**Demographic mechanisms of species’ coexistence in subalpine forests are vulnerable to changing climate and disturbance**

*Target journals: Global Change Biology? Ecology Letters (long shot)?*

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**Introduction**

Global change is reshuffling species assemblies globally, and predicting what that looks like is very difficult. Predicting community assembly is a longstanding problem in ecology, exacerbated by rapidly shifting environmental/disturbance conditions.

Coexistence theory may help in this respect; explicitly considering how environmental requirements intersect with competition and demography

For example, subalpine fir-spruce codominance in mountains of WNA maintained by very specific balance of demographic rates; those are a product of species-specific responses to environment and disturbance regimes. Prior work suggests that coexistence of subalpine fir and Engelmann spruce is maintained by interspecific differences in key life history traits and associated vital rates. Specifically, the faster growth and more prolific regeneration of subalpine fir is balanced by higher survival and longevity of Engelmann spruce, leading to overstory codominance despite fir understory dominance (Andrus et al. 2018). Periodic disturbance may also play an important role in providing canopy gaps in which spruce seedlings can outcompete the more shade-tolerant fir seedlings (Shea 1985).

Evidence from past glacial-interglacial cycles suggests that no-analog communities formed when climates were different/differently distributed than they are now; we also know that this spruce-fir association looked very different. Highlight a couple examples. We know that subalpine fir and Engelmann spruce were not always as closely associated as they are today -- during Pleistocene glaciations, the bulk of Engelmann spruce refugia were in southern interior highlands (AZ mountains, NM plateau, CO plateau), whereas subalpine fir populations were more widely distributed across northern interior basins and coastal refugia (Roberts & Hamann 2015).

Could current and future global change produce conditions under which current species associations are no longer viable? Changing climate and disturbance regimes may “break” these demographic pathways that maintain spruce-fir forest systems, insofar as species have different responses to climate, fire, and host-specific biological disturbance agents.

Evidence from prior ABLA paper suggesting that trajectories of subalpine forests depends on interspecific variation in climate resposnes responses. Our subalpine fir status and trends paper suggested that the future trajectories of subalpine forest communities may depend on interspecific variation in responses to climate change, nondiscriminant forest disturbances (*e.g.,*fire), and host-specific forest disturbances (*e.g.,* biological disturbance agents, BDAs; Perret et al., 2023). This was supported in part by differences we found in the importance of major sources of mortality between regions where subalpine fir was in decline compared to other co-occurring species.

Here we leverage FIA data to investigate whether demographic mechanisms of coexistence for subalpine fir and Engelmann spruce across the two species’ joint distribution in western NA are vulnerable to changing climates and disturbances. We do this by first estimating population trends between 2000-2009 and 2010-2019 for both species where they co-occur, and using a new conceptual framework to categorize these trajectories. We then build a series of hierarchical Bayesian demographic models that estimate the effect of climate types, climate anomalies, and disturbance on individual mortality, regeneration, and recruitment. We use these models to assess whether projected future change scenarios make future coexistence more/less likely.

**Methods**

Forest inventory data

The US Forest Service Forest Inventory and Analysis (FIA) database provides nationally-consistent and randomized forest plot measurements across all forest lands in the United States. In the western United States, plots are remeasured on an average rotation of 10 years, facilitating estimates of decadal-scale changes in forest attributes and tree vital rates. In brief, each FIA plot consists of nested subplots on which adult trees (> 12.7 cm DBH) are inventoried, microplots on which seedlings (<2.54 cm DBH and >15.24 cm height) and saplings (2.54 – 12.7 cm DBH) are inventoried, and macroplots on which large trees are inventoried (in certain Western states; size threshold varies by state). FIA field crews collect a vast array of information, including physical tree measurements, tree damages, putative causes of mortality, and disturbance type and extent. For a complete description of FIA sampling and measurement protocols, refer to the FIA user guide and FIA field manual.

