wildfire and this may help the model better represent evolving fire dynamics under warmer and drier future climates. Predicting fire behavior under novel fuel and weather conditions remains a challenge for mechanistic and phenomenological fire models alike (e.g., Stephens et al., 2022), and there is a significant need for research that will improve our ability to reliably model fire behavior at multiple scales.

Simulated fires showed a weaker power-law fit compared with the empirical fire activity, which followed a more linear trend for fires <10,000 ha (Fig. 4C). The distribution of simulated fires was concave due to a lower relative abundance of intermediate-sized fires (10–1000 ha). This pattern may be attributed to fire spread probabilities in SCRPPLE being calculated based on daily weather values, as the logistic form of the model tends to produce either very high or low spread probabilities. As there is no sub-daily weather to moderate spread rate as the day progresses and no “clock” to initiate the next weather day, diurnal fluctuations in temperature and humidity have limited control

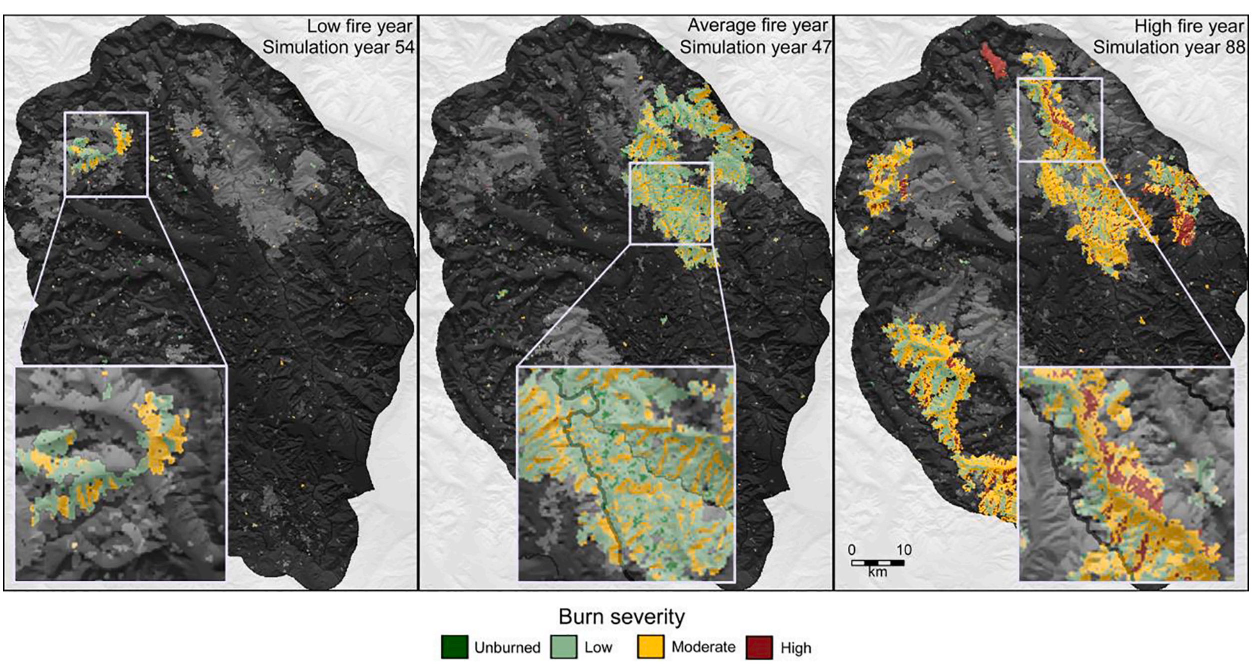

Fig. 9. Fire severity map produced by the SCRPPLE fire extension for LANDIS-II. The map displays all fires for a single simulation year. Severity reflects “site-level severity” derived from the SCRPPLE output maps (“dNBR” beginning in SCRPPLE v3.2). Light gray areas represent the footprint of fires from previous years. Dark lines represent watershed and ecoregion boundaries.

over spread rates and this may have inhibited the production of more intermediate sized fires.

