

Determinants of conifer distributions across peatland to forest gradients in the coastal temperate rainforest of southeast Alaska

Sarah M. Bisbing,^{1*} David J. Cooper,² David V. D'Amore³ and Kristin N. Marshall⁴

¹ Department of Natural Resources Management and Environmental Sciences, California Polytechnic State University, 1 Grand Ave San Luis Obispo, 93407, CA, USA

² Forest and Rangeland Stewardship, Colorado State University, 1472 Campus Mail, Fort Collins, CO, 80523, USA

³ USDA Forest Service, Pacific Northwest Research Station, 11175 Auke Lake Way, Juneau, AK, 99801, USA

⁴ School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA, 98195, USA

ABSTRACT

Wetland determination relies on assumptions that site hydrologic and edaphic conditions limit plant species to certain environments. For example, using species' wetland indicator status for wetland determination assumes that tolerance of wetland conditions best explains distributional patterns. However, abiotic and biotic factors often interact to create complex plant responses across different environments. To evaluate these interactions, we used a hydrologic gradient in the coastal temperate rainforest of southeast Alaska to (1) quantify the primary determinants of conifer distributions, (2) identify thresholds in environmental factors limiting species' success and (3) assess current wetland indicator status of local conifers (*Pinus contorta*, *Picea sitchensis*, and *Tsuga heterophylla*). Data were collected using a hierarchical sampling scheme and analyzed within a Bayesian framework. Topography and hydrologic regime were the primary determinants of distributional patterns, but species were limited by specific microsite factors. Competitively dominant *P. sitchensis* occurred where hydrology, pH, and nitrogen were most favorable for establishment, while stress-tolerant *P. contorta* was competitively excluded from these sites. *Tsuga heterophylla* occurred across the gradient but took advantage of drier conditions, which promoted biomass accumulation. Tree distributions were limited by the interaction between abiotic and biotic factors rather than by abiotic tolerance alone. This knowledge of local and regional drivers of species' distributions and the relative importance of interacting abiotic and biotic drivers provide critical information for land management and regulation. Wetland delineation procedures can be improved through application of the regional empirical limits identified for plant species, as implemented and addressed in this study. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS conifer distributions; hydrologic gradient; coastal temperate rainforest; southeast Alaska

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INTRODUCTION

Wetland determination and delineation in the USA relies on the assumption that hydrologic and edaphic conditions limit plant species to certain environments. For example, using species' wetland indicator status for wetland determination assumes that tolerance of wetland conditions best explains distributional patterns. However, abiotic influences often interact with biotic effects to create complex plant responses in different environments (Kraft *et al.*, 2014). The environment serves as a strong filter to species' occurrence (Cooper, 1982; Tilman, 1982; Vince and Snow, 1984; Chase and Leibold, 2003; Sanderson, *et al.*, 2008), but biotic

factors interact with abiotic stressors to limit or exclude species from habitats that are otherwise suitable (Connell, 1961; Bertness *et al.*, 1999; Crain *et al.*, 2004). Plant species establishment and survival in wetlands requires tolerance of saturated and often nutrient-poor conditions, but it is unlikely that suitable habitat versus unsuitable habitat are differentiated solely by the local environment. Species' distributions are more likely determined by complex gradients of interacting abiotic and biotic stressors.

Stress tolerance and competition are key determinants of plant community composition across a wide range of natural hydrologic gradients. For example, low-marsh dominant *Spartina alterniflora* grows vigorously in New England salt marshes but is excluded from high marsh habitat by *Spartina patens* and *Juncus gerardi* (Bertness and Ellison, 1987). Freshwater marsh plants are absent from salt marsh habitat because of high salinity, while many salt marsh species grow best when transplanted to

*Correspondence to: Sarah M. Bisbing, Department of Natural Resources Management and Environmental Sciences, California Polytechnic State University, 1 Grand Ave, San Luis Obispo, 93407, CA, USA.
E-mail: sbisbing@calpoly.edu

freshwater marshes and released from competition (Crain *et al.*, 2004). Studies along wetness gradients in Pacific Northwest forests suggest that light limitations and competition with fast-growing shrubs exclude tree species from favorable locations (Pabst and Spies, 1999; Waring *et al.*, 2002). Watershed position influences the abundance of *Rubus spectabilis* and determines woody plant distributions in these riparian forests (Sarr and Hibbs, 2006). In the Jura Mountains of Switzerland, competition with *Picea abies* excludes *Pinus uncinata* from dry uplands and from what appears to be its optimal habitat (Freléchoux *et al.*, 2004). These studies demonstrate how abiotic and biotic stressors determine herbaceous and woody plant distributions along environmental gradients.

Identifying the factors limiting species' success is essential when distribution and habitat information is used in land management and regulation, as in the case for wetland regulation by the United States Army Corps of Engineers (USACE). The USACE delineates wetlands by the presence of three indicators: wetland hydrologic regime, hydric soils, and hydrophytic vegetation (Environmental Laboratory, 1987). Site determinations must provide evidence of long-term inundation and/or saturation during the growing season, anaerobic soil conditions, and a predominance of hydrophytes (species tolerant of wetland conditions >50%) (Tiner, 1991; USACE, 2007). The National Wetland Plant List (NWPL; <http://rsgisias.crrel.usace.army.mil/NWPL/>) groups species by their presence or absence in wetland versus upland ecosystems, and classifications assume that tolerance of wetland conditions best explains species distributions across the landscape (Lichvar and Gillrich, 2011). Species assigned obligate status (OBL) are thought to occur in wetlands >99% of the time, while upland (UPL) species occur <1% of the time. Many species are facultative (facultative wetland = 66–99% occurrence in wetlands (FACW), facultative = 33–66% (FAC), or facultative upland = 1–33% (FACU)), occurring in both wetlands and non-wetlands in the same region (Tiner, 1991). Wetland scientists debate facultative rankings, because classification relies on assumptions of species' ecological site preferences and presumed frequency of occurrence in wetlands (Dewey *et al.*, 2006; Lichvar and Gillrich, 2011). The presence of facultative species, particularly when they dominate a community, creates significant challenges to wetland determination, and more information on what controls species' occurrence in wetland versus non-wetland habitats is needed. Furthermore, rankings do not account for competitive interactions that limit species' presence on a site where it would otherwise be successful. These knowledge gaps are major limitations in wetland management and regulation, particularly in regions where wetlands occupy a large portion of the landscape.

Wetlands cover 40% of Alaska's land area (~70 million ha), more than any other region of the USA (Hall *et al.*, 1994). In

the coastal temperate rainforest of southeast Alaska, wetlands dominate the landscape, and hydrologic processes are thought to be the primary determinant of species' distributions (Zoltai and Vitt, 1995; Asada *et al.*, 2003; D'Amore *et al.*, 2012). Plant community composition varies across hydrologic gradients created by topography and landform, and three conifers vary in abundance across this heterogeneous landscape. *Pinus contorta* (Douglas Ex. Louden) ssp. *contorta* (shore pine) grows in wetlands, predominantly fens and bogs. *Picea sitchensis* (Bong. (Carr.)) (Sitka spruce) occurs on steeper forested wetlands and uplands. *Tsuga heterophylla* (Raf. (Sarg)) (western hemlock) grows in wetlands and uplands but dominates forests on the dry end of the hydrologic gradient. All three conifers are classified as FAC or FACU and assumed to occur in both wetlands and uplands.

The coastal temperate rainforest of southeast Alaska is an ideal system for assessing potential drivers of species occurrence along hydrologic gradients. Few studies have evaluated the determinants of tree species distributions under such conditions (Denslow and Battaglia, 2002; Rodríguez-González *et al.*, 2010), and none have focused on conifer species distributions across wetland to upland gradients in the USA. We used this gradient to address the following questions: (1) What are the abiotic and biotic controls on conifer distributions along the wetland to upland gradient? (2) Do local environmental thresholds limit conifer distributions, or are species plastic in their response to the environment? (3) Does the distribution of each species correspond to its wetland indicator status on the NWPL?

