SPATIAL ELEMENTS OF MORTALITY RISK IN OLD-GROWTH FORESTS

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Abstract. For many species of long-lived organisms, such as trees, survival appears to be the most critical vital rate affecting population persistence. However, methods commonly used to quantify tree death, such as relating tree mortality risk solely to diameter growth, almost certainly do not account for important spatial processes. Our goal in this study was to detect and, if present, to quantify the relevance of such processes. For this purpose, we examined purely spatial aspects of mortality for four species, *Abies concolor*, *Abies magnifica*, *Calocedrus decurrens*, and *Pinus lambertiana*, in an old-growth conifer forest in the Sierra Nevada of California, USA. The analysis was performed using data from nine fully mapped long-term monitoring plots.

In three cases, the results unequivocally supported the inclusion of spatial information in models used to predict mortality. For *Abies concolor*, our results suggested that growth rate may not always adequately capture increased mortality risk due to competition. We also found evidence of a facilitative effect for this species, with mortality risk decreasing with proximity to conspecific neighbors. For *Pinus lambertiana*, mortality risk increased with density of conspecific neighbors, in keeping with a mechanism of increased pathogen or insect pressure (i.e., a Janzen-Connell type effect). Finally, we found that models estimating risk of being crushed were strongly improved by the inclusion of a simple index of spatial proximity.

Not only did spatial indices improve models, those improvements were relevant for mortality prediction. For *P. lambertiana*, spatial factors were important for estimation of mortality risk regardless of growth rate. For *A. concolor*, although most of the population fell within spatial conditions in which mortality risk was well described by growth, trees that died occurred outside those conditions in a disproportionate fashion. Furthermore, as stands of *A. concolor* become increasingly dense, such spatial factors are likely to become increasingly important. In general, models that fail to account for spatial pattern are at risk of failure as conditions change.

Key words: Abies concolor; Abies magnifica; Calocedrus decurrens; competition; demography; Pinus lambertiana; Sierra Nevada, California, USA; spatial structure; tree disease; tree mortality.

INTRODUCTION

For many species of long-lived organisms, survival rather than growth or regeneration appears to be the most critical vital rate affecting population persistence (sensu Batista et al. 1998). Indeed, this pattern has been reported for a wide range of species, including a bird of prey (Katzner et al. 2006), a common pond turtle (Congdon et al. 1994), a perennial wetland herb (Pino et al. 2007), and a slow-growing marine invertebrate (Linares et al. 2007). Thus understanding processes that influence the survival of these organisms is crucial to understanding their ecology. However, dying can be a complex event for such organisms and quantifying their mortality risk poses a significant challenge.

One common difficulty in quantifying mortality is incorporating spatial processes. For motile organisms,

such as bear and elk, spatial variation in food availability or predator populations can have important effects on survivorship (e.g., Schwartz et al. 2006, Frair et al. 2007), and in general, population viability is often strongly influenced by spatial relationships (Morozov and Li 2007). With sessile organisms such as plants, spatial effects can be even more direct, since such organisms can only "move" via births and deaths (e.g., Pacala and Deutschman 1995, Bolker et al. 2003). In this paper, we examine spatial elements of mortality risk by specifically addressing their role in the mortality of forest trees.

Trees are long-lived, sessile organisms whose persistence is strongly dependent upon survivorship (Silvertown et al. 1993, Batista et al. 1998). Moreover, tree mortality is a key driver of forest development and change (Hawkes 2000, Keane et al. 2001, Lutz and Halpern 2006). However, the death of a tree often involves many interacting factors, including competition, pathogen and insect attack, mechanical failure, climate-induced environmental stress, and localized

edaphic constraints (Franklin et al. 1987, Waring 1987). Teasing apart the various contributors to a given tree's death can be exceedingly difficult and determining their relative importance even more so. Compounding the difficulty is the fact that tree mortality, in the absence of major disturbance, is a relatively infrequent event. Thus the large number of observations needed to untangle a process such as tree mortality is rarely available.

One typical approach to predicting tree mortality is to develop indices that integrate multiple risk factors. For example, many forest simulation models base mortality risk on the relationship between short-term tree growth rate and the probability of mortality. Deaths unrelated to growth are presumed to be random occurrences (reviewed in Bugmann 2001, Keane et al. 2001). As useful as these simplifications are, it is important to understand what ecological processes they miss and whether and when such omissions matter.

Growth rate alone almost certainly does not fully capture the mortality risks defined by spatial arrangement. In terms of tree-to-tree interaction, spatial elements of tree mortality risk can be broken into four broad categories: increased risk of stress mortality due to resource competition; increased risk of pathogen or insect attack due to the proximity of like neighbors; increased risk of mechanical damage due to the proximity of large neighbors; and decreased risk of mortality due to resource sharing with like neighbors (i.e., facilitative effect).

The spatial aspects of mortality risk posed by resource competition have been well explored in temperate forests. Many studies have shown a relationship between tree density and mortality (e.g., Eid and Tuhus 2001, Temesgen and Mitchell 2005, Bravo-Oviedo et al. 2006), and in theory, diameter growth should respond strongly to competition, allowing growth rate to describe the mortality risk. Many forest models (e.g., SORTIE; Pacala et al. 1996) in fact quantify nonrandom mortality risk entirely from growth rate as determined by the competitive environment. Growth rate does respond to competition (e.g., Biging and Dobbertin 1992), but does diameter growth completely capture the pressures represented by competition? If two trees have the same growth rate in differing competitive environments is the mortality risk the same? Results from several temperate forests (Monserud 1976, Umeki 2002, Yang et al. 2003) suggest the possibility that a competition index might provide information beyond that found in diameter growth.

Threats posed by tree diseases and insects also have a spatial element not captured by growth rate. While slow-growing trees are often more susceptible to such agents, many insects and disease-causing organisms are species or genus specific (Wood et al. 2003). Therefore, in a manner similar to that described for seedlings by the Janzen-Connell hypothesis (Janzen 1970), proximity to conspecific or congeneric neighbors might increase risk of attack regardless of growth rate. Schenk et al. (1977,

1980), for instance, developed risk indices for *Abies grandis* and *Pinus contorta* that incorporated host availability and found that the abundance of conspecific trees increased risk of attack by bark beetles. In tropical forests, Peters (2003) also found an increase in mortality risk with the numbers of conspecific neighbors.

