Spatially nonrandom tree mortality and ingrowth maintain equilibrium pattern in an old-growth *Pseudotsuga–Tsuga* forest

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Abstract. Mortality processes in old-growth forests are generally assumed to be driven by gap-scale disturbance, with only a limited role ascribed to density-dependent mortality, but these assumptions are rarely tested with data sets incorporating repeated measurements. Using a 12-ha spatially explicit plot censused 13 years apart in an approximately 500-year-old *Pseudotsuga–Tsuga* forest, we demonstrate significant density-dependent mortality and spatially aggregated tree recruitment. However, the combined effect of these strongly nonrandom demographic processes was to maintain tree patterns in a state of dynamic equilibrium. Density-dependent mortality was most pronounced for the dominant late-successional species, *Tsuga heterophylla*. The long-lived, early-seral *Pseudotsuga menziesii* experienced an annual stem mortality rate of 0.84% and no new recruitment. Late-seral species *Tsuga* and *Abies amabilis* had nearly balanced demographic rates of ingrowth and mortality. The 2.34% mortality rate for *Taxus brevifolia* was higher than expected, notably less than ingrowth, and strongly affected by proximity to *Tsuga*. Large-diameter *Tsuga* structured both the regenerating conspecific and heterospecific cohorts with recruitment of *Tsuga* and *Abies* unlikely in neighborhoods crowded with large-diameter competitors ($P < 0.001$). Density-dependent competitive interactions strongly shape forest communities even five centuries after stand initiation, underscoring the dynamic nature of even equilibrial old-growth forests.

Key words: Abies amabilis; long-term data sets; Pseudotsuga menziesii; Taxus brevifolia; tree mortality; Tsuga heterophylla; Wind River Forest Dynamics Plot.

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Introduction

Detecting and understanding changes in forest composition and structure is critical to understanding how forests are responding to environmental variability and change, but subtle changes can often be missed by insufficient sample size or temporal interval. With demographic rates of annual ingrowth and mortality averaging <1% to 3% in old-growth forests (Larson and Franklin 2010, Runkle 2013), changes to less abundant species or subpopulations may be impossible to detect with small numbers of individuals or short periods of observation. Furthermore, even when demographic rates of ingrowth and mortality are balanced, forest structure and tree spatial patterns may be changing (Getzin et al. 2006, Das et al. 2011).

Most conceptual models of temperate old-growth forest dynamics assume that change is primarily driven by small-scale disturbances such as wind, insects, and pathogens (operating without Janzen-Connell effects, but see Das et al. [2008]), and that competitive density-dependent mortality has ceased to play a major role, with the remaining large trees widely spaced and permissive of understory regeneration (Franklin et al. 2002). In contrast, He and Duncan (2000) and Getzin et al. (2006) inferred density-dependent mortality in old-growth conifer forests, but their studies were based on pattern analysis of a single census. Work from mature and old-growth *Pinus resinosa* (red pine) forests in northern Minnesota (Aakala et al. 2012, Silver et al. 2013) found no evidence for density-dependent mortality, and Das et al. (2011) found only modest support for competitive density-dependent mortality in mixed-conifer forests.

In our previous work using the initial surveys of two permanent 25.6-ha plots (Lutz et al. 2012, 2013), we proposed a generally limited role for competitive mortality as a driver of tree spatial patterns in old-growth conifer forests. But we also found spatial segregation of understory and canopy trees (Larson and Franklin 2006), especially for large-diameter *Tsuga*

heterophylla (Raf.) Sarg., suggesting that those individuals could influence forest dynamics through competitive interactions (Lutz et al. 2013). Based on that work, we expected ingrowth to be strongly suppressed in the neighborhood of large-diameter *Tsuga*. This hypothesis is supported by Getzin et al. (2006), who found evidence for strong intraspecific competition based on spatial relationship of live and dead *Tsuga* at their Vancouver Island study site, and by Stewart (1986), who found limited understory tree recruitment when the main canopy was dominated by *Tsuga*.

In the current study, we predicted that *Tsuga*, especially the large-diameter subpopulation, act as strong organizers of spatially structured tree demography at decadal scales, particularly on ingrowth of shade-tolerant species. Using a 12-ha old-growth *Pseudotsuga–Tsuga* forest plot sampled at a 13-year interval (1999–2012), we addressed three questions: (1) Were there significant demographic changes in shade-intolerant and shade-tolerant tree species, (2) notwithstanding constant demography (a balance of ingrowth and mortality), did spatial patterning of the forest trees change due to nonrandom mortality and ingrowth, and (3) what species and subpopulations caused changes in spatial pattern? Further, because of the apparent contradictions in the literature (e.g., Getzin et al. 2006, Silver et al. 2013), we specifically tested the prediction of competitive density-dependent mortality, and also tested our hypothesis (Lutz et al. 2013) of competitive inhibition of tree recruitment by large-diameter trees.