METHODS

Study region

This study was conducted in Juneau, AK, USA, in the north-central portion of the Alexander Archipelago (58°26' 40"N, 134°13'47"W), which is bounded by the Juneau Icefield to the east and the Lynn Canal to the west (Kelly *et al.*, 2007). Regional climate is hypermaritime, consisting of mild, wet winters and cool, wet summers (Carrara *et al.*, 2007). Juneau's mean annual precipitation is 150 cm but can exceed 225 cm, with rain falling an average of 230 days a year (Carrara *et al.*, 2007; Kelly *et al.*, 2007). The landscape transitions from the Pacific Ocean into steep glaciated mountains and includes glacier-fed rivers, *Sphagnum*-dominated peatlands and conifer forests (Alaback, 1982; DellaSala *et al.*, 2011). Palustrine wetlands, which include inland wetlands not adjacent to large lakes or streams, are the most commonly mapped ecosystems within the region. These ecosystems dominate valley bottoms, with vegetation transitioning into upland forests on steep slopes (US Department of Agriculture

(USDA), 1997; Fellman and D'Amore, 2007). Palustrine wetlands are characterized by the dominant-plant life form and classified as emergent (PEM), scrub-shrub (PSS) or forested (PFO). Scrub-shrub and forested wetlands have woody vegetation cover >30% but are distinguished by tree heights of <6 m for PSS and >6 m for PFO. Soils of palustrine wetland sites are histosols and spodosols (D'Amore *et al.*, 2012). Glacial till comprises the top metre of the soil profile on upland sites and influences drainage (Swanston, 1969; Collins, 1974; Alaback, 1982).

Site selection and installation

National Wetland Inventory (NWI) maps (Cowardin *et al.*, 1979) were imported into ArcGIS 9.2 (ESRI, Redlands, CA, USA) and partitioned by PEM, PSS, PFO and upland (U) sites. Three study sites were randomly selected from each NWI class using the generalized random tessellation stratified (GRTS) selection process. This spatially balanced, probability-based survey was implemented in R 2.9.2 (R Core Team, 2008) using the *spsurvey* package, the GRTS function, and equal probability selection (Stevens and Olsen, 2004; Detenbeck *et al.*, 2005). This process produced a list of randomly-dispersed sites for each NWI class, which were visited in selection order and excluded only if misclassified or human-modified. Study sites ($N=12$) were

installed across Juneau and Douglas Island (Figure 1), capturing all NWI classes (Figure 2). Sampling represented a statistical population of inference of about 1200 km², but factors driving distributions likely occur across a much larger geographical region.

To capture within-site environmental heterogeneity, each site was stratified into four topographically distinct sample units, and one groundwater-monitoring well was installed at each unit. Data were collected on elevation, aspect, slope, landform position and presence/absence of each tree species (Table I). Over a four-year period, we quantified the following: occurrence and biomass of each tree species, depth to groundwater, pH, soil ammonium-N, soil nitrate-N, and transmitted light (%). Groundwater measurements were summarized as annual and growing season maximum, minimum and mean depth to water, number of growing season days when the water table was within the rooting zone (≤ 20 cm from soil surface) (Coutts and Philipson, 1978, Wang *et al.*, 2002) and standard deviation of growing season water table depth. Further details on sampling methods and data processing are in Appendix S1.

Statistical analysis

To simultaneously consider the influence of abiotic and biotic variables on species distributions at multiple spatial

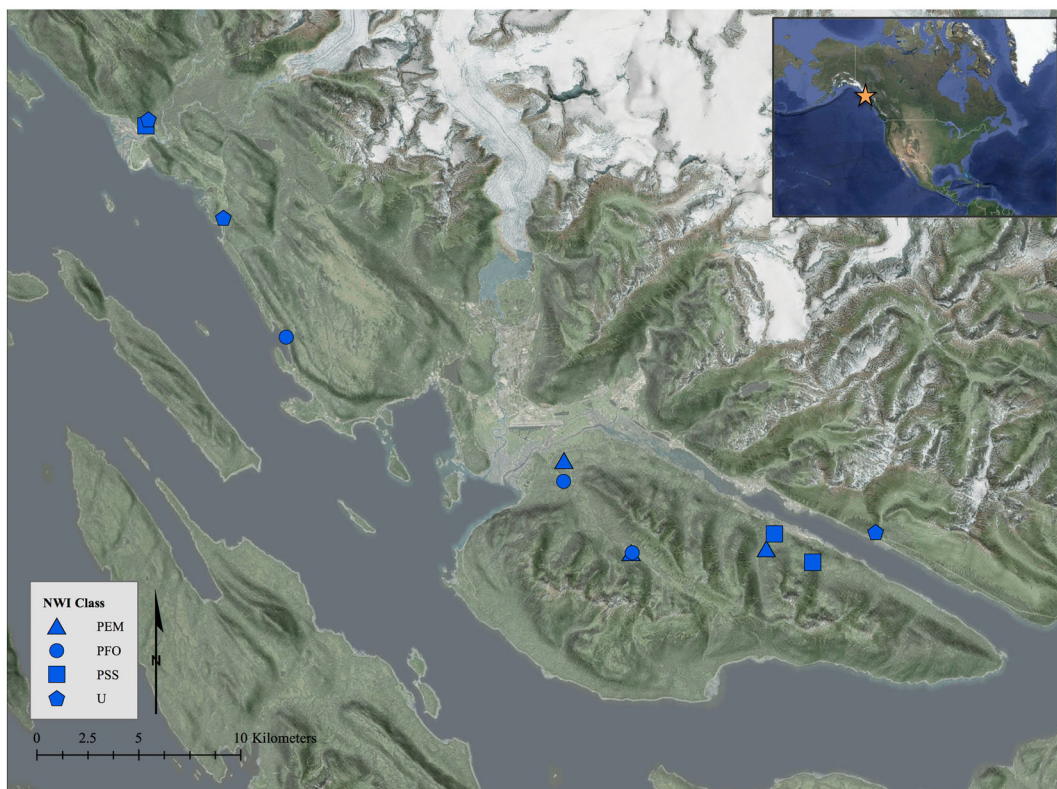


Figure 1. Map illustrating the distribution of sites across the Juneau–Douglas Island Complex of southeast Alaska, USA. PEM, palustrine emergent wetland; PSS, palustrine scrub-shrub wetland; PFO, palustrine forested wetland; U, upland forest.

