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Death and *Taxus*: the contribution of mechanical damage to the multiple factors associated with *Taxus brevifolia* mortality

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Abstract

Background Recent increases in tree mortality are often attributed to climate, but climate extremes may just be the last of many stressors that have unfolded over many years resulting in tree death. Potentially it is only those trees weakened by mechanical damage or attacks by insects or fungi that are susceptible to climate-mediated mortality, whereas vigorous trees resist periods of unfavorable climate. Although previous studies have explored immediate and catastrophic effects of mechanical damage via blowdowns and stem breakage, few have investigated the delayed effects of mechanical damage on mortality. *Taxus* is a shade-tolerant genus of subcanopy trees or shrubs distributed throughout the northern hemisphere. Populations of *Taxus* are in decline worldwide but owing to the tenacity of *Taxus* in the face of stressors, this decline is poorly understood. Here, we provide spatial evidence that cumulative stress interactions, particularly mechanical damage, contribute to *Taxus* mortality.

Methods We examined 14 years of annual demographic data from the 27.2 ha Wind River Forest Dynamics Plot (WFDP), where woody stems, snags, and deadwood have been tagged, mapped and identified to species. We analyzed the multiple factors associated with tree death, including mechanical damage, pathogens, suppression, beetles, animal damage, and their combinations. We performed spatial pattern analyses with the pair correlation function to investigate the prevalence of density-dependent mortality, effects of neighboring large-diameter trees, and effects of nearby snag fall and deadwood.

Results In 2011, there were 29,827 trees within the WFDP of which 2119 were *Taxus*. Between 2011 and 2024, *Taxus* declined to 1523 trees (mean annual mortality of 2.79% yr^{-1}). *Taxus* mortality was not influenced by intraspecific density dependence or the presence of snags but was mainly driven by mechanical damage, pathogens, and suppression. Dead *Taxus* were strongly associated with deadwood within 2 m of the bole. Structural equation modeling showed that mechanical damage likely increased the vulnerability of *Taxus* to pathogen infection and exposure to drier gap areas.

Conclusions These results suggest that *Taxus* mortality is rarely due to a single event, but a cumulative process of interacting stressors initiated by falling wood and often culminating in death by other stressors—potentially many years later. The association of newly dead trees with deadwood suggests that falling snags likely contributed to past crown damage, initiating or accelerating a decline spiral. The results emphasize that previous mechanical damage—evidenced by mapped and persistent deadwood—can disproportionately affect tree species, influencing successional dynamics.

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Keywords Deadwood, Decline spiral, Mechanical mortality, Smithsonian ForestGEO, Snag, *Taxus brevifolia*, Wind River Forest Dynamics Plot

Introduction

Tree mortality can rapidly alter forest composition, structure, and functioning (Franklin et al. 1987; Chao et al. 2009; Holzwarth et al. 2013; Birch et al. 2019). Tree mortality can be influenced and accelerated by rising temperature, declining precipitation, and drought (Hutyra et al. 2005; Allen et al. 2010; Germain and Lutz 2022). However, mortality and mortality-driven successional processes are not driven by climate alone—death can result from immediate mechanical damage (i.e., windthrow or stem breakage) or from cumulative stressors that can weaken tree vigor or from the combined effects of insects, pathogens, mechanical damage, and unfavorable local tree neighborhoods (Birch et al. 2019).

The process of tree mortality often unfolds over many years as the effect of small injuries compounds (Manion 1981). The Manion's "decline disease spiral" model (Manion 1981) posits that initial injuries predispose an individual to further factors associated with death, and after time, mortality results from the sequential contribution of various factors from which the tree is unable to recover. These mortality processes are a long-term series of interactions involving both biological (Manion 1981) and mechanical factors (Lutz and Halpern 2006; Larson and Franklin 2010; Das et al. 2016). In this conceptualization, an initially negative factor, which could be competition-related or related to an acute injury, renders the tree less able to compete for limited resources. This lesser ability to mobilize resources (compared to the pre-injury state) may result in the tree being unable to mobilize sufficient chemical defenses against pathogens or repair mechanical damage through primary or epicormic branch growth. Once a tree loses its competitive ability, it may be ultimately excluded from the forest ecosystem (Iszkuło et al. 2012), but it is important to consider that the actual tree mortality may occur many years after the onset of the decline spiral.

Mechanical damage from wind or snow can cause treefall that directly injures neighboring trees or indirectly alters the surrounding environment (Valinger et al. 1993). Although mechanical damage was not emphasized in Manion (1981), it has been identified as a significant cause of mortality in western forests in United States (Lutz and Halpern 2006; Larson and Franklin 2010). Direct physical damage, including injuries to the crown, branches, and bole, can weaken trees (Lutz and Halpern 2006; Larson and Franklin 2010; Das et al. 2016), leading to reduced vigor and increased the risk of pathogen infection (Manion 1981; Marçais and Bréda 2006). Trees may not die immediately, but repairing mechanical damage requires considerable energy (Anderegg et al. 2012). Indirect damage can also occur when small or large gaps are created in a tree's local neighborhood, allowing more light penetration that in turn increases air and soil temperature and reduces humidity compared to non-gap areas (Chen et al. 1992, 1995).

Fully mapped areas of forest can reveal complex interactions between trees including those resulting in population fluctuations and mortality (Franklin et al. 1985; Kenkel 1988; Kenkel et al. 1997; O'Dwyer et al. 2025). Spatial point pattern analyses of these mapped areas can provide evidence for intra- and interspecific competition, as well as the association between existing structures (i.e., large trees or gaps) and mortality and recruitment (Raventós et al. 2010; Lutz et al. 2014; Erfanifard et al. 2018; Birch et al. 2019; Birch and Lutz 2023). Mortality processes are often reflected in tree distribution patterns with the principal categories of patterns being aggregation, randomness, and regularity. Complex relationships between tree neighborhoods and mortality may require large numbers of individuals to achieve significant results (Wiegand and Moloney 2013; Baddeley et al. 2015).