The risk of a tree being crushed by neighboring trees (i.e., when one tree falls on top of another and crushes it) also has an obvious spatial association at least partly independent of growth rate: a given tree's risk of being crushed should be affected by the number of large trees close enough to crush it. While soil and topographic factors also influence the risk of crushing, we should still be able to discern a purely tree-to-tree-based mechanism. As for facilitative effects, it is certainly possible that trees can reduce the risk of mortality through root grafting or mychorrizal associations (e.g., Dickie et al. 2005), though we found no evidence in the literature suggesting such an effect for the species in our study.

Our goal in this study was to detect and, if present, to quantify the importance of spatial elements of mortality risk for forest trees. Specifically, we wished to test for the importance of spatial processes not captured well by commonly used methods (e.g., average recent growth). For this purpose, we used a long-term, spatially explicit data set from forests in the Sierra Nevada of California, USA. This data set not only gave us a robust sampling of mortality from an old-growth forest but also the ability to model mortality risk for four dominant conifer species with differing life-history characteristics. For each species, we developed indices to test for the effect of spatial risk factors unrelated to growth rate. In each case, the performance of models that included spatial indices was compared against those without them. In addition, because strong model improvement does not necessarily translate into strong biological effects, we assessed the importance of these spatial indices in determining mortality risk across the range of values observed in the population.

METHODS

Species and sites

We examined four tree species in the Sierra Nevada conifer forests: *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir), *Abies magnifica* A. Murr. (red fir), *Calocedrus decurrens* Torr. (incense cedar), and *Pinus lambertiana* Dougl. (sugar pine). *Abies concolor* and *C. decurrens* are ranked as shade tolerant. *Abies magnifica* is considered slightly less tolerant than *A. concolor*, and *P. lambertiana* is considered mid-tolerant (Burns and Honkala 1990). The study sites are located in the Sierra Nevada conifer forest in Sequoia National Park (118°35′ W, 36°35′ N). Data from nine fully mapped monitoring plots were used for this study, ranging in elevation from 1600 to 2500 m. The plots were checked annually for mortality, with growth measured and new recruitment mapped every five years (for details see Appendix A).

Indices

Mean recent annual growth rate was calculated for each tree for each plot by taking the diameter measurement closest to the start of the given mortality census period, subtracting the prior diameter, and then dividing by the number of years between measurements. If a tree died before the second five-year diameter measurement, its growth rate was determined from its diameter at death and the number of years since the last measurement. Tree size was taken as the diameter measured at the most recent forest inventory prior to the census period.

To estimate resource competition, we chose one simple and one complex index, calculating the index in a 10-m radius around the subject tree (see Appendix B for a discussion of the method by which neighborhood size was chosen). The simple index was a count of the number of trees. For our more complex measure we chose the Hegyi index (Biging and Dobbertin 1992), which takes into account the distance of the competitor to the subject tree as well as the sizes of the trees:

$$H = \sum_{j \neq i} \frac{DBH_j}{DBH_i \times (Dist_{ij} + 1)} \tag{1}$$

where dbh$_i$ (dbh, diameter at breast height measured at 1.37 m above the ground surface) is the diameter of the subject tree, dbh$_j$ is the diameter of a competitor tree, and Dist$_{ij}$ is the distance between the subject and competitor trees. As different species can have different competitive effects (Canham et al. 2006), we also calculated a species-weighted Hegyi index in which the competitive contribution from each competitor was weighted by relative canopy density (see Appendix B). Competition indices were calculated for the beginning of the mortality census period considered (see *Full mortality model development*). To correct for edge effects, competition indices were weighted using an area-weighted edge correction: for trees that were within 10 m of the plot edge, index values were divided by the proportion of a 10 m radius circle centered on the tree that would lie inside the plot boundaries. For example, if only 30% of the 10 m radius circle centered around a given tree would be within the plot, the raw index value for that tree was divided by 0.30.

To estimate increased risk of biotic attack due to like neighbors, we calculated both density- and distance-related indices. Density indices included densities of conspecific and congeneric trees. All density measurements were made in a 10-m radius around the subject tree and corrected for edge effects using an area-weighted correction. Distance indices included distance to nearest conspecific or congeneric neighbors and mean distance to the nearest three conspecific or congeneric neighbors. Due to plot size, distance was restricted to a maximum of 30 m with the index set at 30 m in cases in which a neighbor was farther away. For mean distances, if the distances to any of the nearest neighbors were over 30 m, the distance to that neighbor was set at 30 m. Analyses were also run using 50-m and 100-m maximum distances with no substantial effect on the results. Edge effects were corrected using a toroidal edge correction (Bailey and Gatrell 1995).

Since many tree-killing bark beetles in these forests generally only attack trees above a certain minimum size (Wood et al. 2003), we also calculated species- and genus-specific density and distance indices considering only susceptible trees (i.e., all trees with a dbh > 12.7 cm, "pole-sized" trees or larger). This definition of susceptibility is based on the approximate minimum-sized tree that bark beetle species in these forests would attack, as determined by reported values (Furniss et al. 1977, Wood et al. 2003). Only susceptible trees were considered as subject trees or neighbor trees to calculate a given index. For comparison, we also calculated the non-species-specific density using only susceptible trees.

To examine the spatial component of mechanical agents of mortality, we focused on the risks associated with being crushed by a neighbor. We postulated that the risk of being crushed would increase with the number of trees residing nearby that were capable of crushing the given subject tree. We used two indices. For a very simple index, we used the same density index described above for measuring resource competition (number of trees within a 10-m radius around the tree). We then developed a more complex crushing index by counting the number of trees of equal or greater size to the subject tree that were close enough to crush the subject tree given their height. Heights were calculated using allometric equations developed for the model FACET (Urban et al. 2000), substituting equations for similar species for those species not described by FACET. Only pole-size trees or larger, as defined above, were considered as potential "crushers."

Although we did not develop separate indices to measure facilitative effects, the indices developed above serve that purpose already. For example, if a tree were less likely to die when close to conspecific neighbors, that would indicate possible facilitation.

