

Diameter limits impede restoration of historical conditions in dry mixed-conifer forests of eastern Oregon, USA

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Abstract. The U.S. Forest Service is reconsidering policies that limit the size of trees that can be removed in the course of restoration treatments in dry forests of eastern Oregon. To evaluate the effects of diameter limits on the ability of managers to meet restoration objectives, we used an existing network of long-term research plots to summarize historical and contemporary structure and composition of mixed-conifer forests within a one million-ha study area in eastern Oregon. Then, we used a novel thinning simulation procedure to quantify the degree to which thinning using different diameter limits restored stands to historical conditions. Contemporary mixed-conifer forests within the study area are significantly denser, have more basal area, and have a greater proportion of shade-tolerant species than historical conditions. Our simulations of thinning under current policy that prohibits cutting of trees ≥ 53 cm show that a quarter of mixed-conifer stands cannot be restored to within the historical range of basal area or density. Those stands that could be restored to within historical basal area ranges still had a substantially higher component of shade-tolerant trees than historical stands. Permitting larger shade-tolerant trees to be removed allowed restoration of all or most of stands to within historical structural and compositional ranges. Forest conditions in the late 1800s may not necessarily provide the best template for management because climate and disturbance projections suggest that eastern Oregon forests will be less well suited to shade-tolerant species in the future. Adapting stands to future conditions will require robust monitoring of forest structural and compositional response to restoration treatments.

Key words: 21-inch rule; climate change adaptation; co-production of research; diameter limits; Douglas-fir; eastside screens; grand fir; ponderosa pine; restoration; shade-intolerant; shade-tolerant; simulations; thinning; western larch; western white pine.

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INTRODUCTION

Policies that prohibit cutting of trees larger than a certain diameter were widely adopted by U.S. Forest Service (USFS) managers during the 1990s to satisfy social and legal demands to

conserve old-growth habitat (Abella et al. 2006). In eastern Oregon, USFS policy prohibits cutting live trees ≥ 53 cm diameter at breast height (DBH). This policy, commonly referred to as the “21-inch rule,” was adopted in 1995 as an interim measure for one year pending adoption of a new

ecosystem management plan for eastern Oregon national forests (USDA 1995). Scientists and managers have long recognized that the 21-inch is an imperfect tool for protecting old-growth trees because it fails to protect small old trees and prevents removal of young but large trees that compete with old trees (Merschel et al. 2019). However, no replacement policy process has ever been completed, and the 21-inch rule remains agency policy to the present day, more than two decades past its intended expiration.

Since adoption of the 21-inch rule, climate change has accelerated wildfire-, insect-, and drought-related mortality of old-growth trees in eastern Oregon and throughout the American West (Littell et al. 2009, van Mantgem et al. 2009, Reilly and Spies 2016, Reilly et al. 2017). An important old-growth conservation strategy is mechanical thinning of stands to reduce competition around old-growth trees and make them more resistant to uncharacteristically severe drought, insect, and fire effects (Fettig et al. 2007, Millar and Stephenson 2015). An increasing number of shade-tolerant trees that recruited into eastern Oregon forest stands in the absence of fire are ≥ 53 cm, and scientists and managers are concerned that the 21-inch rule limits the ability to adapt stands to future climate and disturbance stressors (Stine et al. 2014, Johnston 2017, Spies et al. 2018).

In this paper, we report the results of a simulation study co-produced in partnership with USFS managers and collaborative stakeholder groups to determine the degree to which timber harvest using different diameter limits can restore historical structure and composition within a large forest landscape in eastern Oregon. We began by summarizing dendroecological reconstructions of historical forest structure and composition. Then, we simulated thinning using a variety of diameter limits on cutting and compared the resulting structure and composition to historical reconstructions. This investigation is timely because the USFS recently launched a National Environmental Policy Act (NEPA) planning effort that will adapt the 21-inch rule to reflect the best available science about the effects of diameter limits on forest restoration efforts (USDA 2020). Restoring historical structural and compositional configurations is a common goal of managers and stakeholder groups because

historical forests are thought to be more resilient to a wide range of climate and disturbance stressors than contemporary forests (Jackson and Hobbs 2009, Franklin et al. 2018, Merschel et al. 2019).

Cutting of larger trees is controversial, particularly in mixed-conifer stands with complex structure and a wide range of different tree species and age classes (Blicharska and Mikusiński 2014, Franklin et al. 2014). Co-production of research involving university scientists, managers, and stakeholders about the effects of controversial management actions like cutting of larger trees has the potential to build social license for management, increase the capacity of collaborative governance structures, and accelerate the pace and scale of forest restoration treatments (Butler et al. 2015, Urgenson 2017). We intend for this use-inspired research to provide managers and stakeholders insights that will assist in the development of socially acceptable, legally defensible, and scientifically sound strategies for conserving old-growth within mixed-conifer forests of eastern Oregon (Keeler et al. 2017).