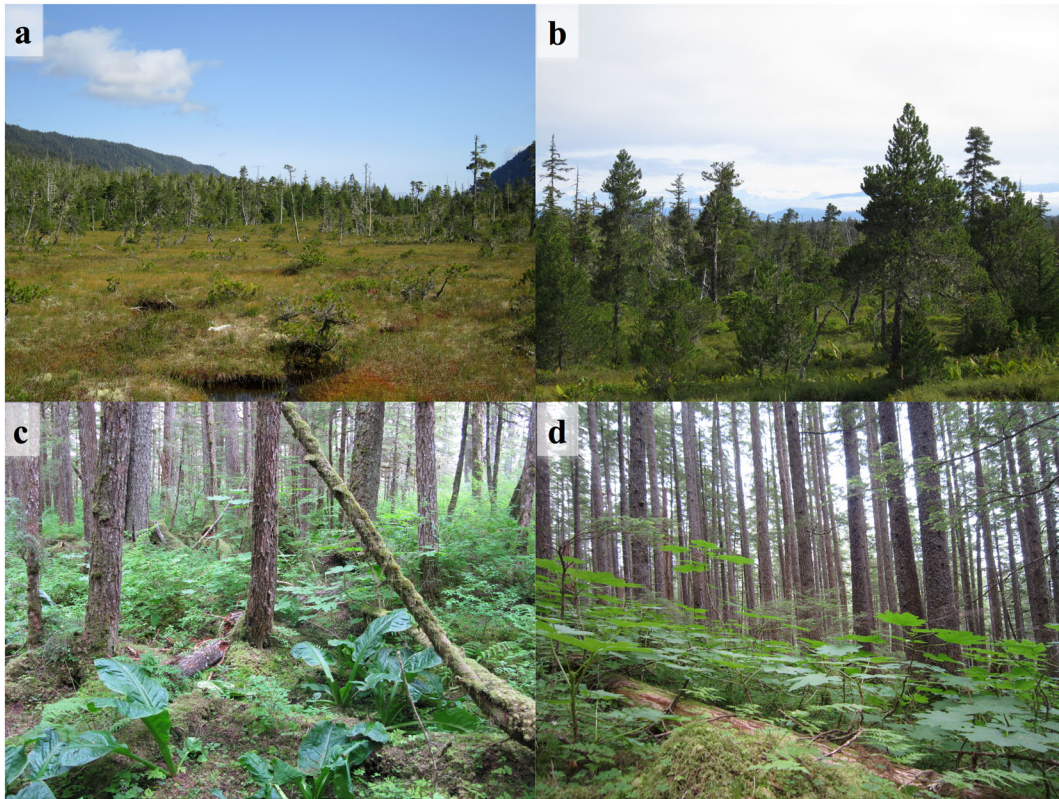


Figure 2. Representative National Wetland Inventory (NWI) ecosystem types in the coastal temperate rainforest of southeast Alaska, including palustrine emergent (a), palustrine scrub-shrub (b), palustrine forested (c), and upland (d) sites.

scales, we analyzed data using a Bayesian framework. Prior to fitting models, we examined the dataset for well-level and site-level spatial autocorrelation and correlations among predictor variables (See Appendix S2 for details). The number of growing season days when the water table was within the rooting zone (depth to water < 20cm, DTW₂₀) was minimally correlated (<0.65, Bothwell *et al.*, 2012) to other predictor variables and used in analysis. Initial assessments of covariance suggested that relationships between *P. sitchensis* and *T. heterophylla* biomass and DTW₂₀ were quadratic, indicating that biomass was highest within a narrow range of saturation and declined above or below this range. We used both linear and quadratic terms in biomass models.

We fit Bayesian hierarchical generalized linear mixed models to assess the relative importance of abiotic and biotic factors in determining tree species' occurrence and in limiting biomass (Diez and Pulliam, 2007). The hierarchical structure allowed for predictions at three spatial scales (well, site, and NWI class) and included uncertainty using random effects. Separate models were developed for predicting occurrence and biomass of each tree species (*P. contorta*, *P. sitchensis* and *T. heterophylla*).

Occurrence was modelled under a binary Bernoulli process, $Y_i \sim \text{Bernoulli}(\phi_i)$, where Y_i represents species occurrence at each well i , and ϕ_i is the estimated

probability of occurrence at each well. For each species, estimated probabilities of occurrence were related to linear predictors as

$$\log\left(\frac{\phi_i}{1 - \phi_i}\right) = \beta X_i \quad (1)$$

where β is a vector of regression coefficients, and X_i is a vector of well-level abiotic and biotic predictors. Depth to water (DTW₂₀), nitrate-N, and ammonium-N were included as potential abiotic predictors. Transmitted light (%) was used as a surrogate for the biotic effects of competition on species' occurrence.

Biomass was modelled as a normal distribution, $Y_i \sim \text{Normal}(\mu_i, \sigma_2)$ where Y_i represents species biomass at each well i . For each species, estimated probabilities of biomass were related to linear predictors as

$$\mu_i = \beta X_i + a_i + \rho_i \quad (2)$$

In this model, a_i is a random effect for site, and ρ_i is a random effect for NWI class. Both were normal random variables, such that $a_i \sim \text{Normal}(0, \sigma_s)$, where σ_s represents the variance among sites and $\rho_i \sim \text{Normal}(0, \sigma_t)$, where σ_t represents the variance among NWI classes. Nitrate-N, ammonium-N, pH and both linear and quadratic terms for DTW₂₀ were included as potential abiotic predictors.

Table I. Descriptions of each site in Juneau, Alaska, including National Wetland Inventory (NWI) class, location, landscape features, and tree species' occurrence (0/1).

Site name	NWI class	Latitude	Longitude	Elevation (m)	Aspect	Slope	Landform position	PICO presence (0/1)	PISI presence (0/1)	TSHE presence (0/1)
FAA	PEM	58.33578	-134.56222	52	North	0	Flat lowland	1	0	1
Water Tower	PEM	58.27284	-134.42079	211	North	5	Sloping lowland	1	0	1
Ski Area Fen	PEM	58.28849	-134.53043	278	West	10	Sloping lowland	1	0	1
Eagle River	PSS	58.52952	-134.81861	11	Southeast	0	Flat lowland	1	1	1
Water Tower	PSS	58.27801	-134.41075	130	South	0	Sloping lowland	1	0	1
Mt. Jumbo	PSS	58.26144	-134.38673	203	North	0-5	Sloping lowland	1	0	1
Tee Harbor	PFO	58.42273	-134.75595	48	West	5-10	Smooth hillslope	0	1	1
Fish Creek	PFO	58.32709	-134.56751	61	South	5	Sloping lowland	0	1	1
Ski Area PFO	PFO	58.28835	-134.52925	306	West	15	Smooth hillslope	0	1	1
Eagle River	U	58.41010	-134.61721	52	South	20	Smooth hillslope	0	1	1
Peterson	U	58.48095	-134.77828	77	North	20	Smooth hillslope	0	1	1
Sheep Creek	U	58.26595	-134.32890	122	Southeast	20	Mountain	0	1	1

PICO, *Pinus contorta* ssp. *contorta*; PISI, *Picea sitchensis*; TSHE, *Tsuga heterophylla*; PEM, palustrine emergent wetland; PSS, palustrine scrub; PFO, palustrine forested wetland; U, upland; FAA, Federal Aviation.

Biomass of other tree species (Mg/ha) was used as a surrogate for the biotic effects of competition on species' biomass (Waring and Running, 1998), which was assumed to be a reasonable substitute for the effects of competition.

All models were fit using flat, non-informative priors (gamma (0.01, 0.01) for inverse residual variance, Normal (0, 100) for regression coefficients, and uniform (0, 10) for random effects (Gelman, 2006). All continuous covariates were standardized. We used posterior probability densities of regression coefficients to determine whether to retain coefficients in the final model. If the 95% credible interval for the parameter did not include zero, we considered the effect of that covariate non-zero and correlated to species occurrence and/or biomass. Model-fitting procedures are detailed in Appendix S2.

We estimated Bayesian R^2 at each level of the model to quantify the proportion of variance explained across this hierarchical scale. Both marginal and conditional R^2 were calculated using medians of the parameter posteriors; marginal R^2 includes the variance explained by fixed effects, while conditional R^2 includes the proportion of variation explained by both fixed and random effects (Nakagawa and Schielzeth, 2013). We also calculated variance partition coefficients (Goldstein *et al.*, 2002) to describe unexplained variation across this hierarchical sampling schema.

RESULTS

The abiotic and biotic environment

Forest community composition varied as a function of topography, and site hydrologic regime was linked to landscape position. Wetlands extended from the lowest landscape position to hillslopes, where drainage became sufficient to support upland forests. Mean annual depth to water was distinguishable between but highly variable within NWI classes (Figure 3). Although most sites met the minimum requirements of their assigned class (Cowardin *et al.*, 1979), including percent canopy cover and period of inundation, ecological conditions varied, particularly within PSS and PFO classes (Table II).

