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ORIGINAL RESEARCH

Remotely sensed forest habitat structures improve regional species conservation

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Abstract

Recent studies show that light detection and ranging (LiDAR) derived habitat variables significantly increase the performance and accuracy of species distribution models (SDMs). In particular, the structure of complex habitats such as forest can be accurately parametrized by an area-wide, LiDAR-based vegetation profile. However, evidence of specific applications of such models in real-world conservation management still remains sparse. Here, we developed a resource selection SDM for hazel grouse (*Bonasa bonasia* L.) in a Swiss nature park with the aim to map habitat suitability and to inform the park management about habitat improvement measures. We used remote sensing, particularly LiDAR to derive ecologically relevant forest vegetation characteristics at the local scale and used them as predictors in an ensemble SDM approach. The predicted habitat suitability was mainly affected by local, fine grained vegetation structure. Average vegetation height, shrub density and canopy height variation contributed most to the habitat quality for hazel grouse. This clearly shows how LiDAR provides the means to develop ecologically interpretable predictor variables of forest habitat structure and that these predictors can be used to reliably map local-scale habitat quality, indicated by high model performance scores (median AUC of 0.918). This improves spatial conservation planning, and at the same time, provides meaningful information to derive habitat improvement measures that can be implemented in the field by foresters. Hazel grouse occurrence in the park is restricted to a few highly suitable, disjunct habitat patches. Therefore, conservation management should increase the connectivity of suitable habitat with the aim to stimulate an increase and better exchange of individuals in the regional hazel grouse population. Habitat improvements can be achieved by forestry measures that regularly integrate early successional forest stages into production forests. They should contain stands with a shrub density of around 30% as well as heterogeneous stands in terms of vegetation height.

Introduction

During the last two decades, species distribution models (SDMs) and habitat suitability maps have become an increasingly important tool to understand the ecology and occurrence of species and to support their conservation (Guisan and Thuiller 2005; Guisan et al. 2013). SDMs are used to assess the effects of environmental and land use

changes on species richness and distribution (Zaniewski et al. 2002; Jeschke and Strayer 2008; Braunisch et al. 2014; Vogeler et al. 2014; Breiner et al. 2015), to investigate specific habitat requirements of species (Vierling et al. 2011; Farrell et al. 2013; Zellweger et al. 2013) or as basis for priority site selection in species conservation management (Bässler et al. 2011; Flaherty et al. 2014). A matter of primary interest is the relative importance of ecological

parameters that are the causal, driving factors for a species distribution (Guisan and Zimmermann 2000). It depends on habitat availability that is driven by different habitat characteristics at multiple spatial extents and grains (Meyer and Thuiller 2006). Coarse environmental factors (e.g. climate, macro-topography) are important predictors of species distribution at the landscape scale (Franklin 2009). They show a good correlation with observed species distributions but have often no direct physiological relevance for a species' performance (Guisan and Zimmermann 2000). Hence, the relative importance of coarse environment factors remain controversial at smaller scales (Field et al. 2009), in particular for mobile species. At the small scale, species distributions are likely driven by local, fine-grained habitat conditions (Farrell et al. 2013) such as vegetation composition and structure (Zellweger et al. 2016). They provide nutrition and cover, and therefore control the regional and local distribution of a species (Franklin 2009). Especially in forest-dominated landscapes, animal species largely depend on the distribution, composition and abundance of vegetation elements (MacArthur and MacArthur 1961; Davies and Asner 2014). Vegetation elements such as trees, shrubs and logs and their spatial arrangement and heterogeneity are directly associated with the diversity and availability of resources, shelter, as well as breeding and hiding sites which constitute a large variety of ecological niches (MacArthur and MacArthur 1961; Stein et al. 2014). Composition refers to the identity of plant species and their proportion and variability in a certain area (Franklin 2009). Hence, fine-grained three-dimensional (3D) vegetation data are considered to be good resource based predictors for assessing habitats of forest animal species (Davies and Asner 2014).

Recent developments in remote sensing technologies, particular in light detection and ranging (LiDAR), facilitate the accurate quantification and contiguous measurement of the 3D habitat structure from fine-scaled plots to entire landscapes (Vierling et al. 2008; Davies and Asner 2014; Zellweger et al. 2014). Based on single tree crowns, LiDAR is able to quantify small scaled alterations in forest characteristics caused by site effects or natural and anthropogenic disturbances (Davies and Asner 2014). LiDAR has thus spurred interest in modelling habitat suitability for forest species (Ackers et al. 2015) and provides an excellent opportunity to assess how species are affected by vegetation structure (Davies and Asner 2014; Zellweger et al. 2014). LiDAR offers the opportunity to develop resource selection habitat models at local and regional scales (Zellweger et al. 2014). Moreover, LiDAR-based habitat variables of 3D forest structure represent gradients of biotic habitat characteristics which are shaped by forest management (Hyyppä et al. 2008). The growing availability of detailed information of vegetation structure

and its relationship to habitat quality supports evidence-based decisions in conservation and an improved integration of biodiversity conservation in forest planning (Bergen et al. 2009; Zellweger et al. 2014, 2016).

