Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning

Rupert Seidl,[1,3] Werner Rammer,[1] and Thomas A. Spies[2]

[1]*Institute of Silviculture, Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria*
[2]*USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331 USA*

Abstract. Disturbances are key drivers of forest ecosystem dynamics, and forests are well adapted to their natural disturbance regimes. However, as a result of climate change, disturbance frequency is expected to increase in the future in many regions. It is not yet clear how such changes might affect forest ecosystems, and which mechanisms contribute to (current and future) disturbance resilience. We studied a 6364-ha landscape in the western Cascades of Oregon, USA, to investigate how patches of remnant old-growth trees (as one important class of biological legacies) affect the resilience of forest ecosystems to disturbance. Using the spatially explicit, individual-based, forest landscape model iLand, we analyzed the effect of three different levels of remnant patches (0%, 12%, and 24% of the landscape) on 500-year recovery trajectories after a large, high-severity wildfire. In addition, we evaluated how three different levels of fire frequency modulate the effects of initial legacies. We found that remnant live trees enhanced the recovery of total ecosystem carbon (TEC) stocks after disturbance, increased structural complexity of forest canopies, and facilitated the recolonization of late-seral species (LSS). Legacy effects were most persistent for indicators of species composition (still significant 500 years after disturbance), while TEC (i.e., a measure of ecosystem functioning) was least affected, with no significant differences among legacy scenarios after 236 years. Compounding disturbances were found to dampen legacy effects on all indicators, and higher initial legacy levels resulted in elevated fire severity in the second half of the study period. Overall, disturbance frequency had a stronger effect on ecosystem properties than the initial level of remnant old-growth trees. A doubling of the historically observed fire frequency to a mean fire return interval of 131 years reduced TEC by 10.5% and lowered the presence of LSS on the landscape by 18.1% on average, demonstrating that an increase in disturbance frequency (a potential climate change effect) may considerably alter the structure, composition, and functioning of forest landscapes. Our results indicate that live tree legacies are an important component of disturbance resilience, underlining the potential of retention forestry to address challenges in ecosystem management.

Key words: biological legacy; canopy structural diversity; ecosystem carbon storage; fire frequency; H. J. Andrews Experimental Forest; iLand model; natural disturbance; remnant live trees; species succession; tree species diversity.

INTRODUCTION

Forest disturbances are discrete events that cause tree mortality and destruction of plant biomass (Pickett and White 1985, Seidl et al. 2011*a*). Disturbances from agents such as wildfire, bark beetles, or strong winds are common throughout the world's forests (Johnson and Miyanishi 2006). In Europe's forest ecosystems, for instance, damage from the two most important abiotic and biotic disturbance agents (wind and bark beetles) are together responsible for a loss of 0.13% of the standing tree volume on average per year (Schelhaas et al. 2003). Yet, forests are remarkably resilient to such disturbances. They are natural processes of forest

ecosystem dynamics (Franklin et al. 2002), and forest species have evolved with and are adapted to the locally prevalent disturbance regime (Gutschick and BassiriRad 2003). Forest ecosystems thus have strong capacity to maintain processes under natural disturbance regimes, supporting the recovery of structural and compositional characteristics functionally equivalent to pre-disturbance states, a quality referred to as resilience (Holling 1996).

Understanding and quantifying the resilience to disturbance is increasingly important for forest ecosystem management, as disturbance regimes have been altered across many parts of the globe recently (Westerling et al. 2006, Seidl et al. 2011*b*). Recent bark beetle outbreaks in western North America, for instance, have exceeded the frequencies, impacts, and ranges observed over the last 125 years (Raffa et al. 2008). Also, the observed frequency of extreme fire years has increased

markedly in recent decades (Westerling et al. 2006). Contributing to this intensification are factors related to changes in forest management but also climatic changes (Seidl et al. 2011b), highlighting that disturbances are highly climate sensitive processes (Dale et al. 2001, Turner 2010). The changes in the climate system expected for the future have the potential to further intensify disturbance regimes (Seidl et al. 2009, Rogers et al. 2011). Model simulations for the Greater Yellowstone area, for instance, indicate that historically rare extreme fire years could be occurring regularly by the end of the 21st century as a result of climate change (Westerling et al. 2011). Increasing the resilience of ecosystems to such climate-mediated changes in the disturbance regime is thus important for foresters and conservation managers (Spies et al. 2012, Stephens et al. 2013). A prerequisite for taking action in this regard is an improved understanding of the processes and drivers of ecosystem resilience to disturbance.

Recent advances in understanding the resilience of forest ecosystems to disturbance have identified several important factors contributing to this ecosystem property. The considerable ability of early-seral species to disperse and colonize recently disturbed forests, in combination with seed banks in the soil and crown, serotiny, and resprouting ability contributes to often swift recolonization of disturbed sites (Perry 1994, Yang et al. 2005). Furthermore, diversity in species results in diverse responses to disturbance, mitigating the risk of a complete loss in ecosystem functioning. Heterogeneity in space, both with regard to disturbance impacts and ecosystem responses, also contributes to retaining structural and compositional components of forest ecosystems (Turner et al. 2013). Biological legacies, defined as organisms, organic materials, and patterns that persist through a disturbance (Franklin et al. 2000, 2002), are an important component of ecological heterogeneity. They influence the rate and trajectory of post-disturbance development (Lindenmayer et al. 2008) and thus contribute to the resilience of forest ecosystems. In particular, the abundance and spatial arrangement of survivors has been proposed as one of the pivotal factors determining succession and recovery after disturbance (Turner et al. 1998). Here we focus on this particularly important class of legacies, investigating the role of remnant patches of surviving trees on disturbance resilience (rate of recovery, return to equivalent ecosystem state) in forest ecosystems. We selected this class of legacies as our study object not only for their ecological relevance but also because they are an important consideration in ecosystem management. Salvage logging, i.e., the removal of (live and dead) legacy trees, is a standard procedure in many forest ecosystems that is now receiving considerable criticism for its ecological impacts (Lindenmayer et al. 2008). Furthermore, the concept of live-tree retention is increasingly viewed as a valuable approach to achieve the multiple objectives of forest ecosystem management (Franklin et al. 2007, Gustafsson et al. 2012).

The ecological roles and effect of remnant live trees, referred to simply as remnants or survivors in the remainder of this contribution, have become a focus of study in recent years (e.g., Wimberly and Spies 2001, Keeton and Franklin 2005). They can act as seed source for the recolonization of disturbed patches, can limit soil erosion and the loss of nutrients, and can speed up successional development. A recent study of hurricane disturbance, for instance, suggests that it often is the survivors rather than the invaders that control forest development after disturbance (Plotkin et al. 2013). In some systems, legacies have been associated with path dependence, i.e., inducing alternative successional trajectories after disturbance (Johnstone and Chapin 2006, Harvey and Holzman 2014). A quantitative assessment of the effects of live tree legacies based on empirical data is, however, often complicated by decreasing information on remnants (amount, spatial distribution) with increasing time since disturbance, inhibiting an assessment of persistence of such legacy effects in long-lived forest ecosystems. A further aspect complicating the investigation of legacy effects is the impact of compounding disturbance events, i.e., multiple disturbances affecting the same area over time. If disturbances are increasing in frequency and intensity due to climate change, as some studies suggest, these cumulative effects might become more prominent (see Kulakowski et al. 2013). The role of legacies in such multi-disturbance settings is not yet clear, as they can speed up ecological recovery and thus aid resilience (e.g., Keeton and Franklin 2005), but can also increase the severity of subsequent disturbances, e.g., due to an increased fuel load and altered forest structure (e.g., Thompson and Spies 2010).