We queried the FIA database for plots that had been remeasured during the 2010-2019 inventory period, and contained both subalpine fir and Engelmann spruce. Following Perret *et al.* 2023, we included all plots that contained at least one individual of both species with a DBH > 2.54 cm. We intentionally retained plots that only contained dead individuals of either or both species, in order to avoid excluding plots that had experienced high mortality rates since the previous measurement. Every plot we included in our analyses could be linked back to a previous plot measurement; because Wyoming transitioned to the annualized sampling design later than other western States, initial plot measurements in the state came from the previous periodic survey design. In total, this yielded 2,972 plots with two measurements between the 2000-2009 and 2010-2019 inventory periods, containing 34,989 subalpine fir individuals and 27,944 Engelmann spruce individuals.

Population trajectories

The FIA program uses a randomized sampling design that facilitates post-stratified estimation of multiple forest attributes. We used standard FIA estimation procedures (Bechtold & Patterson), modified from implementation in the rFIA package (Stanke), to estimate decadal changes in the abundance and basal area of both subalpine fir and Engelmann spruce within ecoregion subsections (Bailey) occupied by both species. Changes in either abundance or basal area can be caused by a variety of processes, including stand development, disturbance-related turnover, or mortality. To disentangle these processes, we combined abundance and basal area estimates for each species using a binary categorization scheme (Figure 1; Perret *et al.* 2023) with four population trajectory categories: *densification* (increases in both basal area and abundance), *development* (declining abundance but increasing basal area), *turnover* (increasing abundance but declining basal area)*,* and *decline* (decreases in both basal area and abundance). In cases where change estimates were statistically indistinguishable from zero (*i.e.,* sampling error was equal or greater to the magnitude of the change), we treated the estimate as though it were positive.

Continued codominance of Engelmann spruce and subalpine fir requires positive population trajectories (*i.e.,* *development* or *densification*, described above) for both species. In contrast, if one species is experiencing turnover or decline, the spruce-fir system is vulnerable to a shift to single-species dominance or other compositional changes. We used the single-species population trajectories described above to categorize these possibilities (Figure 1) after the post-disturbance reorganization schema presented by Seidl & Turner (2021). These possibilities include: (1) *persistence/resilience* – both species are either undergoing changes corresponding with normal stand development or are actively increasing in density; (2) *structural change* – one or both species have experienced significant turnover of individuals, indicating that future trajectories may depend on post-disturbance recovery and survival of new recruits; (3) *compositional change* – one species is in decline while the other is either undergoing normal stand development or increasing in density, suggesting that one species will become dominant over the other; and (4) *replacement* – indicating that both species are in decline, and the system may be replaced entirely.

Demographic models

We built a series of statistical models for each species predicting individual mortality, seedling presence, and recruitment presence as the linear combination of several predictor variables and their interactions. Because each response variable is a binary state (*i.e.,* the presence or absence of mortality, seedlings, or recruitment), each model is a binomial generalized linear mixed model with a logit link function that we implemented in a Bayesian framework with non-informative priors. We used the ‘brms’ package (cit) in the RX.X.X statistical programming environment (R Core Team, 2023) to build all of our models.

*Climate data*

Past work has demonstrated tree demography in temperate regions is strongly influenced by aspects of the local climate related to moisture availability (Littlefield, Davis, Babst, etc). However, at regional or continental scales, spatial variation in mean climatic conditions also plays an important role in structuring biogeographical patterns in forest systems, including local responses to temporal climatic variation (cits, Klesse, Perret). We balanced these different influences in our demographic models by including climate predictors reflecting underlying mean climatic conditions, as well as predictors reflecting local climate anomalies. Specifically, we used historical climate data from ClimateNA (Wang et al) to calculate the mean annual temperature, mean annual precipitation, and mean climatic moisture deficit for each FIA plot in our dataset during a reference period comprising the 30 years preceding each site’s initial measurement. We then calculated the maximum mean annual temperature and climatic moisture deficit anomalies each plot experienced between its initial measurement and remeasurement (approximately 10 years) relative to the reference period means. These maximum anomalies were converted to z-scores using variation observed during the reference period, following the procedures of Littlefield *et al.* (2020) and Davis *et al.* (2023). These anomalies capture the maximum degree to which climatic conditions at each FIA plot departed from historical baselines during the period reflecting our population trajectory estimates. In all our demographic models, we incorporated interactions between climate anomalies and reference mean conditions, which allows for regional variation in demographic responses to local temporal climatic variation.