Study Area

The study site is located in the *Pseudotsuga–Tsuga* (Douglas-fir/western hemlock) forest in the T. T. Munger Research Natural Area of the Gifford Pinchot National Forest in western Washington State, USA (45.82° N, 121.96° W) between 352 m and 379 m elevation. Tree composition is primarily conifers consisting of the shade-tolerant *Tsuga heterophylla*, *Taxus brevifolia* Nutt., *Thuja plicata* Donn ex D. Don, and *Abies amabilis* Douglas ex J. Forbes, and the shade-intolerant *Pseudotsuga menziesii* (Mirb.) Franco. *Pseudotsuga* constitutes about two-thirds of the largest trees, with a maximum age about 500 years (inferred from ring counts on stumps in adjacent clearcuts; Franklin and DeBell 1988). Plant nomenclature follows Flora of North America (Flora of North America Editorial Committee 1993+). Following disturbance, the archetypical successional sequence involves establishment of a relatively even-aged *Pseudotsuga* cohort, intense intra-cohort competition and density-dependent mortality, gap creation, and subsequent recruitment of shade-tolerant species, especially *Tsuga* (e.g., Franklin et al. 2002).

Methods

Field sampling

In 1999, a 12-ha permanent forest plot (400 × 300 m) was established in which all live and dead trees ≥5 cm dbh (diameter at breast height; 1.3 m above the forest floor) were identified to species, mapped, and tagged (Chen et al. 2004). In 2010, the 12-ha plot was overlain and incorporated into a 25.6-ha plot (800 × 320 m) during the establishment of the Wind River Forest Dynamics Plot (Lutz et al. 2013; see Plate 1). Within the new 25.6-ha plot, all live trees and shrubs ≥1 cm dbh and all snags ≥10 cm were identified, mapped, and tagged, noting tag numbers from the 1999 survey to facilitate merging the two data sets. In 2012, we located and reconciled all trees, snags, and downed stems from the 1999 data set that were not present in the 2010 data set.

Analyses

We generated annually compounded demographic rates for mortality and ingrowth. We similarly generated the annual basal area increment for those trees that were alive in both censuses. To examine changes in tree spatial patterns (Appendix: Fig. A1), we used the univariate, bivariate, and multi-type forms of the pair correlation function, $g(r)$, to quantify at inter-tree distance r the spatial patterns of tree mortality and ingrowth, and spatial relationships between mapped tree subpopulations represented as marked point patterns (Wiegand and Moloney 2004). The pair correlation function is defined as

$$g(r) = \frac{K'(r)}{2\pi r}$$

where $K'(r)$ is the derivative of Ripley's K function. The bivariate form, $g_{i,j}(r)$, quantifies spatial relationships between points of type i and j; the multi-type form, $g_{i,\cdot}(r)$, characterizes relationships between points of type i and all other types. Values of $g(r) > 1$ indicate spatial aggregation, while values <1 suggest spatial uniformity. All analyses were performed in the statistical program R version 3.0.0 (R Development Core Team 2013) and used functions in the spatstat library (Baddeley and Turner 2005). Estimates of $g(r)$ used isotropic edge correction; details on estimation are provided in the spatstat documentation (Baddeley and Turner 2005).

