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Using airborne laser scanning to predict plant species richness and assess conservation threats in the oil sands region of Alberta's boreal forest

Lingfeng Mao[a,*], Jacqueline Dennett[a], Christopher W. Bater[b], Piotr Tompalski[c], Nicholas C. Coops[c], Dan Farr[d], Monica Kohler[e], Barry White[b], John J. Stadt[b], Scott E. Nielsen[a]

[a] Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1, Canada
[b] Forest Management Branch, Forestry Division, Alberta Agriculture and Forestry, Edmonton, Alberta T5K 2M4, Canada
[c] Department of Forest Resource Management, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada
[d] Environmental Monitoring and Science Division, Government of Alberta, 10th Floor, 9888 Jasper Avenue NW, Edmonton, Alberta T5J 5C6, Canada
[e] Alberta Biodiversity Monitoring Institute, CW 405 Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

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ABSTRACT

Timely and cost-effective monitoring of biodiversity across large areas is a major challenge, yet an important component of monitoring programs that inform policy and conservation strategies. Recent advances in Airborne Laser Scanning (ALS) provide new opportunities to simultaneously measure vegetation structure and terrain morphology at fine spatial scales. However, there is limited research on whether ALS metrics correlate with biodiversity measures. Here we used vascular plant data from 283 quarter-hectare (50 m × 50 m) plots from the boreal forest in northeast Alberta, Canada, to evaluate the potential for ALS-derived metrics to explain species richness patterns for vascular plants, as well as for four growth forms: herbaceous (including forbs and graminoids) and woody plants. We found canopy height from ALS was the most consistent and important (positive) factor related to local patterns in vascular plant species richness. Multivariate regression models of ALS-derived metrics explained 20–35% of the variation in species richness among vascular plants and the four subclasses. When considering the current distribution of *in situ* oil sands leases in the region, vascular plant richness inside of the leases is higher than outside. Areas delineated for woodland caribou conservation had lower average plant richness suggesting that it will do little to protect hotspots of vascular plant diversity in Alberta's boreal forest. Our results highlight the value of using fine-scale measures of ALS-derived vegetation structure to explain, predict, and potentially monitor local plant diversity for a high latitude forested ecosystem.

1. Introduction

Given recent and projected trends in climate change and human disturbance, biodiversity threats continue to be a major conservation concern (Sala et al., 2000; Thuiller, 2007). In order to understand trends in biodiversity and subsequently prioritize conservation efforts, it is essential to better understand environment-biodiversity relationships and to derive efficient methods for monitoring biodiversity change (Araújo and Rahbek, 2006; Kreft and Jetz, 2007). Taxonomic richness of species (alpha diversity), most often obtained directly from field surveys, is the most typical measure of biodiversity (Thuiller, 2007). However, it is not practical to monitor biodiversity in this way across large regions. A major challenge in managing biodiversity is therefore to link biodiversity measures at local scales to cost-effective monitoring across large areas (Mairota et al., 2015). Appropriate surrogates for direct assessments of biodiversity are therefore needed.

Advances in remote sensing technology have created opportunities for monitoring habitat and vegetation structure at local to global scales, leading to potentially better, more economical, and faster alternatives to field surveys (Pimm et al., 2015).

Although some studies suggest that multispectral passive optical sensors can be used to predict biodiversity at large scales (Coops et al., 2008; John et al., 2008; Zhang et al., 2016), most passive spectrum-derived satellite indices do not consider vertical structure of vegetation (except for the forest canopy height in open canopy forests, see Montesano et al., 2017), a key driver of biodiversity at local scales (MacArthur and MacArthur, 1961; Bergen et al., 2009). Moreover, new insights and methods are needed to recognize that vegetation structure and species composition differ even in two adjoining sites sharing a consistent regional species pool (Cook et al., 2002). Indeed, the physical structure of vegetation has long been noted by scientists to explain variation in species diversity, particularly for animals, in part because it

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relates to possible mechanisms of ecological complexity and niche partitioning (MacArthur and MacArthur, 1961; Kalko and Handley, 2001). However, metrics related to vertical distribution and stratification of vegetation have historically been feasible only through collection of field data (Baker and Wilson, 2000) and thus limiting their application to local case studies.

Recent advances in Airborne Laser Scanning (ALS) technology now provide opportunities for measuring and monitoring the structure and complexity of vegetation across larger areas. This includes measures of canopy cover, height class distribution of vegetation, and maximum canopy height (Bergen et al., 2009). These metrics of vegetation structure have been used to predict the richness of mammals, bats, vertebrates, particularly for birds (Bradbury et al., 2005; Clawges et al., 2008;Vierling et al., 2008; Davies and Asner, 2014; Coops et al., 2016; Davies et al., 2016) with little done to assess whether ALS metrics explain local patterns in plant diversity.

Plant diversity at local scales (i.e., community level) is known to be affected by many different factors, including biome-scale environmental conditions or regional-to-local factors of topography, environmental heterogeneity, vegetation type, and vegetation structure (e.g., Moser et al., 2005; Kreft and Jetz, 2007; Fine, 2015). In particular, vegetation structure (e.g. canopy height) is considered to be an important factor shaping plant diversity (Wolf et al., 2012; Gatti et al., 2017). Exploring the factors affecting plant diversity at the community level therefore requires understanding of both regional climate factors and local environmental variables, including those that can be measured by ALS, i.e. vegetation structure metrics such as canopy height, percent of returns above a specified height, and return proportion at specified height intervals. Here, we use 283 plant biodiversity plots from the boreal forest in northeast Alberta, Canada, an area undergoing rapid landscape change due to oil sands developments, to examine whether ALS vegetation and terrain measurements, in combination with other environmental variables, relate to patterns of plant species richness. Establishing this relationship will enable landscape-scale predictions of conservation values.

