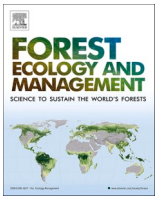
Forest Ecology and Management 561 (2024) 121814

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Ecological forestry treatments affect fine-scale attributes within large experimental units to influence tree growth, vigor, and mortality in ponderosa pine/white fir forests in California, U.S.

Christopher E. Looney [a,*], Emily G. Brodie [b,1], Christopher J. Fettig [a], Martin W. Ritchie [c], Eric E. Knapp [c]

[a] USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, USA
[b] USDA Forest Service, Pacific Southwest Research Station (ORISE Program), 3644 Avtech Parkway, Redding, CA 96002, USA
[c] USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA

ARTICLE INFO

Keywords:
Ecological forestry
Forest structure
Species mixture effects
Individual-tree modeling
Mixed-conifer forest
Forest restoration

ABSTRACT

Ecological forestry experiments typicaly use large treatment units and silvicultural prescriptions that commonly increase within-unit heterogeneity in structural complexity and species composition in large treatment units. Increased heterogeneity influences processes affecting tree responses (e.g., competition) that operate at the neighborhood-level, posing challenges to analysis and interpretation. To investigate whether examining within-unit heterogeneity offers a more meaningful evaluation of project success than comparing categorical treatment effects, we used 20-year data from the Goosenest Adaptive Management Area (AMA) ecological forestry experiment in northern California, U.S. Designed to evaluate management alternatives for reducing fuels and accelerating development of late-seral forest characteristics in ponderosa pine (*Pinus ponderosa*)/white fir (*Abies concolor*) mixed-conifer forests, the Goosenest AMA study consists of (1) an untreated Control, (2) a Big Tree treatment using thinning from below to favor retention of large trees of any species, (3) a Pine Emphasis treatment combining thinning from below with radial thinning to favor percent ponderosa pine while increasing structural complexity, and (4) a Pine Emphasis with Fire treatment with added post-thinning prescribed burns. Our objectives were to evaluate 1) how treatments affect within-unit variation in neighborhood competition, structural complexity, and tree species composition, and 2) whether categorical treatment effects versus within-unit variation in competition, complexity, and composition influence individual-tree basal area increment (BAI), vigor as indicated by live crown ratio (ΔLCR), and tree mortality. To accomplish this, we developed and compared a series of generalized linear mixed models. Our analysis included the first investigation into whether fuel-reduction treatments alter tree species mixture-effects in ponderosa pine/white fir mixed-conifer forests. We found that all treatments similarly reduced neighborhood competition relative to the Control. The two Pine Emphasis treatments promoted greater variation in neighborhood competition and higher Percent pine relative to the Big Tree treatment, consistent with restoration objectives. Reduced neighborhood competition improved both ponderosa pine and white fir BAI. Reduced neighborhood competition helped to offset or reverse crown vigor decline in ponderosa pine and white fir, respectively. Species-mixture effects were negative for both small and large ponderosa pine BAI. For white-fir, trees grew faster in neighborhoods with a higher percentage of pine but the probability of mortality increased. Categorical treatment differences consistently reduced ponderosa pine and white fir mortality, except for the Pine Emphasis with Fire treatment, which increased white fir mortality. Our findings suggest that restoring historical ponderosa-pine forest reference conditions could accelerate the development of fire-resistant ponderosa pine tree sizes and sustain large pine growth.

* Corresponding author.
E-mail address: christopher.looney@usda.gov (C.E. Looney).
[1] Current affiliation: California Department of Fire and Forestry, Grass Valley, CA

https://doi.org/10.1016/j.foreco.2024.121814
Received 2 August 2023; Received in revised form 18 January 2024; Accepted 26 February 2024
0378-1127/Published by Elsevier B.V.

1. Introduction

Effective silvicultural approaches for mitigating disturbance impacts while enhancing ecosystem services are needed to restore dry mixed-conifer forests in the western U.S. (Addington et al., 2018; North et al., 2009). Traditional silvicultural field experiments, which use small (e.g., <4 ha) relatively homogeneous plots to maximize uniformity (Curtis and Marshall, 2005), are inherently limited in their ability to address complex natural resource questions. Ecological forestry provides an alternative approach for testing the potential of altering the continuity, complexity, timing, and context of traditional silvicultural systems to achieve diverse objectives (Palik et al., 2020). To accomplish this, ecological forestry typically uses large experimental units that may encompass one or more stands and silvicultural prescriptions that commonly increase within-stand heterogeneity in structural complexity and tree species composition (Franklin et al., 2007; North et al., 2009), posing a challenge to formal comparison of cross-treatment effects. Examining within-stand variation in factors such as neighborhood competition, structural complexity, and tree species composition may offer more meaningful evaluations of project success than simply focusing on treatment-level averages (Puettmann et al., 2012; Roberts and Harrington, 2008).

Silvicultural thinning prescriptions commonly seek to reduce stand density. In the case of ecological forestry, prescriptions also often call for varying within-stand density (e.g., Knapp et al., 2012), blurring the traditional concept of stands as relatively homogeneous management units (O'Hara and Nagel, 2013). Varying within-stand density affects processes governing tree responses that are increasingly understood to operate in neighborhoods of proximate competitors (Coates et al., 2009; Pommerening et al., 2021). In particular, the influence of tree competition on individual-tree growth, vigor, and mortality is more effectively quantified in terms of the relative size and distances to neighboring trees (Larocque et al., 2012). Although tree performance is commonly more responsive to neighborhood conditions (Pommerening et al., 2021), there are key exceptions. These include disturbances such as forest insect outbreaks that overwhelm local variations in stand structure (Fettig et al., 2007) and water-limited forests, such as ponderosa pine (*Pinus ponderosa*)-Jeffrey pine (*Pinus jeffreyi*) forests in the western U.S., where local density may not influence the growth of large, old trees (Erickson and Waring, 2014; Hood et al., 2018).

In addition to altering density, ecological forestry prescriptions commonly emphasize enhancing structural complexity, defined as variation in the horizontal or vertical arrangement of forest biomass, to achieve multiple ecosystem benefits (Churchill et al., 2013; Palik et al., 2020). Enhancing structural complexity can provide habitat for a great range of animal, plant, and fungi species (Bauhus et al., 2009). The creation of gaps can reduce canopy bulk density and crown fire risk (Agee and Skinner, 2005; Churchill et al., 2013), while greater variation in tree sizes may reduce susceptibility to disturbances such as wind and bark beetles (Fettig et al., 2007; Hanewinkel et al., 2014). In mature stands, greater structural complexity is associated with the growth of taller trees (Zeller and Pretzsch, 2019), which, in turn, is a predictor of lower tree mortality risk from insect outbreaks (Dobbertin, 2005). Structurally complex stands also support greater variation in crown length, which is associated with faster tree growth and reduced tree mortality risk (O'Hara and Nagel, 2006). Enhancing structural complexity may potentially benefit tree vigor and carbon sequestration and storage under climate change, although long-term, experimental studies of structural-complexity effects on factors such as tree vigor or tree mortality in mature forests are comparatively rare (e.g., Zhang et al., 2008). Understanding how tree size modulates treatment effects on tree vigor and mortality can help anticipate treatment effects on structural complexity (Forrester, 2019).

Ecological forestry prescriptions may also seek to alter tree species composition to reverse shifts associated with historical logging practices or altered disturbance regimes (Covington et al., 1997; Holland et al., 2019) or foster positive interactions among tree species, which have been shown to increase tree growth and carbon sequestration in mixed vs. pure stands in forests worldwide (Feng et al., 2022; Jactel et al., 2018). Positive tree species-mixture effects can reflect a range of interactions (Forrester and Bauhus, 2016). For example, complementarity in tree species' functional traits such as crown shape may reduce competition to promote more efficient use of resources, in this case, light (Ishii and Asano, 2010), or facilitation may occur through improved litter quality or nutrition to increase tree vigor or stand productivity (Bauhus et al., 2017). Tree species-mixture effects are not universally positive, but can range from positive to negative depending on forest type and modulating stand and site factors, including topographic, climatic, and edaphic conditions (Mina et al., 2018). For example, tree species-mixture effects may situationally exacerbate tree mortality from drought stress in water-limited forests (Grossiord, 2020). Tree species-mixture effects are contingent on neighborhood competition and therefore are commonly weak in understocked stands, strongest at moderate stand densities, and overwhelmed by competitive interactions in highly overstocked stands (Bauhus et al., 2017; Feng et al., 2022). Tree size has also been shown to play an important role in determining tree species-mixture effects (D'Amato and Puettmann, 2004; Madrigal-González et al., 2016). Thus, thinning treatments can either accentuate or erase tree species-mixture effects depending on pretreatment stand density and treatment prescription (Bauhus et al., 2017). Whereas the influence of treatment on tree species-mixture effects on tree performance has been studied in mature European forests (Bauhus et al., 2017), research into how forest restoration treatments affect these interactions is lacking in western U.S. forests.

In the ponderosa pine/white fir (*Abies concolor*) mixed-conifer forests of California, U.S., a combination of fire exclusion and historical harvesting practices have led to tree densification and homogenization of forest structure (Safford and Stevens, 2017), while favoring fire-sensitive species such as white fir (Brodie et al., 2023; Collins et al., 2016). Restoration is complicated by the fact that studies to date on species-mixture effects in ponderosa pine/mixed-conifer stands have been primarily observational (Koontz et al., 2021; Long and Shaw, 2010; Looney et al., 2020) or focused on young plantations (Seidel, 1985). An observational study of ponderosa pine-dominated forest inventory plots from the Intermountain West, U.S. found no evidence of differences in stand growth between structurally or compositionally simple and complex stands (Long and Shaw, 2010). In California, a study of forest inventory plots not subject to recent fire or silvicultural treatment found that individual ponderosa pine basal area increment and live crown ratio were negatively correlated with stand-level functional diversity, while true fir live crown ratio increased in compositionally diverse stands (Looney et al. 2023). Results from other studies in California indicate that stands with a lower proportion of ponderosa pine have lower likelihoods of infestation by western pine beetle (*Dendroctonus brevicomis*) (Koontz et al., 2021), while white fir growing with neighbors of different tree species experienced elevated mortality (Das et al., 2008).

Previous studies in ponderosa pine-dominated mixed-confier forests in the western U.S. have examined the effects of fuel-reduction treatments on structural complexity (e.g.; Korb et al., 2012; Ritter et al., 2022), overstory and understory composition (e.g., Fulé et al., 2002; Schwilk et al., 2009), and tree responses to stand density and competition reduction (e.g., Bernal et al., 2023; Fiedler et al., 2010). However, no study to date has investigated the influence of fuel-reduction treatments on tree species-mixture effects on individual tree performance. Nor has the relative importance of reducing competition, promoting structural complexity, and restoring tree species composition when seeking to enhance retained-tree growth, vigor, and survival been resolved.

Our efforts examine 20-yr results from the Goosenest Adaptive Management Area (AMA) study, which was experimentally treated to evaluate common management alternatives for xeric, east-side, forests in the Cascade Range of California (Ritchie, 2005). The Goosenest AMA

study provides an expansive (~1200 ha), long-term, manipulative investigation into the effects on ponderosa pine/white fir mixed-conifer forests of altering stand density, structural complexity, and tree species composition, as well as introducing post-treatment prescribed fire. The study compared an untreated control and three approaches for accelerating the development of historical late-seral forest characteristics while simultaneously reducing fuels. Each approach incorporated thinning from below: 1) to uniformly reduce stand density and favor large tree retention with no species preference, 2) to increase structural complexity and favor pine over shade-tolerant species by also incorporating radial thinning around dominant and co-dominant pines, and 3) to reduce fuels by adding prescribed burning after thinning in a manner identical to 2 (Ritchie, 2005).

