Demographic status, trajectory, and stressors of *Pinus lambertiana* across the western USA

# Abstract

Sugar pine (*Pinus lambertiana*) is the largest Pinus species, an important timber species, and a component of several dry conifer forest types of western North America, in particular the extensive Sierra Nevada mixed conifer forest. The species faces several challenges in the Anthropocene, including a disrupted fire regime, an invasive pathogen, forest structure changes, and drought with ensuing bark beetle epidemics. Managers are concerned about the conservation outlook for sugar pine, but it is unclear where and how to best invest conservation resources. In this study, we use data from the US Forest Service's Forest Inventory and Analysis dataset to assess how these various stressors shape the vital rates (survival, growth, and fecundity) of sugar pine across the vast majority of its range. We synthesize the vital rate functions by constructing an integral projection model which predicts the effects of various stressors on the asymptotic population growth rate. The analysis reveals that wildfire and forest density are key drivers of the demographic rates of sugar pine across its range. Fire has strong negative effects on survival and reduces the growth of surviving large trees, resulting in a negative asymptotic population growth rate on burned sites. Conversely, lower than average forest density (neighborhood basal area) results in a positive population growth rate via beneficial effects on growth and fecundity. These results highlight the value of fire hazard mitigation, particularly where it also reduces forest density, in the conservation of this important species.

# Introduction

Novel Anthropogenic stressors threaten species but may be amenable to management (Millar and Stephenson, 2015; Hessburg *et al.*, 2021). However, conservation resources are scarce, so it is often necessary to prioritize some stressors over others (North *et al.*, 2009, 2019; Panek *et al.*, 2012). Demographic models built around large-scale longitudinal datasets (such as the Forest Inventory and Analysis, or FIA, dataset) can provide detailed insight into how stressors impact species of concern across wide geographic ranges (Davis *et al.*, 2019; Shriver *et al.*, 2021). In this paper, we fit vital rate models including the effects of key stressors. By comparing their effects on vital rates and demographic summary statistics (such as the asymptotic population growth rate), we can assess the relative importance of the stressors and highlight the mechanisms by which they influence the population trajectory. Findings from such demographic analyses can provide crucial information about how best to prioritize varied stressors in making management decisions (Shriver *et al.*, 2019; Bradford *et al.*, 2022; McCauley *et al.*, 2022).

Like many other plant and animal species, Sugar pine faces numerous challenges in the Anthropocene, and managers and policymakers are concerned about the future status of the species (Kinloch Jr., Marosy and Huddleston, 1996). Sugar pine (*Pinus lambertiana*) is the largest Pinus species, an important timber species, and a component of several dry western conifer forest types. In the extensive Sierra Nevada Mixed Conifer forest, sugar pine typically composes 5-25% of basal area (Kinloch and Scheuner, 1990; Safford and Stevens, 2017; Bohlman, Safford and Skinner, 2021). Its range extends through much of the North American Mediterranean zone throughout mountain ranges in California, central Oregon, and a small population in northwestern Mexico but with the heart of its range located in California. Sugar pine seeds are an important food source for animal species (Fowells and Schubert, 1956; Murray and Tomback, 2010), and mature sugar pines are large-diameter trees which play a key role in the structure and function of ecosystems they occur in (Lutz *et al.*, 2013, 2018, 2020). However, sugar pines face numerous challenges in the Anthropocene.

First, disruptions to the fire regime have challenged sugar pine. Sugar pine is a fire-tolerant species with moderate shade intolerance (Yeaton, 1983, 1984; Bohlman, Safford and Skinner, 2021) and persisted in frequent fire forest types with mean fire return intervals of at most 11-16 years (Safford and Stevens, 2017; Bohlman, Safford and Skinner, 2021). Sugar pine has traits associated with a fire-surviving strategy (Schwilk and Ackerly, 2001), whereby large adults survive wildfires and provide offspring that can take advantage of reduced competition for light and water in the postfire environment. However, intensive historical logging and fire suppression in the 20th century have altered forest structure and a warming climate have increased the area affected by high severity fire within sugar pine’s range (Safford and Stevens, 2017; Stevens *et al.*, 2017; Parks and Abatzoglou, 2020; Bohlman, Safford and Skinner, 2021). This novel fire regime has increased the proportion of the sugar pine’s range where there are no surviving adult conifers to produce the next generation, threatening not just sugar pine but the mixed conifer forest type as a whole (Steel, Safford and Viers, 2015; Shive *et al.*, 2018; Coop *et al.*, 2020).

Second, an invasive fungal pathogen, *Cronartium ribicola* (white pine blister rust; WPBR) has spread across much of sugar pine’s range since its introduction to North America in the early 20th century and has caused substantial mortality (Van Mantgem *et al.*, 2004; Maloney *et al.*, 2011; Dudney *et al.*, 2020). WPBR affects white pines (subgenus *Strobus*, excluding the pinyon pines in subsection *Cembroides*) by parasitizing foliage, shoots, inner bark, and outer xylem, causing the formation of cankers which can reduce vigor and kill outright by girdling the stem (Geils, Hummer and Hunt, 2010). The epidemic in the western United States has been severe enough to cause the related species, *Pinus albicaulis*, to be listed as endangered (Mahalovich and Stritch, 2013), and there has been considerable concern about the outlook for sugar pine as well (Kinloch Jr., Marosy and Huddleston, 1996).

Third, there is evidence that the modern densified forest structure threatens sugar pine in numerous ways. Effective fire suppression, which was instituted across much of sugar pine’s range in the 20th century, has resulted in an overall densification of these forests (Stephens *et al.*, 2015; Safford and Stevens, 2017; Bohlman, Safford and Skinner, 2021; North *et al.*, 2022). Sugar pine is only moderately shade tolerant (Yeaton, 1983; Bohlman, Safford and Skinner, 2021) and there is evidence that it is outcompeted by species such as *Abies concolor* and *Calodecrus decurrens* under modern dense canopies. Species composition (especially of younger cohorts) has shifted towards shade-tolerant firs and incense-cedar (Ansley and Battles, 1998; Levine *et al.*, 2016). There is also evidence that the densified forest structure has reduced the vigor of adult sugar pines, thus reducing their ability to resist other stresses (Young *et al.*, 2017; Restaino *et al.*, 2019; Furniss *et al.*, 2021; North *et al.*, 2022).

Finally, the changing climate may increase the duration and severity of droughts and associated bark beetle epidemics, which are already causing mass mortality events in sugar pine’s range (Fettig *et al.*, 2019; Stephenson *et al.*, 2019; Steel *et al.*, 2021). Once these epidemics are underway, bark beetles tend to preferentially target large and reproductively-valuable sugar pines, independent of individuals’ stress (Stephenson *et al.*, 2019), exacerbating the impact of this stressor on the demographic outlook for sugar pine. Drought can also kill trees, especially small individuals, more directly via hydraulic failure and/or carbon starvation (Moran *et al.*, 2019).

Given these numerous challenges, there are widespread concerns about the future of the species (Kinloch Jr., Marosy and Huddleston, 1996). Management options to benefit sugar pine are available, ranging from restoration thinning and prescribed fire to restore forest structure (Stephens *et al.*, 2009; Restaino *et al.*, 2019; Steel *et al.*, 2021) to out planting seedlings with genetic resistance to WPBR (Aitken and Whitlock, 2013; North *et al.*, 2019). However, many of these options are expensive. In a context where natural resource management funding is constrained, it is important to understand the status and demographic outlook for sugar pine as a species. This study seeks to inform decisions about when and where to prioritize management actions to conserve sugar pine. To that end, we address two questions:

1. What is the current trajectory of abundance across the range-wide ensemble of sugar pine populations?
2. What is the relative importance of the various stressors acting on sugar pine?

# Methods

## Study Area

The area of interest for this study is that part of the range of sugar pine which is within the contiguous United States (Figure 1), which is the vast majority of the species’ range (excluding only an isolated population in Baja California). The range of sugar pine in the United States extends from 33.7°N to 45.3°N throughout much of the Sierra Nevada and Klamath mountains, and parts of the Transverse, Peninsular, and Southern Cascades ranges in the US states of California and Oregon. Sugar pine is widely distributed throughout this range as an important element of the mixed conifer forest belt at elevations ranging from 1000 m to 2700 m, depending on latitude (Safford and Stevens, 2017). The climate throughout this range is Mediterranean, with a cool-wet season and a warm-dry season (Safford and Stevens, 2017).

## Inventory Data

The Forest Inventory and Analysis (FIA) plots are part of a US Forest Service-run nationwide inventory network operating in its current form since 2001 (Bechtold and Patterson, 2005). Here, we use 1,221 FIA plots from California and Oregon where live sugar pine was present at initial measurement from 2001-2009 or remeasurement from 2010-2019 (we used version number 1.8.0.03 of the FIA database). The geographic coordinates listed for the FIA plots are not exact; to preserve plot integrity, the plot coordinates are randomly perturbed, and some plot locations are swapped. Most perturbations are to a random location within 0.8 km of the true location, and all perturbations are to within 1.6 km of the actual location. Between 0 and 10 percent of plot locations are swapped with a similar plot in the same county. FIA plots are placed on a hexagonal grid with a density of approximately 1 plot per 2429 ha. Each plot is revisited approximately once every 10 years, which we treat as the census interval for the purpose of calculating vital rates and constructing an IPM. Of the 1,102 plots used for this study, 90% had an inventory interval from 9.6 to 10.3 years, with a mean interval of 10.0 years, a minimum interval of 7.9 years, and a maximum interval of 12.3 years. Each included plot was remeasured one time in this study, so we have one census interval per plot, with the initial censuses taking place from 2001-2009 and the remeasurements from 2011-2019. On each FIA plot, trees >= 12.7 cm diameter at breast height (1.37 m, DBH) are inventoried on four 168 m2 permanent subplots. Small trees from 2.54-12.7 cm DBH are inventoried on four 13.5 m2 microplots, and large trees (>= 70.0 cm or >= 91.4 cm DBH, depending on the plot) on four 1012 m2 macroplots. Data inventoried for each individual stem include the species, live/dead status, DBH, and a “damage agent” code indicating whether some agent (e.g. white pine blister rust) is visibly affecting the individual’s health. Trees which are individually inventoried (all stems ≥ 2.54 cm DBH) are physically tagged to facilitate relocation of specific individuals at remeasurement. The survival or death of 3,530 sugar pine individuals was tracked to estimate the parameters of the survival function, and growth of the 2,821 surviving individuals was used to estimate the parameters of the growth function. The number of new recruits (stems with DBH between 2.54 cm and 12.7 cm which were not present on the microplot at initial census, but appeared in the second census) was calculated on 967 plots with sugar pine present at initial census to estimate the fecundity, the number of new recruits per existing individual. We included harvested trees as mortalities in the survival data for two reasons. First, our goal is to understand the actual population dynamics of sugar pine across its range, inclusive of mortality caused by harvests. Second, the prevalence of postfire salvage harvests on some land ownerships across the range of sugar pine make it likely that some mortalities caused by fire, competition, drought, or disease were later harvested, and we wanted to include these mortalities in vital rates estimation.

In addition to the tree-level data collected, the FIA program also records information about forest conditions, including the presence of significant disturbances (e.g., fire), the ecological subsection the plot is located within, and the nominal GPS coordinates of the plot center.

To assess the current trajectory of sugar pine abundance across its range, we calculated the per-plot basal area and stem densities for individuals greater than 2.54 cm DBH on every plot where sugar pine was present at initial measurement or remeasurement (1,221 plots). Across-plot means and standard errors were calculated and plotted for both basal area and stem density.

## Climate Data

To assess the level of drought sugar pine individuals were exposed to, we extracted monthly climatic water deficit (CWD) estimates for each nominal plot location from the TerraClimate dataset (Abatzoglou *et al.*, 2018). CWD is a measure of evaporative demand not met by available water (Stephenson, 1998). The TerraClimate dataset provides modeled estimates of CWD at approximately 4km resolution for years 1958-2020. The 4 km resolution approximately matches the degree of fuzzing associated with the nominal FIA plot locations, so that fuzzing is unlikely to add substantial error in the estimation of CWD experienced at the true plot location. Mean growing season (May-October) CWD estimates for each year between a plot’s initial measurement and its revisit provide a proxy for the drought stress experienced by individuals between the two censuses. The annual mean growing season CWD estimates were summarized in two ways: First, the 20-year mean of the annual CWD estimates provides a measure of the usual climatic dryness characteristic of each site, enabling the comparison of typically-wetter vs. typically-drier locations across space. Second, the 90th percentile of the annual departures from the site-specific mean CWD provide a measure of the most severe drought (departure from usual climatic conditions) experienced by each plot location between the initial observation and the remeasurement.

## Vital Rates Models

Survival, growth, and fecundity functions were independently estimated based on the observed data. The model for survival is:

Equation 1

Equation 2

where is an integer indicating the live/dead status (1 if live, 0 if dead) of individual at the revisit measurement, approximately 10 years after initial measurement), is the probability of survival from initial measurement to remeasurement, is a row vector of covariates (described below) for individual , is a column vector of fixed effect coefficients for the survival sub model, is a vector of plot-level random effects indexed by the plot for individual with , and is a vector of ecoregion subsection-level random effects indexed by the ecoregion subsection for individual with .

The fixed effects covariates for each individual in the row vector are: The intercept (), the DBH in meters at initial measurement (), the squared DBH (), a binary flag indicating whether the individual’s plot experienced a fire at least 0.404 ha in size that killed or damaged at least 25% of trees between initial measurement and remeasurement (), a binary flag indicating whether any trees in the individual’s plot displayed signs of white pine blister rust infection at initial measurement (), the plot-level basal area at initial measurement (), the plot-level 90th percentile of growing season departure from mean climatic water deficit () between initial measurement and remeasurement, the plot-level growing season mean climatic water deficit over the period 2000-2020 (), and interactions between and and all other variables (, , , *,* , , , , , and ). Continuous variables other than and (, , and ) were centered and scaled to have 0 mean and unit variance across all subplots. We measured size on the meter scale so that size was on a similar scale as the other explanatory variables, which was necessary to avoid divergent transitions in the Hamiltonian monte carlo parameter estimation described below.

The model for growth is:

Equation 3

Equation 4

where is the DBH in meters of individual at remeasurement drawn from a truncated normal distribution (to prevent excluded-by-sampling-design size below 2.54 cm DBH), is the residual variance, is a row vector of the fixed effects covariates, and the other parameters are as defined for the survival sub model, though here indexed to indicate that they are the parameters specifically for the growth sub model. The fixed effect covariates for the growth model are the same as those for the survival model.

The response distribution for the fecundity model is:

Equation 5

where is the observed count of new recruits (individuals between 2.54 cm and 12.7 cm DBH which were newly present at the followup census) on plot . is the area-standardized occurrence rate of new recruits on plot at remeasurement, gives the total plot area surveyed for individuals between 2.54 cm and 12.7 cm DBH, and is the dispersion parameter for the negative binomial distribution.

The area-standardized occurrence rate of new recruits, , is the sum of the fecundity of each of 99 size classes (2.54 to 250.4 cm DBH in 2.54 cm wide bins):

Equation 6

where is the fecundity (the number of new recruits produced per existing individual) and is the area-standardized occurrence rate of individuals in the th size class at the initial census. The low frequencies of new recruits in the data (942 of the 967 observed plots had no new recruits) precluded estimation of a more complex fecundity function which would have allowed fecundity rates to vary by individual sizes and/or the presence of stressors, as with the survival and growth functions. Instead, we estimate a simple overall fecundity rate using an intercept-only linear model with a log link:

Equation 7

where is the intercept for the log-scale linear predictor of fecundity.

Model data was prepared using the tidyverse package in R Version 4.1.1, and Bayesian parameter estimation was performed using Hamiltonion Monte Carlo as implemented in stan version 2.28.2 and the cmdstanr package. The sampler was run in four chains for 2000 iterations per chain (discarding the first 1000 iterations as warmup). The prior distribution specified for all parameters was (with variance terms restricted to positive values) except for the negative binomial dispersion parameter , which received a prior following Shriver et al. 2021.

## Model Validation

The basic diagnostics provided by cmdrstan (R-hat values, trace plots, per-chain posterior density plots, posterior pair plots, and assessment of divergences) were inspected for evidence of convergence and between-chain consistency or signs of difficulty estimating parameters. 10% of plots were randomly held out the training dataset used to estimate parameters, and were only used to assess the out-of-sample predictive performance of the model. For both the training and validation data sets, the central tendency and spread of data simulated using posterior parameter values (posterior predictions) were compared to the true observed values of individual growth and individual survival to assess whether model results were consistent with real data. Likewise, we compared histograms of observed vs. simulated counts using the estimated fecundity rate to assess whether model results were consistent with real data.

## Evaluation of vital rate functions and integral projection models

Once parameters were estimated and model validity checked, the fitted model for vital rate functions was used to assess the impact of the various stressors (fire, WPBR, stand density, drought, and site dryness) on the vital rates of growth and survival. Idealized explanatory data were constructed representing a suite of environmental scenarios correspond to situations where a single stressor is present (in the case of the discrete explanatory variables and ) or elevated/depressed by one standard deviation (in the case of the continuous variables , , and ), while other stressors are absent or held at their mean value (0 for scaled variables). Given these environmental contexts, vital rates for individuals ranging in size from 0.0254-2.0 m DBH were predicted using the parameters from each posterior sample, and the predicted response plotted against DBH and stressor. Median posterior random effect values for ecoregions in survival, growth, and fecundity functions were mapped to understand regional-scale patterns in vital rates not explained by the fixed effects.