The boreal forest is the largest terrestrial biome on the earth, playing a major role in global biodiversity conservation and ecosystem function (Melillo et al., 1993; Näsholm et al., 1998). The biome is, however, sensitive to global climate change and human disturbance (Sala et al., 2000; Larsson and Danell, 2001). Understanding biodiversity patterns (e.g. biodiversity hotspots) in the boreal forest, as well as their relationships with local to regional factors, is one key step for managing biological conservation and monitoring change due to exogenous (e.g. climate change) and endogenous (e.g. habitat fragmentation) threats. This includes a better understanding of the implications of exploration and extraction of oil in Alberta's oil sands (Rooney et al., 2012), the world's largest oil reserve (Sherrington, 2005), on plant biodiversity hotspots. And to explore whether the locations of plant biodiversity hotspots overlap with those of other major conservation objectives, in particular areas of woodland caribou (*Rangifer tarandus*) habitat, which represent the current focus of conservation initiatives in Canada's boreal forest (Schneider et al., 2010).

2. Materials and methods

2.1. Materials

2.1.1. Study area

The study area was located in the boreal forest of northeast Alberta, Canada ranging in latitude from 55.3° N to 57° N (Fig. 1). This area is part of the Boreal Forest Natural Region, which includes the lower portion of the Athabasca River and Lake Athabasca (Natural Regions Committee, 2006). Elevations in the area range from 231 m to 863 m a.s.l., with annual precipitation and mean annual temperatures ranging from 430 mm to 492 mm and from −1.2 °C to 0.3 °C, respectively. On the uplands, soils are typically Brunisols, while wetland areas are
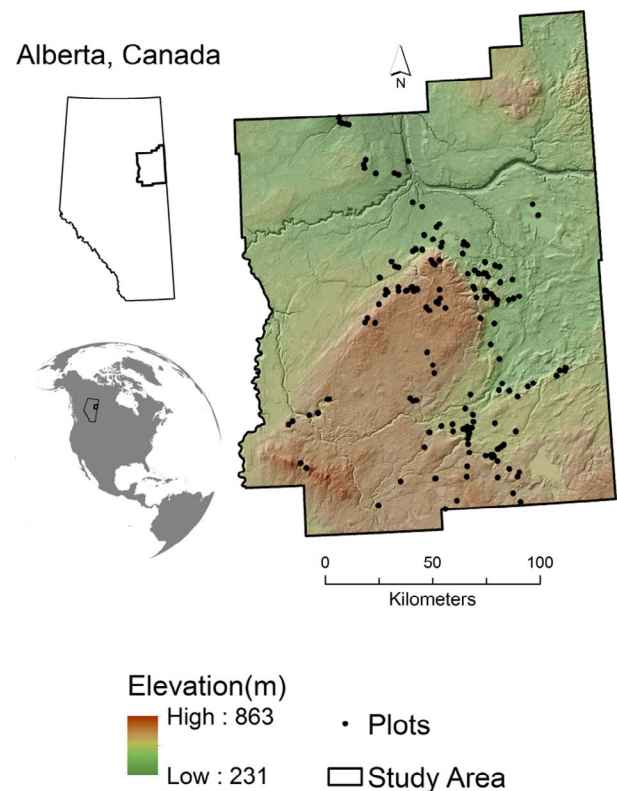

Fig. 1. Study area in Alberta, Canada and plot locations.

Mesisols, Organics, Gleysols, and Grey Luvisols. Forests in the area are comprised of a mosaic of deciduous, mixed wood and coniferous stands, with upland stands dominated by *Populus, Picea,* and *Pinus* species., while lowland areas are represented by fens, swamps, and bogs (Natural Regions Committee, 2006; Zhang et al., 2014).

2.1.2. Plot data

Plot data were collected in the summers of 2012–2015 with a plot size of 50 m × 50 m (0.25 ha) based on stratified random sampling. Vascular plants were identified to species in each plot and recorded as present/absence data. Unknown specimens were collected and identified later in the lab to species. See Zhang et al. (2014) for more details on field methods. In total, 602 plots were completed, but only 283 plots overlapped with ALS data (spatial coverage limited) on both vegetation structure and topography-derived variables and thus were used in this study. Since the underlying drivers and assembly mechanisms of plant diversity may differ across growth forms (Mao et al., 2013), all plants were classified into five growth forms (subdivisions) based on records from Floras (http://www.efloras.org/). These subdivisions included (1) all vascular plants, (2) herbaceous plants (further separated to (3) forbs and (4) graminoids), and (5) woody plants. Only native species were considered in this paper. Non-native species were infrequently encountered and included only sparse cover of a small number of species (e.g. *Taraxacum officinale* in upland sites). It should be noted, however, that plots were not placed directly on human disturbances, such as vegetated well sites, pipelines, or clearcuts, but were in the region of general forest disturbances and habitat fragmentation. Therefore, we are not testing here the direct effect of footprints from industrial practices on plant richness, but rather what factors affect natural patterns of plant diversity and where does that diversity occur within the broader region.

