

Compound disease and wildfire disturbances alter opportunities for seedling regeneration in resprouter-dominated forests

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Abstract. Human-altered disturbance regimes and changing climatic conditions can reduce seed availability and suitable microsites, limiting seedling regeneration in recovering forest systems. Thus, resprouting plants, which can persist in situ, are expected to expand in dominance in many disturbance-prone forests. However, resprouters may also be challenged by changing regimes, and the mechanisms determining facultative seedling recruitment by resprouting species, which will determine both the future spread and current persistence of these populations, are poorly understood. In the resprouter-dominated forests of coastal California, interactions between wildfire and an emerging disease, sudden oak death (SOD), alter disturbance severity and tree mortality, which may shift forest regeneration trajectories. We examine this set of compound disturbances to (1) assess the influence of seed limitation, biotic competition, and abiotic conditions on seedling regeneration in resprouting populations; (2) investigate whether disease-fire interactions alter postfire seedling regeneration, which have implications for future disease dynamics and shifts in forest composition. Following a wildfire that impacted a preexisting plot network in SOD-affected forests, we monitored seedling abundances and survival over eight years. With pre- and postfire data, we assessed relationships between regeneration dynamics and disturbance severity, biotic, and abiotic variables, using Bayesian generalized linear models and mixed models. Our results indicate that postfire seedling regeneration by resprouting species was shaped by contrasting mechanisms reflecting seed limitation and competitive release. Seedling abundances declined with decreasing postfire survival of mature, conspecific stems, while belowground survival of resprouting genets had no effect. However, where seed sources persisted, seedling abundances and survival generally increased with the prefire severity of disease impacts, suggesting that decreased competition with adults may enhance seedling recruitment in this resprouter-dominated system. Species' regeneration responses varied with their relative susceptibility to SOD and suggest compositional shifts, which will determine future disease management and forest restoration actions. These results additionally highlight that mechanisms related to biotic competition, seed limitation, and opportunities for seedling recruitment beneath mature canopies may determine possible shifts in the occurrence of resprouting traits. This result has broad applications to other systems impacted by human-altered regimes where asexual persistence may be predicted to be a beneficial life history strategy.

Key words: disturbance interactions; emerging infectious disease; seedling regeneration; sudden oak death; vegetative reproduction; wildfire.

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INTRODUCTION

Anthropogenic activities have rapidly altered the frequency, severity, extent, and timing of many historical regimes in forest systems (Turner 2010). Under changing regimes, the persistence of tree populations will depend on processes that compensate for tree mortality, such as post-disturbance regeneration (Lloret et al. 2011). However, altered perturbations can cause mismatch between modern disturbances and the life history strategies present in communities that are well-adapted to past disturbance regimes (Johnstone et al. 2016). Such mismatches can result in reduced or failed recruitment and may prompt post-disturbance restoration actions. For instance, in forests dominated by obligate seed-producing species, larger or more severe disturbances, compound disturbances, and changing climatic conditions can reduce subsequent seedling regeneration by decreasing the occurrence of mature, seed-producing trees or microsites hospitable to seedling survival (Johnstone et al. 2010, Harvey et al. 2013, 2016, Enright et al. 2015, Stevens-Rumann et al. 2017, Davis et al. 2018).

Consequently, many studies suggest the dominance of resprouting species (as well as plants with canopy or soil seed banks) may increase with changing forest disturbance regimes (Kulakowski et al. 2013, Coop et al. 2016, Welch et al. 2016, Davis et al. 2018). Mature resprouting plants can persist and regrow in situ following damage, without requiring dispersal and survival through other ecological filters acting on seedlings (Bond and Midgley 2003). However, altered disturbances can also cause increased aboveground and belowground mortality of resprouting trees, following more severe fires (Simler et al. 2018), more frequent disturbance (Fairman et al. 2017), drought (Worrall et al. 2010), and emergence of new diseases (Rizzo and Garbolotto 2003, Simler-Williamson et al. 2019). Under these rapidly changing disturbance regimes, facultative seedling recruitment by resprouting species will influence both (1) where existing resprouting populations will persist, if

altered disturbances cause increased resprouter mortality, and (2) where resprouting species may colonize new sites, become more dominant, or increasingly hinder seedling regeneration by other species, as hypothesized for some disturbance-prone systems. However, the mechanisms determining facultative seedling regeneration in many predominantly asexual tree populations remain poorly understood (Gill et al. 2017), though this process will be essential for understanding possible compositional shifts in disturbance-prone systems. Frameworks and observational studies have proposed that gap availability and competition with surviving, resprouting adults may broadly determine the evolution, fitness, and distribution of seeding traits and sexual regeneration (Pausas and Keeley 2014, Keeley et al. 2016).

Here, we investigate the mechanisms constraining postfire seedling regeneration in a forest system dominated by resprouting species and their relationship to an altered disturbance regime. In the fire-prone coastal forests of Big Sur, California, the foundational tree species all resprout, exhibit high levels of belowground survival following disturbance, and, more rarely, recruit new individuals from seed (Simler et al. 2018). However, anthropogenic activities have introduced a novel biotic disturbance to these forests (Rizzo and Garbolotto 2003). An emerging disease, sudden oak death (SOD), causes aboveground and belowground mortality in several susceptible, typically long-lived host tree populations, with impacts that vary widely among species (Rizzo and Garbolotto 2003, Davidson et al. 2005). Further, fuels created by SOD-related mortality interact with subsequent wildfires and alter fire severity (Metz et al. 2011), increasing mortality of trees' aboveground stems (Metz et al. 2013) and belowground genets (Simler et al. 2018). It remains poorly understood whether gaps created by this novel biotic disturbance will be filled by new recruitment from seed and whether less-susceptible species will occupy these openings, facilitating compositional shifts. Previous research suggests that, in SOD-

impacted forests that have not been impacted by recent fire, seedling recruitment by disease-tolerant or non-susceptible species is limited (Ramage et al. 2011).