Taxus brevifolia Nutt., our focal species, is a non-resinous evergreen genus belonging to the Taxaceae Gray (Spjut 1999). *Taxus* L. is a widely distributed genus in the northern hemisphere, including Europe (*Taxus baccata* L.–European yew), North America (*T. canadensis* Marshell–Canada yew, *T. brevifolia*–Pacific yew, *T. floridana* Nutt.–Florida yew, *T. globosa* Schltdl.–Mexican yew) and Asia (*T. chinensis* Rehd.–China yew, *T. contorta* Griff–West Himalayan yew, *T. cupidata* Zucc.–Japanese yew, *T. florinii* Spjut–Florin yew, *T. mairei* (Lemée & H.Lév.) S. Y. Hu–Maire yew, *T. wallichiana* Zucc.–East Himalayan yew, and *T. calcicola* L. M. Gao) (IUCN 2024; Royal Botanic Gardens, Kew 2024; Thakur and Kanwal 2024). *Taxus* has considerable economic value due to the secondary compounds in their bark and leaves, which are used in cancer treatment (Fuchs and Johnson 1978; Gomes et al. 2020). Despite their importance, six out of the 12 recognized *Taxus* species are currently threatened (IUCN 2024), with declining populations driven by early anthropogenic exploitation and environmental changes. *Taxus* is a highly shade-tolerant genus (Mitchell 1998;

Windels and Flaspohler 2011), well adapted to low-light environments, but sensitive to drought (Thomas and Garcia-Marti 2015; Germain and Lutz 2020) and herbivory (Holmes et al. 2009). Recovery following disturbance and drought is typically slow (Busing et al. 1995).

Our objective was to unravel the underlying mechanisms of the mortality for *Taxus* in late-seral forests. Specifically, we examined (1) whether high tree neighborhood density increased mortality via competition, (2) whether mechanical damage was directly associated with mortality, and (3) whether mechanical mortality was indirectly associated with mortality, showing the potential to increase vulnerability to drought as well as attacks by insect and fungal enemies.

Methods

Study site

We used *Taxus* population data in Wind River Forest Dynamics Plot (WFDP; Lutz et al. 2013), a 535-year-old forest located 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). Elevation ranges from 352 to 379 m with mean annual temperature of 10.7 °C, and mean annual precipitation is 2493 mm. There is very little precipitation between June and September, and the droughtiness of the summer dry season has shown an increasing trend from 2000 to 2024, but without statistical significance due to the high interannual variation (Figure S1b). The vegetation is characterized as *Pseudotsuga-Tsuga* (Douglas-fir/western hemlock) forest. The most abundant woody stems (by stem density) include *Acer circinatum* Pursh, *Tsuga heterophylla* (Raf.) Sarg., *Abies amabilis* Douglas ex J. Forbes, *Taxus brevifolia*, *Vaccinium parvifolium* Sm., *Corylus cornuta* var. *californica* Marshall, *Pseudotsuga menziesii* (Mirbel) Franco, *Rhododendron macrophyllum* D. Don ex G. Don, *Thuja plicata* Donn ex D. Don, and *Cornus nuttallii* Audubon ex Torr. & A. Gray. The majority of basal area (85%) is contributed by *Tsuga* and *Pseudotsuga* (Lutz et al. 2013). Plant nomenclature follows Flora of North America Editorial Committee (1993).

Data collection

The WFDP was established at 25.6 ha in 2010–2011 and was subsequently increased in area to 27.2 ha in 2016. All woody stems ≥ 1 cm at breast height (1.37 m above the ground—the historical height of measurement in the Pacific Northwest (Pinchot 1903; Magarik 2021)) were tagged, mapped, and identified to species following the protocols of the Smithsonian Forest Global Earth Observation network (ForestGEO; Davies et al. 2021). Full remeasurement of all stems took place in 2016 and 2021, and tree mortality and recruitment were assessed annually, early in the growing season, from 2012 to 2024 (Lutz 2015). Annual examination of the multiple causes of mortality in early spring allows differentiation between beetle activity that was proximate to mortality and activity that was post-mortem (Lutz 2015). Similarly, annual examinations capture pathogenic fungi that contributed to mortality, whereas longer intervals (i.e., a more standard 5-year interval between forest censuses) may not be able to differentiate between pathogenic activity and post-mortem decomposition (Lutz and Halpern 2006). For details of the field identification of the factors associated with mortality, see Supplemental Information. In addition to the dynamics of living stems, snags and deadwood were also tracked (Lutz et al. 2021), with all deadwood originating from the main stem of trees ≥ 10 cm being mapped, including deadwood that fell to the ground before plot inception in 2010/2011 (Janík et al. 2018). Newly created deadwood was assessed and mapped annually.

To address the multiple factors contributing to *Taxus* mortality, field crews performed pathology exams on newly dead trees to assess the factors associated with tree death, including those arising from mechanical causes, pathogens, suppression, beetle attack, and animal damage. Field crews removed bark from dead trees and roots to identify beetles and root rot pathogens. We consolidated the detailed mortality factors into mechanical mortality, pathogens, suppression, bark beetles, and their combinations.