To understand the demographic implications of the estimated survival, growth, and fecundity rates we constructed a suite of integral projection models. For each environmental scenario (as described above) and posterior draw we generated an integral projection model transition kernel**.** Each transition model kernel is a discretized integral projection model kernel describing the rates of transition from each size classes (each 2.54 cm DBH wide) into size classes over the course of a single 10 year census interval, which includes fecundity as well as growth and survival. The elements of this matrix are a function of the parameters for the survival, growth, and fecundity functions and the data describing scenario-specific covariates, as described below. A separate exists for each plot and posterior draw . The elements of for each plot and draw are given by:

Equation

where is the proportion of surviving individuals in class which grow into class during the census interval on plot using the th draw of growth parameters, is the proportion of individuals in size class which will survive the 10-year census interval on plot using the th draw of the survival parameters, is the probability that a new recruit will transition into size class by the end of the 10 year interval, and is the number of new recruits generated per existing individual using draw of the fecundity parameters (which we refer to as the fecundity, following Shriver et al. 2021).

Following the recommendations of Doak et al. (2021), the continuous growth kernel described in Equation 3 is discretized into size class transition probabilities using the cumulative density function difference method. That is, is the probability that an individual on plot with DBH equal to the midpoint of size class will have a DBH at remeasurement somewhere between the upper and lower bounds of size class , and is given by:

Equation

where is the cumulative probability density function of a normal distribution with mean and variance evaluated at the upper bound of size class (), the lower bound of size class (), or 0.0254 (the minimum modeled size). This is an exact method for calculating the area under the probability density function for the growth kernel and normalizing it by that portion of the kernel which is in the modeled size range. is calculated for each draw , plot , and size class from Equation 4 using the midpoint DBH of size class and the environmental covariates associated with plot . Because our objective was to better understand the influence of the stressors (fixed effects) on vital rates, we assume that both the plot random effect and the ecoregion random effect are equal to 0.

Likewise, is calculated using Equation 2 to predict the proportion of surviving individuals whose DBH is equal to the midpoint of size class on plot (using parameter values from draw ). We used the observed size distribution of new recruits to calculate the proportion of new recruits falling into each 2.54 cm bin, giving . Eviction from the largest size class is avoided by setting an extremely high upper size bound for the largest class, such that portion of individuals growing beyond the maximum bound is numerically indistinguishable from 0.

The largest real eigenvalue of each full transition matrix corresponds to the asymptotic population growth rate for posterior draw and environmental context . The distribution of for each environmental context was plotted to understand how the presence or absence of different stressors is expected to shape the asymptotic population growth rate of sugar pine.

We also used the constructed transition kernels to project the average population trends over the course of a single census interval:

where is the vector giving the projected stem density of individuals in each of the 99 size classes for draw and scenario , is the transition kernel for draw and scenario , and is the vector giving the mean (across all real plots) stem densities of individuals in each of the 99 size classes. These projected size distributions were summed to get a total stem density projection for each draw and scenario to better understand how the various stressors contributed to the observed trends in abundance on the FIA plots.

# Results

## Trends in Abundance

The abundance of sugar pine on plots where it was present at either census declined between initial censuses (2004-2009) and remeasurements (2014-2019; Figure 2). Basal area declined from a mean of 4.55 m2/ha (standard error 0.18 m2/ha) to a mean of 4.22 (0.17) m2/ha. Stem density declined from a 221.8 (21.5) stems/ha to 199.3 (17.9) stems/ha. Because these figures include only plots where sugar pine was present, they should be interpreted as upper bounds on the actual density of sugar pine across its range. Rather than estimate true abundance, they provide insight into the relative change in abundance across the decade between initial measurement and remeasurement.

## Vital Rates Model Validation

Diagnostics for mixing, convergence, R-hat, and transitions all indicated that the model fitting algorithm performed well. Comparisons of posterior distributions with prior distributions showed that the posterior was strongly informed by the data, rather than the prior, for most parameters (Supplementary Materials). The exception, where the posterior was only weakly informed by the data, were the estimates for the interactions of WPBR with size and quadratic size affecting survival. This uncertainty regarding interactions involving WPBR was likely due to the relatively low frequency of WPBR presence in the data. Posterior predictions generated using the posterior parameter samples and the training data as explanatory variables were consistent with the true values observed in the training data, with the true values nearly always falling within the range of variation predicted by the model (Supplementary Materials). The survival model appeared slightly underconfident, in that true survival rates were slightly lower than predicted survival rates for , and true survival rates were slightly higher than predicted survival rates for . The frequency distribution of simulated new recruit counts closely matched the observed frequency distribution of recruit counts. Simulations generated using the posterior parameter samples and the held-out validation data as explanatory variables were broadly consistent with the true values observed in the validation data (Supplementary Materials).

## Survival

There was a strong positive effect of size on survival, with a negative quadratic effect (Table 1): Median posterior predicted 10-year survival rates increased from approximately 80% for stems with 0 m DBH up to a maximum of 96.5% for stems with 0.91 m DBH, before falling off for the largest stems (Figure 3), though with relatively large uncertainty because there were few extremely large individuals. There was a strong negative main effect of fire, a positive interaction between fire and size, and a negative interaction between fire and squared size, indicating that fire substantially reduced survival, particularly for the smallest and largest trees (Figure 3). There were moderate negative effects of WPBR and basal area on survival. Other effects were weak or uncertain (their 90% credible intervals overlapped 0).

## Individual Size (growth)

The posterior median for the intercept of the model for size at the second census was 0.018, with a 90% credible interval from 0.014 to 0.022 (Table 2). The effect of initial size was, as expected, very close to 1, and the quadratic effect of initial size was negative. Together, these results indicate that the smallest and largest trees grew approximately 2.5 cm DBH in the 10 years between initial and follow-up census, with midsize trees (initial DBH ~70 cm) growing faster, at around 4.4 cm in 10 years (Figure 4). White pine blister rust actually increased the growth of the smallest stems, perhaps due to cankers increasing stem diameter. By contrast, basal area reduced the growth of small stems but not large ones. Site dryness also had a negative main effect and a positive interaction with initial size, plus a negative interaction with quadratic size: For the smallest and largest stems growth was lower on dry sites, whereas for stems between approximately 40 cm and 110 cm DBH growth was higher on dry sites. Other effects were weak or uncertain.

## Fecundity

The posterior median value for the intercept of the fecundity model was -2.92, with a 90% CI from -3.29 to -2.56 (Table 3). These figures indicate that the average number of new recruits produced per existing tree in 10 years was 0.05 (0.04-0.08).

## 10-year Projections

Total stem densities were projected to decline over the duration of a single census under nearly all hypothetical scenarios, the only exception being the low basal area scenario (Figure 5). The decline was particularly severe in the burned scenario, followed by the WPBR scenario. Declines were predicted even for undisturbed plots, with similar declines in the high BA, high drought, and high site dryness scenarios.

## Asymptotic Population Growth Rates

Figure 6 shows the posterior distribution of the asymptotic population growth rate () predicted from IPMs built on a variety of hypothetical scenarios. In each scenario, each posterior sample of the parameters is used to calculate a transition matrix for a population of sugar pines on an idealized plot where the fixed effect covariates (other than size) for the vital rate models are held to specific values representing each scenario. For each of the nine scenarios, one transition matrix is constructed using the parameter values from each of the 4,000 posterior draws. The dominant eigenvalue of each matrix gives the estimate of for that scenario and draw.

In the undisturbed scenario, categorical stressors (fire and WPBR) were absent, while continuous stressors (BA, drought, and site dryness) were held at zero (their scaled means). Under these circumstances, the asymptotic growth rate is near or slightly below one, with a median posterior value of of 0.980 and a 90% credible interval from 0.953 to 1.005 (Figure 6, Supplementary Table 1). Where fire is present, is strongly reduced (median 0.643, CI 0.521 to 0.788). Where WPBR is present, the posterior distribution for is below 1 (median 0.948, CI 0.857 to 0.994). When basal area is lower than average, there posterior distribution of is near or slightly above above one (median 1.002, CI 0.974 to 1.029). By contrast, when basal area is higher than average the posterior distribution of is below one (median 0.946, CI 0.912 to 0.977) and is clearly lower than the undisturbed scenario. For sites experiencing low amounts of drought, the median is 0.991 and the 90% CI of straddles one, while for sites experiencing high drought the posterior distribution of is below one (median 0.967, 90% CI from 0.933 to 0.998). Likewise, on particularly dry sites the posterior distribution of is below one (median 0.953, 90% CI from 0.918 to 0.986). Fire had the clearest effect on , followed by WPBR and high basal area, and then drought and site dryness. However, the posterior median value of was below one even in the undisturbed scenario, suggesting that even under “unstressed” conditions the population of sugar pine may be declining.

# Discussion

This study is the first range-wide assessment of stressors impacting the vital rates and population dynamics of sugar pine. We found the abundance of sugar pine to be slightly declining in terms of both basal area and stem density. This observed decline was consistent with the asymptotic population growth rates and the 10-year stem density projections, both of which projected the abundance of sugar pine to decline even in the undisturbed scenario (Figure 5 and Figure 6). The analysis described here allows direct comparison of the influence of fire, WPBR, stand density, short-term drought, and long-term site dryness, providing valuable guidance for managers seeking to prioritize efforts to prevent further decline.

The results of this study highlight fire as a key stressor negatively impacting demographic rates of sugar pine. Fire strongly reduced survival of individual trees, particularly small ones. This finding is broadly consistent with the existing literature, which has documented many cases of negative (and size-dependent) impacts of fire on survival of sugar pine (Van Mantgem *et al.*, 2004; Hood, Smith and Cluck, 2010; Nesmith *et al.*, 2015; Furniss *et al.*, 2018; Dudney *et al.*, 2020). Fire can also injure surviving trees, reducing their growth rate as seen in this study and others (Foster *et al.*, 2020). Reduced growth rates may have particularly strong effects on the asymptotic population growth rate in species where large / old individuals disproportionately contribute to reproduction (Shriver *et al.*, 2019); Sugar pine is one such species, though we were unable to estimate a relationship between size and fecundity in this study. The literature suggests that a core way in which fire influences the population dynamics of sugar pine is by killing large high-fecundity individuals (Van Mantgem *et al.*, 2004). The most extreme form of this dynamic results in so-called type conversion, where high severity fire locally extirpates sugar pine and other mixed conifer species, resulting in the loss of mixed conifer forest generally (Shive *et al.*, 2018; North *et al.*, 2019; Coop *et al.*, 2020).

In this study, fire’s effects on survival, growth, and fecundity combine to result in posterior values well below one for burned plots (Figure 6), and sharp declines in stem density projected for a single census interval (Figure 5). However, we caution that the asymptotic population growth rates presented in this study should not be interpreted as predictions, because in reality fire is unlikely to repeatedly occur on the same site during every census interval. Instead, the asymptotic population growth rates give some insight into the overall influence of each stressor on population dynamics, which is supplemented by the single-step projections. Existing literature has shown that most trees killed by fire die within 1 year of the fire (Furniss *et al.*, 2018) and mortality rates in stands affected by prescribed fire returned to background levels approximately six years postfire (van Mantgem *et al.*, 2011), suggesting that the negative effects of fire on survival are transient. However, there is abundant evidence that the ecological footprint of fire, in particular high severity wildfire, is increasing throughout the range of sugar pine because of climate changes and biomass accumulation resulting from fire suppression (Parks and Abatzoglou, 2020; Alizadeh *et al.*, 2021). Given this context and the results of this study, it is clear that the disrupted fire regime is a core threat facing sugar pine.

Though their effects were less severe than those of fire, both WPBR and densification negatively impacted sugar pine’s population dynamics in this study. The data here show that WPBR negatively impacted survival (Figure 3). Numerous other studies have shown that blister rust tends to kill smaller trees (Van Mantgem *et al.*, 2004) and negatively affects survival rates of sugar pine and other vulnerable species (Maloney *et al.*, 2011; Dudney *et al.*, 2020). The presence of WPBR on individual trees (and thus on their plots) may be difficult to detect (Dudney *et al.*, 2020), and is likely that WPBR was only detected in this study where it has caused a particularly severe infection in a sampled tree. There are two likely effects of this sampling bias towards under detection: Our data may underreport the true prevalence of WPBR and overestimate the true impact of its presence on a subplot.

This study also found that relatively high neighborhood density (basal area) resulted in lower rates of survival (Figure 3) and for small individuals, growth (Figure 4). There is extensive evidence in the literature that high neighborhood density and other proxies for competition negatively impact sugar pine survival (Van Mantgem *et al.*, 2004; Maloney *et al.*, 2011; Levine *et al.*, 2016) and growth (Latham and Tappeiner, 2002; Das, 2012; Eitzel *et al.*, 2013; Steel *et al.*, 2021). Though we were unable to estimate how stressors affected fecundity, the literature suggests that competition may result in decreased reproduction due to stress of parent trees or decreased survival and/or growth of new recruits (Schubert, 1956; York *et al.*, 2004, 2012; Van Mantgem, Stephenson and Keeley, 2006; Angell, Waring and Graves, 2014; Levine *et al.*, 2016; Moran *et al.*, 2019). In this study, high neighborhood basal area and presence of WPBR both reduced the expected asymptotic growth rate relative to an unstressed site, though negative impacts were weaker than that of fire (Figure 6, Supplementary Table 1). However, reducing neighborhood basal area to one standard deviation below the mean had positive effects on (Figure 6).

This study found that long-term site dryness had clearer effects on population dynamics than did drought (departure from average climate), with site dryness having a negative impact on the growth of the largest and smallest trees. However, the asymptotic population growth rate was below one for populations on dry sites and those experiencing drought (Supplementary Table 1), as it was for the undisturbed scenario. Other literature has emphasized the role of moisture stress in increased mortality rates and reduced growth among sugar pine directly and indirectly via decreased ability of trees to resist mountain pine beetle (Das *et al.*, 2007, 2013; Van Mantgem and Stephenson, 2007; Paz-Kagan *et al.*, 2017; Restaino *et al.*, 2019; Bohner and Diez, 2021), though see Furniss et al. (2021) which found that stand density played a more important role than climate variables in shaping mortality dynamics after fire and/or drought. Stephenson et al. (2019) examined the role of mountain pine beetle as the primary mortality agent taking advantage of widespread stress among sugar pine populations affected by drought, a finding supported by other assessments of the relationship between drought and bark beetles (Fettig *et al.*, 2019; Slack, Kane and Knapp, 2021). Intermittent droughts and/or long-term mean climatic conditions may particularly challenge small trees, causing recruitment failures even on sites where adult trees are able to persist (Bell, Bradford and Lauenroth, 2014; Maloney, 2014; Davis *et al.*, 2019; Moran *et al.*, 2019; Stewart *et al.*, 2021). However, we did not find strong effects of drought on survival. Though the extreme drought from 2012-2016 resulted in beetle epidemics that caused massive mortality among sugar pine (Stephenson *et al.*, 2019), drought may be a necessary but not sufficient condition for causing such epidemics, with some droughts not resulting in widespread mortality.

One unexplained but troubling finding of this study was the declining survival rates observed for the largest sugar pines (Figure 3). One possible explanation is bark beetles, which are a driver of mortality for these trees: Once an outbreak is underway, beetles often preferentially kill large individuals (Stephenson *et al.*, 2019), and localized beetle outbreaks could explain the low survival of the largest trees in our data. However, this finding is based on relatively few data points and should be interpreted with caution. This uncertainty regarding the outlook for the largest individuals, which are an important ecological resource (Lutz *et al.*, 2018), highlights a need for further research.

An important limitation of this study is that we did not test for interaction between stressors in shaping vital rates of sugar pine. We did not test for interactions because including numerous three-way interactions between size and two stressors would have resulted in difficult-to-interpret vital rate models. The literature suggests that a variety such interactions may be important. For example, moisture stress increases the likelihood of regeneration failure, which may be a particularly acute problem in postfire landscapes where seed sources and shade trees may be limited (Davis *et al.*, 2019; Stewart *et al.*, 2021). A warmer and dryer climate may provide some relief from WPBR for sugar pine, as the disease’s climatic envelope shifts upslope away from existing populations of sugar pine (Maloney, 2011; Dudney *et al.*, 2021). A relationship between fire exclusion, stand density, and WPBR infection has been suggested (Dudney *et al.*, 2020), but evidence is mixed with some studies finding that conspecific basal area was an important driver of sugar pine mortality (Das *et al.*, 2008) but others failing to find evidence linking fire exclusion to elevated rates of WPBR infection (Van Mantgem *et al.*, 2004; Dudney *et al.*, 2020). Stress caused by drought and/or competition may decrease trees’ ability to resist wildfire (Nesmith *et al.*, 2015; Furniss *et al.*, 2018, 2021; van Mantgem *et al.*, 2018; Van Mantgem *et al.*, 2020), and beetle epidemics may kill off the largest and most fire-resistant individuals (Stephenson *et al.*, 2019; Steel *et al.*, 2021). Drought and density both alter the fuelbed in ways that may increase the intensity of wildfires (Hicke *et al.*, 2012; Stephens *et al.*, 2018; Wayman and Safford, 2021). Likewise, wildfires may decrease trees’ ability to resist bark beetles, facilitating epidemic outbreaks in the event of a post-fire drought (Davis, Hood and Bentz, 2012; Furniss *et al.*, 2021). Competition tends to reduce trees’ ability to resist drought and beetle epidemics (Young *et al.*, 2017; Furniss *et al.*, 2021; Bradford *et al.*, 2022). Finally, there is potential for stressors to mitigate one another, primarily by a mechanism where mortality caused by one stressor results in less competitive stress and increased resilience to other stressors (van Mantgem *et al.*, 2016; Voelker *et al.*, 2019; North *et al.*, 2022). For example, wildfire could reduce basal area, leaving the surviving trees better able to resist drought over the long term. Exploring how stressors are likely to interact and shape population dynamics is another goal for future research.

