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Environmental landscape determinants of maximum forest canopy height of boreal forests

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Abstract

Aims
Canopy height is a key driver of forest biodiversity and carbon cycling. Accurate estimates of canopy height are needed for assessing mechanisms relating to ecological patterns and processes of tree height limitations. At global scales forest canopy height patterns are largely controlled by climate, while local variation at fine scales is due to differences in disturbance history and local patterns in environmental conditions. The relative effect of local environmental drivers on canopy height is poorly understood partly due to gaps in data on canopy height and methods for examining limiting factors. Here, we used airborne laser scanning (ALS) data on vegetation structure of boreal forests to examine the effects of environmental factors on potential maximum forest canopy height.

Methods
Relationships between maximum canopy height from ALS measures and environmental variables were examined to assess factors limiting tree height. Specifically, we used quantile regression at the 0.90 quantile to relate maximum canopy height with environmental characteristics of climate (i.e. mean annual temperature [MAT] and mean annual precipitation), terrain (i.e. slope) and depth-to-water (DTW) across a 33 000 km^2 multiple use boreal forest landscape in northeast Alberta, Canada.

Important Findings
Maximum canopy height was positively associated with MAT, terrain slope and terrain-derived DTW, collectively explaining 33.2% of the variation in heights. The strongest explanatory variable was DTW explaining 26% of canopy height variation with peatland forests having naturally shorter maximum canopy heights, but also more sites currently at their maximum potential height. In contrast, the most productive forests (i.e. mesic to xeric upland forests) had the fewest sites at their potential maximum height, illustrating the effects of long-term forest management, wildfires and general anthropogenic footprints on reducing the extent and abundance of older, taller forest habitat in Alberta's boreal forest.

Keywords: forest succession, vegetation structure, quantile regression, remote sensing, airborne laser scanning (ALS)

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INTRODUCTION

As one of the main metrics of vertical forest structure, canopy height is a key predictor of aboveground biomass, primary productivity and biodiversity (Anderson *et al.* 2006; Goetz *et al.* 2007; Lefsky *et al.* 2005; Thomas *et al.* 2008). Increases in human disturbance (e.g. industrial harvesting), and more generally rapid global change (e.g. wildfires and climate change), have resulted in widespread losses of old-growth and intact forests (Hansen *et al.* 2013; Harvey 2016; Johnson *et al.* 1995; Spies *et al.* 2006). One forest biome where intact forests are still common is the boreal forest, with 43.8% considered globally intact (Melillo *et al.* 1993; Potapov *et al.* 2008). Natural disturbances in the boreal biome are prevalent and widespread, with fire being the most dominant factor in the western boreal forests in Canada (Stocks *et al.* 2002). Canopy heights for many sites have not therefore reached their potential maximum height with many sites being in early stages of secondary forest succession. Since canopy height plays an important role in forest ecosystem services and is an indicator of old forests and thus habitat to some old forest specialists, it is important to know the location, extent and dynamics of forests that are at their potential maximum height. This information can then be used to help guide conservation strategies that protect older forests and models of carbon cycling, and wildlife habitat.

At broad spatial scales, plant and forest canopy height are known to be related to climatic factors and historical conditions (Moles *et al.* 2009; Tao *et al.* 2016; Zhang *et al.* 2016). However, at more local scales plant and canopy height are affected by site-level variation in soils, terrain and water availability (Falster and Westoby 2003; Koch *et al.* 2004). Variation in maximum individual plant (canopy) height differs due to, (i) climate measured over large scales (e.g. Tao *et al.* 2016); (ii) species composition with certain species occurring in specific habitats (Guisan and Zimmermann 2000) together with the height variations in species (Falster and Westoby 2003; Moles *et al.* 2009); and (iii) the intra- and inter-specific variations of individual heights in forest communities due to forest succession (age), nutrient and energy availabilities and biological actions (e.g. light competition; Falster and Westoby 2003). Local factors both directly and indirectly affect species occurrence and maximum potential canopy height. For example, water availability directly affects the occurrence of different tree species and their subsequent canopy heights (Koch *et al.* 2004; Tao *et al.* 2016), while the slope indirectly affects the distribution of species (Guisan and Zimmermann 2000). Although climate and disturbance history relate to broad-scale patterns in tree heights, less is known about the environmental determinants of canopy heights at finer scales. Methods are also needed to predict maximum canopy height for different sites given environmental conditions and thus rapidly identify sites with potential old-growth forest characteristics to target monitoring and protection. With the developments of moderate-resolution satellite technology and its rapid delivery and cost-effectiveness, large scale monitoring of forests is now feasible (Hansen *et al.* 2013). Until recently, the mostly commonly utilized remote sensing tools were passive optical sensors. Unless used in a photogrammetric environment, these products presented a fundamentally two-dimensional representation of vegetation structure (Pettorelli *et al.* 2014). Direct measures of canopy height can now, however, be made using airborne laser scanning (ALS) technologies (Coops *et al.* 2007, 2016).