METHODS

Research was conducted within mixed-conifer forests stands across the Ochoco and Malheur National Forests of eastern Oregon, the ancestral homeland of the Northern Paiute, Cayuse, and Umatilla people. We limited our historical reconstructions and simulation analysis to mixed-conifer stands because of the strong interest on the part of USFS managers and collaborative partners in developing silvicultural strategies for this forest type (Lindsay and Johnston 2020). Mixed-conifer forests in this study area contain both shade-intolerant western larch (*Larix occidentalis*) and ponderosa pine (*Pinus ponderosa*) and relatively shade-tolerant Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*; Simpson 2007). Following previous research and Forest Service planning documents, we defined mixed-conifer stands as all grand fir potential vegetation types identified by plant association guides (Johnson and Clausnitzer 1992). Mixed-conifer forests, which are found on higher elevation sites with deeper ashy soils, make up ~40% of the total forested area of our 1.03 million-ha study area (Fig. 1).

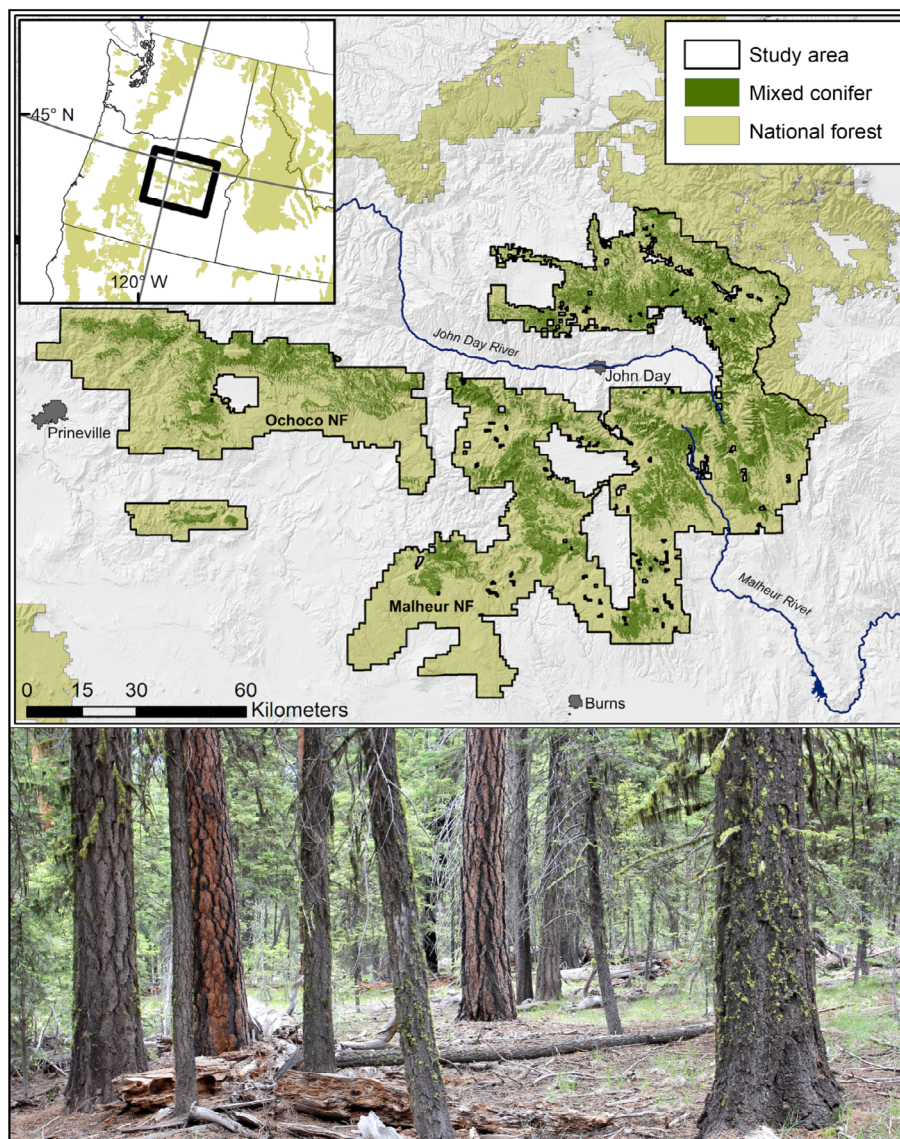


Fig. 1. Map of the study area and photograph of a representative mixed-conifer forest within one of the stands where simulated thinning occurred (the Elk 16 planning area on the Malheur National Forest).