The results of this study provide clear guidance for managers interested in conserving sugar pine. This study’s findings, which point at fire, WPBR, and neighborhood basal area as major stressors of sugar pine, suggest that fuel treatments with a density reduction component could substantially benefit sugar pine populations. Fuel treatments to reduce or rearrange the dead biomass which fuels wildfires have been proven to reduce the hazard of severe wildfire (Stephens and Moghaddas, 2005; Foster *et al.*, 2020), and in many cases have the co-benefit of reducing basal area (Hessburg *et al.*, 2016; North *et al.*, 2021). Our findings, and other studies examining the effects of prescribed fire on sugar pine mortality (Van Mantgem *et al.*, 2004; Steel *et al.*, 2021), suggest that managers should be deliberate in their application of prescribed fire to reduce wildfire hazard and consider measures such as raking or local density reduction to protect individual trees where pre-fire fuels are abundant (Nesmith *et al.*, 2010; Furniss *et al.*, 2021). Mechanical fuel treatments will provide some protection from wildfire and can be applied in combination with timber harvests, for a dual benefit of reducing wildfire hazard and competition (Collins *et al.*, 2014; Restaino *et al.*, 2019). On burned landscapes, managers can take advantage of established programs producing WPBR-resistant seedlings in reforestation efforts aimed at restoring sugar pine on landscapes impacted by high severity fire (Kinloch *et al.*, 2018). Investments in artificial regeneration should likewise be made deliberately and secured with follow up treatments for wildfire hazard (North *et al.*, 2019) and pruning to limit the effects of WPBR (Bronson, Petrick and Danchok, 2018). The findings of this study indicate that managers can substantially benefit sugar pine populations by investing resources in addressing the tractable challenges posed by fire, densification, and white pine blister rust.

# References

Abatzoglou, J. T. *et al.* (2018) ‘TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015’, *Scientific Data*, 5, pp. 1–12. doi: 10.1038/sdata.2017.191.

Aitken, S. N. and Whitlock, M. C. (2013) ‘Assisted Gene Flow to Facilitate Local Adaptation to Climate Change’, *Annual Review of Ecology, evolution, and Systematics*, 44, pp. 367–88. doi: 10.1146/annurev-ecolsys-110512-135747.

Alizadeh, M. R. *et al.* (2021) ‘Warming enabled upslope advance in western US forest fires’, *Proceedings of the National Academy of Sciences of the United States of America*, 118(22), pp. 1–14. doi: 10.1073/pnas.2009717118.

Angell, N., Waring, K. M. and Graves, T. A. (2014) ‘Predicting height growth of sugar pine regeneration using stand and individual tree characteristics’, *Forestry*, 87(1), pp. 85–97. doi: 10.1093/forestry/cpt028.

Ansley, J.-A. S. and Battles, J. J. (1998) ‘Forest Composition , Structure , and Change in an Old-Growth Mixed Conifer Forest in the Northern Sierra Nevada Author ( s ): Jolie-Anne S . Ansley and John J . Battles Published by : Torrey Botanical Society Stable URL : http://www.jstor.org/stable/29972’, *The Journal of the Torrey Botanical Society*, 125(4), pp. 297–308.

Bechtold, W. A. and Patterson, P. L. (2005) ‘The Enhanced Forest Inventory and Analysis Program — National Sampling Design and Estimation Procedures’, *USDA General Technical Report*, SRS-80, p. 85.

Bell, D. M., Bradford, J. B. and Lauenroth, W. K. (2014) ‘Early indicators of change: Divergent climate envelopes between tree life stages imply range shifts in the western United States’, *Global Ecology and Biogeography*, 23(2), pp. 168–180. doi: 10.1111/geb.12109.

Bohlman, G. N., Safford, H. D. and Skinner, C. N. (2021) ‘Natural range of variation for yellow pine and mixed-conifer forests in northwestern California and southwestern Oregon’, *Gen. Tech. Rep. PSW-GTR-273. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station. 146 p.*, 273(November).

Bohner, T. and Diez, J. (2021) ‘Tree resistance and recovery from drought mediated by multiple abiotic and biotic processes across a large geographic gradient’, *Science of The Total Environment*, 789, p. 147744. doi: 10.1016/j.scitotenv.2021.147744.

Bradford, J. B. *et al.* (2022) ‘Tree mortality response to drought-density interactions suggests opportunities to enhance drought resistance’, *Journal of Applied Ecology*, 59(2), pp. 549–559. doi: 10.1111/1365-2664.14073.

Bronson, J., Petrick, J. and Danchok, R. (2018) ‘Efficacy of Early Pruning to Reduce the Incidence of White Pine Blister Rust on Sugar Pine ( Pinus lambertiana )’, pp. 205–208.

Collins, B. M. *et al.* (2014) ‘Beyond Reducing Fire Hazard’, *Ecological Applications*, 24(8), pp. 1879–1886. doi: 10.1890/14-0971.1.

Coop, J. D. *et al.* (2020) ‘Wildfire-Driven Forest Conversion in Western North American Landscapes’, *BioScience*, 70(8), pp. 659–673. doi: 10.1093/biosci/biaa061.

Das, A. *et al.* (2008) ‘Spatial elements of mortality risk in old-growth forests’, *Ecology*, 89(6), pp. 1744–1756. doi: 10.1890/07-0524.1.

Das, A. (2012) ‘The effect of size and competition on tree growth rate in old-growth coniferous forests’, *Canadian Journal of Forest Research*, 42(11), pp. 1983–1995. doi: 10.1139/x2012-142.

Das, A. J. *et al.* (2007) ‘The relationship between tree growth patterns and likelihood of mortality: A study of two tree species in the Sierra Nevada’, *Canadian Journal of Forest Research*, 37(3), pp. 580–597. doi: 10.1139/X06-262.

Das, A. J. *et al.* (2013) ‘Climatic Correlates of Tree Mortality in Water- and Energy-Limited Forests’, *PLoS ONE*, 8(7). doi: 10.1371/journal.pone.0069917.

Davis, K. T. *et al.* (2019) ‘Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration’, *Proceedings of the National Academy of Sciences of the United States of America*, 116(13), pp. 6193–6198. doi: 10.1073/pnas.1815107116.

Davis, R. S., Hood, S. and Bentz, B. J. (2012) ‘Fire-injured ponderosa pine provide a pulsed resource for bark beetles’, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 42(12), pp. 2022–2036. doi: 10.1139/x2012-147.

Dudney, J. *et al.* (2021) ‘Nonlinear shifts in infectious rust disease due to climate change’, *Nature Communications*, 12(1). doi: 10.1038/s41467-021-25182-6.

Dudney, J. C. *et al.* (2020) ‘Compounding effects of white pine blister rust, mountain pine beetle, and fire threaten four white pine species’, *Ecosphere*, 11(October), p. e03263. doi: 10.1002/ecs2.3263.

Eitzel, M. *et al.* (2013) ‘Estimating tree growth from complex forest monitoring data’, *Ecological Applications*, 23(6), pp. 1288–1296. doi: 10.1890/12-0504.1.

Fettig, C. J. *et al.* (2019) ‘Tree mortality following drought in the central and southern Sierra Nevada, California, U.S.’, *Forest Ecology and Management*, 432(August 2018), pp. 164–178. doi: 10.1016/j.foreco.2018.09.006.

Foster, D. E. *et al.* (2020) ‘Potential wildfire and carbon stability in frequent-fire forests in the Sierra Nevada: trade-offs from a long-term study’, *Ecosphere*, 11(8). doi: 10.1002/ecs2.3198.

Fowells, H. A. and Schubert, G. H. (1956) ‘Seed crops of forest trees in the pine region of California’, *USDA Technical Bulletin*, 1150(1150), pp. 1–48.

Furniss, T. J. *et al.* (2018) ‘Multi-scale assessment of post-fire tree mortality models’, *International Journal of Wildland Fire*, p. in press. doi: 10.1071/WF18031.

Furniss, T. J. *et al.* (2021) ‘Crowding, climate, and the case for social distancing among trees’, *Ecological Applications*, (June 2021), pp. 1–14. doi: 10.1002/eap.2507.

Geils, B. W., Hummer, K. E. and Hunt, R. S. (2010) ‘White pines, Ribes, and blister rust: A review and synthesis’, *Forest Pathology*, 40(3–4), pp. 147–185. doi: 10.1111/j.1439-0329.2010.00654.x.

Harry, D. E., Jenkinson, J. L. and Kinloch, B. B. (1983) ‘Early Growth of Sugar Pine from an Elevational Transect’, *Forest Science*, 29(3), pp. 660–669. Available at: http://www.ingentaconnect.com/content/saf/fs/1983/00000029/00000003/art00027.

Hessburg, P. F. *et al.* (2016) ‘Tamm Review: Management of mixed-severity fire regime forests in Oregon, Washington, and Northern California’, *Forest Ecology and Management*, 366, pp. 221–250. doi: 10.1016/j.foreco.2016.01.034.

Hessburg, P. F. *et al.* (2021) ‘Wildfire and climate change adaptation of western North American forests: a case for intentional management’, *Ecological Applications*, 0(0). doi: 10.1002/eap.2432.

Hicke, J. A. *et al.* (2012) ‘Effects of bark beetle-caused tree mortality on wildfire’, *Forest Ecology and Management*, 271, pp. 81–90. doi: 10.1016/j.foreco.2012.02.005.

Hood, S. M., Smith, S. L. and Cluck, D. R. (2010) ‘Predicting mortality for five California conifers following wildfire’, *Forest Ecology and Management*, 260(5), pp. 750–762. doi: 10.1016/j.foreco.2010.05.033.

Kinloch, B. B. *et al.* (2018) ‘Patterns of Variation in Blister Rust Resistance in Sugar Pine ( Pinus lambertiana )’, in *Schoettle, Anna W.; Sniezko, Richard A.; Kliejunas, John T., eds. 2018. Proceedings of the IUFRO joint conference: Genetics of five-needle pines, rusts of forest trees, and Strobusphere; 2014 June 15–20; Fort Collins, CO. Proc. RMRS-P-76. Fort Collins, CO*, pp. 124–128.

Kinloch, B. B. and Scheuner, W. H. (1990) ‘Pinus lambertiana Dougl.’, in *Silvics of North America 1*, pp. 370–380.

Kinloch Jr., B. B., Marosy, M. and Huddleston, M. E. (1996) ‘Sugar pine: status, values, and roles in ecosystems: Proceedings of a symposium presented by the California Sugar Pine Management Committee’, p. 225.

Latham, P. and Tappeiner, J. (2002) ‘Response of old-growth conifers to reduction in stand density in western Oregon forests’, *Tree Physiology*, 22(2–3), pp. 137–146. doi: 10.1093/treephys/22.2-3.137.

Levine, C. R. *et al.* (2016) ‘Long-term demographic trends in a fire-suppressed mixed-conifer forest’, *Canadian Journal of Forest Research*, 46(5), pp. 745–752. doi: 10.1139/cjfr-2015-0406.

Lutz, J. A. *et al.* (2013) ‘The importance of large-diameter trees to forest structural heterogeneity’, *PLoS ONE*, 8(12). doi: 10.1371/journal.pone.0082784.

Lutz, J. A. *et al.* (2018) ‘Global importance of large-diameter trees’, *Global Ecology and Biogeography*, 27(7), pp. 849–864. doi: 10.1111/geb.12747.

Lutz, J. A. *et al.* (2020) ‘Large-diameter trees dominate snag and surface biomass following reintroduced fire’, *Ecological Processes*, 9(1). doi: 10.1186/s13717-020-00243-8.

Mahalovich, M. and Stritch, L. (2013) ‘Pinus albicaulis. The IUCN Red List of Threatened Species 2013’. Available at: https://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T39049A2885918.en.

Maloney, P. E. (2011) ‘Incidence and distribution of white pine blister rust in the high-elevation forests of California’, *Forest Pathology*, 41(4), pp. 308–316. doi: 10.1111/j.1439-0329.2011.00732.x.

Maloney, P. E. *et al.* (2011) ‘Population biology of sugar pine (Pinus lambertiana Dougl.) with reference to historical disturbances in the Lake Tahoe Basin: Implications for restoration’, *Forest Ecology and Management*, 262(5), pp. 770–779. doi: 10.1016/j.foreco.2011.05.011.

Maloney, P. E. (2014) ‘The multivariate underpinnings of recruitment for three Pinus species in montane forests of the Sierra Nevada, USA’, *Plant Ecology*, 215(2), pp. 261–274. doi: 10.1007/s11258-013-0295-6.

van Mantgem, P. J. *et al.* (2011) ‘Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California’, *Forest Ecology and Management*, 261(6), pp. 989–994. doi: 10.1016/j.foreco.2010.12.013.

van Mantgem, P. J. *et al.* (2016) ‘Does Prescribed Fire Promote Resistance To Drought in Low Elevation Forests of the Sierra Nevada, California, Usa?’, *Fire Ecology*, 12(1), pp. 5–15. doi: 10.4996/fireecology.1201013.

van Mantgem, P. J. *et al.* (2018) ‘Pre-fire drought and competition mediate post-fire conifer mortality in western U.S. National Parks’, *Ecological Applications*, 28(7), pp. 1730–1739. doi: 10.1002/eap.1778.

Van Mantgem, P. J. *et al.* (2004) ‘Effects of an introduced pathogen and fire exclusion on the demography of sugar pine’, *Ecological Applications*, 14(5), pp. 1590–1602. doi: 10.1890/03-5109.

Van Mantgem, P. J. *et al.* (2020) ‘The influence of pre-fire growth patterns on post-fire tree mortality for common conifers in western US parks’, *International Journal of Wildland Fire*, 29(6), pp. 513–518. doi: 10.1071/WF19020.

Van Mantgem, P. J. and Stephenson, N. L. (2007) ‘Apparent climatically induced increase of tree mortality rates in a temperate forest’, *Ecology Letters*, 10(10), pp. 909–916. doi: 10.1111/j.1461-0248.2007.01080.x.

Van Mantgem, P. J., Stephenson, N. L. and Keeley, J. E. (2006) ‘Forest reproduction along a climatic gradient in the Sierra Nevada, California’, *Forest Ecology and Management*, 225(1–3), pp. 391–399. doi: 10.1016/j.foreco.2006.01.015.

McCauley, L. A. *et al.* (2022) ‘Landscape-scale forest restoration decreases vulnerability to drought mortality under climate change in southwest USA ponderosa forest’, *Forest Ecology and Management*, 509(February), p. 120088. doi: 10.1016/j.foreco.2022.120088.

Millar, C. I. and Stephenson, N. L. (2015) ‘Temperate forest health in an era of emerging megadisturbance’, *Science*, 349(6250), pp. 823–826. doi: 10.1126/science.aaa9933.

Moran, E. V. *et al.* (2019) ‘Negative impacts of summer heat on Sierra Nevada tree seedlings’, *Ecosphere*, 10(6). doi: 10.1002/ecs2.2776.

Murray, M. P. and Tomback, D. F. (2010) ‘Clark’s nutcrackers harvest sugar pine seeds from cones’, *Western North American Naturalist*, 70(3), pp. 413–414. doi: 10.3398/064.070.0314.

Nesmith, J. C. B. *et al.* (2010) ‘The effects of raking on sugar pine mortality following prescribed fire in sequoia and kings canyon national parks, California, USA’, *Fire Ecology*, 6(3), pp. 97–116. doi: 10.4996/fireecology.0603097.

Nesmith, J. C. B. *et al.* (2015) ‘The influence of prefire tree growth and crown condition on postfire mortality of sugar pine following prescribed fire in Sequoia National Park’, *Canadian Journal of Forest Research*, 45(7), pp. 910–919. doi: 10.1139/cjfr-2014-0449.

North, M. *et al.* (2009) ‘An ecosystem management strategy for Sierran mixed- conifer forests’, *USDA Forest Service, Pacific Southwest Research Station, General Technical Report*, (March), p. PSW-GTR-220.

North, M. P. *et al.* (2019) ‘Tamm Review: Reforestation for resilience in dry western U.S. forests’, *Forest Ecology and Management*, 432(July 2018), pp. 209–224. doi: 10.1016/j.foreco.2018.09.007.

North, M. P. *et al.* (2021) ‘Pyrosilviculture needed for landscape resilience of dry western United States forests’, *Journal of Forestry*, pp. 1–25. doi: 10.1093/jofore/fvab026.

North, M. P. *et al.* (2022) ‘Operational resilience in western US frequent-fire forests’, *Forest Ecology and Management*, 507(November 2021), p. 120004. doi: 10.1016/j.foreco.2021.120004.

Panek, J. A. *et al.* (2012) ‘A natural resource condition assessment for Sequoia and Kings Canyon National Parks’, *Natural Resource Report NPS/SEKI/NRR—2012*.

Parks, S. A. and Abatzoglou, J. T. (2020) ‘Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017’, *Geophysical Research Letters*, 47(22), pp. 1–10. doi: 10.1029/2020GL089858.

Paz-Kagan, T. *et al.* (2017) ‘What mediates tree mortality during drought in the southern Sierra Nevada’, *Ecological Applications*, 27(8), pp. 2443–2457. doi: 10.1002/eap.1620.

Restaino, C. *et al.* (2019) ‘Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada , USA’, *Ecological Applications*, 29(December 2017), pp. 1–14. doi: 10.1002/eap.1902.

Safford, H. D. and Stevens, J. T. (2017) ‘Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the bioregional assessment area, including the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests’, *Gen. Tech. Rep. PSW-GTR-2562*, (October), pp. 1–151.

Schubert, G. H. (1956) *Effect of fertilizer on cone production of sugar pine*.

Schwilk, D. W. and Ackerly, D. D. (2001) ‘Flammability and Serotiny as Strategies : Correlated Evolution in Pines evolution correlated as strategies : and serotiny Flammability in pines’, *Oikos*, 94, pp. 326–336.

