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Understanding the dynamics of species distributions under climate change: linking empirical evidence, ecological theory, and statistical models

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UNDERSTANDING THE DYNAMICS OF SPECIES DISTRIBUTIONS UNDER CLIMATE CHANGE: LINKING EMPIRICAL EVIDENCE, ECOLOGICAL THEORY, AND STATISTICAL MODELS

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Understanding the dynamics of species distributions under climate change: linking empirical evidence, ecological theory, and statistical models

Chair: Solomon Z. Dobrowski

ABSTRACT

Climate change is threatening biota all over the world through dictating changes in species distributions. The ability to predict the effects of climate on species distributions requires an understanding of how climatic and disturbance factors relate to species distributions. I examined the relationship between climate, disturbance, and geographic distributions of vascular plants in the western United States.

Within the mountain ranges of California, woody plants have largely shifted their distributions downhill during the 20th century. These shifts were strongly related to observed changes in climatic water balance, consistent with theoretical predictions. Downhill shifts were most prominent for species occurring at higher elevations where environmental conditions were marginal. Downhill shifts were observed at nested spatial scales where changes in climatic conditions were consistent, but at all scales were unrelated to species ecological traits.

Niche models based entirely on climatic variables were highly accurate both within and across time periods. The inclusion of fire occurrence as an additional explanatory variable did not affect model likelihood or niche model transferability, due primarily to climatic influences on fire occurrence. Departure from historical return interval influenced total model likelihood when it was included as an additional explanatory variable for species adapted to high frequency return intervals, but did not improve model transferability for most species.

Regeneration of tree species occurred within a narrower range of climatic conditions than adults. Species with greater niche breadth displayed greater differences between adult and regeneration niches. Both adults and juveniles displayed higher sensitivity to climatic variables representing mortality risk than to variables representing growth potential. Spatially explicit models of regeneration indicated overestimation of tree ranges based on niche models and the potential for future range contractions. These results were consistent across species.

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INTRODUCTION AND OBJECTIVES

Understanding the factors governing the distribution of species is arguably the most central tenant of ecology. Beginning with the seminal works of Grinnell (1917) and Hutchinson (1957) ecologists have adopted the species niche concept as fundamental to basic and applied ecology. Using the niche concept as a theoretical foundation, many ecologists have leveraged spatially explicit information on species occurrences and climatic conditions to develop correlative models relating the two (Elith and Leathwick 2009). These models, often referred to as species distribution or environmental niche models, have been used in a variety of contexts but are arguably most popular for developing predictions of the potential impacts of climate change on the future distributions of species. When used in this context, these models form the basis for many large-scale predictions of species loss and turnover resulting from climate change (Thomas et al. 2004, Lawler et al. 2010). Because of the widespread concern over the potential impacts of climate change on biota, and the dire consequences projected by many species distribution models (SDM), there has been great interest in understanding the behavior of these models and their utility for predicting the impacts of future climatic change.

Most studies that have assessed the utility of SDMs have focused on issues related to model development, including the choice of statistical algorithm and the characteristics of input data (Elith et al. 2006, Anderson and Raza 2010). However, there has been relatively little effort made to link ecological theory to these models as a means of evaluating their ability to predict climate change impacts, nor have sufficient efforts been made to understand the potential utility of broad-scale species occurrence data for understanding ecological processes beyond developing predicting of suitable climatic conditions in an SDM framework. The few studies that have evaluated the impacts of ecological phenomena on SDMs have found that such factors can influence the accuracy of SDMs. For example, several studies have suggested that the dispersal capacity of a species can directly influence the accuracy of SDM predictions, with higher model accuracies found for species with a greater capacity to track climate (Kharouba et al. 2009, Dobrowski et al. 2011). However, our understanding of how correlative models of suitable climatic conditions can be affected by extraneous ecological phenomena remains limited. It has been suggested that a more thorough understanding of such factors is needed if ecologists are to continue using the SDM framework as a means of assessing the potential impacts of climate change on biota (Franklin 2010). Providing a more explicit link between fundamental ecological principles and the SDM paradigm has the dual benefit of potentially providing more realistic predictions of species distributions and providing a mechanism by which basic ecological questions can be addressed using SDMs.

OBJECTIVES

This primary objective of this dissertation is to improve our understanding of SDM predictions across time and the ecological inferences gained from the application of these models. Because these models are often used to guide conservation planning actions, this dissertation has direct relevance for both research and management applications. Specifically, my objectives are to:

1) Document climatically induced shifts in the geographic distribution of vascular plants within the mountain ranges of California

2) Quantify the influence of mechanistic processes on spatial patterns of vascular plant occurrence and how these processes affect our ability to predict future geographic distributions

3) Empirically test for evidence of large-scale ontogenetic niche differences in long-lived vascular plants and demonstrate their effects on SDM-based predictions of suitable habitat

These three chapters each provide a unique, and to date largely unexplored, link between fundamental ecological principles and SDMs. First I provide evidence of shifting species distributions in my study area (Chapter 1). I show that unexpected shifts in species distributions can be directly related to physiologically relevant climatic parameters, and that these patterns can hold across a range of spatial scales. In this case, I demonstrate that climatic factors with direct physiological links to vascular plant growth and survival can be used to explain seemingly inconsistent shifts in species distributions. Second, I demonstrate the effects of mechanistic processes on species distributions and SDM predictions (Chapter 2). Despite many criticisms of SDMs for being too simplistic and failing to account for mechanistic processes, I show that the occurrence of wildfire, and its recent departure from historic temporal patterns, has little to add to models of the distributions of vascular plant species once climatic conditions are accounted for. I provide evidence that this disturbance agent is itself climatically mediated and in this case provides little explanatory power for predicting the occurrence of plant species on the landscape. Lastly, I show that demographic differences in niche characteristics are evident at large spatial scales (Chapter 3). I use data from throughout the western United States to provide empirical evidence that plant regeneration occurs under a different set of environmental conditions than do adults. I demonstrate that failure to account for demographic differences in environmental tolerances can lead to overly optimistic predictions of future climatic suitability.

DISSERTATION FORMAT

Each chapter in this dissertation is formatted for submission to a specific peer-reviewed journal. Co-authors for journal submission are indicated on the first page of each chapter. In those cases where the manuscript has already been published, in whole or in part, or submitted to a specific journal a footnote on the first page denotes the outlet. Hereafter I use the collective “we” throughout this dissertation to acknowledge the work done by collaborators that contributed each chapter.

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CHAPTER 1

RECENT SHIFTS IN THE ALTITUDINAL DISTRIBUTION OF VASCULAR PLANTS IN CALIFORNIA

Crimmins, S.M., S.Z. Dobrowski, J.A. Greenberg, J.T. Abatzoglou, and A.R. Mynsberge. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331:324 – 327.

ABSTRACT

Recent climate change has induced many well-documented shifts in species distributions. Often, observed upslope shifts are attributed to warming temperatures, leading to the widespread assumption that biota will ubiquitously shift their distributions upslope as global temperatures continue to increase. Conversely, downslope shifts have been considered anomalous and generally unrelated to changing climate. The widespread assumption of upslope shifts is contingent upon temperature being the primary factor driving distributions. However, coupled climatic metrics that account for both energy and water are known to be directly linked to distributions in vascular plants. Here, we use two temporally independent datasets on the distributions of vascular plants in the mountains of California, an area that has experienced varying changes in temperature and climatic water balance, to examine how plant species distributions have changed during the 20th century. We found widespread evidence of downslope shifts in species' optimum elevations ($n = 64$, $\bar{x} = 88.2$ m downslope) across our study area. We found evidence of downhill shifts in both upper and lower elevation margins and little evidence of changes in the range of elevations occupied, suggesting shifts across the entire altitudinal distribution. The shifts we observed appear to be driven by widespread decreases in climatic water deficit. Our results are the first to document downslope shifts in species' distributions linked to climate change and suggest that the de facto assumption of upslope shifts in response to global warming should be questioned.

INTRODUCTION

Global temperatures increased by approximately 0.6 °C during the 20th century and are projected to increase by as much as 5.8 °C by the end of the 21st century (IPCC 2007). The biological impacts of this climatic change have been widespread and are projected to continue as temperatures continue to rise. Among the most commonly observed of these impacts are changes in the geographic distributions of species (Parmesan 2006). Researchers have found evidence of poleward shifts in latitude for a variety of mobile taxa including insects (Parmesan et al. 1999, Hickling et al. 2005) and birds (Hill et al. 1998, Thomas and Lennon 1999). For sessile organisms like plants, uphill shifts in elevation have been observed (Lenoir et al. 2008, Harsch et al. 2009). This change is generally thought to correspond with cooler temperatures, and thus reduced heat stress, occurring at higher elevations. Under this paradigm, as temperatures increase, plant species are expected to shift their distributions uphill to track isoclines of temperature. However, even in areas that have experienced widespread and substantial warming there is evidence of some species shifting their distributions downhill, suggesting that alternative drivers of species distributions may warrant consideration when predicting distributional shifts (Lenoir et al. 2010).

The widespread assumption that temperature is the primary factor describing species' distributions ignores the fact that the distributions of many species, particularly those of vascular plants, are highly constrained by both available energy and water (Stephenson 1990, 1998). Subsequently, temperature alone may serve as an inadequate metric for understanding and predicting shifts in plant species distributions under changing climate. Despite widespread climatic warming, there is a growing body of evidence demonstrating stasis and downhill shifts in species distributions for a variety of taxa (Archaux 2004, Lenoir et al. 2008, Popy et al. 2010).

Such seemingly inconsistent results are often attributed to non-climatic drivers such as competitive interactions (Lenoir et al. 2010), human induced landscape modification (Archaux 2004), time lags (Popy et al. 2010), or idiosyncratic responses of individual species (Millar et al. 2004), with little consideration given to alternative climatic influences such as water balance. Because of this somewhat dogmatic focus on temperature as the primary driver of distributional shifts there has been limited progress in understanding the influences of other components of climatic change on shifts in species' distributions.

The mountain ranges of central and northern California have experienced substantial climatic warming during the 20th century, and consequently many climatically induced changes in vegetation have already occurred. These include changes in growth patterns (Millar et al. 2004), dominance (Thorne et al. 2008), and tree mortality (Millar et al. 2007), with many such changes predicted to continue as temperatures increase (Battles et al. 2008). However, along with rising temperatures this region has also experienced substantial increases in precipitation that have led to reduced climatic water deficit (Crimmins et al. 2011, Dobrowski et al. 2011a). Under these circumstances we may not expect plant species distributions to shift uphill, as enhanced growing conditions would actually be found at lower elevations. Rather, distributions would be expected to shift downhill owing to the tight coupling between vegetation distribution and climatic water balance (Stephenson 1990, 1998). Many floristic communities in this region are thought to be especially vulnerable to climate change (Loarie et al. 2008), highlighting the need for evaluations of recent climate change impacts in this region.

Most studies of climatically induced shifts in species distributions have been continental in scale (Parmesan et al. 1999), with smaller scale studies typically occurring across entire mountain ranges or geographic regions (Lenoir et al. 2008). It is generally unknown if large-scale (e.g. regional) climate change impacts can be detected at smaller (e.g. watershed) scales. It is important to determine if climate change impacts, which are generally thought to manifest at large scales corresponding to broad synoptic climatic patterns, can be scaled to smaller spatial extents. Studies of climate change impacts at spatial scales relevant to management could provide much needed guidance for developing climate change mitigation and conservation strategies. Likewise, if climate change impacts detected at smaller spatial scales are indicative of regional patterns, the results of such studies could be useful for regional, national, or even international climate change mitigation and conservation planning strategies. Here, we present a multi-scale analysis of 20th century changes in plant species altitudinal distributions within the dominant mountain ranges of central and northern California using temporally independent datasets of plant species' distributions.

METHODS

Study area

We defined our broad study area as the Northwest, Cascade Ranges, Sierra Nevada, and Central Western ecoregions (Hickman 1993) within central and northern California (Figure 1). This region encompassed an area of 177,000 km^2 and represented the majority of the mountainous regions in the state north of 35° latitude. These ecoregions were chosen because of the availability and abundance of vegetation survey data (see below) and long-term weather station data. This region is considered a biodiversity hotspot due to its abundance of endemic flora and is an area of great conservation concern (Loarie et al. 2008). Additionally, this region has experienced substantial climate change during the 20th century, making it an ideal setting for studying the impacts of climatic change on vascular plants (Figure 1).

Climate data

We used gridded (800 m) monthly normal (i.e. monthly average) climate data developed by the Parameter-elevation Regression on Independent Slopes Model (PRISM) (Daly et al. 2008). Monthly normals for climatic parameters were averaged across 30 year historical (1905–1935) and modern (1975–2005) time frames, providing mean climatic values for the previous 3 decades prior to vegetation data collection (see above). Climate surfaces were downscaled to a resolution of 400 m using dynamic lapse rate estimates (Keane and Holsinger 2006). Downscaling of climate surfaces was conducted because of the strong influence of physiography on air temperature in the region (Dobrowski et al. 2009) and previous research demonstrating that small-scale factors can influence the distribution of sensitive species (Ashcroft et al. 2009). Clear sky radiation was modeled for the study area at a 400 m resolution. Potential evapotranspiration (PET) was calculated via the Penman-Monteith method using downscaled climate data, radiation maps, and wind maps from the National Renewable Energy Laboratory (Allen et al. 1998). Climatic water deficit was calculated as the annual difference between PET and precipitation. We created a continuous surface of 20th century change in deficit by subtracting historical values from modern values (Figure 1).

Species distribution data

We used species distribution data from two separate time periods to estimate change in the altitudinal position of vascular plant species. First, we used plot data from the Wieslander Vegetation Type Mapping (VTM) project (Kelly et al. 2005), representing approximately 14,000 plots throughout the state (Figure 2). The VTM project was originally designed to map the vegetative communities of California, with plot data collected between 1928 and 1940 (Wieslander 1935a, 1935b). Individual plots comprised virtually complete vascular plant inventories and have been digitized to a spatial accuracy of 200 m (Kelly et al. 2005). Although the VTM sampling design was not a true presence/absence survey, these data are widely used for modeling the historic distribution of plant species in California (Syphard and Franklin 2010, Dobrowski et al. 2011b) and likely only suffer from false absences for only the rarest species.

We also compiled data from a variety of sources to develop a collection of approximately 33,000 modern vegetation plots measured in the 2000's. Sources for modern data included, among others, the US Forest Service, National Park Service, California Fish and Game, US Bureau of Land Management, US Geological Survey, and university researchers including the authors (Figure 2). As with historic VTM plots, species presence/absence data were extracted from each georeferenced plot location. Hereafter we refer to these data as "historical" (~1930's) and "modern" (~2000's) respectively. The majority of survey plots in both datasets were located on publicly owned lands where anthropogenic influences on land use would be minimal.

Sample stratification

Because plot data in the two data sets were not collected in the same manner or with the same objectives, and because of the substantial environmental heterogeneity within our study area, there existed the possibility for geographic bias between the two data sets. For example, climatic parameters such as temperature and precipitation can exhibit substantial variation with respect to latitude and longitude, especially in mountainous regions such as California that are strongly influenced by oceanic circulation patterns (Abatzoglou et al. 2009). Ideally, the distributions of sampling locations between the two time periods would be close enough to mimic re-sampling of the historical locations. However, the disjunct and patchy distributions of sampling locations between the two time periods precluded us from using such an approach (Figure 2). Instead, we chose to eliminate bias along environmental gradients across our broad study area. We used a subsampling procedure in which we randomly selected an equal number of plots from each time period from 20 equal-width bins based on climatic water deficit. We also subsampled the original datasets in 20-equal width bins based on elevation and again by mean annual temperature using 1° C width bins (Lenoir et al. 2008). Results were similar across these subsampled datasets, therefore we only present results at the broad scale from the sampling procedure based on climatic water deficit. This procedure left us with a balanced sample of 8,747 survey plots in each time period.

Within the Sierra Nevada ecoregion (63,000 km^2) survey plots were abundant and well distributed in both time periods. Therefore, within this ecoregion we conducted a geographic, rather than environmental, bias removal approach. We divided the latitudinal and longitudinal ranges of our study area into six equidistant sections, creating 36 equal area sections across the ecoregion. Within each of these sections, we randomly sampled an equal number of plots from each dataset. This procedure effectively removed geographic bias associated with latitude and longitude and left us with a balanced sample of 4,331 plots in each time period. By doing this any potential influence associated with geographic lapse rates in climate were removed. We repeated this procedure within each of the six Jepson subecoregions (Hickman 1993) occurring within the Sierra Nevada (Figure 2) as survey plots were also well distributed within these smaller extents (range 5,860–17,550 km^2). This procedure differed from that for the entire ecoregion in that our subsampling used three equal width bins of latitude and longitude, resulting in nine equal area sections within which plots were randomly sampled. We also replicated the bias removal procedure conducted at the broad study area scale based on climatic water deficit and found qualitatively similar results (not shown).

Analysis

We modeled the altitudinal position of vascular plant species within each time period using a variety of metrics. We used metrics of central tendency as well as upper and lower altitudinal margins because these areas are thought to represent differential responses to climate change and have different implications for conservation (Hampe and Petit 2005, Shoo et al. 2006). First, we used logistic regression to calculate the optimum elevation of each species, which is the elevation with the maximum probability of occurrence (Lenoir et al. 2008). We chose this metric as a measure of central tendency because it is substantially more robust to variability in sampling intensity than other metrics such as means or medians (ter Braak and Looman 1986, Zadrozny 2004). We calculated optimum elevations only for species that had sufficient representation (≥ 50 occurrences) and exhibited unimodal response curves in each time period. For these species we also estimated the upper and lower altitudinal margins as the 90th and 10th percentile of the altitudinal range covered by the species following Lenoir et al. (2009). We also calculated the tolerance of each species, which is an estimate of the range of elevations in which a species occurs (Oksanen et al. 2001, Lenoir et al. 2008).

We calculated change in elevation as the difference between the historical and modern estimates. We tested for overall changes in altitudinal position using paired *t*-tests for each metric. The entire analysis procedure was also conducted within the Sierra Nevada and each of the six Jepson subecoregions (Hickman 1993) occurring within it to determine if patterns were consistent across nested spatial scales. We examined the effects of species traits on elevation shifts using a Kruskal-Wallis test. Traits examined included lifeform (tree, shrub), dispersal mechanism (wind, animal, gravity, ballistic), and level of fire adaptation (Dobrowski et al. 2011b).

To test whether or not species were tracking optimal environmental conditions, we used a similar approach as that described above to test for changes in optimum water balance. We used spatially explicit estimates of annual climatic water deficit (Stephenson 1990, 1998) from 30-year time frames prior to vegetation data collection (1905–1935, 1975–2005) to represent historical and modern metrics of water balance (Dobrowski et al. 2011a). If species in our study area were shifting their distributions to track changes in water balance, we would expect to see no net change in water balance of sites occupied by a species between time periods. We used similar approaches to those described above for calculating optimum climatic water deficit and temporal shifts in optimums.

RESULTS

Entire study area

We retained 64 species within our study area with sufficient sample size and unimodal response curves. Overall, these species exhibited a significant downhill shift in optimum elevation between time periods ($\bar{x}$ = -88.2 m, t = -2.49, df = 63, P = 0.016) with a higher proportion (p) shifting their distributions downhill (p = 0.72, 95% CI = 0.59–0.82) than uphill (p = 0.28, 95% CI = 0.18–0.41) (Figure 3). We found no significant changes in optimum climatic water deficit ($\bar{x}$ = -11.1 mm, t = -0.20, df = 45, P = 0.843), with similar proportions of species shifting their distributions towards drier (p = 0.41, 95% CI = 0.27–0.57) and wetter conditions (p = 0.59, 95% CI = 0.43–0.73). We found no evidence of changes in species' tolerance ($\bar{x}$ = -5.4 m, t = -0.38, df = 63, P = 0.7) (Figure 3). Upper and lower elevation margins exhibited non-significant (P > 0.05) uphill shifts due to modern plots occurring an average of 296 m higher than historical plots (P < 0.0001). When correcting for differences in elevation between the two datasets both upper (

$\bar{x}$ = -115.8 m, t = -4.14, df = 57, $P < 0.001$) and lower ($\bar{x}$ = -141.0 m, t = -4.10, df = 57, $P < 0.001$) elevation margins exhibited substantial downhill shifts (Figure 3).

Sierra Nevada ecoregion

We retained 40 species in the Sierra Nevada ecoregion with sufficient sample size and unimodal response curves with respect to elevation for our analysis. Overall, optimum elevations for these species within the Sierra Nevada shifted significantly downhill ($\bar{x}$ = -71.2 m, t = -2.76, df = 39, P = 0.009) with a higher proportion shifting their distributions downhill (p = 0.7, 95% CI = 0.53–0.83) than uphill (p = 0.3, 95% CI = 0.17–0.47) (Figure 4). Again, we found no evidence of changes in species' tolerance ($\bar{x}$ = -10.3 m, t = -0.66, df = 39, P = 0.5) (Figure 4). Upper elevation margins exhibited a moderate but non-significant shifts downhill ($\bar{x}$ = -36.4 m, t = -1.34, df = 39, P = 0.19) with similar proportions shifting their altitudinal margins uphill (p = 0.65, 95% CI = 0.48–0.79) and downhill (p = 0.35, 95% CI = 0.21–0.52) (Figure 4). Lower elevation margins displayed similar results, with a non-significant shift downhill ($\bar{x}$ = -14.9 m, t = -0.53, df = 39, P = 0.597) and similar proportions shifting their lower margins uphill (p = 0.575, 95% CI = 0.41–0.73) and downhill (p = 0.425, 95% CI = 0.27–0.59) (Figure 4). Shifts in elevation metrics were unrelated to any species traits ($P > 0.05$ in all cases).

Contrary to our expectation, we found that species optimum climatic water deficits exhibited moderate evidence of increases ($\bar{x}$ = -30.2 mm, t = 2.33, df = 36, P = 0.07) within the ecoregion, although three species were not included due to a lack of unimodal response curves. We also found that a greater proportion of species shifted their distributions towards drier (p = 0.78, 95% CI = 0.61–0.90) than wetter conditions (p = 0.22, 95% CI = 0.10–0.39).

Subecoregions

The two southernmost subecoregions (sSNH, sSNF) did not retain a sufficient number of sampling locations after our bias removal to generate optimum elevation estimates, therefore all results at the subecoregion scale are from the four central and northern Sierra Nevada subecoregions. The pattern of elevation shifts at the subecoregion scale was similar to that found at the study area and ecoregion scale, with a general trend of downhill shifts in elevation, particularly in optimum elevation (Figure 5). However, the results within each subecoregion were less clear than those at larger scales due to the limited number of species retained within each subecoregion. When results were pooled among subecoregions, we found strong evidence of downhill shifts in optimum elevation ($\bar{x}$ = -41.7 m, t = -2.59, df = 53, P = 0.012), lower elevation ($\bar{x}$ = -70.1 m, t = -3.55, df = 53, $P < 0.001$), and upper elevations ($\bar{x}$ = -26.2 m, t = -2.02, df = 53, P = 0.048) (Figure 6). When using our pooled data we did find evidence of moderate decreases in species' tolerance ($\bar{x}$ = -27.1 m, t = -3.48, df = 53, P = 0.001) (Figure 6). Shifts in elevation were unrelated to species traits ($P > 0.05$ in all cases). We were unable to calculate optimum water deficit values for most species within subecoregions due to a lack of unimodal response curves, therefore we used median water deficit values to represent species level environmental conditions. We did not detect changes in median water balance using our pooled data ($\bar{x}$ = 0.5 mm, t = 0.12, df = 53, P = 0.91).

DISCUSSION

We found widespread evidence of downhill shifts in plant distributions in the central and northern mountain ranges of California. This is not entirely surprising, as climatic changes between the time periods we investigated led to decreases in climatic water deficit throughout most of this region (Crimmins et al. 2011, Dobrowski et al. 2011a). Given the strong influence that climatic water deficit has on vascular plant distributions (Stephenson 1990, 1998), these downhill shifts are what one might expect in regions where increases in evaporative demand are outpaced by increases in available moisture. The fact that our results were unrelated to individual species' traits suggests that a widespread driver, such as climate, is responsible for these shifts. One line of evidence to support this conclusion is that species occurring at higher elevations exhibited larger downhill shifts (Figure 7). Because of the nonlinear relationship between elevation and vapor pressure deficit, cooler and wetter sites found at higher elevations are expected to exhibited greater sensitivity to changes in precipitation compared to warmer and drier sites at lower elevations. Thus, the observed changes in climate throughout our study area would be expected to exhibit a greater influence on higher elevation sites. Observational studies from this region have found increases in the density of young tree cohorts at lower elevations, providing further support for downhill shifts in overall distributions (Millar et al. 2004, Eckert and Eckert 2007).

Most previous studies of climatic influences on elevational position of plants have focused only on changes in one point along the entire altitudinal gradient, often represented by a range limit. This study represents one of the few attempts to examine shifts in altitudinal position at upper, lower, and central elevations (e.g. Lenoir et al. 2009). The significant shifts in optimum elevations we observed suggest population level changes in altitudinal distributions (Shoo et al. 2006). At the upper and lower altitudinal range margins we found evidence of downhill shifts at all scales, although not with the consistency they were observed for optimum elevations. This is not entirely surprising, as range margins are generally thought to be much more dynamic and subject to transient influences than the center of a range (Gaston 2003).

However, the consistency with which downhill shifts were observed among elevation metrics and across scales suggests that downhill shifts are occurring across the entire altitudinal ranges of many species within our study area. Our evidence of downhill shifts at both upper and lower range margins suggests that the altitudinal ranges of many species may not be experiencing contraction or expansion, but rather a uniform shift. This is supported by species tolerance values generally remaining unchanged. This is in contrast to many other studies that have demonstrated expansions and contractions in distributions related to climate change (Chen et al. 2011).

Our findings of downhill shifts are contrary to the widespread assumption of uphill shifts in species distributions resulting from increasing temperatures (Walther et al. 2002, Parmesan 2006). Several studies have found evidence contrary to this widely held assumption (Archaux 2004, Lenoir et al. 2008), suggesting that the influence of climate on species geographic distributions may be quite complex. In our study area, substantial changes in precipitation occurred between the two study periods that resulted in widespread decreases in climatic water deficit despite warming temperatures (Dobrowski et al. 2011a). Because water balance is known to have a direct effect on the geographic distributions of vascular plants (Stephenson 1990, 1998), this is a plausible explanation for our observed downhill shifts. This is supported by our general finding of species exhibiting only small changes in optimum climatic water deficit at one study scale and no change at the other two, although this could represent a lagged response to climatic warming. It has been suggested that climatic parameters other than temperature may explain downhill shifts in species distributions despite increasing temperatures (Lenoir et al. 2010), although few studies have provided empirical evidence of such relationships. The lack of shifts in species-level optimum water balance values, especially when coupled with their concomitant shifts in elevation, provide strong support for climatic factors other than mean temperature driving species distributions. In our study area, tracking of temperature isoclines would have required species to shift their distributions substantially uphill, the opposite direction in which most species actually moved. Although we cannot infer a causal relationship between climatic water balance and species altitudinal position from our study, our results do provide further evidence that the influence of climate on biota can be complex.

We found that climate change impacts occurring in California are evident at spatial scales that span an order of magnitude. Several recent studies have found large scale shifts in the altitudinal distributions of vascular plants (e.g. Lenoir et al. 2008). Because these shifts have occurred at such large scales they are generally attributed to climate change, which is thought to be the only factor that could act at such geographic scales. Our results indicate that some of these large-scale climate change impacts can be detectable at more localized scales. This suggests that the results from localized or small-scale studies of climate change impacts can be relevant to large-scale conservation planning actions or policy initiatives. Similarly, findings from large-scale studies may be applicable at local scales where on-the-ground conservation actions are more likely to occur. However, it is important to note that the most likely causal driver of the observed shifts in species distributions in our study, decreases in climatic water deficit, was evident across our study area at all scales. If climatic drivers at more localized scales show disparate trends from regional patterns it is quite possible that localized effects may not mimic those detected across broader regions. Thus, it is important to consider the spatial patterns of climate change when attempting to scale the results of a single study up to broader or down to more localized domains.

The assumption that rising temperatures will lead to nearly ubiquitous uphill shifts in species distributions is common among ecologists (Parmesan and Yohe 2003, Walther et al. 2005, Parmesan 2006). For species with direct physiological limitations to temperature this assumption may be valid, but for many species the coupled availability of water and energy is far more important than temperature alone (Stephenson 1990, 1998). It has previously been suggested that climatic parameters other than mean temperature may explain seemingly incongruous shifts in species distributions (Lenoir et al. 2010), although no previous studies have attempted to link such shifts to alternative climatic parameters. Our results suggest that careful consideration of relevant climatic parameters is critical to understanding the effects of climate change on biota. Beyond simply understanding the effects of climate change, these results should also provide caution to those attempting to predict the effects of climate change, such as those employing climatic envelope models to project species distributions under future climatic scenarios (Pearson and Dawson 2003). In most cases these studies do not consider physiologically relevant climatic parameters, and instead utilize widely available gridded climate surfaces such as mean, minimum, and maximum temperature. Clearly, such metrics are not relevant to all species, and only through the use of appropriate climatic parameters can ecologists hope to fully understand the consequences of a rapidly changing climate.

