

Can't see the trees for the forest: complex factors influence tree survival in a temperate second growth forest

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Abstract. Forest decline is a widespread, well-recognized problem, but studies reporting decreases in tree survival have been largely limited to relatively rare old-growth forests or low-diversity systems, and to models which are species-aggregated or cannot easily accommodate yearly climate variables. We created survival models for a multispecies second-growth forest in the Sierra Nevada of California using a hierarchical state-space framework. We accounted for a mosaic of measurement intervals and random plot variation, and we directly included yearly stand development variables alongside climate variables and topographic proxies for nutrient, water, and light availability. Our model captured the expected dependence of survival on tree size, but revealed different relationships between size and survival for each species. At the community level, including stand development variables accounted for decreasing survival time trends, but species-specific models demonstrated a diversity of factors influencing survival, including time trends, fundamental niche limitations, and the impact of competition. Our results on time trends and competitive performance showed local exceptions to existing theories of Sierran forest dynamics, with some shade-tolerant species increasing in survival over time and others performing better than expected under more crowded conditions. Within species, low survival was concentrated in susceptible subsets of our population and single estimates of annual survival rates did not reflect this heterogeneity in survival.

Key words: *Abies concolor*; *Calocedrus decurrens*; forest inventory; hierarchical state-space model; mixed-conifer; *Notholithocarpus densiflorus*; *Pinus lambertiana*; *Pinus ponderosa*; *Pseudotsuga menziesii*; *Quercus kelloggii*; Sierra Nevada; tree mortality.

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INTRODUCTION

Concern about forest decline is high given extensive forest insect outbreaks, rising levels of pollution, and recent increases in global temperature and greater variability in precipitation (Likens and Franklin 2009, FAO 2010, Zeppel et

al. 2013). This concern is motivated by the important suite of ecosystem services provided by forest trees as foundation species (Ellison et al. 2005). A number of studies and reviews have highlighted regional (van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013) and global (Allen et al. 2010, Wang et al. 2012) decreases in

tree survival, particularly in large trees (Dolanc et al. 2013, McIntyre et al. 2015), and some of these studies implicate climate change. In the arid West of the United States, studies of declining tree survival focus on old-growth forests, where endogenous changes in forest structure and species composition are minimal and assumed not to influence demographic trends (van Mantgem and Stephenson 2007, van Mantgem et al. 2009, but see Lutz et al. 2014). While old-growth forests are particularly important because they hold great ecological and social significance, they represent only 36% of the global forest (FAO 2010) and are particularly rare in temperate regions. For example, only 6% of forests in the United States are classified as primary (FAO 2010). Thus, most forests are simultaneously developing following a significant disturbance as well as potentially responding to long-term perturbations in the global environment. Under these circumstances, it is essential to disentangle the impact of trends in environmental conditions (e.g., climate change) from the impact of trends in stand development (Luo and Chen 2013). To date, the few studies that incorporate stand dynamics into mortality assessments focus on boreal forests following wildfire (Thorpe and Daniels 2012, Luo and Chen 2013) or only address the demographic link indirectly via correlation (Lutz and Halpern 2006). To better understand temperate tree survival in the face of increasing threats, we investigated a productive, second-growth mixed conifer forest in California.

To further understand the complex factors influencing tree survival in more diverse systems, we also explore both species-aggregated models and species-specific models. Studies of forest decline typically aggregate species together (van Mantgem and Stephenson 2007, van Mantgem et al. 2009) or fit models for systems with one (Hurst et al. 2011, Uzoh and Mori 2012) or only a few species (Thorpe and Daniels 2012, Luo and Chen 2013). Decline of forest trees at the community level (e.g., species-aggregated) is important for evaluating the risk to fundamental forest ecosystem services. However, species-specific models of tree survival reveal ecological principles at play, reveal dangers to particular species of cultural and commercial interest, and improve parameterization of individual-based

forest simulators and gap models (Bigler and Bugmann 2004, Larocque et al. 2011). Trends in survival at a coarser, community-level scale could mask trends at a finer, species-specific scale—but trends at both scales could be ecologically, culturally, and economically important.

Finally, intraspecific heterogeneity in survival may be important. Survival processes are spatially complex (Das et al. 2011), and small trees (Drobyshev et al. 2009) or trees in crowded stands (Das et al. 2007) may have a reduced chance of survival relative to their larger counterparts in less crowded stands. The concept of a single annual survival probability (e.g., Sheil et al. 1995) becomes less meaningful for a heterogeneous population: a high ‘mean’ annual survival may miss susceptible subsets of the population with substantially lower survival (Sheil and May 1996). The influence of susceptible individuals can be important in applications of survival models, e.g., population models where individual quality can have a strong impact on population-level results (Ellner and Rees 2006). As Clark et al. (2012) point out, survival happens at the scale of individuals, but we are concerned with the species and landscape scale. In this study we pay special attention to the drivers of mortality for susceptible subsets of our population.

Specifically, we ask the following questions regarding tree survival in a temperate second-growth forest: (1) Is there evidence for an unexplained linear time trend (referred to as a ‘secular trend’) in survival even when accounting for the confounding trend in stand development, and does climate change account for such a trend? (2) How strongly do species-specific results differ from species-aggregated results, and how much do species differ from each other in their responses to explanatory variables? (3) Within a species, how heterogeneous is survival and what are the drivers of that heterogeneity?

To address these questions, we turn to forest inventory data. These data can introduce their own complexities: for example, census intervals are often greater than one year and are also variable, causing uncertainty in identifying when a tree died during the interval (Nord-Larsen 2006). This problem is complicated by the potential for individuals to be ‘lost’ and then found again in a later inventory (see Moustakas

and Evans 2015 and references for clever uses of the mark-recapture framework to address this problem). These problems lead to a fundamental difficulty in modeling the influence of annual variables on survival (Thorpe and Daniels 2012, Luo and Chen 2013), including climate or stand development. Hierarchical state-space models address these challenges by explicitly modeling the latent unmeasured survival status of the tree in each year (Clark et al. 2012). If the uneven census intervals provide some information in most years, this model structure may be able to borrow across data-poor years in order to investigate the possibility of time trends in survival while incorporating yearly changes in stand characteristics.