*Mortality models*

The annualized FIA sampling design was implemented in most western US states in 2000, and entails remeasuring each FIA plot on approximately 10 year rotations. For the vast majority of plots, there thus exists an initial measurement between 2000 and 2009, and a single remeasurement between 2010 and 2019. This limits the temporal resolution of any demographic rate (*e.g.,* mortality, growth, recruitment) estimated using FIA remeasurement data. While FIA field crews do assign an estimated year to every observed instance of tree mortality, the accuracy of that estimate likely varies widely depending on mortality agent, stand characteristics, tree species, and region. We thus modeled mortality over the entire remeasurement period, *i.e.,* the decadal probability of mortality.

We filtered FIA tree data to select remeasured subalpine fir and Engelmann spruce from the 2,972 plots on which they cooccurred that were alive at initial measurement and recorded as dead or alive at the second measurement (N = 34,989 subalpine fir and 27,944 Engelmann spruce). For each species, we modeled a tree’s status (*i.e.,* live or dead) at remeasurement using a binomial generalized linear mixed model with individual-, plot-, and landscape-level predictors. The model structures were as follows:

where the survival *S* of individual *i* in plot *p* nested in ecoregion *r* at time *t2* is modeled as a linear function of a fixed intercept b0 modified by a random term g1 varying between ecoregions *r*, and predictors varying between individuals *i*, plots *p,* and ecoregions *r*. Individual-level predictors include the diameter (*DIA*), crown ratio (*CR*), and damage status (*DAM*) of tree *i* at time *t1*. Damage status was coded as 0 if the tree was undamaged, and 1 if any fire, insect, or disease damage was recorded. Plot-level predictors included climate normals *CN* during the 30-year reference period preceding the initial plot measurement, recent climate anomalies *CA* observed between time *t1* and time *t2,* and their interactions. The index *j* indicates the climate normal variable (mean annual temperature or mean annual precipitation), whereas the index *k* indicates the climate anomaly variable (mean annual temperature or climatic moisture deficit). We also included the total stand basal area (*BAH*) within each plot at *t*1. Landscape-level predictors include the proportion of spruce-fir forest in each ecoregion impacted by fire mortality *AF* or biological disturbance agent mortality *AB* between time *t1* and time *t2*. These proportions were calculated using the FIA sampling design, after Perret *et al.* (2023). The model also included selected cross-scale interactions, namely between tree size *DIA,* climate anomalies *CA*, and disturbed area *AF* and *AB*. β4, β5, and β6 terms represent vectors of model-estimated coefficients corresponding to the indices for each covariate and interactions between covariates. The models were implemented in a Bayesian framework with uninformative priors using the ‘brms’ R package (Burkner 2021).

*Regeneration models*

FIA field procedures define seedlings as individual trees with a diameter of less than 2.54 cm and a height of at least 15 cm. Seedlings are inventoried on smaller microplots nested within subplots; because of this, seedling density estimates have more uncertainty than those for adults, and may be unreliable when there is high spatial heterogeneity. We thus chose to model subalpine fir and Engelmann spruce regeneration using seedling presence rather than seedling densities. For each species, we used a binomial generalized linear mixed model to predict the probability of seedling presence at an FIA plot at its remeasurement:

where seedling presence *R* in plot *p* nested in ecoregion *r* at time *t2*is modeled as a linear function of a fixed intercept b0 modified by a random term g1 and several predictor variables. These include the severity of fire disturbance (*SEV*) on a plot between t2 and t1, calculated as the proportion of adult trees of all species living on the plot at t1 that had died due to fire (according to FIA field crew assignments) by t2. Other predictors included total stand basal area (*BAH*) and reference period climate normals (*CN*) and remeasurement period climate anomalies (*CA*), as described for the mortality models above.