We began by summarizing historical structure and composition in 17 plots that fell within mixed-conifer forests from a network of 35 dendroecological reconstruction plots established in the course of past research. As described in previously published work, these reconstruction plots were located in unmanaged stands using random stratified selection procedures to ensure sampling intensity reflected the extent of different forest types (Johnston 2017, Johnston et al.

2018). Reconstructions of historical conditions were accomplished by coring all live trees and sawing partial cross sections from all dead trees within each 0.1-ha circular plot. These samples were visually crossdated, and each tree ring was measured to 0.001 mm precision and converted to basal area increment. Historical tree basal area was estimated as the sum of basal area established prior to a reference year of 1880 after accounting for differences in bark thickness over

time, different sampling heights on tree boles, and the shrinkage of wood samples from water loss. Historical forest density was estimated as the sum of all live and dead trees present in plots that were ≥ 10 cm DBH in 1880. Reconstructions for the full range of forest types within the study area were first reported in Johnston et al. (2018) and Johnston (2017), which contain more detail about methods and accuracy of reconstructions.

We used 1880 as a reference year because the last fire that occurred in most mixed-conifer stands within the study area occurred between 1880 and 1900 and because heavy grazing that altered fire patterns began in the 1870s (Johnston et al. 2017). We bootstrapped 95% confidence intervals for mean historical basal area and forest density calculated from reconstruction plots, and then compared those historical estimates with 95% confidence intervals for mean basal area and density of trees ≥ 10 cm from 336 0.1-ha contemporary long-term monitoring plots that fell within mixed-conifer forests. These long-term monitoring plots were randomly located within randomly selected 3000–24,000-ha NEPA planning areas found across the Malheur and Ochoco National Forests. These plots, which were measured between 2015 and 2018, are designed to quantify changes to forest structure and composition that result from restoration treatments and natural disturbances and provide an unbiased estimate of contemporary forest conditions across the study area. Most reconstruction plots were located in the immediate vicinity of contemporary monitoring plots or in nearby stands

and were similar with respect to slope, elevation, aspect, and plant association (Table 1).

We conducted thinning simulations on trees within contemporary monitoring plots. We constructed 25 composite forest stands that were 1 ha in size by randomly drawing with replacement from among a pool of contemporary plots found within each planning area for a total of 200 composite stands. Simulated thinning was designed to reduce basal area within these stands to between 11 m²/ha and 16 m²/ha. We selected this basal area range because it is slightly wider than basal area targets for typical thinning operations within the study area and we wanted to be conservative about drawing conclusions about the effects of different diameter caps on restoration objectives at a landscape scale. This basal area range encompasses the higher range of confidence intervals for estimates of historical stand basal area, ensuring that we do not overstate the degree to which thinning under different diameter caps fails to restore historical conditions.

Modern restoration thinning operations cannot be simulated simply by removing random trees. Typical silvicultural prescriptions within the study area call for a range of young and mature trees of different species to be cut, but the objective is to thin from below, preferentially removing most of the smaller and shade-tolerant trees before larger trees are cut to meet stand basal area targets. Selecting trees for removal in real-world thinning operation is thus partly a matter of chance but with the probability of a tree being removed significantly influenced by its size and species. To emulate these preferences for tree removal within our simulation framework, we assigned harvest probabilities to different tree species and size classes that reflect preferences for removal found in USFS silvicultural prescriptions (see, for instance, USDA 2018; Table 2).

We developed six different diameter limit scenarios with input from USFS silviculturists and members of local collaborative stakeholder groups. These scenarios ranged from a strict 53 cm diameter cap on cutting for all species (current USFS policy, i.e., the 21-inch rule) to a scenario in which no diameter cap was applied and the only constraint on simulated cutting was harvest probabilities. Intermediate scenarios applied progressively larger diameter caps (Table 3). The tight cap scenario applied slightly

Table 1. Plant associations of mixed-conifer plots used in historical reconstructions and simulated thinning.

Plant association	Reconstruction plots (%; <i>n</i> = 17)	Contemporary plots (%; <i>n</i> = 336)
Grand fir/pine grass (<i>Calamagrostis rubescens</i>)	35	35
Grand fir/twinflower (<i>Linnaea borealis</i>)	29	21
Grand fir/elk sedge (<i>Carex geyeri</i>)	29	20
Grand fir/grouse whortleberry (<i>Vaccinium scoparium</i>)	6	10
Other	0	14

Note: No other plant associations accounted for more than 2% of the plots analyzed.

Table 2. Tree removal probabilities applied to all simulated thinning scenarios.

