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, in 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 (Hyypä 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 successions stages with pioneer plant communities. Pioneer woody plants with buts and catkins are the most important food components of hazel grouse in the winter habitat. A rich and divers 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 (Cada 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...
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
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 (see text for details).

| 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     | 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                 |

*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.*
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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 curve (AUC) (see Segurado and Araújo 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 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
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; Dymytrova et al. 2016). Moreover, the expected effects of the most important factors on habitat suitability were consistent with previous studies.
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 understory (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 understory (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 were 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 were 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 temporarily 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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References

Ackers, S. H., R. J. Davis, K. A. Olsen, and K. M. Dugger. 2015. The evolution of mapping habitat for northern spotted owls (Strix occidentalis caurina): a comparison of photo-interpreted, Landsat-based, and lidar-based habitat maps. Remote Sens. Environ. 156, 361–373.

Allouche, O., T. Asaf, and K. Ronen. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232.

Amt für Wald des Kantons Bern. 2013. LiDAR-Daten Kanton Bern. Available at: http://files.be.ch/lwe/agi/geoportal/geo/lpi/LBEROH_2012_01_LANG_DE.pdf (accessed 20 July 2016).

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. J. Biogeogr. 33, 1677–1688.

Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends Ecol. Evolutionology Evol. 22, 42–47.

Association Parc régional Chasseral. 2015. Projet 2016-2019, Demande d’aides financières globales pour la gestion du Parc régional Chasseral, Rapport version du 21 janvier 2015, 182 pp.

Bae, S., B. Reineking, M. Ewald, and J. Mueller. 2014. Comparison of airborne lidar, aerial photography, and field surveys to model the habitat suitability of a cryptic forest species – the hazel grouse. Int. J. Remote Sens. 35, 6469–6489.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution

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models: how, where and how many? Methods Ecol. Evol. 3, 327–338.
Bässler, C., J. Stadler, J. Müller, B. Förster, A. Göttlein, and R. Brandl. 2011. LiDAR as a rapid tool to predict forest habitat types in Natura 2000 networks. Biodivers. Conserv. 20, 465–481.
Bergen, K. M., S. J. Goetz, R. O. Dubayah, G. M. Henebry, C. T. Hunsaker, M. L. Imhoff, et al. 2009. Remote sensing of vegetation 3-D structure for biodiversity and habitat: review and implications for lidar and radar spaceborne missions. J. Geophys. Res. Biogeosci. 114, 1–13.
Bergmann, H.-H., S. Klaus, F. Müller, W. Scherzinger, J. E. Swenson, and J. Wiesner. 1996. Die Haselhühner. Magdeburg, Westarp Wissenschaften. 278 pp.
Blattner, M. 1998. Der Arealschwund des Haselhuhns (Bonasa bonasia) in der Norwestschweiz. Ornithol. Beob. 95, 11–38.
Bollmann, K., A. Bergamini, B. Senn-Irlet, M. Nobis, P. Duelli, and C. Scheidegger. 2009. Konzepte, Instrumente und Herausforderungen bei der Förderung der Biodiversität im Wald | Concepts, instruments and challenges for the conservation of biodiversity in the forest. Schweiz Z Forstwes. 160, 53–67.
Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecol. Model. 157, 281–300.
Braunisch, V., J. Coppes, R. Arlettaz, R. Suchant, F. Zellweger, and K. Bollmann. 2014. Temperate mountain forest biodiversity under climate change: compensating negative effects by increasing structural complexity. PLoS ONE 9, e97718.
Breiner, F. T., A. Guisan, A. Bergamini, and M. P. Nobis. 2015. Overcoming limitations of modelling rare species by using ensembles of small models. Methods Ecol. Evol. 6, 1210–1218.
Buissou, L., W. Thuiller, N. Casajus, S. Lek, and G. Grenouillet. 2010. Uncertainty in ensemble forecasting of species distribution. Glob. Change Biol. 16, 1145–1157.
Burkhalter, J., and J. Sager. 2003. Laubwald – Mischwald – Nadelwald. Wald differenzierung mit digitalen Satellitendaten. Arealstatistik der Schweiz, Neuchâtel, Bundesamt für Statistik der Schweiz. 112 pp.
Čada, V., R. C. Morrissey, Z. Michalová, R. Bačé, P. Janda, and M. Svoboda. 2016. Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. For. Ecol. Manage. 363, 169–178.
Davies, A. B., and G. P. Asner. 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends Ecol. Evol. 29, 681–691.
Dymytrova, L., S. Stofer, C. Ginzler, F. T. Breiner, and C. Scheidegger. 2016. Forest-structure data improve distribution models of threatened habitat specialists: implications for conservation of epiphytic lichens in forest landscapes. Biol. Cons. 196, 31–38.
Elith, J., and C. H. Graham. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. Ecoscropy 32, 66–77.
Elith, J., S. Ferrier, F. Huettmann, and J. Leathwick. 2005. The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. Ecol. Model. 186, 280–289.
Falkowski, M. J., J. S. Evans, S. Martinuzzi, P. E. Gessler, and A. T. Hudak. 2009. Characterizing forest succession with lidar data: an evaluation for the Inland Northwest, USA. Remote Sens. Environ. 113, 946–956.
Farrell, S. L., B. A. Collier, K. L. Skow, A. M. Long, A. J. Campomizzi, M. L. Morrison, et al. 2013. Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. Ecosphere 4, 1–18.
Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, J. A. F. Diniz-Filho, J. F. Guégan, et al. 2009. Spatial species-richness gradients across scales: a meta-analysis. J. Biogeogr. 36, 132–147.
Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Glob. Ecol. Biogeogr. 16, 265–280.
Flaherty, S., P. W. W. Lurz, and G. Patenaude. 2014. Use of LiDAR in the conservation management of the endangered red squirrel (Sciurus vulgaris L.). J. Appl. Remote Sens. 8, 1–15.
Franklin, J.. 2009. Mapping species distributions- spatial inferences and prediction Cambridge University Press, Cambridge. 320 pp.
Gimmi, U., M. Bürgi, and M. Stuber. 2008. Reconstructing anthropogenic disturbance regimes in forest ecosystems: a case study from the Swiss Rhone valley. Ecosystems 11, 113–124.
Goetz, S., D. Steinberg, R. Dubayah, and B. Blair. 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. Remote Sens. Environ. 108, 254–263.
Gottschalk, T. K., B. Aue, S. Hotes, and K. Ekschmitt. 2011. Influence of grain size on species-habitat models. Ecol. Model. 222, 3403–3412.
Graf, R. F., K. Bollmann, W. Suter, and H. Bugmann. 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. Landscape Ecol. 20, 703–717.
Grossmann, H.. 1927. Die Waldweide in der Schweiz. Dissertation Eidg. Technische Hochschule Zürich, Zürich. 124 pp.
Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.

Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tulloch, et al. 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435.

He, K. S., B. A. Bradley, A. F. Cord, D. Rocchiini, M.-N. Tuanmu, S. Schmid, et al. 2015. Will remote sensing shape the next generation of species distribution models? Remote Sens. Ecol. Conserv. 1, 1–18.

Hirzel, A. H., G. Le Lay, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199, 142–152.

Holbrook, J. D., K. T. Vierling, L. A. Vierling, A. T. Hudak, and P. Adam. 2015. Occupancy of red-naped sapsuckers in a coniferous forest: using LiDAR to understand effects of vegetation structure and disturbance. Ecol. Evol. 5, 5383–5393.

Hyvöppä, J., H. Hyvöppä, D. Leckie, F. Gougeon, X. Yu, and M. Maltamo. 2008. Review of methods of small-footprint airborne laser scanning for extracting forest inventory data in boreal forests. Int. J. Remote Sens. 29, 1339–1366.

Isenburg, M. 2014. LAStools – efficient tools for LiDAR processing. Version 140301. Available at: http://lastools.org (accessed 28 January 2014).

Jeschke, J. M., and D. L. Strayer. 2008. Usefulness of bioclimatic models for studying climate change and invasive species. Ann. N. Y. Acad. Sci. 1134, 1–24.

Jones-Farrand, D. T., T. M. Fearer, W. E. Thogmartin, F. R. Thompson, M. D. Nelson, and J. M. Tirpak. 2011. Comparison of statistical and theoretical habitat models for conservation planning: The benefit of ensemble prediction. Ecol. Appl. 21, 2269–2282.

Keller, V., R. Ayé, W. Müller, R. Spaar, and N. Zhinden. 2010. Die prioritären Vogelarten der Schweiz: Revision 2010. Ornithol. Beob. 107, 265–285.

Kirby, K. J., and C. Watkins. 2015. Europe’s changing woods and forests: from wildwood to managed landscape. CAB International, Wallingford. 363 pp.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42, 594–598.

