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Accelerated tree mortality after a half-century of stability in an old-growth forest: Insights from a 72-year study

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ABSTRACT

Although considered a relatively stable successional stage, old-growth forests can be dynamic, owing to both endogenous (life history, population dynamics) and exogenous (disturbance, global change) processes. Given the long timescales involved, direct tests of basic theories regarding old-growth development, or detecting global-change impacts, are scarce – often relying on space-for-time substitutions instead. Using a 72-year-long dataset in a ~500-year-old temperate forest in the western Cascades, USA, we examined how population, community, and ecosystem states and processes changed over time – encompassing periods of relatively stable climate (1947–1980s) and rapid climate change (1990s-2019). An initial population of 4597 trees was assessed every 4–8 years for growth, recruitment, and mortality across a 478-hectare forest.

For the first half-century of observation, system dynamics were notably consistent with successional theory absent significant disturbance. The long-lived, shade-intolerant species (*Pseudotsuga menziesii*) attenuated slowly (from 53% to 47% of basal area), while the principal shade-tolerant species (*Tsuga heterophylla*, *Abies amabilis*) proportionally increased. Overstory gap formation/expansion and understory tree recruitment progressed, while overall mortality rates, basal area, and aboveground woody biomass were largely stable. Beginning in the 2000s, dynamics departed from theoretical patterns: markedly higher mortality rates among shade-tolerant species – coinciding with increasing climatic water deficit – catalyzed declines in basal area and live biomass (partly buffered by dead-wood biomass). Shade-tolerant tree regeneration surged, suggesting higher turnover and impacts to vertical structure. Whether recent shifts are transient or sustained is yet uncertain. Long-term datasets are crucial to tracking endogenous and exogenous changes to forest development in the global change era.

1. Introduction

Temperate old-growth forests and the ecosystem services they provide have been a major focal point of forest management and conservation for the last several decades (Thomas et al., 1988; Spies TA, SL Duncan., 2008; Davis et al., 2022; Pelz et al., 2023). The manner in which old-growth forests fill a broad range of functions – wildlife habitat, carbon storage, wood fiber, clean water, socio-cultural values, among others – is not static but changes over time with continual structural development. Despite their advanced age, which may range from ~200–1000 + years, old-growth forests are inherently dynamic systems that, even where conserved, can undergo substantial change. These changes may be driven by either endogenous (demography and succession) or exogenous (disturbance or global change) processes (Wang et al., 2015; Zhang et al., 2015). Discerning these drivers is key to understanding the resilience and adaptability of old-growth forests in a

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time of global change (Clark et al., 2016; McDowell et al., 2020; Binkley, 2023).

Forest compositional and structural development (succession) occurs at multiple levels of organization (population, community, ecosystem) and involves multiple processes (recruitment, growth, stem/crown breakage, mortality, decomposition). Although certain aspects of population, community, and ecosystem structure are thought to be relatively stable in old-growth forests (e.g., recruitment balanced with mortality, with biomass largely constant; Odum 1969, Harmon et al. 2004), attainment of such equilibria in forests with long-lived species can take many decades or even centuries (Woods, 2000; Franklin et al., 2002; Li et al., 2026). Moreover, these developments can occur simply with time, and/or be accelerated, slowed, or altered by site conditions (Larson et al., 2008; Donato et al., 2012) and intermediate disturbances (e.g., low/moderate-severity fire, wind events) that can open the canopy and influence tree cohort establishment (e.g., Zenner, 2005; Tepley et al., 2014; Frances et al., 2023). The long temporal scales needed to observe these processes often hinders the ability to test predictions of successional theory, or to understand how global change may drive divergences from theory-based expectations. Studies empirically testing forest successional theory are surprisingly rare – particularly for the later (old-growth) stages of stand development. Moreover, there is remarkably little data on actual long-term change, measured on the same locale and same individuals (see, e.g., Franklin and DeBell, 1988; Woods, 2009; Harmon and Pabst, 2015; Brzeziecki et al., 2020; Woods et al., 2021; Idoate-Lacasia et al., 2025), which avoids the potential pitfalls of pseudo-chronosequence inference (Johnson and Miyanishi, 2008).

Expected changes in old-growth forests depend on the ecological level examined. Structurally, dynamics are thought to be characterized by vertical and horizontal diversification (i.e., gap formation and expansion, canopy layering). At the population and community levels, old-growth stages are considered to develop toward increasing abundance of, and eventual dominance by, shade-tolerant species that continually regenerate in the understory, with balanced growth and mortality (self-replacement) maintaining a 'reverse-J' or rotated sigmoid diameter distribution (Bormann and Likens, 1994; Zhang et al., 2001). In systems with very long-lived pioneer species, this theoretical steady-state mosaic can be elusive: directional change in species composition can continue for many centuries (>700 years), meaning a very slow progression toward shade-tolerant dominance (Munger, 1940; Woods, 2000; Franklin et al., 2002). Mortality rates, a key driver of structural change (Franklin et al., 1987) and biomass storage (Acker et al., 2002), are generally considered to be low and relatively stable in old forests (Larson and Franklin, 2010). Overall, old forests are thought to be characterized by relatively low demographic rates and relatively high structural and compositional stability (e.g., Andrus et al., 2018). At the ecosystem level, classical concepts (Odum, 1969; Bormann and Likens, 1994) suggest stand-level biomass (i.e. carbon storage) accumulates rapidly through the early and middle developmental stages, then stabilizes in old-growth forests where inputs eventually equal outputs, including for living and dead components. Biomass may also change with evolving species composition in old forests, as shade-tolerant species may not reach the same stature as pioneer dominants. This old-growth stability (or slight decrease) is debated, however: studies based on reanalysis of net-ecosystem production (NEP) and flux data posit that older forests continue to accumulate carbon stores (Luyssaert et al., 2008), while others challenge this assertion and methodology (Gundersen et al., 2021). This debate underscores the need for direct empirical assessment with long-term measurements in old-growth forests.

While most foundational work on forest development was conducted within a largely stable climatic regime, the current era of climatic change highlights a need to detect and understand novel alterations to stand dynamics (McDowell et al., 2020). Long-term climatic change, which in many regions entails warming, drying, and/or increased climatic water deficit (Littell et al., 2010), could influence processes at various ecosystem levels (Clark et al., 2016). At the population-community levels, warming and drying can alter rates of recruitment, growth, and mortality depending on whether these are most limited by water or energy availability (Van Mantgem et al., 2009; Das et al., 2013; Ford et al., 2017; Bell et al., 2020; Andrus et al., 2021; Vieira et al., 2024). Climate change may also disrupt species interactions, including with mutualists, pathogens, phytophagous insects, and parasites, leading to variable and potentially abrupt changes to tree vital rates (Germain and Lutz, 2022; Xu et al., 2026). Ecosystem-level impacts of increased climatic water deficit could occur as direct changes to inputs (i.e., net primary production, NPP) and/or outputs (i.e., mortality and decomposition), or indirectly via changes to the components involved in these fluxes (i.e., the species, sizes of components, or types and distribution of pools (live versus dead)). These impacts depend on which factors have previously limited vital rates, and also the degree to which various changes may modulate each other (e.g., reduced live biomass being buffered by increased dead biomass storage).

The moist temperate forests of the western Cascade Range in the Pacific Northwest, USA, have been a globally significant locus of research on forest succession, and pose unique uncertainties regarding potential climate impacts. Moderated by a maritime climate, these biomass-rich forests are sometimes considered relatively buffered or 'high-inertia' systems, in which change may occur mainly when catalyzed by altered fire activity (Turner et al., 2013; Halofsky et al., 2018). However, despite abundant annual precipitation, seasonal summer drought is substantial; this drought period has intensified in recent years and is associated with increased mortality of key tree species (e.g., Andrus et al., 2024). Punctuated shifts in regional forest assemblages with changing climate and fire activity are well documented to have occurred over the Holocene (e.g., Whitlock, 1992; Walsh et al., 2015; Reilly et al., 2021), and projections suggest increasing drought in the western Cascades may increasingly select against drought-intolerant species (Hudec et al., 2019; Germain and Lutz, 2020).

We used a rare data set spanning 72 years (1947–2019) in a ~500-year-old temperate forest in the western Cascade Range of Washington state, USA, to examine long-term changes in the forest state and processes at the population, community, and ecosystem levels. The dataset encompasses a period in which climate was relatively stable (1947–1980s) and in which climate was changing (1990s−2019), thus assessing a relatively stable stage of succession both before and during a significant shift in a fundamental ecosystem driver. This analysis extends that of DeBell and Franklin (1987) and Franklin and DeBell (1988), comprising not only a much longer timeframe but a substantially larger set of plots and trees tracked. We examined the degree to which decadal changes in the forest were consistent with either (1) successional theory largely presuming stable climate, or (2) departures from theory-based predictions in a manner consistent with climate change impacts, such as altered stand dynamics that track with changing drought conditions. If (1), we expected slow progression toward increasing shade-tolerant dominance, increasing horizontal diversification, mortality balanced with ingrowth, and relative stability in overall structure such as stem densities, basal area, and aboveground biomass. Conversely, (2) would be supported by altered vital rates (e.g., mortality) (e.g., Andrus et al., 2024) – causing departures from theoretical predictions, altered balance between growth and mortality, and less stability in ecosystem structure.