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Figure 1: Change in mean annual temperature (A), potential evapotranspiration (B), annual precipitation (C), and climatic water deficit (D) in California from the early (1905–1935) to late (1975–2005) twentieth century.

Figure 2: Distribution of sample plots in historical (ca. 1935) and modern (ca. 2005) time frame prior to bias removal. Plots from the USFS Forest Inventory and Analysis plots (*n* = 3,740) are not shown but regions containing the plots are highlighted in yellow. Abbreviations refer to Jepson subecoregions: cSNH – Central High Sierra Nevada, cSNF – Central Sierra Nevada Foothills, nSNH – Northern High Sierra Nevada, nSNF – Northern Sierra Nevada Foothills, sSNH – Southern High Sierra Nevada, sSNF – Southern Sierra Nevada Foothills.

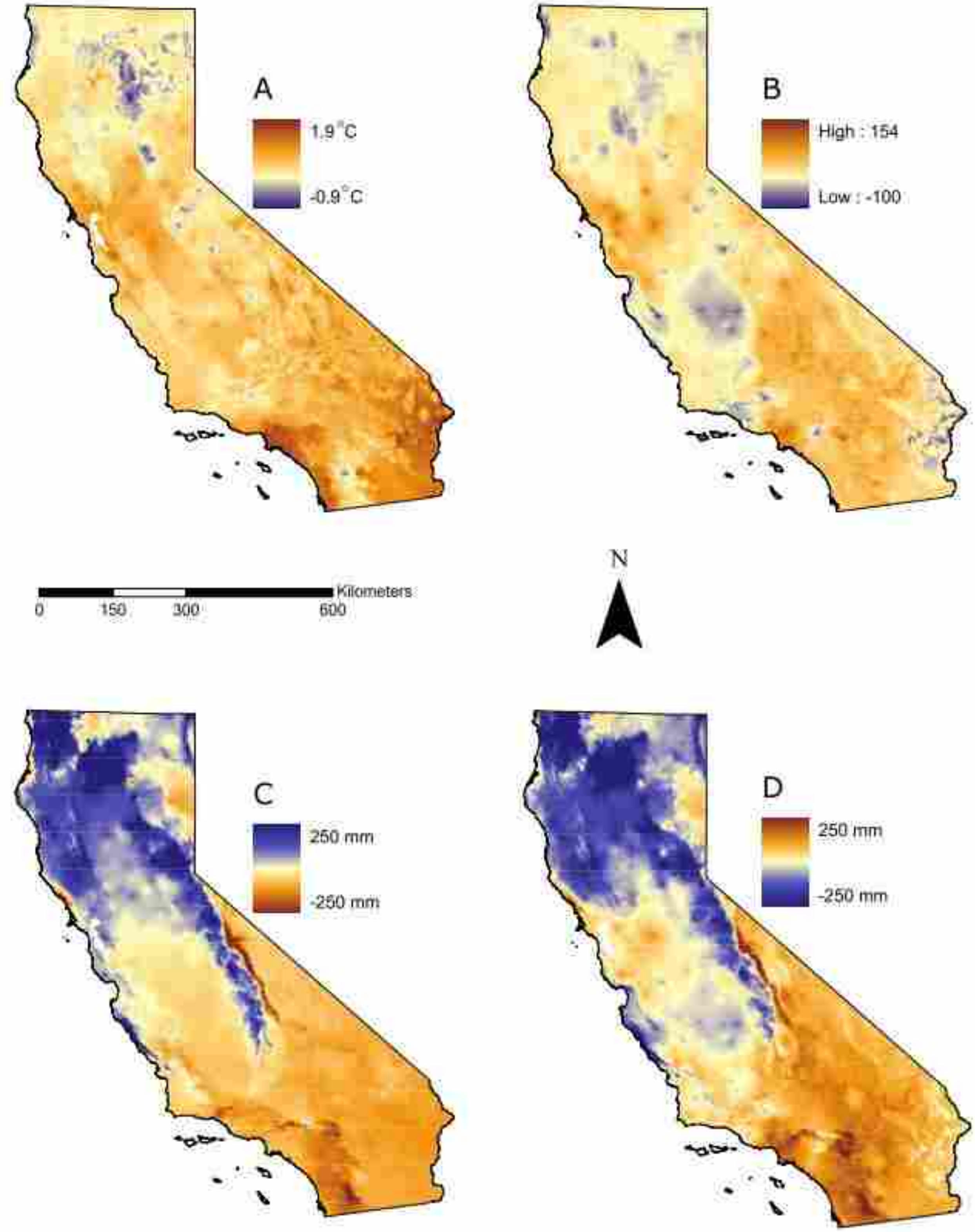
Figure 3: Scatterplots of species-specific historic position versus modern position for optimum elevation (A), lower elevation (B), upper elevation (C), and tolerance (D) from the entire study area.

Figure 4: Scatterplots of species-specific historic position versus modern position for optimum elevation (A), lower elevation (B), upper elevation (C), and tolerance (D) within the Sierra Nevada ecoregion.

Figure 5: Boxplot of species-specific shifts in optimum, upper, and lower elevations within subecoregions. Asterisks indicated level of significance (* $p = 0.15$, ** $p = 0.1$, *** $p = 0.05$) from paired t-tests of historic versus modern elevations. Width of boxes is proportional to sample size (cSNF = 7, cSNH = 17, nSNF = 8, nSNH = 22).

Figure 6: Scatterplots of species-specific historic position versus modern position for optimum elevation (A), lower elevation (B), upper elevation (C), and tolerance (D) from pooled subecoregions.

Figure 7: Scatterplot of shift in optimum elevation (m) versus historical (ca. 1935) altitudinal position across entire study area (A), within the Sierra Nevada ecoregion (B), and within subecoregions (C). Note that within C, species may be included more than once if they occurred in multiple subecoregions. Solid line represents linear regression model with 95% CI (dashed lines). Linear regression models were highly significant ($P < 0.01$) in each case.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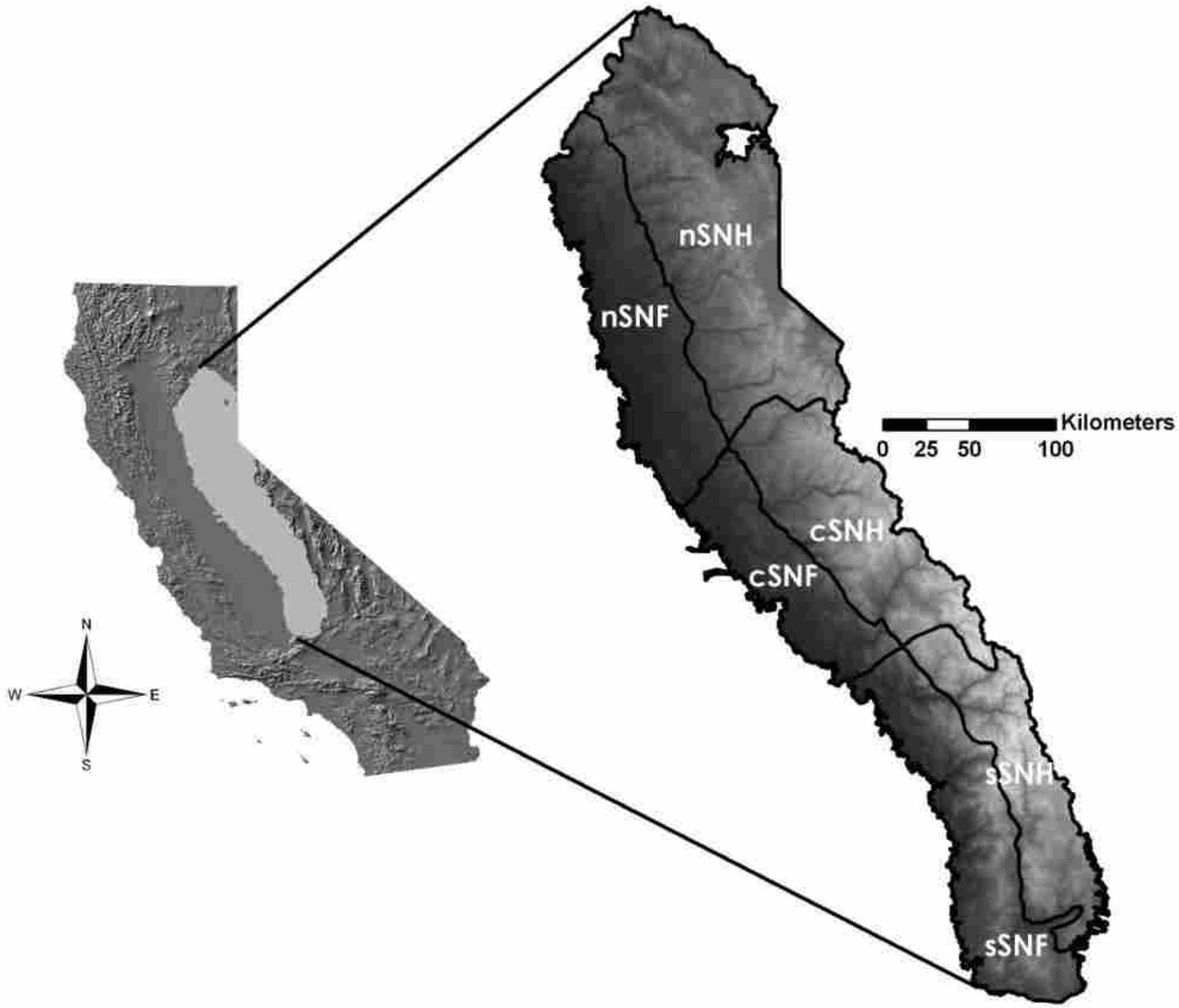
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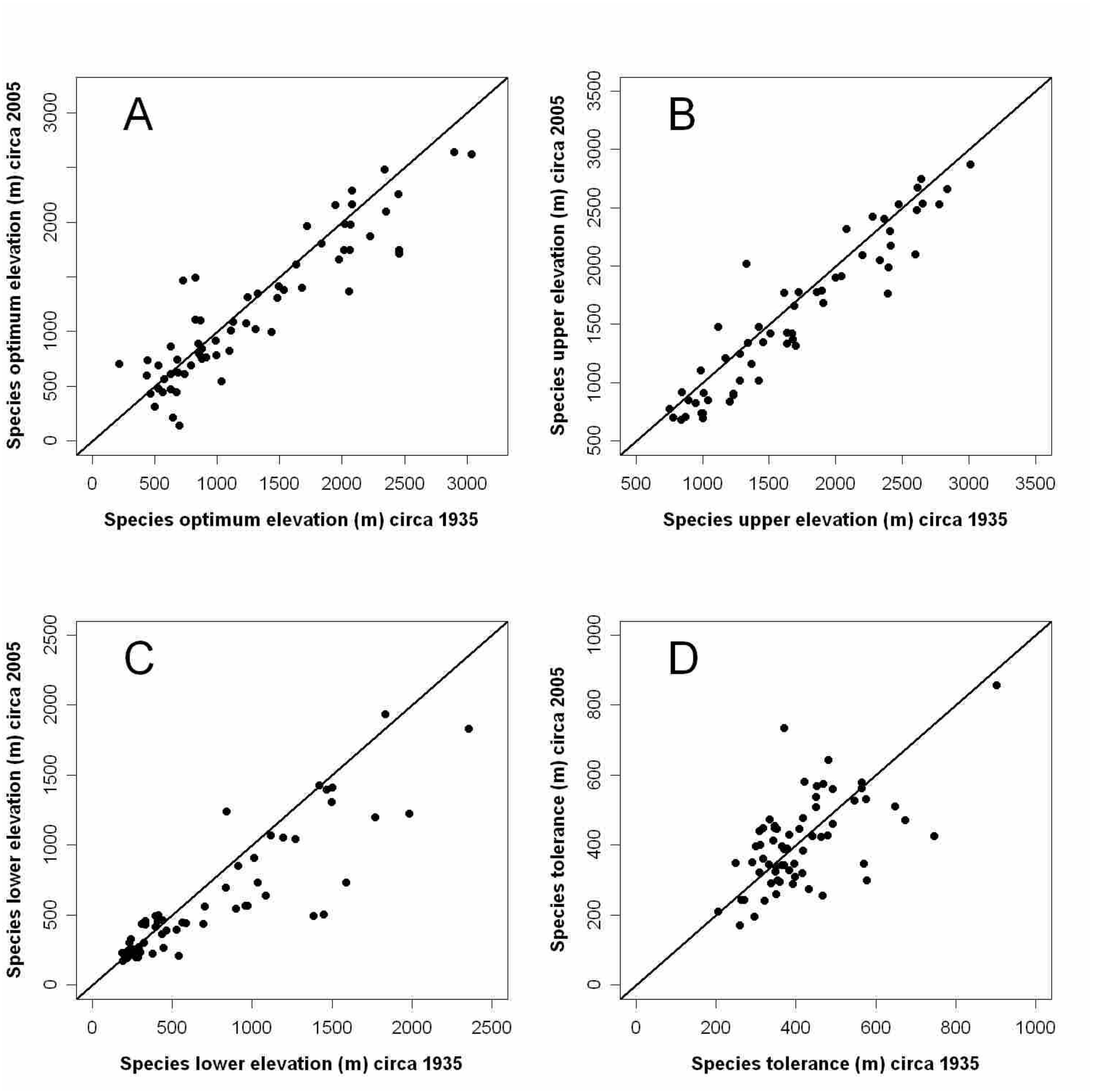
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C
Species lower elevation (m) circa 2005
Species lower elevation (m) circa 1935
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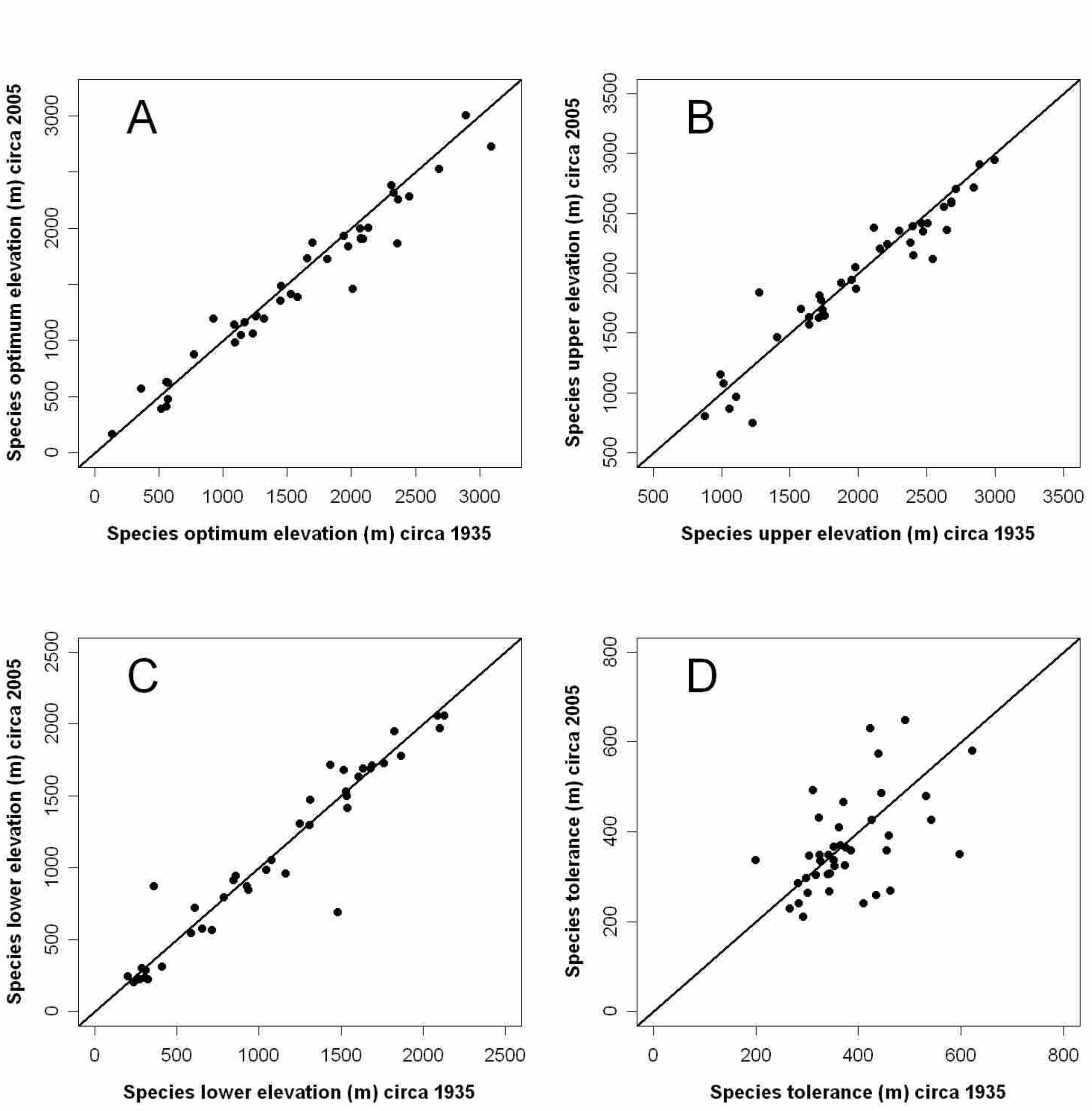
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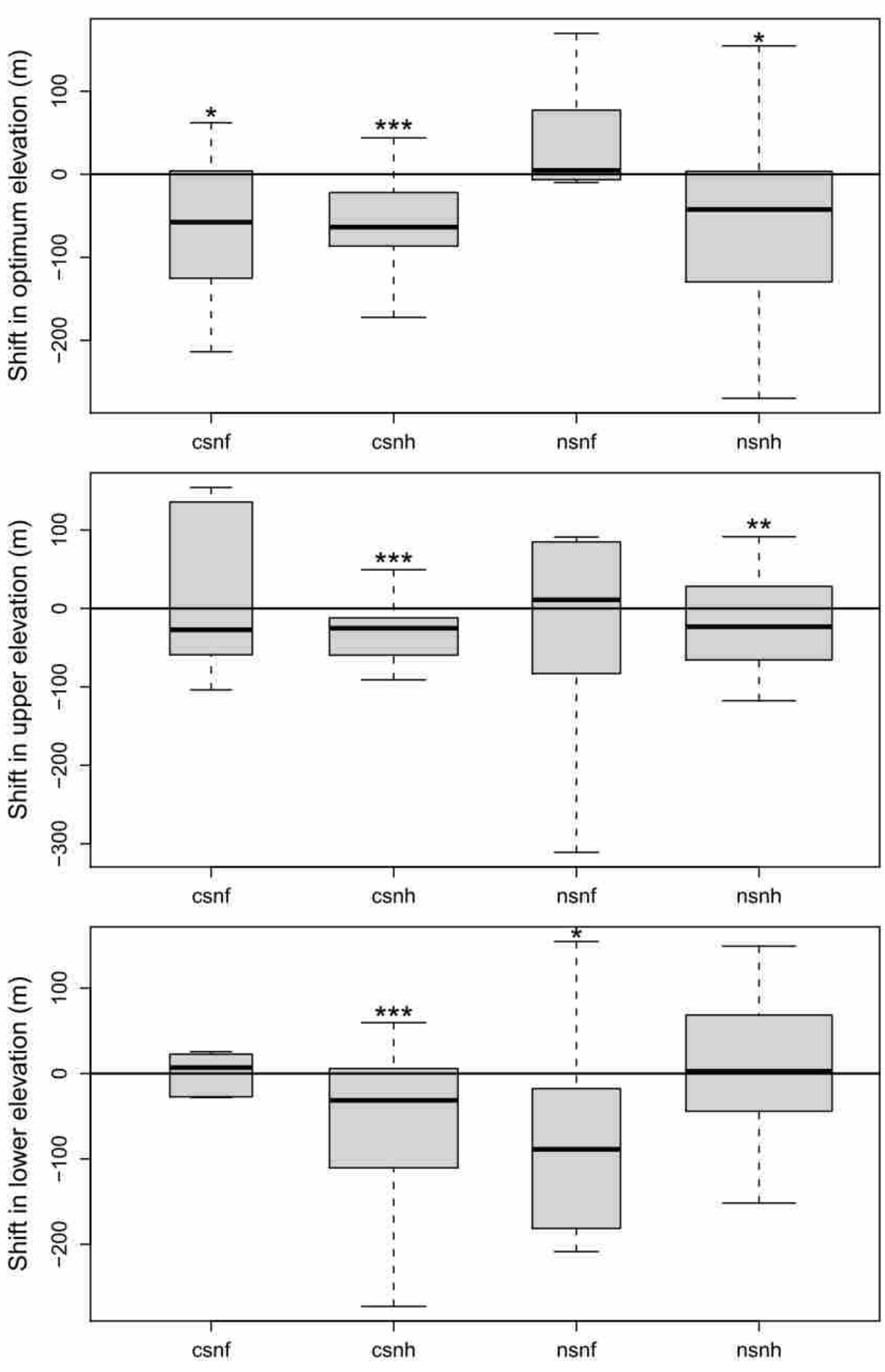
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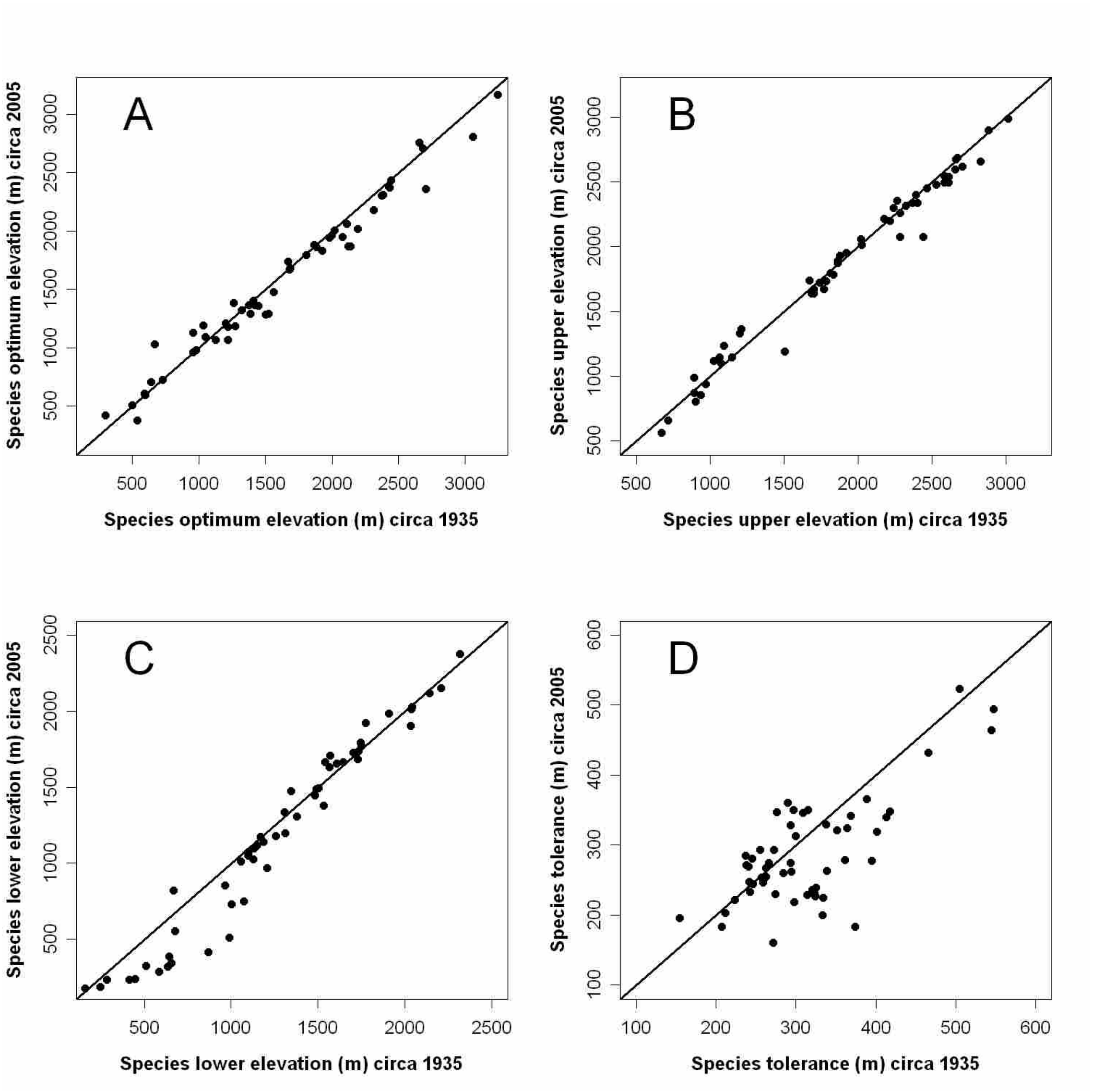
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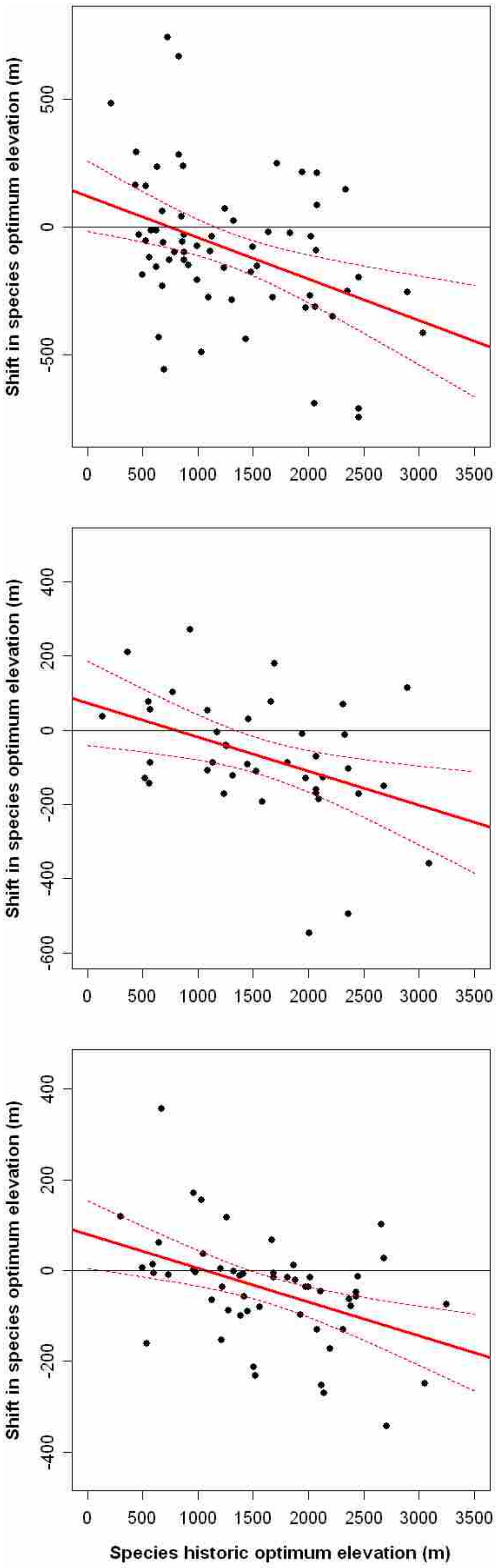
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Shift in species optimum elevation (m)
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Species historic optimum elevation (m)

CHAPTER 2

CAN FIRE OCCURRENCE DATA IMPROVE SPECIES DISTRIBUTION MODEL PROJECTIONS THROUGH TIME?

Crimmins, S.M., S.Z. Dobrowski, A.R. Mynsberge, and H.D. Safford. IN PREP. Can fire occurrence data improve species distribution model projections through time? *Formatted for Ecological Applications*

Abstract: Correlative species distribution models (SDM) are widely used in studies of climate change impacts, yet are often criticized for failing to incorporate mechanistic processes that can influence species distributions. Here, we use two temporally independent datasets of vascular plant distributions, climate data, and fire atlas data to examine the influence of disturbance on SDM projection accuracy through time in the mountain ranges of California. We used hierarchical partitioning to examine the influence of fire occurrence on the distribution of 145 vascular plant species, and built a suite of SDMs to examine how the inclusion of fire occurrence and departure from historical fire return intervals as predictors affected SDM projection accuracy. Fire occurrence provided the least explanatory power for predicting species' distributions in both time periods, but provided marginal explanatory power for species whose regeneration is tied closely to fire. Fire return interval departure had greater explanatory power for calibrating modern SDMs than fire occurrence but did not improve model accuracy when evaluated against data used to build the models. Fire occurrence and fire return interval departure were strongly related to the climatic covariates used in SDM development, suggesting that improvements in model accuracy may not be expected due to limited additional explanatory power. Our results suggest that the inclusion of coarse-scale measures of disturbance in SDMs may not be critical for generating predictions of potential species distributions under climate change, particularly for disturbance processes that are largely mediated by climate.