The hazel grouse is a small, sedentary forest grouse that strongly depends on multi-layered forests with structurally diverse stands (Bergmann et al. 1996; Maumary et al. 2007). The species inhabits territories ranging from 10 to 20 ha in coniferous and mixed deciduous forests in the Eurasian boreal forest and in mountain forests of Central and Eastern Europe (Bergmann et al. 1996; Maumary et al. 2007). Used forest stands are partly composed by early succession stages with pioneer plant communities. Pioneer woody plants with butts and catkins are the most important food components of hazel grouse in the winter habitat. A rich and diverse composed shrub layer complies with the species requirement for nutritious and well digestible food. Beside, interspersed dense, coniferous stands reduce the probability of depredation by forest-dwelling raptors and carnivores (Wiesner et al. 1977; Bergmann et al. 1996).

Hazel grouse is listed as a priority breeding bird species for conservation action plans in Switzerland because of its Red List status (NT) and the relative high species abundance in relation to the international situation (Keller et al. 2010). Between 1970 and 1990, a strong decline and range contraction of hazel grouse occurred in Central Europe (Bergmann et al. 1996). Regional populations decreased between 20 and 50% (Maumary et al. 2007). Changes in silvicultural practices caused landscape modification and habitat fragmentation which are considered to be the main factors for the population decline (Bergmann et al. 1996). In the 18th and 19th centuries, silvicultural practices such as planting of conifers, extensive livestock grazing and small-scaled stand harvesting (Kirby and Watkins 2015) have improved habitat conditions for hazel grouse (Bergmann et al. 1996; Blattner 1998; Storch 2007). These anthropogenic modifications of forest ecosystems had important long-term impacts on the vegetation (Gimmi et al. 2008) and often produced structurally diverse and multi-layered forests (Montadert and Leonard 2003). Later, in the second half of the 20th century, forest conversion often resulted in uniform, structurally poor stands (Storch 2007; Savill 2015) that are dominated by uniform single layered high forests with a lack of young successional stages (Bollmann et al. 2009; Savill 2015). In Switzerland, hazel grouse is nowadays restricted to mountain forests in the Alps and partly in the Jura mountains (Maumary et al. 2007). There, the heterogeneous topography causes small-scale changes in site conditions and forest structural complexity (Čada et al. 2016) and thus, is considered to have a high landscape potential as hazel grouse habitat.

To inform the park management about appropriate, spatially explicit species conservation measures, we

