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Habitat assessment for forest dwelling species using LiDAR remote sensing: Capercaillie in the Alps

Roland F. Graf a,b,*, Lukas Mathys c,d, Kurt Bollmann c

- ^a ZHAW Zurich University of Applied Sciences, Unit Wildlife- and Landscape Management, Postfach, CH-8820 Wädenswil, Switzerland
- ^b UFZ Helmholtz Centre for Environmental Research, Department of Ecological Modelling, Permoserstrasse 15, D–04318 Leipzig, Germany
- ^c Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

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ABSTRACT

Large-scale information on habitat suitability is indispensable for planning management actions to further endangered species with large-spatial requirements. So far, remote sensing based habitat variables mostly included environmental and land cover data derived from passive sensors, but lacked information on vegetation structure. This is a serious constraint for the management of endangered species with specific structural requirements. Light detection and ranging (LiDAR), in contrast to passive remote sensing techniques, may bridge this gap in structural information at the landscape scale. We investigated the potential of LiDAR data to quantify habitat suitability for capercaillie (Tetrao urogallus), an endangered forest grouse in Central Europe, in a forest reserve of 17.7 km². We used continuous variables of horizontal and vertical stand structure from first and last pulse LiDAR data and presenceabsence information from field work to model habitat suitability with generalized linear models (GLM). The two final habitat suitability models explained the observed presence-absence pattern moderately well (AUC of 0.71 and 0.77) with horizontal structure explaining better than vertical structure. Relative tree canopy cover was the most important variable with intermediate values indicating highest habitat suitability. As such, LiDAR allowed us to translate the results from habitat modeling at the landscape scale to effective management recommendations at the local scale at a level of detail that hitherto was unavailable for large areas. LiDAR thus enabled us to integrate individual habitat preferences at the scale of entire populations and thus offers great potential for effective habitat monitoring and management of endangered species.

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1. Introduction

The knowledge of habitat requirements and distributions of endangered species is a primary prerequisite for conserving biodiversity (Rushton et al., 2004). Species distribution models relate the spatial distribution of a species to its present environment and have become a widespread tool in conservation biology (Guisan and Zimmermann, 2000). They are often used to predict species distributions over large areas (landscape, region, continent) and are well-suited for identifying priority areas in large-scale conservation concepts (e.g., Mladenoff and Sickley, 1998; Corsi et al., 1999; Graf et al., 2004; Braunisch and Suchant, 2007). However, more detailed

E-mail address: roland.graf@alumni.ethz.ch (R.F. Graf).

information about the habitat suitability within priority areas are generally needed to define the sites, timing and type of required management actions. From this arises a common dilemma in analyses of habitat requirements and species distributions: models should ideally be realistic, precise and general at the same time (Guisan and Zimmermann, 2000) making them valid for application outside the area where they were calibrated. These requirements are best met if habitat suitability models predict the species' occurrence with the factors that causally describe its habitat use (Boyce et al., 2007; Guisan and Zimmermann, 2000). However, such direct explanatory variables are often not available consistently over large areas relevant for entire animal populations (Karl et al., 1999). Remote sensing may thus hold the key in habitat modeling to bridge the gap between precision, generality and reality.

Remote sensing techniques are indispensable for assessing habitats consistently over large areas. So far, mainly passive sensors were used to assess habitats from local to regional, continental and global scales (Verner et al., 1986; Turner et al.,

^d Sigmaplan, Thunstrasse 91, CH-3006 Bern, Switzerland

^{*} Corresponding author at: ZHAW Zurich University of Applied Sciences, Unit Wildlife- and Landscape Management, Postfach, CH-8820 Wädenswil, Switzerland. Tel.: +41 58 934 55 78.