We examine the annual survival probabilities for seven tree species in a second-growth temperate forest in the Sierra Nevada of California. Using a state-space model, we incorporate stand structure, tree size, climate, and resource availability proxies, as well as spatial heterogeneity among plots. With this model, we are able to appropriately represent the complexity of forest tree inventory data and to include many different drivers of survival, enabling us to address our proposed questions.

METHODS

Study site, species, and variables

Data for this study come from Blodgett Forest Research Station (BFRS), located near Georgetown, California, USA on the western slope of the Sierra Nevada (38°52' N, 120°40' W). The forests at BFRS are dominated by a mix of five conifer species: white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), and ponderosa pine (*Pinus ponderosa*). Two hardwood species are also common: California black oak (*Quercus kelloggii*) and tanoak (*Notholithocarpus densiflorus*). Elevation ranges from 1100 to 1410 m. The loamy-sandy soils are underlain by Mesozoic, granitic material and are predominantly classified as the Holland and Musick series (Olson and Helms 1996). Total annual precipitation averages about 1600 mm, falling mainly between September and May. The average minimum daily temperature in January is 0.6°C and the average maximum daily tempera-

ture in July is 28.3°C.

BFRS is an actively managed commercial timberland that has been subjected to fire suppression for the last 90 years, reflecting a management history common to many forests in California (Laudenslayer and Darr 1990). Our work focused on the reserve compartments (stands 11–45 ha in size) that have not been managed with the exception of fire suppression since the initial clear-cut harvests were completed early in the 20th century (Olson and Helms 1996). Fire was a common ecosystem process at BFRS before the policy of fire suppression began early in the 20th century (Stephens and Collins 2004).

All compartments are sampled by a grid of permanent inventory plots 0.04 ha in size. Each plot is surveyed periodically but not always in the same year, creating a mosaic of measurement intervals ranging from 3 to 14 years. Altogether, inventories account for the time period from 1976 to 2010. Crews measure the diameter at breast height (DBH; breast height = 1.37 m) of living trees greater than 11.4 cm DBH and record information on standing dead trees. Smaller trees (greater than 0.254 cm DBH) are tracked in subplots.

We include all of the native canopy tree species in this study. Black oak (*Q. kelloggii*) and tanoak (*N. densiflorus*) are both fire-adapted hardwoods capable of vigorous vegetative resprouting, though black oak is extremely shade-intolerant while tanoak is considered shade tolerant (Niinemets and Valladares 2006). Ponderosa pine (*P. ponderosa*) and sugar pine (*P. lambertiana*) also rely on disturbance: ponderosa pine is capable of surviving low-intensity fires due to thicker bark, and sugar pine recruits well in forest gaps (Burns and Honkala 1990). As the fire regime has shifted from frequent, low-intensity fires set by native peoples (Stephens et al. 2007 and references) to fire suppression, these species have become less abundant at BFRS. White fir (*A. concolor*) and incense-cedar (*C. decurrens*), on the other hand, are shade-tolerant (Niinemets and Valladares 2006) and have become the main canopy constituents at BFRS. Douglas-fir (*P. menziesii*) has intermediate shade-tolerance and also benefits from more frequent fire (Burns and Honkala 1990), but still remains an important component at BFRS. By stem count, the most abundant

species are incense-cedar, Douglas-fir, white fir, and ponderosa pine. These species together comprise 88.9% of the stems in the control plots. Less abundant are sugar pine, black oak, and tanoak; these species account for another 9.5% of stems (Table 1).

In order to assess the relative impact of different biotic and abiotic factors on tree survival, our models include variables representing competition, tree size, climate, and topographic proxies for nutrient, light, and water availability. We include two biotic variables: tree size (DBH in cm) and plot basal area (m^2/ha). Plot basal area is calculated using the cross-sectional area at breast height of all trees in the plot, divided by the area of the plot. The second-growth forest at BFRS has undergone heavy density-dependent mortality (Battles et al. 2008), with plot basal area increasing over time through our inventory period (Appendix A). When a tree was identified as dead in a census, no size was recorded in the database. There are several ways to estimate a missing size, but model results proved not to be sensitive to the different methods; ultimately we extrapolated individual size from its final measurement until the year it was discovered dead using a simple linear model of size as a function of time (see Appendix B). Each tree's size and plot's basal area were interpolated over time using smoothing splines (Wood 2006). See Olson and Helms (1996) for more information on inventory procedures.

We include three topographic variables (measured at the plot level) as proxies for resource availability (i.e., light, nutrients, and water): insolation, topographic slope, and elevation. Annual insolation (Wh/m^2) is calculated from a $1/3$ arc second digital elevation model from the USGS Seamless Map Database (USGS 2011), using the solar radiation calculator in ArcGIS 9.3 (ESRI 2011). Topographic slope (in percent) is measured in the field using a clinometer, and elevation (m) is measured from a topographic map to the nearest 3.05 m. We also include annual climatic water deficit, as well as year (to test for a secular time trend in survival). Annual water deficit is calculated in mm from weather records at BFRS, using AET 1.0 (Gavin 2007) and a modified Thornthwaite method; note that deficit is a negative number and more negative numbers indicate more stressful conditions.

Deficit incorporates precipitation and temperature variables and has been correlated with tree survival in Sierran forests (van Mantgem and Stephenson 2007). Because trees are measured in summer, we use the climatic water deficit from the previous year in our model as the drought stress from the previous summer is most likely to affect tree survival in the current year (McDowell et al. 2008). Water deficit at BFRS is slightly increasing with time (becoming more negative: $-1.06 \text{ mm}/\text{year}$, $p = 0.29$), but the trend is not significant. The topographic variables and biotic variables are largely uncorrelated with each other; see Appendix A: Table A2.

We recognize that there are many possible climate variables, as well as many possible stand development variables and individual tree variables (Monserud and Sterba 1999). To make modeling tractable, we have chosen representative variables to account for the range of factors which have been shown to relate to tree survival: tree size reflects canopy position at BFRS (Eitzel et al. 2013), plot basal area is a good representation of crowding (Lines et al. 2010), and many studies in Mediterranean forests use annual climatic water deficit to represent climate effects (van Mantgem and Stephenson 2007, Thorne et al. 2012, McIntyre et al. 2015). See Appendix A for more information on these explanatory variables (including summary statistics in Table A1 and plots in Figs. A1 and A2) and Eitzel et al. (2013) for details and more information on data auditing.