2.1.3. Airborne laser scanning metrics and environmental variables

Airborne laser scanning data were generated from aerial surveys conducted between 2005 and 2013. Point densities averaged 1.9

returns/m^2 with the data processed using the "area-based" technique (Reutebuch et al., 2005; Wulder et al., 2008). Specifically, ALS point clouds were processed with FUSION software (McGaughey, 2014) to derive vegetation height and canopy metrics (Coops et al., 2016). Most generally, ALS data can be divided into three different forest vegetation attributes that relate to the horizontal and vertical vegetation structure: (1) canopy height at different percentiles; (2) percent of returns above a specified height of the ground to indicate vegetation cover at that height stratum; and (3) return proportion at specified height intervals or variability of return heights to indicate vertical structure (McGaughey, 2014; Coops et al., 2016). Since many of these metrics are highly correlated with each other, we selected a suite of variables that we considered to have greater ecological meaning to biodiversity. For example, canopy height can be positively associated with plant diversity at broad scales since a larger volume of vegetation could potentially hold more heterogeneous environment for more different species (Wolf et al., 2012; Gatti et al., 2017), and the vertical stratification of vegetation could partly present the drivers of biodiversity in forest communities, such as the characteristics of forest gaps and the complexity and diversity of available habitats (MacArthur and MacArthur, 1961; Brokaw and Busing, 2000). Previous research has demonstrated that metrics based on first returns are more stable than those based on all returns (Goodwin et al., 2006; Næsset, 2009; Bater et al., 2011). We considered the following nine lidar-derived variables: the 95th percentile of observed first return heights above ground to represent canopy height, percentage of first returns above 1.37 m (i.e. breast height) represent percent canopy coverage, percentage of first returns above mean height, proportion of first returns for the height strata of: below 0.15 m and between 0.15 m to 1.37 m, 1.37 m to 5 m, 5 m to 10 m, 10 m to 20 m, and 20 m to 30 m (Table 1). Particularly, the proportion of first returns below 0.15 m represents a proportion of non-vegetation and low herbaceous coverage areas, while the other strata represents the vertical proportions of vegetation at the specific heights. We used LiDAR-derived canopy height at the 95th percentile of observed heights to measure the maximum height of vegetation at a site rather than using maximum height measured by LiDAR. This reduced sampling bias from extreme conditions (e.g., birds in flight, communication towers, etc.) or possible errors from LiDAR returns (Kane et al., 2010; Bolton et al., 2013).

Water availability at a site, soil moisture, and local disturbances caused by flood erosion are considered to be important factors shaping local biodiversity (Nilsson et al., 1999; Sala et al., 2000; Xiong et al., 2003). To indicate the effects of water availability on plant richness at each plot, depth to water (DTW) was estimated for the same study region using 'Wet Areas Mapping' (WAM) data derived from ALS point clouds (http://watershed.for.unb.ca). Depth to water is an index that indicates the vertical distance (elevation) to available water, thus indicating drier to wetter conditions of the soil (Murphy et al., 2007; White et al., 2012; Oltean et al., 2016). Terrain variability within a site is also a factor influencing local patterns in plant richness (Webb et al., 1999). We used terrain slope within plots to represent the effects of topography, including its effects on promoting environmental heterogeneity within a site. Terrain slope was calculated using ALS-derived digital terrain model (DTM) at a 50 m spatial resolution to match our plot data on species richness.

Mean annual precipitation (MAP) and mean annual temperature (MAT) were used to account for the effect of broad-scale environmental variability in the size of the local species pool (Gaston, 2000; Kreft and Jetz, 2007). Mean annual precipitation and MAT were extracted for each plot using climate normals from Climate-AB data (http://tinyurl. com/ClimateAB). We note that because of the regional geographic extent of the study (the distance between the furthest plots is *ca.* 150 km) and the lack of mountainous terrain in the area, climate variables did not substantially vary across the region, but they did indicate general temperature and moisture gradients from colder and wetter to warmer and drier conditions.

2.1.4. Relationships between plant biodiversity hotspots, oil sands, and woodland caribou

Here we assess the threats to plant biodiversity hotspots from oil sands developments, as well as the effectiveness of woodland caribou (*Rangifer tarandus*) conservation in protecting these hotspots. To do this we compared plant species richness for sample plot locations inside active oil sands leases versus areas outside of active leases. Sites within lease boundaries represent natural forest conditions surrounding *in-situ* developments and are potentially impacted by edge or indirect effects, not by the footprint itself. Second, we compared sample plot locations of plant richness for areas inside versus outside of woodland caribou range, given that woodland caribou represent the main focus of conservation and restoration in Canada's boreal forest (Schneider et al., 2010), but little is known about the effectiveness of caribou in conserving other taxa. To map locations of caribou habitat, we used caribou range maps from Alberta Environment and Parks (http://aep. alberta.ca). These ranges are utilized for recovery monitoring and conservation initiatives. Oil sands lease boundaries were current to 2013 and based on data from Alberta Environment and Parks (http://

Table 1

Simultaneous Autoregressive (SAR) univariate models of species richness for total vascular plants, herbaceous plants, woody plants, forbs, and graminoids against each explanatory variable. The pseudo-r squares (r^2) of SAR models are given in the table, and symbols in brackets represent the trends of relationships between species richness and variables. *p-value* is the significance of coefficients. AIC is Akaike Information Criterion. CH, canopy height; PR1.37 and PRmean, the percentages of returns above 1.37 m and mean height, respectively; P0–0.15, P 0.15–1.37, P1.37–5, P5–10, P10–20, P20–30 represent the return proportion at 0–0.15 m, 0.15–1.37 m, 1.37–5 m, 5–10 m, 10–20 m and 20–30 m, respectively; MAP, mean annual precipitation; MAT, mean annual temperature; Slope, the terrain slope of the plot; DTW, the depth to water at the plot. The two most supported models (lowest AIC) for each growth form are shown in bold.