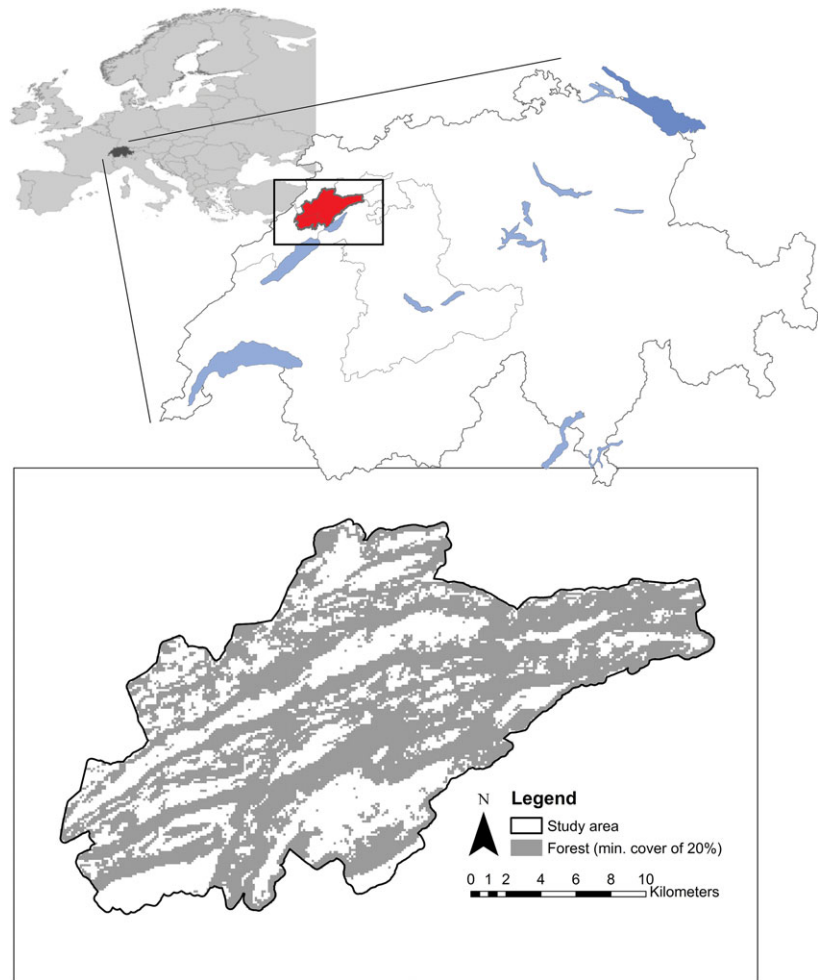


Figure 1. Location of the *Parc régional Chasseral* in Switzerland. The park is located in the Jura mountains of the Cantons of Bern (BE) and Neuchâtel (NE). ©Netzwerke Schweizer Pärke 01/2012 EB - Swisstopo 5704002947.

developed a resource selection SDM for the hazel grouse in the *Parc régional Chasseral*. Our objectives were to (1) derive biotic variables from remote sensing, especially LiDAR datasets, to assess the importance of specific forest vegetation parameters for the distribution of hazel grouse at the local scale, and (2) to spatially evaluate forests in term of habitat suitability at the landscape scale for evidence-based priority site selection and active forest habitat management.

Materials and Methods

Study area

We used the *Parc régional Chasseral* as study area with an additional buffer zone of 250 m to reduce edge effect on predictive variables along the border. The park is located in the Jura mountains in the north-western part of Switzerland (47°8'N, 7°3'E) and covers an area of 387 km² (Fig. 1). The elevation ranges from 429 m to 1607 m a.s.l.

at the top of the Chasseral, a mountain chain in the center of the park (Association Parc régional Chasseral 2015). The oceanic climate provides a mean annual precipitation of 1289 mm (peaks in summer and winter) and a mean annual temperature of 6.3°C with a maximum of 15.1°C in July and a minimum of −1.4°C in January (MeteoSchweiz 2016). The landscape is characterized by parallel mountain chains and a mosaic of forests, pastures, farmlands and settlements. Forests are clustered as three forest belts in east-west direction. Historically, the natural timberline has been pushed down through pastoralism on the gentle areas in the higher zones of the mountain chains. Forest composition changes from predominantly deciduous forest in low areas to coniferous dominated forest at higher elevations (Zbinden 1979).

Species data

We used 212 species presence points provided by the park authorities and the Swiss Ornithological Institute from the

Table 1. Environmental predictor variables for developing the resource selection SDM for the hazel grouse in the *Parc régional Chasseral*. We analyzed the species-habitat relationship at a grain size of 125 m. Some variables were processed with higher resolution (pixel size listed in brackets) and thereafter up-scaled for the data analysis and modelling process. In the last column, the expected relationship between the predictor variable and the habitat suitability for hazel grouse derived from literature is given as: positive, positive linear relationship; unimodal, unimodal relationship; cat. 3, peak at conifer-dominated mixed forest.

Variable name	Description	Unit	Resolution [m]	Source	Expected relationship
Average vegetation height	Average height of all vegetation return heights above 0.5 m	m	125	LiDAR	Unimodal
Canopy height variation	Standard deviation of canopy heights based on the 90th height percentile (see text for details)	m	125 (5)	LiDAR	Positive
Shrub density	Number of vegetation height below 5 m divided by the total number of all returns, including terrain points (Morsdorf et al. 2006)	%	125	LiDAR	Unimodal
Sum of small gaps	Sum of squares with a canopy height below 1.3 m, based on the 90th height percentile (see text for details)	Count	125 (5)	LiDAR	Unimodal
Length of forest edges	Boundary length between forest, shrub forest, open forest to non-forest (see text for details)	m	125	Swisstopo	Positive
Forest type	Classification of forest stands in four categories:(1) deciduous forest, (2) deciduous-dominated mixed forest, (3) conifer-dominated mixed forest, and (4) conifer forest (see text for details)	Category	125 (25)	Landsat	cat.3

time period between autumn 2011 and spring 2015. Presence data from the park were derived from a multi-year field survey, launched 2013 by the park management. To reduce the workload for the field survey, clusters of four aggregated grid cells (250×250 m each) were visually classified with aerial photographs according to their habitat suitability potential for hazel grouse. Grid cells with low percentage of forests (<20%) or high proportion of cliffs/settlements were excluded. 50 out of 83 clusters were randomly chosen and surveyed for species presence in the winter. Because this field survey covered only those parts of the park with moderate to good habitat suitability and only winter data, we complemented our species data with presence data from the Swiss Ornithological Institute ($N = 2$). We considered only species presence data that were recorded during the months of December to August, thus excluding the period of juvenile dispersal (Bergmann et al. 1996).