*Recruitment models*

Previous work on subalpine fir population trends has demonstrated that sapling recruitment presents a critical demographic bottleneck for the species across its distribution (Perret *et al.* 2023). However, saplings are defined by FIA field protocol as trees with a diameter between 2.54 and 12.7 cm, and are inventoried on microplots similarly to seedlings. We thus chose to model sapling recruitment similarly to seedling regeneration; as the presence or absence of new sapling recruits recorded on the microplot at remeasurement. \*\*sentence about splitting seedlings/saplings getting at different demographic processes?\*\* Sapling recruitment models were structured identically to seedling regeneration models (equation 2).

Future Projections

**Preliminary results**

*Population estimation and categorization*

When we categorize ecoregion subsections using this scheme, as in Figure 2a, we find that 38.4% of the species’ shared distribution falls in the *persistence/resilience* category, 13.0% in the *structural change* category, 38.6% in *compositional change,* and 10.1% in *replacement*. This suggests that, based on population trends estimated between 2000-2009 and 2010-2019 inventory periods, it is unlikely that subalpine fir-Engelmann spruce systems will persist across ~50% of their current distribution. The major sources of mortality for each species differ between categories, shown in Figure 2b. Notably, insect mortality dominates across all categories except *persistence/resilience* for Engelmann spruce, probably reflecting severe spruce beetle outbreaks in parts of the species’ range. Subalpine fir mortality from insects and diseases is fairly consistent across categories, ranging from 2-3 trees per hectare for diseases and 1-3 trees per hectare for insects. Fire mortality was more variable, however, and was the dominant mortality agent for subalpine fir in the *compositional change* and *replacement* categories. Mortality is more evenly distributed between fire, disease, and insect agents for subalpine fir, except in the *replacement* category, where it seems to be mostly driven by fire. These differences suggest that global change drivers that indirectly cause mortality by acting on these proximate mortality agents may impact the two species differently across their shared distribution.

*Mortality models*

**Effects**

ABLA – negative effect of mean temps on survival but positive effect of temperature anomalies (check interactions between anomalies and refs), super strong negative effect of fire area (with anom interactions), moderate tree size effect that interacts with lots of terms significantly. Negative effect of previous BAH on mortality (which is strange).

PIEN – no significant tree size effect! Small/moderate positive effect of temp anoms, very negative effect of CMD anoms (and strong interaction). No effect of MAT reference, moderate neg effect of MAP reference, check interactions with anoms. Strong fire area effect. Strong disturbance x anomaly interactions. Positive effect of previous BAH on mortality, but the effect is pretty weak.

*Regeneration models*

**Effects**

ABLA – no effect of previous BAH on seedling presence (makes sense, shade tolerant). Strong negative effect of temp anomalies (gets more negative in warmer regions), weak negative effect of CMD anomalies.

PIEN – strong negative effect of previous BAH on seedling presence (makes sense, less shade tolerant). Effect of MAT anomalies strongly dependent on reference temperature; strongly positive in cold areas, strongly negative in hot areas.