In the near term, landscape simulation modeling is our best tool for studying the spatial and temporal effects of disturbance legacies (for a recent review on disturbance modeling, see Seidl et al. [2011a]). Landscape models dynamically simulate the effects of disturbances on ecosystems properties, and are designed to assess long-term (i.e., multiple decades to centuries) effects of and structural and spatial patterns created by disturbance on ecosystem dynamics (Scheller and Mladenoff 2007). A prime strength of simulation modeling is the ability to examine alternative scenarios. In the context of legacy effects, scenarios can be used to address uncertainties both with regard to past (e.g., legacies of past disturbance) and future (e.g., changing disturbance regimes) conditions (Wimberly and Spies 2001, Seidl et al. 2009). Furthermore, simulation modeling provides a means to disentangle compounding disturbance impacts by studying the effect of different agents/scenarios separately as well as in combination (Temperli et al. 2013). Here we used a simulation approach to study the effects of remnant trees on trajectories of forest development over long time periods

while controlling for different levels of compounding disturbance. Our main objective was to study the landscape-level effects of survivors after high-severity fire on recovery and resilience of forest structure, composition, and functioning. We hypothesize that (1) due to the slow generational turnover and dispersal limitations of late-seral species, legacy effects on recovery are greatest for forest composition (Turner et al. 1998), while we expect ecosystem functioning to be least sensitive to legacies as a result of functional redundancy (see also Peters et al. 2013); (2) an increase in disturbance frequency will decreases the persistence of biological legacies and thus reduce the effect of legacies on the recovery of forest structure, composition, and functioning; and (3) different initial levels of survivors and subsequent disturbance induce path dependence in post-disturbance forest dynamics and lead to alternative states of the system (Johnstone and Chapin 2006, Harvey and Holzman 2014).

MATERIAL AND METHODS

Material

The H. J. Andrews Experimental Forest.—The study landscape chosen to investigate these questions is the H. J. Andrews Experimental Forest (HJA), located in the western Cascades of Oregon, USA (44.2° N, 122.2° W). HJA is a 6364-ha watershed characterized by complex mountain topography. Its well-drained soils are derived from aeolian volcanic materials, colluvium, and residual materials from Tertiary basalts and andesites. The climatic conditions are characterized by mild and wet winters and cool and dry summers, with mean monthly temperatures ranging from 1°C in January to 18°C in July. Precipitation falls mainly in the winter and increases with elevation, from approximately 2300 mm at the bottom of the watershed (410 m above sea level) to >3500 mm at high elevations (the highest peak at HJA, Lookout Mountain, is 1630 m above sea level). Forests are dominated by Douglas-fir (*Psuedotsuga menziesii* (Mirb.) Franco), which is in the lower reaches associated with western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). Higher elevation forests contain noble fir (*Abies procera* Rehd.) and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) in addition to Douglas-fir and western hemlock. Low- and mid-elevation forests at HJA are among the most productive in the world, with canopy heights in excess of 75 m and total ecosystem carbon (C) storages >1.0 Gg C/ha (Smithwick et al. 2002).

Climate and soil data.—A climate time series with daily resolution was available for the period 1973–2001 from the PRIMET weather station located in the lower reaches of the landscape (Daly and McKee 2013). In addition, grids of monthly temperature, precipitation, and radiation variation over the landscape (100 m horizontal resolution; Daly 2005, Daly and Smith 2005*a*, *b*) have been previously used to determine

homogeneous climate regions ($n = 113$ climate regions) for the 6364-ha HJA landscape (Seidl et al. 2012*b*). A spatially distributed daily climate time series for these climate regions was constructed using monthly differences to the PRIMET location. To extend this time series to a 500-year data set for simulation (years 1501–2000) stratified sampling with replacement was used, applying the Pacific Decadal Oscillation as stratification criterion (see Seidl et al. [2012*b*] for details). The change in atmospheric CO_2 concentration over the respective time period was taken from Meinshausen et al. (2011). Quantitative soil data was available from 326 soil profiles for the landscape (Dyrness 2001), which were imputed to soil mapping units (soil series × slope class; Dyrness et al. 2005) to achieve full spatial coverage. C and nitrogen (N) pools for the forest floor and mineral soil, sand, silt, and clay content, and effective rooting depth were extracted from soil profile data. A proxy of nutrient availability (plant-available N per hectare per year) was derived from total soil N levels (Seidl et al. 2012*a*).

Disturbance regime and biological legacies.—The disturbance history of the HJA and surrounding areas has been extensively studied by means of dendroecology (Teensma 1987, Weisberg 1998, Giglia 2004, Tepley 2010, Tepley et al. 2013). From these studies, there is strong evidence that a landscape-level high-severity fire event occurred approximately in the year 1500. This event serves as the starting point for our analysis of post-disturbance legacies. The extent of remnant live tree patches surviving this event were reconstructed following the analysis of Giglia (2004), who estimated based on 874 sample sites in the greater HJA region that on average 12% of the current landscape are "super-old-growth" forests, i.e., they predate the landscape-scale fire event of 1500. For the most likely spatial distribution of these survivors, we followed the analysis of Tepley (2010), who mapped the probability of such forest types based on climatic and topographic variables using nonparametric multiplicative regression. According to this analysis, survivors of the 1500 burn mostly persisted along streams and in topographically sheltered positions. Forest structure and composition in these remnants was not explicitly reconstructed but was assumed to correspond to current observations in old-growth forests at HJA in the respective vegetation zone (Harmon and Franklin 2012). For the period 1501–2000 the mean fire size at HJA was reconstructed to be 965 ha from dendroecological studies (Teensma 1987, Weisberg 1998). The landscape-scale mean fire return interval was estimated to 262 years, varying from 349 years in lower elevation forest types to 198 years in high elevation areas of the landscape.

Methods

The iLand simulation model.—To assess legacy effects on century-scale post-disturbance ecosystem trajectories, we used iLand, the individual-based forest land-

scape and disturbance model (Seidl et al. 2012a). iLand is an individual-based model, using an approach rooted in ecological field theory (see Berger et al. 2008) to simulating the resource competition of trees explicitly in time and space. To make these tree-level interactions computationally scalable to the landscape scale, process-based interference patterns are applied within a hierarchical multi-scale framework of resource use and limitation in iLand (Seidl et al. 2012a). Generalized physiological principles are applied to model individual tree growth (using a light use efficiency approach) and mortality (by carbon starvation) based on the resources captured by an individual. Allocation to tree compartments is modeled based on empirical allometric ratios (Duursma et al. 2007), with trees dynamically adapting their individual allocation strategy based on their local environment (Seidl et al. 2012a). Seed dispersal is simulated in a spatially explicit manner based on the distribution of mature trees over the landscape as well as their species-specific dispersal strategies. When seeds are available at a site, regeneration is simulated at 2-m horizontal resolution by means of a phenology-based establishment probability as well as the local light availability (Seidl et al. 2012a). iLand is a species-specific model, and is currently parameterized for 10 tree species in the Pacific Northwest and four central European tree species. iLand also includes a soil and decomposition module to simulate closed ecosystem C and N cycles (Kätterer and Andrén 2001). Separate pools for standing and downed deadwood, litter, and soil organic matter are distinguished in the model. A detailed description of iLand is given by Seidl et al. (2012a, b). In addition, extensive technical model documentation as well as the model code and executable can be obtained online (see Seidl and Rammer 2014).

iLand has been evaluated for our study area in previous studies. The model was found capable of reproducing the productivity patterns observed over wide environmental gradients in Oregon, and successfully simulated observed stand structure and mortality patterns in old-growth forests at the HJA (Seidl et al. 2012a). Furthermore, landscape-level evaluation against remote sensing-based estimates indicated that iLand realistically simulates forest structure and composition at the HJA (Seidl et al. 2012b). Simulated total ecosystem C stocks (TEC) were found to be well in line with expectations from field-based studies (Seidl et al. 2012b).

