



Remotely sensed forest structural complexity predicts multi species occurrence at the landscape scale



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ABSTRACT

Along with plant species composition forest structural complexity is an important determinant of forest biodiversity, but difficult to predict in space from field data. We analyzed forest structural complexity based on a comprehensive set of variables derived from nationally available, area-wide remote sensing, particularly LiDAR data. We generated variables related to vertical and horizontal structural heterogeneity, as well as site factors potentially indicating the abundance of weakened trees or snags. We used them to predict the occurrence of four bird species with narrow and complementary structural habitat requirements, together being indicative of structurally diverse forests. Presence/absence data of Capercaillie (*Tetrao urogallus*), Hazel Grouse (*Bonasa bonasia*), Three-toed Woodpecker (*Picooides tridactylus*) and Pygmy Owl (*Glaucidium passerinum*) from three biogeographic mountain regions in Switzerland were used to calibrate species distribution models (boosted regression trees BRT) for each species individually, as well as for the sympatric occurrence of at least three of the four target species. The predictive deviances explained (D^2) and the AUC values obtained from cross-validation ranged from 15.5% to 63.1% and 0.77% to 0.97% respectively. Sympatric species occurrence reflecting overall forest structural complexity was predicted best, with an outstanding accuracy. To support management and monitoring schemes we identified variable threshold effects based on partial dependence plots. Variables related to vertical foliage distributions were most important, followed by horizontal structural attributes such as canopy height variations, forest edges and gaps. Site factors such as topographic position improved all models and were most important for the species depending on weakened trees and dead wood. We conclude that recent advances in remote sensing allow for large-scale determination of forest structural characteristics suitable for developing species and habitat distribution models of considerable generality, while keeping an unprecedented level of detail. Our approach allows forest managers to amend regional and countrywide management plans with reliable maps depicting areas of high forest structural complexity and habitat quality, which will facilitate the integration of conservation-relevant information into multifunctional forestry.

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1. Introduction

Maintaining structural complexity is an important need to halt ecosystem simplification and the loss of biodiversity in managed temperate forests (Franklin, 1988; Hunter, 1999). Quantifying forest structure to better understand biodiversity patterns and to support multifunctional forest management is thus a fundamental task to conserve biological diversity (Lindenmayer et al., 2000). Forest structure is generally described with measures of the

vertical and horizontal distribution of forest vegetation elements (Franklin et al., 2002). More specifically, several combinations of structural attributes related to variation in foliage arrangement, canopy cover, tree diameter, tree height, tree spacing, tree species, stand biomass, understory vegetation, and deadwood have been proposed as indices of forest structural complexity at the stand scale (McElhinny et al., 2005). A broad range of structural attributes is expected to promote the abundance and diversity of species by creating a large variety of ecological niches, themselves providing cover, nutrition and breeding sites for many species and individuals (MacArthur, 1958; Hunter, 1999).

Measures of structural complexity are traditionally derived from field data, however, gathering such data is labor-intensive and usually limited to sample plots. Thus, area-wide predictions

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are not feasible and consistency issues often confine integrating data across multiple regions. Recent developments in remote sensing, such as the emergence of national LiDAR (Light Detection And Ranging) datasets, provide alternative ways to consistently quantify forest and habitat structures across large areas at an unprecedented level of detail (Lefsky et al., 2002; Hyypä et al., 2008). There is a growing body of literature describing the application of LiDAR-derived variables of forest structure to explain animal–habitat relationships (Bradbury et al., 2005; Vierling et al., 2008). Based on the foliage height diversity (FHD) concept, which was proposed by MacArthur and MacArthur (1961) to show that bird species diversity is positively associated with the vertical distribution of foliage among the forest vegetation layers, direct LiDAR measurements representing the vertical complexity of canopy elements, for example, explained the multi-year prevalence of a Neotropical bird species (Goetz et al., 2010). LiDAR metrics of vegetation height, density or volume as well as variables based on single tree crowns have been found to be good predictors of species distributions and habitat suitability (Hill et al., 2004; Seavy et al., 2009; Swatantran et al., 2012) and were identified as indicators of avian species diversity (e.g. Goetz et al., 2007; Lesak et al., 2011). LiDAR variables of canopy height variation and light availability in the lower forest strata also performed well in predicting the distribution and assemblages of arthropods (Müller and Brandl, 2009; Vierling et al., 2011), and explained the occurrence and activity of bats (Jung et al., 2012). To complement direct variables of forest structure, a number of studies included topography-related variables and combined LiDAR data with radar and multi-spectral satellite data, such as variations of the normalized difference vegetation index (NDVI) (e.g. Goetz et al., 2010; Swatantran et al., 2012).

Most studies using airborne-LiDAR data to explain species–habitat relationships employed relatively high-resolution data for both the dependent and independent variables (e.g. point counts and/or plot areas ranging from 100 s to 10,000 s of m²) across relatively small spatial extents (e.g. national parks or forest reserves). Thus, their level of precision comes at the cost of decreased generality, which is a major concern in forest and predictive habitat distribution modeling (Guisan and Zimmermann, 2000). The potential of LiDAR to optimize the trade-off between precision and generality based on landscape-level analysis of forest structural complexity and habitat quality across larger plot areas (e.g. km²) and extents (e.g. several biogeographic regions) has remained largely unexplored. At the landscape level, structure-based indicators representing between-stand heterogeneity, structural complexity, or structural variation patterns caused by disturbance (e.g. from wind, snow, fire, insects) are considered relevant biodiversity surrogates, but difficult to measure in the field (Lindenmayer et al., 2000). Methods and metrics utilizing national LiDAR data may provide a promising route to quantifying such forest landscape characteristics and build habitat and species distribution models of considerable generality.