Spatial variability of soil saturation was important in the distribution of tree species. Over the four-year sampling period, PEM and PSS water tables rarely dropped below the plant root zone (DTW₂₀), while water tables in U sites never rose into this zone (Figure 3). The water table was <20 cm from the soil surface in PEM and PSS sites for an average of 121 (±10) and 102 (±30) days of the 138-day Juneau growing season from 2009–2013 (Table II), with drawdown occurring during June and July each year (Figure 3a and b). Hydrologic regime was more highly variable in PFO and U sites (Figure 3c and d), but patterns emerged in rooting-zone saturation, occurring on average for 74 days (±46) in PFO sites and never

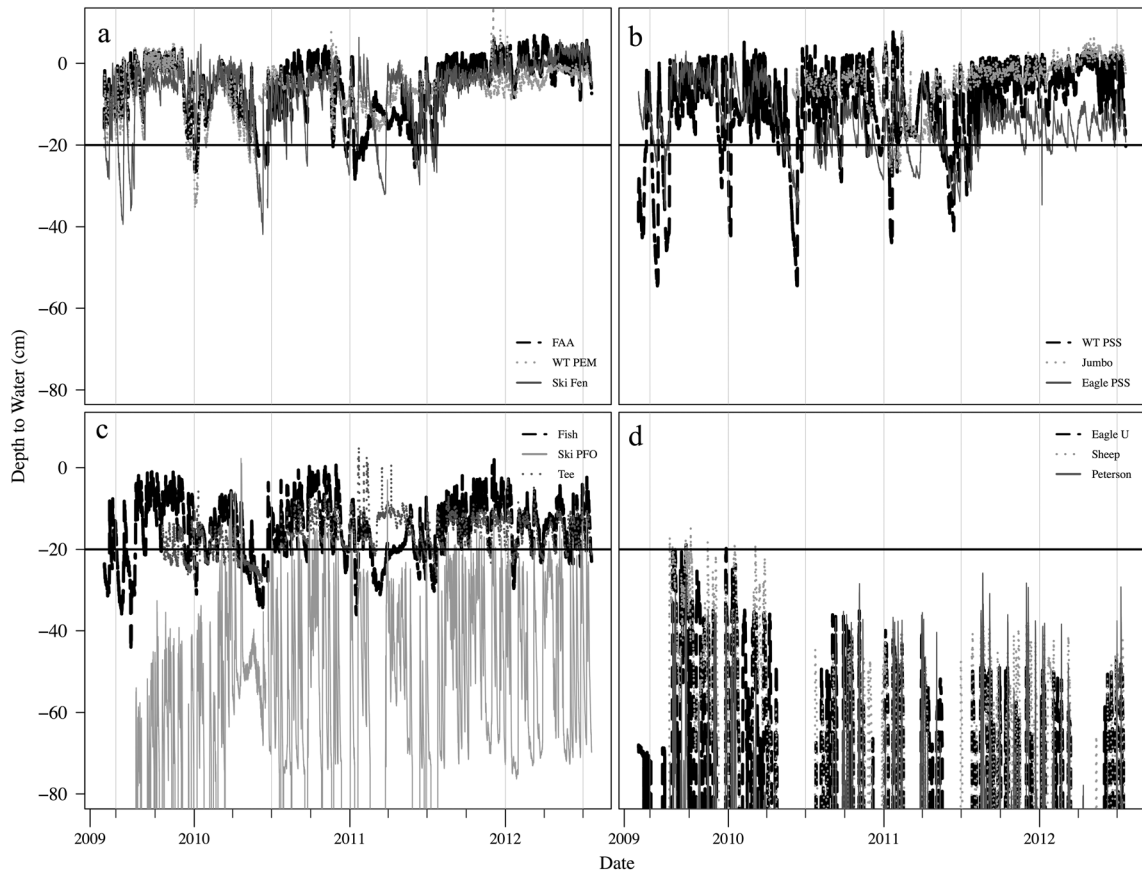


Figure 3. Hydrologic data from June 2009 through July 2013 in palustrine emergent (a), palustrine scrub-shrub (b), palustrine forested (c), and upland (d) sites in southeast Alaska.

reaching the root zone in U sites (0 of 138 days). The Ski Area PFO water table rose during precipitation events and responded more like a U than a PFO (Figure 3c). Increases in the water table at U sites were ephemeral and driven by large precipitation events or sustained periods of snowmelt. Depth to the water table exceeded 1 m for the majority of each growing season (Figure 3d), and drawdown closely followed the end of precipitation events.

Hydrologic regime influenced pH and development of forest biomass (Table II, Figure 4). Emergent and scrub-shrub wetlands were peatlands with high water tables and $\text{pH} < 5.0$ (Table II). Forested wetlands were peat-accumulating with high water tables and were less acid, $\text{pH} > 5$. Upland sites were well drained with pH similar to rain or slightly more alkaline, $\text{pH} > 5.6$. Upland pH was more basic with deeper mean growing season water tables (Figure 4a) and lower percentages of transmitted light (Figure 4b), which corresponded to greater overstory biomass and increased canopy cover (Figure 4a and d). *Tsuga heterophylla* accounted for the majority of the overstory biomass and closed canopy in PFO and U sites (Figure 4d).

The occurrence and biomass of each conifer varied across the gradient. *Pinus contorta* occurred only in peat-accumulating PEM and PSS sites (Figure 4c), with its highest

biomass on two PSS sites (Table II, Water Tower and Mt. Jumbo). *P. sitchensis* was absent or represented by a few individuals in PEM and PSS sites (Figure 4c). Its biomass was higher on sites with greater water table depth and was closely tied to landscape position and slope (Tables I and II). *Tsuga heterophylla* occurred on every site along the gradient, but biomass was higher on sites with a greater depth to the water table and steeper slope (Figure 4c and Table II).

Species' distributions

Pinus contorta, *P. sitchensis* and *T. heterophylla* distributions were explained by different abiotic and biotic variables (Figure 5), but the number of days with water in the rooting zone (DTW_{20}) was highly correlated with species' occurrence and biomass for all but *P. contorta* occurrence (Figure 5; 95% credible interval, CI). The mean predicted probability of occurrence of *P. contorta* was less than 0.05 until DTW_{20} exceeded 48, and its probability of occurrence increased with increases in DTW_{20} (up to 0.85 [0.15, 0.99] at 137 days, Figure 6). For *P. sitchensis*, predictions of occurrence (Figure 6) exceeded 0.95 until DTW_{20} was greater than 107 days. Beyond this point, probability of occurrence declined and fell below 0.05 when DTW_{20} was

Table II. Mean and standard error (±SE) of abiotic and biotic characteristics of each study site, including tree species biomass, depth to groundwater (cm below surface), groundwater pH, soil nitrogen, and percent transmitted light.

