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# Stand diversity increases pine resistance and resilience to compound disturbance

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## Abstract

**Background** Drought, fire, and insects are increasing mortality of pine species throughout the northern temperate zone as climate change progresses. Tree survival may be enhanced by forest diversity, with growth rates often higher in mixed stands, but whether tree defenses are likewise aided remains in question. We tested how forest diversity-productivity patterns relate to growth and defense over three centuries of climate change, competition, wildfire, and bark beetle attack. We used detailed census data from a fully mapped 25.6-ha forest dynamics plot in California, USA to conduct a spatially explicit, dendroecological assessment of large-diameter *Pinus lambertiana* survival following fire reintroduction. Our structural equation models investigated direct and indirect pathways by which growth, defense, and forest composition together mediated pine resistance and resilience.

**Results** In the historical era of frequent, mixed-severity fire (pre-1900), trees that were ultimately resistant or susceptible to the post-fire bark beetle epidemic all showed similar growth and defenses, as measured by axial resin duct traits. During the era of fire exclusion (1901–2012), however, susceptible trees had slower growth. Following fire re-entry in 2013, both growth and defense declined precipitously for susceptible trees, resulting in fatal bark beetle attack. Spatial analysis showed that monodominant crowding by shade-tolerant competitors contributed to the long-term stress that prevented susceptible trees from recuperating defenses quickly following fire re-entry. For beetle-resistant trees, however, we found positive feedbacks between diversity, growth, and survival: trees in species-rich communities had higher growth rates pre-fire, which promoted a rapid recuperation of defenses following fire that helped trees resist bark beetle attack. Overall, this associational resistance outweighed associational susceptibility (+8.6% vs. –6.4% change in individual tree survival odds), suggesting a relaxation effect that ultimately allowed 58% of large pines to survive.

**Conclusions** Though climate change threatens forest biodiversity, biodiversity is key to forest climate adaptation in return. Our findings demonstrate centennial-scale feedbacks by which forest diversity increases pine resistance and resilience to climate-amplified disturbances. The spatially explicit, dendroecological framework provides new insights into diversity-productivity theory, while also informing climate-adaptive forest management by identifying thresholds of tree density and richness that maximize large pine survival.

**Keywords** Associational resistance, Bark beetles, Drought, Diversity-productivity, Fire, Pine, Smithsonian ForestGEO, Yosemite Forest Dynamics Plot

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## Resumen

**Antecedentes** Sequías, incendios, e insectos están incrementando la mortalidad de especies de pino a través de toda la región templada del norte de los EEUU, a medida que avanza el Cambio Climático. La supervivencia de árboles puede aumentarse con la diversidad forestal, con productividades muchas veces más altas en rodales mixtos, aunque el cómo se promueve la defensa de esos árboles permanece aún irresuelta. Probamos cómo los patrones de productividad y diversidad se relacionan con el crecimiento y la defensa del bosque en tres centurias de Cambio Climático, competencia, fuegos y ataques del escarabajo de la corteza. Usamos datos de censos detallados de un rodal mapeado completamente, sobre la dinámica del rodal en una parcela de 25,6 ha en California, EEUU, para conducir un trabajo espacialmente explícito de dendro-ecología en la supervivencia de árboles de *Pinus lambertiana* de gran diámetro luego de la reintroducción del fuego. Nuestro modelo de ecuación estructural investigó los caminos directos e indirectos por los cuales el crecimiento, las defensas, y la composición del bosque todos juntos median la resistencia y resiliencia de los pinos.

**Resultados** En la era histórica de los fuegos de severidad mixta (pre-1900), los árboles que eran tanto resistentes como susceptibles al ataque post fuego del escarabajo de la corteza mostraban defensas y crecimiento similares, medidos por los ductos de resina axiales. Durante la era de la exclusión del fuego (1901–2012), sin embargo, los árboles susceptibles tuvieron menores crecimientos. Luego de la reintroducción del fuego en 2013, tanto el crecimiento como las defensas declinaron precipitadamente en los árboles susceptibles, resultando en ataques fatales del escarabajo de la corteza. Los análisis espaciales revelaron que las copas mono-dominantes de árboles competidores tolerantes a la sombra, contribuyeron al estrés de largo plazo que les impidió a los árboles susceptibles de poder recuperar rápidamente sus defensas luego de la reintroducción del fuego. Para los árboles resistentes al escarabajo de la corteza, encontramos retroalimentaciones positivas entre diversidad, crecimiento y supervivencia: los árboles en comunidades ricas en especies tuvieron tasas de crecimiento más altas previo al fuego, lo que promovió una rápida recuperación de sus defensas luego de un incendio y ayudaron a esos árboles a resistir el ataque del escarabajo de la corteza. Por sobre todo, esta resistencia asociativa superó a la susceptibilidad asociativa (+ 8,6 vs -6,49% de cambio en la probabilidad de supervivencia individual de árboles), lo que sugiere un efecto de relajación que permitió sobrevivir al 58% de los pinos más grandes.

**Conclusiones** Aunque el Cambio Climático amenaza la diversidad forestal, la biodiversidad es, de manera recíproca, un factor clave para la adaptación climática de los bosques. Nuestros hallazgos demuestran una retroalimentación a escala de centuria y por la cual la diversidad forestal aumenta la resistencia y resiliencia de los pinos a los disturbios climáticos amplificadas. El marco dendro- ecológico espacialmente explícito, provee de nuevas perspectivas en la teoría de la diversidad-productividad, mientras que la vez informa sobre el manejo forestal climático-adaptativo mediante la identificación de límites en la densidad y riqueza de árboles que maximiza la supervivencia de los pinos más grandes.

## Background

Fire exclusion has created forests that are more dense, structurally homogeneous, and with a greater proportion of shade-tolerant understory tree species (Scholl and Taylor 2010). In addition to being more vulnerable to high-severity fire and bark beetle outbreaks (Fettig et al. 2007; Stephens et al. 2018), fire-excluded forests often show reduced biodiversity as well (Knapp et al. 2013a; Stephens et al. 2021). Yet, trees growing in higher diversity stands will often, all else equal, grow faster and have higher survival than those in monodominant stands, indicating positive diversity-productivity relationships (Zhang et al. 2012; Forrester and Bauhus 2016; Liang et al. 2016). It is unclear whether diversity-productivity relationships have been maintained in fire-excluded forests and, if not, whether this is one mechanism explaining higher insect-related mortality.

A prominent element of positive diversity-productivity relationships is associational resistance (Barbosa et al. 2009), or the observation that trees in diverse stands are often less susceptible to host-specific herbivorous insects (Jactel and Brockerhoff 2007; Sousa-Silva et al. 2018). The most impactful host-specific insects targeting western conifers are bark beetles (Coleoptera: Scolytidae): in the western USA, bark beetles killed more tree canopy area than did wildfire over recent decades (1997–2012; Hicke et al. 2016). Forest diversity may reduce insect *attack* rates by masking the visual and chemical cues relied upon by insects to find preferred hosts (plant apparency hypothesis; Huber and Borden 2001; Himanen et al. 2010; Castagneyrol et al. 2013). Reduced insect attack is also observed due to reduced host frequency (resource concentration hypothesis; Kareiva 1983) and accumulation of insect natural enemies (enemies hypothesis; Russell

1989). Forest diversity can also influence insect *success* rates by moderating resource abundances via competitive and mycorrhizal interactions, therefore contributing to the tree defense capacities necessary to combat insect attack (Bennett et al. 2005; Slack et al. 2017; Buonanduci et al. 2020).

Though monodominant and fire-excluded stands are often more susceptible to bark beetles due to higher host availability (Fettig and McKelvey 2010), individual-tree susceptibility depends, ultimately, on trees' ability to defend. The primary line of conifer defense against bark beetles is oleoresin (i.e., resin), which creates a physical barrier to entry and contains terpenoids that are toxic to insects and microbes (Phillips and Croteau 1999; Raffa 2014). Resin is crucial for combatting attack by bark beetles and their fungal symbionts (Ferrenberg et al. 2014; DeRose et al. 2017), and can also prevent pathogen invasion following physical damage (e.g., post-fire; Bonello et al. 2006; Hood et al. 2015). Trees' ability to defend against bark beetles can be compromised by water stress during drought (Gaylord et al. 2013; Stephenson et al. 2019), rendering pathways of associational resistance that prevent bark beetle attack increasingly important as drought severity and frequency increase due to climate change (Dai 2013; Germain and Lutz 2020).