5.2.2. Fire severity

A key advance made in SCRPPLE is the development of multi-level severity algorithms: fire severity (i.e., ecological impact of fire) is modeled at both individual cohort- (trees within a cell) and at the site- or cell-level. Site-level severity is output in maps roughly approximating values of dNBR (Robbins et al., 2022), facilitating empirical validations of ecologically meaningful aspects of fire behavior such as patch size distributions and spatial patterns in severity (Figs. 7–9; Table 2). These spatial metrics are central to the ecological function of fire (Agee, 1998; Collins et al., 2017), and the sophistication of the severity algorithms is a notable strength of the SCRPPLE fire model. These severity models contained within SCRPPLE are interrelated: site-level severity, which is modeled as a function of climate, fuels, and windspeed, is fed into the cohort mortality model as an independent variable. This approach captures both bottom-up and top-down controls on fire severity (e.g., Povak et al., 2020b), and for this reason it is functionally appropriate. However, the relationship between these models is inverted; in reality, fine-scale severity (mortality of individual trees and patches) drives variability in dNBR (severity as detected with satellite imagery at the 30 m scale; Morgan et al., 2014; Harvey et al., 2019; Furniss et al., 2020a). Although the current model structure is functional, modifying the severity algorithms such that broad-scale biogeoclimatic variables predict fire intensity, which would then serve as a predictor for cohort mortality, which in turn would be used to model site-level severity, would help the model structure better reflect the process of fire at these different scales.

5.2.3. The problem of validation

Despite the growing number of studies that have explicitly validated aspects of LANDIS-II (Tables 1 and 2), not all new FLM applications are sufficiently validated or the validation methods may remain unpublished. In these cases, readers and researchers who are not personally familiar with the model developers are left to simply trust that the model application is credible. The calibration and validation methods we describe in this study rely on publicly available, full coverage datasets and are therefore generalizable to any other landscape where similar data exist. We suggest these methods serve as a set of benchmark practices that others may use to inform their own model initialization methods. These methods were developed to balance rigor with practicality; while more intensive validation methods may be necessary in specific contexts, not all FLM users will have the resources to validate all aspects of their model with the maximal level of statistical rigor. Instead, we found that visually evaluating goodness-of-fit to numerous ecologically meaningful metrics may be a good middle ground that is a viable way for new model users to validate model behavior and demonstrate the credibility of new model applications.

Based on our synthesis of prior LANDIS-II validation efforts and the results of this study, we suggest a few best practices for establishing and evaluating the credibility of any given FLM application:

(1) When applying a FLM model to a new study domain many parameters may be inherited from previously developed models, but key parameters should be calibrated. This process should begin with sensitivity analyses (either formal or informal; e.g., Simons-Legaard et al., 2015; McKenzie et al., 2019) to determine which critical parameters will be the focus of calibration efforts. Calibration then involves setting initial parameters, comparing model outputs to empirical data or independent models, tuning one or several parameters, and re-running the model. This process is repeated for each parameter (or set of related parameters) deemed critical during the initial sensitivity analyses. Such an iterative calibration procedure can halt when model behavior is a reasonable representation of the processes of interest, as over-tuning cannot compensate for a residual amount of persistent uncertainty due to the fact that process-based simulation models are approximations, not replicas, of reality.

(2) After calibration, system-level dynamics of the model should be more formally validated, and the results made available for others to examine (e.g., through publication). If model outputs are highly variable, multiple simulations may be averaged to account for various sources of stochasticity within the model. Although some qualitative validation is done throughout the calibration process, this validation step may involve more rigorous goodness-of-fit tests, comparing model outputs to different data sources, or a more extensive evaluation of simulated landscapes using several different summary metrics (Tables 1 and 2).

(3) When using a previous FLM application to address a new research topic, the validation methods and assumptions of the initial model developers should be reconsidered for any new application. Additional validation may be necessary if prior efforts were insufficient, or if they are not directly relevant to the new research topic. Validity of the model in a prior context does not guarantee the validity of the model in all future contexts. If each iteration of a given model instance was validated in a new way, established models will become more robust and reliable with usage.

These guidelines are already employed by many who use LANDIS-II and other FLMs, but we articulate them here to provide a resource for the modeling community that may assist future modeler developers in implementing rigorous, transparent, and repeatable methodology for calibrating and validating newly calibrated forest landscape models.