State-space model

In our state-space formulation, we explicitly model the unknown yearly status of individual trees; because tree status is a discrete state, our model falls in the category of hidden Markov models. This model structure represents our ignorance of when the tree died between inventories. In this sense, our approach is similar to a mark-recapture model as seen in wildlife applications (Gimenez et al. 2007), but with perfect detection. As our plots are not mapped, we choose to model spatial heterogeneity in the forest using a random plot effect.

We model the alive/dead status z for tree i within plot j in year $(t + 1)$ as a Bernoulli random variable where 1 is 'alive,' conditional on status at time t , in the following way:

Table 1. Species abundances and number of records for all species at Blodgett Forest Research Station (including sub-canopy species as well as canopy species featured in the paper).

Code	Species name	Common name	Trees	Plots	Years	Records
All	...	all species	3319	109	34	9000
IC	<i>Calocedrus decurrens</i>	incense-cedar	1378	98	34	3733
WF	<i>Abies concolor</i>	white fir	846	93	34	2224
DF	<i>Pseudotsuga menziesii</i>	Douglas-fir	395	69	34	1110
PP	<i>Pinus ponderosa</i>	ponderosa pine	332	75	34	955
TO	<i>Notholithocarpus densiflorus</i>	tanoak	110	15	25	284
BO	<i>Quercus kelloggii</i>	black oak	104	29	34	292
SP	<i>Pinus lambertiana</i>	sugar pine	101	39	34	271
YW	<i>Taxus brevifolia</i>	Pacific yew	18	2	24	42
CH	<i>Chrysolepis</i> spp.	chinquapin	16	5	29	43
DW	<i>Cornus nuttallii</i>	Pacific dogwood	9	3	11	18
AL	<i>Alnus</i> spp.	alder	7	3	24	21
MD	<i>Arbutus menziesii</i>	Pacific madrone	3	2	25	7

$$z_{ij}(t+1) \sim \text{Bern}(\phi_{ij}(t)z_{ij}(t)) \quad (1)$$

where $\phi_{ij}(t)$ is the probability of survival from year t to year $t+1$. Multiplying by the status at the previous time ensures that dead trees stay dead. The $z_{ij}(t+1)$ are conditionally independent (given parameters) over (i, j) .

The full model for the biotic and abiotic factors influencing survival probability is

$$\begin{aligned} \logit(\phi_{ij}(t)) &= \beta_{0j} + \sum_k \beta^k x_{ij}^k(t) \\ \beta_{0j} &= b + p_j \end{aligned} \quad (2)$$

where b is an overall mean survival for an average tree, and p_j is a random effect for plot j with $p_j \sim N(0, \sigma_p^2)$. The p_j are independently and identically distributed across plots. k indexes one of the explanatory variables (it is not an exponent): insolation (x_j^{insol}), topographic slope (x_j^{slope}), and elevation (x_j^{elev}) are all measured at plot level; plot basal area ($x_j^{\text{ba}}(t)$) is measured at plot and year level; tree size ($x_{ij}^{\text{DBH}}(t)$) is measured at the tree and year level; and annual water deficit is measured at year level ($x^{\text{def}}(t-1)$). The β^k are coefficients for each of these explanatory variables. In order to test for a secular time trend, β^t , we also include the measurement year $x^t = t$.

Survival depends monotonically on most of these covariates. For example, we expect tree survival to decrease with more stressful conditions (e.g., more severe water deficit or increasing plot basal area) so a linear relationship with the logit of survival is reasonable. For several of the other covariates (elevation, insolation, and topographic slope), the ranges of these variables at

BFRS are small relative to the range of the variables for our study species' fundamental niches (see Eitzel et al. 2013; Appendix H). A linear relationship between these variables and the logit of survival is appropriate over a small range of values. Neither of these assumptions apply to tree size, however. To allow a more flexible survival relationship with size, we have both a linear (β^{DBH}) and quadratic (β^{DBH^2}) term for tree diameter. Finally, we are explicitly testing for a linear time trend in survival. See Appendix C: Fig. C1 for a diagram representing the relationship of model components to each other.

We standardized (centered and scaled) the explanatory variables; centering improves the mixing of the MCMC sampler and clarifies interpretation, while scaling allows the relative impact of variables within a species to be assessed (Gelman and Hill 2007). When comparing between species, we have returned the parameter estimates to their original scale but left them centered. See Appendix C for algebra regarding standardizing and rescaling these parameter estimates.

To fit the state-space models in a Bayesian framework, we used Markov chain Monte Carlo (MCMC) estimation techniques in OpenBUGS (Lunn et al. 2009), run through R2WinBUGS (Sturtz et al. 2005) in R (R Development Core Team 2009), and coda (Plummer et al. 2010) to calculate credible intervals. We chose weakly informative (effectively uninformative) priors: the random effect standard deviation σ_p was uniform from zero to 100, and the priors for the β^k s were normal with precision 10^{-6} . For survival of an average tree $\text{expit}(b)$ ('expit' is the inverse

logit, the transformation required to return to the probability scale), care in parameterization of priors was required. Due to the nonlinearity of the logit, a prior which is flat on the scale of the linear predictors (e.g., b) is U-shaped on the probability scale ($\text{expit}(b)$). Because tree survival is high, the estimated mean survival can be quite close to one, where the nonlinearity has the strongest effect (Van Dongen 2006). Therefore, as in Buoro et al. (2012), we used a uniform distribution from zero to one for $\text{expit}(b)$ rather than a normal distribution for b . We assessed the sensitivity of parameter estimate posteriors to these choices of prior distributions, and confirmed the appropriateness of our choices (Appendix C).

We validated a simple version of this model (with only an intercept, b) against maximum-likelihood implementations of a typical mortality calculation, m , after Sheil et al. (1995, see Appendix D for details of this model and its estimation). The mortality rate for an average tree is simply the complement of annual survival probability, or for the simple state-space model: $1 - \phi = 1 - \text{expit}(b)$. We also use this simple estimate of mortality, m , to compare with the results of the more complex models, as most forest mortality studies use calculations like Sheil's.

Model selection

Due to the lengthy run times for each model and the number of candidate variables, it was not feasible to fit all possible models, requiring us to take a stepwise approach. Backward stepwise selection from full models was also not feasible due to poor mixing and computational limitations. Poor mixing is likely to be caused by heavy parameterization in the full models, especially for year-level variables (e.g., annual climatic water deficit) for which the response variable is sparse in some years. Therefore, we took a forward stepwise selection approach to navigating possible models. Although forward selection has limitations in some situations, it has been shown to often have similar predictive accuracy to other model selection strategies (Murtaugh 2009).