In a biodiversity conservation context, an ideal suite of variables representing structural complexity needs to reflect observed relationships with faunal diversity. While a number of studies used LiDAR-derived variables of forest structure to examine patterns of avian, mostly passerine diversity, the performance of such variables to predict the sympatric occurrence of bird species with specific, well-known and complementary structural requirements has not been analyzed so far. Such predictors may comprehensively represent forest structural complexity and cover a large breadth of species, providing that the target species complement each other in terms of their specialization to different structural characteristics, forest successional stages, trophic levels and resource requirements.

We studied four rare and sedentary mountain bird species meeting the above criteria: Capercaillie (*Tetrao urogallus*), Hazel Grouse (*Bonasa bonasia*), Three-toed Woodpecker (*Picoides tridactylus*) and Pygmy Owl (*Glaucidium passerinum*). Capercaillie is a large forest grouse usually found in structurally rich, semi-open coniferous old-growth (Bollmann et al., 2005). It is considered an umbrella species for the autochthonous montane and subalpine forest species communities (Suter et al., 2002; Pakkala et al., 2003) and has considerable spatial requirements with home range sizes ranging from 100 to 1000 ha (Storch, 1995). Hazel Grouse inhabits early succession stages with pioneer plant communities as well as small rejuvenation areas embedded in old-growth forests, with territories typically ranging from 10 to 40 ha (Bergmann et al., 1996; Schaublin and Bollmann, 2011). Given the Capercaillie's and Hazel Grouse's narrow structural habitat requirements, we expect heterogeneity in vertical and horizontal forest structure to be an important determinant of their habitat qualities.

The insectivorous Three-toed Woodpecker has been proposed as an indicator species of structurally rich coniferous forests with old-growth attributes such as substantial volumes of dead wood, an important resource of forest biodiversity in general (Bütler et al., 2004; Roberge and Angelstam, 2006). Local disturbances and low productivity sites rendering the required snags and weakened trees thus form optimal habitats. Three-toed Woodpeckers have a home range size of ca. 100 ha and are considered a keystone species supplying forest stands with tree-cavities that serve secondary users as nesting or roosting holes (Pechacek and d'Oleire-Oltmanns, 2004). Pygmy Owls are secondary cavity nesters and occupy territories of a few hundred hectares. They depend on key habitat structures such as abundant old trees or snags providing hollows for nesting and fodder storage or interior edges to optimize hunting for their prey, mostly small birds and mammals (Glutz von Blotzheim, 1980; Strom and Sonerud, 2001). Along with heterogeneity of vertical and horizontal structure, we expect site factors affecting the abundance of weakened trees and snags, such as topography, to have a comparably strong effect on the habitat quality for these two species.

The aim of this study is to evaluate the potential of nationally available remote sensing data, particularly LiDAR, for the assessment of forest structural complexity on the landscape level across a broad range of mountain forest conditions. Our objectives were: (1) to derive a set of variables representing the complexity of vertical and horizontal forest structure and complement it with variables of vegetation density and topographic site factors, (2) test the capacity of these variables to predict the occurrence of each of the four target bird species as well as (3) the sympatric occurrence of at least three of these species, representing overall structural complexity.

2. Material and methods

2.1. Study area

This study was carried out in three biogeographic mountain regions covering 21,620 km² of Switzerland: the Swiss Jura, the Northern Prealps and the Eastern Central Alps (Fig. 1a). These regions represent mountain forest ecosystems from low to high elevations and comprise a broad range of the ecological niches realized by the study species, which is expected to improve the generality of the results (Graf et al., 2006). The general landscape composition in all three regions is characterized by forests, pasture grasslands, settlements and unproductive areas, such as bare rock.

In the Swiss Jura, elevations do not reach the tree-line and forests form semi-continuous habitats interrupted by pasture grasslands. In the Northern Prealps, the upper natural tree-line lies at

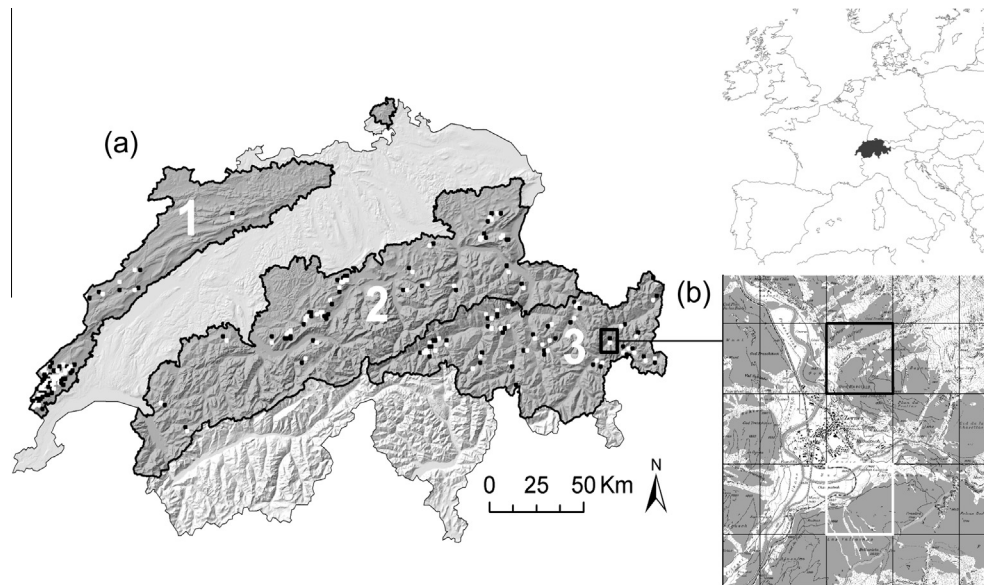


Fig. 1. Study area and sampling design. The study area (a) consists of three biogeographic mountain regions in Switzerland: Jura (1), Northern Prealps (2) and Central Eastern Alps (3). Dots indicate species presence (white) and absence (black) cells. The map (swisstopo, 2012) extract in (b) shows the sampling design including the km² reference grid and a presence (white frame) and an absence (black frame) sampling cell with forest cover and rivers in gray.