Predictor variables and expected relationships

We developed six forest predictor variables that were considered to influence the local-scale habitat conditions and thus, the habitat use of hazel grouse (Table 1). The variable length of forest edges represents the length of forest boundary (m) between forest and non-forest cover based on a forest cover GIS dataset provided by swisstopo (Zellweger et al. 2013; swisstopo 2014). An increasing length is expected to increase hazel grouse

suitability due to the promotion of light demanding trees next to hiding options of dense forest stands. The variable forest type was derived from satellite images (Landsat-5, Thematic Mapper, WMG25, BFS GEOSTAT) by an automated maximum likelihood classification (Burkhalter and Sager 2003). Forest type had at a resolution of 25 m (pixel extent). It was classified in four categories: (1) deciduous forest, (2) deciduous-dominated mixed forest, (3) conifer-dominated mixed forest, and (4) conifer forest, whereas conifer-dominated forests is assumed to suit best for hazel grouse (Bergmann et al. 1996). Graf et al. (2005) confirmed the high accuracy of this classification.

The LiDAR variables were derived from discrete multiple return airborne LiDAR data recorded between May 2010 and April 2011, during leaf-off conditions. They originate from two flight missions with two different sensors (Leica Scanner ALS60, Optech Gemini 166 KHz) due to the fact that the study area included two different political and administrative areas (cantons). The minimum point density was 4 points/m² (echo) with a minimum vertical and horizontal accuracy $\leq \pm 0.3$ m and $\leq \pm 1.0$ m, respectively (Système d'information du territoire neuchâtelois 2010, Amt für Wald des Kantons Bern 2013). The raw point cloud data was pre-processed using a suite of *LAStools* algorithms (Isenburg 2014) to derive the normalized vegetation heights above ground. We used the *LAScanopy* tool to calculate average vegetation height, canopy height and a proxy for shrub density (see below) based on grids with a 5 m pixel size. We used the 5 m

grids, which approximates a single-tree crown projection, to integrate fine-scale variability of the heterogeneous forest characteristics and to increase the accuracy of the forest/non-forest classification. To this end we aggregated each 5 m grid to a 125 m grid by using either the mean or standard deviation as described below. The aggregation at a raster of 125 m was chosen because small harvesting interventions of approx. 1 ha are wide spread in the Swiss high montane and sup-alpine forests, including the *Parc régional Chasseral*. We only considered 5 m pixels that were covered by forest, as derived from the forest cover dataset mentioned above, and considered all vegetation return heights between 0.5 and 55 m to reduce biases from potentially misclassified points.

We used the average vegetation height to represent the successional stage (see Müller and Brandl 2009), assuming a positive effect of early successional stages due to hazel grouse's preference toward young forest stages (Bergmann et al. 1996; Mathys et al. 2006; Schäublin and Bollmann 2011). The effect of average vegetation height on hazel grouse occurrence should thus show an optimum at low to medium values. Canopy height variation was defined as the standard deviation of the 90th percentile of the vegetation return heights (Zellweger et al. 2016) and represents important aspects of the physiognomy of the vegetation indicating the horizontal structural heterogeneity (Falkowski et al. 2009). Hazel grouse is linked to structurally diverse forests and avoids single layered forest stands (Mathys et al. 2006; Müller et al. 2009a; Bässler et al. 2011). We thus expect a positive linear relationship between hazel grouse occurrence and canopy height variation. Shrub layer and its composition are key factors influencing habitat suitability for hazel grouse, for example, by providing food resources and cover from predators (Sachot et al. 2003; Mathys et al. 2006; Müller et al. 2009b; Schäublin and Bollmann 2011; Zellweger et al. 2014). Therefore, an intermediate shrub cover is assumed to support hazel grouse territories best. We calculated a proxy for shrub density by using the ratio of vegetation heights between 0.5 and 5 m divided by the total number of all vegetation heights. Forest gaps were reported in many studies as an important predictor of hazel grouse occurrence (Saari et al. 1998; Mulhauser 2003; Sachot et al. 2003; Müller et al. 2009b) as an intermediate number of gaps within a single cell should provide feeding options next to hiding places and thus supports hazel grouse habitat. Using the 90th percentile of the vegetation return heights, a gap was defined as a 5 m reference pixel with a maximum canopy height of 1.3 m. The height cutoff of 1.3 m allowed for examining the lowest layers of forest stands which include important food resources like berry bushes (Mulhauser 2003).

