

Landscape-scale patterns in tree occupancy and abundance in subarctic Alaska

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Abstract. Recent studies suggest that climate warming in interior Alaska may result in major shifts from spruce-dominated forests to broadleaf-dominated forests or even grasslands. To quantify patterns in tree distribution and abundance and to investigate the potential for changes in forest dynamics through time, we initiated a spatially extensive vegetation monitoring program covering 1.28 million ha in Denali National Park and Preserve (DNPP). Using a probabilistic sampling design, we collected field measurements throughout the study area to develop spatially explicit Bayesian hierarchical models of tree occupancy and abundance. These models demonstrated a strong partitioning of the landscape among the six tree species in DNPP, and allowed us to account for and examine residual spatial autocorrelation in our data. Tree distributions were governed by two primary ecological gradients: (1) the gradient from low elevation, poorly drained, permafrost-influenced sites with shallow active layers and low soil pH (dominated by *Picea mariana*) to deeply thawed and more productive sites at mid-elevation with higher soil pH on mineral substrate (dominated by *Picea glauca*); and (2) the gradient from older, less recently disturbed sites dominated by conifers to those recently affected by disturbance in the form of fire and flooding with increased occupancy and abundance of broadleaf species. We found that the establishment of broadleaf species was largely dependent on disturbance, and mixed forests and pure stands of broadleaf trees were relatively rare and occurred in localized areas. Contrary to recent work in nearby areas of interior Alaska, our results suggest that *P. glauca* distribution may actually increase in DNPP under warming conditions rather than decline as previously predicted, as *P. glauca* expands into areas formerly underlain by permafrost. We found no evidence of a shift to broadleaf forests in DNPP, particularly in the poorly drained basin landscape positions that may be resistant to such changes. Overall, our results indicate that probabilistic sampling conducted at a landscape scale can improve inference relative to the habitat associations driving the distribution and abundance of trees in the boreal forest and the potential effects of climate change on them.

Key words: Alaska; *Betula neoalaskana*; boreal forest; Denali National Park and Preserve; landscape-scale pattern; *Larix laricina*; *Picea glauca*; *Picea mariana*; *Populus balsamifera*; *Populus tremuloides*; species–environment; vegetation monitoring.

INTRODUCTION

The boreal forest is the second largest terrestrial biome on Earth (Saugier et al. 2001), representing ~14% of the vegetation cover (McGuire et al. 1995) and 29% of the total forested area (Kuusela 1990). However, the boreal forest contains fewer species than any other forested biome (Pastor and Mladenoff 1992), and only six native tree species occur in interior Alaska (Chapin et al. 2006a). Even small changes in the distribution and abundance patterns of a boreal-forest tree species can be important because of the large geographic extent and relative simplicity of this vast ecosystem. Such incremental changes may ultimately alter boreal ecosystems

beyond a threshold and result in significant ecological transformations over large areas (Chapin et al. 2004).

Changes in boreal-forest tree species composition could have numerous important and cascading ecological effects, including changes in the albedo of the land surface that affects the climate system (Betts and Ball 1997, Chapin et al. 2000, McGuire and Chapin 2006) and variation in the amount and quality of primary productivity and litterfall (Flanagan and Van Cleve 1983, Van Cleve et al. 1983). Boreal-forest tree composition also affects habitat attributes for most resident animal life, from insects (Werner 1983, Werner et al. 2006) and birds (Schieck and Song 2006), to large ungulates (Pearson et al. 1995, Weixelman et al. 1998). Since the 1960s, the mean annual temperature in Alaska has increased by 1.9°C, with most of the warming occurring in the winter (Karl et al. 2009), while the surface water balance (precipitation minus potential

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evapotranspiration) has decreased by 5.5 mm/yr in northern interior Alaska between 1960 and 2001 (Hinzman et al. 2005). Because seasonality, temperature, and net evapotranspiration affect the physiology and distribution of boreal tree species, changing climate norms will likely alter the future distribution and abundance of boreal-forest tree species (Chapin et al. 2004).

The response of Alaska's boreal forest to a changing climate has recently attracted attention due to the potential for dramatic shifts in the landscape mosaic (ACIA 2005, Chapin et al. 2008, 2010). The four primary hypotheses for forest change in this region include: (1) landscape-scale conversion of conifer forests to broadleaf-dominated ecosystems resulting from increased fire frequency or severity (Rupp et al. 2000, Johnstone et al. 2010b, Shenoy et al. 2011); (2) the potential diminution of both white spruce (*Picea glauca*) and black spruce (*P. mariana*) across much of their current ranges due to temperature induced drought stress (Barber et al. 2000, ACIA 2005, McGuire et al. 2010, Beck et al. 2011); (3) a concomitant invasion of white spruce into previously treeless landscape positions, thereby converting tundra to forest over wide areas (Cooper 1986, Suarez et al. 1999, Lloyd et al. 2002, Lloyd and Fastie 2003, Stueve et al. 2011); and (4) potential increases in phytophagous insect outbreaks due to a warming climate resulting in changes to forest structure (see Volney and Fleming 2000, ACIA 2005). Whether these hypothesized changes in Alaska's boreal forests occur depends largely on how tree species respond to a changing physical environment over large areas. Determining the ecological controls over patterns of tree species occurrence and abundance over spatially extensive study areas is thus crucial for informing predictions about prospective changes to Alaska's ecosystems.

Most of the available field data describing habitat preferences and patterns in the spatial distribution and abundance of tree species in interior Alaska come from studies undertaken in limited areas at subjectively selected and/or relatively accessible sites near population centers (e.g., Viereck et al. 1983, Dyrness et al. 1989, Wirth et al. 2008, although see Yarie 1981). While this information is valuable for describing species habitat preferences, studies with nonrandom selection of sample sites can have significantly different results than studies with randomly chosen sample sites (Michalcová et al. 2011). Furthermore, conclusions from studies conducted within small study areas can be influenced by localized site conditions, such as disturbance history (Fastie et al. 2003), and these observations cannot legitimately be extrapolated to larger, unsampled regions without risk of biased conclusions (Powell et al. 2011), especially since species composition can be controlled by different factors at varying scales (Hollingsworth et al. 2006). The historic patterns in human disturbance of forests in interior Alaska, in particular, was nonrandom in both time and space (e.g., logging, fire frequency), and may

have significantly affected current patterns of forest composition in some parts of interior Alaska, particularly those along rivers and near settlements where most of the existing forest research has taken place (Roessler 1997, Fastie et al. 2003).

We selected a 1.28-million-hectare study area encompassing the northern portion of Denali National Park and Preserve (DNPP) to examine landscape-scale patterns in tree occurrence and abundance in the interior Alaskan boreal forest according to an unbiased design. All habitats within the sampling frame could be included in the sample, providing the opportunity to draw direct inferences to the entire region. Our approach integrated spatial clustering of samples with a rigorous geospatial analytical framework that allowed us to formally assess the effects of residual spatial pattern in this data set. This design made possible timely, cost-effective, and logistically feasible sampling of large numbers of plots in a remote area with substantial barriers to access. This project was implemented throughout the Central Alaska Network (MacCluskie et al. 2005) as part of the National Park Service's long-term Inventory and Monitoring program (Roland et al. 2004). From 2001 to 2010, we systematically sampled sites throughout the study area. The sample design captured the primary gradients in terrain and habitat variability, while also providing an unbiased sample with inference at a large spatial extent.

A primary goal of this project was to make a baseline, landscape-scale assessment of the important habitat attributes for all six tree species that occur in interior Alaska: Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), tamarack (*Larix laricina*), black spruce (*Picea mariana*), and white spruce (*Picea glauca*). Relative to this goal, we had three specific objectives: (1) summarize forest community attributes, including spatial patterns in species composition, structure, seedling recruitment, and mortality of trees; (2) develop spatially explicit statistical models describing relationships between habitat characteristics and occupancy and abundance of the six tree species occurring in the study area; and (3) use the identified habitat relationships for each species to evaluate the relevance of the major hypotheses concerning potential changes in the boreal forest of interior Alaska to DNPP. We expected that using a probabilistic sampling design at the landscape scale would allow us to meet these objectives and provide a foundation for future work investigating broad-scale changes in the boreal forest in DNPP and other areas in Alaska.

METHODS

Study area

Our study area encompasses 12 800 km² (1.28 million ha) in DNPP in south-central interior Alaska, USA (Fig. 1). The area spans 160 km east to west and 80 km north to south, with a center near 63°41' N, 150°25' W.

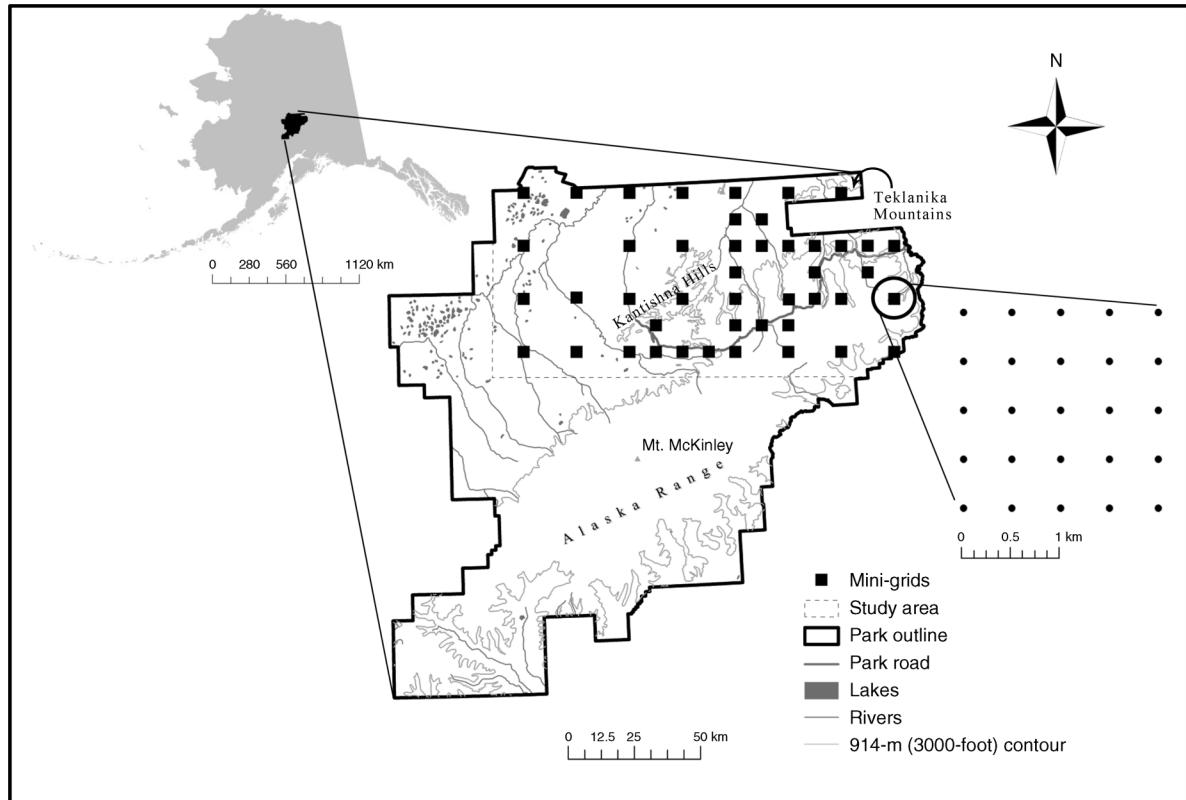


FIG. 1. The location of Denali National Park and Preserve (DNPP) within Alaska, USA, including a map of DNPP with a schematic diagram of the sampling design showing the location of each sampled mini-grid in DNPP, and a diagram of the layout of a mini-grid (five rows of five plots spaced 500 m apart).

There is a single 148-km road located in the central part of the study area. Terrain varies dramatically and includes steep Alaska Range peaks >2400 m elevation above sea level in the south, which grade into surrounding foothill ranges and uplands to the north, and finally debase into extensive lowland basins in the extreme northern and western regions of DNPP. Numerous braided rivers that drain the Alaska Range have deposited thick glacially derived alluvium throughout the northern lowlands of DNPP. The study area also contains satellite ranges including the Kantishna Hills and Teklanika Mountains. These lower summits create additional topographic heterogeneity in the northeast part of the study area, as do isolated schist domes that rise from the lowlands along the northern edge of DNPP.

The geology in DNPP is complex, with a mix of bedrock types forming the mountains and various quaternary sediments blanketing the apron of uplands below the ranges and the lowland basins beyond. The surficial geology of the Alaska Range portion of the study area is composed mostly of sedimentary or meta-sedimentary rock (Reed and Nelson 1980, Jones et al. 1983, Csejtey et al. 1992), while the Kantishna Hills, Teklanika Mountains, and the “outer range” on the northern boundary are dominated by schistose surficial

geology (Reed and Nelson 1980, Jones et al. 1983, Csejtey et al. 1992). Glacial drift and outwash from Pleistocene glaciers forms the uplands in proximity to the Alaska Range, whereas loess deposits of Pleistocene origin mantle the uplands in the northern and western areas of DNPP (Clark and Duffy 2006). The basin lowlands are dominated by alluvium and areas of loess and relict sandsheets (Clark and Duffy 2006). Permafrost underlies much of the northern lowland terrain outside of the thawed bands along river corridors. Permafrost is sporadic in south-exposed terrain and at high elevations that receive deeper snowpacks and warmer winter temperatures (Clark and Duffy 2006).

The area has a continental climate characterized by long, cold, dry winters with short, relatively warm summers. The mean annual temperature at DNPP headquarters, located in the northeast region of our study area (63°43' N, 148°58' W; 628 m elevation; Fig. 1), was -3°C , with a mean high of 20°C in July and a mean low of -22°C in January during the period from 1971 to 2000 (Shulski and Wendler 2007). The mean annual precipitation was 38.1 cm at the DNPP headquarters for 1971 to 2000 (Shulski and Wendler 2007), with the majority of this falling during June through August (Sousanes 2008). The average annual

snowfall was 206 cm, with the heaviest snowfall during November and December (Sousanes 2008).

Sampling design

We established permanent vegetation plots throughout the study area according to a two-stage systematic grid-sampling design (Roland et al. 2004). First, we generated a “macro-grid” at 10-km intervals throughout the study area using a random starting point. At each grid point we established a secondary “mini-grid” consisting of five rows of five plots spaced 500 m apart (Fig. 1). We sampled a systematic subset of these 10-km mini-grids, such that a regular 20-km systematic grid sample was obtained across the study area, with one exception. We augmented this sample with additional mini-grids located within a 6-km buffer along both sides of the DNPP road and in a region north of the road, based on logistical considerations (Roland et al. 2004).

At each of the 25 points within a mini-grid, we established a circular plot 16 m in diameter (200 m²). We did not move plots to accommodate local obstructions or vegetation patterns, although plots with extremely difficult access (e.g., on a cliff or in a river) were usually not sampled. Within each plot we recorded measurements of all trees present. We counted “seedlings” (individual trees <1.37 m in height) in four 4-m² quadrats, with one quadrat arrayed along each arm of two bisecting transects in the plot oriented to the cardinal directions crossing at the plot center. At each plot we measured a suite of topographic and edaphic variables and recorded evidence of fire history, flooding, or geomorphic activity. Data associated with this paper can be found in the Supplement.

Tree variables

We recorded both the occurrence and basal area (abundance) of tree species within each of the plots according to the following procedure: For all individuals ≥ 12 cm diameter at breast height (dbh; 1.37 m) we recorded species, condition class (live/dead), dbh, and location within the plot; for saplings (individuals <12 cm dbh, but >1.37 m in height) we recorded dbh, species, and condition class; for seedlings (individuals <1.37 m in height) we counted individuals in the four 4-m² quadrats per plot, which were then tallied by species and condition class. We recorded the occurrence of all tree species within each plot. This set of observations allowed us to quantify the occurrence (presence/absence), density (stems per hectare), and abundance (basal area [BA]; m² of bole per hectare at breast height) of each tree species within each size class.