about 1800 m above sea level (m a.s.l.) and mountain tops with elevations around 3000 m a.s.l. occasionally disrupt the potential natural forest cover. The climatic conditions in the Jura and Northern Prealps are mostly oceanic with cold-temperate winters, wet summer months and precipitation rates from 2000 to 3000 mm yr⁻¹. The natural tree species composition varies along the altitudinal gradient, with European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) dominating the montane altitudinal belt, while Norway spruce (*Picea abies*) and mountain pine (*Pinus mugo*) are dominant in the subalpine belt. The Eastern Central Alps are characterized by high relief over short distances, with mountains reaching elevations of up to 4000 m a.s.l. The forests in this region occur in belts around mountain ranges, and the upper tree-line is at ca 2300 m a.s.l. This region has a continental climate with cold winters, warm and dry summers and precipitation rates from 800 to 2000 mm yr⁻¹. Compared to Jura and Northern Prealps, a larger proportion of larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) makes out the tree species composition in the Eastern Central Alps.

2.2. Species data and study design

We compared used versus unused habitat based on a paired species presence/absence approach. The pairs of cells with species presence and absence were delineated using a national reference grid with a cell size of 1 km² (Fig. 1b).

Species presence data included multi-year species evidence taken from the database of the Swiss Ornithological Institute and the grouse database of the Swiss Federal Research Institute WSL. Species specialists and qualified ornithologists reported direct (i.e. sightings) and indirect (i.e. feathers and/or droppings) evidence, which were validated by experts from the Swiss Ornithological Institute and the WSL, and allocated to the respective km² cell. Presence cell selection was restricted to cells with at least three years of observation between 2006 and 2010. We applied a stratified random sampling design to select the presence cells. In each study region, the presence cells represent the altitudinal gradient and the distribution range of each species. The 1-km²-resolution approximates the home range size of the study species, which is

generally recommended for studying species–habitat relationships.

We defined pseudo-absence cells (from now on referred to as absence cells) as cells with no reported species evidence between 2000 and 2010. Because our aim was to study only forest-dominated landscapes, we restricted our analysis to cells with more than 50% forest cover, as delineated by the digital mapping product Vector25 (swisstopo, 2012). Pairs of presence and absence cells were located in the same valley within dispersal distance, in our case set to a maximum of 4 km. Thereby, we accounted for the underlying idea that absence cells could potentially be used by the species but are unused due to suboptimal habitat characteristics. Considering the two criteria above, we randomly selected an absence cell at least one but not more than three grid cells apart from a particular presence cell, whereas the closest potential absence cell was prioritized (Fig. 1b).

Our sample sizes for the analysis amounted to 51 pairs ($n = 102$) for Capercaillie, 73 pairs ($n = 146$) for Hazel Grouse, 61 pairs ($n = 122$) for Three-toed Woodpecker, 56 pairs ($n = 112$) for Pygmy Owl and 40 pairs ($n = 80$) for sympatric occurrence of at least three species. We chose the occurrence of at least three species to represent sympatric occurrence because the sample size for simultaneous occurrence of all four species would have been too small for the analysis (11 pairs). The numbers of species presence within the sympatric occurrence pairs were 27 for Capercaillie, 37 for Hazel Grouse, 35 for Three-toed Woodpecker and 31 for Pygmy Owl, and all possible species combinations were evenly represented.

2.3. Predictor variables

2.3.1. LiDAR data

We derived 23 variables from a nationally available first and last return LiDAR dataset acquired at a nominal footprint size in the range of small-footprint laser scanning (i.e. several decimetres). The mean point density for our sampled areas was 1.4 m⁻² and the standard deviation of height accuracy was 1.5 m in forested areas, as reported by the data provider. Data was delivered in the form of classified point clouds for the digital terrain model (DTM) and the digital surface model (DSM) (swisstopo, 2011).

Vertical complexity – to account for the species' preferences with respect to vertical foliage distributions we used the terrain corrected vegetation point cloud (heights of laser echoes in DSM minus interpolated DTM heights) to derive height quartiles in the form of a multi-layer raster grid (Fig. 2). We calculated the multi-layer raster based on a 50×50 m pixel grid, with the vegetation heights in each pixel box being subdivided into 4 layers, indicating the quartiles. For each km^2 cell, we computed the mean quartile heights and the standard deviation (SD) thereof, over all pixel boxes. The SD of the four quartile heights were included separately in the set of predictor variables (Table 1). They measure how evenly the vegetation heights are distributed within each km^2 cell and thus represent spatial variability of vertical structure. Mature or old-growth forests with a continuously rich vertical structure promoted by periodical natural disturbance are therefore expected to exhibit smaller standard deviations of the quartile heights than forest landscapes showing distinctive patterns of stand level management (Fig. 2).

To complement our measurements of vertical structure we developed a single index for multi-storied forest profiles. For this purpose we used the mean quartile heights to calculate the range (in meters) between the second and third mean quartile height and divided it by the fourth mean quartile height (Table 1).