*Recruitment models*

**Effects**

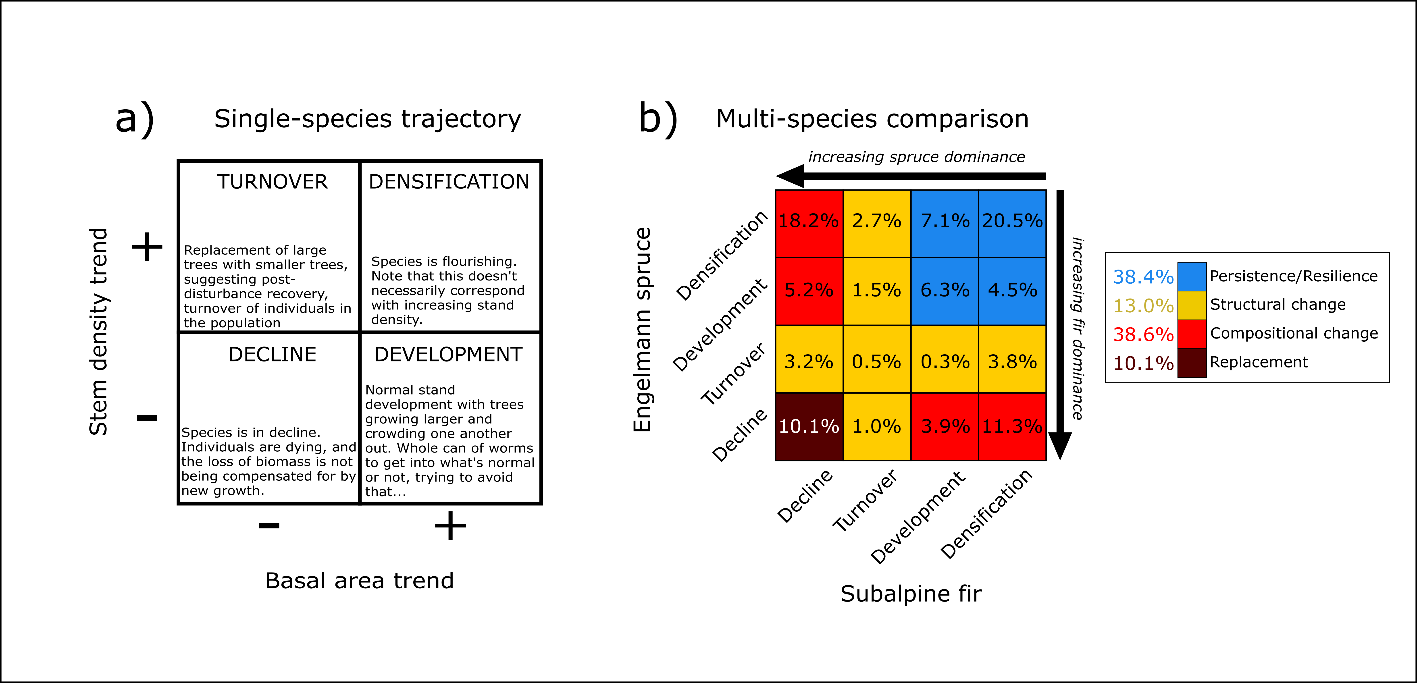
ABLA – strong negative effect of temp anoms at all references for ABLA (more negative in warmer refs).

PIEN – not much of a temp anom effect.