2. Methods

2.1. Study area

The T.T. Munger Research Natural Area (Munger RNA), a portion of the Gifford Pinchot National Forest reserved for scientific study, comprises 478 ha of forest dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) in the western Cascade Range

of southern Washington State, USA (45° 49' N; 121° 57' W) (Fig. 1). The site was selected for protection in 1926 as an archetypal representative of the widespread old-growth Douglas-fir/western hemlock forests found west of the Cascade crest (Munger, 1946). The Munger RNA is situated on the lower slopes of an inactive Quaternary shield volcano (Trout Creek Hill); soils are well-drained sandy loams developed in young volcanic tephra deposited over basalt bedrock. Topography is flat to gentle (<15% slope) and elevation ranges from 325 to 650 m above sea level. The climate is characterized by mild wet winters and warm dry summers. Modeled mean temperature range (1971–2000) in the Munger RNA was 10–27°C in July (17°C mean daily range) and −2–4°C in January (6°C mean daily range); mean annual precipitation was 2493 mm with 73% of precipitation falling outside the summer growing season (1 Nov to 31 Mar), much of it as snow (Daly et al., 2008; Lutz et al., 2013). Mean annual peak snow accumulations historically were up to 50 cm of snow water equivalent (SWE), with 1 April snow depth of 50–100 cm; however, depths have been less recently, with projections for no April 1 snowpack by mid-century (Germain and Lutz, 2022). Strong seasonality in precipitation often yields a growing-season drought, mediated in normal or wet years by soil water storage (Lutz et al., 2010, 2013).

Vegetation characteristics are described in detail by Shaw et al. (2004) and Lutz et al. (2013). In brief, the site spans wet to dry *Tsuga heterophylla* plant associations as well as some cooler Pacific silver fir (*Abies amabilis*) associations; most of the RNA is transitional between the *Tsuga heterophylla/Polystichum munitum* and *Abies amabilis/Gaultheria shallon* habitat types (Franklin and DeBell, 1988). Major tree species include Douglas-fir, western hemlock, Pacific silver fir, western redcedar (*Thuja plicata*), western white pine (*Pinus monticola*), and Pacific yew (*Taxus brevifolia*). *Abies procera* and *A. grandis* have a minor presence in the surrounding forest, but not significantly in plots. The understory is composed of mainly shade-adapted woody and herbaceous perennials, with tall shrubs (principally *Acer circinatum* and *Rhododendron macrophyllum*) forming a distinct understory layer, and low shrubs (<1 m tall), ferns, and bryophytes covering much of the forest floor (Lutz et al., 2013).

The forest of the Munger RNA is thought to have originated after a stand-replacing wildfire (or a series of such fires) around the year 1500 (Shaw et al., 2004), with no known evidence of surface fire occurrence since. Radiocarbon dating of soil macro-charcoal in the Munger RNA provides evidence of multiple fire events with calibrated ages (95% prob.) of 6178 ± 21 yr BP, 6523 ± 145 yr BP, 45,097 ± 536 yr BP, and 47,450 ± 684 yr BP (Šamonil et al., 2026). The primary disturbance regime of the northwestern Cascades includes infrequent stand-replacement fires at intervals of several centuries, commonly with one or more short-interval reburns, and, in some sites, other non-stand-replacing fires later in stand development (Agee, 1993). After stand establishment and tree dominance of a site, intermediate disturbances that open or diversify the canopy during succession can include wind, fungi/disease, low/moderate-severity fires, and endemic insects. Primary biotic agents include native bark beetles (*Dendroctonus, Scolytus*), structural root rots (*Phellinus, Phaeolus*), and root pathogens (*Armillaria*). While various developmental pathways exist, the general successional trend in this Pacific slope Western Hemlock Zone typically begins with initial establishment of several of the main species complement of the vegetation zone, but rapid dominance in both density and biomass by the relatively shade-intolerant and long-lived (400–1000 + years) Douglas-fir (along with the shorter-lived western white pine) and, over time, increasing importance of shade-tolerant western hemlock, Pacific silver fir, and western redcedar (Franklin and Dyrness, 1988).

The current stand in the Munger RNA is in the "horizontal diversification" stage of advanced old-growth structure, exhibiting both vertical and horizontal structural complexity (Franklin et al., 2002) (Fig. 1). The main overstory canopy reaches ~60–70 m height, with large gaps and clumps in the horizontal dimension and shade-tolerant trees forming a vertically continuous height distribution. No significant timber harvest has occurred in the RNA.

2.2. Field sampling

A series of permanent tree demography and mortality plots was established in the RNA in 1947. These originally consisted of strips of 40 × 100-m rectangular plots wherein only mortality of trees > 45.7 cm diameter at breast height (dbh) was tallied and blazed; and nested circular demography plots centered in every other mortality plot, in which trees were tagged and tracked for ingrowth, growth, and mortality (0.02

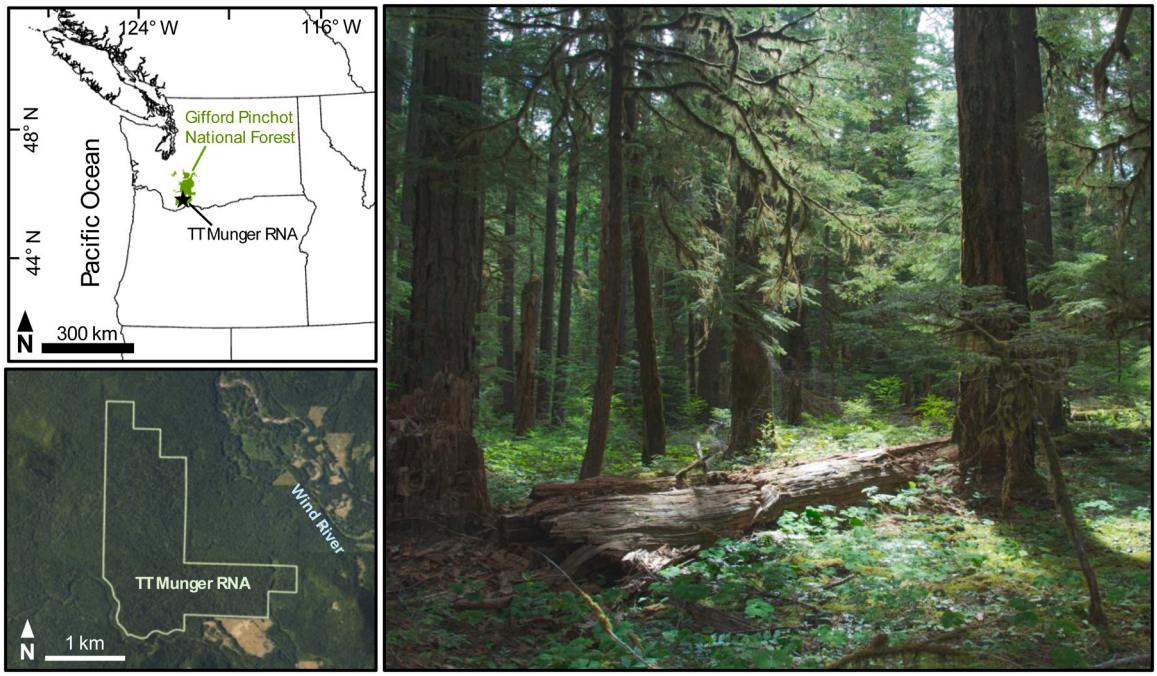

Fig. 1. Study location and interior view of the T.T. Munger Research Natural Area (RNA). Stand photo taken in 2023, by J. Lutz.

and 0.08 ha circles for trees 6.0–25.4 cm and >25.4 cm dbh, respectively). Plots were visited at 6-year intervals through 1983, after which intervals ranged from 4 to 8 years but averaged 6 years. In 1991, measurements in the 40 × 100 m rectangular plots were expanded to include tagging and demographic tracking of all trees > 45.7 cm dbh. For the present analysis, the dataset was distilled to the following: all trees 6.0–25.4 cm dbh were assessed in 0.02-ha circular plots; all trees 25.4–45.7 cm dbh were assessed in 0.08-ha concentric circular plots; and all trees > 45.7 cm dbh were assessed in 40 × 100 m rectangular plots. See Appendix 1 for plot diagram and layout. The count of plots that have been continuously measured through modern years is 93 large rectangular plots and 46 sets of nested circular plots, tracking a sample initially consisting of 4597 individual trees. To be more generalizable, we use approximate stand ages of 450 and 520 years in this paper to reflect the first and most recent measurements, rather than solely calendar years. Data are on file with the joint US Forest Service/Oregon State University Permanent Sample Plot Program (http://pnwpsp.forestry.oregonstate.edu).

2.3. Data analysis

Because large trees (>45.7 cm) were measured on the 40 × 100-m plots starting only in 1991, we reconstructed that component of 1947–1983 forest structure by "growth-regressing" large trees for earlier periods – applying an annual subtraction to both live and dead-tallied large trees in the 40 × 100-m plots based on mean growth rates of extant large trees in the circular plots (~0.5–1.5 cm yr^{-1} depending on species) (Bible, 2001). While imperfect, this approach is reasonable because it is only for large trees (>45.7 cm), which reduces issues with diameter increments inherently changing with tree size.

In addition to computing demographic and structural metrics (stem densities, mean tree sizes, basal area) by species through time, we computed annual stem mortality rates (M) for each species on a percentage basis using the method employed by Franklin and DeBell (1988):

$$M = 100*(1\text{-}P(S_t)^{1/t}) \quad (1)$$

where $P(S_t)$ is the proportion of a population (by stem count) remaining during a measurement interval, and t is the length of the interval in years (see also Sheil et al., 1995). Specific mortality agents were not recorded with enough consistency over the measurement period to support analysis of their trends.

We evaluated the degree to which horizontal diversification processes have been moving the stand to a patchier spatial distribution. Although the plot data were not spatially explicit in terms of stem mapping, we could assess whether the density of Douglas-fir has become more variable among plots (higher coefficient of variation [standard deviation as a percentage of the mean]), as well as the proportion of plots with little or no Douglas-fir present (signifying development or expansion of large gaps).

