Forest Ecology and Management 377 (2016) 46–54

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Airborne laser scanning for modelling understory shrub abundance and productivity

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ARTICLE INFO

Article history:
Received 10 March 2016
Received in revised form 20 June 2016
Accepted 21 June 2016

Keywords:
Airborne laser scanning (ALS)
Light detection and ranging (LiDAR)
Species-habitat modelling
Grizzly bear (*Ursus arctos*)
Understory vegetation

ABSTRACT

Fiber production is no longer the sole objective of forest management, with increasing importance placed on other goods and services, such as maintaining habitat quality and stand successional development. Evaluating habitat quality and understory composition across complex landscapes remains a challenge for forest and wildlife managers, but is essential for ensuring the stability of vulnerable species. In this study we investigate whether forest stand structure, as measured by airborne laser scanning (ALS), can be used to predict the abundance and fruit production (fruit count) for Canada buffaloberry (*Shepherdia canadensis*), huckleberry (*Vaccinium membranaceum*), and saskatoon (*Amelanchier alnifolia*) shrubs in southwest Alberta, Canada. We combine ALS, climate, and terrain data to build random forest models of species abundance and fruit productivity, trained on data from 322 field plots. ALS data was processed into a suite of stand structure variables, under the hypothesis that models incorporating stand structure will be more powerful than models without for describing understory shrub abundance and reproduction (fruit productivity). ALS data improved model fit for saskatoon and huckleberry abundance models, with total explained variance (r^2) ranging from 37.6 to 59.4%. Inclusion of ALS data improved explained variance between 0% and 16%, suggesting that saskatoon and huckleberry in particular were associated with overstory vegetation structure. Despite the importance of ALS in further improving explanation of shrub abundance and fruit production, terrain factors were the dominant factor affecting regional and local variation in species abundance and fruit production.

1. Introduction

Airborne laser scanning (ALS) is an emerging tool being used by ecologists to remotely measure subtle differences in the three-dimensional physical features of vegetation. Spaceborne remote sensing instruments have been used extensively for tracking spatial and temporal changes in land cover and vegetation (Turner et al., 2003). However, two-dimensional (2D) satellite imagery is limited in resolution compared with light detection and ranging (LiDAR) (Lefsky et al., 2002 1999; Wulder et al., 2008) systems, which use return times of emitted light to produce estimates of distance. Technological systems developed over the last decade have made high-resolution 3D remote sensing of forest structural features possible and increasingly economical. These aircraft-mounted LiDAR systems are known as ALS, although LiDAR and ALS terms are often used interchangeably. ALS has become an effective operational technology that provides forest managers with information useful for forest inventory and monitoring (Nelson et al., 2006; Wulder et al., 2013). The majority of ALS-derived stand attributes, like volume, basal area, and biomass, are based on height percentiles and proportions, as well as other descriptive statistics like the mean or standard deviation of point height values. As laser pulses are able to pass through canopy openings, ALS is capable of characterizing vertical structure of the forest stands (Coops et al., 2007), a useful application for forest inventory and monitoring (Næsset et al., 2004; Nelson et al., 2006). Several novel ecological applications have included fine-scale assessments of natural forest regeneration (Falkowski et al., 2009), avian habitat quality assessment (Clawges et al., 2008), insect defoliation monitoring (Solberg et al., 2006) and improved distribution models of key grizzly bear (*Ursus arctos*) forage species (Nijland et al., 2014). A review of LiDAR applications in animal and habitat ecology is provided by Davies and Asner (2014).

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http://dx.doi.org/10.1016/j.foreco.2016.06.037
0378-1127/

ALS offers the possibility of remotely detecting understory plant species on the basis of three-dimensional canopy structure. In an early study, Korpela (2008) predicted the distribution of understory lichens from using discrete-return ALS. Martinuzzi et al. (2009) used ALS to predict presence/absence of an understory shrub layer, with classification accuracies above 80%. These innovative studies led to more advanced characterization of understory vegetation using ALS, including: mapping percentage of understory vegetation cover in ponderosa pine (*Pinus ponderosa*) forests using ALS intensity measures (Wing et al., 2012); detection and mapping of Chinese privet (*Ligustrum sinense*), an invasive plant species, using a combination of ALS and multispectral satellite imagery (Singh et al., 2015); and fine-scale predictions of understory plant species distribution (Nijland et al., 2014) from a suite of ALS metrics. However, to our knowledge, no studies have attempted to model fine-scale understory species abundance or productivity using ALS data. High-resolution characterization of stand structure may be a keystone tool in facilitating the evolution of local-scale models of species abundance.