We hypothesize that this set of compound disturbances may shift opportunities for postfire seedling regeneration by both altering seed availability via increased tree mortality and decreasing competition with surviving adults via increased gap openings. In this work, we assess the importance of these hypothesized mechanisms using a natural experiment created when the 2008 Basin Complex and Chalk wildfires burned across a preexisting long-term study in the SOD-impacted forests of Big Sur, California. We collected pre- and postfire measurements of forest structure and regeneration, allowing us to examine postfire sexual recruitment along gradients of disturbance severity. We address three experimental questions: (1) Do compound disturbances (disease and fire) alter opportunities for postfire facultative seedling regeneration in resprouter-dominated forests? (2) How do parent-tree survival, competition with neighboring trees, and abiotic factors influence postfire seedling recruitment by resprouting species? and (3) Do SOD-susceptible and non-susceptible species' postfire regeneration responses differ in relationship to their epidemiological roles, suggesting compositional shifts?

This work has broad applications to both the management of SOD and other plant communities impacted by human-altered disturbance regimes. Postfire seedling regeneration represents a clear, but poorly understood, form of ecosystem resilience in this system, determining whether changing patterns of genet mortality will be balanced by recruitment, and, if so, which species will occupy these novel gaps. Depending on species' epidemiological roles, compositional shifts will determine future SOD severity, disease and fuel management actions, and forest restoration objectives (Metz et al. 2017). Additionally, in other changing environments, the processes by which seedlings of resprouting species colonize new gaps, disperse to new sites, and survive to recruit will improve our understanding of potential shifts in resprouter occurrence and how this may enhance or erode system resilience. This work represents a contribution to our limited knowledge of the

processes that may determine resprouting seedling establishment in communities impacted by altered disturbances.

METHODS

Study system

We conducted this study in mixed evergreen and coast redwood forests in the coastal Big Sur region of Monterey County, California. By basal area, the most common tree species in this region's redwood forests are coast redwood (*Sequoia sempervirens*, which dominates the canopy), tanoak (*Notholithocarpus densiflorus*), California bay laurel (*Umbellularia californica*), coast live oak (*Quercus agrifolia*), Shreve's oak (*Q. parvula*), and Pacific Madrone (*Arbutus menziesii*; Appendix S1: Table S1). Species will hereafter be referred to by these common names. The mixed evergreen forest type is codominated by these same species, excluding coast redwood. Each of these most common tree species can resprout, exhibit high belowground survival rates, and regrow vigorously postfire (Henson and Usner 1996, Simler et al. 2018). These species also can facultatively reproduce from seed (Henson and Usner 1996). Though top-killed resprouting plants do not retain the ability to produce seeds immediately following disturbance, survivors regain sexual maturity as they regrow, making their contribution to seed availability unclear. These forests experience a mixed-severity fire regime, and though no clear record of fire history exists for Big Sur, the fire return interval in neighboring regions is thought to range between 5 and 75 yr, with a mean of 24 yr (Mensing et al. 1999).

Phytophthora ramorum, the introduced oomycete pathogen that causes SOD, infects over 100 species, with impacts that vary widely among hosts (Rizzo and Garbolotto 2003, Davidson et al. 2005). *Phytophthora ramorum* kills both the aboveground stems and belowground genets of tanoak and susceptible oak species (including coast live oak and Shreve's oak); however, bay laurel, a non-susceptible host, is the most significant agent of disease spread in California and develops foliar infections that disperse the pathogen via wind-driven rain splash, with occasional long-distance dispersal (Grünwald et al. 2012). Tanoak twig infections also spread inoculum,

albeit less prolifically, but coast live oak and Shreve's oak are thought to be dead-end hosts (Davidson et al. 2005).

Forest monitoring network design and prefire sampling

We established a network of 500-m² circular plots in redwood and mixed evergreen forests in 2006 and 2007, one to two years before the Basin and Chalk fires ignited (Appendix S1: Fig. S1). These plots were originally designed to examine the emerging SOD epidemic and were stratified to represent variation in pathogen occurrence, topography, climate, and fire history. During initial plot establishment, we tagged all living or dead woody stems (including shrubs) >1 cm in diameter at breast height (dbh), recording dbh, location, and species identity.

We characterized prefire SOD-related impacts in several ways (Table 1). We collected samples from symptomatic hosts in each plot and cultured them in the laboratory on an oomycete-

selective medium to confirm the presence of *P. ramorum* via morphological identification (Rizzo et al. 2002). Within each plot, we recorded all standing dead hosts and the volume of fallen host stems (or coarse woody debris; CWD) >20 cm in diameter. Plots were categorized into one of three disease categories, based on the progression of these dead hosts (Metz et al. 2013). Plots in the early or no disease stage had not yet experienced any host mortality. The middle stage represents plots where more than one-third of the dead host basal area was recently killed, standing, and still retained dead leaves, and in the late stage, more than two-thirds of host mortality was older, lacking leaves and fine twigs.

Sampling postfire regeneration

From June to September 2008, the Basin Complex and Chalk fires burned more than 111,000 ha in Big Sur, impacting >40% of these previously measured plots. To assess impacts of prefire disease history on postfire regeneration,

Table 1. Candidate variables for fixed effects considered in seedling abundance and mortality models.

Mechanism	Variable	Description of data collected
Fire and disease-related disturbance history	Prefire standing dead SOD hosts	Basal area of dead hosts (cm ²) in infested plots, from 2006 to 2007 surveys
	Prefire SOD-host CWD	Volume of dead hosts (cm ³ /plot) in infested plots, from 2006 to 2007 surveys
	Disease stage	Plots are categorized as early, middle, or late disease stage based on the percentage of hosts within the plot that have been recently killed by SOD or have fallen to the ground (Metz et al. 2013)
	Fire-related tree mortality	Basal area (cm ² /plot) killed in 2008 Basin Complex fires
	Distance to edge of burned patch	Distance (m) between plot center and edge of burned perimeter
	Fire × disease interaction	Interaction between fire-related mortality and disease stage
Biotic site factors	Surviving conspecific basal area postfire	Basal area (cm ² /plot) of stems that survived the fire for focal species
	Resprouting conspecific basal area postfire	Basal area (cm ² /plot) of stems that recruited postfire for focal species
	Postfire shrub cover	Basal area of understory shrubs (based on the individual's largest stem). Common groups included <i>Ceanothus</i> spp., <i>Heteromeles</i> spp., and <i>Arctostaphylos</i> spp
	Forest type	Plot's location in either coast redwood or mixed evergreen type
Abiotic site factors	Mean annual precipitation	In mm/year, calculated from PRISM for the 5 yr postfire
	Plot slope	Noted in degrees

CWD, coarse woody debris; SOD, sudden oak death.

we revisited 20 burned redwood and 25 mixed evergreen plots to collect the same measurements recorded in prefire surveys, at two sampling periods, in 2010–2011 and in 2013–2014, visiting redwood plots in the first year and mixed evergreen in the second during each period. We remeasured the growth, mortality, recruitment, and infection status of all previously monitored and new woody stems >1 cm in dbh.

