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Climate-driven ponderosa pine dieback and regionally variable pathogen pressure across the western United States

Michael D. McKee [a], Kelly S. Burns [a,b], Ashley Hawkins [c], Christine K. McTavish [d], Maria Newcomb [e], Mee-Sook Kim [f], Ned B. Klopfenstein [g], Thomas S. Davis [h], Jane E. Stewart [a,*]

[a] Colorado State University, Department of Agricultural Biology, Fort Collins, CO, 80523, USA
[b] Forest Health Protection, Rocky Mountain Region, USDA Forest Service, Golden, CO, 80401, USA
[c] Forest Health Protection, Pacific Southwest Region, USDA Forest Service, Redding, CA, 96002, USA
[d] Forest Health Protection, Intermountain Region, USDA Forest Service, Boise, ID, 83709, USA
[e] Forest Health Protection, Northern Region, USDA Forest Service, Missoula, MT, 59804, USA
[f] USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR, 97331, USA
[g] USDA Forest Service, Rocky Mountain Research Station, Moscow, ID, 83843, USA
[h] Colorado State University, Dept. of Forest and Rangeland Stewardship, Warner College of Natural Resources, Fort Collins, CO, 80523, USA

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ABSTRACT

Ponderosa pine (*Pinus ponderosa*) is a foundational species in dry-forest landscapes across western North America. Ongoing warming and aridification intensify climatic stress across its native range. Prior research on ponderosa pine health is regional in scope and focuses on single disturbances, leaving the combined influence of climate, stand structure, and biotic agents on dieback and mortality poorly understood. To address these knowledge gaps, we surveyed sites across California, Colorado, Idaho, Montana, and Wyoming during 2024 and 2025. At each site, we characterized stand conditions, assessed tree health, and collected tissue samples for pathogen identification. Long-term changes in climate were also recorded at each site to test associations between tree health and biotic and abiotic factors. Recent climate trends included reduced precipitation, elevated mean temperatures, and changes in vapor pressure deficit, indicating the potential for climatic stress on trees. Of the 324 trees surveyed, 25.8% had detections of pathogens and symptoms consistent with pathogen infection. Pathogens were composed of two functional groups: (1) needle and branch pathogens, including the widely distributed endophyte, *Sydowia polyspora*, primarily associated with trees of moderately poor health status, and (2) vascular stain fungi that were strongly linked to recent mortality. Only *S. polyspora* showed significant relationships with abiotic conditions in generalized linear models, while non-metric multidimensional scaling revealed clear geographic structuring of pathogen assemblages. In summary, our study suggests that climatic stress is associated with increases in host vulnerability to biotic agents, while fungal pathogens exhibit distinct associations with moderate decline and recent mortality.

1. Introduction

Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) is a foundational conifer species across western North America, providing timber, wildlife habitat, and recreational value (Shinneman et al., 2016). Over recent decades, warmer temperatures and regional aridification have intensified atmospheric water demand and altered moisture regimes (Karimzadeh et al., 2025). These shifting conditions can cause tree stress and heighten tree susceptibility to biotic pressures (Abatzoglou and Williams, 2016; Allen et al., 2010; Littell et al., 2009). Although increased background tree mortality has been documented across forests of the western USA (van Mantgem et al., 2009), the specific contribution of pathogens to canopy dieback and mortality of ponderosa pine remains poorly characterized, representing a knowledge gap in forest health management. It is not established whether emerging ponderosa pine dieback and mortality is associated with only abiotic factors or some combination of heightened environmental stress and subsequent damage from biotic agents. A better understanding of

* Corresponding author.
E-mail address: Jane.Stewart@colostate.edu (J.E. Stewart).

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interactions between environmental stressors and secondary pathogens could lead to more effective, region-specific management strategies that promote forest resilience.

Often, tree death is an ecological process that includes exposure to some combination of predisposing, inciting, and contributing factors (Gea-Izquierdo et al., 2019). Anthropogenic warming has resulted in elevated environmental stress on ponderosa pine by reducing winter snowpack and/or increasing summer transpiration demands (Abatzoglou and Williams, 2016), presumably widely predisposing forest trees to subsequent inciting and contributing mortality factors. For instance, chronic parasitism by dwarf mistletoe (*Arceuthobium* spp.) reduces growth and stand vigor (Hoffman et al., 2007; Shaw and Agne, 2017), and mistletoe-infected trees are often more sensitive to subsequent water-stress events (Stanton, 2007). Similarly, Heterobasidion root disease, caused by *Heterobasidion irregulare occidentale* Garbelotto & Otrosina and Armillaria root disease can further compound drought stress and eventually lead to mortality (Filip et al., 2024; Oester et al., 2018). Many insects can act as inciting and contributing factors as well. For example, defoliation events by the pandora moth (*Coloradia pandora* C.A.Blake) can depress radial growth in ponderosa pine and when coincident with drought or fire, entire stands can be impacted (Ciesla et al., 2010; O'Neill et al., 2023). Native bark beetles like western pine beetle (*Dendroctonus brevicomis* LeConte) and mountain pine beetle (*D. ponderosae* Hopkins) increase in abundance following heat and drought, as climatic stress reduces host defenses while simultaneously enhancing beetle development and survival (Evangelista et al., 2011, Kolb et al., 2016, Thomson and Shrimpton, 1984). Ponderosa pine infected by mistletoe can be selectively attacked by *Ips* spp. and other insects, further contributing to the decline in tree health (Kenaley et al., 2006). Together, these biotic agents that are already present in low numbers in natural stands can interact with changing climate factors that result in increased damage and disease prevalence and severity, amplifying localized ponderosa pine dieback and mortality risk.