6. Conclusion

Process-based forest landscape models (FLMs) are indispensable tools for forecasting forest dynamics under changing disturbance and climatic regimes. When properly calibrated and validated, these models can reliably simulate empirical trends in forest biomass, fire spread and severity, and vegetation-disturbance patch dynamics. Validation is a critical step as new simulation models are built and as existing models are adapted to address new research questions. In this study, we synthesize the strengths and shortcomings of various validation methods to give readers, researchers, and end users consistent terminology with which to evaluate FLMs. We demonstrated generalizable calibration methods based on publicly available, full-coverage datasets, and established benchmark validation practices based on ecologically relevant summary metrics. These advances lower the barrier to adapting LANDIS-II to new landscapes, and will enhance the overall rigor of LANDIS-II modeling by synthesizing various validation methods that can be used to demonstrate the credibility of forest landscape models.

CRediT authorship contribution statement

Tucker Furniss: Conceptualization, methodology, analysis, writing, editing, and visualization. **Paul Hessburg:** Funding acquisition, conceptualization, methodology, editing, and supervision. **Nicholas Povak:** Conceptualization, methodology, editing, and supervision. **R. Brion Salter:** Conceptualization, methodology, and editing. **Mark Wigmosta:** Funding acquisition, conceptualization, methodology, and editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.110099.

References

Abatzoglou, J.T., Brown, T.J., 2012. A comparison of statistical downscaling methods suited for wildfire applications. Int. J. Climatol. 32 (5), 772–780. https://doi.org/10.1002/joc.2312.

Agee, J.K., 1998. The landscape ecology of western forest fire regimes. Northwest Sci. 72 (24), 12.

Baddeley, A., Rubak, E., 2015. Spatial point patterns: methodology and applications with R. Chapman and Hall/CRC Press, London.

Boulanger, Y., Arseneault, D., Boucher, Y., Gauthier, S., Cyr, D., Taylor, A.R., Price, D.T., Dupuis, S., 2019. Climate change will affect the ability of forest management to reduce gaps between current and presettlement forest composition in southeastern Canada. Landsc. Ecol. 34 (1), 159–174. https://doi.org/10.1007/s10980-018-0761-6.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America, Vol. 1 Conifers. Page Pp. 675. No. Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C.

Cansler, C.A., McKenzie, D., 2014. Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. Ecol. Appl. 24 (5), 1037–1056. https://doi.org/10.1890/13-1077.1.

Cassell, B.A., Scheller, R.M., Lucash, M.S., Hurteau, M.D., Loudermilk, E.L., 2019. Widespread severe wildfires under climate change lead to increased forest homogeneity in dry mixed-conifer forests. Ecosphere 10 (11), e02934. https://doi.org/10.1002/ecs2.2934.

Collins, B.M., Stevens, J.T., Miller, J.D., Stephens, S.L., Brown, P.M., North, M.P., 2017. Alternative characterization of forest fire regimes: incorporating spatial patterns. Landsc. Ecol. 32 (8), 1543–1552. https://doi.org/10.1007/s10980-017-0528-5.

Connolly, S.R., Keith, S.A., Colwell, R.K., Rahbek, C., 2017. Process, mechanism, and modeling in macroecology. Trends Ecol. Evol. 32 (11), 835–844. https://doi.org/10.1016/j.tree.2017.08.011 (Amst.).

Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Ritter, S.M., Hoffman, C.M., 2022. Extreme fire spread events and area burned under recent and future climate in the western USA. Glob. Ecol. Biogeogr. https://doi.org/10.1111/geb.13496.

Creutzburg, M.K., Scheller, R.M., Lucash, M.S., LeDuc, S.D., Johnson, M.G., 2017. Forest management scenarios in a changing climate: trade-offs between carbon, timber, and old forest. Ecol. Appl. 27 (2), 503–518. https://doi.org/10.1002/eap.1460.

Dixon, Gary E., 2002. *Essential FVS: A user's guide to the Forest Vegetation Simulator*. US Department of Agriculture, Forest Service, Forest Management Service Center, Fort Collins, CO, USA.

Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B., Howard, S., 2007. A project for monitoring trends in burn severity. Fire Ecol. 3 (1), 3–21. https://doi.org/10.4996/fireecology.0301003.

Flanagan, S.A., Bhotika, S., Hawley, C., Starr, G., Wiesner, S., Hiers, J.K., O'Brien, J.J., Goodrick, S., Callaham, M.A., Scheller, R.M., Klepzig, K.D., Taylor, R.S., Loudermilk, E.L., 2019. Quantifying carbon and species dynamics under different fire regimes in a southeastern U.S. pineland. Ecosphere 10 (6), e02772. https://doi.org/10.1002/ecs2.2772.