We conducted exploratory analyses of the overall change in tree patterns, spatial pattern of mortality, spatial relationships between dead and surviving trees, and spatial patterns of tree ingrowth. We quantified the net change (i.e., arising from the combined effect of mortality and ingrowth) in tree patterns from 1999 to 2012 with the summary statistic $g_{2012}(r) - g_{1999}(r)$. The expected value of this statistic under random mortality and ingrowth is zero; positive values indicate that tree patterns became more aggregated; negative values indicate that tree patterns became more uniform. We used $g_{d,d}(r)$ to determine if mortality was aggregated within the initial live tree population and $g_{d,l}(r)$ to evaluate if dead (d) and surviving trees (live, l) were segregated or attracted (Raventós et al. 2010). Patterns of ingrowth were quantified using the inhomogeneous (inh) pair correlation function, $g_{inh}(r)$, because of the
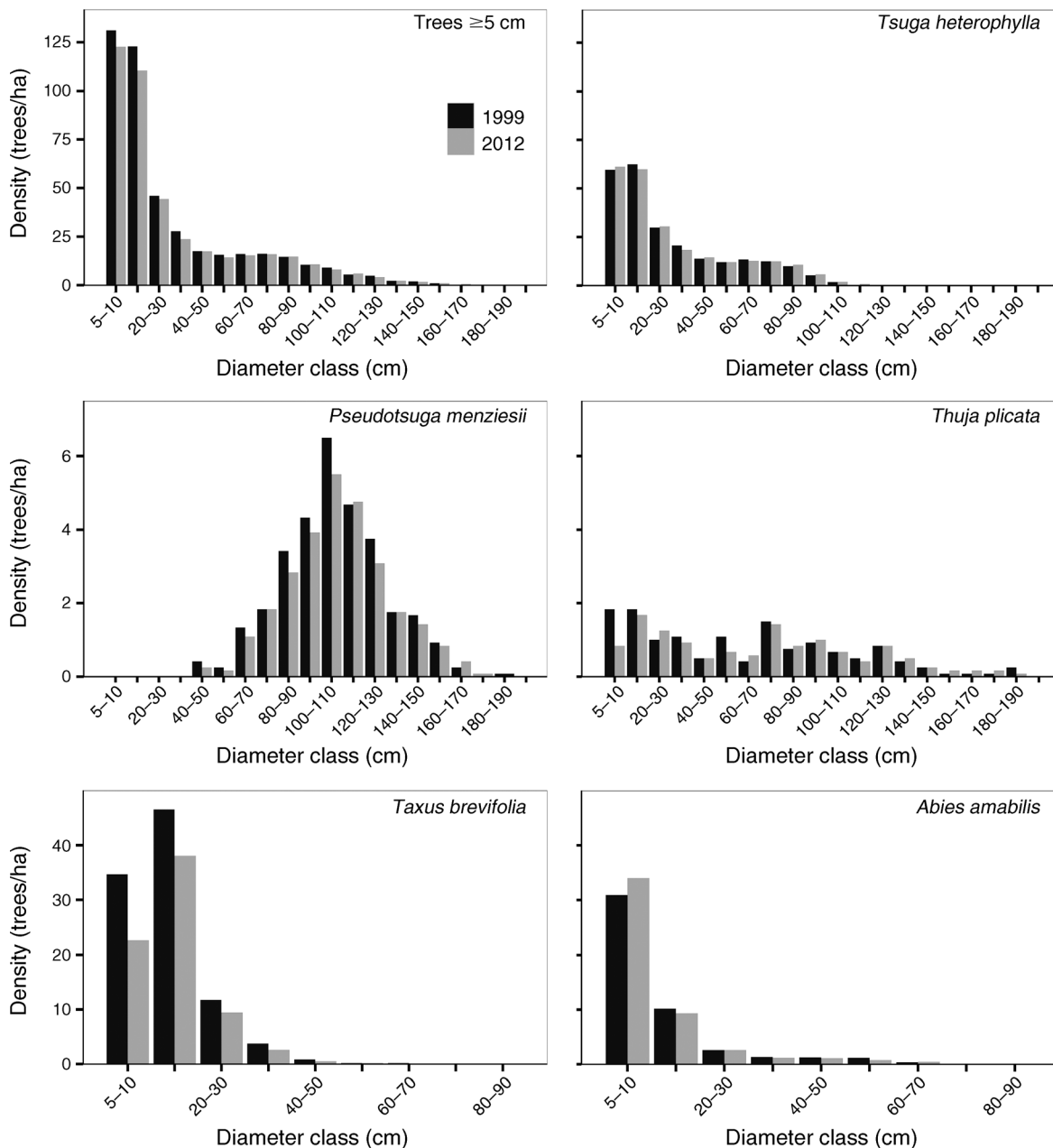
FIG. 1. Diameter distributions for all trees ≥5 cm dbh and those species with $n \geq 150$ present in 1999 and 2012 in the T. T. Munger Research Natural Area of the Gifford Pinchot National Forest in western Washington State, USA.

obvious heterogeneity of ingrowth across the plot (Baddeley et al. 2000, Das et al. 2011). We simulated random mortality using random labeling (Goreaud and Pélissier 2003) and random ingrowth as an inhomogeneous Poisson process with intensity estimated from observed ingrowth locations.

We used two different statistics and the null model of random mortality (Goreaud and Pélissier 2003) to test for density-dependent competitive mortality. First, we assessed if the initial neighborhoods of surviving trees differed from those of trees that died during the study

period using $g_{i,.}(r)$. Under random mortality $g_{d,all}(r) - g_{1,all} = 0$ (Yu et al. 2009, Jacquemyn et al. 2010). If mortality is density-dependent, then $g_{d,all}(r) - g_{1,all} > 0$, indicating that trees that died had more crowded initial neighborhoods than trees that survived. Competitive density-dependent mortality is expected to cause the pattern of live trees to become more uniform through time (Das et al. 2011, Aakala et al. 2012, Silver et al. 2013). Therefore, we quantified the change in pattern of surviving trees due to mortality. If mortality is random then the initial (live + dead trees in 2012) and final (live

TABLE 1. Tree demography between 1999 and 2012 in the 12-ha study site in the T. T. Munger Research Natural Area of the Gifford Pinchot National Forest, Washington State, USA.