The genus, *Pinus*, constitutively produces large amounts of resin stored throughout a network of resin ducts in the primary and secondary xylem and can also be induced to produce resin systemically upon bark beetle attack (Wu and Hu 1997). This abundance of defense capacity likely reflects *Pinus*' coevolution with two of the most destructive insect genera worldwide, *Dendroctonus* and *Ips* (Raffa et al. 2008; Mason et al. 2019), and fire (Kolb et al. 2007). As such, *Pinus* is at the crux of drought, fire, and insect compound disturbances and has been consequently declining across the northern temperate region (Lutz et al. 2009; Haynes et al. 2014; García de la Serrana et al. 2015; Sangüesa-Barreda et al. 2015; Li et al. 2020; Pandit et al. 2020). Identifying ecological processes that protect large-diameter *Pinus* from future outbreaks will provide actionable information to maintain these important carbon stores (Lindenmayer et al. 2012; Stephenson et al. 2014).

Here, we utilize a spatially explicit dendroecological dataset to test whether positive diversity-productivity relationships persist through three centuries of fire exclusion, climate change, and large-scale compound disturbance in the Sierra Nevada, CA, USA. We examine the direct and indirect effects of fire, drought, and bark beetles in a previously fire-excluded forest to (1) parse how growth and defense differentially contribute to diversity-productivity relationships; (2) identify forest stand characteristics governing associational resistance and

susceptibility; and (3) quantify whether forest diversity, overall, contributed to tree survival during compound disturbance. We focused our efforts on growth and axial resin duct production dependence on forest diversity and density for *Pinus lambertiana* Douglas, an iconic gymnosperm residing in historically fire-prone montane forests of the Sierra Nevada. We then assessed whether growth or defense benefits to *Pinus* growing in diverse communities, if they exist, translated into enhanced survival during a bark beetle outbreak.

## Methods

### Study area

The study area was the Yosemite Forest Dynamics Plot (YFDP), located in Yosemite National Park, CA, USA (Lutz et al. 2012, 2013). The YFDP is part of the Smithsonian ForestGEO network (Anderson-Teixeira et al. 2015; Davies et al. 2021), with every tree  $\geq 1$  cm diameter at breast height (DBH) mapped, measured, and identified. Since 2011, the YFDP has served as a natural experiment for compound disturbances by tracking growth and survival of 34,458 trees within a 25.6-ha contiguous area exposed to overlapping fire, drought, and bark beetle disturbances. The fire regime at the YFDP prior to Euro-American settlement was one of low- to moderate-severity fires occurring at a mean fire return interval of 30 years in the YFDP (Barth et al. 2015). This return interval was longer than characteristic for this vegetation type (12 years; Scholl and Taylor 2010), most likely because of its generally north-facing aspect. The last fire to burn through the YFDP prior to the onset of fire exclusion was in the year 1900 (Barth et al. 2015).

The YFDP is located in the *Abies concolor*/*Pinus lambertiana* vegetation zone of the central Sierra Nevada, where the distribution and abundance of woody vegetation is jointly determined by climate and fire (Lutz et al. 2010; van Wagtenonk et al. 2020). Common tree species include the gymnosperms *Abies lowiana* (Gordon) A. Murray (previously *Abies concolor* (Gordon & Glendinning) Hildebrand; shade tolerant, subdominant), *Calocedrus decurrens* (Torrey) Florin (shade tolerant, co- to subdominant), and *Pinus lambertiana* Douglas (shade intolerant, dominant); and subdominant angiosperms *Cornus nuttallii* Audubon and *Quercus kelloggii* Newberry. Prominent shrubs include *Arctostaphylos patula* Greene, *Ceanothus cordulatus* Kellogg, *Ceanothus integerrimus* Hooker & Arnott, *Ceanothus parvifolius* Trelease, *Chrysolepis sempervirens* (Kellogg) Hjelmquist, *Corylus cornuta* ssp. *californica* (A. de Candolle) E. Murray, and *Prunus emarginata* (Douglas) Eaton. Nomenclature follows Flora of North America Editorial Committee (1993+) (Flora of North America Editorial Committee 1993).

The YFDP experienced severe drought spanning 2012 to 2015: in spring of 2015, the snow water equivalent was at 5% of its historical average, a level that has not been observed for over 3000 years (Belmecheri et al. 2016; Table 1). Coinciding with drought, the YFDP burned in September 2013 in a management-ignited backfire set to control the spread of the Rim Fire (Lutz et al. 2017). The satellite-derived fire severity within the YFDP showed mostly a mixture of low- to moderate-severity (Blomdahl et al. 2019) generally characteristic of fires in Yosemite since 1975 (van Wagtenonk and Lutz 2007). Within the YFDP, fire severity was generally indistinguishable from the majority of the Rim Fire footprint within Yosemite (Kane et al. 2015), but much less severe than the high-severity effects on the adjacent Stanislaus National Forest (Lydersen et al. 2014). Surface fuel consumption, including consumption of duff mounds near larger-diameter trees, was approximately 90% (Cansler et al. 2019), but unburned surface area in patches  $\geq 1 \text{ m}^2$  was 5% (Blomdahl et al. 2019). Elevated bark beetle activity followed the fire, reaching incipient-epidemic levels between the years 2014 and 2016 (Furniss et al. 2020, 2022).

All trees were measured for diameter in 2009–2010, 2014, and 2019. We revisited each tree annually from 2011 to 2019 (Lutz 2015) and conducted pathology exams of newly dead trees, which were considered dead if no live foliage, buds, or photosynthetic stems were evident. Pathology exams entailed exposing the phloem and sapwood of the stem and root crown using a hatchet. Our immediate post-fire pathology exams in May 2014 measured direct fire effects: crown scorch and consumption were estimated ocularly as a proportion of total pre-fire live crown volume, bole scorch height was measured with a TruPulse laser, and bole consumption was recorded as a proportion of tree basal diameter. Fire-caused mortality was assumed for conifers with 100% crown scorch or consumption and was verified through physical examination of phloem and sapwood of the stem and root crown for those with  $< 100\%$  crown death. Subsequent pathology exams from 2015 to 2019 captured delayed fire- and bark

beetle-related mortality. We identified bark beetles as the primary cause of mortality when the tree showed signs of invasion externally (e.g., pitching, entry, and exit holes) and internally (e.g., live beetles or larvae present, abundant bark beetle galleries visible under bark). All pathology exams detailed predisposing factors (e.g., crushing) and multiple mortality causes when applicable, which were ordered from most proximate to least proximate based on the annually resolved field observations (e.g., fire damage in 2014, beetle attack and final mortality in 2017). See Germain and Lutz (2021a, their Appendix S1) for a full description of pathology exam methods.

We randomly selected 80 bark beetle-resistant and 80 beetle-susceptible *Pinus* trees that were  $\geq 80 \text{ cm}$  DBH in 2019 from which to sample annual growth and defense. Both resistant and susceptible tree groups were represented by an equivalent range of tree diameters (Additional file 1: Fig. S1). Selected trees met all the following criteria: resistant trees were those still alive in the summer of 2019; susceptible trees were those that were alive in 2014 (immediately post-fire) but that died due to bark beetles (*Dendroctonus ponderosae* Hopkins and/or *Dendroctonus valens* LeConte) between 2015 and 2019; though these trees may have endured fire damage, annual surveys in the 5 years following fire indicated these trees survived the fire and that bark beetles were the most proximate cause of mortality. Because *P. lambertiana* is the only host for *Dendroctonus* spp. in the YFDP, we consider these beetles host-specific for the purposes of this study. Of resistant trees, 19% showed evidence of bark beetle attack during the 5 years post-fire (pitching, bark beetle frass, entry and exit holes, bark beetles). Trees were not sampled from rocky ridges or riparian draws to avoid possibly confounding effects of unique water status, nutrients, and altered fire intensity in these areas (North et al. 2009; van Wagtenonk et al. 2020). Topographical strata were determined by calculating 50-m<sup>2</sup> topographic position index (TPI; Fig. 1), then defining ridges as  $> 80\text{th}$  percentile (2.2 TPI) and draws as  $< 20\text{th}$  percentile ( $-2.3$  TPI). We verified that this stratification controlled for prevailing edaphic controls on tree neighborhoods through additional soil and topographic tests (see [Tree neighborhoods](#), below).