Shive, K. L. *et al.* (2018) ‘From the stand scale to the landscape scale: predicting the spatial patterns of forest regeneration after disturbance’, *Ecological Applications*, 28(6), pp. 1626–1639. doi: 10.1002/eap.1756.

Shriver, R. K. *et al.* (2019) ‘Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance’, *Ecology Letters*, 22(9), pp. 1357–1366. doi: 10.1111/ele.13291.

Shriver, R. K. *et al.* (2021) ‘Quantifying the demographic vulnerabilities of dry woodlands to climate and competition using range‐wide monitoring data’, *Ecology*, 0(0), pp. 1–12. doi: 10.1002/ecy.3425.

Slack, A. W., Kane, J. M. and Knapp, E. E. (2021) ‘Growth and defense inform large sugar pine ( Pinus lambertiana ) mortality in a fire ‐ excluded forest of the central Sierra Nevada’, *Trees*, (0123456789). doi: 10.1007/s00468-021-02098-8.

Steel, Z. *et al.* (2021) ‘Do Forest Fuel Reduction Treatments Confer Resistance to Beetle Infestation and Drought Mortality?’, *Ecosphere*, 12(January). doi: 10.1002/ecs2.3344.

Steel, Z. L., Safford, H. D. and Viers, J. H. (2015) ‘The fire frequency-severity relationship and the legacy of fire suppression in California forests http://www.esajournals.org/doi/pdf/10.1890/ES14-00224.1’, *Ecosphere*, 6(1). doi: 10.1890/ES14-00224.1.

Stephens, S. C. L. S. *et al.* (2015) ‘Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada’, *Ecosphere*, 6(May), pp. 1–63.

Stephens, S. L. *et al.* (2009) ‘Fire Treatment Effects on Vegetation Structure , Fuels , and Potential Fire Severity in Western U . S . Forests’, *Ecological Applications*, 19(2), pp. 305–320. doi: 10.1890/07-1755.1.

Stephens, S. L. *et al.* (2018) ‘Drought, Tree Mortality, and Wildfire in Forests Adapted to Frequent Fire’, *BioScience*, XX(X), pp. 1–12. doi: 10.1093/biosci/bix146.

Stephens, S. L. and Moghaddas, J. J. (2005) ‘Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest’, *Forest Ecology and Management*, 215(1–3), pp. 21–36. doi: 10.1016/j.foreco.2005.03.070.

Stephenson, N. L. (1998) ‘Actual evapotranspiration and deficit: Biologically meaningful correlates of vegetation distribution across spatial scales’, *Journal of Biogeography*, 25(5), pp. 855–870. doi: 10.1046/j.1365-2699.1998.00233.x.

Stephenson, N. L. *et al.* (2019) ‘Which trees die during drought? The key role of insect host-tree selection’, *Journal of Ecology*, 107(5), pp. 2383–2401. doi: 10.1111/1365-2745.13176.

Stevens, J. T. *et al.* (2017) ‘Changing spatial patterns of stand-replacing fire in California conifer forests’, *Forest Ecology and Management*, 406(August), pp. 28–36. doi: 10.1016/j.foreco.2017.08.051.

Stewart, J. A. E. *et al.* (2021) ‘Effects of postfire climate and seed availability on postfire conifer regeneration’, *Ecological Applications*, 31(3), pp. 1–14. doi: 10.1002/eap.2280.

Voelker, S. L. *et al.* (2019) ‘Fire deficits have increased drought sensitivity in dry conifer forests: Fire frequency and tree-ring carbon isotope evidence from Central Oregon’, *Global Change Biology*, 25(4), pp. 1247–1262. doi: 10.1111/gcb.14543.

Wayman, R. B. and Safford, H. D. (2021) ‘Recent bark beetle outbreaks influence wildfire severity in mixed-conifer forests of the Sierra Nevada, California, USA’, *Ecological Applications*, 31(3), pp. 1–19. doi: 10.1002/eap.2287.

Yeaton, R. I. (1983) ‘The Successional Replacement of Ponderosa Pine by Sugar Pine in the Sierra Nevada Author ( s ): Richard I . Yeaton Source : Bulletin of the Torrey Botanical Club , Jul . - Sep ., 1983 , Vol . 110 , No . 3 ( Jul . - Published by : Torrey Botanical Society ’, 110(3), pp. 292–297.

Yeaton, R. I. (1984) ‘Aspects of the Population Biology of Sugar Pine ( Pinus lambertiana Dougl .) on an Elevational Gradient in the Sierra Nevada of Central California’, *The American Midland Naturalist*, 111(1), pp. 126–137. Available at: https://www.jstor.org/stable/2425550.

York, R. A. *et al.* (2004) ‘Group selection management in conifer forests: Relationships between opening size and tree growth’, *Canadian Journal of Forest Research*, 34(3), pp. 630–641. doi: 10.1139/x03-222.

York, R. A. *et al.* (2012) ‘A gap-based approach for regenerating pine species and reducing surface fuels in multi-aged mixed conifer stands in the Sierra Nevada, California’, *Forestry*, 85(2), pp. 203–213. doi: 10.1093/forestry/cpr058.

Young, D. J. N. *et al.* (2017) ‘Long-term climate and competition explain forest mortality patterns under extreme drought’, *Ecology Letters*, 20(1), pp. 78–86. doi: 10.1111/ele.12711.

# Tables

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameter** | **Mean** | **Median** | **StDev** | **q5** | **q95** | **rhat** | **ess\_bulk** | **ess\_tail** |
| **Intercept** | 1.59 | 1.58 | 0.26 | 1.17 | 2.01 | 1.00 | 1456.24 | 2098.04 |
| **DBH (m)** | 4.00 | 3.99 | 0.79 | 2.68 | 5.34 | 1.00 | 1336.35 | 2155.84 |
| **DBH^2 (m)** | -2.29 | -2.28 | 0.56 | -3.22 | -1.36 | 1.00 | 1397.96 | 2151.10 |
| **Fire** | -4.07 | -4.06 | 0.59 | -5.05 | -3.11 | 1.00 | 1629.72 | 2176.19 |
| **WPBR** | -1.05 | -1.04 | 0.56 | -1.99 | -0.13 | 1.00 | 1582.57 | 2456.43 |
| **Basal Area** | -0.65 | -0.65 | 0.23 | -1.03 | -0.27 | 1.00 | 1641.95 | 2121.95 |
| **Drought** | -0.18 | -0.18 | 0.21 | -0.52 | 0.16 | 1.00 | 1333.50 | 2379.36 |
| **Site Dryness** | -0.34 | -0.34 | 0.23 | -0.73 | 0.04 | 1.00 | 1502.16 | 2478.08 |
| **DBH x Fire** | 3.67 | 3.62 | 1.51 | 1.22 | 6.16 | 1.00 | 1432.73 | 2296.75 |
| **DBH^2 x Fire** | -1.64 | -1.63 | 0.96 | -3.24 | -0.10 | 1.00 | 1401.16 | 2199.19 |
| **DBH x WPBR** | -0.04 | 0.00 | 1.84 | -3.06 | 2.98 | 1.00 | 2131.47 | 2735.02 |
| **DBH^2 x WPBR** | 0.56 | 0.54 | 1.40 | -1.66 | 2.94 | 1.00 | 2393.36 | 2598.78 |
| **DBH x BA** | 0.71 | 0.70 | 0.57 | -0.23 | 1.65 | 1.00 | 1458.07 | 1935.68 |
| **DBH^2 x BA** | -0.08 | -0.08 | 0.33 | -0.62 | 0.45 | 1.00 | 1490.06 | 2207.10 |
| **DBH x Drought** | -0.02 | -0.02 | 0.60 | -1.01 | 0.95 | 1.00 | 1497.81 | 2284.53 |
| **DBH^2 x Drought** | 0.08 | 0.08 | 0.41 | -0.58 | 0.79 | 1.00 | 1565.87 | 2268.01 |
| **DBH x Dryness** | 0.66 | 0.64 | 0.69 | -0.44 | 1.80 | 1.00 | 1414.52 | 2218.03 |
| **DBH^2 x Dryness** | -0.64 | -0.62 | 0.49 | -1.46 | 0.15 | 1.00 | 1426.39 | 2469.34 |
| **SD Plots** | 2.00 | 2.00 | 0.16 | 1.76 | 2.26 | 1.00 | 1193.61 | 2227.74 |
| **SD Ecoregions** | 0.28 | 0.26 | 0.19 | 0.03 | 0.61 | 1.01 | 403.37 | 997.11 |

Table :Summary of results for survival sub model, giving the mean, median, standard deviation, 5th percentile, and 95th percentile of posterior samples for each parameter, plus diagnostics R-hat, effective sample size (bulk), and effective sample size (tail).

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameter** | **Mean** | **Median** | **StDev** | **q5** | **q95** | **rhat** | **ess\_bulk** | **ess\_tail** |
| **Intercept** | 0.018 | 0.018 | 0.003 | 0.014 | 0.022 | 1.00 | 1932.23 | 2370.47 |
| **DBH (m)** | 1.076 | 1.076 | 0.006 | 1.067 | 1.086 | 1.00 | 3524.26 | 3051.14 |
| **DBH^2 (m)** | -0.056 | -0.056 | 0.004 | -0.063 | -0.049 | 1.00 | 3626.18 | 3225.29 |
| **Fire** | -0.007 | -0.007 | 0.007 | -0.019 | 0.005 | 1.00 | 2513.11 | 2712.72 |
| **WPBR** | 0.011 | 0.011 | 0.005 | 0.003 | 0.020 | 1.00 | 2895.99 | 2856.91 |
| **Basal Area** | -0.013 | -0.013 | 0.002 | -0.017 | -0.010 | 1.00 | 4376.90 | 3496.19 |
| **Drought** | -0.002 | -0.002 | 0.002 | -0.005 | 0.000 | 1.00 | 3798.53 | 3164.24 |
| **Site Dryness** | -0.007 | -0.007 | 0.002 | -0.010 | -0.003 | 1.00 | 3209.21 | 3237.66 |
| **DBH x Fire** | -0.012 | -0.012 | 0.018 | -0.042 | 0.018 | 1.00 | 2332.80 | 2469.12 |
| **DBH^2 x Fire** | 0.007 | 0.007 | 0.011 | -0.011 | 0.024 | 1.00 | 2432.29 | 2427.42 |
| **DBH x WPBR** | -0.012 | -0.012 | 0.016 | -0.038 | 0.015 | 1.00 | 3008.42 | 2767.14 |
| **DBH^2 x WPBR** | 0.000 | 0.000 | 0.011 | -0.018 | 0.018 | 1.00 | 3138.79 | 2684.75 |
| **DBH x BA** | 0.018 | 0.018 | 0.005 | 0.010 | 0.025 | 1.00 | 4579.41 | 3151.88 |
| **DBH^2 x BA** | -0.003 | -0.003 | 0.003 | -0.008 | 0.001 | 1.00 | 4548.37 | 2823.81 |
| **DBH x Drought** | 0.003 | 0.002 | 0.005 | -0.006 | 0.011 | 1.00 | 4215.27 | 3110.52 |
| **DBH^2 x Drought** | 0.002 | 0.002 | 0.004 | -0.004 | 0.007 | 1.00 | 4124.82 | 3026.97 |
| **DBH x Dryness** | 0.024 | 0.024 | 0.006 | 0.015 | 0.034 | 1.00 | 3594.70 | 2575.45 |
| **DBH^2 x Dryness** | -0.016 | -0.016 | 0.004 | -0.023 | -0.010 | 1.00 | 3577.96 | 2781.10 |
| **SD Plots** | 0.017 | 0.017 | 0.001 | 0.016 | 0.018 | 1.00 | 1346.76 | 2286.28 |

Table 2: Summary of results for growth sub model, giving the mean, median, standard deviation, 5th percentile, and 95th percentile of posterior samples for each parameter, plus diagnostics R-hat, effective sample size (bulk), and effective sample size (tail).

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameter** | **Mean** | **Median** | **StDev** | **q5** | **q95** | **rhat** | **ess\_bulk** | **ess\_tail** |
| **Intercept** | -2.93 | -2.92 | 0.22 | -3.29 | -2.56 | 1.00 | 2564.66 | 2375.05 |
| **NB Dispersion** | 0.06 | 0.06 | 0.03 | 0.03 | 0.12 | 1.00 | 2990.07 | 2402.26 |

Table 3: Summary of results for recruitment sub model, giving the mean, median, standard deviation, 5th percentile, and 95th percentile of posterior samples for each parameter, plus diagnostics R-hat, effective sample size (bulk), and effective sample size (tail).

# Figures

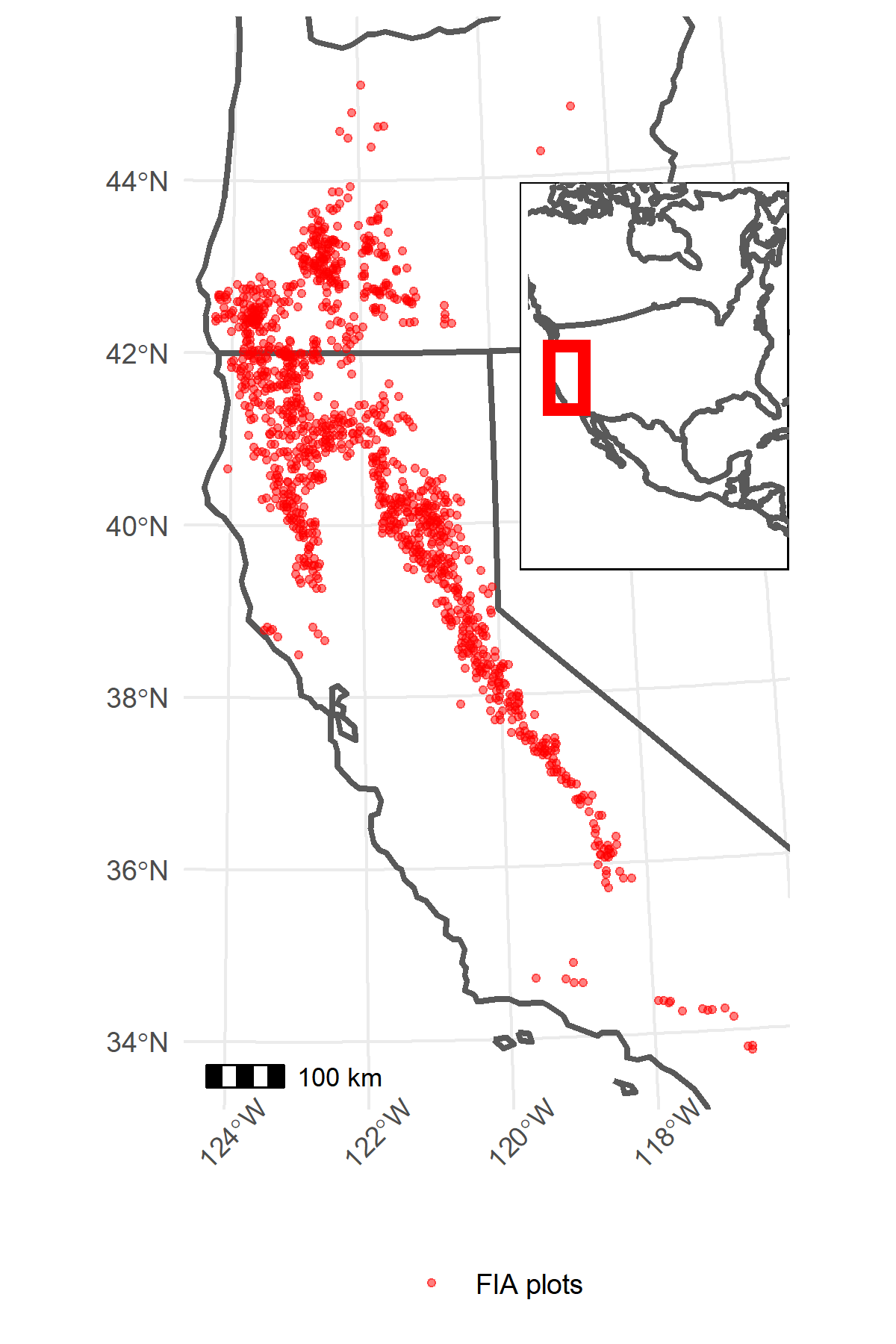


Figure 1: 1,221 Forest Inventory and Analysis (FIA) plots where live sugar pine was present at initial measurement (2001-2009) or remeasurement (2010-2019) with US state borders. Plot locations based on the nominal, rather than true, coordinates. Inset shows position relative to North America and national borders.