We used the data from tree observations in two ways: (1) to fit spatial statistical models identifying relationships between landscape characteristics and tree occupancy and abundance using a subset of plots for which we had complete covariate data ($n = 907$); and (2) to summarize important attributes of the tree community across the entire study area by species, including spatial

patterns in mean tree abundance, tree size class distributions, co-occurrence, plot-level tree species richness, seedling recruitment, and tree mortality ($n = 1107$). We summarized patterns in seedling and sapling recruitment in two ways: (1) We classified forested plots by the composition of the overstory and calculated the mean seedling and sapling densities for each species in these stand types; and (2) we calculated the mean seedling and sapling densities for all species based on the fire history status of the plots in which the seedlings and saplings grew (recently burned, old burn or no evidence of burn).

Predictor variables

We selected 19 environmental and habitat predictor variables that we expected to explain major sources of variation in occurrence and abundance of the six tree species in the study area (Table 1). We determined the spatial location and elevation of each plot using a global positioning system (GPS) unit (GeoExplorer3; Trimble, Sunnyvale, California, USA). Plot coordinates were differentially corrected upon return from the field with Pathfinder Office software (Trimble, Sunnyvale, California, USA). Following differential correction, >91% of GPS coordinates had horizontal precision of ≤ 4 m, and the maximum horizontal precision was 9 m. Similarly, vertical precision of GPS coordinates was ≤ 4 m for >91% of plots with a maximum vertical precision of 14 m. Slope angle and aspect for the plot were measured in degrees using a clinometer and compass, respectively. We calculated two uncorrelated measures of slope aspect: southness and eastness (following Pereira and Itami 1991). This transformation results in values for these measures ranging continuously between -1 and 1 , with maximum values for southness and eastness occurring on slopes with aspects of 180° and 90° , respectively. Sites with slope angles < 4 degrees were considered to be flat and were assigned 0 for both southness and eastness.

Estimates of the annual solar radiation receipts for each plot were made using the Solar Analyst tool in ArcGIS 10.0 (Dubayah and Rich 1995), which uses numerous variables including slope angle, aspect, latitude, sun angle, and surrounding topography to determine insolation receipts of a topographic surface (Rich et al. 1994). We used the United States Geological Survey 60-m digital elevation model (DEM) from the National Elevation Dataset (NED) to calculate estimates of solar radiation receipts. We also used ArcGIS 10.0 to extract soil lithology type and permafrost status of the soil unit for each plot from the spatial data layer of the Denali Soil Map (Clark and Duffy 2006). Any recent geomorphic disturbance or flooding that would have removed or precluded trees from becoming established in the 10 years preceding sampling was also recorded for each plot. The three types of geomorphic disturbance identified were: slope processes (active slide or debris deposition removing trees), fluvial disturbance

TABLE 1. Environmental factors for plots sampled in Denali National Park and Preserve (DNPP), Alaska, USA, that were used to develop spatial models of tree species occurrence and abundance.

Variable	Description	Units	Mean	Median	Minimum	Maximum
Topographic factors						
Elevation	elevation at plot center	m	739	760	153	1641
Slope	slope angle	degrees	10.5	7.0	0	42
Southness	$\cos(\pi \times \text{aspect} + 180)/180$	none	0.041	0	-1	1
Eastness	$\sin(\pi \times \text{aspect}/180)$	none	-0.015	0	-1	1
Annual solar radiation	solar radiation	WH/m ² †	8.1×10^5	8.1×10^5	1.6×10^5	14.2×10^5
Edaphic factors						
Active-layer depth	mean depth of 16 depths/plot	cm	50.1	48.4	0	106
Live mat depth	depth of live mat (e.g., moss)	cm	4.0	3.5	0	38.5
Soil organic layer (SOL)	depth of soil organic layer	cm	13.3	11.5	0	30
pH	reaction of the soil sample	pH	4.99	4.74	3.49	7.81
Gravel	percentage of soil sample >2 mm	%	16.5	8.99	0	100
Total carbon	percentage of carbon	%	13.3	6.6	0.1	59.3
Total nitrogen	percentage of nitrogen	%	0.6	0.4	0.01	3.1
Soil moisture	percentage of soil moisture from sample	%	121	55	1	1045
Soil temperature	mean soil temperature at 10 cm	°C	5.0	4.3	-1.0	25.7
Soil map factors						
Permafrost status	soil unit permafrost status	3 classes	NA	NA	NA	NA
Lithology	soil unit lithology status	6 classes	NA	NA	NA	NA
Total disturbance	recent disturbance of plot	binary	0.09	0	0	1
Fire factors						
Evidence of fire	evidence of fire in plot	binary	0.08	0	0	1
Fire age	age of fire affecting plot	3 classes	NA	NA	NA	NA

Note: These values summarize the 907-plot data set used to build spatial models; NA indicates data are not applicable.

† Units for solar radiation are the sum of watt hours per square meter; calculated using tool in ArcGIS 10.0 (Dubayah and Rich 1995).

(plot disturbed by running water), and inundation (plot location occupied by standing water). Because of the relative rarity of each of these types, we combined them into a single binary predictor called “total disturbance” and categorized sites as either disturbed or undisturbed.

We collected edaphic data for each plot at four soils observation points 1 m beyond the plot perimeter in each cardinal direction. At each point, we exposed a small soil pit (30–40 cm), and the depth of the litter, living, and soil organic (duff) layers (SOL) were measured and averaged for the plot. Soil temperature was recorded at a depth of 10 cm at four soils observation points, and a mean soil temperature was derived for each plot. We also collected a soil sample from the uppermost mineral horizon below the duff layer (10–15 cm depth) and combined them to form a composite sample for the plot. If there was significant variation among two or more of the samples, multiple samples were taken, one for each type. These samples were placed in an airtight sample bag and kept cool until transport out of the field, whereupon they were immediately frozen.

Soil samples remained frozen until they were processed at the University of Alaska Fairbanks Agriculture and Forestry Experiment Station Soils Laboratory (Palmer, Alaska, USA). Soil moisture content was determined gravimetrically by adding the percentage of moisture lost from the sample in two steps: (1) field sample mass to air-dried sample mass and (2) air-dried

sample mass to oven-dried mass. Air-dried samples were sieved to 2 mm, and the coarse fragment was weighed to determine the percentage of gravel. A separate subsample was used to measure soil reaction (pH) using a 1:1 soil to water ratio. The percentage of total carbon (TC) and total nitrogen (TN) in the sieved, air-dried sample were determined using an elemental analyzer (LECO CHN-1000; LECO, St. Joseph, Michigan, USA).

We classified the fire history of each plot using two methods: (1) We consulted the Alaska Fire Service spatial data layer containing all mapped fire perimeters for the study area from 1940 to 2010 (see Kasischke et al. 2010) to determine the ages of fires affecting our plots; and (2) we recorded direct evidence of fire in each plot including the presence of standing, fire-killed snags with evident charcoal, presence of charred logs or stumps, presence of charred organic horizons in surface soil, and presence of multiple, ground-level fire scars on snags or live trees. Because no fires occurred within our plots during the period between 1958 and 1982, we were able to separate each plot into one of three classes: no evidence of fire in last ~100 years, plots affected by recent fires since 1982 (determined from GIS fire perimeter dates), and plots with evidence of older fires. These three readily differentiated fire age classes correspond with broad differences in stand age (unburned, recent, and old fires) and were used as a classification variable for analyses.

Statistical analysis

We used a two-part model (Zuur et al. 2009) to separately identify significant covariates related to probability of occurrence (hereafter occupancy) and tree abundance (i.e., basal area) for each tree species. We used the term “occupancy” to represent the proportion of the sample area where each species was present, following the basic terminology used in the occupancy modeling literature (see MacKenzie et al. 2006). In this study, a species could occupy a sampling location but have no basal area (i.e., individuals <1.37 m tall), assuming that detection probability (p) was 1.0 for all trees within plots. This allowed zeros to occur in the abundance part of the model, but because $p = 1.0$, they were of known origin. Therefore, we did not use a zero-inflated mixture model approach (see Zuur et al. 2009). We assumed that occupancy followed a binomial distribution and selected a negative binomial distribution over a Poisson for the abundance model to help account for overdispersion. Occupied sites generally had low abundances, although the distribution of abundance values had a long right-hand tail. The negative binomial distribution includes an additional parameter that relaxes the assumption of a mean equal to the variance of the Poisson, providing a better fit to this portion of the distribution. We used generalized linear regression models (GLMs) to identify important environmental predictors for each process (Table 1) and selected among competing models for each part using AIC. Model fitting and model selection were completed using program R 2.13.1 (R Development Core Team 2012). We used the proportional reduction in deviance (deviance of the best approximating model/deviance of the intercept-only model) as a measure of the amount of variation explained by our best approximating model.

For the occupancy model, our sample consisted of those plots from the larger sample with complete covariate measurements ($n = 907$). Covariates were considered in two broad classes: landscape-level and site-level characteristics (Table 1). At the landscape scale, we expected terrain characteristics to explain more of the variation in broad patterns of occupancy and abundance, while local edaphic characteristics would explain patterns at the site level. A similar approach was used for the abundance data, which consisted of the subset of plots occupied by a given species. The number of sites occupied by each species varied, but sample sizes were adequate for tree abundance analysis only for *P. glauca* ($n = 289$), *P. mariana* ($n = 242$), and *B. neolaskana* ($n = 117$). We considered various combinations of covariates for each species, but assumed a priori that terrain variables integrating multiple habitat attributes such as elevation, slope, aspect, permafrost, and lithology would be more important than local edaphic variables such as soil temperature, pH, soil moisture, disturbance, and soil depth. This resulted in a two-tiered approach to model selection where we selected among the landscape predictors first, and then

added various combinations of the site-level predictors to arrive at the best approximating model overall.

We expected that some of the covariates we considered might be highly correlated with one another, possibly affecting inference. To address this potential problem, we computed the correlation matrix for the covariates under consideration and did not include any two covariates in the same model if the correlation coefficient was >0.75 . We also used the HH package (Heiberger 2011) to calculate the variance inflation factor (VIF) for the best approximating model for each species to ensure collinearity was not affecting our results. The VIF represents a measure of the severity of the multicollinearity in the data, and as a general rule, a VIF of <10 is considered to be acceptable, although lower values are preferred (e.g., O'Brien 2007). These two diagnostics ensured that correlations among covariates did not influence our results or their interpretation.

After selecting the best approximating model for each species, we added spatial random effects to both the occupancy and abundance portions using Bayesian methods implemented in the geoRglm package (Christensen and Ribeiro 2002). We needed fairly informative and proper priors for the occupancy models' spatial random effects' spatial range and signal variance parameters to ensure well-identified posteriors and more stable convergence of the sampling algorithm (e.g., Berger et al. 2001). Our choice of priors and associated hyperparameters was informed through exploratory analysis by first fitting a fully spatial model without covariates to the data assuming a spherical covariance model, an exponential prior on the correlation parameter, and a scaled inverse chi-squared prior on signal variance parameter (see Christensen and Ribeiro 2002, Diggle and Ribeiro 2010). The posteriors from these analyses were used to form compact priors for the spatial components of the full model including covariates. Diffuse priors were used for all remaining parameters in the spatial abundance models. We ran two Markov chain Monte Carlo chains for one million iterations each and monitored convergence using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). After convergence was reached, we discarded the initial iterations as burn-in, using the remaining values from the posterior to construct 95% credible intervals for each parameter. We then identified those that included 0 after accounting for spatial autocorrelation and adjusted our inference accordingly. In this way we were able to formally address any remaining spatial autocorrelation among the model residuals without undue risk of overfitting. We denoted the changes in model structure in the results to highlight the reduction in apparent model complexity when spatial autocorrelation is formally addressed during analysis. We used the results from the spatial analysis to construct all figures based on statistical modeling results.

TABLE 2. Statistics for frequency of occurrence, mean live basal area (BA), standard deviation (SD), coefficient of variation (CV), and maximum BA of all tree species in DNPP, based on all plots and a subset of plots with full set of predictor variables used in species modeling.

Species	Full plot data set ($n = 1107$)					Subset of plots used in models ($n = 907$)				
	Frequency (%)	Basal area, BA (m^2/ha)				Frequency (%)	Basal area, BA (m^2/ha)			
		Mean	SD	CV	Maximum		Mean	SD	CV	Maximum
Conifer										
PICGLA	30.6	1.9	6.21	3.3	66.3	32.0	2.08	6.61	3.2	66.3
PICMAR	24.4	1.0	3.27	3.2	40.8	26.7	1.17	3.50	3.0	40.8
LARLAR	10.2	0.02	0.14	7.8	2.9	11.9	0.02	0.15	7.4	2.9
Broadleaf										
BETNEO	11.7	0.63	3.46	5.5	35.8	13.0	0.74	3.80	5.1	35.8
POPBAL	5.8	0.20	2.38	11.9	52.7	6.9	0.24	2.63	10.8	52.7
POPTRE	3.2	0.05	0.643	13.3	11.6	3.6	0.05	0.60	12.9	10.8
All species	52.2	3.8	8.73	2.3	71.4	56.7	4.3	9.32	2.16	71.4

Note: Species codes are as follows: PICGLA, *Picea glauca*; PICMAR, *Picea mariana*; LARLAR, *Larix laricina*; BETNEO, *Betula neoalaskana*; POPBAL, *Populus balsamifera*; and POPTRE, *Populus tremuloides*.

RESULTS

We examined 1107 plots within 45 mini-grids throughout the study area for tree occurrence (Fig. 1), and after excluding plots with incomplete covariate information, 907 plots were included in our quantitative analyses of the relationships between environmental covariates and the tree species response variables (Table 2). The patterns of variation in occurrence and abundance among species were similar in the full vs. reduced data sets (Tables 2 and 3). Therefore, we used the full data set to describe general patterns of tree distribution, diversity, recruitment, and mortality because this data set offered the most complete representation of the study area for these descriptions. Results describing quantitative relationships between occupancy and abundance and environmental covariates were based on the 907 plots for which we had complete data (see Tables 2 and 3).

Overall summary

Our plots ranged in elevation from 153 m to 1803 m above sea level, and slope angles ranged from flat to 67

degrees, including the full range of aspects (Table 1). Our sample included widely varying edaphic conditions, including poorly drained, acidic soils with thick SOL and continuous permafrost, to deep, well-drained mineral soils formed from alluvium and colluvium. Also present were shallow soils underlain by bedrock in hilly and mountainous areas. Vegetation types represented in the sample included conifer, broadleaf, and mixed forests of widely varying canopy closures; scrub vegetation dominated by various mixtures of willow (*Salix* spp.), alder (*Alnus* spp.), and ericaceous taxa; wet graminoid meadows and tussock bogs; boreal and subalpine forb-rich meadows; and alpine tundra dominated by dwarf shrubs, graminoids, or lichens. Barren areas such as open gravel bars, fell-fields, and scree slopes also occurred.

The landscape of the study area was relatively open, with 52.2% of the plots containing at least one individual of the six tree species (Table 2), and combined live tree basal area exceeded 15 m^2/ha in only 97 (17%) of the 578 plots with trees. For comparison with nearby forested study plots, the total tree BA in the *Picea mariana* stand

TABLE 3. Values for mean seedling (individual trees <1.37 m tall) density, standard deviation (SD), and coefficient of variation (CV) in vegetation plots in DNPP.

Species	All plots ($n = 1107$), seedling density (stems/ha)				Subset of plots used in models ($n = 907$), seedling density (stems/ha)			
	Mean	SD	CV	Maximum	Mean	SD	CV	Maximum
Conifer								
PICGLA	406	2 075	5	43 125	431	2 194	5	43 125
PICMAR	2922	9 055	3	118 750	3433	9 675	3	118 750
LARLAR	431	2 545	6	37 500	524	2 803	5	37 500
Broadleaf								
BETNEO	413	5 724	14	161 250	500	6 320	13	161 250
POPBAL	195	1 612	8	33 125	238	1 779	5	33 125
POPTRE	154	1 453	9	26 250	172	1 545	9	26 250
All species	4521	12 375	3	161 250	5297	13 331	3	161 250

Note: See Table 2 for species codes.