Presence – pseudo-absence approach

We predicted the habitat suitability of hazel grouse using a presence–pseudo-absence data approach (Guisan and Zimmermann 2000; Araújo and Guisan 2006; Soberón 2007). Cells were defined as 'presence' if they contained at least one hazel grouse record, as described above. We used 10 000 randomly selected background cells as pseudo-absence data and weighted them in the way that the weighted sum of presence equals the weighted sum of absences (Barbet-Massin et al. 2012). Pseudo-absences were defined as cells with no reported species evidence between winter 2011 and winter 2015 and assumed to be locations which could potentially be reached, occupied and used by hazel grouse.

Ensemble modelling and statistical analyses

We analyzed the species-habitat relationship of hazel grouse by using a cell size of 125 m. A raster with 125 m cell size represents an optimal trade-off between representing a substantial part of hazel grouse territory and a level of detail required for a proactive stand-level forest and conservation management. Only grid cells which have a minimum forest proportion of 20% were considered for modelling.

We calculated an ensemble prediction using seven standard species distribution model algorithms. To consider model variability, to reduce uncertainty of different modelling algorithms and to improve reliability of the model predictions, we averaged the outcomes of the single modelling algorithm weighted by the area under the receiver operating characteristic curve (AUC) (see Segurado and Araujo 2004; Araújo and New 2007; Elith and Graham 2009; Buisson et al. 2010; Jones-Farrand et al. 2011; Breiner et al. 2015). We fitted the ensemble prediction with generalized linear models (GLMs), generalized boosted models (GBMs), maximum entropy (MAXENT), artificial neural network (ANN), flexible discriminant analysis (FDA), multiple adaptive regression splines (MARS) and random forest (RF). Various parameter values were tuned for the single algorithms (e.g. feature types for MAXENT) by keeping the parameters with the best cross-validated model performance in terms of AUC. To tune and calibrate the models of the individual modelling algorithms and to generate the ensemble prediction of habitat suitability, we used the R package *BIOMOD2* (version 3.3-3/r713) (Thuiller et al. 2015).

The predictive performance of the ensemble models was assessed using a 5-fold cross-validation procedure with 10 repetitions. Model accuracy was evaluated based on the Area under the Curve (AUC) (Fielding and Bell

1997), True Skill Statistic (TSS) (Allouche et al. 2006) and the Continuous Boyce Index (CBI) (Boyce et al. 2002; Hirzel et al. 2006). To evaluate the contributions of the individual predictors, we calculated the relative importance of each predictor based on a variable randomization procedure as implemented in BIOMOD (Thuiller et al. 2009) and calculated the response curves to infer the direction and shape of the predictor effect on hazel grouse habitat suitability (Elith et al. 2005; Thuiller et al. 2009).

Results

Model performance and predictor contribution

The predictive performance of the ensemble model was outstanding for the three evaluation indices. The cross-validated median AUC, TSS and CBI values were 0.92, 0.73 and 0.84, respectively (Fig. 2).

Average vegetation height was the most important predictor for habitat suitability, followed by shrub density and canopy height variation (Table 2). All three predictors were derived from LiDAR. The length of forest edges reached a similar predictor contribution as canopy height

Table 2. Median predictor contribution of the ensemble model for the hazel grouse in the *Parc régional Chasseral*.

Median predictor contribution	Value
Average vegetation height	0.502
Canopy height variation	0.264
Shrub density	0.338
Sum of small gaps	0.062
Length of forest edges	0.212
Forest type	0.120

variation. Forest type was the second least important predictor with a contribution less than half of that of canopy height variation. The sum of small gaps made a small contribution to the SDM.

Predictor response curves

Average vegetation height and shrub density both showed unimodal responses, with optima from 5 to 10 m and 30%, respectively (Fig. 3). Canopy height variation had an optimum at values around 4 m. However, the unimodal response curve was less evident compared to average vegetation height or shrub density. The expected positive linear relationship between length of forest edges