2003). But, habitat data derived from passive sensors are based on spectral characteristics of the target objects and thus lack information on structure. This shortcoming in structural habitat information is particularly critical in forest ecosystems, where many species depend on structural characteristics of forest stands (Degraaf et al., 1998). LiDAR data, in contrast to passive remote sensing techniques and SAR/InSAR, is rich in three-dimensional structural information at appropriate spatial scales (Hyde et al., 2006) that may bridge the gap between local precision and reality, and landscape generality. LiDAR has been used to quantify structural properties of the forest ecosystem (Næsset, 2002; Lefsky et al., 2002; Zimble et al., 2003; Riaño et al., 2003), as well as to describe relationships between birds and forest characteristics (Hinsley et al., 2002; Hill et al., 2004; Bradbury et al., 2005; Goetz et al., 2007). Effective habitat management needs to differentiate spatially with respect to structural variables to address appropriate habitat aspects and initiate relevant management actions.

Capercaillie (Tetrao urogallus, Tetraonidae, Aves) is an endangered forest grouse in Central Europe that indicates for both structural diversity of its habitat and the associated species community (Suter et al., 2002; Pakkala et al., 2003). The species mainly occurs in conifer or conifer-dominated mixed stands (Klaus et al., 1986; Sachot et al., 2003). Important habitat features are intermediate canopy cover (e.g., Gjerde, 1991; Suchant, 2002; Sachot et al., 2003) and rich ground vegetation cover (e.g., Schroth, 1992; Bollmann et al., 2005) ideally dominated with bilberry (Storch, 1993). Capercaillie combines these specific habitat preferences with large-spatial requirements (average size of home range 5.5 km²; Storch, 1995) making it highly susceptible to landscape and forest structure changes. Over the past decades. capercaillie populations have declined seriously in Central Europe and the occupied range has contracted (Storch, 2000; Mollet et al., 2003). Habitat loss and degradation, increased predation pressure, disturbance by humans and climate change probably are the main reasons for the species' decline (e.g., Klaus, 1991; Storch, 2000). Conservation measures to halt the overall decline of capercaillie have rarely succeeded, probably because they were local in scope and neglected population processes operating at the landscape scale (Storch, 2002; Graf et al., 2007). Therefore, a reliable measure of present habitat suitability for large areas would help substantially to effectively manage capercaillie habitat at the relevant scale of entire populations.

The main aim of this paper was to evaluate the potential of LiDAR data to quantify habitat suitability for capercaillie at the scale of entire populations. Our objectives were (1) to develop habitat suitability models based on LiDAR and species presenceabsence data for a forest reserve in north-eastern Switzerland, (2) to identify areas that deviate from optimal habitat conditions thus where actions for habitat improvement should be considered and (3) to evaluate the potential of our method to monitor habitat suitability for capercaillie on large areas with relatively low effort.

2. Methods

2.1. Study area and design

This study was conducted in the Swiss Pre-Alps (47°8′N, 9°12′E) in the canton of St. Gall (Fig. 1). The study area comprises 17.7 km² of an extensively managed cultural landscape. It is dominated by forests (55%), mires (16%), and alpine pastures and rocky area (29%; Ehrbar, 2006a). The study area was declared as a Special Forest Reserve in 2006 with the goal to conserve the local capercaillie population by an adapted forest management (Ehrbar, 2006b). Before, an extensive forest management with selective single or group wise tree cutting was the general harvesting type. The forest reserve is situated in the higher montane and subalpine zone between 1050 m and 1800 m a.s.l. Nine forest types have been delineated in the forest reserve. The Adenostylo alliariae-Abieti-Fagetum typicum and the Vaccinio myrtilli-Abieti-Piceetum sphagnetosum are the two most abundant (Ehrbar, 2006a). In general, forest stands are dominated by Common beech (Fagus sylvatica) in the lower and Norway spruce (Picea abies) and Silver fir (Abies alba) in the higher areas.