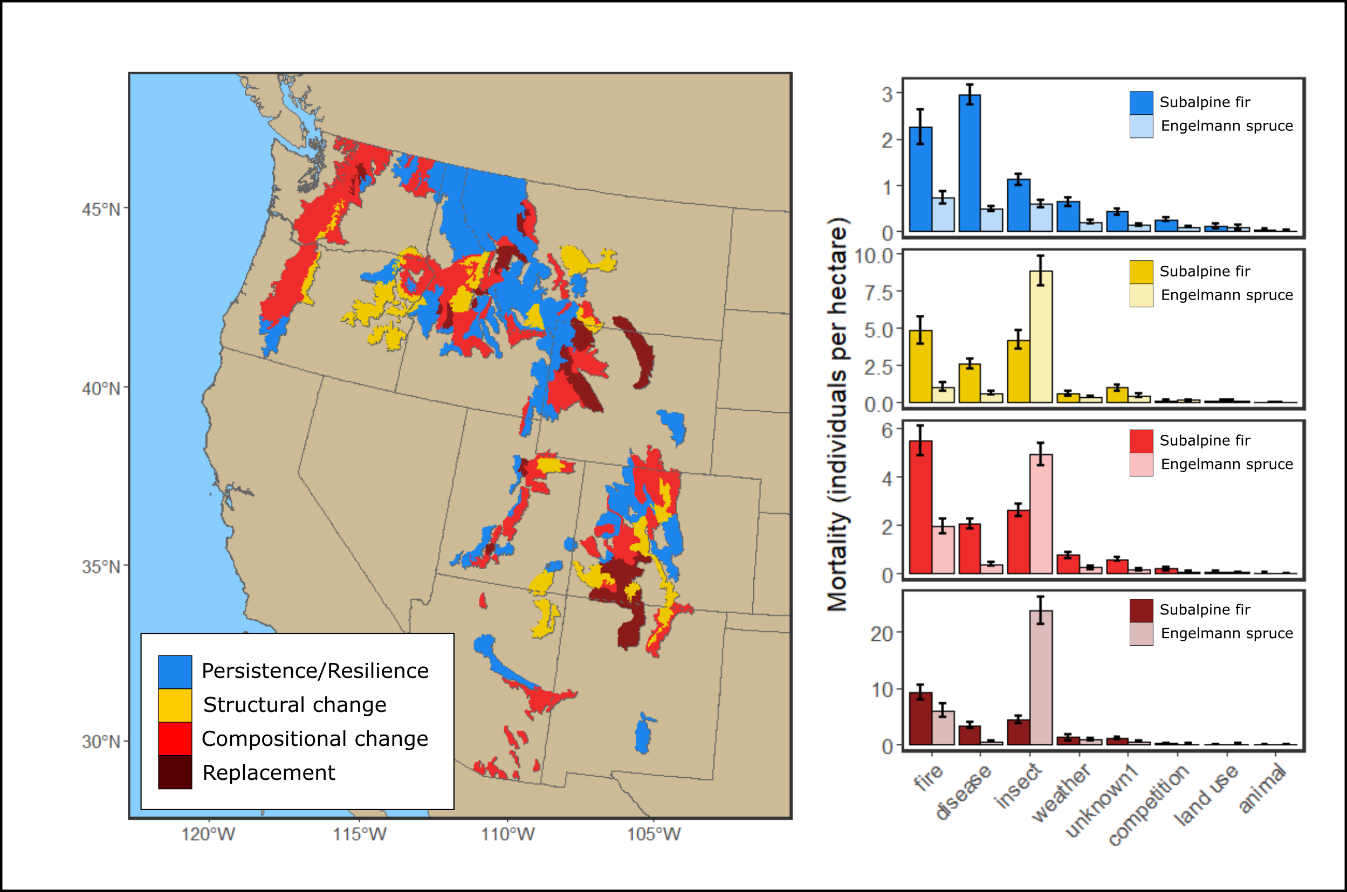
Mortality and regeneration models are still in development. Mortality models are binomial GLMMs with the response variable being tree status (*i.e.,* alive or dead) at the second plot visit for trees that were alive during the initial inventory (*i.e.,* individual probability of survival over a 10-year period). The model incorporates predictors at three levels of organization: tree (tree size, crown ratio, and the presence/absence of insect or disease damage), plot (climate normal and recent anomalies, stand density), and landscape (proportion of ecoregion subsection impacted by fire and biological disturbances); as well as cross-scale interactions (*e.g.,* between tree size, climate anomalies, and disturbance) and ecoregion subsection-level random intercepts. I built a separate model for each species, though I also explored joint models that incorporate interactions between species identity and various other predictors, or species-level random effects; ultimately, separate models performed better and are easier to interpret. I’ve been evaluating model performance in a variety of ways – in short, the models evaluate well at larger scales of organization (*e.g.,* at ecoregion subsection scales), though differentiation between living and dead trees is more difficult at individual scale. The single best predictor of mortality is whether a plot burned between remeasurements; I opted to omit this from the model in order to make larger-scale predictions without trying to model the probability of fire itself.