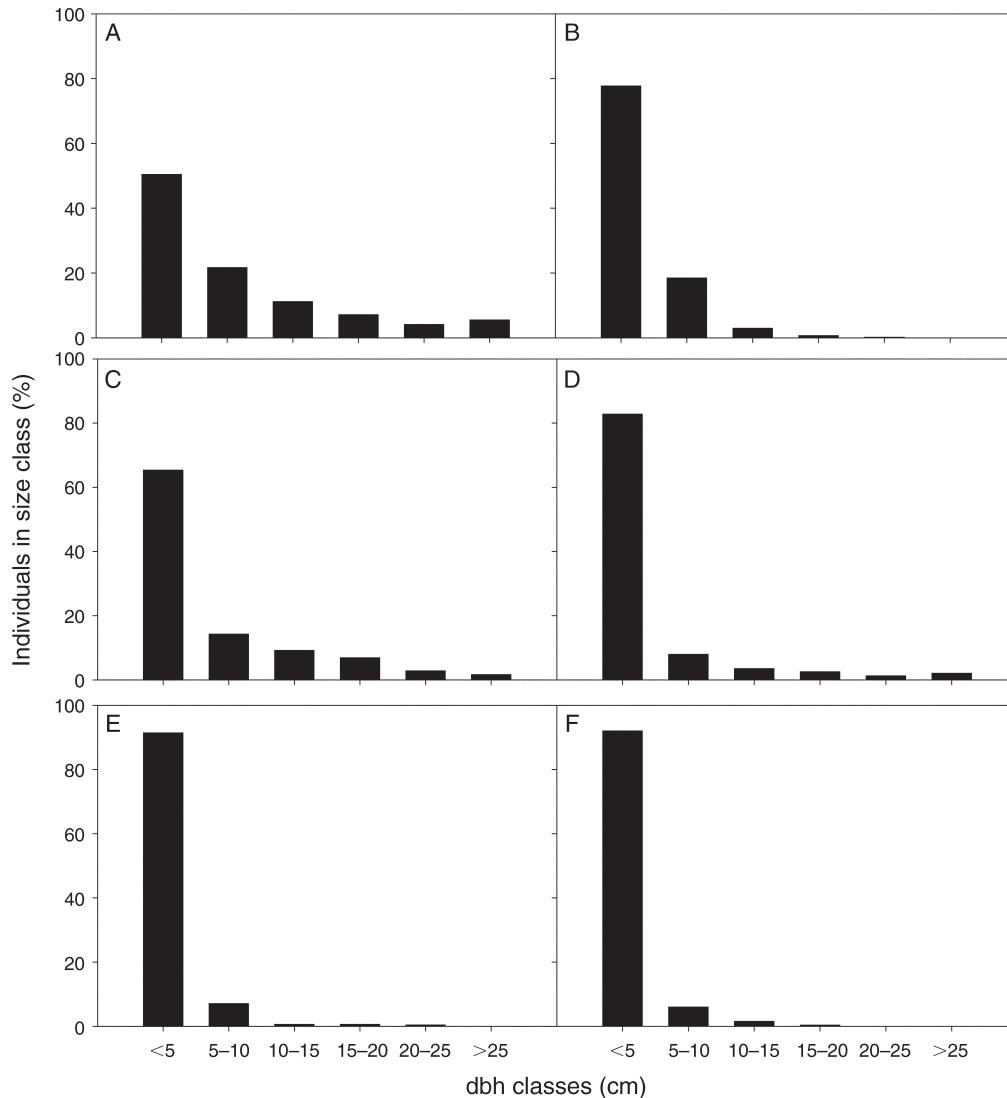


FIG. 2. Size class histograms for six tree species occurring in 1107 plots in DNPP showing the percentages of the total number of individuals for each species divided among six diameter size classes: (A) *Picea glauca*, $n = 4076$; (B) *Picea mariana*, $n = 13\,571$; (C) *Betula neolaskana*, $n = 2453$; (D) *Larix laricina*, $n = 523$; (E) *Populus balsamifera*, $n = 1282$; and (F) *Populus tremuloides*, $n = 1618$.

(FP5A) of the Bonanza Creek LTER was $15.1\text{ m}^2/\text{ha}$, whereas other mature forest stands in Bonanza Creek all had total tree BA of $30\text{ m}^2/\text{ha}$ or greater (Hollingsworth 1997). Mean total tree BA across the DNPP plots was $3.8\text{ m}^2/\text{ha}$ (Table 2). Closed-canopy forests occurred in scattered locations and were restricted primarily to deeply thawed alluvial terraces and warm exposures up to about 750 m elevation. On average, trees occurring in the plots were small, for example, only 291 out of the 23 434 live trees measured during this study measured 25 cm dbh or larger (1.2% of the total). *Picea glauca*, *B. neolaskana*, and *P. balsamifera* were the only species with individuals of >25 cm dbh, and the size class distributions for the other three species were all strongly skewed to the smallest size classes (Fig. 2). In fact, $>90\%$ of the individuals measured for *P. mariana*, *L. laricina*,

P. balsamifera, and *P. tremuloides*, were smaller than 10 cm dbh (Fig. 2).

General character of the forest mosaic

Occurrence and abundance varied substantially among the six species (Table 2) in the forests of DNPP. The two *Picea* species were nearly ubiquitous in treed areas of DNPP, with a member of one of these two species occurring in 93% of the plots that supported at least one tree. *P. glauca* was both the most frequently recorded species, occurring in 30.6% of plots, and the most abundant species, with a mean BA of $1.9\text{ m}^2/\text{ha}$. *P. mariana* occurred in 24.4% of plots with a mean BA of $1.0\text{ m}^2/\text{ha}$, while *B. neolaskana* occurred in 11.7% of the plots with a mean BA of $0.63\text{ m}^2/\text{ha}$. *L. laricina* occurred in 10.2% of plots, but had very low mean BA of $0.02\text{ m}^2/$

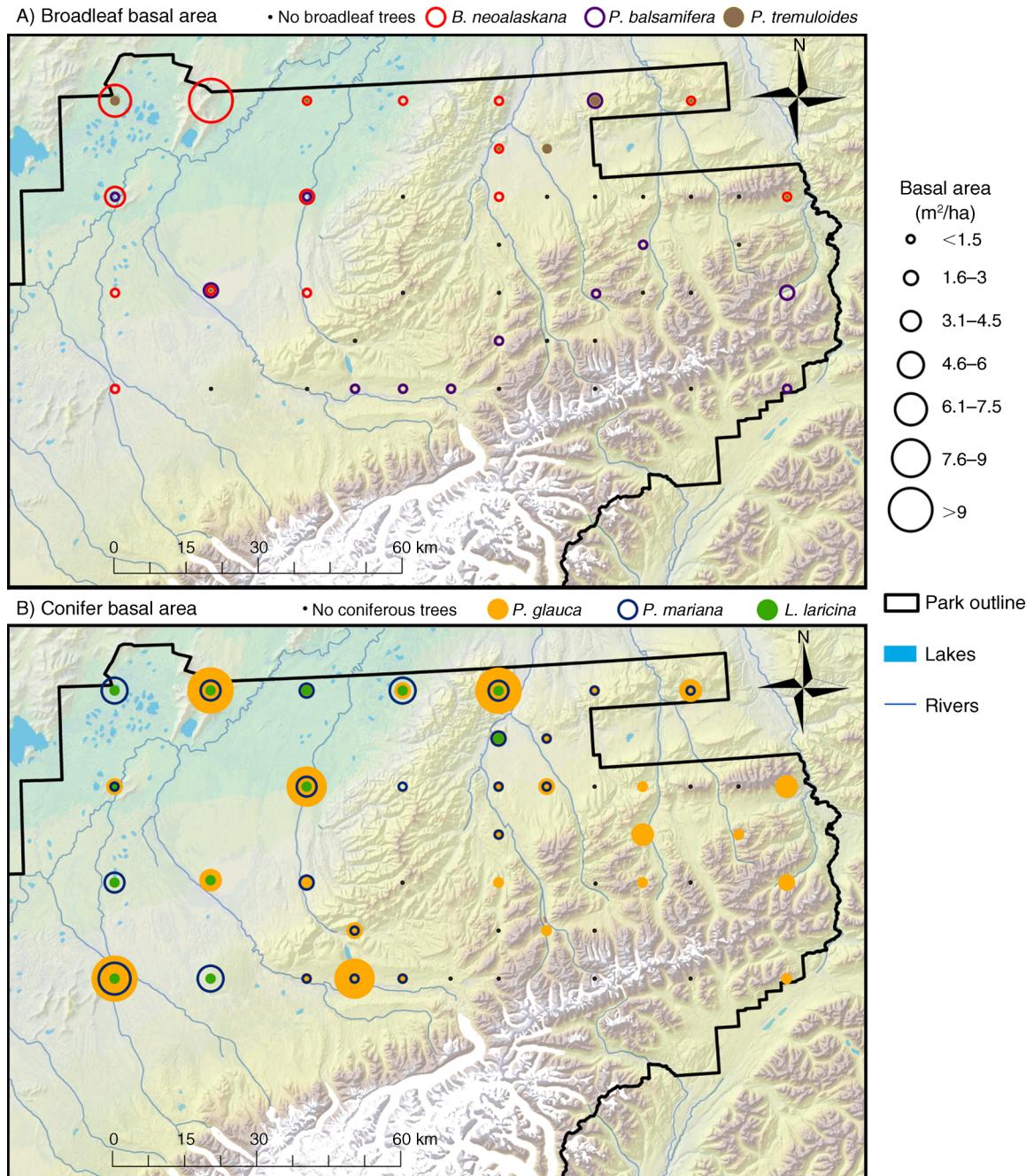


FIG. 3. Maps of the study area showing the spatial variation in mean basal area across 45 mini-grids for (A) three broadleaf tree species and (B) three conifer tree species in DNPP.

ha because of the small size of the live trees in the sample. *Populus balsamifera* and *P. tremuloides* were relatively minor components of the tree community in DNPP, occurring in 5.8% and 3.2% of the plots, respectively, with corresponding mean basal areas of 0.2 m²/ha and 0.05 m²/ha.

The tree species showed high spatial variation in mean abundance patterns (Fig. 3). *Picea glauca* was the

most widespread species, occurring in plots spanning the full range of both latitude and longitude of the study area. *Picea mariana* occurred at relatively high mean BA only in the northern and western parts of the study area and was generally restricted to the lowland basins (Fig. 3B). *Larix laricina* showed a limited distribution, occurring within a subset of the lowland area inhabited by *P. mariana*. *Betula neoalaskana*

TABLE 4. Direction of significant relationships between environmental covariates and occupancy probability in the best approximating models including adjustments made after fitting spatial random effects models for six tree species, and all species combined, in DNPP.

Covariate	Conifer			Broadleaf			All species
	PICGLA	PICMAR	LARLAR	BETNEO	POPTRE	POPBAL	
Proportional reduction in deviance	0.31	0.63	0.62	0.66	0.51	0.38	0.44
Terrain variables							
Elevation	+	-	-	-	+	+	-
Elevation ²	-	[-]			-	-	
Slope	+	+		+			[+]
Slope ²	-	-				[+]	-
Southness					+		
Eastness	+						[+]
Annual radiation	+		-				+
Soil unit permafrost	-			[-]			-
Soil unit lithology	[+]						
Local edaphic variables							
Evidence of fire in plot	[+]		[-]				
Recent burn (since 1982)				+	+	[+]	
Old burn (before 1958)				+	+		
Living mat depth		[+]	[+]	[-]			
Soil organic layer depth		+	+	-		[-]	
Active-layer depth		-	-	+			-
Soil pH	+	-		-			
Percentage of gravel		[-]			+		
Carbon content				[-]			
Total disturbance	-						
Soil temperature						+	
Soil moisture	-					-	

Notes: A plus sign (+) indicates a significant positive influence on occupancy, a minus (-) indicates a negative influence on occupancy, and no sign indicates the variable was not included in the model or that the 95% confidence interval included zero. Square brackets enclosing the sign indicate the 95% credible interval overlapped 0 after the addition of spatial random effects. See Table 2 for species codes.

occurred in high mean BA only in the far northwest corner of the study area, with sporadic occurrences outside of this region (Fig. 3A). *Populus tremuloides* never occurred at high mean abundance, but showed a clustered occurrence pattern in the northern portion of the study area. *Populus balsamifera* occurred in a larger number of mini-grids than *P. tremuloides*, spread throughout the middle and southern half of the sample, and was primarily restricted to river terrace environments or recently disturbed steep slopes. Coniferous tree species dominated the forested segment of the landscape: Of the 455 plots with tree basal area >0, only 16.9% had higher total abundance (BA) of broadleaf species than coniferous species.

Model diagnostics

The calculated VIF for all covariates for all species was <5.2 and most were much lower than 5.0, suggesting that multi-collinearity did not affect our results. The addition of spatial random effects to the top model for each species caused some of the habitat relationships that were previously identified as statistically significant to become not significant (see Table 4). This change in significance, and the magnitude of the parameters associated with the spatial random effects, suggests that some spatial autocorrelation remains after considering the available covariates, particularly for *P. glauca* (Table 5). This implies that one or more

important predictors of patterns of occupancy and abundance on the landscape were not included in our set of variables for some species.

Patterns in tree occupancy

Overall tree occupancy in DNPP was positively correlated with annual solar radiation and was negatively influenced by increasing elevation, soil units with continuous permafrost, and active-layer depth (Table 4, Fig. 4). Tree occupancy was high (probability >0.90) over a wide range of site conditions, although it declined precipitously above 750 m elevation, according to our model (Fig. 4A). Peak overall tree occupancy was predicted to be highest on sites below 750 m with high solar radiation receipts and thin SOL (Table 4, Fig. 4A).

The dominant tree species *P. glauca* and *P. mariana* showed markedly contrasting responses to site conditions (Table 4, Figs. 4–7). The two *Picea* species only shared one similar significant covariate response: They both had peak occupancy probability at moderate slope angles of ~20 degrees, with decreasing occupancy probabilities in both steeper and shallower slopes. The ecological conditions of the slopes that the two dominant tree species preferred, however, were considerably different (Figs. 5–7). Specifically, *P. glauca* was most likely to occur at mid-elevations in sites with high radiation receipts, high soil pH, and underlain by soils without continuous permafrost (with highest preference

TABLE 5. Parameter values used to construct priors for the signal variance (σ^2) of the spatial models for each species and all trees combined for both the occupancy and abundance analyses within DNPP.