Understory shrub productivity is particularly important for grizzly bear populations, and years of low fruit abundance are associated with an increase in grizzly bear mortality through human-wildlife conflict (Mattson et al., 1992). This may be partially ameliorated through human intervention to increase understory resource availability (Braid and Nielsen, 2015), or through climate change, which is projected to result in expanded suitable shrub habitat for some species (Roberts et al., 2014). Huckleberry (*Vaccinium membranaceum*) and Canada buffaloberry (*Shepherdia canadensis*) both represent important grizzly bear food sources (Feldhamer et al., 2003; Munro et al., 2006), while saskatoon (*Amelanchier alnifolia*) represents an important recreational food source (Arnason et al., 1981), has cultural value for First Nations peoples (Arnason et al., 1981), and serves as a secondary grizzly bear food source (Hamer and Herrero, 1987). Fire suppression has hindered growth of many understory shrubs by limiting the availability of forest openings (Hamer and Herrero, 1987), and anthropogenic disturbances may provide an alternative to fire-regulated openings by opening the canopy. However, clearcuts alone do not guarantee fruiting shrub habitat (Nielsen et al., 2004). Further knowledge on the landscape distribution of key fruiting shrub habitat could inform wildlife habitat improvements through silviculture management, such as targeting clearcuts for shrub planting or enhancements (Braid and Nielsen, 2015) or thinning in order to maximize the productivity of anthropogenic openings by encouraging understory shrub growth.

The most common method for predicting food availability is to use species distribution modelling (SDMs) to empirically relate observed presence of specific species to climatic variables, terrain variables, and other environmental variables. While species distribution modelling using climate data has found success, the resultant occupancy models do not provide an effective proxy for grizzly bear habitat quality, since they do not account for quantity or quality of available resources (Nielsen et al., 2010). While predicting site productivity is understandably difficult, improved availability of high-resolution spatial information (i.e. climatic data, ALS data, etc.) and advancements in powerful model-building methodologies provide a framework to examine and describe habitat quality in terms of factors such as fruit production in shrubs at individual sites.

Huckleberry and buffaloberry distribution are associated with low to moderate canopy cover, specific local terrain conditions (Braid and Nielsen, 2015), and low to moderate stand structural complexity (McKenzie et al., 2011). However, defining optimal canopy conditions for maximum berry production is challenging, since the relationship between canopy structure and fruiting shrub abundance depends on local landscape conditions, including soil moisture, elevation, and aspect (Nielsen et al., 2004). Interestingly, Brown and Parker (1994) provide compelling evidence that vertical stand structure, and corresponding leaf area density, is a more realistic determinant of light transmittance than simple crown closure. It is apparent that detailed information on vertical stand structure is necessary for accurate predictions of understory shrub composition and abundance. ALS technologies excel at measuring this type of spatial variation, and their capabilities in remotely measuring vertical stand structure exceed that of satellite-derived vegetative indices (Nijland et al., 2015).

In this study we investigated the usefulness of ALS data for modelling abundance of three fruiting shrubs. To do so, we combined field plot observations of three fruiting shrub species with high-resolution climate, terrain, and a suite of ALS metrics describing three-dimensional stand structure. We built models of species abundance and fruit production for these fruiting shrubs in an area of key grizzly bear habitat in southwest Alberta, Canada. We tested the hypothesis that models built with the inclusion of stand structure data (as measured by ALS) will outperform models built on terrain and climate data alone at predicting understory shrub abundance and reproduction (fruit productivity). Knowledge of this relationship could be used to inform forest management practices that could enhance site conditions, leading to increases in shrub abundance and fruit productivity.

2. Methods

2.1. Ecological and climate data

Sampling of bear foods was conducted for thirteen fruiting species across a 5065 km^2 study area in southwestern Alberta (Braid and Nielsen, 2015, Fig. 1). The study area, located approximately 125 km north of Waterton Lakes Nation Park, features variable mountainous topography and plant communities. Three hundred and twenty-two field plots were sampled for grizzly bear foods in 2012 (early July to mid-August) and 2013 (late May to mid-August), with plot locations stratified by elevation and Alberta Vegetation Inventory classes (Government of Alberta, 2005). Understory shrubs known to form part of regional grizzly bear diets were sampled in 50 m by 2 m transect belts. We recorded percent cover and fruit counts (density) for each of the three focal shrub species. The study area is characterized by variable topography and a variety of plant communities, including open and closed stands of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Avies lasiocarpa*), and lodgepole pine (*Pinus contorta*). Further information on the sampling methodology and study area is provided by Braid and Nielsen (2015).

Canada buffaloberry, mountain huckleberry, and saskatoon were selected for modelling here based on their importance for grizzly bear diets and their common occurrence in sample plots (n = 27–114). Coverage and fruit counts varied greatly between buffaloberry (maximum 20.4% cover and 4616 fruit/100 m^2), saskatoon (maximum 40.6% cover and 6300 fruit/100 m^2), and mountain huckleberry (maximum 51.4% cover and 7800 fruit/100 m^2). While saskatoon represents a less important component of the Alberta grizzly bear's diet (Hamer et al., 1991), it was included here based on amount of data available (common across plots), its value for other wildlife and humans, and the fact that it is the tallest of the three species of shrubs, providing a gradient in heights from which to assess the value of ALS in predicting shrub abundance and fruit production.