Within each plot, we recorded the abundance and species identity of all seedlings, classified as trees smaller than 50 cm in height (Appendix S1: Table S2). In 2013 and 2014, we established three 4-m² quadrats within each plot, located 7 m from its center at 120° intervals. Within each quadrat, we banded each seedling present and recorded its species identity, height, and diameter at the base of the stem and the start of the developing burl. If quadrats did not contain 10 seedlings from each species present, we haphazardly selected additional individuals for monitoring within the plot. After two years, we returned to each plot and recorded each banded seedling's status (alive or dead). During these surveys, we also identified previously unbanded individuals in each quadrat to determine new recruitment rates (Table 2). Four plots were not revisited because they burned in the 2016 Soberanes Fire.

For this study, we specifically wanted to examine recruitment from seed. We conducted an additional survey to determine what proportion of seedlings (individuals <50 cm in height) were prefire recruits that had survived belowground, rather than new, postfire recruits. We compared xylem rings from aboveground and belowground cross sections taken from 358 seedlings excavated from the study area. We determined

that only a small proportion of individuals that we classified as seedlings in burned areas are likely to have established prefire, suggesting these data primarily reflect patterns of postfire recruitment, rather than persistence. These methods are described in the supporting information (Appendix S1: Table S3, Figs. S2, S3).

Statistical analysis

We assessed how prefire disease history, postfire survival of possible seed sources, and abiotic conditions influenced (1) postfire seedling abundances within plots in 2013–2014 and (2) seedling survival probabilities, between 2013–2014 and 2015–2016. We conducted analyses for the most common species present: coast redwood, tanoak, California bay laurel, Pacific madrone, coast live oak, and Shreve's oak. We analyzed coast live and Shreve's oak seedlings together because these *Quercus* species are known to hybridize (Dodd et al. 2002), limiting our ability to visually discern between them.

Using Bayesian generalized linear models for each species, we modeled plot-level seedling counts 5–6 yr postfire (abundance, $n = 45$ plots) (using a negative binomial link function (with mean μ and dispersion parameter ϕ)):

$$\mu = \alpha + \beta \times X,$$

Abundance \sim Negative Binomial (μ , ϕ)

We constructed μ as a function of an intercept (α) and an array of plot-level variables (X with parameter β), representing our hypotheses about determinants of seedling regeneration (Table 1). To examine the importance of seed

Table 2. Mean counts of new seedling recruitment per 500-m² plot 2–3 yr postfire and 7–8 yr postfire.

Species	Redwood forest		Mixed evergreen forest	
	New recruits 2–3 yr postfire (SD)	New recruits 7–8 yr postfire (SD)	New recruits 2–3 yr postfire (SD)	New recruits 7–8 yr postfire (SD)
Coast redwood	6753.50 (17994.6)	6.25 (15.26)	156.00 (780.00)	0.00 (0.00)
Pacific madrone	139.25 (323.05)	2.08 (9.32)	129.84 (483.64)	3.33 (11.54)
Tanoak	56.25 (158.31)	12.50 (55.90)	30.80 (96.21)	5.00 (13.82)
Coast live and Shreve's oak	9.30 (18.38)	6.25 (20.39)	21.28 (25.43)	19.00 (40.00)
Bay laurel	1.05 (1.36)	8.33 (17.10)	3.08 (3.24)	3.33 (11.54)

Note: 7–8 yr postfire counts are estimates, calculated from the number of new seedlings appearing in three 4-m² quadrats within each plot between sampling points ($n = 123$ quadrats within 41 plots).

sources, we included the total basal area of mature conspecific stems that survived postfire. We included new basal area from resprouting conspecifics separately to determine whether top-killed individuals (which regain sexual maturity as they regrow) contribute to postfire seedling recruitment, as we had observed some resprouting individuals developing seeds during the later sampling points. Basal areas for coast live and Shreve's oak were combined for these variables. To assess the impact of disease history, we included either the plot's prefire disease stage or variables for total prefire basal area of standing dead hosts and volume of host CWD. These variable groups were assessed in separate models, due to collinearity. We also included forest type, basal area of shrub species at the plot level, slope, and estimated postfire mean annual precipitation for each plot (obtained from the PRISM climate model) to address potential conflation of other biotic or abiotic factors with disease and fire effects (Daly et al. 1997).

We constructed full models containing all (sufficiently uncorrelated) variables describing our hypotheses and sequentially removed variables. We compared models using leave-one-out cross-validation information criteria (LOOIC), calculated with Pareto smoothed importance sampling, evaluating on the basis of differences in expected log pointwise predictive density (ELPD), and presenting the model with the lowest LOOIC (Vehtari et al. 2016). We considered the use of zero-inflated negative binomial models, but comparisons of LOOIC scores suggested little improvement over negative binomial models (Appendix S1: Fig. S4, Tables S4–S5).