Forest fire modeling.—An aspect that has hitherto been missing from the model, yet is important for the analysis of legacy effects in this study, is the ability to simulate forest fire regimes based on climate, vegetation properties, and landscape characteristics such as topography. To that end, we incorporated a dynamic forest fire module into iLand, based on previous experiences in modeling wildfire in forest landscape vegetation simulators. Fire ignition is modeled following the approach of Keane et al. (2011), accounting for fuel availability, fire

weather (characterized by the Keetch Byram drought index, KBDI [Keetch and Byram 1968]), fire suppression, and historical fire probability. Fire spread is simulated at 20-m horizontal resolution using a cellular automaton approach (e.g., Wimberly 2002). Transition probabilities are modified for the effects of wind, slope, fuel, and land type (Keane et al. 2011). Fire intensity and severity are modeled following the approach by Schumacher et al. (2006), accounting for fuel availability, fuel moisture, as well as tree size- and species-specific resistance. Fire intensity, frequently approximated via scorch height, is modeled as percent crown kill, depending on fuel availability and moisture as well as stand structure (Schumacher et al. 2006). Individual-tree mortality probability is subsequently derived from percent crown kill in conjunction with bark thickness (Ryan and Reinhardt 1988). Fires go extinct in the model either through an extinction probability applied to individual-cell spread, or when the maximum fire size, drawn from an exponential fire size distribution, is reached (Wimberly and Kennedy 2008, Keane et al. 2011). A detailed description of the iLand fire module is given in Appendix A. For the current study, the fire module was parameterized based on reconstructions of the fire regime at the HJA (Teensma 1987, Weisberg 1998). We tested the model's ability to reproduce the reconstructed fire regime with regard to fire severity, fire size, and spatial differences in fire frequency. Details on parameterization and evaluation of the iLand fire module can be found in Appendix B.

Study design and analysis

In addition to the reconstructed survivors of the year 1500 burn (scenario L1) two alternative legacy scenarios were studied, including a no-legacy scenario (L0) and a scenario with twice the historically reconstructed level of survival (L2). The no-legacy scenario L0 equals complete disturbance (i.e., 100% severity). Scenario L2 on the other hand assumed that remnant trees survived on 24% of the landscape (i.e., twice the level of remnants as in scenario L1). The spatial pattern of the legacy area under L2 was determined in the same way as for L1, i.e., using super-old-growth probabilities estimated by Tepley (2010), albeit with a higher cutoff value. It has to be noted that survivors in both L1 and L2 are mostly concentrated in a small number of large unburned patches, rather than being dispersed homogeneously over the landscape. Seed input from outside the landscape boundaries was assumed in the simulations of all scenarios.

In order to assess how compounding disturbances modulate the effect of different levels of remnants, and to determine if and how initial survivors influence subsequent disturbances, we also investigated three different scenarios of subsequent disturbance frequency. In addition to the historically reconstructed mean fire return interval of 262 years (F1), we studied scenarios of doubled fire frequency (F2) and no subsequent distur-

bance (F0). For all fire scenarios, only the fire return interval was modified, while all other simulation parameters (e.g., mean fire size, extinction probability) were kept constant. Furthermore, the spatial differences in fire return intervals across the landscape were retained in all fire scenarios (see Appendix B). It is important to note, however, that the actual occurrence, spread, size, and severity of fires was dynamically simulated with iLand. Interactions between initial survival and subsequent disturbance severity are thus an emergent property of the simulations. We simulated all combinations of legacy levels (L*) and disturbance frequencies (F*; Table 1), and simulations were run for 500 years without management interventions. In order to account for the stochasticity of the dynamically simulated fire scenarios, 25 replicated runs were conducted for all scenarios (except L*F0, in which subsequent disturbances were omitted).

Our main goal was to study the effect of these legacy and disturbance scenarios on the resilience of the studied landscape. Given the wide variety of different definitions of resilience (Brand and Jax 2007) we clarify below how we define the term. We focused on two aspects of resilience, loosely corresponding to the properties referred to as engineering resilience and ecological resilience by Holling (1996). First, we assess the recovery trajectories of selected ecosystem indicators (i.e., their development over time) after widespread high-severity fire in year 1500, and assess how remnant patches of live trees and subsequent wildfires alter these trajectories. In particular we ask if increased legacy levels speed ecosystem recovery from large-scale disturbance (cf. engineering resilience). Second, we ask if our legacy and disturbance scenarios lead to different ecosystem states as jointly defined by indicators of ecosystem structure, composition, and function. This analysis allows us to pursue the question of whether these scenarios lead to divergence of the ecosystem in phase space. (cf. ecological resilience).

With regard to ecosystem functioning, we focused on total ecosystem C storage (TEC), including C in living and dead vegetation components as well as in the soil (up to a maximum soil depth of 100 cm). Carbon cycling is an important indicator of ecosystem functioning (Waring and Running 2007) and is gaining importance also in the context of climate change mitigation (McKinley et al. 2011). As an indicator of vegetation structure, we selected the rumple index (RI) of canopy complexity. The rumple index is the ratio of the canopy surface area to the projected surface ground area (Parker et al. 2004), and was calculated at the level of 100-m grid cells based on simulated canopy top heights mapped at 10-m horizontal resolution. RI was recently proposed as a powerful composite index to describe vegetation structure and distinguish different stages of forest development over large areas (Kane et al. 2011). As indicator of compositional recovery we selected the presence of late-seral species (i.e., western hemlock,

TABLE 1. Overview of the legacy and disturbance scenario combinations studied and the acronyms used to identify them.

Initial survivors (percentage of landscape)	Subsequent mean fire return interval (yr)		
	∞	262†	131
0	L0F0	L0F1	L0F2
12†	L1F0	L1F1	L1F2
24	L2F0	L2F1	L2F2

† Historic level.

western red cedar, Pacific silver fir, and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.)) >4 m in height (LSS). All three indicators (TEC, RI, and LSS) were analyzed at the level of 100-m grid cells, and averaged over the 6364-ha HJA landscape for time series analyses. In order to provide additional information on species succession, we analyzed spatiotemporal patterning of early-seral patches (LSS <33% based on stem number of individuals >4 m height), mixed (33–66% LSS), and late-seral patches (>66% LSS). Landscape-level patch diversity with regard to these three patch types was calculated using the Simpson diversity index, which describes the probability that any two grid cells selected at random would be in different seral stages (McGarigal et al. 2002). Furthermore, tree species diversity (over all simulated species, which, in addition to the four late-seral species mentioned above, include Douglas-fir, Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), noble fir, grand fir (*Abies grandis* Lindl.), bigleaf maple (*Acer macrophyllum* Pursh), and red alder (*Alnus rubra* Bong.)) was assessed at the stand level (100m grid) using the same diversity index.