Keywords: California, disturbance, fire, niche, SDM, species distribution model, transferability

INTRODUCTION

Understanding the factors that determine biogeographic patterns has been a central tenet of ecological studies for decades (Grinnell 1917). Although early efforts to describe the relationships between species distributions and environmental factors were largely qualitative, ecologists today employ a wide variety of techniques for evaluating and describing these patterns (Elith and Leathwick 2009). In recent decades, species distribution models (SDMs) have become widely implemented for the study and description of biogeographic patterns. These models use observed species occurrences and spatially explicit environmental data to build probabilistic models of suitable habitat across the landscape (Austin 2002). Today, these models are widely applied to a variety of topics including invasive species biology (Urban et al. 2007), conservation planning (Araújo et al. 2011), and tests of ecological theory (Broennimann et al. 2007). However, perhaps the most common application of SDMs is in predicting the effects of climate change on species distributions (Thuiller 2004). As the availability of species distribution and climate data continues to increase, it is likely that these models will continue to be widely used in ecological studies.

Although commonly used among ecologists, SDMs are also the subject of widespread criticism (Hampe 2004). Because the results of SDMs are often used to guide conservation planning or climate change mitigation efforts, it is not surprising that substantial efforts have been made to understand the factors affecting SDM performance (Araújo and Luoto 2007, Thuiller et al. 2008). Yet despite these criticisms, SDMs are still considered to be an appropriate tool for many ecological studies (Pearson and Dawson 2003). One criticism that could limit the predictive accuracy of SDMs, and one whose effects have rarely been investigated, is that they typically fail to incorporate disturbance processes that can strongly influence biogeographic patterns (Austin 2002). It has been suggested that disturbance can disrupt the relationship between species occurrence and environmental factors (Cassini 2011), and that accounting for such processes is critical for the field of conservation biogeography (Franklin 2010).

Fire is one such disturbance that is often strongly related to the spatial patterns of vascular plants on the landscape (Franklin et al. 2004). In systems where fire represents the dominant natural disturbance mechanism, such as in many of the mountain ranges of California, fire differentially affects the survival and recruitment of individual species, with some succumbing to fire-induced mortality while others require the occurrence of fire to facilitate germination (Hickman 1993). Fire occurrence has also been linked to patterns of vegetation community shifts in portions of California (Callaway and Davis 1993), further indicating its influence on plant communities. There is abundant indirect evidence from studies in regions with Mediterranean climates, such as California, to suggest that fire-related covariates could influence SDM predictions. For example, previous studies have shown that species-specific adaptation to fire is strongly related to SDM accuracy when using internally validated (i.e. within a single time period) or temporally independent data (Syphard and Franklin 2010, Dobrowski et al. 2011b). Similarly, simulations of potential vegetation indicate that fire occurrence has a strong influence on broad-scale vegetation distribution and structure in both Mediterranean climates and globally (Bond et al. 2003, 2005). However, in one of the few studies to empirically assess the influence of fire related covariates on SDMs, Tucker et al. (2012) found that the inclusion of fire-related covariates in SDMs provided relatively little additional explanatory power for species occurrence in South African plant communities, like California a Mediterranean-climate region with strong ecological and evolutionary influences of fire.

A potential confounding factor when considering the occurrence of fire as a covariate in SDMs is that in many regions the current fire regime differs substantially from the historical fire regime. In regions with altered fire regimes, contemporary occurrence of fire is likely not representative of the long-term fire conditions under which local species evolved. This means that, especially for species with distributions tightly coupled to historical patterns in fire occurrence, current fire regimes may overlap only the periphery of, or be entirely beyond, the fundamental niche of these species (i.e. Hutchinson's [1957] "n-dimensional hypervolume"). These departures in fire regime can be the result of change in climatic factors influencing fire occurrence and/or changes in anthropogenic influences on the fire regime, in either positive or negative directions (Whitlock et al. 2003), yet it is largely unknown as to how these departures may affect SDMs. For example, California has experienced large changes in fire regime, including ignition rates, fire frequency, and area burned, resulting from anthropogenic activities (Syphard et al. 2007). Thus, in some systems, it is reasonable to assume that incorporating departure from historical fire regimes into SDMs may prove more useful than incorporating contemporary fire occurrence.

Despite previous research efforts and the extensive literature debating the utility of correlative SDMs that ignore mechanistic processes, to date no studies have addressed the basic question: Does including covariates describing disturbance patterns improve SDM projections under climate change? Relatively little work has been done to directly address this question, and what little work has been done using empirical data has occurred within a single time period. Previous studies focused on species' response to fire have provided ancillary evidence to suggest that the inclusion of fire as a predictor in SDM development could improve projections (Dobrowski et al. 2011b) but a direct assessment of this is still lacking. Thus we have little information on how the inclusion of fire-related covariates influences SDM projections through time.

METHODS

Study area

We conducted our study in the major mountain ranges of California, USA, an area of approximately 220,000 km^2. This region represents an excellent area for investigating the effects of climate change on biota and our subsequent abilities to model these changes. The study region has experienced substantial and spatially variable changes in climate and hydrology and contains major elevational, latitudinal, and longitudinal gradients (Crimmins et al. 2011, Dobrowski et al. 2011a). The region has been identified as a global biodiversity hotspot, and predicting the effects of climate change on the region's endemic flora is of great conservation concern (Loarie et al. 2008). There is evidence to suggest that species distributions within this region have shifted as a result of recent climate change (Tingley et al. 2009, Crimmins et al. 2011). Additionally, fire represents arguably the most important natural disturbance mechanism to plant species in this region (Figure 1), with more than 65,000 km^2 burned (including areas with multiple fires) in the state during our two primary study periods (see below).

Species data

We used two temporally independent datasets of vascular plant species distributions from our study area to develop and test SDMs. The first dataset is a collection of approximately 14,000 survey locations collected in the 1930's as part of the US Forest Service's Vegetation Type Map (VTM) Project (Wieslander 1935a, 1935b). VTM plots were 800 m^2 in size and plot locations have been digitized and georeferenced with an accuracy of +/- 200 m (Kelly et al. 2005). The second dataset represented approximately 33,000 survey locations compiled from a variety of sources that have been collected since 2000. Further details about these inventories are provided in Crimmins et al. (2011) and Dobrowski et al. (2011b). We extracted species presence-absence data from both datasets for a suite of species that were sufficiently represented ($\geq$ 30 occurrences) in each dataset. This left us with 144 species for which we were able to build and evaluate SDMs.

We categorized species by their adaptation to fire, the primary natural disturbance agent in our study area. We used published studies of species' ecology and expert opinion to assign each species to one of three adaptation levels: (1) fire evaders, (2) fire resisters, and (3) fire endurers and avoiders (Agee 1998; we refer to group 3 as "avoiders" throughout). Fire evaders are species that exhibit regeneration syndromes that are thought to have evolved in response to fire, including fire obligate seeding and serotiny; these are mostly species adapted to high intensity fire regimes, where the adult plant is often killed. Fire resisters are species that tend to survive fire through adaptations conferring resistance to low or moderate intensity fires, such as thick bark or self-pruning of lower branches; resisters do not possess specialized regeneration syndromes tied to fire and they tend to be rare or absent in areas characterized by high intensity fires. Fire endurers are resprouting species whose aboveground parts are usually killed by moderate or high intensity fire; the ability to resprout is nearly universal in woody plants and is considered a generalized adaptation to a variety of disturbances that remove or consume aboveground biomass (Bond and van Wilgen 1996). Fire avoiders are species without any adaptations to fire or similar disturbances; these species are rare in Mediterranean climate regions like California. In the fire evader group, we included species that exhibit both fire-stimulated germination and postfire resprouting ("facultative" species), and in the resisters group we included fire resistant species that sprout (e.g., *Quercus* spp.) or not (e.g., *Pinus* spp.).

Climate and fire data

We developed a suite of four climatic predictor variables that we hypothesized would exhibit direct influence on species distributions. We used 800-m resolution climate data from two time periods approximately representing 30-year time frames prior to vegetation data collection (1906–1935, 1976–2005). We used two climatic variables from the Parameter-elevation Regression on Independent Slopes Model (PRISM) (Daly et al. 2008) dataset, maximum temperature and minimum temperature. We also used two hydrologic variables that have been shown both theoretically and empirically to affect vascular plant distributions; actual evapotranspiration and annual climatic water deficit (Stephenson 1990, 1998). These variables were estimated at a monthly time-step and then summed within each year and averaged across the 30-year periods to represent average annual conditions for the entire time period. The hydrologic variables were developed using a modified climatic water balance model (Lutz et al. 2010) that accounts for atmospheric demand, snowmelt and soil moisture storage on a monthly time-step. For additional information see Dobrowski et al. (2012). Fire perimeters were acquired from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP; http://frap.cdf.ca.gov/). For each vegetation survey location we determined if a fire perimeter from the same 30-year time periods used in our climate summaries overlapped the survey location. We also tabulated the total number of fire occurrences at each sampling locations during the 30-year time periods and used this value as a covariate in SDMs. However, these results did not differ from those when including simple binary occurrence of fire (Appendix A). To evaluate the effects of departure from historical fire regime on SDMs we used a recently developed dataset on the departure in fire return interval between the 20th century and pre-European settlement conditions for all national forests in California (Safford and Van de Water, in review). From this we extracted the departure in mean fire return interval for all modern survey locations that occurred on US Forest Service lands, the area covered by the fire return interval departure map. Because this map did not cover our entire study area, analyses based on fire return interval departure were conducted using a subset ($n = 116$) of the 144 species for which we had sufficient occurrence data.

Hierarchical partitioning

We evaluated the influence of covariates, including fire, on explained deviance in species distributions using hierarchical partitioning (Chevan and Sutherland 1991). Hierarchical partitioning is an approach that quantifies the contribution of a given explanatory variable to the explanation of a dependent variable, in our case species presence or absence. Importantly, it allows for the contribution to be partitioned into the component that is shared jointly with other explanatory variables and the individual component that is unique to that predictor. The independent contribution of the variable is calculated by quantifying the effect of the variable in all possible models that can be constructed from the entire set of explanatory variables, while the joint contribution is that contribution that is shared among explanatory variables. We conducted hierarchical partitioning using the hier.part package in the R programming language (R Development Core Team 2011). We used generalized linear models (GLM) with a binomial distribution and calculated the contribution of each explanatory variable to goodness-of-fit, using log-likelihoods as our measure of fit. We modeled each species separately in each of the two time periods when including fire occurrence as a covariate and in the modern time period when including fire return interval departure.

Species distribution models

Although our hierarchical partitioning allows us to decompose the influence of individual covariates on measures of model fit, it does little to describe how incorporation of new covariates affects actual prediction accuracy of SDMs. Because we sought to explore the influence of fire on various classes of SDMs, we used a suite of different model algorithms to build our predictive models. First, we developed generalized linear models (GLM) of species presence-absence using logistic regression. We used a step-wise variable selection procedure based on minimization of AIC scores (Burnham and Anderson 2002). Using this procedure, each variable could be dropped or fit as a linear, second order, or third order polynomial. Second, we developed generalized additive models (GAM) as an example of a semi-parametric regression approach (Hastie and Tibshirani 1990). We again used stepwise variable selection procedure based on AIC scores where each variable could be dropped, fit as a linear term, or fit as a cubic spline with three degrees of freedom. Third, we developed boosted regression trees (BRT) as an example of a relatively new machine learning approach (De'ath 2007). BRT models were built using 2000 trees with a shrinkage parameter of 0.01, a 0.5 bag fraction, and an interaction depth of 3 (Elith et al. 2008). We derived out-of-bag estimates of the optimal number of boosting iterations, which we then used to predict probability of occurrence. Finally, we developed random forest (RF) models as another example from the machine learning community (Breiman 2001, Cutler et al. 2007). RF models were developed using independent bootstrap samples to grow 750 trees for each species (Cutler et al. 2007). For each species the probability of occurrence was determined as the proportion of presence votes from the 750 trees. We built one set of models using only our four climatic variables, and one set of models that also included fire occurrence as a predictor. We developed models using 75% of the historical data and tested the models on the remaining 25% of the historical data and all of the modern data. We refer to results from tests using the withheld 25% of the historical data as internal evaluations while the results using data from the modern time frame as independent evaluations. Because of the temporal scale of our fire return interval data we were not able to develop models in the historical time period using these data, and thus could not evaluate their effects on model projections across time (i.e. independent evaluations). However, we were able to evaluate the influence of fire return interval departure on internal evaluations in our modern data, using a randomly selected 75% of the modern data to build models and testing it on the remaining 25%. Because these data did not cover our entire study area we were only able to conduct these evaluations for a subset (n = 116) of our overall group of species.

We evaluated SDMs using multiple criteria. First, we used the area under the ROC curve (AUC) as a threshold independent measure of SDM accuracy (Fielding and Bell 1997). AUC is a commonly used metric for describing SDM accuracy (Elith et al. 2006) because it avoids the somewhat arbitrary issue of choosing a prediction threshold. However, it has been suggested that AUC may be a misleading measure of SDM accuracy (Lobo et al. 2008). Therefore, we also chose to use binary classifications of species presence or absence and confusion matrices to assess model accuracy. We used the sensitivity-specificity equality approach to select our prediction thresholds (Cantor et al. 1999). This approach places equal weight on sensitivity and specificity and performs well when compared to other commonly used threshold selection criteria (Liu et al. 2005). We converted our predicted probabilities of occurrence into binary presence-absence predictions for each species at each sampling location and assigned each prediction one of the four possible entries into a confusion matrix. We expressed false positive (FP; errors of commission) and false negative (FN; errors of omission) error rates as the proportion of true absences or presences that were incorrectly classified. We quantified the effect of fire on SDM projection accuracy by calculating the change in each accuracy metric (AUC, FP rate, FN rate) when going from a model without fire as a predictor to one including fire as a predictor using both internal and external model evaluations. Because previous research has indicated that species' response to fire can influence SDM projection accuracy (Dobrowski et al. 2011b), we summarized results from hierarchical partitioning and SDM evaluations within each of the three fire response groups.

RESULTS

Hierarchical partitioning

In general, the occurrence of fire provided little explanatory power relative to the climatic variables used in SDMs. When examined across all 144 species the joint and individual contributions of fire occurrence to the log-Likelihood were the lowest of all explanatory variables, a pattern that was evident regardless of time period (Figure 2). The individual explanatory power of fire occurrence was similar between time periods ($P = 0.99$), in each case accounting for <6% of the total variation explained by the model. The patterns in explanatory power among other predictors differed between time periods but were consistently greater than fire (Figure 2). Patterns of explanatory power differed when examined within individual fire adaptation groups. For fire avoiders and resisters fire occurrence yielded the least explanatory power in either time period (Figure 2). For fire evaders the occurrence of fire provided the least explanatory power in the historical time period, but the third strongest in the modern time period, surpassing the explanatory power of AET and maximum temperature (Figure 2). For all fire adaptation groups in both time periods the individual contribution of fire occurrence amounted to less than 10% of the total explanatory power. Patterns of explanatory power for other variables differed between time periods within each of the fire adaptation groups, with temperature related variables showing a general increase in predictive power while hydrologic variables showed a general decrease (Figure 2).

Compared to fire occurrence, fire interval departure did offer additional explanatory power, with an individual contribution to the total explained variability of approximately 10%

when examined across all species. However, as with fire occurrence this was the lowest among all predictors (Figure 3). Patterns of explanatory power for the avoiders and evaders groups were similar to those found when using fire occurrence, with the explanatory power of fire return interval departure exceeding that of AET and maximum temperature for the evaders while retaining the lowest explanatory power among the avoiders. For the resisters, fire return interval departure yielded the second highest individual contribution to total model likelihood, explaining approximately 16% of the total variation in species occurrence.

Species distribution model accuracy

Our models that excluded fire occurrence performed well when evaluated internally, with an average AUC of 0.91 across all five model algorithms (Table 1). When validated with contemporary data, average AUC of models excluding fire occurrence dropped to 0.80. The random forest model exhibited the largest decrease in AUC when projected into the modern time period (Table 1). FP and FN error rates both increased when SDMs were projected into the future, with FP rates increasing to a larger degree than FN rates (Table 1).

When evaluated internally, models including fire occurrence yielded small but non-significant ($P > 0.1$) increases in overall model accuracy compared to models excluding fire across all 144 species (Table 1). Changes in accuracy metrics varied among model algorithms but in each case were not significant (Table 1). When evaluated with temporally independent data the inclusion of fire occurrence in SDMs had no discernible effects on model accuracy, with no significant changes in any accuracy metric when examined across all 144 species (Table 1). When examined within fire adaptation categories, the inclusion of fire generally did not improve any metric of projection accuracy (Figure 4). The lone exception was AUC for the evaders group, which exhibited a small but significant ($P < 0.01$) increase. When evaluated against temporally independent data, the inclusion of fire occurrence yielded no discernible changes in any accuracy metric within any of the fire adaptation groups (Figure 4). The inclusion of fire return interval departure yielded no discernible changes in any accuracy metric within any of the fire adaptation groups (Figure 5).

DISCUSSION

Disturbance-related variables are typically absent from species distribution models, a point that has been highlighted in critical evaluations of SDMs (Austin 2002). Although SDMs are widely criticized for this lack of mechanistic processes, empirical evaluations of its effects on model accuracy are rare. We conducted our study in a region with a dominant natural disturbance mechanism (fire) that is generally thought to exert a strong influence on plant distributions (Keeley and Fotheringham 2001). Because of this we hypothesized that fire occurrence would be an important predictor of species distributions and that its inclusion would improve SDM projection accuracy. Contrary to our expectations, we found that fire occurrence yielded very little additional explanatory power relative to climatic variables and generally did not improve model accuracy. We had also hypothesized that using fire return interval departure as a covariate in our models might yield additional explanatory power compared to observed fire occurrence. Our hierarchical partitioning results confirmed this hypothesis, with a relative contribution to total explanatory power of about 15% compared to 8% when using fire occurrence. However, this increase in explanatory contribution had little effect on metrics of model accuracy.

In a related study, Tucker et al. (2012) also found that variables related to fire regime yielded little explanatory power. Their study was conducted in the Cape Floristic Region of South Africa, an area with similar climatic patterns and evolutionary forces as much of our study area, which may help explain the similarity in our results. Tucker et al. (2012) found that the influence of fire related variables on SDMs was not related to species' adaptation to fire, which they attributed to limited statistical power due to a small number of species included in their analysis (*n* = 27). Our results are similar to those of Tucker et al. (2012) in that we generally found that fire occurrence yielded little explanatory power. However, our results did differ from those of Tucker et al. (2012) somewhat in that we found what appears to be a pattern of improved SDM accuracy for fire evading species when including fire occurrence, and to some extent fire return interval departure, as a variable in our models (Figures 4 and 5). Although the improvement in model accuracy was not statistically significant, the pattern does match what we would expect for species that are dependent upon fire for regeneration. Although our overall sample size was large (*n* = 144), we did not have a large number of species that exhibited specialized regeneration responses to fire in our study (*n* = 41) suggesting that our results may also be limited by sample size issues. Additional studies with a greater number of disturbance-linked species would greatly improve our understanding of disturbance mechanisms on SDM performance.

A potentially parsimonious explanation for the general lack of influence of fire occurrence on species distributions is that the occurrence of fire itself is not independent of climate. Wildfire regimes are largely determined by climatic factors (Westerling et al. 2003), which could have limited their predictive power in our models. For example, using the same climatic variables as in our SDMs to build logistic models (GLM) of fire occurrence at the vegetation survey locations instead of species occurrence yields an AUC value of >0.78 in both time periods, suggesting that the occurrence of fires in our study area was largely determined by the climatic parameters used in our SDMs and thus provided limited additional explanatory power. This is not entirely surprising, as previous research has documented the strong influence of long-term climate on the relative probability of fire occurrence in the western United States (Parisien et al. 2012). Similarly, climatic models of fire return interval departure yielded relatively high levels of predictive power ($r^2 = 0.5$) as well. Even though fire return interval departure is driven primarily by fire suppression efforts, the success of these efforts is dependent to a great extent on variables related to weather and climate, such as drought, fuel moisture, temperature, precipitation, and wind patterns (Miller et al. 2012). It is entirely possible that other disturbance mechanisms unrelated to long-term climate may prove useful for SDM studies, however our results suggest that, particularly for relatively short-term projections, climatically mediated disturbance mechanisms may be of limited utility in improving SDM projections.

Although was fire was prevalent in our study area, with 15.6% and 17.6% of our historical and modern plots having at least one fire occurrence during our 30-year time frames respectively, our data come from a time period in which fire suppression was widespread throughout our study area. Thus, the fire regimes represented in our data do not represent the natural fire regimes that developed in the region prior to large-scale anthropogenic alterations of the system and the fire regime under which many of these species have adapted. Because of this it is not entirely surprising that including contemporary fire occurrence data in our models had little effect on their accuracy. Given that large-scale fire suppression is likely to continue in the near future, and thus continued alterations of the natural historical fire regime will occur, our results are very pertinent to short-term predictions of future species distributions. The lack of influence of fire return interval departure on SDM accuracy, despite its increased contribution to explained variation, may be an artifact of the relatively short time frame (30 yr.) used in our analysis. Fire regimes, and species adaptations to them, have developed over evolutionary time-scales. Thus, departures from historical fire regimes may have a strong influence on species distribution, but at a time-scale greater than that of our study. Paleoecological studies may prove very informative for understanding the long-term influence of altered disturbance regimes on species distributions (Svenning et al. 2011).

Another issue to consider regarding the inclusion of disturbance related covariates in SDMs is that of large-scale distributional patterns versus small-scale occupancy dynamics. Although we found that disturbance had little effect on broad-scale species distributions in this study, disturbance may be important when considering temporal changes in site-level occupancy patterns. For example, propagules of fire evading species dispersing into previously unoccupied habitat cannot generally germinate in the absence of a fire event, regardless of climatic suitability. Thus, the actual occurrence of a fire at a specific site can serve as the mechanism determining whether or not a site is occupied by a particular species despite the site being climatically “suitable” habitat. This dynamic would be very important at range margins, where transient metapopulation dynamics that are poorly represented by correlative SDMs may exhibit stronger influence on site level occupancy dynamics than long-term climatic conditions. Thus, it is important to consider issues of both temporal- and spatial-scale when developing SDMs using disturbance related covariates. The issue of temporal scaling may have influenced our findings because of our use of 30-year time frames to quantify fire occurrence. Using this approach, we were not able to differentiate between plots that had burned 30 years prior to sampling or two years prior. If a fire occurred at a plot near the beginning of our 30-year window, this would allow ample time for regeneration of any species that were killed by fire. Thus, the timing of vegetation sampling relative to that of fire occurrence may have substantial consequences for understanding site-level occupancy dynamics. That our results when using the count of the total number of fires during our 30-year time frames (results not shown) did not differ from those when using binary fire occurrence suggests that our results are likely robust to this issue, however hybrid modeling approaches that incorporate climate envelope models with dynamic metapopulation models may be a promising approach for incorporating disturbance mechanisms into predictions of species distribution under climate change (Anderson et al. 2009).

The motivation behind including disturbance related variables in SDMs is that they represent mechanistic processes that can directly affect the survival and reproduction of organisms, whereas many long-term climatic factors commonly used in SDMs (e.g. mean annual temperature) do not. An important yet overlooked caveat to this discussion is that it presumes that patterns of disturbance, both spatially and temporally, carry information that is independent of the climate factors used in SDM development. It is nearly impossible to argue that fire does not have a direct influence on plant distributions through its differential effects on mortality and regeneration. Likewise, it is also difficult to argue that, in many situations, SDMs that do not include disturbance related variables yield accurate predictions of species distributions (see Table 1). Our relatively good measures of SDM accuracy across time (AUC >0.8) occurred in a system historically dominated by disturbance, yet the inclusion of this disturbance yielded no discernible improvement on SDM performance. Because the disturbance mechanism of interest in our system is largely governed by the same climatic parameters used in SDM development, it may be unnecessary to include it in modeling efforts. For other disturbance processes that are not related to climate, the decision of whether to include them in SDMs will depend upon a variety of factors including the availability of spatially explicit disturbance data and the accuracy of future projections of disturbance regimes.

There are several practical limitations to including disturbance mechanisms into SDMs used for conservation planning. First, it requires a detailed knowledge of the life-history requirements of the species of interest in order to properly incorporate the disturbance process into the model (Franklin 2010). For example, it has been suggested that fire occurrence in fire dominated systems is more likely to affect demographic patterns and abundances of vascular plants than their broad-scale distribution patterns (Tucker et al. 2012). Many species that require the occurrence of fire for germination also have life spans longer than the interval between our two study periods. For these species, it seems reasonable to assume that areas that frequently burn may support higher densities, but that because of their longevity these species can occur in many areas that have not experienced recent fire activity. This also relates to the issue of detectability, as many of these species can lay dormant in seed banks for extended periods of time until fire occurrence promotes germination. Second, it requires spatially explicit estimates of the disturbance process and, ideally, projections of the disturbance into the future. For many disturbance processes such data are difficult to attain, and projections of disturbance processes into the future carry large uncertainty in their predictions (Flannigan et al. 2009). In the absence of such data, it has been suggested that modeling demographic ratios rather than simple occurrences in non-equilibrium environments can accurately capture the effects of disturbance by separating its differential effects on survival and recruitment (Cassini 2011). However, this approach requires information that is typically unavailable in most datasets. Obviously, the inclusion of anthropogenic disturbance mechanisms will be critical for the building accurate SDMs in regions with a rapidly expanding human footprint. However, our results indicate that, in certain situations, SDMs that do not include disturbance mechanisms can yield accurate projections of species distributions under climate change.

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SUPPLEMENTAL MATERIAL

Appendix A

Hierarchical partitioning and SDM accuracy results when considering number of fires as an ordinal predictor.

Appendix B

Change in model accuracy metrics for alternative SDM algorithms.

Table 1: Accuracy statistics for 145 species distribution models with and without fire occurrence as a predictor variable (FP = false positive error rate; FN = false negative error rate).

	Fire not included						Fire included as binary predictor					
	Internal Evaluation			External Evaluation			Internal Evaluation			External Evaluation		
Model	AUC	FP	FN	AUC	FP	FN	AUC	FP	FN	AUC	FP	FN
GLM	0.888	0.176	0.209	0.829	0.383	0.210	0.891	0.171	0.209	0.826	0.377	0.214
GAM	0.895	0.172	0.199	0.834	0.279	0.268	0.898	0.167	0.197	0.830	0.318	0.237
GBM	0.925	0.202	0.174	0.803	0.284	0.349	0.926	0.186	0.175	0.804	0.284	0.347
RF	0.975	0.209	0.056	0.781	0.536	0.152	0.975	0.181	0.056	0.788	0.493	0.168
CT	0.877	0.298	0.162	0.742	0.439	0.230	0.878	0.302	0.168	0.742	0.444	0.223

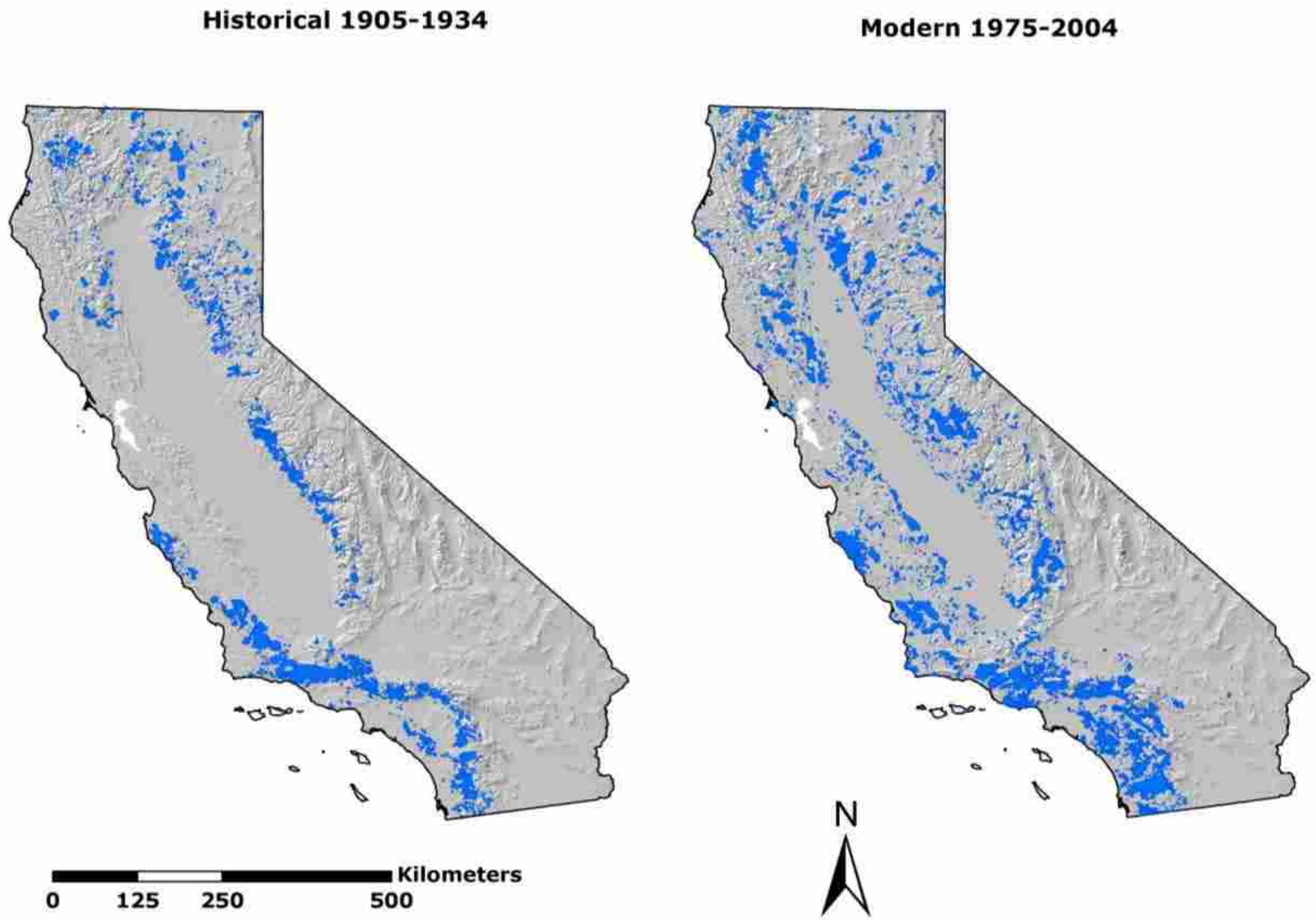
Figure 1: Map of study area showing fire perimeters (blue) from historical (1905–1934) and modern (1975–2004) time periods.

