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 (particularly of small individuals) 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 strongly 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

1. This study as an example of using national inventory data to build demographic models which inform management decisions about anthropogenic stressors
   1. Novel Anthropogenic stressors threaten species, but may be amenable to management
   2. They may be amenable to management, but conservation resources are scarce, so is often necessary to prioritize some stressors over others
   3. Demographic models built around large-scale longitudinal datasets (such as FIA) can provide detailed insight how stressors impact species of concern across wide geographic ranges.
   4. By including multiple stressors in the model and 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 the highlight the mechanisms by which they influence the population trajectory.
   5. Findings from these analyses can provide crucial information about how best to prioritize varied stressors in making management decisions.

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 most of the growing stock located in California. Sugar pine seeds are an important food source for animal species (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.*, 2018). 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).

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 relative importance of the various stressors acting on sugar pine?
2. What are the current population dynamics across the range-wide ensemble of sugar pine populations?

# 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 1,102 FIA plots from California and Oregon where live sugar pine was present at initial measurement from 2001-2010 (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. 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 salvage harvests on some land ownerships across the range of sugar pine make it likely that some mortalities caused by fire, drought, or disease were later harvested.

The smallest stems surveyed (height ≥ 0.15 m and DBH < 2.54 cm) are not inventoried as individuals but tallied by species and remain untagged. Thus, the individuals which are untagged at the time of the second census are either new recruits (i.e., they were not present at the initial measurement) or were not tagged due to small size at initial measurement (i.e., they were present at the initial measurement). An embedded integral projection model, described below, allowed us to use the counts of untagged individuals < 2.54 cm DBH on each plot to estimate the parameters of the fecundity function despite fecundity being only indirectly observed through these counts. Only 379 plots were used to estimate the fecundity parameters, because the sampling protocol for tallying seedlings (individuals < 2.54 cm DBH) has changed over time, and we restricted analysis to plots where both initial and remeasurement observations use the latest protocol (FIA manual version >= 2.0).

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.

## 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 Model

The modelling approach for this study broadly follows that described in Shriver et al. (2021). In short, this study models three vital demographic rates for sugar pine as functions of individual states and environmental covariates. The vital rates modeled are survival, growth, and fecundity. Survival and growth of individuals are directly observed as data, but fecundity is only indirectly observed through the count of untagged individuals at remeasurement (which includes both new recruits and small survivors). The three sub models were analyzed as a single model, so that the findings of the survival and growth sub models could inform the fecundity model; see below for details.

The sub 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.

The sub 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 biologically impossible negative size), 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, except that a quadratic effect of initial size (and the associated interactions) were omitted because the Hamiltonian Monte Carlo sampling algorithm experienced divergent transitions when attempting to fit models including a quadratic effect of initial size on size at remeasurement. Visual data exploration did not reveal any evidence of a quadratic effect of initial size on size at remeasurement.

As noted in Shriver et al. (2021), analysis of recruitment is complicated by the fact that seedlings (stems whose height >= 0.15 m and DBH < 0.0254 m) are not individually surveyed and tagged, but instead tallied by species. Thus, there is uncertainty as to which of the seedlings present at remeasurement are true new recruits (vs. individuals which were already present at the initial measurement). We followed the approach of Shriver et al. (2021) to address this issue by building a recruitment model which is itself an integral projection model describing the survival, growth, and recruitment of seedlings. In this way, the number of new seedlings on each plot can be estimated as a latent state based on a count of all seedlings at remeasurement and the estimated (from the survival and growth sub models) rates of growth and survival among pre-existing seedlings.

The response distribution for the fecundity sub model is:

Equation 5

where is the observed count of seedlings on plot at remeasurement, which includes both new recruits and individuals which were present but untagged due to their small size at the initial measurement. is a vector containing the area-standardized occurrence rates of 100 0.0254 m wide DBH size classes (ranging from 0 to 2.54 m) on plot at remeasurement, is the first element of and is the area-standardized occurrence rate of seedlings (size class 1) at remeasurement, gives the total plot area surveyed for seedlings, and is the dispersion parameter for the negative binomial distribution. The largest observed individual in the data is 2.45 m.

The area-standardized occurrence rates of all size classes at remeasurement, , is the product of an integral projection model transition kernel and the area-standardized occurrence rates of the same size classes at initial measurement:

Equation 6

where each is a discretized integral projection model kernel describing the rates of transition from each of size classes into size classes, 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 plot-specific covariates, as described below. A separate exists for each plot . is the vector giving the area-standardized occurrence rates of individuals in each of the 100 size classes at initial measurement on plot , which are observed data. The elements of for each plot are given by:

Equation 7

where is the proportion of surviving individuals in class which grow into class during the census interval on plot , is the probability that an individual in size class will survive the 10-year census interval on plot , 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 in size class plot (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 8

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 (the minimum possible 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 plot and size class from Equation 4 using the midpoint DBH of size class and the environmental covariates associated with plot . Note that because we are modelling the count of untagged individuals, which by the sampling design must have been in size class 1 at initial measurement, there are no untagged individuals growing from other size classes into size class 1, so when .

Likewise, is calculated using Equation 2 to predict the survival of an individual whose DBH is equal to the midpoint of size class on plot . Shriver et al. (2021) estimated using a normalized gaussian kernel but had difficulty estimating the mean and variance of this recruit size kernel. During model testing for this study, attempting to estimate the parameters for this kernel resulted in divergent transitions in the Hamiltonian Monte Carlo algorithm described below. Rather than attempt to estimate the mean and variance of a gaussian recruitment size kernel, we assume that all true new recruits during the 10 year census interval fell into the seedling size class (size class 1) at remeasurement census, based on existing literature documenting growth rates for sugar pine seedlings (Harry, Jenkinson and Kinloch, 1983; York *et al.*, 2004; Angell, Waring and Graves, 2014) and the fact that new recruits have, on average, 5 years to grow until being observed in the remeasurement census. Therefore, we use .

Finally, the parameter of primary interest in the recruitment sub model is , the fecundity of individuals in size class on plot :

Equation 9

where is a row vector of fixed effects covariates for size class on plot , again using the midpoint DBH of size class to approximate the size of an individual in class . The covariates and parameters are as described for the survival sub model, with a quadratic effect of size and associated interactions, though here indexed by to indicate that these are the parameters for the fecundity sub model. A random effect for plot was not included in the fecundity sub model because there is only one observation (count of untagged individuals at remeasurement) per plot.

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. Other R packages used for data acquisition, data management, and plotting include: here, sf, spdata, bayesplot, posterior, units, raster, ggplot2, USAboundaries, truncnorm, cowplot, foreach, and doParallel.

## 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, individual survival, and plot-level count of seedlings to assess whether model results were consistent with real data.

## Evaluation of vital rate functions and integral projection model

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, survival, and fecundity. 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 0-2.54 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.

For this paper, three suites of IPMs were constructed. The first suite of IPMs was used for estimating the parameters for the fecundity function, and is described above. In the second suite of IPMs, w each draw of posterior parameter values to generate an integral projection model kernel and compute posterior asymptotic growth rates under the suite of idealized environmental scenarios described above. The structure of the integral projection models for the second suite mostly mirrors that used in the parameter estimation stage, using the same 100 size classes and vital rate discretization to construct a unique transition kernel for each environmental context and posterior sample .

The first difference between the construction of the IPM for results interpretation and the IPM used in parameter estimation is that, because we are interested in all individuals and not just untagged ones, the growth kernel is simplified to:

Equation 10

with the same variable meanings as in Equation 8. The second difference is that random effects were omitted to better understand the effects of the stressors, which are represented by the fixed effects. 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 idealized plot . 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.

# Results

## 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, the interaction of size with fire affecting fecundity, and the interaction between size and WPBR affecting fecundity. This uncertainty regarding fecundity parameters was likely due to the fact that fecundity was not directly observed, and the 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 p\_s < 0.8, and true survival rates were slightly higher than predicted survival rates for p\_s > 0.8. Some plots with relatively high predicted seedling counts actually had few or no seedlings (which was within the expected range of variation). 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 was slightly under-predicted, though again within the expected range of variation. For the growth model, the central tendency and expected variation in posterior predictions agreed well with both the training and validation data.

## 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 rapidly falling off for the largest stems to just 5.6% for a stem with 2.50 m DBH (Figure 2), though with relatively large uncertainty because there were few extremely large individuals. The rapid declines in survival for the largest individuals are striking but in line with the data, where of the 5 individuals larger than 2.00 m, only two survived to remeasurement. There was a strong negative main effect of fire and a positive interaction between fire and size, indicating that fire substantially reduced survival, particularly for smaller trees (Figure 2). There were moderate negative effects of WPBR and basal area on survival, and a positive interaction between basal area and size. 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 0.038, with a 90% credible interval from 0.034 to 0.041 (Table 2). The effect of initial size was, as expected, very close to 1. Together, these results indicate that the smallest trees trees grew an average 3.8 cm DBH in the 10 years between initial and follow-up census, with larger trees growing slightly more (Figure 3). Fire had weak or no effect on growth of the smallest trees, but did reduce the growth of larger stems. By contrast, basal area reduced the growth of small stems but not large ones. Site dryness had a negative main effect and a positive interaction with initial size: For the smallest stems growth was lower on dry sites, whereas for stems above approximately 0.60 m growth was higher on dry sites. Other effects were weak or uncertain.

## Fecundity

As with survival, there was a positive effect of size on fecundity and a negative quadratic effect of size (Table 3). The predicted number of new seedlings in a 10-year census per existing individual climbed from 0.02 for individuals of 0 m DBH to a maximum of 1.14 for individuals of 1.74 m DBH, before declining to 0.53 for individuals of 2.5m DBH (Figure 4). Fecundity was slightly higher on drier sites, except for the largest individuals. There was a positive interaction between WPBR and size on fecundity and a negative interaction between squared size and WPBR, though there was considerable uncertainty about the magnitudes of each: The relationship between size and fecundity was steeper on plots with WPBR. By contrast, basal area had a negative interaction with size and a positive interaction with squared size, so the relationship between size and fecundity was less steep on plots with high basal area. Other effects were weak or uncertain.

## Asymptotic Population Growth Rates

Figure 5 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 0 (their scaled means). Under these circumstances, the asymptotic growth rate is above 1, with a median posterior value of of 1.04 and a 90% credible interval from 1.01 to 1.07 (Figure 5, Supplementary Table 1). Where fire is present, is strongly reduced (median 0.61, CI 0.51 to 0.70). Where WPBR is present, the posterior distribution for straddles 1, but is generally lower than that of the undisturbed scenario (median 0.99, CI 0.90 to 1.06). When basal area is lower than average, there posterior distribution of is well above one (median 1.09, CI 1.06 to 1.13). By contrast, when basal area is higher than average the posterior distribution of straddles one (median 0.98, CI 0.94 to 1.02) and is clearly lower than the undisturbed scenario. For sites experiencing low amounts of drought, the median and 90% CI of is above 1, while for sites experiencing high drought the posterior distribution of straddles one (median 1.03, 90% CI from 0.99 to 1.08). Likewise, on particularly dry sites the posterior distribution of straddles 1 (median 1.04, 90% CI from 0.99 to 1.09). Fire had the clearest effect on , followed by WPBR and high basal area, and then drought and site dryness.

# Discussion

This study is the first range-wide assessment of stressors impacting the vital rates and population dynamics of sugar pine. 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 conserve sugar pine.