To assess the impacts of compound disturbance on the longer-term success of established seedlings, we used a hierarchical structure to model seedling mortality between 2013–2014 and 2015–2016. Mortality was modeled as the outcome of a Bernoulli trial with probability p , for an individual (i), of a given species (k), within its plot (j) ($n = 1046$ seedlings from 41 plots across five species):

$$\text{logit}(p_{[i]}) = \alpha + \alpha_{j[i]} + \alpha_{s[i]} + \beta \times \text{height}_{[i]},$$

$$\alpha_j \sim \text{Normal}((\gamma \times U_j), \sigma_j),$$

$$\alpha_k \sim \text{Normal}(0, \sigma_k),$$

$$\text{Mortality}_i \sim \text{Bernoulli}(p_i)$$

We constructed mortality probability as a function of a mean intercept (α), a varying intercept component for plot identity (α_j), a varying intercept component for species (α_k), and the effect of seedling size (height, with parameter β), to account for the fact that larger individuals may be less vulnerable to stressors. Species-level effects were distributed with standard deviation σ_s . We constructed plot-level effects (α_j , with standard deviation σ_j) as a function of an array of plot-level variables (U_j with parameters γ), reflecting our hypotheses. To assess the impacts of compound disturbance on seedling survival, we included variables for prefire standing dead host basal area, prefire volume of host CWD, and postfire tree mortality. In addition, we included shrub basal area, slope, and postfire mean annual temperature, hypothesizing that these variables may characterize additional stressors for seedlings.

All parameters were assigned weakly informative regularizing priors, to avoid overfitting. Half-Cauchy priors were assigned to the variance terms. Model code can be found via GitHub at <https://doi.org/10.5281/zenodo.3523289>. Variables were centered, standardized, and assessed for covariance. We inferred models using the Rstan package (Stan Development Team 2018), which integrates the Stan statistical language with the R environment (R Core Team 2016) and uses a Markov Chain Monte Carlo (MCMC) sampler. For each model, we ran four MCMC chains, each with 2,000 samples in posterior distributions (in addition to a 500 iteration burn-in). We checked effective sample size and model convergence, indicated by Gelman-Rubin statistics and stable, well-mixed chains (Gelman and Rubin 1992). We assessed fit using graphical posterior predictive checks (Appendix S1: Fig. S4). We considered parameter estimates with 90% credible intervals not overlapping with zero to have important effects on the outcome.

RESULTS

Postfire seedling abundances were predicted by prefire disease severity, survival of mature conspecific stems, and other abiotic and biotic

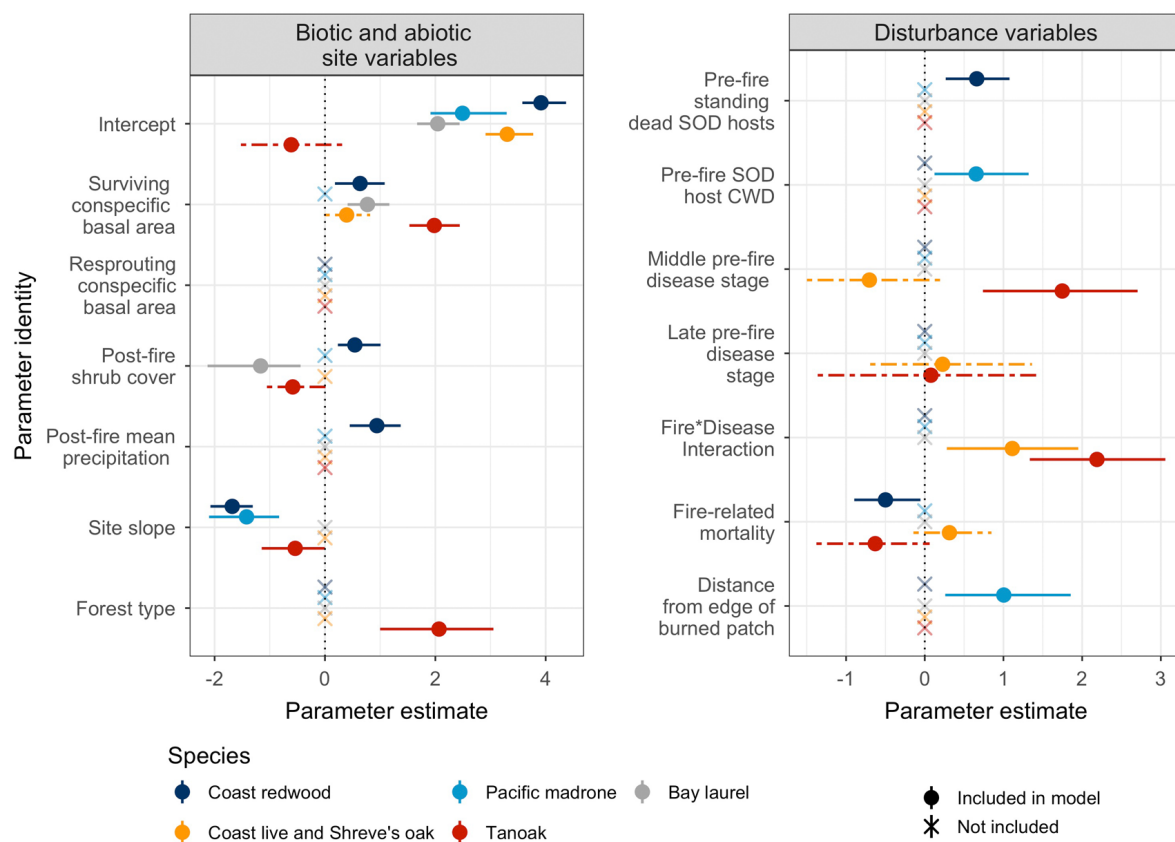


Fig. 1. Posterior parameter estimates from Bayesian generalized linear negative binomial models of postfire seedling regeneration for each species. Warm colors indicate highly susceptible hosts, cool colors indicate tolerant, non-sporulating hosts that do not experience measurable sudden oak death (SOD) impacts, and sporulating-tolerant hosts are shown in gray. Circles represent mean estimates. Parameters whose 90% credible intervals (indicated by lines) include zero were not considered important predictors and are shown with dotted lines. Parameters that were not included in the model with the lowest leave-one-out cross-validation information criteria score are shown with an X. The parameter for forest type represents redwood forest, compared with mixed evergreen.

factors, with important variation among species (Fig. 1). The inclusion of candidate predictors improved seedling abundance models' LOOIC scores over the null models, with only a small improvement in the oak species model ($\Delta\text{ELPD} = -21.41$, $\text{SE} = 4.76$ for tanoak, $\Delta\text{ELPD} = -25.00$, $\text{SE} = 10.50$ for redwood, $\Delta\text{ELPD} = -9.39$, $\text{SE} = 3.91$ for bay laurel, $\Delta\text{ELPD} = -7.18$, $\text{SE} = 2.88$ for madrone, and $\Delta\text{ELPD} = -5.31$, $\text{SE} = 3.91$ for oak species).