Full mortality model development

We used the data from the plots to perform a cohort study, tracking a population of live trees from one starting point and recording all the mortalities in that population over the period considered without regard to cause of mortality. For *A. concolor, C. decurrens,* and *P. lambertiana,* we chose a census period between 1997 and 2005 and for *A. magnifica* we chose the period from 1998 to 2005 (see Appendix B for sample sizes and a description of the manner in which census period was chosen). We then used the characteristics of each tree at the start of the period (growth rate, size, and spatial indices) to estimate the association of those characteristics with mortality risk. Using plots established in different years presented a difficulty with regard to the use of newly recruited trees, which were only recorded

and mapped every five years. If the start of the census period fell between measurement periods for a given plot then only a portion of the newly recruited trees in those plots would truly have reached breast height (recruited) by the start of the monitoring period. We addressed this temporal asynchrony by bootstrapping to estimate recruitment between measurement intervals. Specifically, we randomly selected a number of trees equal to the proportion that should have recruited by the start of the period assuming a constant recruitment rate, performing the analysis 100 times and averaging the results (see Appendix B for details).

Mortality probability was modeled using the logistic function:

$$\pi(x) = \frac{e^{g(x)}}{1 + e^{g(x)}} \qquad (2)$$

where $\pi(x)$ is mortality probability and $g(x)$ is a linear function of predictor variables. For example a model with growth rate and size as predictors would have $g(x) = \beta_0 + \beta_1 \times$ growth rate $+ \beta_2 \times$ size, where β_0 is the intercept and β_1 and β_2 are fitted parameters. As a shorthand, we will refer to $g(x)$ by listing the included indices. For example, the size and growth rate model would be g(growth rate, size). Models were fit using the lrm function in the Splus 6.2 Design library (Insightful Corporation, Seattle, Washington, USA).

All models for the full mortality analysis were built on a base model that included size and mean recent growth, g(growth rate, size), to account for these variables before assessing the effect of a given spatial variable. Each of the spatial indices was added separately to the base model to generate a set of comparison models (e.g., g(growth rate, size, Hegyi index), g(growth rate, size, local density)), resulting in 11 models for all species except *C. decurrens*, which had eight due to the lack of congenerics. We also performed a separate analysis considering only pole-sized trees or larger and using the additional pole size indices described above (see *Indices*), resulting in a total of 18 models for all species except *C. decurrens*, which had 11. We will refer to this analysis as the "pole" analysis hereafter, while referring to the analysis that includes all trees as the "all-size" analysis.

In order to compare the models within each set, we used Akaike's information criterion (AIC; Burnham and Anderson 1998). The AIC values were calculated for each model as well as AIC difference values (ΔAIC: the difference in AIC values between a given model and the model with the lowest AIC value) and Akaike weights (w_i, a measure of the proportional likelihood that the ith model is the best model). We also calculated an evidence ratio, comparing our spatial models with the base model, where the evidence ratio is $w_{\text{spatial}}/w_{\text{base}}$. The evidence ratio measures how much stronger the evidence for one model is compared to another. As a guide, based upon Burnham and Anderson's (1998) rules of thumb for ΔAIC values, an evidence ratio less than 2.7 would be considered very little evidence while a value of 7.4

would be considered much stronger evidence. In general, we considered evidence ratios greater than 5.0 as reasonable evidence for model improvement.

Although model fitting was not our goal (our goal was to assess the potential importance of spatial risk factors not tied to growth rate), we did calculate several fit statistics as a guide to the adequacy of our models. For each model we calculated the area under the receiver operating characteristic curve (ROC), the variance inflation factor (VIF), and the unweighted sum-of-squares fit statistic. The ROC is a threshold-independent measure of model discrimination (ability to distinguish live and dead trees) in which 0.5 indicates no discrimination, 0.7–<0.8 acceptable discrimination, and 0.8–0.9 excellent discrimination (Hosmer and Lemeshow 2000). The VIF was used to check for multicollinearity (Neter et al. 1996). The unweighted sum of squares test was used as a general measure of fit (see Copas 1989, Hosmer et al. 1997).

Crush mortality model development

We performed a separate subanalysis for mechanical mortality using the subset of trees that had been crushed by other trees. We limited our cause-specific analysis to this agent because field identification of crushed trees was obvious and the ultimate cause of the failure certain. In contrast, most biotic mortality factors can be difficult to identify and easily missed by field crews (e.g., root rots belowground and beetle attacks high on the tree stem are easily overlooked). In short, we examined our ability to assess the risk of a tree being crushed by analyzing the differences between those trees that were crushed and those not over the census period.

In performing this analysis we did not include recent growth rate, as there was no obvious and direct mechanism that would relate slow growth of a given tree to its risk of being crushed by another tree. Therefore, the following variables were considered for logistic models of crushing risk: size, local density, and crushing index. We considered all one- and two-variable models formed from the combination of these variables with the only restriction being that crushing index and local density were never placed in the same model. The AIC statistics were calculated as for the full mortality models. For evidence ratios, we compared each model to a model that included only size, making the g(size) model the effective base model. Model diagnostics (ROC, VIF, unweighted sum of squares) were calculated as for the full mortality models.

Because growth rate was not used as a predictor for this analysis, there was no need for a re-measurement of diameter prior to the census period. We were therefore able to use a longer census period: 1993–2005. We made no distinction among species, because risk of being crushed should be relatively independent of species. In addition, splitting by species would have resulted in small sample sizes since crush mortality was relatively rare, with an annual rate over the period of ~0.15%/yr

(compared to rates varying between 0.66%/yr and 4.84%/yr for all mortality; Appendix B). *Sequoiadendron giganteum* were not considered as subject trees as their presence in model building tended to result in poor fits, likely due to their extreme size (mean dbh = 219 cm). However, *Sequoiadendron giganteum* were considered when calculating the crushing index for other species. The resulting sample (9115 trees, 8957 survivors, 158 crush-related mortalities) was tracked for crushing-related mortality using plot mortality evaluations. Newly recruited trees were ignored as these posed no crushing risk.

Results

Unweighted sum-of-squares analyses and VIF results generally indicated acceptable fit with no problematic multicollinearity and never indicated such problems for the top-ranked models. For potentially the most problematic case, the relationship between growth rate and competition, we found that, using linear models, competition never accounted for more than 12% of the variance in growth for any species.