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, as seen in the strong effect of individual size on 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 below one for burned plots (Figure 5). Fire was the only stressor which reduced the 90% credible interval of the posterior distribution of to below one (Supplementary Table 1), indicating a strong influence of fire on population dynamics. 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. 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, potentially with a greater effect on small trees (Figure 2). 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 growth (Figure 3) and survival of small individuals (Figure 1). 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). It is unclear from our data whether the negative impact of density on fecundity of trees between 0.50 and 2.00 m DBH is a result of decreased reproduction due to stress of parent trees, or decreased survival and/or growth of new recruits due to competition, but both dynamics are plausible (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 5), and the credible intervals for in both the high basal area and WPBR scenarios included 1 (Supplementary Table 1). However, reducing neighborhood basal area to one standard deviation below the mean had positive effects on (Figure 5).

A surprising result of this study is that drought and climate related variables had relatively weak impacts on sugar pine’s vital rates and asymptotic population growth rate. 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). This study found a weak negative effect of drought on survival (Figure 2, Table 1) and a size-dependent effect of site dryness on growth, where smaller stems grew slower on dry sites and larger stems grew faster on dry sites (Figure 3, Table 2). However, neither effect was strong enough to substantially reduce the asymptotic population growth rate relative to the unstressed scenario (Figure 5, Supplementary Table 1). 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. In addition, though the resolution of the terraClimate data is similar to the scale at which plot coordinates are fuzzed, the fuzzing and swapping of plot coordinates likely introduced error between the true drought and site dryness experienced on a plot and the measured drought and site dryness appearing in our data. This noisy measurement of climate conditions could result in an underestimation of the true effects of drought and site dryness.

One unexplained but troubling finding of this study was the low survival rates observed for the largest sugar pines (Figure 2). Bark beetles 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. 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). 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 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.

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# Tables

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameter** | **Mean** | **Median** | **StDev** | **q5** | **q95** | **rhat** | **ess\_bulk** | **ess\_tail** |
| **Intercept** | 1.39 | 1.38 | 0.26 | 0.97 | 1.82 | 1.00 | 1218.79 | 1859.83 |
| **DBH (m)** | 4.31 | 4.29 | 0.77 | 3.05 | 5.58 | 1.00 | 1225.93 | 1840.31 |
| **DBH^2 (m)** | -2.40 | -2.39 | 0.55 | -3.29 | -1.50 | 1.00 | 1320.76 | 2096.45 |
| **Fire** | -3.51 | -3.50 | 0.56 | -4.45 | -2.61 | 1.00 | 1364.76 | 2179.64 |
| **WPBR** | -0.96 | -0.96 | 0.55 | -1.87 | -0.05 | 1.00 | 1279.53 | 2174.54 |
| **Basal Area** | -0.81 | -0.81 | 0.22 | -1.18 | -0.45 | 1.00 | 1463.60 | 2170.85 |
| **Drought** | -0.34 | -0.34 | 0.20 | -0.68 | -0.01 | 1.00 | 1113.71 | 1900.59 |
| **Site Dryness** | -0.33 | -0.33 | 0.23 | -0.70 | 0.05 | 1.00 | 1429.15 | 2287.44 |
| **DBH x Fire** | 2.40 | 2.38 | 1.45 | 0.10 | 4.78 | 1.00 | 1291.53 | 2079.10 |
| **DBH^2 x Fire** | -1.10 | -1.08 | 0.92 | -2.64 | 0.35 | 1.00 | 1386.52 | 2235.70 |
| **DBH x WPBR** | 0.83 | 0.82 | 1.68 | -1.89 | 3.62 | 1.00 | 1482.98 | 2079.69 |
| **DBH^2 x WPBR** | -0.42 | -0.40 | 1.20 | -2.39 | 1.57 | 1.00 | 1592.54 | 2189.01 |
| **DBH x BA** | 0.94 | 0.93 | 0.55 | 0.04 | 1.83 | 1.00 | 1528.47 | 2091.84 |
| **DBH^2 x BA** | -0.17 | -0.17 | 0.32 | -0.68 | 0.36 | 1.00 | 1630.07 | 2358.15 |
| **DBH x Drought** | 0.49 | 0.49 | 0.58 | -0.46 | 1.44 | 1.00 | 1260.66 | 2100.02 |
| **DBH^2 x Drought** | -0.19 | -0.18 | 0.40 | -0.85 | 0.48 | 1.00 | 1394.84 | 2170.48 |
| **DBH x Dryness** | 0.60 | 0.61 | 0.67 | -0.53 | 1.69 | 1.00 | 1202.08 | 2221.01 |
| **DBH^2 x Dryness** | -0.56 | -0.57 | 0.46 | -1.31 | 0.20 | 1.00 | 1280.66 | 2221.16 |
| **SD Plots** | 2.04 | 2.03 | 0.16 | 1.79 | 2.32 | 1.00 | 1120.85 | 2021.54 |
| **SD Ecoregions** | 0.27 | 0.25 | 0.17 | 0.02 | 0.57 | 1.02 | 317.97 | 977.47 |

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** | 0.038 | 0.038 | 0.002 | 0.034 | 0.041 | 1.00 | 976.04 | 1615.67 |
| **DBH (m)** | 1.001 | 1.001 | 0.002 | 0.998 | 1.004 | 1.00 | 3598.48 | 3670.58 |
| **Fire** | -0.006 | -0.006 | 0.005 | -0.014 | 0.002 | 1.00 | 2076.59 | 2646.10 |
| **WPBR** | 0.006 | 0.006 | 0.004 | -0.001 | 0.013 | 1.00 | 1641.70 | 2659.93 |
| **Basal Area** | -0.004 | -0.004 | 0.001 | -0.007 | -0.002 | 1.00 | 2558.93 | 3202.40 |
| **Drought** | 0.000 | 0.000 | 0.001 | -0.003 | 0.002 | 1.00 | 2233.77 | 2778.53 |
| **Site Dryness** | -0.004 | -0.004 | 0.002 | -0.007 | -0.001 | 1.00 | 1981.64 | 2584.46 |
| **DBH x Fire** | -0.008 | -0.008 | 0.005 | -0.017 | 0.000 | 1.00 | 2463.56 | 2561.93 |
| **DBH x WPBR** | -0.004 | -0.005 | 0.005 | -0.013 | 0.004 | 1.00 | 2633.02 | 2602.77 |
| **DBH x BA** | 0.002 | 0.002 | 0.002 | -0.001 | 0.005 | 1.00 | 3683.91 | 3249.29 |
| **DBH x Drought** | 0.001 | 0.001 | 0.002 | -0.002 | 0.004 | 1.00 | 3419.86 | 3362.41 |
| **DBH x Dryness** | 0.006 | 0.006 | 0.002 | 0.004 | 0.009 | 1.00 | 3868.52 | 3515.61 |
| **SD Plots** | 0.018 | 0.018 | 0.001 | 0.017 | 0.019 | 1.00 | 1162.46 | 2109.90 |
| **SD Ecoregions** | 0.012 | 0.012 | 0.002 | 0.009 | 0.015 | 1.00 | 935.99 | 1395.57 |
| **SD Residual** | 0.022 | 0.022 | 0.000 | 0.021 | 0.022 | 1.00 | 2054.00 | 2747.82 |

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** | -3.65 | -3.63 | 0.39 | -4.32 | -3.01 | 1.00 | 1457.36 | 1998.09 |
| **DBH (m)** | 4.38 | 4.38 | 0.68 | 3.28 | 5.52 | 1.00 | 1452.09 | 1771.06 |
| **DBH^2 (m)** | -1.27 | -1.27 | 0.29 | -1.75 | -0.80 | 1.00 | 1638.78 | 2025.90 |
| **Fire** | -0.27 | -0.20 | 1.02 | -2.03 | 1.30 | 1.00 | 1798.17 | 2444.86 |
| **WPBR** | -2.14 | -2.08 | 1.45 | -4.67 | 0.13 | 1.00 | 2005.95 | 1710.63 |
| **Basal Area** | 0.40 | 0.40 | 0.31 | -0.10 | 0.93 | 1.00 | 1817.20 | 2445.80 |
| **Drought** | 0.07 | 0.05 | 0.23 | -0.31 | 0.45 | 1.00 | 1962.79 | 2208.44 |
| **Site Dryness** | 0.80 | 0.80 | 0.31 | 0.31 | 1.33 | 1.00 | 1735.81 | 2291.06 |
| **DBH x Fire** | 0.37 | 0.42 | 2.14 | -3.18 | 3.86 | 1.00 | 1513.14 | 2242.98 |
| **DBH^2 x Fire** | 0.04 | 0.02 | 0.91 | -1.42 | 1.54 | 1.00 | 1618.22 | 2513.76 |
| **DBH x WPBR** | 4.95 | 4.84 | 2.62 | 0.80 | 9.38 | 1.00 | 1667.46 | 1534.56 |
| **DBH^2 x WPBR** | -2.19 | -2.15 | 1.17 | -4.23 | -0.34 | 1.00 | 1851.86 | 2202.04 |
| **DBH x BA** | -1.33 | -1.33 | 0.68 | -2.43 | -0.19 | 1.00 | 1352.48 | 2404.24 |
| **DBH^2 x BA** | 0.50 | 0.50 | 0.30 | 0.01 | 1.00 | 1.00 | 1485.97 | 2159.68 |
| **DBH x Drought** | 0.49 | 0.49 | 0.50 | -0.36 | 1.30 | 1.00 | 1592.82 | 2356.51 |
| **DBH^2 x Drought** | -0.26 | -0.26 | 0.23 | -0.64 | 0.13 | 1.00 | 1805.73 | 2694.80 |
| **DBH x Dryness** | -0.32 | -0.33 | 0.63 | -1.36 | 0.72 | 1.00 | 1562.24 | 1894.60 |
| **DBH^2 x Dryness** | -0.08 | -0.08 | 0.29 | -0.55 | 0.40 | 1.00 | 1812.10 | 2451.13 |
| **SD Ecoregions** | 0.88 | 0.85 | 0.24 | 0.51 | 1.30 | 1.00 | 1264.58 | 1891.26 |
| **NB Dispersion** | 0.45 | 0.44 | 0.07 | 0.35 | 0.57 | 1.00 | 3248.49 | 2768.46 |