Species	Family	Trees						Basal area						
				Ingrowth		Mortality					Ingrowth		Mortality	
		1999 (no. trees)	2012 (no. trees)	No. trees	Rate	No. trees	Rate	1999 (m^2)	2010 (m^2)	Growth rate	Area (m^2)	Rate	Area (m^2)	Rate
Abies amabilis	Pinaceae	574	593	132	1.60	113	1.67	13.77	12.38	0.97	0.36	0.20	2.91	1.81
Abies grandis†	Pinaceae	46	30	⋯	⋯	16	3.23	7.76	5.70	0.82	⋯	⋯	2.55	3.01
Abies procera†	Pinaceae	7	7	⋯	⋯	⋯	⋯	2.24	2.23‡	0.05	⋯	⋯	⋯	⋯
Alnus rubra	Betulaceae	3	5	2	4.01	⋯	⋯	0.06	0.05‡	3.75	0.01	1.09	⋯	⋯
Cornus nuttallii	Cornaceae	57	58	17	2.03	16	2.50	0.41	0.35	1.52	0.06	1.03	0.14	3.04
Pinus monticola	Pinaceae	7	2	⋯	⋯	5	9.19	4.10	0.95	0.122	⋯	⋯	3.17	10.81
Pseudotsuga menziesii	Pinaceae	374	335	⋯	⋯	39	0.84	349.42	319.19	0.234	⋯	⋯	37.61	0.87
Taxus brevifolia	Taxaceae	1173	877	15	0.10	311	2.34	24.72	18.36	0.38	0.07	0.02	4.87	1.67
Thuja plicata	Cupressaceae	169	156	⋯	⋯	13	0.61	80.51	85.12	0.90	⋯	⋯	0.47	0.05
Tsuga heterophylla	Pinaceae	2900	2894	206	0.53	212	0.58	374.45	387.87	0.79	0.62	0.01	16.51	0.34
All species		5310	4957	372	0.52	725	1.12	857.44	832.20	0.63	1.12	0.01	68.23	0.63

Notes: Ingrowth, mortality, and growth rates reflect annually compounded rates (expressed as a percent). Growth rate was calculated using those trees where $dbh_{2012} - dbh_{1999} \geq -1$ cm, with dbh representing diameter at breast height. Ellipses indicate "no data."

† *Abies grandis* and *Abies procera* were not pooled with *Abies amabilis* in the spatial analyses.

‡ Overall basal area of *Abies procera* and *Alnus rubra* declined because of mechanical damage to one tree for each species. Growth rates were calculated based on the undamaged individuals.

only in 2012) patterns will not differ: $g_{1,1}(r) - g_{1+d,1+d}(r) = 0$. If mortality is density-dependent, causing the pattern of surviving trees to become more uniform, then $g_{1,1}(r) - g_{1+d,1+d}(r) < 0$ We similarly evaluated if ingrowth changed the pattern of trees that survived to 2012 with $g_{1+ing,1+ing}(r) - g_{1,1}(r)$. If ingrowth caused the pattern of surviving trees to become more aggregated, then $g_{1+ing,1+ing}(r) - g_{1,1}(r) > 0$.

We used the null model of population independence (simulated by toroidal displacement of the ingrowth population [Goreaud and Pélissier 2003]) with $g_{i,j}(r)$ to test the predictions that large-diameter (≥ 70 cm dbh) *Tsuga heterophylla*, in particular, and large-diameter trees in general, constrain the spatial pattern of ingrowth through asymmetrical competition (Larson and Franklin 2006, Lutz et al. 2013). If large-diameter trees (lrg) suppress ingrowth, then $g_{lrg,ing}(r) < 0$.

Monte Carlo methods with the respective null models were used for exploratory analysis and plotting, and also combined with the goodness-of-fit (GoF) test of Loosmore and Ford (2006) for formal inference ($n = 2000$ simulations for each analysis). All GoF tests were performed at distances of 9 m, our estimate of the effective tree neighborhood for temperate old-growth conifer forests (Das et al. 2011, Larson et al. 2012), and the scale up to which we expect density-dependent competitive processes to occur and resultant changes of tree patterns to manifest. We only considered individual species with $n \geq 150$ individuals in both 1999 and 2012.

RESULTS

Between 1999 and 2012, tree composition changed little in absolute terms, with slight declines in both the numbers of trees and basal area of most species (Fig. 1, Table 1). The initial cohort of shade intolerant *Pseudotsuga* declined as expected. However, there were also large declines in the very shade-tolerant *Taxus*. Increases in basal area were limited to the shade-tolerant *Thuja* and *Tsuga*. Mortality and ingrowth rates were relatively balanced in demographic terms (Table 1), but *Pinus monticola* and *Abies grandis* experienced declines of larger diameter trees (Table 1).