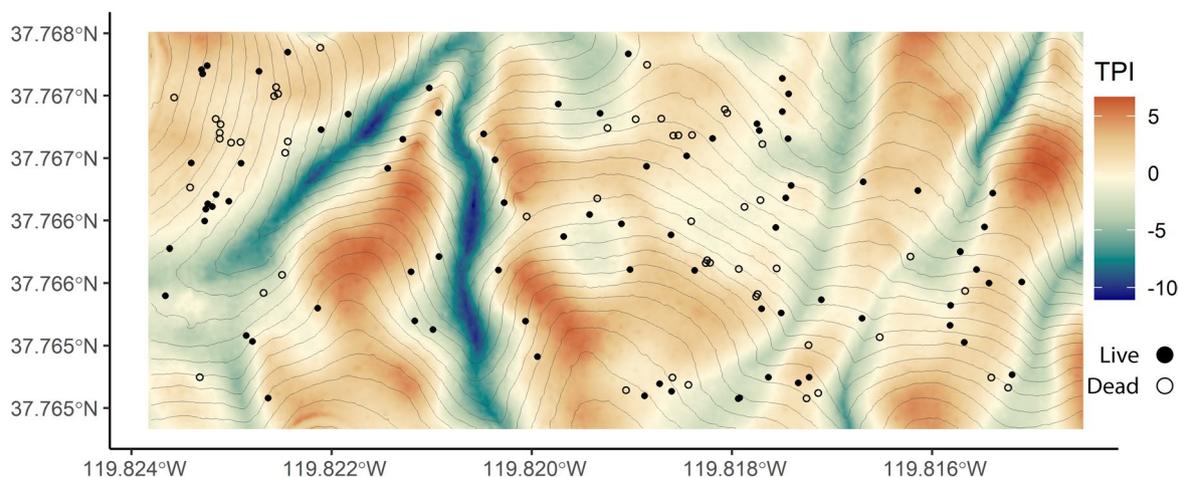
An increment borer was used to extract one, 5.15-mm wide  $\times$  30-cm long core from each sampled tree, approximately 1 m above the soil surface. Cores were visually inspected upon sampling and trees were re-sampled if initial cores were too rotten to identify rings. Increment borers were cleaned with steel wool and disinfected with a diluted Lysol solution between each tree to prevent disease transmission. Cores were dried, mounted, and sanded progressively from 220 grit to 30 microns using standard dendrochronological techniques (Speer 2010).

**Table 1** Timeline of the compound disturbance in Yosemite, CA, USA. Temporal overlap between these three disturbances, combined with spatial heterogeneity of fire effects and bark beetle activity, allow investigation of the interactions between varying levels in disturbance severity alongside pre- and post-fire comparisons

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2012–2015: Sustained period of drought.
2013: Fire reintroduction — the Rim Fire burns with mixed severity.
2014–2019: Bark beetles invade, reaching incipient-epidemic levels by 2016.

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**Fig. 1** Map of the Yosemite Forest Dynamics Plot from which *Pinus lambertiana* was sampled, where a low topographic position index (TPI) represents concavity and a high TPI represents convexity. *Pinus* was not sampled from ridges (> 80<sup>th</sup> percentile; 2.2 TPI) or draws (< 20<sup>th</sup> percentile; -2.3 TPI). Lines represent 5-m contours

Mounted cores were scanned as high-resolution images (3000 dpi).

Of the originally sampled 160 trees, 30 cores could not be crossdated due to severe stem rot (final live  $n=80$ , dead  $n=50$ ). Ring boundaries were assigned and radial growth measured to  $\pm 0.001$  mm accuracy using Cybis' *CooRecorder* and *CDendro* software [version 9.6] (Larsson and Larsson 2017). All cores were visually crossdated before being evaluated for possible errors using the package *dplR* [version 1.7.2] (Bunn 2008). Live trees were used to crossdate dead trees and determine their final year of growth. Dead trees produced terminal growth rings between 0 and 3 years preceding evidence of death observed in the field, which was deduced from annual mortality surveys (Germain and Lutz 2021a, their Appendix S1). We compared our chronologies (the robust bi-weight mean of live vs. dead trees built on pre-whitened ring widths; Germain and Lutz 2021b, c) with five *Pinus* chronologies and one *Calocedrus decurrens* (Torrey) Florin chronology to verify crossdating accuracy and identify missing rings (Additional file 1: Table S1).

To control for temporal variability in tree diameter, ring width was converted to basal area increment (BAI;  $\text{mm}^2 \text{ year}^{-1}$ ) using backwards calculations from DBH measured at the time of coring. We note that bark thickness was not measured directly and therefore contributes some uncertainty to the BAI estimates; yet, we do not expect a systematic difference in bark thickness between live and dead trees given the similar range of tree diameters (closely correlated with bark thickness) captured in both live and dead tree populations. Because of the mature stature of the trees, combined with the fact that our coring depth did not hit pith, we observed no

age-related growth trends and did not further detrend growth data for analysis.

To quantify defenses, we followed the methods outlined by Hood and Sala (Hood and Sala 2015). We identified and measured annual resin ducts in core images using the ellipse tool in *ImageJ* [version 1.53e] (Rasband 2012). We delineated a 350-px-wide area down the center of each core within which to measure resin ducts to control for slightly different core widths. We cross-verified resin duct measurements twice for consistency and accuracy and calculated six metrics of resin duct production: average individual duct area ( $\text{mm}^2 \text{ n}^{-1}$ ), annual duct area ( $\text{mm}^2 \text{ year}^{-1}$ ), annual duct density ( $\text{n year}^{-1}$ ), and each of these raw metrics relativized by ring width (Table 2, Hood and Sala 2015). Welch's *T*-tests were performed on unstandardized, mean values for growth, defense, and diameter (see the Results: "Growth and defense" section) to compare live and dead trees in the pre-fire and post-fire periods (2009–2013 and 2014–2019, respectively) for descriptive statistics.

### Tree neighborhoods

We calculated live density and basal area of each woody species present in the stand using a mirrored edge correction to account for edge effects. We examined the effect of neighbor size by including the density and basal area of large ( $\text{DBH} \geq 60$  cm), medium ( $10 \text{ cm} \leq \text{DBH} \leq 60$  cm), small ( $1 \text{ cm} \leq \text{DBH} < 10$  cm), and all neighbors ( $\text{DBH} \geq 1$  cm). We measured the nearest distance to a susceptible *Pinus* and resistant *Pinus*, the proportion of neighboring *Pinus* that were killed by bark beetles, and basal area of bark beetle-killed *Pinus* in the neighborhood (as a proxy for local bark beetle attack

**Table 2** Summary of growth and defense metrics obtained from dead and live tree cores. Basal area increment and annual duct area were used for growth and defense metrics in statistical models. Diameter at breast height was recorded in 2019 for live trees and in the year of mortality for dead trees (between 2014 and 2019). All summary statistics were calculated at the tree-level (for which time periods varied as a function of the core sample), then summarized at the population-level secondarily here

	Live				Dead			
	Min	Median	Max	SD	Min	Median	Max	SD
Core sample (years)	1709	1874	2019	53.9	1591	1848	2019	76.5
Diameter at breast height (cm)	80.1	111.0	171.0	23.0	84.6	121.1	154.6	19.3
Ring width (mm)	0.10	1.79	9.17	0.69	0.42	1.47	7.10	0.67
Basal area increment (mm <sup>2</sup> )	1.3	47.4	348.7	17.2	1.4	40.6	191.2	15.5
Average individual duct area (mm <sup>2</sup> n <sup>-1</sup> )	0.004	0.260	0.100	0.008	0.005	0.290	0.210	0.010
Annual duct area (mm <sup>2</sup> year <sup>-1</sup> )	0	0.039	0.306	0.040	0	0.034	0.339	0.040
Annual duct density (n year <sup>-1</sup> )	0	1	14	1.4	0	1	10	1.3
Relative individual duct area (mm <sup>2</sup> n <sup>-1</sup> ring-mm <sup>-2</sup> )	0.0005	0.0047	0.0710	0.0028	0.0005	0.0064	0.2388	0.0047
Relative annual duct area (mm <sup>2</sup> ring-mm <sup>-2</sup> )	0	0.0068	0.1540	0.0093	0	0.0073	0.9550	0.0135
Relative annual duct density (n ring-mm <sup>-2</sup> )	0	0.26	5.24	0.33	0	0.25	32.16	0.45

rates for focal trees). Finally, we characterized diversity using the number of different woody species (richness) and the standard deviation of tree DBH within each neighborhood (i.e., old-growth index; Spies et al. 1991). Neighborhood metrics were calculated annually to capture changes in neighborhood structure and composition arising from annually resolved tree mortality and recruitment.

The density, basal area, distance, and diversity metrics were calculated at 5, 10, 20, and 30-m radii from focal trees, where focal trees were the cored *Pinus*. We conducted two preliminary analyses using Random forests to determine (1) the optimal radial distance within which to quantify neighborhoods, and (2) which of the neighborhood variables were most predictive of *Pinus* survival. We then conducted multivariate multiple regression to test whether neighborhood effects were confounded with underlying variability in site conditions, where edaphic variables included topographic position (relative concavity or convexity of the site; used to stratify initial sampling), slope, aspect, soil nitrogen (NH<sub>4</sub> mg kg<sup>-1</sup>), soil phosphorus (mg kg<sup>-1</sup>), total exchangeable bases (cmolc kg<sup>-1</sup>), and effective cation exchange capacity (cmolc kg<sup>-1</sup>; Tamjidi and Lutz 2020). Welch’s *T*-tests were performed to compare live and dead trees for descriptive statistics in the pre-fire and post-fire periods (2009–2013 and 2014–2019, respectively; *Results: Neighborhoods*).