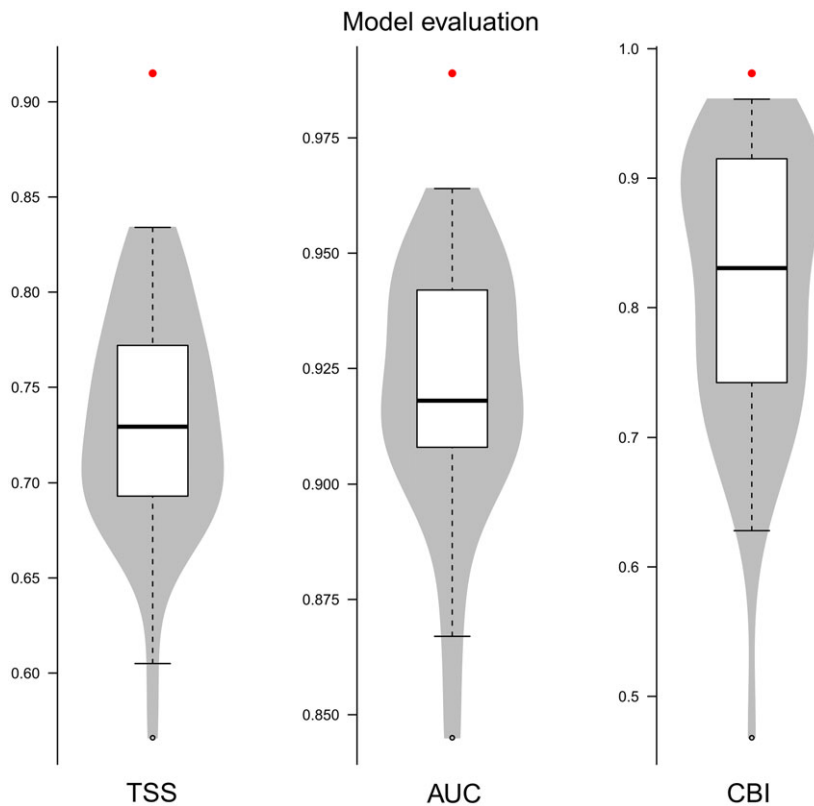


Figure 2. Violin boxplot for model evaluation. The plot is combining boxplot information with information from kernel density estimation (grey shade). The model evaluation is based on 10 times repeated 5-fold cross-validation for three different evaluation scores. Red points indicate the evaluation scores of not cross-validated models using the entire data for calibration and evaluation. TSS, true skill statistic; AUC, area under the curve; CBI, continuous boyce index.

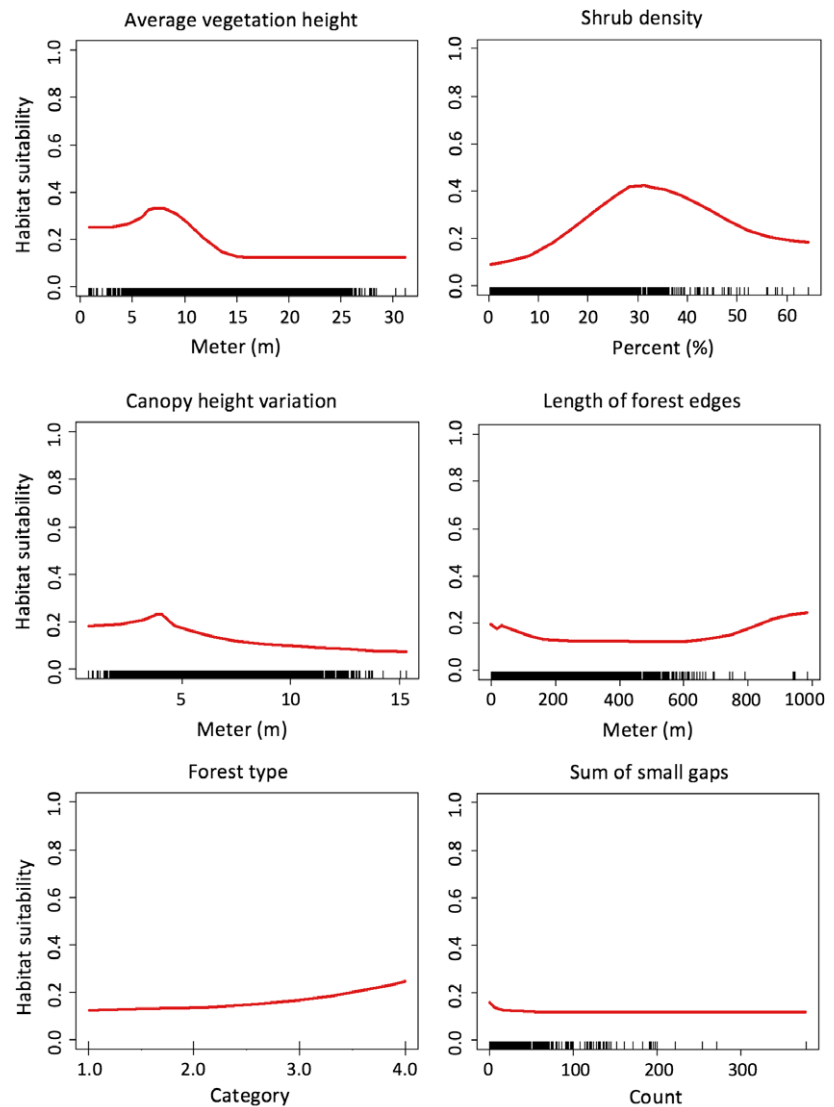


Figure 3. Response curves of the six predictor variables used in the ensemble model: increasing values on the y-axis indicate that the probability of hazel grouse presence responded positively, decreasing values the opposite. The x-axis shows the data range of predictor variable measurements in the study area.