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

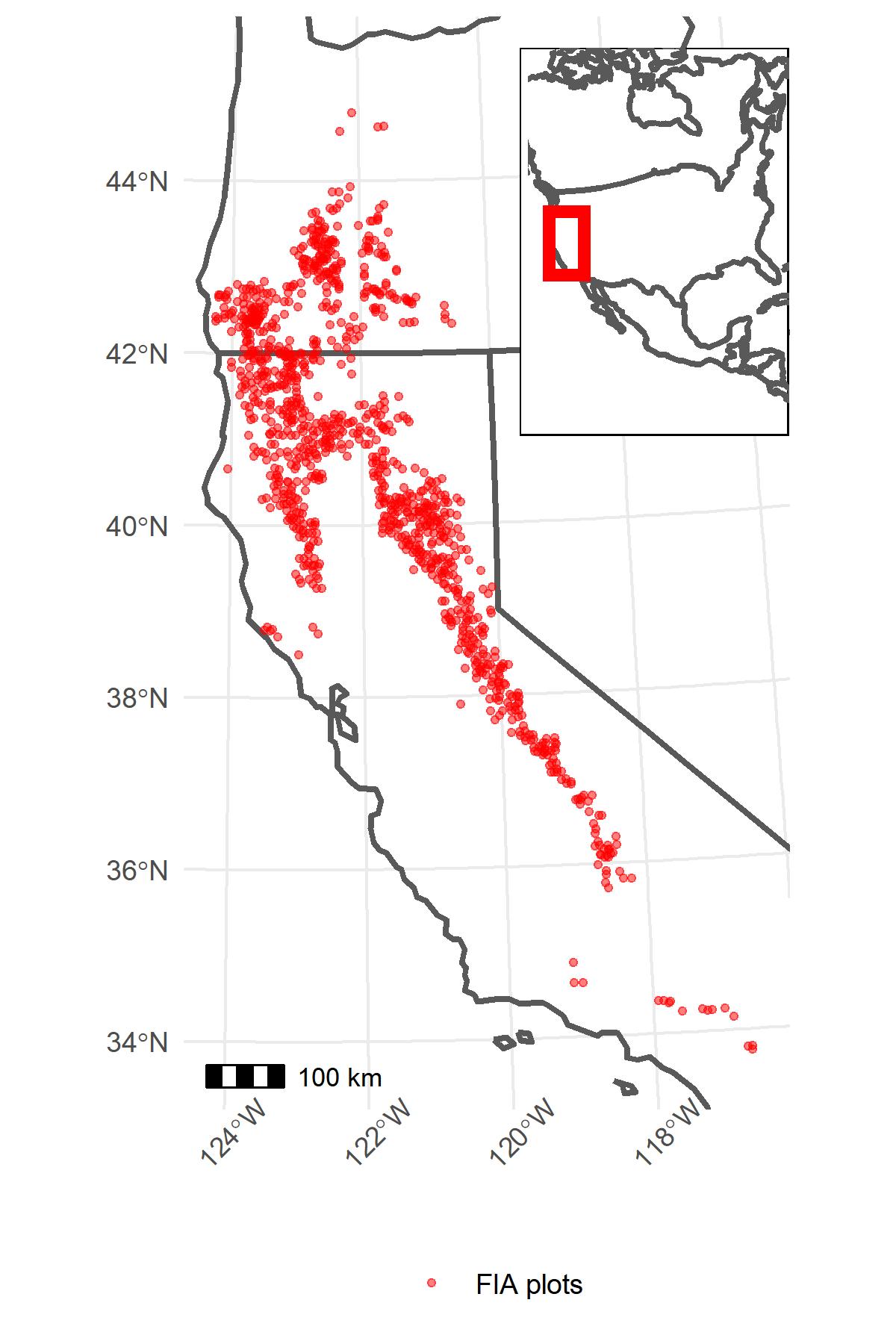


Figure 1: 1,102 Forest Inventory and Analysis (FIA) plots where live sugar pine was present at initial measurement (2001-2010) with US state borders. Plot locations based on the nominal, rather than true, coordinates. Inset shows position relative to North America and national borders.

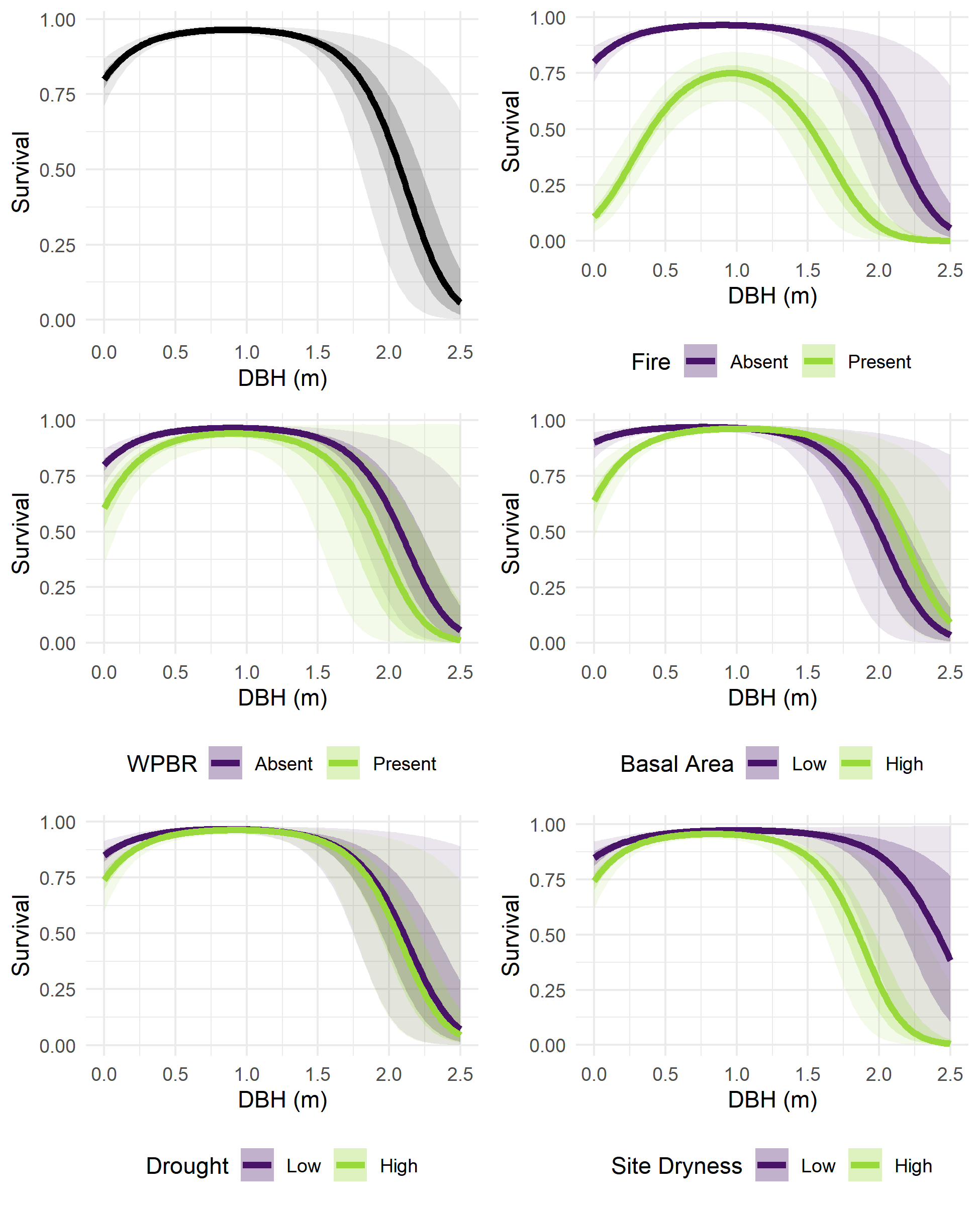


Figure 2: Fixed effects of initial DBH, fire, WPBR, neighborhood basal area, drought, and site dryness on survival. In the top left panel, probability of survival (Y-axis) is predicted for stems of various initial size (X-axis), holding other variables at “Absent” (for fire and WPBR) or 0 (scaled mean, 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, resulting in relatively wide uncertainty about the survival of stems larger than 1.25m.

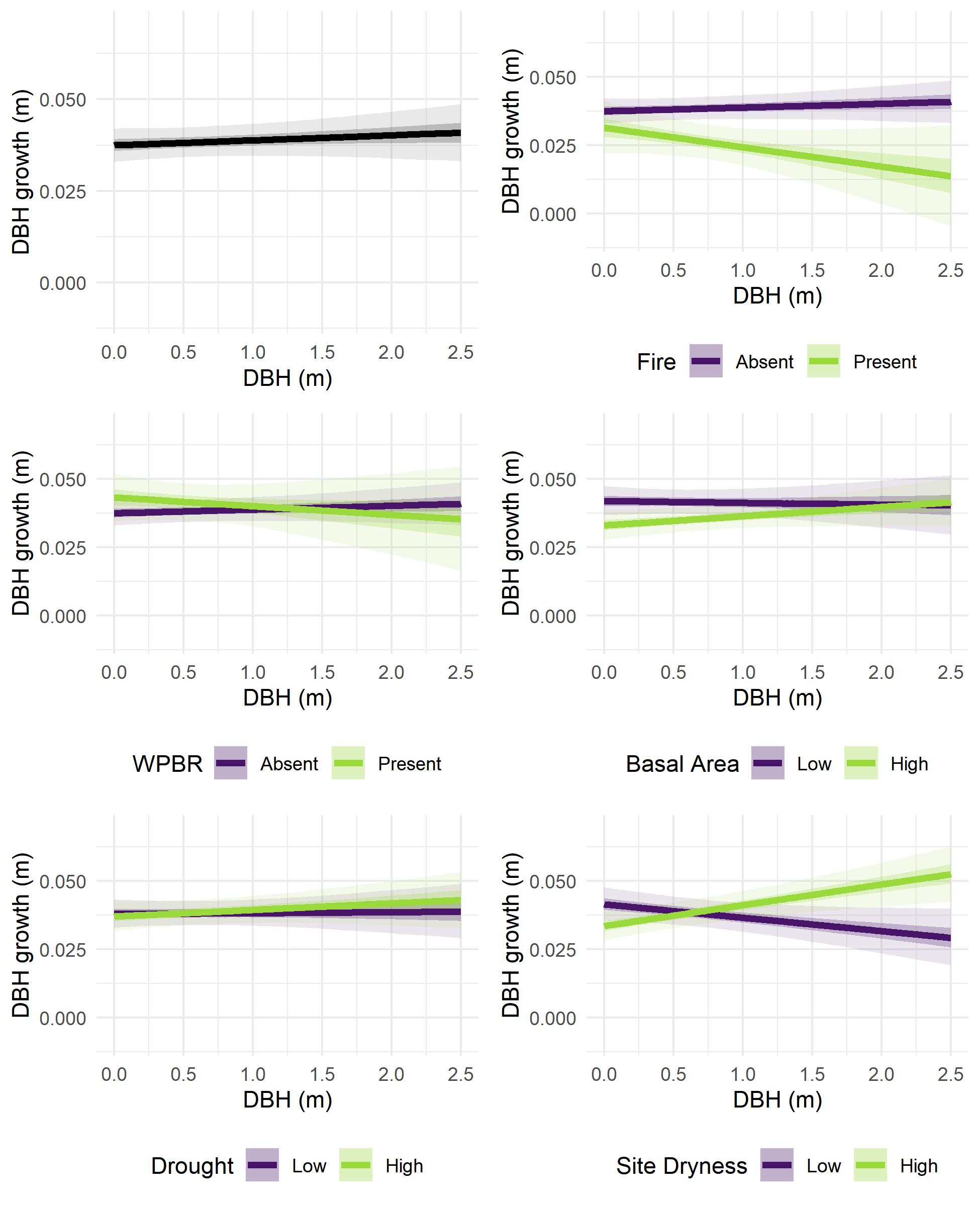


Figure 3: Fixed effects of initial DBH, fire, WPBR, neighborhood basal area, drought, and site dryness on growth. In the top left panel, DBH growth over the 10 years between censuses (Y-axis) is predicted for stems of various initial size (X-axis), holding other variables at “Absent” (for fire and WPBR) 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.