Tree spatial patterns (for all species pooled) experienced no net change from 1999 to 2012, despite strongly nonrandom tree mortality and ingrowth (Fig. 2A). Mortality was aggregated up to ~30 m, and again at ~45 m, with the strongest aggregation apparent at distances <7 m (Fig. 2B; Appendix: Fig. A2). No spatial relationships were evident between live and dead trees for all species pooled or for individual species (Appendix: Fig. A3). At the tree neighborhood scale (≤9 m), we found evidence for density-dependent mortality for all species pooled (GoF test, $P < 0.001$; Fig. 2C). This density-dependent mortality caused the spatial distribution of surviving trees to become significantly more uniform by 2012 (GoF test, $P < 0.001$; Fig. 2D). The increasing spatial uniformity caused by density-dependent mortality was offset by strongly aggregated ingrowth (Fig. 2E), especially of *Tsuga* (Appendix: Fig. A4). Ingrowth caused the pattern of trees that survived to 2012 to become more aggregated (Fig. 2F), with both *Abies* and *Tsuga* contributing to this shift (Appendix: Fig. A5), ultimately maintaining tree patterns in dynamic equilibrium over the 13-year study period (Fig. 2A).

The density-dependent mortality detected at the community level appears largely attributable to *Tsuga heterophylla*. Intraspecific density-dependent mortality of
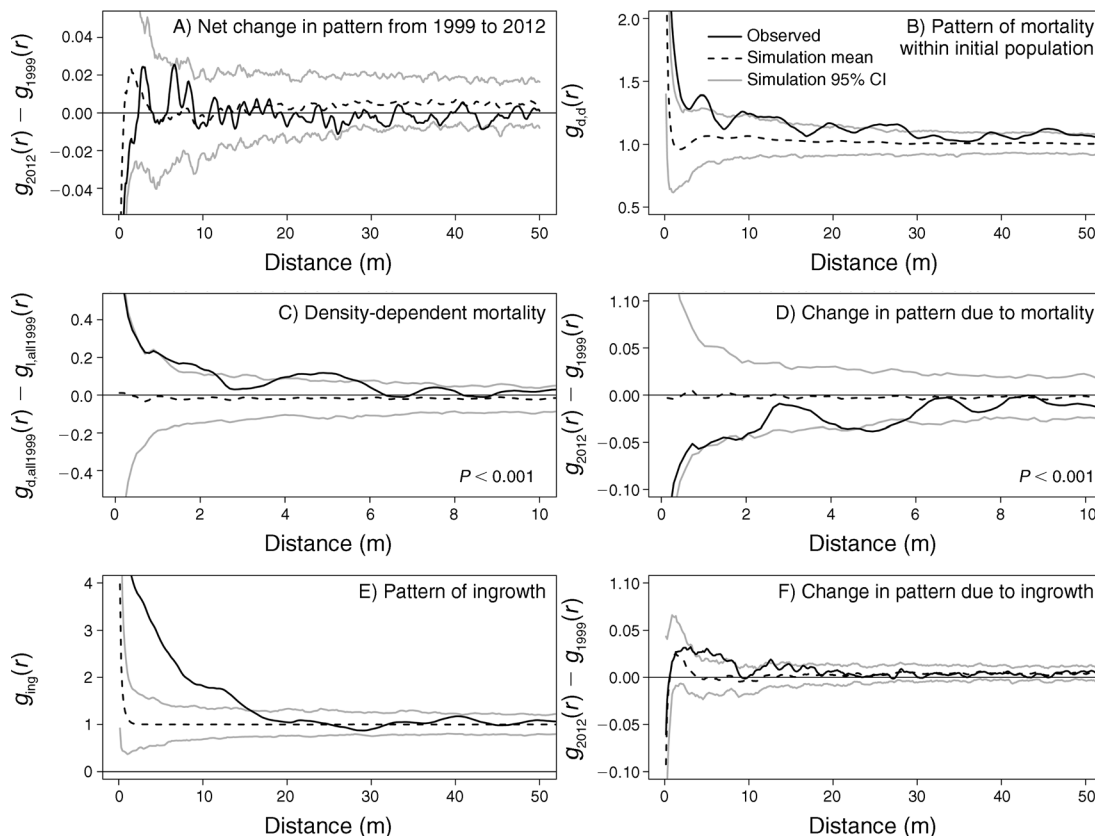
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Fig. 2. Overall changes in tree patterns, and patterns of mortality and ingrowth, 1999–2012. (A) Net change in pattern resulting from combined mortality and ingrowth. Values above (below) the simulation envelope indicate that the pattern became more aggregated (uniform) during the study. (B) Spatial pattern of mortality conditioned on the initial pattern of live trees. Values above (below) the simulation envelope indicate aggregated (dispersed) mortality. (C) Density-dependent mortality. Values above (below) the simulation envelope indicate that the initial 1999 neighborhoods of trees that died by 2012 were more (less) crowded the initial neighborhoods of trees that survived to 2012. (D) Change in pattern due to mortality. Values above (below) the simulation envelope indicate that the pattern of surviving trees became more aggregated (dispersed) due to mortality. (E) Spatial pattern of ingrowth. Values above (below) the simulation envelope indicate that ingrowth is more aggregated (dispersed) than expected. (F) Change in pattern due to ingrowth. Values above (below) the simulation envelope indicate that the pattern of surviving trees became more aggregated (dispersed) due to ingrowth. For each panel, the function "g" is the pair correlation function at inter-tree distance "r"; subscript abbreviations are: d, dead; l, live; and ing, ingrowth. P values are based on the goodness-of-fit test of Loosmore and Ford (2006).