Here, we demonstrate an approach that uses quantile regression of ALS-derived canopy height data (i.e. the maximum values) for the boreal forest of northeast Alberta, Canada. Quantile regression is a useful method for isolating different components of data, including factors limiting maximum observed values (Cade and Noon 2003). Here, we specifically investigated factors limiting maximum vegetation (canopy) heights, thereby effectively ignoring young successional forests that can occur across any range of environmental conditions due to local disturbance history. This approach therefore focuses directly on conditions and sites that limit or promote maximum possible height with the aim of demonstrating a cost-efficient method for identifying and monitoring the dynamics of forests, including those sites that have canopy height characteristics indicative of potential old forests.

METHODS

Study area

The study area is located in northeast Alberta, Canada, with an area of 33 000 km^2. The area is characterized as boreal forests dominated by *Picea*, *Pinus* and *Populus* species (Zhang *et al.* 2014). Latitude across the study area ranges from 55.25°N to 57.38°N with longitude ranging from 110.00°W to 112.80°W (Fig. 1). Climatic and elevation differences are relatively small with differences in climate mainly due to local variation in elevation that ranges from 231 to 863 m (Fig. 1). Climatically, the area is characterized as being continental with warm summers and cold winters. Mean annual temperatures (MATs) for the area is −0.4°C, while mean annual precipitation (MAP) is 460 mm (http://tinyurl.com/ClimateAB). Except for major

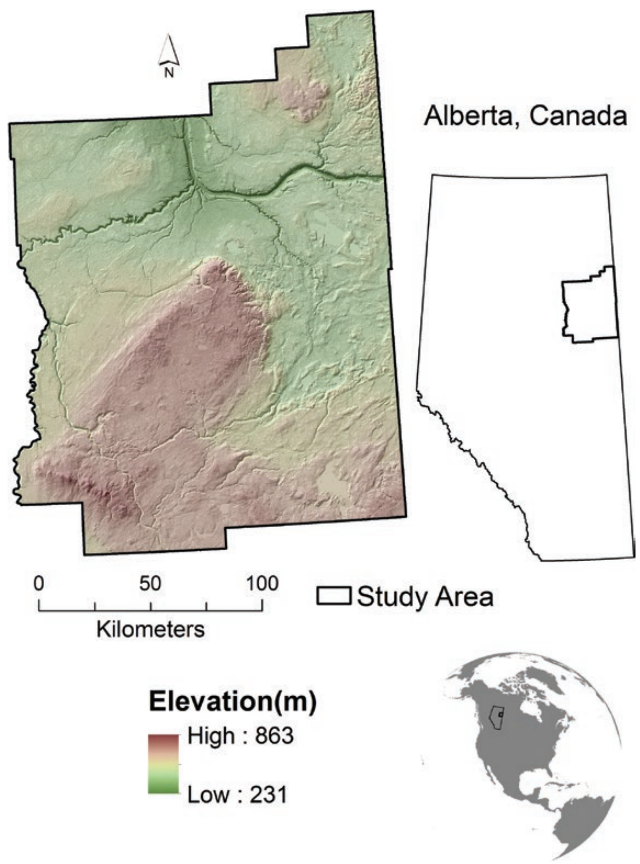

Figure 1: map of the study area illustrating variations in terrain within the boreal forest of northeast Alberta, Canada.

river valleys, glacial moraines, small vegetated dunes and the edges of the Stoney Mountain plateau, much of the area is flat (Fig. 1) with large expanses of forested peatlands being common (Halsey *et al.* 1995).