Variables	Vascular			Herbaceous			Woody			Forbs			Graminoids		
	r^2	AIC	*p*-value	r^2	AIC	*p*-value	r^2	AIC	*p*-value	r^2	AIC	*p*-value	r^2	AIC	*p*-value
MAP	0.155(−)	**387.0**	0.000	0.122(−)	**539.0**	0.000	0.098(−)	**221.1**	0.000	0.192(−)	568.3	0.000	0.025(−)	597.2	0.034
MAT	0.054(+)	418.9	0.000	0.063(+)	557.3	0.000	0.029(+)	241.8	0.006	0.083(+)	604.1	0.000	0.021(+)	598.6	0.099
CH	0.100(+)	**404.9**	0.000	0.069(+)	**555.5**	0.000	0.111(+)	**216.8**	0.000	0.149(+)	**583.1**	0.000	0.054(−)	588.6	0.000
PR1.37	0.049(+)	420.4	0.001	0.028(+)	567.7	0.029	0.058(+)	233.3	0.000	0.090(+)	602.1	0.000	0.088(−)	578.3	0.000
PRmean	0.045(+)	421.8	0.002	0.025(+)	568.6	0.051	0.053(+)	234.6	0.000	0.084(+)	603.9	0.000	0.094(−)	576.4	0.000
DTW	0.019(+)	429.4	0.130	0.012(+)	572.3	0.834	0.033(+)	240.5	0.005	0.030(+)	620.2	0.011	0.112(+)	**570.7**	0.000
Slope	0.036(+)	424.3	0.005	0.021(+)	569.7	0.093	0.060(+)	232.7	0.000	0.036(+)	618.3	0.003	0.024(+)	597.6	0.054
P0–0.15	0.074(−)	413.1	0.000	0.047(−)	562.2	0.001	0.072(−)	228.9	0.000	0.135(−)	587.6	0.000	0.062(+)	586.3	0.000
P0.15–1.37	0.011(−)	431.6	0.887	0.013(+)	572.1	0.607	0.009(−)	247.7	0.463	0.012(−)	625.3	0.269	0.108(+)	**572.1**	0.000
P1.37–5	0.011(−)	431.5	0.752	0.013(−)	571.9	0.477	0.007(+)	248.1	0.749	0.008(−)	626.4	0.685	0.013(+)	600.6	0.475
P5–10	0.024(+)	428.0	0.055	0.013(+)	572.0	0.514	0.041(+)	238.4	0.002	0.028(+)	620.7	0.015	0.034(−)	594.7	0.011
P10–20	0.068(+)	414.7	0.000	0.043(+)	563.2	0.002	0.077(+)	227.4	0.000	0.109(+)	596.2	0.000	0.068(−)	584.4	0.000
P20–30	0.056(+)	418.3	0.000	0.050(+)	561.2	0.001	0.042(+)	238.0	0.001	0.095(+)	600.5	0.000	0.046(−)	591.2	0.001

osip.alberta.ca). Surface mine leases were removed from comparisons and predictive maps of plant richness to account for the amount and severity of disturbance within mines. Active oil sands surface mining is devoid of vegetation and we considered these mining leases to have no conservation value in the near-term. Instead, we focus on *in situ* oil sands developments where bitumen is extracted from sub-surface wells and represent overall a larger combined footprint than that of the more well-known oil sands surface mines.

2.2. Statistical analysis

Natural logarithm, $\log_{10}$ or square-root transformations were used to normalize ALS and environmental variables exhibiting highly skewed distributions, while a natural logarithm transformation was used to normalize species richness values. All statistical analyses were performed in R program (R Core Team, 2015). Simultaneous Auto-regressive (SAR) models with a spatial error model were used to account for spatial autocorrelation in plots (Kissling and Carl, 2008). Richness of total vascular plants, herbaceous plants, forbs, graminoids, and woody plants were then regressed against ALS metrics and environmental variables using SAR models. SAR models were estimated using the package 'spdep' (Bivand et al., 2013; Bivand and Piras, 2015). We first used spatial autoregressive one-predictor regression to examine the effects of individual factors (Table 1). We also used Moran's I index to assess the residuals of SAR models in our analyses (Legendre and Legendre, 2012). We then used multivariate regression models of plant richness against different combinations of those variables to assess overall relationships. Pearson correlations among all ALS metrics and environmental variables were first examined to avoid multi-collinearity in multivariate regression models. Where variable pairs had correlation coefficients $|r| > 0.7$ (Table S1), the one with more ecological relevance and higher explanatory power for single factor regression models was kept (Dormann et al., 2013). After considering all variable correlations, the following uncorrelated variables were considered in models: mean annual precipitation (MAP), mean annual temperature (MAT), the 95th percentile of canopy height (CH), the proportion of first returns below 0.15 m (P0–0.15), proportion of first returns between 0.15 m and 1.37 m (P0.15–1.37), proportion of first returns between 1.37 m and 5 m (P1.37–5), proportion of first returns between 5 m and 10 m (P5–10), depth to water (DTW), and slope of plots (Slope). Since responses of biodiversity to environmental variables are not always linear (Gaston, 2000), we assessed quadratic effects for all ALS metrics by comparing linear and quadratic effects of all investigated ALS metrics using Akaike Information Criterion (AIC) (Tables 1 and S2). It has been proposed that if the ΔAIC between two models is smaller than 2, both models could be considered as having similar support (Burnham and Anderson, 1998; Mazerolle, 2004). Thus, if the AIC of a regression model with a linear response was more than 2 AIC points larger than a quadratic response, the model with a quadratic function was used (Tables 1 and S2). As a result, the quadratic of P5–10 was considered for explaining richness of vascular, herbaceous, woody and forb plants, while P0.15–1.37 and P1.37–5 were considered for graminoids (Table S2; Fig. S2). Since different combinations of canopy height and depth-to-water could potentially indicate types of forest habitats in this area, we also assessed the interactive effect canopy height and depth to water (i.e. CH × DTW). Finally, AIC was used to rank support among models with competing variable combinations. The model with the lowest AIC was considered the most parsimonious model and the results from this model were reported (Table 2). Akaike weights (*w*) were estimated for each variable based on the full set of models to compare relative importance of each variable (Burnham and Anderson, 2002).