Species	Common name	Code	Removal probability			
			13–25 cm	26–38 cm	39–51 cm	>52 cm
<i>Abies grandis</i>	Grand fir	ABGR	0.95	0.85	0.75	0.55
<i>Pseudotsuga menziesii</i>	Douglas-fir	PSME	0.80	0.70	0.60	0.40
<i>Pinus ponderosa</i>	Ponderosa pine	PIPO	0.50	0.20	0.05	0.01
<i>Larix occidentalis</i>	Western larch	LAOC	0.10	0.05	0.01	0.01
<i>Pinus contorta</i>	Lodgepole pine	PICO	0.95	0.80	0.15	0.01
<i>Juniperus occidentalis</i>	Western juniper	JUOC	0.95	0.90	0.85	0.01
<i>Picea engelmannii</i>	Engelmann spruce	PIEN	0.75	0.60	0.40	0.30
<i>Cercocarpus ledifolius</i>	Curl-leaf mtn. mahogany	CELE	0.01	0.01	0.01	0.01
<i>Pinus monticola</i>	Western white pine	PIMO	0.01	0.01	0.01	0.01

Table 3. Simulated thinning scenarios.

Scenario	Diameter cap (cm)								
	ABGR	PSME	PIPO	LAOC	PICO	JUOC	PIEN	CELE	PIMO
21-inch rule	53	53	53	53	53	53	53	53	53
Tight cap	64	64	53	53	64	64	76	13	13
Loose cap	76	76	64	64	64	64	76	13	13
Shade-intolerant cap	...	...	64	64	64	64	76	13	13
Minor species cap	...	...	...	...	64	64	76	13	13
No cap	...	...	...	...	...	...	...	...	...

'...' indicates that there is no diameter cap for that scenario.

larger diameter caps on cutting of shade-tolerant species and the same diameter cap as current policy on shade-intolerant species. The loose cap scenario applied somewhat higher diameter caps than the tight cap scenario. A shade-intolerant cap scenario only applied loose diameter caps to shade-intolerant species or species that are relatively rare (i.e., lodgepole pine) or declining in abundance (i.e., western white pine). A minor species cap only applied loose diameter caps to rare/declining species. Given that the Forest Service is currently considering policy change that would eliminate the 21-inch in favor of looser caps or no diameter cap, the range of scenarios we evaluate represents the full range of reasonable policy alternatives.

The custom thinning simulated code we wrote for R version 3.6.1 (R Core Team 2020) selected trees for removal within each 1-ha composite stand by comparing the assigned harvest probability for each tree to a randomly generated value from a uniform distribution between zero and one. If the randomly generated number was lower than the probability of harvest, and the tree was

smaller than the established diameter cap, the tree was cut, or removed from the data set. This procedure was applied to all trees within each composite stand until one of two outcomes was reached. First, stand basal area reached 11 m²/ha to 16 m²/ha. Second, the simulation failed when stand basal area could not be cut below 16 m²/ha because the only trees left available to cut were above any given diameter limits. We calculated the proportion of failed simulations and summarized average residual structure and composition of all stands in which the simulation achieved the target basal area (Fig. 2).

RESULTS

Dramatic change in the structure and composition of mixed-conifer forests occurred between the historical reference (1880) and contemporary (2015–2018) periods. Average stand basal area in contemporary plots was 149% greater than average stand basal area in reconstruction plots. Density of trees >10 cm in contemporary plots was 210% greater than in reconstruction plots. There

