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ARTICLE

Influence of elevation and site productivity on conifer distributions across Alaskan temperate rainforests

J.P. Caouette, E.A. Steel, P.E. Hennon, P.G. Cunningham, C.A. Pohl, and B.A. Schrader

Abstract: We investigated the influence of landscape factors on the distribution and life stage stability of coastal tree species near the northern limit of their ranges. Using data from 1465 forest inventory plots, we estimated probability of occurrence and basal area of six common conifer species across three broad latitudinal regions of coastal Alaska. By also comparing models across life stages of each species (seedlings, saplings, mature trees, and dead trees), we explored trends in population stability at this leading edge of climate change. Elevation had a stronger influence on the probability of tree species occurrence than on basal area; site productivity impacted both estimated odds of presence and estimated basal area for most species in at least some regions. Interestingly, there were fairly dramatic differences across species in the degree to which the modeled probability of occurrence differed across the four life stages. Western redcedar (*Thuja plicata* Donn ex D. Don), for example, showed relatively stable distributions but other species appear to be in flux, e.g., yellow-cedar (*Callitropsis nootkatensis* (D. Don) D.P. Little), which has experienced widespread mortality at low elevations. Differential effects of elevation on live versus dead basal area suggest that mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) and yellow-cedar are shifting upslope in some regions and that Sitka spruce (*Picea sitchensis* (Bong.) Carrière) is shifting downslope in the Northwest region.

Key words: landscape, elevation, species distribution models, climate, biogeography.

Résumé : Nous avons étudié l'influence des caractéristiques du paysage sur la distribution et la stabilité des étapes de vie des espèces côtières arborescentes à proximité de la limite septentrionale de leur aire de répartition. À l'aide de données provenant de 1465 placettes d'inventaire forestier, nous avons estimé la probabilité d'occurrence et la surface terrière de six espèces communes de conifère à travers trois vastes régions latitudinales de la zone côtière de l'Alaska. En comparant aussi des modèles des étapes de vie de chaque espèce (semis, gaule, arbre mature et arbre mort), nous avons exploré les tendances de la stabilité des populations là où le changement climatique est le plus prononcé. L'altitude avait une plus forte influence que la surface terrière sur la probabilité d'occurrence d'une espèce; la productivité de la station avait un impact à la fois sur les chances estimées de présence et sur la surface terrière estimée de la plupart des espèces au moins dans certaines régions. Il est intéressant de noter qu'il y avait des différences assez marquées parmi les espèces dans l'ampleur avec laquelle la probabilité modélisée d'occurrence différait pour l'ensemble des quatre étapes de vie. À titre d'exemple, la distribution du thuya géant (*Thuja plicata* Donn ex D. Don) était relativement stable mais d'autres espèces semblaient être en pleine évolution : le cyprès de Nootka (*Callitropsis nootkatensis* (D. Don) D.P. Little) par exemple qui a connu une mortalité généralisée à faible altitude. Les différents effets de l'altitude sur la surface terrière vivante versus morte indiquent que la pruche subalpine (*Tsuga mertensiana* (Bong.) Carrière) et le cyprès de Nootka migrent vers le haut des pentes dans certaines régions et que l'épicéa de Sitka (*Picea sitchensis* (Bong.) Carrière) migre vers le bas des pentes dans la région du nord–ouest. [Traduit par la Rédaction]

Mots-clés : paysage, altitude, modèles de distribution des espèces, climat, biogéographie.

Introduction

Conifer forests in coastal Alaska at the current northern extent of temperate rainforests in North America are experiencing a variety of landscape-scale pressures related to global climate change, expanding human development, and increasing recreation demands (Haufler et al. 2010). Understanding resiliency of these forests in the face of these pressures is critical; yet, our knowledge of landscape dynamics within these forests is limited. Emerging issues in this region include maintaining ecosystem integrity, protecting cultural resources and values, and providing functioning wildlife habitats, as well as identifying potential commodity uses of forestlands (Oakes et al. 2015). An understanding of macroscale physical and climatic predictors of species distribution and productivity is essential for managing these unique and important forests. Comparisons of realized species niches across life stages provide a first indication of whether and in what ways species distributions may already be shifting. Such macroscale

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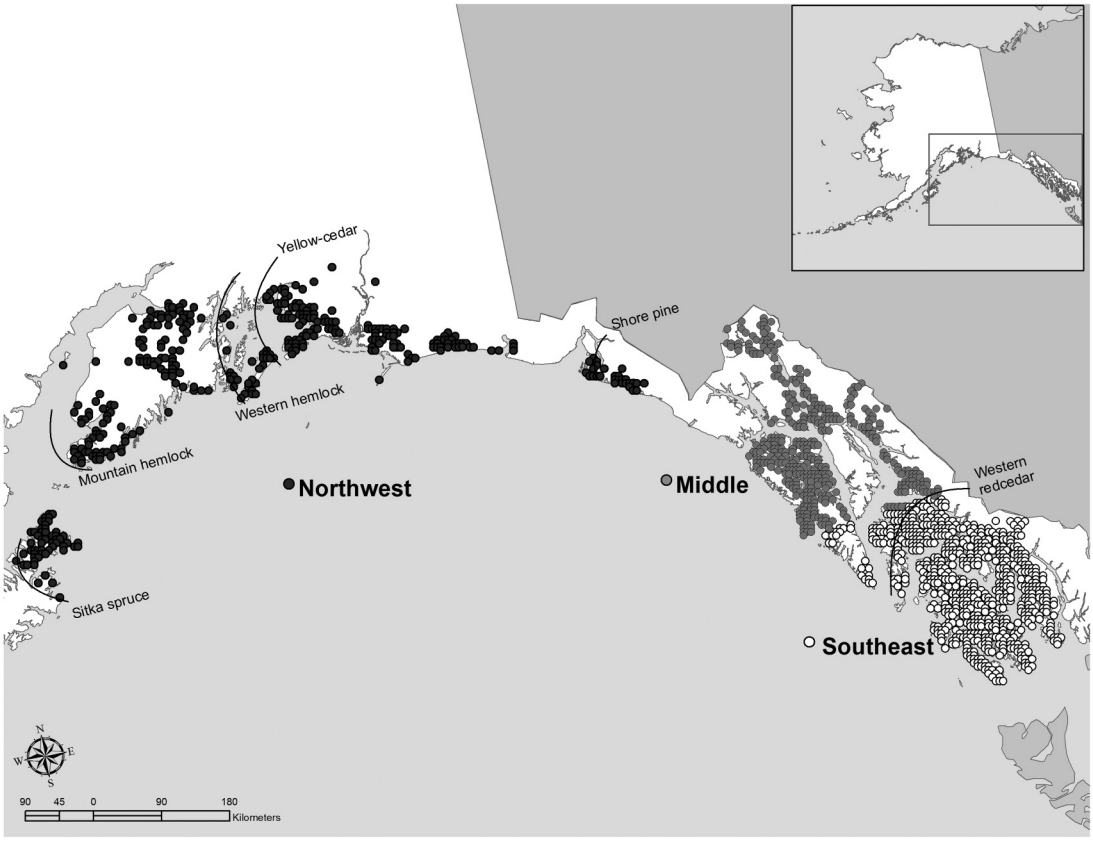
*In memorium. This study was initiated by the late John Caouette (1964–2010) of The Nature Conservancy. John's tireless efforts to synthesize and gather support for the idea, to find, organize, and clean the data, and to provide early reports has been an inspiration to the co-workers and collaborators he left behind. John's enthusiasm and drive for this project provided the co-authors of this report with the motivation to carry his work forward in the wake of his untimely death in October 2010.

Fig. 1. Map of coastal Alaska indicating the location of forest inventory and analysis (FIA) plots, north or northwestern limits for each of the main tree species, and the regions (Northwest, Middle, and Southeast) used in our analysis.



models can also provide a first step toward a more comprehensive modeling framework that might eventually untangle mechanistic relationships at finer scales (Pearson and Dawson 2003).