**Climate**

We obtained monthly time series of climatic water deficit (deficit) from the TerraClimate dataset via Google Earth Engine at a 4-km spatial resolution and spanning 1958 to 2019 (Abatzoglou et al. 2018). This measure of drought

was chosen based on regional analyses informing our a priori understanding that the water balance, rather than precipitation or temperature alone, influences conifer growth and survival in the Sierra Nevada (Stephenson 1998; Lutz et al. 2010). The 2012–2015 drought was captured by deficit values: maximum monthly deficit ranged from 1799 to 1945 mm H<sub>2</sub>O year<sup>-1</sup> during this time (compared to the prior 30-year average, 1666 mm H<sub>2</sub>O year<sup>-1</sup>). Maximum monthly deficit in subsequent years (2016–2019) ranged between 1743 and 1777 mm H<sub>2</sub>O year<sup>-1</sup>. All analyses were performed in R [version 4.1.2] (R development core team 2019).

**Statistical analysis**

We built a multilevel moderated mediation structural equation model (SEM) that tested the direct and indirect mechanisms by which forest characteristics altered bark beetle success rates (i.e., tree survival) across heterogeneous drought and fire disturbances. Because the analysis was performed on years following first fire re-entry (2014–2019), the sample depth for tree growth and defense was saturated (Additional file 1: Figs. S2, S3). We performed piecewise SEM (i.e., confirmatory path analysis), which uses local estimation of each linear regression (i.e., path) rather than global estimation of all paths simultaneously (Lefcheck 2016). This allowed for the fitting of a wide range of variable distributions, including our binomial survival response and multilevel data structure. As an extension of linear regression, SEM allows greater flexibility to examine interactions between variables through both moderation and mediation. Much like interactions in simple linear models, *moderation* alters the direction or strength of a relationship between two

variables. Conversely, *mediation* characterizes the mechanism by which an indirect effect occurs between two variables. Serial mediation refers to an indirect effect that is mediated by two or more variables, and moderated mediation happens when an indirect relationship is also moderated by a third exogenous predictor. The multilevel structure reflects within-tree variability (i.e., growth, defense, and drought over time), while between-tree variability was sampled by tree neighborhoods and fire damage. All mediated relationships were therefore cross-level interactions. Analysis was performed using the package `semEff` [version 0.6.0] (Murphy 2021) and cross-verified using the package `piecewiseSEM` [version 2.1.2] (Lefcheck 2016; Murphy 2021).

To account for temporal and spatial autocorrelation, we employed nonparametric bootstrapping on the standardized effects (1000 resamples) using the `bootEff` function in the `semEff` [version 0.6.0] package (Murphy 2021). For temporal autocorrelation, resampling occurred with replacement at the group-level, as individual observations were not independent. We therefore allowed correlated errors between (1) repeated measures over time for each tree, and (2) BAI and duct area per year within the same tree. We then ran Global Moran's *I* tests using the `oce` package (Kelley et al. 2022) to detect significant spatial autocorrelation of covariates, which was found for *Abies* density and richness ( $P$ -values < 0.01), but not bole scorch ( $P$ -value = 0.49; see also van Mantgem and Schwilk 2009). We allowed correlated errors for these spatially correlated covariates during the non-parametric bootstrapping step as well.

The SEM predicted tree survival as a function of (1) the direct effects of biotic factors in the 5 years following fire: 30-m post-fire woody species richness, 10-m post-fire *Abies* density, 10-m post-fire basal area of bark beetle-killed *Pinus* (proxy for beetle attack rates), BAI (growth), and resin duct area (defense); (2) the indirect effects of single and serial mediation processes among these five factors, and (3) the moderation of each direct and indirect effect by drought (i.e., maximum monthly deficit) and fire damage (bole scorch). Neighborhood metrics were calculated annually to capture changes in neighborhood structure and composition arising from annually resolved tree mortality and recruitment (spanning 2014 to 2019). Predictors were standardized across all trees using the *z*-score transformation. The hypotheses underlying each moderation and mediation interaction are described below:

**Stage 1 — Direct effects of predictors on survival**

Overall, we expect direct effects of tree neighborhoods on *Pinus* survival to be less predictive than indirect effects. We expect tree survival (i.e., low beetle success

rate) to depend on tree growth and defense, which are in turn governed by direct and indirect biotic and abiotic factors (see single and serial mediation, below). The direct effects of beetle attack on tree survival represent mass attacks that overwhelm and thus circumvent tree defensive capacity. Negative covariance between growth and defense indicates a growth-defense trade-off. In the presence of such an observation, we expect that tree survival would be more benefited by defense than by growth. We expect the relationships between tree growth/defense and survival to be moderated by drought and fire damage: these two stressors may increase the relative importance of factors not considered by the model (e.g., hydraulic conductivity), thus weakening the relationship between tree defense and survival.

**Stage 2 — Indirect effects via single mediation: neighborhood effect on survival is mediated by tree growth and defense**

We expect tree neighborhoods to have indirect effects on tree growth and defense: if there is lower competitive stress due to lower density of neighbors, *Pinus* will have higher photosynthetic rates to support increased growth and constitutive defenses. We expect the relationships between neighborhoods and tree growth/defense to be moderated by drought and fire damage: these two stressors may strengthen competitive interactions and weaken the facilitative effects of diversity, reducing growth and defenses as a result.

**Stage 3 (full model) — Indirect effects via serial mediation: neighborhood effect on survival is mediated by tree growth and defense, which are themselves mediated by bark beetle attack rates**

We expect that tree neighborhood indirect effects on tree growth and defense are mediated by beetle attack rates: if there are fewer beetles attacking due to higher tree diversity, *Pinus* will be able to invest more carbon in growth, as less will be required for defense. We may expect the opposite to be true for density: if there are more beetles attacking due to vulnerability arising from competitive stress, *Pinus* will be induced to allocate carbon to defense rather than growth. We expect the relationships between neighborhoods and beetle attack rates to be moderated by drought and fire damage: these two stressors may induce *Pinus* to emit an altered volatile chemical profile that increases beetles' detection probabilities (Jenkins et al. 2014), weakening the relationship between neighborhoods and beetle attack. Likewise, we expect the relationships between beetle attack rates and tree growth/defense to be moderated by drought and fire damage: these two stressors may further induce *Pinus* to invest in defenses (Hood et al. 2015), strengthening the

relationship between beetle attack rates and defense relative to growth.

## Results

Direct mortality from the Rim Fire reduced total stand density by 72.4% (1402.8 stems ha<sup>-1</sup> in 2013 to 387.4 stems ha<sup>-1</sup> in 2014), and delayed fire effects over the 5 years post-fire further decreased density by 28.4% (277.4 stems ha<sup>-1</sup> in 2019). The stand density in 2019 was still more than double the estimated historical density (i.e., pre-1900; historical = 109.5–114.1 stems ha<sup>-1</sup>; Barth et al. 2015 their Table B.1). However, including delayed effects, the fire returned large *Pinus* and small *Abies* densities to historical levels: *Pinus* ≥ 100 cm DBH dropped from 13.4 stems ha<sup>-1</sup> to 7.2 stems ha<sup>-1</sup> (historical = 6.9–8.0 stems ha<sup>-1</sup>) and *Abies* ≤ 10 cm DBH dropped from 612.2 stems ha<sup>-1</sup> to 14.3 stems ha<sup>-1</sup> (historical = 9.4–14.3 stems ha<sup>-1</sup>). Of the *Pinus* with DBH > 80 cm (the coring cohort), 1.8% died pre-fire; 1.8% were killed during the fire; and 42.3% of the initial cohort were killed in the 5 years post-fire.

## Growth and defense

Growth differed the most between groups during the era of fire exclusion (1901–2012): trees that ultimately died from bark beetles following the 2013 Rim Fire and concomitant drought were the trees that responded poorly to fire suppression following the 1900 fire (less growth; Fig. 2). Susceptible trees showed massive growth declines following the Rim Fire. On average over the series, susceptible trees had 17% smaller median ring width and 8% smaller BAI compared to resistant trees (Fig. 2). Within-series growth variability was similar for both groups (Table 2), but there was greater inter-series variability for susceptible trees than resistant trees. Cores contained between 69 and 427 rings. Susceptible trees had a greater variance in ring number (SD = 76.5 vs 53.9 rings, respectively), generally having more numerous, smaller rings. At the time of sampling, tree DBH ranged from 80.1 to 170.6 cm, meaning the 30-cm long cores sampled between 18 and 37% of the total tree diameter. There were no detectable differences in DBH between resistant and susceptible groups at the time of sampling (Additional file 1: Fig. S1).