Choosing a criterion to rank candidate variables to add to the model in our selection process is not straightforward in a Bayesian framework, and the common choice of the deviance infor-

mation criterion (DIC) is controversial for models like ours with many latent states and random effects (Celeux et al. 2006, Millar 2009, Kery and Schaub 2012; Appendix E). Therefore we referred directly to posterior densities for a criterion to use in selecting the variable x^k : at each step, we add the variable whose β^k posterior is most separated from zero. We represent 'separation from zero' using a tail probability analogous to a two-tailed p-value (Bochkina and Richardson 2007). This method is a way to determine which equal-tailed credible interval barely includes zero. This metric is justified because it will be similar to a p-value, which, when comparing single variable additions, will be ranked in the same order as AIC differences (Murtaugh 2014; Appendix E). We break tail probability ties by choosing the variable with the larger mean effect size.

We proceeded using our tail probability criterion by fitting separate models with each individual variable by itself, choosing the variable with the smallest tail probability, and then fitting another round of models with that variable and each of the others. To determine when to stop adding variables, we used a traditional 5% threshold, but typically also went one step beyond that and checked one additional variable (and the result usually agreed with the 16% threshold more typical of AIC reasoning in these cases; de Valpine 2014). We emphasize that we are not engaged in significance testing, especially conditioned on model selection, but rather that we are approximating the AIC ordering from Bayesian posteriors for single-variable additions. We also compared our results with DIC for our models where DIC should be least problematic and found that our final model in that case did have the lowest DIC among all the models we calculated as part of the forward selection (Appendix E). To select the plot random effect standard deviation, we used slightly different criteria and model selection strategies (Appendix F).

We fitted models for incense-cedar, Douglas-fir, white fir, ponderosa pine, sugar pine, black oak, and tanoak, as well as for all species aggregated together. We referred to intermediate models in the model selection procedure to investigate confounding between secular trends and stand development (Question 1). We used

the results of the model selection procedure to compare between species-aggregated results and individual-species results and to compare among individual-species results (Question 2). In order to address heterogeneity within each species (Question 3), we transformed models back to the probability scale to examine the range of survival probabilities for trees under different conditions. We also compared the survival estimates for an average tree from a simple model with only one parameter (b) to the same parameter in more complex models created during model selection (which include random plot effects and other variables). However, differences between the survival of an average tree, $\text{expit}(b)$, in a simple state-space model with one parameter and the same parameter in the complex models may be partly attributable to the nonlinearity of the logit and Jensen's inequality (see *Discussion: Heterogeneity and susceptible subsets* for more information on this mathematical issue). We therefore focus on comparisons from within the complex models in our discussion rather than comparisons between simple models and complex models.

RESULTS

Question 1: secular time trends and stand development

For the species-aggregated result, including plot basal area in the model rendered the time trend non-significant: the posterior heavily overlapped zero (Fig. 1A), and the model selection procedure did not select this variable once plot basal area was included. Single-species models for white fir, Douglas-fir, black oak, and tanoak showed no evidence of a significant time trend at any time in the model selection process. The other three species showed more interesting results, however. Ponderosa pine did not initially show a time trend, but when tree size and topographic slope were included in the model, the time trend emerged and was selected for the best model for this species (Fig. 1B). Adding basal area to the best model for ponderosa pine rendered the time trend not significant, but still within the AIC-like selection criteria (de Valpine 2014). In the case of incense-cedar, the time trend became less significant with the addition of size and then not significant when basal area was

added (though as with ponderosa pine, using the AIC-like threshold, the time trend would still be retained; Fig. 1C). For sugar pine (Fig. 1D), the time trend was significant when initially added during the model selection procedure, and remained separated from zero when tree size and plot basal area were included in later models.

Question 2: species-aggregated results vs species-specific results, and differences between species-specific results

For the most part, species-aggregated results did not mirror species-specific results (Table 2). The only variable which was consistent between species-aggregated models and individual-species models was the increasing linear size effect. Species-aggregated models did demonstrate the importance of the quadratic size effect and the effect of plot basal area, but these effects were not consistent across all individual-species models. The species-aggregated models entirely missed the importance of other variables to individual species (e.g., elevation for tanoak). In some cases, species-aggregated parameter estimates appeared to be an average of species-specific results (Fig. 2A, C), but even here the species-aggregated result missed meaningful details, e.g., incense-cedar's plot basal area effect was very different from the species-aggregated results (Fig. 2B).

All species individually showed a significant and increasing linear trend in survival for larger trees, and none of them showed an effect of annual water deficit (Table 2, Fig. 2). For all other variables, however, each species had a different response (Table 2, Fig. 3; Appendix G). For several variables, only one species responded (i.e., insolation for white fir, elevation for tanoak, plot basal area for incense-cedar), and for other variables, species had opposite responses. The quadratic size term modifying the linear increase in survival for larger trees was positive for white fir and negative for ponderosa pine and black oak. Topographic slope had a positive effect on ponderosa pine survival and a negative effect on tanoak. Finally, the secular time trend was negative for ponderosa pine and positive for sugar pine.