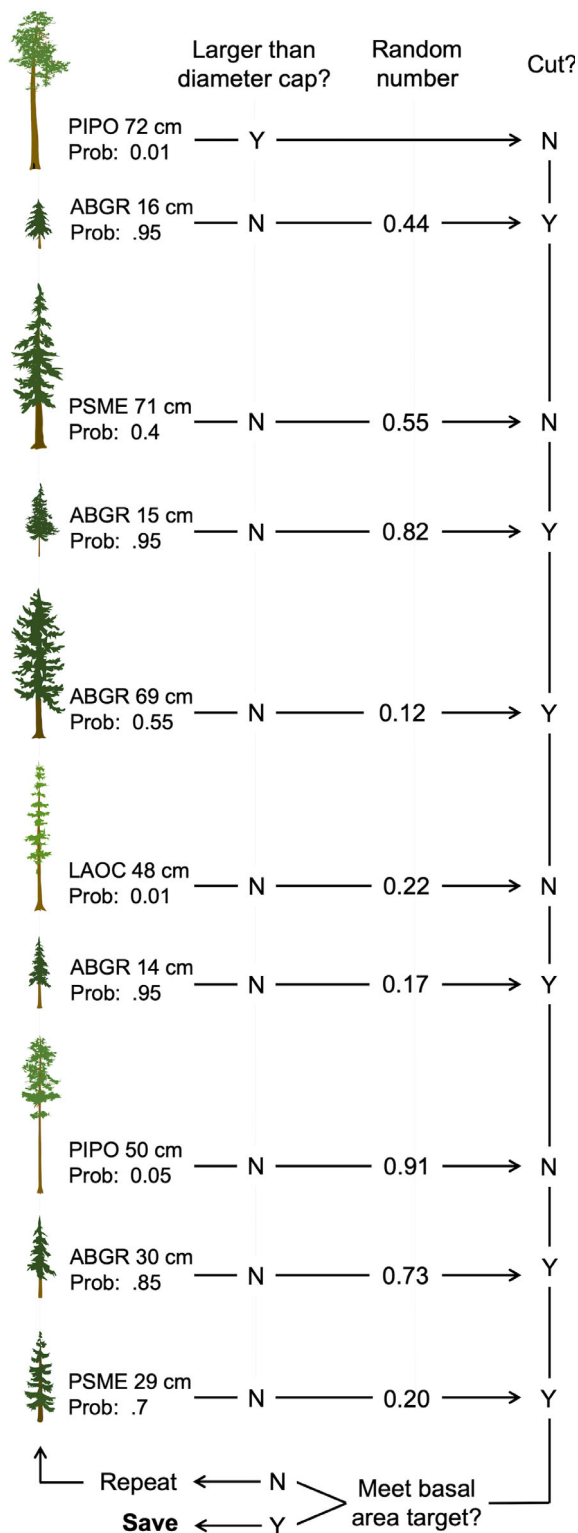


Fig. 2. Simulation procedures. This figure illustrates a

were 16.5 trees/ha that were ≥ 53 cm in reconstruction plots in 1880 and 28.3 trees/ha that were ≥ 53 cm in contemporary plots in 2015–2018, although there was slight overlap in 95% confidence intervals for historical and contemporary estimates of trees of this size class (Fig. 3). There were equally dramatic shifts in species composition over time. Relatively shade-tolerant Douglas-fir and grand fir made up 8% and 14%, respectively, of historical mixed-conifer basal area, and 19% and 45%, respectively, of contemporary stands. Shade-intolerant ponderosa pine made up 45% of historical mixed-conifer stand basal area and 25% of basal area of contemporary stands. Shade-intolerant western larch made up 26% of basal area of historical stands and only 8% of basal area of contemporary stands. Western white pine accounted for 6% of historical stand basal area but only 0.03% of contemporary stand basal area.

Simulated thinning under six diameter limit scenarios resulted in stands with somewhat similar structural characteristics (Table 4, Fig. 4). Residual forest density for all scenarios ranged from 95 trees/ha to 105 trees/ha, which were slightly below historical densities because thinning from below cutting preferences resulted in basal area targets being met through retention of larger rather than smaller trees. Predictably, the 21-inch rule scenario resulted in retention of the greatest numbers of trees ≥ 53 cm (24 trees/ha), which is at the upper limit of the historical density of trees of this size class. Intermediate diameter cap scenarios and the no diameter cap scenario resulted in retention of approximately

(Fig. 2. continued)

small part (ten trees) of a simulated thinning procedure for a composite 1 ha stand thinned under the shade-intolerant cap scenario. Tree removal probabilities (“Prob”) are designed to emulate preferences for tree removal found in USFS silvicultural prescriptions. If a random number generated by the simulation procedure is lower than the probability for tree removal, then the tree is cut or removed from the dataset. Removal probabilities are all that govern simulated cutting in the no diameter cap thinning scenario. Abbreviations are LAOC, *Larix occidentalis* (western larch); PIPO, *Pinus ponderosa* (ponderosa pine); PSME, *Pseudotsuga menziesii* (Douglas-fir); and ABGR, *Abies grandis* (grand fir).