To explore potential relationships between mortality and climate drivers, we evaluated Spearman rank correlation coefficients between mortality rates and climatic water deficit for each measurement period, by species and size class. Climatic water deficit was chosen for analysis because of its relevance to plant drought stress incorporating temperature, precipitation, and snowpack collectively – particularly for the dry growing season months when deficit accumulates in this region (see also Germain and Lutz, 2020). Deficit data were derived from a Thornthwaite-type water balance model Thornwaite., (1948), Lutz et al., (2010)). Monthly climatic water deficit values were summed by year; this annual summed deficit was then averaged over each measurement interval to evaluate how relatively wet or dry each period was. Preliminary analysis showed that using maximum deficit during each measurement interval yielded equivalent results as using the average.

Live aboveground woody biomass (stem, branch, bark) was computed for each tree at each measurement interval, using whole-tree allometric equations built from and for the full range of tree sizes in the study (adapted from Jenkins et al., 2004; Sillett et al., 2018; R. Van Pelt, unpublished data), with an adjustment to exclude foliage at the stand scale based on Harmon et al. (2004) (see Appendix 2). Dead biomass was accounted by converting live biomass to dead for each individual tree that died, then tracking its biomass over time using species-specific overall decomposition constants for dead wood from site-specific data (Sollins, 1982; Janisch and Harmon, 2002; stand-level average $k = 0.026$ yr^{-1}, see Appendix 2). This dead biomass recruitment was added to an estimated pool existing in 1947 (start of measurements) derived from the live:dead ratio from early in the measurement period (Sollins, 1982; Janisch and Harmon, 2002). We ran a sensitivity analysis to test how varying the decomposition constant by ±20% changed outcomes for overall biomass dynamics (Appendix 2). Annualized net primary productivity of aboveground woody tissues (NPP_{AW}) for each measurement period was computed as gross growth of stem, branch, and bark mass – comprising growth of extant trees and ingrowth of new trees.

To test for significant changes in temporal trends in the climate and mortality data, we used moving Wilcoxon tests, in which the time series is iteratively split into before-and-after periods using each possible temporal break point (excluding bookends with <3 data points in the before or after), and the before and after values compared using a simple rank test. This is essentially a permutation test of the probability, given only random variation, of getting after-break values as extreme as those observed in the actual data. The test identifies the temporal break point with the most extreme test statistic U and the associated *P*-value. We show here the before-versus-after median values for any species and size class having a $U < 4$ and $P < 0.10$.

3. Results

3.1. Overall stand structure

3.1.1. Total stem density, basal area, mean tree size

Overall stem density changed little over the measurement period (420–468 stems ha^{-1}, Table 1; Fig. 2). Stand diameter distributions also remained similar; however there was a slight shift away from medium size classes and toward the larger and the smallest size classes (Fig. 3). Except for a slight decline initially due to western white pine mortality, overall stand basal area remained largely constant from age 450–500 yr, between ~66–68 m^2 ha^{-1} (Fig. 4), after which overall stand basal area exhibited the steepest observed declines (Fig. 4). Overall mean tree diameter across the stand remained relatively flat, being 40.5 cm at age 450 yr and 38.3 cm at age 520 yr (Table 1).

3.1.2. Horizontal diversification

The distribution of Douglas-fir among plots became patchier over time, with the coefficient of variation in Douglas-fir density among plots increasing from 51% to 61% over the measurement period. The frequency of plots with < 10 Douglas-fir ha^{-1} present – i.e., 0.4-hectare-scale overstory gap areas largely dominated by shade-tolerants – increased from 2% of plots at stand age 450 yr to 10% of plots at stand age 520 yr (Fig. 5).

3.2. Population and community dynamics

3.2.1. Recruitment

Recruitment varied largely between ~3–7 trees ha^{-1} yr^{-1} for most of the measurement period (Fig. 6). Relatively shade-intolerant Douglas-fir and western white pine effectively did not recruit during the entire period, while most shade-tolerant species continually regenerated – especially western hemlock and Pacific silver fir which each recruited ~1–3 trees ha^{-1} yr^{-1} over most of the observation period (Fig. 6). The main exception to the above was western redcedar, the only shade-

Table 1
Tree density (trees ha^{-1}) by size class, basal area, mean dbh, and plot-frequency for each species in 1947 and 2019 (stand age ~450 and 520).

Species	Year	Mean dbh (cm)	Basal area (m^2 ha^{-1})	Trees ha^{-1} by diameter class					Frequency (% of plots)
				6–25 cm	25–45 cm	45–100 cm	> 100 cm	Total	
Douglas-fir	1947	88.0	36.7	2.2	3.0	35.9	16.7	57.7	100
	2019	100.3	29.2	2.2	0.5	14.9	17.9	35.5	100
western hemlock	1947	33.7	21.1	135	43.8	41.2	1.2	221	100
	2019	34.6	24.0	150	29.1	43.8	2.7	226	99
Pacific silver fir	1947	19.9	4.4	93.5	14.1	6.2	0.1	114	82
	2019	17.2	3.4	96.7	10.9	3.7	0.0	111	71
western redcedar	1947	70.8	3.3	2.2	1.4	2.8	1.5	7.9	30
	2019	92.7	3.7	0.0	1.1	2.0	2.1	5.2	33
western white pine	1947	64.2	1.9	1.1	0.5	3.7	0.4	5.7	71
	2019	84.6	0.2	0.0	0.0	0.2	0.1	0.3	10
Pacific yew	1947	13.9	1.2	58.7	3.3	0.2	0.0	62.1	34
	2019	18.7	1.3	34.8	6.3	0.5	0.0	41.5	39
Total	1947	40.5	68.6	292	66.0	90.0	19.8	468	100
	2019	38.3	61.9	302	48.7	65.0	22.8	420	100

tolerant to not recruit during the entire period. The two highest recruitment rates for both western hemlock and Pacific silver fir occurred after 2004 (Fig. 6).

3.2.2. Mortality rates

The stand-wide annual stem mortality rate stayed within a relatively narrow range (~0.5–1% stems yr^{-1}) over the measurement period, except for two sharp spikes around 2% after the year 2000 (Fig. 7o). These spikes increased the period-wide mean annual mortality rate to 1.05% (Table 2) even though the stand-level rate averaged 0.86% over most of the measurement period (Fig. 7o). Mortality was highest for small trees (Table 2). Trends in overall stand mortality were driven mainly by the most abundant species, western hemlock and Pacific silver fir (Fig. 7c-f).

Across the measurement period, mean annual stem mortality rate was highest for western white pine at 4.1%, followed by Pacific silver fir (1.57%) and Pacific yew (1.13%), then by western hemlock and Douglas-fir (0.82% each) (Table 2, Fig. 7). Western redcedar had by far the lowest mean annual mortality, at 0.52% (Table 2, Fig. 7). Excepting western redcedar, much of the shade-tolerant layer of the stand turned over during the 72 years, with 38–75% of western hemlock and Pacific silver fir stems present at stand age 450 yr being lost to mortality by stand age 520 yr (Table 2). Turnover was highest in the smallest size classes (Table 2). Mortality was essentially replaced by recruitment for western hemlock and Pacific silver fir, less so for Pacific yew and western redcedar (Table 2).

By species (Fig. 7), annual stem mortality rates for most of the measurement period ranged from relatively consistent across intervals (Douglas-fir, western hemlock, western redcedar), to broadly cyclical (Pacific silver fir), to climbing with cyclicity (Pacific yew), to initially high before declining (western white pine). A key trend was substantial increases in large hemlock and small silver fir mortality, and lower cedar mortality, beginning around 1998–2004 (Table 3).

Climatic water deficit exhibited a significant inflection point to higher levels starting in 1998, and stand-wide stem mortality rates exhibited a similar inflection starting in 2004 (Table 3). Median deficit for the intervals reflecting 1998–2019 (100 mm) was 1.4x the median deficit from 1947 to 1997 (71 mm). Likewise, median annual stand-level mortality rate for the intervals reflecting 2004–2019 (1.89% yr^{-1}) was 2.1x of that from 1947 to 2003 (0.90% yr^{-1}) (Table 3). There were suggestive positive correlations between mean climatic water deficit during a given measurement interval and mortality rates of large hemlocks, as well as small (and all) silver firs (Fig. 8, Table 4).

3.2.3. Community development

Douglas-fir remained the most dominant species by basal area at stand age 450 and 520 yr (Table 1, Fig. 4) – an outcome of larger mean tree size offsetting declining stem density (Fig. 4). Decreasing Douglas-fir dominance was detectable but slow: it composed 53% of overall stand basal area at age 450 yr, and still 47% at age 520 yr (Table 1, Fig. 4). Basal area of Douglas-fir was much higher than western hemlock at age 450 yr (36.7 versus 21.1 m^2 ha^{-1}, respectively), but was closer to parity by age 520 yr (29.2 versus 24.0 m^2 ha^{-1}, respectively) (Table 1). In terms of continued shade-intolerant species presence, while western white pine has largely disappeared (Tables 1–2, Figs. 2,4), at current rates Douglas-fir will continue to dominate the overstory for some time. Absent major disturbance, applying the time-to-extinction formula from Franklin and DeBell (1988) and using the range of mortality rates observed over all the measurement intervals (Table 2), the estimated time to extinction for Douglas-fir in the stand is an additional 400–820 years (mean 560 yr) – i.e. stand age ~900–1300 yr (mean 1080 yr).

Most trends in stand density were driven by western hemlock and Pacific silver fir (Fig. 2), which together composed 72% of stems at stand age 450, increasing to 81% of stems by age 520 (Table 1). These species maintained similar mean diameters and densities over time (Table 1, Fig. 2) – reflecting a general balance between mortality and growth/recruitment over the bulk of the measurement period (Table 2). Other shade-tolerant species (western redcedar, Pacific yew) experienced similar dynamics to shade-intolerants (growth, mortality, little new recruitment), with relatively large increases in mean diameter and decreases in stem densities (Tables 1–2, Fig. 2). The late decline in overall stand basal area was driven by reductions in western hemlock (Fig. 4), which changed from increasing to decreasing basal area starting in 2004.