ALS and canopy height

Canopy height was assessed using ALS data acquired for the region over a 10-year period with most data gathered between 2007 and 2014. Point cloud data averaged 1.9 returns/m^2 and summarized to a 30-m spatial resolution using FUSION software (McGaughey 2014). To reduce the influence of sampling bias from possible errors and extreme conditions in ALS surveys (Bolton *et al.* 2013; Kane *et al.* 2010), we used the 95th percentile of canopy height to represent the maximum height of forest vegetation for each 30-m grid cell. To confirm that these values were reasonable, we checked the maximum height records in the *Flora of North American* for the tree species distributed in the study area (search online: www.flora.org). All trees in the area have a known maximum potential height of 40 m or less (e.g. *Populus balsamifera* is 40 m, *Populus tremuloides* is 35 m, *Pinus banksiana* is 27 m, *Larix laricina* is 20 m, *Picea glauca* is 30 m, *Picea mariana* is 25 m and *Betula papyrifera* is 30 m), so we assumed that rare grid cells that had canopy heights greater than 40 m (< 0.01%; Fig. 2A) were noise and removed. A forest mask was used to restrict analyses to only forested sites based on a land cover classification for the area from the Alberta Biodiversity Monitoring Institute (Alberta Wall-to-wall Land Cover Map circa 2010; http://www.abmi.ca). Overall, 75.8% of the area was covered by forests with coniferous forests, broadleaf forests and mixed forests being 73.7%, 13.2% and 13.1%, respectively. It should be noted that some early seral forests in this classification were considered shrub land due to recent fires and since they were not classified as forests they were also removed from the analysis. However, because we only focused our analyses on the 90th centile of possible canopy heights in quantile regression, these masked early seral forests did not affect model relationships.

Environmental variables

To represent potential environmental factors that affect maximum forest height, we considered variables from previous research (Moles *et al.* 2009; Tao *et al.* 2016; Zhang *et al.* 2016) and local site characteristics to include two climate variables, MAT and MAP, the slope of the cell (Slope) as a terrain variable which affects soils and fire regimes and thus the distribution of species, and depth-to-water (DTW) as a water available variable. Climatic data were obtained from Climate-AB data (http://tinyurl.com/ClimateAB) and interpolated to a 1-km spatial resolution. Slope data were derived from a 1-m bare ground ALS digital elevation model generalized to a 30 m scale to match our canopy height grid data. DTW data were used from the 'Wet Areas Mapping' project (http://watershed.for.unb.ca/research/wet-areas-mapping) and again derived from the same bare ground ALS returns at a 1 m initial resolution and again generalized to a 30-m spatial resolution to match canopy height data. DTW is an index of water availability with higher values representing drier conditions (Murphy *et al.* 2007; Oltean *et al.* 2016).

Statistical analyses

We first $\log_{10}$-transformed the canopy height, MAP, slope and DTW to get normal distributions. To estimate environment-maximum canopy height relationships, we randomly selected 100 000 samples from the 30 million total study area cells. As previously described, stand-replacing disturbances (natural or anthropogenic) are common to the area and thus environment-maximum canopy height relationships were explored using quantile regression at a 0.90 percentile. In model selection, we first explored the effects of single variables on the variation in maximum canopy height across the region by regressing the 0.90 quantile maximum canopy height versus MAT, MAP, slope and DTW. This was repeated at the 0.75 and 0.99 percentiles to ensure stability of responses (Fig. 2).

A multivariate quantile regression was then fit using variables having high univariate explanatory power. Model predictions were used to estimate potential maximum canopy height across the region given local and regional environmental conditions regardless of recent disturbances. We then estimated the difference between observed maximum canopy heights and predicted maximum potential canopy height to identify sites having canopy heights at or above the 90th percentile expected for a site given its environmental conditions. In effect, this allowed the threshold canopy height to vary by forest type, for instance, treed peatlands would have a lower threshold height than upland mixed forests. This threshold map then illustrated sites at their potential maximum canopy height. Conversely, all remaining sites lower than the thresholds were considered successional forests represented by disturbed, early seral or moderate-aged stands. All analyses were performed in R (R Core Team 2015) with the quantile regression package 'quantreg' (Koenker 2016). To account for possible interactions between the variables and the non-linear quadratic effects of individual variables, interactions and quadratic terms with high explanatory power and ecological meanings were included in the multivariate model. Specifically, we tested the limitations of temperature and precipitation on maximum canopy height by the multivariate 0.90 quantile model through model interactions. The interactive effect of DTW and precipitation was also tested (Fig. 3) since we expect that water limitation from precipitation will matter less for trees when the site is close to the water table. Meanwhile, locally weighted polynomial regression (Cleveland 1981) was used to derive the trends of predicted maximum canopy height predicted at a site based on MAT/MAP, slope and DTW using the R function 'lowess' with the smoother span $f = 0.2$ (see online supplementary Fig. S2).