Full mortality model analysis

Abies concolor.—The all-size analysis for *A. concolor* showed strong evidence of improvement for models with two types of spatial variables: competition indices and distance to nearest conspecific or congeneric neighbor (Table 1). Support for model improvement by adding either Hegyi index was overwhelming, and support for model improvement with distance to nearest conspecific or congeneric neighbors was also very strong. For trees larger than 12.7 cm (Table 2), pole-sized and larger, distance to nearest conspecific or congeneric neighbor still showed strong evidence for model improvement but the competition index no longer provided any improvement, suggesting that improvements due to the competition index were restricted to smaller trees. The ROC results showed acceptable discrimination for all models (Tables 2 and 3).

Across the full range of variation, the competition index had a dramatic effect on *A. concolor* mortality probability (Fig. 1a), particularly at slow growth rates. However, the impact of the competition index was most evident in the extreme cases. When the extremes were trimmed (i.e., the highest 2.5% and lowest 2.5% of the values for each independent variable were deleted), diameter growth had a much stronger effect on most trees (Fig. 1b).

The mortality probability increased with neighbor distance, suggesting that, at a given growth rate, *A. concolor* were more likely to die when growing farther from other *Abies* (Fig. 1c–f). As with the competition index, the effect was quite strong across the full range of the variable (Fig. 1c, e). However, growth rate had a stronger effect on mortality risk than conspecific or congeneric neighbor distance for the vast majority of the trees sampled (Fig. 1d, f). In short, neighbor distance was important primarily at the extremes.

Abies magnifica.—All-size models for *A. magnifica* showed no convincing evidence of improvement with the addition of spatial variables (Table 1). For pole-sized trees, only distance to the nearest conspecific neighbor provided any improvement (Table 2), with the best variable being a pole-specific index. Discrimination was acceptable for all models (Tables 1 and 2). The mortality probability for the best model in the pole analysis was strongly affected by the conspecific neighbor distance at the extreme ranges, particularly at slow growth, and its effect remained comparable to growth rate, though weaker, even for the trimmed ranges (see Appendix C).

Calocedrus decurrens.—Rankings for the all-size models for *C. decurrens* showed moderate support for improvement with the addition of a local density variable. In contrast, the base model was the best model for the pole-sized trees (Tables 1 and 2). These results suggest that improvements were restricted to smaller trees (i.e., <12.7 cm dbh). Discrimination was excellent for all models (Tables 1 and 2). For the best models, growth rate again had a more pronounced effect than competition index for the majority of the population (see Appendix C).

Pinus lambertiana.—The *P. lambertiana* models showed strong evidence for model improvement with the inclusion of conspecific density in the all-size models (Table 1) and overwhelming evidence for improvement in the pole analysis. In addition, the pole analysis showed very strong evidence for model improvement with the inclusion of distance to nearest conspecific or congeneric neighbors (Table 2). The ROC values for all of the all-size models were relatively poor, and none showed marked improvement with the addition of spatial variables. In contrast, the pole analysis showed clear improvement in discrimination with the addition of spatial variables.

The mortality probability increased with conspecific or congeneric density and decreased with distance to conspecific or congeneric neighbors (Fig. 2). For both the all-size and pole analyses, density resulted in stronger models than neighbor distance, indicating that numbers of close neighbors presented a clearer risk than simple proximity. The increased model improvement with spatial variables for the pole analysis provided evidence that spatial factors were more important for larger trees. Examination of the best-ranked all-tree and pole analysis models for each type of index (Fig. 2) demonstrates that spatial variables had a comparable effect to growth rate even for the trimmed ranges. Unlike the other species, spatial variables appeared to have a pronounced effect on mortality probability for *P. lambertiana* even at fast growth rates.

Crush-related mortality analysis

A model containing size and crushing index outperformed all other models (Table 3). The crushing index

TABLE 1.   Model rankings and the area under the receiver operating characteristic curve (ROC) for full mortality models for trees of all sizes.

Model: $g(x)$	ΔAIC	AIC weight	Evidence ratio	ROC
Abies concolor				
Hegyi index	0.00	0.64	33 006 047.53	0.788
Hegyi index (species weighted)	1.16	0.36	18 444 430.34	0.788
Distance 3 conspecifics	29.93	0.00	10.47	0.785
Distance conspecific	30.25	0.00	8.90	0.784
Distance 3 congenerics	30.52	0.00	7.78	0.785
Distance congeneric	32.06	0.00	3.60	0.784
Local density	32.18	0.00	3.39	0.779
Conspecific density	34.21	0.00	1.23	0.780
Base model	34.62	0.00	1.00	0.782
Congeneric density	35.06	0.00	0.80	0.780
Abies magnifica				
Distance congeneric	0.00	0.26	1.60	0.708
Base model	0.95	0.16	1.00	0.706
Hegyi index (species weighted)	1.74	0.11	0.67	0.706
Hegyi index	1.79	0.10	0.65	0.705
Distance 3 conspecifics	2.69	0.07	0.42	0.713
Congeneric density	2.78	0.06	0.40	0.710
Conspecific density	2.80	0.06	0.40	0.706
Local density	2.86	0.06	0.38	0.707
Distance 3 congenerics	2.91	0.06	0.37	0.707
Distance conspecific	2.92	0.06	0.37	0.707
Calocedrus decurrens				
Local density	0.00	0.57	4.88	0.835
Conspecific density	3.07	0.12	1.05	0.824
Base model	3.17	0.12	1.00	0.824
Distance conspecific	4.64	0.06	0.48	0.824
Distance 3 conspecifics	5.14	0.04	0.37	0.824
Hegyi index (species weighted)	5.16	0.04	0.37	0.824
Hegyi index	5.16	0.04	0.37	0.824
Pinus lambertiana				
Conspecific density	0.00	0.66	18.05	0.661
Congeneric density	3.35	0.12	3.39	0.653
Distance 3 conspecifics	5.69	0.04	1.05	0.650
Base model	5.79	0.04	1.00	0.647
Distance 3 congenerics	6.12	0.03	0.84	0.649
Distance conspecific	6.15	0.03	0.84	0.649
Local density	6.51	0.03	0.70	0.645
Distance congeneric	6.60	0.02	0.67	0.649
Hegyi index	7.26	0.02	0.48	0.651
Hegyi index (species weighted)	7.36	0.02	0.46	0.651

Notes: All models are built on the base model g(size, growth rate), with the listed spatial variable added to it. Models are listed in order of AIC rank. The evidence ratio is the ratio of the Akaike weight of the given model to the base model. Note then that larger evidence ratios suggest better models. All AIC results shown are derived from the average of 100 trials (see *Methods* and Appendix B). The study was conducted in the Sierra Nevada conifer forest, California, USA.

provided clear improvement to a model that included tree size only, while density did not appear to offer any improvement. Overall, the annual probability of being crushed was low, with the highest possible annual probability of being crushed only 0.8% for even the most extreme combination of variables (Fig. 3). Discrimination was relatively poor for all models.