In previous analyses, Graf et al. (2005) investigated the distribution of capercaillie at the scale of the entire country using predictive habitat suitability models. These raster-based models included no variables on present forest structure and composition and thus identified only potentially suitable capercaillie habitat. Yet, the habitat suitability models showed large potential for capercaillie in our study area with a mean probability of capercaillie occurrence

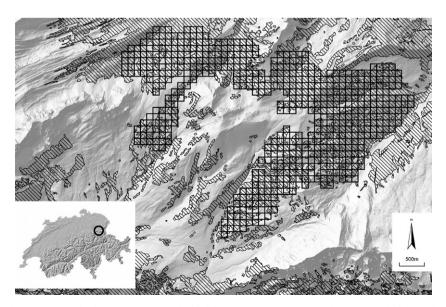


Fig. 1. Study area located in northeastern Switzerland (circle center in embedded figure) where we investigated the potential of LiDAR data to improve habitat suitability prediction for capercaillie. Modeled grid cells and forest distribution (hatched areas) are superimposed on the hillshaded DTM (Vector25-Forest, DTM-AV © 2006 swisstopo DV033492).

of 0.87 and the majority of the cells with values higher than 0.5 (97.1%) and 0.8 (77.1%). The country-wide models among other data sources have been used to define the borders of the Forest Reserve of Amden (Ehrbar, 2006a), i.e. the study area investigated here.

2.2. Species data

The study area includes the habitat of one of the most important capercaillie populations of Switzerland in the north-eastern Pre-Alps (Bollmann, 2006). 20-25 adult males are estimated to live in the area (Jacob et al., submitted for publication). The large majority of presence-absence data stem from a systematic grid sampling that took place twice in April/May and July/August 2006 during the lekking and late breeding period (Imhof, 2007). During the surveys, all indirect (faeces, traces, feathers) and direct (observations) evidence of capercaillie were assessed. This is a standard method to assess presence-absence of woodland grouse species (Sachot et al., 2003; Storch, 2002). The observers were trained before they started the survey to guarantee for a high level of detection and standardization. They assessed species presence data in grid cells of $125 \text{ m} \times 125 \text{ m}$ (N = 589). The area of a cell represents the average area of a forest stand in the study area. We defined the status of a cell as "presence" if we had at least one record of the species otherwise we set the status as "absence". We complemented the presence data set with a database from the forest service (unpublished data) that consists of random observations of the species presence since 1990. This resulted in a total number of presence cells of 227, i.e. 38.5% of the study area.

2.3. Explanatory variables

Raw LiDAR terrain and surface point data (DTM/DSM-AV © 2008 swisstopo DV033492) was acquired through TerraPoint ALTMS 2536 at an average flight height of ca. 1000 m above ground. Average spatial point density in both datasets was 1 point for 2 m² at a nominal footprint of 1.2 m as reported by the data provider. Also, standard deviation of height was lower than 0.5 m for terrain points and between 0.5 m (open land) and 1.5 m (vegetated land) for surface points. Raw terrain and surface height points were then converted to a triangulated irregular network and linearly interpolated to produce a gridded terrain, DTM, and surface model, DSM, with a cell size of 2.5 m. Based on the height difference between DSM and DTM a normalized digital surface model, NDSM, was created. The NDSM contained the surface height of all objects in the study area, i.e. trees and houses. To create a tree canopy height model, TCHM, we defined a tree as woody vegetation \geq 3 m. We thus recoded all cells of the NDSM to the normalized height for cells ≥ 3 m, but not of infrastructure (as known from the infrastructure layer of Vector25 © 2008 swisstopo DV033492).

Structural tree canopy variables relevant to capercaillie habitat requirements (Table 1) were derived from aggregated height information based on the TCHM applying a moving window of $125 \, \text{m} \times 125 \, \text{m}$ (Mathys, 2005). Relative fraction of tree canopy represents a measure for capercaillie preference in horizontal stand structure, i.e. for intermediate canopy cover (e.g., Gjerde, 1991; Sjöberg, 1996; Storch, 2002) and mean and standard deviation of tree canopy height for capercaillie preference in vertical stand structure. Capercaillie prefer multistoried forests to uniform, even-aged stands (e.g., Leclercq, 1987; Suchant, 2002; Suter et al., 2002) and use the cover of low-branched trees (Bollmann et al., 2005). Finally, density of tree canopy edges demonstrably is an important explanatory variable of capercaillie habitat (Stein, 1974; Klaus, 1991; Bollmann et al., 2005, 2008). Consequently, we used contour length per raster cell on TCHM at