Species	Prior		Posterior	
	σ^2 mean	σ^2 df	ϕ	σ^2
Occupancy				
<i>P. glauca</i>	2	10	16.9 (11.3–23.3)	9.7 (4.5–20.7)
<i>P. mariana</i>	2	10	8.2 (3.5–14.5)	2.9 (1.4–5.9)
<i>B. neoalaskana</i>	30	20	8.0 (4.0–14.8)	32.0 (16.3–59.4)
<i>P. tremuloides</i>	20	20	5.4 (2.5–10.8)	26.0 (12.9–53.4)
<i>P. balsamifera</i>	10	20	6.5 (1.8–13.3)	16.2 (7.5–31.7)
<i>L. laricina</i>	5	25	4.3 (1.1–10.6)	5.5 (3.1–9.6)
All trees	7	20	7.6 (4.5–11.6)	6.5 (4.1–10.5)
Abundance				
<i>P. glauca</i>	2	1	4.3 (1.7–6.9)	8.8 (3.7–13.9)
<i>P. mariana</i>	2	1	1.1 (0–2.9)	1.0 (0.3–1.7)
<i>B. neoalaskana</i>	20	1	0.3 (0–0.8)	2.6 (1.5–3.7)
All trees	5	1	4.4 (2.2–6.7)	4.1 (2.3–5.9)

Notes: Posterior values indicate the estimated mean values and 95% credible intervals of the correlation (ϕ) and the signal variance (σ^2) parameters after convergence of the spatial models was achieved. The largest distance between sampled points was 153.6 km. See Table 2 for full species names.

for soil units with only sporadic permafrost). In addition, *P. glauca* responded positively to increasing eastness and negatively to both increasing soil moisture and disturbance (Table 4). *Picea mariana* occupancy, on the other hand, was declined precipitously with increasing elevation (Table 4, Fig. 4) and responded negatively to increasing thaw depth of the active layer and soil pH, and was positively correlated with increasing SOL depth (Table 4, Figs. 5–7). In general, *P. mariana* had the highest occupancy in the coldest, wettest edaphic conditions suitable for tree growth in this landscape, while *P. glauca* was mostly absent from sites with these conditions (compare *P. glauca* occupancy probabilities in Fig. 5A vs. 5B). Although a member of one of the two *Picea* species occurred in 93% of all plots containing a tree in DNPP, the two species occurred together in just 13% of the plots occupied by at least one *Picea* individual, demonstrating a low level of overlap in occupancy between the two *Picea* species.

The three broadleaf tree species sorted into different positions across the primary forest habitat gradient from warmer, well-drained, and productive sites characterized by high *P. glauca* occupancy to sites with shallowly thawed, cold soils, and impeded drainage characterized by high *P. mariana* occupancy (Table 4, Figs. 5–7). The response of *B. neoalaskana* occupancy was intermediate between the two *Picea* species and was strongly related to fire history. The best approximating model showed that *B. neoalaskana* occurred more often on sites with increasing slope, low soil pH, a deeper active layer, and shallower SOL (Table 4, Figs. 6 and 7). A primary difference in the occupancy response of *B. neoalaskana* in comparison to both of the dominant conifer species was its clear association with burned sites, showing increased occupancy probabilities in both new and old burns (Table 4, Fig. 8B).

Peak occupancy of *P. tremuloides* occurred in the warmest and driest forest conditions in DNPP, and occupancy probability of this species responded positively in mid-elevation, south-facing sites with gravelly (mineral) soil and thin SOL (Table 4, Fig. 5). The clearest contrast between *P. tremuloides* and *P. glauca*, which overlapped in their topographically defined habitat preferences, was the strong association of *P. tremuloides* with burned sites (Table 4, Fig. 8A). *Populus tremuloides*, even more so than *B. neoalaskana*, showed increased occupancy probabilities in both new and old burns (Fig. 8) as compared sites without evidence of fire. Fitting of the spatial model for *P. tremuloides* resulted in no adjustments to the best approximating nonspatial model.

The third broadleaf tree species, *P. balsamifera*, was strongly associated with river terraces and gravel bars DNPP. According to the best model, this species was most likely to occur at mid-elevation sites, with warmer soil temperatures, and well-drained surface soil conditions (Table 4). The coarse, well-drained mineral surface soil with exposed sand and cobbles characteristic of gravel bars were warmer and drier at the surface than well-vegetated areas in surrounding terrain, corresponding to observed patterns of distribution in DNPP.

Occupancy of *L. laricina*, the rarest coniferous tree in DNPP, showed a similar set of responses to the covariates as *P. mariana* (Table 4, Figs. 5–7). High occupancy probabilities for this species were restricted to the lowest elevations and to situations with low annual radiation receipts, shallowly thawed soils, deep SOL, and low soil PH. (Table 4, Figs. 5–7). Although it had similar preferences as *P. mariana*, *L. laricina* had an idiosyncratic and interrupted distribution within DNPP, occurring in many fewer plots than did *P. mariana*

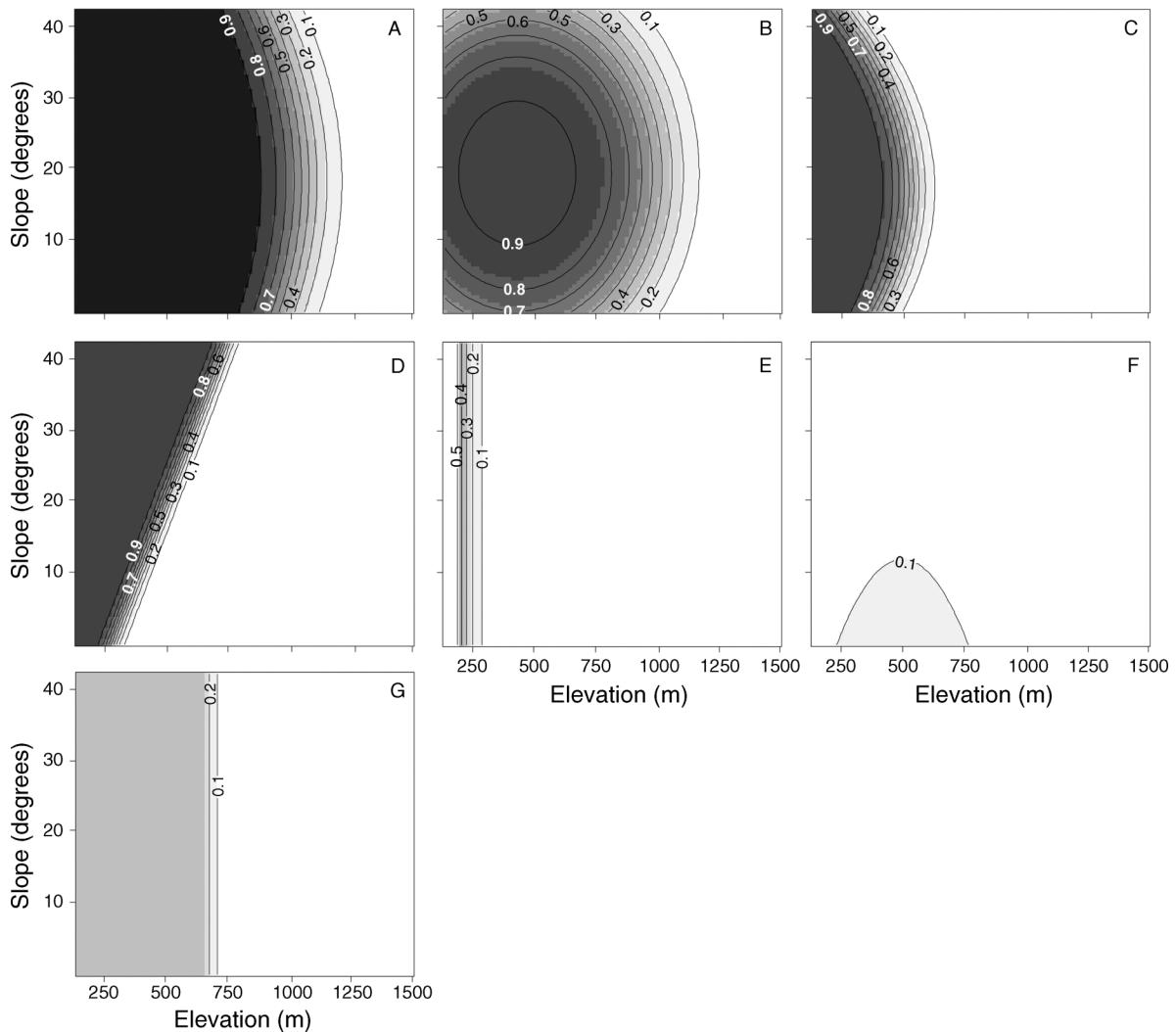


FIG. 4. Contour plots indicating occupancy probability (darker shading represents higher probability of occupancy) across the observed ranges of slope and elevation for (A) all species combined, (B) *P. glauca*, (C) *P. mariana*, (D) *B. nealaskana*, (E) *L. laricina*, (F) *P. balsamifera*, and (G) *P. tremuloides*. Because the model parameters vary for each species, graphs are based on the mean parameter values from the best approximating model for each species, except as follows: (A, B) sporadic permafrost and maximum annual radiation, (D) recently burned, (F) high soil temperature (mean + 2 SD = 12.2°C), and (G) recently burned.

(10.2% of plots vs. 24.4% for *P. mariana*; Tables 2 and 4, Figs. 4–7).

Although there was overlap in the occupancy responses among several pairs of tree species in DNPP (particularly *P. mariana* and *L. laricina*) in relation to major landscape gradients, our models generally revealed distinctly individualistic responses to unique sets of covariates by members of the tree flora (Table 4, Figs. 4–8). Species with similar responses to topographically controlled site conditions (e.g., *P. glauca* and *P. tremuloides*) showed contrasting responses to disturbance vectors. In general, occupancy of the broadleaf species was strongly associated with disturbance processes in this landscape, and all two of these species showed a positive influence of recent fire on occupancy (Table 4, Figs. 5 and 6). Another factor related to fire,

increasing SOL thickness, also had a negative influence on occupancy of both *B. nealaskana* and *P. tremuloides*. It is interesting to note that the nonspatial model indicated both a positive response to recent burn, and negative response to increasing SOL for occupancy of the third broadleaf species (*P. balsamifera*) also, although the model including spatial random effects indicated these trends were nonsignificant.

Patterns in tree abundance

Overall tree abundance was highest at mid-elevations and positively associated with well-drained soils in south-exposed terrain and in soil units without continuous permafrost, and was negatively associated with SOL depth and increasing soil moisture (Table 6). Not surprisingly, recent disturbances from either geomorphic

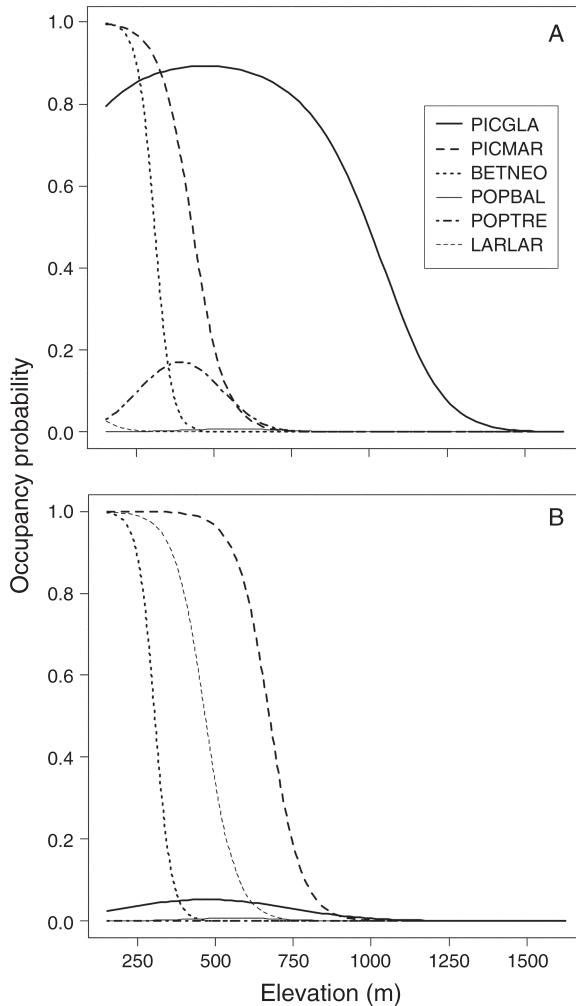


FIG. 5. The occupancy probability of each species across the observed range of elevation from (A) warmer sites (unburned, discontinuous permafrost, high annual radiation [mean + 2 SD], high soil pH [mean + 2 SD], and shallow soil organic layer [SOL; 2 cm]) and (B) colder sites (unburned, discontinuous permafrost, low annual radiation [mean - 2 SD], low soil pH [3.5], and deep SOL [30 cm]). Species codes are as follows: PICGLA, *Picea glauca*; PICMAR, *Picea mariana*; BETNEO, *Betula neoalaskana*; POPBAL, *Populus balsamifera*; POPTRE, *Populus tremuloides*; and LARLAR, *Larix laricina*.

activity or fire reduced overall tree abundance at a site (Table 6, Fig. 9A). According to the best approximating model, maximum overall tree abundance in DNPP was predicted to occur between ~280 m and 450 m elevation on stable, south-exposed slopes that had not recently burned, but had relatively thin SOL (Table 6, Fig. 9A).

Patterns of abundance for *P. glauca*, *P. mariana*, and *B. neoalaskana* (Table 6, Fig. 9) differed from occupancy patterns for these species (Tables 4 and 6, Figs. 4 and 8). Predicted *P. glauca* abundance peaked at similar elevation to peak occupancy for this species, at ~450 m to 500 m. The structure of the abundance model for

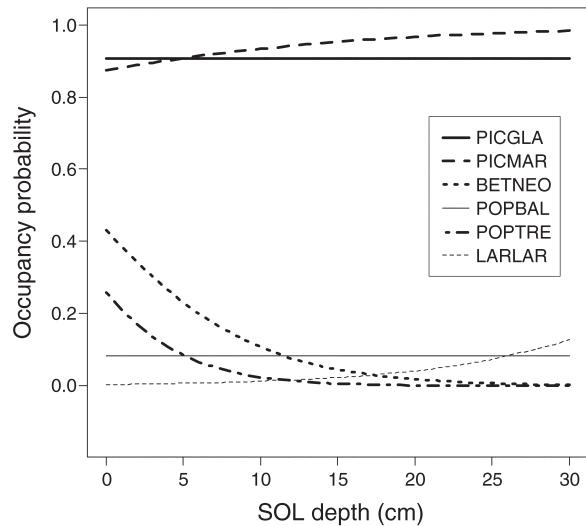


FIG. 6. The predicted relationship between occupancy of the six tree species and SOL depth in DNPP. Because the model parameters vary for each species, graphs are based on the mean parameter values from the best approximating model for each species, except as follows: *P. glauca*, sporadic permafrost and maximum annual radiation; *B. neoalaskana*, recently burned; *P. balsamifera*, high soil temperature (mean + 2 SD); and *P. tremuloides*, recently burned. See Fig. 5 for species codes.

P. glauca was substantially similar to the occupancy model for this species, with occupancy and abundance responding positively to increasing slope angle and factors associated with increased insolation (annual radiation, southness). *Picea glauca* occupancy and

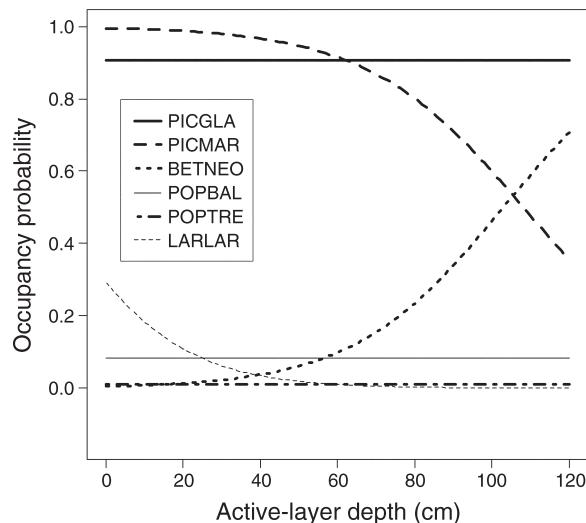


FIG. 7. The predicted relationship between occupancy of the six tree species and active-layer depth in DNPP. Because the model parameters vary for each species, graphs are based on the mean parameter values from the best approximating model for each species except as follows: *P. glauca*, sporadic permafrost and maximum annual radiation; *B. neoalaskana*, recently burned; *P. balsamifera*, high soil temperature (mean + 2 SD); and *P. tremuloides*, recently burned. See Fig. 5 for species codes.