Climate surfaces were from Roberts et al. (2014), which provided data from the 1961–1990 baseline period at a resolution of 300 m. This dataset is based on historical climate records interpolated using PRISM down-sampling (Daly et al., 2008) via the

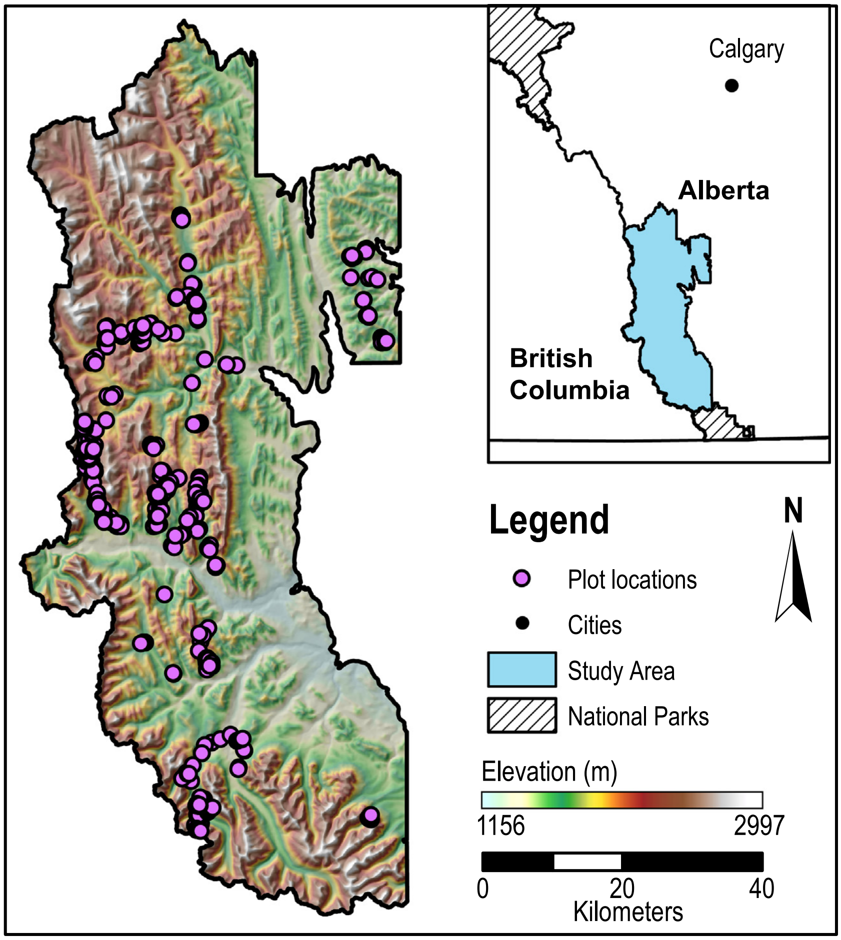

Fig. 1. Study area location in southwestern Alberta, Canada.

ClimateWNA software package (Wang et al., 2012), and includes derived climate variables such as evaporative demand, number of frost-free days, and continentality. We used a 30 m resolution digital elevation model (DEM) to derive topographic/radiative predictor variables, including potential direct incident radiation (PDIR), heat load index (HLI), and compound topographic index (CTI).

2.2. Software

The ALS point clouds were processed into height grid metrics using FUSION software (McGaughey, 2012). All other modelling, analysis, and data processing were done in the R programming environment (R Core Team, 2015). Models were produced using the *caret* package (Kuhn, 2008) and the *randomForest* package (Liaw and Wiener, 2002). Map predictions were prepared in the ArcGIS software package.

2.3. Airborne laser scanning data

ALS data for the study area were provided by the Government of Albert's Forest Management Branch. The majority of the ALS data were collected between 2006 and 2009 using sensors capable of detecting four returns per pulse and with a mean point density of 1.4 returns/m^2 (sd = 0.5 returns/m^2). The ALS point cloud data were normalized to height above ground level and processed using standard processing routines available in FUSION (McGaughey, 2012). We used FUSION to produce a suite 110 height and structure metrics, describing elements such as canopy height, mean return height, variation in return height, and density of returns in key strata (such as 0.15–1.37 m). ALS point cloud data were processed twice, first over field plot centers at a resolution of 25 m for model building, and then across the entire study area at a resolution of 30 m. Models built on field plot data were used to make abundance and fruit productivity predictions at a 30 m resolution.

From an initial dataset of 110 height metrics, variables with no *a priori* biological linkage (such pulse return intensity metrics) or variables that were not reproducible (such as maximum height metrics or pulse return count metrics) were discarded, resulting in 48 candidate variables. These 48 candidates were further reduced to 9 variables during model building. We only used first returns ALS metrics, since other studies have found significant, non-reproducible variation when using multi-return data (Bater et al., 2011; Korpela et al., 2012). Note that all references to "return height" refer to pulse return elevation, normalized to height above ground level.

2.4. Random forest modelling

We generated all predictions using random forest, an ensemble classification and regression tree technique (Breiman, 2001). Model accuracy was assessed using percent variance explained, which is a pseudo R^2, and is calculated from out-of-bag error rates. This assesses the model against a held-out test data set, similar to cross-validation, which provides a simple measure of model performance using a replicated test (held out) set. The default of 500 trees produced inconsistent model fit, so a total of 3000 trees were grown for each model.