Likewise, prolonged environmental stress could elicit pathogenesis in otherwise latent infections. For example, many endophytic fungi persist asymptomatically in healthy ponderosa pines but may damage their hosts when conditions change. For example, *Diplodia sapinea* (Fr.) Fuckel is a stress-responsive pathogen capable of causing shoot blight and cankers, and occasionally mortality, under drier, warmer conditions (Stanosz et al., 2001; Wingfield et al., 2025). Similarly, *Sydowia polyspora* (Bref. & Tavel) E.Müll. is a widely distributed foliar endophyte but may become pathogenic following host stress (Ridout and Newcombe, 2018), while *Cytospora* spp. act as opportunistic canker fungi that capitalize on low vigor or wounding of their hosts (Desprez-Loustau et al., 2006). For most pathogens affecting ponderosa pine, the extent to which disease incidence and severity are influenced by environmental factors and host stress remains unknown. However, linking predisposing factors, such as aridity and temperature, to damage could inform which stands may be at risk of future impacts, and why.

Most prior research on ponderosa pine health focuses on individual biotic or abiotic factors in a single stand or region, with studies rarely accounting for interactions between inciting and contributing factors across large landscapes of ponderosa pine. As a result, generalizable, field-based datasets that assess tree health and integrate biotic pathogen pressures with climate data are lacking. We tested the hypothesis that both abiotic and microbial biotic agents, and their interactions, contribute to ponderosa pine dieback and mortality. This study (i) evaluates the abiotic and pathogenic biotic agents associated with ponderosa pine health across the western USA, (ii) tests associations between pathogen prevalence, disease severity, and climate variables, and (iii) characterizes regional differences among pathogens observed on ponderosa pine.

2. Material and methods

2.1. Study area and sampling design

Field plots were established to collect tree health data and samples from symptomatic ponderosa pine across five states—California, Colorado, Idaho, Montana, and Wyoming—where damage had been reported. USDA Forest Service, Forest Health Protection (FHP) collaborators were consulted about ponderosa pine health in their designated regions. A drought index was created for forests with reported damage using weather and climate data from PRISM Group (https://prism.oregonstate.edu/) to identify areas with potential precipitation anomalies. Thirty years of precipitation data (1994–2024) were collected for each forest recommended for survey by FHP at a 4-km resolution, after which 5-year (2020–2024) and 25-year (1994–2019) averages were calculated for each 4-km grid cell (16 km^2) and then subtracted (5-year average minus minus 25-year average) to identify areas with precipitation anomalies. Areas with less precipitation on average in the recent 5 years (2020–2024) were targeted for sampling over areas with the same or more precipitation.

Plot surveys and sampling occurred in the summers of 2024 and 2025. Each plot consisted of three, 30.5-m transects that converged at a center tree and ran south, northeast, and northwest. Geographic coordinates, slope, and aspect were measured at plot center. All trees with a height above 1.37 m within 1.5 m of either side of transects were assessed. Tree data collected included species, health score, and diameter at breast height (DBH; 1.37 m). Health scores were recorded on a 1–5 scale based on the following criteria: (1) healthy: $<$ 15% damage to crown/stem, (2) declining: 16–50% damage to crown/stem, (3) dying: $>$ 50% damage to crown/stem, (4) recently dead: no green needles, red needles/fine twigs present, (5) grey dead: fine twigs, no needles. Signs and symptoms of disease and damage, such as insects or fire, were also recorded. For trees at least 1.37 m tall and with health scores ranging from 2 to 4, multiple samples were collected for lab analysis, including branches, needles from the lower to mid crown using pole pruners, cones, and/or drill shavings for the pinewood nematode (PWN), *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle. Slope and aspect were also taken at plot center each location to characterize site factors. Basal area was calculated from DBH of individual trees using the standard formula $BA = \pi(DBH/2)^2$, summed across all trees in the plot.

Healthy trees were not sampled but were still given an ID, health score, and DBH was recorded. Further, to focus on microbial biotic agents, areas with significant bark beetle mortality were avoided for surveys.

2.2. Identification and frequency of abiotic and microbial biotic agents

Field samples were processed in the laboratory to identify associated pathogens. Methods varied by sample type. Symptomatic needles with banding or flecking were cut into ca. 5-mm long pieces or were cut along the margin of healthy and infected tissue. A total of 6–8 pieces per sample were surface disinfected in 70% ethanol for 60 s, 1% bleach (0.06% NaOCl) for 3 min, placed in sterile water for 30 s, briefly air dried in a laminar flow hood, and then placed on ½-strength potato dextrose agar (PDA) (Hardy Diagnostics; Santa Maria, CA) medium. Plates were sealed with parafilm and placed in the dark at 20℃. Needle samples with fruiting bodies were also surface disinfected and placed in a humidity chamber (empty petri dish with a sterile filter paper) for 2–3 days, before placing samples on ½-strength PDA.

A slightly modified workflow was followed for wood and cone samples. Wood samples were obtained by scraping the outer surface of bark to expose necrotic lesions. Small wood chips (ca. 3–4 pieces; 5–10 mm in size) for each sample were excised along the margin of healthy and infected tissue. Samples were surface disinfected by placing them into 70% ethanol for 60 s, 1% bleach for 5 mins, and sterile water for 30 s. These samples were dried briefly and placed on ½-strength PDA.

Cone samples were only collected from trees suspected of having Diplodia Tip and Shoot Blight (DTSB). For pathogen isolation, 2–3 scales from each cone were surface disinfected in 70% ethanol for 30 s, 1% bleach for 1 min, and sterile water for 30 s. The samples were dried and placed in a humidity chamber at 23 °C for 2–3 days, before they were then placed on ½-strength PDA.