3.3. Ecosystem dynamics

3.3.1. Woody biomass production and mortality

NPP_{AW} was largely consistent through time, staying around 3–4 Mg ha^{-1} yr^{-1}, while woody biomass mortality was more variable, ranging from ~3–7 Mg ha^{-1} yr^{-1} (Table 5).

3.3.2. Biomass trends over time

Aboveground woody biomass was both high (~730–780 Mg ha^{-1}) and relatively stable from stand age 450–520, with 2019 total (live+dead) biomass being 93% of that present in 1947 (Fig. 9). Before the mortality inflection point in 2004 (Table 3), both live and total biomass were mostly stable, with increases in western hemlock live biomass nearly offsetting losses of Douglas-fir live biomass (Fig. 9). After 2004, live biomass began declining much more abruptly, averaging −3.1 Mg ha^{-1} yr^{-1}, ~3x faster than the −1.1 Mg ha^{-1} yr^{-1} prior to 2004 (Table 5) – owing largely to hemlock live biomass declining for the first time (Fig. 9). Biomass remained dominated by Douglas-fir (60–67% of stand total) throughout the measurement period (Fig. 9).

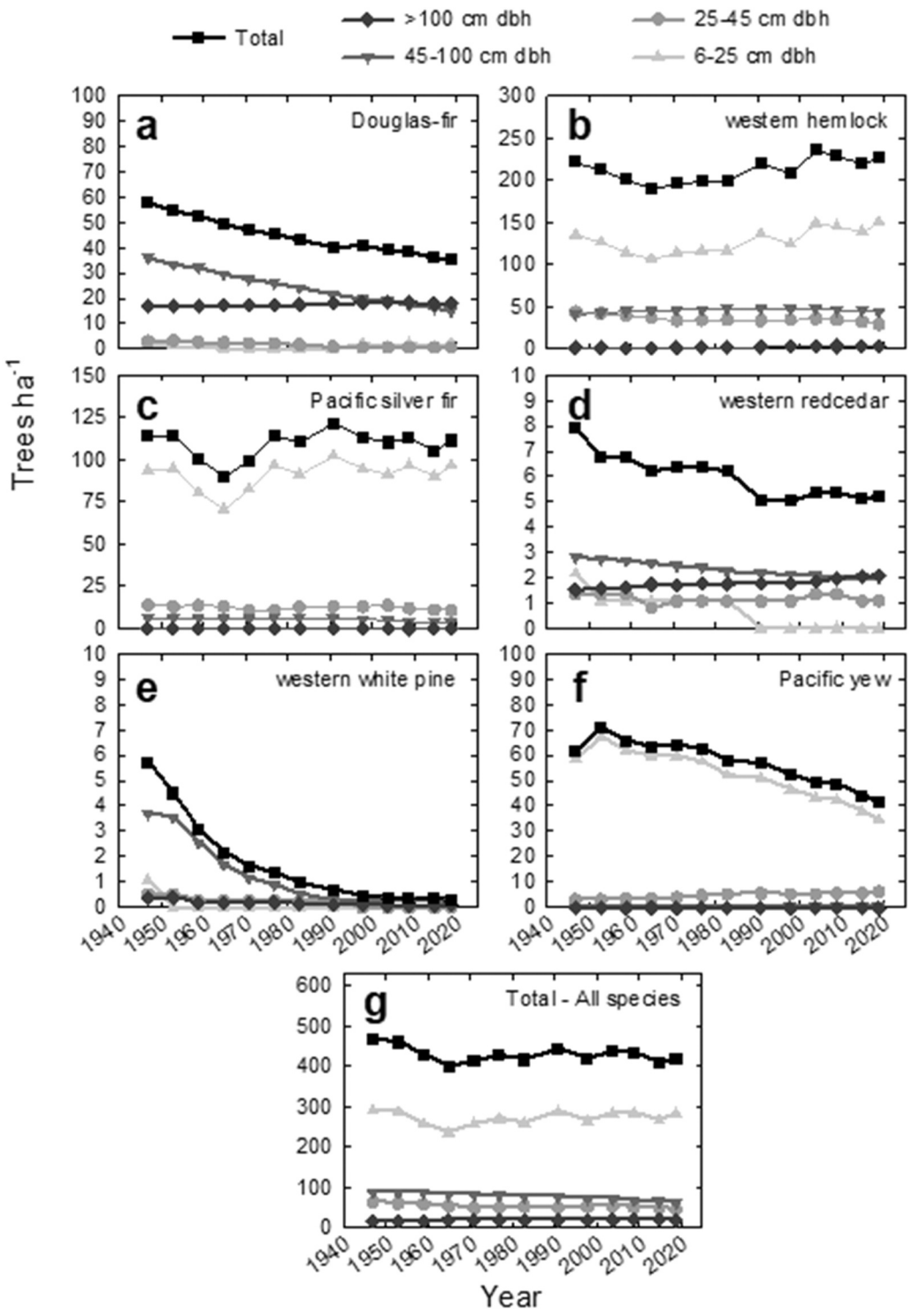

Fig. 2. Tree densities over time, by species and size class (stand age ~450–520). Note different y-axis scales.

3.3.3. *Dead biomass*

Compared to live woody biomass, total woody biomass (live+dead) did not decrease or change among measurement intervals as much, due to the buffering effects of dead biomass, given much of the biomass of trees that died remained despite some decomposition loss (Fig. 9). Live biomass declined by 14.8% over the measurement period, while total biomass declined by only 6.9% (Fig. 8). The dead:live biomass ratio increased markedly after 2004 (mean 0.28 through 2004, 0.33 after 2004; Fig. 10).

4. Discussion

Observations of 72 years of change in a 500-year-old temperate old-growth forest supported many core tenets of forest successional theory – with some departures from expectations in recent decades in ways consistent with changing climatic impacts. The following discussion first addresses patterns observed prior to an apparent inflection point in the early 2000s, then addresses trends in the latest decades.

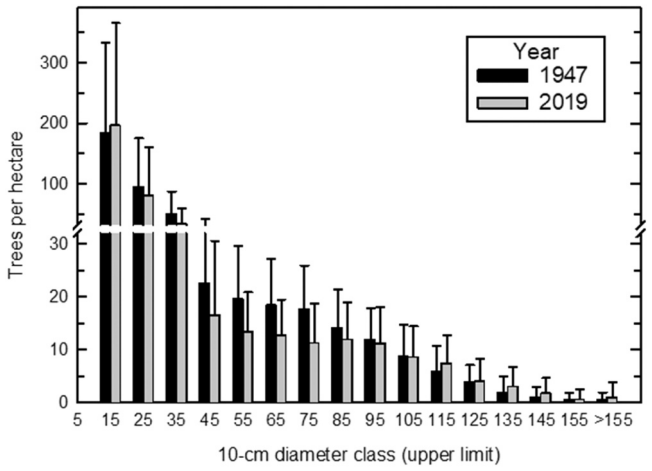

Fig. 3. Size-class distributions across all tree species in 1947 and 2019 (stand age ~450 and 520). Data are mean and standard deviation among plots within the stand for each diameter class.

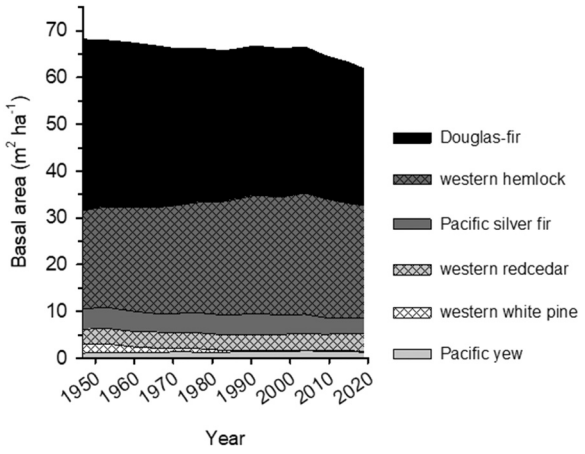

Fig. 4. Changes in live basal area of trees (m^2 ha^{-1}) between 1947 and 2019 (stand age ~450–520).

4.1. Overall stand structure

4.1.1. Total stem density, basal area, mean tree size

The first theory-based prediction we evaluated was that overall structural metrics such as total stem density, total basal area, and mean tree size would be essentially constant in this advanced stage of stand development, when theory posits that recruitment and growth effectively balance out mortality (Bormann and Likens, 1994; Franklin et al., 2002). These predictions were largely borne out.

Maintenance of a reverse-J or rotated sigmoid stem-size distribution (Fig. 3), staying within a notably narrow range over seven decades (Fig. 2, Table 1), suggests a quasi-steady state in the overall organization of stems. Increased bimodality in the stem distribution (Fig. 3) occurred even though medium-sized Douglas-fir (45–100 cm dbh) were slightly more likely to die than grow into the largest size class (>100 cm dbh) (Tables 1–2, Fig. 2). This finding suggests the largest Douglas-firs (>100 cm) still possess the most resistance to mortality agents such as root rot fungi, insects, and drought stress. Stem dynamics among the most abundant shade-tolerant species (stable or cyclical for western hemlock and Pacific silver fir, through 2004) – reflected more steady state, self-replacing populations.

The slight decline in total basal area early in the measurement period is consistent with some predictions relating to the die-out of pioneer species (Bormann and Likens, 1994; Binkley, 2023), and was driven mainly by the attenuation of the last remaining western white pines – a shorter-lived shade-intolerant pioneer that commonly persists no more than ~300–500 years (Graham, 1990) (see mortality section below).