Differences in the trajectories of individual indicators were evaluated by comparing the timing of recovery to particular levels. Significance was tested by means of a Kruskal-Wallis test, and Wilcoxon signed-rank sum tests were used for comparisons between individual scenarios (25 simulation replicates). Applying the parametric equivalents of these tests (ANOVA, Student's t test) yielded similar results (data not shown). Differences in trajectories over all scenarios were further analyzed by means of Tukey's honest significant differences method. Furthermore, trajectories were evaluated with regard to their recovery rates (i.e., annualized changes in indicator values) using the same testing framework. To test for differences in system state the three dimensions ecosystem functioning (TEC), structure (RI), and composition (LSS) were analyzed jointly. Potential scenario differences in phase space were first analyzed using a MANOVA over all scenarios, testing for a significant influence of legacy and fire scenarios. Subsequently, we tested for individual differences between scenarios using the squared Mahalanobis distance as evaluation metric. The R Project for
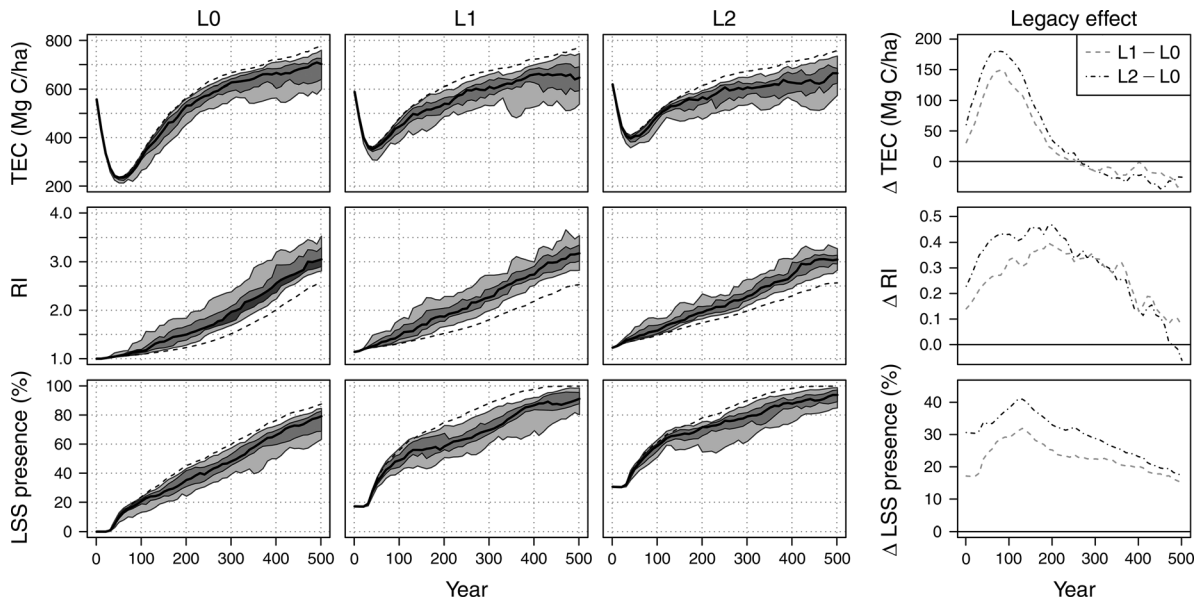
FIG. 1. Trajectories of ecosystem functioning (total ecosystem carbon, TEC), structure (rumple index, RI [see *Materials and methods: Study design and analysis*]), and composition (presence of late-seral species, LSS) for the 6364-ha H. J. Andrews Experimental Forest landscape under different scenarios of initial legacy (L0, no legacies; L1, remnant trees on 12% of the landscape; L2, remnant trees on 24% of the landscape). For a mean fire return interval of 262 years (scenario F1) the median (heavy line), interquartile range (dark gray area) and 5th–95th percentile range (light gray area) of 25 replicated runs are shown, while the dashed line indicates simulation results assuming undisturbed recovery (i.e., no wildfires burning during the 500-year study period). To assist the visual evaluation of legacy effects, the differences (Δ) of L1 and L2 to L0 (mean trajectories under the F1 disturbance scenario) are shown in the last column of the figure.

Statistical Computing was used for all analyses (R Development Core Team 2011).

RESULTS

The effect of live tree legacy

We first analyzed the effect of initial survivors on post-disturbance recovery trajectories, controlling for the effect of subsequent, compounding disturbances by assuming no fire (i.e., setting the fire return interval to infinite, scenarios L*F0). A distinct legacy effect (i.e., different recovery trajectory in legacy scenarios compared to the no-legacy scenario) was evident for all indicators investigated (Fig. 1). Remnants had a strong mitigating effect on TEC loss after disturbance, compared to the no-legacy simulations. In the initial years after disturbance, the TEC levels dropped in all scenarios, indicating that the landscape was a C source to the atmosphere in those years. While the initial TEC level in L0 was only 31.1 Mg C/ha lower than in L1 (−5.3%, see Appendix C: Table C1), the minimum TEC stock fell to more than three times lower values in L0 compared to the historic legacy scenario L1 (123.2 Mg C/ha or −34.2% lower). The rate of landscape-scale C loss in the first 50 years after disturbance was 49.9% greater in L0 compared to L1 (Table C2). Also, the inflection point of the landscape reverting from a C source to a C sink was reached approximately 10 years earlier in L1 than in the no-legacy scenario L0. Structural diversity was considerably increased by

remnant old-growth patches compared to L0, and the recolonization with late-seral species was accelerated by the initial presence of LSS in these remnant patches. After 100 years, RI and LSS were 1.2 and 2.3 times higher, respectively, in the historic legacy scenario L1 compared to the no-legacy run (L0). Their recovery rates exceeded those of the L0 scenario by a factor of 1.86 and 1.62, respectively, over the same period of time (Table C2). While there was a strong difference between no legacy and the historically observed level of survivors (remnants on 12% of the landscape), a doubling of survivor patches (L2) generally showed diminishing effects on the TEC, RI, and LSS indicators.

Our simulations indicate that legacy effects influence the recovery trajectories of forest ecosystems over long timescales, with legacy effects persisting for several centuries. One-hundred years after disturbance, the recovery of TEC under scenario L1 was still 54 years ahead of the no-legacy scenario. Even more dramatically, RI and LSS reached the respective levels of scenario L1 with a delay of 137 and 175 years in scenario L0. The TEC trajectories of the different legacy scenarios converged after 236 years (differences less than ±5%), indicating that after this period ecosystem functioning was no longer affected by the initial level of survivors. RI trajectories only converged close to the end of the simulation period (year 446), suggesting that legacy effects on vegetation structure persist for almost twice as long as those on ecosystem functioning. The effects of

TABLE 2. Indicators of ecosystem functioning (total ecosystem carbon, TEC), structure (rumple index, RI [see *Materials and methods: Study design and analysis*]), and composition (presence of late seral species, LSS) for different initial legacy level (L0–L2) and subsequent fire frequency scenarios (F0–F2).