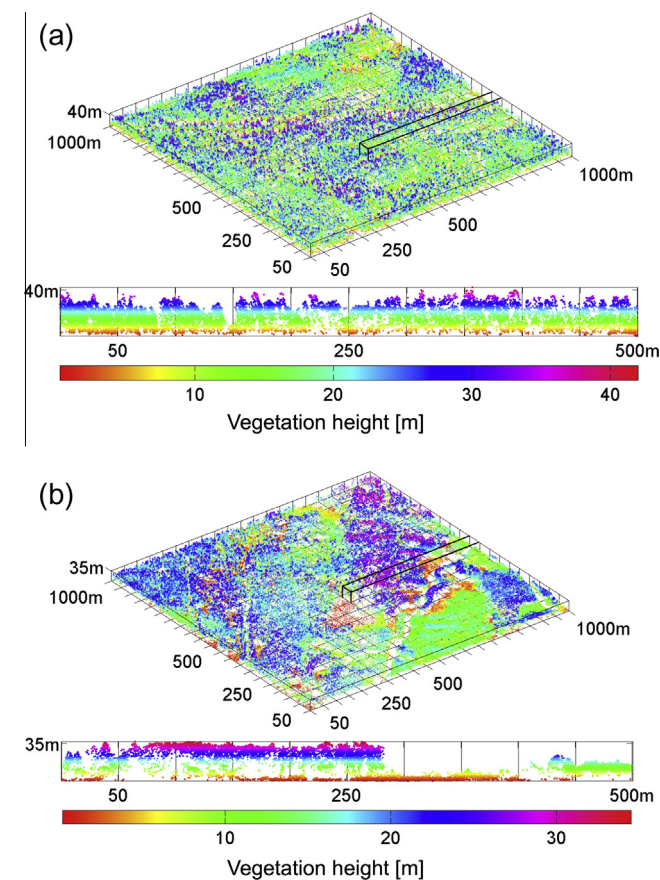


Fig. 2. Terrain corrected vegetation heights for 2 km^2 sampling cells with contrasting vertical distribution profiles shown along two $500 \text{ m} \times 500 \text{ m}$ transect bars located in each cell (emphasized black lines). The km^2 sampling cells were gridded with a $50 \text{ m} \times 50 \text{ m}$ raster and the vegetation heights (xyz -coordinates of laser returns) in each pixel box were used to calculate the height quartiles. The vegetation heights in (a) are distributed comparably evenly and continuously among the pixel boxes, whereas the profile shown in (b) is characterized by vertically homogeneous stands in different development stages and heights, resulting in a high standard deviation of quartile heights between the pixel boxes.

Horizontal complexity – the species requirements in terms of horizontal structural heterogeneity was accounted for by interpolating the terrain corrected vegetation heights to form a continuous Canopy Height Model (CHM) with a resolution of 3 m, representing an average tree crown projection in spruce (*Picea abies*) dominated mountain forests (Fig. 3). For further analysis in FRAGSTATS – an open source software designed for the analysis of spatial patterns of landscape structure (McGarigal et al., 2002) – we classified the CHM into four height classes as indicated in Fig. 3.

We derived potential indicators of forest structural complexity using FRAGSTATS metrics at patch, class and landscape levels (McGarigal et al., 2002) (Table 1). Patch level metrics represent the density of key structural features, such as small forest gaps, and served as a basis to compute class and landscape metrics. The class level metrics indicate the abundance, size and variability of different successional stages as represented by the vegetation height classes. Further, we measured the proximity of patches belonging to the same height class as well as their degree of aggregation because we expected this to influence habitat characteristics, such as resource availability and flight distance. Landscape metrics were mainly used to quantify ecotones by calculating the density of transitions to non-forest patches, as well as between different vegetation height patches.

2.3.2. Topography-related variables

In addition to the direct measurements of vertical and horizontal forest structure, we considered three topographic site factors (Table 1). Forest structure is affected by slope or the topographic position in relation to the surrounding terrain because these site factors influence edaphic characteristics (e.g. soil temperature, moisture, depth and nutrient status) and exposure to disturbance. We hypothesize that positive values of the topographic position index as well as increasing slopes may be proxies for higher abundances of weakened or dead trees, which are crucial elements of Three-toed Woodpecker habitat. We further considered the global radiation because it also influences soil characteristics (e.g. temperature and water content), as well as the energy balance and thus forest vegetation physiology and structure (Kimmmins, 2004).

All three topographic site factors were derived from the digital 25 m grain size terrain model provided by swisstopo (DHM25© 2004, DV033594). The algorithms applied are referenced in Table 1. We only considered pixel values in forests, as delineated by the digital mapping product Vector25 (swisstopo, 2012). Because our aim was to represent the general topographic situation in a km^2 presence/absence cell, we aggregated the pixel values to a grain size of one ha, using the mean per ha to calculate a mean and SD per km^2 cell.

2.3.3. SPOT satellite images

We complemented our predictor set with data from a mosaic of multi-spectral SPOT-5 satellite images recorded between May and September 2004–2006 on a 10 m resolution. We implemented the preprocessed normalized difference vegetation index (NDVI) layer used by Camathias et al. (2013), which was corrected for shadows, illumination and atmospheric effects. Here we use NDVI as a proxy for vegetation density (Goetz et al., 2010) and expect that periodically disturbed forests with large amounts of dead wood or structurally complex and relatively sparse mire forests will exert lower NDVI values than dense production forests. In accordance with the topography-related variables, we only considered pixels in forested areas and aggregated the pixel values to 1 ha to calculate a mean and SD per km^2 cell (Table 1).

Table 1
Description of predictor variables. Canopy Height Model (CHM) classes according to Fig. 3.