The relatively constant mean tree diameter in the stand was an emergent balance of differing trends among species and life history traits

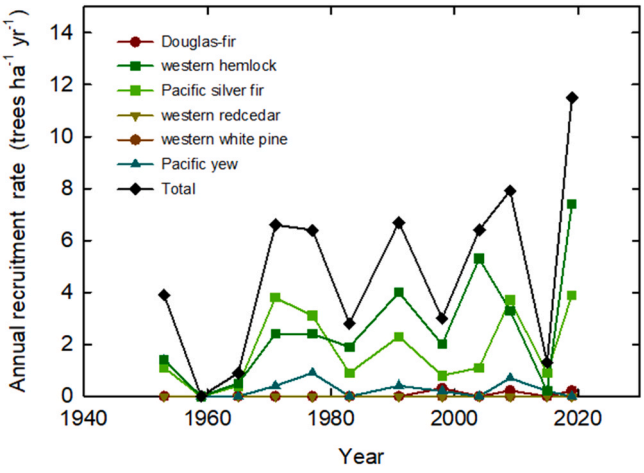

Fig. 6. Annualized recruitment rates over time, by species. Data reflect newly recruited individuals in the smallest size class only (6.0–25.4 cm dbh) and do not assess any later mortality in subsequent measurement intervals (see Table 2 for long-term net recruitment across all size classes over time).

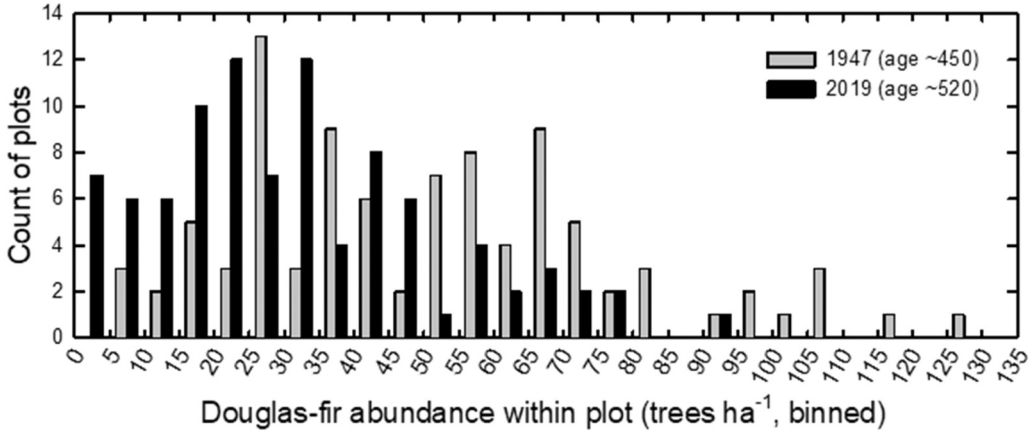

Fig. 5. Frequency distribution of plots by Douglas-fir abundance, compared between 1947 and 2019 (stand ages ~450 and 520).

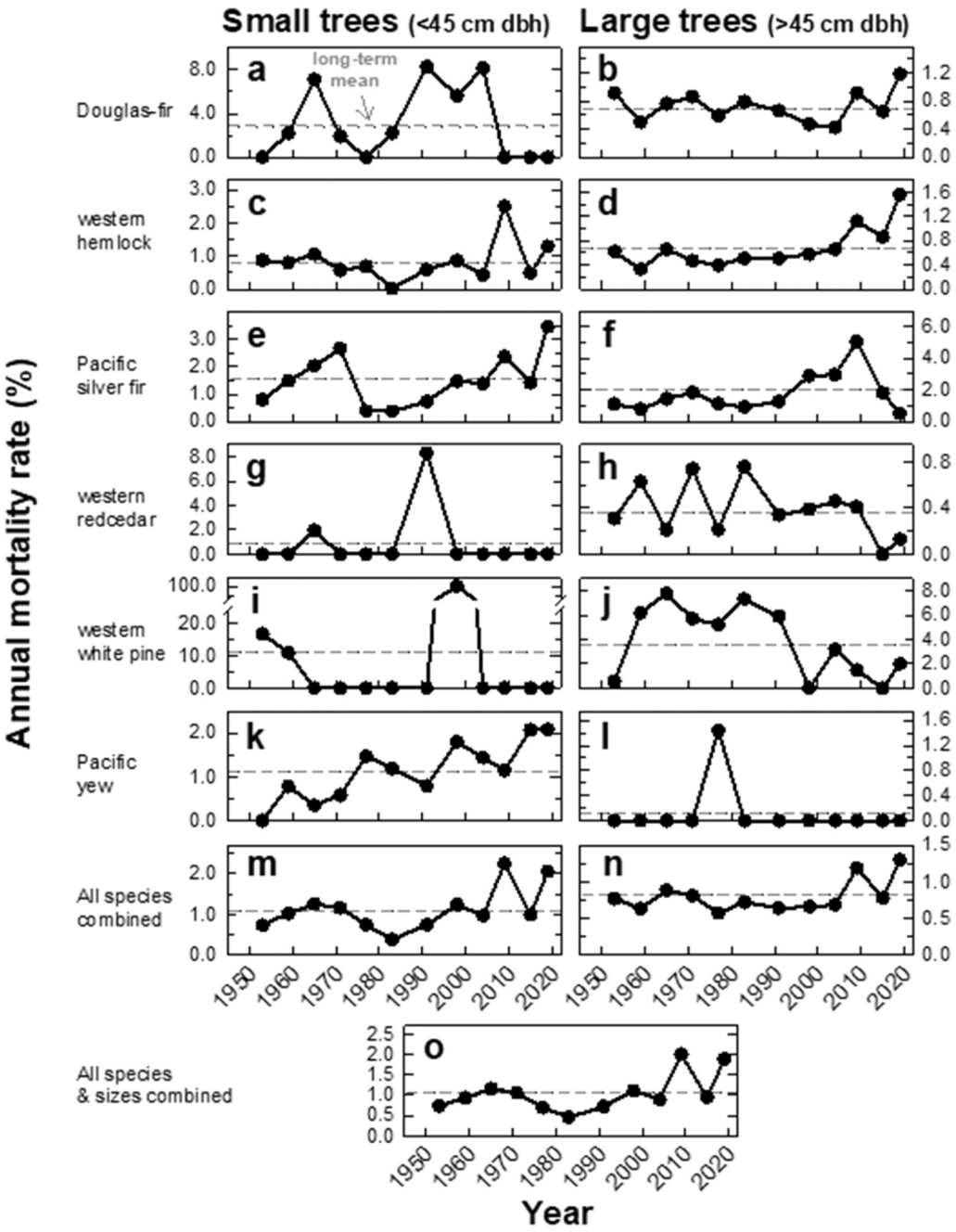

Fig. 7. Stem mortality rates over time, by species and size class, 1947–2019 (stand age ~450–520). Note different y-axis scales.

(Table 1). Species that did not regenerate under the closed canopy (especially pioneer shade-intolerants) increased in mean diameter, while the most numerous trees in the stand (shade-tolerant western hemlock and Pacific silver fir) remained similar or declined slightly (Table 1). These two trends essentially balanced each other over the measurement interval.

4.1.2. *Horizontal diversification*

A rarely-tested prediction of successional theory is the horizontal diversification process, wherein the gap structure of an advanced-stage old-growth stand should broaden into larger structural units over time (Franklin et al., 2002; Van Pelt, 2025). Although this dataset was not spatial, a key indicator of this process is variability in Douglas-fir density among plots, particularly at the low-density end – i.e., patches with little or no Douglas-fir that indicate overstory gaps (Franklin et al., 2002; Van Pelt, 2025). Although no 0.4-hectare plots were yet completely devoid of Douglas-fir during the measurement period (Table 1), the downward shift in its density distribution and several-fold greater representation of plots with few Douglas-fir remaining (Fig. 5) are consistent with the horizontal diversification process. Patches with very low Douglas-fir representation are increasingly dominated by shade-tolerant trees of varying age, creating distinct structural units. With the slow attenuation of Douglas-fir from the stand overall, this process of horizontal diversification appears likely to continue defining spatial stand development for several centuries (Franklin and Van Pelt, 2004).

4.2. *Population and community dynamics*

4.2.1. *Recruitment*

The continual new tree establishment observed over the 72 years

Table 2
Mortality rates and recruitment for the entire 72-year period (1947–2019, stand age ~450–520).

Species	Mean annual % mortality	% mortality of initial sample population	Mortality by diameter class (dead trees ha^{-1}) for 72-year measurement period (1947–2019)					Recruitment (trees ha^{-1})
			6–25 cm	25–45 cm	45–100 cm	> 100 cm	Total	
Douglas-fir	0.82	40	2.2	2.4	13.4	8.0	26.0	3.3
western hemlock	0.82	38	71.7	23.1	20.6	1.6	117	135
Pacific silver fir	1.57	75	88.0	14.7	6.9	0.1	110	85.7
western redcedar	0.52	25	1.1	0.3	0.9	0.2	2.5	1.5
western white pine	4.14	93	1.1	0.5	3.8	0.4	5.9	0.0
Pacific yew	1.13	49	41.3	1.9	0.0	0.0	43.2	18.0
Total	1.05	43	205	42.9	45.6	10.3	304	244
Mean annual % mortality			1.13	1.14	0.84	0.70	1.05	
% mortality of initial sample population			52	49	43	38	40	

*Recruitment = ingrowth of individuals of any size class that had attained the minimum dbh for inclusion in the relevant subplot, not present in 1947 but present as of 2019.

(Fig. 6) is consistent with successional theory positing increasing shade-tolerant recruitment and relative abundance over time. Although somewhat punctuated (similar to observations by Acker et al. 2002), new recruitment was generally consistent over time, occurring without significant disturbance.