Flatley, W.T., Fulé, P.Z., 2016. Are historical fire regimes compatible with future climate? Implications for forest restoration. Ecosphere 7 (10), e01471. https://doi.org/10.1002/ecs2.1471.

Furniss, T.J., Das, A.J., Mantgem, P.J., Stephenson, N.L., Lutz, J.A., 2022. Crowding, climate, and the case for social distancing among trees. Ecol. Appl. e2507. https://doi.org/10.1002/eap.2507.

Furniss, T.J., Kane, V.R., Larson, A.J., Lutz, J.A., 2020a. Detecting tree mortality with Landsat-derived spectral indices: improving ecological accuracy by examining uncertainty. Remote Sens. Environ. 237, 111497 https://doi.org/10.1016/j.rse.2019.111497.

Furniss, T.J., Larson, A.J., Kane, V.R., Lutz, J.A., 2020b. Wildfire and drought moderate the spatial elements of tree mortality. Ecosphere 11 (8), e03214. https://doi.org/10.1002/ecs2.3214.

Gustafson, E.J., 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landsc. Ecol. 28 (8), 1429–1437. https://doi.org/10.1007/s10980-013-9927-4.

Hagmann, R.K., Hessburg, P.F., Prichard, S.J., Povak, N.A., Brown, P.M., Fulé, P.Z., Keane, R.E., Knapp, E.E., Lydersen, J.M., Metlen, K.L., Reilly, M.J., Sánchez Meador, A.J., Stephens, S.L., Stevens, J.T., Taylor, A.H., Yocom, L.L., Battaglia, M.A., Churchill, D.J., Daniels, L.D., Falk, D.A., Henson, P., Johnston, J.D., Krawchuk, M.A., Levine, C.R., Meigs, G.W., Merschel, A.G., North, M.P., Safford, H.D., Swetnam, T. W., Waltz, A.E.M., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecol. Appl. 31 (8), e02431.

Hargrove, W.W., and F.M. Hoffman. 2004. A flux atlas for representativeness and statistical extrapolation of the AmeriFlux network. ORNL Technical Memorandum, No. ORNL/TM-2004/112, Oak Ridge National Laboratory. Available online at: https://www.geobabble.org/flux-ecoregions.

Hargrove, W.W., Pickering, J., 1992. Pseudoreplication: a sine qua non for regional ecology. Landsc. Ecol. 6 (4), 251–258. https://doi.org/10.1007/BF00129703.

Harvey, B.J., Andrus, R.A., Anderson, S.C., 2019. Incorporating biophysical gradients and uncertainty into burn severity maps in a temperate fire-prone forested region. Ecosphere 10 (2), e02600. https://doi.org/10.1002/ecs2.2600.

Haugo, R.D., Kellogg, B.S., Cansler, C.A., Kolden, C.A., Kemp, K.B., Robertson, J.C., Metlen, K.L., Vaillant, N.M., Restaino, C.M., 2019. The missing fire: quantifying human exclusion of wildfire in Pacific Northwest forests, USA. Ecosphere 10 (4), e02702. https://doi.org/10.1002/ecs2.2702.

He, H.S., Yang, J., Shifley, S.R., Thompson, F.R., 2011. Challenges of forest landscape modeling—simulating large landscapes and validating results. Landsc. Urban Plan. 100 (4), 400–402.

Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of Inland Northwest United States forests, 1800–2000. For. Ecol. Manag. 178 (1–2), 23–59. https://doi.org/10.1016/S0378-1127(03)00052-5.

Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. For. Ecol. Manag. 211, 117–139. https://doi.org/10.1016/j.foreco.2005.02.016.

Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., Prichard, S.J., North, M.P., Collins, B.M., Hurteau, M.D., Larson, A.J., Allen, C.D., Stephens, S.L., Rivera-Huerta, H., Stevens-Rumann, C.S., Daniels, L.D., Gedalof, Z., Gray, R.W., Kane, V.R., Churchill, D.J., Hagmann, R.K., Spies, T.A., Cansler, C.A., Belote, R.T., Veblen, T.T., Battaglia, M.A., Hoffman, C., Skinner, C.N., Safford, H.D., Salter, R.B., 2019. Climate, environment, and disturbance history govern resilience of western North American forests. Front. Ecol. Evol. 7, 239. https://doi.org/10.3389/fevo.2019.00239.