To assess the effects of locations of *in situ* oil sands leases and the effectiveness of woodland caribou conservation as an umbrella for areas of high plant biodiversity, we overlaid predicted plant species richness with oil sand leases (Fig. S3) and woodland caribou ranges (Fig. S4). We also directly compared plant richness from field data among treatment categories (leased vs. non-leased; caribou vs. no caribou) using two-sample t-tests of log10 transformed species richness (Fig. 3).

3. Results

3.1. Relationships of species richness across growth forms

Richness of all native vascular, woody, herbaceous, forb and graminoid plants in the boreal forests of Alberta were positively correlated with each other (Table S1). However, richness of graminoids was less significantly correlated with the other growth forms. For instance, the Pearson correlation between richness of woody plants and graminoids was 0.52, while the correlation for richness of forb and vascular plants was 0.93 (Table S1).

3.2. Results of univariate responses in plant richness

Total species richness of vascular plants was significantly positively associated with mean annual temperature (MAT), canopy height (CH), the percentages of LiDAR returns above 1.37 m (PR1.37), mean canopy height (PRmean), the slope of plots (Slope), the return proportion within 10–20 m (P10–20) and within 20–30 m (P20–30) (Table 1; Fig. S1). In contrast, mean annual precipitation (MAP) and the return proportion below 0.15 m were significantly negatively associated with total species richness (Table 1). Richness of vascular plants was not significantly related to depth to water (DTW), the return proportion within 0.15–1.37 m (P0.15–1.37), within 1.37–5 m (P1.37–5), and within 5 m to 10 m (P5–10) (Table 1). Of the variables assessed, MAP and CH were the two strongest predictors of richness having the lowest AICs and individually explaining 15.5% and 10.0% (*pseudo r²*) of the variation in vascular plant richness, respectively. MAP and CH were also the most supported predictors in single-regression models for herbaceous, forb, and woody plant richness, but not for richness of graminoids, which was better explained by DTW and the return proportion within 0.15–1.37 m (P0.15–P1.37) (Table 1). Mean annual precipitation (MAP) was consistently negatively associated with richness of herbaceous, forb, graminoid, and woody plants, explaining 12.2%, 19.2%, 2.5%, and 9.8% of the variation, respectively. Canopy height was negatively associated with richness of graminoids, but only explaining 5.4% of the variation (Table 1; Fig. S1). Unlike total vascular, herbaceous, woody, and forb plant richness, plant richness of graminoids was negatively associated with depth to water explaining 11.2% of the variation (Table 1; Fig. S1). Comparing results of linear and quadratic responses, quadratic relationships for P5–10 significantly explained richness of vascular, herbaceous, woody, and forb plants (Tables 1 and S2; Fig. S2). In contrast, for graminoids, the quadratic terms were significant for P0.15–P1.37 and P1.37–5. The interactive effect of canopy height and depth to water (CH × DTW) explained 6.5% of the variation in richness of graminoids.

3.3. Results of multivariate simultaneous autoregressive models of plant richness

Simultaneous Autoregressive (SAR) multivariate models explained 19.5–35.0% (*pseudo-r²*) of species richness across the five growth forms of plants based on combinations of ALS vegetation metrics and other environmental variables (Table 2). In multivariate regression models, canopy height (CH) remained the most consistent and important variable overall explaining species richness for all growth forms except graminoids. Non-linear quadratic responses of P5–10 were also important for forbs, woody species, and total vascular plants. Depth to water was negatively associated with richness of total vascular, herbaceous, graminoid, and forb plants. Consistent with single-predictor regression models, MAP was an important predictor of plant richness and was included in the most supported models (lowest AIC values) for

Table 2
Simultaneous Autoregressive (SAR) multivariate models of richness of vascular plants, herbaceous plants, woody plants, forbs and graminoids against combinations of explanatory variables. The combinations with the lowest AIC (Akaike Information Criterion) were considered the most parsimonious models with the z-value for each coefficient given in the table. Pseudo r^2 of the most supported model for all five growth forms are reported. The Akaike weight (w) is by summing the weights of all models including a specific variable (combination of thirteen variables) and used to indicate the relative importance of those individual variables. CH, canopy height; P0.15, P0.15–1.37, P1.37–5 and P5–10 represent the return proportion at 0–0.15 m, 0.15–1.37 m, 1.37–5 m and 5–10 m, respectively; MAP, mean annual precipitation; MAT, mean annual temperature; Slope, the slope of the plot; DTW, the depth to water; CH × DTW, the interactive effects of CH and DTW. The two highest values of w for each growth form are in bold.