Of the various resource management objectives that require detailed spatial information on tree species, perhaps none is as compelling as understanding climate effects and how species are or are not adapting to change. There is growing appreciation of how climate has shaped forests historically and concern for how existing forests will be impacted by a rapidly changing climate. Because climate change is likely to affect each tree species in a unique manner, it is essential to understand the distribution and habitat requirements of individual tree species in addition to composite plant communities (Iverson et al. 2008; Woodall et al. 2009). Methods for predicting future responses in forests such as bioclimatic envelopes or climate profiles (e.g., Hamann and Wang 2006; Rehfeldt et al. 2006) are founded on current factors influencing the spatial distributions of forest tree species.

Species distribution models (SDMs) are frequently used to predict occurrence and abundance of organisms in landscapes where ground plot data are incomplete or where remote sensing cannot adequately identify species. SDMs are used in forest management to estimate species ranges and distributional limits, prioritize restoration and management activities, quantify available resources in a particular area, or identify regions of active management, e.g., where species diversity might be particularly high or where a native species might be particularly vulnerable to competition from an invasive species (Peterson 2003). Models range in complexity from bioclimatic envelopes that are typically constructed on the relationships between coarse species distributions and climate variables to fine-scale species distribution models, which may include disturbances, soils, and other available information (Booth et al. 1988). Biotic factors such as interspecies competition, herbivory, and pathogens are rarely explicitly included because of the intricacy of interactions (Elith and Leathwick 2009); however, these biotic factors are often implicitly included via effects on plot data (Schroeder et al. 2010).

The coastal temperate rainforests of Alaska (Fig. 1) are largely intact ecosystems and offer an ideal setting to explore natural processes driving the distribution and success of individual tree species. These forests are relatively unique in western North America in that large areas have had no previous logging history; fire is rare and has played a minimal role in contemporary forest development in all but a few areas (Alaback 1982). Although there has been considerable attention to forests stressed by drought and other effects of climate change on the trailing edge of tree species ranges (Mátyás 2010), there is a need to study forests at the latitudinal and elevational leading edge of range shifts. The six most common conifer species in the area reach the northern extent of their respective natural ranges at particular latitudes in southeastern Alaska or a location to the northwest along the Gulf of Alaska (Fig. 1). Therefore, on-the-ground patterns reflect natural processes driving species distribution and basal area growth at distributional extremes where range shifts, potentially due to climate, are most likely to be detected.

Vegetation in this northernmost extent of the coastal temperate rainforest is still recovering and migrating in response to the last glacial retreat millennia ago, as well as responding to current effects of climate change (Peteet 1991). Responses to climate change and other disturbances can include changes in occupancy of particular sites. Responses can also include changes in vigor, growth rates, and density. Basal area, a commonly measured stand-level descriptor of forest structure, can be considered an imperfect index of these types of responses (Cade 1997). We note that occupancy and basal area reflect different ecological pro-

cesses and likely respond to different suites of environmental variables (Nielson et al. 2005). Conservation and management of forested ecosystems responding to a changing climate rely on accurate descriptions of current tree species distributions across large spatial extents, fine-scale estimates, and estimates of how those geographic patterns may be changing over time. As a prime example, yellow-cedar (*Callitropsis nootkatensis* (D. Don) D.P. Little) has experienced intense mortality in the region related to changes in snow cover with climate change (Hennon et al. 2012). Broadscale models involving life stages of each of the tree species can help inform how their distributions may be changing.

With changing climates, temperature can be a driving factor in determining treeline (Grace et al. 2002) and is a contributing factor at the trailing edge of species ranges (Mátyás 2010). Across the coastal Alaskan temperate rain forest, tree species composition also appears to be controlled at a finer scale by site productivity, which is primarily related to soil drainage in this region (Neiland 1971; Alaback 1982; Hennon et al. 1990). For example, shore pine (*Pinus contorta* var. *contorta* Douglas ex Loudon) is known to be common in less productive wet, boggy soils, the cedars and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) are most competitive at intermediate drainage, and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) dominate the most productive, well drained sites. These tendencies as well as the mixed composition of most forests are recognized in local plant association guides (e.g., DeMeo et al. 1992; Develice et al. 1999) but have not been interpreted across broad spatial extents in the context of latitude, elevation, and climate change.

Acquiring empirical data on shifts in tree species distributions at the leading edge of climate change is difficult. Accurate fine-scale data for many drivers of vegetation dynamics (e.g., seasonal temperature extremes, water availability, and soils) are generally unavailable across the range of coastal Alaskan landscapes. Fortunately, the USDA Forest Service's Forest Inventory and Analysis (FIA) program collects data from a large systematic sample of forested plots across the region (Barrett and Christensen 2011). These data include species presence and absence, basal area by species, number of seedlings and saplings (as judged from size class data) by species, and a simple site productivity classification (productive versus unproductive soils). Elevation data are also widely available. Elevation and site productivity are static and do not change over time, at least not on time scales of management relevance. Changes in the relationships between trees and these static, landscape features are therefore potential descriptors of changes in realized species distributions.

In this study, we take a simple, transparent, and easily comparable approach to quantifying landscape-scale factors that influence tree species distributions across the temperate rainforests of coastal Alaska. We address the following questions:

(*i*) How is elevation, a stationary surrogate for climatic conditions, related to the distribution and basal area of six common coastal Alaskan tree species and does that relationship differ across three major geographic regions?
(*ii*) Does site productivity have an additional impact on either occupancy or basal area for the six tree species or across the three geographic regions?
(*iii*) By comparing models for live trees, dead trees, and regeneration, can we see a shift in the relationship of stationary factors to species distributions over time? Are there indications that some species' relationship to elevation may be changing?

We focused on only two stationary predictors of tree species occupancy and basal area over a vast geographic area, namely elevation and site productivity. By modeling presence versus absence independently of basal area, we distinguished between factors associated with these two distinct life history stages: seedling establishment and tree growth. Independent models for each of six species and across each of three geographic regions allowed explicit comparisons of the effects of our two stationary predictors on multiple species and areas within the leading edge of climate change. Independent models for different life stages of each tree species provided a quantitative estimate of how relationships between observed tree distributions and stationary landscape conditions may be shifting.

Methods

Region

We segregated the coastal rainforest in Alaska into three regions (Fig. 1). Forests along the Gulf of Alaska west to Kodiak Island were considered to be in the Northwest region. This region is the coldest and has historically had the most snowfall. Weather stations here (station numbers: 509685 and 509941) report mean annual maximum temperatures in 1949–2012 of 6.0 and 7.8 °C and mean annual snowfalls of 4702 and 5664 mm. Forests on the upper panhandle were classified as being in the Middle region. Weather stations in this region (station numbers: 503490, 503695, and 504092) report mean annual maximum temperatures of 8.8, 9.1, and 9.3 °C and mean annual snowfalls of 3081, 2210, and 1892 mm in 1949–2012. Forests on the lower panhandle were classified as being in the Southeast region. Weather stations in the Southeast region (station numbers: 509919, 504590, and 502227) reported mean annual maximum temperatures as high as 9.7–10.6 °C and mean annual snowfalls of only 572–1473 mm in 1949–2012. The northern or northwest limits of tree species are known to extend differentially into these regions.