Previous efforts at the Goosenest AMA study, the most recent of which examined ~14-year post-treatment data (Ritchie, 2020), found faster tree growth and reduced tree mortality in treated units but no substantial differences among treatments (Ritchie and Harcksen, 2005). Such results are hardly unexpected given that all treatments involved similar thinning-from-below prescriptions. We focus on within-unit heterogeneity to help identify the extent to which fine-scale variation modulates treatment effectiveness (Puettmann et al., 2012). Our objectives were to determine 1) how treatments affect within-unit variation in neighborhood competition, structural complexity, and tree species composition, and 2) whether categorical treatment effects versus within-unit variation in neighborhood competition, structural complexity, and tree species composition influence individual-tree growth as indicated by basal area increment (BAI), vigor as indicated by change in live crown ratio (ΔLCR), and tree mortality. We built into this analysis the first investigation into whether fuel-reduction treatments can alter tree-species mixture effects on subsequent tree performance in ponderosa pine/white-fir mixed-conifer forests. Our goal was to provide a better understanding of how future forest ecological silviculture treatments can be optimized to promote development and retention of ecologically valuable, large ponderosa pine while sustaining overall tree growth, vigor, and survival.

2. Methods

2.1. Study area and experimental design

One of several Adaptive Management Areas under the Northwest Forest Plan, the Goosenest AMA was established on Klamath National Forest near Tennant, Siskiyou County, California and includes a long-term silvicultural study initiated in 1998 (Ritchie, 2005). Located on a moderately productive site northeast of Mount Shasta, California the study area is characteristic of interior ponderosa pine forests in the Cascade Range. Soils are volcanic, with a pumice layer posing a barrier to artificial regeneration success without site preparation. The climate is continental and Mediterranean, with precipitation largely occurring in the form of snow in winter. After ponderosa pine, white fir is the second most plentiful tree species, with lower abundances of sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), lodgepole pine (*Pinus contorta*), and red fir (*Abies magnifica*). Stands were high-grade logged in the 1920–1930s prior to acquisition by the USDA Forest Service, with harvesting focused on pine removal.

The Goosenest AMA study consists of twenty 40-ha experimental units inclusive of an untreated control and three treatment alternatives: 1) A Large Tree treatment sought to release large trees of any species from competition and change the diameter class distribution. Treatment involved thinning from below to a 5.5-m tree spacing, with trees removed solely based on size without consideration of species. This treatment is comparable to contemporary restoration treatments (Ritchie, 2020). 2) A Pine Emphasis treatment sought to restore the historical relative abundance of ponderosa pine (i.e., with at least 80 percent of basal area represented by ponderosa pine), while enhancing structural complexity through a combination of radial thinning around retained trees and installation of canopy gaps through group selection. All codominant and dominant pines were retained during marking, resulting in an irregular spatial distribution of retained trees despite the radial thinning policy. Group selection gaps, artificially regenerated with ponderosa pine, varied in size from 0.2 to 1.4 ha and comprised a cumulative target of 15 percent of stand area. Where possible, gaps were centered on concentrations of white fir. Gaps were planted with bare-root ponderosa pine (2−0) at an effective spacing of 3.4 m in 2000–2002 following harvest. Site preparation with ripping enhanced early survival of seedlings by turning over the upper pumice soil profile (Ritchie, 2005). 3) A Pine Emphasis with Fire treatment identical to the Pine Emphasis treatment, except for the addition of prescribed burns after thinning in 2001 and again in 2010, sought to reduce surface and ladder fuels, raise canopy base heights, and decrease natural tree regeneration, particularly of fire-sensitive fir (Ritchie, 2020). Burns were performed in fall following early seasonal rains to moisten fuels and moderate fire behavior. Burns used tree-centered spot firing in 2001 and strip head firing in 2010. Burn prescriptions called for not igniting within group selection openings, and the low flammability of shrubs within canopy gaps in 2010 also assisted with the goal of excluding fire from these areas, resulting in low mortality of planted pines. Fuel consumption was otherwise less than desired due to weather and fuel moisture conditions. The four treatments were applied in a completely randomized design (n = 5/treatment). Due to the large scale of this project, timber harvests were executed during multiple years (1998–2000). Overall stand-level statistics are summarized for each treatment in Table 1.

2.2. Vegetation monitoring

A monitoring plot network was established within each experimental unit prior to treatment implementation. This plot network consists of precision-survey grid points at a density of approximately 0.5 plots/ha. Pretreatment vegetation sampling was collected in 1996 using a variable-radius design and so is not directly comparable to post-treatment vegetation sampling on a plot-level basis (Ritchie, 2005). Post-treatment measurements were conducted in 2002, 2005, 2013, and 2019. Our

Table 1
Mean 2005–2019 site, stand and tree characteristics for the Goosenest AMA study (mean ± standard deviation).

Characteristic	Control	Big Tree	Pine Emphasis	Pine + Fire
Number of units	5	5	5	5
Number of plots	90	91	89	91
Number live trees*	2201	753	772	654
Mortality (%)‡	14.0 (4.2)	9.1 (5.4)	11.7 (6.9)	14.1 (7.9)
Elevation (m)	1617.2 (79.4)	1554.4 (48.7)	1588.2 (51.7)	1624.9 (77.7)
Heat load	0.77 (0.03)	0.77 (0.03)	0.77 (0.01)	0.77 (0.03)
DBH (cm)	36.9 (3.2)	46.8 (1.9)	46.6 (2.9)	47. 5 (1.9)
Height (m)	23 (5.8)	23.5 (3.0)	23.7 (4.4)	24.1 (4.6)
CI (trees ha^{-1})	447.6 (87.6)	188.8 (17.0)	219.7 (33.4)	176.5 (50.6)
LCR	0.54 (0.05)	0.7 (0.07)	0.66 (0.07)	0.65 (0.05)
SCI	0.032 (0.004)	0.016 (0.004)	0.019 (0.003)	0.018 (0.002)
Percent pine	41.9 (10.9)	53.5 (17.3)	60.8 (19.6)	65.4 (21.7)
TPH	598.6 (111.9)	135.6 (15.8)	163.7 (21.9)	124.4 (30.0)
SDI (trees ha^{-1})	1205.0 (189.0)	428.9 (39.9)	475.1 (40.9)	390.1 (107.5)
Basal area (m^2 ha^{-1})	74.1 (12.8)	28.7 (2.7)	31.8 (2.1)	26.3 (7.4)

Note: *Initial sample of live trees entering the study in 2005. ‡ cumulative mortality between 2005 and 2019. Abbreviations are as follows: DBH=diameter at breast height (1.37 m), CI=stand density index (additive method) of plot neighbor trees larger than a given focal tree, LCR = live crown ratio, SCI= structural complexity index, TPH= trees per hectare, SDI= stand density index (additive method).

effort focuses on data from 2013 and 2019, which had similar observation windows and dated since the second prescribed burn in 2010 in the Pine Emphasis with Fire treatment.

At each sampling point, vegetation was monitored within a nested fixed-radius sample plot design. Overstory trees (>29 cm diameter at breast height, DBH) and midstory trees (9.1 cm < DBH <29 cm) were assessed for survival, damage, mortality risk rating, DBH, total height, and height to live crown base within 0.081 and 0.02-ha plots, respectively. Total height was measured to the height of the tallest live branch junction in the case of trees with dead tops. Height to live crown base was based on an average adjusted for large canopy gaps or unevenness following procedures detailed in Schomaker (2007). DBH was assessed at 1.37 m in height. While trees are attributable to a given sample plot they are not mapped within a plot, making this dataset only coarsely spatially explicit.

2.3. Analytical approach and variables

To address our first research question, we examined how treatments influenced the within-unit responses of plot-level neighborhood competition, structural complexity, and tree species composition. We sought to establish whether treatment effects translated into substantial differences in tree neighborhoods. We were also interested in establishing whether these fine-scale characteristics of treatment varied over time. To address our second research question, we modeled individual-tree performance, defined in terms of BAI, ΔLCR, and mortality, as a function of either unit-level treatment or plot-level factors. We followed an individual-tree modeling approach to flexibly integrate treatment, plot, and tree-level data. We used the original Goosenest AMA treatment categories to represent the unit-level treatment variable. Treatment and other variables are detailed in Table 2.

For our individual-tree models, we divided species into "ponderosa pine" and "white fir" categories and analyzed each category separately to avoid complex three-way covariate x treatment x tree species interaction models. We made this choice based on 2019 counts of live trees showing that white fir comprised 95 percent of non-ponderosa pine species to strengthen inferences regarding the impacts of biotic tree mortality agents on white fir, specifically bark beetles, which differ from species affecting other non-ponderosa pine species such as incense-cedar, sugar pine, and lodgepole pine (Das et al., 2011; Fettig, 2016). These species categories are consistent with the original design goals of Goosenest AMA study, which focused on ponderosa pine separately from shade-tolerant tree species.

To evaluate individual-tree performance, we used periodic annual basal area increment (BAI) as our growth response variable. We integrated BAI over a single 2005–2019 period based on outside-bark diameters, focusing on trees with positive BAI and initial (2005) DBH > 11.4 cm. We dropped 9 tree records (0.2%) from this analysis due to non-positive BAI. To indicate individual-tree vigor, we selected compacted live crown ratio (LCR), based on average tree height to live crown base, adjusted for large canopy gaps or lopsided crowns following procedures detailed in Schomaker et al. (2007). Live crown ratio is associated with reduced tree mortality odds and is a strong predictor of growth rate (Zarnoch et al., 2004). We calculated the periodic change in LCR to yield ΔLCR over the entire 2005–2019 period. Mortality was coded as a binary variable (0=live, 1=dead). For BAI and LCR models, we included all trees with an initial DBH > 11.4 cm that were alive at the end of each observation period. For mortality models, we included all live trees > 11.4 cm DBH as of 2005.

We controlled for variation in plot-level site quality in individual-tree models through the incorporation of elevation and heat load. The Goosenest AMA spanned 330 m of elevation and 7.6 km of distance, making it likely that tree performance was affected by variations in site quality, which may also alter species interactions (Lu et al., 2018) and the development of structural complexity (Larson et al., 2008). Elevation serves as an indicator of local temperature and precipitation, while heat load integrates site slope, aspect, and latitude to summarize relative site insolation (McCune, 2007). We calculated elevation, slope, and aspect for each plot based on a 10-m resolution (1/3rd arc-second) digital elevation model (U.S. Geological Survey, 2016) in QGIS v. 3.16 (Quantum GIS Development Team, 2020). Heat load and elevation represented average conditions within the 0.081-ha monitoring plots.

Initial tree size controlled for size-related variations in individual-tree performance, while also potentially providing insights into how covariates altered performance across diameter distributions. We used initial DBH in BAI and mortality models. For BAI models, we followed the approach of Uzoh and Oliver (2008) and Ritchie (2020) by including both log-transformed and squared DBH terms to account for a typical peak in the diameter increment-DBH relationship at moderate tree sizes. We modeled tree mortality as a function of both linear and quadratic DBH to account for the typically "U-shaped" mortality-DBH relationship (Yang et al., 2003). We used initial tree height in ΔLCR models (Ritchie and Hann, 1987). We also included initial LCR as a predictor to normalize change relative to initial tree vigor (Crookston and Dixon, 2005; Zarnoch et al., 2004). While LCR is a commonly used predictor in mortality modeling (Crookston and Dixon, 2005; Zarnoch et al., 2004), we excluded LCR as a predictor in BAI models as including this variable can lead to problematic levels of collinearity.

Table 2
Variables used in basal area increment, live crown ratio change, and mortality modeling.