Site name	NWI Class	PICO biomass (Mg/ha)	PISI biomass (Mg/ha)	TSHE biomass (Mg/ha)	Mean annual depth to water (cm below surface)	Mean growing season depth to water (cm below surface)	Mean growing season days depth to water > -20 (cm)	Groundwater pH	NH ₄ (ug/g dry soil)	NO ₃ (ug/g dry soil)	Transmitted light (%)
FAA	PEM	17.67 (±0.62)	0	0.53 (±0.14)	6.25 (±3.70)	12.76 (±2.79)	123 (±7)	4.12 (±0.05)	14.71 (±1.2)	10.87 (±1.28)	96.19 (±0.33)
Water Tower	PEM	27.86 (±2.40)	0	3.37 (±2.24)	5.32 (±1.73)	5.61 (±1.12)	123 (±15)	4.92 (±0.12)	28.81 (±10.76)	12.99 (±7.00)	83.85 (±6.57)
Ski Area	Fen	6.97 (±2.52)	0	1.29 (±0.44)	7.22 (±4.30)	16.04 (±1.27)	117 (±8)	4.81 (±0.03)	16.53 (±2.31)	15.14 (±3.61)	80.01 (±5.06)
Eagle River	PSS	2.71 (±1.42)	4.27 (±0.96)	3.97 (±1.41)	14.64 (±3.65)	20.98 (±2.14)	64 (±13)	4.35 (±0.07)	17.84 (±6.53)	24.04 (±6.03)	86.94 (±1.40)
Water Tower	PSS	48.41 (±0.84)	0	2.52 (±0.62)	11.07 (±5.4)	21.61 (±1.98)	109 (±3)	4.57 (±0.06)	10.58 (±2.73)	13.05 (±3.86)	57.49 (±7.44)
Mt Jumbo	PSS	37.35 (±2.80)	0	4.48 (±0.81)	4.66 (±3.10)	5.47 (±2.53)	132 (±8)	4.38 (±0.15)	42.19 (±2.51)	10.47 (±1.80)	85.91 (±4.14)
Tee Harbor	PFO	0	68.07 (±16.43)	267.61 (±22.63)	16.51 (±2.30)	20.03 (±5.73)	108 (±5)	5.41 (±0.08)	72.42 (±29.11)	5.20 (±0.32)	13.33 (±1.10)
Fish Creek	PFO	0	91.35 (±28.48)	267.58 (±10.71)	15.49 (±3.70)	21.37 (±3.23)	105 (±5)	5.84 (±0.13)	95.53 (±26.59)	5.05 (±0.90)	19.02 (±2.52)
Ski Area	PFO	0	75.27 (±10.61)	335.95 (±12.91)	62.10 (±13.50)	79.8 (±9.6)	9 (±2)	4.96 (±0.08)	12.48 (±3.82)	3.22 (±0.46)	15.16 (±1.13)
Eagle River	U	0	96.42 (±9.02)	307.33 (±5.83)	84.05 (±12.03)	94.76 (±7.93)	0	5.86 (±0.17)	23.49 (±8.40)	4.04 (±0.95)	18.53 (±2.60)
Peterson	U	0	31.18 (±13.30)	585.50 (±93.85)	95.69 (±7.20)	101 (±1.00)	0	5.88 (±0.17)	8.04 (±1.15)	4.55 (±0.73)	11.87 (±0.45)
Sheep Creek	U	0	213.62 (±38.85)	451.36 (±63.43)	79.04 (±13.47)	93.06 (±3.67)	0	5.95 (±0.14)	38.42 (±26.21)	9.39 (±3.22)	15.88 (±0.47)

PICO, *Pinus contorta* ssp. *contorta*; PISI, *Picea sitchensis*; TSHE, *Tsuga heterophylla*; PEM, palustrine emergent wetland; PSS, palustrine scrub-shrub wetland; PFO, palustrine forested wetland; U, upland.

* Out of 138 day growing season, defined as 15 May through 30 September.

greater than 130 days. *Tsuga heterophylla* was predicted to occur across all sites, with mean predicted probability of occurrence exceeding 0.99 over the entire range of DTW₂₀ observed. Thresholds were identified for *P. contorta* and *P. sitchensis* occurrence at greater than 45 and less than 100 DTW₂₀, respectively. Credible intervals were much wider for *P. contorta*, suggesting that rooting-zone saturation was less important for its occurrence than for *P. sitchensis*.

Pinus contorta occurrence and biomass were best explained by shade intolerance and competitive ability. Occurrence was positively correlated with percent of transmitted light, while its biomass was negatively correlated with *P. sitchensis* biomass (Figure 5; 95% CI). *Pinus contorta* was absent from sites until transmitted light exceeded 40%, which corresponded to reductions in *P. sitchensis* and *T. heterophylla* biomass. *Pinus contorta* biomass was also negatively correlated with the quadratic water-table variable, indicating that biomass accumulation is closely tied to the number of growing season days when the water table falls below the rooting zone. This species was absent from sites where the depth to water exceeded 25 cm, at which point *P. sitchensis* and *T. heterophylla* increased (Figure 4c).

Picea sitchensis and *T. heterophylla* occurrence and biomass were best explained by DTW₂₀ and pH. Rooting zone saturation was the most influential variable in *P. sitchensis* occurrence. With the exception of a few established individuals in Eagle PSS, this species was absent when the water table was within the rooting zone (DTW₂₀) and lower soil nitrate-N concentrations occurred (Figure 5, 95% CI). Occurrence was positively associated with concentrations of soil ammonium-N (95% CI). The best predictors of *P. sitchensis* biomass were the quadratic water table variable and pH, with the quadratic term indicating that biomass was highest under a narrow range of conditions (DTW > -100 cm, Table II) and declining above or below this range. *Tsuga heterophylla* presence was positively associated with soil ammonium-N concentrations, which was the strongest predictor of occurrence. Occurrence was negatively associated with wetland conditions, including DTW₂₀ and a high percentage of transmitted light (Figure 5, 95% CI). Biomass of *T. heterophylla* was best explained by the quadratic water table variable and pH. Its biomass was highest when water table depth exceeded -100 cm but was predicted to decline above or below this threshold. Positive parameter estimates (Figure 5, 95% CI) indicate that this optimal range is driven by a lower water table and a higher pH. Both *P. sitchensis* and *T. heterophylla* biomasses were negligible on sites where the depth to water was less than 25 cm (Figure 4c).

Occurrence models outperformed biomass models in explaining species' distributions (Table III). Occurrence models explained 95%, 99%, and 89% of the variation in *P. contorta*, *P. sitchensis* and *T. heterophylla* presence (marginal R², Table III). Tree species' presence and absence

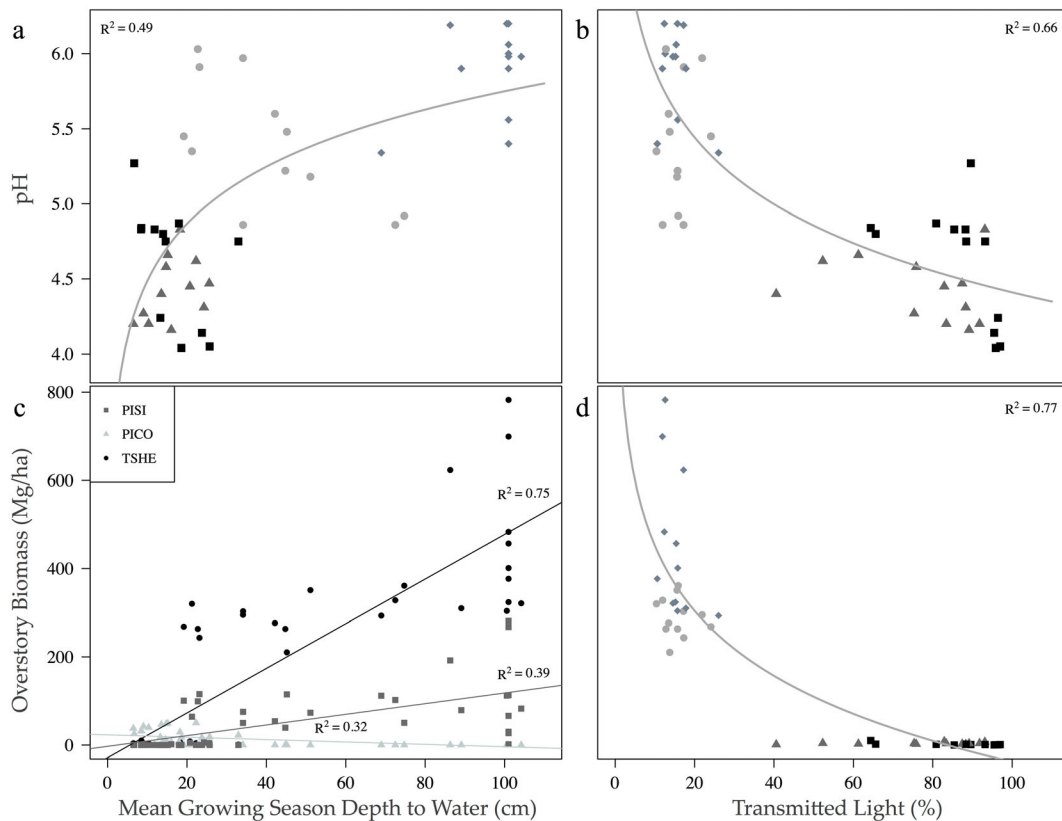


Figure 4. Well-level site ecological data from palustrine emergent (dark grey triangles), palustrine scrub-shrub (black squares), palustrine forested (light grey circles), and upland (slate grey diamonds) sites in southeast Alaska. Figures illustrate the relationships between pH and mean growing-season depth to water (a), pH and percent of transmitted light (b), overstory biomass by tree species and mean growing season depth to water (c), and *Tsuga heterophylla* (TSHE) biomass and percent of transmitted light (d). Symbols in Figure 1c represent well-level data by species rather than well-level data by National Wetland Inventory (NWI) class. PICO, *Pinus contorta* ssp. *contorta*; PISI, *Picea sitchensis*.