Hessburg, P.F., Salter, R.B., James, K.M., 2007. *Re*-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landsc. Ecol. 22 (S1), 5–24. https://doi.org/10.1007/s10980-007-9098-2.

Hessburg, P.F., Salter, R.B., Richmond, M.B., Smith, B.G., 2000. Ecological subregions of the interior Columbia Basin, USA. Appl. Veg. Sci. 3 (2), 163–180. https://doi.org/10.2307/1478995.

Hessburg, P.F., Smith, B.G., Salter, R.B., 1999. Detecting change in forest spatial patterns from reference conditions. Ecol. Appl. 9 (4), 1232–1252. https://doi.org/10.1890/1051-0761(1999)009[1232:DCIFSP]2.0.CO;2.

Hessburg, P.F., Spies, T.A., Perry, D.A., Skinner, C.N., Taylor, A.H., Brown, P.M., Stephens, S.L., Larson, A.J., Churchill, D.J., Povak, N.A., Singleton, P.H., McComb, B., Zielinski, W.J., Collins, B.M., Salter, R.B., Keane, J.J., Franklin, J.F., Riegel, G., 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. For. Ecol. Manag. 366, 221–250. https://doi.org/10.1016/j.foreco.2016.01.034.

Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. Landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42, 1648–1657.

Hijmans, R.J. 2021. Raster: geographic data analysis and modeling.

Hilborn, R., Mangel, M., 2013. The Ecological Detective. Princeton University Press. https://doi.org/10.1515/9781400847310.

Jeronimo, S.M.A., Kane, V.R., Churchill, D.J., Lutz, J.A., North, M.P., Asner, G.P., Franklin, J.F., 2019. Forest structure and pattern vary by climate and landform across active-fire landscapes in the montane Sierra Nevada. For. Ecol. Manag. 437, 70–86. https://doi.org/10.1016/j.foreco.2019.01.033.

Jin, W., He, H.S., Thompson, F.R., 2016. Are more complex physiological models of forest ecosystems better choices for plot and regional predictions? Environ. Model. Softw. 75, 1–14. https://doi.org/10.1016/j.envsoft.2015.10.004.

Keane, R.E., Cary, G.J., Davies, I.D., Flannigan, M.D., Gardner, R.H., Lavorel, S., Lenihan, J.M., Li, C., Rupp, T.S., 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecol. Model. 179 (1), 3–27. https://doi.org/10.1016/j.ecolmodel.2004.03.015.

Keane, R.E., Loehman, R.A., Holsinger, L.M., Falk, D.A., Higuera, P., Hood, S.M., Hessburg, P.F., 2018. Use of landscape simulation modeling to quantify resilience for ecological applications. Ecosphere 9 (9). https://doi.org/10.1002/ecs2.2414 e02414.

Pagesin Keane, R.E., Loehman, R., Clark, J., Smithwick, E.A.H., Miller, C., Perera, A.H., Sturtevant, B.R., Buse, L.J., 2015. Exploring interactions among multiple disturbance agents in forest landscapes: simulating effects of fire, beetles, and disease under climate change, editors. Simulation Modeling of Forest Landscape Disturbances. Springer International Publishing, Cham, pp. 201–231.

Keane, R.E., Parsons, R.A., Hessburg, P.F., 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. Ecol. Model. 151 (1), 29–49. https://doi.org/10.1016/S0304-3800(01)00470-7.

Keyser, A.R., Krofcheck, D.J., Remy, C.C., Allen, C.D., Hurteau, M.D., 2020. Simulated increases in fire activity reinforce shrub conversion in a southwestern US forest. Ecosystems 23 (8), 1702–1713. https://doi.org/10.1007/s10021-020-00498-4.

Keyser, C., Dixon, G., 2008. East Cascades (EC) Variant Overview. Page 68. Internal Rep. US Department of Agriculture, Forest Service, Forest Management Service Center, Fort Collins, CO, USA.

Krofcheck, D.J., Hurteau, M.D., Scheller, R.M., Loudermilk, E.L., 2017. Restoring surface fire stabilizes forest carbon under extreme fire weather in the Sierra Nevada. Ecosphere 8 (1), e01663. https://doi.org/10.1002/ecs2.1663.

Larson, A.J., Churchill, D., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. For. Ecol. Manag. 267, 74–92. https://doi.org/10.1016/j.foreco.2011.11.038.