DISCUSSION

Our results demonstrate that the spatial arrangement of trees provide information about the likelihood of mortality even after growth-related mortality risk is taken into account. In other words, tree diameter growth does not capture all the nonrandom risk factors

associated with tree mortality in temperate forests. In three cases, *P. lambertiana*, *A. concolor*, and the crush analysis, the results unequivocally support the inclusion of spatial information in models used to assess mortality risk. Moreover these improvements lead to relevant ecological insights.

For *P. lambertiana*, proximity to conspecific or congeneric neighbors clearly increased the risk of mortality. This result was consistent with a mechanism in which risk of biotic attack, such as that from bark beetles and root rots, increases in the presence of like neighbors (Janzen-Connell type effect). Spatial indices capturing this effect had large impacts on the estimation of mortality risk regardless of growth rate, for both the

TABLE 2. Model rankings and the area under the receiver operating characteristic curve (ROC) for full mortality models for pole-sized or larger trees.

Model: $g(x)$	ΔAIC	AIC weight	Evidence ratio	ROC
Abies concolor				
Distance 3 congenerics (pole)	0.00	0.18	7.78	0.758
Distance conspecific (pole)	0.51	0.14	6.02	0.753
Distance congeneric (pole)	0.94	0.11	4.87	0.755
Distance conspecific	1.14	0.10	4.40	0.749
Distance 3 congenerics	1.54	0.08	3.60	0.750
Distance 3 conspecifics (pole)	1.60	0.08	3.49	0.753
Distance 3 conspecifics	1.69	0.08	3.34	0.748
Distance congeneric	1.74	0.07	3.27	0.753
Local density (pole)	3.16	0.04	1.60	0.747
Base model	4.10	0.02	1.00	0.746
Local density	4.17	0.02	0.97	0.746
Congeneric density (pole)	4.75	0.02	0.72	0.746
Conspecific density (pole)	4.98	0.01	0.65	0.747
Congeneric density	5.08	0.01	0.61	0.746
Conspecific density	5.42	0.01	0.52	0.746
Hegyi index	5.84	0.01	0.42	0.745
Hegyi index (species weighted)	6.08	0.01	0.37	0.745
Abies magnifica				
Distance conspecific (pole)	0.00	0.21	2.96	0.754
Distance 3 conspecifics	1.76	0.09	1.23	0.749
Distance 3 conspecifics (pole)	1.99	0.08	1.09	0.750
Base model	2.17	0.07	1.00	0.749
Hegyi index	2.17	0.07	1.00	0.759
Distance conspecific	2.25	0.07	0.96	0.748
Hegyi index (species weighted)	2.26	0.07	0.95	0.759
Conspecific density	2.31	0.07	0.93	0.753
Distance 3 congenerics	3.34	0.04	0.56	0.750
Congeneric density	3.50	0.04	0.52	0.751
Local density	3.62	0.03	0.49	0.754
Distance 3 congenerics (pole)	3.88	0.03	0.42	0.751
Distance congeneric	3.97	0.03	0.41	0.745
Distance congeneric (pole)	3.98	0.03	0.40	0.745
Conspecific density (pole)	4.14	0.03	0.37	0.750
Congeneric density (pole)	4.16	0.03	0.37	0.749
Local density (pole)	4.17	0.03	0.37	0.750
Calocedrus decurrens				
Base model	0.00	0.19	1.00	0.816
Distance 3 conspecifics	1.12	0.11	0.57	0.819
Conspecific density	1.51	0.09	0.47	0.816
Conspecific density (pole)	1.65	0.08	0.44	0.816
Local density	1.73	0.08	0.42	0.816
Hegyi index (species weighted)	1.87	0.08	0.39	0.817
Distance conspecific	1.88	0.08	0.39	0.818
Local density (pole)	1.94	0.07	0.38	0.816
Distance 3 conspecifics (pole)	1.94	0.07	0.38	0.816
Hegyi index	1.95	0.07	0.38	0.817
Distance conspecific (pole)	1.97	0.07	0.37	0.817
Pinus lambertiana				
Conspecific density (pole)	0.00	0.46	40 702.54	0.736
Conspecific density	1.00	0.28	24 702.13	0.731
Congeneric density (pole)	1.94	0.18	15 455.33	0.730
Congeneric density	3.63	0.08	6630.22	0.719
Distance 3 conspecifics (pole)	12.99	0.00	61.43	0.711
Distance 3 congenerics (pole)	15.67	0.00	16.13	0.700
Distance 3 conspecifics	16.50	0.00	10.63	0.689
Distance 3 congenerics	17.63	0.00	6.04	0.686
Distance conspecific (pole)	17.96	0.00	5.13	0.695
Distance congeneric (pole)	19.87	0.00	1.98	0.686
Distance conspecific	20.37	0.00	1.54	0.677
Distance congeneric	20.78	0.00	1.25	0.675
Base model	21.23	0.00	1.00	0.664
Hegyi index	21.73	0.00	0.78	0.677
Hegyi index (species weighted)	21.78	0.00	0.76	0.677
Local density	22.51	0.00	0.53	0.665
Local density (pole)	23.21	0.00	0.37	0.664

Notes: All models are built on the base model, g(size, growth rate), with the listed spatial variable added to it. Models are listed in order of AIC rank.

full and the trimmed population, with spatial indices for pole-sized trees improving model discrimination from poor to acceptable (Fig. 2, Table 2). In short, variables beyond growth rate were necessary to adequately assess mortality risk for this species.

For *A. concolor*, the addition of a competition index to a model with size and diameter growth rate strongly improved mortality risk estimation. This result suggests that growth rate may not always fully capture the risk posed by resource competition. In addition, mortality risk for this species decreased with proximity to like neighbors, a result consistent with a facilitative effect. In both instances, spatial indices had the strongest impact at the extremes of the spatial index and at the slowest growth rates (Fig. 1).