After incubating branch, needle, and cone samples placed in ½-strenght PDA and fungal growth was evident, fungi were sub-cultured further onto ½ strength PDA and placed in storage at at 4°C for subsequent DNA extractions

Molecular Identification. DNA was extracted from cultures by scraping mycelium, placing it into a 0.2-mL, PCR strip tube with a 5% Chelex 100 resin solution, mixing for 30 s using a pipette tip, and then placing it in a thermocycler for 20 mins at 98°C (Kozhar et al., 2023). For each DNA sample, the internal transcribed spacer region (ITS) of rDNA was amplified using polymerase chain reaction (PCR) using the primers ITS1 and ITS4 and following the protocol of White et al. (1990). Products were run on a 2% agrose gel to confirm amplification and sent to Eurofins Genomics, LLC for Sanger sequencing. The DNA sequences were then compared to the NCBI database using the BLAST algorithm via Geneious Prime (Version 2025.2). Species identity was assessed based on a pairwise identity > 95%, query coverage > 95% and a E value ≈ 0. The top result from the BLAST search was recorded, and representative culture samples were stored in 20% glycerol at −80°C at Colorado State University, Fort Collins, CO.

For wood shavings or increment cores taken to test for pine wilt disease caused by the PWN), DNA was extracted using Chelex 100 resin (Bio-Rad Laboratories, Hercules, CA) and 2% polyvinylpyrrolidone (PVP) (PVP-40; MP Biomedicals, Solon, OH) to help reduce phenolic compounds in the extraction solution (Walsh et al., 1991; Heikrujam et al., 2020). Ca. 0.01 g shavings or increment wood core materials was added to 200 μl of the 5% Chelex and 2% PVP solution. Samples were then incubated at 98°C for 30 min. Samples were tested for PWN using a commercial *B. xylophilus* detection kit (Nippon Gene Co. Ltd., Tokyo, Japan; Kikuchi et al., 2009).

2.3. Quantification of health and pathogen frequency

Pathogen detections were summarized across plots and states. For each tree, pathogen occurrence was recorded as a binary variable (presence/absence). Counts of each pathogen were reported and visualized overall and by state.

To quantify dieback and mortality of ponderosa pine across states, the frequency of ordinal health classes (1−5) were summarized for all trees surveyed within transects at each site. To determine if tree health was independent of geographic location, a Chi-squared (X^2) test of independence was conducted using the frequency of health scores. Statistical significance was assessed at $\alpha = 0.05$.

To determine if individual pathogens were significantly associated with symptom severity, Fisher's exact tests were conducted on the subset of symptomatic trees that underwent laboratory analysis. Analyses were restricted to trees with health scores ≥ 2 and severity was dichotomized as moderate (2−3) or dead (4−5) for statistical stability and simplicity. Effect size was summarized as the odds ratio (OR) for mortality associated with the presence or absence of each biotic agent, with 95% confidence intervals calculated on the log scale. To account for multiple comparisons, the false discovery rate was controlled using the Benjamini–Hochberg (BH) method, with q-values ≤ 0.05 considered statistically significant (Benjamini & Hochberg, 1995). The analysis was repeated on the state level with BH adjustment applied separately.

2.4. Climate and stand structure associations with tree health and pathogens

To assess the effects of abiotic factors, weather and climate data from PRISM were collected for each site. Using a 4-km resolution, average precipitation (Avppt; cm), minimum, mean, and maximum temperature (Tmin, Tmean, Tmax; °C), and minimum and maximum vapor pressure deficit (VPDmin and VPDmax; hPa) were downloaded for the past 30 years (1994–2024). Differences in climate between the most recent 5 years and the past 25 years were analyzed. Site-specific averages for each variable were calculated separately for the 5-year (2020–2024) and 25-year (1994–2019) periods. The 5-year average was subtracted from the 25-year average to quantify recent changes. To quantify the variability across sites within states, standard deviations were calculated for the mean climate anomalies across states.

All data handling, summarization, statistics, and graphics were scripted in R (v4.4.1; R Core Team, 2024). Data summaries used functions in the tidyverse (cite: dplyr, tidyr) and executed in base R. Figures were produced with ggplot2 (patchwork for multi-panel layouts), networks with igraph/ggraph, and tables were generated with gt and openxlsx2.

A site-level correlation analysis was conducted to determine the effects of abiotic and site factors on tree health using tree health (health score; response variable), stand-structure, and climate predictors (anomaly data from the difference of 5- and 25-year averages). Predictors were Tmin, Tmean, Tmax, VPDmin, VPDmax, Avppt, DBH (cm), basal area, elevation (m), and aspect eastness (sin) and northness (cos). Pathogen variables were excluded from the analyses because survey/testing was preferential to symptomatic trees, making prevalence estimates unreliable for comparison across sites. Spearman pairwise correlations were tested among all numeric predictors, and p-values were adjusted for multiple testing using the BH false discovery rate (FDR) procedure. Correlation coefficients (ρ), raw p-values (P), and FDR-corrected p-values (P_FDR) were reported.

Generalized linear models (GLMs) were used to evaluate associations between abiotic site conditions and pathogen incidence. Separate models were fit for *Sydowia polyspora*, *Diplodia sapinea*, *Leptographium* spp., and *Ophiostoma* spp. For each pathogen, incidence was modeled as the number of infected trees out of the total live trees surveyed at a site. All models included the same nine predictors of site conditions, including elevation, basal area, DBH, Avppt, Tmin, Tmean, Tmax, VPDmin, and VPDmax. Predictor significance was evaluated using Wald tests. For visualization, partial-effect curves were generated for four predictors per pathogen, selecting either the significant predictors ($P < 0.05$) or, when none were significant, the four predictors with the lowest p-values.

2.5. Regional difference in pathogen community composition

Non-metric multidimensional scaling (NMDS) was used to visualize differences in pathogen community composition among sites. Pathogen count data were collated by site, and pathogens with total abundance of less than five detections across all sites were removed. Pathogen counts were used to calculate Bray–Curtis dissimilarities, and a two-dimensional NMDS solution was generated with multiple random starts to ensure stable ordination.