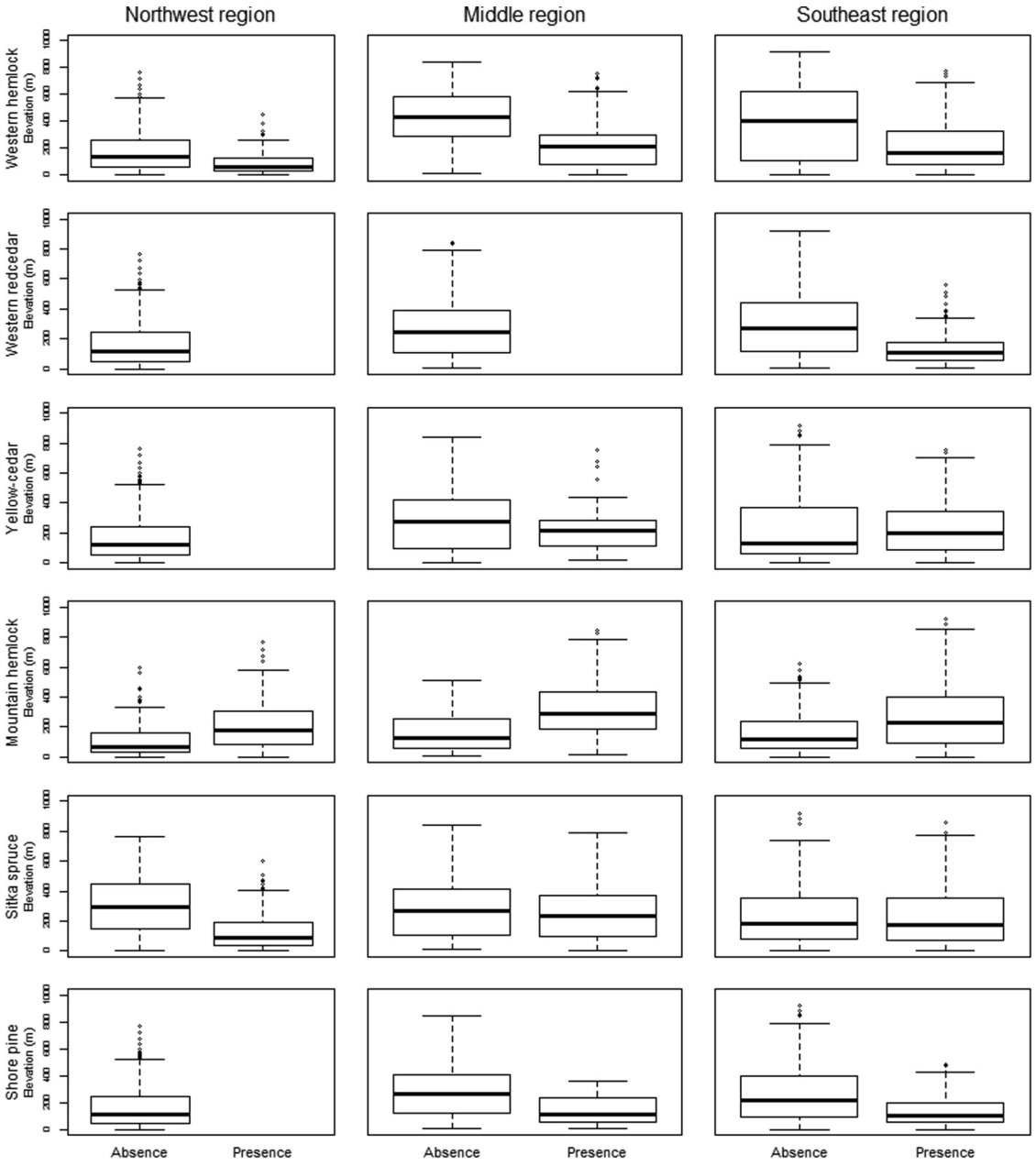
Moderated by the Pacific Ocean that delivers year-round precipitation (Harris et al. 1974; Alaback 1982), a hypermaritime climate has influenced forest structure and composition of coastal Alaska. Terrain is mountainous and has had an active glacial history. These are conifer-dominated ecosystems of low tree species diversity. We studied the six most abundant tree species, with western hemlock as the most common species and lesser amounts of Sitka spruce, yellow-cedar, western redcedar (*Thuja plicata* Donn ex D. Don), mountain hemlock, and shore pine. Other conifer tree species occur but are either less common or distributed around the fringes of coastal Alaska.

Vegetation data

We used 1465 vegetation plots in unmanaged stands: 376 in the Northwest region, 388 in the Middle region, and 701 in the Southeast region. These did not include plots identified as being in timber harvest areas, which were omitted to avoid direct effects of forest management on species composition and existing basal area. Plots used were distributed fairly well across all three broad geographic regions (Fig. 1). Any large geographic gaps without plots were generally in a national park or in USDA Forest Service wilderness areas.

Live and dead standing trees >12.7 cm (5 inches) in diameter were recorded from 0.017 ha (1/24 acre) circular plots from 1995 to 2003 (Barrett and Christensen 2011). Saplings (diameter, 2.5–12.7 cm) and seedlings (diameter, <2.5 cm but >15 cm tall) were recorded from 0.0013 ha (1/300 acre) nested microplots. Note that these are size class distinctions and do not necessarily reflect life stages. Designation of site productivity was made by evaluations of tree heights and site index. Plots judged to have the ability to produce 1.4 $m^3 \cdot ha^{-1}$ of wood or more annually were labeled "productive", and those that did not meet this threshold were labelled "unproductive" (USDA Forest Service 1972). Individual plots that were designated with "mixed productivity" were omitted from analyses where productivity class was a bivariate independent variable. Shore pine and another subspecies (lodgepole pine, *Pinus contorta* var *latifolia* Engelm. ex S. Watson) are not distinguished in FIA data; however, shore pine is by far the more common and widespread.

Fig. 2. Distribution of elevation (m) for plots in which each of six tree species was present versus absent by region. The solid line indicates the median value, boxes identify the center quartiles of the data, and whiskers designate 1.5 times the interquartile range. Presence data were not plotted for a particular region and species if there were less than five plots in which the species was present in that region.



Statistical analysis

We built independent models of tree distribution and basal area as a function of landscape-scale stationary predictors (elevation and site productivity) for each of the six primary tree species listed above and across each of the three regions of coastal Alaska described above. This data-partitioning approach enabled simple interpretation of results and comparisons across regions and species despite extreme natural imbalances in design; some species are not present in some regions. Because of the large number of zeros in the data and because the factors influencing early seedling establishment (probability of presence) may be different from those influencing later tree responses to climate (basal area where present), we modeled distribution and basal area of each tree species separately using a two-step modeling process akin to a hurdle model. Hurdle models have been successfully used on a wide range of problems (e.g., Steel et al. 2012). In the first step, we built a logistic regression model to explain presence–absence patterns or distribution of tree species. In the second step, we modeled the basal area of each species.

To examine relationships between elevation and species distribution, we constructed logistic models in which tree presence was a function of elevation. Coefficients from logistic models were transformed for display to show the change in the odds of presence for a 100 m gain in elevation. Models to predict basal area used a log-transformed response and a normal distribution. For these models, the raw regression coefficient is displayed, which does not have a simple ecological definition but can be interpreted as a general positive or negative change with increasing elevation. To explore the effects of site productivity, we eliminated sites with mixed productivity classification and refit the models. We then added an indicator variable of site productivity (unproductive versus productive) to the above models and also an

interaction term (elevation × productivity). We note that the indicator variable denotes a change in site classification from unproductive to productive. Again, coefficients for the logistic model are transformed to display the change in odds when considering an unproductive site versus a productive site. Raw coefficients are displayed for the log linear model. To explore the third question of indications that the relationship to elevation may be changing over time for some species, we used additional information on presence and absence of seedlings, saplings, and dead trees in each plot, as well as basal area of dead trees in each plot. We created independent models of presence–absence for live trees, dead trees, seedlings, and saplings, as well as independent models of log(basal area) for dead trees and live trees. Life stage models were built using the original data set with all site productivity classes included.

Because of the large sample size and the exploratory nature of these analyses, we did not test for significance in a formal manner. We instead compared parameter estimates and their associated confidence intervals. Where confidence intervals overlapped with zero, we note that the relationship was indistinguishable from zero, and where confidence intervals did not overlap with zero, we conclude that a relationship likely exists. Where confidence intervals failed to overlap with each other or with zero, we conclude that observed relationships are different from one another.

Results

The presence of tree species in FIA plots in the three regions corresponded well to previously published natural information on ranges of four of the species (Fig. 1). For example, inventory plots detected western redcedar as being restricted to the Southeast region (it occurred on four plots just north of this border), which marks its northern extent (Andersen 1953). Small populations of shore pine and yellow-cedar are known to extend far into the Northwest region (Peteet (1991) and Hennon and Trummer (2001), respectively); however, these species were not detected in FIA plots included in our analyses in this region.