Multi-stage modelling was used to estimate abundance and fruit production of the three species of interest. Three model stages were developed, each conditional on the prior stages: (1) occupancy (presence/absence) was estimated using logistic regression models, developed by Braid and Nielsen (2015) and used to constrain predictions of abundance and fruit production (next two stages) to where it was predicted present; (2) random forest regression was used to model shrub abundance (log transformed) conditional on presence (non-zero counts); and (3) random forest regression was used to model fruit productivity (log transformed), conditional on presence, with log abundance from the second stage also considered as one of the model candidate variables since abundance of shrubs at a site should relate to total fruit production. Species abundance models were parameterized using counts of individuals for saskatoon and buffaloberry, and percent transect cover for huckleberry. Models of fruit production were parameterized using fruit abundance on each transect, and were not separated by year, but instead were built to produce estimates of average fruit production among years. Spatial predictions of shrub abundance (density or cover) and fruit abundance (density) were estimated for the study area, conditional on predicted presence by occupancy models, and compared against distribution predictions from Braid and Nielsen (2015).

Straightforward interpretation of a random forest model is impractical, since tree-building is stochastic and involves an exceedingly large number of regression trees (Breiman, 2001). We used linear regression (Fig. 2) to evaluate the strength and direction of the relationship between important ALS variables and shrub abundance or fruit productivity. However, it remains important to understand the effects of individual variables on the model response. This is accomplished using the random forest variable importance measure (Liaw and Wiener, 2002). For each tree, the mean square error (MSE) is computed on the out-of-bag data, and compared against the MSE when each predictor variable is permuted. The difference in accuracy is averaged across all trees, and normalized by the standard error. Variable importance can be ranked by the corresponding loss in accuracy when a specific variable is permuted.

Variable selection was conducted in order to identify the most significant ALS variables for each species and to attain a parsimonious model. We adapt the protocol outlined by Díaz-Uriarte and de Andrés (2006), performing variable selection by iteratively removing the least important variables while avoiding high correlation among final predictor variables. This was essential because random forest algorithms automatically distribute importance among correlated predictors, reducing their apparent contribution. From 48 candidate ALS variables, a correlation matrix was used to identify groups of highly-correlated variables ($r > 0.75$), and highly-correlated pairs were avoided. Random forest variable importance measures were used to further reduce candidate variables, resulting in nine ALS variables that were selected for final inclusion in shrub abundance and fruit models.

We controlled for multicollinearity in 28 climate and terrain variables by recursively eliminating the variable with the highest variance inflation factor, leaving a final set of three terrain variables and between six to eight climate variables. As a final model

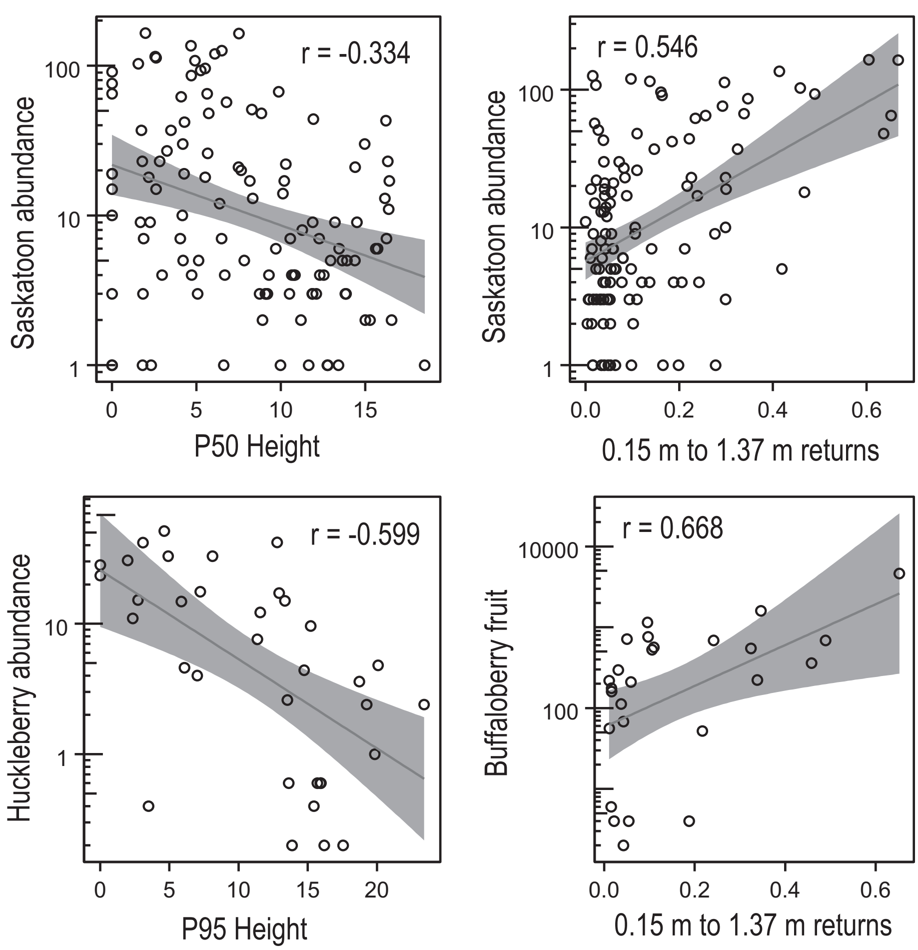

Fig. 2. Linear regression between observed abundance/fruit productivity and commonly-selected ALS variables. Pearson's r statistic calculated with $p < 0.05$. All abundance and fruit productivity values are per 100 m^2.