Tsuga ($P = 0.025$; Appendix: Fig. A6) caused surviving *Tsuga* to become more uniformly distributed ($P = 0.041$; Appendix: Fig. A7). But, *Tsuga* also suffered heterospecific density-dependent mortality ($P = 0.015$; Appendix: Fig. A8), as did *Taxus* ($P = 0.002$; Appendix: Fig. A8). *Tsuga* were apparently strong competitors against *Taxus* and *Thuja*. *Taxus* that died had more *Tsuga* in their initial (1999) neighborhoods than did *Taxus* that survived ($P < 0.001$; Appendix: Fig. A9); and dying *Thuja* had more large-diameter *Tsuga* in their initial neighborhoods than did *Thuja* that survived ($P = 0.026$; Appendix: Fig. A10). No evidence for conspecific or heterospecific density-dependent mortality was found for either *Abies* or *Pseudotsuga* (Appendix: Figs. A6–A10).

Overstory trees ≥ 70 cm dbh of *Tsuga* ($n = 344$) and all other species combined ($n = 402$) inhibited recruitment of new individuals into the tagged tree population. Locations of *Tsuga* ingrowth, *Abies* ingrowth, and ingrowth of

all species combined were spatially segregated from large-diameter trees (Fig. 3). The inhibitory effect of large-diameter *Tsuga* on ingrowth was stronger than that of large-diameter stems of other species (Fig. 3).

Discussion

Overall changes in the abundance of species generally followed our expectations. The decline of *Pseudotsuga* matched predictions for this forest type: a gradual loss of the shade-intolerant pioneer cohort (Franklin et al. 2002). Declines in *Pinus monticola* were mostly due to endemic activity of *Dendroctonus ponderosae* (mountain pine beetle), and potentially to past infection with *Cronartium ribicola* (white pine blister rust), as inferred from visits to those trees in 2012. Demographic rates of ingrowth and mortality were almost perfectly balanced for the shade-tolerant species *Tsuga* and *Abies*. Mortality of *Taxus* was surprising because the 2.34% per year
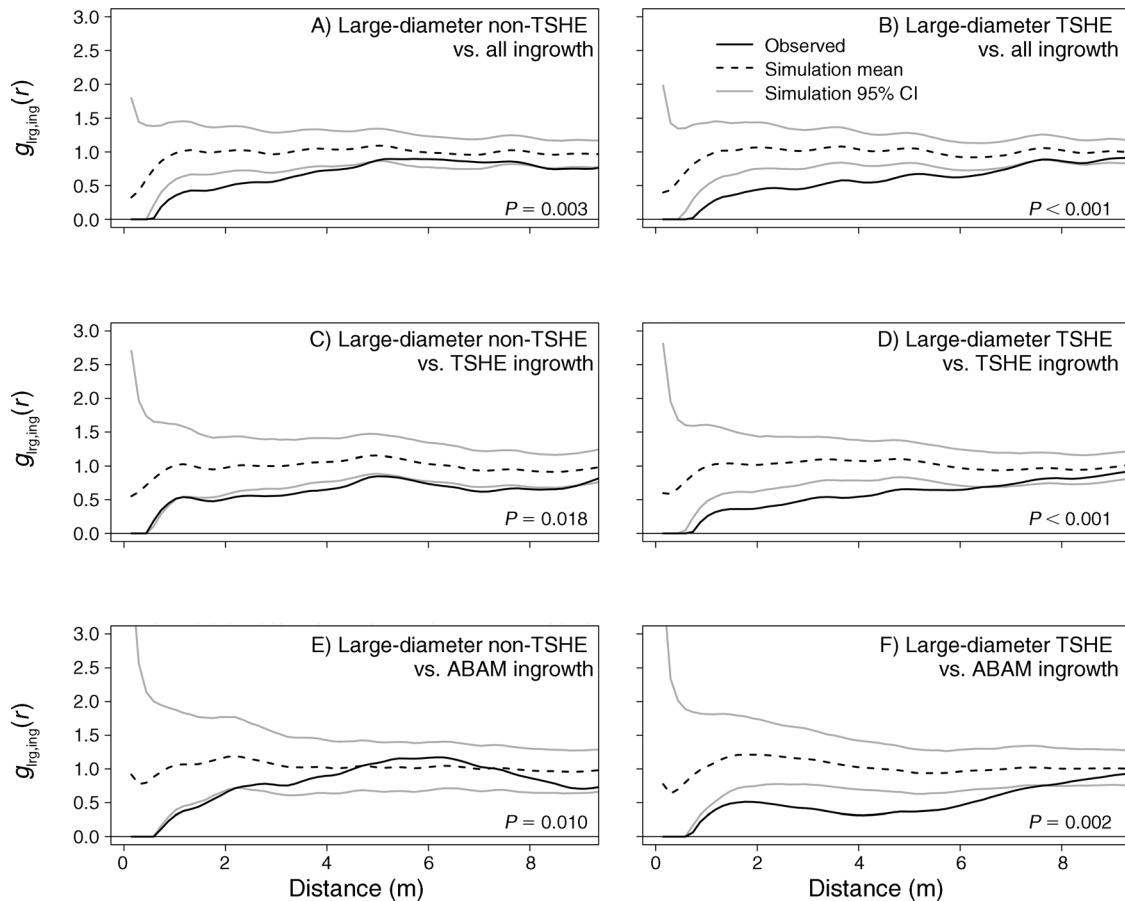
FIG. 3. Spatial relationships between ingrowth (trees reaching 5 cm dbh between 1999 and 2012) and large-diameter (≥70 cm dbh; lrg) trees. In all panels, values above (below) the simulation envelope indicate attraction (segregation) between large-diameter trees and ingrowth. Species abbreviations: all, all species pooled; TSHE, *Tsuga heterophylla*; and ABAM, *Abies amabilis*. *P* values are based on the goodness-of-fit test of Loosmore and Ford (2006).