Variable group	Variable (abbreviation)	Unit	Definition
LiDAR – vertical complexity	SD quartiles (SDQTL)	m	Standard deviation for each height quartile across all pixel boxes of the multi-layer raster (see text for details)
	Multi-storied profile (MSP)	(index)	Index representing the vertical distribution range within the 2nd and 3rd height quartile (see text for details). Low index values indicate a more evenly distributed vertical vegetation texture, high values single- or two-layered profiles
LiDAR – horizontal complexity	Patch area (AREA)	ha	Mean patch area for understory, midstory and canopy CHM class. Class level metric
	Forest gap density (GAP)	Gaps/ha	Sum of forest gaps, i.e. non-forest patches <1 ha, divided by total forest area in ha. Patch level metric
	% of landscape (PLAND)	%	Percentage of landscape (1 km ²) for patches of understory, midstory and canopy CHM class. Class level metric
Clumpy (CLMP)	Clumpy (CLMP)	(index)	Clumpy Index for patches of understory, midstory and canopy CHM class. Class level metric
	Nearest neighbor (NN)	m	Mean nearest neighbor distances for patches of understory, midstory and canopy CHM class. Class level metric
Edge density (ED)	Edge density (ED)	m/ha	Density of edges (pixel transitions) between two CHM classes, i.e. non-forest/understory, non-forest/midstory, non-forest/canopy, understory/canopy. Landscape level metric
	Canopy height heterogeneity (CHH)	m	Total length of edges (pixel transitions) between understory, midstory and canopy CHM class. Landscape level metric
Topography-related variables	Topographic position (TPI)	(index)	Mean and SD of the Topographic Position Index. Measures the exposure of a site in relation to the surrounding terrain. Positive values: Ridges and hilltops; negative values: sinks, gullies and valley bottoms (Zimmermann and Roberts, 2001). Algorithm applied: Zimmermann (2000)
	Slope (SLP)	degrees	Mean and SD of slope. Algorithm applied: slope function in ArcGIS (v 10.1)
SPOT-satellite images	Solar radiation (SRAD)	kJ/m ²	Monthly mean and SD of potential global clear sky solar radiation during the months April–October. Algorithm applied: Kumar et al. (1997)
	NDVI (NDVI)	(index)	Mean and SD of the normalized difference vegetation index

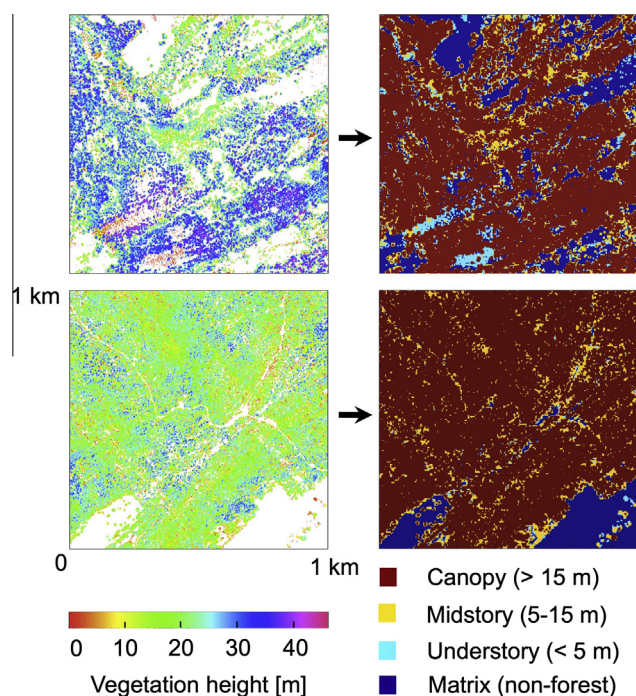


Fig. 3. Orthogonal projection of terrain corrected vegetation heights (left) and classified Canopy Height Models (CHM, 3 m resolution) (right) for a 1 km² presence (top) and absence cell (bottom).

2.4. Data analysis

We used boosted regression trees (BRT) to model species presence as a function of the predictor variables, as well as the squared terms of predictors with potentially unimodal responses. BRT are an advanced machine learning-based regression modeling technique that is ranked among the best performing species

distribution modeling algorithms (Elith et al., 2006). It can handle any variable type (e.g. numeric, binary, categorical), is insensitive to outliers, controls for over-fitting and automatically models typical ecological features such as nonlinearities and interactions (Friedman, 2002; Elith et al., 2008).

We fitted BRT models in R using the `gbm` function in the `dismo` package (Hijmans et al., 2011) and custom written code by Elith et al. (2008). The settings for the model parameters (tree complexity, learning rate and number of trees) were defined in accordance with recommendations by Elith et al. (2008) and optimized by comparing model performance for a range of different parameter combinations. The five most parsimonious final models were identified by the simplification procedure proposed by Elith et al. (2008) which involves sequential removal of least important predictor variables based on cross-validated prediction accuracy.

The relative importance of each predictor variable was determined based on how often a variable was selected and on the model improvement as a result of the selections. We chose a threshold-based approach to visualize the fitted functions using partial dependence plots, which indicate the effect of each predictor variable on the response variable after taking into account the average effect of all other predictors in the model (Elith et al., 2008). The residuals of each final model were checked for spatial independence by calculating correlograms and Moran's I coefficients over various lag distances and no statistically significant spatial autocorrelation was found.

The predictive performance of each model was determined based on ten-fold cross validation. We calculated two evaluation measures: the percentage of explained predictive deviance (D^2) and the area under the receiver operating characteristic curve (AUC). The AUC value is a threshold-independent measure that indicates the model's ability to discriminate between presence and absence cells (Fielding and Bell, 1997). AUC values >0.7 indicate acceptable, 0.8–0.9 excellent, and >0.9 outstanding model discrimination (Hosmer and Lemeshow, 2000).

3. Results

3.1. Model performance

We developed BRT models for all four species individually, as well as for the sympatric occurrence of at least three species. Model predictive performance based on AUC values ranged from outstanding (sympatric occurrence, Capercaillie) to excellent (Hazel Grouse, Three-toed Woodpecker), and acceptable (Pygmy Owl) (Table 2). The range of the explained predictive deviance varied considerably among the five models, with highest values for sympatric occurrence and Capercaillie, supporting the outstanding predictive power of these two models. All the five models showed a high robustness, as interpreted from the standard errors.