Question 3: heterogeneity within a species

A single annual survival probability did not

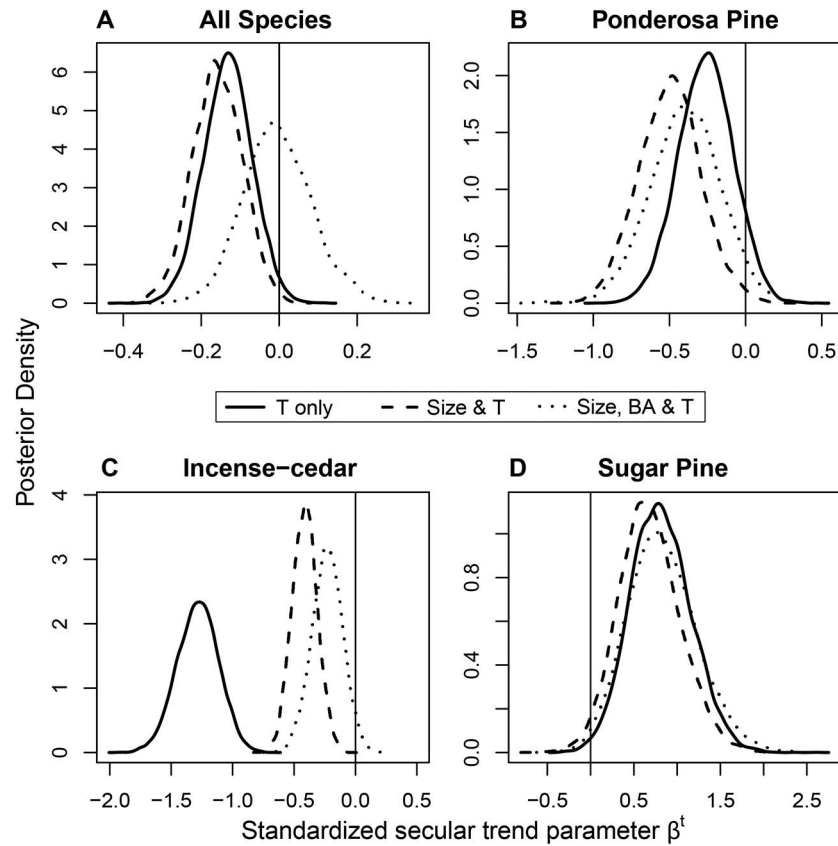


Fig. 1. Parameter posteriors for the time trend in different models for all species aggregated together (A), ponderosa pine (B), incense-cedar (C), and sugar pine (D). Solid lines indicate models with only a time trend, while dashed lines represent models with tree size (including the quadratic term if selected for that species) along with the time trend, and dotted lines indicate models with size, basal area, and the time trend. For ponderosa pine, the topographic slope is also included in the latter two models as it was consistently important in the model selection.

represent the heterogeneous effects of tree size and other variables on survival (Fig. 3, Table 3). Table 3 compares m calculations with results from our simple state-space model for each

individual species as well as for all species aggregated. The annual mortality rate for an average tree, $1 - \expit(b)$, for the simple state-space model is estimated in the same way as the

Table 2. Summary of model selection results for each parameter and species.

Species	β^{DBH}	β^{DBH^2}	β^{ba}	β^{insol}	β^{elev}	β^{slope}	β^t	β^{def}
All species	+	—	—
Incense-cedar	+	...	—
White Fir	+	+	...	+
Douglas-fir	+
Ponderosa Pine	+	—	+	—	...
Sugar Pine	+	+	...
Black Oak	+	—
Tanoak	+	—	—

Notes: An arrow indicates the sign of the coefficient β^k for variable k ; “+” indicates a positive β_k coefficient and “—” indicates a negative β_k coefficient for variable k ; “...” indicates that the variable was not selected in the final model for that species.

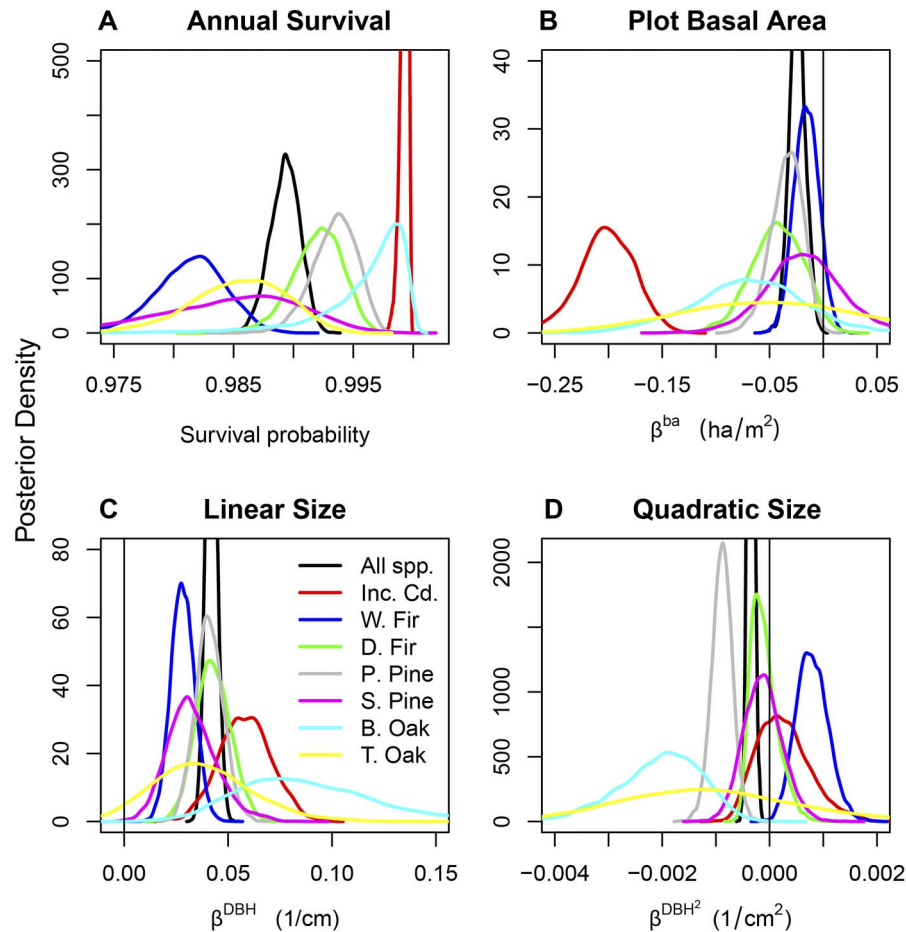


Fig. 2. Rescaled parameter posteriors from similar models for all species. These models include a random plot effect, size (linear and quadratic), and basal area. For tanoak, basal area and size posteriors are from separate models (tanoak's survival for an average tree, $expit(b)$, in (A) is from the basal area model). Posteriors have been rescaled in order to compare estimates between species. (A) Survival of an average tree in an average plot ($expit(b)$) for each species. Panels (B–D) show estimates of the effects of basal area (B), linear size term (C), and quadratic size term (D).

more complex state-space models detailed in *Methods: State-space model*. The simple state-space model and m calculations should and do agree closely for each species. We also show the results for the annual mortality probability from a model with a plot effect and no explanatory variables, indicating mortality for high-mortality (low survival, $1 - [expit(b - \sigma_p)]$), mean mortality ($1 - expit(b)$), and low-mortality (high survival, $1 - [expit(b + \sigma_p)]$) plots. Finally, we include in Table 3 the mortality rate associated with an average tree $1 - expit(b)$ in the final model for each species. Survival increased (mortality decreased) for the hypothetical mean tree as the

model became more complex. For example, in ponderosa pine, the single estimate of survival probability for an average tree $expit(b)$ (98.4% from a model without plot and explanatory variables; 99.3% for the final model; see Table 3) did not reflect the range of survival shown in Fig. 3: from 65.4% for small trees (1.52 cm DBH) on shallow slopes to 99.8% for medium-sized trees (71.09 cm DBH) on steep slopes. Other species showed similar heterogeneity in survival due to size and other variables (Fig. 3; Appendix G).