documented here is three to eight times higher than previously documented for this slow-growing, stress-tolerant species in similar old-growth forests (Franklin and DeBell 1988, Busing and Spies 1995, Larson and Franklin 2010). We speculate that much of this mortality occurred as a result of several consecutive dry summers in the study period, which undoubtedly compounded the effects of density-dependent processes, particularly competitive interactions with *Tsuga* (Appendix: Fig. A9).

Forest-wide tree spatial patterns were maintained in a dynamic equilibrium by strongly nonrandom demographic processes: density-dependent mortality and spatially aggregated recruitment into the tree size class. Mortality of the pioneer *Pseudotsuga* population was aggregated at moderate scales, with no density-dependence apparent, as proposed by Franklin et al. (2002). In contrast, competitive density-dependent mortality is occurring within the population of the dominant late-successional species *Tsuga*, likely concentrated in tree clumps developing in old canopy gaps (Appendix: Fig. A1B), as postulated by

Franklin et al. (2002). But, because *Tsuga* ingrowth was spatially aggregated, the overall pattern was maintained.

This 13-year study of spatially explicit tree demography revealed the role of *Tsuga heterophylla* as a strong organizer of tree population and community dynamics through intra- and interspecific competitive interactions that give rise to negative density-dependent survival and recruitment. Analysis of this long-term data set supported our prediction that large-diameter *Tsuga* would suppress tree recruitment in their immediate neighborhood, which was based on prior analysis of spatial relationships between large and small stems (Stewart 1986, Getzin et al. 2006, Larson and Franklin 2006, Lutz et al. 2013). We did not anticipate, however, that the competitive effects of *Tsuga* would also manifest conspecific and, in the case of *Thuja* and *Taxus*, heterospecific density-dependent mortality, because previous long-term studies have emphasized the importance of noncompetitive mortality agents in temperate old-growth forests (Franklin and DeBell 1988, Larson and Franklin 2010).
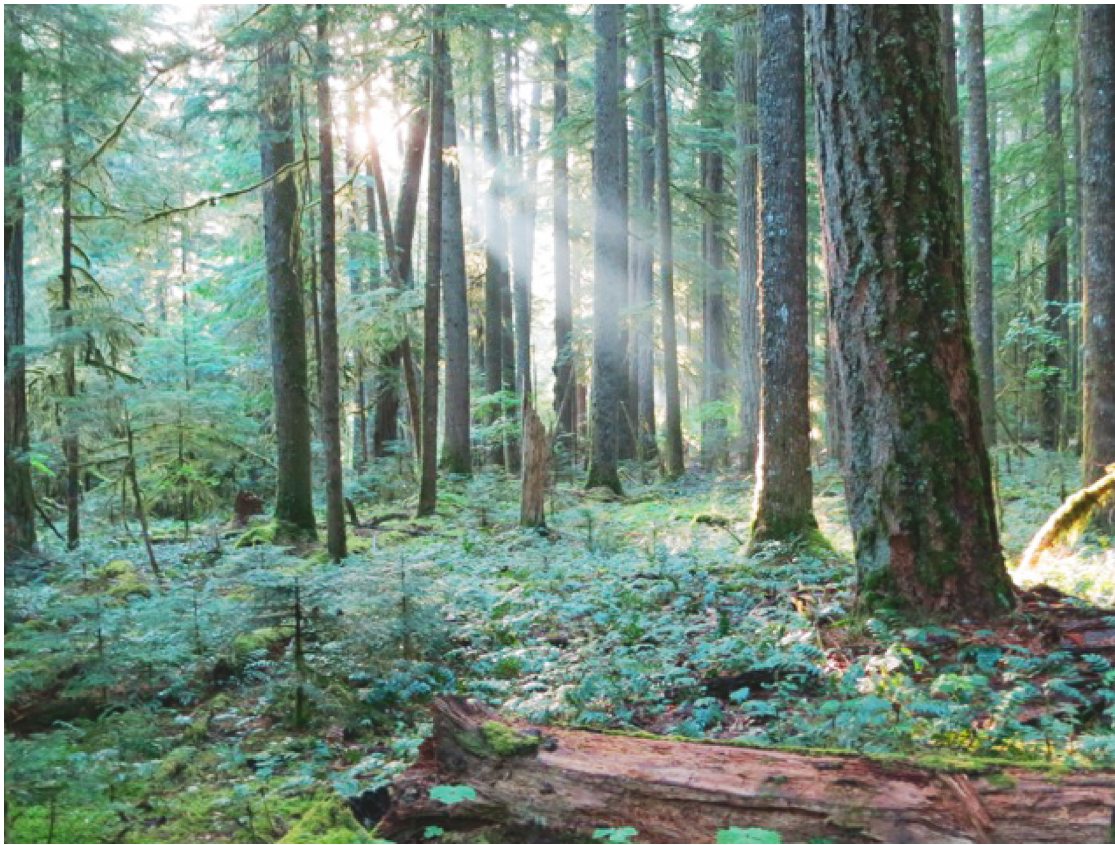
PLATE 1. The *Pseudotsuga-Tsuga* forest of the Wind River Forest Dynamics Plot includes most of the plant community types defined for the *Tsuga heterophylla* Zone (Franklin and Dyrness 1988) and a gradient of productivities leading to diverse structure throughout the plot (Larson et al. 2008). Here, a shade-intolerant *Pseudotsuga* (right foreground) is accompanied by shade-tolerant *Tsuga* amid an understory of *Acer circinatum*, regenerating *Tsuga* and *Abies amabilis*, *Mahonia nervosa*, moss, and large woody debris. Photo credit: J. A. Lutz.