3. Results

3.1. Biotic and abiotic agents associated with ponderosa pine dieback and mortality

During 2024 and 2025, 26 plots were established across northern California (CA; 9), Colorado (CO; 6), Idaho (ID; 4), Montana (MT; 4), and southern Wyoming (WY; 3). A total of 404 trees were examined, and 80% (ca. 324) were ponderosa pine. Other species surveyed included Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) (42), Juniper (*Juniperus* sp.) (20), black oak (*Quercus velutina* Lam.) (13), and common manzanita (*Arctostaphylos manzanita* Parry) (ca. 5). The average DBH for ponderosa pine was 28.1 cm with an average health score of 2.3. Elevation ranged from 990 m to 2638 m and was 2166 m on

average. Most plots were on southeast-facing slopes (44%), and the most common site disturbance was fire with five sites (19.2%) experiencing fire in previous years.

Tree health distributions differed among states (Fig. 1**A**). CA had most surveyed ponderosa pines (n = 159) and was dominated by healthy trees (health score 1; 53%). However, CA also had more dead trees (health score 4–5; 30.6%) than dying trees (health score 2–3; 15.6%). CO (n = 104) also showed a preponderance of healthy trees, with a higher proportion of individuals in health classes 2–3 (51.4%) compared to CA. ID (n = 53) contained 47% healthy trees and 43% were in health classes 2–3 (43.4%). MT (n = 31) and WY (n = 35) showed relatively higher proportions of trees in class 2–3 (51.6% and 42.9%, respectively) with very few dead trees (health class 4–5; 0% and 2.9%, respectively). Overall, in most states, healthy trees made up almost 50% of the trees surveyed, but the relative proportion of health scores in categories 2–3 and 4–5 varied regionally. The Chi-squared test indicated a statistically significant relationship between the state and the distribution of health scores ($X^2 = 83.77$, df = 16, $P < 0.001$).

Of the 324 ponderosa pine surveyed, 99 (25.8%) exhibited symptoms consistent with pathogen infection. In all states, detections were dominated by *S. polyspora*, which was the most observed taxon. Other consistently observed pathogens included *D. sapinea*, *Leptographium* spp., *Cytospora* spp., *Ophiostoma* spp., and *Endocronartium harknessii* (J. P. Moore) Y. Hirats. f. (causal agent of western gall rust). Rarely observed taxa with typically less than 5 detections across all sites, included *Biscogniauxia mediterranea* (De Not.) Kuntze, *B. xylophilus*, *Cenangium ferruginosum* Fr., *Epicocum nigrum* Link, *Lophodermium baculiferum* (Fr.) Chevall., and *Thyronectria pinicola* (Alb. & Schwein.) Seeler.

Geographical differences were observed in pathogen distribution (Fig. 1**B**). As in the overall findings, *S. polyspora* was found in all states and was most frequently detected in CO, ID, MT, and WY (56.7%, 36.8%, 47.4%, and 52.9%, respectively). CA ponderosa pine had a unique pathogen profile, with *Leptographium* spp. (31.8%) as the most detected pathogen, followed by *D. sapinea*, *Ophiostoma* spp., and *E. harknessii* (27.3%, 20.5%, and 13.6%, respectively). *Cytospora* spp. was identified consistently across CO and WY at moderate frequencies (23.3% and 29.4%, respectively), while *Elytroderma deformans* (Weir) Darker and *Arceuthobium* sp. (dwarf mistletoe) were localized in ID (31.6%) and CO (13.3%), respectively. Rarely observed taxa were infrequent in every state panel and in several cases, absent from most