Legacy and fire frequency	Years 1–100	Years 401–500	Years 1–500
Functioning, TEC (Mg C/ha)			
L0			
F0	316.3[ab]	745.5[ab]	568.0[abdefgh]
F1	307.5[b] (290.9–315.7)	663.7[a] (571.6–727.1)	518.6[b] (457.2–558.2)
F2	272.6[a] (253.3–286.2)	588.9[bc] (508.5–667.0)	466.8[c] (406.1–522.4)
L1			
F0	428.2[cde]	743.9[ab]	614.3[degh]
F1	411.4[c] (381.2–426.7)	642.4[a] (531.1–724.3)	548.0[egh] (474.6–599.5)
F2	401.5[c] (363.0–424.0)	556.4[c] (475.8–671.4)	490.7[f] (417.6–556.5)
L2			
F0	467.8[de]	733.1[ab]	621.5[gh]
F1	450.3[d] (419.5–466.7)	631.6[ab] (535.3–709.7)	559.1[h] (494.6–605.4)
F2	437.0[e] (400.4–460.9)	553.3[c] (456.2–656.9)	494.4[af] (414.4–560.5)
Structure, RI (dimensionless)			
L0			
F0	1.04[a]	2.31[a]	1.53[a]
F1	1.07[a] (1.04–1.13)	2.89[bc] (2.59–3.33)	1.88[a] (1.66–2.22)
F2	1.10[a] (1.05–1.17)	3.34[d] (3.08–3.67)	2.21[b] (1.95–2.50)
L1			
F0	1.23[ab]	2.38[ac]	1.74[a]
F1	1.30[b] (1.23–1.43)	3.01[b] (2.71–3.38)	2.15[b] (1.90–2.46)
F2	1.34[b] (1.24–1.52)	3.32[d] (2.99–3.63)	2.38[c] (2.12–2.67)
L2			
F0	1.36[bcd]	2.46[ace]	1.89[ab]
F1	1.43[c] (1.35–1.57)	2.96[be] (2.65–3.24)	2.18[b] (1.99–2.42)
F2	1.50[d] (1.38–1.66)	3.26[d] (2.98–3.60)	2.46[c] (2.21–2.75)
Composition, LSS (%)			
L0			
F0	8.6[a]	82.5[abcdef]	49.4[abe]
F1	7.8[a] (4.9–9.6)	70.2[be] (57.0–78.9)	40.8[b] (31.4–47.6)
F2	8.1[a] (5.0–10.3)	56.0[c] (45.4–67.6)	33.4[c] (24.7–41.9)
L1			
F0	32.6[bc]	99.4[abdef]	74.8[df]
F1	30.5[b] (27.0–33.4)	87.8[df] (74.7–96.0)	63.5[ef] (52.9–72.0)
F2	28.9[b] (21.8–32.8)	70.8[e] (53.4–86.2)	52.0[g] (37.8–63.5)
L2			
F0	42.7[de]	99.5[abdef]	78.3[df]
F1	40.9[d] (37.6–43.4)	90.2[f] (80.9–97.1)	70.3[d] (60.9–76.7)
F2	39.5[ce] (35.0–43.1)	73.1[abe] (50.6–89.4)	58.2[a] (43.2–70.4)

Notes: See Table 1 for scenario details. Values are landscape-scale means and, for scenarios F1 and F2, mean values over 25 replicated simulations are reported (5th–95th percentile range in parenthesis). Different superscript letters indicate statistical difference between scenarios within the respective time periods at $\alpha = 0.05$ as determined by Tukey's honest significant difference method.

initial disturbance remnants on species composition even exceeded the time frame of the simulation. After 500 years, the presence and distribution of late-seral species still differed between legacy scenarios (L1, L2) and no-legacy scenarios (L0). Over all simulations, Kruskall-Wallis tests indicated that legacy scenarios significantly differed with regard to TEC, RI, and LSS ($P < 0.05$ for the 500-year averages of all indicators).

The role of disturbance frequency

Including historical (F1) and increased (F2) fire frequencies in the simulation of recovery trajectories resulted in lower levels of total ecosystem C storage at the landscape scale and slowed the spread of late-seral species in the landscape, compared to undisturbed runs assuming infinite fire return intervals (Table 2). The structural complexity of the landscape (RI), on the other hand, was higher in scenario F1 than in F0. TEC and LSS were −10.8% and −15.1% lower under the historical fire frequency scenario (L1) than the no-fire scenario, while RI was 23.6% higher, on average over the 500-year simulation period ($P < 0.001$ for all three indicators). These effects further intensified for all indicators when a doubling of the fire frequency was assumed under scenario F2 (Table 2).

TABLE 3.   Mean fire severity in scenarios of different initial survival (L0–2) and subsequent fire frequency (F1, F2).

Fire frequency and legacy	Years 1–100	Years 101–200	Years 201–300	Years 301–400	Years 401–500
F1					
L0	78.4 ± 19.6	53.7 ± 21.9	39.3 ± 19.0	36.6 ± 21.5	45.4 ± 21.5
L1	60.0 ± 27.1	49.0 ± 18.6	37.7 ± 18.4	46.2 ± 20.0	45.7 ± 18.3
L2	52.5 ± 29.6	46.7 ± 18.6	42.8 ± 23.4	48.1 ± 20.7	50.5 ± 20.5
F2					
L0	78.8 ± 19.4	47.7 ± 22.8	33.6 ± 20.3	32.4 ± 20.1	35.1 ± 19.8
L1	56.5 ± 29.0	46.5 ± 20.9	37.7 ± 21.3	38.1 ± 20.9	40.5 ± 20.3
. L2	53.4 ± 26.7	48.1 ± 19.2	40.5 ± 22.5	37.4 ± 22.5	39.3 ± 22.4

Notes: Severity is reported as the mean percentage of basal area killed by wildfire within the simulated fire perimeters. Values are means ± SD over all fires of the 25 replicated simulations.

The magnitude and persistence of legacy effects on TEC were significantly reduced when subsequent disturbance by wildfire was simulated (Fig. 1). Under the F0 scenarios, the average TEC stocks over 500 years were +46.3 Mg C/ha (+8.2%) higher in the legacy runs (L1) compared to no-legacy simulations (L0). However, this difference was reduced to +29.4 Mg C/ha (+5.7% greater than L0) for the historically observed fire-frequency scenario (F1). Increased fire frequency (F2) further reduced the effect of disturbance remnants on TEC. For RI and LSS, the impact of subsequent fire on the effect of initial legacies was considerably weaker than for TEC (Table 2). However, a significant effect of survivors on the first 100 years of post-disturbance recovery was evident for all indicators when realistic fire return intervals were considered (Table 2). In other words, subsequent fires did not erase the positive effect of initial survivors on recovery from the 1500 burn for all three ecosystem indicators.

The influence of initial survivors on subsequent disturbance

However, in the simulations considering the full interactions between initial survivors and subsequent fires, a negative effect of legacy on recovery was evident: landscape-scale TEC levels in the legacy scenarios were lower than in the no-legacies scenario in the last 234 years of the simulation (Fig. 1). A comparison to the undisturbed runs, which do not show this behavior, indicate that accelerated successional development is not the main driver behind this effect. A more detailed analysis revealed this to be the result of the interaction between remnant trees and subsequent disturbance severity. Due to an increased vertical diversification (e.g., ladder fuels) and a higher share of late-seral species (which have thin bark and are more susceptible to fire), simulated fire severities in legacy runs were elevated compared to the no-legacy (L0) runs in the second half of the study period (Table 3). In turn, the delayed development in the no-legacies scenario (lower crown height and smaller tree diameter/bark thickness in scenario L0) resulted in considerably higher fire severity in the first 100 years of the simulation, compared to the two legacy scenarios. Remnant patches of old-growth trees thus reduced the severity of reburns in our simulations. In summary, our results indicate that subsequent, compounding disturbances do not only modulate the effect of initial survivors on ecosystem dynamics, but are themselves affected by the amount and distribution of legacies from previous disturbances.