Relationship of elevation with distribution and basal area of six common Alaska tree species

Looking across all FIA plots in a region, the patterns of occupancy as a function of elevation differed across species and across regions (Fig. 2). The percentage of plots in which a particular species was present varied dramatically with elevation for most species (Fig. 3).

Western hemlock, western redcedar, and shore pine were more likely to be present in plots at lower elevations and absent in plots at higher elevations in those regions where the species occurred (Fig. 2). Mountain hemlock followed the opposite tendency. It was generally found at higher elevations across all regions (Figs. 2 and 3). Presence of Sitka spruce was unrelated to elevation in the Middle and Southeast regions in our sample, suggesting that it was similarly present across the elevation range. It was, however, more common at low elevations in the Northwest region (Fig. 2). Basal area of each species (where present) did not vary by elevation (Fig. 4). The only exception was mountain hemlock in the Middle region, where there was an indication of greater basal area at higher elevations.

Model coefficients describe how either probability of species presence or basal area differs as a function of elevation. They supported and quantified what we observed in Figs. 2–4. Most elevation coefficients were significantly different from zero when predicting presence–absence (Fig. 5). For most species, the coefficient for the presence–absence model was negative, indicating reduced odds of being present as elevation increases. The exception was mountain hemlock, which had a large positive coefficient for elevation in all regions; the odds of this species being present in an FIA plot increased with elevation. In the Middle region, for example, we estimate that the odds of mountain hemlock presence nearly double for every increase in 100 m of elevation over the observed range. Sitka spruce was the one species to show a dramatic interaction with region. The transformed elevation coefficient was effectively one, indicating no effect of elevation on the odds of presence in a particular FIA plot for both the Middle and Southeast regions, but it was strongly negative in the Northwest region.

There were fewer strong relationships between elevation and basal area (where a species was present) (Fig. 5). Western hemlock and mountain hemlock again had opposite relationships with elevation; basal area of western hemlock was reduced as elevation increased and basal area of mountain hemlock increased with increasing elevation, though model coefficients for the Northwest region were indistinguishable from zero (Fig. 5). There was again an interaction between elevation and region for Sitka spruce with a negative effect of elevation on basal area only in the Northwest region. There was an indication that basal area of western redcedar tends to be lower at higher elevations.

Fig. 3. Percentage of sites with species present across 150 m elevation classes for each of the six common conifer species and each of the three regions. TSHE, western hemlock; THPL, western redcedar; CANO, yellow-cedar; TSME, mountain hemlock; PISI, Sitka spruce; PICO, shore pine.

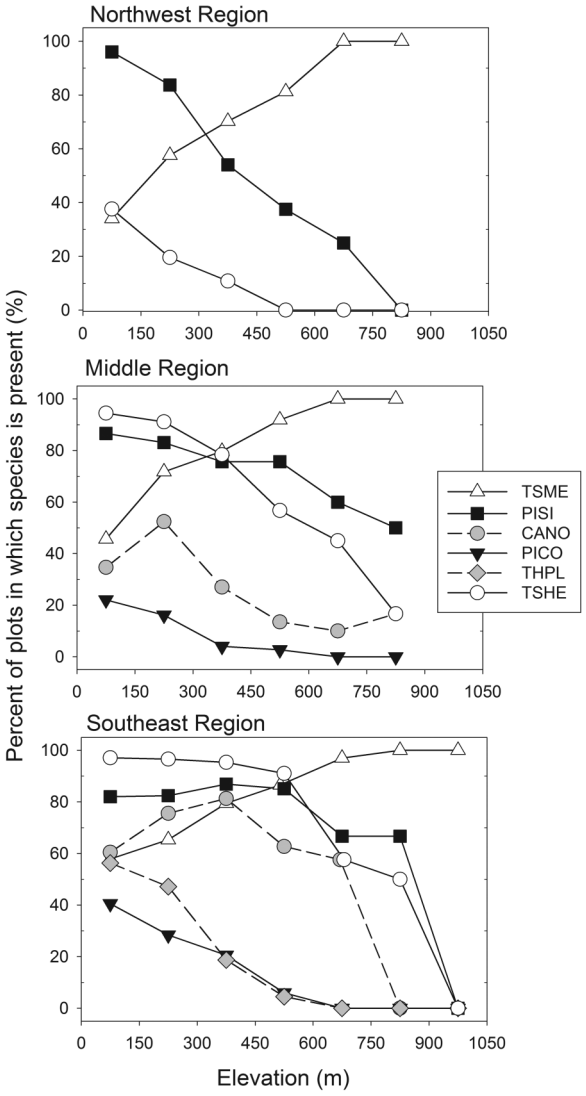
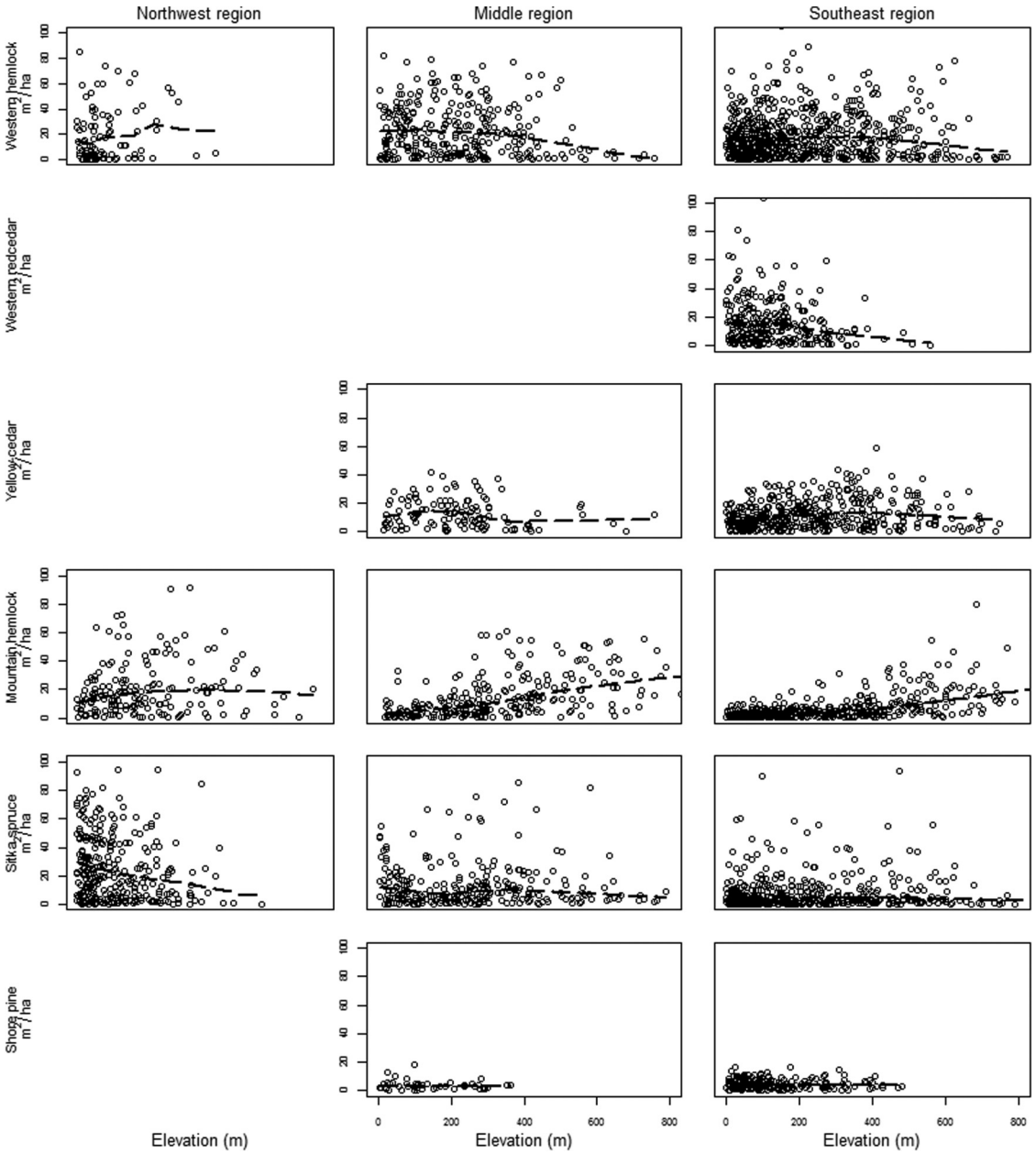


Fig. 4. Basal area ($m^2 \cdot ha^{-1}$) by elevation (m) across six species and three regions for plots in which the species was present. Dashed lines describe a locally weighted scatterplot smoothing for visual inspection of trends. Data were not plotted for a particular region and species if there were less than five plots in which the species was present in that region.