Basal area of surviving conspecific stems was an important positive predictor of postfire seedling abundances in coast redwood, tanoak, and bay laurel (Figs. 2, 3). For oak species, this

parameter also had a generally positive impact on seedling abundances, with a 90% credible interval that overlapped with zero (Figs. 2, 3). Pacific madrone did not show a clear relationship between surviving mature seed sources and seedling abundances. Postfire resprout recruitment from conspecific individuals surviving belowground was not an important predictor across all models (Fig. 2).

Prefire disease history also influenced seedling abundances, with important variation among species' responses to SOD-fire interactions (Figs. 1, 3). Redwood seedlings were more abundant in areas with greater prefire standing SOD-

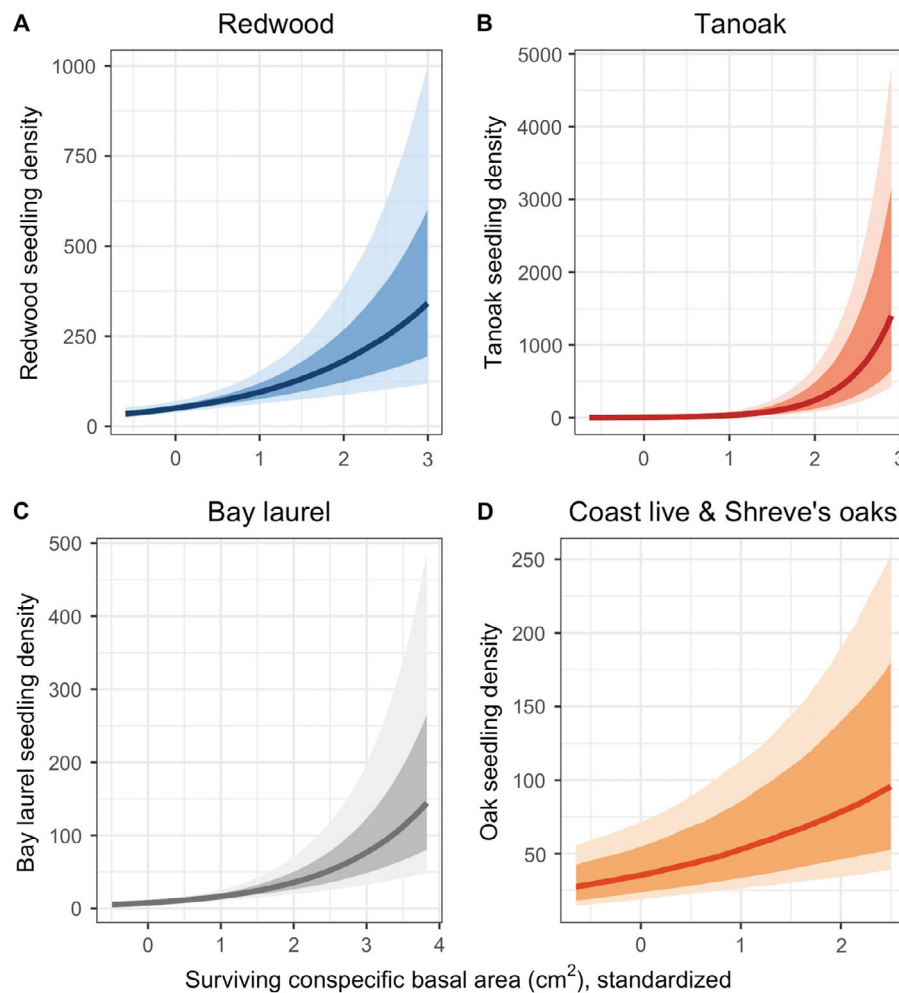


Fig. 2. The marginal effects of surviving, mature conspecific basal on postfire seedling abundances for redwood (A), tanoak (B), California bay laurel (C), and oak species (D) from models depicted in Figure 1 with all other variables held at their means. Surviving conspecific basal area (on the x -axis) has been centered and scaled across the range of values observed in the study.

host mortality. Tanoak seedling abundances increased in burned areas that were in the middle stages of disease prefire, and the interaction between fire-related tree mortality and mid-stage disease impacts also increased oak and tanoak seedling occurrence. Pacific madrone regeneration increased with greater prefire volume of host CWD and with distance to the edge of burned perimeter. Disease-related variables were not important predictors of seedling abundances of bay laurel. Further, we did not observe any clear nonzero negative impacts of SOD history on postfire regeneration.

Other biotic and abiotic variables inconsistently impacted seedling occurrence. Site slope was negatively related to seedling abundance for redwood, tanoak, and madrone, and postfire shrub basal area had variable effects on seedling abundances (Fig. 1). Postfire mean annual precipitation was only positively correlated with redwood seedling abundances and was not included in other selected models.

Variables describing seedling size, site factors, and prefire SOD impacts improved prediction of postfire seedling mortality ($\Delta\text{ELPD} = -33.6$, $\text{SE} = 8.7$, compared with the