Variable	Category	Level	Description	Units
		Response variables		
CI	Response	Plot	sum of live tree SDI of plot neighbor trees larger than a given focal tree	25 cm tree equivalents ha^{-1}
SCI	Response	Plot	Structural complexity index	ratio
Percent pine	Response	Plot	Percent relative ponderosa pine stand density index	percent
BAI	Response	Tree	periodic annual basal area increment	cm^2 tree yr^{-1}
LCR	Response	Tree	compacted live crown ratio	ratio
Mortality	Response	Tree	tree status (0=live, 1= dead)	binary
		Predictor variables		
Trt	Treatment	stand	GAMA treatment	factor
Year	Year	stand	Measurement year (2005, 2013, 2019)	factor
Htl	Site quality	plot	heat load as a function of latitude, aspect, slope	unitless
El	Site quality	plot	elevation above sea level	m
DBH	Tree size	tree	initial tree diameter at breast height	cm
Ht	Tree size	tree	initial tree total height	m
CI	Neighborhood	neighborhood	sum of live tree SDI of plot neighbor trees larger than a given focal tree	25 cm tree equivalents ha^{-1}
SCI	Neighborhood	plot	Structural complexity index	ratio
Percent pine	Neighborhood	plot	Percent relative ponderosa pine stand density index	percent

We represented neighborhood competition (CI) using an individual-tree, distance-independent competition index (Larocque et al., 2012). To address our first research question, this index was averaged to the plot level to summarize plot-level neighborhood competition. To address our second research question, this index was integrated into individual-tree modeling. Quantifying neighborhood competition also served to represent horizontal variation (del Río et al., 2016) in local stand density. After a preliminary comparison with Wykoff's (1990) basal area level competition index and total plot-level SDI, we selected the SDIL competition index of del Río et al., (2014), which is based on plot-level SDI (Reineke, 1933), to represent neighborhood competition in models for all three responses (Supplementary Table S1). We modified this index to use the summation SDI method of Long and Daniel (1990). This distance-independent index is conceptually similar to basal area level in that it considers only plot neighbors larger than each subject tree to be competitors:

$$CI = \sum_{j=1\ D_j>D_i}^{n} \left(\frac{D_j}{25}\right)^{1.605}$$

where D_i is the diameter of target tree i, Dj is the diameter of plot neighbor tree j, and n is the total number of plot neighbors. Given the nested monitoring plot design, this index was calculated for fixed neighborhoods of 0.081 ha for overstory trees and 0.02 ha for midstory trees.

We calculated an index of local structural complexity to serve as both a plot-level response in support of our first research question and as a predictor of tree performance in support of our second research question. We used one minus the ratio of additive SDI (Long and Daniel, 1990) to traditional SDI (Reineke, 1933) as a structural complexity index (SCI) of plot-level conditions as of 2005 (Ducey, 2009). This index is an indicator of vertical tree distribution patterns (del Río et al., 2016). Lower values of SCI, as rescaled, indicate uniform or normal diameter distributions, while higher values indicate more complex diameter distributions such as bimodal or negative exponential (Ducey, 2009).

We calculated plot-level tree species composition to serve as both a plot-level response in support of our first research question, and as a predictor of tree performance for our second research question. We calculated tree-species composition (Percent pine) in terms of relative additive SDI of ponderosa pine as of 2005, in keeping with the objective of the original experiment to increase relative abundance of ponderosa pine in the Pine Emphasis and Pine Emphasis with Fire treatments (Ritchie, 2005). All other pine species, including sugar pine and lodgepole pine, were pooled with true firs and incense-cedar in these calculations.

2.4. Model building, statistical procedures, and model selection

2.4.1. Treatment effects on within-unit neighborhood competition, structural complexity, and species composition

To address our first research question, we built three *a priori* alternative hypothesis models to examine how treatment influenced each of the within-unit responses of 1) neighborhood competition (CI), 2) structural complexity (SCI), and 3) species composition (Percent pine; Table A1). Our null model for each response included only the intercept and random effects. Our first alternative model included only the fixed effect of treatment. Our second alternative model included the fixed effects of both year and treatment. Our third alternative included the fixed effects of year, treatment, and the year x treatment interaction to account for potential changes in treatment effects over time. We aggregated CI to the plot level to make models comparable with SCI and Percent pine. Year was treated as a factor variable due to our having only three comparably spaced measurement years. Random effects included plot nested within unit to account for repeated measures on the same plots.

2.4.2. Tree responses to categorical treatment effects vs. within-unit variation in neighborhood competition, structural complexity, and species composition

To address our second research question, we used an individual-tree modeling approach to investigate the relative influence of categorical treatment effects versus within-unit variation in neighborhood competition, structural complexity, and tree species composition influence on individual-tree BAI, ΔLCR, and mortality. We built 11 increasingly complex *a priori* alternative hypothesis models for each response, creating separate sets of models for ponderosa pine and white fir (Table A1). Our general model form was analogous to the approach of Uzoh and Oliver (2008), which predicts ponderosa pine diameter increment as a function of slope, aspect, stand density, neighborhood competition, and tree size. In our null model, BAI, ΔLCR, and mortality varied with the fixed effects of heat load, elevation, and initial tree size. Our first alternative model investigated whether responses varied with the categorical predictor of treatment. To evaluate whether local variations in competition altered tree responses, our second alternative model included the main effect of CI. Our third alternative included the main effect of CI and the CI x initiation size interaction to investigate whether competitive interactions were consistent across the ranges of tree sizes. Our fourth alternative model included the main effects of treatment, CI, and SCI to investigate the role of structural complexity, quantified in terms of vertical tree distributions, via SCI, while controlling for potential covariation between neighborhood competition and SCI due to the influence of group selections in the Pine Emphasis treatments. Our fifth alternative further investigated whether neighborhood competition altered the influence of local SCI through inclusion of CI, SCI, and the CI x SCI interaction. Our sixth alternative included the main effects of CI, SCI, and the SCI x initial tree size interaction to examine whether the influence of structural complexity was consistent across the range of tree sizes. Our seventh alternative model included the main effects of CI and % Pine to investigate potential species-mixture effects while controlling for potential covariation between % Pine and local density due to retention of dominant and codominant pines regardless of spacing in Pine Emphasis treatments (Ritchie, 2005). Our eighth alternative included the main effects of CI, % Pine, and the CI x % Pine interaction to investigate whether competition altered species mixture effects. Our ninth alternative investigated whether mixture effects were contingent on initial tree size by including the main effects of CI, % Pine, and the % Pine x initial tree size interaction. Our tenth alternative model included the main effects of treatment, CI, % Pine, and SCI to evaluate whether potential species-mixture effects were confounded with structural complexity (del Río et al., 2016). To investigate whether local variation in structural complexity modified species mixture effects, our eleventh alternative model included the main effects of treatment, CI, % Pine, SCI, and the % Pine x SCI interaction. Individual-tree models included the random effect of sample plot nested within unit to account for spatially autocorrelated responses among trees sharing the same sample plot.

2.4.3. Statistical procedures and model selection

All statistical analyses were conducted in R (R Core Team, 2022). We used the glmmTMB package (Magnusson et al., 2018) to perform all generalized linear mixed modeling. For within-unit analysis in support of our first research question, we analyzed the response variables, SCI and Percent pine, by applying square-root and arcsine transformation, respectively. For individual-tree BAI, we used a log link to the Gamma distribution to model these right-skewed data. We did not find it necessary to transform ΔLCR. For binary mortality data, we used a logit link to the binomial distribution.

We fit models with maximum likelihood estimation to focus inference on fixed effects. We used the default "nlminb" optimizer in glmmTMB except for tree mortality models, where we used the "BFGS" optimizer to help achieve convergence. We plotted boxplots of raw data and simulated residuals to graphically verify model assumptions of

homogeneous variances, normality of residuals, and the appropriateness of error distributions using both conventional (CI, SCI, Percent pine, and BAI models) and simulated residuals plots (Hartig, 2018). We plotted predictors against residuals to diagnose issues with linearity. Diagnostics and boxplots of raw data prompted us to an error structure accommodating heterogeneous variances by treatment for the plot-level responses of CI, SCI, and Percent pine (Zuur et al., 2009). Except for height and diameter, predictor variables were not highly correlated ($r < 0.5$), and height and diameter were never included simultaneously in models (Table A1). Variance inflation factors (VIF) did not exceed 6 for retained BAI models, indicating moderate collinearity (James et al., 2013). We dropped BAI Hypothesis model #4 (BAI as a function of CI and the CI x DBH interaction, in addition to null model terms) due to problematic collinearity for both ponderosa and white fir (VIF >10; James et al., 2013). We found that VIF did not exceed 3 in LCR or mortality models.

We used the information-theoretic approach to evaluate evidence for alternative hypothesis models (Burnham and Anderson, 2002), using corrected Akaike's information criterion (Sugiura, 1978). We considered alternative hypothesis models plausible if ΔAICc values were within 6 units distance of the best-approximating model and represented at least a 2 ΔAICc reduction per added parameter compared to simpler nested models (Burnham and Anderson, 2002; Richards, 2008). We used the MuMin package (Bartoń, 2017) to perform model comparisons. We present *pseudo*-R^2 results from the mgcv package (Wood, 2012) purely for descriptive purposes and relied on AICc for statistical inference.

We used AICc for inference but calculated conditional (combined fixed and random effects) pseudo-R^2 for each model with substantial AICc support for descriptive purposes. In the event of substantial evidence for a treatment main effect, we also interpreted differences among treatments using Tukey's HSD post-hoc test at $\alpha = 0.05$. For plot-level CI, SCI, and Percent pine models with heterogenous variances by treatment, we used the Games-Howell post-hoc test. We used the MuMIn package (Bartoń, 2017) to perform multi-model inference for all models and the multcomp package for multiple comparisons (Hothorn et al., 2023). We calculated pseudo-R^2 statistics for BAI using Nakagawa and Schielzeth's (2013) method. The emmeans package (Lenth, 2018) was used to perform post-hoc testing. Predictor variables were converted to Z-scores to aid interpretation of relative effect sizes as well as reduce collinearity and help model convergence.

Model interpretation focused on the effect size and sign of covariates in terms of main effects and interaction coefficients. A positive term for Percent pine in individual-tree models signified a positive species composition effect for the other conifers and a negative species composition effect for ponderosa pine, relative to pure plots of either species group. In the event of substantial evidence supporting treatment interactions with covariates, we interpreted covariates as contingent on treatment rather than interpreting these main effects. We used the sjPlot package (Lüdecke and Schwemmer, 2017) to summarize model effects and interpret interactions.

3. Results

3.1. Treatment effects on within-unit neighborhood competition, structural complexity, and species composition

The best-approximating model of within-unit neighborhood CI, summarized to the local plot-level, contained the fixed effects of treatment, year, and the treatment x year interaction (Table 3). CI was consistently highest in the Control, increasing between 2005 and 2019 and displaying higher within-category variability relative to the other treatments. In the Big Tree treatment, CI was lower relative to the Control and showed lower variability relative to the Control, Pine Emphasis, and Pine Emphasis with Fire treatments. Mean CI was lower in all treatments relative to the Control, while not significantly different from each other (Fig. 1). Treatments did not show consistent trends in CI over time. No other competing model was plausible for this response.

Table 3
Summary of plausible model comparison results for within-unit responses.

Response	Hypothesis model	logLik	ΔAICc	R^2
CI	~Trt + Year + Trt * Year	-5713.3	0.0	0.5
CI	~Intercept-only	-5788.8	128.4	0
SCI	~Trt + Year + Trt * Year	2180.4	0.0	0.12
SCI	~Intercept-only	2146.6	45.0	0
Percent pine	~Trt + Year + Trt * Year	576.1	0.0	0.13
Percent pine	~Intercept-only	545.8	38.0	0

Note: Please see Table S2 in Supplementary Material for complete model comparison results. Abbreviations are as follows: LogLik = log-likelihood, ΔAICc = corrected Akaike's information criterion, R^2 = coefficient of determination. See Table 2 for model term abbreviations and Table A1 for the list of hypotheses.