Both resistant and susceptible trees increased duct density, with parallel increases in total duct area, during the era of fire exclusion (1901–2012; Fig. 3). Resistant trees showed slightly more resin ducts than susceptible trees, but density converged in the past three decades. Susceptible trees' ducts tended to be larger than those of resistant trees, but this difference also converged. Differences in duct density and size struck a balance such that resistant and susceptible

trees produced similar total annual duct area. Because susceptible trees had lower annual growth but equal duct area as resistant trees in the years following the Rim Fire (2014–2019), susceptible trees showed higher relative annual duct area ( $P = 0.007$ ) and relative area per duct ( $P < 0.001$ ). These relative metrics were driven by differences in ring width, yet our goal was to model the separate effects of disturbance and stand structure on growth and defense. We therefore included annual duct area (the best synthesis of duct density and size) and growth separately in statistical models.

All except five bark beetle-susceptible trees produced no growth nor defenses in the 1 to 2 years post-fire. Susceptible trees produced less duct area with severe fire damage; resistant trees produced higher defenses independent of fire damage. In the pre-fire record, resistant trees maintained high growth rates and duct production, while susceptible trees showed decreasing growth (Fig. 2).

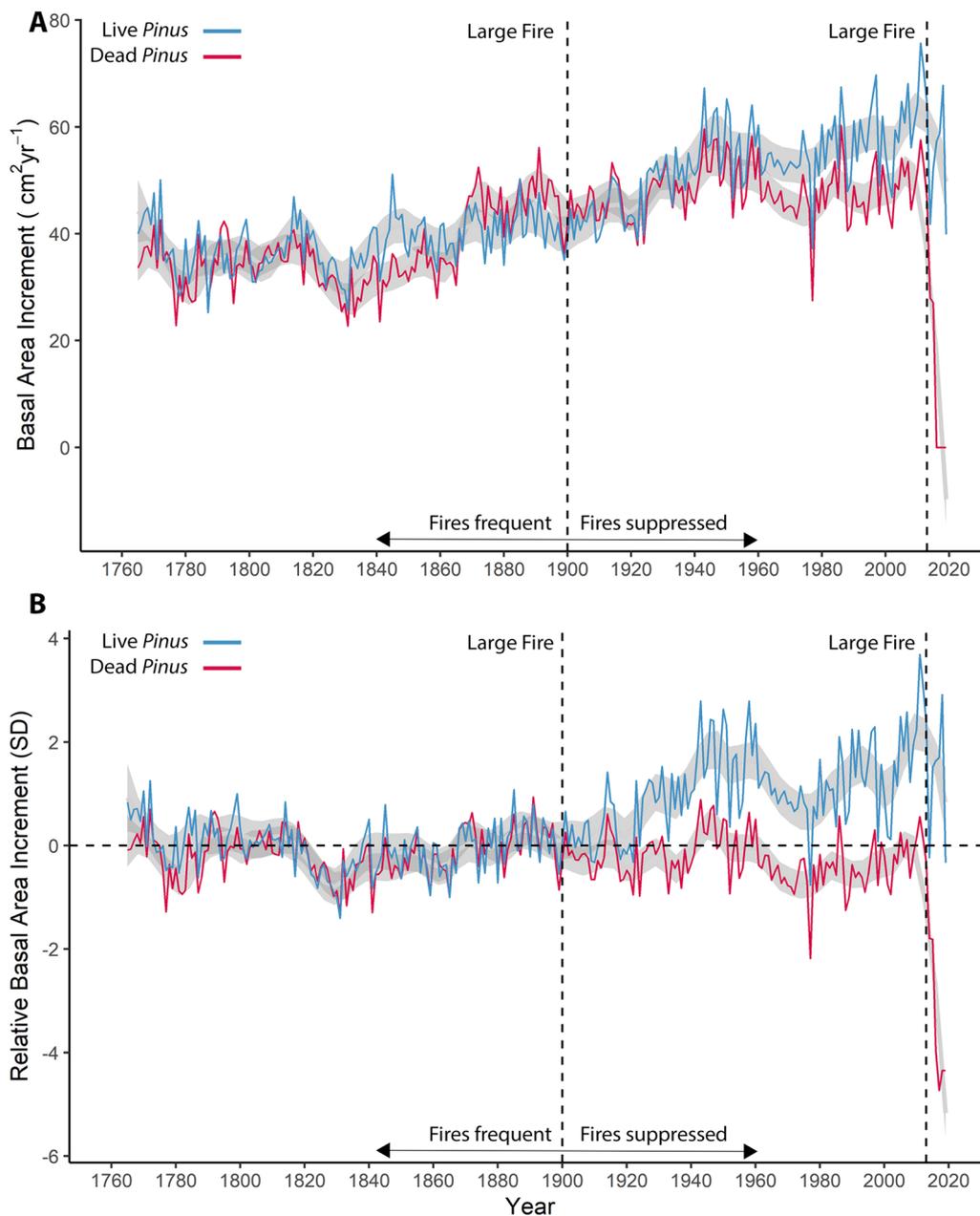
## Tree neighborhoods

Close-range basal area of bark beetle-killed *Pinus* (10 m) was associated with subsequent *Pinus* mortality, while the basal area of live *Pinus* at a close range was not (Additional file 1: Fig. S4). Within a 10-m radius, lower densities of small-diameter *Abies* (1 cm ≤ DBH < 10 cm), large-diameter *Pinus* (DBH ≥ 60 cm), and lower total basal area and density (DBH ≥ 1 cm) during the pre-fire period were associated with *Pinus* post-fire survival (Additional file 1: Fig. S5). Within a 30-m radius, neighborhood species richness was higher for resistant trees pre- and post-fire; along with higher *Cornus* and shrub pre-fire density (Additional file 1: Fig. S6; high variability). Structural diversity (old-growth index) did not differ between resistant and susceptible trees during the fire exclusion nor post-fire periods (Additional file 1: Fig. S6).

Species richness at 30-m was not correlated with 10-m total density ( $p = 0.2$ ), *Abies* density ( $p = 0.9$ ), large *Pinus* density ( $p = 0.2$ ), or large *Pinus* living basal area ( $p = 0.1$ ). Small *Abies* density was slightly higher when richness was higher ( $p < 0.001$ ; +0.6 small *Abies* per additional species richness, maximum 7.8 more small *Abies*). Higher *Abies* densities were found on sites with slightly more nitrogen, while the highest richness was on slightly steeper slopes.

## Statistical analysis

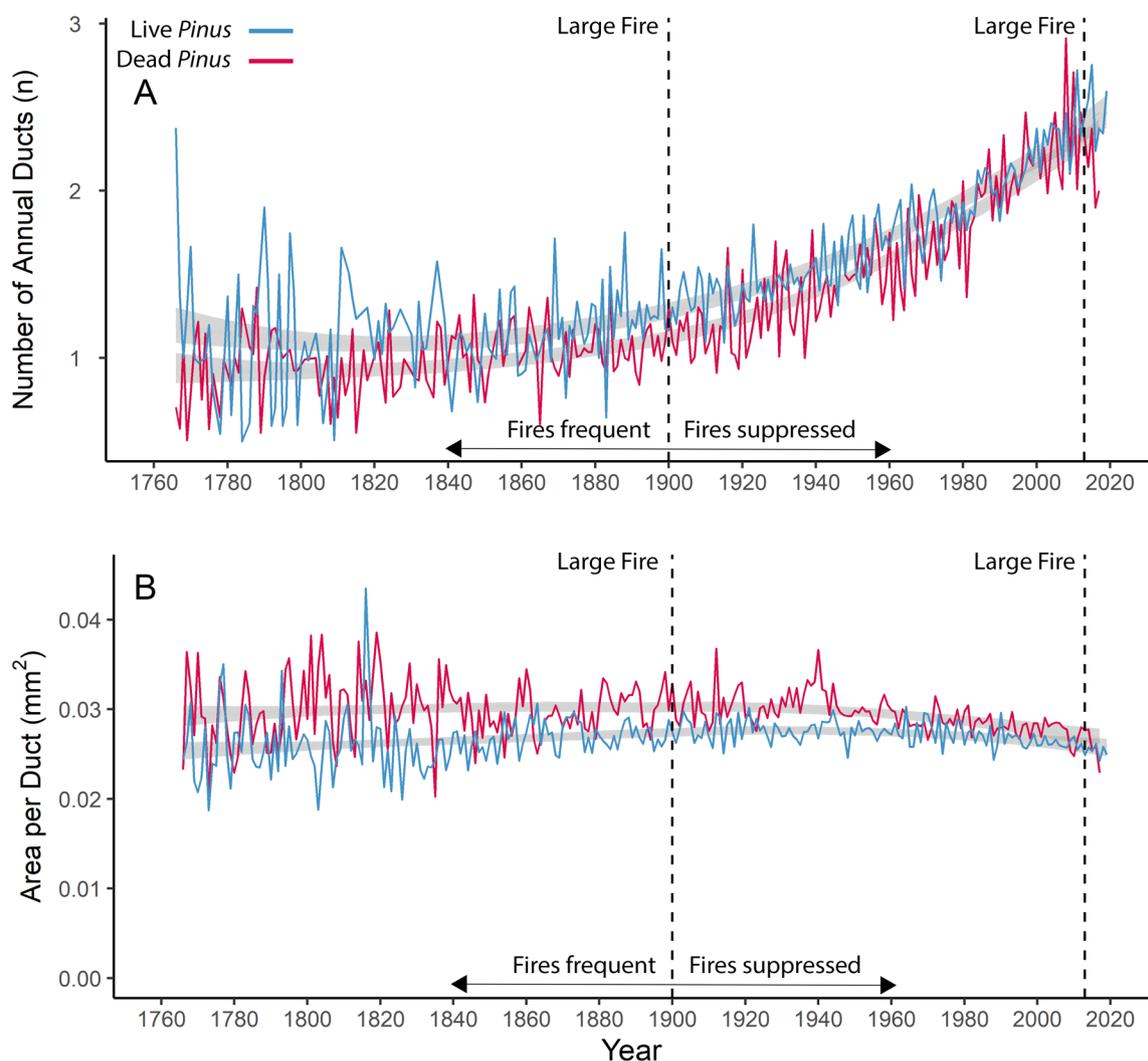
SEM predicted *Pinus* survival with very high accuracy (94.6% specificity, 94.0% sensitivity, 94.6% total accuracy). As expected, indirect effects outweighed direct effects of tree neighborhoods on *Pinus* survival (Fig. 4, Additional file 1: Tables S2, S3). On average, associational resistance (i.e., species richness effects) increased survival by