were correctly assigned by posterior predictions >90% of the time for *P. contorta* and *P. sitchensis* (Table III). The low predictive power of *T. heterophylla* occurrence (Table III) was likely a function of its presence on all sites. The addition of random effects for site and NWI class improved predictive power of biomass models (conditional R^2 , Table III), but importance of these variables indicated that unmeasured variation at these levels was important in explaining biomass. After accounting for fixed effects, *P. contorta* and *P. sitchensis* biomass varied more across sites than NWI class (Figure 7), while *T. heterophylla* biomass varied more across NWI class than sites. Variance partition coefficients identified NWI class as the greatest source of unexplained variation for *P. contorta* and *P. sitchensis* biomass, but the greatest source of unexplained variation in *T. heterophylla* occurred at the well level (Table IV).

DISCUSSION

Abiotic and biotic influences on conifer distributions

Dynamic interactions between abiotic and biotic factors explain the distribution of conifers in the coastal temperate

rainforest of southeast Alaska. Growing-season soil saturation and light limitations created by other conifers act together to determine species' presence or absence, while pH and hydrologic variability control biomass accumulation. Local abiotic factors strongly influence occurrence and biomass, but these factors interact with biotic drivers to filter potential species and determine the forest community. This study identifies abiotic and biotic limits of conifer distributions along wetland to upland gradients and quantifies tolerance thresholds for the local species. Our analysis allowed us to identify local niche requirements for each tree species, including quantified values for the limits of depth to groundwater, pH, soil nitrogen and light.

Our study was grounded on the concept that the landscape strongly influences plant distributions (Beatty, 1984; Vivian-Smith, 1997; Hutchinson *et al.*, 1999). Microtopographic variation and heterogeneous terrain control the distribution of water and duration of soil saturation, and hydrologic regime can limit species' occurrence (Vitt and Chee, 1990; Zoltai and Vitt, 1995; Asada *et al.*, 2003). The coastal temperate rainforest of southeast Alaska amplifies the common transition from wet to dry ecosystems, as continuous precipitation influences vegetation across the entire wetland

CONIFER DISTRIBUTIONS ACROSS HYDROLOGIC GRADIENTS IN THE TEMPERATE RAINFOREST

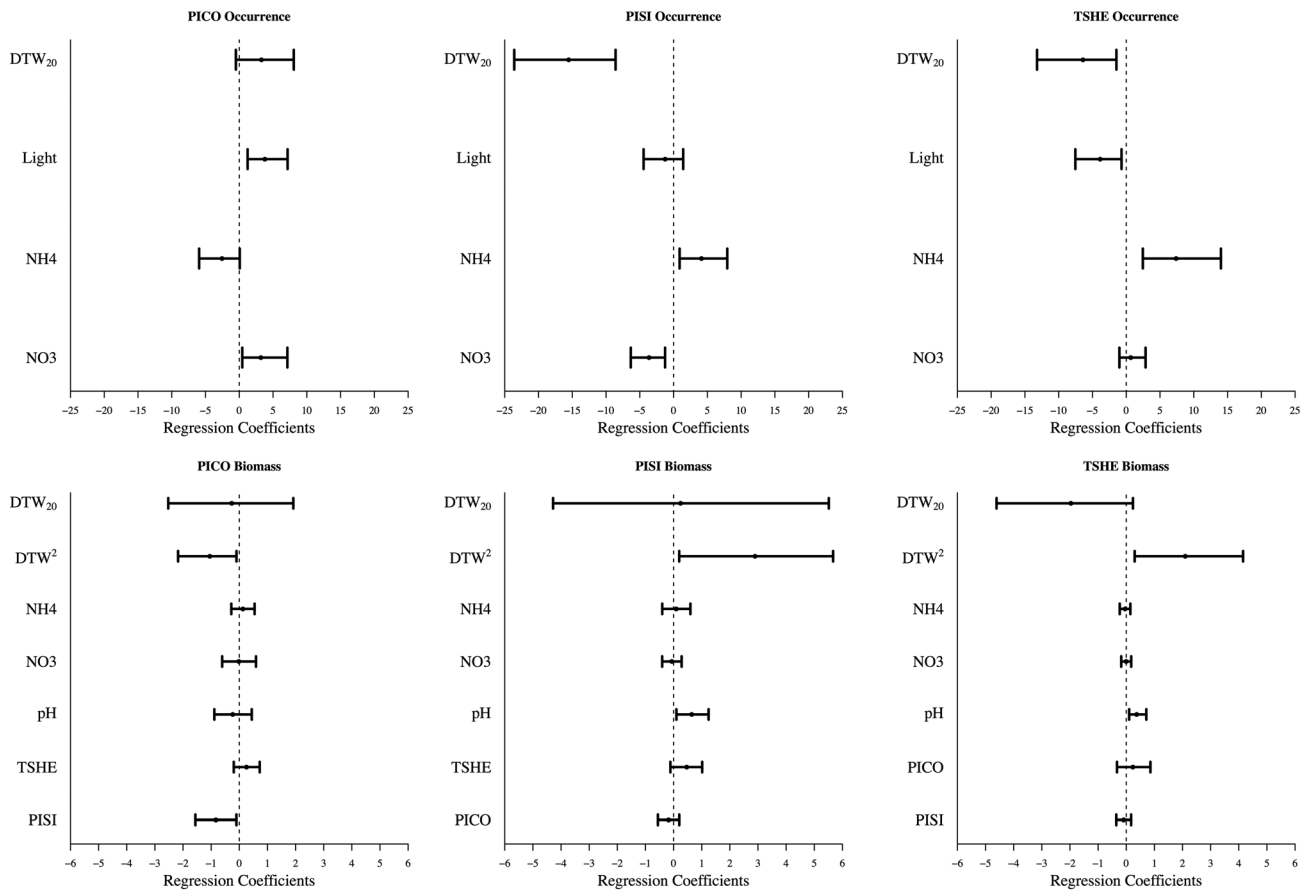


Figure 5. Posterior estimates of regression coefficients from Bayesian hierarchical models. The top row shows model output from occurrence models, and the bottom row shows output from biomass models. Points represent the mean values, and lines display the 95% credible interval. We considered those variables with intervals that did not cross the vertical zero line as non-zero. DTW/DTW₂₀, depth to water in rooting zone (>20 cm); DTW², quadratic depth to water; PICO, *Pinus contorta* ssp. *contorta*; PISI, *Picea sitchensis*; TSHE, *Tsuga heterophylla*.

to upland gradient (Neiland, 1971; D'Amore *et al.*, 2012). The timing, duration, and extent of soil saturation influence pH, oxygen levels, and nutrient availability, as well as the accumulation of organic matter. These products of hydrologic regime set the stage for the distribution of species across this landscape.

While hydrologic regime is the major abiotic influence on plant occurrence and biomass in southeast Alaska, hydrology alone did not explain distributional patterns. Occurrence was not coupled to a specific hydrologic regime nor was biomass of co-occurring species controlled by the same limiting factor. Rather, conifer distributions were driven by complex interactions between abiotic and biotic stressors. Abiotic factors filtered the local species pool and determined which conifers survived and persisted along the wetland to upland gradient. The resulting forest community further influenced the local environment by altering light availability, ecosystem productivity, and nitrogen inputs (Beatty, 1984; Xiong *et al.*, 2003; D'Amore and Bisbing, *unpublished data*), and facilitating interspecies competition for these resources (Davis *et al.*, 1998, 1999). Although abiotic and biotic limitations are not

always sequential steps in community assembly (Kraft *et al.*, 2014), the saturated, nutrient-poor conditions of local emergent wetlands act as a selective force and limit tree establishment. Tolerance of the local environment was the primary determinant of conifer occurrence, but abiotic and biotic interactions together defined forest community composition and plant zonation. These concepts had previously been explored for herbaceous plant communities (Weiher and Keddy, 1999; Seabloom *et al.*, 2001; Crain *et al.*, 2004; Cornwell and Ackerly, 2009) but were poorly understood for conifer species occurring across natural hydrologic gradients.