Leenhouts, B., 1998. Assessment of biomass burning in the conterminous United States. Conserv. Ecol. 2 (1), 1–22.

Liang, S., Hurteau, M.D., Westerling, A.L., 2018. Large-scale restoration increases carbon stability under projected climate and wildfire regimes. Front. Ecol. Environ. 16 (4), 207–212. https://doi.org/10.1002/fee.1791.

Ling, P.-.Y., Prince, S., Baiocchi, G., Dymond, C., Xi, W., Hurtt, G., 2020. Impact of fire and harvest on forest ecosystem services in a species-rich area in the southern Appalachians. Ecosphere 11 (6), e03150. https://doi.org/10.1002/ecs2.3150.

Loehman, R., Flatley, W., Holsinger, L., Thode, A., 2018. Can land management buffer impacts of climate changes and altered fire regimes on ecosystems of the southwestern United States? Forests 9 (4), 192. https://doi.org/10.3390/f9040192.

Loudermilk, E.L., Scheller, R.M., Weisberg, P.J., Yang, J., Dilts, T.E., Karam, S.L., Skinner, C., 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate–fire interactions. Glob. Chang. Biol. 19 (11), 3502–3515. https://doi.org/10.1111/gcb.12310.

Lutz, J.A., 2015. The evolution of long-term data for forestry: large temperate research plots in an era of global change. Northwest Sci. 89 (3), 255–269. https://doi.org/10.3955/046.089.0306.

Ma, J., Xiao, X., Bu, R., Doughty, R., Hu, Y., Chen, B., Li, X., Zhao, B., 2017. Application of the space-for-time substitution method in validating long-term biomass predictions of a forest landscape model. Environ. Model. Softw. 94, 127–139. https://doi.org/10.1016/j.envsoft.2017.04.004.

Martin, K.L., Hurteau, M.D., Hungate, B.A., Koch, G.W., North, M.P., 2015. Carbon tradeoffs of restoration and provision of endangered species habitat in a fire-maintained forest. Ecosystems 18 (1), 76–88. https://doi.org/10.1007/s10021-014-9813-1.

McKenzie, D., Kennedy, M.C., 2012. Power laws reveal phase transitions in landscape controls of fire regimes. Nat. Commun. 3 (1), 726. https://doi.org/10.1038/ncomms1731.

McKenzie, P.F., Duveneck, M.J., Morreale, L.L., Thompson, J.R., 2019. Local and global parameter sensitivity within an ecophysiologically based forest landscape model. Environ. Model. Softw. 117, 1–13. https://doi.org/10.1016/j.envsoft.2019.03.002.

Mladenoff, D.J., 2004. LANDIS and forest landscape models. Ecol. Model. 180 (1), 7–19. https://doi.org/10.1016/j.ecolmodel.2004.03.016.

Morgan, P., Keane, R.E., Dillon, G.K., Jain, T.B., Hudak, A.T., Karau, E.C., Sikkink, P.G., Holden, Z.A., Strand, E.K., 2014. Challenges of assessing fire and burn severity using field measures, remote sensing and modelling. Int. J. Wildland Fire 23 (8), 1045–1060. https://doi.org/10.1071/WF13058.

Pagesin Moritz, M.A., Hessburg, P.F., Povak, N.A., McKenzie, D., Miller, C., Falk, D.A., 2011. Native fire regimes and landscape resilience (Eds.). The Landscape Ecology of Fire. Springer Netherlands, Dordrecht, Netherlands, pp. 51–86.

Oreskes, N., Shrader-Frechette, K., Belitz, K., 1994. Verification, validation, and confirmation of numerical models in the earth sciences. Science 263 (5147), 641–646.

Otto, S.P., Day, T., 2011. A Biologist's Guide to Mathematical Modeling in Ecology and Evolution. Princeton University Press.

Parks, S.A., Miller, C., Parisien, M.-A., Holsinger, L.M., Dobrowski, S.Z., 2015. Wildland fire deficit and surplus in the western United States, 1984–2012. Ecosphere 6 (12), 1–13. https://doi.org/10.1890/ES15-00294.1.

Parton, W., 1996. The CENTURY Model. Pages 283–291 Evaluation of Soil Organic Matter Models. Springer.

Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. R J. 10 (1), 439–446. https://doi.org/10.32614/RJ-2018-009.