Demography

We classified *Taxus* into four diameter classes: 1 cm ≤ DBH < 5 cm, 5 cm ≤ DBH < 15 cm, 15 cm ≤ DBH < 25 cm, and DBH ≥ 25 cm, following Busing et al. (1995). For the non-*Taxus* species, we defined large trees as having a diameter ≥ 60 cm, based on (Lutz et al. 2018, 2021). Trees of non-*Taxus* species < 60 cm DBH were classified as small trees.

Mortality and recruitment rates from 2012 to 2024 were calculated:

$$\text{Annual mortality rate}: m = \left[1 - \left(\frac{N_0 - N_m}{N_0}\right)^{1/t}\right] \times 100 \quad (1)$$

$$\text{Annual recruitment rate}: r = \left[\left(\frac{N_0 + N_r}{N_0}\right)^{\frac{1}{t}} - 1\right] \times 100 \quad (2)$$

where t is the time of the census interval in years; N_0 represents the population at the previous census t–1; N_m is the number of trees that died in the interval; N_r is the number of trees that recruited at time t. We also calculated the local extinction time (t_{ex}), which was assumed

to be equal to the time for 99% of the cohort to die, it was derived from the mortality rate (m):

$$t_{ex} = \frac{\ln(0.01)}{\ln(1 - \frac{m}{100})} \quad (3)$$

Associations among mortality factors

To test the associations among mechanical damage, pathogen infection, suppression, insect and animal factors contributing to *Taxus* mortality across different diameter classes, we developed a multilevel structural equation model (SEM; Lefcheck 2016). We used a piecewise SEM with generalized linear models (GLMs), employing Gaussian and binomial distributions to fit the data type of each factor affecting *Taxus* mortality. The Gaussian distribution was used to detect the relationship between each mortality factor on different diameter classes, while the binomial distribution was used to test the relationship among mortality factors. The SEM model also allowed examination of the moderation and mediation effects within and between GLMs. Moderation evaluates the direction and strength of the relationship between dependent and independents variables, while mediation assesses the indirect effect of one variable on another through a third variable.

To evaluate whether mechanical damage initiated a cascade of fungal and insect-related stressors leading to *Taxus* mortality, we constructed three SEMs to test the causal pathways. First, we tested whether each mortality factor was associated with different diameter classes of *Taxus* mortality. Second, we evaluated the possibility that mechanical damage serves as the initial injury, triggering an increased risk of suppression and fungal infection. Third, we assessed whether pathogen infection was directly influenced by mechanical damage but also indirectly driven by tree suppression resulting from mechanical damage.

Spatial patterns

To examine the spatial correlates of *Taxus* mortality within different local neighborhoods, we used the univariate, bivariate and multi-type point pattern of the pair correlation function $g(r)$. The pair correlation function is defined as:

$$g(r) = \frac{K'(r)}{2\pi r} \quad (4)$$

where $K'(r)$ represents the derivative of Ripley's K function and r is the distance from the focal tree. Preliminary analysis showed that the distribution of *Taxus* and other species were not homogenous, so the inhomogeneous forms of each pair correlation function were used (Baddeley et al. 2015). We applied the univariate point pattern process to examine the spatial distribution of live *Taxus,* where $g(r) > 0$ indicates spatial aggregation, $g(r) = 0$ indicates a random distribution, and $g(r) < 0$ indicates a regular (or dispersed) distribution (Taylor and Halpern 1991; Perry et al. 2009).

Next, we used the multi-type point pattern analysis to evaluate density dependency between dead *Taxus* and the live *Taxus*. Random labeling was used to assess posteriori process within the data (Kenkel 1988; Goreaud and Pélissier 2003). In this context, $g_{d,d}(r) > 0$ indicates an aggregation of dead trees, $g_{d,d}(r) = 0$ represents a random distribution, and $g_{d,d}(r) < 0$ indicates repulsion among dead trees. Under a random mortality $g_{d,all}(r) - g_{l,all}(r) = 0$. If the mortality indicates negative density dependency, $g_{d,all}(r) - g_{l,all}(r) > 0$ indicates that trees that died were more crowded than surviving trees. Conversely, if mortality is positive density dependent, $g_{d,all}(r) - g_{l,all}(r) < 0$ indicates that trees that died were less crowded than surviving trees.

Last, the bivariate point pattern was used to test the relationship between two independent categories (Lotwick and Silverman 1982). Specifically, we assessed the relationship between all dead (or live) *Taxus* and the variables j including the large (or small) diameter dead (or live) trees and all deadwood. We applied a toroidal shift approach that randomized one pattern while fixing the other, maintaining internal structure but removing spatial dependence. Large and small tree locations were fixed when shifting *Taxus* positions, whereas dead *Taxus* were fixed when randomizing deadwood. $g_{d,j}(r) > 0$ shows a positive relationship between dead *Taxus* and the variable j; $g_{d,j}(r) < 0$ indicates a negative relationship between the dead *Taxus* and variable j; $g_{d,j}(r) = 0$ represents two variables unrelated in space.

We calculated the nearest distance from deadwood pieces to dead *Taxus* and used that nearest distance as the location of the deadwood. We then calculated the diameter of the deadwood at its nearest point, selecting those with diameter ≥ 25 cm (diameter sensitivity analysis; Figure S3).

All analysis were conducted in R version 4.4.1 (R Core Team 2024). For spatial pattern analyses, we used the *spatstat* package (Baddeley and Turner 2005). The *ppp()* function was used to create the point patterns, and *quadrat.test ()* was employed to test the homogeneity or inhomogeneity of point patterns. The univariate point pattern was analyzed using *pcfinhom()*, random labels were generated by *pcfdot.inhom()* with *rlabel()* for random label simulation, and the bivariate point pattern was generated by *pcfcross.inhom()* with *rshift()* for shifting simulation. All simulation for the randomness were performed 99 times using *envelope()* with Ripley's edge correction. For

testing associations among factors, we built models using *glmer ()* from the *lme4* package. The *piecewiseSEM* package was used to structure the models through *psem()* for piecewise structural equation modeling (Table 1).