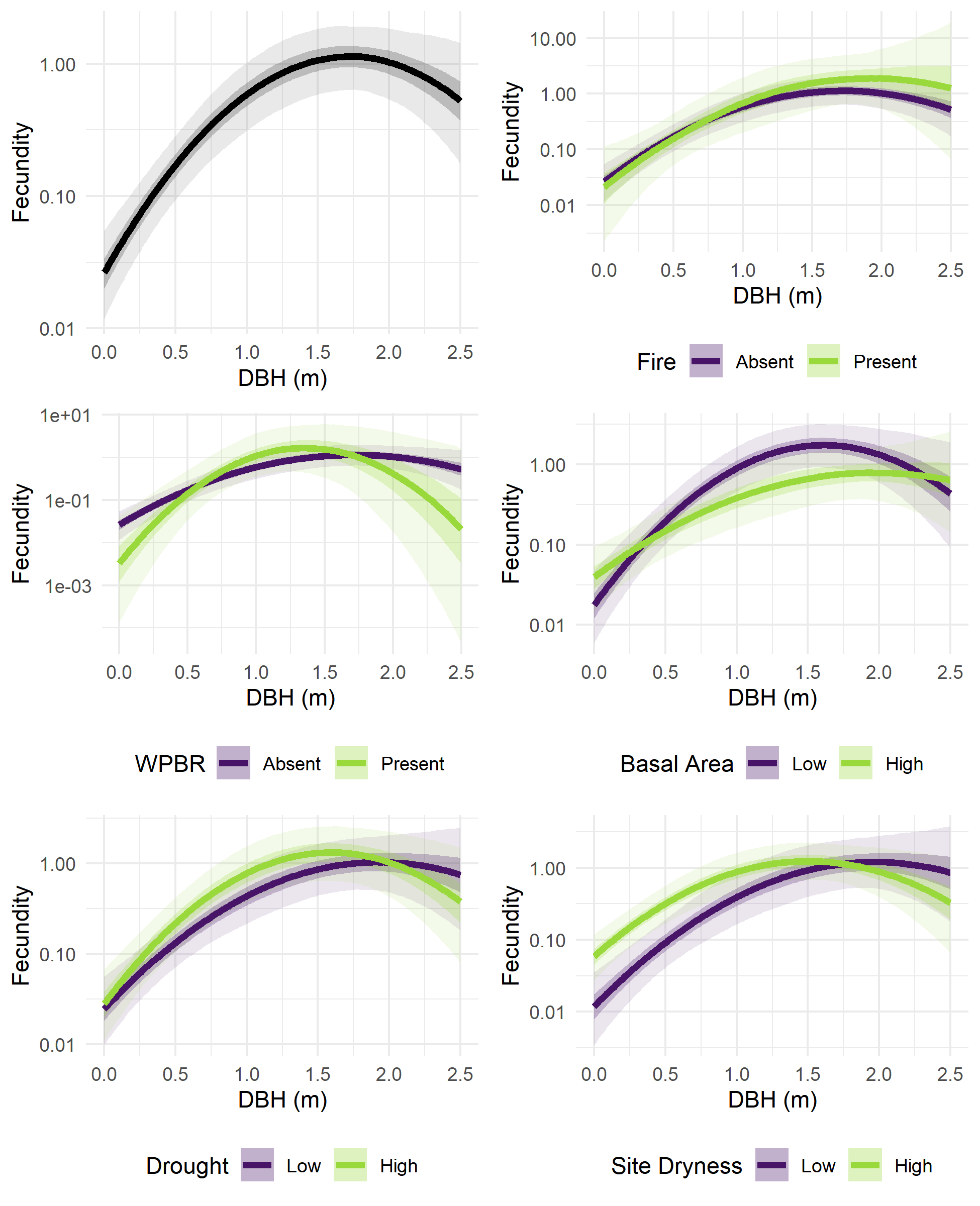


Figure 4: Fixed effects of initial DBH, fire, WPBR, neighborhood basal area, drought, and site dryness on fecundity. In the top left panel, fecundity (Y-axis) is predicted for stems of various initial size (X-axis), holding other variables at “Absent” (for fire and WPBR) or 0 (scaled mean, for basal area, drought, and site dryness). In the other panels, fecundity 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. Note the varying scales and log10 scaling on the Y-axis.

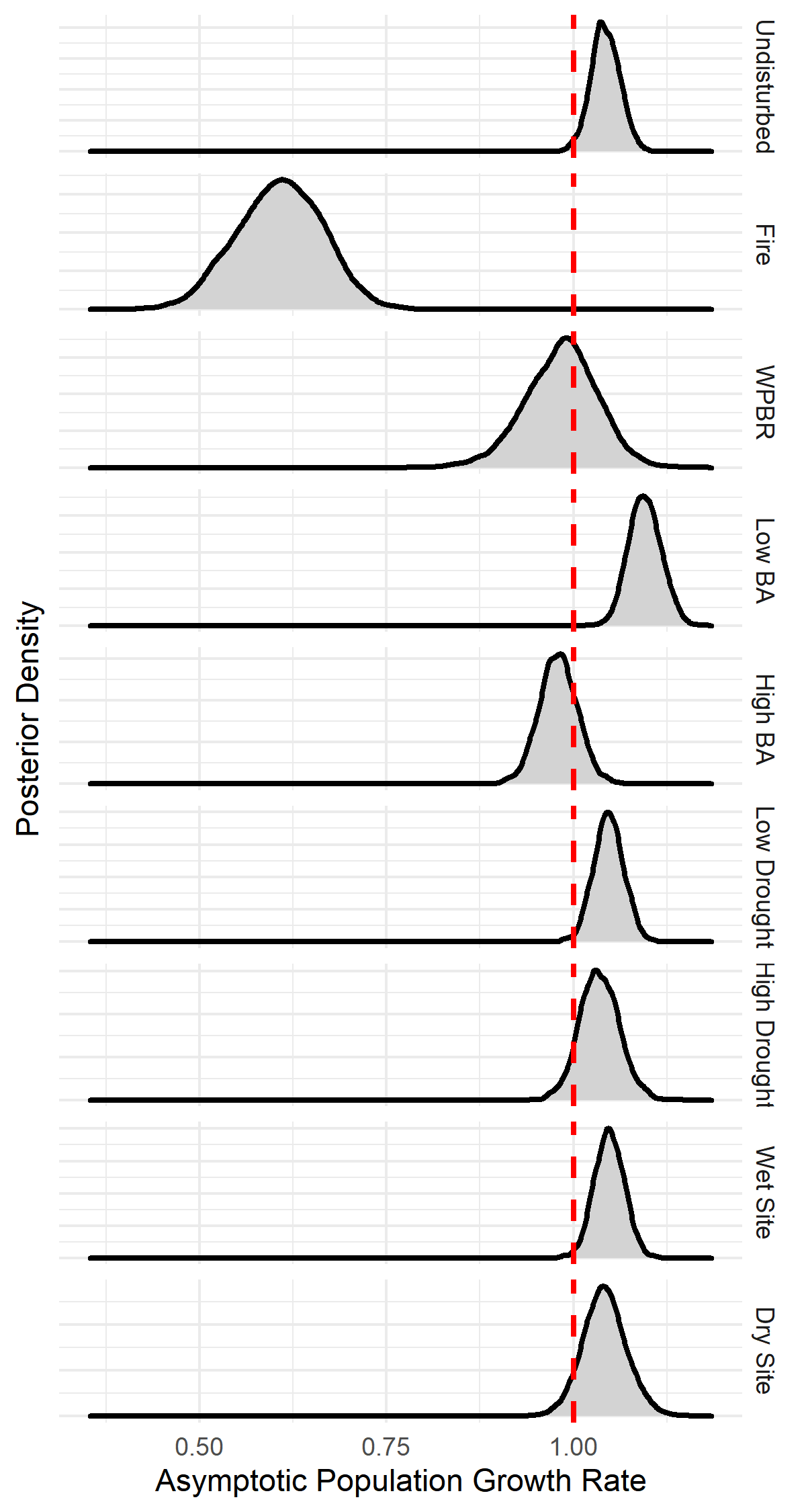
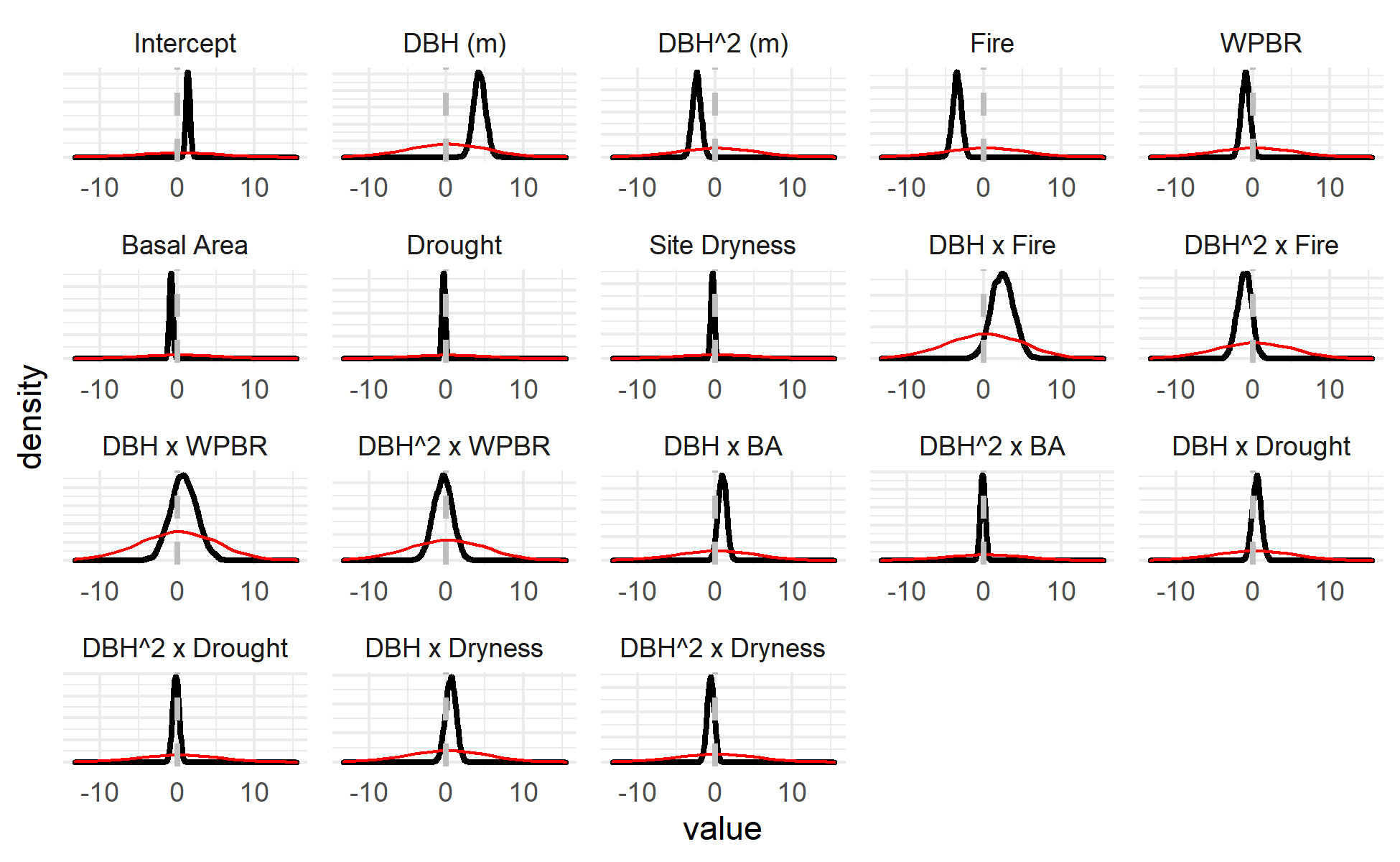
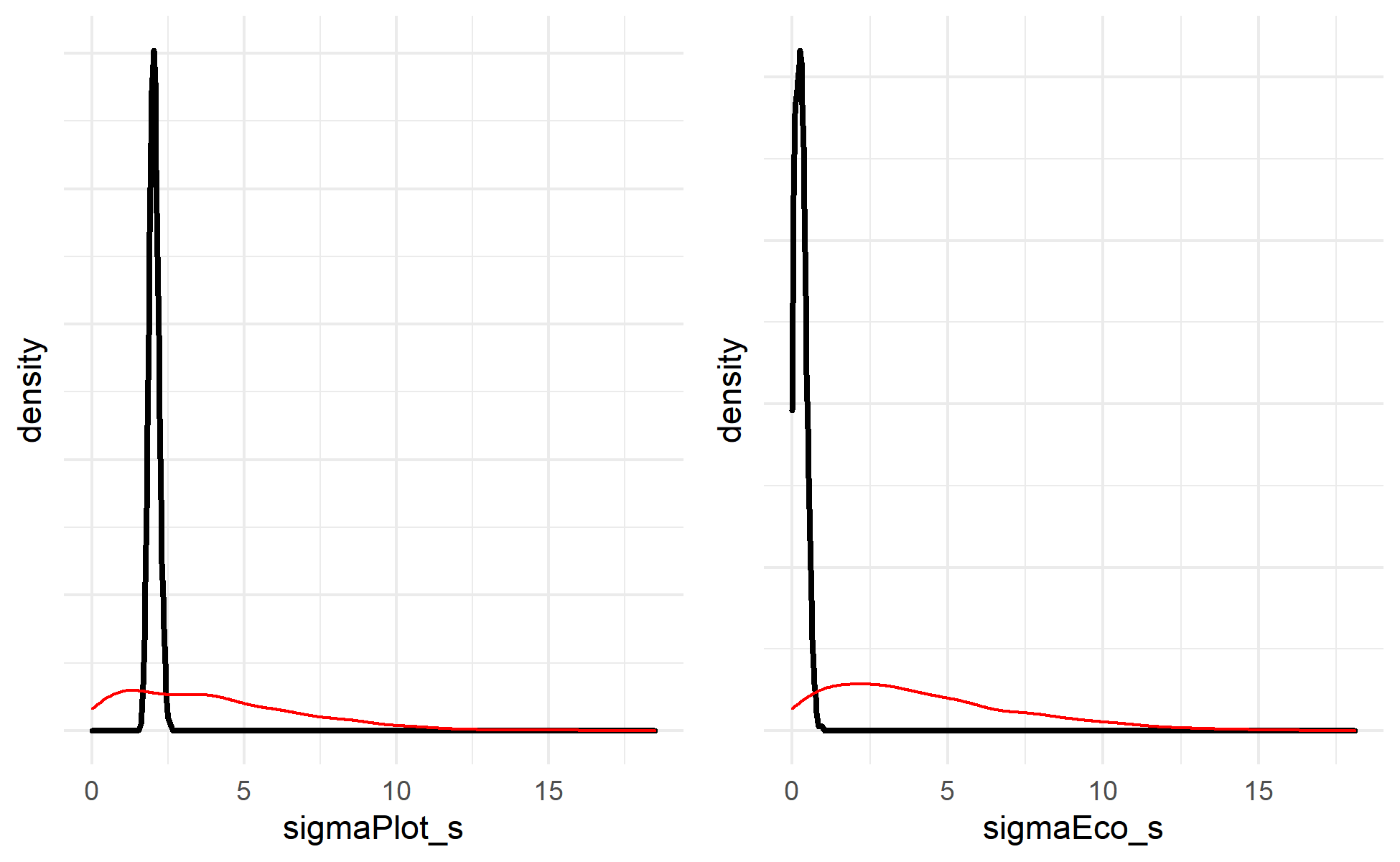