3.2. Relative influence and effect of predictor variables

Predictor variable contributions to the total deviance explained in the five BRT models ranged from 7% to 24% (Table 2), with the LiDAR-based measures together always accounting for more than 50% of the overall contributions. Variables directly derived from the LiDAR point cloud (vertical complexity) were the most important group, whereby the standard deviation within the 2nd and 3rd quartile and the multi-storied profile index accounted for most of the contribution. These three variables were retained by four of five final models, however, in the Pygmy Owl model they were less important. Variables based on the interpolated CHM (horizontal complexity) formed the second main source of explained deviance. In this group, the distance to the nearest neighbor of midstory patches was the most important predictor and retained by all models except for the Three-toed Woodpecker model. Edge and forest gap densities were most important in the Hazel Grouse and Pygmy Owl models and were not retained by the sympatric occurrence model. The mean topographic position index and the mean NDVI contributed to all five models, however, NDVI variability, as expressed by the standard deviation (SD), was only important in

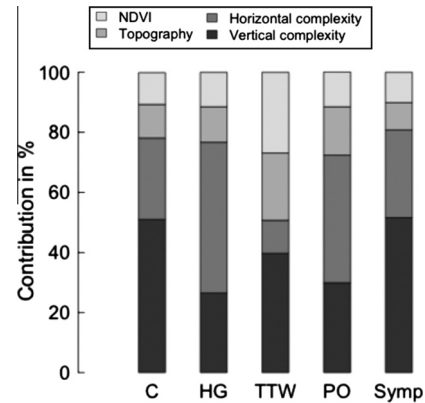


Fig. 4. Predictor variable group contribution to total deviance explained in the five final BRT models. C = Capercaillie, HG = Hazel Grouse, TTW = Three-toed Woodpecker, PO = Pygmy Owl, Symp = Sympatric occurrence.

the Three-toed Woodpecker model. Topography-related variables and the NDVI were substantially more important in the Three-toed Woodpecker model than in the other models, although the Pygmy Owl model also responded comparably stronger to topography (Fig. 4). Half of the explained deviance in the Hazel Grouse model stems from CHM-derived variables, whereby such variables only marginally contributed to the Three-toed Woodpecker model. Both the Capercaillie and sympatric occurrence models show similar patterns of variable group contributions, with vertical complexity accounting for half of the explained deviance.

We represent the partial responses of the predictor variables by reporting the fitted response curves for the sympatric occurrence model only (Fig. 5), because the variables in this model are good representatives for the other models. The two most important variables, SD 2nd quartile and the nearest neighbor of midstory patches, had clear threshold values at 6 m and just below 10 m respectively. Thus, habitat quality, as represented by probability

Table 2

Performance of the five final BRT models in terms of predictive deviance explained (D^2) and area under the receiver operating characteristics curve (AUC) as well as the contribution of the predictor variables (in percent) to the total deviance explained. For D^2 and AUC means and standard errors (SE) calculated from ten cross-validation replicates are provided.

	Model name				
	Capercaillie	Hazel Grouse	Three-toed Woodpecker	Pygmy Owl	Sympatric occurrence
<i>Predictive performance</i>					
D^2	43.6 (2.7)	29.0 (1.9)	27.7 (1.8)	15.5 (1.8)	63.1 (1.8)
AUC	0.92 (0.02)	0.84 (0.01)	0.84 (0.02)	0.77 (0.02)	0.97 (0.01)
<i>Variable contribution in %</i>					
<i>LiDAR – vertical complexity</i>					
SD 1st quartile				14.4	
SD 2nd quartile	15.3		19.2	15.5	24.1
SD 3rd quartile	11.7	12.7	8.1		10.8
SD 4th quartile	13.4				
Multi-storied profile	10.6	13.8	12.4		16.7
<i>LiDAR – horizontal complexity</i>					
Nearest neighbor midstory	19.8	11.7		17.3	21.2
Nearest neighbor canopy					8.0
% of landscape understory		6.9			
Edge density non-forest/midstory			11.0		
Edge density non-forest/canopy	7.3	9.3		15.5	
Forest gap density		13.7		9.7	
Canopy height heterogeneity		8.6			
<i>Topography-related variables</i>					
Mean topographic position	11.2	11.8	15.5	16.1	9.1
Mean solar radiation			6.9		
<i>SPOT satellite images</i>					
Mean NDVI	10.6	11.5	15.9	11.6	10.1
SD NDVI			11.0		

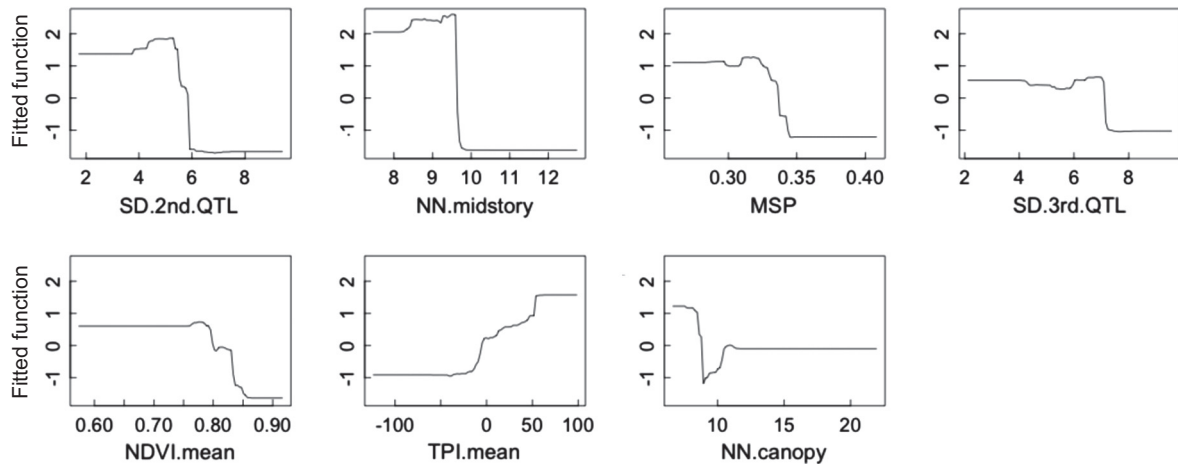


Fig. 5. Partial dependence plots showing the fitted functions for each of the predictor variables retained by the sympatric occurrence BRT model. The graphs show the effect of a particular variable on the response variable: increasing fitted function values indicate that species presence/absence responded positively, decreasing values the opposite. Values on the y-axis are uniformly scaled so that the relative importance of the variables can be visually compared.

of species presence, strongly increased for values below these thresholds. For all other variables except topographic position, the direction of the effect on the response variable was the same, however, less distinctive. The effect of the mean topographic position index is characterized by a more or less gradual increase in the fitted function, which means that species presence was affected positively by increasing values.