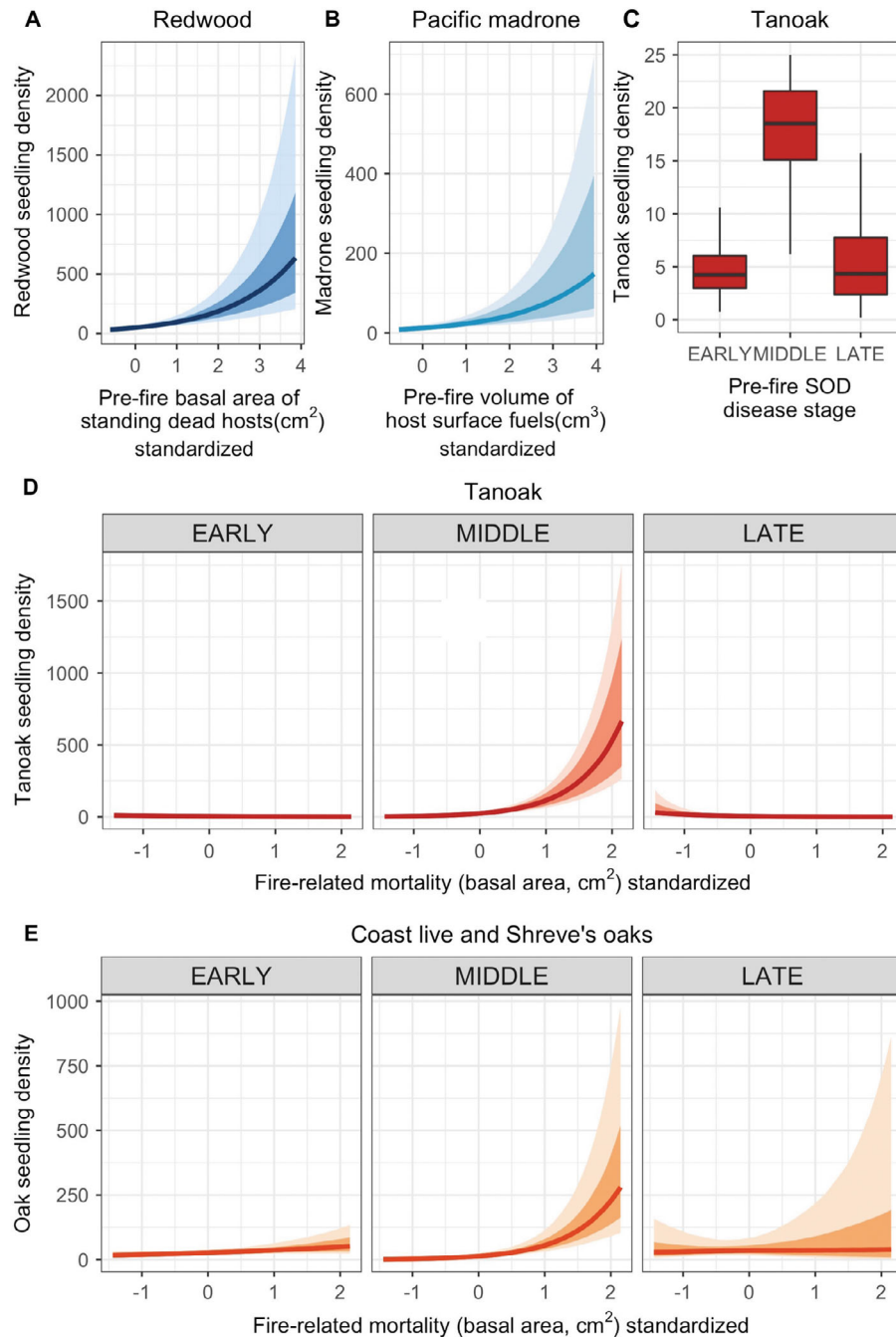


Fig. 3. Marginal effects of prefire disease impacts on postfire seedling abundances for redwood (A), Pacific madrone (B), tanoak (C, D), and *Quercus* species (E), with other variables held at their means. Panels (D) and (E) show the marginal effect of the interaction between disease stage and fire-related tree mortality. Variables have been centered and scaled across the range of values observed in the study.

null model). Over the 2-yr monitoring period, increasing prefire mortality due to SOD and seedling height was negatively related to the probability of seedling mortality, while survival

decreased at steeper sites (Fig. 4). Seedling mortality also weakly decreased in areas with greater postfire tree mortality and in redwood forests (sampled in 2015), relative to mixed