The within-unit SCI response to treatment was also contingent on year in the best-supported model, which contained the fixed effects of treatment, year, and the treatment x year interaction (Table 3). Under this interaction, SCI was consistently higher (indicative of greater structural complexity) in the Control than in any other treatment, while increasing over the 2005–2019 period relative to the three other treatments. Mean SCI was comparable among the Big Tree, Pine Emphasis, and Pine Emphasis with Fire treatments, with SCI exhibiting a slight negative trend in treated stands. We did not find support for any alternative model.

The best-approximating model of within-unit Percent pine contained the fixed effects of treatment, year, and the treatment x year interaction (Table 3). Percent pine was lower in the Control, relative to the Big Tree, Pine Emphasis, and Pine Emphasis with Fire treatments, and declined over time. Percent pine in the Big Tree treatment was intermediate between the Control and Pine Emphasis treatment, increasing with time since treatment but continuing to overlap the Control in 2019. Percent pine in the Pine Emphasis treatment was higher than in the Big Tree treatment and showed clear separation from the Control in 2013 and 2019. The Pine Emphasis with Fire treatment featured the highest mean Percent pine, with relative density consistently shifting towards greater pine relative density in 2013 and 2019. No other Percent pine model was plausible.

3.2. Individual-tree responses to categorical treatment effects vs. within-unit variation in neighborhood competition, structural complexity, and species composition

The best-approximating model of 2005–2019 BAI for ponderosa pine featured the CI and Percent pine main effects, the DBH x Percent pine interaction, and null model terms of elevation, heat load, DBH, and CI (Table 4). Under the DBH x Percent pine interaction, the BAI of ponderosa pine peaked at approximately 60 cm DBH on plots with low Percent pine. On plots with high Percent pine, BAI peaked at 75 cm DBH (Fig. 2). The BAI of both small and large ponderosa pines on high Percent pine plots was higher relative to ponderosa pines on low Percent pine plots, while intermediate-sized ponderosa pines showed similar maximum BAI regardless of composition. BAI did not substantially vary with the null model terms of elevation or heat load while declining steeply with CI. No other ponderosa pine structural complexity model was plausible.

The best approximating model of ponderosa pine 2005–2019 ΔLCR included the main effect of CI, as well as the null model terms of heat load, elevation, initial total height, and initial LCR (Table 4). Ponderosa pines under minimal CI displayed neutral ΔLCR, signifying no change in crown vigor. Ponderosa pine ΔLCR shifted to negative with increasing CI (Fig. 3), signifying declining crown vigor. ΔLCR did not substantially vary with elevation or heat load, while declining with initial height and initial LCR. No other ΔLCR model was plausible for ponderosa pine.

Mean ΔLCR was negative in the Control, signifying declining crown condition. Mean ΔLCR was positive in the Big Tree, Pine Emphasis, and

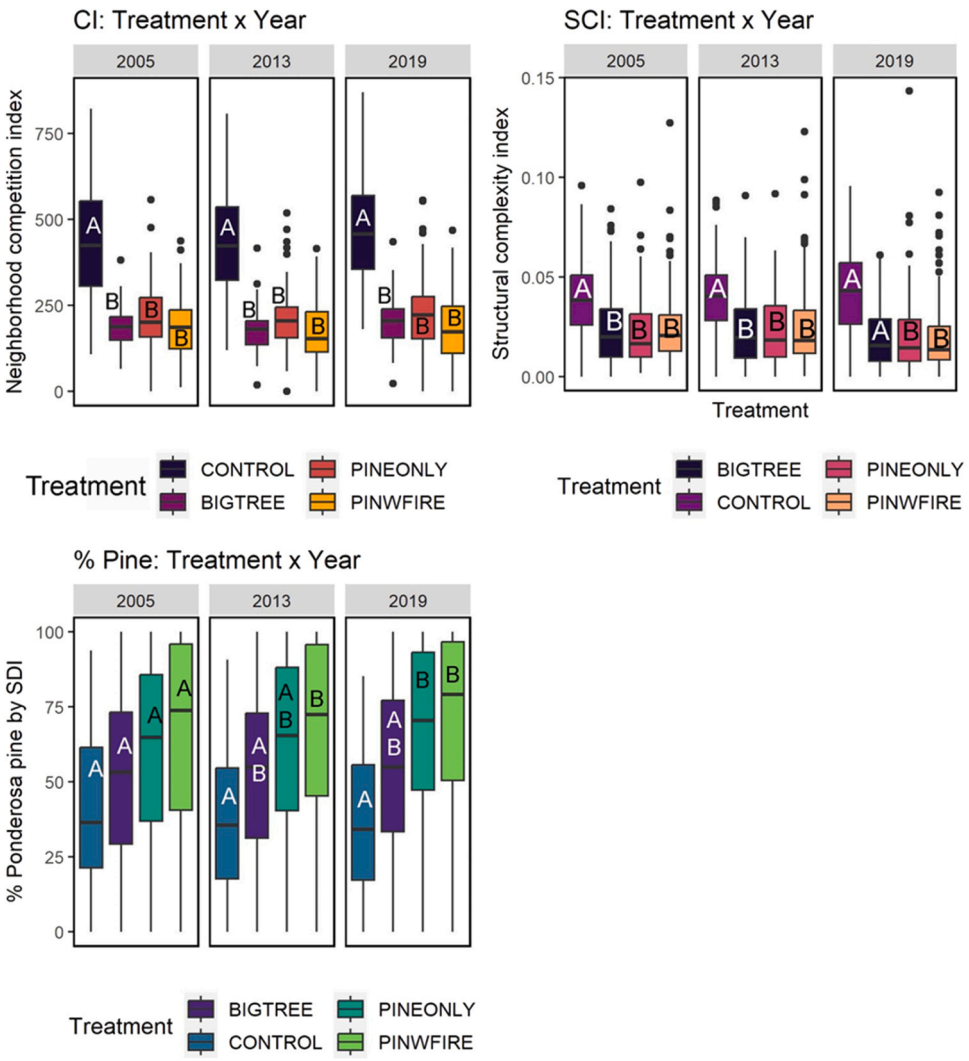


Fig. 1. Boxplots of plot-level covariates (competition index, CI; structural complexity index, SCI; Percent pine, percent ponderosa pine relative stand density index) as a function of treatment and year of sampling. All three variables were found to show strong evidence of variation in response to treatment and sample year.

Pine Emphasis with Fire treatments, signifying improving crown condition (Fig. 3). The three treatments showed comparable mean ΔLCR. Among the null model terms, ΔLCR was neutral with respect to heat load while declining with elevation, initial height, and initial LCR. No other model was plausible for white fir.

The best-supported species mixture model of 2005–2019 ponderosa pine mortality included the main effect of treatment as well as the null model terms of elevation, heat load, DBH, and initial LCR (Table 4). Under this model, mortality odds for ponderosa pine were elevated in the Control relative to the Big Tree, Pine Emphasis, and Pine Emphasis with Fire treatments (Fig. 4). No significant differences were observed among treatments, all of which had low odds (mean <1%) of mortality (Fig. 4). Mortality odds increased with the null model terms of heat load and elevation, while remaining neutral relative to CI. Mortality showed a U-shaped relationship with DBH, with mortality odds lowest for intermediate-sized ponderosa pines. No other model had substantial AIC support.

The best-supported model of 2005–2019 white fir mortality included the main effect of Percent pine, as well as the null model terms of elevation, heat load, DBH, and CI (Table 4). Under this model, white fir mortality odds increased with Percent pine (Fig. 4). Mortality odds remained neutral relative to the null model term of heat load, declined with elevation, did not substantially vary with DBH or CI, and declined with LCR. A plausible alternative model provided support for the categorical treatment effect (ΔAICc=4.8). No other white fir mortality model was plausible.

4. Discussion

The large spatial scale and long-term nature of the Goosenest AMA ecological forestry experiment afforded a unique opportunity to investigate how alternative thinning treatments not only affect within-unit neighborhood competition, structural complexity, and tree species composition, but how experimentally manipulating these factors alters within-unit individual-tree performance. We discuss below how treatments influenced within-unit variation in neighborhood competition, stand structure, and tree species composition, and how such fine-scale variation was commonly more consequential to individual-tree responses than categorical treatment effects.

4.1. Treatment effects on within-unit neighborhood competition, structural complexity, and species composition

Neighborhood tree competition in treated units, as indicated by CI, showed little change or slight declines between 2005 and 2013 before recovering by 2019, while neighborhood tree competition in the Control consistently increased over time. Because our competition index considered both local stand density and individual tree size, initial post-

Table 4
Summary of plausible model comparison results for tree-level responses.

Species group	Response	Hypothesis model	logLik	ΔAICc	R^2
Ponderosa	BAI	~Htl + El + log(DBH) + DBH2 + CI + Percent pine + DBH x Percent pine	-8740.8	0.0	0.41
Ponderosa	BAI	~Htl + El + log(DBH) + DBH2	-8843.3	195.1	0.33
White fir	BAI	~Htl + El + log(DBH) + DBH2+ CI x log(DBH) + CI x DBH2	-6711.9	0.0	0.66
White fir	BAI	~Htl + El + log(DBH) + DBH2 + CI + Percent pine + CI x Percent pine	-6711.6	1.6	0.66
White fir	BAI	~Htl + El + log(DBH) + DBH2	-6804.7	386.5	0.59
Ponderosa	ΔLCR	~Htl + El + Ht + LCR1 + CI	2269.2	0.0	0.18
Ponderosa	ΔLCR	~Htl + El + Ht + LCR1	2246.1	40.0	0.16
White fir	ΔLCR	~Htl + El + Ht + LCR1 + Trt	1312.3	0.0	0.46
White fir	ΔLCR	~Htl + El + Ht + LCR1	1284.7	49.1	0.18
Ponderosa	Mortality	~Htl + El + DBH + DBH2 + LCR1+ Trt	-579.6	0.0	0.28
Ponderosa	Mortality	~Htl + El + DBH + DBH2 + LCR1	-592.3	10.1	0.19
White fir	Mortality	~Htl + El + DBH + DBH2 + LCR1+ CI + Percent pine	-586.5	0.0	0.10
White fir	Mortality	~Htl + El + DBH + DBH2 + LCR1+ Trt	-587.4	4.1	0.11
White fir	Mortality	~Htl + El + DBH + DBH2 + LCR1	-592.4	7.8	0.09

Note: Please see Tables S3, S4, and S5 in Supplementary Material for complete model comparison results. Abbreviations are as follows: LogLik = log-likelihood, ΔAICc = corrected Akaike's information criterion, R^2 = coefficient of determination. See Table 2 for model term abbreviations and Table A1 for the full list of hypotheses.

treatment contrasts in CI under the Big Tree, Pine Emphasis, and Pine Emphasis with Fire treatments relative to the Control partly reflect local stand density reductions, and the removal of small, suppressed trees. Puettmann et al. (2012) recommended evaluating whether ecological forestry treatments promote within-stand heterogeneity where appropriate as a criterion of success. During initial model diagnostics, we noted that CI displayed heterogeneous variances by treatment, which primarily reflected higher variability in CI in the Control. However, evidence of greater variation in CI is also evident in the two Pine Emphasis treatments (with and without-fire) compared to the Big Tree treatment, despite the three treatments sharing similar mean values of CI. Consistent with the Goosenest AMA treatment objective to accelerate the development of late-seral habitat, greater variation in neighborhood competition within the Pine Emphasis treatments would be expected to promote the development of key characteristics associated with late seral habitat, such as greater size class diversity, variation in canopy heights, and snag recruitment (Bauhus et al., 2009; Vogeler et al., 2013).