Although the majority of the *A. concolor* population was in circumstances in which growth rate alone captured most of the risk of mortality (Fig. 1), trees that died occurred outside that common range of conditions in a disproportionate fashion. For example, while only 2.5% of the population had a Hegyi index higher than the maximum of the trimmed range (Fig. 1), 11.1% of trees that died had a Hegyi index higher than that range. Therefore, if population density increased, *A. concolor* mortality would likely increase in a nonlinear fashion. This concern is far from academic because fire exclusion in Sierran conifer forests can lead to increases in tree density, with *A. concolor* comprising a large part of that increase (Parsons and DeBenedetti 1979, Ansley and Battles 1998). Such an effect would be entirely missed by a growth-rate-only model, even if that model worked quite well in less competitive conditions. In essence, to understand mortality processes and to evaluate how they will be affected by environmental changes, we need to understand population dynamics even at the extremes.

For the crushed tree analysis, our results indicate that mechanical damage cannot be presumed to be entirely random. The addition of a simple spatial index dramatically improved model performance over a model with tree size alone. Although mechanical damage is a relatively small contributor to overall forest mortality, the inclusion of spatial information still improved our understanding of its operation.

Our results also provide guidance in understanding when a particular mortality mechanism may not be adequately captured by growth rate. Although this study was largely phenomenological, we can still make biologically informed observations about why different species showed different sensitivity to spatial indices. For instance, indices designed to reflect resource competition improved mortality models for the smaller individuals of shade-tolerant species such as *A. concolor* and to a lesser extent *C. decurrens*. As shade-tolerant trees (Niinemets and Valladares 2006), both species can persist in subcanopy environments and presumably survive long periods of slow growth, perhaps resulting in less predictive power for growth rate in the most extreme

TABLE 3. Crush mortality model Akaike information criterion (AIC) rankings and the area under the receiver operating characteristic curve (ROC) values.

Model: $g(x)$	ΔAIC	AIC weight	Evidence ratio	ROC
g(size, crush index)	0.00	1.00	2623.39	0.680
g(size)	15.74	0.00	1.00	0.640
g(size, local density)	17.47	0.00	0.42	0.643
g(crush index)	29.24	0.00	0.00	0.623
g(local density)	70.46	0.00	0.00	0.504

Notes: See *Methods* for variable explanations. Models are listed in order of AIC rank. The evidence ratio is the ratio of the Akaike weight of the given model to the g(size) model.

conditions. Put simply, in very competitive environments growth rate may level off to some minimum, but increased competition would still affect resource availability and therefore likelihood of mortality.

We can also see from these results that mortality risk increased in the presence of conspecific neighbors for *P. lambertiana* but not the other three species. The explanation may lie in the specific relationships these species have with biotic mortality agents. For instance, *P. lambertiana* are susceptible to attack by biotic agents, including species-specific root rots (Rizzo and Slaughter 2001) and beetles that release aggregation pheromones (Wood 1982), that are likely to spread more vigorously in areas where densities of *P. lambertiana* are high. *Pinus lambertiana* are also under pressure from the nonnative pathogen *Cronartium ribicola* that attacks only five-needled pines (van Mantgem et al. 2004). While the complicated two-host life cycle of the pathogen does not involve tree-to-tree transmission (Edmonds et al. 2000), abundance of one host might still have an effect on disease prevalence and tree mortality. In contrast, *C. decurrens* does not have any strong tree-damaging insects that kill it in these forests (North et al. 2002), and infection by root rots appeared to be uncommon in these plots (A. Das, *personal observation*). For *A. concolor* and *A. magnifica*, the major tree-killing insect, *Scolytus ventralis* (Wood et al. 2003), tends to attack already weakened trees and is not known to have an aggregating pheromone (Macias-Samano et al. 1998). Furthermore, though fir species do suffer from *Heterobasidon annosum* root rot infections, the disease is more frequently a heart rot than a cambial rot in these species (Slaughter et al. 1991, Wood et al. 2003), perhaps dampening the effect of root rot centers. For all three of these species (*A. concolor*, *A. magnifica*, *C. decurrens*), therefore, the lack of obvious increased mortality risk from closer conspecific neighbors is understandable.