Conifer distributions along wetland to upland gradients appear to be driven by a range of adaptive strategies, including competitive dominance, stress tolerance, and phenotypic plasticity (Tilman, 1982; Grime, 2002; Grime and Mackey, 2002). Species able to tolerate interspecific competition were most productive at the drier end of the gradient because of their inability to survive in saturated soils (Grace and Tilman, 1990; Campbell and Grime, 1992; Crain *et al.*, 2004). Sites with stable water tables near the surface were dominated by *Sphagnum* spp. mosses that, by

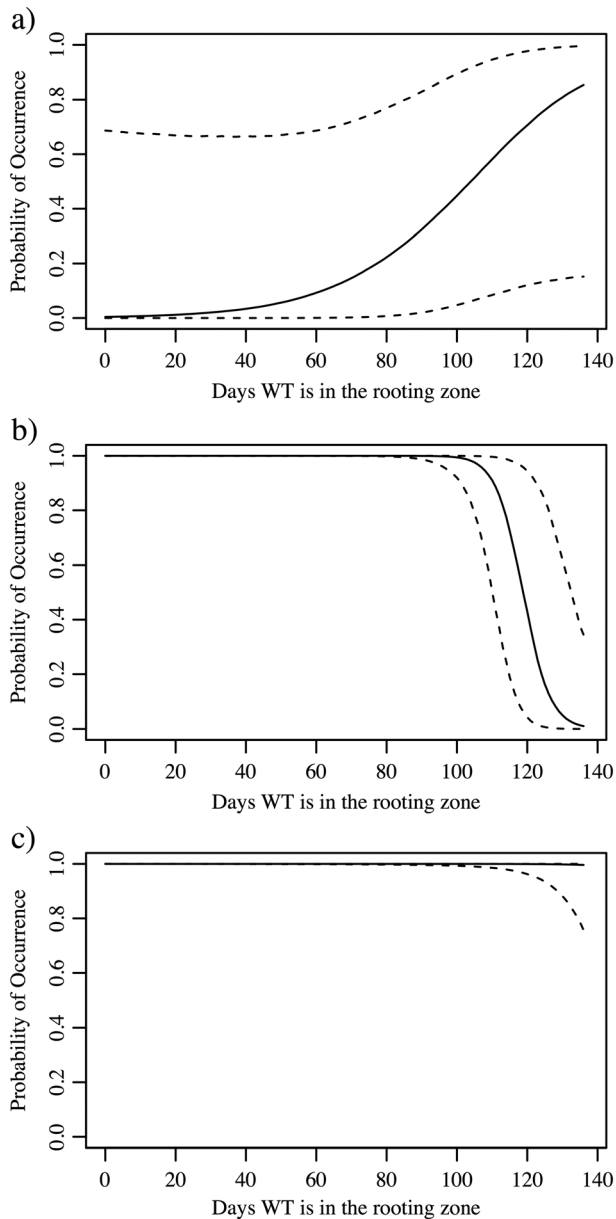


Figure 6. The predicted probability of occurrence of (a) *Pinus contorta ssp. contorta*, (b) *Picea sitchensis*, and (c) *Tsuga heterophylla* over the gradient in the number of days during the growing season when the water table was within the root zone (≤ 20 cm from soil surface) while fixing all other predictors at their mean values. Solid lines represent posterior estimates of regression coefficients from Bayesian hierarchical models and dashed lines display the 90% credible interval.

ion exchange mechanisms (Clymo, 1963, 1964), drive the site pH from 4.0 to 4.5, limiting occurrence of *P. sitchensis* and aboveground biomass accumulation of all conifers. Conversely, *Sphagnum* spp. mosses were mostly absent from sites with water tables fluctuating in and out of the rooting zone, where pH was > 5 and conifers dominated the vegetation. The physical landscape produced the template for the accumulation of water and development of anaerobic soil conditions, which created the first limitation

to tree species establishment. These abiotic conditions limit plant community composition to tolerant or phenotypically plastic species in coastal (D'Amore *et al.*, 2010) and boreal forested peatlands (Chapin *et al.*, 2004a, b), while interacting abiotic and biotic factors limit productivity across wetland to upland gradients.

Response of Alaskan conifers

Competitively dominant *P. sitchensis* occurred where the abiotic conditions of depth to water, pH, and soil nitrogen were favorable for tree establishment and growth. Stress-tolerant *P. contorta* was more susceptible to biotic stressors and competitively excluded from well-drained sites. Higher water tables, lower nitrogen, and low pH did not hinder *P. contorta* occurrence. Its distribution was limited to saturated, nutrient-poor wetlands because of light limitations in PFO and U sites created by a dense *P. sitchensis* and *T. heterophylla* canopy. In the absence of interspecific competition, *P. contorta* would be capable of inhabiting the entire gradient explored here (Bisbing, unpublished data). However, competition narrows its distribution by displacing it from its potential optimum in well-drained sites and forcing it to occupy wetland habitats where other conifers are limited in productivity. This distribution pattern is characteristic of *P. contorta* across its entire range, with each subspecies (*bolanderi*, *contorta*, *latifolia* and *murrayana*) growing under harsher conditions than co-occurring conifers. For example, subspecies *contorta* grows in coastal sand dunes, rocky seaside cliffs, and peatlands from British Columbia to its southern extent in California (Lotan and Critchfield, 1990). Although competition and light availability have been hypothesized as determinants of *P. contorta ssp. contorta* occurrence (Lotan and Critchfield, 1990), its ecological requirements had not been previously quantified as they have been for subspecies *latifolia* (Chen *et al.*, 1996; Schoettle and Smith, 1999). Our study provides support for the intolerance and limitation of *P. contorta ssp. contorta* by competition and the limitation of *P. sitchensis* more by abiotic conditions, such as persistent saturated soil conditions within the root zone (Coutts and Philipson, 1978).

Highly plastic *T. heterophylla* transcended hydrologic limitations, taking advantage of favorable conditions that promoted biomass accumulation while also tolerating wet conditions that limited growth. The intermediate shade tolerance of this species allowed it to occupy a range of sites (Malavasi and Perry, 1993), but soil saturation and low pH limited productivity in PEM and PSS wetlands. One potential explanation for *T. heterophylla* occurrence in wetlands is that germination is closely tied to specific environmental conditions that create aerobic microsites. It is also possible that dry summers result in a water table deep enough to allow establishment in typically inhospitable

Table III. Model summaries of occurrence and abundance for each species. Marginal R^2 is the proportion of variance explained by fixed effects. Conditional R^2 is the proportion of variance explained by fixed and random effects. Assignment statistics assess the proportion of the time the model correctly assigns the presence/absence data. Results assess model performance across all levels of the hierarchy: well, site, and National Wetland Inventory (NWI) class.

	Occurrence models			Biomass models	
	Marginal R^2	Correctly assigned presence	Correctly assigned absence	Marginal R^2	Conditional R^2
PICO	0.95	0.97	0.96	0.10	0.84
PISI	0.99	0.95	0.94	0.08	0.69
TSHE	0.89	0.88	0.63	0.03	0.50

PICO, *Pinus contorta* ssp. *contorta*; PISI, *Picea sitchensis*; TSHE, *Tsuga heterophylla*.