building step, the remaining 19 climatic, terrain and ALS variables, were used to fit a random forest model for each species' abundance and fruit production. The least important variables were iteratively removed until further removal would increase the out-of-bag (OOB) error rate. This resulted in the selection of a parsimonious model with up to three ALS variables and up to four climatic or topographic variables. We tested our hypothesis by comparing the percent explained variance of models fit on climate/terrain alone against models fit with both ALS and terrain/climate. The change in explained variance from incorporating ALS data was used to measure the influence of stand structure on understory characteristics.

3. Results

Models were able to explain a large proportion of the observed variance in abundance, with variance explained (calculated on the OOB sample) of 37.6% for saskatoon and 59.4% for huckleberry (Table 2). ALS data did not significantly improve models of saskatoon fruit production over models built on climate alone, although models still had high model fit (46.0% explained variance). Huckleberry fruit abundance also had high model fit (44.1% explained variance). Buffaloberry fruit models had weak model fit (15.79% explained variance), and buffaloberry abundance models failed to predict data (0% variance explained). Overall, the inclusion of ALS improved explained variance by 16% for saskatoon abundance, 0% for saskatoon fruit productivity, 6% for huckleberry abundance, 4% for huckleberry fruit productivity, 0% for buffaloberry abundance, and 16% for buffaloberry fruit productivity. Models built on ALS data alone with no climatic or terrain data were still reasonable in explaining shrub abundance, explaining 13.7% of abundance in saskatoon and 23.5% of the abundance in huckleberry (Table 2).

All three species responded to a terrain-derived local heat load index (HLI), including strong influences on saskatoon abundance, huckleberry abundance, huckleberry fruit productivity, and buffaloberry fruit productivity (Table 2). Overall, ALS data were an

Table 1
Variables considered for modelling shrub abundance and fruit production.

Variable	Category	Description
BFFP	Climate	Beginning of frost-free period
EFFP	Climate	Ending of frost-free period
EREF	Climate	Reference atmospheric evaporative demand
PPT_SM	Climate	Summer precipitation
PPT_WT	Climate	Winter precipitation
TD	Climate	Continentality (MWMT – MCMT)
TMAX	Climate	Maximum temperature
EMT	Climate	Extreme minimum temperature (30 year period)
MAR	Climate	Mean annual solar radiation
PDIR	Terrain	Potential direct incident radiation
HLI	Terrain	Heat load index
CTI	Terrain	Compound topographic Index
Height SD	ALS	Standard deviation of return height (elevation), "vegetation height variability"
Height P50	ALS	50th percentile of returns height (elevation), "median vegetation height"
Height P60	ALS	60th percentile of returns height (elevation), "60th percentile vegetation height"
Height P95	ALS	95th percentile of returns height (elevation), "maximum canopy height"
Canopy relief ratio	ALS	Relative height of canopy above ground
% first returns > 1.37 m	ALS	Percentage of returns greater than 1.37 m "canopy strata cover"
0.15–1.37 m prop	ALS	Proportion of returns between 0.15 m and 1.37 m "shrub strata cover"

Table 2
Variables selected by random forest variable importance, and total variance explained of each model. Primary models are bolded, while models used for assessment of variables families are not.

Model	Variables	Variance explained
Saskatoon	**HLI, CTI, Height P50, 0.15–1.37 m prop**	**37.59%**
Saskatoon climate/terrain	PDIR, MAP, PPT_WT, CTI, TD	21.18%
Saskatoon ALS only	0.15–1.37 m prop, Height P50, % first returns > 1.37 m, Height P_95	13.65%
Saskatoon fruit	**Abundance, EMT, MAR, 0.15–1.37 m prop, CTI, BFFP**	**46.09%**
Saskatoon fruit climate/terrain	Abundance, EMT, MAR, CTI, BFFP	45.89%
Saskatoon fruit ALS only	Abundance, Height SD, 0.15–1.37 m prop, Height P60, Height P50	30.38%
Huckleberry	**Height_P95, HLI, PPT_WT, MAR**	**59.36%**
Huckleberry climate/terrain	PPT_WT, MAR, HLI, PPT_SM	52.87%
Huckleberry ALS only	Height P95, Height P60, Height P50, Height SD	23.50%
Huckleberry fruit	**Abundance, HLI, % first returns > 1.37 m, EFFP, TD**	**44.07%**
Huckleberry fruit climate/terrain	Abundance, HLI, CTI, PPT_WT, PPT_SM, BFFP	39.99%
Huckleberry fruit ALS only	Abundance, canopy relief ratio, Height P95, Height SD,% first returns > 1.37 m	37.88%
Buffaloberry	**Height_P50, Height_P95, Height SD, HLI, EREF, BFFP**	**0%**
Buffaloberry fruit	**HLI, 0.15–1.37 m prop, % first returns > 1.37 m, PDIR, Height SD, Abundance**	**15.79%**
Buffaloberry fruit climate/terrain	PDIR, HLI, BFFP, EREF	0%
Buffaloberry fruit ALS only	% first returns > 1.37 m, 0.15–1.37 m prop, Height SD	0%