Results

Forest dynamics in the Wind River Forest Dynamics Plot

In 2024, there were 1,523 live *Taxus* trees in the WFDP, with an average DBH of 14 cm and a maximum DBH of 69 cm. The 1% largest diameter of *Taxus* was 46.1 cm. From 2012 to 2024, 671 *Taxus* died; average DBH of dead trees was 12.5 cm (maximum 69 cm DBH; Fig. 1).

Taxus showed the highest mortality of all principal species in the WFDP with annual mortality between 1.38% and 4.18%, gradually increasing over time (Table 2). The overall annual mortality rate from 2011 to 2024 was 2.79%. If current rates continue, with no change in recruitment or mortality factors, *Taxus* will be locally extirpated in 163 years.

Mortality factors for *Taxus*

Mechanical damage accounted for 49.3% of *Taxus* mortality, pathogen infection contributed 58.4% (with 32% being *Armillaria ostoyae* (Romagn.) Herink), and suppression accounted for 25.6% (Fig. 2). There was strong

Table 1 Tests used for different categories of ecological processes and the interpretation for each function

Function	Description	Results
Univariate		
$g_{live\ Taxus}(r)$	Testing the spatial pattern of *Taxus*	Figure 3a
Bivariate		
Simulation: random labeling		
$g_{dead\ Taxus,\ all\ Taxus}(r)$-$g_{live\ Taxus,\ all\ Taxus}(r)$	Conspecific negative density dependence of *Taxus*	Figure 3b
Simulation: Random shifting		
$g_{live\ Taxus,\ live\ small}(r)$	Testing the aggregation of surrounding small trees (fixed variable) from the live *Taxus* (shifting variable)	Figure 3c
$g_{dead\ Taxus,\ live\ small}(r)$	Testing the aggregation of surrounding small trees (fixed variable) from the dead *Taxus* (shifting variable)	Figure 3d
$g_{dead\ Taxus,\ live\ large}(r)$	Relationship between dead *Taxus* (shifting variable) and large diameter trees (fixed variable)	Figure 3e
$g_{dead\ Taxus,\ dead\ large}(r)$	Relationship between dead *Taxus* (shifting variable) and dead large trees (fixed variable)	Figure 3f
$g_{live\ Taxus,\ dead\ wood}(r)$	Relationship between live *Taxus* (fixed variable) and deadwood (shifting variable)	Figure 4a
$g_{dead\ Taxus,\ dead\ wood}(r)$	Relationship between dead *Taxus* (fixed variable) and deadwood (shifting variable)	Figure 4b

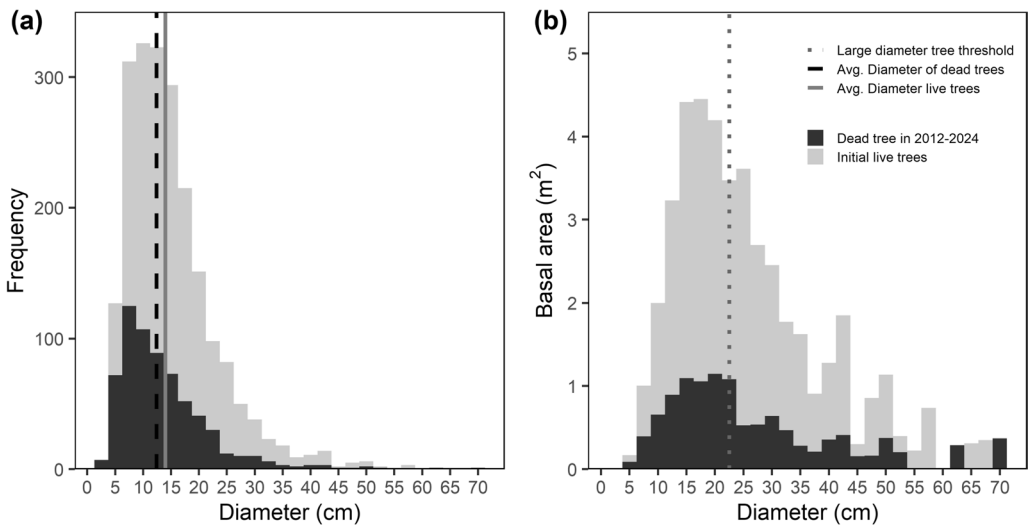


Fig. 1 Diameter distribution of *Taxus* from 2010 to 2024 in the Wind River Forest Dynamics Plot, Washington, USA. **a** trees in each centimeter diameter class; **b** basal area (m^2) in each centimeter diameter class. Black bars indicate trees that died between 2011 and 2024 ($n = 671$); and grey bars indicate those trees alive at the initial survey in 2010/2011($n = 2119$)

Table 2 Population dynamics of *Taxus* with diameter at breast height ≥ 1 cm from 2012 to 2024 in Wind River Forest Dynamics Plot, Washington State, USA. BA: Basal area