Despite differences in marking guidelines among treatments, mean values of our within-unit indicator of vertical structural complexity, SCI, were similar among the Big Tree, Pine Emphasis, and Pine Emphasis with Fire treatments. Lack of a positive trend in SCI in the Pine Emphasis treatments over time, particularly the Pine Emphasis with Fire, is noteworthy. SCI is sensitive to tree diameter distributions deviating from the normal (Ducey, 2009), but we would have expected planted group selections to influence diameter distributions after 2013, when planted pines began to recruit above our minimum measurement size threshold (Ritchie, 2020).

Compositional contrasts between treated and untreated stands were slower to emerge compared to trends in SCI or CI. Even at 8–14 years post-treatment, the only statistically significant difference that emerged was between the Pine Emphasis with Fire treatment and the Control. The gradual ingrowth of planted ponderosa pines may have postponed the emergence of clear contrasts in composition, and further reductions of fire-sensitive fir likely contributed to the Pine Emphasis with Fire treatment achieving clear compositional distinctions from the Control. Overall, our findings support previous research suggesting that the reintroduction of fire is an important step towards restoring historical forest composition in ponderosa pine/dry mixed-conifer forests (Brodie et al., 2023; Huffman et al., 2018; Korb et al., 2012).

4.2. *BAI response to categorical treatment effects vs. within-unit variation in neighborhood competition, structural complexity, and species composition*

In agreement with the recent ecological understanding that processes

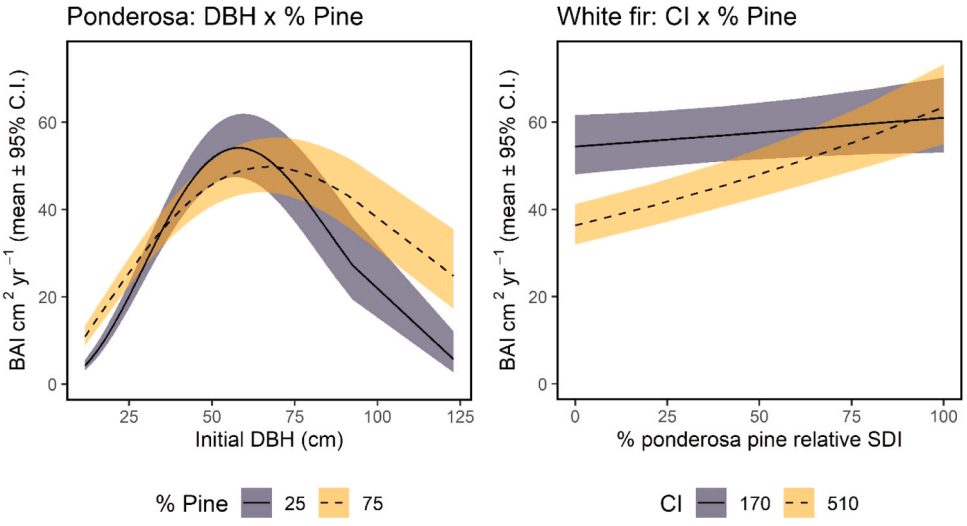


Fig. 2. Plots illustrating predicted values of basal area increment (BAI) based on the plausible models for ponderosa pine and white fir, focusing on the best-supported fixed factor of interest to this study, relative density by SDI of ponderosa pine (Percent pine). All other predictors are held at their mean values. The plot for ponderosa pine (left) depicts the Percent pine x initial DBH interaction, with Percent pine displayed at the 25th and 75th percentile values for this covariate. The plot for white fir (right) depicts the Percent pine x neighborhood competition index (CI) interaction, calculated for the 25th and 75th percentile values of CI. Lines show mean predicted values with 95 percent confidence envelopes. Please note that y-axis scaling is consistent by species.

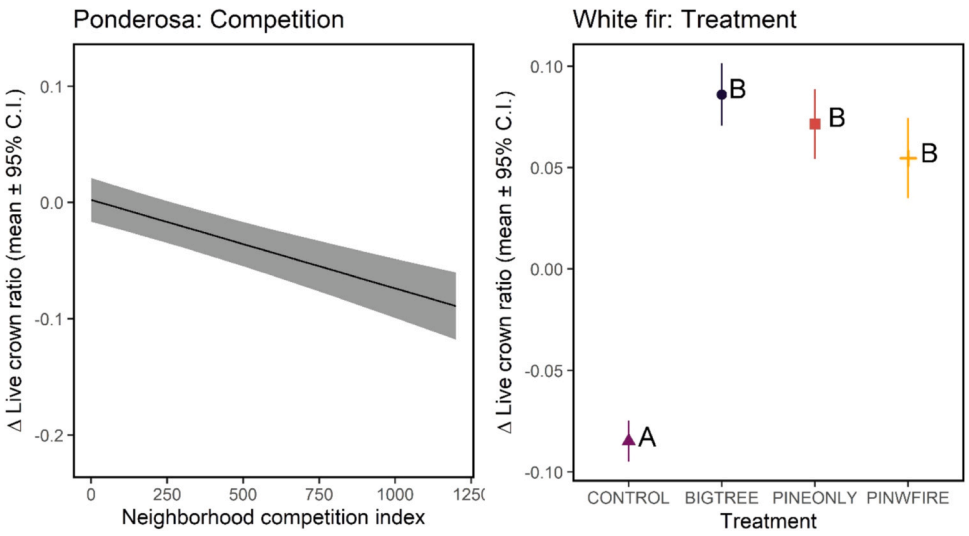


Fig. 3. Predicted values of the change in live crown ratio (ΔLCR) based on the plausible models for ponderosa pine and white fir, focusing on the best-supported fixed factors of interest to this study: competition index (CI) and treatment. All other predictors are held constant at their mean values. In the left panel, points depict mean predicted means while error bars display 95 percent confidence intervals. Letters indicate the results of Tukey's HSD post-hoc comparisons among treatments. Treatment means not sharing the same letter are significantly different at the α=0.05 level. In the right panel, lines show mean predicted values with 95 percent confidence envelopes. All other predictors are held at their mean values.

affecting tree performance commonly operate at the level of tree neighborhoods (Pommerening et al., 2021), within-unit variations in neighborhood competition and composition were more consequential for individual-tree BAI than unit-level treatment effects. Previous studies have found mixed support for a role of neighborhood competition in influencing ponderosa pine growth. Erickson and Waring (2014) found that ponderosa pine BAI responded positively to restoration treatments, but not to neighborhood competition, in trees originating prior to European settlement on the north rim of the Grand Canyon, Arizona, U.S. Zald et al. (2022) similarly found that overall thinning and burning treatment effects exerted a stronger influence on individual-tree BAI than neighborhood competition in mixed-conifer forests of the southern Sierra Nevada, California. In contrast, a study in mixed-conifer forests in the central Sierra Nevada found both plot level-treatment effects and neighborhood competition to be important indicators of tree growth (Knapp et al., 2021).

We found no evidence that differences in structural complexity fostered by treatment affected the BAI of ponderosa pine or white fir. Our individual-tree results are consistent with those of observational studies that found no clear differences in productivity or growth efficiency between even-aged and uneven-aged ponderosa pine stands (Ex and Smith, 2014; O'Hara and Nagel, 2006). In California Sierra Nevada mixed-conifer forests of which ponderosa pine was a small component, Knapp et al. (2021) similarly found comparable individual-tree and stand-level growth in high and low diversity stands following density-reduction treatments. Our findings suggest that thinning can flexibly promote individual-tree growth in ponderosa pine-dominated stands across a range of residual structural diversity.

Tree size modulated the effect of local species composition in ponderosa pine, with lower plot-level Percent pine associated with reduced growth of both small and large pines. In contrast, a previous observational study of mixed-conifer forests across California found that higher functional diversity reduced ponderosa pine BAI regardless of DBH (Looney et al., 2023). Our finding of reduced growth in small ponderosa pine is consistent with previous studies that found positive tree species-mixture effects are most evident in large trees (Bigelow et al., 2023; D'Amato and Puettmann, 2004; Madrigal-González et al., 2016). In contrast, species-mixture effects on white fir BAI were contingent on neighborhood competition, with white fir BAI increasing with Percent pine under high CI and remaining neutral under low CI. This finding is in agreement with the general understanding that positive species mixture effects are strongest at moderate-high stand densities (Bauhus et al., 2017). Our finding that reducing competition weakens positive species-mixture effects in white fir suggests that thinning has the potential to help reinforce species selection for ponderosa pine in restored California mixed-conifer forests.

4.3. LCR response to categorical treatment effects vs. within-unit variation in neighborhood competition, structural complexity, and species composition

We found that reducing neighborhood competition was important for sustaining crown vigor in ponderosa pine, whereas reducing overall stand density was important for improving white fir crown vigor. These results are consistent with previous research that found thinning and burning treatments slowed ponderosa pine crown recession (Crotteau and Keyes, 2020), although post-thinning absolute improvements in overall live crown ratio are not universally detectable (Hood et al., 2018). The lower responsiveness of pine versus fir to stand density reduction reflects the rapid recession of pine crowns in dense stands (Oliver, 1990), whereas the more shade-tolerant white fir maintains longer crown lengths and has poorer self-pruning ability (Stevens et al., 2020). Our LCR results suggest that reducing tree density may be a more important consideration than restoring composition or structural complexity for the purposes of promoting crown vigor in ponderosa pine and white fir.

4.4. Mortality response to categorical treatment effects vs. within-unit variation in neighborhood competition, structural complexity, and species composition

Treatments achieved equivalent success in reducing retained-tree mortality odds in ponderosa pine relative to the Control. Previous studies have found delayed ponderosa pine mortality following prescribed fire (Kolb et al., 2007; Stephens and Finney, 2002), which the authors speculate may be due to heavy duff accumulations that contribute to lethal basal girdling and secondary bark beetle attack. Yet at the Goosenest AMA study, the lack of elevated mortality in the Pine Emphasis with Fire treatment relative to the two unburned treatments suggests prescribed fire effects on survival were negligible. The