important factor across most models. Saskatoon abundance was negatively associated with 50th percentile of height and positively associated with proportion of returns between 0.15 m and 1.37 m (Fig. 2). Huckleberry abundance was negatively associated with the 95th percentile of returns height (Fig. 2). While our buffaloberry fruit productivity model was relatively weak (Table 2), there was nonetheless a significant relationship between buffaloberry fruit productivity and proportion of returns between 0.15 m and 1.37 m (Fig. 2). Predictably, abundance of shrubs (log count data for saskatoon, log percent cover for huckleberry) was the most important predictor of fruit production (Table 2).

Modelled spatial predictions illustrate dense populations of saskatoon in the central-south and northeast portion of the study area, with similar patterns in fruit production (Fig. 3). Occupancy models from Braid and Nielsen (2015) predicted little to no saskatoon in the northwest of the study region. Despite this, the

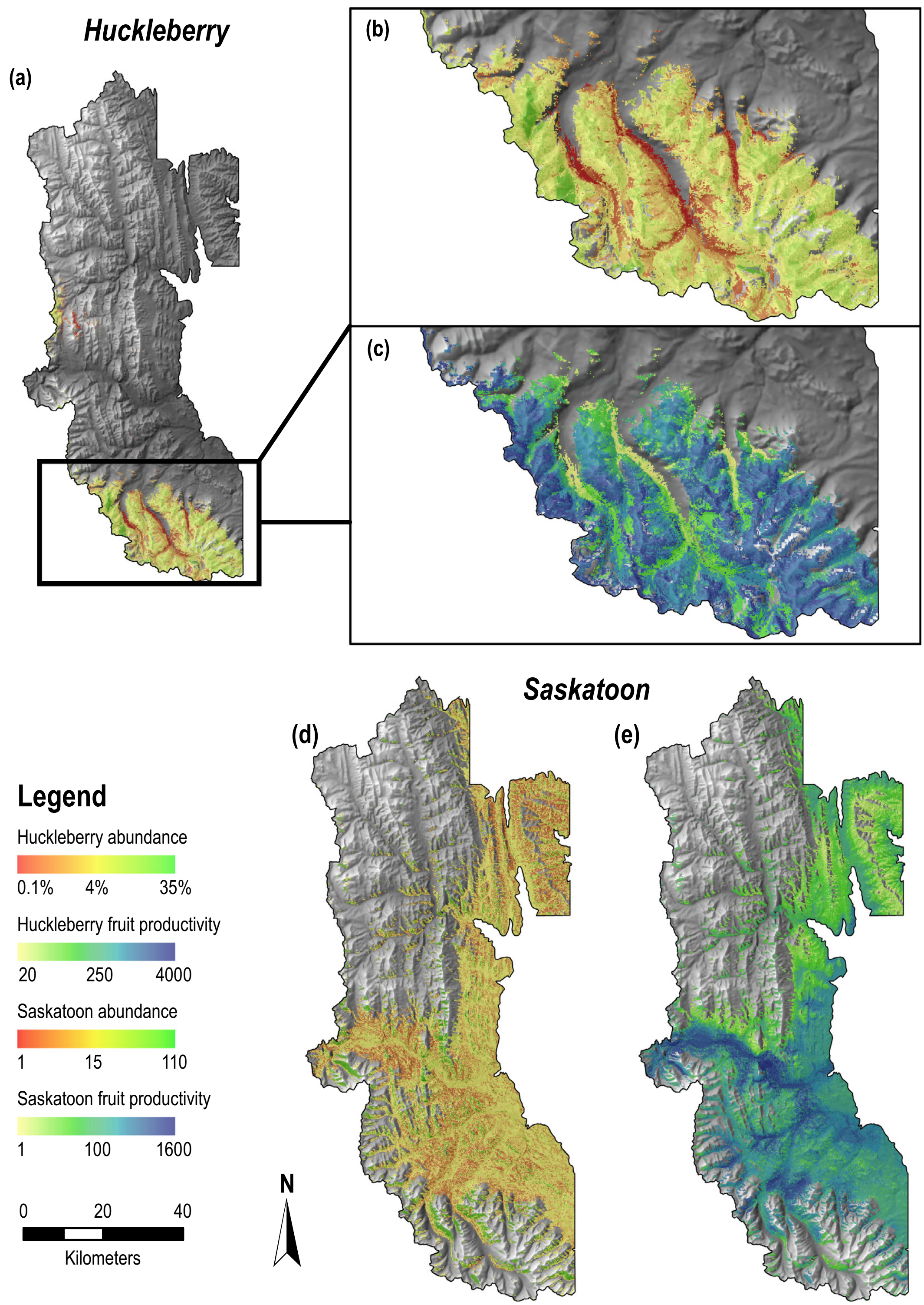

Fig. 3. Model predictions of shrub and fruit abundance where predict present. Predictions are shown for (a) huckleberry abundance (% cover), (b) huckleberry abundance (% cover), (c) huckleberry fruit productivity (per 100 m^2), (d) saskatoon abundance (stem density per 100 m^2), and (e) saskatoon fruit productivity (per 100 m^2).