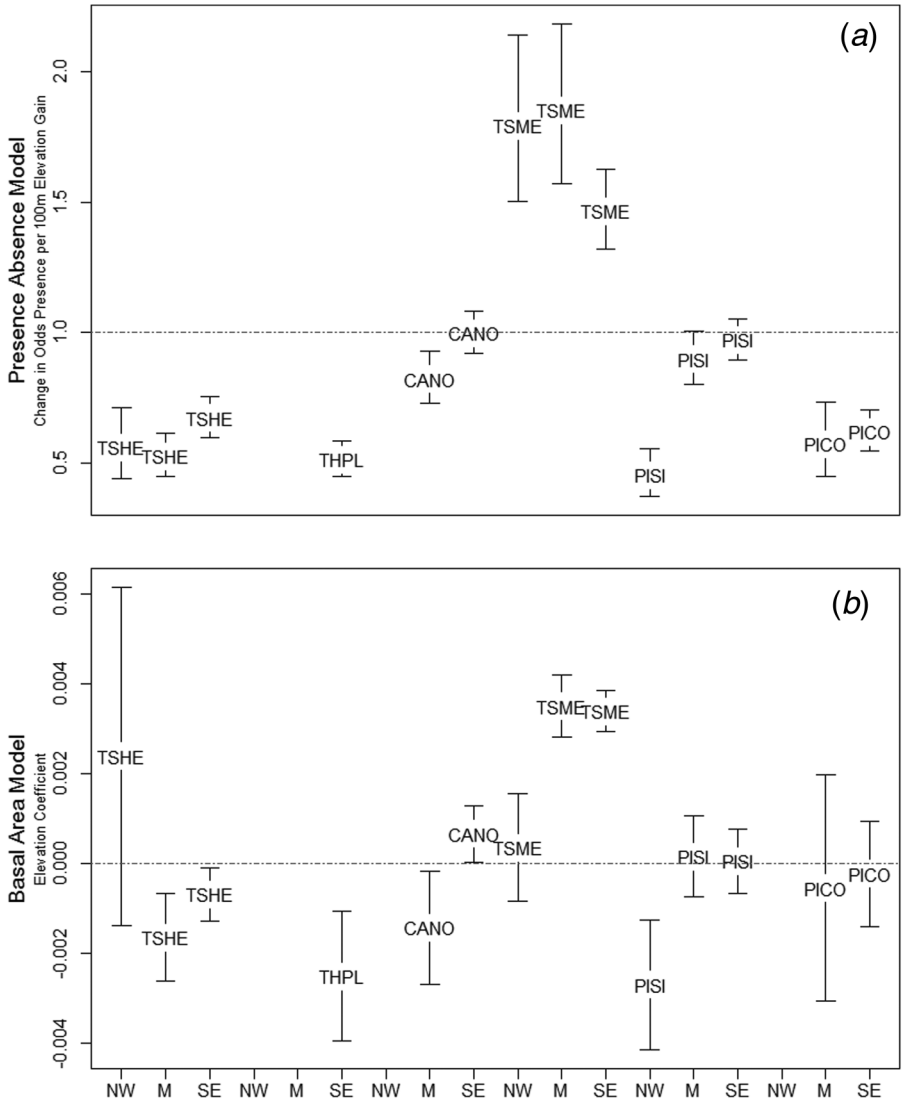
Relationship of site productivity to distribution and basal area

When added to a model that already contains elevation, an indicator of site productivity (unproductive versus productive) generally had additional explanatory power for both species presence or absence and basal area (Fig. 6). The odds of western hemlock and Sitka spruce presence were higher in productive areas. Other species were more likely to be present in unproductive areas. The two cedar species, for example, showed a reduced probability of presence on productive sites after accounting for the effect of elevation (Fig. 6).

Where species were present, site productivity classification also had a strong effect on basal area for Sitka spruce and western hemlock; however, there were indications of regional differences in how western hemlock responded to site productivity. There were also regional differences in how yellow-cedar responded to site productivity, with site productivity having a notable positive relationship with basal area in the Middle region but not in the Southeast region. Western redcedar basal area was positively correlated with site productivity in the one region where it was present (Southeast region). There was no apparent effect of site productivity on basal area of mountain hemlock or shore pine in any region though both species are frequently present on unproductive sites (Table 1).

There were few noteworthy interactions between site productivity and elevation when predicting species presence/absence. The only exceptions were yellow-cedar (in the Southeast and Middle regions), western redcedar (in the Southeast region) and western hemlock (in the Northwest region). In these cases, there was an indication that the effect of elevation differed across productivity classes. For example, yellow-cedar presence had a strongly negative relationship with elevation at unproductive sites in both

Fig. 5. Effects of elevation on species presence or absence and on basal area, where present. (*a*) For presence and absence, transformed coefficients representing the change in odds of species presence for a 100 m gain in elevation are presented. (*b*) For basal area, coefficients describe the effect of a change in elevation on log(basal area) using a linear regression model assuming normal errors. Species: TSHE, western hemlock; THPL, western redcedar; CANO, yellow-cedar; TSME, mountain hemlock; PISI, Sitka spruce; PICO, shore pine. Whiskers describe 95% confidence intervals around each parameter estimate. Regions: NW, Northwest; M, Middle; SE, Southeast.



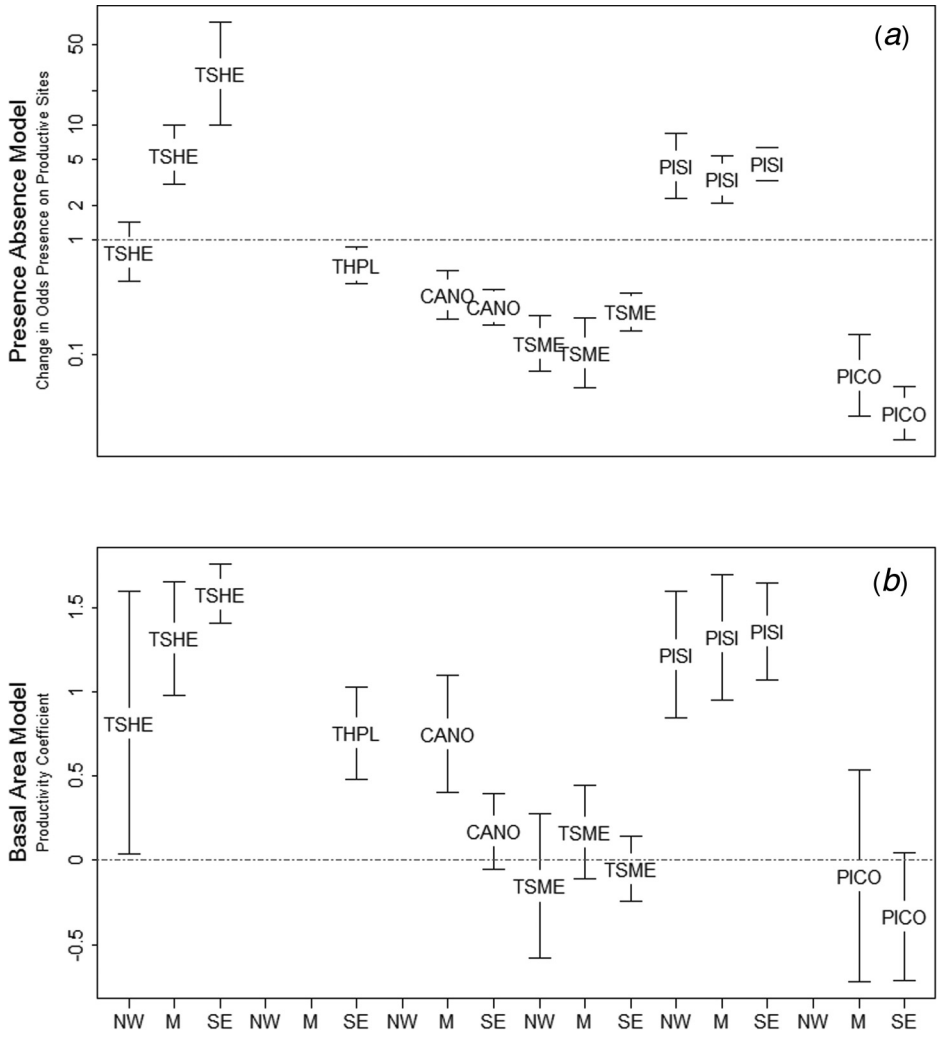
the Southeast and Middle regions; at productive sites, there was a marginally negative relationship with elevation in the Middle region and a fairly positive relationship with elevation in the Southeast region. Western redcedar presence probability in the Southeast region and western hemlock presence probability in the Northwest region were also more negatively associated with elevation at unproductive than at productive sites. There were no significant interactions when predicting the logarithm of basal area. Due to the limited number of coefficients that could be distinguished from zero, these results are not displayed.