Variables	Vascular		Herbaceous		Woody		Forbs		Graminoids	
	z-value	w	z-value	w	z-value	w	z-value	w	z-value	w
MAP	−6.44	**0.996**	−3.97	**0.982**	−8.61	**1.000**	−7.66	**1.000**	−2.55	0.697
P0.15−1.37	3.12	**0.899**	3.21	**0.960**	2.67	**0.799**	2.90	0.942		0.494
CH	3.15	0.859	3.40	0.951	2.90	0.785	3.28	0.874		0.366
DTW	−3.04	0.688	−3.49	0.931		0.469	−3.04	0.794	−4.42	**0.913**
Slope		0.344		0.291	2.10	0.794		0.279		0.365
P0.15	−2.42	0.833	−3.06	0.900		0.433	−4.88	**1.000**		0.333
MAT	2.55	0.617	2.11	0.578		0.357	5.39	0.984		0.417
P1.37–5	−2.78	0.819	−2.76	0.904	−1.61	0.500	−3.42	0.988		0.438
P5–10	1.65	0.386		0.353	2.05	0.418		0.346	2.07	0.575
P0.15–1.37^2									−4.94	**0.919**
P1.37–5^2									2.42	0.601
P5–10^2		0.379		0.364		0.384		0.358		
CH × DTW		0.479		0.390	−2.64	0.791		0.419		0.361
Model performance										
pseudo r^2	0.240		0.223		0.222		0.350		0.195	

all growth forms, with MAP being inversely related to species richness. Predictions from multivariate SAR models suggested that plant richness was highest in the major river valleys for total vascular plants and herbaceous, woody, and forb species (Fig. 2a–e), while species richness of graminoids was highest in the flattest parts of the study area, representing fens and bogs (Fig. 2d).

3.4. Relationships between plant biodiversity hotspots, oil sands, and woodland caribou

The t-tests demonstrated that log10-scaled richness of vascular, woody, and forb plants were significantly different between plots inside and outside of caribou ranges ($p < 0.05$) with caribou ranges having lower plant richness (Fig. 3). Significant difference in plant richness were also found for plots inside versus outside of oil sands leases, except for richness of woody plants, with richness slightly higher inside leases than outside of leases (Fig. 3). These results also reflected regional patterns based on predicted maps of plant richness, although substantial variation was evident among oil sands leases (Fig. S3). As observed in predictive maps of multivariate SAR models, most caribou ranges occurred in areas with relatively low plant diversity. Thus, conservation of caribou ranges will not act as a surrogate to conserve those areas of highest vascular plant species richness (i.e. richness hotspots) (Fig. S4).

4. Discussion

Our results demonstrate that climate, vertical structure of vegetation, and terrain-derived slope and depth to water explained (*ca.* 20–35%) local patterns in native plant species richness. However, the effects of local variables on plant diversity differed across plant growth forms (Tables 1 and 2; Fig. S1). Overall, canopy height and mean annual precipitation (MAP) were the best predictors of vascular, herbaceous, forb, and woody plant richness (Tables 1 and 2).

Many hypotheses have been suggested to explain spatial patterns in plant richness at global and regional scales (Auerbach and Shmida, 1987; Kreft and Jetz, 2007; Fine, 2015). Determinants of biodiversity may, however, change with spatial scale (Auerbach and Shmida, 1987; Gaston, 2000). Although our study plots were located within a relatively narrow geographic area of one ecosystem – the boreal forest (Fig. 1), factors affecting large scale processes would be expected to influence regional species richness and thus richness of the plant

community (Eriksson, 1993). To examine this question further, we explored the effects of mean annual precipitation (MAP) and mean annual temperature (MAT) on the spatial variation in plant species richness of all vascular plants and the four growth forms of herbaceous, woody, forb, and graminoids. Our results demonstrated that, at a community level, these two variables significantly explained local variation in plant diversity (Table 1). For multivariate regression models, precipitation was consistently selected in models predicting richness of vascular plants and the four growth forms. MAP and MAT are considered two key factors in the water-energy hypothesis of global biodiversity patterns (Hawkins et al., 2003; Kreft and Jetz, 2007). However, in our research, precipitation was negatively related to plant richness (Table 1), while temperature was positively related to plant richness across all growth forms. This supports previous studies suggesting that plant diversity in colder regions is primary limited by energy inputs where water availability is not a key limitation (Hawkins et al., 2003).

We measured local environmental conditions using ALS-derived measures of vegetation structure (height and cover) and terrain characteristics to assess their influence in explaining local patterns in plant diversity. Remote sensing data are usually linked to measures of productivity and canopy cover which are known to be related to species assembly and richness (Gillman and Wright, 2006; John et al., 2008). We found that ALS metrics describing vegetation density (e.g. the percentage of returns above 1.37 m), and especially describing vegetation height, were useful predictors of plant diversity at local (community) scales (Table 1; Table 2).

ALS-derived canopy cover has been previously demonstrated as a useful descriptor of vegetation structure (Coops et al., 2007; Smart et al., 2012). Our results further demonstrated that the effects of canopy on plant diversity differed among plant growth forms. The two related variables, i.e. the percentage of returns above 1.37 m (PR 1.37) and percentage of returns above mean height (PRmean), were positively associated with species richness of total vascular, forb, herbaceous, and woody plants, but negatively associated with species richness of graminoids. As would be expected, more open habitats had a higher capacity to maintain graminoid-rich communities, while older and more productive forests were more suitable for maintaining total vascular species and herbaceous, forb, and woody plants.