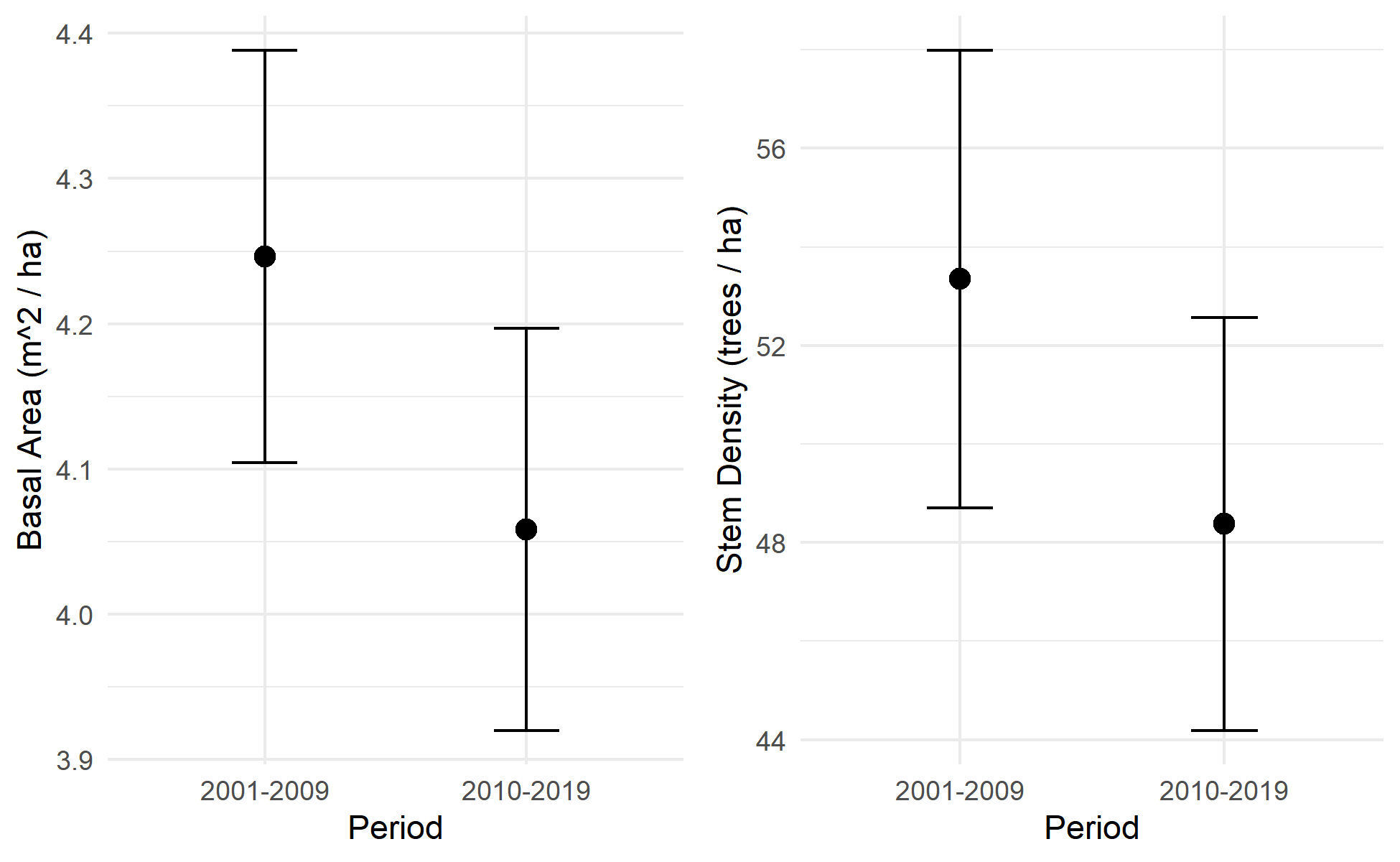


Figure : Changes in plot-level basal area and stems per hectare for 1,221 plots where sugar pine was present at initial measurement (2001-2009) or remeasurement (2010-2019). Points are means and error bars are +/- one standard error across plots. Totals include only stems greater than or equal to 2.54 cm DBH.

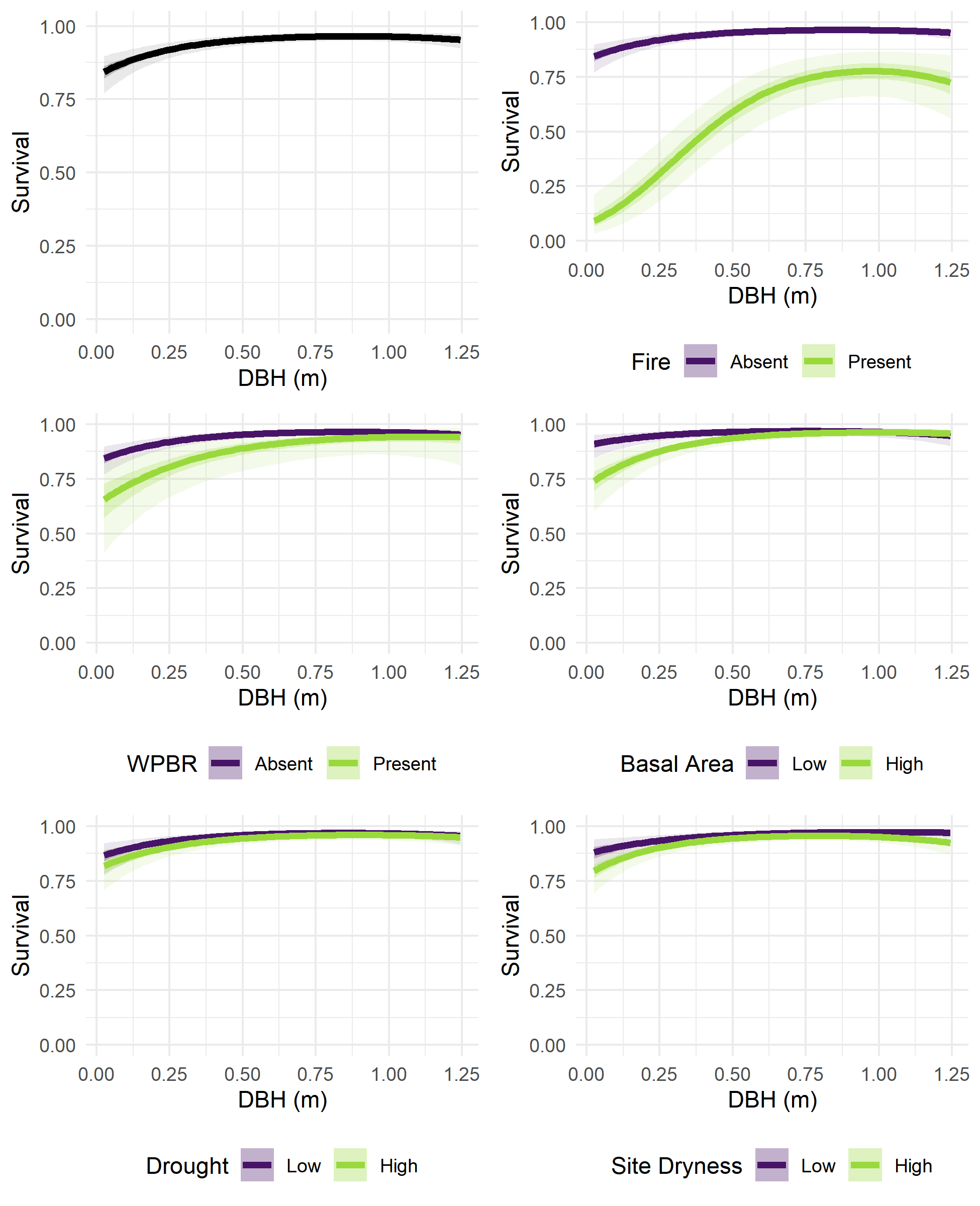


Figure 3: Fixed effects of initial DBH, fire, WPBR, neighborhood basal area, drought, and site dryness on 10-year survival probability. In the top left panel, probability of survival (Y-axis) is predicted for stems of various initial size (X-axis), holding other variables at “Absent” (for fire and WPBR) or 0 (scaled mean, for basal area, drought, and site dryness). In the other panels, probability of survival is predicted for stems of various sizes and across two levels of each other explanatory variable: with or without disturbance, or at high (1.0) or low (-1.0) values for scaled continuous variables. Predictions were generated using the posterior samples for model parameters, resulting in a range of predicted survival for each set of explanatory variable values. Lines show the median predicted survival, darker ribbons show a 50% credible interval, and lighter ribbons show a 95% credible interval. Random effects were held at 0. 1.25 m is approximately the 95th percentile DBH of trees used to train the model.

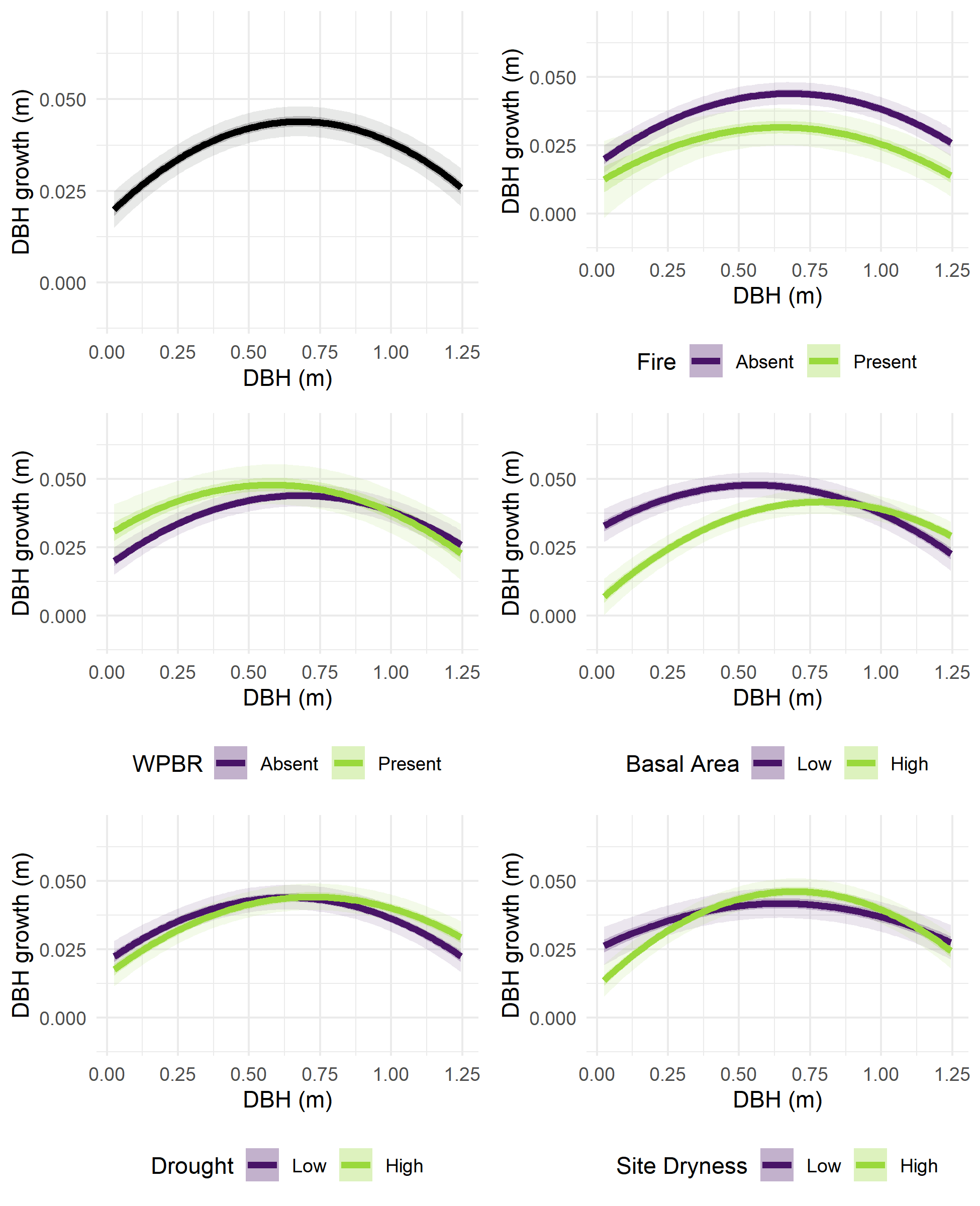


Figure 4: Fixed effects of initial DBH, fire, WPBR, neighborhood basal area, drought, and site dryness on 10-year diameter growth. In the top left panel, DBH growth over the 10 years between censuses (Y-axis) is predicted for stems of various initial size (X-axis), holding other variables at “Absent” (for fire and WPBR) or 0 (scaled mean, for basal area, drought, and site dryness). In the other panels, growth is predicted for stems of various sizes and across two levels of each other explanatory variable: with or without disturbance, or at high (1.0) or low (-1.0) values for scaled continuous variables. Predictions were generated using the posterior samples for model parameters, resulting in a range of predicted survival for each set of explanatory variable values. Lines show the median predicted survival, darker ribbons show a 50% credible interval, and lighter ribbons show a 95% credible interval. Random effects were held at 0.

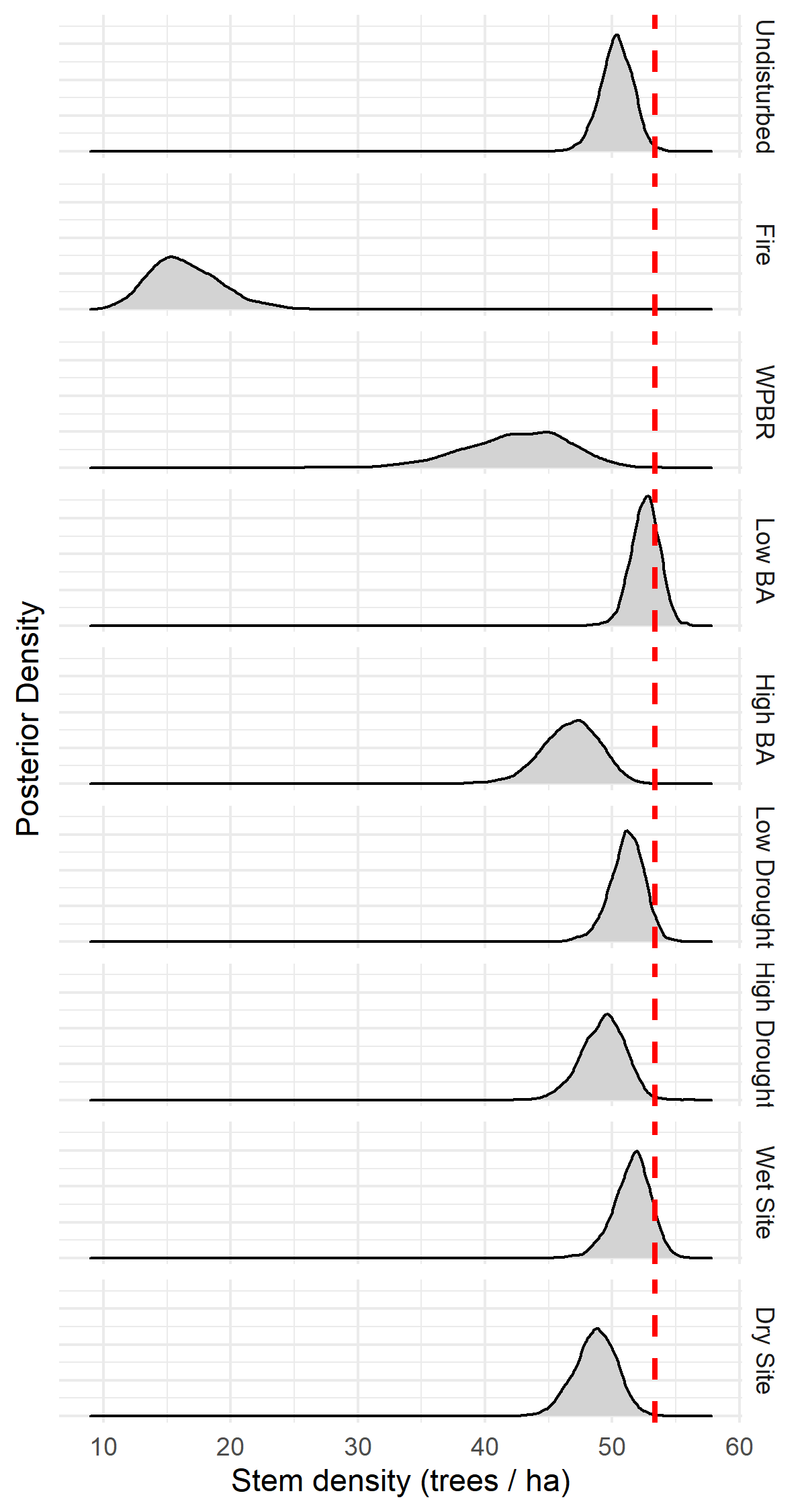


Figure : Posterior distribution of projected stem density (starting with observed mean density) under a variety of hypothetical scenarios, each corresponding to the presence or absence of a specific stressor. In the “Undisturbed” scenario, all fixed effect covariates other than the intercept are held at 0 (representing the absence of fire and WPBR, and basal area, drought, and site dryness at average levels). In each other scenario, a single stressor is set to TRUE (for fire and WPBR), -1 (low levels of basal area, drought, or site dryness), or +1 (high levels of basal area, drought, or site dryness). Random effect values are held at 0, representing an average plot in an average ecoregion.