Since the canopy height-environment relationships may scale dependent, we also tested the univariate linear and quadratic quantile regression relationships at larger scales of 100, 200 and 500 m spatial resolutions. Results for these other

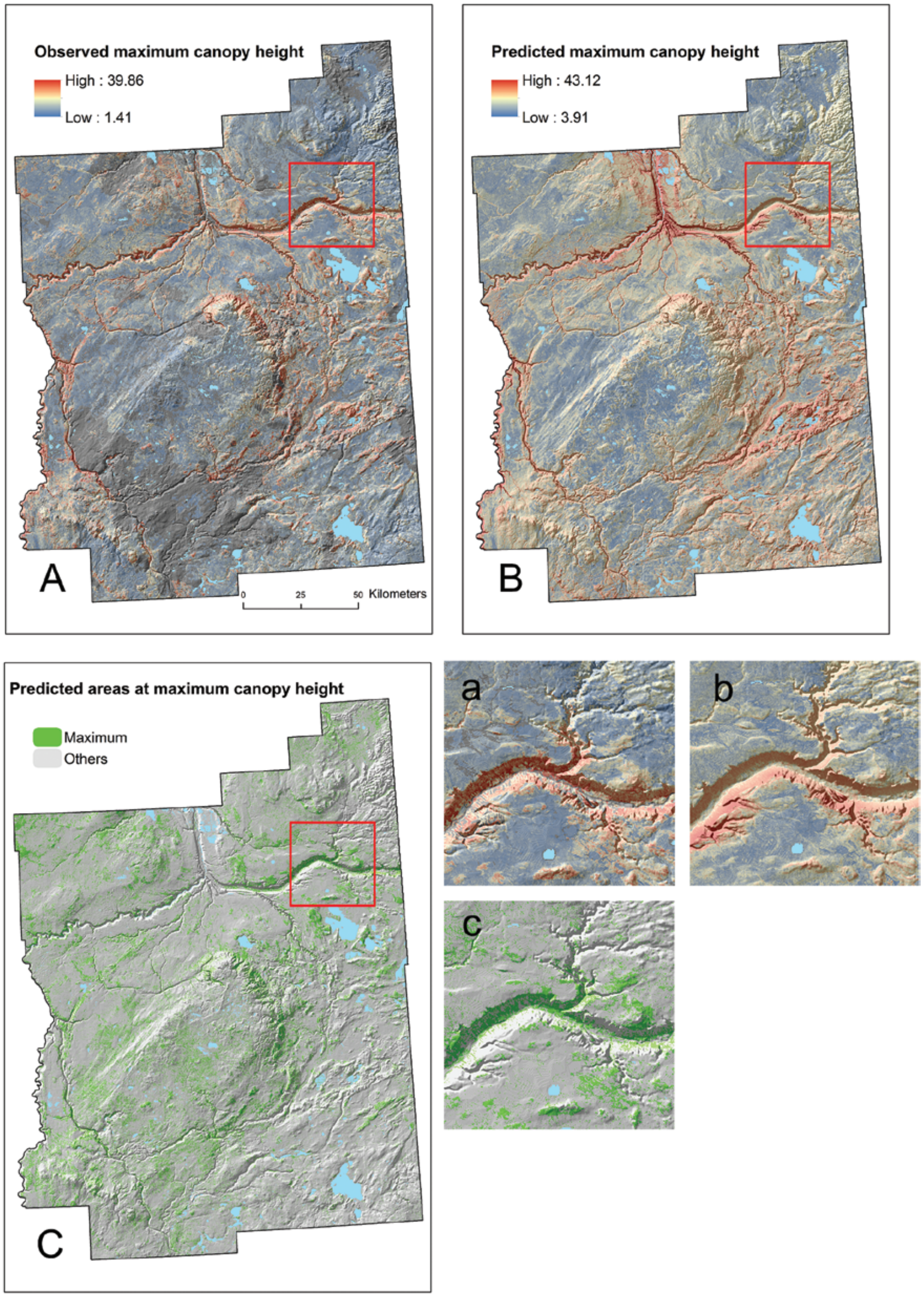

Figure 2: maps of ALS-derived maximum canopy height (**A**), predicted maximum canopy height from a multivariate 0.90 quantile regression model using mean annual temperature, slope and depth-to-water (**B**) and predicted locations of forests with potential maximum canopy height (**C**). And, the detailed maps showed in bottom right corner for the areas in the red boxes (a, b and c for the areas in A, B and C, respectively.).

scales are not reported here, but are instead shown in online supplementary Table S1.