Figure 5: Posterior distribution of asymptotic population growth rate () under a variety of hypothetical scenarios, each corresponding to the presence or absence of a specific stressor. In the “Undisturbed” scenario, all fixed effect covariates other than the intercept are held at 0 (representing the 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. The bounds of the figure have been restricted for readability of scenarios other than “Low BA.”

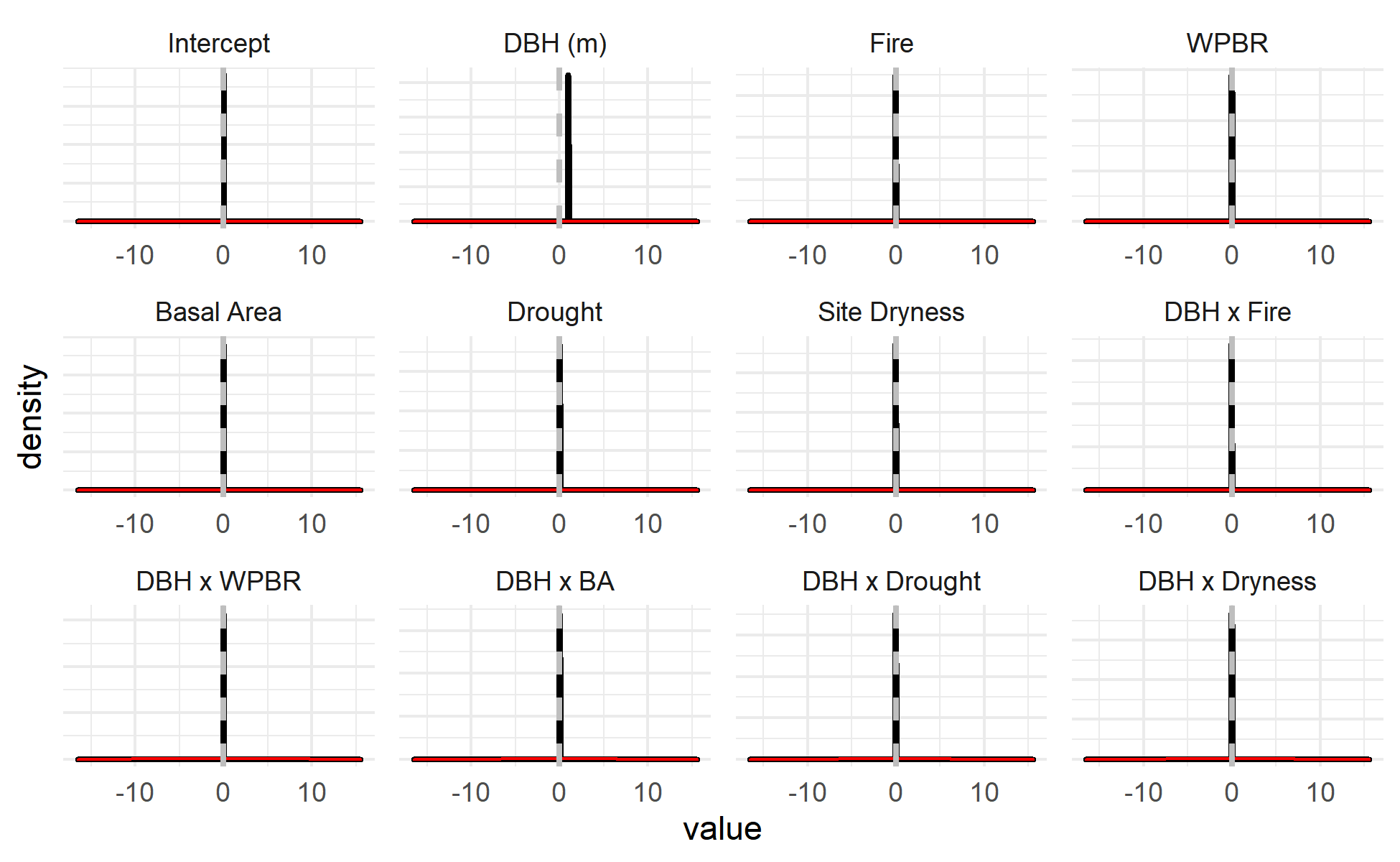
# Supplementary Materials



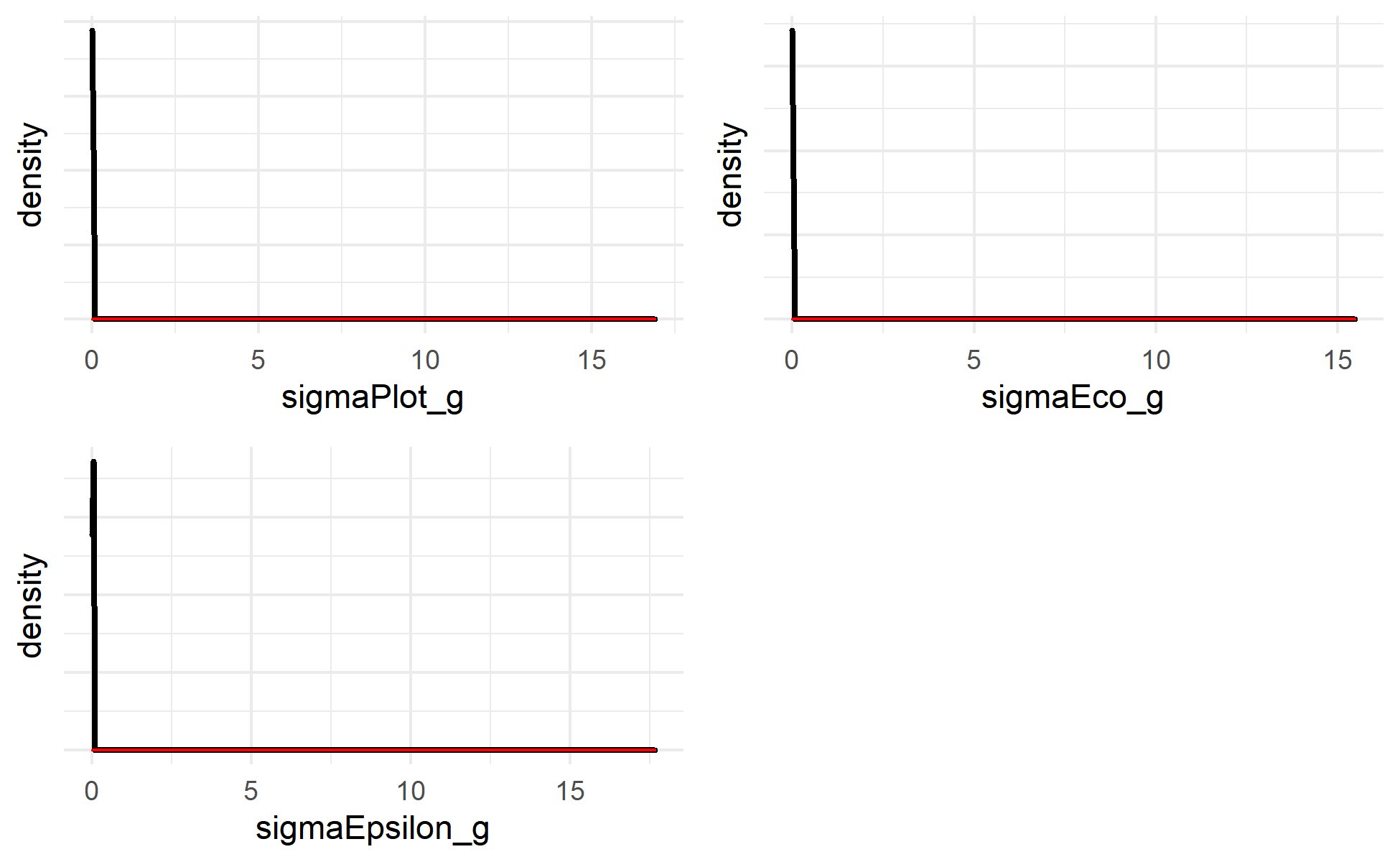
Supplementary Figure 1: Posterior distributions (black) and prior distributions (red) for , the fixed effect coefficients for survival. The magnitude of the discrepancy between the two indicates the extent to which the posterior distribution was informed by the data, rather than the prior.