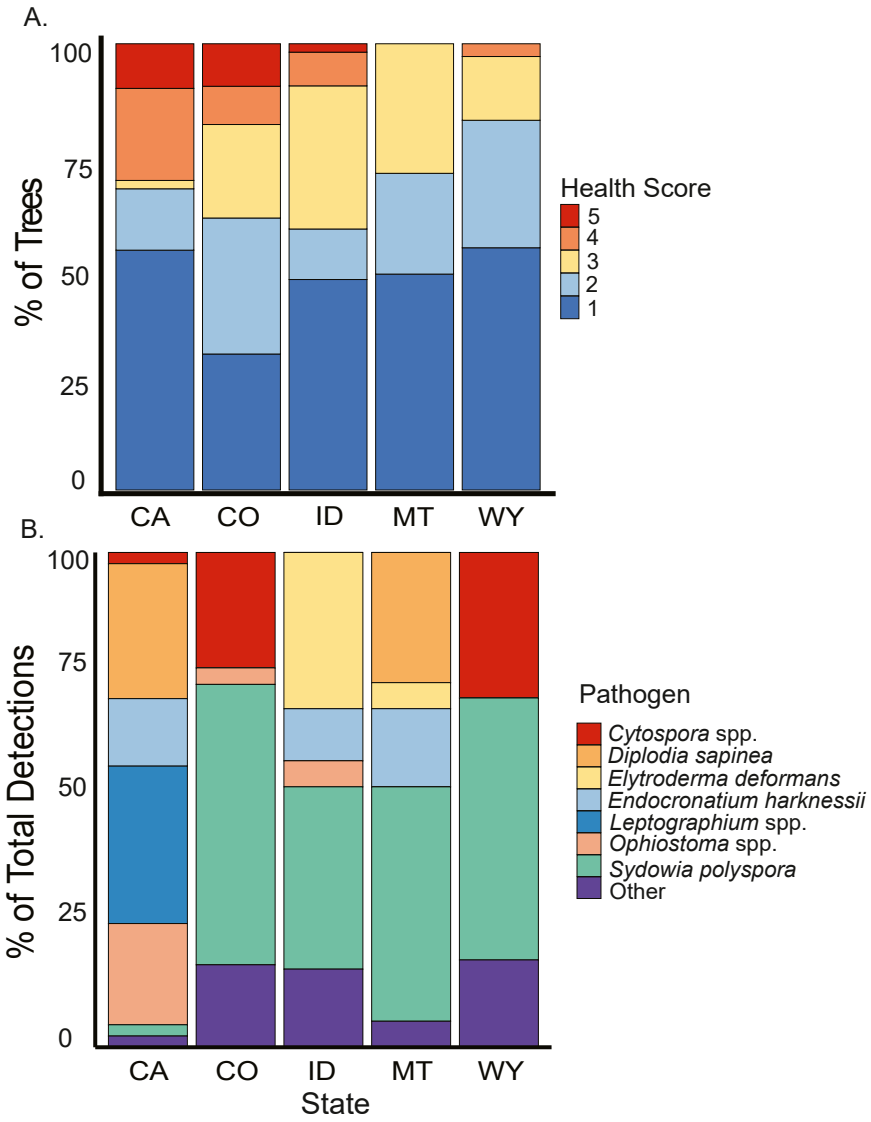


Fig. 1. A. Frequency (%) of tree health for ponderosa pine (*Pinus ponderosa*) stratified by state. CA=California (n = 159), CO=Colorado (n = 104), ID=Idaho (n = 53), MT=Montana (n = 31), WY=Wyoming (n = 35). Fig. 1**B**. Frequency (%) of pathogens found on ponderosa pine (*Pinus ponderosa*) stratified by state. CA=California, CO=Colorado, ID=Idaho, MT=Montana, WY=Wyoming.

states surveyed

Analysis of the subset of symptomatic trees that underwent laboratory analysis revealed significant associations between pathogen detections and symptom severity across all sites. *S. polyspora* was significantly negatively associated with dead trees (health scores 4–5) and occurred more frequently in moderately affected stands (mean health scores 2–3) (P_FDR = 0.02; Table 1). The probability of dead trees on a site was substantially lower when *S. polyspora* was present.

In contrast, *Leptographium* spp. and *Ophiostoma* spp. exhibited strong positive associations with dead trees (health scores 4–5) following Benjamini–Hochberg correction (both P_FDR < 0.001; Table 1). Both taxa were detected significantly more frequently in dead trees than in trees with moderate symptoms, consistent with their suspected roles in host decline and mortality.

On the state level, patterns among tree health scores and pathogens were highly variable. In CA, *D. sapinea* was significantly associated with moderately healthy stands (mean health scores 2–3) and was present in 28.0% of trees but only 4.1% of dead trees. There was a significantly lower probability of tree death when *D. sapinea* was present (OR = 0.11, 95% CI: 0.02–0.58; P_FDR = 0.039; Table S1). For the remaining pathogens, no other state-level associations were present after the FDR correction (P_FDR < 0.05).

3.2. Associations among climate, stand structure, and tree health

When comparing climate data from the past 5 years to the past 25 years, consistent trends emerged across all climate variables and all states. Avppt declined at all sites during the past 5 years (Fig. 2**A**). CA sites had the most significant change, with an average deficit of −16.46 cm (±8.33 cm) per site. CO and WY had average losses of −4.95 cm (±1.54 cm) and −5.01 cm (±0.65 cm), respectively. ID and MT sites had the smallest reductions, averaging −3.92 cm (±1.30 cm) and −3.32 cm (±0.54 cm), respectively.

Changes in Tmean also varied by region. Sites in CA, CO, and WY all experienced an increase in average temperature over the past 5 years. WY sites had the largest increase, averaging 0.29°C (±0.02°C), followed by CA at 0.21°C (±0.14°C) and CO at 0.17°C (±0.09°C). In contrast, Tmean in ID remained relatively stable, with only a 0.006°C (±0.09°C) increase, while MT sites experienced a decrease of −0.13°C (±0.11°C) (Fig. 2**B**). The VPDmax increased at 23 of the 26 sites; only three sites, two in CO and one in MT, saw a decrease. In contrast, VPDmin exhibited greater variability. More than half of the CA sites experienced a decrease in VPDmin, while three showed an increase. Nearly all sites in ID and MT had declines in VPDmin, whereas all CO and WY sites experienced increases in VPDmin (Fig. 2**C & 2D**).

Across all site-level comparisons, tree health worsened as temperature and VPD variables increased. Mean health was moderately correlated with several climate variables (Table 2). Although some of these associations did not meet the conventional FDR-corrected α = 0.05 threshold, most remained below P < 0.10, indicating consistent, directional trends after accounting for multiple testing. No strong negative correlations were observed between tree health and any climatic or structural variable. Basal area, elevation, and aspect metrics showed weak and non-significant associations with health (Table S2). Additionally, multiple fungal pathogens were identified in 26 trees (6.8%), which were in poorer health than the overall populations with an average health score of 2.9.

GLMs revealed differing levels of association between pathogen incidence and associated site factors across the four focal pathogens. *S. polyspora* exhibited the strongest and most interpretable relationships, with significantly higher incidence at sites at greater elevations ($p = 0.02$) and with larger mean DBH trees (P = 0.01), but significantly lower incidence in stands with higher basal areas (P = 0.0004) (Table 3; Supplementary Fig. S1). VPDmax also showed a positive association with *S. polyspora* incidence (P = 0.04). In contrast, *D. sapinea*, *Leptographium* spp., and *Ophiostoma* spp. showed no statistically significant associations with any site variables, and had large confidence intervals, indicating weak predictive value and suggesting that site-level climate and stand structure characteristics do not meaningfully explain their occurrence in this dataset.

Table 1
Results of the pathogen focus subset Fisher's exact test between pathogen presence and disease severity.