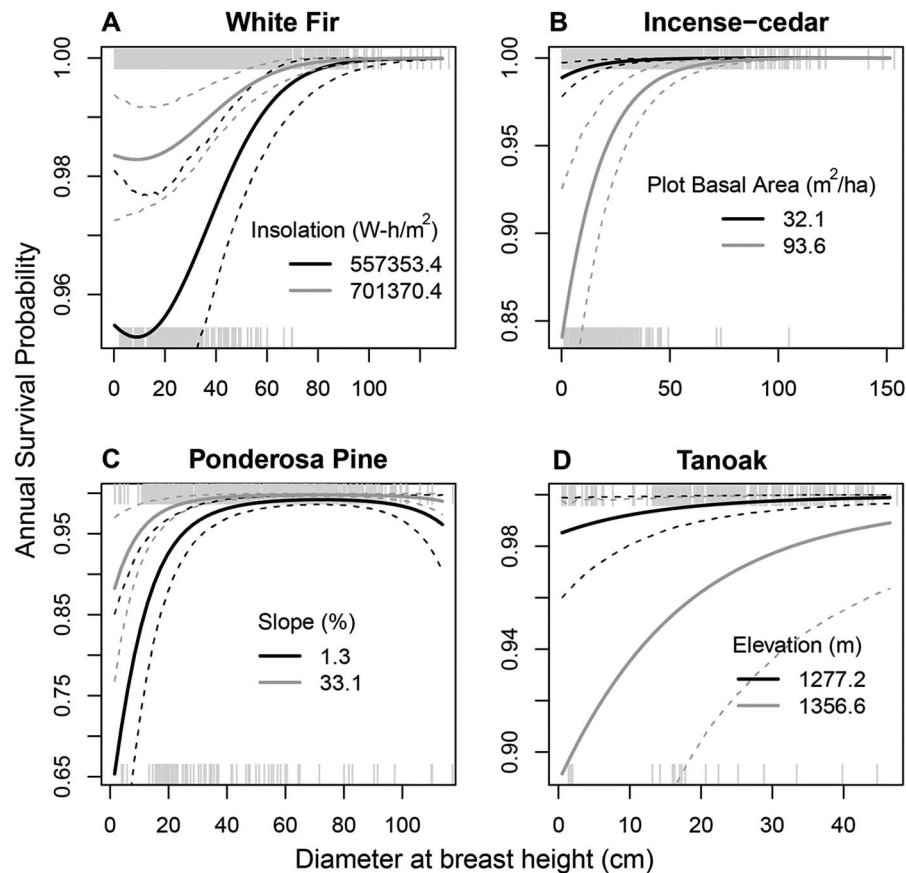


Fig. 3. Size relationships with survival probability for four species: white fir (A), incense-cedar (B), ponderosa pine (C), tanoak (D). Black and dark gray lines show the effects of high and low values of additional variables for each species: insolation (A), plot basal area (B), topographic slope (C), elevation (D). Black lines are two standard deviations below the mean value of the variable, and dark gray are two standard deviations above. Dashed lines indicate 95% credible intervals due to uncertainty in other parameters. Data are shown as light gray tick-marks with live trees at the top of the plot and dead trees at the bottom. The parameter estimates in these figures are from 'full models' including all the forward-selected variables, as indicated in Table 2 (see Appendix G for other species and variables).

Table 3. Comparison of annual mortality rates (in percent) from different models.

Species	Maximum likelihood	Bayesian state-space models				
		<i>expit(b)</i> only	With plot effect			Final model
			Low	Mean	High	
All species	1.79 (1.62, 1.95)	1.79 (1.66, 1.9)	0.7 (0.53, 0.87)	1.5 (1.27, 1.75)	3.12 (2.56, 3.77)	1.07 (0.83, 1.32)
Incense-cedar	1.81 (1.56, 2.08)	1.82 (1.64, 2.01)	0.52 (0.29, 0.73)	1.44 (1.06, 1.84)	3.92 (2.78, 5.16)	1.06 (0.71, 1.44)
White fir	2.14 (1.78, 2.54)	2.14 (1.87, 2.41)	0.67 (0.41, 0.96)	1.69 (1.26, 2.15)	4.11 (3, 5.43)	2.13 (1.51, 2.73)
Douglas-fir	1.39 (1.01, 1.87)	1.41 (1.12, 1.73)	0.63 (0.24, 1.09)	1.13 (0.72, 1.55)	2.1 (1.39, 2.93)	0.99 (0.62, 1.39)
Ponderosa pine	1.62 (1.19, 2.12)	1.63 (1.31, 1.98)	0.55 (0.22, 0.91)	1.43 (0.91, 1.94)	3.7 (2.15, 5.56)	0.72 (0.38, 1.08)
Tanoak	1.28 (0.61, 2.32)	1.37 (0.79, 2)	0.49(0, 1.32)	2 (0.05, 4.09)	12.26 (0.67, 76.17)	0.9 (0.23, 1.65)
Black oak	1.21 (0.61, 2.1)	1.25 (0.75, 1.8)	0.15 (0, 0.46)	1.17(0.09, 2.49)	14.15 (0.97, 50.92)	0.46 (0.02, 1.2)
Sugar pine	2.3 (1.34, 3.61)	2.37 (1.58, 3.18)	1.09 (0.11, 2.11)	2.2 (1.09, 3.31)	4.96 (1.89, 9.5)	1.53 (0.55, 2.51)

Notes: For the simple *m* calculation, the numbers in parentheses are 95% confidence intervals. For all other models, the numbers in parentheses are 95% credible intervals.