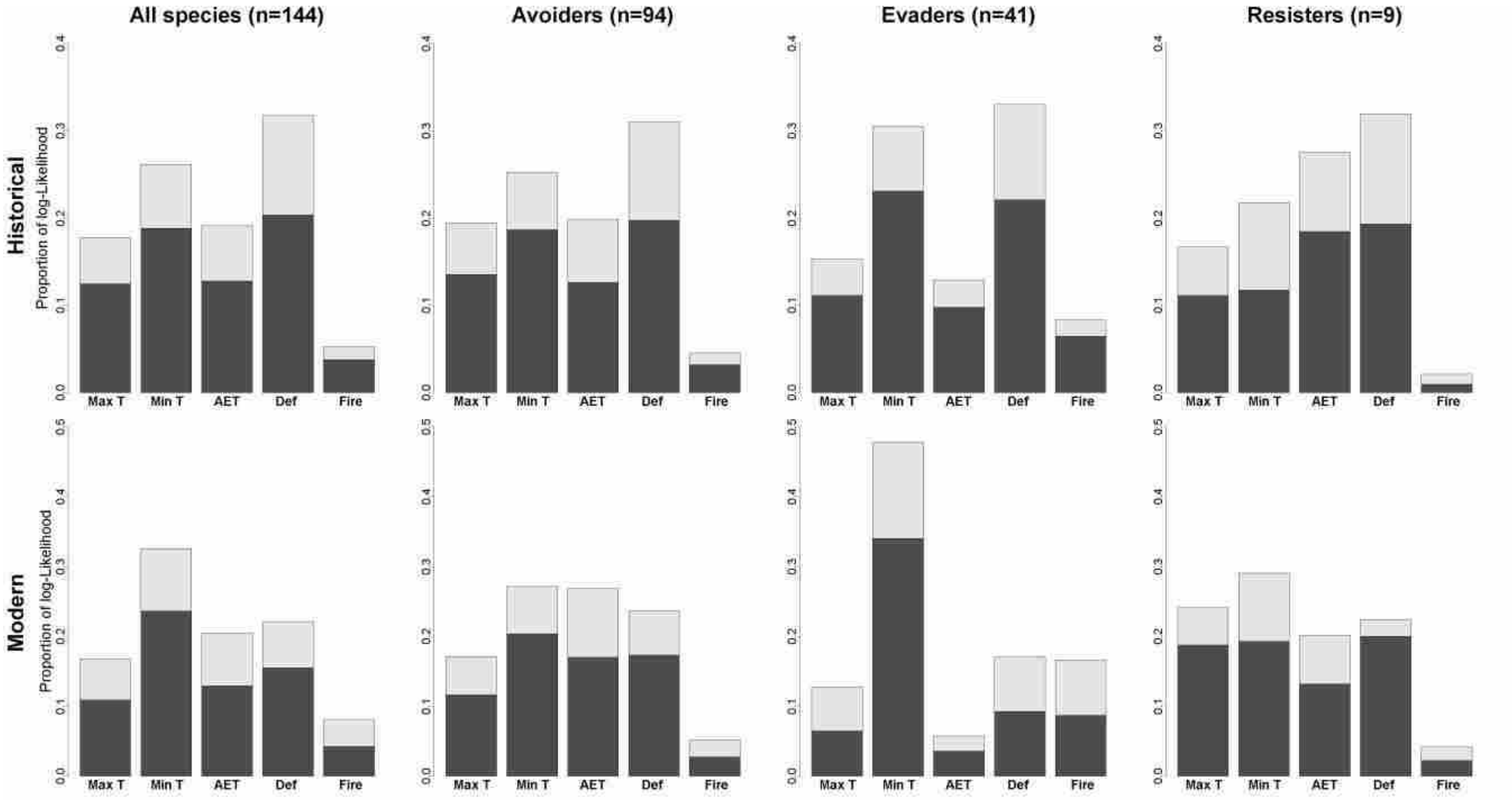
Figure 2: Stacked barplots of joint (light grey) and individual (dark grey) contributions of predictors from hierarchical partitioning. Models were calibrated with historical (1905–1934) and modern (1975–2004) data for all species and within fire adaptation groups. Fire category represents binary fire occurrence.

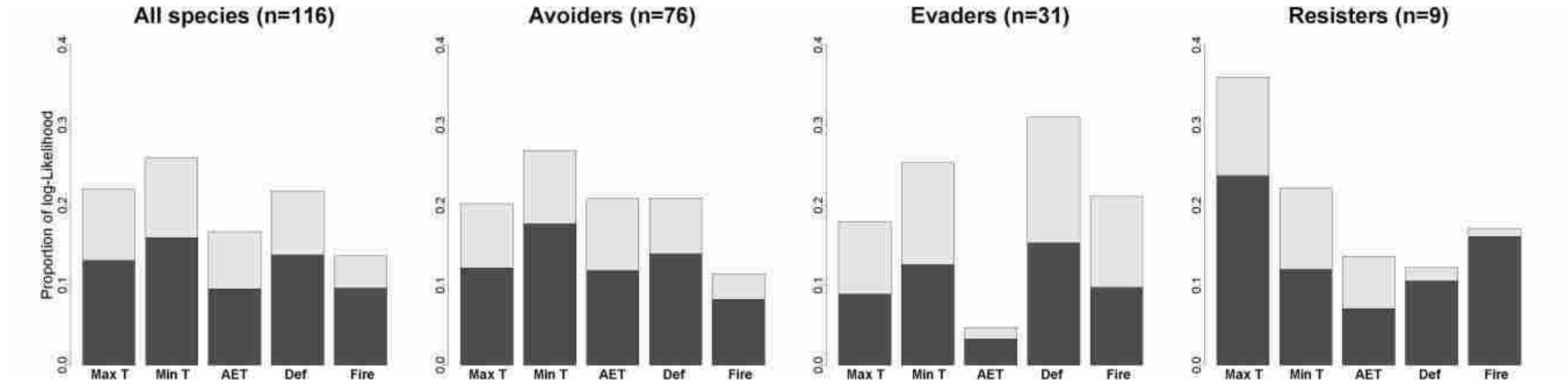
Figure 3: Stacked barplots of joint (light grey) and individual (dark grey) contributions of predictors from hierarchical partitioning. Models were calibrated with modern (1975–2004) data from national forest lands in California for a subset of species with sufficient data. Fire category represents fire return interval departure.

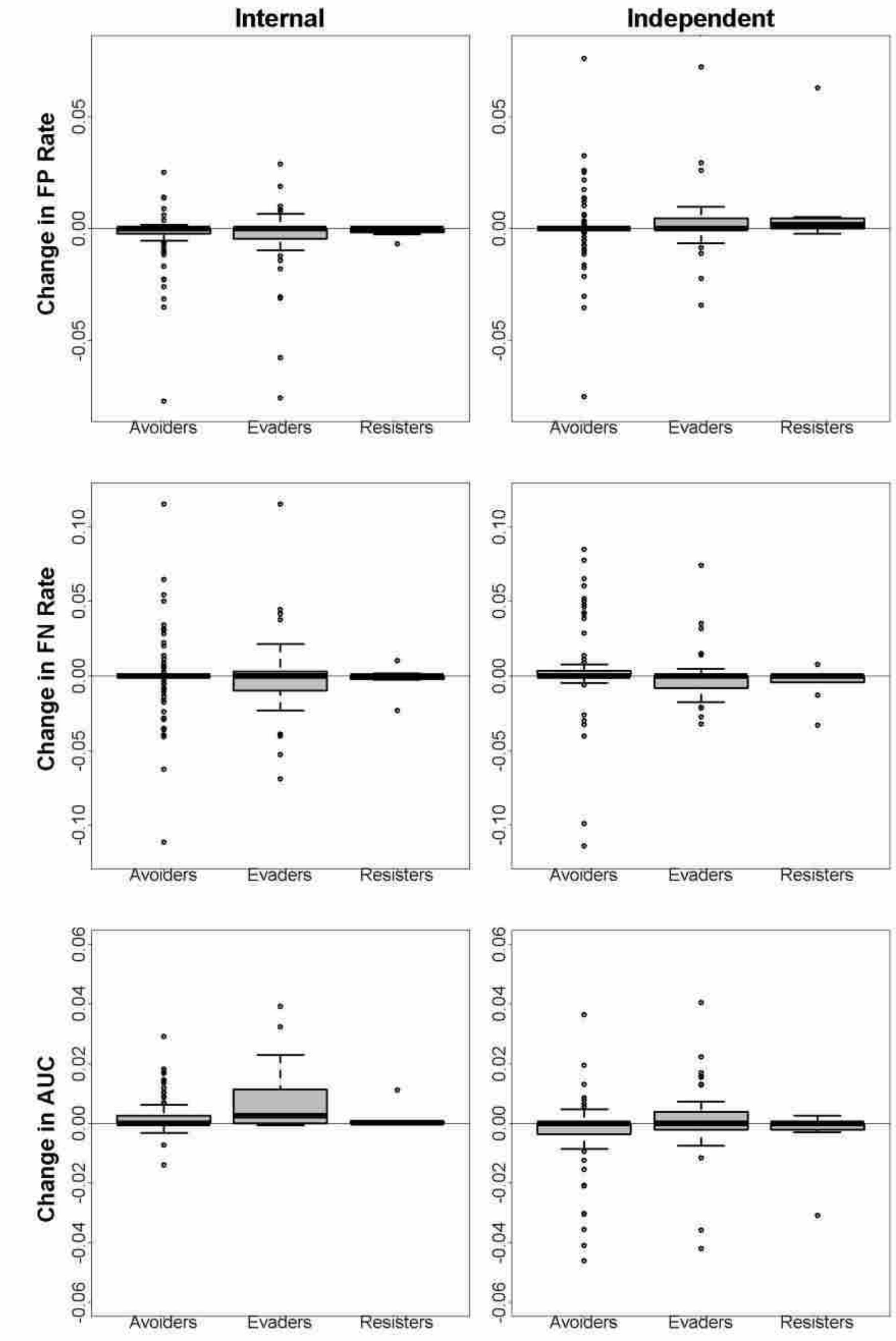
Figure 4: Change in SDM accuracy metrics from internal (t_1 models against t_1 data) and independent (t_1 models against t_2 data) evaluations within fire response groups when adding fire occurrence as a binary predictor variable in a generalized linear model (GLM). Results were similar across SDM algorithms (Appendix B).

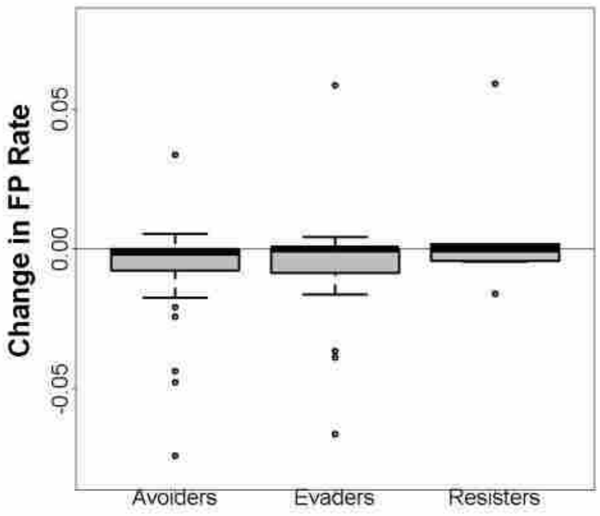
Figure 5: Change in SDM accuracy metrics from internal (t_2 models against t_2 data) evaluations for a subset of species within fire response groups when adding fire return interval departure as a predictor variable in a generalized linear model (GLM). Results were similar across SDM algorithms (Appendix B).

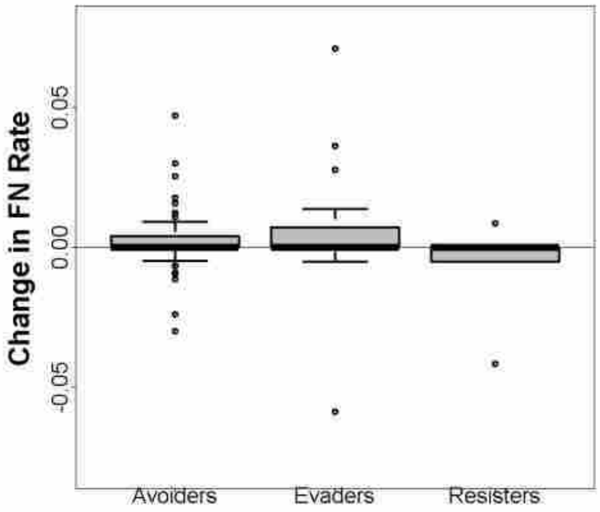

Historical 1905-1934
Modern 1975-2004
0
125
250
500
Kilometers
N

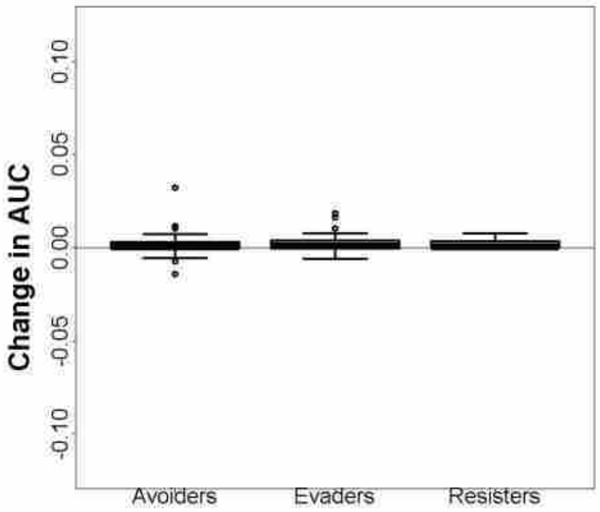

All species (n=144)
Avoiders (n=94)
Evaders (n=41)
Resisters (n=9)
Historical
Modern
Proportion of log-Likelihood
0.0
0.1
0.2
0.3
0.4
0.5
Max T
Min T
AET
Def
Fire


All species (n=116)
Avoiders (n=76)
Evaders (n=31)
Resisters (n=9)
Proportion of log-Likelihood
0.0
0.1
0.2
0.3
0.4
Max T
Min T
AET
Def
Fire


Internal
Independent
Change in FP Rate
Change in FN Rate
Change in AUC
0.05
0.00
-0.05
0.10
0.05
0.00
-0.05
-0.10
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
Avoiders
Evaders
Resisters


Change in FP Rate
0.05
0.00
-0.05
Avoiders
Evaders
Resisters


Change in FN Rate
0.05
0.00
-0.05
Avoiders
Evaders
Resisters


Change in AUC
0.10
0.05
0.00
-0.05
-0.10
Avoiders
Evaders
Resisters

APPENDIX A. Results when considering number of fires as an ordinal predictor.

Figure A1: Stacked barplots of joint (light grey) and individual (dark grey) contributions of predictors from hierarchical partitioning. Models were calibrated with historical (1905–1934) and modern (1975–2004) data for all species and within fire adaptation groups. Fire category represents ordinal fire count.

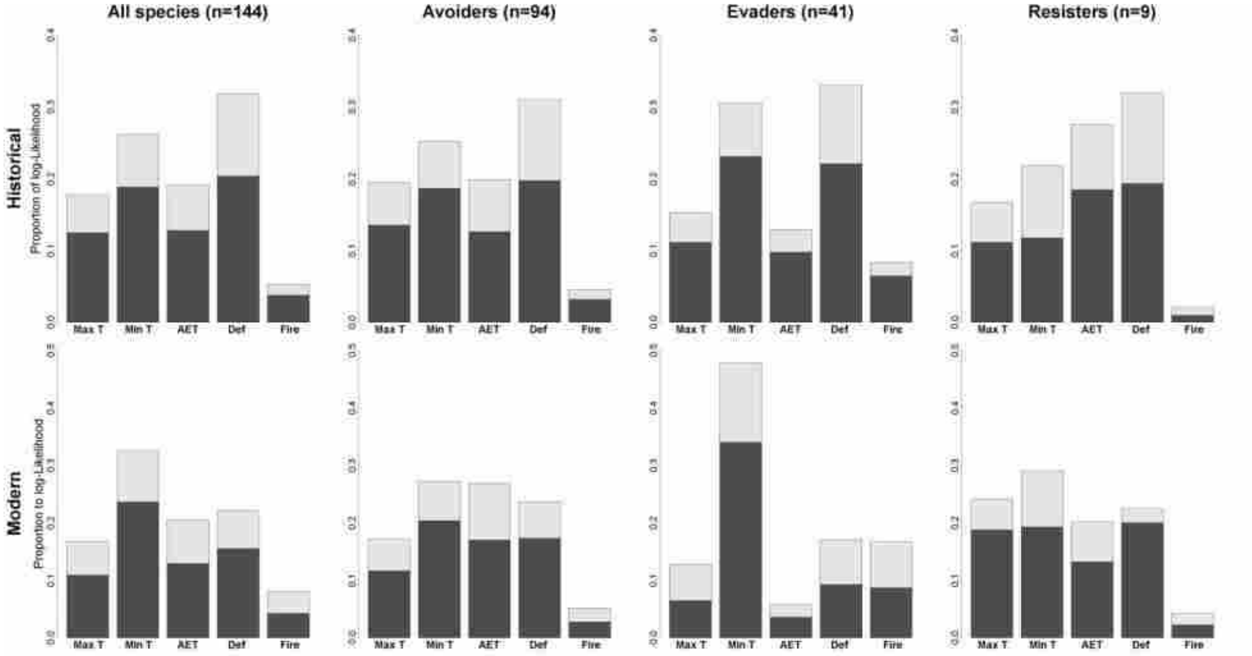
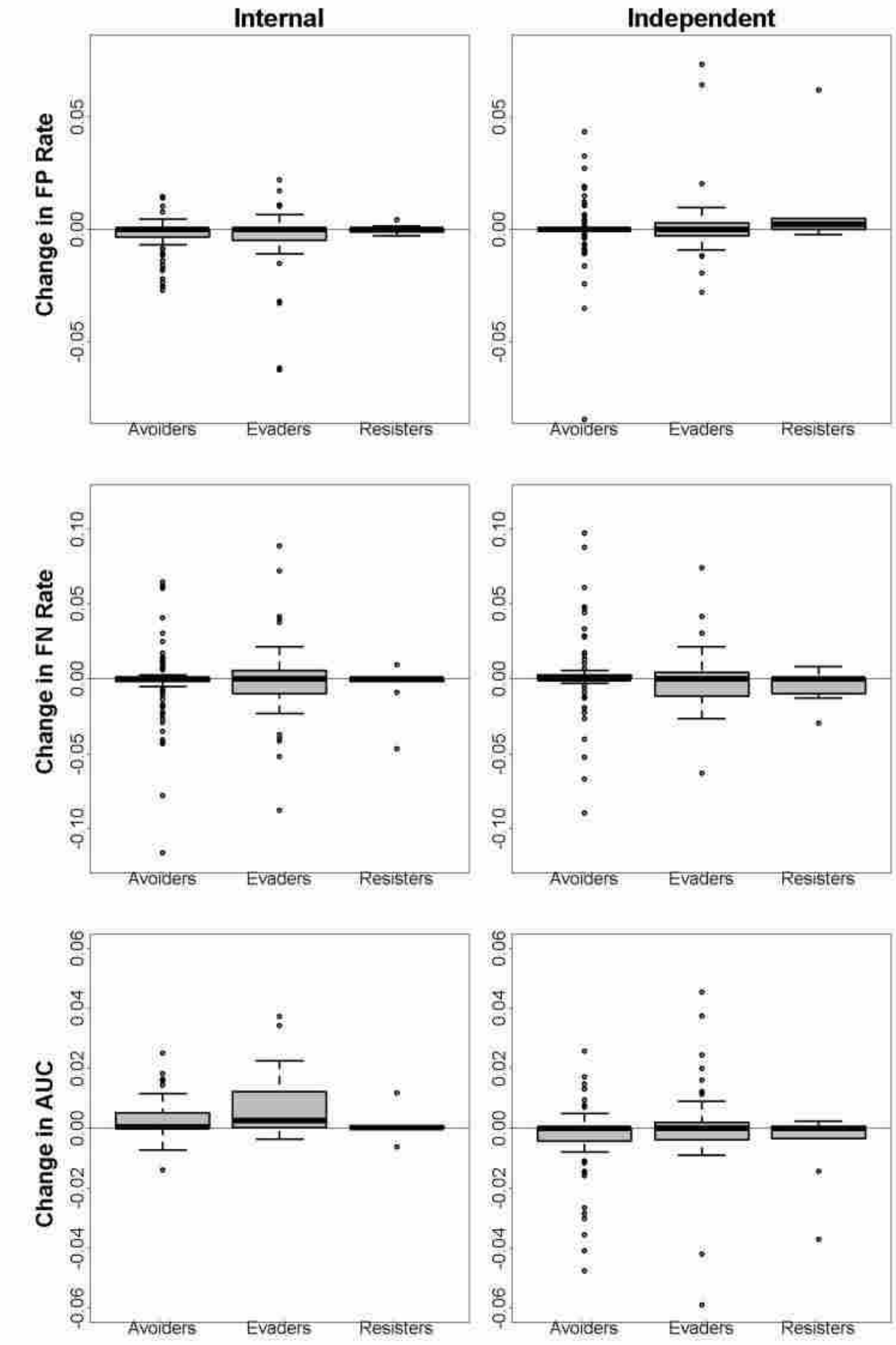


Figure A2: Change in SDM accuracy metrics from internal (t_1 models against t_1 data) and independent (t_1 models against t_2 data) evaluations within fire response groups when adding fire count as an ordinal predictor variable in a generalized linear model (GLM).



APPENDIX B. Change in model accuracy for alternative SDM algorithms.

Figure B1: Change in SDM accuracy metrics from internal (t_1 models against t_1 data) and independent (t_1 models against t_2 data) evaluations within fire response groups when adding fire occurrence as a binary predictor variable in a generalized additive model (GAM).

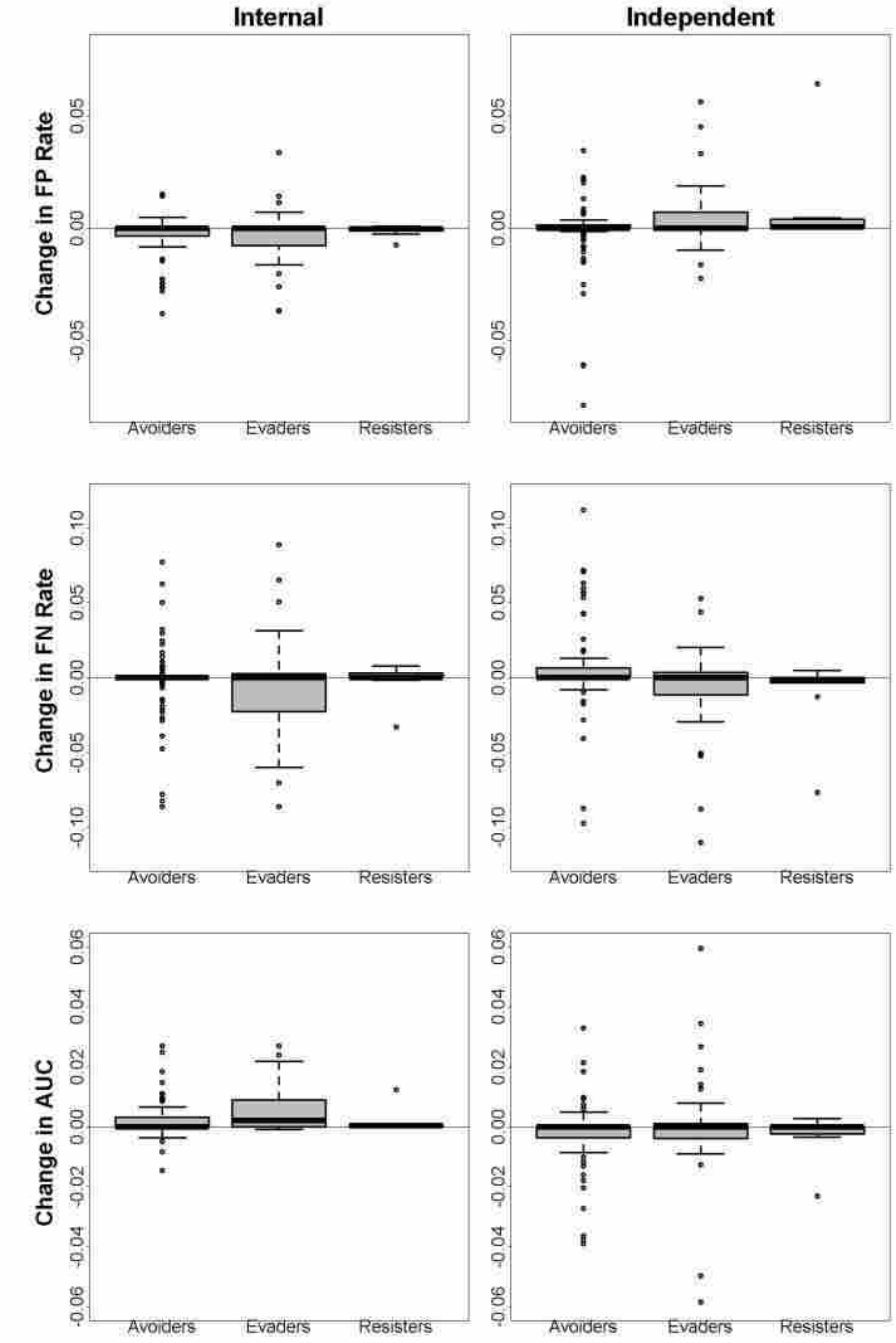


Figure B2: Change in SDM accuracy metrics from internal (t_1 models against t_1 data) and independent (t_1 models against t_2 data) evaluations within fire response groups when adding fire occurrence as a binary predictor variable in a gradient boosting model (GBM).