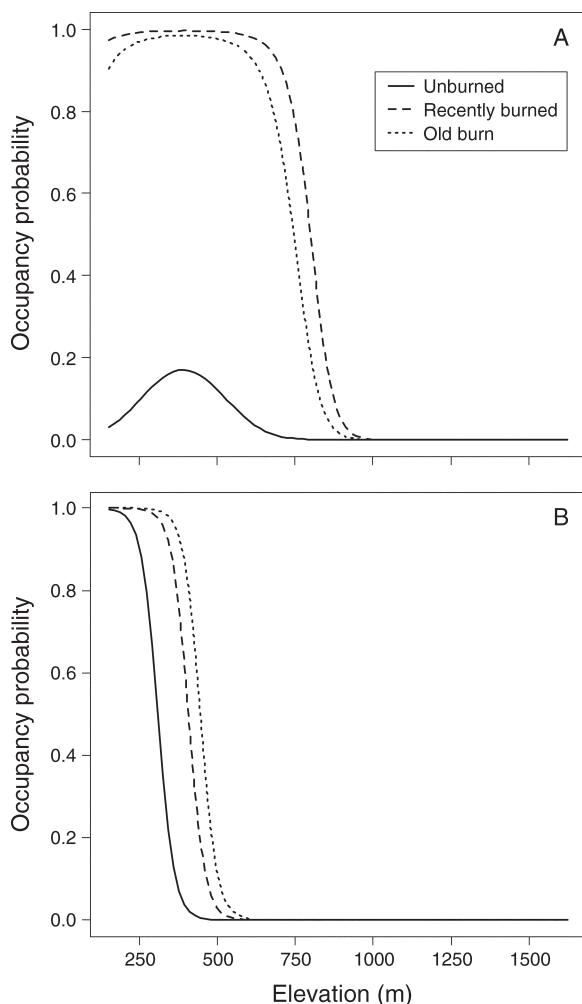


FIG. 8. The occupancy probability of (A) *P. tremuloides* and (B) *B. neoalaskana* across the observed range of elevation in unburned areas, recently burned areas (since 1982), and old burns (before 1958) in DNPP. For display purposes, most parameters were set to mean values, except: SOL was shallow (2 cm), *P. tremuloides* was south-facing, and *B. neoalaskana* was high soil pH (mean + 2 SD).

abundance both responded negatively to increasing soil moisture.

Picea mariana abundance, in contrast, showed a different set of responses to covariates than did occupancy for this species (Tables 4 and 6). Specifically, *P. mariana* abundance was highest at mid-elevations with peak abundance at ~300 m, in contrast to the occupancy response for this species which peaked at the lowest elevations in DNPP, with declining occupancy probability in relation to increasing elevation (Table 6, Fig. 9C). In addition, *P. mariana* abundance was positively correlated with depth of the living mat and negatively correlated with the percentage of soil C (Table 6). *Picea mariana* had sharply lower abundance in recent burns as compared to plots without evidence of fire or old burns, but occupancy of this species was

unaffected by fire within this data set (Tables 4 and 6, Fig. 9C).

Predicted abundance for *B. neoalaskana* was highest at elevations of ~475 m, which coincided with relatively low predicted occupancy for this species (Figs. 4 and 9D). Increasing slope was not a significant predictor of *B. neoalaskana* abundance (Table 6), which contrasts with strong positive response of *B. neoalaskana* occupancy to increasing slope (Table 4, Fig. 4). *Betula neoalaskana* abundance was positively correlated with increased thaw depth of the active layer and negatively correlated with increasing SOL depth, two variables that were also significant predictors of *B. neoalaskana* occupancy. *Betula neoalaskana* showed a substantial increase in abundance in old burns relative to both recently burned plots and those without evidence of fire (Table 6, Fig. 9D), in contrast to the responses observed for abundance of the two *Picea* spp.

Inference based on spatial models

Inference based on both the occupancy and abundance results was affected by the addition of the spatial model components. Several covariates selected as important predictors during the nonspatial analyses were not supported after the addition of the spatial terms, suggesting that more structure had been included

TABLE 6. Association between significant environmental covariates and abundance (BA) of three dominant tree species, as well as all species combined, in DNPP.

Covariate	<i>P. glauca</i>	<i>P. mariana</i>	<i>B. neoalaskana</i>	All species
Proportional reduction in deviance	0.32	0.30	0.52	0.43
Terrain variables				
Elevation	+	+	+	+
Elevation ²	-	-	-	-
Slope	+			[+]
Slope ²				
Southness	+			+
Eastness				
Soil unit permafrost				-
Local edaphic variables				
Evidence of fire in plot				
Burned since 1982	[-]	-	-	-
Burned prior to 1958			+	[+]
Living mat depth	+	+		[+]
Soil organic layer depth			-	-
Active-layer depth			+	
Soil pH	[+]			
Percentage of gravel	[-]			[-]
Carbon content		-		
Total disturbance				-
Soil temperature				
Soil moisture	-			-

Note: A plus sign (+) indicates a positive influence on abundance, a minus (-) indicates a negative influence on abundance, and no sign indicates the variable was not included in the model or that the 95% confidence interval included zero.

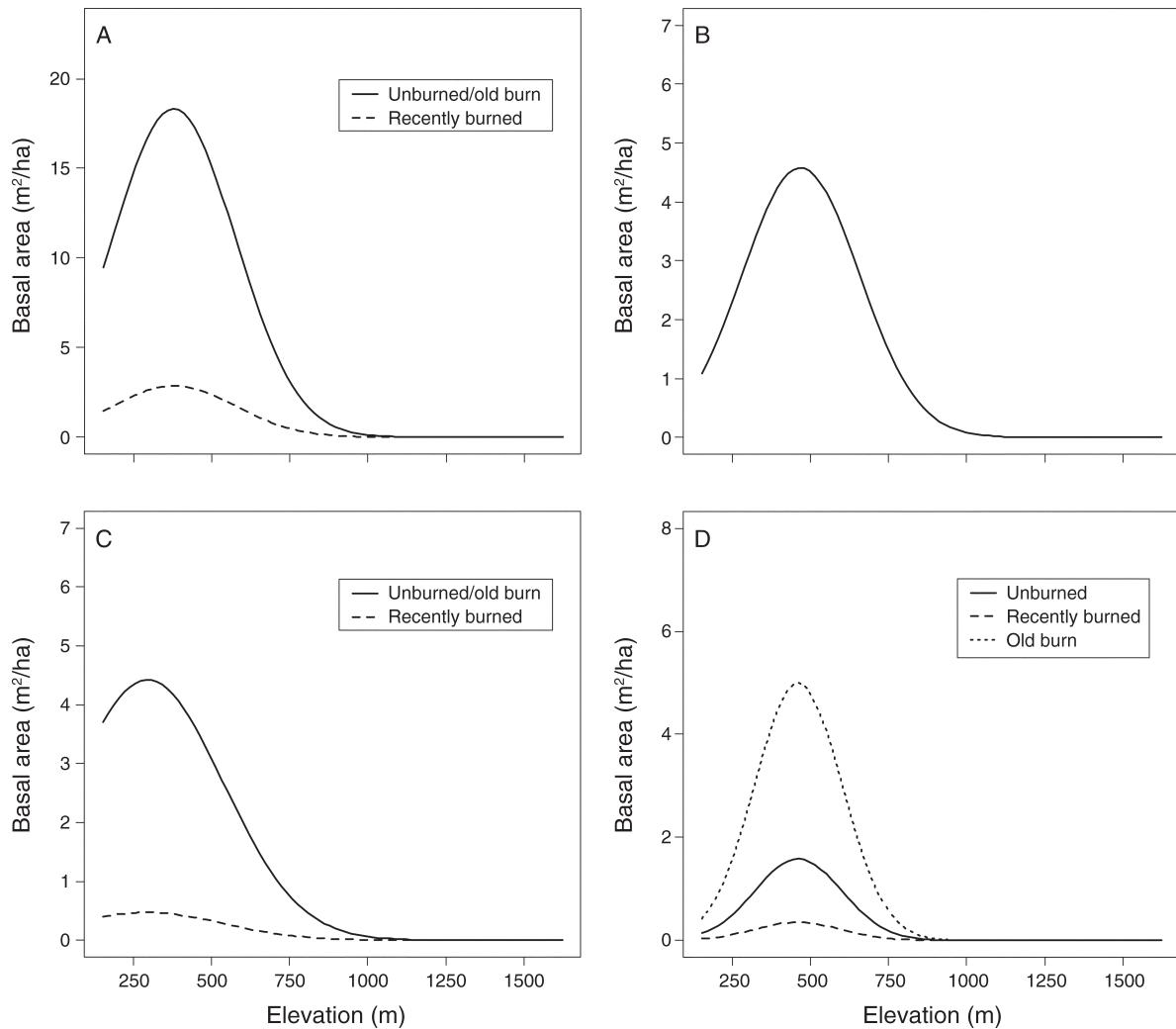


FIG. 9. The predicted relationship between basal area and elevation for (A) all tree species, (B) *P. glauca*, (C) *P. mariana*, and (D) *B. neoalaskana* in DNPP. For display purposes, most parameters were set to mean values, except: all trees, sporadic permafrost, undisturbed, and south-facing; and *P. glauca*, south-facing, moisture at the lower quartile, and living mat depth and slope at the upper quartile.

than could be supported by the available data (see Tables 4 and 6). Changes in model structure were more substantial for the occupancy portion of the models than for the abundance portions. Estimates of the spatial terms indicated that the *P. glauca* model had residual spatial autocorrelation extending across a longer distance (ϕ) for both occupancy and abundance (Table 5) and the occupancy models for broadleaf species had stronger patchiness (σ^2) over a shorter range. The extent of the spatial autocorrelation in occupancy for the remaining species appeared to be confined to a distance approximately equal to the spatial resolution of the mini-grid. For abundance, residual spatial autocorrelation was low and did not influence model structures substantially for *B. neoalaskana* and *P. mariana*. The abundance model for *P. glauca*, on the other hand, contained relatively more residual spatial autocorrela-

tion indicating that potentially important predictors influencing the abundance of this species may have been omitted (Table 5).

Patterns in stand diversity

Forest canopy composition was simple in DNPP, with 53% of the plots with trees containing only a single tree species, 31% of treed plots containing just two tree species, and only 16% of the plots with trees supported three or more tree species growing together (Fig. 10). Plots containing multiple tree species were most common at the lowest elevations (<300 m) in the study area, with only two plots at elevations higher than 900 m containing more than a single tree species (Fig. 10). Certain species pairs occurred together relatively frequently, whereas other pairs of species rarely occurred in the same plot (Table 7). For example, 97% of the plots

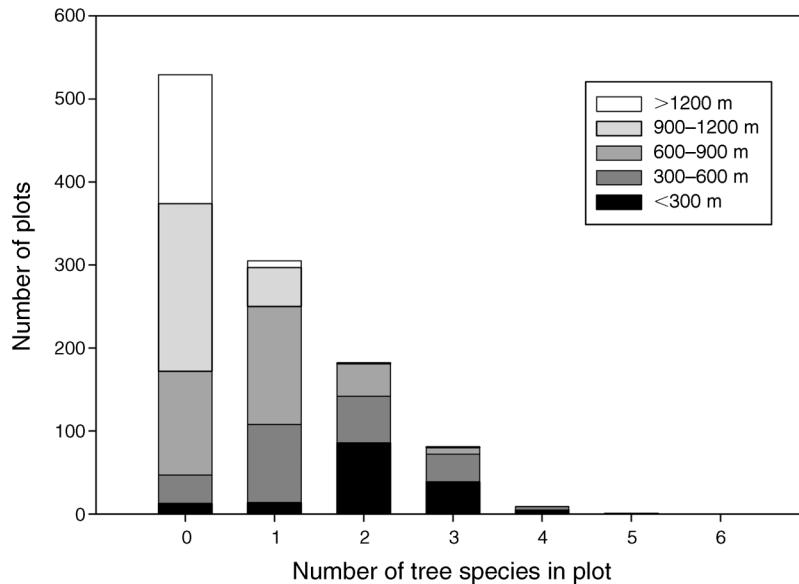


FIG. 10. The number of plots sampled in DNPP containing from zero to five tree species ($n = 1107$). Shades of gray represent the different elevation intervals. Note that plots with multiple species are restricted to the lowest elevation strata.

containing individuals of *L. laricina* also contained individuals of *P. mariana*. Similarly, *P. glauca* occurred in 74% of the plots where *P. tremuloides* was recorded. In contrast, *P. balsamifera* and *P. tremuloides* each occurred in only 0.7% and 2.6%, respectively, of the plots in which *P. mariana* occurred. Not surprisingly, the pairs of species which had the largest percentages of co-occurrence (for example, *L. laricina* and *P. mariana*, and *P. glauca* and *P. tremuloides*) also shared the most similar responses to the covariates within our occupancy models. Similarly, species with sharply contrasting responses to covariates in the occupancy models (for example, *L. laricina* vs. both *Populus* spp.) were spatially segregated due to contrasting ecological preferences. *Picea glauca* occurred as the sole tree species in ~58% of the plots where it was recorded, which was the highest percentage for any species, while *B. neoalaskana* and *L. laricina* rarely occurred as the sole tree species in a plot with only 5% and 1%, respectively.

Patterns in tree recruitment

Trees in DNPP exhibited different patterns of variation in seedling density among species than in

abundance of larger individuals (Table 8). Specifically, mean seedling density of *P. mariana* was almost an order of magnitude higher than the mean seedling densities of the other tree species, even though this species was less abundant overall than *P. glauca*. *Betula neoalaskana*, *L. laricina*, and *P. glauca* had similar seedling densities across the study area. *Populus balsamifera* and *P. tremuloides* had the lowest mean plot seedling densities, with 195 and 154 seedlings/ha, respectively. There was a positive association between a species' presence in the canopy and mean seedling density of that species in the understory (Table 8). For example, the mean density of *P. mariana* seedlings was high in all stand types where this species occurred in the overstory, including pure *P. mariana* stands, and mixtures of *P. mariana* with *L. laricina*, *B. neoalaskana*, and *P. glauca*, but was approximately an order of magnitude lower in stands without *P. mariana* in the overstory. There were no *P. mariana* seedlings in the stands dominated by *Populus* spp. or mixed stands of *Populus* spp. and *P. glauca*.

Thirty-seven of the plots in this sample were classified as recently burned (i.e., fires occurred in the years since 1982) and 33 plots were located in old burns (fires

TABLE 7. Patterns in co-occurrence of species within 1107 plots in DNPP.

Species	Sole species	<i>P. glauca</i>	<i>P. mariana</i>	<i>L. laricina</i>	<i>B. neoalaskana</i>	<i>P. balsamifera</i>	<i>P. tremuloides</i>
<i>P. glauca</i>	57.8	100.0	20.9	4.7	18.3	10.6	7.7
<i>P. mariana</i>	26.3	26.3	100.0	40.7	33.7	0.7	2.6
<i>L. laricina</i>	0.9	14.2	97.3	100.0	31.0	1.8	2.7
<i>B. neoalaskana</i>	4.6	47.6	70.0	26.9	100.0	4.6	6.9
<i>P. balsamifera</i>	42.2	56.3	3.1	3.1	9.4	100.0	40.6
<i>P. tremuloides</i>	11.4	74.3	20.0	8.6	25.7	34.3	100.0

Note: Numbers indicate the percentage of plots in which the species in the row heading co-occurred with the species in the column heading (as a percentage of the total number of plots in which the species in the row heading is present); the first column presents the percentage of plots in which that species occurred as the sole tree species in the plot.

TABLE 8. Mean seedling densities for six tree species in relation to the species composition of the overstory dominants in DNPP.