Perry, D.A., Hessburg, P.F., Skinner, C.N., Spies, T.A., Stephens, S.L., Taylor, A.H., Franklin, J.F., McComb, B., Riegel, G., 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. For. Ecol. Manag. 262 (5), 703–717. https://doi.org/10.1016/j.foreco.2011.05.004.

Petter, G., Mairota, P., Albrich, K., Bebi, P., Brůna, J., Bugmann, H., Haffenden, A., Scheller, R.M., Schmatz, D.R., Seidl, R., Speich, M., Vacchiano, G., Lischke, H., 2020. How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. Environ. Model. Softw. 134, 104844 https://doi.org/10.1016/j.envsoft.2020.104844.

Povak, N., Furniss, T.J., Hessburg, P.F., Salter, R.B., Wigmosta, M., Duan, Z., LeFevre, M., 2022. Evaluating basin-scale forest adaptation scenarios: wildfire, streamflow, biomass, and economic recovery synergies and trade-offs. Front. For. Glob. Chang. 5, 805179 https://doi.org/10.3389/ffgc.2022.805179.

Povak, N.A., Hessburg, P.F., Salter, R.B., 2018. Evidence for scale-dependent topographic controls on wildfire spread. Ecosphere 9 (10), e02443. https://doi.org/10.1002/ecs2.2443.

Povak, N.A., Kane, V.R., Collins, B.M., Lydersen, J.M., Kane, J.T., 2020a. Multi-scaled drivers of severity patterns vary across land ownerships for the 2013 Rim Fire, California. Landsc. Ecol. 35 (2), 293–318. https://doi.org/10.1007/s10980-019-00947-z.

Povak, N.A., Salter, R.B., Hessburg, P.F., Prichard, S.J., Gray, R.W., 2020b. Fire-fire and fire-vegetation dynamics: lessons from REBURN modeling. Ecosystems.

R. Core Team. R: a language and environment for statistical computing. R foundation for statistical computing. https://www.r-project.org/.

Rastetter, E.B., 1996. Validating models of ecosystem response to global change. Bioscience 46 (3), 190–198. https://doi.org/10.2307/1312740.

Reilly, M.J., Dunn, C.J., Meigs, G.W., Spies, T.A., Kennedy, R.E., Bailey, J.D., Briggs, K., 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). Ecosphere 8 (3), e01695. https://doi.org/10.1002/ecs2.1695.

Riley, K.L., Grenfell, I.C., Finney, M.A., Wiener, J.M., 2021. TreeMap, a tree-level model of conterminous US forests circa 2014 produced by imputation of FIA plot data. Sci. Data 8 (1), 11. https://doi.org/10.1038/s41597-020-00782-x.

Robbins, Z.J., Loudermilk, E.L., Reilly, M.J., O'Brien, J.J., Jones, K., Gerstle, C.T., Scheller, R.M., 2022. Delayed fire mortality has long-term ecological effects across the Southern Appalachian landscape. Ecosphere 13 (6), e4153. https://doi.org/10.1002/ecs2.4153.

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11 (s1), e15–e24. https://doi.org/10.1890/120329.

Rykiel, E.J., 1996. Testing ecological models: the meaning of validation. Ecol. Model. 90 (3), 229–244. https://doi.org/10.1016/0304-3800(95)00152-2.

Sargent, R.G., Sheppard, S., Pooch, U., Pegden, D., 1984. A tutorial on verification and validation of simulation models (Eds.). In: Proceedings of the 1984 Winter Simulation Conference. IEEE, pp. 115–122, 84CH2098-2, pp.

Sargent, R.G., 2013. Verification and validation of simulation models. J. Simul. 7 (1), 12–24. https://doi.org/10.1057/jos.2012.20.

Scheller, R., Kretchun, A., Hawbaker, T.J., Henne, P.D., 2019. A landscape model of variable social-ecological fire regimes. Ecol. Model. 401, 85–93. https://doi.org/10.1016/j.ecolmodel.2019.03.022.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol. Model. 201 (3–4), 409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009.

Scheller, R.M., Hua, D., Bolstad, P.V., Birdsey, R.A., Mladenoff, D.J., 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic forests. Ecol. Model. 222 (1), 144–153. https://doi.org/10.1016/j.ecolmodel.2010.09.009.