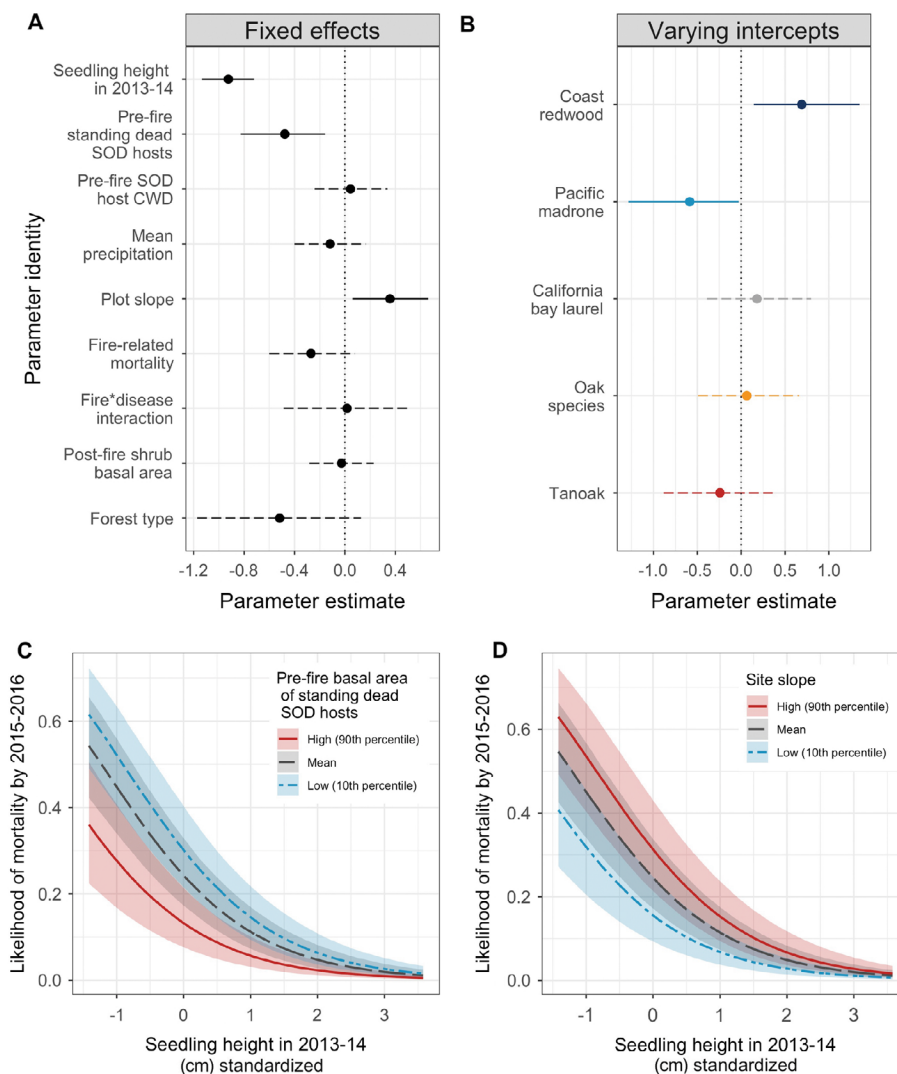


Fig. 4. Posterior parameter estimates for fixed effects (A) and varying intercepts (B) from a Bayesian generalized linear Bernoulli mixed model of seedling mortality between 2013–2014 and 2015–2016. Circles and lines denote mean estimates and the 90% credible interval, respectively. Parameters with 90% credible intervals including zero are shown with dotted lines. Marginal effects are plotted with other variables held at their means (C–D). Seedling height (C–D), prefire basal area of dead sudden oak death (SOD) hosts (C), and site slope (D) had non-zero effects on mortality probability for monitored seedlings. The parameter for forest type describes redwood forest, compared with mixed evergreen. Variables have been centered and scaled across the range of values observed in the study.

evergreen plots (sampled in 2016; Fig. 4A). Redwood seedlings experienced higher mortality, and madrone seedlings displayed lower mortality probabilities than other species, based on comparison of species-level varying intercept effects (Fig. 4B).

Annual rates of new seedling recruitment 2–3 and 7–8 yr postfire, which were based on plot-level seedling counts or estimated from new individuals identified within 4-m² quadrats during 2015–2016 surveys, are presented in Table 2.

DISCUSSION

In resprouter-dominated forests impacted by disease and wildfire, postfire seedling regeneration was influenced by surviving mature seed sources, stand-level competition, and abiotic factors. Seedlings were generally more abundant with increased survival of conspecific stems but were not influenced by resprouting genets, suggesting that the legacies determined by postfire aboveground survival will shape initial seedling regeneration trajectories. Yet where seed sources persisted, measurements of prefire SOD severity also resulted in increased seedling regeneration, indicating potential competitive release of seedlings associated with disease impacts and increased gap openings. Compound disturbances may accelerate stand turnover and create novel opportunities for the recruitment of new genetic individuals in these populations comprised of long-lived genets. However, declines in mature seed sources may reduce these opportunities for highly susceptible hosts, intensifying forest compositional changes associated with SOD.

Possible shifts in forest composition indicated by this analysis may determine future disease dynamics and inform forest management actions designed to minimize SOD impacts and SOD-related fuel accumulation. In addition, the mechanisms determining seedling regeneration by resprouting species have broader applications to projections of how altered disturbances may change selection pressures on plant life history traits or generate shifts in community composition, with implications for post-disturbance restoration efforts.

Dispersal constraints on seedling regeneration by resprouters

Though top-killed trees gradually regain the ability to produce seeds following aboveground damage (Henson and Usner 1996), 5–6 yr post-fire, seedling establishment was predominantly related to aboveground survival of mature parent stems, rather than conspecific resprouting (Figs. 1, 2). By 8–9 yr postfire, rates of new recruitment had slowed for the most abundant species but had not completely halted (Table 2). Together, these results indicate that immediate

postfire patterns of stem survival determine which seeds will fill novel gaps created by disease and fire. In heavily SOD-impacted areas, tanoak and oak mortality reduce these postfire seed sources, and elevated fire severity due to the accumulation of disease-related fuels can additionally increase stem mortality for other species, such as coast redwood (Metz et al. 2013). This may further limit seed dispersal, as indicated by the generally negative relationship between fire-related mortality and redwood seedling occurrence (Fig. 1).

Seedling establishment for oak species and Pacific madrone was not as strongly related to surviving aboveground seed sources (Fig. 1). These species are important wildlife food sources, but are less common than other forest components, such as tanoak (Keeley 1991, Rizzo and Garbolotto 2003). Assisted dispersal in combination with reduced overall density may explain weaker relationships between these species' abundances and local survival of parent trees.

Impacts of disease-related mortality and competition on seedling regeneration

Yet, after incorporating possible dispersal limitations, prefire disease impacts generally increased opportunities for seedling establishment in this resprouter-dominated system (Figs. 1, 3, 4). These increases in seedling occurrence and survival may be explained by the effects of disease and disease-fire interactions on gap availability and competition with neighboring adult trees.

Following fire, top-killed resprouting trees in this system typically persist at high rates (ranging from ~80% to 100% across size classes; Simler et al. 2018). However, SOD can cause complete belowground mortality of tanoak and oak genets, and elevated substrate fire severity in SOD-impacted stands has been associated with increased post-fire belowground mortality in resprouting species (Metz et al. 2013, Simler et al. 2018). Thus, the impacts of SOD and SOD-fire interactions represent important shifts in gap formation and competition, given increased mortality of typically persistent genets. Several proposed frameworks suggest that the relative occurrence of resprouters and obligate seeders in fire-prone systems is influenced by productivity,

disturbance, and how each influence adult survival relative to juvenile recruitment (Clarke et al. 2013, Pausas and Keeley 2014, Zeppel et al. 2015). Low gap availability and high competition from surviving resprouters, especially in resource-rich environments that allow for rapid regrowth via vegetative reproduction, may limit opportunities for sexual recruitment and select against reseeding strategies (Pausas and Keeley 2014).

Thus, where seed sources persisted, we propose that prefire disease effects reduced competition and created novel opportunities for seedling recruitment, with impacts that varied with species' epidemiological roles (Figs. 2, 3). In SOD-impacted forests, postfire tanoak and oak seedling abundances increased in stands that were characterized by the middle disease stage, when a significant portion of neighboring trees had been killed, but some seed sources still likely persisted (Figs. 2, 3). No positive effect was observed in areas impacted by the later stages of disease, where conspecific seed sources may have been completely removed. By contrast, the abundance of coast redwood and Pacific madrone seedlings, which are not killed by the disease and will not experience disease-related seed limitation, increased as prefire host mortality accumulated (as measured by standing basal area and CWD), likely due to reduced stand competition (Figs. 2, 3). In addition to these mechanisms, accumulated host CWD can increase substrate burn severity (Metz et al. 2011), which could facilitate germination by species that favor exposed mineral soils, such as Pacific madrone or coast redwood (Fig. 2, Tappeiner et al. 1986).