**Fig. 2** *Pinus lambertiana* basal area increment (BAI) chronologies for live and dead trees (A) and the z-scores of live and dead tree BAI (B), where each was standardized by the group average BAI during the historical period with an intact frequent fire regime (pre-1900). Curves falling above zero in B indicate trees grew faster than their historical average, while curves below zero indicate slower than historical growth. The last large fire in 1900 marked the beginning of fire suppression efforts. Live and dead tree growth was similar during the pre-1900 period when the historic frequent fire regime was still intact (mean fire return interval 30 years). During the era of fire exclusion (1901–2012), trees that would ultimately die from bark beetles following the 2013 Rim Fire grew more slowly than trees that would survive and often grew slower than they did historically. Together, these patterns indicate less resilience to the structural and compositional changes resulting from fire exclusion. Curves begin at 1765, after which sampling depth was  $\geq 10$  individuals per live and dead category (Additional file 1: Fig. S2, S3). Mean fire return intervals derived from Barth et al. (2015). The 95% confidence intervals are shown in gray

8.6%, while associational susceptibility (i.e., *Abies* density effects) decreased survival by 6.4%. Trees that grew faster survived, regardless of the duct area produced.

The highest bark beetle attack rates were near fire-damaged *Pinus* in monodominant, high *Abies* density neighborhoods, while the lowest bark beetle attack rates



**Fig. 3** *Pinus lambertiana* annual resin duct density (A), and area per duct (B) with 95% confidence intervals shown in gray. Duct density has been increasing over the past 260 years for live and dead trees alike. Duct area (not shown) follows the same trajectory as duct density. During the post-1900 era of fire exclusion (mean fire return interval 65 years), trees that would ultimately die from bark beetles following the 2013 Rim Fire showed reduced growth yet sustained resin duct production, resulting in a higher duct area:ring width ratio. Curves begin at 1765, after which sampling depth was  $\geq 10$  individuals per live and dead category (Additional file 1: Fig. S2, S3)

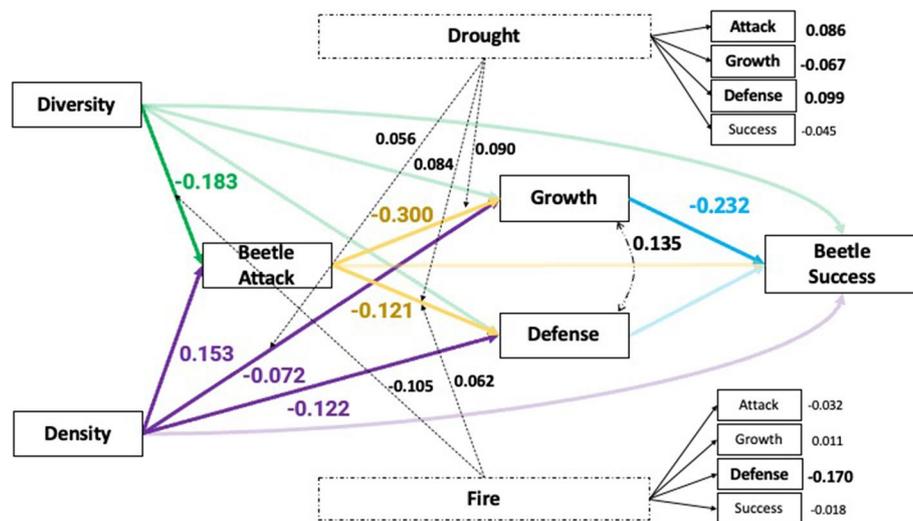
were near fire-damaged trees in diverse neighborhoods (Fig. 5). Diversity was not correlated with *Abies* density nor overall density. Growth rates were highest during wetter years and for trees with low local bark beetle attack rates, few *Abies* neighbors, and diverse neighborhoods. Defenses were highest for trees with low fire damage, low local bark beetle attack rates, few *Abies* neighbors, and diverse neighborhoods. Yet, defenses were not predictive of tree survival.

Higher diversity decreased local bark beetle attack rates, which indirectly increased *Pinus* growth and survival. Fire strengthened the ability of diverse neighborhoods to reduce bark beetle attack, leading to increased

growth and survival for burned *Pinus* when diversity was high. Conversely, fire damage led to greater bark beetle attack, less growth, and lower survival when *Pinus* grew in monodominant neighborhoods. Drought and *Abies* density decreased growth and increased bark beetle attack rates, both indirectly reducing *Pinus* survival as well.

**Discussion**

Forests that historically burned with high frequency need fire to remain resilient to climate changes and to prevent catastrophic wildfire (e.g., Hagsmann et al. 2021), but reintroducing fire to these long fire-excluded areas

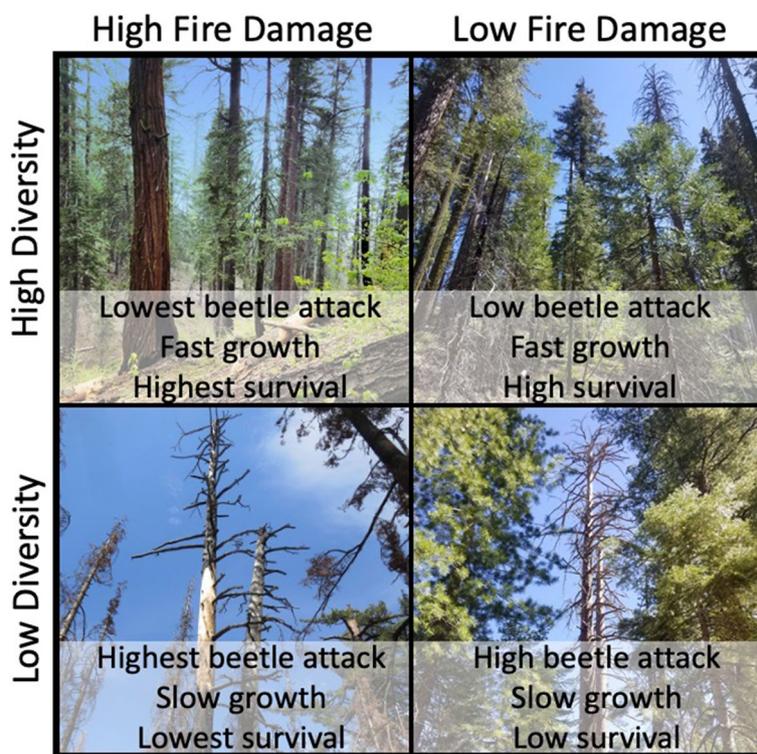


**Fig. 4** Results from the multilevel moderated mediation structural equation model testing the mechanisms underpinning bark beetle attack/success and tree constitutive/induced defenses in a compound disturbance environment. Paths represent hypothesized causal relationships. Bark beetle success rate is measured as *Pinus* survival or mortality due to bark beetles. Bark beetle attack rate is approximated by total bark beetle-killed *Pinus* BA within a 10-m radius. Density is *Abies concolor* within 10-m radius, and diversity is species richness within a 30-m radius. Dashed lines connecting two factors indicate a covariance. Dashed lines connecting a factor to a path (i.e., drought and fire effects) indicate a moderation interaction. Drought and fire moderated paths independently from one another, though this is not depicted in the figure for esthetic parsimony. Within-tree variability (level 1) was sampled by growth, defense, and drought over time; between-tree variability (level 2) was sampled by all other factors. Thus, all mediated (i.e., indirect) relationships are represented as cross-level interactions. Transparent arrows indicate a non-significant effect. To calculate the total moderation effect, direct effects of moderators are also shown for each variable (included when significant, shown here in bold). All parameters except survival (binomial) were standardized across trees using the z-score transformation; thus, coefficients may be interpreted as in simple linear regression (change in the response value per single SD increase in predictor)