Dominant species	No. plots	LARLAR	PICMAR	BETNEO	PICGLA	POPTRE	POPBAL
PICMAR or LARLAR	137	2397	15 589	81	18	0	0
PICMAR–BETNEO	15	125	7 625	2500	83	125	0
PICMAR–BETNEO–PICGLA	16	0	6 680	664	508	0	0
PICMAR–PICGLA	17	221	7 500	0	478	0	0
BETNEO or PICGLA–BETNEO	38	0	724	5444	1053	132	0
PICGLA	104	0	204	12	2037	138	294
POPsp or PICGLA/POPsp	29	0	0	0	1681	1466	1940

Notes: Plots were assigned to categories based upon the dominant tree species occurring in each plot (all tree species occurring in abundance of $>0.5 \text{ m}^2/\text{ha}$ BA were listed in the dominant species category). The mean seedling density was calculated across all plots with the combination of dominant species shown. Forest dominant types are arranged along a gradient of site types, from those generally occurring on cold/wet sites (containing *P. mariana*) to those occurring in well-drained and warm sites (containing *Populus* spp.). See Table 2 for species codes; POPsp indicates *P. balsamifera* and/or *P. tremuloides*.

occurred prior to 1958). Recent fires occurred in plots within six mini-grids in the years 1982, 1986, 1990, 1991, 1997, and 2002) and plots showing evidence of old burns occurred within 11 mini-grids. Most of the recently burned plots originally supported *P. mariana*-dominated stands (although 11 of 37 had *P. glauca* or other as pre-burn dominant). We cannot characterize the composition of pre-burn stands for the older burns with sufficient confidence to report here.

There were apparent trends in the mean densities of seedlings and saplings in relation to fire age classes

(Table 9) and in the relative responses of conifer species as compared to the broadleaved-tree species in relation to burn age classes within DNPP (Fig. 11), although plot-to-plot variation in seedling and sapling densities were high. *Picea mariana* had the highest mean densities of seedlings in plots within all three burn classes (unburned, recently burned, and old burn) by a large margin, with mean density of 3426 stems/ha in unburned plots, 16 706 in recent burns, and 4805 stems/ha in old burns (Table 9). The other two conifer species, *L. laricina* and *P. glauca*, had the second and third highest

TABLE 9. Means and standard deviations (SD) for mean seedling and sapling densities of six tree species in plots for three burn classes in DNPP.

Species and burn class	Seedling density (stems/ha)		Seedling frequency (% of plots)	Sapling density (stems/ha)		Sapling frequency (% of plots)
	Mean	SD		Mean	SD	
Conifer						
PICGLA						
0	523	2 393	17	180	692	27
1	1 064	3 632	27	162	425	22
2	938	1 688	38	459	642	63
PICMAR						
0	3 426	8 861	24	846	2077	28
1	16 706	24 762	59	284	642	32
2	4 805	8 402	38	1416	2575	53
LARLAR						
0	558	2 924	9	32	150	10
1	1 470	3 527	27	59	228	19
2	684	3 867	3	11	44	6
Broadleaf						
BETNEO						
0	407	6 473	3	97	603	9
1	3 851	12 405	38	265	525	35
2	684	1 914	28	712	1547	59
POPBAL						
0	234	1 842	5	71	574	4
1	1 301	3 256	24	230	543	30
2	0	0	0	3	18	3
POPTRE						
0	137	1 587	2	66	1027	1
1	1 233	2 851	24	651	1965	30
2	801	2 351	16	196	691	13

Notes: Burn classes are: 0, no evidence of fire; 1, recently burned plots; and 2, old burns. Data presented are for the set of 788 plots below 1000 m elevation because fires are extremely rare above 1000 m in DNPP. Sample sizes for the burn classes below 1000 m elevation were as follows: 719 with no evidence of fire, 37 recently burned, and 32 old burns. See Table 2 for species codes.

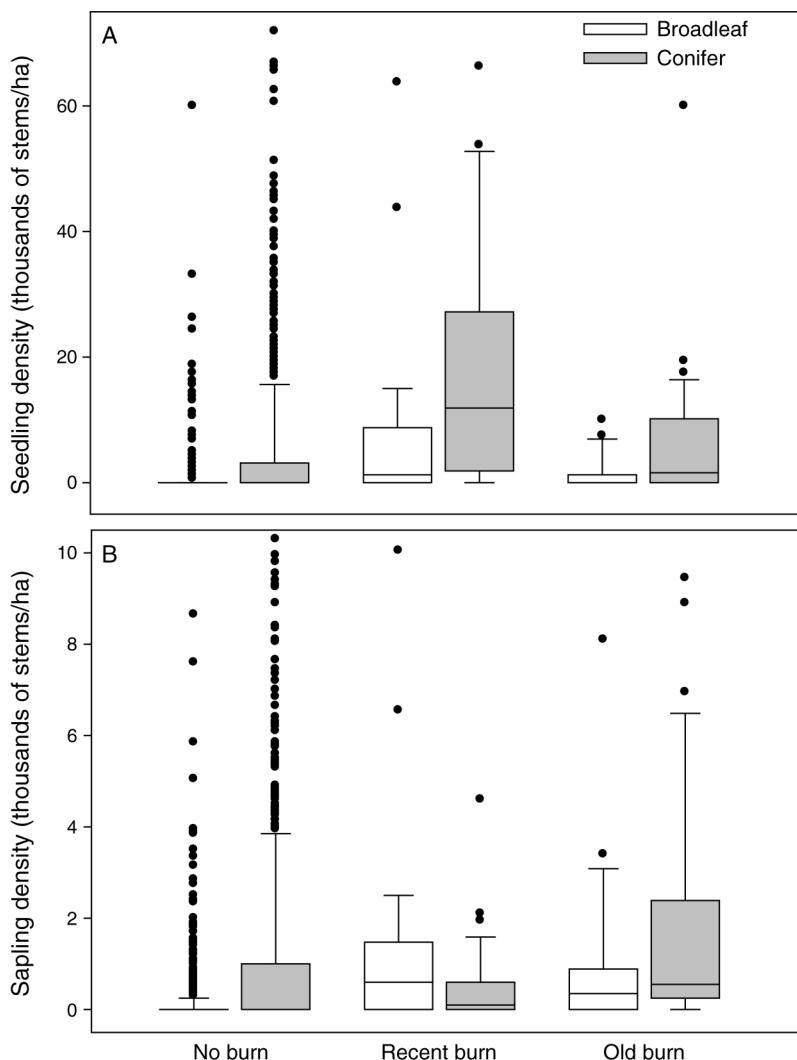


FIG. 11. Box and whisker plots showing the range and median of (A) seedling and (B) sapling densities for broadleaf and conifer species in unburned plots ($N = 719$), recently burned plots ($N = 37$), and old burns ($N = 32$) for plots below 1000 m elevation in DNPP. The center line within the box marks the median value, the top and bottom of the box indicate the 75th and 25th percentile, respectively. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, respectively. Outliers, indicated by points above the whiskers, are observations for plot seedling and sapling density values beyond the 90th percentile. Outlier seedling density values greater than 100 000 stems/ha and outlier sapling density values greater than 10 000 stems/ha were omitted for display purposes.

mean seedling densities in unburned plots with 558 stems/ha and 523 stems/ha, respectively. In recently burned plots, however, *B. neolaskana* had the second highest mean density with 3851 stems/ha, followed by *L. laricina*, *P. balsamifera*, and *P. tremuloides*, with mean densities of 1470, 1301, and 1233 stems/ha, respectively. In contrast, *P. glauca* had the second highest mean seedling density in plots located in old burns with 938 stems/ha, followed by *P. tremuloides* and *B. neolaskana* with 801 and 684 stems/ha, respectively.

The mean seedling densities observed in recently burned plots for the broadleaf species, *B. neolaskana*, *P. tremuloides*, and *P. balsamifera*, were factors of 9.5, 9.0, and 5.6, respectively, higher than for mean densities

for these species in plots without evidence of fire (Table 9, Fig. 11). Although conifer species generally showed a smaller relative increase in seedling density in recently burned plots as compared to their densities in unburned plots, *P. mariana* seedling density in recent burns was a factor of 4.9 higher than was observed in unburned plots (Table 9). Mean densities for *P. glauca* and *L. laricina* were just 2.0 and 2.6 higher, respectively, than the mean densities for these species observed in unburned plots. Mean seedling densities in old burns, in contrast, were only slightly higher than mean values for the unburned plots for all species, except for *P. balsamifera* seedlings, which were absent from plots situated in old burns (Table 9).

TABLE 10. Mean densities and associated standard deviations (SD) for seedlings and saplings found in the plots with two forms of recent disturbance in DNPP that were below 1000 m elevation for fluvially disturbed plots ($n = 46$) and plots located in slope disturbances ($n = 4$).

Disturbance type and species	Seedling density (stems/ha)		Sapling density (stems/ha)	
	Mean	SD	Mean	SD
Fluvial				
<i>P. glauca</i>	1019	6354	24	78
<i>P. mariana</i>	0	0	1	7
<i>L. laricina</i>	0	0	0	0
<i>B. neoalaskana</i>	27	184	0	0
<i>P. balsamifera</i>	1821	5729	26	132
<i>P. tremuloides</i>	0	0	0	0
Slope				
<i>P. glauca</i>	156	312	38	75
<i>P. mariana</i>	0	0	13	25
<i>L. laricina</i>	0	0	0	0
<i>B. neoalaskana</i>	0	0	0	0
<i>P. balsamifera</i>	625	884	125	250
<i>P. tremuloides</i>	0	0	0	0

Frequency of occurrence of individuals in the seedling and sapling size classes for broadleaf tree species were uniformly negligible in our unburned plots, and uniformly elevated (by nearly an order of magnitude for *B. neoalaskana* and *P. tremuloides*) in plots located in both recent burns and old burns (Table 9). The dominant conifers *P. mariana* and *P. glauca* had the highest mean densities of saplings (individuals >1.37 m tall and <12 cm dbh) in unburned plots across DNPP, with 846 stems/ha and 180 stems/ha, respectively (Table 9). *Populus tremuloides* had the highest mean sapling density in recently burned plots with 651 stems/ha, and given the variability in these data, mean sapling densities in new burns for *P. mariana*, *B. neoalaskana*, *P. balsamifera* were essentially the same with 284, 265, and 230 stems/ha, respectively (Table 9). Species with the highest sapling densities in old burns were *P. mariana*, with 1416 stems/ha and *B. neoalaskana* with 712 stems/ha.

Fifty-one plots were located in recently disturbed fluvial deposits and 97 showed evidence of recent slope-process disturbance such as a slide or slump feature (Table 10). Seedling and sapling densities were highly variable among plots within these disturbance classes (Table 10), but showed marked contrast to the patterns

that we observed for the fire-disturbed plots. Specifically, the sets of plots undergoing primary succession following disturbance by water and slope processes were colonized almost exclusively by individuals of *P. balsamifera* and *P. glauca* (Table 10).

Patterns in tree mortality

The percentage of standing trees that were dead varied from 8.6% of the individuals of *P. tremuloides* to 60% of *L. laricina* individuals (Table 11). In general, tree mortality was low throughout the study area, except for burned plots and the conspicuous study area-wide mortality of *L. laricina*. The other two species with somewhat elevated mortality percentages were *P. mariana* and *P. balsamifera*, with overall mortality percentages of 15.9% and 19.2%, respectively, but these species were differentially affected by fire. Excluding the 1115 dead trees in burned plots (presumably killed by fire), the mortality percentage of *P. mariana* would have been ~9%, and excluding the 68 dead *P. balsamifera* killed by fire, its percentage would have been ~15%.

DISCUSSION

We used field data, collected using a probabilistic study design over a 1.28 million ha area, to construct

TABLE 11. Numbers of total, live, and dead individuals >1.37 m tall for six species, and the percentage of standing trees that were dead in 1107 plots in DNPP.

Species	Total no. individuals	No. live	No. dead	Standing mortality (%)
<i>B. neoalaskana</i>	2 800	2 453	347	12.4
<i>L. laricina</i>	1 306	523	783	60.0
<i>P. glauca</i>	4 567	4 076	491	10.8
<i>P. mariana</i>	16 133	13 571	2562	15.9
<i>P. balsamifera</i>	1 587	1 282	305	19.2
<i>P. tremuloides</i>	1 770	1 618	152	8.6
All species combined	28 163	23 523	4640	16.5

spatially explicit Bayesian hierarchical models describing relationships between tree occupancy and abundance and terrain, edaphic, and disturbance factors. We also used this unique, spatially extensive data set to describe general patterns of recruitment, mortality, and species co-occurrence and tree diversity in DNPP. Although the general habitat preferences of tree species in interior Alaska have been described within spatially restricted study areas (e.g., Viereck et al. 1983, Dyrness et al. 1989, Kurkowski et al. 2008, Wirth et al. 2008, although see Yarie 1981 and Yarie and Billings 2002), we investigated tree distribution throughout the landscape in a larger and previously unstudied area, capturing broader gradients in topography and site type than have previously been examined in the literature. Using this unique data set and a rigorous geostatistical modeling approach, we have established a quantitative baseline that will provide a landscape-scale spatial context for intensive, site-specific studies of forest dynamics in interior Alaska and will allow comparisons with other studies in the boreal forest.

General character of the forest mosaic

The relative openness of the canopy we observed in DNPP has two primary explanations. First, a large fraction of the extensive bottomlands were occupied by open bogs or sparse *P. mariana* woodland in cold, waterlogged soils supporting small, slow-growing trees (Clark and Duffy 2006). Due to suboptimal habitat conditions, tree abundances in these areas were relatively low. Van Cleve et al. (1983) observed a similar pattern near Fairbanks in interior Alaska. Closed forests and large diameter trees were generally restricted to river terraces and south-exposed, well-drained positions in sloping terrain without recent disturbance. These conditions were relatively rare, and dense stands of large trees occurred infrequently (Table 2). Second, because our sample was selected systematically across all habitats within the study area including areas above treeline, numerous treeless plots were included. This decreased the mean number of trees per plot substantially as compared to a sampling design targeting only forested sites, but allowed inference across the entire landscape.

The forest mosaic in DNPP was dominated by coniferous species, with 83% of treed plots having higher total combined abundance of conifer species as compared to combined broadleaf tree BA. Exceptions to conifer species dominance in DNPP occurred in response to disturbance and patches of broadleaf and mixed forest were generally restricted to areas of relatively recent burns, south-exposed hilly terrain, and river terraces.

Statistical models

The lack of influence of local edaphic factors on overall tree occupancy was a result of the strong partitioning of the landscape among species, with high

occupancy of *P. mariana* and *L. laricina* in wet, organic soils with shallow active layers, and high occupancy of the other species (particularly *P. glauca* and *B. neoalaskana*) on mineral soil with deeper active layers and better drainage (Table 4). This partitioning of tree habitat among species resulted in a forest mosaic composed primarily of one- or two-species stands at the 200-m² scale of our plots, consistent with hierarchical patch dynamic theory (Wu and Loucks 1995). Plots situated below 1000 m were infrequently devoid of trees, although poorly drained lowland sites supported very low tree abundance.

Patterns in tree occupancy

Occupancy of the six tree species varied according to species-specific responses to unique sets of environmental covariates, and we observed strong spatial segregation of stand dominant tree species based on topographic factors, edaphic attributes, and disturbance history. Our models suggest two primary gradients along which tree species were arrayed in DNPP. The first was largely controlled by the influence of topography on site conditions (solar radiation, active-layer depth, soil drainage, and reaction), and the second was related to site history and succession following disturbance. The primary gradient in ordering tree species occupancy was the transition from cold, poorly drained sites with shallowly thawed active layer, low pH, and deep SOL (generally associated with basin landscape positions and north-exposed terrain) to more productive sites on mineral soil with deeply thawed active layer, thin SOL, and located in mid-elevations in generally south-exposed (high insolation) terrain or alluvial terrace situations. Superimposed on this topographically driven gradient in forest structure and composition were the influences of fire and flooding, the two primary vectors of forest disturbance in boreal Alaska.