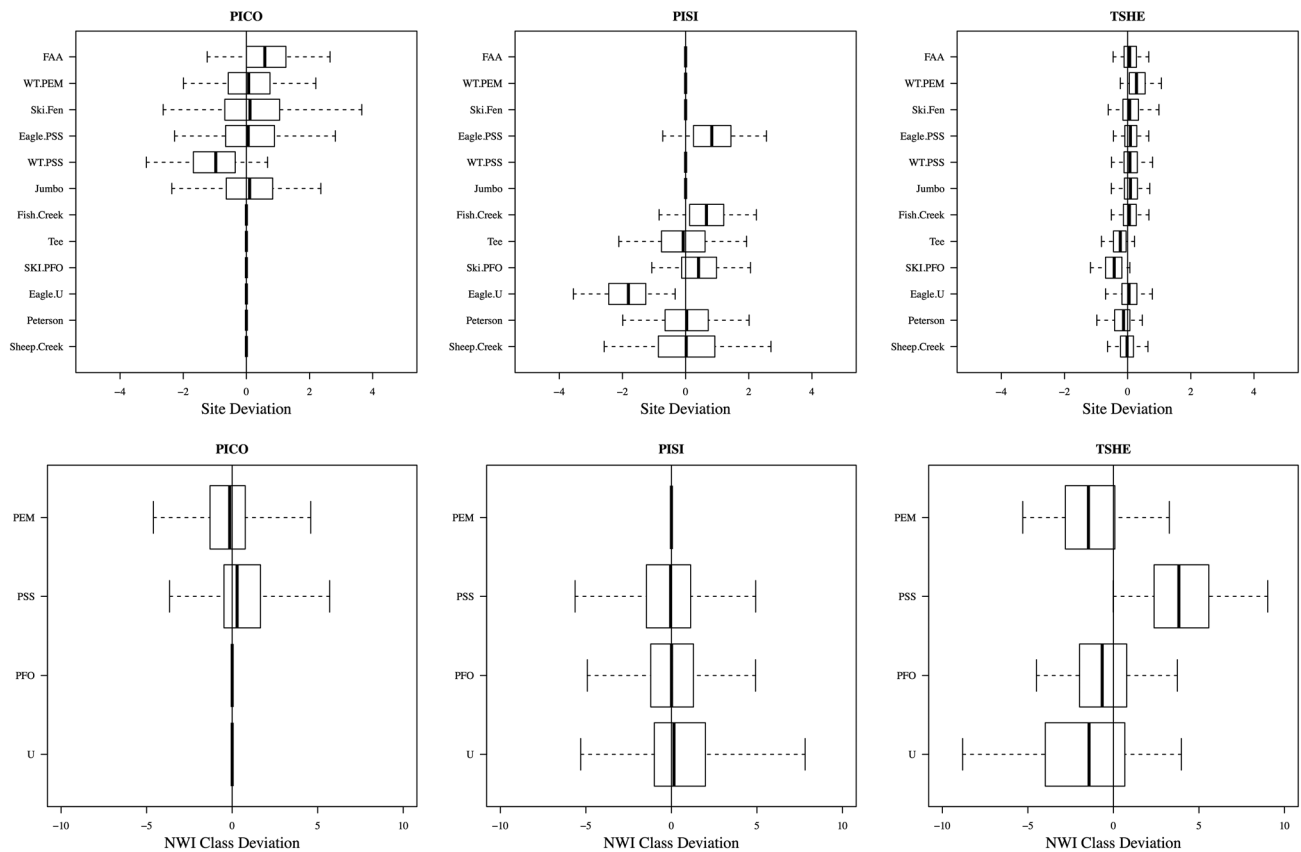


Figure 7. Posterior distributions of site and National Wetland Inventory (NWI) class random effects from biomass models. Black bars represent predicted means; boxes display 25th and 75th percentiles; whiskers show the 95% credible interval. We considered variables with intervals that did not cross the vertical zero line as non-zero. Site effects are presented in the top row, and NWI class effects are displayed in the bottom row. PICO, *Pinus contorta* ssp. *contorta*; PISI, *Picea sitchensis*; TSHE, *Tsuga heterophylla*; PEM, palustrine emergent wetland; PSS, palustrine scrub-shrub wetland; PFO, palustrine forested wetland; U, upland.

PEM and PSS wetlands. Across the region, *T. heterophylla* occurs in all ecosystems found along this wetland to upland gradient but is limited in biomass accumulation by local abiotic conditions.

Indicator status of Alaskan tree species

The close association of each conifer with specific abiotic and biotic factors can be used to evaluate NWPL rankings in

particular wetland or upland niches in the Alaska region and beyond. Our findings narrow the potential tolerance range for each species and suggest both a subspecies and regionally based evaluation of wetland plant rankings. The limited tolerance of *P. sitchensis* to saturated conditions and its dominance in well-drained sites support its classification as a FACU species. Despite occasional occurrence in wetlands, it does not meet the minimum occurrence threshold (34–66%) for classification as a FAC species.

Table IV. Variance partition coefficients (VPCs) by species for well, site, and NWI class in the biomass models. VPCs explain how variance is partitioned for each model and represent the amount of unexplained variation at each spatial scale.

	PICO	PISI	TSHE
Well	0.18	0.34	0.52
Site	0.20	0.13	0.10
NWI Class	0.62	0.53	0.38

PICO, *Pinus contorta* ssp. *contorta*; PISI, *Picea sitchensis*; TSHE, *Tsuga heterophylla*; NWI, National Wetland Inventory.

Pinus contorta is a wetland indicator and would fit the definition of FACW or OBL wetland species in southeast Alaska. This ranking is not necessarily related to this species' preference for saturated conditions but rather its inability to compete with *P. sitchensis* and *T. heterophylla* on well-drained sites. The low tolerance of this subspecies to competition makes it a strong indicator of emergent and scrub-shrub wetlands in southeast Alaska and an inhabitant of drier upland sites and rocky cliffs at the southern extent of its distribution (Lotan and Critchfield, 1990). Our research and knowledge of this species' distribution lead us to suggest that *P. contorta* wetland plant rankings be separated into subspecies designations for the Alaska region. Subspecies *contorta* is best identified as FACW or OBL, while subspecies *latifolia* is better classified as FACU or U. Finally, *T. heterophylla* occurrence and success across the entire gradient make it hard to categorize. *Tsuga heterophylla* is classified as FAC for Alaska, suggesting it is successful in all habitat types along the wetland to upland gradient. This species could retain its FAC designation but best fits the FACU ranking in the coastal temperate rainforest, as it is a dominant species of upland forests and a minor component of emergent and scrub-shrub wetland ecosystems in southeast Alaska.

Next steps

One limitation of our research is its focus on established forest communities. Species' occurrence and biomass are a function of exposure not only to environmental stressors over the lifetime of individuals but also to conditions at the time of establishment. Early life stages are poorly understood and minimally studied, as in the case for the conifer species presented here. Dendrochronology, aerial photo analysis and field studies can be used collectively to identify patterns of past and current establishment. Given our minimal understanding of tree species' ecological requirements for establishment and the uncertainties associated with climate change predictions for the region, future research should address this critical gap in knowledge.

CONCLUSIONS

This research is the first to quantify the drivers of conifer species' distributions across a wetland to upland gradient and to identify the primary determinants of tree species occurrence and biomass in the coastal temperate rainforest of southeast Alaska. Collectively, results highlight the importance of ecological and hydrologic interactions. Landscapes strongly control hydrologic regime, which in turn, alters the local environment and determines plant community composition. The local plant community can alter the local environment through organic matter accumulation, controlling pH, rooting depth, light availability, and the creation of micro-topographic variation. These feedbacks between abiotic and biotic processes directly shape tree species distributions across several spatial scales and hydrologic gradients. Understanding the role of each factor and the interactions among processes is essential to describing a species' niche and in determining drivers of its distribution. This knowledge of local and regional drivers of species' distributions and the relative importance of interacting abiotic and biotic drivers provides critical information for land management and regulation. Wetland delineation procedures can be improved through application of the empirical limits identified for each species, as implemented and addressed in this study. Distinct zones of species abundance also provide a template for future research into potential species' range shifts as environmental conditions change over time.

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