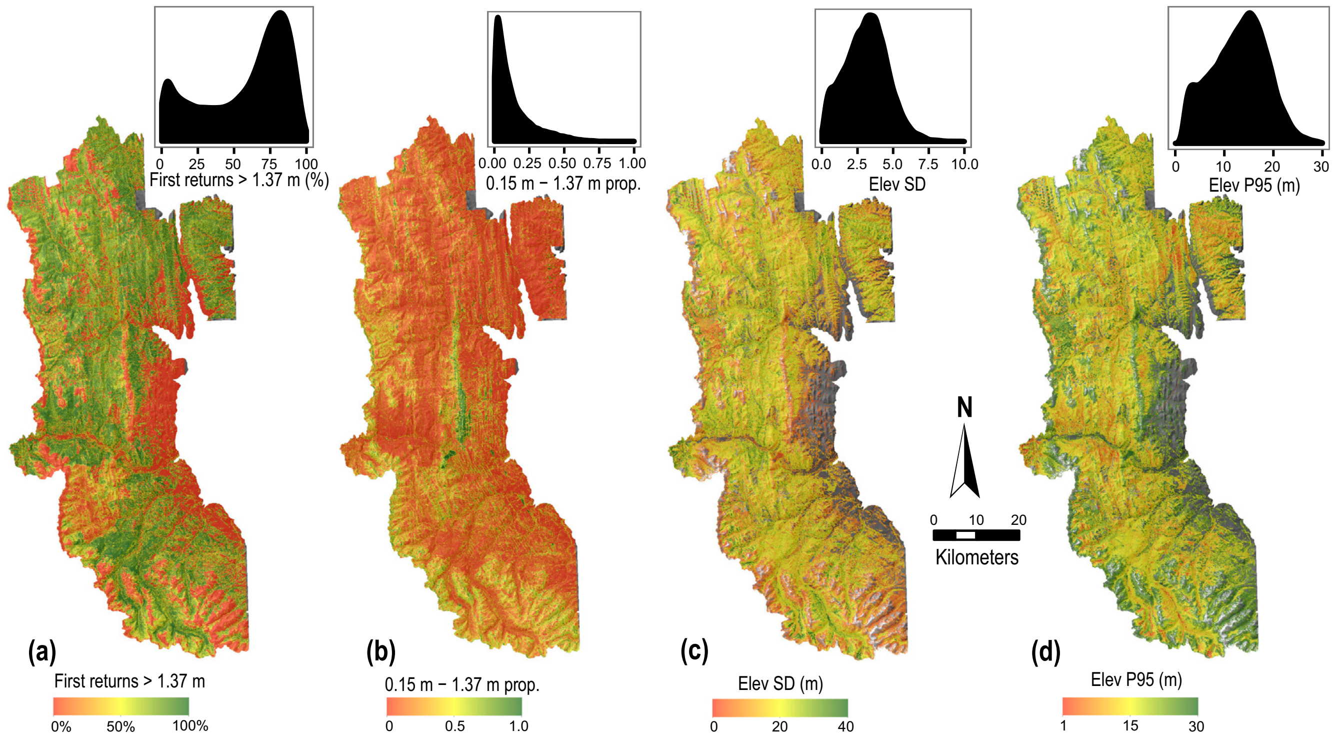

Fig. 4. Selected ALS variables across the study area. Stand structure values are shown for: (a) proportion of returns greater than 1.37 m; (b) percentage of returns from 0.15 m to 1.37 m; (c) standard deviation of return height; and (d) 95th percentile of returns height. Gray areas indicate no data (no points above 1.37 m).

abundance models identified isolated patches of saskatoon with moderate stem densities in the northwest where terrain conditions were favorable, with the highest predicted abundance on south-facing slopes at mid to high elevations. Some areas are projected to have over 100 individual shrubs/100 m^2 with up to 160,000 berries/100 m^2.

Occupancy predictions predicted that huckleberry would be restricted to the southern regions of the study area near the British Columbia border (Fig. 3). Within these regions, abundance is predicted to be lower in the bottoms of large valleys, while abundance was predicted to be moderate to high on high-elevation slopes, particularly southeast-facing slopes. Some areas of particularly high abundance of huckleberry were estimated to have up to 35% cover and total fruit abundance of up to 4000 berries/100 m^2.

Processed ALS data detected variations in stand structure and disturbances including linear features, forest openings, and barren areas (Fig. 4). ALS data were not available in a few areas of the study area due to prohibitive flying conditions, most commonly at the highest elevations. First returns greater than 1.37 m featured a bimodal distribution, likely corresponding to forested and open sites.