DISCUSSION

We have succeeded in both modeling data with uneven sampling intervals and in incorporating yearly stand development variables in order to test for climate effects and secular trends. The ecological generalizations of our results are generally consistent with current understanding of forest dynamics. We expect tree mortality to increase as a forest develops (i.e., self-thinning; Reineke 1933); we expect tree survival to generally increase with size (i.e., the Type 3 mortality curve typically observed for trees; Harcombe 1987); we are not surprised that trees of different species have different drivers of mortality (classic life history and coexistence theory; Condit et al. 1995); and we expect survival in populations to be heterogeneous (Vaupel and Yashin 1985, Sheil and May 1996). The inter- and intra-specific details of these processes sometimes diverge from current understanding, however. The answers to our questions point to a complex story, demonstrating the need for a rich set of species-specific models which incorporate stand development variables and tree size as well as climate variables, time trends, and topographic variables.

Time trends and climate effects

Our species-aggregated models are most similar in structure to the existing models of survival trends for this region (van Mantgem and Stephenson 2007), though existing models were created for old-growth forests. In our second-growth forest, the secular time trend for the species-aggregated models is elusive, disappearing once basal area is included, while for some individual species the trend is robust (Fig. 1). Our results imply that incorporating stand development in a second-growth forest accounts for decreasing survival at the community level (Thorpe and Daniels 2012), but that the story is more complex for individual species. Though there is no sign of an annual water deficit effect at our site (unlike van Mantgem and Stephenson 2007), in some ways this is unsurprising, as BFRS's weather records do not yet show a strong climate trend (Appendix A), and drought stress can take long time periods to play out (Bond-Lamberty et al. 2014). If BFRS begins to experience increasing climatic water deficit as

climate warming proceeds, a negative secular trend in survival may emerge for more species and a species-specific annual climatic water deficit effect may become more pronounced. We have developed an appropriate and sensitive model which will be able to detect these effects as the dynamics of the system unfold.

Where a secular time trend was selected for individual species, however, it does not always agree with existing thinking about the roles of these species in forest community dynamics. In these forests, a century of fire exclusion has resulted in increasing abundances of shade-tolerant fir and cedar at the expense of shade-intolerant pines, which require large canopy gaps such as those created by flare-ups during mixed-severity fires in order to regenerate successfully (York et al. 2013). Stands are increasingly characterized by larger numbers of small diameter trees (primarily white fir, Douglas-fir, and incense-cedar), increased canopy cover, and decreased gap size and gap abundance (Minnich et al. 1995, McIntyre et al. 2015). These structural qualities provide a positive feedback for increasing fir survival and decreasing pine survival. Our models do indicate that ponderosa pine's survival is decreasing, but sugar pine shows an increase in survival. This unexpected result is particularly intriguing given that white pine blister rust *Cronartium ribicola* has been found in the Sierra Nevada. One possible explanation for this difference between expectations and results is the dominance of local factors which overwhelm generalized knowledge about the species or forest type. Perhaps sugar pine survival improves as a consequence of the decline of its congener, ponderosa pine. Alternatively local factors and past land use history may be at play. For example, the infection level of white pine blister rust may not be as strong at BFRS as reported for other mixed conifer forests in the Sierra Nevada (van Mantgem et al. 2004, Das 2006). If so, BFRS may become a refuge for the species as it declines elsewhere. In the face of climate change and species range shifts, cryptic local refugia may become critical to preventing extinction (Hampe et al. 2013).

Species differences in survival

Even in a second-growth forest exhibiting strong density-dependent mortality (Lutz and

Halpern 2006), there is a diversity of responses to different factors controlling survival (Figs. 2 and 3). Of all our explanatory variables, tree size has the most consistent impact on survival, as in Hurst et al. (2011), but each species has a different relationship with size (Lines et al. 2010). Unsurprisingly, all species, both individually and aggregated, generally show higher survival for larger trees as evidenced by the significant positive linear term. Each species, however, shows very different details beyond that overall increase of survival with size. Some species show a sharper decline in survival for smaller trees than others, and only two species show a relative decline in the survival of the largest individuals as noted in other studies in the region (Dolanc et al. 2013), evidenced by a significant negative quadratic term (Table 2, Fig. 2). White fir has an unusual positive quadratic effect, indicating higher survival for very small individuals, lower survival for medium-sized individuals, and then much higher survival for larger individuals—but overall has very high survival (Fig. 3). This result may indicate that a more complex functional form is required to capture the subtleties of white fir's survival as a function of size (perhaps cubic or higher order polynomials, or a nonparametric relationship, which is beyond the scope of this study). Ponderosa pine has much lower survival for smaller individuals than the other species. Tanoak's negative response to elevation is consistent with its current observed range limits: at BFRS, tanoak is at the high-elevation limit of its range (Burns and Honkala 1990).

Species' responses to plot basal area, on the other hand, show some surprising relationships. Plot basal area is increasing at BFRS (Appendix A), and reflects increasing competition for resources, which in theory should affect all of the canopy species. Taking shade intolerance as an indication of competitive sensitivity, based on Niinemets and Valladares (2006), we expect the following ranking from least shade-tolerant (competitively weakest) to most shade-tolerant (competitively strongest): black oak, ponderosa pine, sugar pine, Douglas-fir, incense-cedar, tanoak, and white fir. Directly comparing basal area effects for all species (in a model with size and basal area, regardless of the best model; Fig. 2B), black oak does show a relatively larger

negative effect (basal area effect = -0.069 ; see Fig. 2), Douglas-fir an intermediate effect (-0.043), and white fir the smallest negative effect (-0.016), as in Niinemets and Valladares (2006). Surprisingly, however, incense-cedar shows the largest negative effect (-0.202), while tanoak is unusually intolerant of greater basal area (-0.047) and ponderosa pine (-0.034) and sugar pine (-0.018) are unusually tolerant relative to the other species. Note that the strong impact of basal area on incense-cedar would not have been apparent if we had limited ourselves to species-aggregated models (basal area effect = -0.024). As suggested for the unexpected time trends, the explanation for this unanticipated ranking could be that the local context at BFRS changes the usual competitive landscape for these species. This result demonstrates the importance of creating statistical models appropriate for forest inventory data to enable estimation of local tree demographics. If local context is important to survival, growth, and fecundity, then customized data from different locales will be necessary to plan effective management. Forest inventories are notoriously idiosyncratic, so a model like ours provides an example of how to proceed in order to learn about a specific system from complex tree census data.