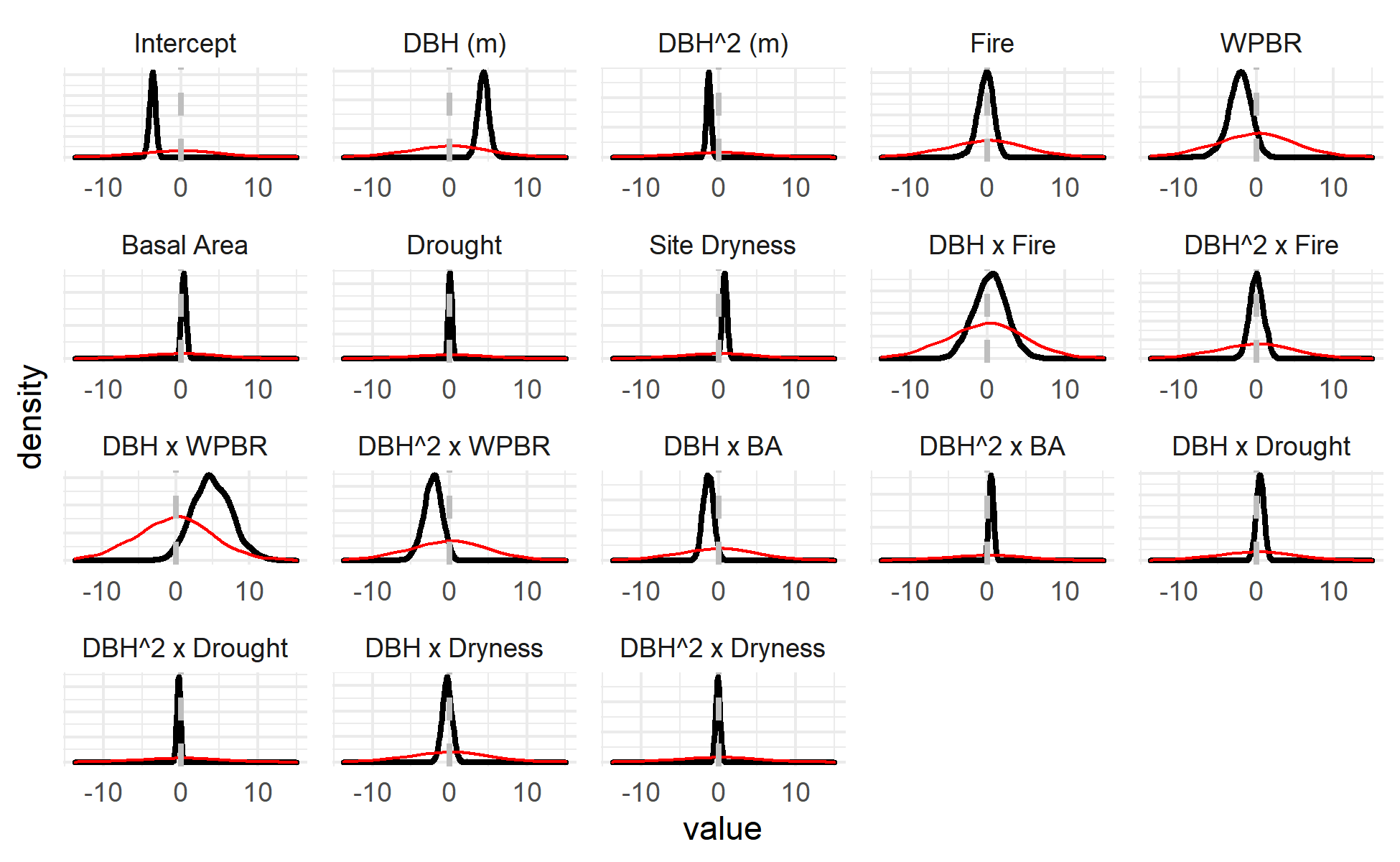
Supplementary Figure 2: Posterior distributions (black) against prior distributions (red) for the standard deviations of the plot and ecoregion random effects in the survival model.



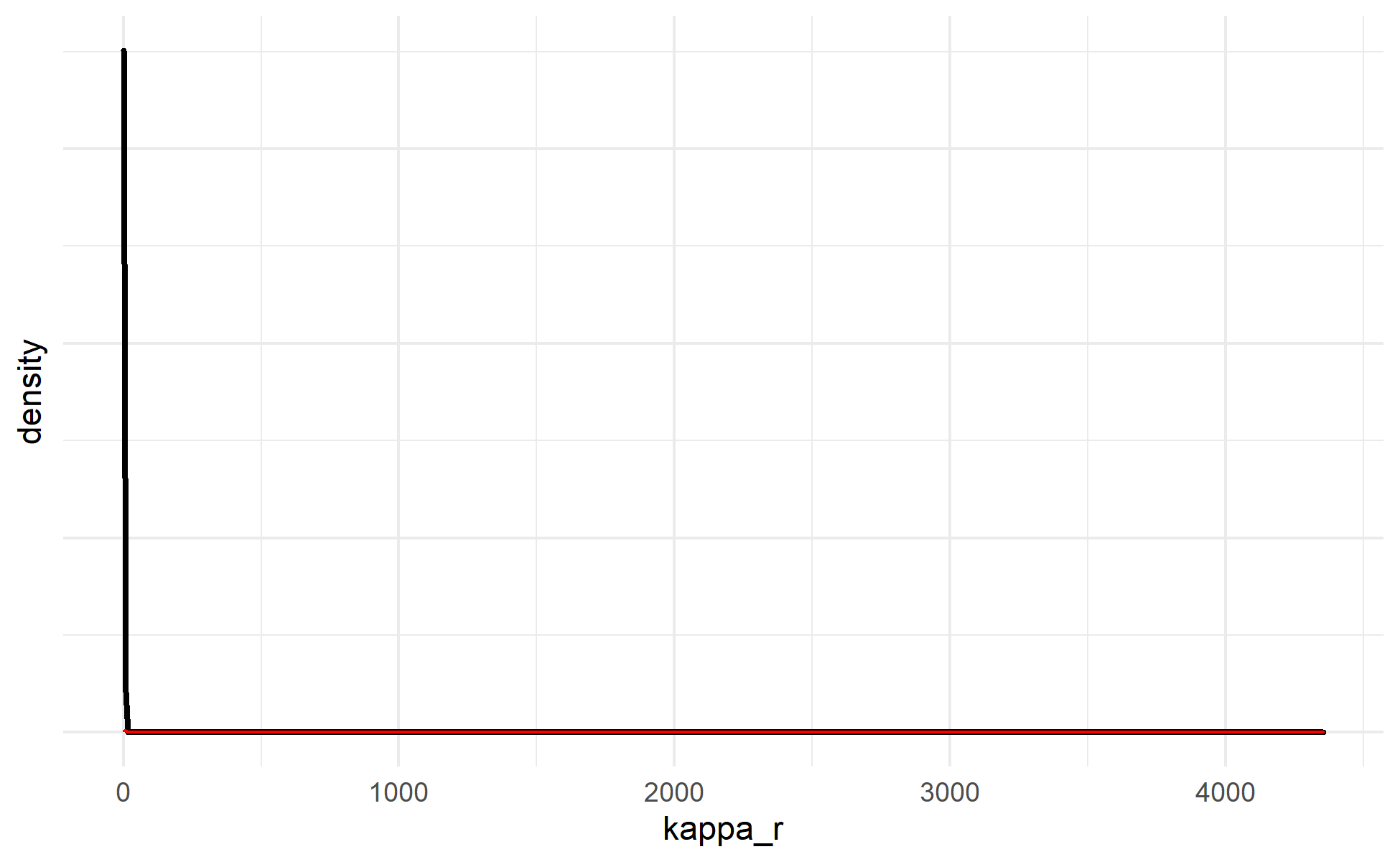
Supplementary Figure 3: Posterior distributions (black) against prior distributions (red) for fixed effect coefficients in the growth model.



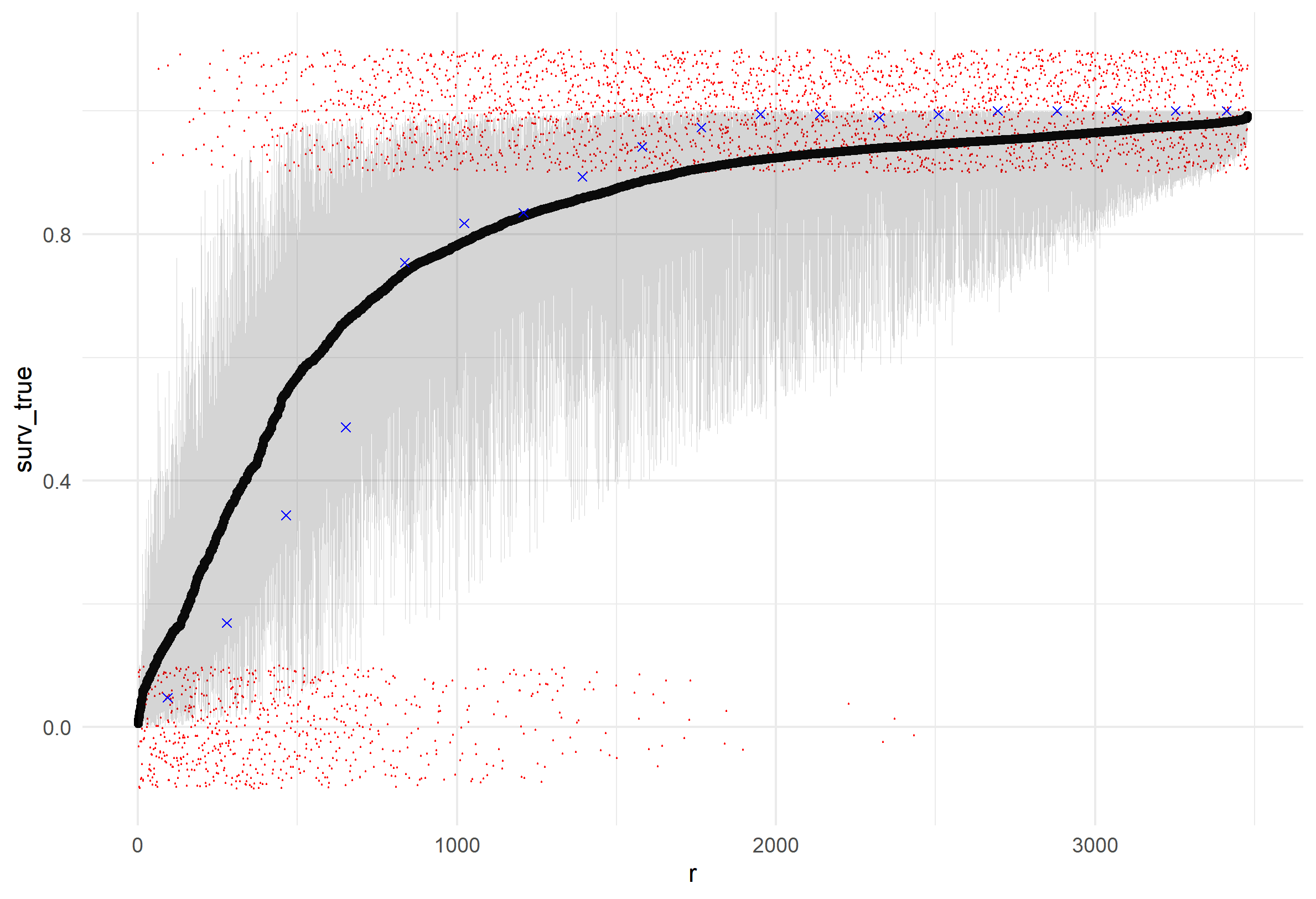
Supplementary Figure 4: Posterior distributions (black, along Y axis) against prior distributions (red, along X axis) for the standard deviations of the plot random effect, the ecoregion random effect, and the residuals in the growth model.