However, the apparent facilitative effect indicated by the decreased mortality risk from proximity to conspecific neighbors for *A. concolor* and possibly *A. magnifica* was surprising. All indications prior to our analysis suggested these species should either be at increased risk with increased conspecific density (due to various diseases) or perhaps show no noticeable relationship.
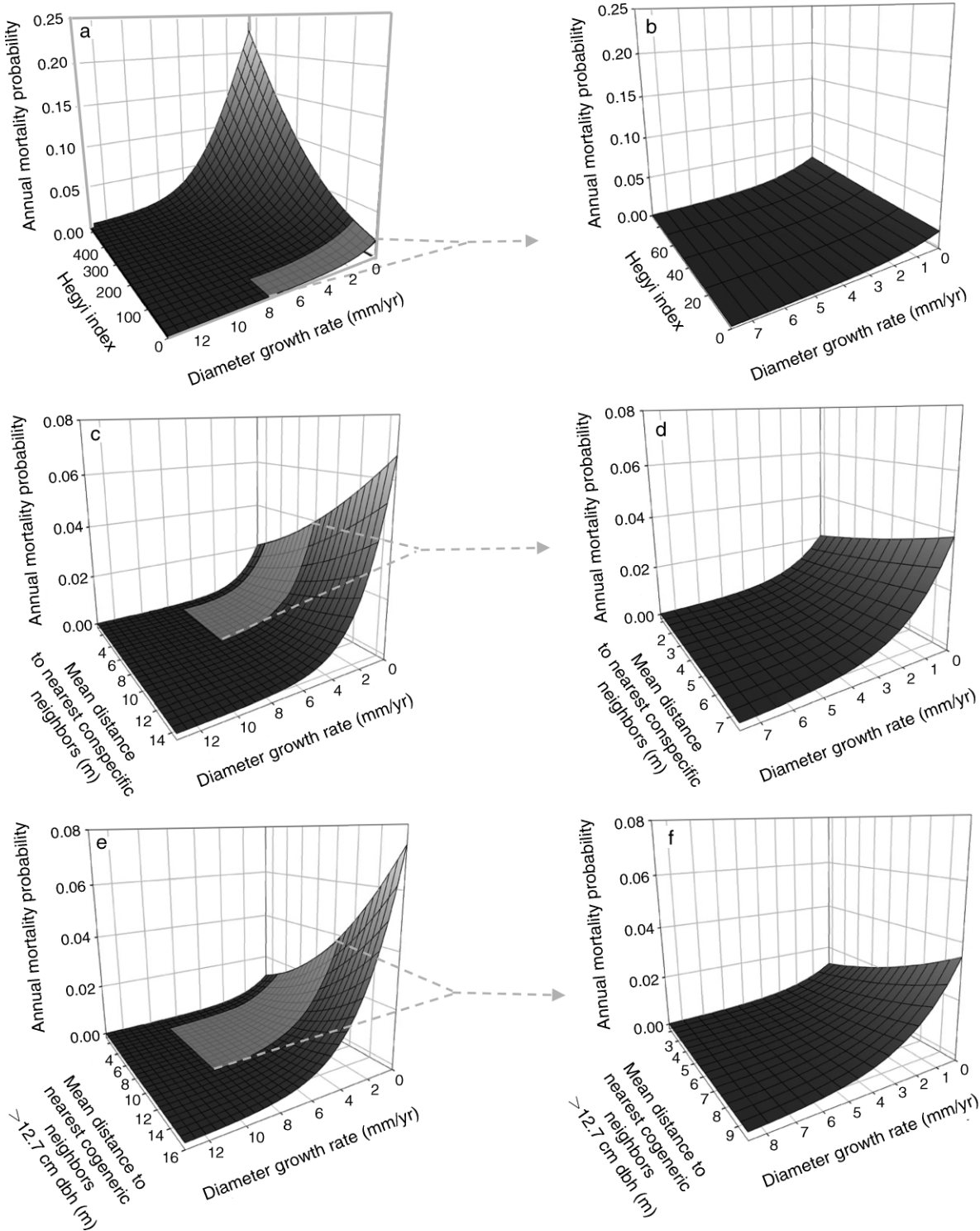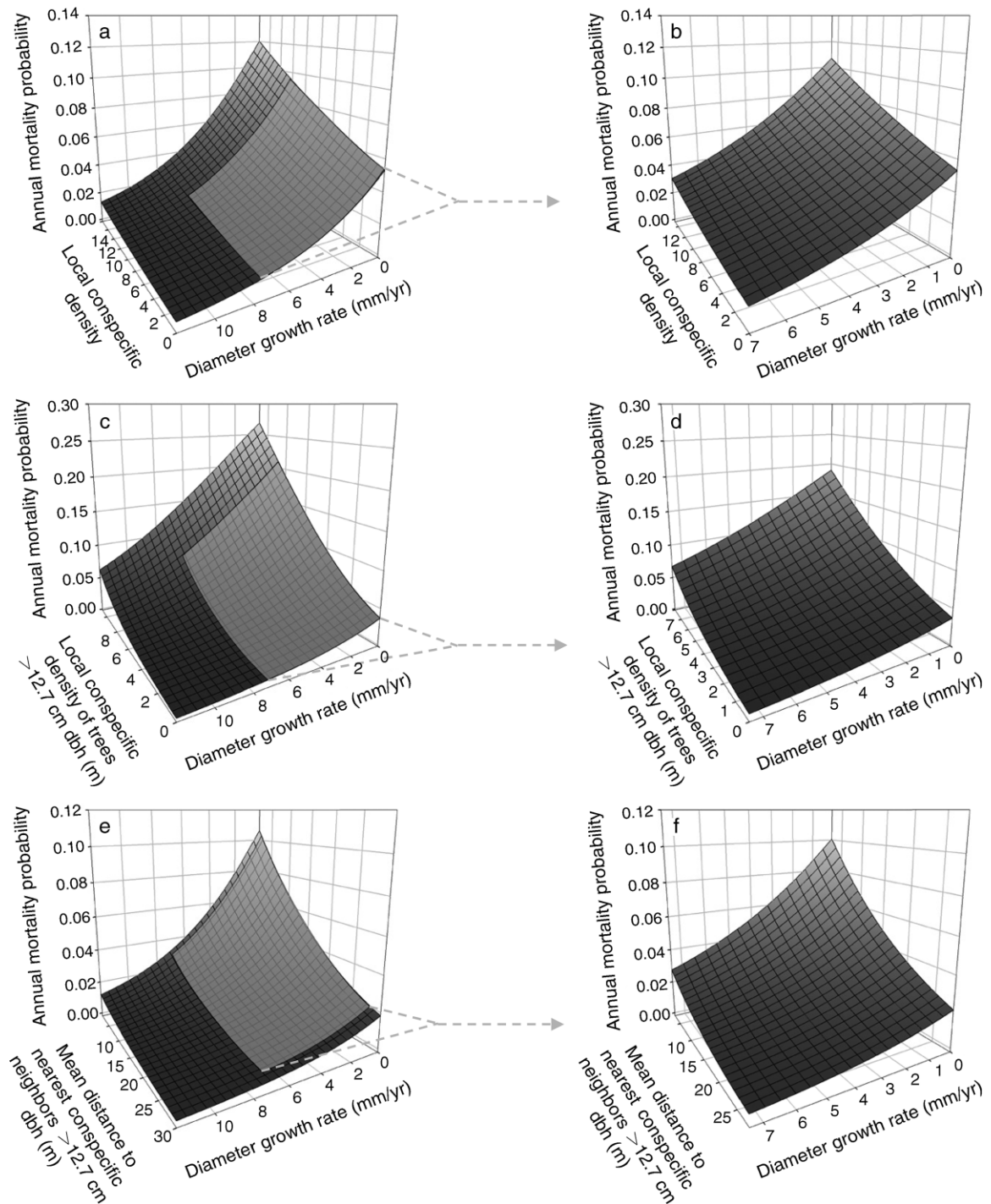
FIG. 1. Mortality probability plots for three *Abies concolor* models with size held constant at the mean value. All mortality probabilities have been normalized to an annual time step. (a, c, e) Probability surfaces for the full range of values found in the population for each variable. (b, d, f) Probability surfaces for the range of values of each variable found in the population after the highest 2.5% and the lowest 2.5% values have been trimmed. (a, b) Hegyi index vs. growth rate for the all-sizes model; (c, d) mean distance to nearest three conspecific neighbors vs. growth rate for the all-sizes model; (e, f) mean distance to nearest three congeneric neighbors vs. growth rate for pole-sized and larger trees. The study was conducted in the Sierra Nevada conifer forest, California, USA.