and the expected unimodal relationship of sum of small gaps with hazel grouse habitat suitability was not found. Forest type increased habitat suitability toward rising proportions of conifer trees. However, the expected optimum at conifer-dominated forests (i.e. category 3) was not found.

Habitat suitability map

Habitat suitability was predicted in a range from 0 (no suitable habitat) to 1 (very suitable habitat). Less than 5% of cells were predicted with suitability values higher than 0.6. Most of them were aggregated to habitat patches distributed across most regions of the park (Fig. 4). The two largest patches with highly suitable cells were located in the western part of the park and along the upper tree line

on the southern slope of the Chasseral mountain chain in the center of the park. Beside other small patches with high suitability, the main part of the park was predicted to be less suitable.

Discussion

Remote sensing and biotic variables

Our SDM was based exclusively on remotely sensed biotic variables describing forest characteristics. The outstanding predictive power of the model indicates that remote sensing is a valuable tool to derive habitat parameters for forest species at the local scale which confirms recent findings (Tattoni et al. 2012; Holbrook et al. 2015; Dymytrva et al. 2016). Moreover, the expected effects of the most important

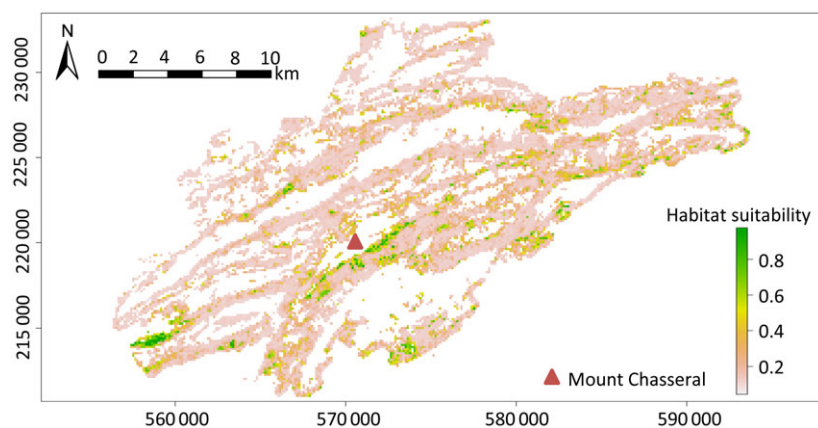


Figure 4. Predicted habitat suitability in the Parc régional Chasseral illustrated with values from 0 to 1. Cells with green or greenish colors implied areas with high suitability for hazel grouse. Intermediate habitat suitability is indicated in yellow and areas with low suitability in reddish. The x- and y-axis represent the coordinate system (CH1903_LV03).

predictors, that is, average vegetation height and shrub density, on the habitat suitability and the results match perfectly. This clearly shows how we can use LiDAR to derive ecologically meaningful variables of forest habitat structure. The fact that the models' outstanding predictive power is solely based on biotic vegetation variables implies that small scale habitat suitability is driven by local, fine-grained vegetation conditions (Farrell et al. 2013; Zellweger et al. 2016). Especially for habitat specialists, such as hazel grouse, that depend on small-scaled habitat features and are sensitive to anthropogenic land-use change, the distribution and abundance of habitat within the overall distribution range tend to be strongly influenced by fine grained habitat metrics (Meyer and Thuiller 2006; Gottschalk et al. 2011; Farrell et al. 2013).