Census (year)	Area (ha)	*Taxus* trees	Density (trees ha^{-1})	BA (m^2 ha^{-1})	Mortality			Recruitment		
					Density (trees ha^{-1})	BA (m^2 ha^{-1})	Rate (%)	Density (trees ha^{-1})	BA (m^2 ha^{-1})	Rate
2010/2011	25.6	2119	83	1.68						
2012†	25.6	2050	80	1.68	3	0.04	1.99	0	0.00	0.00
2013	25.6	2008	78	1.65	2	0.03	2.05	0	0.00	0.00
2014	25.6	1972	77	1.62	1	0.03	1.79	0	0.00	0.00
2015	25.6	1900	74	1.57	3	0.06	3.65	0	0.00	0.00
2016	27.2	1714	70	1.55	2††	0.03††	2.79††	0	0.00	0.00
2017	27.2	1850	68	1.49	2	0.03	3.34	0	0.00	0.00
2018	27.2	1770	65	1.44	3	0.05	4.43	< 1	< 0.01	0.11
2019	27.2	1735	64	1.41	1	0.03	1.98	0	0.00	0.00
2020	27.2	1712	63	1.39	1	0.02	1.38	< 1	< 0.01	0.06
2021	27.2	1680	62	1.38	1	0.02	1.99	< 1	< 0.01	0.12
2022	27.2	1652	61	1.34	1	0.03	1.73	< 1	< 0.01	0.06
2023	27.2	1582	58	1.30	3	0.04	4.30	0	0.00	0.00
2024	27.2	1522	56	1.25	2	0.05	3.86	< 1	< 0.01	0.06

† Mortality and recruitment in 2012 were calculated based on a two-year interval for the 12.8 ha of the WFDP first censused in 2010 and based on a one-year interval for the 12.8 ha censused in 2011 with the separate rates being combined on an equal-area basis

†† As part of the 2016 census, the WFDP was extended 20 m to the north (from 25.6 ha to 27.2 ha). Mortality for 2016 was calculated based on the 2015 population in the original 25.6 ha

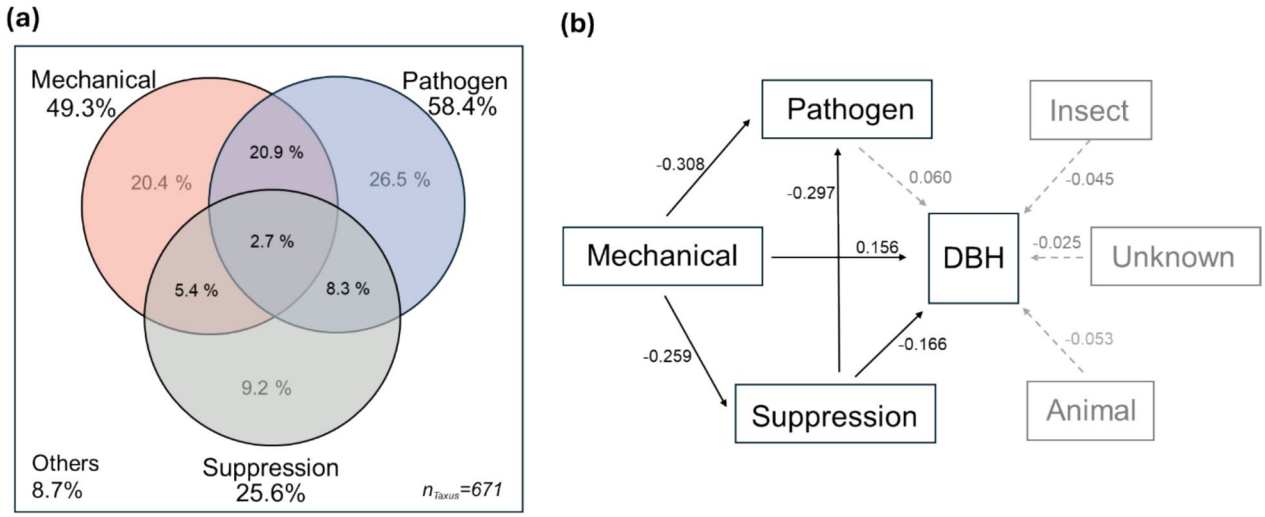


Fig. 2 Association of the multiple factors contributing to *Taxus* mortality. **a** Proportions of *Taxus* mortality are attributed to three major factors, showing both pure effect and joint effects; **b** Structural equation model shows the relationships among mortality factors, and their impact on *Taxus* mortality across different diameters. Trees affected by multiple combinations of factors may experience overlapping influences, resulting in percentages that may exceed 100%

association among mechanical damage, pathogen infection, and suppression (Fig. 2). Specifically, 29.0% of mechanical damage was associated with other factors; 31.9% of pathogen-related mortality overlapped with other factors; and 16.4% of suppression was linked to other factors (Fig. 2a). Overall, there was ~ 50% probability of mechanical mortality being associated with other factors, leading to the negative interactions among the factors (Fig. 2b). Mortality patterns varied by tree diameter (Fig. 2). Mechanical damage accounted

Table 3 Mortality factors and population dynamics for each diameter class of dead *Taxus* between 2012 and 2024 in the Wind River Forest Dynamics Plot, Washington, USA

Diameter class (cm)	Dynamic		Mortality factors (%)						
	Initial live *Taxus*	Annual mortality rate (%)	*N*	Mechanical	Pathogen	Suppression	Insect	Animal	Unknown
1–5	125	5.86	77	31.2 (24)	48.1 (37)	46.8 (36)	1.3 (1)	2.6 (2)	13.0 (10)
5–15	1246	2.88	402	47.5 (191)	57.1 (229)	28.4 (114)	0.2 (1)	0.2 (1)	9.0 (36)
15–25	558	2.34	147	58.5 (86)	66.7 (98)	13.6 (20)	–	–	4.1 (6)
≥ 25	190	1.90	45	66.7 (30)	62.2 (28)	4.4 (2)	–	–	4.4 (2)
Total	2119	2.79	671	49.3 (331)	58.4 (392)	25.6 (172)	0.3 (2)	0.4 (3)	8.0 (54)

† Each tree may have multiple factors associated with mortality, resulting in percentages that may exceed 100%

for 66.7% of *Taxus* mortality in large-diameter trees (DBH ≥ 25 cm), the highest percentage for mechanical damage (Table 3). Suppression, on the other hand, was more prevalent in the mortality of small-diameter trees (1 cm ≤ DBH < 5 cm), although most small-trees mortality was also associated with pathogens. However, pathogens were not linked to mortality in any specific diameter class.