4.2.2. Mortality

The overall stem mortality rates of ~0.5–1% per annum observed in this old-growth stand for most of the 72-year period were generally consistent with those from other studies (Table 2, Fig. 7, Bible, 2001; Luo and Chen, 2013; Larson and Franklin, 2010; Acker et al., 2023; Idoate-Lacasia et al., 2025). The collective mortality regime of the stand could be described as slow loss of the pioneer overstory, with both recruitment and substantial turnover of the shade-tolerant layer. This continual mortality among the shade-tolerant layer is an important driver of spatial heterogeneity in old-growth forests (Larson et al., 2015). That western redcedar was the primary exception to the latter dynamic is consistent with findings from other studies reporting very low mortality rates for this species in old forests (Larson and Franklin, 2010).

Despite a relatively narrow and consistent stand-wide mortality rate, important temporal variations occurred (Fig. 7). The broadly cyclical pattern of Pacific silver fir mortality may be associated with pathogen or insect cycles (DeBell and Franklin, 1987) – including, perhaps, the introduction of non-native balsam wooly adelgid to the region which caused a known spike of Pacific silver fir mortality in the area in the mid-1900s (Johnson et al., 1963). The increasing Pacific yew mortality over time, and the high mortality rate of western white pine (a shorter-lived pioneer species) highlight that mortality in this 500-year--old stand is not simply steady state; rather there are still directional changes in certain elements of the population – which are not completely density-independent and partly reflect continued spatial interactions among live trees (Woods, 2000; He and Duncan, 2003; Lutz et al., 2014) or impacts of falling or fallen dead trees (Larson and Franklin, 2010; Ku and Lutz, 2025). Cyclicity and non-stationarity in mortality rates also highlight how mortality-driven changes in stand structure and function are often punctuated rather than gradual (Harmon and Pabst, 2015).

Confidently identifying causes of mortality in forests surveyed at longer than annual intervals is often difficult because some evidence rapidly decomposes. Here, plots were revisited every 4–8 years, introducing uncertainty in attribution of proximate mortality causes (>50% of mortality trees causes were recorded as an unknown cause). Although field assignment of mortality causes was not consistent enough to support formal analysis, it has been possible to ascertain key mortality agents for some species, with these conclusions consistent with nearby studies having annually-resolved mortality data (Lutz et al., 2021; Ku and Lutz, 2025).

Mortality of old-growth Douglas-fir is generally due to one of three identifiable factors (Bible, 2001). The first and most important is mechanical failure due to butt rot by the native velvet top fungus (*Phaeolus schweinitzii*), which observations suggest caused about 2/3 of Douglas-fir mortality. This heartwood rot results in breakage near ground level, with little or no roots exposed and torn shreds of sapwood extending above the stump. Douglas-firs killed in this way are often mistaken for windthrown or uprooted trees; wind can precipitate failure of butt-rotted individuals but the main factor is mechanical failure due to rot, and can occur under calm conditions. We were able to retrospectively identify Douglas-firs that died as a result of mechanical failure due to butt rot (Bible, 2001). A second important mortality agent for Douglas-fir is the Douglas-fir bark beetle, which usually kills the tree in a single season and leaves it standing as an intact snag. A third key mortality agent for Douglas-fir is true windthrow, in which significant portions of the root system are uprooted and exposed on the soil surface. Root rots (especially *Phellinus*) can be contributing causes (Šamonil et al., 2022).

Western white pine died mainly from mountain pine beetle attacks, which kill them within a single year, leaving them as snags that persist for several decades. White pine blister rust (*Cronartium ribicola*), an introduced pathogen affecting this species throughout much of its range, was present in some trees but there is not conclusive evidence of it being the sole driver of pine mortality in this stand. Perhaps most importantly, mortality and attenuation of white pine from this stand is consistent with its known 300–500-year lifespan (Graham, 1990).

Identifying causes of mortality for other species, most prominently western hemlock, is more difficult because of the lack of evidence (often), except in the case of trees crushed by branch or stem mortality of other trees (Larson and Franklin, 2010). We have observed many medium and large western hemlock gradually losing leaf area, thinning from the top down, until the trees eventually die. We have also recently observed a few instances of galleries of the native flatheaded fir borer (*Phaenops drummondi*) in standing, newly dead large-diameter western hemlock in the Munger RNA. We speculate that this is due to impacts of warmer and drier conditions, which is supported by the suggestive timing and correlation between drought and mortality of large hemlocks (Fig. 8, Tables 3–4).

4.2.3. Community development

Another key successional-theory prediction we evaluated was increasing dominance of shade-tolerant species (Munger, 1940; Franklin et al., 2002). While the change was incremental, the stand did cross a threshold during the measurement period, wherein a plurality of basal area went from being shade intolerant to shade tolerant – one key milestone that took ~500 years of development. Given the very slow

Table 3
Moving Wilcoxon test results to identify threshold changes (timing, magnitude) in tree population mortality rates and climatic water deficit. Threshold year and before-after medians are shown only when the test statistic (U) ≤ 4 and $P \leq 0.10$. Species/size classes for which < 2 trees ha^{-1} remained in the stand were not tested.

Variable	Threshold year	Median before	Median after	U	*P*
Climatic water deficit	1998	71	100	3	0.028**
– Population mortality rates –					
All species combined	2004	0.90%	1.89%	3	0.064*
All species, large (>45.7 cm)	2004	0.69%	1.19%	2	0.042**
All species, small (<45.7 cm)	2004	0.97%	2.06%	4	0.096*
Douglas-fir	---	---	---	11	0.711
Douglas-fir, large (>45.7 cm)	---	---	---	5.5	0.165
Douglas-fir, small (<45.7 cm)	---	---	---	---	---
western hemlock	---	---	---	6	0.196
western hemlock, large (>45.7 cm)	1998	0.51%	0.99%	0.5	0.004***
western hemlock, small (<45.7 cm)	---	---	---	7	0.267
Pacific silver fir	---	---	---	8	0.149
Pacific silver fir, large (>45.7 cm)	---	---	---	7	0.267
Pacific silver fir, small (<45.7 cm)	---	---	---	5	0.139
western redcedar	2004	0.40%	0.10%	2	0.042**
western redcedar, large (>45.7 cm)	---	---	---	5	0.138
western redcedar, small (<45.7 cm)	---	---	---	---	---
western white pine	---	---	---	---	---
western white pine, large (>45.7 cm)	---	---	---	---	---
western white pine, small (<45.7 cm)	---	---	---	---	---
Pacific yew	1971	0.47%	1.45%	0.5	0.004***
Pacific yew, large (>45.7 cm)	---	---	---	---	---
Pacific yew, small (<45.7 cm)	1971	0.47%	1.46%	0	0.004

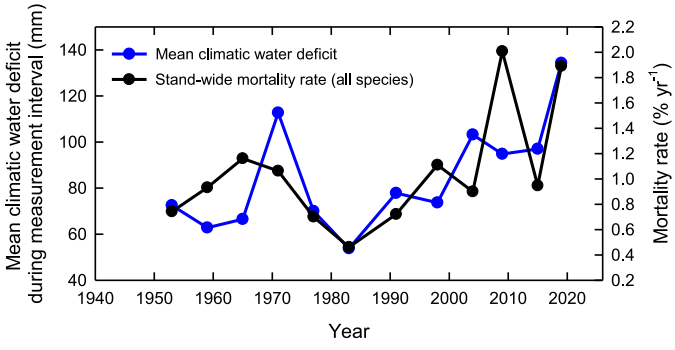

Fig. 8. Comparing trends in climatic water deficit for each measurement period (averaged over the ~6 years) and mortality rates across the stand. See Table 3 for correlations by species and total.

Table 4
Correlations between mortality rates and mean climatic water deficit during a given measurement interval, across the entire measurement period (1947–2019; stand age ~450–520).

Species	Correlation between mortality rate and mean climatic water deficit during measurement interval	
	Spearman *r*	*P*
All species combined	0.48	0.111
All species, large (>45.7 cm)	0.49	0.099*
All species, small (<45.7 cm)	0.43	0.150
Douglas-fir	0.28	0.364
Douglas-fir, large (>45.7 cm)	0.23	0.456
Douglas-fir, small (<45.7 cm)	−0.19	0.527
western hemlock	0.05	0.869
western hemlock, large (>45.7 cm)	0.53	0.071*
western hemlock, small (<45.7 cm)	0.06	0.834
Pacific silver fir	0.62	0.026**
Pacific silver fir, large (>45.7 cm)	0.36	0.233
Pacific silver fir, small (<45.7 cm)	0.54	0.066*
western redcedar	−0.31	0.317
western redcedar, large (>45.7 cm)	−0.24	0.442
western redcedar, small (<45.7 cm)	−0.17	0.572
western white pine	−0.64	0.022**
western white pine, large (>45.7 cm)	−0.50	0.089*
western white pine, small (<45.7 cm)	−0.32	0.295
Pacific yew	0.36	0.233
Pacific yew, large (>45.7 cm)	−0.22	0.484
Pacific yew, small (<45.7 cm)	0.378	0.215

Table 5
Annualized rates (Mg ha^{-1} yr^{-1}) of ecosystem variables relating to aboveground woody biomass, during each measurement interval.

Year	NPP_{AW}	Mortality	Δ Live Mass†	Δ Dead Mass‡	Δ Total Mass
1947	–	–	–	–	–
1953	4.2	−5.8	−1.6	2.3	0.7
1959	3.3	−4.3	−1.1	0.4	−0.6
1965	3.3	−5.0	−1.7	1.0	−0.7
1971	3.0	−5.1	−2.0	0.9	−1.2
1977	2.8	−3.7	−0.9	−0.6	−1.5
1983	2.9	−4.2	−1.4	0.0	−1.3
1991	4.1	−4.0	0.1	−0.1	0.0
1998	2.9	−3.6	−0.6	−0.6	−1.2
2004	2.9	−3.3	−0.4	−0.8	−1.2
2009	3.7	−6.8	−3.1	2.8	−0.3
2015	1.8	−4.4	−2.6	0.1	−2.5
2019	3.3	−7.1	−3.7	2.6	−1.1

* NPP_{AW}, net primary production of aboveground wood, is gross growth of aboveground tree woody tissues (stem, branch, bark) comprising growth of extant trees and ingrowth of new trees.
† Δ Live Mass is net growth of aboveground tree woody tissues; computed as NPP_{AW} minus mortality.
‡ Δ Dead Mass accounts for both recruitment into the dead biomass pool via mortality, and decomposition of carryover wood from prior time point.

attenuation rate of Douglas-fir and the estimated time to its functional extinction in the stand (another 400–820 years, or stand age ~900–1300), the eventual full culmination to pioneer cohort loss (Franklin et al., 2002; Van Pelt, 2025) remains in the distant future, absent significant disturbance or novel stressors that could accelerate this timeline.