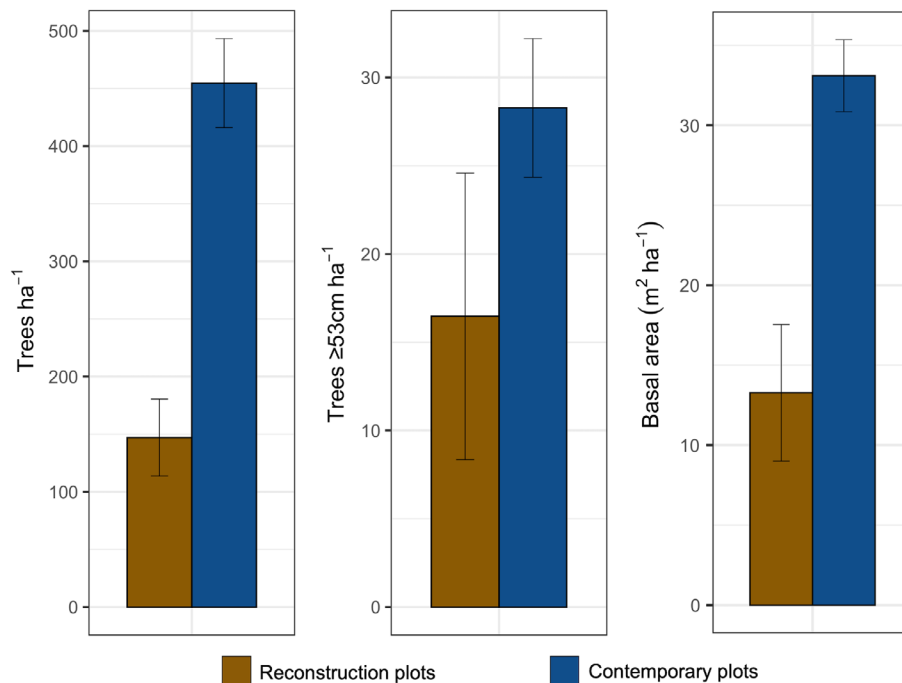


Fig. 3. Historical and contemporary forest structure based on data from mixed-conifer reconstruction plots ($n = 17$) and contemporary monitoring plots ($n = 336$). Historical structure was reconstructed for the year 1880. Contemporary structure was measured in 2015–2018. Error bars represent 95% confidence intervals for the estimates (see Methods).

Table 4. Average structure and composition values for historical and contemporary plots and average structure and composition results from all thinning simulations under each scenario.

	Density Trees/ha	Density large trees Trees ≥ 53 cm/ha	Basal area m ² /ha	Simulation failure % stands	Basal area proportion				
					LAOC	PIPO	PSME	ABGR	Other
Historical (1880)	147 ± 33	16.5 ± 8.1	13.3 ± 4.3	—	0.26	0.45	0.08	0.14	0.06
Contemporary (2015–2018)	455 ± 39	28.3 ± 4.0	33.1 ± 2.3	—	0.08	0.25	0.19	0.45	0.03
21-inch rule	95.1	23.6	14.3	23	0.10	0.46	0.15	0.29	0.01
Tight cap	99.8	19.0	13.9	18.5	0.11	0.50	0.14	0.24	0.01
Loose cap	102.1	17.2	13.8	12	0.12	0.52	0.13	0.21	0.02
Shade intolerant cap	102.0	17.3	13.6	2.5	0.12	0.59	0.11	0.16	0.02
Minor spp. Cap	105.3	17.3	13.6	0	0.12	0.56	0.13	0.17	0.02
No cap	103.6	17.0	13.4	0	0.12	0.56	0.13	0.17	0.02

Note: A simulation failure indicates that a stand could not be thinned to within the basal area target under that thinning scenario (see text).

the same density of trees ≥ 53 cm (17/ha) as the mean historical density for trees of this size class. Residual stand basal area ranged from a mean of 14.3 m²/ha (21-inch rule scenario) to 13.4 m²/ha (no diameter cap scenario), all of which were the same or slightly higher than the historical mean basal area of mixed-conifer forests (Table 4).

The 21-inch rule scenario resulted in residual stands in which an average of 44% of residual basal area consisted of shade-tolerant species (grand fir and Douglas-fir) and 56% shade-intolerant species (larch and ponderosa pine). Looser diameter limit scenarios or the no cap scenario better approximated historical conditions, with