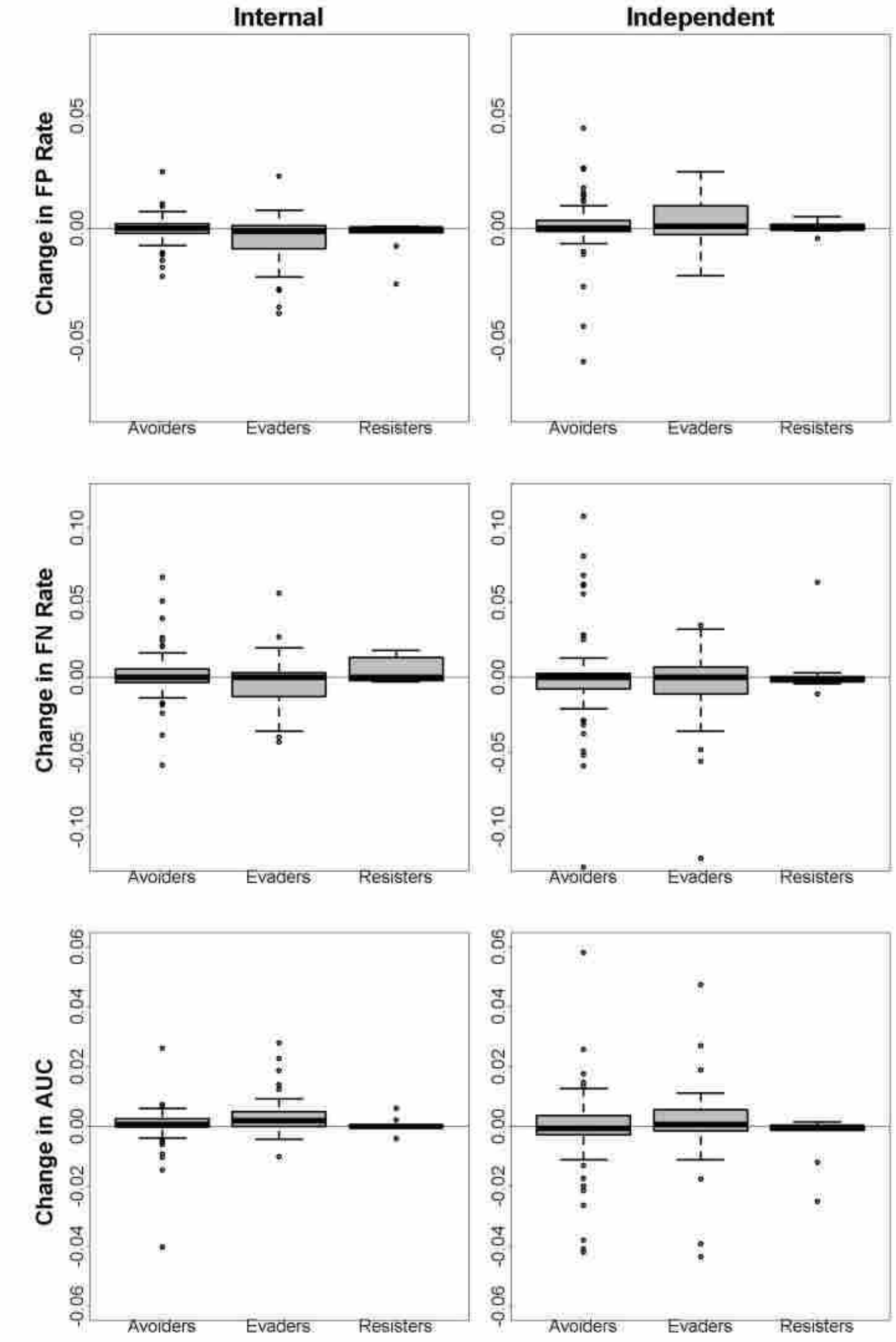


Figure B3: Change in SDM accuracy metrics from internal (t_1 models against t_1 data) and independent (t_1 models against t_2 data) evaluations within fire response groups when adding fire occurrence as a binary predictor variable in a random forest model (RF).

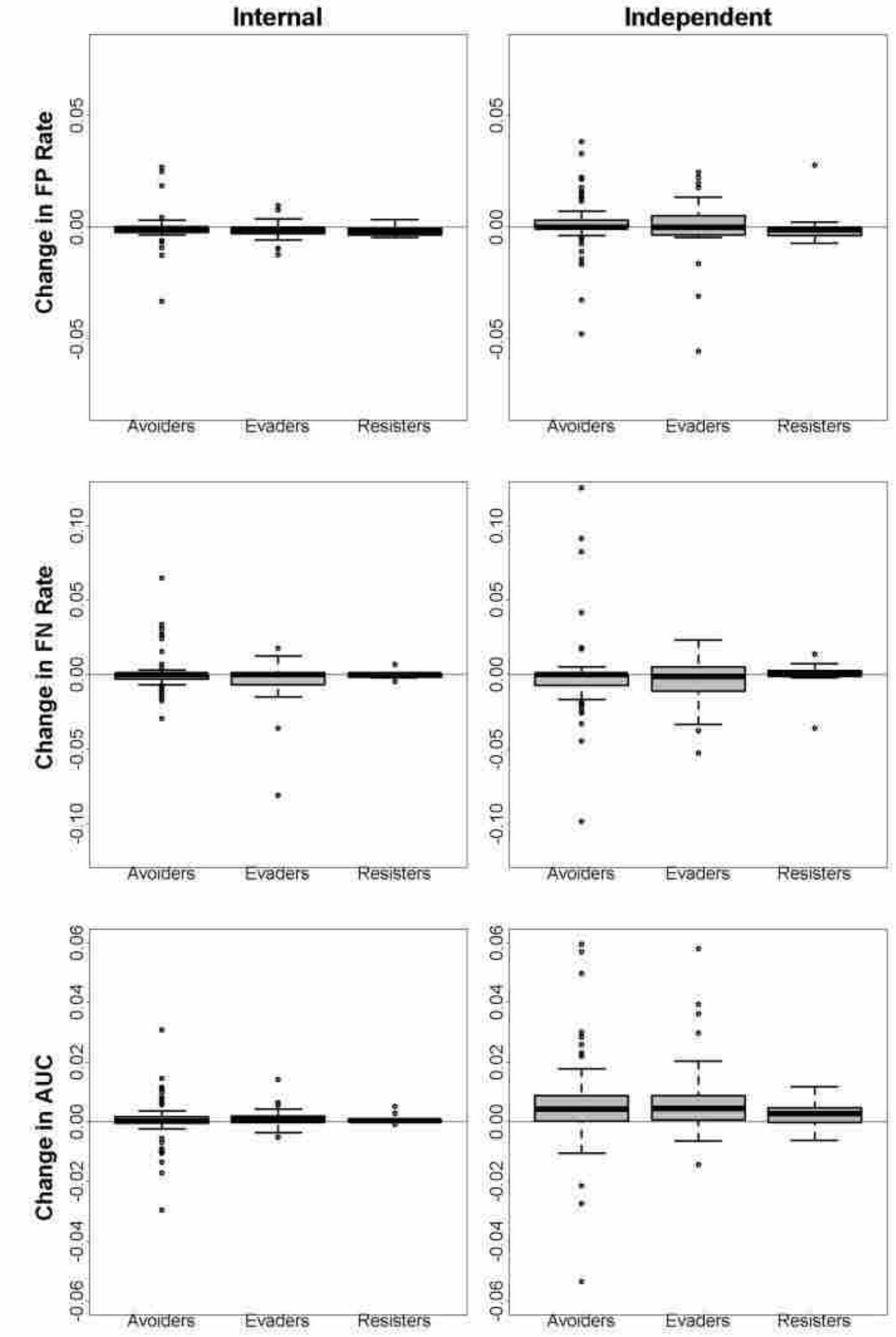


Figure B4: Change in SDM accuracy metrics from internal (t_1 models against t_1 data) and independent (t_1 models against t_2 data) evaluations within fire response groups when adding fire occurrence as a binary predictor variable in a classification tree model (CT).

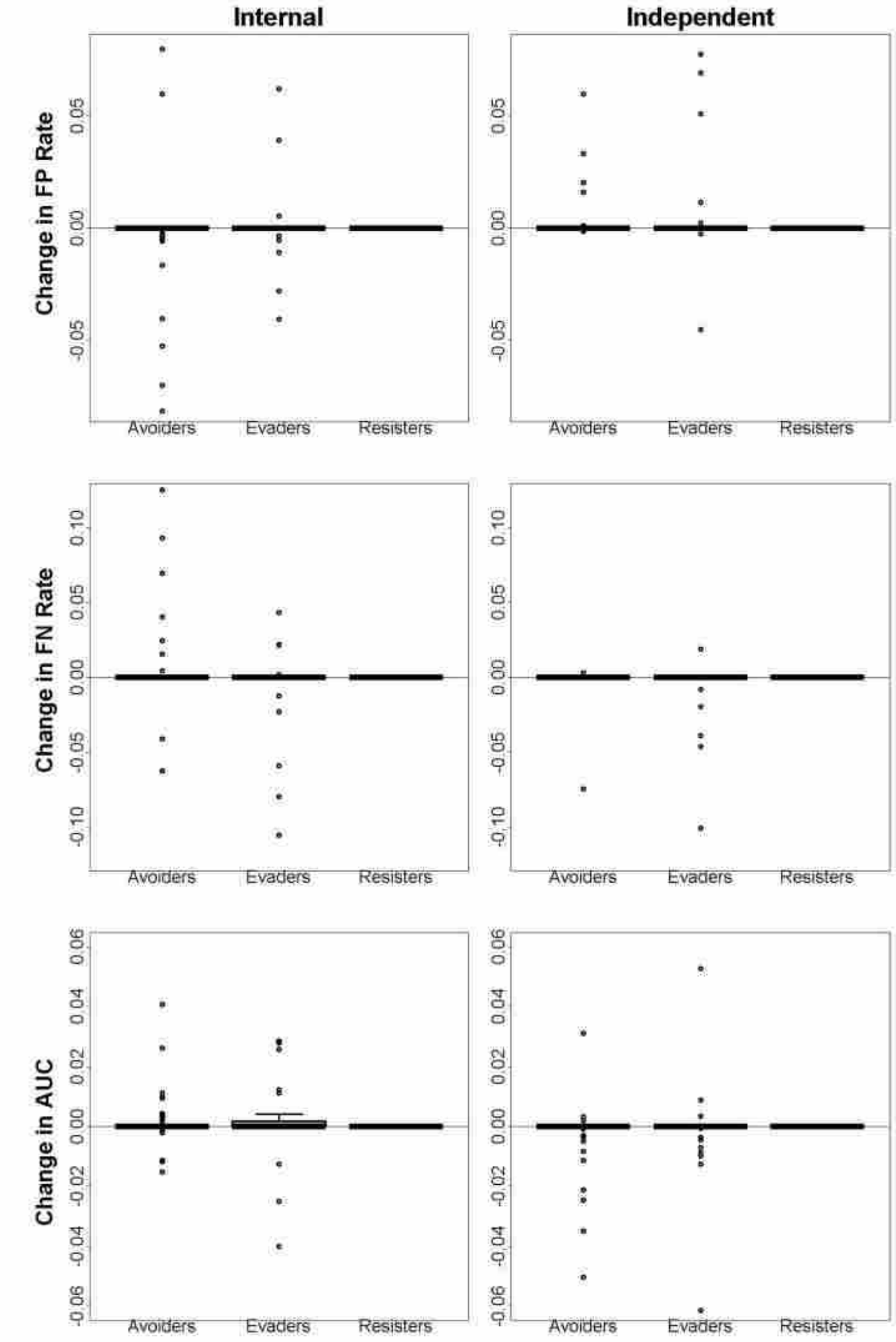


Figure B5: Change in SDM accuracy metrics from internal (t_2 models against t_2 data) evaluations for a subset of species within fire response groups when adding fire return interval departure as a predictor variable in a generalized additive model (GAM).

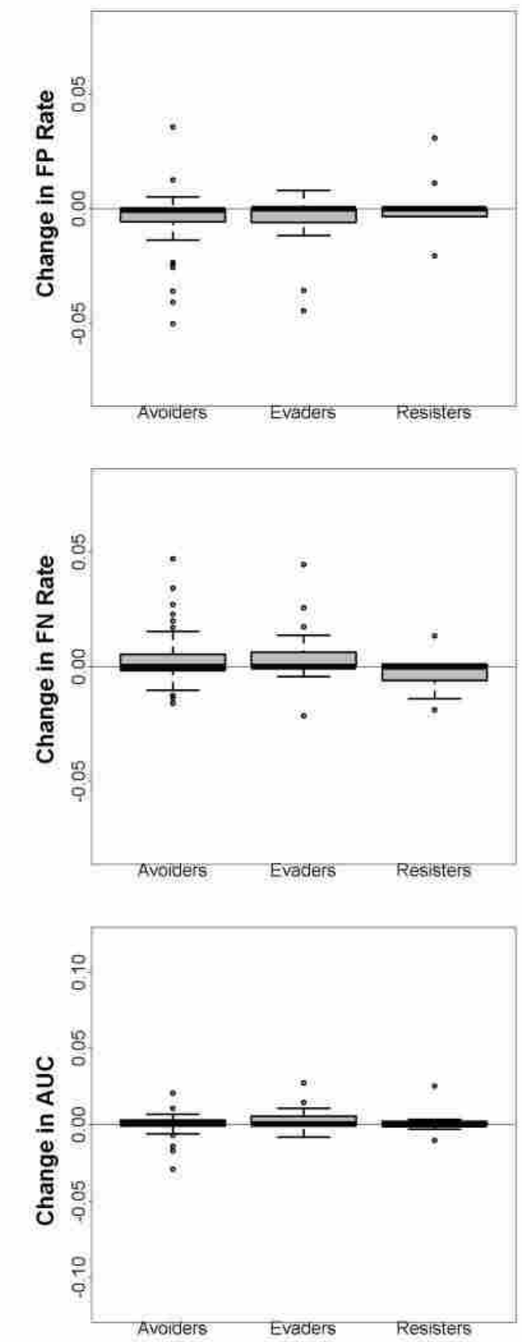


Figure B6: Change in SDM accuracy metrics from internal (t_2 models against t_2 data) evaluations for a subset of species within fire response groups when adding fire return interval departure as a predictor variable in a gradient boosting model (GBM).

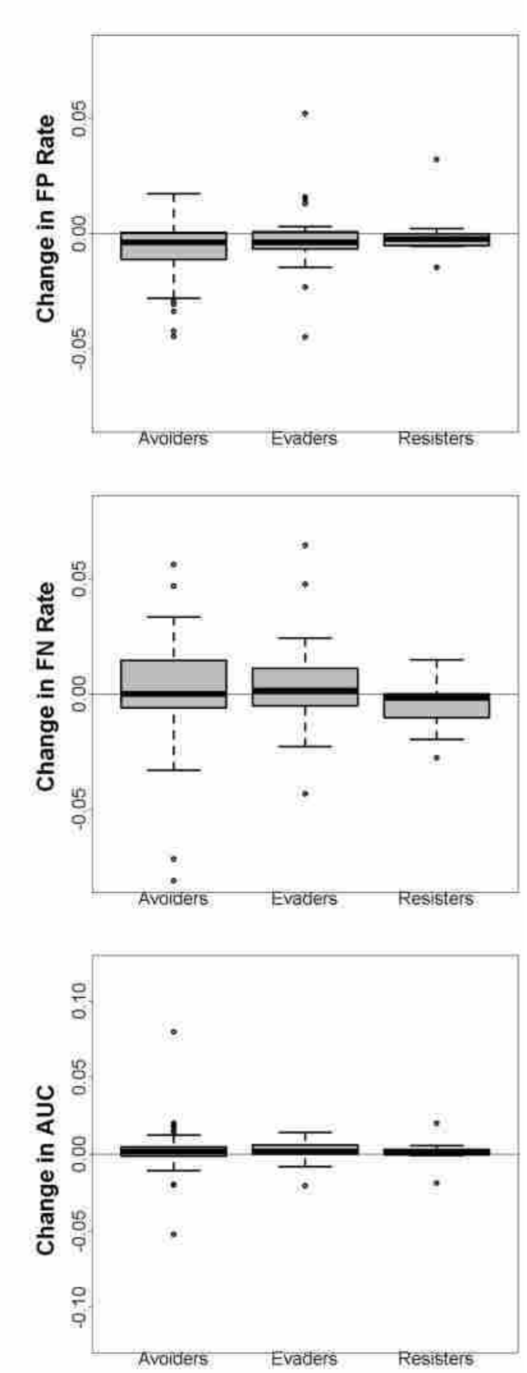


Figure B7: Change in SDM accuracy metrics from internal (t_2 models against t_2 data) evaluations for a subset of species within fire response groups when adding fire return interval departure as a predictor variable in a random forest model (RF).

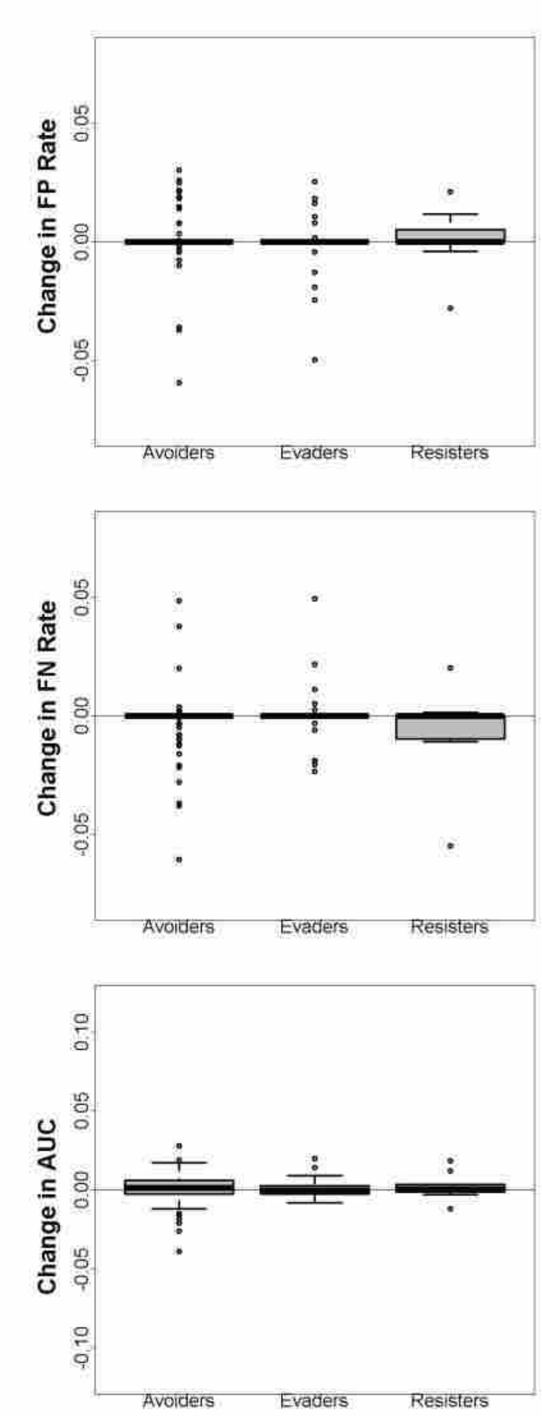
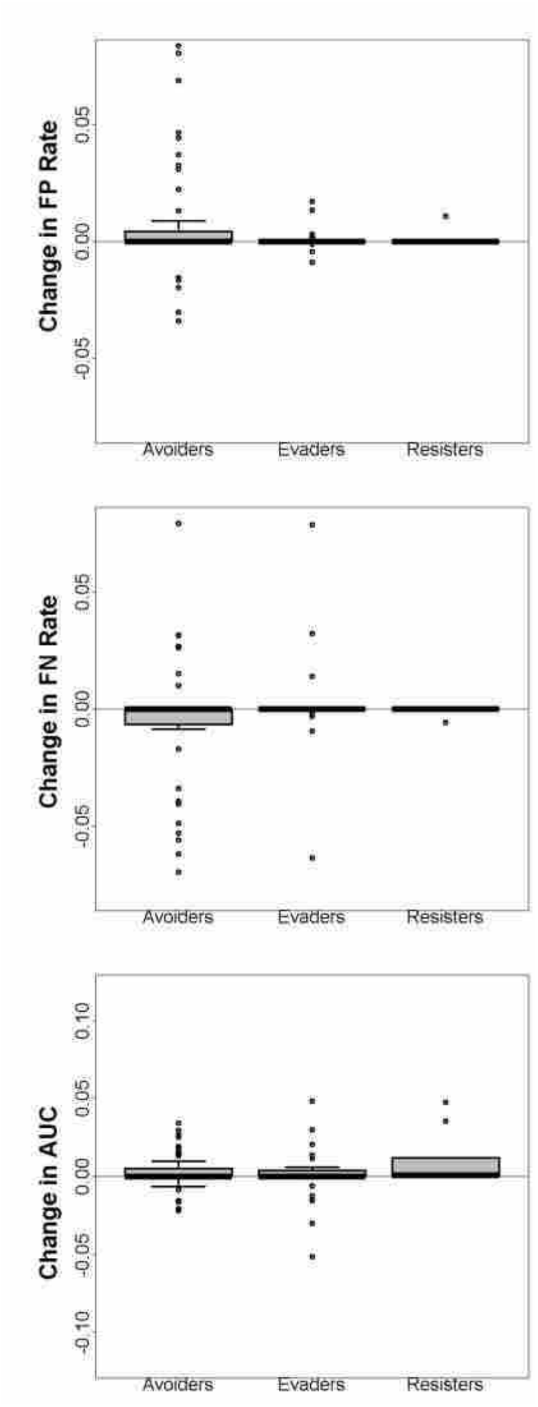


Figure B8: Change in SDM accuracy metrics from internal (t_2 models against t_2 data) evaluations for a subset of species within fire response groups when adding fire return interval departure as a predictor variable in a classification tree model (CT).



CHAPTER 3

LARGE-SCALE EVIDENCE OF DEMOGRAPHIC DIFFERENCES IN THE CLIMATIC NICHE OF WESTERN US TREE SPECIES

Crimmins, S.M., S.Z. Dobrowski, A.R. Mynsberge, and Z.A. Holden. IN PREP. Demographic niche differences suggest future range declines for western US tree species. *Formatted for PLoS ONE*

Abstract: Applications of the environmental niche concept rarely consider demographic factors such as mortality and reproduction that are the putative mechanisms for shifting species' distributions and community composition. The so-called "regeneration niche" of a species is the set of conditions under which that species can reproduce, however for long-lived species such as trees there are potentially many conditions that allow for adult survival but are not conducive to successful reproduction. Inclusion of such areas in estimates of species' niches can lead to biased estimates of environmental tolerances and optimal conditions for population growth, yet empirical data demonstrating this outcome are largely lacking. We used occurrence and demographic data from 62 tree species throughout the western United States to investigate differences in environmental conditions between locations occupied by juveniles and those occupied by adults. Adults consistently occurred in warmer maximum and minimum temperatures than did juveniles, consistent with ubiquitous temperature increases throughout our study region. Niche differences between juveniles and adults for hydrologic variables were greater as species occupied drier environments. Along all climatic gradients examined, juveniles displayed narrower niche breadth than did adults. For several gradients differences between adult and juvenile niche breadth were positively related to overall niche breadth. Differences in optimal conditions and climatic tolerances between adults and juveniles were generally unrelated to species ecological traits. Juveniles and adults had similar patterns of sensitivity to climatic variables. Niche models based on adult occurrences yielded significantly larger estimates of suitable conditions than did models based on juvenile occurrences. Our findings suggest that model projections of climate change impacts on species distributions may be biased for many long-lived sessile organisms such as trees and may overestimate the extent of areas climatically suitable for sustained populations.

Introduction

Understanding how species respond to changing environmental conditions is a central research focus of contemporary ecology [1]. Concern over the potential impacts of climate change on biota has led to widespread interest in the relationship between climatic conditions and species' geographic ranges [2]. This focus of contemporary ecological research has been facilitated by widespread acceptance of the environmental niche concept, where the geographic distribution of a species is defined by the set of environmental conditions that allow for positive population growth [3,4]. Using the niche concept as a foundation, numerous studies have built models of the "realized niche" using available species occurrence and climatic data to generate predictive models of suitable climatic conditions that can be projected based on various climate change and global emissions models [2]. The results of these models form the basis for many conservation actions and provide evidence to suggest that future climate change will have pronounced effects on existing biological systems [5,6].

For many species, the range of environmental conditions that can be tolerated may vary with life-history stage. In some cases this process, often referred to as ontogeny, results in a unique set of conditions that promote reproduction compared to conditions facilitating adult persistence. This particular phenomenon, known as "regeneration niche", was suggested as a means of describing plant community turnover [7]. According to this concept, plant seedlings are tolerant of a relatively narrow range of environmental conditions, and the occurrence of these conditions facilitates plant regeneration and ultimately community turnover. While it has been suggested that ontogeny can serve as a unifying framework for applied ecological restoration [8] there has been surprisingly little theoretical development of this topic since its introduction and few quantitative explorations of relationships between adult and juvenile species occurrences

[9,10]. Specifically, the relationship between the regeneration niche and the adult niche is largely unknown. Jackson et al. [11] provided a conceptual figure describing the hypothetical relationship between the adult and regeneration niche. In this conceptual framework, the regeneration niche is depicted as having narrower tolerances than the adult niche and having optimum conditions offset from those of adults. Although their focus was on the effects of variable environmental conditions on recruitment dynamics [11], their framework remains, to our knowledge, the only purely theoretical representation of the relationship between the adult and regeneration niche and, as such, provides an excellent starting point for examining the relationship between the two. However, their framework does not explicitly account for many of the basic facets of niche theory, which we address here. First, it is important to consider that the fundamental niche is the set of conditions that allow a species "to survive and reproduce" [4]. Thus, only those conditions supporting reproduction should even be considered as part of the fundamental niche of a species, as conditions allowing adult survival in the absence of regeneration do not meet Hutchinson's original definition. Practically speaking, the conditions supporting reproduction define the areas we would expect to support populations in the future and should therefore be the focus of predictive modeling efforts aimed at identifying future suitable climatic conditions. Second, differences in optimal conditions of the fundamental niche [4] between adults and regeneration would most likely result from active niche shifts [12] or from a lack of climatic equilibrium leading to population decline. Because it is extremely difficult to quantify the fundamental niche, and impossible to do using empirical field data [13], a more appropriate representation would be to consider optimal conditions not as those conditions which maximize demographic vital rates but the conditions under which the species is most likely to occur on the landscape. This allows for the regeneration niche to be placed in the

context of the realized niche, which is the most relevant to applied ecologists and is readily quantified from observational data.

Consider two hypothetical species, one in which the regeneration niche is similar to the adult niche and one in which the regeneration niche differs substantially from the adult niche (Figure 1). Species with a greater discrepancy between adult and regeneration niche breadth would likely exhibit higher proportions of their occupied range functioning as sinks compared to species with similar adult and regeneration niche breadths (Figure 1). This suggests that understanding differences between the adult and regeneration niche with regards to environmental tolerances could have substantial effects on population dynamics, as these differences would likely have a strong influence on spatial patterns of population growth and metapopulation dynamics [14]. Another potential issue associated with differences between adult and regeneration niches is that of differing optimal values. Considering our two hypothetical species again, for the first species there is little difference between the optimal values (peaks of the bell curves) between the adult and regeneration niches (Figure 1). For this species, estimates of optimal conditions would be similar. For species with substantially offset optimums, failing to account for ontogenetic differences could lead to poor estimates of optimal conditions for reproduction. For applications that predict the potential future range of species in which reproduction and establishment, and thus population growth, are assumed (such as climate change impact forecasts), failure to account for these ontogenetic differences could lead to costly and ineffective conservation actions. In such applications it might be more appropriate to consider only those conditions which promote regeneration, and thus more closely represent the fundamental niche [4], rather than conditions that support any individuals of the species regardless of regeneration potential. An example of such applications is environmental niche or species distribution modeling, which relate observed species occurrences to environmental data to develop predicted models of suitable conditions [2]. Often these models make no distinction between different developmental stages of an organism, and assume that all instances of species occurrence are suitable for developing predictive models of future distributions. This approach ignores the fact that regeneration may be more representative of suitable conditions while the occurrence of adult individuals is potentially representative of past conditions that have little to do with current population growth or stability.

Despite the large number of studies examining species-environment relationships, and the strong theoretical basis for the regeneration niche concept, there is relatively little empirical evidence to support the concept at large spatial scales [15]. Although ontogeny has long been a topic of interests to animal ecologists [16], it remains relatively unexplored in-situ by plant ecologists. Several researchers have suggested through modeling efforts that climatic impacts on plant reproduction may lead to large-scale contractions at trailing or lower elevation margins [17,18]. Yet most empirical evaluations of the regeneration niche have been based on small-scale experimental studies where environmental conditions are largely controlled [19]. In natural systems, the regeneration niche is often used as a theoretical mechanism for understanding localized processes such as forest gap dynamics [20] or regeneration dynamics of individual species [21]. However, there has been little effort to link these controlled or localized studies to large-scale dynamics, particularly in a changing climate. This lack of large-scale evaluations is surprising given that the regeneration niche hypothesis provides a clear mechanism for understanding climatically induced shifts in species distributions and community turnover. The few large-scale studies examining differences in position between adult trees and seedlings have focused largely on differences in geographic rather than environmental position [9,10]. These studies have found that seedlings tend to occur at higher elevations or latitudes than adults, with the strongest evidence found near the center of the range but with limited evidence for such differences at range margins [9,10,22]. However, to date no studies have focused on examining the relative differences between adult and regeneration niche characteristics, particularly at landscape scales or in the context of climate change.