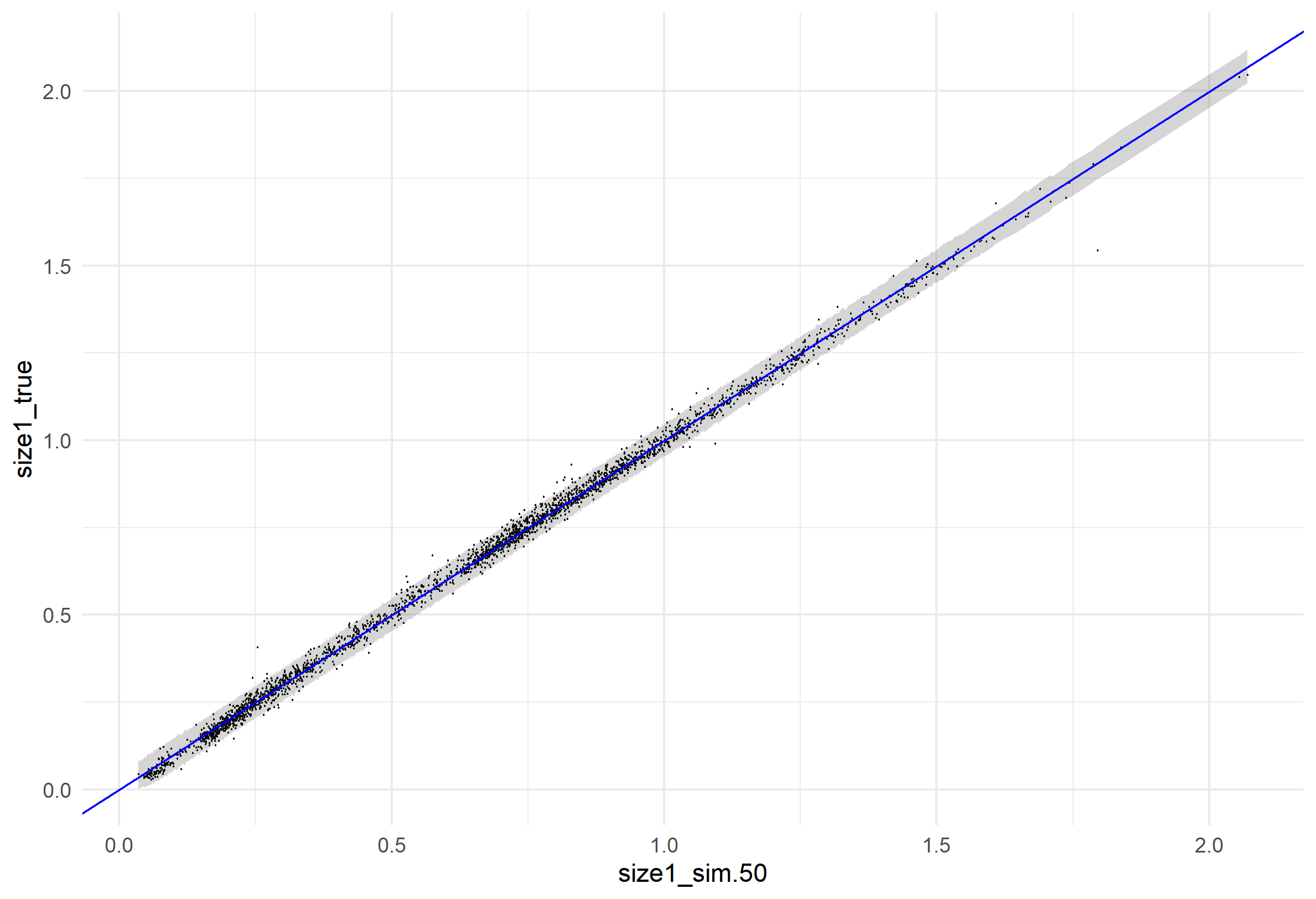
Supplementary Figure 5: Posterior distributions (black) against prior distributions (red) for the fixed effect coefficients affecting fecundity in the recruitment model.



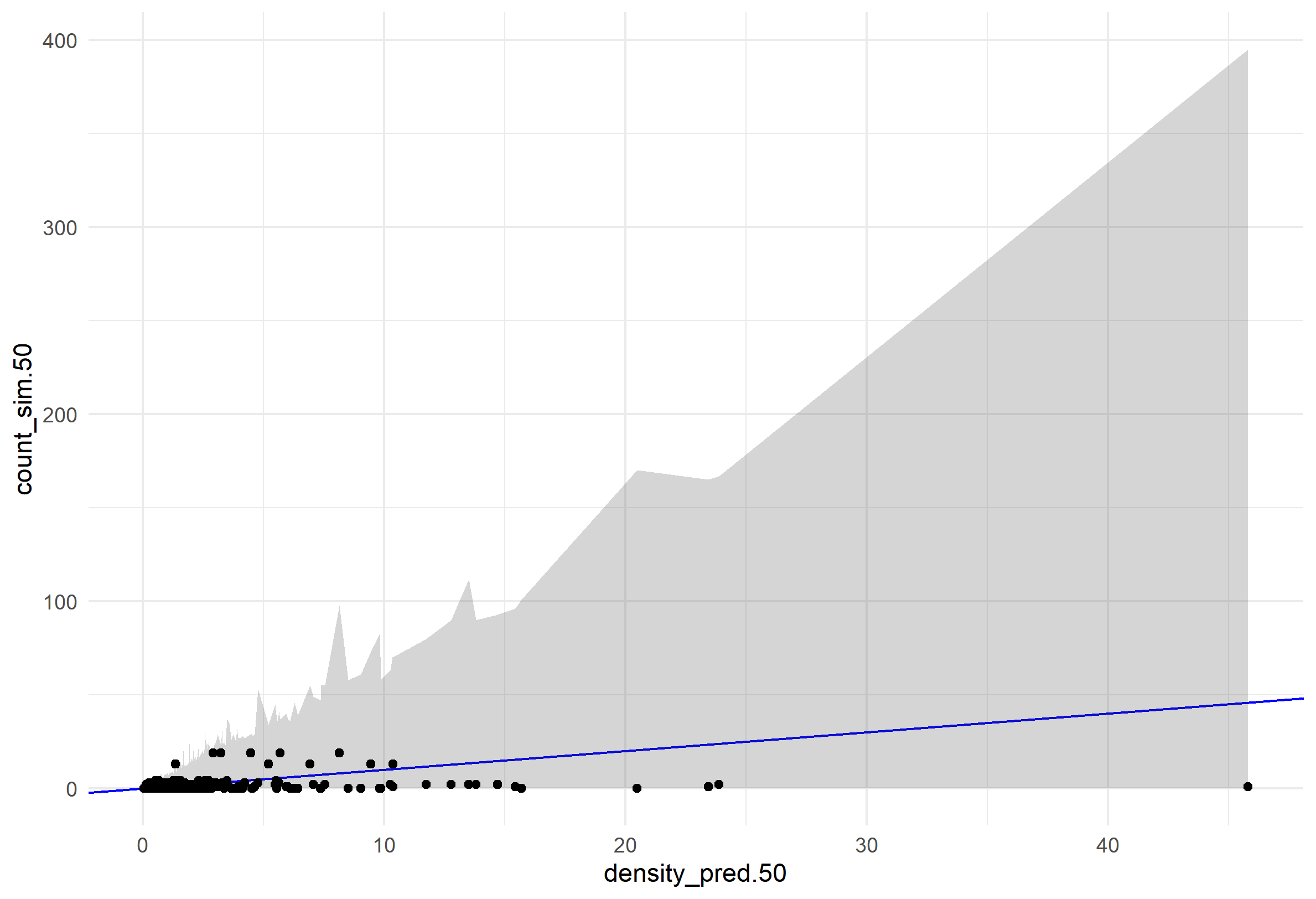
Supplementary Figure 6: Posterior distribution (black, along Y axis) against prior distribution (red, along X axis) for the dispersion term of the negative binomial response in the recruitment model.



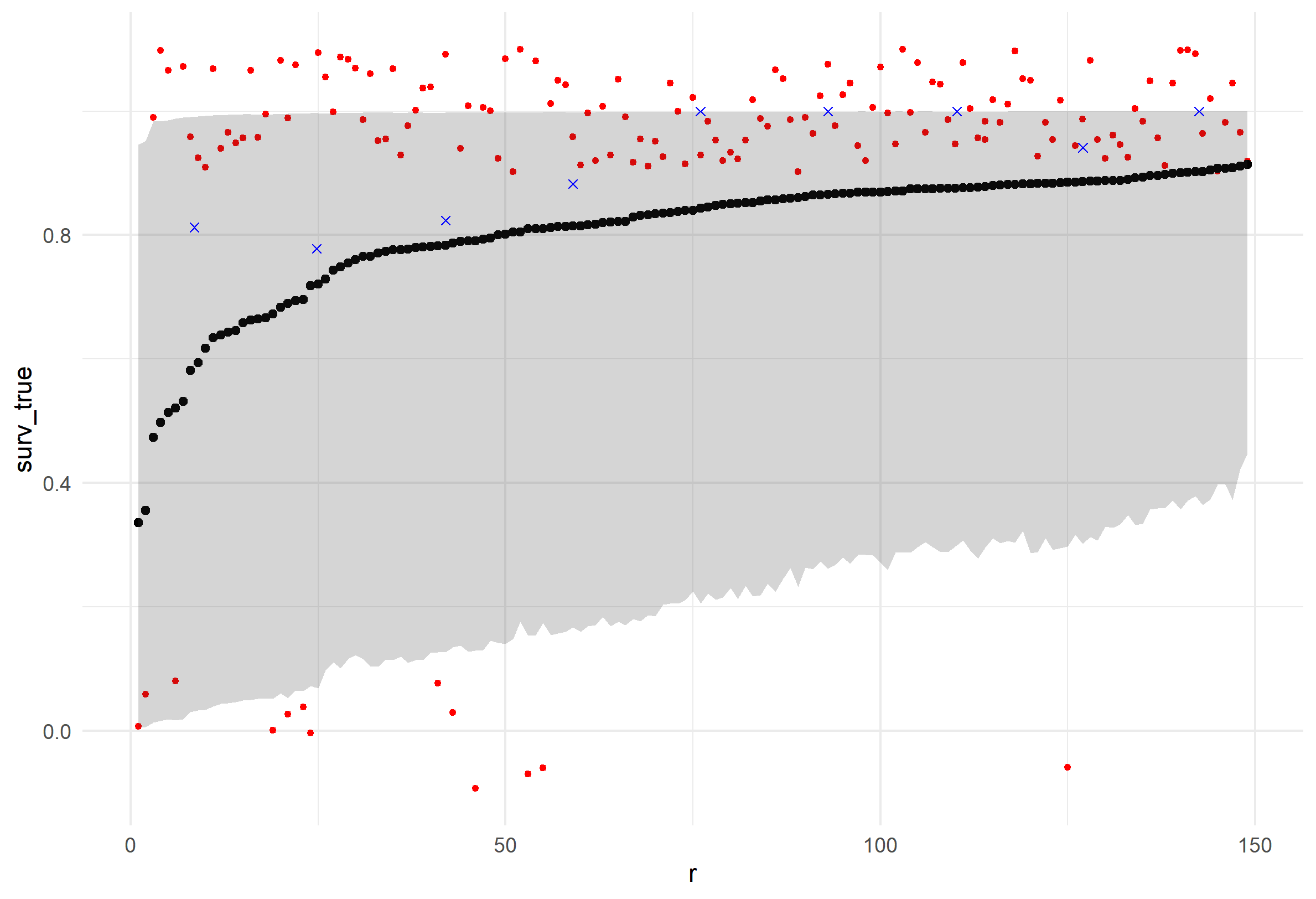
Supplementary Figure 7: Results of posterior retrodictive simulations for survival of individual trees. Posterior samples of the parameters were used to predict the survival probability of each individual tree using Equation 2 and the training data used to fit the model. Individual trees (red points) 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.



