1. Introduction

The composition and structure of forests are changing in response to climate change, shifts to natural disturbance regimes, and increasing industrial development (Brandt et al. 2013). Statistical models linking distribution, abundance, and community structure to select environmental variables are often used to understand how forest birds respond to these habitat changes (Carrillo-Rubio et al. 2014, Engler et al. 2017, He et al. 2015). Many factors influence the predictive capacity of such models, but spatial covariates—and their spatial and temporal resolution—may be key drivers of model accuracy (Franklin 1995, Vaughn and Ormerod 2003).

Avian species distribution models (SDMs) often rely on horizontal environmental covariates derived from traditional digital cartography, e.g. land cover maps and digital forest resource inventories (FRIs). FRIs are commonly used in forestry management planning and function as sources of spatial explanatory variables in avian SDMs (Cumming et al. 2010a, 2010b). While these products may contain detailed information on plant species composition, disturbance history, and canopy height, they often lack data on three-dimensional (3D) habitat structure (e.g. shrub density, vertical heterogeneity, ground surface topography, etc). The 3D structure of forest ecosystems influences both the abundance, distribution, and behavior of birds (Davies and Asner 2014). Different vegetation structures at various heights and densities are key factors that influence where birds perch, feed, and reproduce (Bradbury et al. 2005), by providing shelter from environmental conditions (Carrascal and Diaz 2006), concealment from predators (Gotmark et al. 1995), and creating habitat variation for their insect prey [REF].

Traditionally, 3D structural metrics are obtained through ground-based field measurements. While valuable for explaining variation in the sampled area, such an approach has limited value in predicting where birds will or will not be in unsampled areas. Furthermore, field measurements are typically limited to discrete sampling regimes over relatively narrow spatial extents (Bergen et al. 2009). Developing methods to directly measure the 3D distribution of canopy and sub-canopy structures at varying scales could provide dramatic increases in the predictive accuracy of avian SDMs (Zellweger et al. 2014) and address limitations inherent in SDMs that only use horizontal land cover variables (Davies and Asner 2014, Lefsky et al. 2002).

Airborne LiDAR gathers structural information by measuring the 3D elevation of surface topography and vegetation. A sensor attached to a plane or UAV repeatedly fires laser pulses towards the earths surface recording the echoes reflected from branches, dead woody debris, and foliage (for full overviews of the LiDAR techniques used for collecting habitat structural data, see Leeuwen and Nieuwenhuis (2010) and Vierling et al. (2008)). The height and frequency of returned echoes can generate metrics associated with avian habitat, including those related to plant species composition (Ackers et al. 2015, Zielewska-Buettner et al. 2018), ground topography (Schaffer-Smith et al. 2018, Fritz et al. 2018), terrain wetness (White et al. 2012), and vegetation structure (Renner et al. 2018, Bae et al. 2018, Kortmann et al. 2018). Many of these variables relate to habitat structural properties thought to be selected by birds. (Coops et al. 2016) and (Lefsky et al. 2005) grouped structural metrics into three broad classes: (1) horizontal features similar to many derived from passive optical sensors (e.g. basal-area, connectivity, horizontal structural heterogeneity, and the size, shape, and distribution of patches), (2) overall height and biomass (e.g. canopy height, canopy relief, crown shape, total biomass), and (3) metrics corresponding to the vertical distribution of vegetation (e.g. density of shrub or understory vegetation, vertical structural complexity). Thus LiDAR is likely to improve bird models by introducing new, biologically relevant, spatial covariates at finer resolutions. However, exactly which of the three classes of structural metrics will provide the greatest increase in predictive power are unclear.

While LiDAR is increasingly being used to explore relationships between animals and their habitats (Davies and Asner 2014), the generality of which LiDAR metrics to include has not been fully explored. The number and kind of LiDAR metrics included in avian models varies between studies with some using LiDAR to measure variables already available from other remotely sensed datasets (i.e. tree height), just more precisely. Others have tried developing novel metrics to describe structural elements not available from traditional photogrammetry. The importance of including novel versus more precise measures of structural variables likely depends on a species' niche and life history. For example, Vogeler et al. (2014) examined the relationships between richness of nesting guilds and a suite of height and density metrics and found understory vegetation density was far more important for understanding ground nesters than tree height, and Weisberg et al. (2014) found that measures of habitat heterogeneity are stronger predictors of richness of foliage foragers than ground foragers.

Here, we evaluate the suitability of LiDAR-derived environmental predictor variables for modeling species-habitat relationships in a boreal forest. Specifically, we compare metrics summarized at scales ranging from 1 to 500 m2 for modeling the abundance of songbirds grouped by nesting guild. We assess the results of LiDAR based models against those built using FRI predictors from the Common Attribute Schema for Forest Inventories (CAS-FRI)(Cosco 2011). Objectives are: (1) model the abundance of canopy, understory, and shrub layer nesting songbirds using LiDAR-derived structural metrics, (2) identify the strongest LiDAR based predictors for different nesting guilds, and (3) compare the utility of LiDAR and FRI based predictors in avian SDMs.

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