4. Discussion

We evaluated a set of direct and indirect variables of forest structure to predict the individual and sympatric occurrence of four bird species with narrow and complementary habitat requirements, thus being indicative of forest structural complexity. The results from the sympatric occurrence model indicate that structurally complex forest landscapes harboring the broad range of structural characteristics required by our target species were predicted with an astonishingly high accuracy. This evidences that we have developed a comprehensive set of forest structural indicators reflecting well-established species-habitat relationships, thus providing new insights into the relationship between forest structural attributes and species richness at the landscape scale. Apart from the high performance of the sympatric occurrence model, the Capercaillie model also performed very well, and showed similar variable group contributions. This suggests that Capercaillie may be a suitable surrogate organism for structurally complex forest habitats, which corresponds well with other studies proposing Capercaillie as a potential umbrella species for the autochthonous montane and subalpine forest species communities (Suter et al., 2002; Pakkala et al., 2003).

4.1. Ecological relevance of predictors

The use of detailed three-dimensional information of forest vegetation directly derived from the LiDAR point cloud allowed us to analyze the relationship between vertical forest structure and species richness, originally described by MacArthur and MacArthur (1961) who proposed the concept of foliage height diversity (FHD) to explain forest bird species diversity. For the interpretation of the predictors used in this study it is important to keep in mind that they were calculated for a spatial reference of 1 km², thus representing between-stand variation patterns rather than single stand characteristics. Small standard deviations in the height quartiles represent forest landscapes with

continuously and evenly distributed vegetation elements along the vertical profile, as it is typical for forests with a relatively sparse canopy cover or old-growth forests subject to periodical small-scale disturbance. Thus, small standard deviations of, e.g. the 2nd and 3rd height quartile represent forests with comparably high light availabilities and rich in vegetation elements in the lower and upper middle strata of the forest, which in turn promote important habitat characteristics of our target species, such as hiding or perching opportunities or a rich ground vegetation. On the other hand, forest landscapes dominated by patterns of vertically homogeneous stands in different development stages and heights, which typically result from intensive stand-level management, will exhibit larger standard deviations of the quartile heights (Fig. 2). Thus, our results correspond well with results from field studies investigating in the relationship between vertical forest structural complexity and habitat quality for Capercaillie (Bollmann et al., 2005), Hazel Grouse (Schäublin and Bollmann, 2011) and Three-toed Woodpecker (Pechacek and d'Oleire-Oltmanns, 2004). However, especially when considering specific species rather than species diversity, it is not vertical structure per se that affect avian habitat, since vertical structure may be an indicator of the presence of critical forage species or the abundance of breeding sites (Helmer et al., 2010; Schäublin and Bollmann, 2011).

While multi-storied forest profiles are one of the most commonly used structural attributes to describe forest stand structure in the field (McElhinny et al., 2005), several studies developed indices of vertical complexity from LiDAR data. Goetz et al. (2007) derived a vertical distribution ratio from waveform LiDAR to explain bird species richness across a variety of guilds, and their LiDAR measurements clearly outperformed habitat variables derived from optical sensors. Clawges et al. (2008) used discrete return LiDAR to calculate several versions of the foliage height diversity index according to MacArthur and MacArthur (1961), and showed that their measurements significantly correlated with bird species diversity. Similar to our quartile-based variables, Lesak et al. (2011) used percentile height and density metrics derived from a LiDAR point cloud to model forest songbird species richness. In line with these previous findings, the index of multi-storied profiles used in this study was identified as an important model parameter. However, the results suggest that generalizing the mean quartile heights over forest landscapes of 1 km² to form a single index entails a loss of ecologically valuable information, such as the variability of the quartile heights.

Spatial patterns of horizontal forest structures, such as edge and gap densities or whether trees are distributed randomly, evenly dispersed or aggregated are considered important features directly affecting wildlife habitat and biodiversity (Lindenmayer and Franklin, 2002). Our results confirm that detailed information of canopy height and spatial patterns thereof, as derived from a digital canopy height model, provides adequate and ecologically meaningful forest structural attributes. Forest edges and small gaps, for example, have been shown to be preferred by Hazel Grouse because the increased light availability at such sites favors light demanding, deciduous resource shrubs and trees, while cover against predators is accessible within short distances (Schäublin and Bollmann, 2011). Pygmy Owls, on the other hand, use edges because they offer perches from which they can search for prey in nearby open habitats (e.g. gaps) but also because edge zones potentially harbor higher densities of passerines and small mammals (Strom and Sonerud, 2001). Further, LiDAR-derived tree edge length was also identified as an important model parameter in a Capercaillie habitat assessment (Graf et al., 2009).

We identified variation of canopy height as a further structural attribute of high quality habitat, as indicated by comparably small nearest neighbor distances between patches of intermediate canopy heights as well as high values of our canopy height heterogeneity metric. Varying canopy heights over relatively small areas are typical for periodically disturbed old-growth mountain forests rich in structure, and have previously been used to explain patterns of riparian bird species occurrence (Seavy et al., 2009) as well as the abundance and assemblages of forest passerines (Müller et al., 2009).