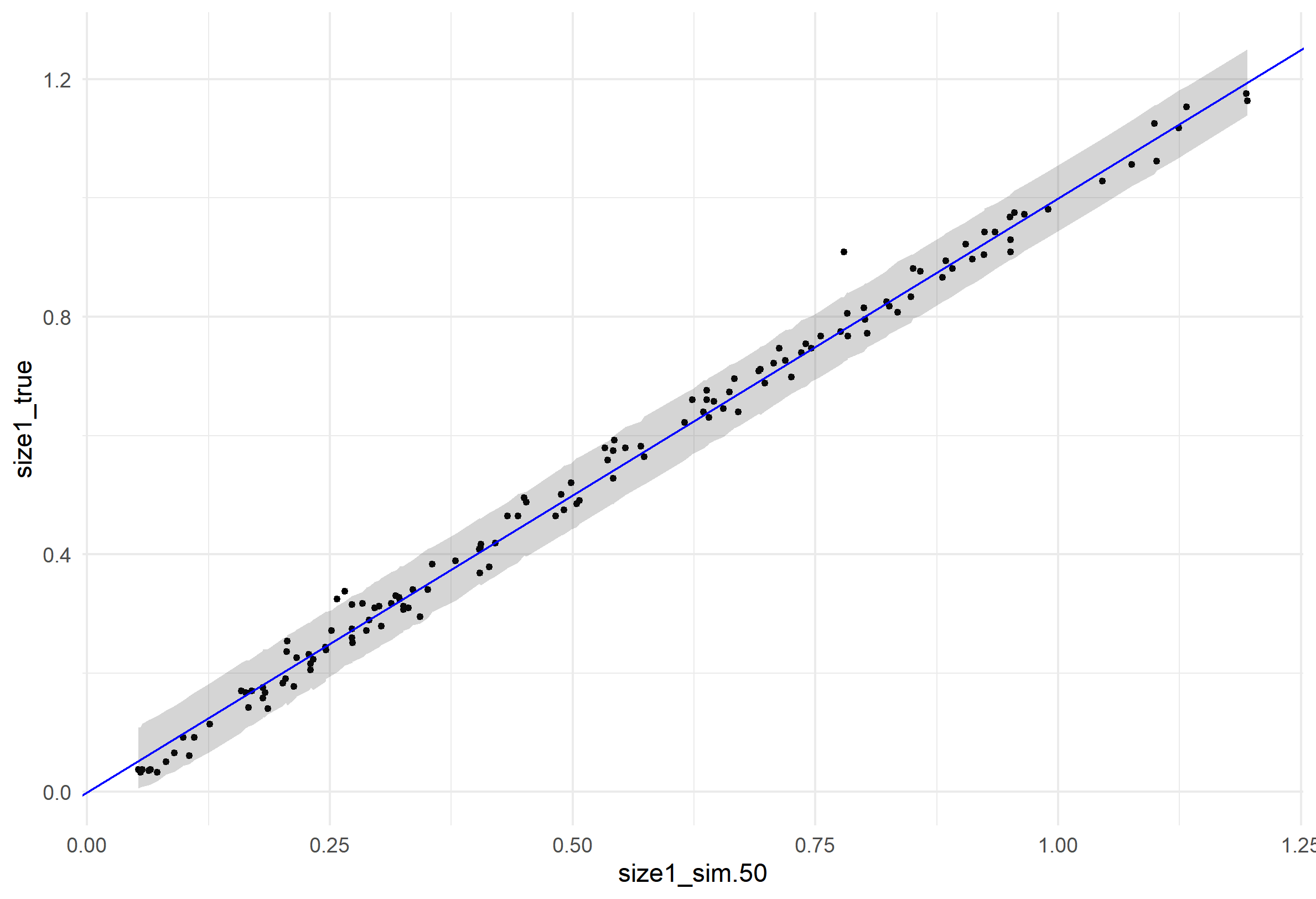
Supplementary Figure 8: Posterior retrodictions for the growth model, using posterior parameter values and the training data. Individual trees (black points) are plotted with their median predicted size at remeasurement along the X-axis, and their true size at remeasurement along the y axis. The blue 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.



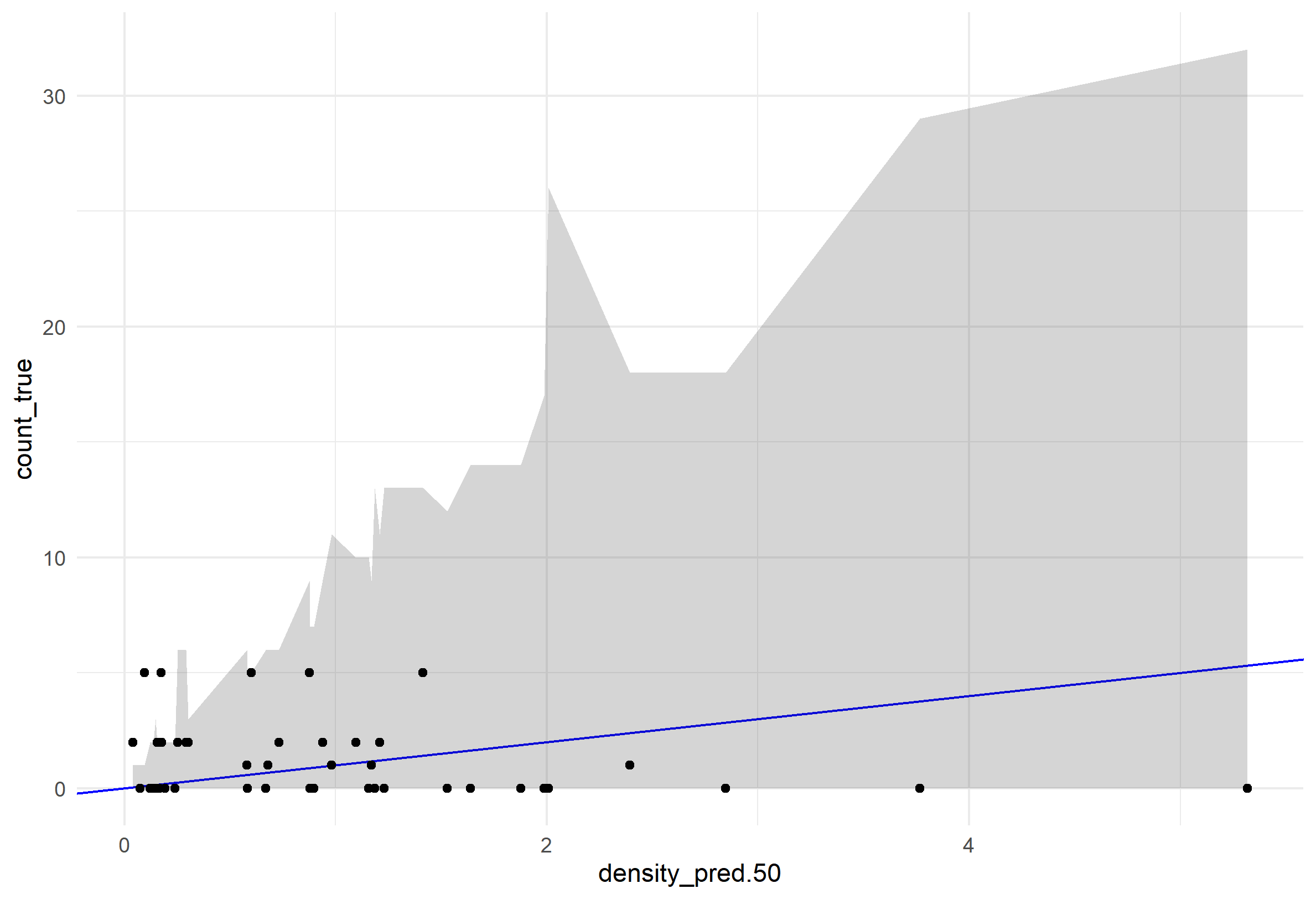
Supplementary Figure 9: Posterior retrodictions for the recruitment model. The black points show the observed count of untagged individuals (new recruits and preexisting small stems) on each subplot on the Y-axis, and the median predicted density on the X-axis. The blue line has slope 1 and intercept 0, i.e. perfect prediction. The bounds of the grey ribbon correspond to the 2.5th and 97.5th percentiles of simulated counts drawn from a negative binomial distribution with location parameter predicted from the posterior distribution of the model. The gray ribbon contains all the true values, indicating that all of the observed counts are consistent with the variability expected from the model.



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. The black points show the observed count of untagged individuals (new recruits and preexisting small stems) on each subplot on the Y-axis, and the median predicted density on the X-axis. The blue line has slope 1 and intercept 0, i.e. perfect prediction. The bounds of the grey ribbon correspond to the 2.5th and 97.5th percentiles of simulated counts drawn from a negative binomial distribution with location parameter predicted from the posterior distribution of the model. The gray ribbon contains all the true values, indicating that all the observed counts are consistent with the variability expected from the model.

|  |  |  |  |
| --- | --- | --- | --- |
| **Scenario** | **Lambda (median)** | **Lambda (5th percentile)** | **Lambda (95th percentile)** |
| **Undisturbed** | 1.04 | 1.01 | 1.07 |
| **Fire** | 0.61 | 0.51 | 0.70 |
| **WPBR** | 0.99 | 0.90 | 1.06 |
| **Low BA** | 1.09 | 1.06 | 1.13 |
| **High BA** | 0.98 | 0.94 | 1.02 |
| **Low Drought** | 1.05 | 1.01 | 1.08 |
| **High Drought** | 1.03 | 0.99 | 1.08 |
| **Wet Site** | 1.05 | 1.02 | 1.08 |
| **Dry Site** | 1.14 | 1.02 | 1.38 |

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.