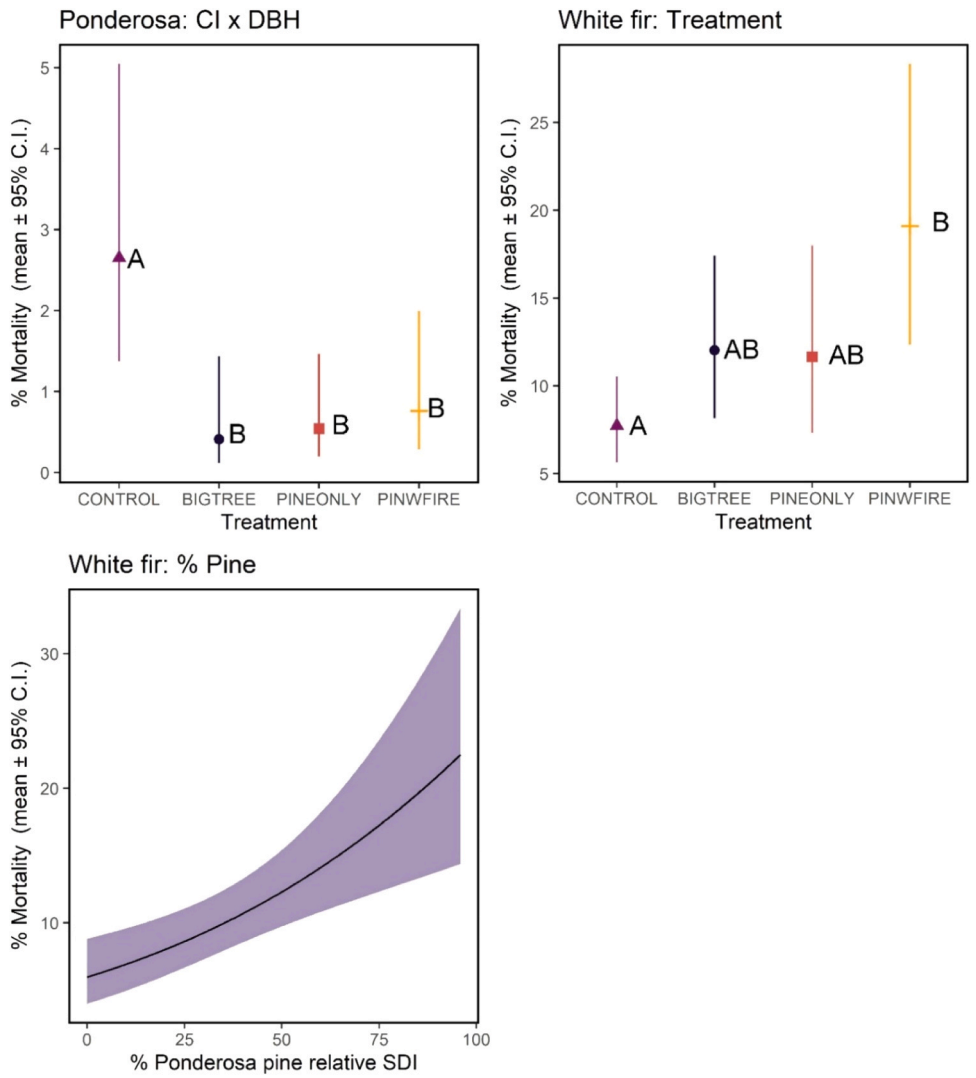


Fig. 4. Predicted values of tree mortality probability (%) based on the plausible models for ponderosa pine and white fir, focusing on the supported fixed factors of interest to this study: treatment and percent ponderosa pine relative density (Percent pine). We display both treatment and Percent pine effects for white fir based on the two plausible models for this species. All other predictors are held constant at their mean values. In the top panels, points depict mean predicted means while error bars display 95 percent confidence intervals. In the bottom panel, lines show mean predicted values with 95 percent confidence envelopes. Letters indicate the results of Tukey's HSD post-hoc comparisons among treatments. Treatment means not sharing the same letter are significantly different at the α=0.05 level.

relatively young age of most trees at the Goosenest AMA may have prevented heavy litter and duff accumulations around large trees. Another factor may have been the use of fire under mild weather conditions (Ritchie, 2020). On Fire and Fire Surrogate plots imbedded within the larger Goosenest AMA units, Fettig et al. (2010) reported that cumulative levels of tree mortality attributed to bark beetles 6–7 years after treatment were low, ranging from <1 (Pine Emphasis) to 3.3 percent (Pine Emphasis with Fire). Most long-term studies indicate that levels of bark beetle-caused tree mortality increase following prescribed burns, but that the effect is limited, short-lived, and concentrated in smaller-diameter trees (Fettig et al., 2022).

Ponderosa pine and white fir mortality were more responsive to categorial treatment effects than neighborhood competition. Thinning ponderosa and mixed-conifer stands to complex structures of individuals, clumps, and openings has been advanced to promote within-stand heterogeneity for bark beetle resistance (Churchill et al., 2013). Our results highlight the continuing relevance of stand density, rather than local density, as a key guide to avoiding tree mortality in ponderosa pine (Fettig, 2016; Zhang et al., 2013). Elevated white fir mortality in the Pine Emphasis with Fire treatment relative to the Control likely signaled greater sensitivity to fire effects in this species. Secondary tree mortality from fir engraver (*Scolytus ventrals*) is commonly related to prescribed fire effects, particularly in smaller-diameter white fir, a result previously documented following the first prescribed burn at the Goosenest AMA study (Fettig et al., 2010).

The elevated mortality odds of white fir under locally higher Percent pine contrast with our finding that white fir under heavy competition grew relatively more quickly in pine-dominated neighborhoods. We found the Percent pine effect remained consistent once accounting for treatment in follow-up modeling, suggesting Percent pine was not confounded with fire-related mortality in the Pine Emphasis with Fire treatment. A landscape scale study using forest inventory data similarly found that mortality of California true fir species increased with stand-level functional diversity, although the effect was modulated by DBH and CI (Looney et al., 2023). Higher white fir mortality in pine--dominated plots may explain our finding of a positive white fir BAI--Percent pine effect under high competition, with white fir in pine-dominated plots responding to release following the recent death of neighboring fir trees. Our contrasting BAI and mortality results for species-mixture effects on white fir illustrate the importance of integrating multiple components of forest change.

Our study has several caveats reflecting the limitations of our

monitoring plot design. The relatively small acreage under group selection (15 percent of stand area) in the Pine Emphasis treatments may have contributed to our not detecting differences in mean plot-level structural complexity when addressing our first research question. Larger plot sizes would have captured more horizontal heterogeneity, while smaller plot sizes or stratified random sampling could have been more effective for sampling group vs. matrix conditions in the two Pine Emphasis treatments. Heat load, which we used to control for variations in local topography when addressing our second research question, was based on within-plot (0.081 ha) conditions and did not incorporate potentially important edge effects. Lack of within-plot spatial data prevented us from confining the scope of our analysis to trees growing in the interior of plots, as well as limited our ability to characterize local topography and tree neighborhoods, particularly for plot-edge trees.

5. Conclusions

The ecologically-based treatments of the Goosenest AMA study were successful in reducing neighborhood competition and restoring ponderosa pine dominance, which in turn affected tree growth, vigor, and survival. Our results have a number of implications for management. If the goal is to shift long-term compositional trends towards ponderosa pine, the Pine Emphasis with Fire treatment could aid in promoting pine growth, crown vigor, and survival, while further reducing the fir component and controlling understory competition through periodic prescribed burning. If managing for even-aged wood products production or habitat guidelines for key species such as the California spotted owl (*Strix occidentalis occidentalis*), where diameter caps commonly preclude the removal of large trees, the Big Tree treatment could provide an effective approach to controlling ladder fuels and promoting retained-tree growth, vigor, and survival regardless of species. However, ladder fuel reduction will be temporary in the absence of fire, due to natural regeneration. Simply reducing stand-level density without manipulating structural complexity or composition would provide an effective tactic for minimizing mortality in ponderosa pine, while improving crown vigor in both ponderosa pine and white fir. For climate change adaptation, mixed-species, uneven-aged management through the Pine Emphasis treatments could present a viable option for bolstering stand resistance and resilience to disturbances that target a single tree species. Alternatively, managing for a patchwork of single-species within-stand units could be used to promote the coexistence of ponderosa pine and white fir in California mixed-conifer forests, while minimizing antagonistic mixture effects between these species.

CRediT authorship contribution statement

Martin W. Ritchie: Data curation, Formal analysis, Funding acquisition, Project administration, Writing – review & editing. **Christopher J. Fettig:** Funding acquisition, Project administration, Writing – original draft, Writing – review & editing. **Eric E. Knapp:** Conceptualization, Funding acquisition, Project administration, Writing – review & editing. **Emily G. Brodie:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Christopher E. Looney:** Conceptualization, Formal analysis, Funding acquisition, Visualization, Writing – original draft.

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.

Acknowledgements

The USDA Forest Service Pacific Southwest Research Station provided support for this research. We thank current and former personnel of the Goosenest Ranger District of the Klamath National Forest and the Pacific Southwest Research Station for their assistance and support over the more than quarter-century of work at the Goosenest Adaptive Management Area.

Appendix

Table A1
List of hypothesis models by research question and response.

Research question	Hypothesis	Response	Varies as a function of:
1	0	CI	~1 (Intercept-only)
1	1	CI	~Trt
1	2	CI	~Trt + Year
1	3	CI	~Trt + Year + Trt x Year
1	0	SCI	~1 (Intercept-only)
1	1	SCI	~Trt
1	2	SCI	~Trt + Year
1	3	SCI	~Trt + Year + Trt x Year
1	0	% Pine	~1 (Intercept-only)
1	1	% Pine	~Trt
1	2	% Pine	~Trt + Year
1	3	% Pine	~Trt + Year + Trt x Year
2	0	log(BAI)	~log(DBH) +DBH^2 + Htl + El
2	1	log(BAI)	~log(DBH) +DBH^2+ Htl + El+ Trt
2	2	log(BAI)	~log(DBH) +DBH2+ Htl + El + CI
2	3	log(BAI)	~log(DBH) +DBH^2+ Htl + Trt + CI + CI x log(DBH) + CI x DBH2
2	4	log(BAI)	~log(DBH) +DBH^2+ El + Htl + CI + SCI
2	5	log(BAI)	~log(DBH) +DBH^2+ Htl + Trt + CI + SCI + SCI x log(DBH) + SCI x DBH2
2	6	log(BAI)	~log(DBH) +DBH^2+ El+ Htl + CI + SCI + SCI x CI
2	7	log(BAI)	~log(DBH) +DBH^2+ Htl + El+ CI + % Pine
2	8	log(BAI)	~log(DBH) +DBH^2+ Htl + Trt + CI + % Pine + % Pine x log(DBH) + % Pine x DBH2
2	9	log(BAI)	~log(DBH) +DBH2+ Htl + El+ CI + % Pine + SCI
2	10	log(BAI)	~log(DBH) +DBH2+ Htl + El+ CI + Trt + % Pine + CI x % Pine
2	11	log(BAI)	~log(DBH) +DBH2+ Htl + El+ CI + Trt + SCI + % Pine + SCI x % Pine
2	0	LCR	~Ht + Htl + El

(*continued on next page*)

Table A1 (*continued*)

Research question	Hypothesis	Response	Varies as a function of:
2	1	LCR	~Ht + Htl + El+ Trt
2	2	LCR	~Ht + Htl + El + CI
2	3	LCR	~Ht+ Htl + Trt + CI + CI x Ht
2	4	LCR	~Ht+ El + Htl + CI + SCI
2	5	LCR	~Ht+ Htl + Trt + CI + SCI + SCI x Ht
2	6	LCR	~Ht+ El+ Htl + CI + SCI + SCI x CI
2	7	LCR	~Ht+ Htl + El+ CI + % Pine
2	8	LCR	~Ht+ Htl + Trt + CI + % Pine + % Pine x Ht
2	9	LCR	~Ht+ Htl + El+ CI + % Pine + SCI
2	10	LCR	~Ht+ Htl + El+ CI + Trt + % Pine + CI x % Pine
2	11	LCR	~Ht+ Htl + El+ CI + Trt + SCI + % Pine + SCI x % Pine
2	0	Mortality	~DBH +DBH2 + Htl + El
2	1	Mortality	~DBH +DBH2+ Htl + El+ Trt
2	2	Mortality	~DBH +DBH2+ Htl + El + CI
2	3	Mortality	~DBH +DBH2+ Htl + Trt + CI + CI x DBH + CI x DBH2
2	4	Mortality	~DBH +DBH2+ El + Htl + CI + SCI
2	5	Mortality	~DBH +DBH2+ Htl + Trt + CI + SCI + SCI x DBH + SCI x DBH2
2	6	Mortality	~DBH +DBH2+ El+ Htl + CI + SCI + SCI x CI
2	7	Mortality	~DBH +DBH2+ Htl + El+ CI + % Pine
2	8	Mortality	~DBH +DBH2+ Htl + Trt + CI + % Pine + % Pine x DBH + % Pine x DBH2
2	9	Mortality	~DBH +DBH2+ Htl + El+ CI + % Pine + SCI
2	10	Mortality	~DBH +DBH2+ Htl + El+ CI + Trt + % Pine + CI x % Pine
2	11	Mortality	~DBH +DBH2+ Htl + El+ CI + Trt + SCI + % Pine + SCI x % Pine

Abbreviations are as follows: CI=Competition index; SCI=Structural complexity index; % Pine = Percent ponderosa pine stand density index; log(BAI)=log-transformed BAI; LCR=live crown ratio; trt=treatment; DBH=diameter at breast height; Ht=height; El=elevation; Htl=heatload. See Table 2 for complete model term descriptions.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121814.