Complementing our LiDAR variable set with topographic site factors and NDVI data improved the predictive power for all five models. However, their relative contribution was considerably higher in the Three-toed Woodpecker model and to a lesser extent also in the Pygmy Owl model. The topographic position in relation to the surrounding terrain affects edaphic characteristics, such as soil temperature, moisture, depth and nutrient status, but also exposure to gravitational disturbances (e.g. snow movements or rock fall) or exposure to wind (Zobel et al., 1976; Kimmins, 2004). Ridges or hill tops, as expressed by high values of the topographic position index, will be exposed to comparably high winds and will in general have dryer, shallower and nutrient poorer soils than sites in sinks, gullies, valleys or toe slopes (Zimmermann and Roberts, 2001). Thus, weakened or dead trees are likely to be more abundant on sites with high index values. Further, trees on equator facing slopes will be exhibited to higher solar radiation and thus warmer soil temperatures and potentially drought stress, making them more susceptible to disturbance agents such as bark beetles that enhance regional forest structural complexity (Wermelinger, 2004). Forests with comparably low NDVI values and thus low vegetation density were favored by all species and particularly improved the Three-toed Woodpecker model, which was further enhanced by spatial variability of the NDVI. This variability was at least partially caused by local disturbance patterns stemming from wind-throws or insect infestations providing important foraging habitats for the Three-toed Woodpecker (Pechacek and d'Oleire-Oltmanns, 2004). In line with White et al. (2012), who modeled coarse woody debris with NDVI after an ice storm, recently disturbed sites with structural legacies such as snags and logs were expected to be temporarily reflected in low NDVI values. Although the forests studied here are dominated by coniferous tree species, larger portions of deciduous canopy tree species (e.g. beech) in lower elevation sites may have increased NDVI values (Van Wagtenonk and Root, 2003). Considering the strong association of Three-toed Woodpeckers to coniferous, especially spruce dominated forests, we assume that mean NDVI values at least partly represented differences in canopy dominance of broadleaf versus coniferous tree species.

4.2. Model generality and precision

The lack of consistent data over large areas is often a major confining factor for the modeling of species and habitat distributions based on predictor variables with direct ecological significance. In consequence, ecologists often use indirect predictors to develop large-scale habitat distribution models. However, the lacking association with direct habitat factors and thus species occurrence may lower the generality of such models (Guisan and Zimmermann, 2000; Graf et al., 2006). We calibrated accurate predictive models mainly based on habitat variables with direct ecological significance and used data from three biogeographically different mountain regions representing a large range of ecological niches realized by the study species. Thus, our results suggest that national LiDAR datasets are highly valuable for optimizing the trade-offs between generality, reality and precision in habitat and species distribution models (Guisan and Zimmermann, 2000), although direct transferability of our models to other European montane and subalpine mountain forests has not been shown due to missing data from outside the calibration range.

Despite the advantages of such datasets, species distribution models strongly depend on the quality and precision of the dependent variable, i.e. the species occurrence data. Our approach involves area-wide species data that incorporate potential sources of uncertainty, e.g. with regard to the precise location of species evidence (i.e. whether the observations allocated to the corresponding 1 km² were located centrally or in the periphery of the cell). This may entail a considerable amount of variability of habitat quality in the presence cells. The effect of this variability on model accuracies may partially be species specific. Capercaillie, for example, has the largest territories of our study species, averaging 550 ha (Storch, 1995). Thus, the surrounding area (and thus the km²-presence cell) where Capercaillie was detected is more likely to constitute suitable habitat, compared to for example Hazel Grouse, who occupy only small territories of 10–40 ha (Bergmann et al., 1996). Apart from the fact that Capercaillie was expected to integrate well due to its narrow habitat requirements in terms of forest structure, this may have added to the comparably high accuracy in the Capercaillie model.

Model prediction accuracies would most likely increase with more precise species data, however, its availability across broad spatial extents is normally restricted. Furthermore, for mobile species such as our target species, area-wide species occurrence data of limited precision, but representatively sampled across multiple regions, may be preferable to precise, systematically sampled data across small extents (Braunisch and Suchant, 2010).

4.3. Limitations, outlook and conclusions

Interpreting variables derived from remote sensing and in particular LiDAR data requires knowledge about the technical background and the assumptions made in the variable extraction process. Different resolutions of interpolated canopy height models, for example, influence the interpretation and may change the explanation strength of variables describing forest structure, such as variability of canopy heights. Canopy height variability measured based on a 0.25 m resolution (sub-tree level), as used by Müller and Brandl (2009) to predict forest beetle assemblages, is associated with the vertical variation of canopy height, whereby a resolution of 3 m (single tree level), as in this study, is more related to the horizontal arrangement of trees or tree groups. This can lead to inconsistencies between different studies and complicates comparison.

Translating remote sensing variables into habitat management recommendations is often difficult and calls for further development. As a starting point, threshold-based variable analysis as

suggested in this study may be a promising way to increase the applicability of such variables in management and monitoring schemes. To enhance forest inventories and account for consistency, it would be desirable to work with LiDAR metrics that correlate well with field-based parameters of forest stand structure. However, such variables may be limited in reflecting observed relationships with faunal diversity, especially on the landscape-level, where important patterns may only emerge from area-wide stand mosaic analysis. Thus, regional forest management aiming at integrating off-reserve conservation planning into multifunctional forestry may especially benefit from innovative possibilities for large-scale assessments of forest structural complexity and habitat quality. To cut costs of repeated LiDAR data acquisition, photogrammetric updates of canopy height models would allow for change detection and could be used to monitor the effects of conservation related forest management practices.

We conclude that the occurrence of bird species with narrow and complementary habitat requirements related to forest structure can accurately be modeled using remote sensing, particularly LiDAR data. However, the accuracy of the models varies considerably depending on the ecology of the target species. Complementing LiDAR with multispectral and topographic data related to vegetation density and exposure to disturbance improved model accuracies, especially for species depending on abundant snags or weakened trees. LiDAR-derived measures of forest structural characteristics and complexity reflected realistic cause-effect relationships across large areas and produced species and habitat distribution models of considerable generality, while keeping a high level of precision. This enables forest managers and conservationists to identify areas of high forest structural complexity and to integrate this information into regional and countrywide management plans.

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