Pathogen	*p*_FDR[A]	Odds Ratio (95% CI)[B]
Leptographium spp.	< 0.001	76 (12.6–878)
Ophiostoma spp.	< 0.001	24 (4.4–255)
Sydowia polyspora	0.02	0.12 (0.01–0.55)

[A] Benjamini–Hochberg corrected *p*-value for significance (p < 0.05)
[B] Odds ratio of severity with 95% confidence interval.

3.3. Regional difference in pathogen communities

The NMDS ordination revealed differences in the pathogen community composition among states (Fig. 3). CA sites clustered tightly along the upper NMDS2 axis (stress = 0.11). CO sites formed a compact cluster, whereas ID sites were more dispersed. MT sites formed a narrower cluster, partially overlapping with ID and CO. WY sites, although few, occupied a distinct position in ordination space and showed minimal overlap with CO.

4. Discussion

Understanding the drivers of ponderosa pine dieback and mortality requires determining the relative roles of recent climatic change, host condition, and pathogen identity. In this study, we evaluated short-term climatic anomalies, stand characteristics, and fungal pathogen communities across 26 sites in the western United States. Our results indicate that recent increases in temperature and atmospheric moisture demand (VPD) are associated with changing host condition. Yet, pathogen incidence patterns were largely independent of climate variables, and pathogen community composition exhibited clear geographic structure. Together, these findings suggest that climate can function as a predisposing stressor that increases host vulnerability (Schoeneweiss, 1975, 1981; Kolb et al., 2019), while local pathogens are associated with either moderately healthy or dying trees.

Across all sampled states, recent 5-year climate conditions differed from long-term averages, with consistent rising temperatures and atmospheric dryness (VPD) alongside decreasing precipitation. The observed climate patterns are consistent with studies linking regional warming and drying to increased stress, greater disturbance vulnerability, and higher mortality in conifers of the western United States (Abatzoglou & Williams, 2016; Littell et al., 2009). Increased heat and atmospheric dryness, accompanied by reduced precipitation, can elevate host stress directly and indirectly, exacerbating disturbance from biotic agents, resulting in reduced tree health and increased mortality (Allen et al., 2010; Weed et al., 2013), and our study concurs with these previous findings.

Tree health assessments showed that more than half of the surveyed trees exhibited crown or stem damage (health score ≥ 2), indicating that worsening host condition is common across all sampled regions. Spearman's rank correlation revealed positive associations between worsening health scores and multiple climate variables, including maximum VPD and mean temperature. Although no climatic predictor remained significant after FDR correction, the consistent positive correlation suggests that atmospheric demand and warming are associated with reduced host health. This pattern aligns with previous studies that demonstrated increasing atmospheric dryness can impair conifer water relations and physiological function (Kolb et al., 2019; Schoeneweiss, 1975, 1981). Structural site variables, such as basal area, DBH, elevation, and aspect, showed weak and non-significant relationships with

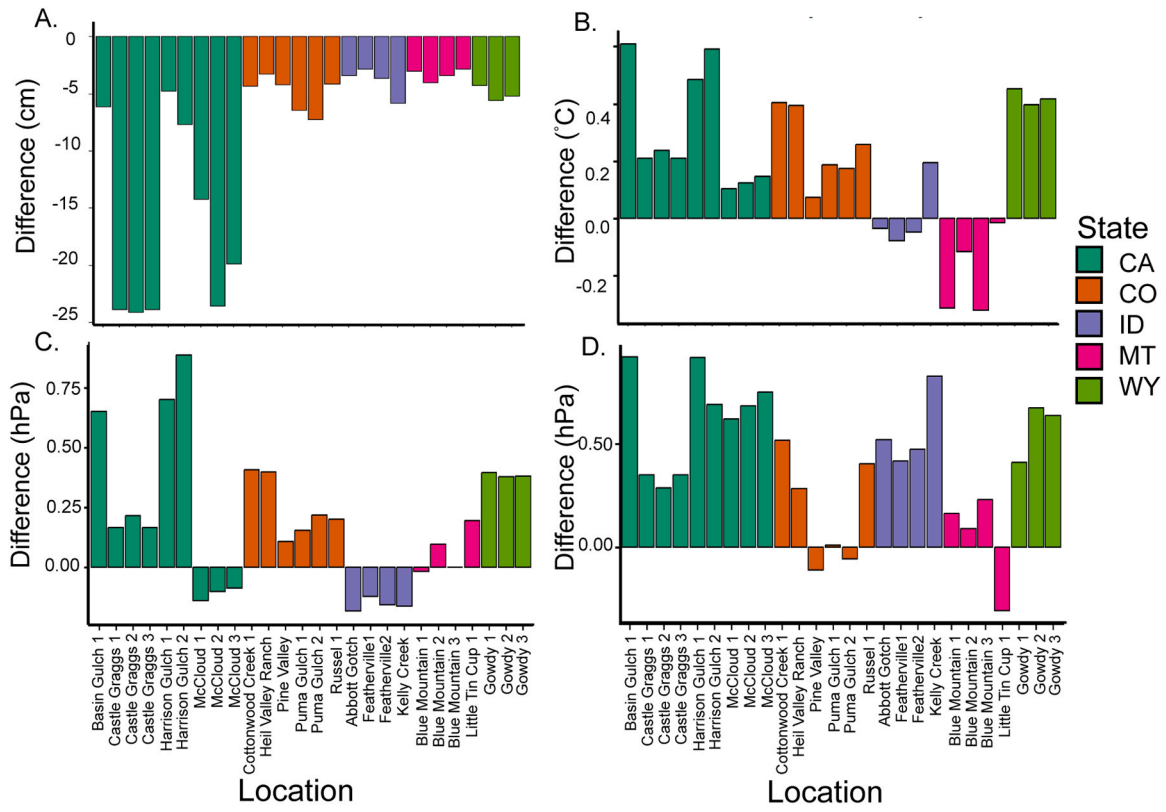


Fig. 2. Recent (2020–2024) annual mean climate anomalies relative to the preceding 25-year period (1994–2019) by site. Panels show (A) annual mean precipitation, (B) annual mean temperature, (C) annual mean minimum vapor pressure deficit, and (D) annual mean maximum vapor pressure deficit.