Stability in relationships with elevation across life stages

Analysis of the relationships between elevation and presence of live trees, dead trees, saplings, and seedlings for each species revealed patterns of distributional stability or change for the six tree species (Fig. 7). The coefficient values can be interpreted as the change in the odds of a species being present for every 100 m increase in elevation by live trees, dead trees, saplings, and seedlings and for each species. Where the coefficients differ across life stages, it is an indication that the relationship of that species' distribution to elevation is shifting over time (Fig. 7). Western hemlock had relatively similar relationships with elevation across life stages in the Northwest and Southeast regions. In the Middle region, smaller trees were more likely to be present at higher elevations than mature and dead trees. In the Southeast region, seedlings of western hemlock were present at somewhat lower elevations than the other life stages. There was a trend for dead yellow-cedar to be found at lower elevations and for live trees and saplings and seedlings to be found at progressively higher elevations; the strongest relationship with elevation was for the dead trees and the weakest relationship with elevation was for seedlings and saplings. Dead mountain hemlock occurred at somewhat lower elevations than other life stages in the Northwest region. The odds of Sitka spruce and shore pine presence as a function of elevation indicated relative stability for the four life stages, except that the odds of live Sitka spruce tree presence was reduced at low elevations in the Northwest region (Fig. 7).

The relationship between basal area and elevation was not dramatically different for dead versus live trees (where present) for

Fig. 6. Regression coefficients for productivity in regression models to describe (*a*) presence or absence using a logistic model and (*b*) log(basal area) using a linear regression model assuming normal errors. Regression coefficients for the logistic model are transformed to describe the change in odds of presence for a productive versus unproductive site. In both cases, the subset of plots classified as "mixed productivity" were not used in model building, and productivity was added to a model that already contained log-transformed elevation. Abbreviations are as defined in Figure 5.



most species and in most regions (Fig. 8). As for the presence–absence models above, we compared the coefficients between live and dead tree basal area within each species to assess whether the relationship of that species' productivity to elevation is stable. As in Figs. 5 and 6, positive values for these coefficients indicate increasing basal area with elevation for live or dead trees; conversely, negative values suggest reduced basal area with increasing elevation. The positive effect of elevation was dramatically stronger for live versus dead basal area for mountain hemlock in both the Middle and Southeast regions. Yellow-cedar, in the Southeast regions, had a slightly positive relationship with elevation for live trees, yet there was no effect of elevation on dead basal area. In interpreting these models, we recognize that dead standing trees used in our analysis may remain standing for various lengths of time in inventory plots according to tree species, elevation, and productivity class, and therefore, differences in parameters estimated across life stages may reflect multiple processes in addition to climate change.

Discussion

Elevation was a strong predictor of the distribution of six common conifer tree species across the expanse of the coastal temperate rainforest in Alaska, an area at the leading edge of climate change. Elevation was, however, a better predictor of occurrence than of basal area. Our simple yet quantitative models of the current realized niche for each species agreed well with published qualitative descriptions of species occurrence across the region (e.g., Hultén 1968; Vierick and Little 2007). Nested within these broad trends, a fine-scale indicator of site productivity refined our predictions of occurrence for almost every species within all relevant regions. For some species and within some regions, site quality also had a significant effect on basal area. By comparing models across life stages, we observed indications, for some species and in some regions, of changing relationships between species distributions and elevation that may be indicative of a changing climate. Interestingly, for other species, we observed no indication of shifting species distributions (Table 1). Our findings can be applied to gain insight into species of particular interest, for example, to understand changes in the distribution of yellow-cedar, which has been impacted across portions of the region throughout the 20th century.

Biogeography and forest management at the leading edge

The broad spatial arrangement of tree species, especially at their northern or northwestern-most range limits in Alaska, is

Table 1. A summary of modeled tree distributions by species, region (NW, Northwest; M, Middle; SE, Southeast), and life stage.

	Western hemlock (TSHE)			Western redcedar (THPL)	Yellow-cedar (CANO)		Mountain hemlock (TSME)			Sitka spruce (PISI)			Shore pine (PICO)	
	NW	M	SE	SE	M	SE	NW	M	SE	NW	M	SE	M	SE
Effect of increasing elevation on probability of presence	↓	↓	↓	↓	↓		↑	↑	↑	↓			↓	↓
Effect of elevation on BA where present (by region)		↓	↓	↓	↓			↑	↑	↓				
Effect of higher site quality on probability of presence		↑	↑	↓	↓	↓	↓	↓	↓	↑	↑	↑	↓	↓
Effect of higher site quality on BA where present	↑	↑	↑	↑	↑					↑	↑	↑		
Interaction between site quality and elevation	PA				PA	PA								
Effect of elevation on probability of presence by life stage						Dead lower	Dead lower			Live lower				
Effect of elevation on BA by life stage							Dead lower	Dead lower						

Note: The regional presence is defined as presence in more than five plots within the region. Arrows describe parameters for which the 95% confidence intervals do not overlap zero. Grey indicates that the 95% confidence interval is extremely close to zero. The direction of the arrow indicates the effect of increasing elevation or of productive site classification. The effect of site productivity classification was assessed in models that already contained elevation. The effects of interactions are summarized simply as presence of a significant interaction between elevation and site productivity in models to predict presence or absence of the species (PA) or basal area (BA). There were no significant interaction effects in models of BA. Results of models describing the effects of elevation on probability of presence by life stage were summarized by describing the life stage that differed from the others.

probably a result of distinct adaptations to particular climate factors, as well as differing migration histories. Therefore, patterns at this leading edge provide a unique opportunity to observe range shifts as a result of climate change and other disturbances. Each of our six tree species has natural ranges that extend far south of Alaska along the Pacific Coast to California (Burns and Honkala 1990). Moisture deficits, possibly combined with fire, may pose the greatest risk of potential range retractions at the trailing edge of climate change in California, as none of these species is tolerant to drought or fire. However, precipitation is not typically limiting at low elevation in the northern portions of these species' ranges. Here, climate may influence the elevational patterns of these trees by affecting their reproductive success and competitive ability more than by imposing heat or drought to exceed their physiological limits.