Table 1Explanatory variables assessed in the forest reserve of Amden to describe capercaillie–habitat relationships

Variable description	Abbreviation	Spatial resolution [ha]
Relative fraction of tree canopy	COVREL (m ²)	1.6
Focal mean of relative fraction of tree	NCOVREL (m ²)	25
canopy for a moving window of 25 ha		
Mean height of tree canopies	HMEAN (m)	1.6
Standard deviation of tree canopy heights	HSTD (m)	1.6
Tree edge length at 10 m height	EDGE10M (m)	1.6
Tree edge length at 20 m height	EDGE20M (m)	1.6
Tree edge length at 30 m height	EDGE30M (m)	1.6
Conifer forest ratio (1: coniferous forest, 0:	CONFOR (index)	25
deciduous forest)		

The variables based on LiDAR data were all prepared at the two scales of 1.6 ha (cell size 125 m) and 25 ha. In previous analyses, we dropped all LiDAR variables at the scale of 25 ha (except NCOVREL) due to strong correlations with retained variables.

the heights of 10 m, 20 m and 30 m, respectively, as proxies for tree edge density. All LiDAR data were processed in the Geographic Information System ESRI ArcInfo 9.1.

The structural relationship between capercaillie habitat preferences and LiDAR probably differs between coniferous and mixed stands (Klaus et al., 1986). To unmix these effects we included conifer forest ratio, an explanatory variable that described forest composition and originated from a passive remote sensing technique. We built this variable from a dataset "Forest type" (WMG25, BFS GEOSTAT) that was originally derived from satellite images (Landsat-5, Thematic Mapper) by an automated maximum likelihood classification. "Forest type" was available in four categories: conifer forest (1), conifer-dominated mixed forest (2), deciduous-dominated mixed forest (3) and deciduous forest (4). To calculate conifer forest ratio we reclassified the forest type categories into values of 1.0 (cat. 1), 0.667 (cat. 2), 0.333 (cat. 3) and 0.0 (cat. 4) and calculated neighborhood means for a window size of 25 ha.

2.4. Statistical analyses

We used capercaillie presence—absence data as the response and the remote sensing data as explanatory variables to build a model of habitat suitability. And we used logistic regression (GLM with binomial error distribution and logit as the link function) to predict the binary response variable. We performed all statistical analyses in the statistical environment R version 2.0.0 (R Development Core Team, 2005) complemented with the additional package Design (Version 2.0-12; Harrel, 2001).

We first used density plots (R-function of main package R 2.4.1; e.g., Venables and Ripley, 1994) to explore the relationship between capercaillie presence-absence response and each explanatory variable separately. In the case of a unimodal response that can be explained with capercaillie ecology (e.g., COVREL), we also included the squared term of the explanatory variable. For all the variables we calculated focal means (neighborhood means) with a window size of 25 ha. Such spatial aggregation should increase the explanatory power of variables (cf. Graf et al., 2005; Guisan and Thuiller, 2005), because capercaillie prefer areas with a high amount of suitable habitat to islands of good habitat embedded in unsuitable stands (Storch, 1995). We only applied one window size (arbitrarily chosen), because the focus of this paper was to measure and monitor habitat suitability at exact locations (but for large areas) in order to provide spatially explicit information on the need of management actions.

Then, we adopted two model approaches: in a first model (CELL-SCALE model), we included all LiDAR based variables at the

cell scale of 1.6 ha making modeling results directly transferable to forest management. In the second model (MIXED-SCALE model), we used all LiDAR based variables at the cell scale but included also the same variables transformed with the focal mean procedure for a window size of 25 ha. This procedure maximized the explanatory power of the habitat suitability model but made the interpretation for management more difficult. As the transformed variables were all highly correlated (Spearman rank correlation >0.7), we used only the relative tree canopy cover (NCOVREL, Table 1). In both approaches, we included conifer forest ratio at the scale of 25 ha as a filter variable to unmix the effects of forest structure on capercaillie habitat suitability between conifer- and deciduous-dominated forests.