Our results generally agreed with established habitat preferences for the tree flora of interior Alaska (Viereck et al. 1983): *Picea mariana* and *L. laricina* were primarily limited to wet, acidic sites with shallow active layers in permafrost terrain; *P. glauca* occurred in relatively well-drained, south-exposed landscape positions with higher pH soils, and preferentially on alluvium; *P. tremuloides* occurred in the warmest, south-exposed sites; and *P. balsamifera* occurred almost exclusively in river terraces and recently deposited alluvium, and more rarely in very steep, disturbed slopes. The occupancy response of *B. neoalaskana* was roughly intermediate between the two dominant conifer species, although the abundance response of *B. neoalaskana* was very similar to that of *P. glauca*. In addition, *B. neoalaskana* was more patchily distributed, generally restricted to lower elevation, and occupancy of this species showed marked positive responses to fire.

We suspect the reduced occupancy probability of the two *Populus* species at the lowest elevations was related to the fact that these two species germinate and establish

most successfully on moist, nutrient-rich mineral soil (Chapin 1986, Perala 1990, Zasada and Phipps 1990). These conditions were rare in the lowland basins of DNPP where thick, acidic SOL mats predominate. The *Populus* species did occur at low elevations in alluvial terraces and floodplains where mineral soil was available and available nutrient levels can be relatively high (Chapin et al. 2006b, Yarie and Van Cleve 2006). Occupancy probabilities of both *Populus* species also showed a negative correlation with SOL depth, further supporting this hypothesis.

The broadleaf tree species were strongly associated with disturbance within the forest mosaic of DNPP, which agrees with earlier work in Alaska's boreal forests (Chapin et al. 2006b, Johnstone and Chapin 2006b, Johnstone et al. 2010b, Shenoy et al. 2011). *Betula neoalaskana* and *P. tremuloides* produce copious quantities of small, wind-borne seeds that benefit from a mineral seedbed following high-severity fire events (Johnstone and Chapin 2006a, b, Greene et al. 2007). High-severity fires can substantially reduce the thickness of the SOL (Johnstone et al. 2010b, Kasischke et al. 2012), and we found the depth of the SOL also had a significant negative influence on the occupancy of *B. neoalaskana* and *P. tremuloides*, supporting this hypothesis for DNPP across a wide area.

A primary contribution of our study is our ability to model occupancy patterns for all six tree species across a large area based on field data with genuine inference to the entire landscape. However, there are also important limitations inherent in our extensive-scale approach. For example, our design did not allow us to address patterns at scales <500 m, the spacing between plots in a mini-grid. One such likely factor influencing *P. glauca* occupancy at local scales in DNPP is the proximity to established mature stands of trees that both ameliorate conditions, and thus facilitate tree establishment, and provide a source of propagules to accomplish this process (Stueve et al. 2011). Furthermore, there are important statistical considerations inherent in an analysis of tree occupancy at the extensive scale of our study, including the existence of residual spatial autocorrelation in the resulting models. Indeed, our occupancy models for *P. glauca* and *P. balsamifera* contained relatively high spatial autocorrelation as compared to models for other tree species. Thus, our results emphasize the importance of choosing appropriate spatial models when analyzing spatially indexed data. This approach has revealed that additional variables beyond those included in our models have influenced patterns in tree occupancy in DNPP, which can serve as the starting point for generating additional hypotheses.

Patterns in tree abundance

The character of sites supporting peak abundance of *P. mariana* shared similarities with sites supporting high *P. glauca* occupancy in that they were at higher elevation, better drained, and more likely to occur in mineral soil

(due to landscape position and reduced C content of soil) than was typical of high-occupancy *P. mariana* sites. *Picea mariana* had higher abundance in sites atypical for occupancy of this species in DNPP as compared to the poorly drained sites where it most frequently occurred. The fact that *P. mariana* reached peak abundance in sites more similar to those with high occupancy of *P. glauca* than those with highest *P. mariana* occupancy suggests competition with *P. glauca* may limit the distribution of *P. mariana*. Areas with high *P. mariana* abundance were also perhaps less affected by shallow permafrost and low soil pH than sites with highest occupancy probability for the species. *Picea mariana* is tolerant of waterlogged soils (Van Cleve et al. 1983, Islam et al. 2003), and we suspect this allowed it to occupy the poorest lowland sites supporting tree growth within the landscape. In addition, *P. mariana*, which is a slow-growing species and well adapted to low-nutrient environments, can tolerate the low N mineralization rates found in the cold soils associated with deep SOL, while other tree species are less competitive under these conditions (Bonan and Van Cleve 1992). The characteristics of these poor sites generally precluded establishment of the other tree species, except for *L. laricina*, which is also tolerant of waterlogged soils (Islam et al. 2003).

Competitive interactions between *P. glauca* and *P. mariana* are likely most common in segments of the landscape where predicted levels of occupancy and abundance were relatively high for both species (e.g., moderate west-facing slopes below 500 m). *P. mariana* is a very slow-growing species that has been shown to exhibit slower growth rates in competition with other species early in succession (Gutsell and Johnson 2002, Wagner and Robinson 2006). Gutsell and Johnson (2002) demonstrated that, across a variety of stand types and tree species mixtures, *P. mariana* consistently exhibited the slowest growth rates of all boreal tree species studied. Similarly, Wirth et al. (2008) found that, even in a set of burned sites typical of *P. mariana* stands in lowland interior Alaska with postfire establishment of both *Picea* spp., *P. glauca* growth in the seedling stage equaled or exceeded that of co-occurring *P. mariana* seedlings. They concluded that in the absence of mortality of the *P. glauca* cohort due to the return of permafrost edaphic conditions over time, *P. glauca* forest would likely replace prefire *P. mariana* stands.

The variables controlling *B. neoalaskana* abundance were similar to those that influenced occupancy of this species, except peak abundance occurred at a higher elevation than peak occupancy. Both occupancy and abundance of this species responded positively to increasing active-layer depth and decreasing SOL depth and were both clearly associated with plots that had burned. *Betula neoalaskana* establishes in high numbers following fire (Johnstone et al. 2010a), likely explaining our results suggesting peak occupancy in recently burned sites, and highest abundance in deeply thawed mid-elevation sites with thin SOL in old burns. Our results

show that, whereas *B. neoalaskana* is able to colonize such areas (probably due to warmer, higher nutrient seedbed conditions following fire), the species generally did not reach high abundance across all sites where it was able to become established, particularly in sites with shallow active layers, impeded drainage, and deep SOL. Instead, *B. neoalaskana* required site conditions similar to those of *P. glauca*, which were more prevalent in the mid-elevations in deeply thawed terrain on mineral soil to produce stands of high abundance in DNPP.

Inference based on spatial models

The changes in model structure we observed after the addition of spatial random effects highlights the importance of addressing residual spatial autocorrelation during analysis. Commonly used analytical techniques assume that all sample points are independent, but we found evidence of spatial autocorrelation, suggesting some lack of independence among points at least within mini-grids, and extending in some cases to adjacent mini-grids. A lack of independence also indicated that one or more important explanatory variables were not included in our model set. For example, our abundance model for *P. glauca* contained a relatively high amount of residual spatial autocorrelation, which we strongly suspect is related to the rare and spatially clustered distribution of high-abundance plots for this species in DNPP. We rarely observed *P. glauca* abundances in excess of 25 m²/ha in DNPP, and these high *P. glauca* abundance plots were spatially clustered, often in low-elevation river terrace situations on deeply thawed alluvium without recent disturbance. Although we did not consider interaction terms in our analysis a priori, we suspect that an interaction term between active-layer depth and soil lithology (alluvium) would be included in a spatial model for *P. glauca* abundance. While this prediction has support in the literature (e.g., Viereck et al. 1983), we have not tested it here. This example points to one benefit of the geospatial modeling approach: Spatial model results can serve as a starting point for the development of additional hypotheses regarding residual pattern revealed by the spatial models. In addition, formally accounting for spatial autocorrelation also strengthens the inference that can be drawn from our results because they are not dependent on the assumption of complete independence among points. This allowed us to be more confident in our conclusions and decreased the chances that our conclusions were spurious.

Patterns in stand diversity and tree recruitment

Two primary successional pathways have been demonstrated for Alaskan boreal forests, the “self-replacement” pathway, in which the dominant species from the pre-disturbance canopy repopulates a site following a disturbance, to the “species dominance relay” model, where succession follows a predictable series of dominant tree species that replace each other

through time (Viereck et al. 1993, Chapin et al. 2006b, Kurkowski et al. 2008). We found evidence for both of these successional pathways in DNPP forests.

The predominance of plots with a single tree species and the fact that the species composition of seedlings and saplings generally mirrored the composition of the forest canopy across the study area support the conclusion that self-replacement was the dominant pathway of forest succession in DNPP. Specifically, the high densities of seedlings and saplings of *P. mariana* in the recently burned plots (many of which were *P. mariana* forest prior to the fire) suggest the primacy of this successional pathway within DNPP. Species dominance relay, on the other hand, is likely to be a more common successional pathway in the sites that experience substantial establishment of broadleaf species following disturbance.

The three broadleaved-tree species were able to occupy sites within this landscape primarily through opportunities provided by disturbance, either by fire, flooding, or slope processes. Our models and observations of variation in seedling and sapling densities indicated that occupancy and abundance of the broadleaf tree species, particularly *B. neoalaskana* and *P. tremuloides*, showed significant positive correlations with occurrence of fire, which agrees with previous studies (Chapin et al. 2006b, Johnstone and Chapin 2006b, Johnstone et al. 2010b, Shenoy et al. 2011). However, very few plots supported pure stands of broadleaved species in DNPP, and in mixed stands, the ability of both *Picea* species to eventually dominate the canopy as the shorter lived broadleaved trees die out has been well established in interior Alaska (Viereck et al. 1983, Chapin et al. 2006b). Although broadleaf saplings outnumbered coniferous saplings in recent burns, combined broadleaf sapling density was much less than conifer sapling densities in old burns within our sample, and even in recent burns the mean density of conifer seedlings was higher than for the broadleaf species. These results suggest, at least in this set of plots, successional trajectories in DNPP favor eventual dominance by conifer species as a result of both the self-replacement and the species dominance relay pathways, although single-cohort mixed broadleaf–conifer stands also occurred. However, a localized exception was reported by Mann and Plug (1999), who described a site on the eastern edge of our study area that experienced an unusual 40–60-year fire return interval in recent centuries (perhaps due to its location near human habitation and anthropogenic fire starts). Youngblood (1995) also reported postfire establishment of mixed conifer–broadleaf stands on south aspects that did not succeed to conifer dominance prior to the subsequent fire near Fairbanks, Alaska.

Hypotheses regarding forest change in interior Alaska

The Alaskan boreal forest is a dynamic ecosystem likely to undergo substantial changes in response to

predicted climate warming in the next century (ACIA 2005). By explicitly quantifying tree species responses to environment across a spatially extensive study area, our results provide useful context to inform predictions about the potential trajectories of forest change in this area. Specifically, our results suggest: (1) Forests in DNPP were dominated by conifer species, and we did not find evidence of incipient conversion to broadleaf ecosystems; (2) *P. glauca* may increase in abundance and distribution in the future due to increased occupancy in newly thawed terrain; (3) *P. glauca* is the primary treeline species in DNPP, and we predict it will continue to increase in abundance and distribution at elevations above 800 m under warming climate conditions; and (4) forests in DNPP may be vulnerable, based on the extent of observed *L. laricina* mortality, to other large-scale tree mortality events caused by insects.

Conversion from conifer to broadleaf forest types

Recent literature has suggested a widespread conversion of the landscape in interior Alaska from conifer to broadleaved-forest ecosystems may occur as a consequence of climate warming (Rupp et al. 2000, Johnstone and Chapin 2006b, Johnstone et al. 2010b, Barrett et al. 2011, Beck et al. 2011, Shenoy et al. 2011). Evidence shows some coniferous forests that have experienced high-severity fires have converted to broadleaved stands in interior Alaska (Johnstone et al. 2010a, b, Barrett et al. 2011), and conifer dominated sites that have experienced a higher frequency of fires also favor postfire establishment of deciduous tree species (Johnstone and Chapin 2006b). Small-seeded, thus farther dispersing and faster growing broadleaved species are favored in postfire seedbeds characterized by bare mineral soil (Johnstone and Chapin 2006b, Greene et al. 2007, Johnstone et al. 2010b); therefore, a pronounced trend towards high-severity and/or frequent fire that consume the SOL and the establishment of additional nearby seed sources could continue this process over large areas.

Our occupancy and abundance models show conifer dominance and strong topographic and edaphic controls over tree distributions at the landscape scale, suggesting that conversion to a predominantly broadleaved ecosystem would likely require a fundamental transformation of the physical attributes of the landscape. In addition, recruitment data from our recently burned plots showed a dominance of conifer self-replacement in postfire seedling and sapling densities. Similarly, a recent fire ecology study in the basin lowlands of DNPP showed a preponderance of conifer self-replacement with little evidence of conversion to broadleaf dominance within three recent large fires located in lowland *P. mariana* habitat (J. Barnes, unpublished data).

A crucial element governing the potential for transformation of the lowlands of DNPP is the interaction of fire frequency and severity with the distribution of SOL. Our models support the idea that increased fire would,

likely benefit broadleaf species by increasing the footprint of early-successional habitats. The few plots with broadleaf dominance in DNPP were located either in mineral alluvium of river terraces or had evidence of a burned SOL layer contained in the surface soil with little to no remaining SOL remaining in evidence. The burned sites with broadleaf dominance were generally located in relatively warm topographic exposures in sloping, hilly terrain on the flanks of domes rising out of the northern lowlands, and few, such sites were observed in the flat and gently rolling basin terrain characterizing highest occupancy probability for *P. mariana* within DNPP. These poorly drained basin landscape positions are more likely to follow a pattern of succession characterized by *P. mariana* self-replacement than moderate-to-well-drained slopes due to the moderating influence of high soil moisture on fire behavior (Johnstone and Chapin 2006b, Kane et al. 2007, and Johnstone et al. 2010b).

During the recent drought years of 2004–2005, fires consumed an average of 17.8 cm of the surface organic horizon in poorly drained *P. mariana* forests in interior Alaska (Kasischke et al. 2012). Using this figure as an estimate for the lowland basin positions in DNPP where organic horizons are sometimes in excess of 40 cm (Clark and Duffy 2006), it would require repeated severe fire events in order to eventually expose a mineral seedbed that would tip the balance conclusively in favor of the broadleaf species within these areas. The combination of high soil moisture and deep SOL in the basin landscape positions suggest this area may be resistant to conversion to broadleaf dominance without a major increase in fire frequency and/or severity. With an estimated fire return interval of 244 years in this ecoregion, at elevations <800 m (Kasischke et al. 2002), it could take centuries for such a conversion to take place. However, new research indicates that annual area burned in Alaska has increased recently, along with a trend of increased consumption of SOL during late season fires (Kasischke et al. 2010, 2012) suggesting an increased potential for this process to occur in DNPP.

For the present, the rarity of *P. tremuloides* forest within the study area suggests that if conversion of conifer forest to *P. tremuloides* woodland is occurring in DNPP, as has been suggested for other areas of interior Alaska, it has been a spatially limited phenomenon to date. Plots in two mini-grids have burned since our initial measurements were made, providing opportunities to document whether type conversion will occur in the future in DNPP.

Potential vulnerability of Picea glauca and Picea mariana to warming in interior Alaska

Recent research has shown declining growth rates of *P. glauca* in mature forest stands in interior Alaska due to temperature induced drought stress in the decades since 1900 (Barber et al. 2000, Lloyd and Fastie 2002, McGuire et al. 2010, Beck et al. 2011). Beck et al.

(2011) suggested that the negative trends in *P. glauca* radial growth and a trend of reduced primary productivity estimated from satellite imagery are indications that an incipient biome shift is underway in interior Alaska. A continuation of these trends, they suggest, would result in a replacement of *Picea* forests in interior Alaska by aspen parkland or possibly a grassland biome. Mature stands in which *P. glauca* occurs in high abundance would be particularly vulnerable due to increased density-dependent competition for water among large trees (Yarie and Van Cleve 2010). The response of *P. glauca* to drought stress, however, may vary depending on landscape position (slope, aspect, elevation) and regional climate (Lloyd and Fastie 2002, Wilmking et al. 2004). Positive responses of *P. glauca* growth to warm summers have been found in the coolest wettest sites, such as the northern and northwest range limits of the boreal forest (Beck et al. 2011), while growth declines were most common in the warmer and drier sites (Lloyd and Fastie 2002), lending support to the replacement hypothesis for certain landscape segments.