Disturbance, legacy, and diversity

Since the most profound and persistent legacy effect was found for species composition (Fig. 1) we further analyzed the effect of initial survival (L*) and subsequent disturbance frequency (F*) on species distribution and diversity. A spatiotemporal analysis of compositional dynamics showed that while the landscape is quickly recolonized by early-seral species within a few decades, old-growth conditions with a substantial share of late-seral species emerge only after a couple of centuries at a significant portion of the landscape (Fig. 2, Appendix C: Fig. C1). Our results indicate that remnant trees facilitate the rate of succession toward late-seral communities (Table C2) by acting as nuclei for the spread of LSS into the post-disturbance landscape. However, the interactions between initial survivors and subsequent disturbance severity (Table 3) also exert a negative feedback on LSS. Under the high frequency fire regime F2, for instance, the no-legacy scenario (L0) was found to have the highest proportion of LSS-dominated patches on the landscape at the end of the study period (Fig. 3).

The effect of initial survivors and subsequent disturbance on diversity warrants further investigation. While we found that the structural diversity of the landscape (RI) increased with legacy level and disturbance frequency (Table 2), species diversity showed a more complex and scale-dependent pattern. Stand-level species diversity increased with an increasing level of remnants via a carry-over effect of the pre-disturbance LSS species (Fig. 3c). Higher fire frequencies, on the other hand, reduced species diversity via a negative selection of fire-prone LSS species (Fig. 3a, c). At the landscape scale, however, trade-offs between accelerated succession and increased fire severity modulated this effect. While our results indicate that the negative effect of increasing fire frequency on late-seral species and
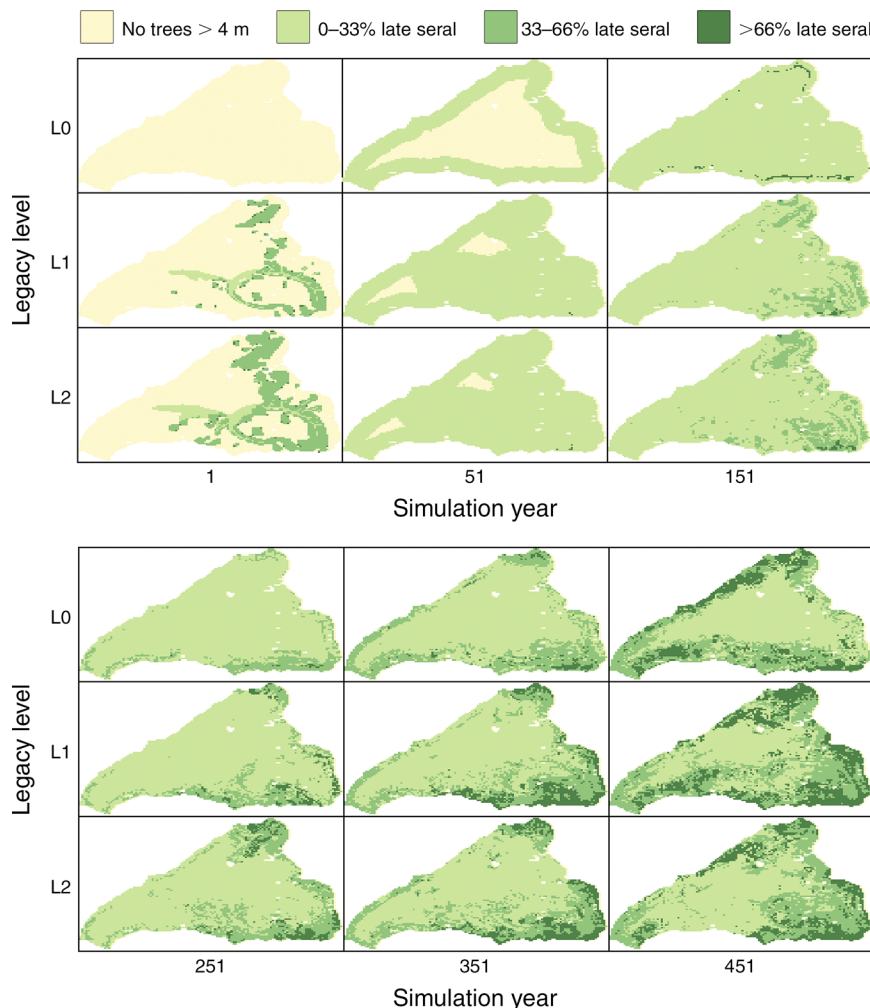
FIG. 2. Maps of the 6364-ha H. J. Andrews Experimental Forest landscape (grain: 100-m grid), showing seral stages for six points in time and three initial legacy levels (L0, no legacies; L1, remnant trees on 12% of the landscape; L2, remnant trees on 24% of the landscape). The values are cell-level means over 25 replicated simulations per series and assume the historically observed mean fire return interval of 262 years (scenario F1). Note that late-seral species proportions are calculated for stocked areas only (trees >4 m in height), and that the persistence of initial survivors beyond the starting year is masked by regenerating early-seral species in areas adjacent to remnant old-growth patches in the spatial aggregation to 100 × 100 m pixels. With regard to the persistence of remnant old-growth patches, see Appendix C: Fig. C1.

species diversity prevails also at the landscape scale, the effect of initial survivors on composition was significantly dampened at this scale (Fig. 3b, d). Overall we found that remnants increase the diversity of ecosystems both with regard to structure and composition. Yet our results also show a stronger effect of increased disturbance frequency on these indicators, with the potential to lastingly change species composition in favor of early-seral and more fire adapted species (e.g., Douglas-fir).

State changes in ecological phase space

Finally, we tested whether the ecosystem recovered to different phase space states in ecosystem structure, composition, and functioning in legacy and fire scenarios. A MANOVA over all legacy and fire scenarios

suggested that ecosystem states in the phase space of TEC, RI, and LSS were significantly different at the end of the 500-year study period ($P < 0.001$). More detailed analyses showed that, within a given fire regime, landscape trajectories for legacy scenarios L1 and L2 were converging over time (Fig. 4), and were no longer significantly different after 500 years (Table C3). This convergence over time is slow, however, particularly with regard to species composition, and subsequent disturbances further delay it. Overall, we found that different disturbance frequencies (F*) had a stronger impact on ecosystem state than different levels of disturbance remnants (L*). Scenario F0 was outside the envelope of F1 and F2 in all legacy scenarios (Fig. 4), indicating that a disturbance-free system is significantly different from systems that are periodically
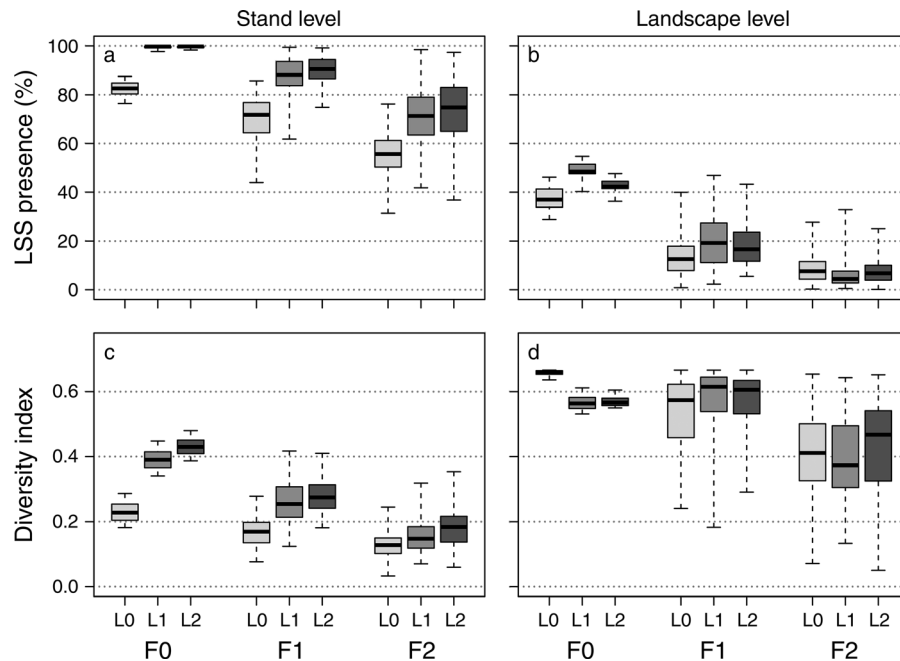
FIG. 3. Effect of initial legacy levels (L0, L1, L2) and subsequent fire scenarios (F0, F1, F2) on stand- and landscape-scale indicators of compositional diversity (years 401–500). (a) Presence of late-seral species >4 m height at the level of 100-m grid cells. (b) Proportion of the landscape dominated by late-seral patches (>66% of all individuals >4 m height are late-seral species). (c) Simpson index of diversity calculated from basal area shares of all tree species present (100 m grid cell level). (d) Landscape-level patch diversity derived by means of a Simpson index over three successional stages (early, mid, late seral). For scenarios F1 and F2, values over 25 replicated simulations are given.