can have unforeseen effects (Harris and Taylor 2015; Becker and Lutz 2016). In many cases, fire reintroduction can elevate bark beetle attack, even after initial thinning (Youngblood et al. 2009; Stark et al. 2013; Steel et al. 2021). Thus, whether first re-entry fire will harm or benefit even the most fire-adapted species is a central question arising from restoration efforts. We found that fire-damaged *Pinus* resisted beetle attack if they were growing in a neighborhood that had high pre-fire woody plant diversity; in contrast, fire-damaged *Pinus* in low-diversity areas were the most susceptible to bark beetle mortality. Our findings complement recent work showing bark beetle activity to be highly dependent on local forest conditions (Buonanduci et al. 2020), even more so than on direct fire effects (Furniss et al. 2022). In fact, fire damage can increase tree defenses (Hood et al. 2015) and the associated density reductions can relax competitive interactions (Feeney et al. 1998; Hood et al. 2016), leading to higher survival of trees able to tolerate fire. Our sample of *Pinus* represented the most fire-tolerant trees in the forest — even with relatively high levels of fire damage, large-diameter *Pinus* can thrive in burned environments. Despite this life history, however, we observed unexpected declines of nearly half the large-diameter cohort due to elevated bark beetle susceptibility arising

from long-term stress in dense, monodominant environments. These findings highlight the important role of forest composition in moderating resilience to compound disturbances.

Managers are increasingly reliant on wildland fire use over large areas in an attempt to restore historic conditions (van Wagtenonk 2007), but it is clear that first re-entry fire does not erase the legacy effects of fire exclusion (Becker and Lutz 2016; Lutz et al. 2020). Although the Rim Fire returned small *Abies* densities to historic levels, the long-term stress (e.g., carbon starvation; Sevanto et al. 2014) caused by these competitors during the century of fire exclusion reduced *Pinus*' resilience to bark beetles post-fire (Van Mantgem et al. 2018). Instead, mechanical thinning pre-fire can promote resilience to compound stressors in fire-suppressed forests by decreasing fire severity and increasing resistance to drought and bark beetles (Agee and Skinner 2005; Fettig et al. 2007; Hood et al. 2016). Whether and how quickly trees can reverse declining trajectories and resist bark beetles following thinning depends on the forest type in question and is still largely unexplored (Harrington and Reukema 1983; Hood et al. 2016; Zald et al. 2022). For Sierra Nevada mixed-conifer forests, our findings suggest that thinning small-diameter *Abies* before fire can



**Fig. 5** Summary of primary findings from the structural equation model showing associational resistance in the post-fire environment. *Pinus lambertiana* growing in areas with high woody species richness (high diversity; 30-m scale) had lower post-fire bark beetle attack rates, faster pre-fire and post-fire growth, and ultimately higher survival in the 5 years post-fire than did *Pinus* in low diversity areas. Of the trees in high-diversity areas, the highest survival was observed for those that sustained fire damage (higher bole scorch), which likely represents moderate-severity fire in the adjacent neighborhood. In contrast, higher fire damage resulted in the lowest survival for *Pinus* growing in low-diversity neighborhoods. Diversity at 30-m was not correlated with competitor density (*Abies*), conspecific density, or overall density. Photo credits: Sara Germain

improve outcomes for large-diameter *Pinus*. Yet, our findings join others in urging discretion when thinning forests in order to maintain pathways of associational resistance that promote tree vigor and defenses: species richness offered survival benefits, even in dense areas (Baleshta et al. 2005; Germain and Lutz 2021a).

Species interactions have the potential to counteract negative climate change effects (Suttle et al. 2007), and, as such, community-level climate responses may hold the key to more comprehensively predicting, mitigating, and adapting to the climate crisis (Germain and Lutz 2021a, 2022). Without accounting for these indirect and interactive effects, models are unlikely to fully anticipate climate change impacts in forests (Allen et al. 2015; Clark et al. 2021; Germain and Lutz 2022). In particular, models reliant on simplistic depictions of delayed fire effects likely overpredict survival of large-diameter trees (Furniss et al. 2019), leading to a concurrent overprediction of carbon storage capacity in mature forests (Stephenson et al. 2014; Piloniot et al. 2022). The first step to addressing these weaknesses is to integrate models capable of more ecological complexity into projections of

future disturbance regimes under climate change (Hessburg et al. 2005; Kasischke et al. 2013). Traditional linear models are only capable of considering moderation interactions and are unable to quantify indirect effects (i.e., mediation). Yet, our SEM analysis revealed these mediation effects to be quite important: diversity decreased bark beetle attack rates, which in turn, improved survival. The ability of complex models like SEM to quantify these indirect mechanisms will be especially useful to managers and ecologists alike when forecasting the future of community interactions and forest disturbances, especially when coupled with tree- and neighborhood-level datasets (Forrester and Pretzsch 2015).

We add to previous work of tree survival during compound disturbances (van Mantgem et al. 2013, 2018) by identifying multiple interacting mechanisms responsible for *Pinus* resistance and resilience. Competition was relaxed in areas crowded by a more diverse assemblage of species (indicated by faster growth; Ammer 2019), ultimately increasing *Pinus* survival and thereby providing evidence for associational resistance. Associational resistance operated along two distinct pathways: decreased

bark beetle attack and decreased bark beetle success. For individual trees, bark beetle attack rates depend on patch-scale beetle population density, which is directly proportional to the basal area of nearby large-diameter *Pinus* killed by bark beetles: higher basal area reflects more available phloem area and thus a greater number of emerging bark beetles (Cole and Amman 1969; Amman 1972). Bark beetles proceed to attack nearby living hosts after emerging from killed trees, resulting in spatially aggregated beetle activity (Furniss et al. 2020; Howe et al. 2022). We found that diversity at a larger spatial scale than *Pinus* clustering (30-m vs. 10-m) reduced this aggregated attack activity (e.g., likely due to host apparency, resource concentration, and/or natural enemies). For trees that were attacked, survival then depended on vigor, which was also aided in diverse communities. Bark beetles may have chosen not to attack nearby healthy trees based on olfactory cues suggesting strong defenses (Wallin and Raffa 2000), but evidence from field observations indicates that *many resistant trees were attacked and survived*. Enhanced vigor in diverse communities therefore appears to have also decreased bark beetle success. Higher richness was not correlated with more productive sites, nor with reduced stem density; moreover, the benefit of diversity emerged at the community level. It is therefore unlikely that species-rich communities reflect differences in local abiotic conditions, and instead, these communities may have promoted long-term tree vigor through greater access to shared mycorrhizal networks (Germain and Lutz 2021a) or relaxed competition. Future research may build upon these findings to pinpoint the exact mechanisms of associational resistance, including how those may differ in fire-excluded vs. fire-restored forests.

Evidence for whether bark beetles target fast- or slow-growing trees is equivocal and appears to depend on species (Ferrenberg et al. 2014), diameter (Buonanduci et al. 2020), and beetle populations (Boone et al. 2011; Howe et al. 2022). The prevailing paradigm is that slow growth can be an indicator of long-term stress that makes trees more susceptible to bark beetles (Hard 1985; Franklin et al. 1987; Nesmith et al. 2015; Cailleret et al. 2017). Yet, bark beetles may target fast-growing, healthy trees because these represent greater nutritive value (Huberty and Denno 2004). Indeed, recent work has indicated that faster-growing trees can be more susceptible to bark beetle-kill (Six et al. 2021), particularly when beetle populations reach incipient levels (Boone et al. 2011; de la Mata et al. 2017; Howe et al. 2022) or during drought (Stephenson et al. 2019). Although we were not able to determine tree ages, our findings support the decline spiral hypothesis of slow-growing trees being more susceptible (Mansion 1991), which is surprising because we would expect

bark beetles to kill healthy trees during the coinciding drought and incipient beetle outbreak observed during the study. This is among the first studies to delineate how associational resistance can prevail even amidst higher risk levels inherent to compound disturbances.