We reduced the variable set applying a three-step procedure in both model approaches: First, we studied bivariate correlations (Spearman's rank correlation). Correlations exceeding 0.7 are critical in logistic regression models (Fielding and Haworth, 1995). We selected relative fraction of tree canopy (COVREL, NCOVREL) actively because it had highest predictive power in univariate analyses and has high relevance for capercaillie habitat suitability. We included all other variables that were not highly correlated with these variables. Second, we reduced the remaining variable set in a stepwise backwards selection (R 2.0.0, STEP function based on AIC; e.g., Crawley, 2002). In a third step, we checked the coefficients of the explanatory variables for plausibility. Additionally, we tested interactions between the variables that were selected for the final model. As the interactions did not improve model fit significantly, we did not include any interaction terms.

We evaluated the final model with the procedure "validate" implemented in the R-package Design (Version 2.0-12; Harrel, 2001). We applied bootstrapping (N = 1000) and reported the corrected indexes of R-square and the threshold-independent area under the receiver operating curve, AUC (Fielding and Bell, 1997). Additionally, we provided threshold-dependent accuracy measures based on the confusion matrix (e.g., Fielding and Bell, 1997). A confusion matrix contrasts the predicted with the observed presences and absences based on a fixed threshold for suitability. We report the correct classification rate (CCR), the positive predictive power (PPP), the negative predictive power (NPP) and Kappa at a threshold of 0.5.

3. Results

The final habitat suitability models relating capercaillie response to LiDAR based explanatory variables were able to further

Table 2Description of the two final habitat suitability models for capercaillie in the forest reserve of Amden; CELL-SCALE model with LiDAR variables at cell scale only, MIXED-SCALE model with LiDAR variables at two scales (1.6 ha, 25 ha)

Model	Variable	Coef.	S.E.	Wald Z	P
CELL-SCALE	Intercept	-1.079E+01	1.3523	-7.98	<0.001
	COVREL	1.251E-01	0.0300	4.18	<0.001
	COVREE	-1.071E-03	0.0003	-3.84	<0.001
	CONFOR	7.868E+00	1.2200	6.45	<0.001
MIXED-SCALE	Intercept	-2.007E+01	2.3638	-8.49	<0.001
	NCOVREL	4.839E-01	0.0864	5.60	<0.001
	NCOVREL ²	-4.740E-03	0.0009	-5.51	<0.001
	EDGE10M	5.619E-04	0.0002	2.74	0.006
	CONFOR	7.647E+00	1.2180	6.28	<0.001

Coefficients of the parameters in the final models (Coef.), standard error (S.E.), Wald statistic (Wald *Z*) and *P*-values (*P*).

differentiate the generally suitable study area (Fig. 2). The CELL-SCALE model using LiDAR data only at cell scale (1.6 ha) attained an AUC = 0.71 and an R^2 = 0.16. Applying a probability threshold of 0.5 to distinguish between suitable (predicted presence) and unsuitable (predicted absence) cells resulted in a correct classification rate CCR = 0.68, positive predictive power PPP = 0.61, negative predictive power NPP = 0.71, and Kappa = 0.29. At the optimized threshold of 0.53, Kappa was slightly higher (Kappa_opt = 0.31). 30% of the area was predicted as suitable, 70% as unsuitable (Fig. 2). The MIXED-SCALE model performed better than the CELL-SCALE model with an AUC = 0.77, R^2 = 0.27. It attained a correct classification rate CCR = 0.70, positive predictive power PPP = 0.62, negative predictive power NPP = 0.75, and Kappa = 0.37 (probability threshold 0.5). At the optimized threshold of 0.41, the measures were slightly higher (CCR = 0.71, Kappa_opt = 0.42). With a suitability threshold of 0.5, 36% of the area was predicted as suitable, 64% as unsuitable.