Habitat structure and hazel grouse occurrence

Our results confirm the importance of forest structure and composition in influencing habitat suitability for forest species in general. We focused on biotic metrics that had a clear foundation in hazel grouse ecology at the local scale and hypothesized the relationship of each variable on the habitat. Our study demonstrates that habitat suitability of hazel grouse is strongly controlled by small scaled forest structure, such as average vegetation height and shrub cover. Vegetation height and its variability are widely used predictors for LiDAR based habitat assessments of forest-dwelling species (Goetz et al. 2007; Davies and Asner 2014; Zellweger et al. 2014) and have also been considered in previous studies to be key habitat elements for hazel grouse (Mathys et al. 2006; Bae et al. 2014). The combination of an optimum vegetation height from 5 to 10 m with moderate deviations in canopy height may represent forests in early successional stages with a slight growth variability. Vertically well-structured forests provide short escape distances between different vegetation

layers and support the hazel grouse's escape behavior from predators (Wiesner et al. 1977; Bergmann et al. 1996). As a distinctive food specialist, hazel grouse is known to depend on buds and catkins of soft-wood species in early successional stages (Bergmann et al. 1996). Therefore, the optimum of around 30% shrub density as the second most important predictor confirms the species requirements for a relatively dense understorey (Sachot et al. 2003; Melin et al. 2016) in both, primeval and in extensively used forests (Wiesner et al. 1977). However, LiDAR is not able to directly identify the species composition in the understorey (Bergen et al. 2009; Yao et al. 2012). Measurements of shrub density with LiDAR-derived predictors cannot distinguish between a shrub layer that is composed of preferred food-plant species or of rejuvenation of other tree species, such as beech (*Fagus sylvatica*). This differentiation is essential for hazel grouse in mountain areas where the incidence of specific food plants tend to be a crucial factor for hazel grouse occurrence (Müller et al. 2009b; Schäublin and Bollmann 2011). The relatively small predictor contributions of length of forest edges, forest type and sum of small gaps indicate that forest horizontal composition tends to be less important for habitat suitability of hazel grouse than aspects of the vertical forest structure. Our conceptual approach to model habitat suitability with a cell approach based on high resolution reference pixels without considering habitat relationships to neighboring cells may have reduced the influence of horizontal forest composition. Therefore, using focal explanatory predictors of forest composition that integrate proximity information of these variables might have improved their contribution to the model (Guisan and Thuiller 2005).

Management implication

Despite a surge in the development of SDMs in this decade and growing model performances based on remote

sensing techniques (He et al. 2015), evidence of the application of these models in real-world conservation management remains sparse (Guisan et al. 2013). Habitat management should be targeted towards cells with high habitat suitability and hazel grouse occurrence to prevent a decline in the regional hazel grouse population. Occurrence cells with low habitat suitability may constitute degraded habitat where the species still persists but does not reproduce (Fischer and Lindenmayer 2007). Our use of fine-grained habitat predictors promote the decision making at the grid scale. Moreover, the biotic variables directly integrate the impact of human land use and habitat management (Hyyppä et al. 2008).

The two largest habitat patches with high suitability located in the western part of the Park perimeter and along the southern slope of the Chasseral mountain chain are the core areas of hazel grouse occurrence within the park. Their habitat should be preserved or restored. The two best suitable patches are completely segregated. As hazel grouse is considered to be sensitive to habitat fragmentation (Rueda et al. 2013), the conservation management should improve the connectivity of these patches by creating stepping stones between. Besides, the park management should increase the total area of suitable habitat in the vicinity of patches and stepping stones such as to provide space for new territories. Structural restoration of less suitable stands comprise measures that promote early successional stages with a shrub density of around 30% and a slight growth variability within the stand. Such stands can be achieved by adequate forestry practices aiming at structurally diverse forest stands with mixed stages of development or by forest browsing by livestock. In former times and partly still today, the core patches were part of summer pastoralism in the higher area (Grossmann 1927; Zbinden 1979; A. Gerber personal communication, March 2016). We suggest that the long-term impact of this practice on forest characteristics is responsible for the highest density of species occurrence in the core patches. Grazing in forests causes a heterogeneous mosaic of ground and shrub vegetation with a higher percentage of early succession pioneer plant communities compared to ungrazed production forests with more dense and uniform stands (Montadert and Leonard 2003; Mayer and Stöckli 2005). Hence, we support an extensive and temporally restricted forest pasture as an alternative to silvicultural measures that aim to improve habitat suitability for hazel grouse by transforming single-layered high forests to multi-storied stands with a well-developed ground and shrub cover which provide important food resources for hazel grouse. Independent of the methodological approach, successful management depends on sufficiently large areas with viable populations that produce enough

emigrants that can colonize nearby suitable habitat patches (Thomas and Kunin 1999).

Conclusion

We show that regional species conservation can substantially benefit from modelling habitat preferences using the growing availability of airborne LiDAR datasets. LiDAR provides the means to develop ecologically interpretable predictor variables of forest habitat structure and allows for high-fidelity mapping of local-scale habitat quality. It thus facilitates spatial planning and priority setting. LiDAR variable based results can be used to derive habitat improvement measures that are meaningful to forest managers who can directly implement them in the field.

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