This study is the first to confirm density-dependent mortality in very old forests through repeat measurements, although other studies (e.g., Getzin et al. 2006) have inferred intraspecific competition from the patterns of live and dead trees. The importance of self-thinning (density-dependent) mortality in young even-aged stands developing after high-severity disturbance is well established (Kenkel 1988, Getzin et al. 2006, Lutz and Halpern 2006, Halpern and Lutz 2013). Studies in maturing forests still undergoing rapid compositional change (e.g., Ward et al. 1996) have shown density-dependent mortality up to two centuries following stand initiation, but our study shows density-dependent mortality in a very old forest where compositional change is low and successional development is largely complete. The limited role of competitive mortality in old-growth Sierra Nevada forests (Das et al. 2011) could be explained by the greater importance of pathogens and insects, a lower relative competitive strength of shade-tolerant species compared to *Tsuga*, or alternatively, that 1-ha to 4-ha plots do not include sufficient numbers of trees to obtain a statistically significant result. The lack of density-dependent mortality

in *Pinus resinosa* forests (Aakala et al. 2012, Silver et al. 2013) could be due to relatively large size and advanced age of the pioneer *Pinus*, consistent with the results for the shade-intolerant pioneer species *Pseudotsuga* documented here (Appendix: Fig. A6).

The finding of strong density-dependent mortality in old-growth forests has implications for forest development in a changing climate (Das et al. 2013). Van Mantgem et al. (2009) demonstrated increasing mortality rates in western United States old-growth forests, but were not able to attribute the causes. Our finding of strong density-dependent mortality, especially when considered alongside the density-dependence and elevated rate of *Taxus* mortality, suggests the imperative of examining the effect of the local tree neighborhood on tree mortality. The interaction of climate variability and tree neighborhood effects will likely be a significant future driver of tree mortality and resultant forest change (Dwyer et al. 2010). Disentangling the relative contributions of climate variability and density-dependent biotic processes to tree mortality will be crucial to understanding how forests may change with changing climate.

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SUPPLEMENTAL MATERIAL

Appendix

Spatial patterns and simulations for all tree species from 1999 to 2012 (*Ecological Archives* E095-181-A1).