Spatial pattern and density dependence

Live *Taxus* were aggregated (Fig. 3a), whereas *Taxus* mortality followed a random distribution relative to the overall *Taxus* population. Density dependence analysis (Fig. 3b) revealed that dead *Taxus* have a negative g (r) within 0.5 m, suggesting that *Taxus* are less likely to die near aggregated live *Taxus* in the forest. Both live and dead *Taxus* were negatively associated with live trees at distances < 3 m, and showed random associations with other small trees (Fig. 3c, d). There was no significant relationship between large-diameter trees and live *Taxus* (Fig. 3e). Dead *Taxus* exhibited a random distribution relative to large-diameter trees (Fig. 3f).

Deadwood

Of the 5,809 pieces of mapped deadwood ≥ 10 cm in diameter, there were 2,505 pieces ≥ 25 cm diameter (Figure S4). Live *Taxus* showed no spatial relationship with deadwood (Fig. 4a). However, dead *Taxus* were highly associated with deadwood (Fig. 4b). Notably, 338 pieces of deadwood ≥ 25 cm diameter were located within a 2-m radius of dead *Taxus*, including 163 pieces that had fallen before the WFDP was established.

Discussion

Spatial analysis showed that the declining *Taxus* population was primarily influenced by the local neighborhood. However, the most significant aspect of the local neighborhood was fallen deadwood rather than competition. *Taxus* experienced high mortality rates in the WFDP, a pattern observed not only in our forest but also in others (Busing et al. 1995; Larson and Franklin 2010; Lutz et al. 2014; Germain and Lutz 2020). If current conditions were to continue, the recent rate of decline is consistent with *Taxus* facing local extirpation within 163 years. However, SEM analysis showed that *Taxus* mortality is heavily influenced by a combination of factors, and the prevalence of these factors may change over centennial timeframes.

Density dependence and neighborhood effects

Competition can be highest in areas with high densities of small trees, leading to strong density-dependent mortality (Gause 1932; Das et al. 2018; Gavina et al. 2018). Negative density dependence is a key process in forest succession (Johnson et al. 2012) of both tropical (Wills and Condit 1999; Zhu et al. 2010) and temperate forests (Yao et al. 2016; Das et al. 2016), the intensity varying through successional stages (Birch et al. 2019). Although *Taxus* were highly aggregated in the WFDP, our results (based on location of tree boles) found no evidence of self-thinning, suggesting that *Taxus* does not undergo the same nature of competitive pressures found with other species. Instead, *Taxus* tends to thrive in relative moist areas, where multiple trees often grow together, suggesting the importance of habitat selection.

Taxus showed a positive density dependent in both conspecific and heterospecific contexts, indicating strong facilitation at short inter-tree distances (Bronstein 2009; Zélé et al. 2018). *Taxus* associated positively with various species, likely because it is long-lived in old-growth systems. In contrast, other shade-tolerant conifers in these *Pseudotsuga/Tsuga* forests, such as *Tsuga heterophylla*, often exhibit strong conspecific negative density dependence (Lutz et al. 2014), likely driven by strong competition for water in the dry summer. Our results show that *Taxus* survives well in the presence of other