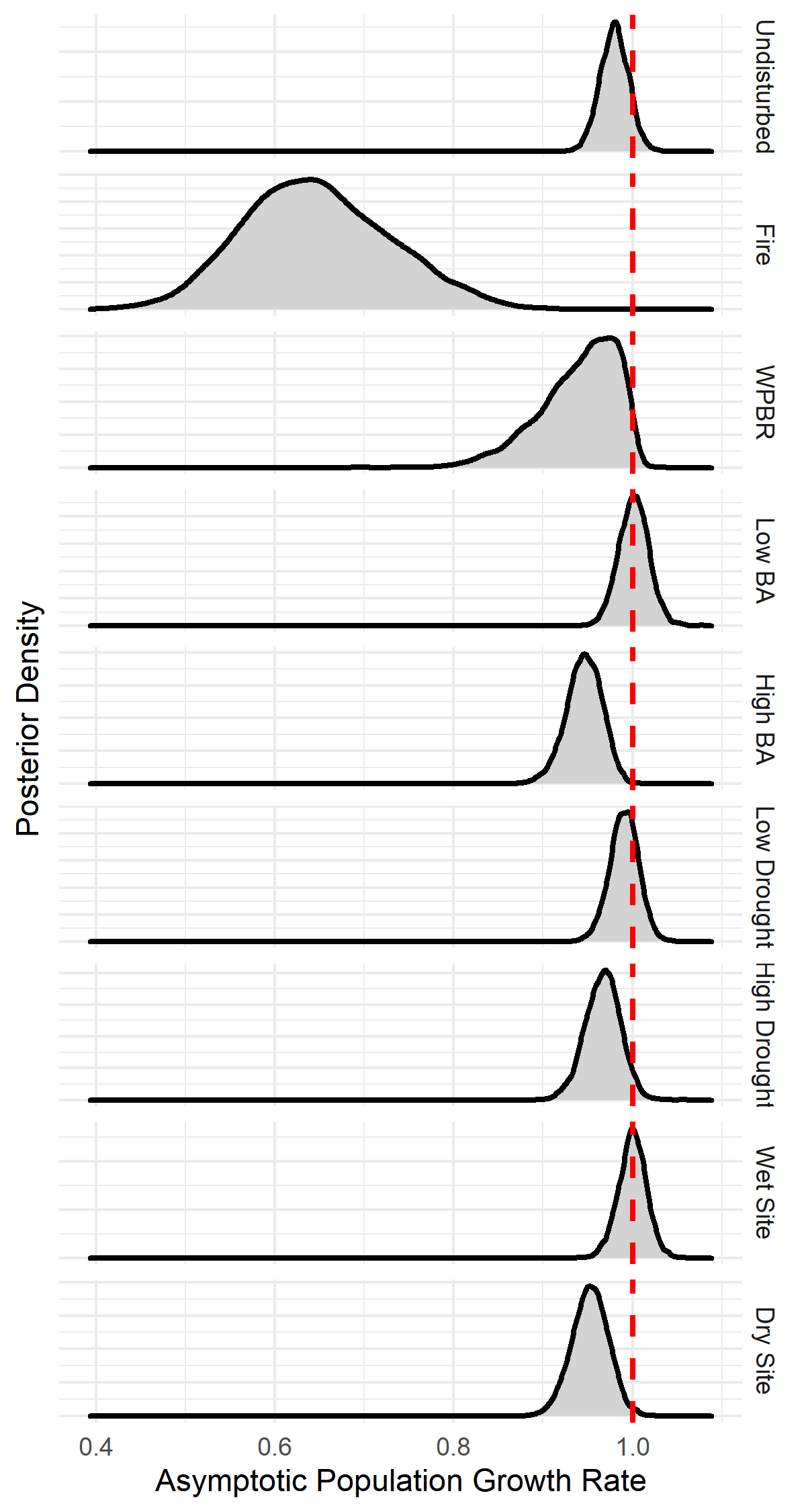
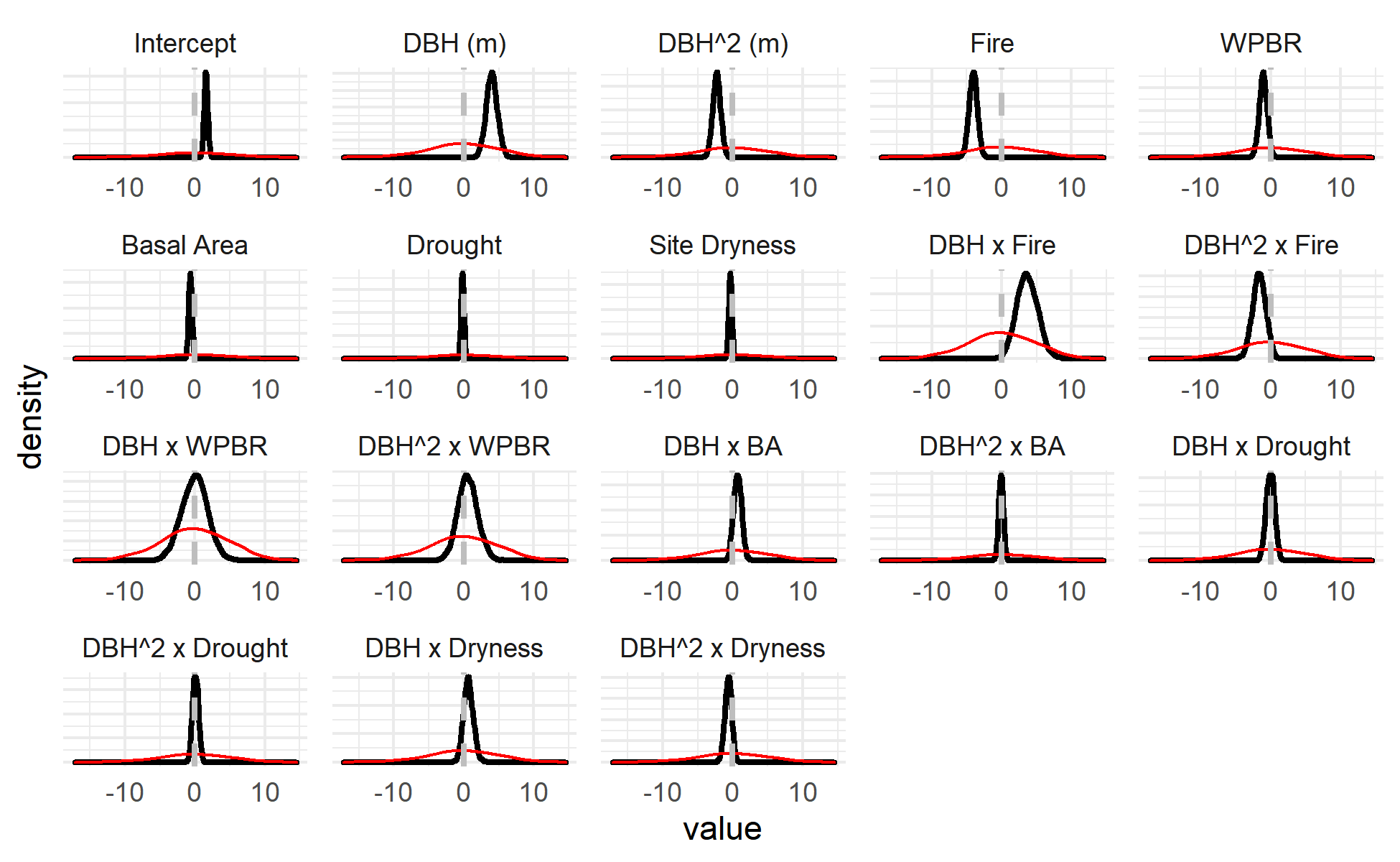
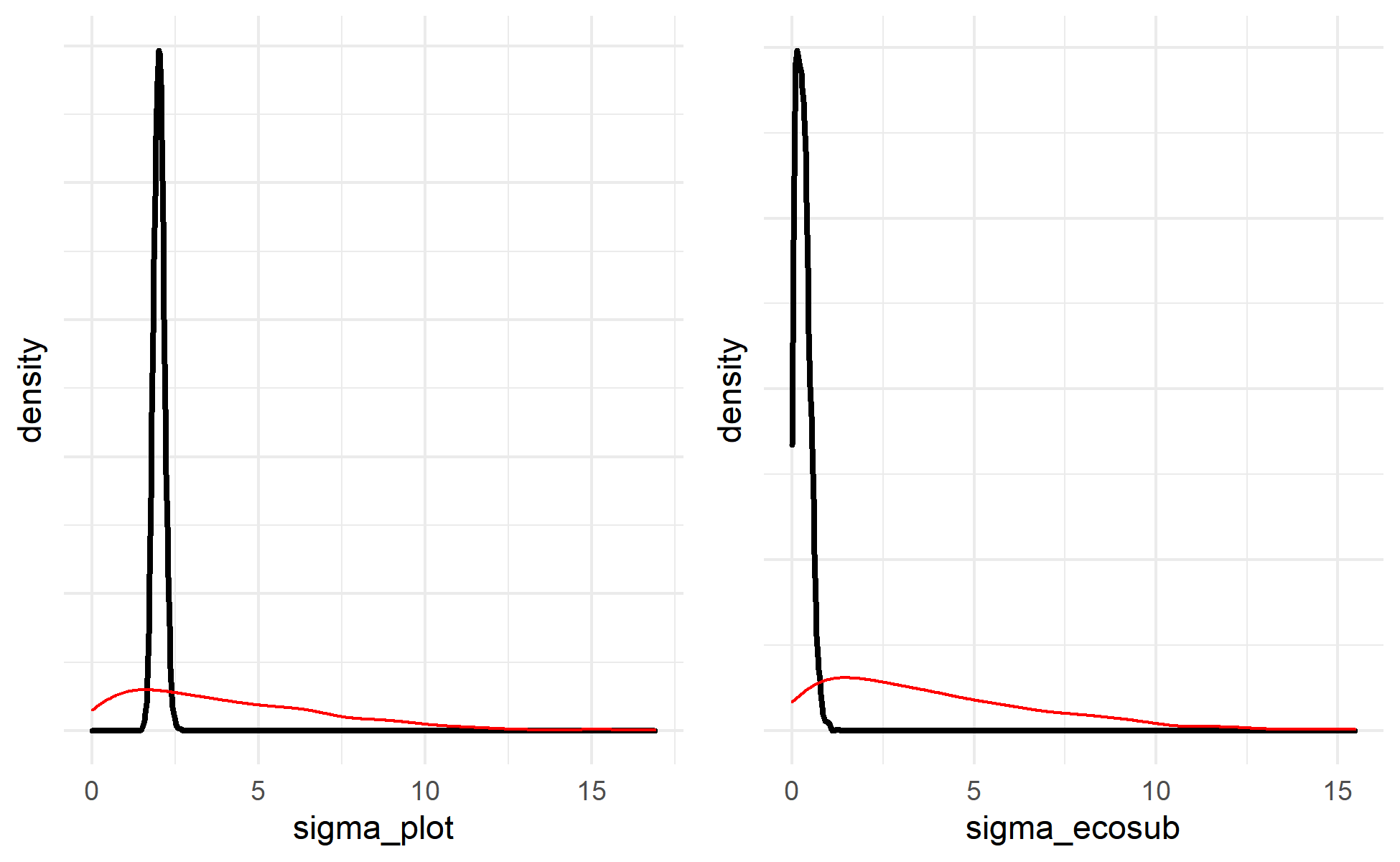


Figure 6: Posterior distribution of asymptotic population growth rate. In the “Undisturbed” scenario, all fixed effect covariates other than the intercept are held at 0 (representing the absence of fire and WPBR, and basal area, drought, and site dryness at average levels). In each other scenario, a single stressor is set to TRUE (for fire and WPBR), -1 (low levels of basal area, drought, or site dryness), or +1 (high levels of basal area, drought, or site dryness). Random effect values are held at 0, representing an average plot in an average ecoregion.

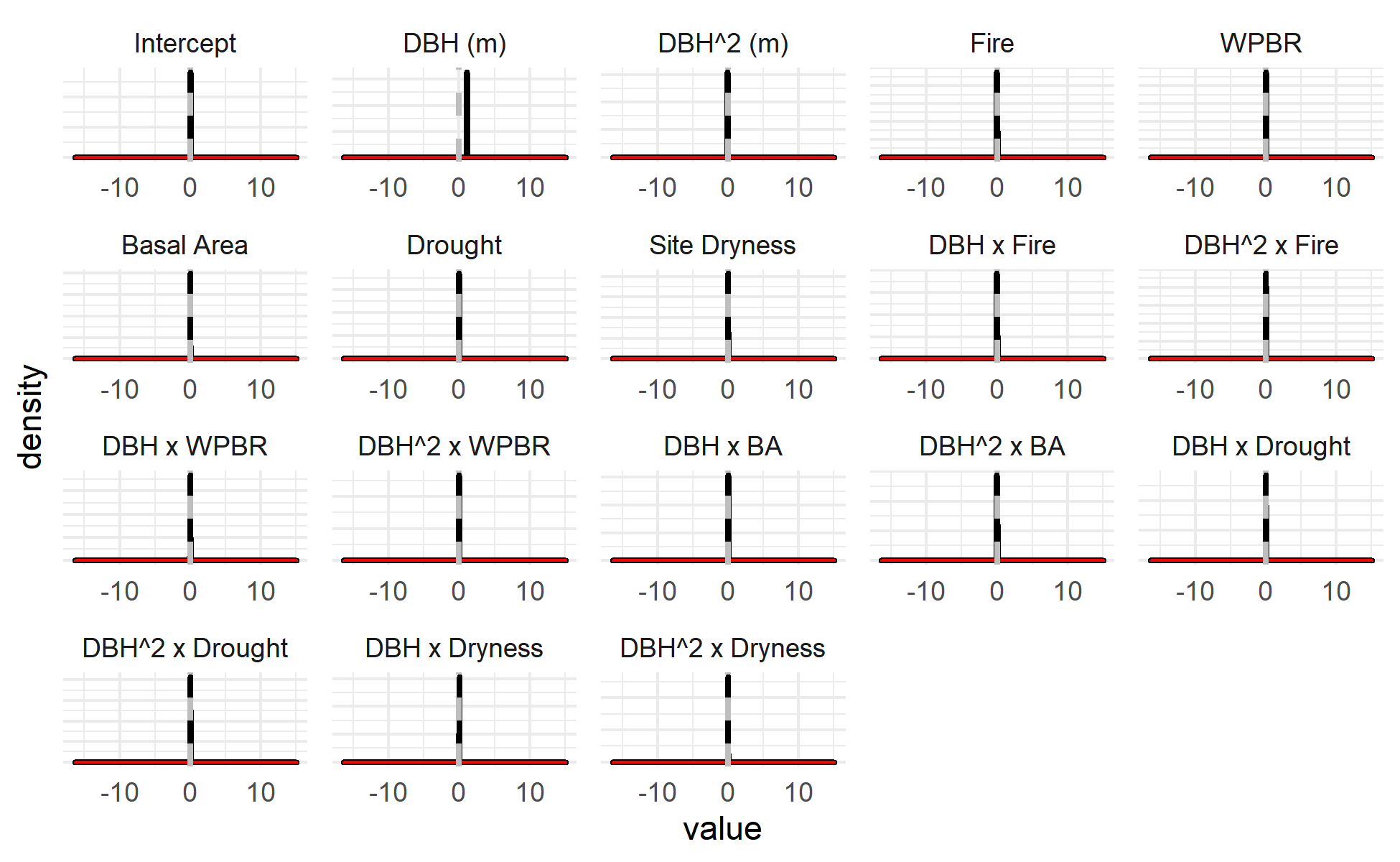
# Supplementary Materials



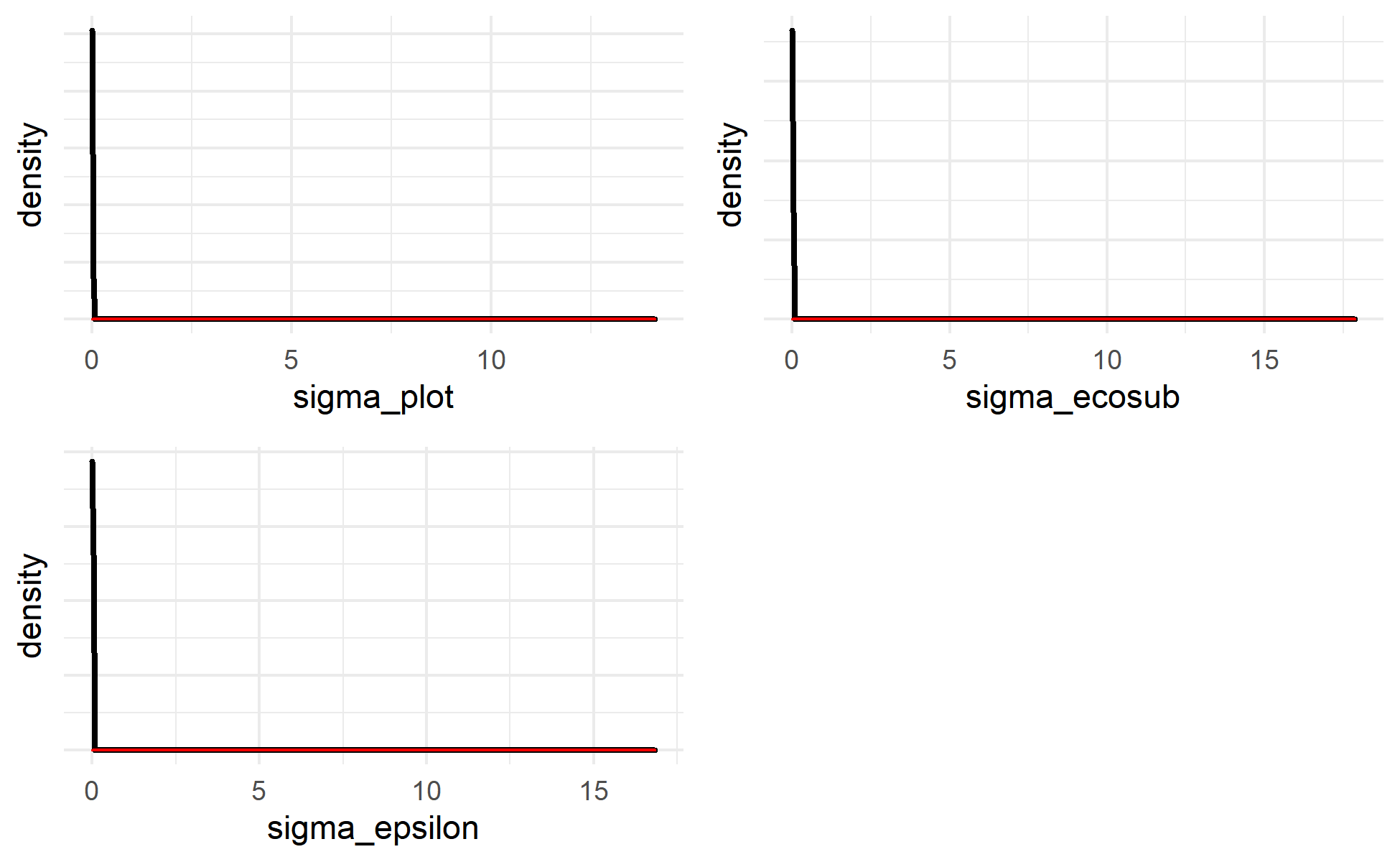
Supplementary Figure 1: Posterior distributions (black) and prior distributions (red) for , the fixed effect coefficients for survival. The magnitude of the discrepancy between the two indicates the extent to which the posterior distribution was informed by the data, rather than the prior.