Lastly, greater prefire mortality of SOD hosts was correlated with increased postfire seedling survival over a two-year period, suggesting that competitive release associated with mortality of neighboring trees may have long-lasting impacts on patterns of recruitment (Fig. 4). Similar compensatory increases in seedling establishment have been observed in other forest systems following acute drought-related tree mortality events (Lloret et al. 2011).

Abiotic factors determining seedling regeneration

We found few consistent relationships between postfire climate and seedling occurrence (Fig. 1);

however, regeneration data were collected during a severe drought in California (2012–2016), and climatic variation among plots may have been dampened by overall severe water stress. Additional research will be required to understand climatic impacts on facultative seedling regeneration and the development of below-ground resources in these resprouting trees, particularly given their distinct patterns of resource allocation, compared with obligate seeders (Zeppel et al. 2015). For several species, seedling regeneration and survival also decreased with increasing site slope (Figs. 1, 4). Slope and soil erosion may be key determinants of where seedlings, especially slow-growing resprouters, may find sufficient stability for establishment in Big Sur's rugged topography.

Implications for the ecosystem impacts and future management of sudden oak death

Overall, variable, species-specific patterns of mortality due to SOD were associated with novel postfire opportunities for sexual recruitment, which may shape compositional shifts in disease-impacted forests. Regeneration in unburned, SOD-impacted redwood forests is largely characterized by pulses of susceptible tanoak seedling recruitment and resprouting from preexisting individuals, which may not be sufficient to reoccupy spaces created by host mortality (Ramage et al. 2011). Limited seedling recruitment by other species in unburned areas may be due to lack of exposed soil, overstory shading, or competition from shrubs or resprouting trees (Ramage et al. 2011). Our results suggest that in fire-prone forests, wildfire may facilitate compositional shifts in SOD-impacted stands, indicated by increasing postfire redwood and madrone recruitment with progressively more severe prefire disease impacts.

However, in one case, SOD's impacts on postfire regeneration did not vary as expected, in relationship to species' epidemiological roles. Cobb et al. (2010) suggested that California bay laurel, a non-susceptible, sporulating host, may increase in prominence in disease-impacted forests because it generates apparent competition for tanoaks and oaks, is not negatively impacted by the disease, and currently occupies a similar sub-canopy position in these forests. Yet, bay laurel was the only focal species that did not exhibit

a positive response to SOD impacts and, among focal species, had the lowest seedling abundances in burned areas (Fig. 2; Appendix S1: Table S2). Bay laurel regeneration is similarly limited in unburned, SOD-impacted areas (Ramage et al. 2011), suggesting that despite its key epidemiological impacts, other non-susceptible species may be better capable of filling gaps created by disease. If non-sporulating hosts, such as Pacific madrone or redwood, were to increase in relative occurrence more consistently than bay laurel following fire, it would be of significant importance to future SOD dynamics and disease management actions. These results indicate that, in this fire-prone system, increases in these non-sporulating hosts may be more likely than widespread expansion of bay laurel.

Changing patterns of gap formation, stand turnover, and seedling success could also impact genetic structure of predominantly asexual populations (Dodd et al. 2013). Within tanoak and oak populations, some individuals exhibit partial resistance to SOD, and sexual regeneration could influence the genetic variation that *P. ramorum* may encounter (Hayden et al. 2013, Cobb et al. 2019). Further, though *P. ramorum* still exists in many burned areas, the Basin and Chalk fires significantly decreased its occurrence (Beh et al. 2012). Separate from the effect of declining parent-tree survival, we did not observe negative impacts of disease history on host seedlings, suggesting that direct infection of new recruits by *P. ramorum* may have minimal impacts in burned areas (Figs. 1, 4). Given the effect of surviving seed sources, prefire SOD impacts, and the reduction in *P. ramorum* occurrence in burned areas, hosts that survived both disturbances may experience temporary disease release and have a disproportionate opportunity to contribute seed to the novel gaps formed by SOD.

Applications for other altered disturbance regimes

In many other fire-prone forest systems in the western United States, resprouting species, which can persist in situ without relying upon aboveground survival, dispersal, and germination, are predicted to be favored by many changing disturbance regimes (Kulakowski et al. 2013, Welch et al. 2016, Davis et al. 2018). Seedling regeneration will determine resprouting species' ability to colonize new areas or increase in

relative abundance. Our results suggest that, following disturbance, low competition environments may generate distinct opportunities for seedling regeneration by species with predominantly asexual life history strategies. However, even for resprouting species, postfire seed sources play an important role in recruitment, especially considering these species' relatively low allocations to seed production (Zeppel et al. 2015). The morphology of many resprouting species prioritizes belowground persistence over aboveground survival in fire. Therefore, dispersal limitations may determine where resprouting populations may expand under changing regimes, especially where post-disturbance recruitment windows are narrow or for species with large seeds that animal dispersers.

To better understand these shifts, we require information about how rapidly resprouting tree species regain the ability to produce seeds following top kill, how regularly advanced regeneration occurs under mature canopies, and how these trajectories of sexual development compare to obligate seeding species. Where fires are sufficiently infrequent, advanced regeneration by resprouters in mature stands may circumvent these dispersal limitations, but seedlings' understory persistence may be limited by resource competition, suitable climatic conditions, and the time required for small individuals to gain the ability to resprout.

Under many human-altered regimes, greater relative occurrence of resprouting species may confer resilience under increasingly severe, large, or frequent disturbance events, but shifts will depend on successful seedling regeneration. Similarly, seedling recruitment will determine turnover in forest composition following the emergence of SOD in the resprouter-dominated coastal forests of the United States. The results of this work suggest that gap availability, competition with surviving, mature vegetation, dispersal limitations, and variation in the rates of sexual development in resprouting populations will underlie potential shifts in the composition of forest species and functional traits.

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DATA AVAILABILITY

Model code and data are available via GitHub from <https://doi.org/10.5281/zenodo.3523289>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2991/full>