The regeneration niche suggests that in a warming climate [23] we would expect areas supporting regeneration of plants to occur in cooler and more mesic environments than adults, as over time previously suitable areas for regeneration will become unsuitable yet retain adults that established themselves during periods of more favorable climate (Figure 1). It is also reasonable to expect that differences between adult and regeneration niches would be most pronounced in more harsh environments, where conditions are only marginally suitable for reproduction to begin with. This may be particularly true in a changing climate, as relict adults can still persist in areas formerly suitable for regeneration but that have now become unsuitable as local climatic conditions have changed. For example, tree seedlings have shallower root systems than adults and occur in layers of the soil that are more susceptible to drying due to evaporation [24]. Thus, we might expect tree seedlings to occupy more mesic environments than adults, particularly in regions characterized by high levels of evaporative demand. It is less clear how ontogenetic differences in niche breadth would relate to the range of conditions occupied by the species. It has been suggested that species with greater niche breadth should be generalist species that will occupy larger geographic ranges than species with narrower environmental tolerances [25]. However, empirical studies have found no such relationship between regeneration niche breadth and range size, and have suggested that plant ranges are ultimately dictated by the distribution of adults [26,27]. If this is the case we might not expect regeneration niche breadth to increase monotonically with adult niche breadth, but rather to exhibit increasing discrepancy in size relative to adult niche breadth as adult niche breadth increases.

Methods

Study Area

Our study occurred in the 11 westernmost states of the continental United States (Figure 2), an area of nearly 3,100,000 km^2. This region is characterized by steep and spatially variable climatic gradients [28]. This area is also characterized by large geographic gradients, including both the highest and lowest elevation points in the contiguous United States.

Species Occurrence Data

We used data on tree species occurrences from the USDA Forest Service's Forest Inventory and Analysis (FIA) program. FIA is a national inventory of forest resources that applies a nationally consistent sampling protocol across all land ownerships with the United States [29]. The FIA program tabulates all adult trees, defined as having a diameter at breast height (dbh) > 12.7 cm, within each sample plot. FIA also tabulates all seedlings in each subplot [29,30]. Hardwood seedlings are defined as any hardwood tree at least 30.5 cm in height with a root collar diameter < 2.5 cm whereas conifer seedlings are defined as any conifer tree that is at least 15.2 cm in height with a root collar diameter < 2.5 cm. Although not strictly measurements of regeneration, we considered these size class designations as a suitable proxy for age and regeneration. We aggregated all subplot data into a single data point representing the entire sampling plot following previous studies that used FIA data [10,22]. Hereafter we refer to seedlings as juveniles. We retained data only from FIA plots sampled since 1999 to ensure that our data represented current forest structure. Year of annual inventory initiation and sampling intensity varies among states, therefore the exact years in which sampling occurred and number of sampled plots varies among states within our study area (Table 1), leaving a total of 33,665 plots. We limited our analyses to species with at least 30 occurrences of both adults and juveniles to ensure adequate statistical representation of both the adult and regeneration niches, and to species with distributions restricted to the western half of North America. We categorized species based on a suite of ecological traits provided by the USDA Natural Resource Conservation Service; these included: fire resistant (yes/no), fire tolerance (low/medium/high), growth rate (slow/moderate/rapid), drought tolerance (low/medium/high), lifespan (short/moderate/long), and seed spread rate (slow/moderate/rapid).

Climate Data

We considered a set of four bioclimatic variables (niche axes) we hypothesized would influence tree distributions. We focused on long-term means rather than anomalies, using monthly normals from the period 1976–2005 at an 800-m resolution. Bioclimatic values at sampling plot locations were generated using a bilinear interpolation and a first-order neighborhood as provided by US Forest Service Spatial Data Services. The variables were minimum temperature (T_{min}) and maximum temperature (T_{max}), from the Parameter-elevation Regression on Independent Slopes Model (PRISM; [31]), and two hydrologic variables known to influence vascular plant distributions in our study region [32,33]. These variables were actual evapotranspiration (AET), and climatic water deficit (DEF) [28]. We considered these variables to represent relevant axes of the realized niche [4]. Three of our variables (T_{min}, T_{max}, DEF) could be considered proximate causes of mortality in plants, while AET is largely reflective of productivity or growth potential [34,35]. Both AET and DEF are integrated variables that account for multiple limiting factors to plants including light, water, and energy [32,33].

Statistical Analyses

Rather than relying on smoothed response functions of optimums to represent niche position, we used the median and mean climatic values from occupied plots for each species and age-class to ensure that species lacking unimodal responses were still included. Previous research examining geographic niche position has found little difference between mean, median, and smoothed optimums [9], thus we felt this approach was justified. We evaluated whether individual species exhibited differences in adult and juvenile niche positions using *t*-tests of climatic values from occupied plots between the two age classes. We tested for community level differences in niche positions between adults and juveniles using paired Wilcoxon signed-rank test median climatic values of sites occupied by adults and seedling of each species. We used medians for this analysis to avoid the influence of outlying values on species-level estimates of niche position. We defined juvenile and adult niche breadth as the range of values from occupied plots for each species along each climatic axis. Paralleling our community level analysis of niche position, we compared niche breadth between juveniles and adults along each climatic axis using paired Wilcoxon signed-rank test of the range of occupied values between adults and juveniles of each species. We evaluated the effects of species traits on differences between adult and juvenile niche position and niche breadth using a suite of Kruskal-Wallis tests with a multiple comparisons procedure [39].

We developed a suite of linear models to determine if differences between adult and juvenile niches were related to niche characteristics. For each climatic axis we modeled differences between adult and juvenile niche position as a function of adult niche position. We used a similar approach for niche breadth, modeling the differences between adult and juvenile niche breadth as a function of total niche breadth.

To evaluate the relative sensitivity of juveniles and adults to different climatic parameters (i.e. plasticity), we computed standardized z-scores for each niche axes across our entire dataset. We then calculated the range of z-scores from occupied sites for each species along each niche axis, where higher values indicate a greater range of environmental conditions tolerated. Thus, species exhibiting a higher z-score range would be considered to have lower sensitivity because they occur in a wider range of conditions. We compared sensitivity among niche axes by visually examining boxplots of z-score ranges.

Niche Models

We developed predictive niche models for adults and juveniles of each species using generalized linear models (GLM). We included all four climatic variables in our models, using a step-wise variable selection procedure based on minimization of AIC scores [36]. Using this procedure, each variable could be dropped, fit as a linear predictor, or a second order polynomial. We randomly selected 75% of our data to build models, using the remaining 25% to evaluate the accuracy of our models. We evaluated model accuracy using the area under the ROC curve (AUC), a metric commonly applied to evaluate the accuracy of niche models when presence and absence data are available [37]. We excluded species for which either adult or juvenile models yielded AUC < 0.8 to reduce spurious effects resulting from inaccurate models. For each remaining species we converted our predicted probability of occurrence to binary presence/absence predictions using the species prevalence as a threshold [39]. For each species we then calculated the total area within our study area predicted as containing adults and the total area predicted to contain juveniles.

Because species' range-filling is limited by dispersal capacity [40] we also compared predicted areas of adult and juvenile occurrence within extant ranges as a more conservative estimate of the potential effects of ontogeny on SDM predictions. We attained range maps for most species from the USGS Geosciences and Environmental Change Science Center (http://esp.cr.usgs.gov/data/little/). Species for which we could not attain range maps were excluded from this analysis, leaving 53 species. We then constrained our projections of adult and juvenile occurrence to the areas within the range extents identified by the species' range maps to identify patterns of predicted occupancy within the range of each species.

Results

Of the 62 species in our dataset, 46 exhibited a statistically significant difference in niche positions between adults and juveniles along at least one climatic axis (Table 2). Statistically significant differences in adult and juvenile niche positions were found for 29, 27, 27, and 24 species along the AET, T_{min}, T_{max}, and DEF climatic axes respectively (Table 2). Along each climatic axis we found evidence of juveniles having niche positions greater or less than adults depending on the individual species (Table 2). Of the species that exhibited significant differences in niche position between adults and juveniles, the proportion exhibiting higher AET values for adults was similar to the proportion exhibiting AET values for juveniles (χ^2 = 0.276 ,

$P = 0.56$). A greater proportion of species had adults with higher T_{max} ($\chi^2 = 18.963$, $P < 0.001$), T_{min} ($\chi^2 = 14.519$, $P < 0.001$), and DEF ($\chi^2 = 10.083$, $P = 0.002$) niche positions than juveniles.

At the community level we found strong evidence for widespread differences in niche position between all juveniles and adults along temperature axes, with juvenile trees on average occurring at significantly ($P < 0.001$) lower maximum ($\Delta T_{max} = 0.21$°C) and minimum ($\Delta T_{min} = 0.28$°C) temperatures than adults. We also found community level evidence for differences in niche position for DEF ($P = 0.006$). However, community level values for AET did not differ between adults and juveniles ($P = 0.45$). Community level metrics of niche breadth indicated that juveniles had significantly narrower ($P < 0.001$) niche breadth than adults along each climatic axis. Differences between adult and juvenile niche position (Appendix I) and breadth (Appendix II) were generally unrelated to species traits, with only five of a possible 48 comparisons showing significant ($P < 0.05$) effects of species traits.

The position of the species-specific niche was unrelated to the differences between adult and juvenile niche positions along T_{min} and T_{max} axes; that is, a higher niche position for juveniles or adults did not indicate a larger or smaller difference in niche position (Figure 3). However, differences along AET and DEF axes were significantly ($P < 0.05$) related to niche position, with greater differences (adult-juvenile) in niche position occurring for species occurring at higher niche position values (Figure 3). Along DEF, T_{min}, and T_{max} axes differences between adult and juvenile niche breadth were significantly ($P < 0.05$) related to species niche breadth, with greater differences occurring for species with larger niche breadth (Figure 4). There was no statistical relationship between difference in adult and juvenile niche position for AET and species niche breadth (Figure 4).

Sensitivity to niche variables was similar between juveniles and adults (Figure 5). Tree species exhibited high sensitivity to DEF, T_{min}, and T_{max} with relatively little variability among species. Conversely, trees exhibited generally low sensitivity to AET, although this relationship exhibited greater variation among species than did other climatic axes (Figure 5).

Four species were removed from our niche model analysis due to poor model fit (AUC < 0.8). Niche models for the 58 remaining species were highly accurate, as measured by AUC, for both adults ($\bar{x} = 0.937$, 95% CI = 0.926 – 0.948) and juveniles ($\bar{x} = 0.925$, 95% CI = 0.913 – 0.938), although accuracy of models for juveniles was significantly lower than those for adults ($P < 0.001$, $t = 3.669$, $df = 57$, paired *t*-test). For 46 of the 58 species (79.3%) the estimated amount of suitable habitat was greater for adults than for juveniles. For these species, the total amount of area predicted to be occupied by adults was on average 30.8% greater than the area predicted to be occupied by juveniles. When averaged across all 58 species, this value dropped to 19.7%, but was still highly significant ($P < 0.001$, $t = 4.993$, $df = 57$, paired *t*-test).

Of the 53 species for which we acquired range maps, 48 (90.6%) had a greater proportion of the extant range predicted to contain adults compared to juveniles. For these species, the total amount of area predicted to be occupied by adults was on average 17.7% greater than the area predicted to be occupied by juveniles. When averaged across all 53 species for which we had range maps, this value dropped to 15.6%.

Discussion

Ontogenetic niche shifts have been widely explored and documented for animals [41], but particularly for long-lived plant species such as trees, the in-situ differences between adult and seedling niches due to ontogenetic changes are poorly understood. We found strong evidence for juveniles occurring in cooler locations than adults regardless of niche position along maximum and minimum temperature axes, and more mesic conditions along the climatic water deficit axis. This finding is consistent with predictions from the regeneration niche concept in a warming climate and would suggest that species distributions in this region may be tracking isoclines of temperature. Our study region has experienced widespread and largely ubiquitous increases in temperature during the 20th century [28], thus our finding of niche shifts along temperature axes is not entirely surprising. Studies that have found relatively consistent differences between adult and seedling geographical position have also attributed these shifts to climate warming [9], whereas studies that have found no such differences suggest that species failing to exhibit differences in seedling and adult distributional patterns are more threatened by climate change than those species that are shifting towards cooler environments [10]. Our findings support the conclusion that climate change can lead to discrepancies in the conditions experienced by adult and juvenile plants, particularly in relation to temperature and drought stress.

Unlike temperature, niche differences along hydrologic axes were a function of niche position. In an examination of 23 tree species from France, Bertrand et al. [42] also found asymmetric niche shifts along a niche axis, observing niche contractions in areas of high nutrient availability and niche shifts in nutrient poor areas. We found that for species occurring in areas with high levels of AET and DEF, juveniles were more likely to occur in locations with lower evaporative demands (i.e. lower water stress), while the opposite was true of species inhabiting areas of low water stress (Figure 3). We would expect that species occurring in areas of high water stress to have juveniles occur in more mesic environments due to their increased susceptibility to drought compared to adults [34]. Conversely, we would not expect such shifts in areas with low water stress, as juveniles in these areas are likely not limited by moisture availability and thus there would be no benefit to establishing in areas with further reduced water stress, and previous studies have demonstrated that the relative importance of climate in structuring species ranges decreases as one moves towards more mesic environments [43]. Previous work from a portion of our study area found unexpected downhill shifts in plant distributions and suggested that these shifts were the result of species tracking optimal hydrologic conditions, and that temporal shifts in geographic position were a function of the geographic area occupied [44,45]. Our results in this study mimic these previous finding and indicate that shifts in geographic or environmental space are likely contingent on the environmental conditions occupied by the species, and not solely on the magnitude and direction of climate change.

We found widespread evidence of juveniles occupying a narrower range of climatic conditions than adults, consistent with theoretical predictions from the regeneration niche concept [11]. Along three of the four niche axes examined, differences between adult and juvenile niche breadth were greater for species with greater niche breadth. For most species it is reasonable to assume that the majority, if not all, of the niche breadth is accounted for in the adult life stage (Figure 1). Thus, species with the greatest niche breadth may be the most prone to overestimates of resilience to climate change, as these species are likely to display the greatest discrepancy between the environmental conditions occupied by adults and the conditions suitable for reproduction. There is conflicting theoretical [25] and empirical [26] work on the relationship between niche breadth and geographic range size. Previous work has suggested that niche breadth decreases with increasing resource availability [46]. Therefore species with greater niche breadth may be expected to occur in resource limited (i.e. marginal) environments, precisely those that will be most severely impacted by climate change. Therefore, our results suggest that species with greater discrepancies between adult and regeneration niche breath, and thus the greatest potential for underestimating risk of climate change from niche model projections, are the most likely to experience detrimental effects of climate change. Given the lack of empirical evidence supporting a relationship between niche breadth and range size [26,27], this indicates that the presence of a large geographic range should not necessarily be taken as a sign of resilience to climate change. However, we caution that a great deal of additional research is needed to understand the factors influencing niche breadth and its relationship to ontogeny and susceptibility to climate change.

Relative sensitivity to climatic variability was similar between adults and juveniles (Figure 7). We found that tree species generally exhibited high sensitivity to temperature, which may largely explain our finding of consistent niche shifts in relation to these niche axes. The effects of acute stressors on plant survival are well documented and provide a mechanistic explanation for our findings [34]. Plants can exhibit a wide variety of adaptations for coping with temperature and drought stress, which often serve as proximate causes of mortality in plants [34]. Such stressors, represented in our study by T_{max}, T_{min}, and DEF, are often considered mechanistic determinants of species ranges [47]. Thus, we would expect that plant species would generally show high sensitivity to such variables. Conversely, AET is more strongly related productivity [35] and growth potential within the range rather than geographic extent of the range. Because of this we would not expect patterns of plant occurrence, as opposed to growth or abundance, to be highly sensitive to a variable such as AET. This is supported by the low values and lack of variability in sensitivity to temperature and DEF exhibited in our study relative to AET. The consistency of the relative pattern of sensitivity between adults and juveniles is encouraging, as this suggests that ontogenetic niche shifts may not be extreme enough to alter the relative influence of climatic factors on specific life-stages. However, it is important to note that our climate data were at a relatively coarse scale (800 m) that may not entirely capture localized variability in climate [48] that could drive site-specific regeneration dynamics. Even so, the consistency we found among species with largely differing ecological requirements suggests that our results are robust to this scaling issue.

Most applications of environmental niche models develop projections of potentially suitable habitat without regard to regeneration potential [e.g. 2]. When used in this manner, these models fail to differentiate between areas suitable for regeneration, and thus long-term population viability, and areas of simple occupancy. In doing so, these models may be limited in their utility for predicting climate change impacts and developing robust conservation strategies. Our niche model projections suggest that estimates of species occupancy developed without regards to regeneration potential will be systematically larger than demographically informed estimates that provide spatially explicit predictions of areas suitable for long-term population viability by supporting regeneration. This pattern was evident for most species, indicating the potential for substantial underestimation of extinction risk due to climate change. This was particularly true for geographically isolated subpopulations or populations at the range margins (Figure 6). These areas likely represent the environmental conditions at the margins of the environmental niche, which in our theoretical model area those areas beyond the range of conditions suitable for regeneration but that still contain adults (Figure 1). Even though most predictive models are designed to most accurately model the mean response, our results support the idea that reduced niche breadth for juveniles can result in constricted geographic predictions of climatically suitable area.

In general we found that species ecological traits had little effect of niche differences between adults and juveniles. It has been suggested that differential adaptations to climate can lead to different levels of climatic dependence for plant reproduction [15]. Although we did not find evidence to support such theories, our results do not preclude species traits from having substantial effects on ontogeny. The traits we used to categorize our study species were not developed specifically to be relevant to our study or the climatic axes we used. It is possible that traits more directly linked to mechanistic processes governing reproduction may be directly relevant, as several studies have linked species traits to differential responses to climate change [49-51]. For example, we did not explicitly account for specific regeneration strategies (e.g. pulsed regeneration) that could have influenced our results. Given that our analyses were limited to a single period in time, we may not have captured regeneration pulses for species that exhibit such reproductive strategies. Further developments of mechanistic links between climate and plant distributions are needed to better understand the potential for species trait effects on ontogeny.

Conclusions

We found strong evidence to support many of the theoretical predictions arising from the regeneration niche concept including different niche positions between adults and juveniles, and reduced niche breadth for juveniles (Figure 1). Both findings have major implications for predicting the dynamics of species distributions under climate change. There is currently great interest in using correlative species distribution models to predict the amount and distribution of suitable environmental conditions under future climatic scenarios [2]. These models are often based on large-scale species occurrence data and typically ignore any ontogenetic differences in environmental tolerances as life-stage specific species occurrence data are often unavailable at such extensive spatial scales. Our findings of differing niche positions and reduced niche breadth for juveniles across such an extensive spatial scale suggests that such modeling efforts may 1) inaccurately represent optimal conditions for reproduction and 2) overestimate the range of conditions in which reproduction will occur. The former could result in accurate predictions of potential distributions, while the latter could results in underestimates of range loss, both of which were evident in our niche model predictions. Although numerous studies have addressed the impacts of modeling approach [52,53], input data [54], and climatic scenario [55] on prediction accuracy from these models, to date relatively little effort has been made to quantify the effects of ontogenetic niche differences despite their clear importance for range shifting species. Although alternative mechanisms could affect the relationship between climate and the occurrence of plant regeneration [e.g. 56], the consistency of our results across such an extensive geographic region and large set of species suggests a ubiquitous explanation such as the regeneration niche hypothesis. Future efforts should focus on quantifying in greater detail the effects of ontogenetic niche differences on predictions of species distributions and, more specifically, on predictions of areas suitable for reproduction and population growth.

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Author Contributions

Conceived the research: SD, ZH, and SC. Acquired the data: SC and SD. Performed the analyses: SC and AM. Wrote the paper: SC, SD, AM, and ZH.

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Figure 1: Theoretical representation of the relationship between the adult niche, regeneration niche, and potential population growth rate for two hypothetical species with similar adult niches. For the first species, the regeneration niche is nearly as wide as the adult niche (A), resulting in a large proportion of occupied areas exhibiting the potential for positive population growth ($\lambda \geq 1$). For the second species, the regeneration niche is much narrower relative to the adult niche (A), resulting in a greater proportion of occupied sites functioning as sinks ($\lambda < 1$). In each case adults have similar responses and tolerances to climate, thus differences in overall population growth rate and viability are driven by characteristics of the regeneration niche. As directional climate change occurs (B), species with narrower regeneration niches compared to adult niches will exhibit greater demographic disequilibrium and proportion of occupied sites with $\lambda < 1$.

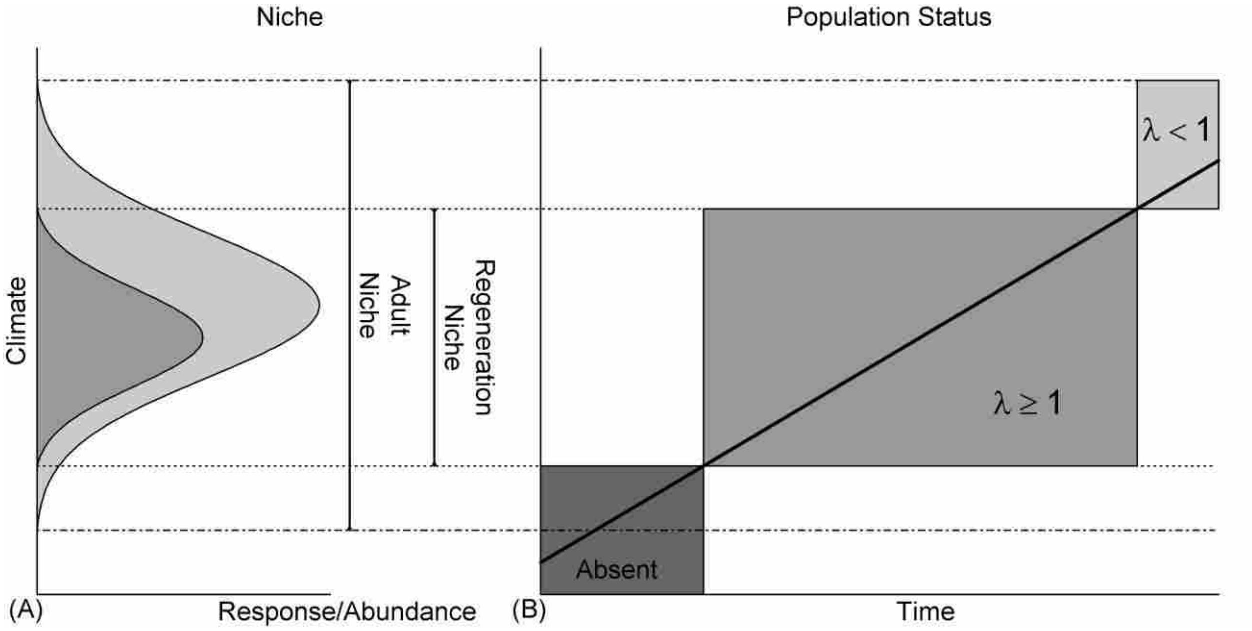
Figure 2: Map of study area.

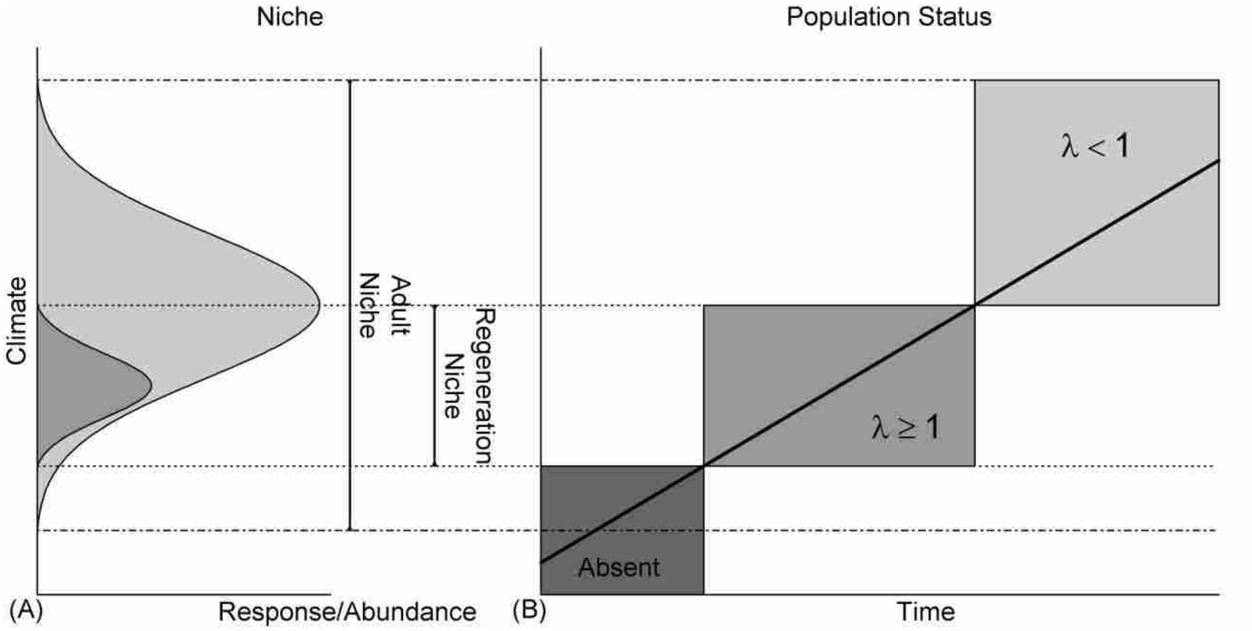
Figure 3: Scatterplots of differences in niche position between adults and juveniles (adult niche position – seedling niche position) versus adult niche position for 64 tree species along four niche axes. Panels are A) AET, B) DEF, C) T_{min}, and D), T_{max}. Solid and dashed red lines are predictions and 95% confidence intervals from a linear model. Model was significant ($P < 0.05$) for AET and DEF (panels A and B). Model significance was unchanged when species identified as statistical outliers (Bonferroni test) were removed. Horizontal black lines represent 0, or no differences between adult and juvenile niche position. Values > 0 along y-axes indicate higher values for adults compared to juveniles.

Figure 4: Scatterplots of differences in niche breadth between adults and juveniles (adult niche breadth – juvenile niche breadth) versus total niche breadth for 64 tree species along four niche axes. Panels are A) AET, B) DEF, C) T_{min}, and D), T_{max}. Solid and dashed red lines are predictions and 95% confidence intervals from a linear model. Model was significant ($P < 0.05$) for DEF, T_{min}, and T_{max} (panels B, C, and D). Horizontal black lines represent 0, or no differences between adult and juvenile niche breadth. Values > 0 along y-axes indicate larger niche breadth for adults compared to juveniles.

Figure 5: Boxplots of z-score range for 62 tree species along four niche axes for sites occupied by adults (A) and juveniles (B). Wider boxplots indicate greater variation among species in sensitivity to a given niche axis.

Figure 6: Predicted suitable area for A) adult *Acer glabrum*, B) juvenile *Acer glabrum*, and C) areas where adults are predicted to occur in the absence of juveniles. *A. glabrum* is widespread in our study area but displays a highly patchy extant distribution. Areas predicted to contain adults but no juveniles occur primarily at range margins or in small, isolated patches.