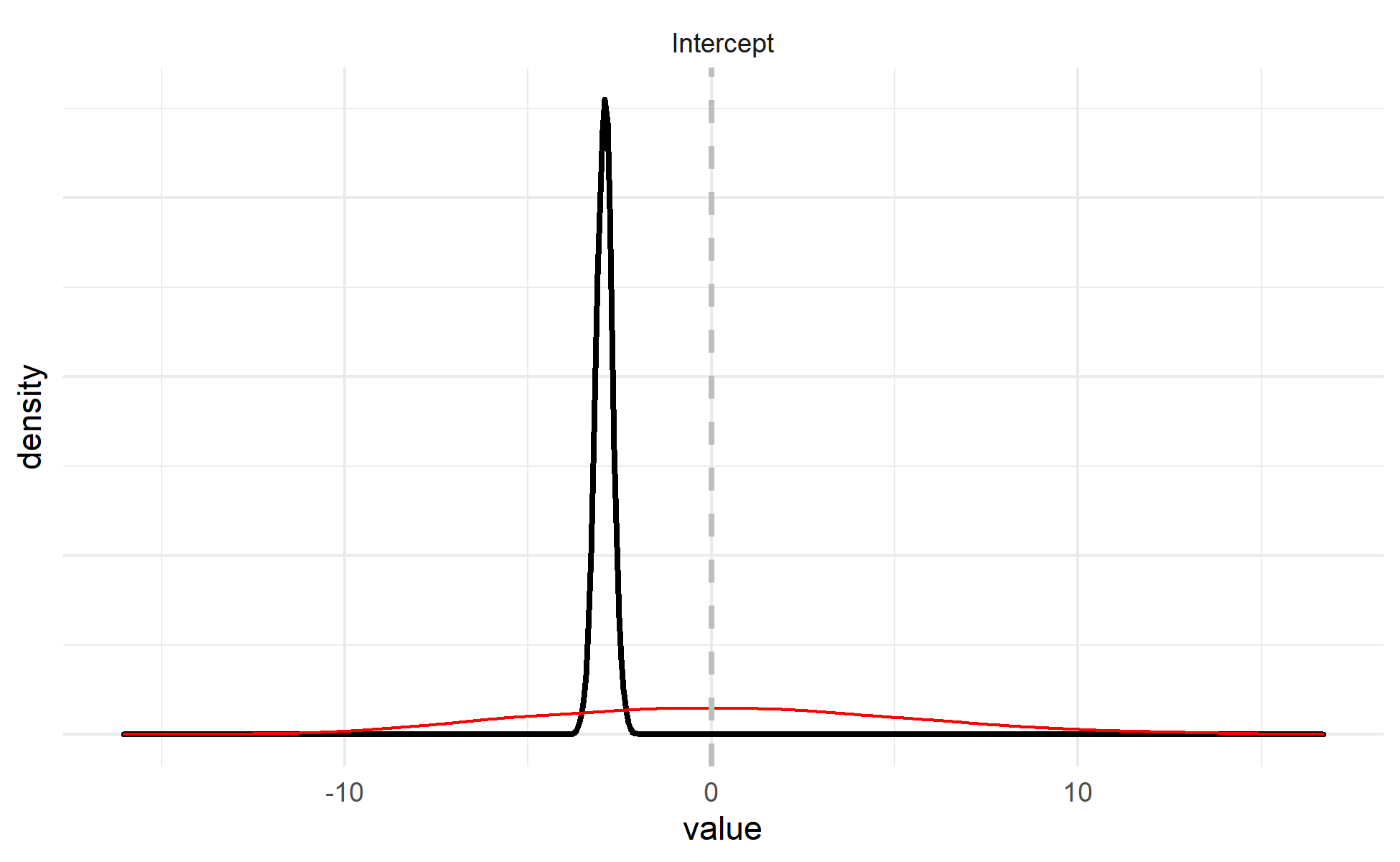
Supplementary Figure 2: Posterior distributions (black) against prior distributions (red) for the standard deviations of the plot and ecoregion random effects in the survival model.



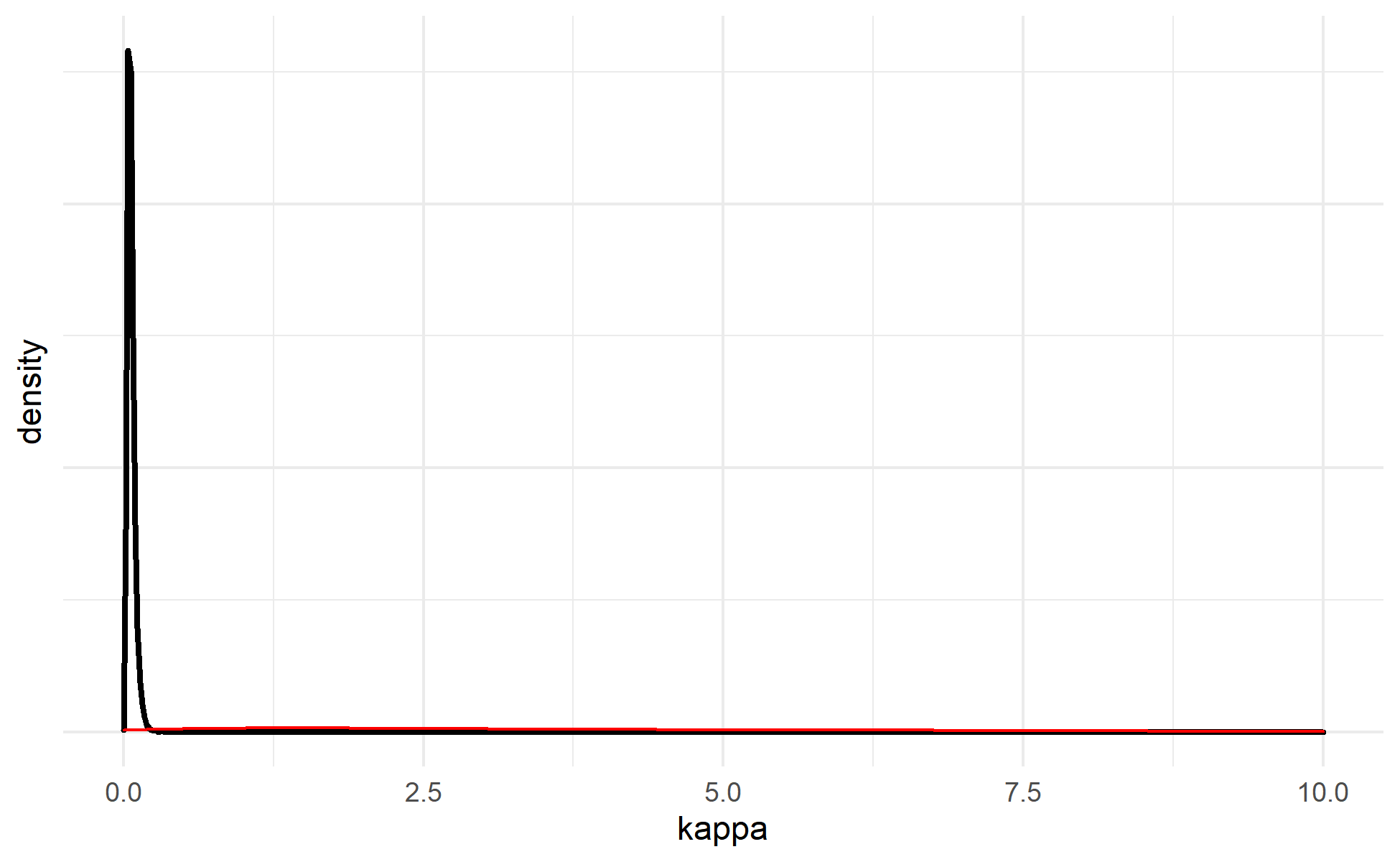
Supplementary Figure 3: Posterior distributions (black) against prior distributions (red) for fixed effect coefficients in the growth model.



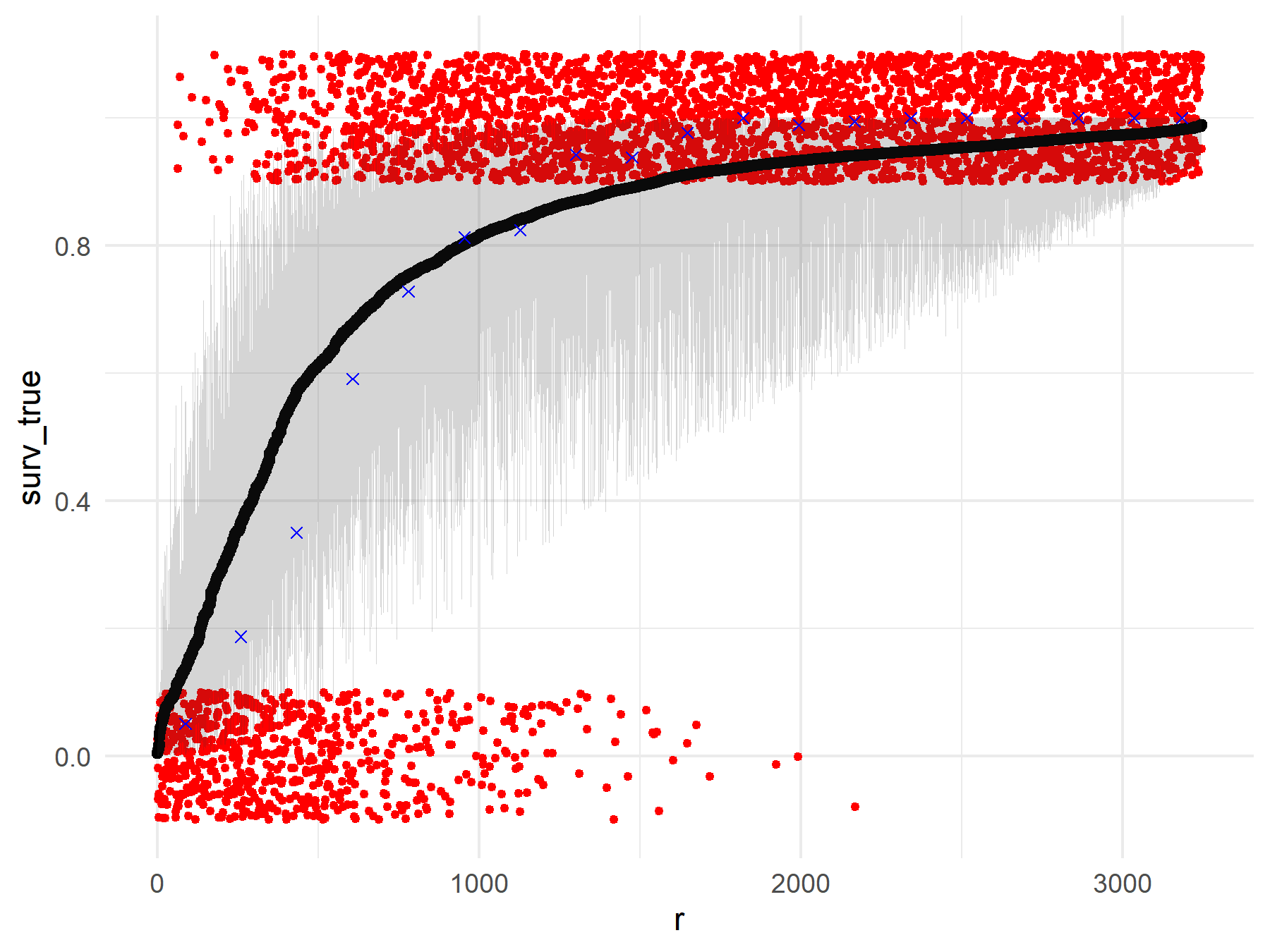
Supplementary Figure 4: Posterior distributions (black, along Y axis) against prior distributions (red, along X axis) for the standard deviations of the plot random effect, the ecoregion random effect, and the residuals in the growth model.



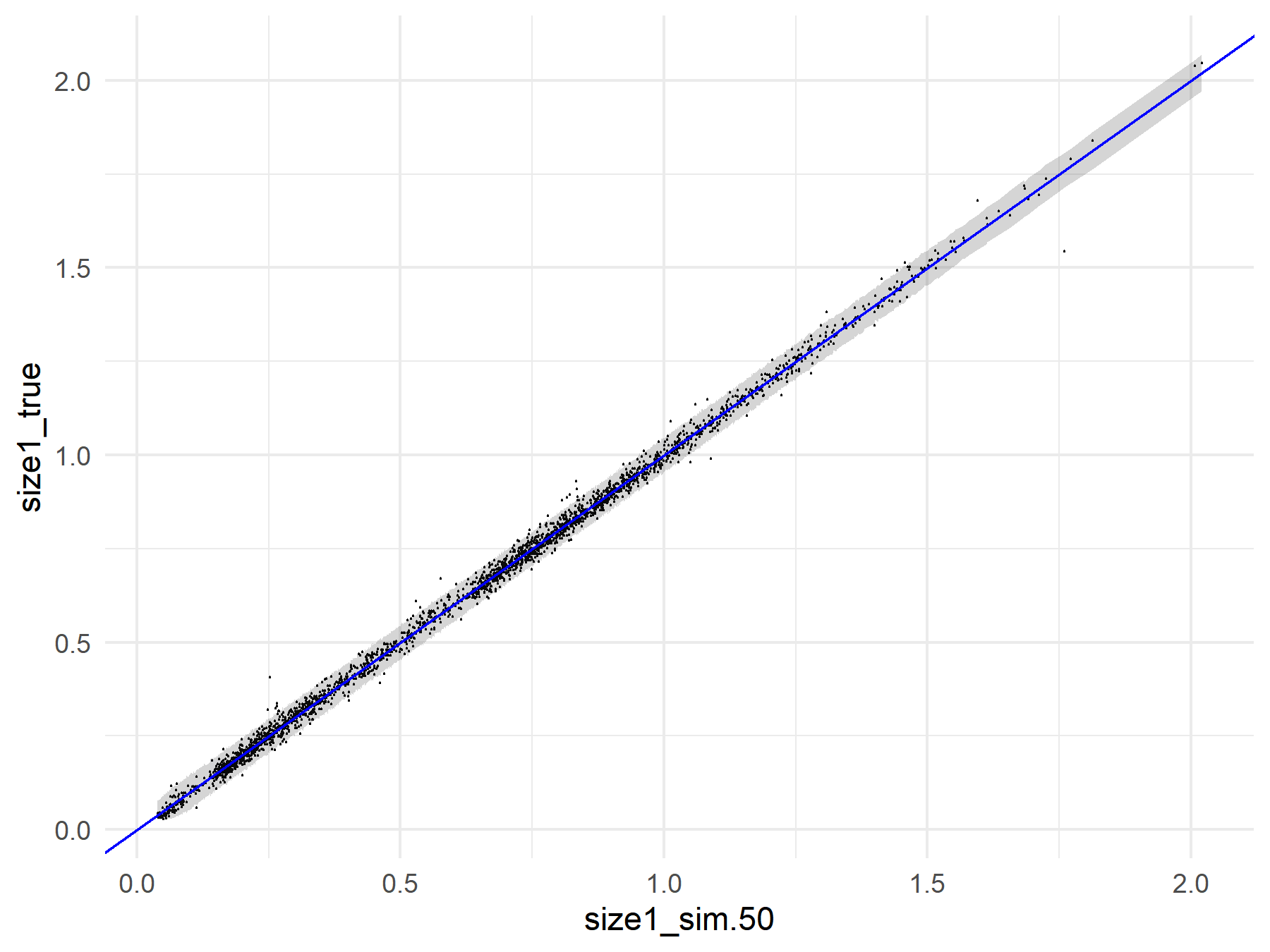
Supplementary Figure 5: Posterior distributions (black) against prior distributions (red) for the fixed effect coefficients affecting fecundity in the recruitment model.