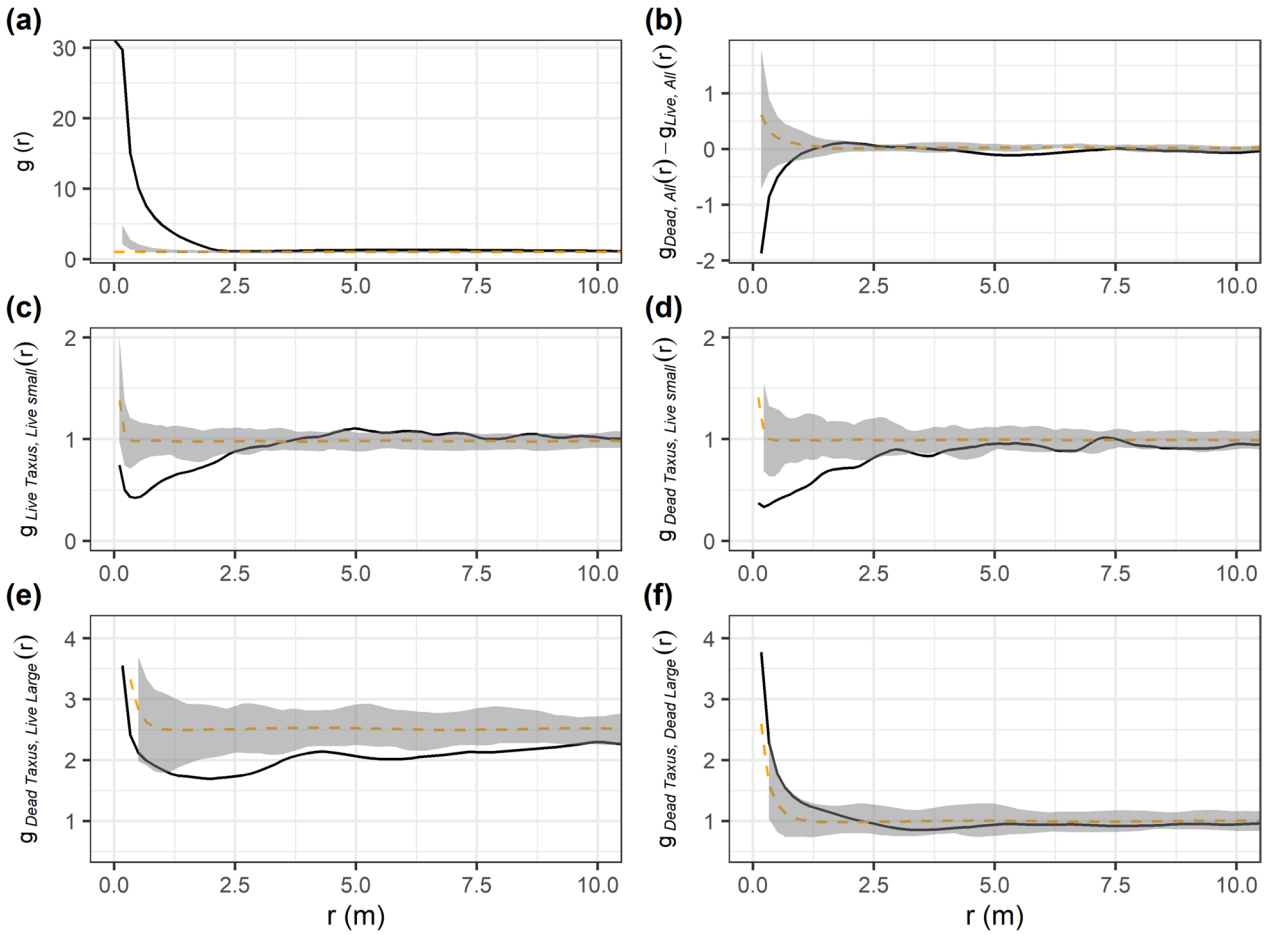


Fig. 3 Spatial pattern of *Taxus* with different neighborhoods in the Wind River Forest Dynamics Plot, Washington, USA. **a** inhomogeneous univariate for all live *Taxus* ($n = 1{,}523$); **b** random labeling testing the density dependency of dead *Taxus* ($n = 671$); **c** bivariate comparison between live *Taxus* ($n = 1{,}523$) and live trees with diameter < 60 cm ($n = 28{,}740$); **d** bivariate comparison between dead *Taxus* ($n = 671$) and live trees with diameter < 60 cm ($n = 28{,}740$); **e** bivariate relationship between dead *Taxus* ($n = 671$) and live large diameter trees (DBH ≥ 60 cm) ($n = 1{,}654$); **f** bivariate relationship between dead *Taxus* ($n = 671$) and dead large diameter trees (DBH ≥ 60 cm) ($n = 795$). Confidence intervals are based on 99 Monte Carlo simulations

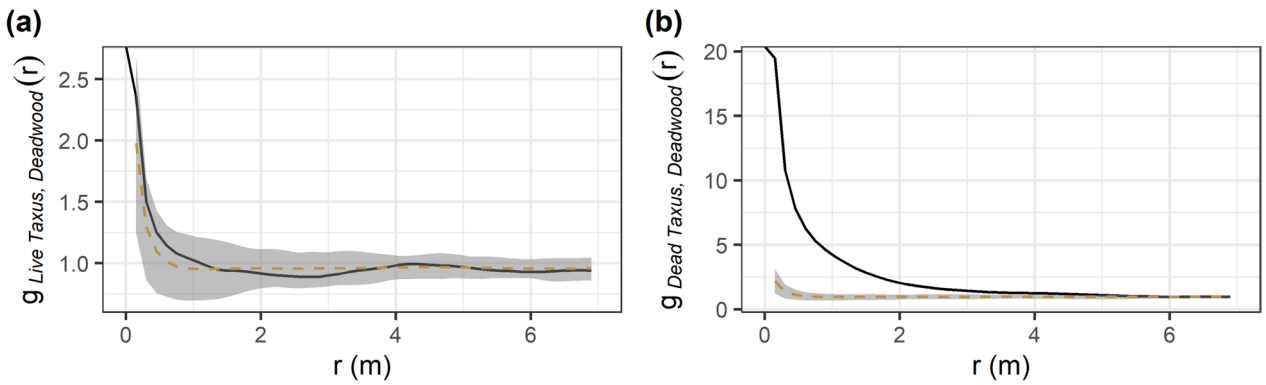


Fig. 4 Bivariate distribution between *Taxus* and deadwood ($n = 2505$) in the Wind River Forest Dynamics Plot, Washington, USA. **a** live *Taxus* ($n = 1523$) were distributed randomly with respect to deadwood; **b** dead *Taxus* ($n = 671$) were associated with deadwood within 2–3 m of the stem and very strong associated at shorter distances

live trees, likely benefiting from favorable microsite conditions, either inherent in their location or created by the surrounding trees (Das et al. 2018). *Taxus* experienced higher mortality in less dense areas, suggesting that the overstory or surrounding trees contributed specific environmental conditions associated with survival, potentially higher humidity (Chen et al. 1995).

Mechanical damage from fallen snags

We found strong evidence that the spatial pattern of dead *Taxus* is closely linked to the distribution of deadwood (Fig. 4). Because the WFDP features relatively high biomass (481 Mg ha^{-1} aboveground live biomass from trees ≥ 10 cm diameter and 74 Mg ha^{-1} snag biomass; Lutz et al. 2021), falling deadwood is plentiful (109 Mg ha^{-1} of bole biomass on the ground; Lutz et al. 2021). Because the canopy of a *Taxus* is much larger than its bole, falling snags are more likely to damage the canopy and reduce its size rather than crushing trees outright. Field-crew-reported mechanical damage accounted for 21.7% of *Taxus* deaths, especially of the large diameter *Taxus*. The mechanical impact of falling deadwood, with some trees breaking immediately and others suffering damage that leads to reduced competition for resources with neighboring trees and a combination of biotic and abiotic stressors (Velázquez and Wiegand 2020; Palm-Hellenurm et al. 2024).