Scheller, R.M., Kretchun, A.M., Loudermilk, E.L., Hurteau, M.D., Weisberg, P.J., Skinner, C., 2018. Interactions among fuel management, species composition, bark beetles, and climate change and the potential effects on forests of the Lake Tahoe basin. Ecosystems 21 (4), 643–656. https://doi.org/10.1007/s10021-017-0175-3.

Scholl, A.E., Taylor, A.H., 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecol. Appl. 20 (2), 362–380.

Serra-Diaz, J.M., Maxwell, C., Lucash, M.S., Scheller, R.M., Laflower, D.M., Miller, A.D., Tepley, A.J., Epstein, H.E., Anderson-Teixeira, K.J., Thompson, J.R., 2018. Disequilibrium of fire-prone forests sets the stage for a rapid decline in conifer dominance during the 21st century. Sci. Rep. 8 (1), 6749. https://doi.org/10.1038/s41598-018-24642-2.

Shifley, S.R., He, H.S., Lischke, H., Wang, W.J., Jin, W., Gustafson, E.J., Thompson, J.R., Thompson, F.R., Dijak, W.D., Yang, J., 2017. The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. Landsc. Ecol. 32 (7), 1307–1325. https://doi.org/10.1007/s10980-017-0540-9.

Shifley, S.R., Rittenhouse, C.D., Millspaugh, J.J., Millspaugh, Joshua, Thompson III, Frank R., 2009. Validation of landscape-scale decision support models that predict vegetation and wildlife dynamics (Eds.). Models for Planning Wildlife Conservation in Large Landscapes. Academic Press, Burlington, MA, USA, pp. 415–448.

Short, K.C.. Spatial wildfire occurrence data for the United States, 1992-2015 [FPA_FOD_20170508]. https://www.fs.usda.gov/rds/archive/catalog/RDS-2013-0009.4.

Simons-Legaard, E., Legaard, K., Weiskittel, A., 2015. Predicting aboveground biomass with LANDIS-II: a global and temporal analysis of parameter sensitivity. Ecol. Model. 313, 325–332. https://doi.org/10.1016/j.ecolmodel.2015.06.033.

Soil Survey Staff, 2020. Gridded National Soil Survey Geographic (gNATSGO) Database for Washington State. United States Department of Agriculture, Natural Resources Conservation Service. Available online at. https://nrcs.app.box.com/v/soils. November 1, 2020 (FY2020 official release).

Stephens, S.L., Bernal, A.A., Collins, B.M., Finney, M.A., Lautenberger, C., Saah, D., 2022. Mass fire behavior created by extensive tree mortality and high tree density not predicted by operational fire behavior models in the southern Sierra Nevada. For. Ecol. Manag. 518, 120258 https://doi.org/10.1016/j.foreco.2022.120258.

Stevens, J.T., Kling, M.M., Schwilk, D.W., Varner, J.M., Kane, J.M., 2020. Biogeography of fire regimes in western U.S. conifer forests: a trait-based approach. Glob. Ecol. Biogeogr. 29 (5), 944–955. https://doi.org/10.1111/geb.13079.
Suárez-Muñoz, M., Mina, M., Salazar, P.C., Navarro-Cerrillo, R.M., Quero, J.L., Bonet-García, F.J., 2021. A step-by-step guide to initialize and calibrate landscape models: a case study in the Mediterranean mountains. Front. Ecol. Evol. 9, 653393 https://doi.org/10.3389/fevo.2021.653393.
Syphard, A.D., Scheller, R.M., Ward, B.C., Spencer, W.D., Strittholt, J.R., 2011. Simulating landscape-scale effects of fuels treatments in the Sierra Nevada, California, USA. Int. J. Wildland Fire 20 (3), 364. https://doi.org/10.1071/WF09125.
Wang, W.J., He, H.S., Spetich, M.A., Shifley, S.R., Thompson, F.R., Dijak, W.D., Wang, Q., 2014. A framework for evaluating forest landscape model predictions using empirical data and knowledge. Environ. Model. Softw. 62, 230–239. https://doi.org/10.1016/j.envsoft.2014.09.003.
Watershed Boundary Dataset for Washington State. 2019. http://datagateway.nrcs.usda.gov.
Wang, X., Wotton, B.M., Cantin, A.S., Parisien, M.-A., Anderson, K., Moore, B., 2017. cffdrs: an R package for the Canadian forest fire danger rating system. Ecol. Process. 6 (1), 5. https://doi.org/10.1186/s13717-017-0070-z.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.