Both final habitat suitability models included explanatory variables from LiDAR (describing horizontal tree structure) and from passive sensors (describing the main forest type; Table 2). The final habitat suitability model using LiDAR data only at cell scale (1.6 ha, CELL-SCALE model) retained two variables (Table 2): (1) relative tree cover (COVREL) and its squared term indicating a unimodal response, and (2) the conifer forest ratio (CONFOR) with a positive relationship to habitat suitability (Fig. 3). Thus, this model simulates the preference of capercaillie for conifer-dominated forests with intermediate canopy cover. The MIXED-SCALE model retained three variables (Table 2): (1) relative tree cover at the scale of 25 ha (NCOVREL) and its squared term indicating a unimodal

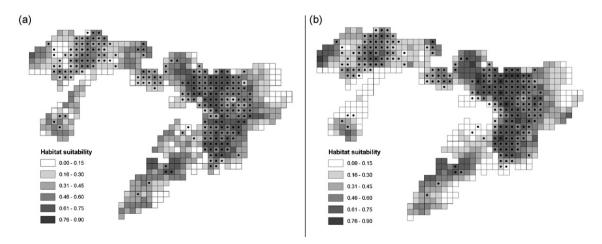


Fig. 2. Grid map of the study area (cell size of 1.6 ha) with modeled habitat suitability and the distribution of observed capercaillie presence (black points). CELL-SCALE model with LiDAR variables at cell scale only (a); MIXED-SCALE model with relative tree cover at scale of 25 ha (b).

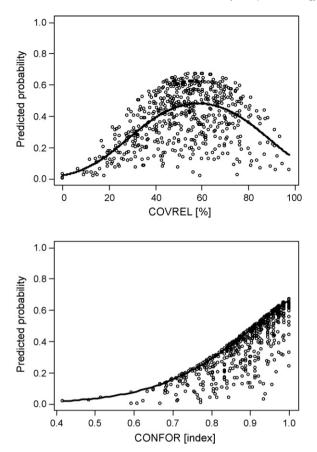


Fig. 3. The variables selected by the final model at cell scale (CELL-SCALE model) are plotted against predicted probability for capercaillie presence. The curves are the simulated responses for the respective variable (where the other variables are set to median).

response, (2) tree edges at 10 m height (EDGE10M) with a positive response, and (3) conifer forest ratio (CONFOR) also with a positive response (Fig. 4). Thus, in our case capercaillie appeared to prefer conifer-dominated stands with intermediate canopy cover and a high amount of interior edges. These capercaillie–habitat relationships are in accordance with those found in field studies (Gjerde, 1991; Klaus, 1991; Schroth, 1992; Suchant, 2002; Bollmann et al., 2005, 2008).

The LiDAR based structural variables differed in spatial pattern to describe capercaillie habitat suitability (Fig. 5). Optimum capercaillie habitat in the study area, i.e. values from uppermost 10% suitable cells, had a mean relative tree cover of 55.9 (S.D. = 7.0) and mean conifer forest ratio of 0.98 (S.D. = 0.01) for the CELL-SCALE model, and a mean relative tree cover of 52.9 (S.D. = 4.7), mean tree edge density at 10 m height of 2326 (S.D. = 333), and a mean conifer forest ratio of 0.98 (S.D. = 0.02) for the MIXED-SCALE model. The directional difference of a cell value to the optimum habitat value was not equal with respect to the explanatory variables. For instance, there were cells with a denser canopy cover (COVREL) than the optimum combined with both low and high density of internal edges at 10 m (EDGE10M).

4. Discussion

4.1. Habitat predictions

The special forest reserve of Amden is a generally suitable area for capercaillie (Graf et al., 2005). Nevertheless, our habitat

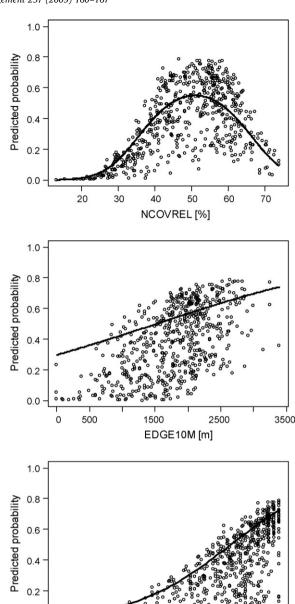


Fig. 4. The variables selected by the final model at mixed scales (MIXED-SCALE model) are plotted against predicted probability for capercaillie presence. The curves are the simulated responses for the respective variable (where the other variables are set to median).