Mechanical damage may also facilitate fungal infection (Cobb and Metz 2017; Idbella et al. 2023). The combination of mechanical damage and pathogens played a significant role in *Taxus* mortality (21.0%; Table S1). Injured trees must allocate resources to repair canopy damage at the expense of their defensive mechanisms, which increases their susceptibility to pathogen infection (Worrall et al. 2005; Krisans et al. 2020). Although *Taxus* has strong defenses, including chemical production and wood properties that limit the spread of infection (Murray and Hansen 1997), it remains vulnerable to pathogens (Taylor 2014). In particular, *Armillaria ostoyae* is a known root rot pathogen affecting *Taxus* and is widespread in *Pseudotsuga–Tsuga* forests (Thomas 1934; Shaw and Kile 1991) In our survey, *A. ostoyae* was associated with 32% of total mortality. Although *A. ostoyae* may infect both healthy and weakened trees (Thomas 1934), open wounds at the base of the bole may provide greater likelihood of infection.

Deadwood-driven gaps create drier microenvironments

Dead trees, whether remaining as standing snags or as deadwood on the ground, can create gaps that influence environmental conditions (McCarthy 2001). Dead *Taxus* clustered around both large snags and areas with high deadwood density, with much stronger aggregation observed in areas with fallen deadwood compared to snags. Therefore, gaps either from deadwood that directly damage *Taxus* or from those that change the microclimate likely both contribute to *Taxus* mortality (Hennon 1995). In the WFDP, wind and snow break weakened trees and expand existing gaps (Foster and Reiners 1986; Bottero et al. 2011). Compared to forest interiors, gap edges experience higher temperature, soil warming and wind speed (Chen et al. 1995), with wind load up to 14 times greater (Panferov and Sogachev 2008). These conditions increase vulnerability to pathogens (Whitney 1989) and further mechanical damage (Worrall et al. 2005) with prolonged climatic water deficit (Figure S1) precluding the rapid recovery of *Taxus* or neighboring trees (Andrew et al. 2016). *Taxus* prefers somewhat shaded environments with higher humidity and is highly sensitive to drought (Mitchell 1998; Germain and Lutz 2020). When gaps form due to fallen deadwood or death of neighboring trees, *Taxus* individuals are exposed to increased sunlight, rising temperature and drought stress, likely reducing their ability to respond to mechanical damage.

Decline disease spiral

The process of the mortality is a series of the accumulation of mortality factors (Manion 1981). The delayed mortality from visible and invisible damage may occur between 5 and 7 years or 10–25 years after the initial event (Greene et al. 1992; Harmon and Pabst 2019; Sato et al. 2017; Harmon and Pabst 2019). *Taxus* is a long-lived, slow-growing species, highly persistent in the face of stressors. The *Taxus* mortality that we observed likely indicates that *Taxus* persists for up to a decade after serious damage. However, if the summer dry season is longer and more severe than typical, drought may kill *Taxus* that have already been damaged by falling deadwood. So, although *Taxus* may exhibit increased mortality in dry periods, the reasons for mortality are more complex.

Deadwood

Deadwood and the processes of mechanical mortality are becoming recognized as a more important component of temperate forests and their development. Beyond the role of deadwood in carbon and nutrient storage, the process of creation and decay of deadwood is itself a dynamic part of forest succession. Snags can exhibit considerable periods of time before they fall, during which branches or bole pieces may fall on sub-canopy trees (Becker and Lutz 2023). Some mechanical mortality creating deadwood is responsible for soil turnover and the exposure of soil substrates (Šamonil et al. 2023). The deadwood itself can contribute to soil microbial activity (Birch et al. 2023; Schreiber et al. 2025; Xue et al. 2025)

and seedling recruitment (Birch and Lutz 2023). Here we show that mechanical damage leading to mortality—evidenced by remaining deadwood—can disproportionately affect individual species, guiding the process of forest succession.

Conclusions

The demographic trend of *Taxus* in the WFDP is decidedly negative. Spatial analysis showed that dense local neighborhoods around *Taxus* were not associated with higher mortality, implying that the decline is not primarily due to competition. However, higher levels of mortality were associated with proximity to deadwood from fallen snags. This mechanical damage, some occurring over a decade before actual mortality, likely increased the risk of pathogen infection and created microhabitats with decreased humidity as well as shearing off branches that directly reduced productivity. We speculate that these mechanically damaged *Taxus* had reduced vigor owing to reduction in leaf area, with concomitantly less ability to allocate photosynthate to either growth or defense. Although drought may be a proximate cause of *Taxus* mortality, *Taxus* illustrates a classic "decline disease spiral" initiated by mechanical damage that plays out over many years.

Abbreviations

DBH	Diameter at breast height (herein 1.37 m above the ground)
GLM	Generalized Linear Model
SEM	Structural Equation Model
WFDP	Wind River Forest Dynamics Plot

Supplementary Information

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Supplementary Material 1.

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Author contributions

JAL conceived the study and established the WFDP. JAL, CCK, and field technicians collected data. CCK analyzed data and wrote the initial manuscript. Both authors contributed to the writing and editing and approved the final document.

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Data availability

Data are archived at the Smithsonian ForestGEO, https://forestgeo.si.edu

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no conflicts of interest.

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