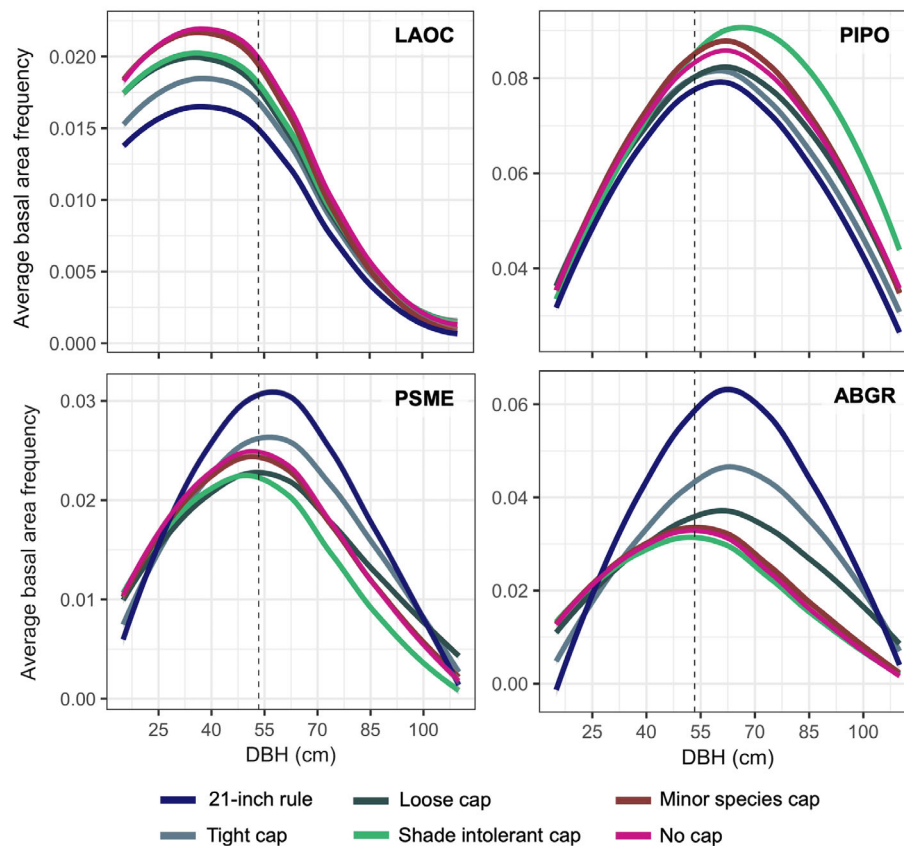


Fig. 4. Average basal area in diameter bins for four major species following simulated thinning under six different diameter cap scenarios. Dashed vertical line indicates 53 cm (21 inches). Structural outcomes of different simulations were relatively similar, except that less shade-tolerant grand fir could be cut under the 21-inch rule scenario. Abbreviations are LAOC, *Larix occidentalis* (western larch); PIPO, *Pinus ponderosa* (ponderosa pine); PSME, *Pseudotsuga menziesii* (Douglas-fir); and ABGR, *Abies grandis* (grand fir).

as little as 27% of residual basal area in shade-tolerant species, which was close to historical shade-tolerant basal area (Table 4, Fig. 5). An important difference between scenarios was in the proportion of stands that could not be cut to within basal area targets. Almost a quarter of stands could not meet basal area targets under the 21-inch rule scenario, while all or almost all stands could be successfully treated if there was no diameter cap or if loose diameter caps were only applied to shade-intolerant species (Table 4).

DISCUSSION

The failure of simulations under the 21-inch rule scenario to thin a quarter of stands to within

the historical range of variability has important implications for managers' ability to meet restoration objectives and adapt forests to future change. Approximately 20% of mixed-conifer forests in the study area are found in wilderness or inventoried roadless areas where mechanical thinning is generally prohibited. Thinning is not permitted in between half- and three-quarters of most planning areas because of legal and operational constraints. If an additional quarter of stands that would otherwise be available for thinning are not restored to structural and compositional targets, it may be difficult to create conditions resilient to drought and contagious disturbances like wildland fire at a landscape scale (Ager et al. 2007, Finney et al. 2008, McDowell and Allen 2015).

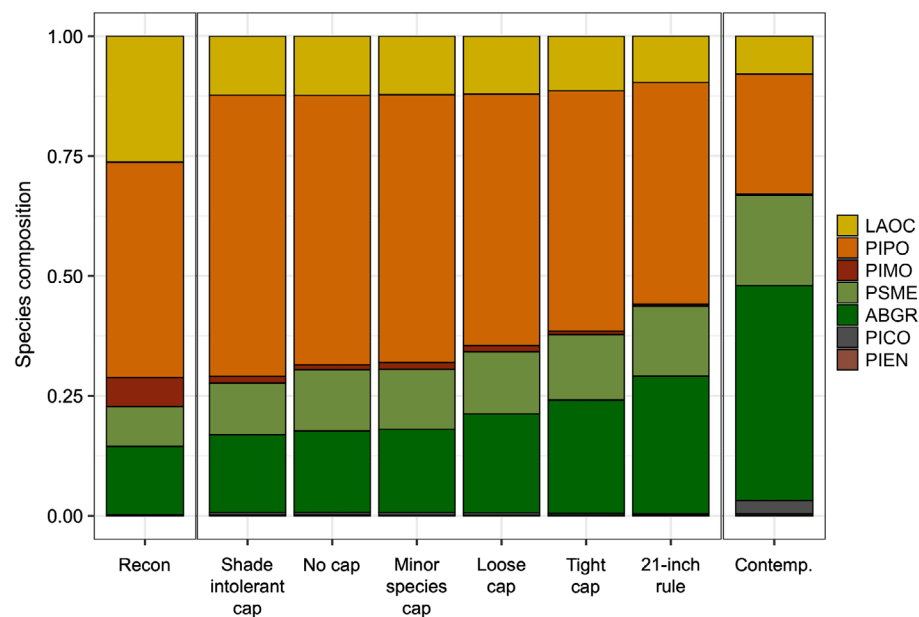


Fig. 5. Average reconstructed historical species composition (far left), average contemporary species composition (far right), and average species composition following simulations under six different diameter cap scenarios. Abbreviations are LAOC, *Larix occidentalis* (western larch); PIPO, *Pinus ponderosa* (ponderosa pine); PSME, *Pseudotsuga menziesii* (Douglas-fir); ABGR, *Abies grandis* (grand fir); PIMO, *Pinus monticola* (western white pine); PICO, *Pinus contorta* (lodgepole pine); and PIEN, *Picea engelmannii* (Engelmann spruce).