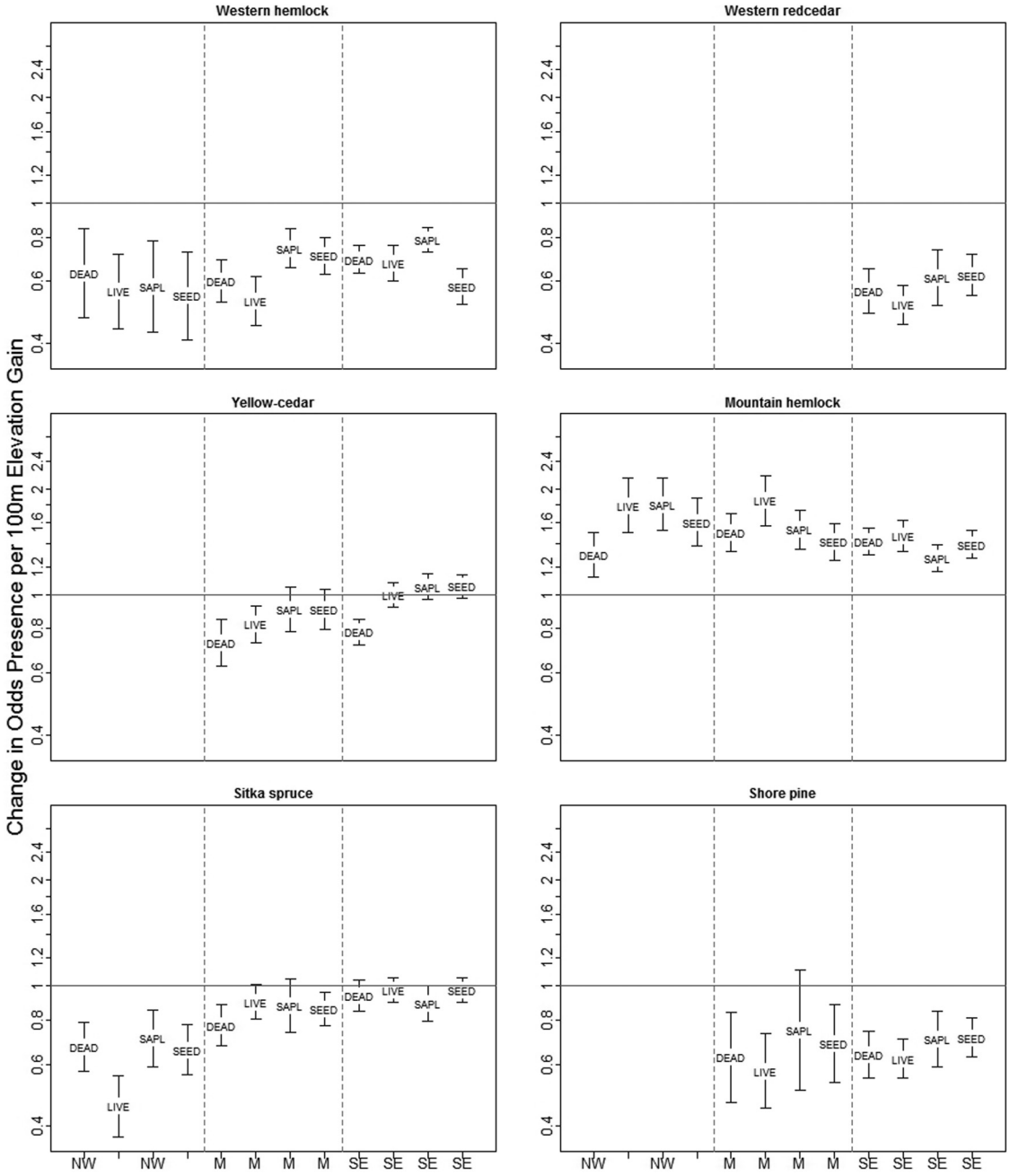
At this leading edge of the climate envelope, elevation was a clear surrogate for latitude. The occurrence of several tree species showed a strong association with elevation. Two of the three species (western redcedar and shore pine) that were most often found at lower elevation also have natural ranges that did not extend far to the northwest into Alaska. The third species, Sitka spruce, which has the most extensive range, had a tendency to occur at low elevations, but this pattern was only present in the most northerly region. Mountain hemlock was most common at higher elevations in all three regions in Alaska. The weaker relationship between basal area and elevation suggests that climate and other factors related to elevation do not substantially affect tree growth, either number or size of stems, in the same way as they affect seedling initiation. The greater basal area of mountain hemlock at higher elevation combined with the negative coefficient for probability of presence on productive sites is consistent with the observation that mountain hemlock is only competitive on low productivity sites at low elevations (Martin et al. 1995).

Given more detailed knowledge of range limits and occurrence by elevation and productivity class, various forest management strategies in coastal Alaska may be employed to favor tree species on particular sites. However, adapting forest management practices at species range edges is in the early stages of development (Milad et al. 2013). With robust distribution models of tree species focusing on patterns at the limits of current species ranges, forest management strategies could be developed for favoring regeneration and competition of species at their current northern or upper elevational limits. Conservation methods might be employed to protect trees at these limits, but various harvesting strategies could also be used to encourage natural regeneration or, in combination with artificial regeneration (planting), to enhance migration (Pedlar et al. 2012). The role of natural disturbance such as windthrow, landslides, and glacial rebound in favoring migration of tree species needs to be investigated and related to active forest management. High-resolution species distribution models and associated GIS layers will undoubtedly be a foundation for developing conservation and management strategies. Our results can serve as inputs to these models, estimating occurrence and abundance where there are no on-the-ground data.

Fine-scale effects of site quality

Site quality or productive potential is tied closely to soil moisture, a function of climate, soils, and microtopography. Site quality, therefore, operates at a fine spatial scale, nested within elevation and climate, to influence the distribution and abundance of tree species. Forest productivity is positively correlated with soil moisture in many forests of the world where water is often limiting (Gholz et al. 1990). The opposite relationship is found in coastal Alaska, where there is abundant year-round precipitation and droughts are relatively rare (Stephens et al. 1969). In coastal Alaska, bogs and other forested peatlands that have developed on gentle slopes or in soils with restricted drainage support less live conifer biomass, more open canopy conditions, and a unique and diverse composition of tree and understory species

Fig. 7. Transformed regression coefficients for elevation in logistic regression models to predict presence or absence by species across life stage and region. Transformed coefficients can be interpreted as the change in odds of presence for a 100 m increase in elevation. Life stages are identified at the center of each bar as dead (DEAD), live (LIVE), sapling (SAPL), or seedling (SEED). Vertical, dotted grey lines visually differentiate the three regions (NW, Northwest; M, Middle; SE, Southeast). Whiskers represent 95% confidence intervals around each parameter estimate.