Overall, canopy height was one of most important factors associated with patterns of plant diversity (positively related) in both univariate and multivariate analyses (Table 1; Table 2). Canopy height may be a surrogate for structural complexity of vegetation (McElhinny et al.,
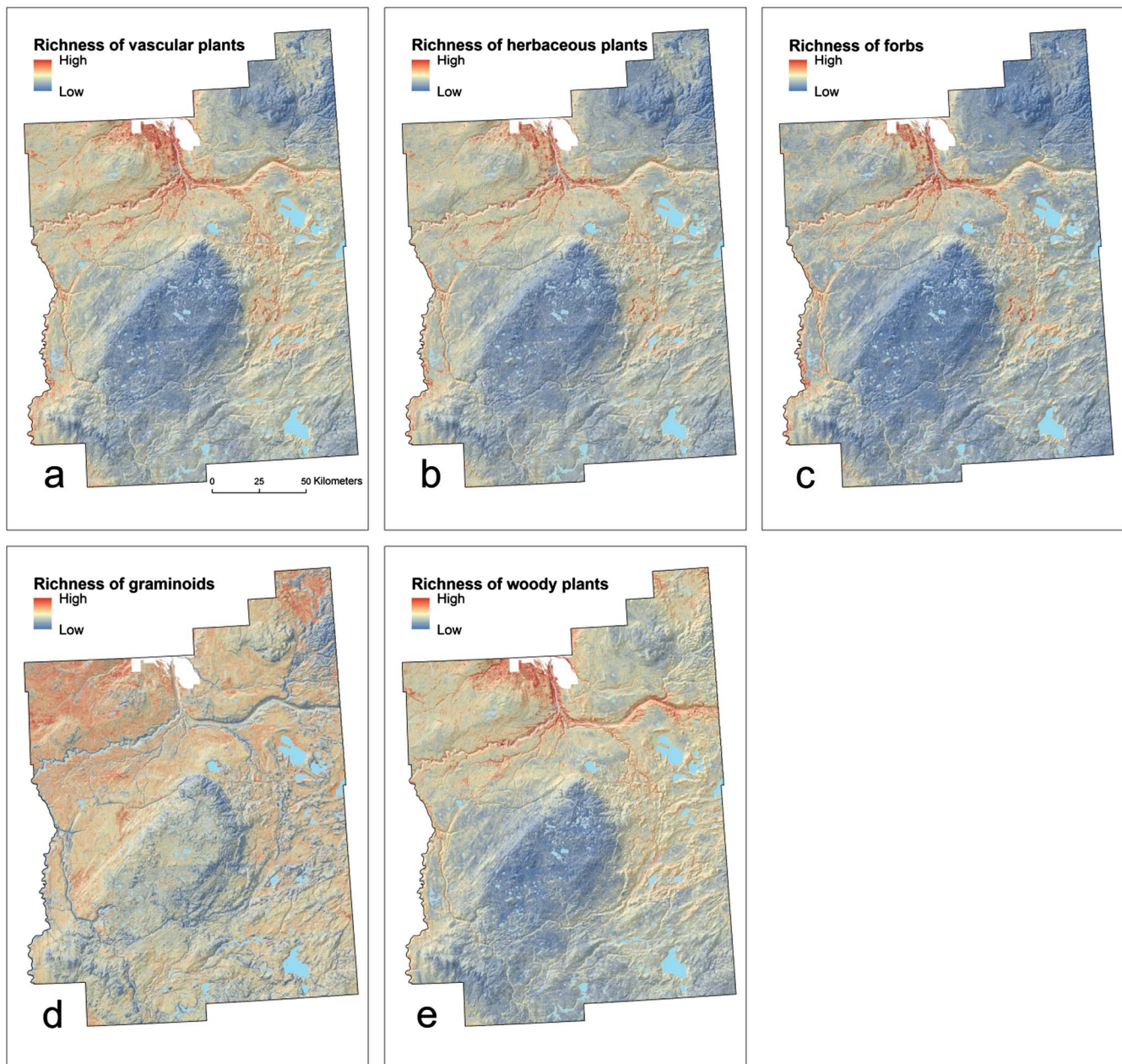
Fig. 2. Predicted species richness for northeast Alberta, Canada based on Simultaneous Autoregressive (SAR) models for richness of vascular (a), herbaceous (b), forb (c), graminoid (d), and woody plants (e). Results indicated that the areas associated with the highest plant richness were in or around river valleys, except for graminoids which peaked in richness in the flattest areas typified as being fens and bogs. Note, oil sands surface mine leases in the far north of the map were removed (white area). Maps with larger size can also be found in the Appendix A.

2005) illustrating a positive association between structural complexity and plant diversity in the boreal forest. More complex structure is well accepted as one of the primary drivers of biodiversity (Wolf et al., 2012; St. Pierre and Kovalenko, 2014; Loke and Todd, 2016). However, most previous studies using LiDAR-derived vegetation structure relate to vertebrates such as birds (e.g., Goetz et al., 2007; Coops et al., 2016), with few studies focused on plant species richness where it is more difficult to argue for a direct increase in niche space due to structural complexity. Light is a basic resource that limits plant growth (Craine and Dybzinski, 2013) and plant communities with taller plant heights potentially provide more possible options for plants in competition for light (Falster and Westoby, 2003). Our results showed ALS-derived canopy height was positively associated with species richness across plots for all growth forms, excluding graminoids, where canopy height was negatively associated with species richness (Table 1). These results