References

Addington, R.N., Aplet, G.H., Battaglia, M.A., Briggs, J.S., Brown, P.M., Cheng, A.S., Dickinson, Y., Feinstein, J.A., Pelz, K.A., Regan, C.M., Thinnes, J., Truex, R., Fornwalt, P.J., Gannon, B., Julian, C.W., Underhill, J.L., Wolk, B., 2018. Principles and practices for the restoration of ponderosa pine and dry mixed-conifer forests of the Colorado Front Range, Gen. Tech. Rep. RMRS-GTR-373. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO. ⟨https://doi.org/10.2737/RMRS-GTR-373⟩.

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments, 211, 83–96 Forest Ecology and Management 211, 83–96. https://doi.org/10.1016/j.foreco.2005.01.034.

Bartoń, K., 2017. MuMln: Multi-Model Inference. R package version 1 (1), 40.

Bauhus, J., Forrester, D.I., Pretzsch, H., Felton, A., Pyttel, P., Benneter, A., 2017. Silvicultural Options for Mixed-Species Stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests: Ecology and Management. Springer, Berlin, Heidelberg, pp. 433–501. https://doi.org/10.1007/978-3-662-54553-9_9.

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. Old forests, new management: the conservation and use of old-growth forests in the 21st century For. Ecol. Manag. 258, 525–537. https://doi.org/10.1016/j.foreco.2009.01.053.

Bernal, A.A., Kane, J.M., Knapp, E.E., Zald, H.S.J., 2023. Tree resistance to drought and bark beetle-associated mortality following thinning and prescribed fire treatments. For. Ecol. Manag. 530, 120758 https://doi.org/10.1016/j.foreco.2022.120758.

Bigelow, S.W., Rollosson, A., Vogel, J., Whelan, A.W., Rother, M., 2023. Hardwoods influence effect of climate and intraspecific competition on growth of woodland longleaf pine trees. Ecosphere 14, e4482. https://doi.org/10.1002/ecs2.4482.

Brodie, E.G., Knapp, E.E., Latimer, A.M., Safford, H.D., Vossmer, M., Bisbing, S.M., 2023. The century-long shadow of fire exclusion: Historical data reveal early and lasting effects of fire regime change on contemporary forest composition. For. Ecol. Manag. 539, 121011 https://doi.org/10.1016/j.foreco.2023.121011.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., Lutz, J.A., 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. For. Ecol. Manag. 291, 442–457. https://doi.org/10.1016/j.foreco.2012.11.007.

Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. 97, 118–130. https://doi.org/10.1111/j.1365-2745.2008.01458.x.

Collins, B.M., Everett, R.G., Stephens, S.L., 2016. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. art51 Ecosphere. https://doi.org/10.1890/ES11-00026.1@10.1002/(ISSN)2150-8925(CAT)VirtualIssue(VI)ECS2.

Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. J. For. 95, 23.

Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: A review of its structure, content, and applications. Comput. Electron. Agric., Decision Support Systems for Forest Management 49, 60–80. https://doi.org/10.1016/j.compag.2005.02.003.

Crotteau, J.S., Keyes, C.R., 2020. Restoration Treatments Improve Overstory Tree Resistance Attributes and Growth in a Ponderosa Pine/Douglas-Fir Forest. Forests 11, 574. https://doi.org/10.3390/f11050574.

Curtis, R.O., Marshall, D.D., 2005. Permanent-plot procedures for silvicultural and yield research, Gen. Tech. Rep. PNW-GTR-634. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. ⟨https://doi.org/10.2737/PNW-GTR-634⟩.

D'Amato, A.W., Puettmann, K.J., 2004. The relative dominance hypothesis explains interaction dynamics in mixed species Alnus rubra/Pseudotsuga menziesii stands. J. Ecol. 92, 450–463. https://doi.org/10.1111/j.0022-0477.2004.00888.x.

Das, A., Battles, J., Mantgem, P.J., van, Stephenson, N.L., 2008. Spatial elements of mortality risk in old-growth forests. Ecology 89, 1744–1756. https://doi.org/10.1890/07-0524.1.

Das, A., Battles, J., Stephenson, N.L., van Mantgem, P.J., 2011. The contribution of competition to tree mortality in old-growth coniferous forests. For. Ecol. Manag. 261, 1203–1213. https://doi.org/10.1016/j.foreco.2010.12.035.

del Río, M., Pretzsch, H., Alberdi, I., Bielak, K., Bravo, F., Brunner, A., Condés, S., Ducey, M.J., Fonseca, T., von Lüpke, N., Pach, M., Peric, S., Perot, T., Souidi, Z., Spathelf, P., Sterba, H., Tijardovic, M., Tomé, M., Vallet, P., Bravo-Oviedo, A., 2016. Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. Eur. J. For. Res. 135, 23–49. https://doi.org/10.1007/s10342-015-0927-6.

Dobbertin, M., 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. Eur. J. For. Res. 124, 319–333. https://doi.org/10.1007/s10342-005-0085-3.

Ducey, M.J., 2009. The ratio of additive and traditional stand density indices. West. J. Appl. For. 24, 5–10. https://doi.org/10.1093/wjaf/24.1.5.

Erickson, C.C., Waring, K.M., 2014. Old Pinus ponderosa growth responses to restoration treatments, climate and drought in a southwestern US landscape. Appl. Veg. Sci. 17, 97–108. https://doi.org/10.1111/avsc.12056.

Ex, S.A., Smith, F.W., 2014. Wood production efficiency and growth dominance in multiaged and even-aged ponderosa pine stands. For. Sci. 60, 149–156. https://doi.org/10.5849/forsci.12-010.

Feng, Y., Schmid, B., Loreau, M., Forrester, D.I., Fei, S., Zhu, Jianxiao, Tang, Z., Zhu, Jiangling, Hong, P., Ji, C., Shi, Y., Su, H., Xiong, X., Xiao, J., Wang, S., Fang, J., 2022. Multispecies forest plantations outyield monocultures across a broad range of conditions. Science 376, 865–868. https://doi.org/10.1126/science.abm6363.