Heterogeneity and susceptible subsets

At BFRS, mortality rates for an average tree (m and $1 - \exp(-b)$), from simple models (1.21–2.3% per year; see Table 3 and Appendix D: Table D1) are similar to reports of background mortality rates in many forests (e.g., Canadian boreal forests: 1.4% per year from Bond-Lamberty et al. [2014], 1–5% per year from Luo and Chen [2013], 1.9–4.9% per year from Peng et al. [2011]; Russian deciduous forests: 1–3% per year from Drobyshev et al. [2009]; New Zealand *Nothofagus* forests: 1.8–2.2% per year from Hurst et al. [2011]).

However, the answers to our questions demonstrate the need for a rich set of species-specific models which incorporate a diversity of factors. For each species, trees under various conditions are more likely to die than others, e.g., those in low-survival plots (see Table 3), of small size (Drobyshev et al. 2009), in high basal area environments (Das et al. 2007), or at the edge of their range (e.g., tanoak at high elevation). The

concept of a single annual survival probability becomes less meaningful for a heterogeneous population: a ‘mean’ annual survival probability may not represent these subsets of the population, whose differences in survival are exposed in a more complex model. The large differences in high- and low-mortality plots illustrate the potential difficulties in using a single number to represent a species’ survival. Sheil and May (1996) indicate that annual mortality probabilities like m will be influenced by temporal variation in mortality processes and census interval lengths. This observation emphasizes the need to use a state-space model to appropriately handle the mosaic of census intervals and test for a time trend. In addition, these simple models mask the lower survival rates of susceptible subsets of the population. Sheil and May (1996) additionally point out that “different species demonstrate varying vulnerabilities when exposed to different environmental phenomena or conditions” and the more heterogeneous the population, the worse the effects on m . Zens and Peart (2003) note that one way to remove bias in survival models is to incorporate covariates into the model. While this is true, we urge caution when comparing the results of models with and without covariates. Given Jensen’s Inequality and the extreme nonlinearity of the logit near zero and one, we expect that the intercept $\text{expit}(b)$ (representing the survival probability of an average tree) will be pushed closer and closer to one and the corresponding mortality closer to zero as we add complexity to the model. This effect is due entirely to mathematics: consider our simple model with only an intercept. It predicts a single survival probability for all trees. Now consider extending the model with one covariate, which has been centered to have mean zero. By virtue of centering the covariate, the mean prediction on the logit scale will be the intercept. However, the mean prediction on the survival probability scale will not be the survival at the intercept: Jensen’s Inequality states that for some distribution of x values, $\text{mean}[f(x)]$ is not equal to $f(\text{mean}[x])$ if $f()$ is nonlinear. Specifically, for the high survival values typical for trees, survival is a concave-down function of the linear predictor from the logit scale, implying that the mean survival of the second model will be below the mean survival at its intercept. Compared to

the simple model, the second model will have a larger estimated intercept parameter to compensate for this effect. Therefore the rising survival of the ‘average’ tree as we compare a simpler and more complicated model is influenced by the nonlinearity of the logit/expit.

This caution regarding Jensen’s Inequality pertains to directly comparing the intercept $\text{expit}(b)$ in simple models and complex models. Within one of the complex models with covariates and plot effects (e.g., the final models for each species), the wide range of survival probabilities for individuals under different conditions indicates that a single estimate does a disservice to the heterogeneity in the system. The predicted size relationships in Fig. 3 show that portions of the population of small size or under other conditions pull the survival curve down, especially for ponderosa pine. In our final models, a single survival rate is potentially misleading. These complex models which include explanatory variables and plot effects are also valuable not only in providing information about the direction and magnitude of those components, but also in providing for better prediction and improving estimates of secular trends.

Accounting for susceptibility via size or plot basal area does not accommodate all the heterogeneity in some species. For example even after including these variables, incense-cedar, Douglas-fir, and ponderosa pine still have plot random effects which are important (Appendix F). In particular, for incense-cedar, which has the strongest plot basal area effect, the species’ plot random effect has the largest standard deviation, potentially indicating spatial dynamics below the plot level, perhaps at the level of a neighborhood (Das et al. 2008).

We have modeled the population-level factors affecting tree survival through individual-based measurements. Individual heterogeneity strongly affects survival processes as lower-quality individuals are removed early on (Vaupel and Yashin 1985), so simple cohort analysis may be misleading (Appendix D). Though we do not model an individual tree quality random effect (Knappe et al. 2011) or individual hazard functions (Zens and Peart 2003), we do include a tree-level variable (size) in our model (Clark et al. 2010). In addition, we have incorporated new individuals throughout the inventory period, so if the

quality of the new recruits is well distributed, we may avoid this cohort problem to some degree. Regardless of the source of individual variation, the importance of susceptible individuals may need to be accounted for in further applications of these results, e.g., structured population models, where individual quality can have a strong impact on population-level results (Ellner and Rees 2006).

CONCLUSIONS

We have shown that survival processes in second-growth temperate forests of the arid West are complex. Heterogeneity appears at every level, as species-specific responses differ from each other and from species-aggregated stories, and susceptible subsets emerge within species. Decreases in survival do occur for some species, but are not as widespread as other studies in old-growth Sierran forests or Canadian boreal forests indicate, and there is no evidence in our models of annual water deficit as a factor in tree survival at BFRS. The best way to assess the true biological significance of species differences in survival would be a full population model for each species (Zuidema et al. 2010). Our models do not estimate recruitment rates (Suarez and Kitzberger 2008), and without modeling recruitment and growth as well, we cannot conclude anything at the population level based on these estimates of survival. Ultimately full population dynamics will determine how changes in survival will affect long-term community dynamics. Another way to expand this work would be to create a multi-level model like ours for all species together which models individual responses and community responses simultaneously (Jackson et al. 2012). Finally, this study is observational rather than experimental. As with many ecoinformatics studies where we are using data for purposes it was not originally intended for, our results are clues pointing to possible relationships which could be more systematically examined.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–G and the Supplement are available online: <http://dx.doi.org/10.1890/ES15-00105.1.sm>