disturbed (Table C3). Furthermore, a doubling of the historic fire return interval in scenario F2 resulted in a trend toward divergent ecosystem states compared to the historic fire frequency scenario F1 in all legacy scenarios (Fig. 4), indicating that intensifying disturbance regimes could considerably change the structure, composition, and functioning of our study landscape.

DISCUSSION AND CONCLUSION

Legacy and resilience

We analyzed the recovery trajectories of a 6364-ha forest landscape by means of simulation modeling to infer the long-term influence of disturbance remnants on the resilience of the ecosystem. Speedy recovery from disturbance is often associated with high resilience in a system (i.e., engineering resilience, see also Virah-Sawmy et al. [2009], Letcher and Chazdon [2009]). Our simulations showed that disturbance remnants significantly accelerate recovery from large-scale, high-severity disturbance, and thus contribute to the resilience of forest ecosystems to disturbance. The main mechanisms via which legacies contributed to increased resilience were (1) a faster revegetation of the landscape with trees, with an accelerated recovery of primary production due to an earlier saturation of leaf area levels (see also Peters et al. 2013); (2) a faster rate of recovery of live C stocks on the landscape in combination with reduced losses of litter and soil C (see also Liu et al. 2011); (3) a "life boat"

function for disturbance-prone late-seral species, facilitating their spread into the post-disturbance early-seral forest, and increasing the tree species diversity at the landscape scale (see Turner et al. 1998); (4) a facilitation of diverse vertical structures, generating regeneration niches for shade-tolerant species and increasing resource utilization (see Seidl et al. 2012b, Hardiman et al. 2013); and (5) a contribution to increased spatial heterogeneity, facilitation of patch diversity, and a differentiated landscape mosaic while decreasing the propensity for early, high-severity reburns (see also Churchill et al. 2013).

However, our results also suggest that the legacy–resilience relationship is more complex than "more survivors = increased resilience." While stand-level species diversity, for instance, was positively influenced by an increasing legacy level, landscape-scale patch diversity showed a variable pattern (Fig. 3). This underscores that multiple levels of scale need to be considered in the assessment of resilience (Johnstone et al. 2010, Seidl et al. 2013). Furthermore, our simulations revealed significant interactions between initial survivors and subsequent fire severity (see also Johnstone et al. 2011). This indicates that factors fostering recovery (e.g., disturbance remnants) with regard to one aspect of ecosystems (e.g., TEC storage) at a particular temporal scale (e.g., short- to mid-term after disturbance) can have the opposite effect at a different time scale (e.g., long-term increase in fire severity with negative effects

on TEC). It is thus important to not only consider individual indicators of (short-term) recovery but to also assess effects on ecological resilience, i.e., the ability of the system to remain within and return to its stability domain when disturbed (Holling 1996). The legacy and fire scenarios analyzed here did not reveal tipping points with regard to the system state. We nonetheless found that in particular the impact of different fire regimes considerably alters the system. From our assessment of selected indicators of ecosystem structure, composition, and functioning it appears that different disturbance regimes hold the potential to send recovery to a significantly different system state. These model-based predictions should be further tested using observational data and experimentation in the future, with a particular focus on possible modulating effects of climatic changes.

Study design and implementation

The complex long-term interactions between initial survivors and subsequent disturbance regimes at different temporal and spatial scales demonstrate the need for tools that are able to capture such interactions. The iLand model used here simulates vegetation dynamics at the individual-tree level, and fire severity and vegetation responses to disturbance are an emergent property of the fully integrated fire module (Appendix A). The use of a simulation approach thus not only allowed us to control for the impact of subsequent disturbances on the legacy effect, but also enabled us to investigate dynamic interactions of vegetation and disturbance dynamics. Furthermore, simulation modeling fosters a long-term perspective in studying forest ecosystems. While previous empirical studies document legacy effects several decades after a disturbance (e.g., Gough et al. 2007, Lorente et al. 2013), we here show that such effects can persist for centuries, and that persistence varies for different ecosystem properties. These findings are consistent with the empirical evidence for succession in the long-lived forests of the western Cascades. For example, Spies and Franklin (1991) found that multivariate components of structure and composition in Douglas-fir/western hemlock forests continued to change with age for 500 years in a chronosequence of stands.

Simulation studies are, however, only as good as the model they are relying on. The simulation tool used here was thoroughly tested for the HJA in previous studies (Seidl et al. 2012a, b). Tests regarding the ability to simulate realistic fire regimes at HJA also yielded promising results (Appendix B). Not least, the levels and dynamics of the selected indicators analyzed in this study conform to data and previous analyses at HJA (Smithwick et al. 2002, Harmon and Franklin 2012). Notwithstanding these successful model evaluation exercises, the simulated responses are limited by the processes and interactions implemented in the model, reflecting a, in parts, still-incomplete system understanding. With regard to the simulation of fire size, for
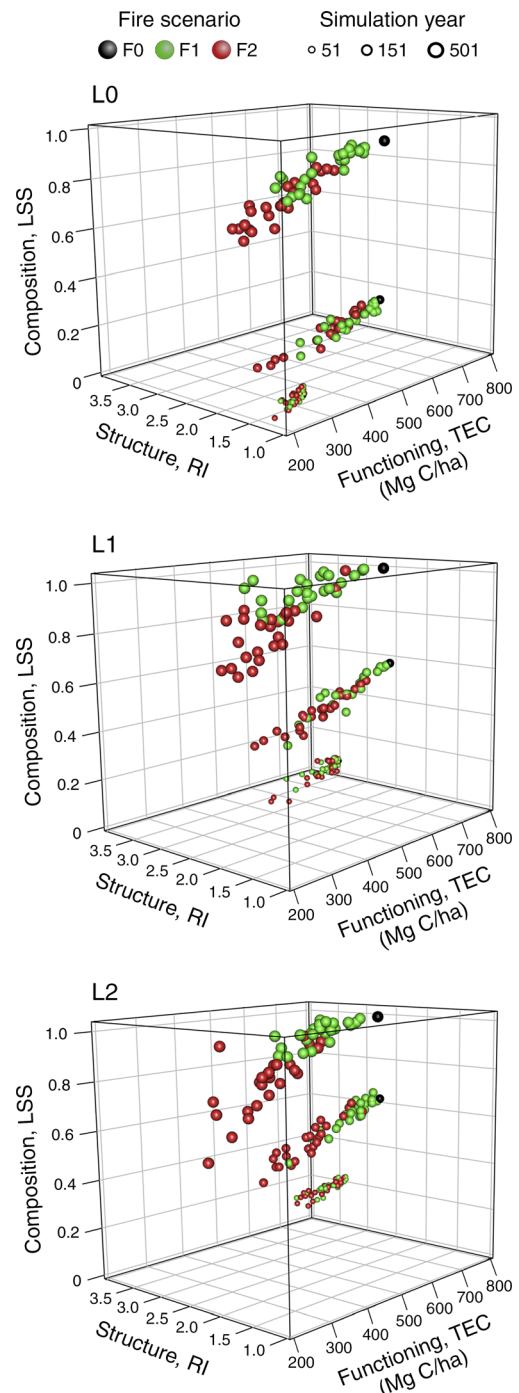