Fettig, C., Borys, R., Dabney, C., 2010. Effects of Fire and Fire Surrogate Treatments on Bark Beetle-Caused Tree Mortality in the Southern Cascades. California. For. Sci. 56, 60–73. https://doi.org/10.1093/forestscience/56.1.60.
Fettig, C.J., 2016. Native Bark Beetles and Wood Borers in Mediterranean Forests of California. In: Paine, T.D., Lieutier, F. (Eds.), Insects and Diseases of Mediterranean Forest Systems. Springer International Publishing, Cham, pp. 499–528. https://doi.org/10.1007/978-3-319-24744-1_18.
Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manag. 238, 24–53. https://doi.org/10.1016/j.foreco.2006.10.011.
Fettig, C.J., Runyon, J.B., Homicz, C.S., James, P.M.A., Ulyshen, M.D., 2022. Fire and Insect Interactions in North American Forests. Curr. For. Rep. 8, 301–316. https://doi.org/10.1007/s40725-022-00170-1.
Fiedler, C.E., Metlen, K.L., Dodson, E.K., 2010. Restoration Treatment Effects on Stand Structure, Tree Growth, and Fire Hazard in a Ponderosa Pine/Douglas-Fir Forest in Montana. For. Sci. 56, 18–31. https://doi.org/10.1093/forestscience/56.1.18.
Forrester, D.I., 2019. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. For. Ecol. Manag. 447, 139–157. https://doi.org/10.1016/j.foreco.2019.05.053.
Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity-productivity relationships in forests. Curr. For. Rep. 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2.
Franklin, J.F., Mitchell, R.J., Palik, B.J., others, 2007. Natural disturbance and stand development principles for ecological forestry, Gen. Tech. Rep. NRS-19. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newton Square, PA. ⟨https://doi.org/10.2737/NRS-GTR-19⟩.
Fulé, P.Z., Covington, W.W., Smith, H.B., Springer, J.D., Heinlein, T.A., Huisinga, K.D., Moore, M.M., 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. For. Ecol. Manag. 170, 19–41. https://doi.org/10.1016/S0378-1127(01)00759-9.
Grossiord, C., 2020. Having the right neighbors: how tree species diversity modulates drought impacts on forests. New Phytol 228, 42–49. https://doi.org/10.1111/nph.15667.
Hanewinkel, M., Kuhn, T., Bugmann, H., Lanz, A., Brang, P., 2014. Vulnerability of uneven-aged forests to storm damage. For. Int. J. For. Res. 87, 525–534. https://doi.org/10.1093/forestry/cpu008.
Hartig, F., 2018. DHARMa: residual diagnostics for hierarchical (Multi-level/mixed) regression models. R package version 0.20.
Holland, A.M., Rutledge, B.T., Jack, S.B., Stober, J.M., 2019. The longleaf pine forest: Long-term monitoring and restoration of a management dependent ecosystem. J. Nat. Conserv. 47, 38–50. https://doi.org/10.1016/j.jnc.2018.11.006.
Hood, S.M., Cluck, D.R., Jones, B.E., Pinnell, S., 2018. Radial and stand-level thinning treatments: 15-year growth response of legacy ponderosa and Jeffrey pine trees. Restor. Ecol. 26, 813–819. https://doi.org/10.1111/rec.12638.
Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S., 2023. multcomp: Simultaneous Inference in General Parametric Models. R package version 1, 4–24.
Huffman, D.W., Crouse, J.E., Sánchez Meador, A.J., Springer, J.D., Stoddard, M.T., 2018. Restoration benefits of re-entry with resource objective wildfire on a ponderosa pine landscape in northern Arizona, USA. For. Ecol. Manag. 408, 16–24. https://doi.org/10.1016/j.foreco.2017.10.032.
Ishii, H., Asano, S., 2010. The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. Ecol. Res. 25, 715–722. https://doi.org/10.1007/s11284-009-0668-4.
Jactel, H., Gritti, E.S., Drössler, L., Forrester, D.I., Mason, W.L., Morin, X., Pretzsch, H., Castagneyrol, B., 2018. Positive biodiversity–productivity relationships in forests: climate matters. Biol. Lett. 14, 20170747. https://doi.org/10.1098/rsbl.2017.0747.
James, G., Witten, D., Hastie, T., Tibshirani, R., 2013. An Introduction to Statistical Learning: with Applications in R, Springer Texts in Statistics. Springer-Verlag, New York. https://doi.org/10.1007/978-1-4614-7138-7.
Knapp, E., North, M., Benech, M., B. Estes, 2012. The variable-density thinning study at Stanislaus-Tuolumne Experimental Forest, in: North, Malcom (Ed.), Managing Sierra Nevada Forests. Gen. Tech. Rep. PSW-GTR-237. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Albany, CA, pp. 127-139. ⟨https://www.fs.usda.gov/research/treesearch/41092⟩.
Knapp, E.E., Bernal, A.A., Kane, J.M., Fettig, C.J., North, M.P., 2021. Variable thinning and prescribed fire influence tree mortality and growth during and after a severe drought. For. Ecol. Manag. 479, 118595 https://doi.org/10.1016/j.foreco.2020.118595.
Kolb, T.E., Agee, J.K., Fulé, P.Z., McDowell, N.G., Pearson, K., Sala, A., Waring, R.H., 2007. Perpetuating old ponderosa pine. For. Ecol. Manag. 249, 141–157. https://doi.org/10.1016/j.foreco.2007.06.002.
Koontz, M.J., Latimer, A.M., Mortenson, L.A., Fettig, C.J., North, M.P., 2021. Cross-scale interaction of host tree size and climatic water deficit governs bark beetle-induced tree mortality. Nat. Commun. 12 https://doi.org/10.1038/s41467-020-20455-y.
Korb, J.E., Fulé, P.Z., Stoddard, M.T., 2012. Forest restoration in a surface fire-dependent ecosystem: An example from a mixed conifer forest, southwestern Colorado, USA. For. Ecol. Manag. 269, 10–18. https://doi.org/10.1016/j.foreco.2012.01.002.
Larocque, G.R., Luckai, N., Adhikary, S.N., Groot, A., Bell, F.W., Sharma, M., 2012. Competition theory — science and application in mixed forest stands: review of experimental and modelling methods and suggestions for future research. Environ. Rev. 21, 71–84. https://doi.org/10.1139/er-2012-0033.
Larson, A.J., Lutz, J.A., Gersonde, R.F., Franklin, J.F., Hietpas, F.F., 2008. Potential Site Productivity Influences the Rate of Forest Structural Development. Ecol. Appl. 18, 899–910. https://doi.org/10.1890/07-1191.1.
Lenth, R.V., Singmann, H., Love, J., Buerkner, P., Herve, M., 2020. Emmeans: Estimated marginal means, aka least-squares means. R package version 1.10.0.
Long, J.N., Daniel, T.W., 1990. Assessment of growing stock in uneven-aged stands. West. J. Appl. For. 5, 93–96. https://doi.org/10.1093/wjaf/5.3.93.
Long, J.N., Shaw, J.D., 2010. The influence of compositional and structural diversity on forest productivity. For. Int. J. For. Res. 83, 121–128. https://doi.org/10.1093/forestry/cpp033.
Looney, C.E., Long, J.W., Fettig, C.J., Fried, J.S., Wood, K.E.A., Audley, J.P., 2023. Functional diversity affects tree vigor, growth, and mortality in mixed-conifer/hardwood forests in California, U.S.A, in the absence of fire. For. Ecol. Manag. 544, 121135 https://doi.org/10.1016/j.foreco.2023.121135.
Looney, C.E., Previant, W.J., Nagel, L.M., 2020. Variations in tree growth provide limited evidence of species mixture effects in Interior West U.S.A. mixed-conifer forests. J. Ecol. https://doi.org/10.1111/1365-2745.13523.
Lu, H., Condés, S., del Río, M., Goudiaby, V., den Ouden, J., Mohren, G.M.J., Schelhaas, M.-J., de Waal, R., Sterck, F.J., 2018. Species and soil effects on overyielding of tree species mixtures in the Netherlands. For. Ecol. Manag. 409, 105–118. https://doi.org/10.1016/j.foreco.2017.11.010.
Madrigal-González, J., Ruiz-Benito, P., Ratcliffe, S., Calatayud, J., Kändler, G., Lehtonen, A., Dahlgren, J., Wirth, C., Zavala, M.A., 2016. Complementarity effects on tree growth are contingent on tree size and climatic conditions across Europe. Sci. Rep. 6, 32233 https://doi.org/10.1038/srep32233.
Magnusson, A., Skaug, H., Berg, C., Kristensen, M., van Bentham, K., Bolker, B., Brooks, M., 2018. glmmTMB: Generalized Linear Mixed Models using Template Model Builder. R package version 0.2.2.0.
McCune, B., 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. J. Veg. Sci. 18, 751–754. https://doi.org/10.1111/j.1654-1103.2007.tb02590.x.
Mina, M., Huber, M.O., Forrester, D.I., Thürig, E., Rohner, B., 2018. Multiple factors modulate tree growth complementarity in Central European mixed forests. J. Ecol. 106, 1106–1119. https://doi.org/10.1111/1365-2745.12846.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.
North, M., Stein, P., O'Hara, K., Zielinski, W., Stephens, S., 2009. An ecosystem management strategy for Sierran mixed-conifer forests, Gen. Tech. Rep. PSW-GTR-220 (Second printing, with addendum). U.S. Dept. of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
O'Hara, K.L., Nagel, L.M., 2013. The Stand: Revisiting a Central Concept in Forestry. J. For. 111, 335–340. https://doi.org/10.5849/jof.12-114.
O'Hara, K.L., Nagel, L.M., 2006. A Functional Comparison of Productivity in Even-Aged and Multiaged Stands: A Synthesis for Pinus ponderosa. For. Sci. 52, 290–303. https://doi.org/10.1093/forestscience/52.3.290.
Oliver, W.W., 1990. Spacing and Shrub Competition Influence 20-Year Development of Planted Ponderosa Pine. West. J. Appl. For. 5, 79–82. https://doi.org/10.1093/wjaf/5.3.79.
Palik, B.J., D'Amato, A.W., Franklin, J.F., Johnson, K.N., 2020. Ecological Silviculture: Foundations and Applications. Waveland Press.
Pommerening, A., Maleki, K., Haufe, J., 2021. Tamm Review: Individual-based forest management or Seeing the trees for the forest. For. Ecol. Manag. 501, 119677 https://doi.org/10.1016/j.foreco.2021.119677.
Puettmann, K.J., Coates, K.D., Messier, C.C., 2012. A critique of silviculture: managing for complexity. Island Press, Washington D.C.
Quantum GIS Development Team, 2020. QGIS Geographic Information System.
R Core Team, 2022. R: A language and environment for statistical computing.
Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.
Richards, S.A., 2008. Dealing with overdispersed count data in applied ecology. J. Appl. Ecol. 45, 218–227. https://doi.org/10.1111/j.1365-2664.2007.01377.x.
Ritchie, M.W., 2020. Effects of thinning and prescribed fire in the Goosenest Adaptive Management Area in northeastern California, in: Pile, L.S., Deal, R.L., Dey, D.C., Gwaze, D., Kabrick, J.M., Palik, B.J., Schuler, T.M. (Eds.), The 2019 National Silviculture Workshop: A Focus on Forest Management-Research Partnerships, Gen. Tech. Rep. NRS-P-193. U.S. Department of Agriculture, Forest Service, Northern Research Station, Madison, WI, pp. 193–206. ⟨https://doi.org/10.2737/NRS-GTR-P-193-paper25⟩.
Ritchie, M.W., 2005. Ecological research at the Goosenest Adaptive Management Area in northeastern California, Gen. Tech. Rep. PSW-GTR-192. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. ⟨https://doi.org/10.2737/PSW-GTR-192⟩.
Ritchie, M.W., Hann, D.W., 1987. Equations for predicting height to crown base for fourteen tree species in southwest Oregon, Research Paper 50. Oregon State University. Forest Research Laboratory, Corvallis, OR.
Ritchie, M.W., Harcksen, K.A., 2005. Accelerating development of late-successional features in second-growth pine stands of the Goosenest Adaptive Management Area, in: Ritchie, M.W., Maguire, D.A., Youngblood, A. (Eds.), Proceedings of the Symposium on Ponderosa Pine: Issues, Trends, and Management, 2004 October 18-21, Klamath Falls, OR., Gen. Tech. Rep PSW-GTR-198. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 81-93. ⟨https://www.fs.usda.gov/psw/publications/documents/psw_gtr198/psw_gtr198.pdf⟩.
Ritter, S.M., Hoffman, C.M., Battaglia, M.A., Jain, T.B., 2022. Restoration and fuel hazard reduction result in equivalent reductions in crown fire behavior in dry conifer forests. Ecol. Appl. 32, e2682 https://doi.org/10.1002/eap.2682.

Roberts, S.D., Harrington, C.A., 2008. Individual tree growth response to variable-density thinning in coastal Pacific Northwest forests. Large-scale experimentation and oak regeneration For. Ecol. Manag. 255, 2771–2781. https://doi.org/10.1016/j.foreco.2008.01.043.

Safford, H.D., Stevens, J.T., 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA, Gen. Tech. Rep. PSW-GTR-256. U.S. Dept. of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA. ⟨https://doi.org/10.2737/PSW-GTR-256⟩.

Schomaker, M.E., Zarnoch, S.J., Bechtold, W.A., Latelle, D.J., Burkman, W.G., Cox, S.M.;, 2007. Crown-condition classification: A guide to data collection and analysis., Gen. Tech. Rep. SRS-102. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. ⟨https://doi.org/10.2737/SRS-GTR-102⟩.

Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C.J., Fiedler, C. E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., Skinner, C.N., Stephens, S.L., Waldrop, T.A., Yaussy, D.A., Youngblood, A., 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecol. Appl. 19, 285–304. https://doi.org/10.1890/07-1747.1.

Seidel, K.W., 1985. A ponderosa pine-grand fir spacing study in central Oregon: results after 10 years, USDA Forest Service PNW Research Note No. 429. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR. ⟨https://doi.org/10.2737/PNW-RN-429⟩.

Stephens, S.L., Finney, M.A., 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For. Ecol. Manag. 162, 261–271. https://doi.org/10.1016/S0378-1127(01)00521-7.

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, 944–955. https://doi.org/10.1111/geb.13079.

Sugiura, N., 1978. Further analysts of the data by Akaike's information criterion and the finite corrections. Commun. Stat. - Theory Methods 7, 13–26. https://doi.org/10.1080/03610927808827599.

U.S. Geological Survey, 2016. The National Map: 3D Elevation Program (3DEP) [WWW Document]. URL ⟨http://nationalmap.gov/3DEP/3dep_prodserv.html⟩ (accessed 12.30.16).

Uzoh, F.C.C., Oliver, W.W., 2008. Individual tree diameter increment model for managed even-aged stands of ponderosa pine throughout the western United States using a multilevel linear mixed effects model. For. Ecol Manage 256 (3), 438–445, 256, 438–445.

Vogeler, J.C., Hudak, A.T., Vierling, L.A., Vierling, K.T., 2013. Lidar-Derived Canopy Architecture Predicts Brown Creeper Occupancy of Two Western Coniferous Forests. The Condor 115, 614–622. https://doi.org/10.1525/cond.2013.110082.

Wood, S., 2012. mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation. R package version 1.9-1.

Wykoff, W.R., 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. For. Sci. 36, 1077–1104.

Yang, Y., Titus, S.J., Huang, S., 2003. Modeling individual tree mortality for white spruce in Alberta. Ecol. Model. 163, 209–222. https://doi.org/10.1016/S0304-3800(03)00008-5.

Zald, H.S.J., Callahan, C.C., Hurteau, M.D., Goodwin, M.J., North, M.P., 2022. Tree growth responses to extreme drought after mechanical thinning and prescribed fire in a Sierra Nevada mixed-conifer forest, USA. For. Ecol. Manag. 510, 120107 https://doi.org/10.1016/j.foreco.2022.120107.

Zarnoch, S.J., Bechtold, W.A., Stolte, K.W., 2004. Using crown condition variables as indicators of forest health. Can. J. For. Res. 34, 1057–1070. https://doi.org/10.1139/x03-277.

Zeller, L., Pretzsch, H., 2019. Effect of forest structure on stand productivity in Central European forests depends on developmental stage and tree species diversity. For. Ecol. Manag. 434, 193–204. https://doi.org/10.1016/j.foreco.2018.12.024.

Zhang, J., Ritchie, M.W., Maguire, D.A., Oliver, W.W., 2013. Thinning ponderosa pine (Pinus ponderosa) stands reduces mortality while maintaining stand productivity. Can. J. For. Res. 43, 311–320. https://doi.org/10.1139/cjfr-2012-0411.

Zhang, J., Ritchie, M.W., Oliver, W.W., 2008. Vegetation responses to stand structure and prescribed fire in an interior ponderosa pine ecosystemThis article is one of a selection of papers from the Special Forum on Ecological Studies in Interior Ponderosa Pine — First Findings from Blacks Mountain Interdisciplinary Research. Can. J. For. Res. 38, 909–918. https://doi.org/10.1139/X07-230.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. GLM and GAM for Absence–Presence and Proportional Data. In: Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. (Eds.), Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer, New York, NY, pp. 245–259. https://doi.org/10.1007/978-0-387-87458-6_10.