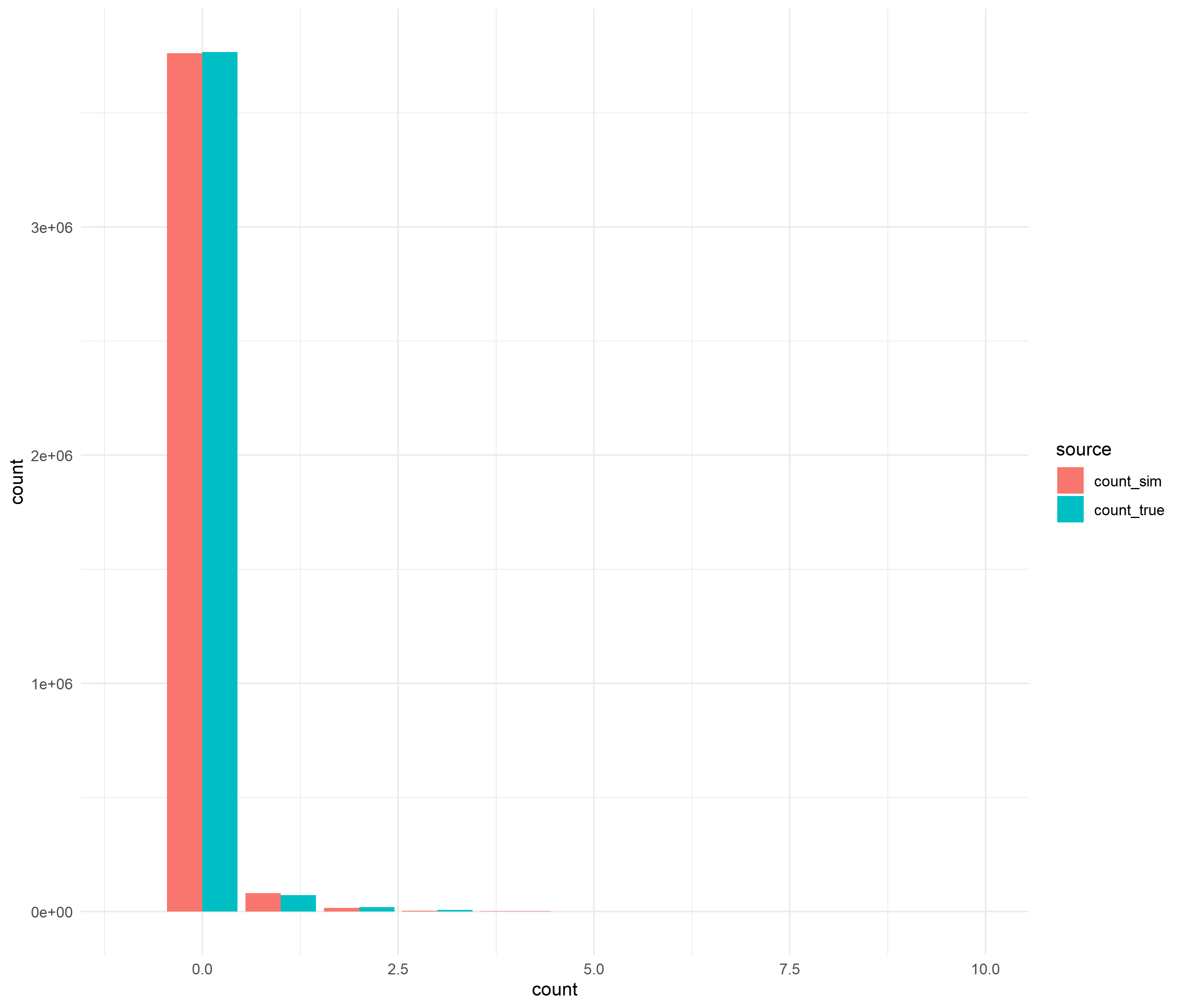
Supplementary Figure 6: Posterior distribution (black, along Y axis) against prior distribution (red, along X axis) for the dispersion term of the negative binomial response in the recruitment model.



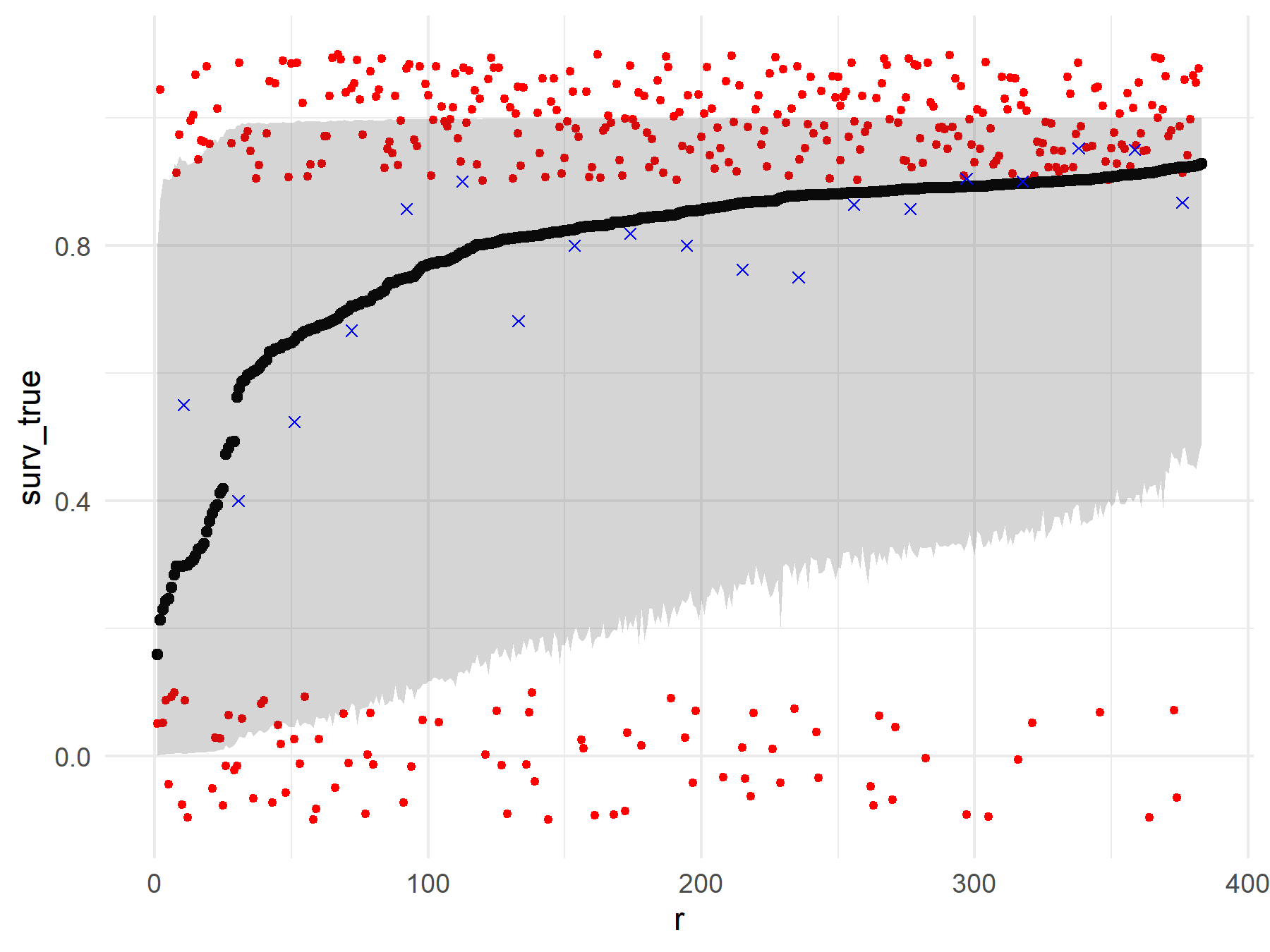
Supplementary Figure 7: Results of posterior retrodictive simulations for survival of individual trees. Posterior samples of the parameters were used to predict the survival probability of each individual tree using Equation 2 and the training data used to fit the model. Individual trees (red points) are ranked along the X-axis by their mean predicted survival probability, and their actual survival (0 or 1) is plotted along the Y-axis (including a jitter for readability). Blue points indicate the actual proportion of individuals in each rank bin which survived. Black points indicate the mean predicted survival for each individual, with a gray ribbon showing a 95% credible interval for survival probability for each individual. The model does a good job ranking trees by their actual survival probability, as shown by the red points. However, the model is slightly under-certain about survival probability, relative to reality: It slightly overpredicts survival for the least-likely-to-survive trees, and slightly underpredicts survival for the most-likely-to-survive trees.



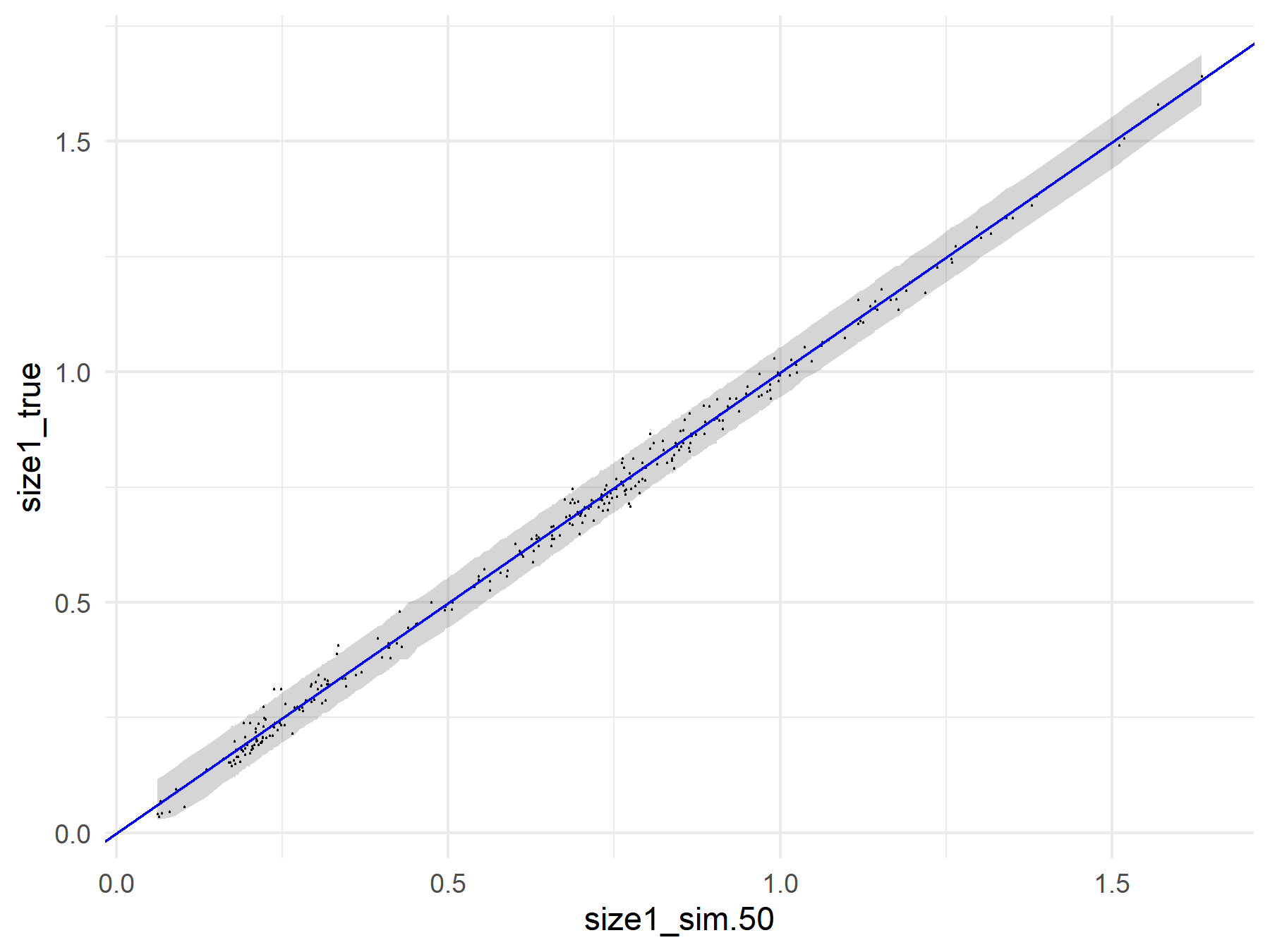
Supplementary Figure 8: Posterior retrodictions for the growth model, using posterior parameter values and the training data. Individual trees (black points) are plotted with their median predicted size at remeasurement along the X-axis, and their true size at remeasurement along the y axis. The blue line has slope 1 and intercept 0, i.e. perfect prediction. The gray ribbon gives a 95% credible interval for size at remeasurement as predicted by the model, and contains nearly all of the true sizes.



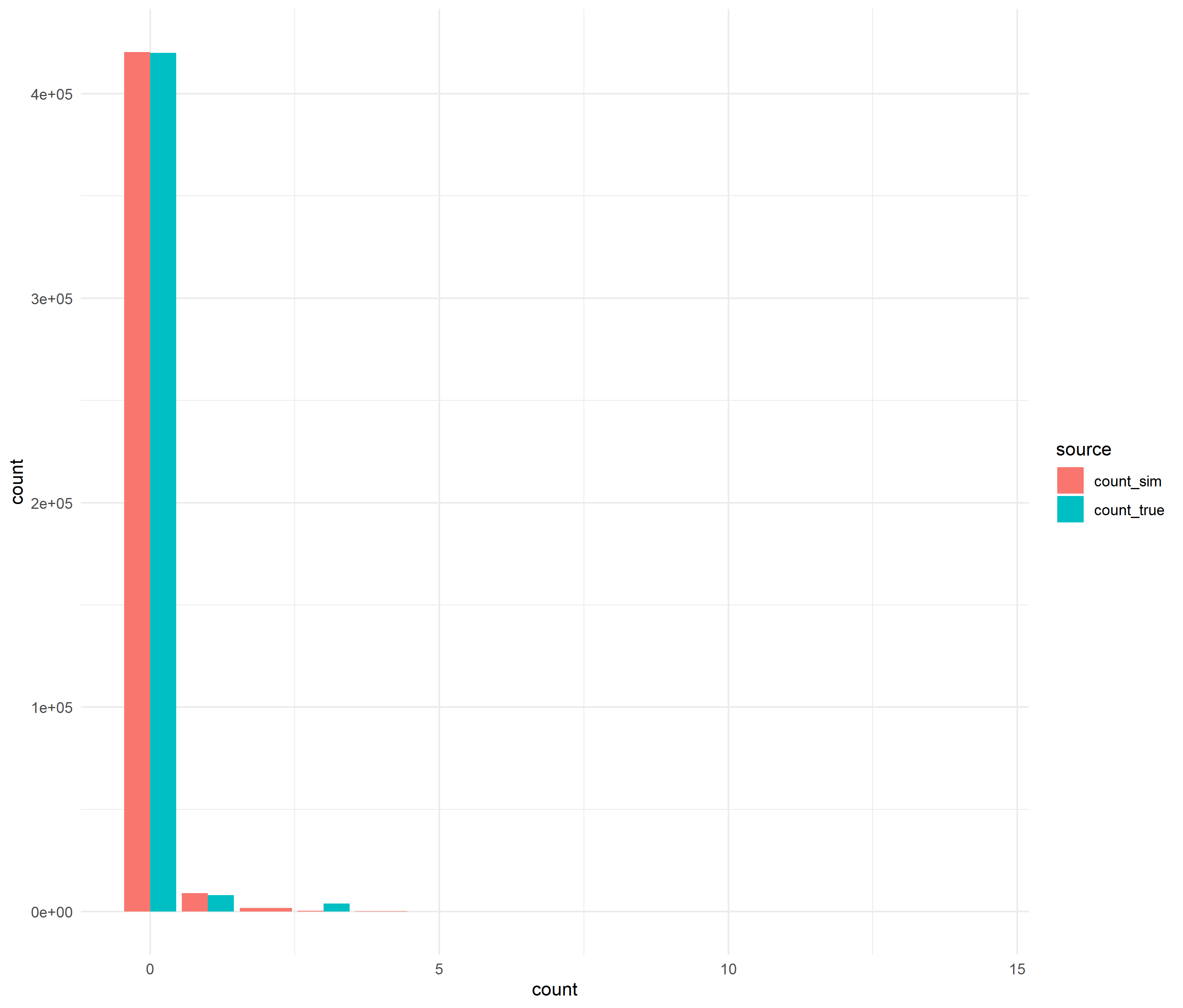
Supplementary Figure 9: Posterior retrodictions for the recruitment model. Histograms of simulated (one simulation per posterior draw) and observed per-plot counts of new recruits are plotted. The frequency distribution of simulated counts (red) closely matches the observed distribution (blue).



Supplementary Figure 10: Results of posterior predictive simulations for survival of individual trees. Posterior samples of the parameters were used to predict the survival probability of each individual tree using Equation 2 and the validation data. Individual trees (red points) are ranked along the X-axis by their mean predicted survival probability, and their actual survival (0 or 1) is plotted along the Y-axis (including a jitter for readability). Blue points indicate the actual proportion of individuals in each rank bin which survived. Black points indicate the mean predicted survival for each individual, with a gray ribbon showing a 95% credible interval for survival probability for each individual.



Supplementary Figure 11: Posterior retrodictions for the growth model, using posterior parameter values and the validation data. Individual trees (black points) are plotted with their median predicted size at remeasurement along the X-axis, and their true size at remeasurement along the y axis. The blue line has slope 1 and intercept 0, i.e. perfect prediction. The gray ribbon gives a 95% credible interval for size at remeasurement as predicted by the model, and contains nearly all of the true sizes.



Supplementary Figure 12: Posterior predictions for the recruitment model, using the out-of-sample validation data. Histograms of simulated (one simulation per posterior draw) and observed per-plot counts of new recruits are plotted. The frequency distribution of simulated counts (red) closely matches the observed distribution (blue).

|  |  |  |  |
| --- | --- | --- | --- |
| **Scenario** | **Lambda (median)** | **Lambda (5th percentile)** | **Lambda (95th percentile)** |
| **Undisturbed** | 0.980 | 0.953 | 1.005 |
| **Fire** | 0.643 | 0.521 | 0.788 |
| **WPBR** | 0.948 | 0.857 | 0.994 |
| **Low BA** | 1.002 | 0.974 | 1.029 |
| **High BA** | 0.946 | 0.912 | 0.977 |
| **Low Drought** | 0.991 | 0.963 | 1.017 |
| **High Drought** | 0.967 | 0.933 | 0.998 |
| **Wet Site** | 1.000 | 0.974 | 1.025 |
| **Dry Site** | 0.953 | 0.918 | 0.986 |

Supplementary Table 1: Summary of posterior distributions of population asymptotic growth rate () under a variety of idealized scenarios. In each scenario, the relevant stressor is either present (for fire and WPBR), elevated (BA, drought, and site dryness), or depressed (BA, drought, and site dryness), while other stressors are held at absent (fire and WPBR) or their mean value (BA, drought, and site dryness). was estimated for each posterior sample by constructing a transition matrix using the posterior sample parameters and the vital rate as described in the methods, and taking the dominant eigenvalue of the transition matrix.