While the most abundant shade-tolerant species exhibited continual establishment and self-replacing dynamics, not all did. Western redcedar experienced almost no new recruitment during the entire measurement period, and uniquely low mortality (Tables 1–2, Figs. 2,6,7), suggesting an earlier window of favorable establishment conditions. Pacific yew followed a less pronounced but similar dynamic. This finding suggests that, for certain shade-tolerant elements, regeneration is associated with discrete periods (events or conditions) during stand development. These

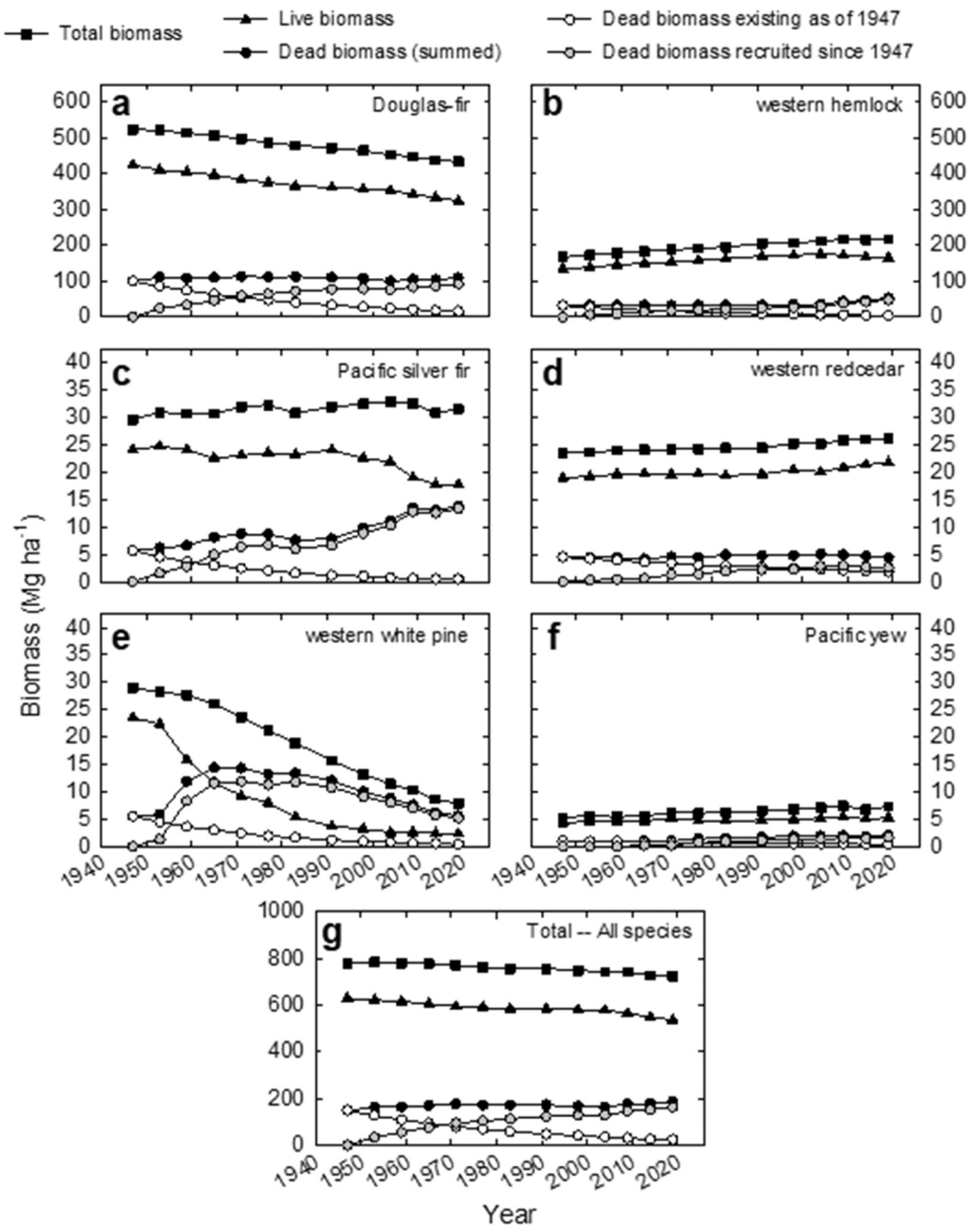

Fig. 9. Trends in live and dead biomass over the 72-year measurement period (stand age ~450–520). Note different y-axis scales.

may include the early stages of canopy opening, remnant legacy seed sources (Keeton and Franklin 2005), or an intermediate disturbance event (Zenner, 2005; Tepley et al., 2013).

4.3. Ecosystem dynamics

Another major theory-based prediction we evaluated was that aboveground biomass would be relatively stable in a 500-year-old stand (Odum, 1969; Acker et al., 2002) – in part due to minimal change in live biomass, and in part due to the buffering effect of dead biomass (Lutz et al., 2021). Prior to the 2000s, this prediction was largely borne out, with relatively little change in total (live+dead) biomass (95.3% net retention of 1947 biomass level through 2004) (Fig. 9, Table 4). While largely stable, the minor decrease during that period is consistent with general expectations of slight biomass decline in very old forests as pioneer trees die (Bormann and Likens, 1994; Binkley, 2023; Kramer et al., 2025). While change in live biomass was slow (92.0% net retention), buffering by dead biomass stored in mortality trees was also a key factor, nearly halving the rate of total biomass change during the measurement period (Figs. 9–10). Given the relatively slow decomposition rate in these systems, this buffering appears to stabilize biomass and carbon stores in old-growth forests for timescales spanning many decades. Moreover, this dataset encompasses only aboveground biomass, not forest floor or soil pools which likely lend further stability to total ecosystem carbon storage than aboveground biomass alone (Harmon et al., 2004; Campell et al., 2004; Lutz et al., 2021).

Our sensitivity analysis on decomposition rates showed the degree of buffering of live biomass losses by dead biomass depends on the decomposition rate. If the rate was 20% less than we assumed, then the offset would be nearly complete; whereas if it was 20% faster, the decline in total biomass would have been essentially parallel to the decline in live biomass (Appendix 2).

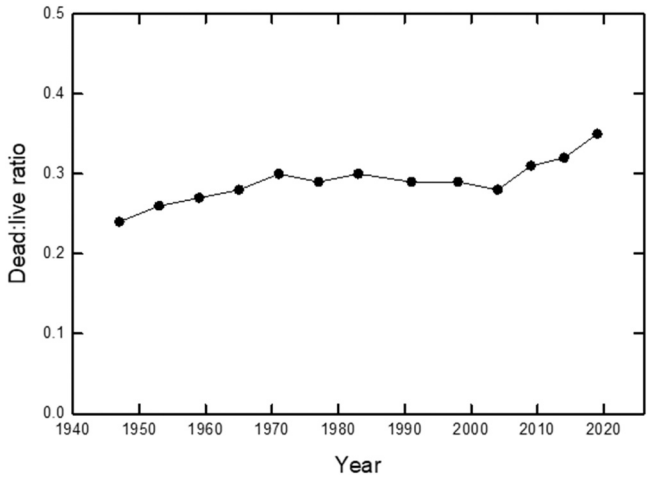

Fig. 10. Dead:live biomass ratio over the 72-year measurement period (stand age ~450–520).

4.4. System dynamism in undisturbed forests

The high production, mortality, and demographic dynamism exhibited by this old-growth forest are similar to those associated with forests experiencing regular exogenous disturbances. Studies in recent decades suggest that, in addition to stand-replacing fires and early-seral reburns, other non-stand-replacing fires later in stand development can be common in parts of the western Cascades (Agee, 1993; Zenner, 2005; Tepley 2013; Johnston et al., 2026). This has led to hypotheses that such fires are *necessary* for establishment of mid- to late-seral shade-tolerant cohorts, and thus development of old-growth structure; however the long-term data in this study demonstrate that is not the case (see also Keeton and Franklin 2005; Zenner, 2005; Tepley et al., 2014 for studies spanning the Washington and Oregon West Cascades). A one-percent annual mortality rate over 80 years can kill a similar number of trees as one or more mixed-severity fires over the same period. In this sense, intermediate disturbances likely affect more the timing of shade-tolerant (and thus old-growth) development – but not whether it occurs. Intermediate exogenous disturbance such as mixed-severity wildfire, windstorms, or irruptive pathogens play an important role in creating, accelerating, and maintaining diversity, even among Western Cascade forests characterized primarily as experiencing low-frequency stand--replacing disturbance (Winter et al., 2002). However, results from this study make abundantly clear that high levels of demographic dynamism and structural development can arise endogenously and be sustained, perhaps indefinitely, without external disturbance.

4.5. Departures from successional predictions in the most recent measurements

Nearly all the structural and demographic dynamics we measured exhibited an inflection point starting in the 2000s, shifting from being consistent with successional-theory predictions to, in some degree, departing from them.