may be due in part to the physiological adaption of plants to different types of habitats with species in the graminoid group represented by the families of Cyperaceae, Poaceae and Juncaceae, which are common to grasslands and peatlands (Edwards et al., 2010). In the case of the boreal forest of Alberta, open habitats are most often peatlands, including graminoid-dominated fens (Rooney et al., 2012). Other vertical measures of vegetation structure were also associated with plant richness (Table 1). For example, species richness of graminoids was positively associated with the proportion of first returns below 15 cm (low ground layer; P0–0.15). In contrast, the relationship between richness of vascular, forb, and woody plants was negatively related to this same ground layer stratum (P0–0.15). These metrics depict characteristics of vertical stratification directly (Coops et al., 2007; Smart et al., 2012), which are related to the complexity of the canopy within the community. The physical structure of vegetation has been proposed as a key
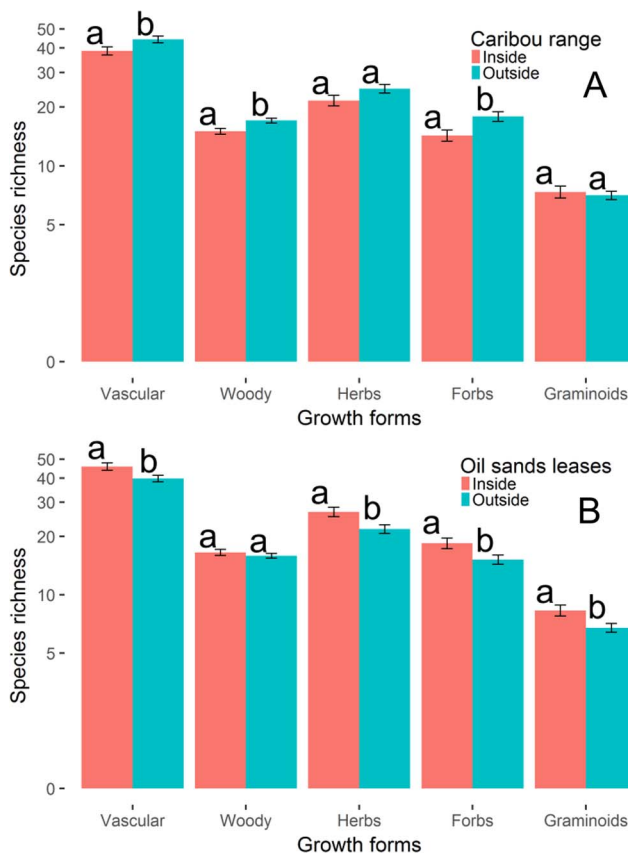
Fig. 3. Boxplots for species richness of vascular plants, herbaceous plants, forbs, graminoids, and woody plants for field plots inside vs. outside of caribou ranges (A) and leased vs. non-leased *in situ* oil sands (B). Richness data were $\log_{10}$-transformed. Different letters indicated that groups are significantly different ($p < 0.05$) from one another based on a *t*-test.

factor limiting diversity of ecosystems, particularly for birds dependent on forest structure (MacArthur and MacArthur, 1961). Our results support the theory that vertical structure of vegetation is associated with plant diversity, not just birds (MacArthur and MacArthur, 1961; Su and Bork, 2007; Bergen et al., 2009).

Our study also demonstrated that hydrological conditions (represented by depth to water) and terrain slope in the boreal forest were associated with local plant diversity (Table 1; Table 2), which is supported by other studies (Webb et al., 1999; Sass et al., 2012). In our study, areas with steeper slopes had higher plant diversity for all growth forms except graminoids. Incised valleys and steeper terrain may therefore be potential hotspots for plant diversity in boreal forests. This supports hypotheses of species diversity-environmental heterogeneity where greater terrain variation results in more microsites and thus niches (Ricklefs, 1977; Hirzel and Le Lay, 2008). Depth to water was negatively correlated with the richness of graminoid species (Tables 1 and 2), again indicating the specificity of many graminoid species to wet environments (i.e. fens).

Environmental and ALS measures used here represent only part of the factors associated with conditions affecting plant richness in the boreal forests. Plant diversity is also affected by other factors not measured in this study including land use, natural disturbances (e.g. fire), soil conditions, and species interactions (Perroni-Ventura et al., 2006; Kouba et al., 2015; Soliveres et al., 2015). Models that incorporate these variables may be more generalizable and have broader application to monitoring. Regardless, ALS-derived measures of vegetation structure show promise in directly measuring vegetation structure and thus indirectly monitoring plant biodiversity (e.g. Su and Bork, 2007) across large (regional) scales. Measures of vegetation structure

are known to relate better to measures of plant diversity than data from multispectral passive optical sensors assessing horizontal features of sites (Krishnaswamy et al., 2009), but this would need to be assessed here to confirm.

One of the most important goals for biodiversity monitoring is to conserve species from threats and set conservation priorities since biodiversity is unevenly distributed in space (Brooks et al., 2006; Freudenberger et al., 2013). *In situ* (non-mineable) oil sands leases were significantly different in plant biodiversity to non-leases for native habitats for all five groups except woody plants with plant richness typically being higher. However, when considering predictions across the region, many of oil sands leases are located in the areas with moderate to relatively lower vascular plant richness. In general, there was a trend towards leases further north having higher total vascular plant richness (Fig. S3). This suggests that the placement of oil sands leases within the landscape is not random with respect to the region's plant biodiversity with some sites having greater conservation value and thus threats. In contrast to oil sands leases, vascular plant richness was lower inside woodland caribou ranges than outside of caribou ranges suggesting that the conservation of caribou, a threatened flagship species for Canada's boreal forest (Weclaw and Hudson, 2004; Festa-Bianchet et al., 2011; Moreau et al., 2012), will have little value for protecting hotspots of vascular plant biodiversity (Fig. S4). Identifying this conservation gap is important for prioritizing future conservation efforts in Canada's boreal forest that extend beyond a single, albeit charismatic, species. Local-scale spatial predictions of plant diversity may also prove effective for initial environmental assessments of future oil sands developments or identifying where proposed developments (e.g. roads, well pads, processing plants) would have the least impact.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.11.017.

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