*Regeneration models*

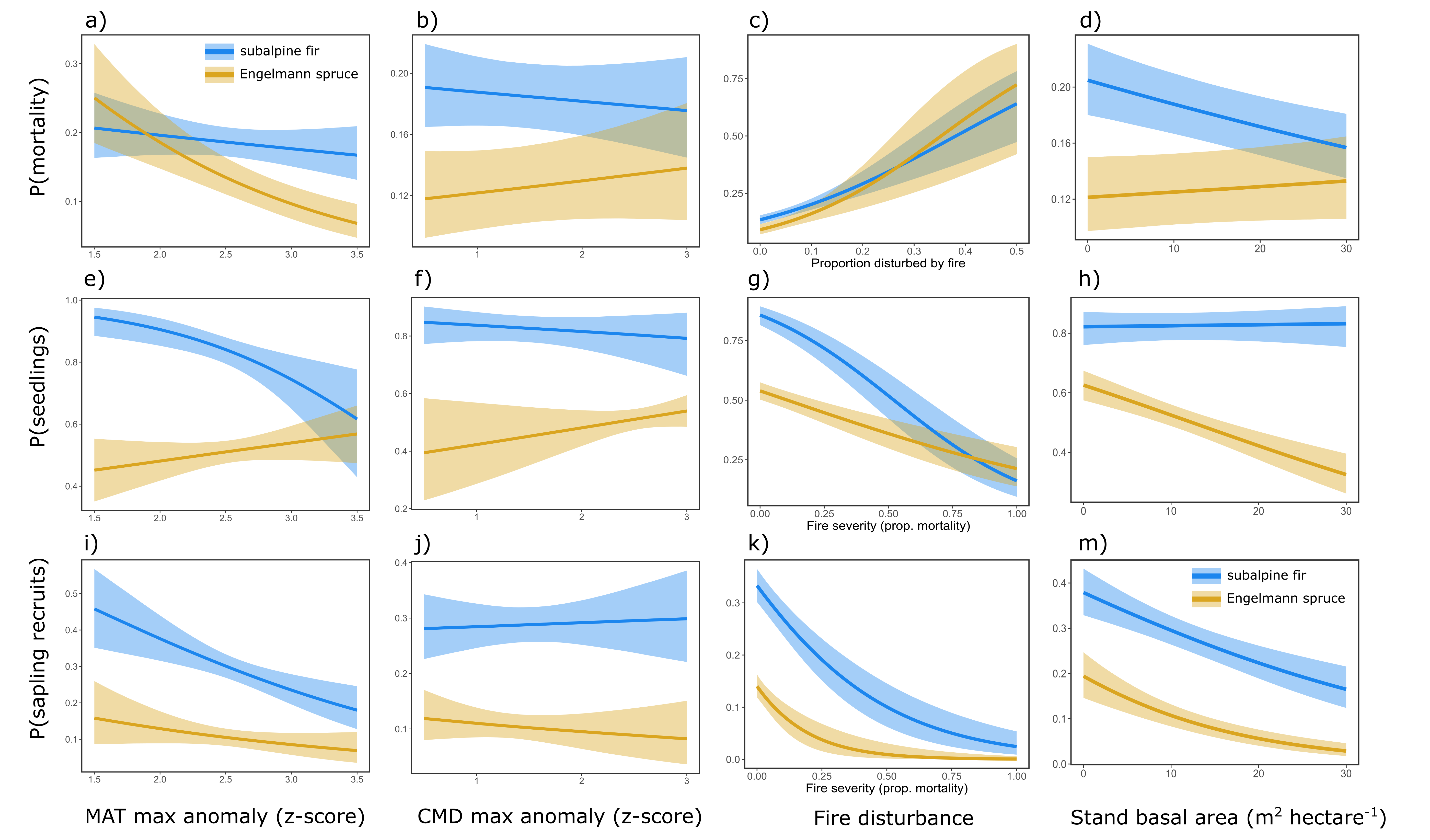
I chose to model regeneration as the probability of seedling presence at the plot level during the most recent inventory period, again using a binomial GLMM. These models are newer and I haven’t yet done as much work evaluating their performance or exploring the estimated effects. They currently incorporate predictors at the plot (climate normal and recent anomalies, estimated fire severity, estimated BDA severity, slope, aspect, elevation) and landscape (proportion of ecoregion impacted by fire or biological disturbances) level. Ideally, climate and disturbance predictors should correspond to those in the mortality models so that predictions from both models can be evaluated jointly.