Niche
Population Status
Climate
Adult Niche
Regeneration Niche
λ < 1
λ ≥ 1
Absent
(A)
Response/Abundance
(B)
Time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Population Status
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Adult Niche
Regeneration Niche
λ < 1
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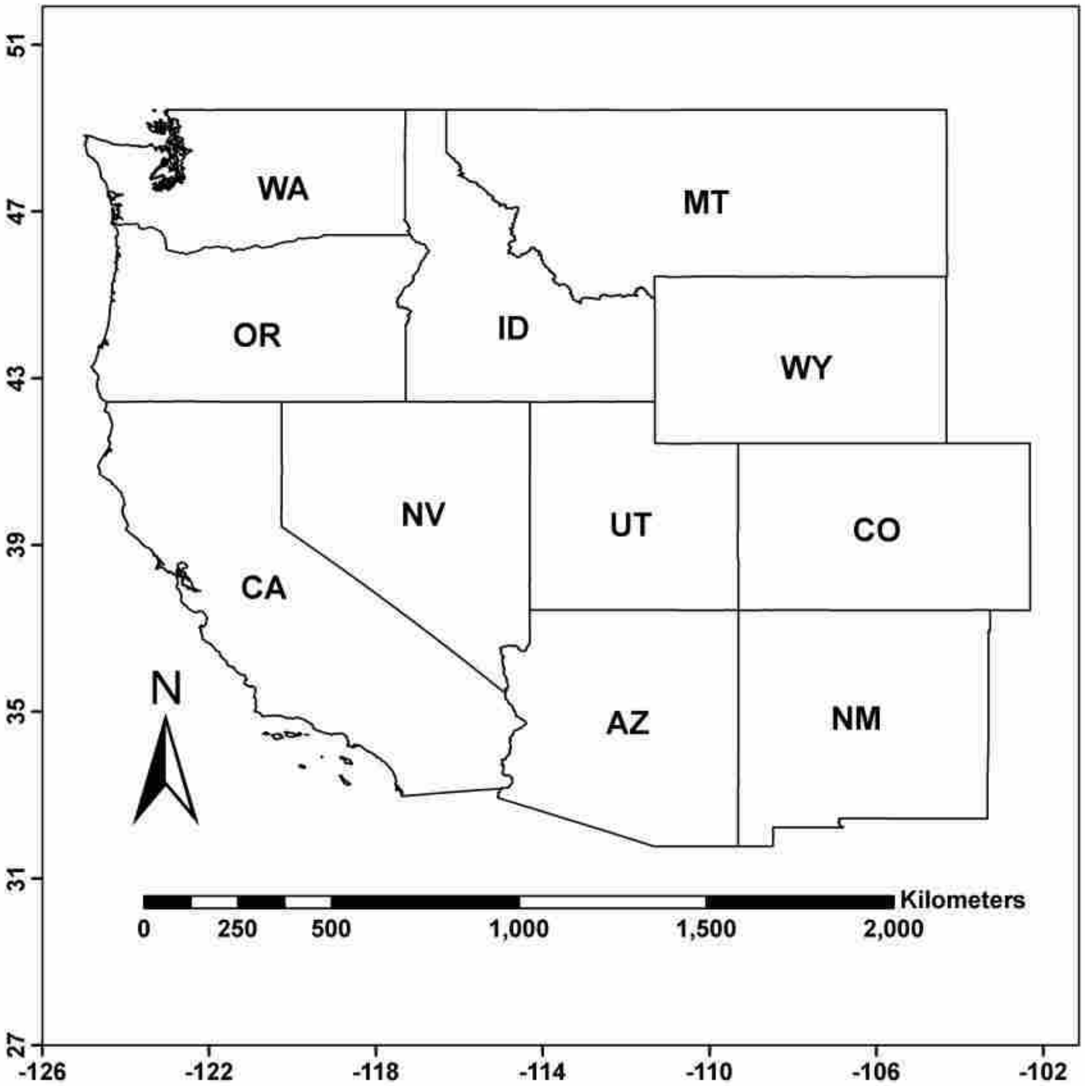
Absent
(A)
Response/Abundance
(B)
Time


WA
MT
OR
ID
WY
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UT
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CA
AZ
NM
N
Kilometers
0
250
500
1,000
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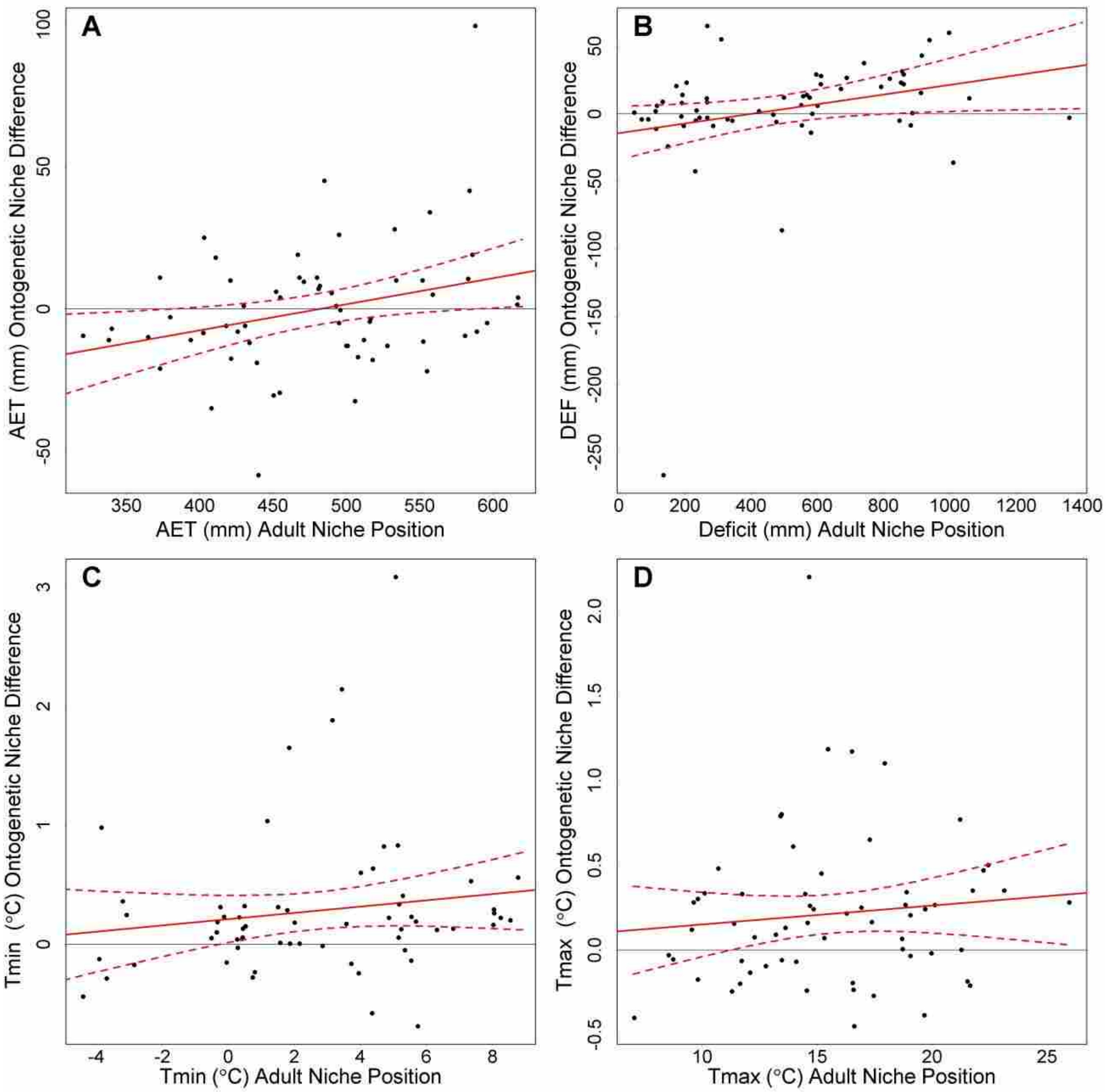
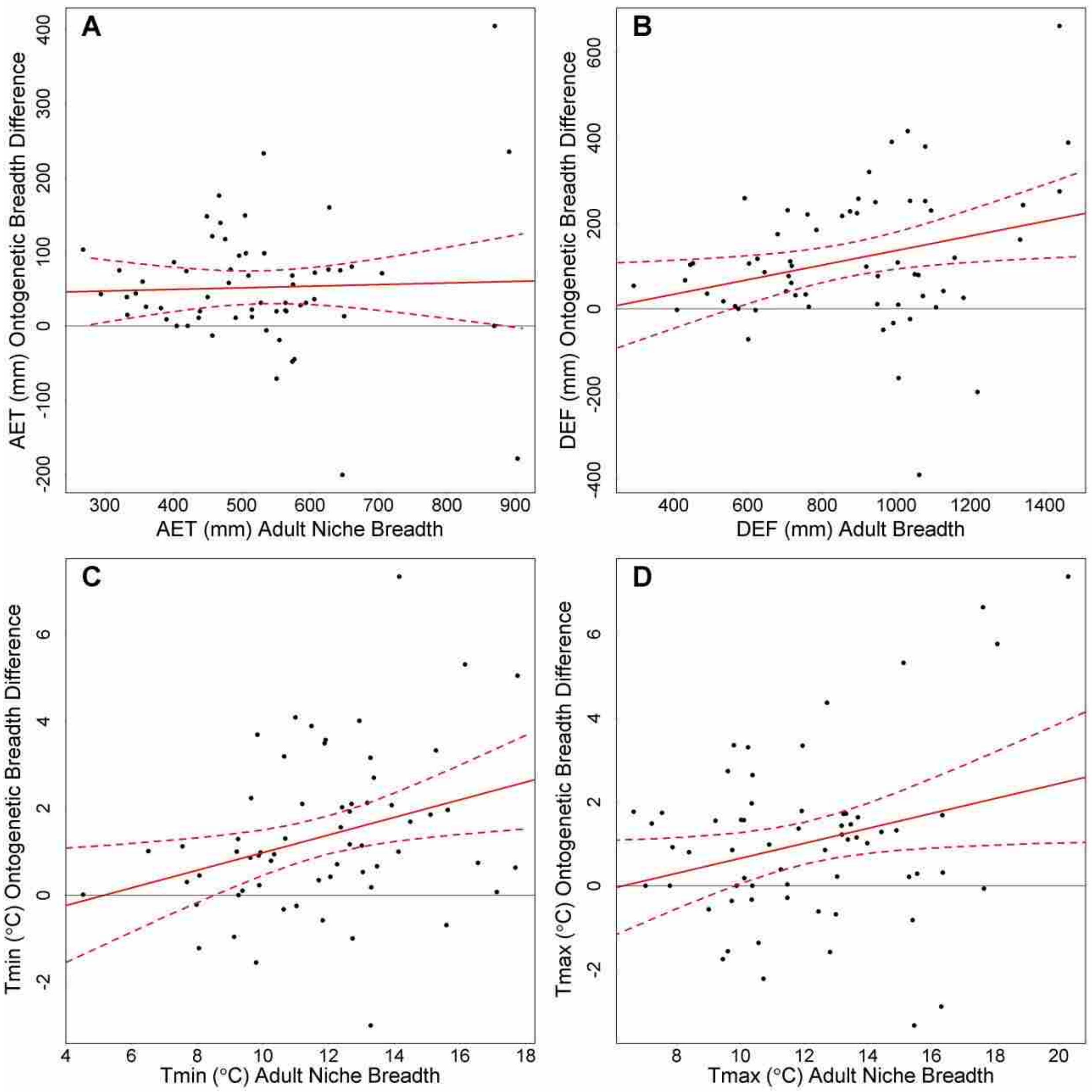
-118
-114
-110
-106
-102


A
AET (mm) Ontogenetic Niche Difference
AET (mm) Adult Niche Position
100
50
0
-50
350
400
450
500
550
600
B
DEF (mm) Ontogenetic Niche Difference
Deficit (mm) Adult Niche Position
50
0
-50
-100
-150
-200
-250
0
200
400
600
800
1000
1200
1400
C
Tmin (°C) Ontogenetic Niche Difference
Tmin (°C) Adult Niche Position
3
2
1
0
-4
-2
0
2
4
6
8
D
Tmax (°C) Ontogenetic Niche Difference
Tmax (°C) Adult Niche Position
2.0
1.5
1.0
0.5
0.0
-0.5
10
15
20
25


A
AET (mm) Ontogenetic Breadth Difference
-200
-100
0
100
200
300
400
300
400
500
600
700
800
900
AET (mm) Adult Niche Breadth
B
DEF (mm) Ontogenetic Breadth Difference
-400
-200
0
200
400
600
400
600
800
1000
1200
1400
DEF (mm) Adult Breadth
C
Tmin (°C) Ontogenetic Breadth Difference
-2
0
2
4
6
4
6
8
10
12
14
16
18
Tmin (°C) Adult Niche Breadth
D
Tmax (°C) Ontogenetic Breadth Difference
-2
0
2
4
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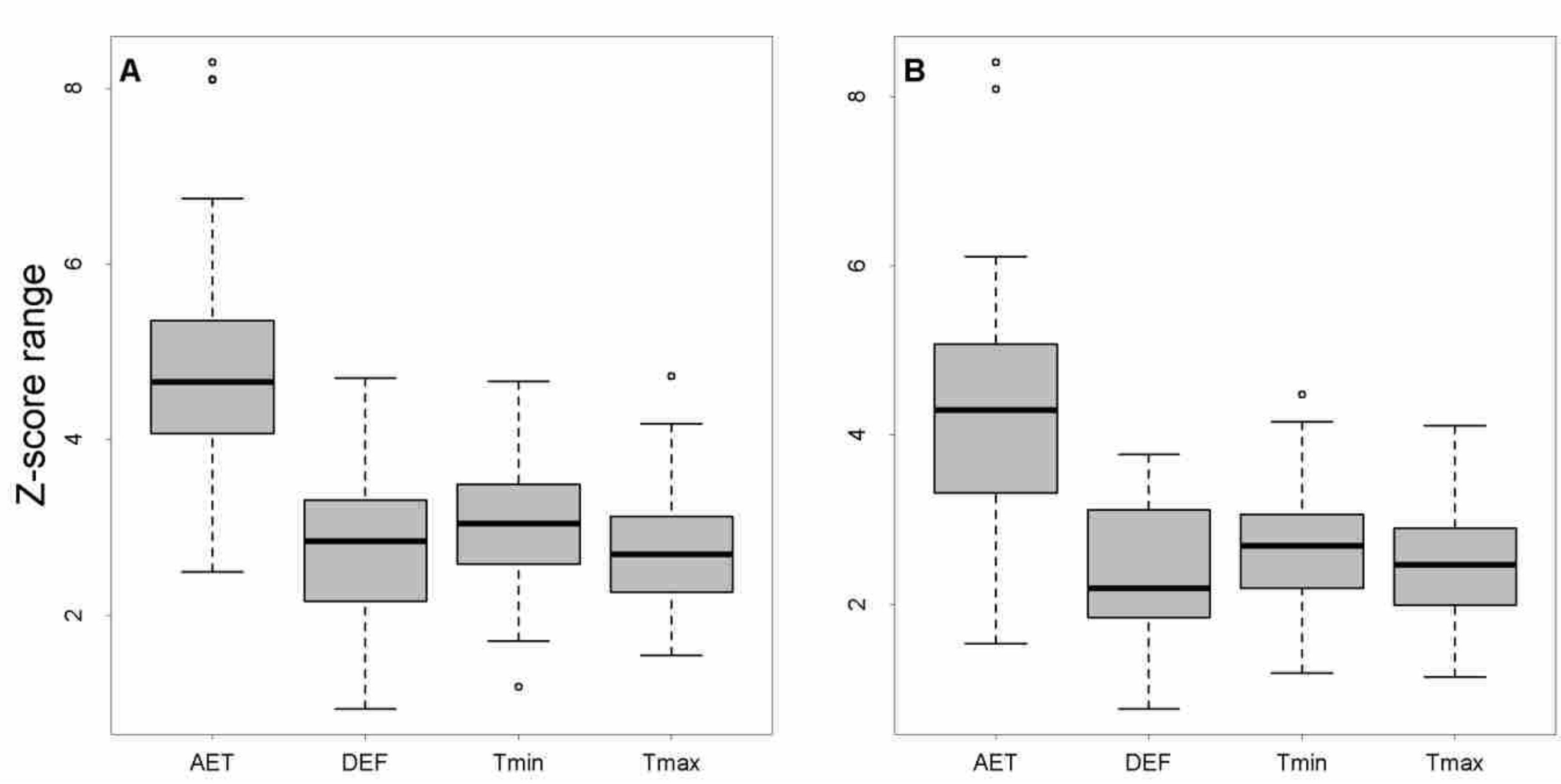
10
12
14
16
18
20
Tmax (°C) Adult Niche Breadth


A
B
Z-score range
2
4
6
8
AET
DEF
Tmin
Tmax

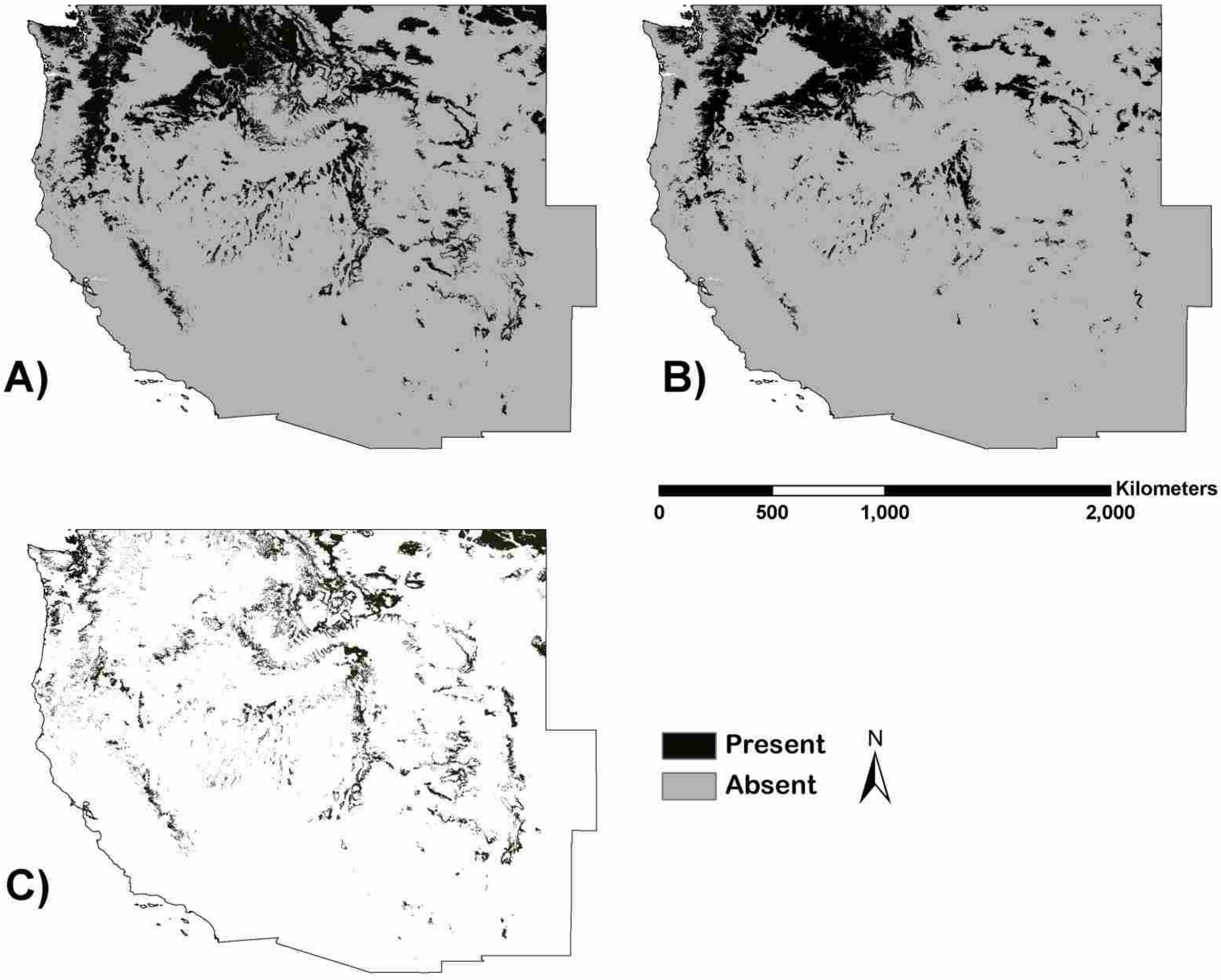

A)
B)
C)
Kilometers
0
500
1,000
2,000
Present
Absent
N

Table 1: Sampling duration and effort within each state.

State	Years	N plots
Arizona (AZ)	2001 – 2009	2913
California (CA)	2002 – 2011	5558
Colorado (CO)	2002 – 2009	3153
Idaho (ID)	2004 – 2009	2234
Montana (MT)	2003 – 2009	3097
Nevada (NV)	2004 – 2005	411
New Mexico (NM)	1999	2542
Oregon (OR)	2002 – 2011	5167
Utah (UT)	2000 – 2009	3224
Washington (WA)	2002 – 2011	3385
Wyoming (WY)	2000	1981

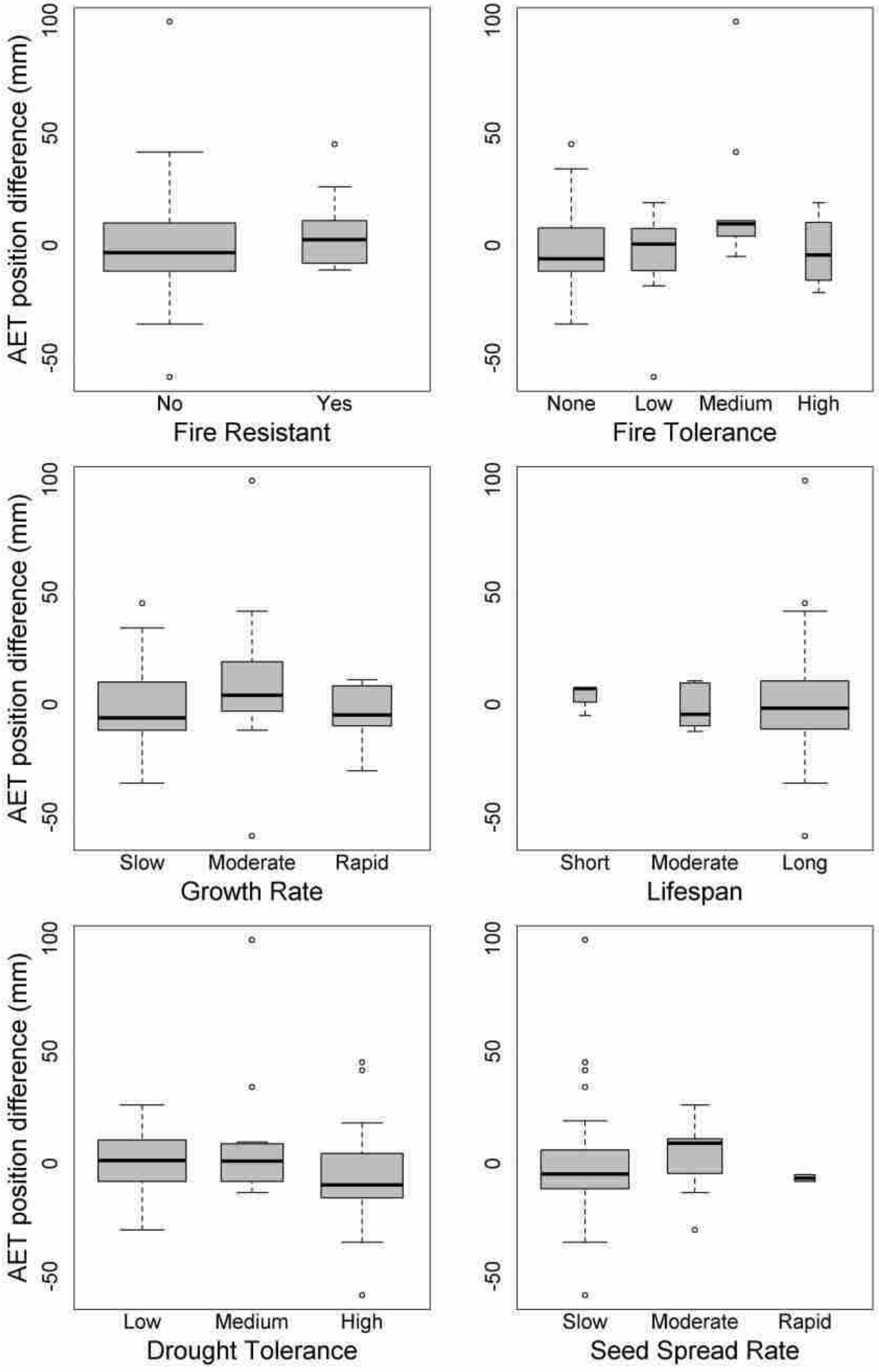
Table 2: Niche positions (mean values of occurrences) for 62 tree species along four climatic niche axes. Values highlighted in grey indicate significant ($P < 0.05$) differences based on *t*-test.

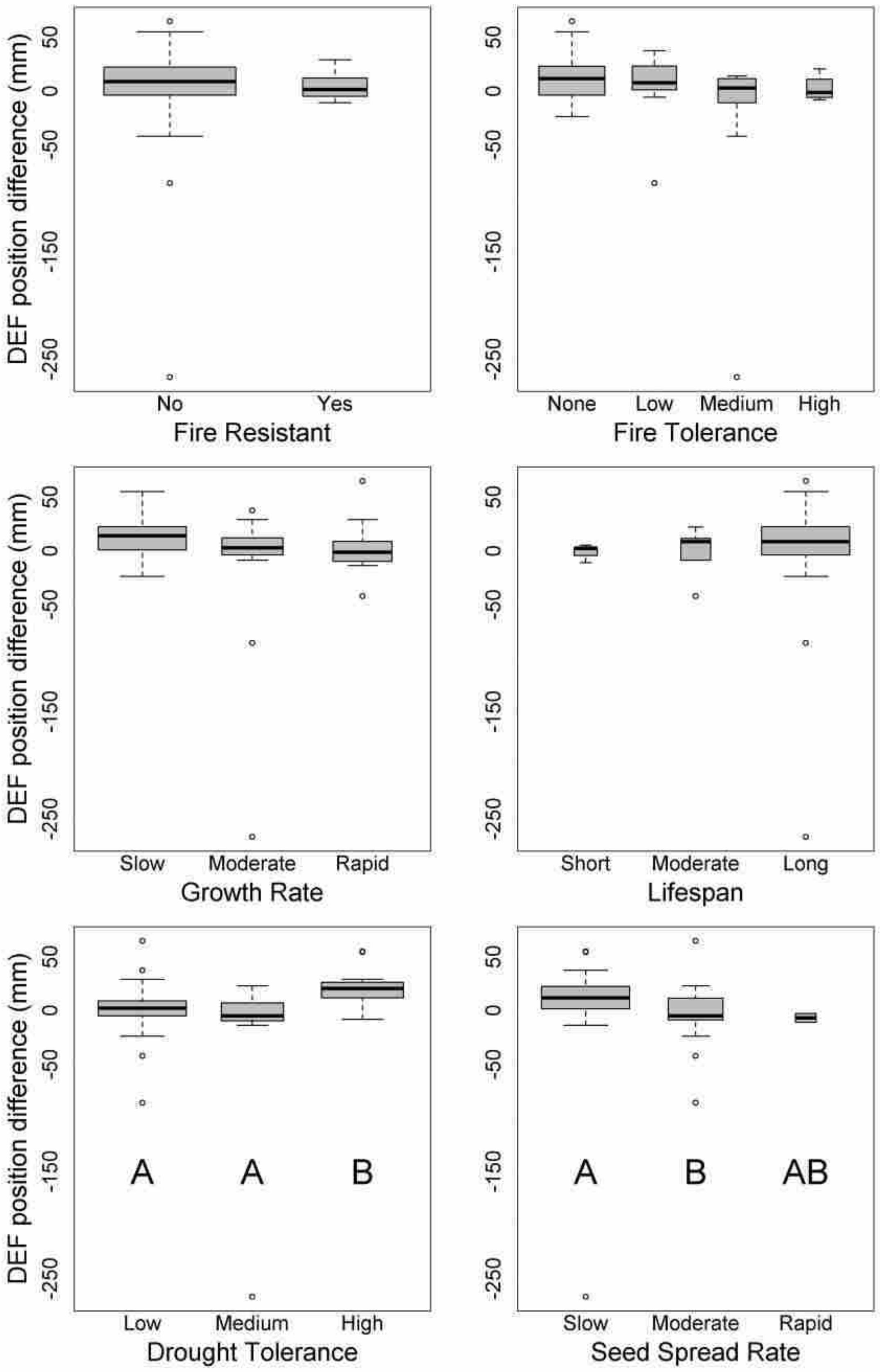
	AET (mm)		DEF (mm)		T_{min} (°C)		T_{max} (°C)	
Species	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Abies amabilis	467	448	89	93	1.5	1.2	10.7	10.2
Abies concolor	482	474	476	482	0.7	1.0	14.1	14.2
Abies grandis	493	492	235	233	0.5	0.4	12.3	12.2
Abies lasiocarpa	418	424	192	178	-3.7	-3.4	8.6	8.6
Abies lasiocarpa arizonica	533	505	189	191	-3.8	-4.8	9.8	9.5
Abies magnifica	403	411	467	467	0.4	0.4	12.8	12.9
Abies procera	496	497	115	109	1.9	1.9	11.3	11.5
Abies shastensis	452	446	268	271	-0.1	-0.4	11.7	11.9
Acer glabrum	471	462	266	255	0.8	1.0	12.1	12.2
Acer grandidentatum	481	474	424	422	0.3	0.1	13.2	13.1
Acer macrophyllum	583	573	231	274	5.2	5.1	16.6	16.8
Aesculus californica	440	499	861	832	8.0	7.8	21.7	21.9
Alrus rubra	596	601	113	124	5.2	5.1	15.3	15.3
Arbutus menziesii	559	554	601	595	5.5	5.7	18.7	18.7
Calocedrus decurrens	517	520	553	562	3.7	3.9	16.6	16.7
Cercocarpus ledifolius	380	383	552	545	-0.2	-0.6	13.5	13.5
Chamaecyparis nootkatensis	421	411	69	73	0.5	0.2	9.6	9.4
Chrysolepis chrysophylla	584	543	329	333	4.7	3.9	16.5	15.4
Cornus nuttallii	586	567	493	579	4.9	4.6	17.5	17.7
Fraxinus latifolia	581	591	267	259	5.7	5.5	17.4	17.2
Juniperus deppeana	506	539	849	854	2.9	2.9	19.1	19.1
Juniperus monosperma	373	394	882	891	2.2	2.2	18.7	18.6
Juniperus occidentalis	340	347	610	588	0.3	0.3	14.7	14.4