RESULTS

Maximum canopy heights were tallest along major river valleys, the edges of major plateaus and glacial moraines (Fig. 2A). General trends in spatial patterns of observed and predicted potential maximum canopy heights were relatively consistent across the area (Fig. 2A and B). Differences between observed and predicted potential maximum canopy heights were used to map locations of maximum potential canopy height as shown in Fig. 2C. Sites that were at or near their potential maximum canopy height were mainly distributed along major river valleys and other major terrain features that would limit natural disturbances such as fire and

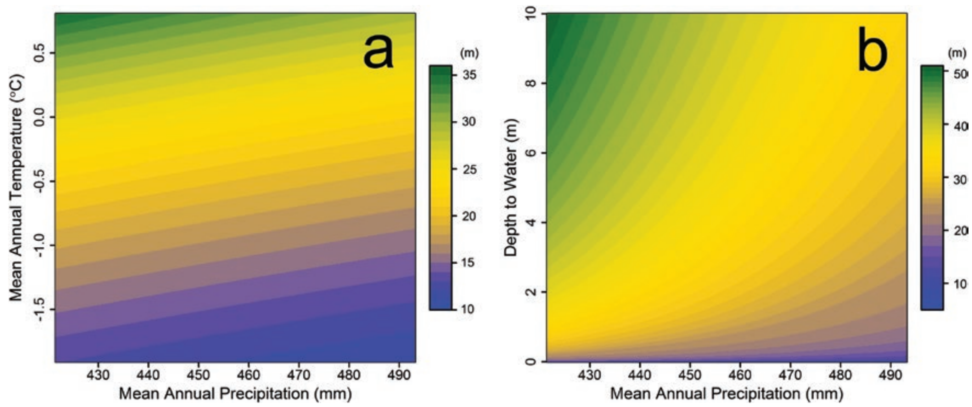

Figure 3: the interactive effects between mean annual temperature (MAT) and mean annual precipitation (MAP, **a**), and the effects between depth-to-water (DTW) and MAP (**b**) on canopy height. Predicted canopy height was based on quantile regression models at 0.90 using MAT and MAP, and DTW and MAP, respectively. The right color scale bars indicate the predicted canopy height.

promote greater rooting depth since they would have moderate to higher DTW.

All univariate quantile regression models were significant, however, explanatory power varied greatly between models. DTW explained 26% of the variation in maximum canopy height, with precipitation, temperature and slope explaining 0.3%, 5.0% and 8.1%, respectively. All relationships, excluding precipitation, were positive. Results from 30, 100, 200 and 500 m spatial resolutions showed the explanatory power of univariate linear and quadratic quantile regression models for these variables with canopy height being generally consistent among scales (see online supplementary Table S1).

Non-linear quadratic responses for DTW further increased model fit with the tallest maximum canopy heights occurring in sites with moderately high DTW (see online supplementary Fig. S1; 26.0% vs. 29.5%). Maximum canopy height was therefore associated with increases in temperature (generally areas of lower elevation), in areas with steep slopes, and more mesic to xeric upland sites (i.e. moderately high DTW). Individually, DTW was by far the most important factor affecting maximum canopy heights. Results of quantile regression models for the environment-maximum canopy height relationships compared between the 0.99 and 0.90 percentiles differed slightly, while regression slopes were more consistent between models at the 0.90 and 0.75 percentiles. The final multivariate quantile regression model that used precipitation, temperature, slope, the quadratic form of DTW, as well as the interaction of DTW and precipitation and temperature and precipitation, explained 33.2% of the variation in canopy height (see online supplementary Table S2).

Taller maximum canopy heights were associated with an interactive effect between areas of low precipitation and high temperature (Fig. 3a). Likewise, the interactive effects between precipitation and DTW demonstrated that maximum canopy height was higher in drier sites with greater DTW and lower precipitation (Fig. 3b). Locally weighted polynomial regressions between predicted maximum canopy height and temperature, precipitation, slope and DTW were consistent with relationships for the observed maximum canopy height and these four variables (Fig. 3; see online supplementary Fig. S2). Notably, with MAP increasing from 420 mm to 450 mm, maximum canopy height decreased dramatically, but was relatively stable between 450 mm to 490 mm (see online supplementary Fig. S2b).