0.7

CONFOR [index]

0.8

0.9

1.0

0.6

0.0

0.4

0.5

suitability models based on LiDAR variables further differentiated the simulated suitability pattern. Three major aspects have to be discussed here to evaluate the quality of this result. First, model performance is no absolute measure (Fielding, 2002), and has to be interpreted on the basis of the primary goal of our study to predict habitat suitability based on local forest structure and composition only. The information of earlier habitat suitability models (Graf et al., 2005) was used to define the borders of the forest reserve that we used as our study area. Thus, the entire study area is potential capercaillie habitat and we know from field work that large parts of the study area provide suitable habitat (Imhof, 2007). Modeling habitat suitability in a generally suitable area is difficult since habitat variation is reduced (Åberg et al., 2000). Nevertheless,

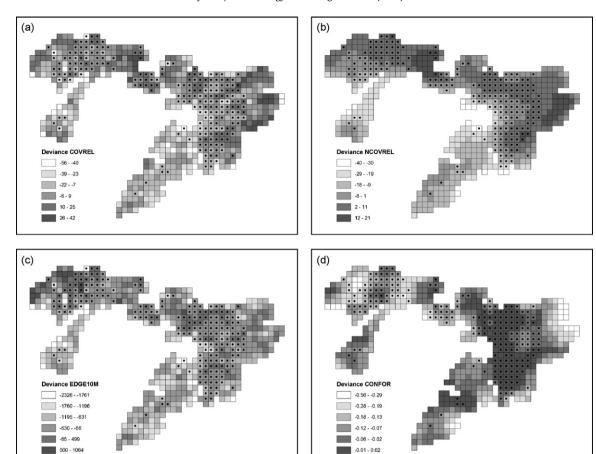


Fig. 5. Difference of explanatory variable values to the mean variable value of the uppermost 10% cells of habitat suitability (Variable value – Mean10perc). Light shading indicates negative values whereas positive values are indicated with dark shading. We show these results for the variables that were selected by the final models: (a) COVREL in the CELL-SCALE model, (b) NCOVREL, (c) EDGE10M, and (d) CONFOR in the MIXED-SCALE model. The range of all four deviance variables is continuous; for appropriate visual interpretation we classified the range in 6 equally sized classes.

our model results show that LiDAR based variables can further differentiate the study area and show a spatially more detailed picture of habitat suitability than was available from large-scale passive sensor data.

Second, forest structure may generally have limited power to explain capercaillie presence-absence at the scale of forest stands, because capercaillie is a mobile species that spends some amount of time also in suboptimal habitats (cf. Graf et al., 2007). Inversely, some areas identified as suitable by the model, may have been classified as "absence", because they were temporarily not used by capercaillie or because their presence was not detected. But our multitemporal data collection strategy should have accounted for this potential error of omission. Also, capercaillie is a species with high cognitive abilities (Klaus et al., 1986) and may use its knowledge of the neighborhood to decide on movement paths and places to stay. This is probably the reason for the mixed scale model to explain better than the CELL-SCALE model. Using focal explanatory variables that summarize information of the neighboring landscape at even larger scale than 25 ha might have further improved model fit (Guisan and Thuiller, 2005), but it would not have supported our aim to give site-specific advice on the type of required management actions. In Graf et al. (2007), the same forest structure variable (open canopy cover) had poor predictive power at the stand scale but explained capercaillie population trend successfully at the scale of local populations. Thus, habitat characteristics that fail to predict the small-scale presenceabsence pattern are obviously required in sufficient quantity to sustain a local population. Our modeling method using LiDAR allows for quantifying such structural characteristics consistently over large areas.