Fig. 4. Simulated system state in the phase space of the three dimensions ecosystem structure, composition, and functioning, represented by rumple index (RI, dimensionless), presence of late-seral species (LSS, proportion of landscape), and total ecosystem carbon (TEC, Mg C/ha), respectively. Panels show three points in time (years 51, 151, 501, differentiated by sphere size) and three initial legacy scenarios (L0, no legacies; L1, historic level of survivors; L2, increased level of survivors), with colors distinguishing scenarios of subsequent fire frequency (black, no fire [F0, 1 replicate]; green, historic fire frequency [F1, 25 replicates], red, increased fire frequency [F2, 25 replicates]).

instance, iLand follows a data-driven approach rather than accounting for the processes influencing fire size explicitly. This means that maximum fire size is currently constrained by the historically reconstructed fire size distribution in the simulations, and dynamic interactions of fire frequency, vegetation, and weather with fire size are neglected, precluding potentially important feedback mechanisms (see Wimberly and Liu 2014).

Our assessment is also limited by the constraint that the model only allows currently occurring tree species at HJA (see Seidl et al. [2012a, b] for details). A profound change in system state in response to increased disturbance frequency, e.g., to mixed conifer forests of fire-adapted species or an open savanna-type system, was thus precluded in our analysis (but see, e.g., Bachelet et al. 2003). Furthermore, the current version of iLand does not include early-seral shrub species such as *Ceanothus* ssp., which have the ability to limit tree regeneration after disturbance, but also influence post-disturbance biogeochemistry via their ability to fix atmospheric nitrogen. Harvey and Holzman (2014), for instance, found alternative successional pathways to be closely linked with shrub cover in their 14-year analyses of post-disturbance succession in a California closed-cone pine forest ecosystem. Finally, while our compositional metric of recovery focused on late successional species it is important to also note that the open, species rich early stages of succession play an important role in ecosystem diversity and function (Swanson et al. 2011).

An important insight for landscape modeling derived from our study is that models disregarding disturbance remnants are likely to produce unrealistic patterns of vegetation composition and distribution (cf. the control scenario L0 in Fig. 2; see also Turner et al. [1998]). We found that while remnant trees on 12% of the landscape facilitated recovery considerably over the no-legacies scenario, a further doubling of the level of survivors had diminishing effects. In this regard it has to be noted that the assumed spatial patterning of remnant patches, which is important for the spatially explicit simulation of seed dispersal and recolonization in iLand, did not differ significantly between L1 and L2 (see Fig. 2). It would thus be interesting to not only evaluate the effect of different levels of survivors but also the role of their spatial distribution (e.g., clustered in patches vs. dispersed) more closely in the future (see, e.g., Churchill et al. 2013). We hypothesize that more dispersed patches of survivors would accelerate successional development, and reduce the persistence of legacy effects particularly for late-seral species presence. Here it must be noted that the spatial development of colonization (Fig. 2) is not only driven by the distribution of initial disturbance survivors, but is also contingent on the delineation of our study landscape. For example, the assumption of seed input from the outside of the landscape creates a clear borderline effect in the simulations. This essentially assumes that the perimeter of the 1500 burn is identical with our landscape boundaries, which is unrealistic. A boundary effect also occurs for simulated wildfires. It would have been preferable to use an explicitly simulated buffer around the core landscape; however, this was precluded by a lack of data for the areas outside the HJA.

Implications for forest ecosystem management

A number of aspects of this study have relevance for forest ecosystem management. First, forests are remarkably resilient ecosystems when they operate within the climate and disturbance regimes to which their component species are adapted. The Douglas-fir/western hemlock forests studied here are adapted in many ways to large-scale high severity fire (such as the 5600-ha high-severity burn in a 6364-ha landscape serving as the starting point for this study), and recovered in time frames that are consistent with the life history characteristics of these long-lived species in our simulations. What is frequently viewed as "catastrophic" by humans thus does not necessarily equate to an ecological calamity, especially when viewed over the extended time frames of forest succession (see also Dale et al. 2005, Müller et al. 2008, Turner 2010). One reason for this resilience is that natural disturbances are rarely complete, especially over large landscapes in diverse mountainous terrain (i.e., disturbance severity is typically <100% [Foster et al. 1998]), and, as shown here, the remaining survivors make an important contribution to the rate and pattern of recovery. In the context of disturbance management this underscores the importance of retaining legacies after disturbance, and balancing the economic benefits of salvage logging (which often removes remnant live trees) with the ecological effects of legacies (Lindenmayer et al. 2008). In this regard, our simulations indicate that disturbance survivors vastly increase the rates of recovery for all three studied ecosystem indicators. However, we also found a decreasing resilience effect of a doubling of the remnant area, which indicates that the spatial distribution of legacies might increase in importance as legacy levels are increased. These ideas are also reflected in the emerging practice of the retention forestry concept, which aims to retain a minimum of 5–10% legacy trees, and suggests an increasingly dispersed pattern of remnants with increasing size of the management unit (Gustafsson et al. 2012).

Despite finding high resilience and identifying mechanisms contributing to it in our simulations our findings also contain a cautionary note for forest management under rapidly changing environmental conditions. As a result of climate change, an increase in disturbance frequency and severity is expected for many parts of the world (Seidl et al. 2009, Rogers et al. 2011, Westerling et al. 2011). Our simulations indicate that a shortened fire return interval would substantially alter recovery trajectories and change the structure, composition, and functioning of the studied forest ecosystem. More

specifically, our analysis suggests that a doubling of the historic fire frequency in forest ecosystems with large amounts of biomass and fuel will reduce long-term ecosystem C storage by >10%, and shift structure and composition to new states significantly different from those under historical disturbance regimes. Moreover, we found that such changes in the disturbance regime have the potential to offset positive effects of legacy and retention. In areas where profound disturbance changes are expected, managers may thus want to consider more proactive adaptive actions, such as to reduce fuel levels and promote structures and species (e.g., large fire-resistant conifers) that will be better adapted to an expected future fire regime, while at the same time managing landscapes in ways that allow ecologically and socially important old-growth forests and associated species to persist as long as possible (Spies et al. 2006). Considering the mounting (environmental and social) pressures on forest ecosystems it is increasingly important to maintain and, where possible, foster their resilience and adaptive capacity. Remnant patches of trees are one important mechanism in this regard, facilitating the recovery of ecosystems after disturbance, and supporting functional, structural, and compositional continuity.

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Supplemental Material

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/14-0255.1.sm

Data Availability

Data associated with this paper have been deposited in the H. J. Andrews Experimental Forest Long-Term Ecological Research data repository: http://andrewsforest.oregonstate.edu/lter/data/abstract.cfm?dbcode=TP125