Table 2
Results of the Spearman's rank correlation analysis between tree health and abiotic factors.

Variable	P[A]	p[B]	p_FDR[C]
Avg VPDmax (hPa)	0.46	0.02	0.06
Avg Tmax (F)	0.46	0.02	0.06
Avg Tmean (F)	0.44	0.02	0.08
Avg VPDmin (hPa)	0.43	0.03	0.08
Avg Tmin (F)	0.42	0.03	0.09
Avg Precipitation (in)	0.40	0.04	0.12

[A] rho (P) is the correlation coefficient and shows directionality of association
[B] p-value for significance ($p < 0.05$)
[C] Benjamini–Hochberg corrected p-value for significance

Table 3
Summary of the top four site factor predictors associated with *Sydowia polyspora* incidence based on binomial generalized linear modeling.

Pathogen	Predictor	β[A]	p[B]	OR[C]	OR CI[D]
Sydowia polyspora	Basal area (m^3)	-0.02	0.0004	0.98	0.97–0.99
	Diameter at breast height (cm)	0.17	0.01	1.18	1.04–1.34
	Elevation (m)	0.0005	0.02	1.00	1.00–1.00
	VPDmax (hPa)	3.25	0.04	25.73	1.20–551.42

[A] β is log-odds change in pathogen incidence per unit increase in the predictor
[B] p-value for statistical significance
[C] Odds Ratio (OR) = multiplicative change in odds of infection per unit increase in the predictor (OR > 1 increases incidence, OR < 1 decreases incidence)
[D] OR 95% CI is the lower and upper bounds of the confidence interval for the odds ratio.

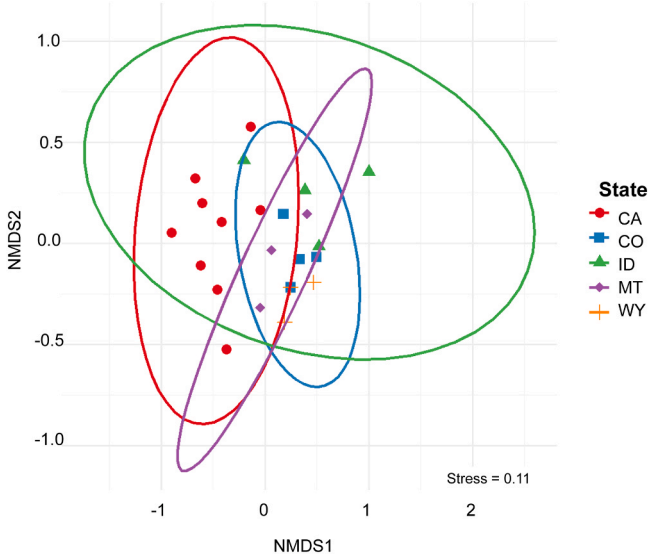


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of pathogen community composition across study sites. Ellipses indicate 95% confidence regions for each state. Points represent individual sites and are colored and shaped by state. The two-dimensional ordination adequately represents patterns in pathogen community composition (stress = 0.11). CA=California, CO=Colorado, ID=Idaho, MT=Montana, WY=Wyoming.

tree health, further supporting that climate stressors are stronger correlates of host condition than structural site variables. Overall, these results suggest that recent climate anomalies are associated with reduced host health across the surveyed regions.

Multiple fungal pathogens were detected across sites, but only four showed associations with tree health. In particular, *Leptographium* spp.

and *Ophiostoma* spp. were significantly associated with dead trees (health scores 4–5), with a substantially higher probability of detection in dead trees compared to moderately healthy trees. Although we deliberately avoided sites with significant bark beetle damage to focus on mortality from pathogens, these fungal pathogens were still found in sites with stressed trees, consistent with their vector-mediated ecology (Six & Wingfield, 2011; Linnakoski et al., 2012; Chang et al., 2017). However, host condition remains important as drought-weakened trees are generally more susceptible to beetle attack when beetle populations are high (Wallin & Raffa, 2004; Raffa et al., 2008; Kolb et al., 2019). Even endemic levels of bark- or wood boring-beetle activity, which can be more difficult to detect, can inoculate trees with ophiostomatoid fungi (Ballard et al., 1982; Six & Wingfield, 2011). Once introduced, rapid sapwood colonization and xylem blockage impose direct hydraulic impedance, leading to health decline and mortality in infected trees (Hansen & Lewis, 1997; Krokene & Solheim, 1998; Arango-Vélez et al., 2016). These factors help to explain the tight linkage of *Leptographium* spp. and *Ophiostoma* spp. with dead or recently dead trees despite our conservative site selection.

In contrast, the presence of *S. polyspora* and *D. sapinea* in a site was negatively associated with dead trees and were frequently found in moderately healthy stands (health scores 2–3). This pattern is consistent with *S. polyspora*'s characterization as a stress-associated endophytic fungus that commonly inhabits host tissues without acting as a primary mortality agent, acting as an indicator of host stress (Sieber, 2007; Ridout and Newcombe, 2018; Talgø et al. 2010). Similarly, *D. sapinea* displayed patterns consistent with opportunistic behavior. Although not broadly associated with mortality across all states, its concentration in moderately affected trees in California aligns with reports that *D. sapinea* intensifies following host stress but does not typically cause mortality independently (Stanosz et al., 2001; Wingfield et al., 2025).