4. Discussion

Our results demonstrate that shrub abundance and fruit productivity are primarily dependent on terrain factors and incoming solar radiation, in agreement with models by Meentemeyer et al. (2011). However, ALS data was a consistently important factor predicting fruit productivity (Table 2), and the inclusion of ALS-derived variables markedly improved fit of abundance models for four of six models. The insignificance of climatic temperature and precipitation variables is notable, as well as the positive association with 0.15–1.37 m return proportion (hereafter "shrub strata cover", see Table 1 for other descriptions) and general negative association with median vegetation height (Fig. 2). Since the growth form of saskatoon is typically 1–6 m in height (Moss, 1983) and lesser at high altitudes, its presence may at least partially drive the values of the ALS vegetation metrics at any given site.

Huckleberry typically grows in Alberta to between 0.5 m and 1.0 m in height (Moss, 1983), making direct detection with ALS difficult. While huckleberry is a moderately shade tolerant species, it grows most vigorously under partial or open canopies (Hamilton and Yearsley, 1988). Berry production also varies inversely with canopy closure beyond partial shading, with dense canopies arresting berry production (Minore et al., 1979). In our study area huckleberry abundance was negatively associated with maximum canopy height as defined by the 95th percentile of returns. The relationship between huckleberry fruit and maximum canopy height is also notable, since fruit abundance is often greatest with some partial shading and decreases with either full sun exposure or moderate to complete shading (Fig. 2). Overall, ALS variables were subordinate to terrain variables in predicting huckleberry shrub abundance, implying that huckleberry abundance is primarily dependent on moisture availability and terrain aspect.

Buffaloberry shrub abundance did not respond to climatic, terrain, or ALS data. It is possible that this was due to true stochastic behavior in their distribution or determining factors that were not captured by the data, such as competition. Despite this, satisfactory environmental models of buffaloberry fruit productivity showed that fruit varied as a result of heat load index and light availability, and had a positive association with shrub strata cover.

Abundance models using field measurements of stand complexity have previously demonstrated effective predictions for specific understory species, with one study of vine maple (*Acer circinatum*) reporting a $R^2 = 0.41$ using linear regression and 52% variance explained using regression tree methods (McKenzie et al., 2011). Our results show that such results can be replicated with the inclusion of both high-resolution ALS data and high-resolution climate data, alleviating the need for costly field measures of stand structural complexity. Models built with ALS data also performed significantly better than models built on climate data alone. It is not possible to determine whether this improvement is because ALS successfully captures the aforementioned variation in canopy cover, or some other systematic environmental variability, although the former seems likely.

We realize the limitations associated with smaller sample sizes for individual shrub species (n = 27–114), although random forest is a particularly powerful technique for small data sets (Cutler et al., 2007). A second potential challenge is the temporal gap between plot observations and collection of ALS data. Temporal differences between the two datasets were normally under five years, but ranged up to a maximum of seven years in some locations with older ALS data. Nijland et al. (2014) showed that such temporal gaps should not represent a significant change in the forest canopy structure or overall height, based on height growth curves for tree species in the region (Chen and Klinka, 2000). Disturbances, including wildfire, logging, avalanches, or wind blowdown, would increase noise in the data, although large-scale disturbances from wildfire and wind blowdown were not known to the area over the period of sampling.

Early seral forests and open forest form ideal fruiting shrub habitat (Martin, 1983; Nielsen et al., 2004), and so targeted harvest with limited retention may facilitate increased understory shrub growth on sites that have faced habitat degradation due to fire suppression. Large clearcuts are not sufficient for encouraging understory growth, since they often fail to emulate early seral stage (Martin, 1983) and high-altitude open-canopy forests (Nielsen et al., 2004) upon which huckleberry relies, depending on the intensity of soil disturbance. ALS is already in widespread use for forest inventory (Næsset et al., 2004; Nelson et al., 2006; White et al., 2013), and ALS-informed models have several potential applications for guiding forest management practices. Our models may inform forest managers by targeting treatments to optimize light transmittance, while it is not practical for forest managers to alter site terrain or moisture characteristics. Targeted harvest at sites that are favorable for shrub growth may even exceed the value of wildfire, which can cause mortality of understory shrub rhizomes and thus reduce overall abundance (Hamilton and Yearsley, 1988). Similarly, disruptive site preparation techniques, such as scarification, can disrupt shrub rhizomes and delay understory regeneration (Haeussler et al., 1999).

In conclusion, this study shows how ALS data can be used to predict abundance and fruit production of understory shrubs across large areas. Local terrain factors were often the most important regional factor affecting shrub and fruit abundance. However, ALS data had a significant contributing effect on understory shrub fruit productivity, indicating that ALS models may be used in combination with high-resolution terrain data to identify favorable understory shrub habitat or areas where forest amendments may produce favorable understory shrub habitat.

Acknowledgements

This work was funded by a Government of Alberta (Agriculture and Forestry) grant to S.E. Nielsen and N.C. Coops. Additional funding for field plot data were from Natural Sciences and Engineering Research Council (NSERC) Discovery grant to S.E. Nielsen and a NSERC-IPS grant (sponsored by the Alberta Conservation Association) to A. Braid. Funding and in-kind support for field work was also provided by Doug Manzer and the Alberta Conservation Association. ALS data were provided by Alberta Agriculture and Forestry. Additional thanks to Andreas Hamann for statistical and modelling advice.

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