Susceptible and resistant trees produced virtually equivalent resin duct size, density, and annual area over the two centuries prior to mortality, leading to the conclusion that past physiological defense characteristics cannot necessarily be used to anticipate tree resistance to bark beetles. Indeed, we found that pre-fire defenses were less important to survival than pre-fire growth. Examination of resin ducts prior to compound disturbance would have erroneously concluded that susceptible and resistant trees were equally likely to survive bark beetle attack, when in fact, long-term stress precluded the resilience of tree defenses following first re-entry fire. More accurate predictions of tree survival during compound disturbances might be captured through simultaneous assessments of tree vigor and chemical defenses, such as terpene concentrations (Delorme and Lieutier 1990), resin flow (Warren et al. 1999), and volatile cues (Gray et al. 2015). Chemical defenses are allocated independently from physical defenses (Mason et al. 2019) and may therefore better reflect tree stress (e.g., Hood and Sala 2015; but see Reichardt et al. 1991). Though resin ducts may be associated with tree survival in some cases (Kane and Kolb 2010; Ferrenberg et al. 2014; Hood and Sala 2015; Slack et al. 2021), we found the strength of this relationship is conditioned on the combined effects of disturbance history, forest structure and composition, and the presence of synergizing stressors.

## Conclusion

The interactive effects of drought, fire, competition, and bark beetles together were responsible for unexpectedly large volumes of biomass loss through delayed mortality of the largest pines in 5 years following the first fire re-entry. Growth and defense declines in susceptible trees immediately post-fire were not entirely explained by higher fire damage: burned trees maintained growth, defense, and survival in diverse neighborhoods. Likewise, post-fire growth and defense declines were not explained by drought alone, as similar declines were not observed during pre-fire periods of severe drought; and competitive stress did not coincide with high bark beetle kill pre-fire. It was only the combined, interactive effects of simultaneous fire damage, water stress, and a history of competition that together governed susceptibility to bark beetles.

Complementing the wealth of literature identifying associational resistance in other forest types, ours is the first study to show tree diversity can reduce insect attack

in a previously fire-excluded forest during compound disturbance. In fact, associational resistance effects outweighed associational susceptibility, ultimately protecting the majority of large-diameter *Pinus* that may have otherwise been targeted by bark beetles post-fire. We highlight that the indirect mechanisms of associational resistance predominated: richness did not directly increase tree survival, but indirectly did so by increasing tree vigor pre-fire and thereby reducing bark beetle attack rates post-fire. Given the phylogenetically conserved nature of growth and defense responses in the genus *Pinus*, particularly those that reside in drier, low-elevation forests, these findings contribute to conservation of pine across the temperate region: building pine forest resilience to compound disturbances hinges on both conserving biodiversity and reducing competitor densities before fire to promote the multiple complementary pathways promoting tree survival.

**Abbreviations**

BAI	Basal area increment
Deficit	Climatic water deficit
DBH	Diameter at breast height
SEM	Structural equation model
TPI	Topographic position index
YFDP	Yosemite Forest Dynamics Plot

**Supplementary Information**

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-024-00283-x>.

Additional file 1: Table S1. Pearson's correlations between the *Pinus lambertiana* chronology developed here (YFDP-PILA; Germain and Lutz 2021a, 2021b), three *Pinus* chronologies from Yosemite National Park (King and Graumlich 2002a, 2002b, 2002c), two *Pinus* chronologies from in the Sierra Nevada region (White 2002, Bigelow et al. 2014), and one *Calocedrus decurrens* chronology from the same study location (YFDP-CADE; Barth et al. 2014). Correlations were performed using a robust biweight mean and pre-whitened chronologies. Tuolumne Grove is <1 km northeast of the YFDP, with slightly lower elevation and wetter habitat. The Merced Grove is ~4 km south-southwest of the YFDP, with slightly lower elevation and wetter habitat. Hodgdon Meadows is ~5 km northwest of the YFDP, with lower elevation and drier habitat. Plumas County is ~260 km north-northwest of the YFDP in northern coastal California. Felkner Ridge is ~310 km northwest of the YFDP in the northern Sierra Nevada mountains. Table S2. Serial mediation model coefficients (logit of mortality odds ratio) and change in mortality odds for the effects of each predictor on *Pinus* survival. Indirect effects were those mediated by a third and/or fourth variable, summarized by Mediation. Richness is number of species within a 30-m radius. *Abies* density is number of *Abies* within a 10-m radius. Beetle attack was measured as the basal area of bark beetle-killed *Pinus* within a 10-m radius. Asterisk (\*) indicates statistical significance at  $\alpha = 0.05$ . Table S3. Moderated mediation model coefficients for the effects of each predictor on each response variable in a serial mediation. Growth is basal area increment; defense is annual duct area; richness is number of species within a 30-m radius; *Abies* is number of *Abies* within a 10-m radius; attack is basal area of beetle-killed *Pinus* within a 10-m radius; fire is bole scorch height; deficit is maximum monthly climatic water deficit. Fire and deficit were moderators (interaction effect), whereas attack, growth, and defense were mediators (indirect pathways connecting richness, density, and tree survival). Asterisk (\*) indicates statistical significance at  $\alpha = 0.05$ . Figure S1. The random sample of live and dead trees captured an equivalent range of tree diameters for both groups (A), meaning there was no systematic

bias towards larger trees (and therefore, more readily targeted by bark beetles) in the dead tree group. However, dead trees showed narrower raw ring widths on average (B), which translated to smaller basal area increment than live trees. Figure S2. Spaghetti plot for live trees. Y axes are labeled with unique tree identifiers, where each line represents the raw ring widths for that tree core. Sample depth was saturated (all individuals included) for management-oriented and mechanism-oriented models. Figure S3. Spaghetti plot for dead trees. Y axes are labeled with unique tree identifiers, where each line represents the raw ring widths for that tree core. Sample depth was saturated (all individuals included) for management-oriented and mechanism-oriented models. Figure S4. Relationship between focal *Pinus* (orange vs. green boxplots) and neighboring *Pinus* (x-axis categories). Panel (A) indicates the nearest distance from focal dead and surviving *Pinus* to the nearest neighboring conspecific, where neighbors were either live or beetle-killed postfire. Panel (B) indicates the association between focal dead and surviving *Pinus* and the total live or beetle-killed conspecific basal area within a 10-m radius. Surviving large-diameter *Pinus* had further distances from both live and dead conspecifics (A). Total conspecific basal area was similar for dead and surviving trees, but surviving trees had a smaller neighboring basal area of beetle-killed *Pinus* following fire (B). Basal area of beetle-kill within 10-m is a representation of the number of beetles emerging from those trees, as larger areas indicate more phloem available for successful beetle reproduction. Surviving trees were therefore exposed to smaller local populations of bark beetles emerging from killed trees. Figure S5. Negative neighborhood characteristics within a 10-m radius of live and dead trees before fire re-entry (2009–2013) and after first re-entry fire (2014–2019). Trees that would eventually be killed by bark beetles following first re-entry fire had higher neighborhood basal area pre-fire (A), higher neighborhood density pre- and post-fire (B), higher large-diameter live *Pinus* density prefire (C), and higher small-diameter live *Abies* density pre- and post-fire (D) than those that survived. Total neighborhood metrics include all woody stems with DBH  $\geq 1$  cm. Large-diameter *Pinus* had DBH  $\geq 60$  cm, and small-diameter *Abies* had 1 cm  $\leq$  DBH < 10 cm. The 10-m radius was chosen through preliminary Random forests tests. Figure S6. Positive neighborhood characteristics within a 30-m radius of live and dead trees before fire re-entry (2009–2013) and after first re-entry fire (2014–2019). Trees that would eventually be killed by bark beetles following first re-entry fire had lower neighborhood richness pre- and post-fire (A), lower shrub neighborhood density pre-fire (B), and lower *Cornus* density pre-fire (C) than those that survived. The two groups did not differ in structural diversity (B; i.e., the standard deviation of all neighbors' DBH). Richness was the number of woody species, including both trees and shrubs.

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**Authors' contributions**

SJG conceived the study, designed analyses, developed the dendroecological datasets, and drafted the manuscript. JAL developed the YFDP dataset as principal investigator of the YFDP. Both authors edited and approved the final manuscript.

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**Availability of data and materials**

Tree data for the Yosemite Forest Dynamics Plot is available from the Smithsonian ForestGEO data portal, <https://forestgeo.si.edu>. Dendroecological data are archived at:

1. Germain, S. J. and J. A. Lutz. Yosemite Forest Dynamics Plot Living Trees – PILA - ITRDB CA728. NOAA National Centers for Environmental Information. <https://www.ncdc.noaa.gov/paleo/study/33853>

2. Germain, S. J. and J. A. Lutz. Yosemite Forest Dynamics Plot Dead Trees – PILA - ITRDB CA727. NOAA National Centers for Environmental Information. <https://www.ncdc.noaa.gov/paleo/study/33852>

**Declarations**

**Ethics approval and consent to participate**

Not applicable.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare that they have no competing interests.

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