Apart from *S. polyspora*, pathogen incidence was not significantly associated with climatic variables. *Leptographium* spp. and *Ophiostoma* spp., despite their strong association with dead trees, showed no significant relationships with site-level climatic or structural predictors. Among the focal pathogens, *S. polyspora* was the only pathogen that had consistent relationships with associated site predictors, including elevation, DBH, basal area, and VPDmax. It was negatively associated with dead trees and found more frequently in moderately affected stands. Typical field symptoms observed included yellow to tan colored bands or spots on the needles rather than extensive crown thinning associated with more aggressive taxa. This combination of patterns distinguishes it from vascular pathogens and suggests an ecological role more consistent with latent colonization or a stress response rather than direct mortality (Sieber, 2007; Ridout and Newcombe, 2018). Within the scope of this dataset, *S. polyspora* appears linked to certain stand characteristics, increased VPD, and intermediate health classes rather than to tree death.

Evidence of geographic structuring of pathogen communities among states was found but in association with climatic factors. CA sites formed a distinct cluster, while CO, ID, MT, and WY exhibited varying degrees of similarity. These findings are consistent with the broader understanding that pathogen assemblages reflect regional climate regimes and biogeographic context (Wan et al., 2022). However, most pathogens did not exhibit significant associations with site-level climate variables, thus the geographic structuring observed here cannot be attributed solely to recent climatic anomalies. Instead, these differences likely arise from biogeographical limits on pathogen distributions and differences in pathogen species ranges among regions. For example, *D. sapinea* has historically been limited to temperate climates because of a preference for warmer temperatures ranging from 25 to 30 °C, to achieve higher inoculum loads (Terhonen et al., 2025).

Several limitations should be considered when interpreting the results of this study. First, although PRISM climate data provides high-quality, long-term climate estimates, topographic variation can be overlooked, potentially obscuring microclimatic conditions in individual stands, especially on mountainous terrain. Second, this study did not incorporate data on insect activity or abundance. Given the strong ecological interactions between bark beetles, root weevils, and fungal pathogens, the absence of insect data limits inferences about biotic interactions driving dieback and mortality. Third, the site selection methods may have introduced sampling bias, as plots were established in landscapes exhibiting visible symptoms of dieback and/or mortality. This could overrepresent stressed stands even though healthy trees were measured within each plot to help mitigate the bias. Finally, regional variation in ponderosa pine subspecies and the presence of closely related Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) in parts of California introduce potential physiological and ecological differences, such as drought tolerance and host specificity to pathogen, that may influence disease dynamics and health outcomes (Willyard et al., 2021). These factors collectively highlight the need for future work integrating climate data that considers topography and represents microclimates within a stand, insect monitoring, and subspecies-level analyses to refine the understanding of ponderosa pine dieback and mortality drivers across the western USA.

Our results indicate that ponderosa pine dieback and mortality across the western USA is primarily associated with recent increases in temperature and higher atmospheric moisture demands that reduce host vigor. Pathogen incidence patterns were largely independent of the climate variables but can still influence the progression and severity of tree health. For this reason, management strategies that prioritize reducing chronic stand-level stress may be more effective than those attempting to control biotic agents after hosts are already stressed. Reducing stand density to reduce competition for soil moisture has been shown to improve tree growth, water status, and resistance to mortality from abiotic or biotic agents (Kolb et al., 2007; Bradford & Bell, 2017). Thinning treatments that retain large, healthy trees and reduce stand density have been shown to increase individual tree resilience during drought and reduce susceptibility to biotic agents by improving host defense capacity (Hood et al., 2016). Additionally, monitoring efforts could be effective when increased following periods of drought or increased atmospheric moisture demand, as these conditions strongly increase mortality risk in conifers (Park Williams et al., 2013; Allen et al., 2015). Because climate conditions and pathogen communities differed among regions, monitoring and management programs may benefit from incorporating region-specific surveillance and treatments that target locally prevalent biotic agents and abiotic issues rather than applying uniform approaches across the range of ponderosa pine. Furthermore, management treatments that promote structural heterogeneity may reduce the risk of stand-level stress responses and improve resilience and recovery following disturbance events (Churchill et al., 2013). Collectively, these findings support a transition in our management methods of ponderosa pine. Instead of a reactive response to tree mortality, an active management strategy focused on physiological resilience will help reduce vulnerability to drought, insects, and disease.

Given that climatic factors were the strongest predictor of tree health, preventing abiotic stress is likely to be the most impactful focus for proactive management. Due to the extensive distribution and importance of ponderosa pine throughout the western United States, continued increases in temperature and atmospheric moisture demand could affect forest resilience at landscape scales. Practices that buffer trees from moisture deficit and heat stress, such as thinning and prescribed burns, can help address the underlying conditions that leave ponderosa pine susceptible to dieback and mortality. While secondary in this framework, management of pathogens in ponderosa pine may benefit from a non-uniform approach. Because pathogen community composition varied across geographical regions, disease monitoring and response may be most effective when tailored to local species assemblages. This is a two-tiered approach where broad abiotic stress reduction is paired with regionally specific pathogen response. This reflects the complexity of ponderosa pine dieback and mortality across the landscape and shows that a durable management solution must be

designed according to individual stands and regions.

CRediT authorship contribution statement

Michael D. McKee: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kelly S. Burns:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Ashley Hawkins:** Writing – review & editing, Methodology. **Christine K. McTavish:** Writing – review & editing, Methodology. **Maria Newcomb:** Writing – review & editing, Methodology, Investigation. **Mee-Sook Kim:** Writing – review & editing, Methodology. **Ned B. Klopfenstein:** Writing – review & editing, Methodology. **Thomas S. Davis:** Writing – review & editing, Methodology, Investigation, Funding acquisition. **Jane E. Stewart:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, 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.2026.124354.

Data availability

Data will be made available on request.

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