FIG. 2. Mortality probability plots for three *Pinus lambertiana* models with size held constant at the mean value. All mortality probabilities have been normalized to an annual time step. (a, c, e) Probability surfaces for the full range of values found in the population for each variable. (b, d, f) Probability surfaces for the range of values for each variable found in the population after the highest 2.5% and the lowest 2.5% values have been trimmed. (a,b) Conspecific density vs. growth rate for the all-sizes model; (c,d) conspecific density vs. growth rate for pole-sized and larger trees; (e,f) mean distance to nearest three conspecific neighbors vs. growth rate for pole-sized and larger trees. Density was measured as the number of trees within a 10-m radius around the subject tree.
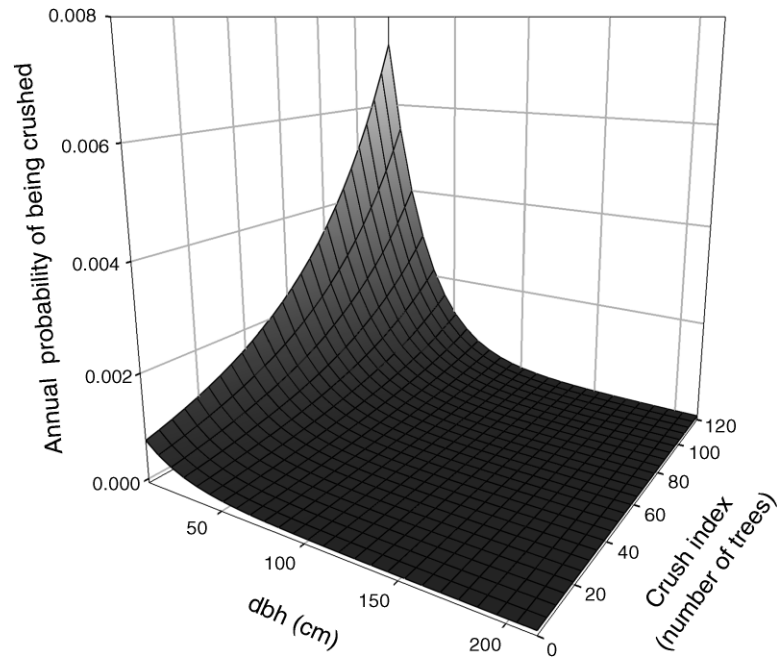
FIG. 3. Probability of being crushed for the top-ranked model (Table 3). Values have been normalized to an annual time step.

One potential explanation is that the sharing of resources through mycorrhizae or root grafting overwhelms any increased risk of biotic attack in a manner not fully captured by growth rate. Mycorrhizae can offset the effects of competition (Perry et al. 1989, Dickie et al. 2005), and stand composition can affect fungal community structure (DeBellis et al. 2006). Perhaps closely spaced firs result in more beneficial sets of mycorrhizal associations. Regardless of the cause, the effect merits further study given the prevalence of *Abies* in these forests.

It is also not immediately clear why improvement due to spatial indices was more equivocal for *C. decurrens* and *A. magnifica*. For *C. decurrens* it may be the paucity of strong biotic mortality agents (North et al. 2002) or that growth rate more adequately captured competition. For *A. magnifica*, it may be that, relative to *A. concolor*, trees of this species were on average in less competitive environments and in closer proximity to conspecifics (i.e., there were not enough trees in extreme environments for our analysis to capture the effect).

Overall, our analyses suggest that by more adequately capturing underlying processes we may be able to gain a greater understanding of how forests will change in response to stressors. Processes left unquantified may well become more important as conditions change, and models that fail to capture these processes will begin to fail in response. For instance, mortality routines that represent competitive effects entirely via growth rate might be inadequate for a species such as *A. concolor* in circumstances of high competition. More broadly, many forest gap models predict rapid, large-scale diebacks with changing climate, but such predictions are unlikely

to be accurate because the mechanisms underlying the mortality functions are too simplistic (Loehle and LeBlanc 1996). Of course adding model complexity should be a guided process, since complex models can be difficult to interpret and inflate the risk of modeling errors (Pacala et al. 1996). For instance, for the forests in this study, stands that contain a significant component of *A. concolor* and *P. lambertiana* are likely to require spatial information for robust modeling while those dominated by *C. decurrens* and *A. magnifica* may not.

We have shown for trees that the quantification of spatial relationships has the potential to improve our understanding of mortality risk, and it is reasonable to expect similar results for other long-lived organisms. But mortality is a temporal as well as a spatial process. In this study, because we only had periodic inventories, we used a fairly simple, short-term growth metric. For trees, we know that examining more detailed temporal indices (e.g., Pedersen 1998, Bigler and Bugmann 2003, 2004, Bigler et al. 2004, Suarez et al. 2004, Das et al. 2007) can also improve mortality prediction. For example we found that for *P. lambertiana*, including long-term growth indices improved our ability to distinguish between live and dead trees by 12.4% (Das et al. 2007). Therefore, we expect that the inclusion of these temporal indices in combination with spatial indices would further improve our overall fits. In general, our results indicate that there is much room for improving our ability to quantify unrecognized or underappreciated mortality processes.

We further suggest that the implications of our analyses have relevance beyond tree population dynamics and forest ecosystems. For example, we have

demonstrated that mortality at the extremes can potentially have a disproportionate effect on population dynamics with changing circumstances and that such an effect could easily be missed with an approach that is too reliant on capturing majority responses. Given the pace of ecological change observed in many ecosystems (sensu Vitousek et al. 1997), it becomes ever more likely that long-lived organisms will encounter extreme conditions in their lifetimes. More generally, since we know that survivorship is critical for projecting populations for long-lived species, quantifying their mortality processes better, both spatially and temporally, will be critical for understanding how such organisms will be affected by environmental change.

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APPENDIX A

Detailed plot and site description (*Ecological Archives* E089-104-A1).

APPENDIX B

Methodological details: defining neighborhood size, creating a species-specific competition index, selecting the census period, and accounting for asynchronous recruitment (*Ecological Archives* E089-104-A2).

APPENDIX C

Mortality probability figures for the best models for *Abies magnifica* and *Calocedrus decurrens* (*Ecological Archives* E089-104-A3).