4.5.1. Drought as driver

The observational nature of this dataset makes determining causal mechanisms uncertain: the recently accelerated mortality rates could be novel and climate-driven, or could be part of cyclical or pulsed population dynamics that are insufficiently reflected in theoretical forest succession models. We posit that, congruent with many similar studies globally (e.g.,Van Mantgem et al., 2009; Luo and Chen, 2013; Brzeziecki et al., 2020; Woods et al., 2021; Andrus et al., 2024), it is more likely to be the former.

While climate change has manifested in other systems decades earlier, in the TT Munger area climatic water deficit only showed consistently elevated levels starting in 1998 (Table 3, Fig. 8). The association between climatic water deficit and mortality rates for the most populous trees (Tables 3–4) – western hemlock and Pacific silver fir, two species which are highly drought intolerant (USDA United States Department of Agriculture., 2025) – suggests increasing summer drought stress is the most salient effect of climate change on stand dynamics. That many trees showed no visual indicators of biotic mortality agents – only slow crown decline and death – is also at least consistent with drought impacts. Seasonal drought is an important driver in the otherwise wet western Cascades (Waring and Franklin, 1979; Franklin and Dyrness, 1988). The concurrent increase in both water deficit and mortality rates in the 2000s (Fig. 8), during a successional stage when *increasing* mortality of major shade-tolerant components is not indicated by theory or other stand development, further supports the notion of climate-driven departure (see also Zhang et al., 2015; Germain and Lutz, 2020). Even with more consistent mortality cause data, tying to drought definitively would be challenging because most trees die of a proximal agent (e.g., insects, fungi, mistletoe) more successfully attacking trees predisposed by drought stress (Bell et al., 2020).

Time lags between increased water deficits and elevated mortality (Figs. 7–8) highlight how several years of cumulative drought stress may be what ultimately triggers widespread tree mortality in a well-established population (Gustafson and Sturtevant, 2012; Ku and Lutz, 2025). This is perhaps reinforced by the lack of mortality response after a single earlier elevated drought period (1965–1970, Fig. 8) as well as the lag between recently elevated drought (starting 1998) and mortality (starting 2004) (Table 3). Such lags, and the punctuated pattern of drought-correlated mortality (Figs. 7–8), suggest there are differing tiers of vulnerability, even within species, in which individuals already stressed, on less ideal or transient microsites (Jones et al., 2025), or with less-developed root systems may die sooner under drier conditions, whereas those less predisposed take longer for drought stress and secondary agents (e.g. insects, fungi) to manifest. Wide oscillation in key system drivers can also be a leading indicator of significant ecological transitions (Brock, Carpenter., 2006); it may be too early to know if this is the case, but it warrants continued observation.

4.5.2. Departure at population and community levels

The post−2004 decline in basal area (driven mainly by western hemlock) was unexpected, as hemlock basal area had been steadily increasing for the entire measurement period before 2004 (Fig. 4). Hemlock mortality was shown to be associated with the combined effects of drought and dwarf mistletoe (*Arceuthobium tsugense*) (Bell et al., 2020) in this stand, in which the latter is common (Swanson et al., 2006).

It is not yet clear whether the recent increase in the smallest measured size class (6–15 cm dbh), driven by a pulse of hemlock recruitment (Figs. 2,6), is a discrete period of in-filling due to pulses of overstory hemlock mortality, or a shift toward a higher-turnover regime among the shade-tolerant layer. Shade-tolerant regeneration pulses can occur without overstory mortality (Acker et al., 2006), and shade-tolerant trees are tied to overstory mortality via increased growth more so than increased establishment (Winter et al., 2002). Either way, persistently altered dynamics of western hemlock would represent a major change in old-growth structural development writ large, as it is the most abundant tree and the main contributor to vertical canopy diversification in old forests of the region. Whether this change continues or is widespread among sites (see Acker et al., 2023) will be key to monitor into the future.

In contrast, western redcedar's relatively stable (or even decreasing) mortality rate in recent intervals (Table 3, Fig. 7) may reflect its high stress tolerance (Antos et al., 2016) in the face of increasing summer drought, and suggests it may play a proportionally greater role in structuring the shade-tolerant layers, if elevated hemlock mortality continues. These observations contrast with observations of widespread

cedar 'dieback' or mortality elsewhere in the region (Zobrist, 2018; Andrus et al., 2024), suggesting that individuals in well-established, closed-canopy forests are less prone to novel drought stress than those in more exposed or developed sites.

4.5.3. Departure at the ecosystem level

Changes in fundamental ecosystem processes such as NPP, mortality and decomposition can influence forest carbon dynamics at multiple time scales (Wharton et al., 2012). The recent elevated biomass mortality rates – particularly for large hemlocks – clearly modified aboveground biomass dynamics; this would be expected since mortality is as important as NPP in determining biomass levels (Acker et al., 2002). The tripling of the annual loss rate of live woody biomass after 2004 means the cumulative loss in the last 15 years of measurements was roughly equal to that of the prior 57 years (Table 5). If these trends in biomass mortality persist, then a substantial (~32%) decline in live biomass is anticipated (Appendix 2). Storage in dead biomass, reflected in part by the uptick in the dead:live ratio near the end of the measurement period (Fig. 10), largely buffered this change for total aboveground woody biomass, which remained comparatively stable even in recent measurement intervals (Fig. 9). Despite this buffering, a persistent increase in biomass mortality rates related to expected intensification of summer drought in the western Cascades (Hudec et al., 2019) could lead to at least a 25% decrease in total wood biomass (Appendix 2). In addition, NPP_{AW} was observed to have declined 10% in the most recent period; if this also persists with increased mortality, then a decline in live and total wood biomass could be 39% and 32%, respectively. Decomposition rates could also change with altered temperature and moisture regimes. If on one hand decomposition rates increase, then total wood stores would decline even more. On the other hand, it seems unlikely that decomposition rates could decline sufficiently (≈50%) to offset the effects of decreased NPP_{AW} and increased mortality rates on total woody biomass (Appendix 2). Given these trends in fundamental ecosystem processes, carbon storage function of this old-growth forest is highly likely to change substantially in the future.

4.6. Study limitations

To our knowledge this is the first study to report accelerated mortality and live biomass decline in an old-growth forest in the Douglas-fir region of the U.S. Pacific Northwest, based upon repeated measurements of long-term permanent (tagged-tree) plots. This phenomenon would have significant impact if widespread. Hence, it is important to consider the degree to which this site might be representative of the broader region. While the TT Munger RNA was selected as an archetype of old-growth Douglas-fir/western hemlock forests, it has some unique features. It is in a valley that is near, and drains south into, the Columbia River Gorge (the only sea-level passage through the Cascade Range), in contrast to the west-facing slopes and valleys in most of the western Cascades. This geography makes the site more subject to continental influences, including warmer and drier summers, than other western Washington Cascade forests to the north. An additional factor is the coarse-textured, somewhat shallow loamy sand/sandy loam young volcanic soil, deposited over basalt bedrock; this somewhat lowers water-holding capacity. Taken together, these conditions may make the site more sensitive to climate change than some other old-growth Douglas-fir/western hemlock forests. It will be important to determine whether observations from this stand are unique versus being a 'leading edge' indicator of drought impacts to similar forests across the broader Douglas-fir region. Numerous permanent sample plots in the region established 45–60 years ago can provide data for such studies.

This study is observational – it is not a controlled experiment. Attribution of changes to a mechanism, such as climate impacts, will necessarily be correlative and other mechanisms cannot be definitively ruled out (though we have described logic and field observations pointing to drought as a likely driver). This approach is similar to a body of research relating recently elevated tree mortality with changing climate (e.g., Van Mantgem et al., 2009; Luo and Chen, 2013; Brzeziecki et al., 2020; Woods et al., 2021; Andrus et al., 2024). Moreover, while the temporal scope and stand type make this dataset uniquely important, it is based on a single stand: the 93 plots do not have spatial independence and are subsamples rather than true replicates (hence the intentionally limited statistical analyses here). This set of observations does not prove generality, which can only be tested by comparing across similar datasets in this and other regions, and with further temporal sampling to distinguish potential climate impacts from possibly cyclical or episodic background dynamics.

5. Conclusion

Classical theory predicts that, without significant disturbance, a forest will eventually attain steady state in recruitment, growth, mortality, net primary production, and biomass storage – while developing toward structural heterogeneity and shade-tolerant dominance. The structural and compositional development, and relative stability in other system attributes, of this ~500-year-old forest were remarkably consistent with these predictions for the bulk of the observation period. These data empirically demonstrate the system dynamism and structural development exhibited by old-growth forests in the absence of, or between, significant disturbances.

The marked inflection point in mortality rates and biomass dynamics in this stand since the onset of intensified drought in the 2000s merits continued attention. The change to the major stand-structuring but drought-sensitive species western hemlock and Pacific silver fir, if continued and/or widespread, could substantially impact old-forest development across multiple scales. Continued observation of this and other old forests will be essential to discerning whether recent climate-correlated changes in mortality and stand dynamics persist, and whether stands like the one studied here are bellwethers or exceptions. Additional work may complement this broad look at stand dynamics by investigating mechanisms, such as agents of tree mortality, better understanding of current and future decomposition rates, and fine-scale species interactions coupled to changing drought stress. Long-term datasets such as this will be crucial to tracking and distinguishing endogenous and externally-driven changes in forest development in the global change era.

CRediT authorship contribution statement

Daniel C. Donato: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mark E. Swanson:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **James A. Lutz:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Andrew J. Larson:** Writing – review & editing, Resources, Methodology, Investigation, Data curation, Conceptualization. **Brian J. Harvey:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Mark E. Harmon:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **James A. Freund:** Writing – review & editing, Resources, Methodology, Investigation. **John L. Campbell:** Writing – review & editing, Investigation. **Jerry F. Franklin:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124012.

Data availability

Research Link Provided

Thornton T Munger Research Natural Area old-growth forest permanent sample plots (MUNA, MUN2) (US Forest Service/Oregon State University Permanent Sample Plot Program)

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