DISCUSSION

It has been proposed that canopy height could be determined by current and historical climate (Tao *et al.* 2016; Zhang *et al.* 2016). In plants, individual maximum height is a fundamental trait known to be influenced by climatic and soil conditions, terrain, the vertical structure of vegetation and competition for light (Falster and Westoby 2003; Koch *et al.* 2004; Moles *et al.* 2009). Although hydraulic limit is known to limit absolute maximum tree height (Koch *et al.* 2004; Midgley 2003; Ryan and Yoder 1997; Ryan *et al.* 2006), tree sizes in our study area are not physiologically restricted by hydraulic deficiency. In this region, excess water availability, typical of treed bogs and fens (forested peatlands), results in shifts in tree composition towards *Larix laricina* and *Picea mariana* where trees are more stunted in their heights. Dry to mesic sites, on the other hand, are more often dominated by the gymnosperms of *Picea alba* and *Pinus banksiana*, and the angiosperm of *Populus tremuloides*. This is supported by higher explained variability in canopy height from DTW illustrating the strong effect of water availability on changing composition and heights of trees. Indeed, we demonstrated here that at local scales, both water-related variables of MAP and DTW were related to canopy heights with both increasing heights of trees under drier conditions (see online supplementary Fig. S1). Thus, boreal forest trees are less water limited than they are temperature limited with respect to maximum possible tree heights. These results are consistent with the conclusions by others that forest canopy height decreases with greater water availability in some areas (Tao *et al.* 2016). Areas with excess water can alter local climates (e.g. more clouds), and subsequently influence the light availability for photosynthesis (Blanke and Cooke 2004; Graham *et al.* 2003).

Our results also demonstrated that both maximum canopy height and the distribution of sites predicted to be at maximum potential canopy height were more likely in areas of deep river valleys and steep hills (see online supplementary Fig. S1A and B). Although some potential sampling errors may exist in the estimation of canopy height in areas of steep terrain using ALS methods, steep sites in the hills and river valleys of this region are drier than in other areas. Indeed, major rivers and lakes in the region are known to create fire breaks, reducing wildfire likelihood and thus promoting local sites of fire refugia with older forests (Nielsen *et al.* 2016). This is particularly important in boreal forests since wildfires are major source of disturbance in this biome (Agee 2005; Larsen 1997). Indeed, over the past 50-year period (1957–2006), 25.8% of the area was burned by wildfires (wildfire maps of Alberta, http://wildfire.alberta.ca/) making it among the most important factor determining patterns in tree heights in the region. Given that the fire return interval in boreal forests can be shorter than the generation time of the trees found within it (Johnson *et al.* 1998), steady-state forests are not typical under natural conditions (Bergeron and Dubue 1988; Larsen 1997), which may explain the distribution (general rarity) of predicted maximum canopy height in this area. Areas of steep terrain are also more likely to be protected from anthropogenic disturbances common to the region (Norton *et al.* 2000; Rooney *et al.* 2012).

Although sites occurring at maximum potential canopy height cannot be assumed to represent 'old growth' forests due to considerations of forest type and conditions (Gauthier *et al.* 1996; Harper *et al.* 2003), we suggest that these sites have greater possibility of containing older trees as our methods adjusted maximum potential height expected for a site based on environmental constraints, and therefore may indicate old-growth stands. Thus, sites determined to be at their potential maximum canopy height using ALS metrics and modeling approaches used here can help identify old-growth forest sites for conservation or monitoring, which is important when considering carbon sequestration (Bradshaw *et al.* 2009; Carey *et al.* 2001; Luyssaert *et al.* 2008) and assessments of habitat for old-growth forest specialist species (Kneeshaw and Gauthier 2003; Venier *et al.* 2014).

CONCLUSION

Our research provides an innovative approach to mapping and understanding environmental limiting factors associated with maximum canopy height in frequently disturbed forests. We found that local ALS-derived site conditions (i.e. slope and DTW) and climate variables explained 33% of the variation in maximum canopy height (90th percentile) across a boreal forest landscape in northeast Alberta, Canada. Areas of conservation value, such as mature or old-growth forest may be identified using this approach, although further work to ground-truth is needed to verify old-growth stands. We believe this approach can be applied to other forest ecosystems and across larger spatial scales to better understand factors limiting tree height and to map potential old-growth forests for conservation.

SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Plant Ecology* online.

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Conflict of interest statement. None declared.

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