The conclusions of this study about the ability of thinning under different diameter cap scenarios to restore historical conditions rests on the assumption that we accurately represent the historical range of variability in forest conditions. Although our estimates of historical structure and composition rely on a relatively small sample size (17 dendroecological reconstruction plots), these plots were located so as to replicate the full range of environmental conditions within the study area (Johnston 2017). The estimates of the historical range of variability presented in this paper are well supported by research from within or nearby our study area, including other dendroecological reconstructions of the Ochoco National Forest (e.g., Merschel et al. 2014), analysis of General Land Office records within the Malheur National Forest (e.g., Johnston et al. 2018), early timber 20th century inventories from the east slope of the Cascades (e.g., Hagmann et al. 2014), and historical accounts within the study area (e.g., Langille 1906). As shown in previous work, validation of our estimates from dendroecological reconstruction plots by other

studies using a wide range of methods provides a high degree of confidence in the historical range of variability we report as a target for restoration efforts (Johnston 2017, Johnston et al. 2018).

Although restoration targets are informed by historical reconstructions (Lindsay and Johnston 2020), post-treatment stand basal area targets within the study are also designed to reduce mortality related to intra-tree competition for resources, which often involves thinning stands to lower basal areas than our basal area targets for simulated thinning (e.g., USDA 2018). The relatively broad range of post-treatment basal area targets adopted for this study (11 m²/ha to 16 m²/ha) are designed to account for the full range of historical conditions we reconstructed and to ensure that we do not overstate the degree to which strict diameter caps on thinning limit the ability of managers to meet restoration objectives. Our thinning simulations are designed to inform managers about the effects of thinning at very broad spatial scales. Individual silvicultural prescriptions that consider site-specific conditions and other management

objectives will be necessary to meet stand-scale restoration objectives.

Restoration targets should not be informed strictly by historical conditions because of changing climate, different land use practices, spread of invasive species, and other considerations (Keane et al. 2009, Kerns et al. 2020). However, future climatic conditions in eastern Oregon are projected to be even less conducive to extensive shade-tolerant tree cover than the historical past (Kerns et al. 2018). Global climate models predict a hotter and drier summer climate in eastern Oregon which is expected to lead to more extensive burned area and larger patches of high severity fire (Mote and Salathe 2010, Littell et al. 2018, Halofsky et al. 2020).

The current structure and composition of mixed-conifer forests are likely maladapted to projected future changes in climate and disturbance regimes. Paleoecological studies from the inland northwest document shifts toward closed canopy *Abies* forests during moister periods with less fire, while ponderosa pine was more extensive during warmer periods with more fire (Long et al. 2011, Whitlock et al. 2011). Shade-tolerant species have greater leaf area and transpire more water, meaning that the same basal area of Douglas-fir or grand fir is associated with greater water use than equivalent area of shade-intolerant species like ponderosa pine (Gersonde and O'Hara 2005, Johnston et al. 2019). Ponderosa pine is also more drought tolerant than Douglas-fir or grand fir by virtue of greater stomatal sensitivity to increasing moisture stress (Lopushinsky 1969, Lopushinsky and Klock 1974). Relatively greater water use efficiency makes shade-intolerant species better adapted to more arid conditions that are projected for the future (Coops et al. 2005). Increases in stand basal area over the last century have reduced drought resistance in eastern Oregon (Voelker et al. 2019). A wide variety of studies have demonstrated that restoring historical competition dynamics, that is, significant reductions in stand basal area, can increase the resistance of stands to drought, insects, and fire disturbance effects associated with a warming climate in eastern Oregon and other dry forests of the western USA (Sohn et al. 2016, Vernon et al. 2018, Tepley et al. 2020, Westlind and Kerns 2020).

In summary, it is likely that management designed to adapt stands to future climate and disturbance regimes will necessitate lower basal

area, lower density, and an even greater proportion of shade-intolerant species than the late 1800s range of variability we reconstructed (Bradford and Bell 2017). In many stands, lowering basal area below the historical range of variability may help to restore the relative abundance of western white pine and western larch, two species that have declined dramatically since fire was excluded from mixed-conifer stands. Both species are light demanding and may require sizeable openings free of competition from shade-tolerant species in order to recruit to the overstory (Jain et al. 2004, Loehman et al. 2011).

The available evidence suggests that restoration of historical conditions is at worst an appropriate intermediate step toward climate change adaptation (Safford et al. 2012). This study demonstrates the value of a well-distributed network of long-term research plots in providing relevant information to managers and stakeholders within a co-production framework. Given uncertainty about the future, the best approach to adapting eastern Oregon forest may be an adaptive management framework that employs long-term monitoring programs to test the degree to which different thinning treatments can maintain trees of different sizes and species over time.

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