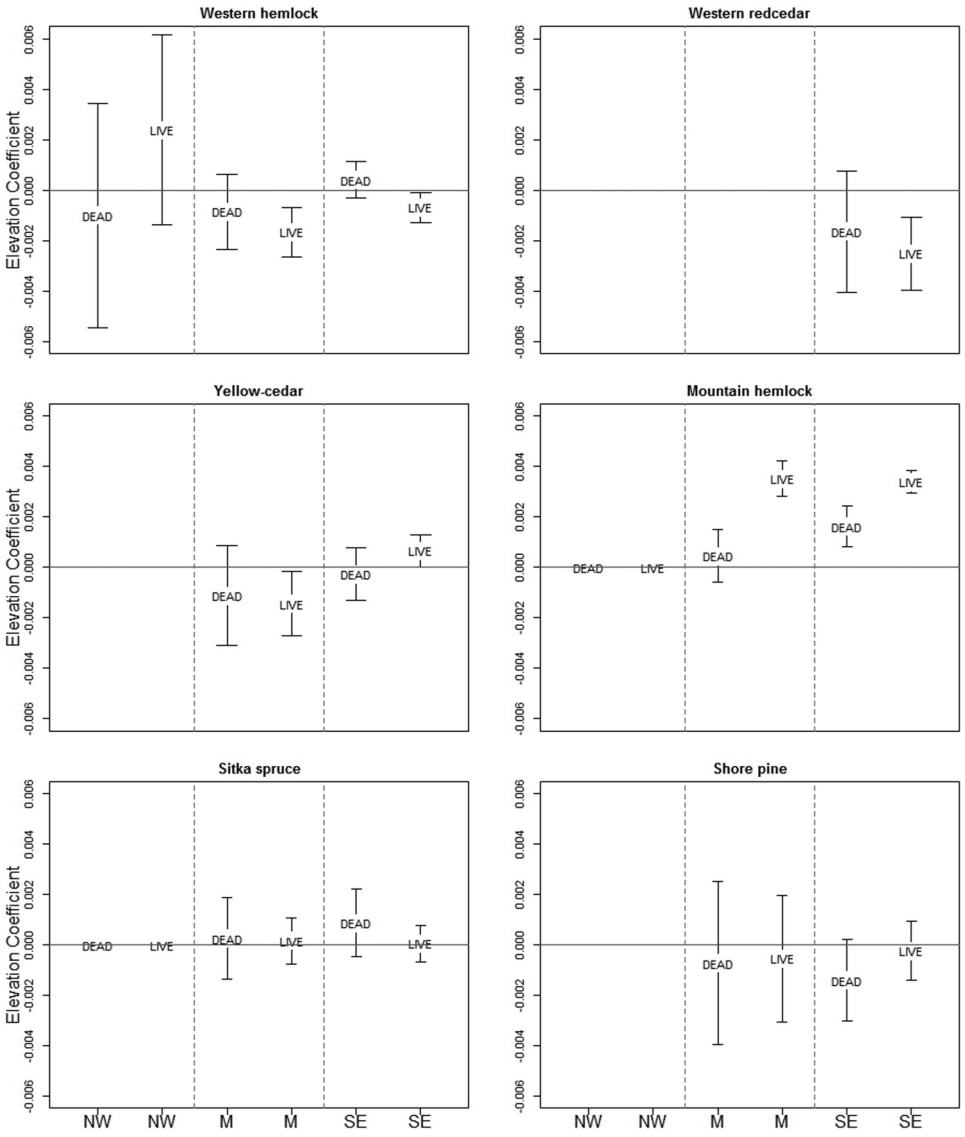
(Neiland 1971). The cedars, mountain hemlock, and particularly shore pine tolerate marginal sites with poor drainage but cannot compete with the faster growing trees on the favorable drained soils (Ruth and Harris 1979). We found western hemlock, western redcedar, yellow-cedar, and Sitka spruce to have higher basal area on productive than unproductive sites, which is consistent with previous observations and plant classification schemes (Neiland 1971; DeMeo et al. 1992; Martin et al. 1995).

Reduced competition can also influence the tendency of particular species to occupy marginal sites. Western hemlock, for example, appeared to expand its niche to less productive conditions in the Northwest region where western redcedar is absent and shore pine and yellow-cedar populations are very limited. Sitka spruce extends even further west beyond the other species on Kodiak and Afognak islands, where it has no competition with conifers in a leading and slowly expanding range edge (Griggs 1934). Improved hydrologic and soils data could be used with forest inventory data to refine our results on how conifers respond across the drainage gradient from bog to upland forest beyond the simple productive–unproductive classes that we used here.

Implications for a species in decline

Yellow-cedar is known to have experienced an intense mortality focused on lower elevations in Alaska (Hennon et al. 2012). In the

Fig. 8. Regression coefficients for elevation in linear regression models assuming normal errors to describe log(basal area) by species across life stage and region. Life stages are identified at the center of each bar as dead versus live. Vertical, dotted grey lines visually differentiate the three regions (NW, Northwest; M, Middle; SE, Southeast). Whiskers describe 95% confidence intervals around each parameter estimate. Where confidence intervals appear to be absent, they are simply smaller than the size of the life stage label.



warmest region of our study, we found that the relationship between elevation and yellow-cedar occurrence differed substantially among life stages (i.e., more dead trees at lower elevation, more regeneration at higher elevation), indicative of an unstable, shifting distribution (Fig. 7). The latitudinal and elevational limits of the intensive yellow-cedar death are considered to be controlled by snow accumulation, with inadequate snow leading to fine-root freezing injury during cold weather in late winter or early spring (Hennon et al. 2012). Snowpack may also protect yellow-cedar regeneration from deer browse by keeping deer populations in check (White et al. 2009) or simply by covering seedlings during the nongrowing season when deer feed on them. These snow effects could explain the more abundant yellow-cedar seedlings that we detected at higher elevation.

Fine-scale site productivity is also important in controlling both the distribution of yellow-cedar and the occurrence of its intensive mortality. We do not have a clear understanding of all the mechanisms that contribute to our finding of varying competitive abilities on sites that are productive (well-drained soils) and unproductive (saturated soils). However, growth of the two cedar species may be favored on saturated soils by having a unique adaptation for acquiring nutrients there through cation mobilization of nitrate (D'Amore et al. 2009).

Our findings suggest that even lands designated for conservation status and not influenced by activities such as road building or timber harvesting may be expected to have dynamic vegetation alteration as species experience shifting distributions, possibly initiated through climate change. Some such protected areas impacted by yellow-cedar mortality are already expressing successional changes as yellow-cedars are replaced by other species such as western hemlock (Oakes et al. 2014). We note that caution should be used in attempting to interpret population dynamics of long-lived tree species from forest plot data because of the possibility of longer term episodic reproduction or mortality (Lertzman 1995) and factors unrelated to climate that can cause tree mortality.

Climate as a factor in future tree species distributions

Shifts across life stages in the relationship between the distribution of particular tree species with respect to latitude and ele-

vation may suggest population expansion or contraction in response to a changing climate. We observed indications of such shifts not only for yellow-cedar, but also for mountain hemlock and Sitka spruce (Table 1), and similar results have been found by others. For example, by comparing the geographic distribution of seedlings and tree biomass from inventory plots in the eastern US, Woodall et al. (2009) found the mean latitude of seedlings to be 20 km north of tree biomass for northern species but southern species appeared static. As in our study, results on life stages should be interpreted cautiously because seedlings and saplings represented size classes and not necessarily recent regeneration. Coldest mean temperature of the month, growing degree days, and moisture indices are useful in predicting vegetation ranges in northern Europe (Sykes and Prentice 1996) and western North America (Shafer et al. 2001). For coastal Alaska, we would add snow accumulation (or snowpack) as an important controlling climate factor of conifer occurrence and abundance.

The climate of coastal Alaska is expected to become warmer and slightly wetter in the next century (Wolken et al. 2011). Forest trees will experience warmer winters, longer growing seasons, and, as the mean winter temperature warms above freezing, considerably reduced snow accumulation in some areas. The region is predicted to have the greatest loss of days below freezing of any area of North America in the 21st century (Meehl et al. 2004) because current winter mean temperatures hover close to the 0 °C freezing threshold. Species reliant on snow for either greater competitive status (mountain hemlock) or protection from direct weather injury (yellow-cedar) are likely to experience diminished suitable habitat. We found both of these species to be associated with higher elevations in Alaska, especially for mountain hemlock. Both tree species have also been projected to lose habitat in British Columbia, as other conifer species from lower elevation would be expected to shift upward (Hamann and Wang 2006). Our study found western hemlock, Sitka spruce, western redcedar, and shore pine to be associated with low elevations in Alaska and have extensive ranges to the south, suggesting that they may be favored by the projected climate during the next century. These tree species may benefit directly by warmer conditions but so could individual insects (e.g., spruce aphid, Powell and Parry (1976)), pathogens (e.g., dwarf mistletoe, Barrett et al. (2012)), and herbivores (e.g., deer, White et al. (2009)) to offset gains in productivity.

The current distributions of forest trees reflect the realized ecological niche of each species, the culmination of their adaptation to environmental factors, competition with other tree species, interaction with other biotic factors, and migration from historic distributions. Untangling these complex interactions will be challenging; however, our quantification of their associations with several stationary factors should form a basis for understanding edaphic and climate niche requirements of coastal conifers. By comparing live versus dead tree basal areas and occupancy across multiple life stages, we revealed possible maladaptation to climate and possible distribution contraction or expansion for some species and not others. Our results provide a convenient glimpse of fluctuating populations across latitude, elevation, and site productivity. Our analysis suggests instability of yellow-cedar, mountain hemlock, and Sitka spruce distributions, whereas western hemlock, western redcedar, and shore pine species appear to have more stable distributions (Table 1). Each of our tree species are found in mixed-species communities, but they are likely to respond individually to climate change, as is suggested by the fossil record (Davis and Shaw 2001). Our models of each independent tree species enable us to begin imagining how communities across whole landscapes might shift and re-arrange under a changing climate.

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