Picea glauca was the most widespread and abundant tree species in DNPP, spanning a wide range of elevations and landscape positions. *Picea glauca* co-occurred with *P. mariana* in cold, wet, lowland sites, and with *P. tremuloides* in the most xeric forest types within the study area. Indeed, *P. glauca* occupancy overlapped substantially with occupancy of all the other tree species in DNPP (although to varying degrees). Populations of *P. glauca* growing in different habitats will likely respond differently to changing climate. *Picea glauca* had higher occupancy and abundance in warmer, well-drained areas with lower soil moisture and higher pH relative to areas of the landscape with deep SOL and cold, wet soils on permafrost in DNPP. These high BA stands of *P. glauca* are potentially at greater risk from drought stress due to their distribution on the landscape. However, DNPP has cooler and wetter summers, on average, than central interior Alaska (Shulski and Wendler 2007), and stands of *P. glauca* in DNPP may therefore be less vulnerable to growth reductions from warming than stands studied in the central interior. Wilmking and Juday (2005) found the frequency of *P. glauca* individuals with positive annual growth response to increased temperatures was correlated with precipitation of the site, and our data suggest a warming and drying landscape could stimulate increased *P. glauca* occupancy in lowland basin sites currently less suitable for this species due to impeded drainage and low soil temperatures. Wirth et al. (2008) suggested *P. glauca* expansion into areas currently occupied by *P. mariana* in interior Alaska would be expected under a warming and drying landscape, and we expect this would be the case in DNPP as well.

An apparent absence of elevated levels of mortality in *P. glauca* further supports the idea that recent conditions, at least, are not causing severe stress to

populations of this species in DNPP. Ultimately, a decrease in *P. glauca* abundance would require increased mortality and/or reduced levels of recruitment in areas currently occupied by this species. In contrast, our data suggest self-replacement of dominant canopy species remains the primary successional pathway in the study area, and *P. glauca* recruitment occurred widely in forests with both broadleaf and conifer canopy dominance. In addition, our model results indicated *P. glauca* had the broadest realized ecological amplitude relative to important landscape gradients of all the tree species in DNPP, suggesting substantial ecological plasticity and potential capacity to respond to changing conditions in comparison to other species that occupied a lower diversity of landscape positions. Support for this idea is provided by Bigras (2005), who showed that slow-growing *P. glauca* genetic families were better able to withstand drought under current conditions and forecasted climate change scenarios, indicating a heritable basis for acclimation to future climate by this species. Whether continued warming will translate into changes in mortality rates or reproductive capacity of *P. glauca* within DNPP is unknown, but our work suggests a net expansion of the species could occur within this landscape. The locations supporting high abundance of the species may change under different climatic conditions, but we do not expect an overall decrease in *P. glauca* on the landscape in DNPP.

Our results agree with recent work that suggested *P. mariana* could suffer range contractions if predicted levels of warming occur (ACIA 2005). This species has negative growth responses to summer warmth in both southern and northern portions of its range (Dang and Lieffers 1989, Brooks et al. 1998, ACIA 2005). Permafrost is warming and degrading across interior Alaska (Osterkamp and Romanovsky 1999, Osterkamp 2005, Hinzman et al. 2006, Osterkamp et al. 2009), and the environments supporting both *P. mariana* and *L. laricina* may thus diminish substantially in the future with continued warming. In the long term, the changed edaphic conditions resulting from permafrost degradation and a warming, drying landscape could facilitate the establishment of faster growing species such as *P. glauca*, which would out-compete *P. mariana* and *L. laricina* under these new conditions. In the short term, however, it is possible increased nutrient turnover and marginally warmer soil conditions in the coldest and wettest sites due to a warmer climate could increase the abundance of established stands of *P. mariana* (ACIA 2005, Bronson and Gower 2010, Drobyshev et al. 2010) in localized areas. A factor potentially balancing projected net habitat loss for *P. mariana* as a result of warming is that drying of interior Alaskan landscapes could facilitate the expansion of this species into sites from which it is currently excluded due to inundation by standing water. Indeed, *P. mariana* commonly occurs in DNPP within a complex mosaic of interspersed wetlands and woodlands where it is often the

primary tree species encroaching into current wetland margins.

Changes in the position and character of treeline

A major focus of research worldwide has been the change in the position and character of alpine and continental treelines in response to changing climate (e.g., Harsch et al. 2009 and Holtmeier 2009). Our study encompasses a uniquely wide range of sites, which span the full range of elevations occupied by trees in this region, including many treeline transitions. Elevation was, not surprisingly, the one variable that was included in all of our occupancy and abundance models for all tree species. Due to its central importance in influencing tree distributions, we examined in detail the responses of the tree flora to elevation in the context of potential changes in these patterns in response to warming. Recent investigations of treeline in Denali and elsewhere in Alaska indicate the establishment of trees (usually *P. glauca*) in formerly treeless areas, possibly presaging the conversion of open shrub tundra landscapes to woodland and forest (Suarez et al. 1999, Lloyd and Fastie 2003, Lloyd 2005, Sullivan and Sveinbjörnsson 2010, Stueve et al. 2011).

All six tree species in DNPP showed a broad pattern of lowest occupancy and abundance at the highest elevations (>1000 m) within the study area. However, there were considerable differences among species in the shape of the relationship between occupancy and elevation, both in the specific zones of optimal elevation for each species, and in the span of elevations with a high probability of occupancy for each species. Three species were most likely to occupy sites above the lowest basin elevation zone in DNPP (*P. glauca*, *P. balsamifera*, and *P. tremuloides*), and the remaining three species had peak occupancy probabilities at the lowest elevations in the study area (<250 m). Increasing elevation negatively influenced tree species occupancy according to the following ranking (from most to least negative responses to elevation): *L. laricina* > *P. mariana* > *B. neoalaskana* > *P. tremuloides* > *P. balsamifera* > *P. glauca*. The relationship of each individual species to elevation can be explained by individualistic species responses to local site conditions, patterns of fire on the landscape (Lloyd et al. 2007), and species-specific dispersal abilities (Wirth et al. 2008).

Experimental work by Hobbie and Chapin (1998) demonstrated that *P. glauca* was the most likely Alaskan tree species (as compared to *B. neoalaskana*, *P. tremuloides*, and *P. balsamifera*) to invade intact upland tundra due to its higher germination and seedling survival rates in these environments. They also found that root growth and nutrient uptake in *P. glauca* seedlings were less sensitive to cold soil temperatures than the other tree species, translating to higher growth rates in tundra. In addition, *P. glauca* has the ability to form a sapling bank far outside of its adult range in part due to long-distance dispersal of seeds (Greene et al.

1999, Wirth et al. 2008). The larger, better provisioned *P. glauca* seeds arriving in high-elevation sites may also be better able to withstand marginal conditions upon germination (Gross 1984, Westoby et al. 1996, Turnbull et al. 1999), allowing a greater number to eventually become established as compared to other species with reduced dispersal ability and smaller, less well-provisioned seeds (e.g., Viereck and Johnston 1990, Reich et al. 1998). We suspect the conspicuously reduced occupancies of the remaining tree species at high elevations are the result of reduced tolerance for alpine conditions and stronger constraints on seedling recruitment due to the absence of fire, and in some cases, reduced tolerance to drought.

It may be more difficult for *P. mariana*, in particular, to become established in higher elevation sites as compared to *P. glauca* for two primary reasons: the rarity of fire (Lloyd et al. 2007) and increased drought in alpine sites (Black and Bliss 1980, Moss and Hermanutz 2009). *Picea mariana* retains its semi-serotinous cones as an aerial seed bank, and following a fire, cones open and release seeds onto the burnt forest floor (Arseneault 2001). Seedling germination and recruitment in this species is enhanced by preparation of the seedbed by fire (Black and Bliss 1980, Greene et al. 2007, Malik et al. 2010). At present, fire seldom occurs above 800 m in interior Alaska (Kasischke et al. 2002), thus reducing the likelihood of recruitment. The sloping and generally well-drained alpine zone may increase drought stress, potentially causing high rates of *P. mariana* seedling mortality (Black and Bliss 1980, Moss and Hermanutz 2009), and the negative influences of low germination rates and reduced survival due to suboptimal conditions in the alpine zone for *P. mariana* are exacerbated by limited dispersal ability because windborne seed dispersal of *P. mariana* is effective up to only 79 m (Viereck and Johnston 1990). This explanation for the limitation of *P. mariana* occupancy at high elevation in DNPP is supported by work in northern Alaska, where *P. mariana* occurred preferentially on older surfaces with deeper SOL and low pH, with reduced density of this species on younger surfaces with thin SOL where *P. glauca* was found to predominate, and where *P. mariana* seedling recruitment only occurred after fires (Lloyd et al. 2007). Similarly, Black and Bliss (1980) found that stand reproduction in *P. mariana* at a site near the arctic treeline in Canada occurred only immediately following fire.

Other studies conducted in central interior Alaska have described treeline forests dominated by *P. mariana* or mixed stands of *P. mariana* and *P. glauca* (Van Cleve et al. 1983, Viereck et al. 1983, Kurkowski et al. 2008). For example, Kurkowski et al. (2008) found that probability of *P. mariana* occupancy was highest (>90%) at elevations up to 770 m in a study area near Fairbanks, including well-stocked stands of *P. mariana* trees at the highest elevations. *Picea mariana* occurred rarely in this elevation band in DNPP, which suggests

geographic variation in habitat attributes for *P. mariana* within interior Alaska that may reflect differences in climate, permafrost distribution, and patterns of SOL depth in relation to elevation due to landscape age or geomorphic regimes. However, these dissimilarities may also be due to the large differences in the spatial extent of existing work as compared to our study. We sampled plots with relatively high densities of *P. mariana* above 600 m elevation in DNPP, but they were rare and spatially clustered. Only one mini-grid at the northern terminus of the Kantishna Hills supported sufficiently extensive *P. mariana* forest at elevations >600 m to represent a similar forest mosaic to those described by Kurkowski et al. (2008). This observation reveals one utility of the current study, which is to help provide a larger scale context for site-specific studies of forest patterns in interior Alaska.

Of the remaining tree species that occur in DNPP, *P. balsamifera* is the only one commonly found at high elevation or at continental treeline sites in the far north (Viereck 1979). In DNPP, *P. balsamifera* most often occurred in plots situated in alluvium close to major braided streams at the base of the Alaska Range escarpment (see Fig. 3), a pattern that was also noted in arctic Alaska north of the Brooks Range (Bockheim et al. 2003). Isolated clones of *P. balsamifera* form the northernmost tree populations in Alaska (Spetzman 1951, Wiggins and Thomas 1962), suggesting a greater tolerance of microclimatic conditions at treeline (e.g., cold air temperatures, short growing seasons) as compared to other tree species in Alaska.

We found that sites above 1200 m in DNPP had negligible *P. glauca* establishment, and this elevation likely represents a rough upper elevation limit for the establishment of *P. glauca* stands under current conditions. A recent study conducted in DNPP within our study area found similar upper tree limits, ~1100 m, in high insolation areas (Stueve et al. 2011). About 13% of the 250 plots that occurred at elevations between 900 m and 1200 m contained individuals of *P. glauca*. Therefore, at least in some high-elevation areas, *P. glauca* reproductive potential exists to further catalyze additional colonization by this species. Indeed, Stueve et al. (2011) documented *P. glauca* upward expansion at elevations between 900 m and 1040 m between 1953 and 2005 in one site near the center of our study area. Additionally, experimental work at subarctic alpine treelines in the Yukon Territory has shown that climate warming may allow *P. glauca* to advance the elevation of treeline or increase in tree density significantly at treeline (Danby and Hik 2007).

Potential for increasing impacts from phytophagous insect outbreaks

Sixty percent of the standing individuals of *L. laricina* >1.37 m tall in the plots were dead, in contrast to much lower mortality percentages for all other tree taxa in the study area. Although we did not specifically evaluate the

cause of death, we attribute this phenomenon to the well-known larch sawfly (*Pristiphora erichsonii*) outbreak that occurred across Alaska in the 1990s (Holsten and Burnside 1997). The extent of *L. laricina* mortality from this event demonstrates the impact an insect outbreak can have on boreal-forest stand composition in Alaska. Because boreal forests have low tree and forest insect diversity, they are naturally subject to periodic large-scale tree mortality from insects (ACIA 2005). A warming climate is expected to result in a greater frequency and extent of insect outbreaks in the boreal forest (ACIA 2005), and future outbreaks affecting other tree species, particularly *P. glauca*, could dramatically affect forest composition and structure throughout DNPP.

CONCLUSIONS

Our primary intent was to quantify the factors governing tree species occupancy and abundance from field data at a landscape scale across an extensive study area as a baseline for future comparisons. Our models provide spatial context for intensive studies of forest dynamics in interior Alaska, and provide useful information for comparisons to other regions of the boreal forest where these tree species occur. Our sampling design provided unbiased coverage of our 1.28 million ha study area and allowed us to examine variation in all six tree species responses across a wide range of environmental predictor variables for an area in interior Alaska not previously reported on in the literature. These models allowed us to quantify clear differences in the distribution of these species along topographic and edaphic gradients, including ranking the responses to elevation in terms of occupancy for each species within a spatially explicit Bayesian hierarchical modeling framework. In addition, these analyses revealed striking variation in the relative influence of disturbance history on the occupancy patterns of these tree species. Direct field measurements collected within a randomized design allowed us to describe the primary gradients governing tree distribution and abundance and quantify patterns in co-occurrence of species and stand composition, seedling and sapling recruitment, and landscape-scale mortality of *L. laricina*.

Our results add a new dimension to the consideration of the principal hypotheses for forest succession and change in interior Alaska from predicted climate warming, including new information collected across a spatial extent with a rigorous sampling design not previously available. We demonstrated this area is currently dominated by coniferous forest with strong physical control of species occupancy and abundance patterns, and found no evidence of an incipient large-scale conversion to broadleaf ecosystems. Indeed, self-replacement of conifer species, particularly *P. mariana*, following forest fire was the rule within the plot network, and mixed and broadleaf dominated stands also usually contained coniferous species suggesting that

the primary successional pathways favor conifers in this landscape. Our results also imply that projected decreases in growth of *P. glauca* in relatively rare mature stands may be offset at the landscape scale by increased occupancy in lowland basins resulting from a warming and drying landscape, and expansion at treeline. We predict *P. glauca* occupancy will expand preferentially in south-exposed terrain and well-drained sites with higher than average pH in the elevation zone above 900 m in DNPP with minimal stand establishment above 1200 m elevation. Future resampling of our plot network, along with similar ongoing projects in two other large park units in interior Alaska (Wrangell-St. Elias National Park and Preserve and Yukon-Charley Rivers National Preserve) will allow us to assess the validity of these predictions at an even larger scale.

Our approach, which combines spatial clustering of samples using an unbiased design, within a rigorous geostatistical analysis framework, has benefits that are worth considering for the design of monitoring programs in remote, logistically challenging, and expensive areas to conduct field research such as DNPP. Clustering of plots into mini-grids allowed us to acquire a multi-scale data set with a larger sample size in considerably less time, at lower cost, and with greater safety, than alternative approaches that require greater travel time per plot sampled. Additionally, a formal evaluation of residual spatial autocorrelation in model structure affords the added benefit of providing insights regarding potentially excluded predictors and makes full use of the available data.

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SUPPLEMENTAL MATERIAL

Supplement

Data used for landscape-scale models ([Ecological Archives M083-001-S1](#)).