Third, more detailed information on vertical stand structure might have improved model fit. Earlier terrestrial analyses of capercaillie habitat identified important variables of stand structure, such as rich ground vegetation cover (e.g., Schroth, 1992) ideally dominated by bilberry (*Vaccinium myrtillus*; Storch, 1993) or lowbranched solitary trees (Bollmann et al., 2005). Such features are not accessible with first and last pulse LiDAR (but see next section).

4.2. LiDAR variable performance

LiDAR based variables describing horizontal stand structure helped to improve the habitat models for capercaillie. Relative tree cover and tree edge densities at 10 m height represented the preference of capercaillie for intermediate canopy cover (Gjerde, 1991; Sjöberg, 1996) and for forests rich in interior edges (Stein, 1974; Klaus, 1991; Bollmann et al., 2005; Imhof, 2007). In literature, we can also find evidence that vertical stand structure affects capercaillie habitat suitability. For instance, a rich understorey cover is an important feature of summer habitat for capercaillie (e.g., Schroth, 1992; Storch, 1993). Also, there is evidence that multistoried forests are preferred over uniform stands (Leclercq, 1987; Schroth, 1992). But our variables of vertical stand structure based on first and last pulse LiDAR, i.e. mean and standard deviation of tree canopy height, could not well explain

capercaillie presence-absence. Probably, the obtained information on vertical structure was not detailed enough, particularly because understorey cover was not included in the raw data. Multiple-return or waveform LiDAR provide much more details on the vertical stand structure including information on the understorey (Lefsky et al., 2002; Goetz et al., 2007) and may thus significantly improve habitat analyses for forest dwelling species in the future.

4.3. Implications for conservation

Habitat models at the landscape scale are most useful for conservation if they include explanatory variables that are directly linked to habitat suitability and available over large areas. Hitherto, large-scale habitat analyses of capercaillie allowed us to identify roughly those areas that are important for capercaillie conservation or areas that might become important for capercaillie in the future (Graf et al., 2004, 2005). However, these models provided no information on present habitat suitability and on management relevant forest characteristics. In this study we improved habitat suitability predictions using variables of present forest structure and composition. From our models, we can generate deficiency maps that identify areas, where forest structure is suboptimal at present, thus where management actions could improve habitat suitability (Fig. 5). These maps illustrate how a specific grid cell deviates from optimum conditions in the study area with respect to management relevant variables. For instance, we can identify too dense forests (with high relative tree cover) where forest management could improve habitat quality by logging. Thus, only now we can determine the type of management actions to improve habitat

In the special case of the forest reserve of Amden, we would not depend on such analyses because detailed data on vegetation structure and composition were assessed during the field work of 2006 (Imhof, 2007). However, capercaillie has large-spatial requirements and cannot be conserved by concentrating efforts on reserves only (Storch, 2003). At the scale of entire countries, habitat models based on passive sensor data can successfully identify those areas that are potentially suitable for capercaillie (Graf et al., 2005). Additional analyses on the spatial arrangement and connectivity of these areas help us to set priorities on those areas that are most important for the survival of the entire population (e.g., Bollmann et al., submitted for publication; Mathys et al., 2006; Mollet et al., 2008; Pascual-Hortal and Saura, 2008). Within the potentially suitable areas with high priority, we need to identify those forest patches, where forestry actions taken to improve capercaillie habitat have the highest effect. Therefore, assessing and monitoring habitat suitability consistently over sufficiently large areas will make conservation more effective. Our results confirm that LiDAR is a promising tool for this task.

5. Conclusions

First and last pulse LiDAR improved predictions of habitat suitability for capercaillie in a generally suitable study area. However, we see the main advances of our study in the spatial differentiation between the different structural stand properties. Capercaillie habitat managers can now spatially address each habitat property separately and take actions more specifically. The study also shows that further model improvement is possible in the vertical structure domain. We thus encourage continuous research in the assessment of explanatory variables for vertical stand structure, as gained from, e.g., multiple-return or waveform LiDAR. Generally, our results show that LiDAR data – once available with country-wide coverage – will enable conservation managers

to assess habitat suitability for forest dwelling species at the scale of entire populations. LiDAR thus offers great potential for effective habitat monitoring and management of endangered species and biodiversity maintenance in general.

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