**Figures**

**Figure 1.** Conceptual diagram of single-species population trajectories (a) and how they combine for two species (b). Panel (a) shows how combinations of basal area and stem density trends suggest differing population trajectories: *decline*, where both basal area and stem density are decreasing; *turnover*, where basal area is decreasing but stem density is increasing; *development*, where increasing basal area and decreasing stem density suggest self-thinning stand development; and *densification*, where both basal area and stem density are increasing. For two species (b), these four categories combine to suggest different likelihoods that species’ coexistence will persist: *persistence/resilience*, where both species are either experiencing stand development or densification; *structural change,* where one of the two species is experiencing high turnover associated with mortality, suggesting that future coexistence depends on increased recruitment and survival; *compositional change*, where one species is in decline and the other is flourishing, suggesting that one species will likely dominate over the other; and *replacement*, in which both species are experiencing population declines concurrently.

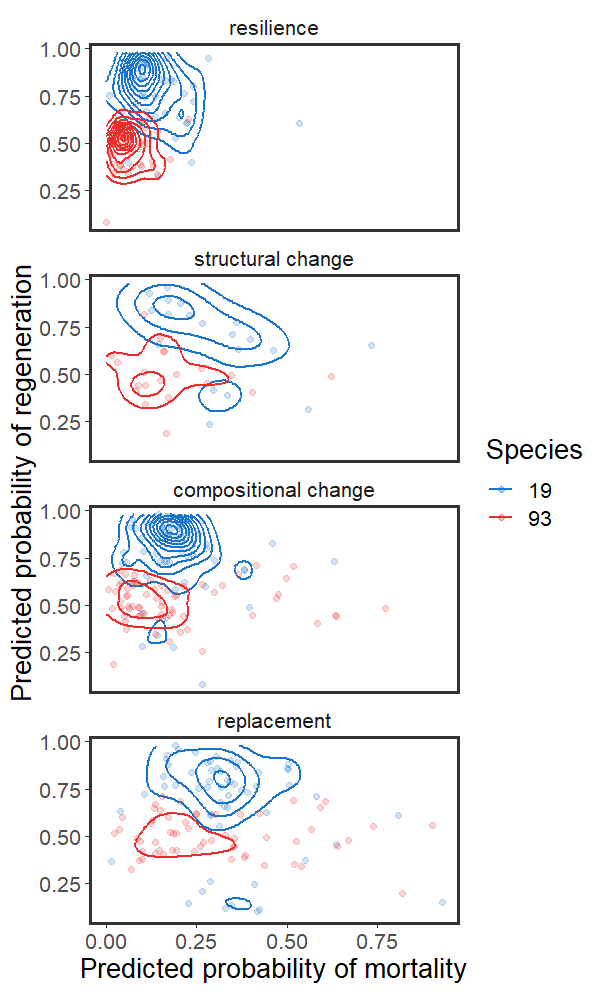
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**Figure 2.** Distribution of different population trajectory categories, as estimated at the ecoregion subsection level across the shared range of subalpine fir and Engelmann spruce (a), and the estimated mortality of both species in each category caused by broad classes of mortality agents (b). Colors correspond with the categories in Figure 1.



**A comparison of a diagram

Description automatically generated with medium confidence**

**Figure 3.** Model-predicted mortality (x-axis) and probability of seedling presence (y-axis) for subalpine fir (blue lines and points) and Engelmann spruce (red lines and points) in each of the population trajectory categories shown in Figure 1. Points indicate the mean predicted rates in an ecoregion subsection, and lines indicate their density distribution.

**A picture containing map

Description automatically generated**

**Figure 4.** Example of using models to project changes in mortality under future scenarios for subalpine fir (a) and Engelmann spruce (b). Maps show the difference between future predicted mortality and current estimated mortality for 2041-2060 under the SSP3-7.0 climate scenario. Predictions assume current landscape levels of disturbance and observed tree sizes.