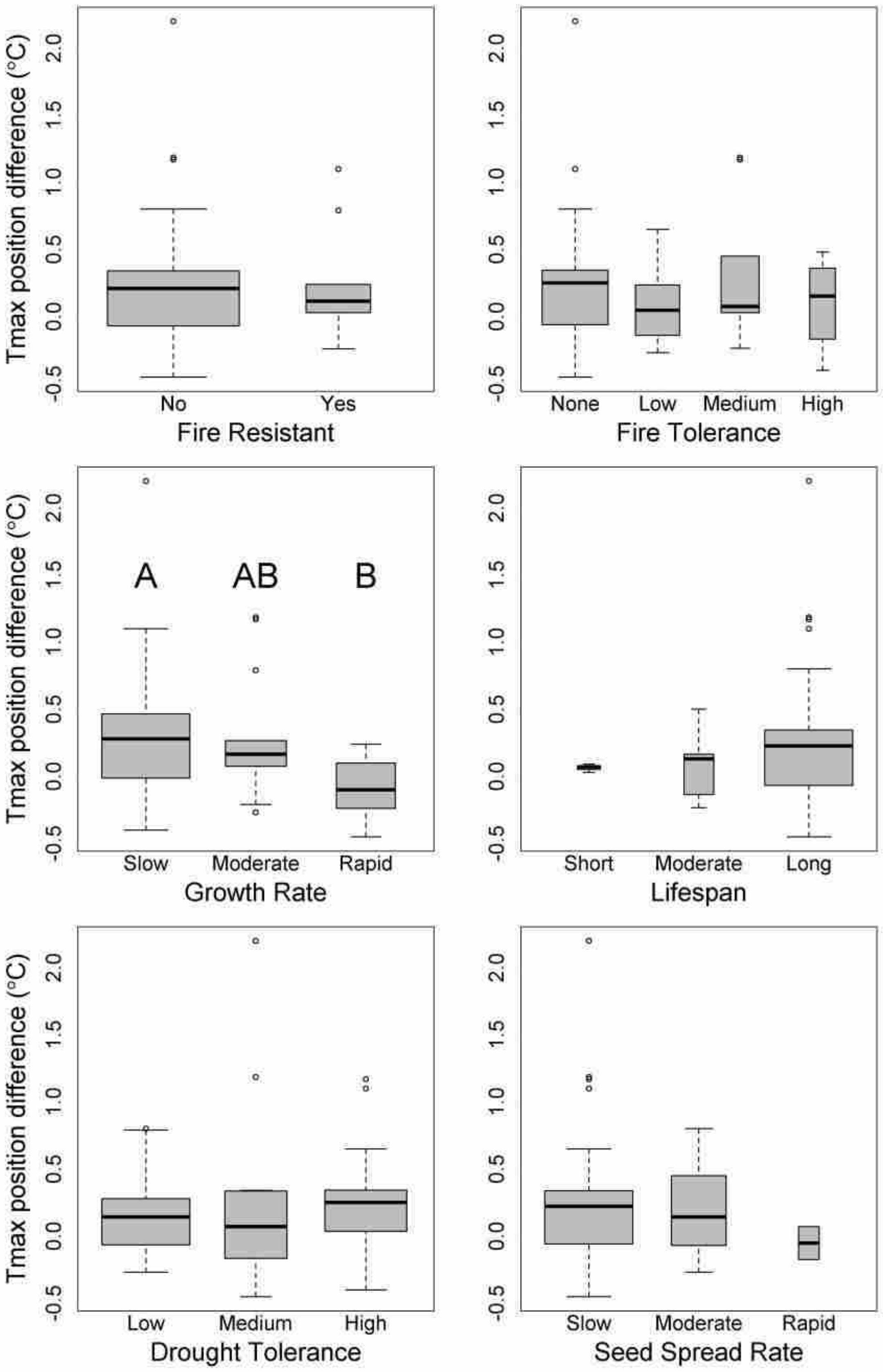
Juniperus osteoperma	338	349	819	793	2.0	1.8	16.9	16.7
Juniperus scopulorum	411	393	557	544	-0.5	-0.6	14.5	14.2
Larix occidentalis	468	457	233	238	-0.3	-0.5	11.4	11.2
Lithocarpus densiflorus	617	613	577	565	6.3	6.2	19.1	18.9
Picea engelmannii	431	437	191	183	-3.9	-3.8	8.7	8.8
Picea pungens	490	485	343	348	-3.2	-3.6	11.7	11.4
Picea sitchensis	617	615	47	46	5.4	5.4	14.9	14.6
Pinus albicaulis	365	375	174	154	-4.4	-4.0	7.1	7.5
Pinus contorta	426	434	244	247	-2.8	-2.7	9.8	10.0
Pinus discolor	495	500	1011	1047	5.7	6.4	21.3	21.3
Pinus edulis	373	362	793	773	1.6	1.6	17.3	16.6
Pinus flexilis	422	439	310	255	-3.1	-3.3	10.1	9.8
Pinus jeffreyi	394	405	585	585	0.4	0.4	14.6	14.8
Pinus lambertiana	500	513	581	595	4.0	4.2	16.6	17.1
Pinus monophylla	321	330	853	830	1.8	1.5	16.3	16.1
Pinus monophylla fallax	501	514	1060	1048	5.2	4.8	21.5	21.7
Pinus monticola	455	484	268	203	-0.1	0.1	11.7	11.8
Pinus ponderosa	455	451	499	487	0.4	0.3	14.6	14.4
Pinus sabiniana	434	446	861	839	8.0	7.9	22.4	21.9
Populus balsamifera	516	521	196	205	1.8	0.2	13.6	13.5
Prosopis velutina	403	378	1361	1364	8.8	8.2	26.0	25.7
Prunus emarginata	588	489	135	402	5.1	2.0	15.5	14.3
Pseudotsuga menziesii	495	469	285	294	1.2	0.1	13.4	12.6
Quercus agrifolia	439	458	916	873	8.3	8.0	21.8	21.4
Quercus arizonica	508	525	913	898	3.6	3.4	20.0	20.0
Quercus chrysolepis	518	536	689	663	5.5	5.3	18.8	18.6
Quercus douglasii	408	443	939	885	8.5	8.3	23.1	22.8
Quercus emoryi	512	523	998	938	5.1	4.3	21.2	20.5
Quercus gambeii	480	469	568	554	0.3	0.2	15.2	14.7
Quercus garryana	485	440	611	583	4.4	3.7	17.9	16.8

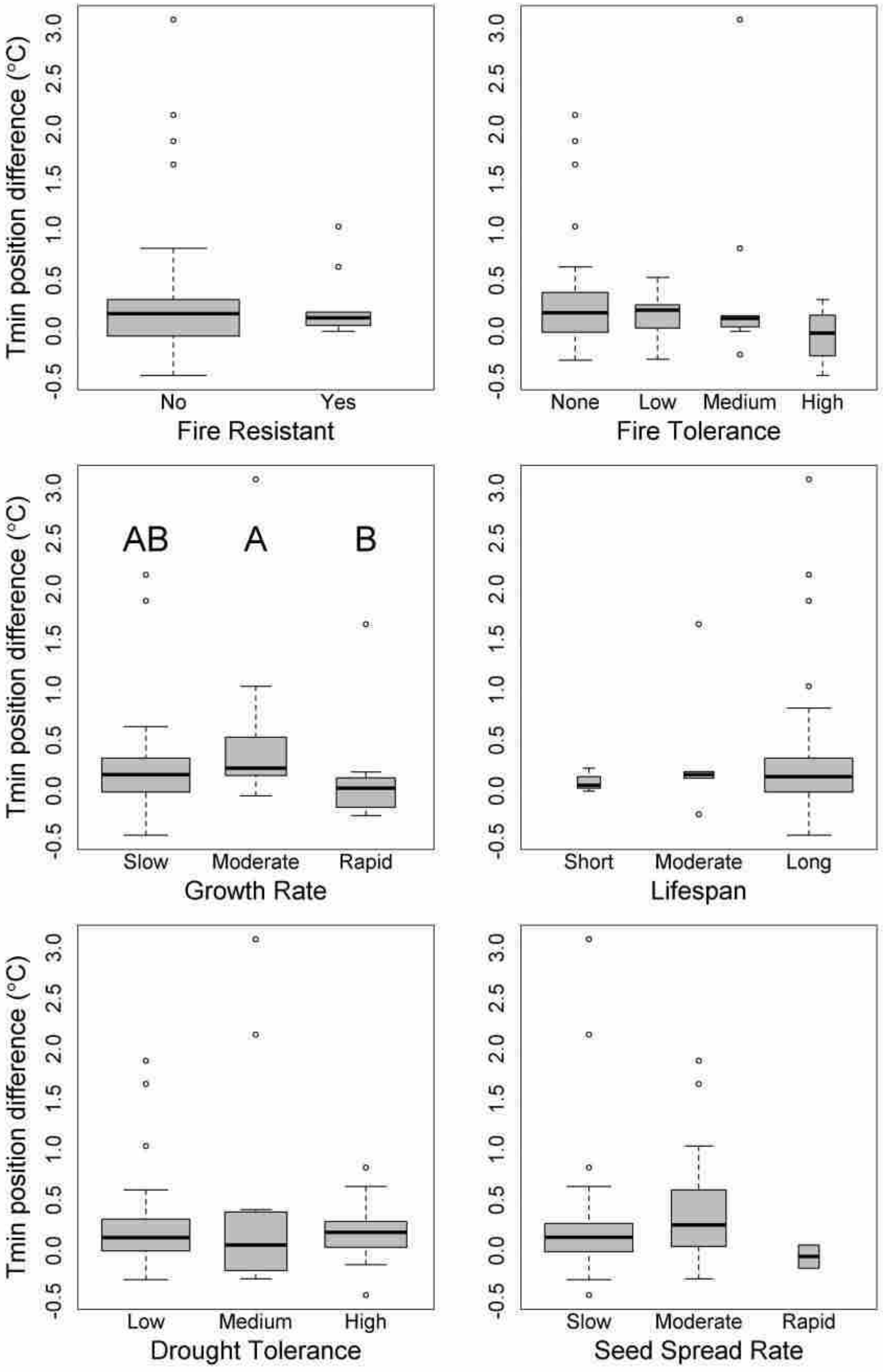
Quercus hypoleucoides	555	577	887	887	4.4	4.9	19.7	20.0
Quercus kelloggii	528	541	672	653	5.3	4.9	18.9	18.6
Quercus wislizeni	451	481	857	825	8.1	7.8	22.2	21.8
Sequoia sempervirens	589	597	597	568	6.8	6.7	19.7	19.5
Taxus brevifolia	557	523	205	182	3.4	1.3	14.7	12.5
Thuja plicata	534	524	149	173	3.2	1.3	13.5	12.7
Tsuga heterophylla	552	542	111	109	4.0	3.4	14.0	13.4
Tsuga mertensiana	430	429	133	124	-0.4	-0.5	9.6	9.4
Umbellularia californica	553	564	741	704	7.4	6.8	20.1	19.9

Appendix I: Boxplots of differences between adult and seedling niche positions by species ecological traits. Width of individual boxes is proportional to sample size within that category. For ecological traits that had a significant ($P < 0.05$) effect on difference in niche position, levels marked with different letters had significant differences.

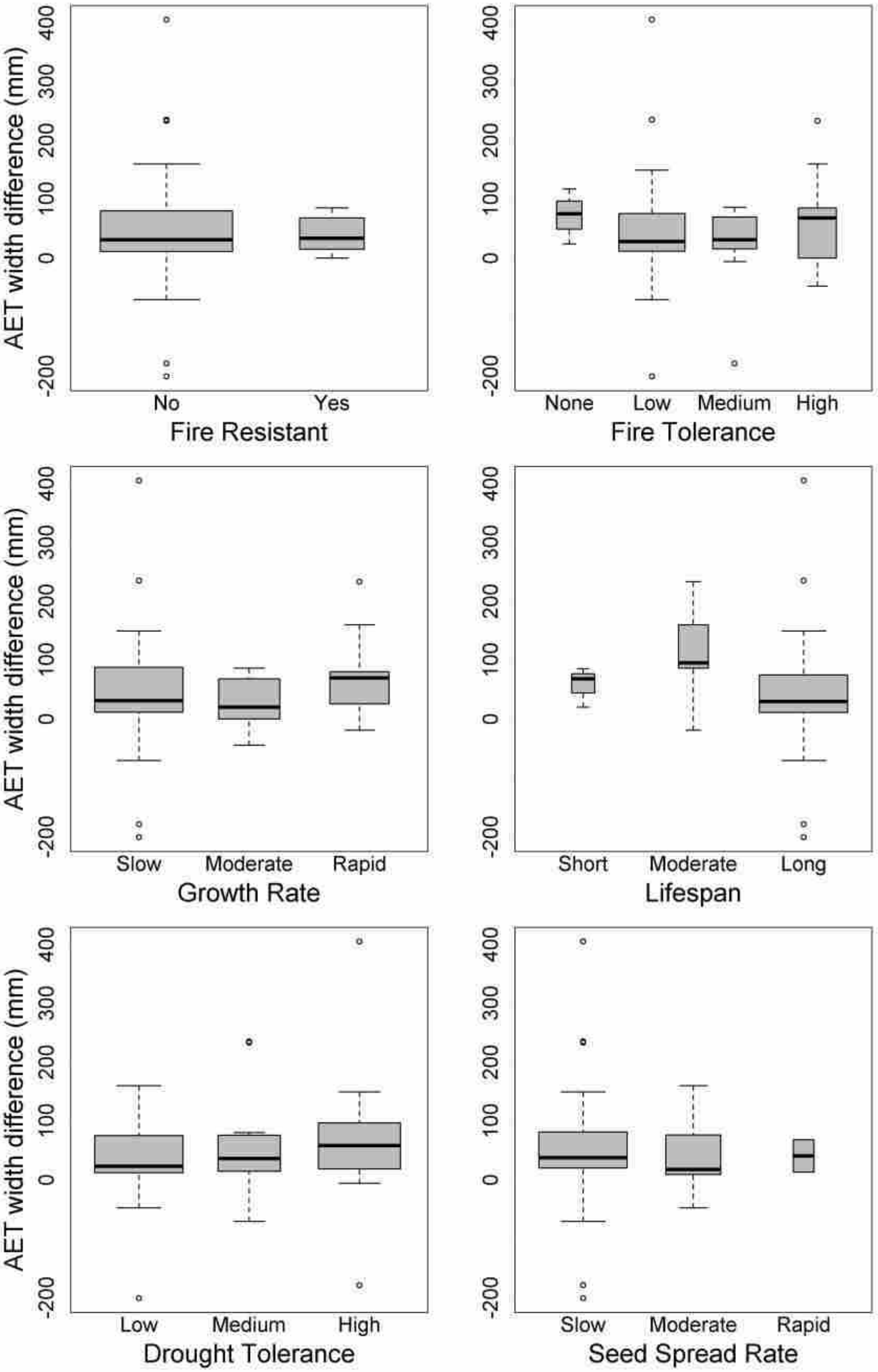

AET position difference (mm)
100
50
0
-50
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
Low
Medium
High
Drought Tolerance
Slow
Moderate
Rapid
Seed Spread Rate

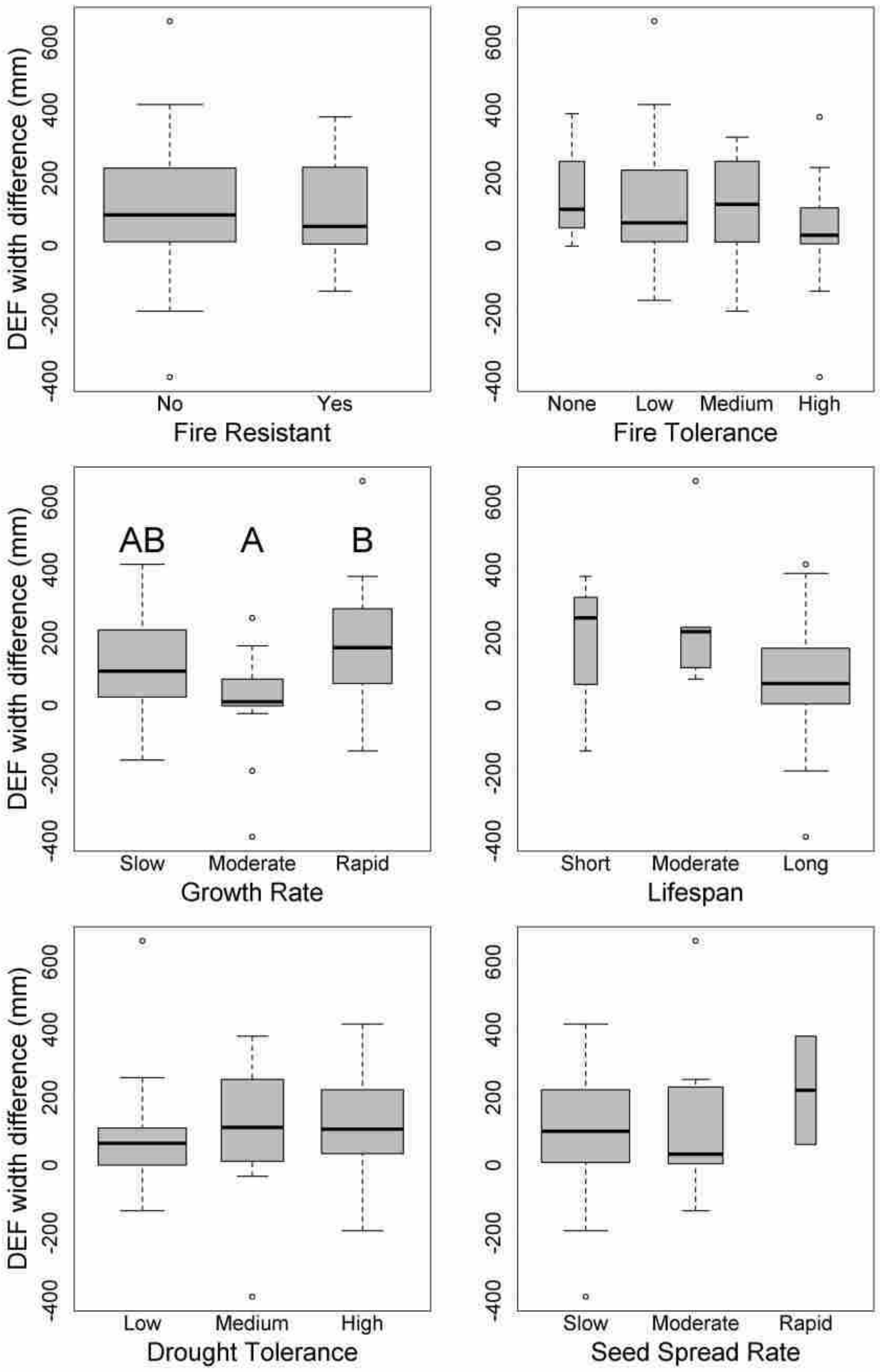

DEF position difference (mm)
50
0
-50
-150
-250
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
A
A
B
Low
Medium
High
Drought Tolerance
A
B
AB
Slow
Moderate
Rapid
Seed Spread Rate

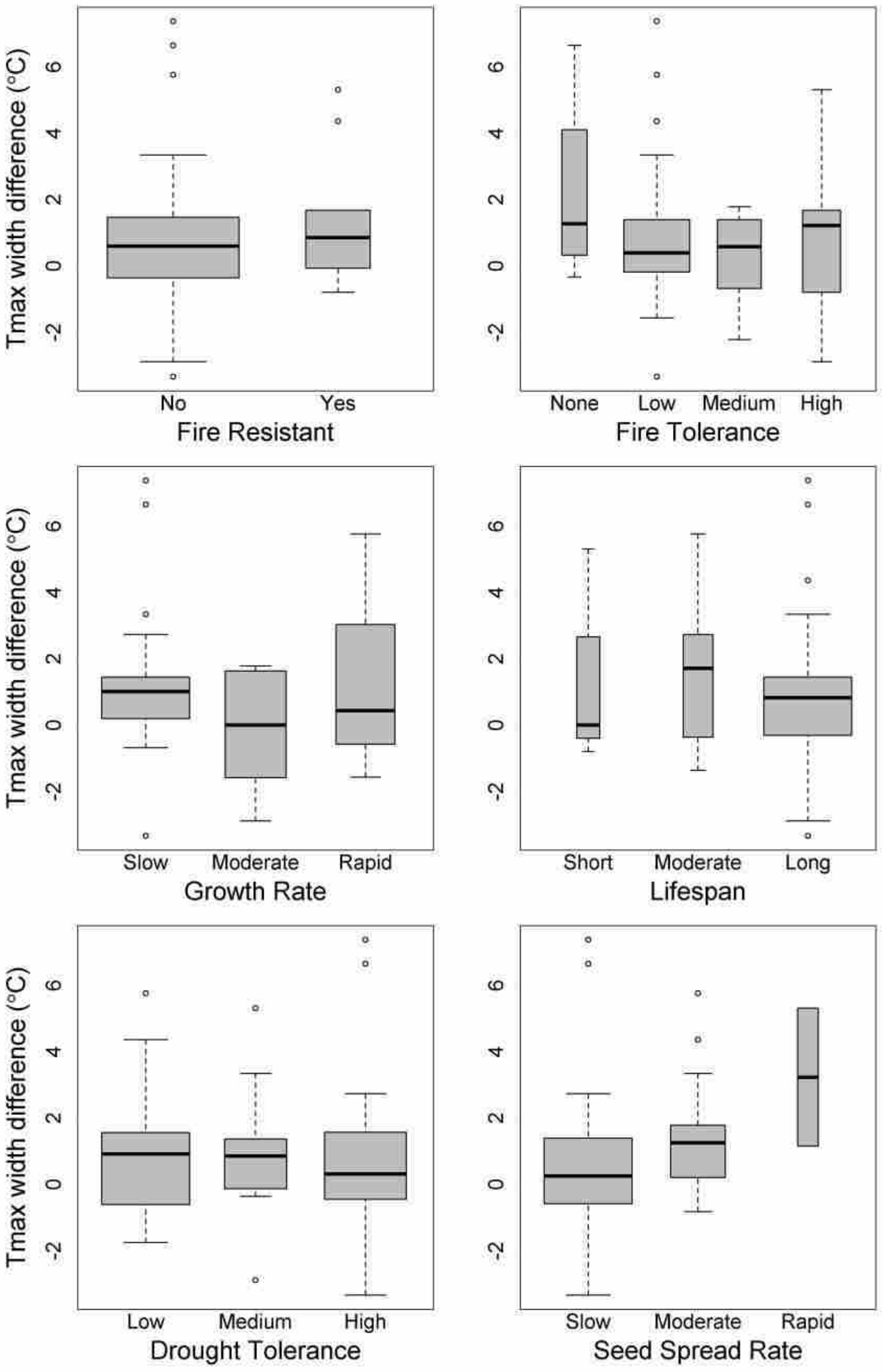

Tmax position difference (°C)
-0.5
0.0
0.5
1.0
1.5
2.0
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
A
AB
B
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
Low
Medium
High
Drought Tolerance
Slow
Moderate
Rapid
Seed Spread Rate

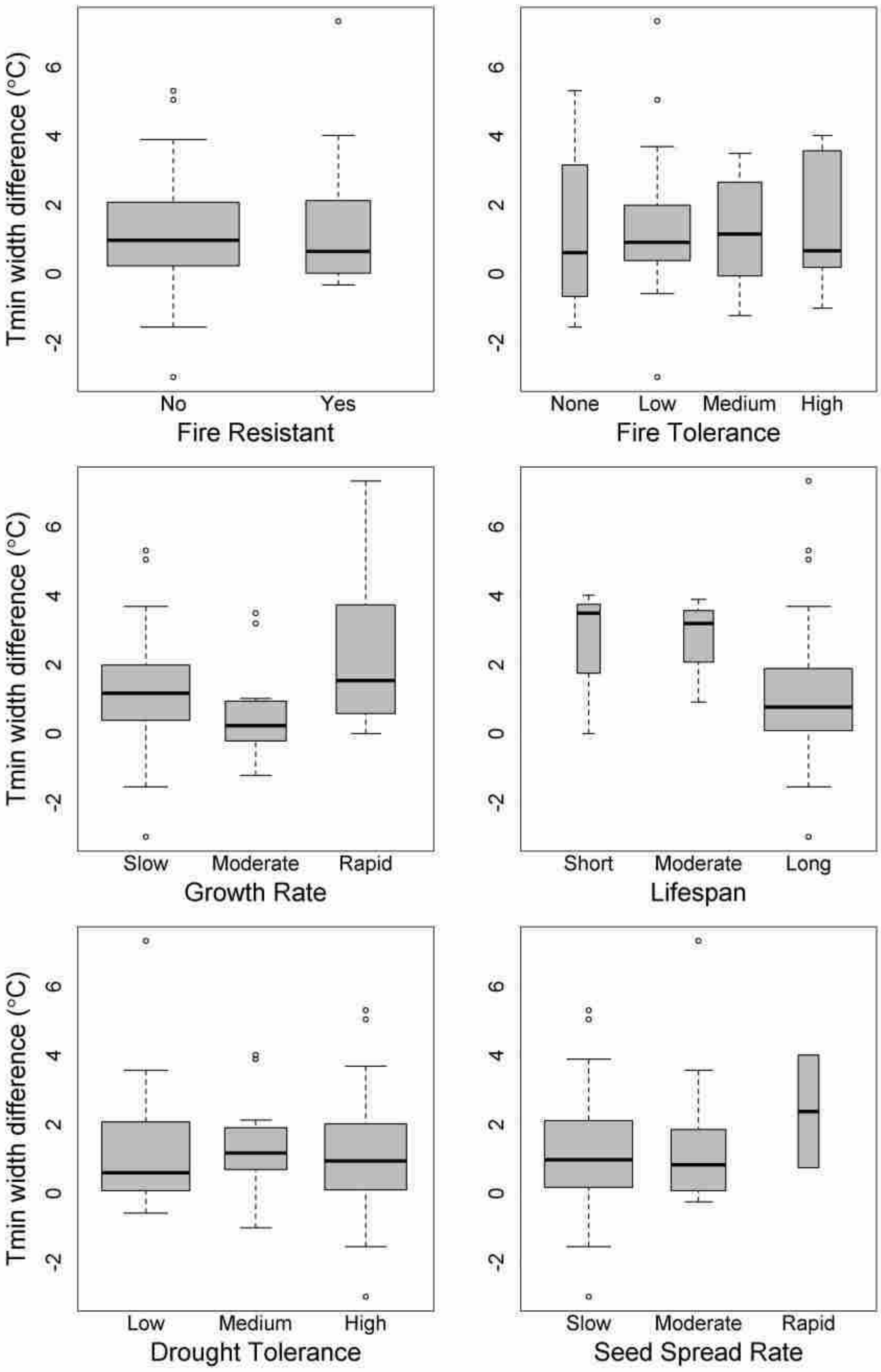

Tmin position difference (°C)
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
AB
A
B
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
Low
Medium
High
Drought Tolerance
Slow
Moderate
Rapid
Seed Spread Rate

Appendix II: Boxplots of differences between adult and seedling niche breadths by species ecological traits. Width of individual boxes is proportional to sample size within that category. For ecological traits that had a significant ($P < 0.05$) effect on difference in niche breadth, levels marked with different letters had significant differences.


AET width difference (mm)
-200
0
100
200
300
400
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
Low
Medium
High
Drought Tolerance
Slow
Moderate
Rapid
Seed Spread Rate


DEF width difference (mm)
600
400
200
0
-200
-400
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
AB
A
B
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
Low
Medium
High
Drought Tolerance
Slow
Moderate
Rapid
Seed Spread Rate


Tmax width difference (°C)
-2
0
2
4
6
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
Low
Medium
High
Drought Tolerance
Slow
Moderate
Rapid
Seed Spread Rate


Tmin width difference (°C)
-2
0
2
4
6
No
Yes
Fire Resistant
None
Low
Medium
High
Fire Tolerance
Slow
Moderate
Rapid
Growth Rate
Short
Moderate
Long
Lifespan
Low
Medium
High
Drought Tolerance
Slow
Moderate
Rapid
Seed Spread Rate