Mathys, L., N. E. Zimmermann, N. Zhinden, and W. Suter. 2006. Identifying habitat suitability for hazel grouse Bonasa bonasia at the landscape scale. Wildlife Biol. 12, 357–366.

Maumary, L., L. Vallotton, and P. Knaus. 2007. Die Vögel der Schweiz. Schweizerische Vogelwarte Sempach, und Nos Oiseaux, Montmollin, Sempach. 848 pp.

Mayer, A. C., and V. Stöckli. 2005. Long-term impact of cattle grazing on subalpine forest development and efficiency of snow avalanche protection. Arct. Antarct. Alp. Res. 37, 521–526.

Melin, M., L. Mehtätalo, J. Miettinen, S. Tossavainen, and P. Packalen. 2016. Forest structure as a determinant of grouse brood occurrence – an analysis linking LiDAR data with presence/absence field data. For. Ecol. Manage. 380, 202–211.

MeteoSchweiz. 2016. Klimanormwerte Chaumont. http://www.meteoschweiz.admin.ch/product/output/climate-data/climate-diagrams-normal-values-station-processing/CHM/climsheet_CHM_np6190_d.pdf.html (accessed 20 July 2016).

Meyer, C. B., and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. Divers. Distrib. 12, 288–297.

Montadert, M., and P. Leonard. 2003. Survival in an expanding hazel grouse Bonasa bonasia population in the southeastern French Alps. Wildlife Biol. 9, 357–364.

Morsdorf, F., B. Kötz, E. Meier, K. I. Itten, and B. Allgöwer. 2006. Estimation of LAI and fractional cover from small footprint airborne laser scanning data based on gap fraction. Remote Sens. Environ. 104, 50–61.

Mulhauser, B. 2003. Survival of the hazel grouse Bonasa bonasia rupelstri in the Jura mountains: Between board and lodging. Bulletin de la Société Neuchâteloise des Sciences Naturelles 126, 55–70.

Müller, J., and R. Brandl. 2009. Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. J. Appl. Ecol. 46, 897–905.

Müller, J., C. Moning, C. Bässler, M. Heurich, and R. Brandl. 2009a. Using airborne laser scanning to model potential abundance and assemblages of forest passerines. Basic Appl. Ecol. 10, 671–681.

Müller, D., B. Schröder, and J. Müller. 2009b. Modelling habitat selection of the cryptic hazel grouse Bonasa bonasia in a montane forest. J. Ornithol. 150, 717–732.

Rueda, M., B. A. Hawkins, I. Morales-Castilla, R. M. Vidanes, M. Ferrero, and M. Á. Rodríguez. 2013. Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds. Glob. Ecol. Biogeogr. 22, 1282–1292.

Saari, L., J. Åberg, and J. E. Swenson. 1998. Factors influencing the dynamics of occurrence of the hazel grouse in a fine-grained managed landscape. Conserv. Biol. 12, 586–592.

Sachat, S., N. Perrin, and C. Neet. 2003. Winter habitat selection by two sympatric forest grouse in western Switzerland: implications for conservation. Biol. Cons. 112, 373–382.

Savill, P. 2015. High forest management and the rise of even-aged stands. In: K. J. Kirby, C. Watkins. Pp. 93–106. Europe’s changing Woods and Forests – From Wildwood to managed landscape. CAB International, Boston.

Schäublin, S., and K. Bollmann. 2011. Winter habitat selection and conservation of hazel grouse (Bonasa bonasia) in mountain forests. J. Ornithol. 152, 179–192.
Segurado, P., and M. B. Araujo. 2004. An evaluation of methods for modelling species distributions. *J. Biogeogr.* **31**, 1555–1568.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **10**, 1115–1123.

Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **17**, 866–880.

Storch, I. (compiler). 2007. *Grouse: status survey and conservation action plan 2006–2010*. IUCN and Fordingbridge, UK, World Pheasant Association, Gland, Switzerland. 114 pp.

swisstopo. 2014. VECTORS25. http://www.swisstopo.admin.ch/internet/swiss-topo/de/home/products/landscape/vector25.html (accessed 28 January 2014).

Système d’information du territoire neuchâtelois. 2010. Relevé altimétrique 3D 2010 du canton de Neuchâtel - basé sur la technologie de balayage laser aéroporté (laserscanning). www.ne.ch/autorites/DDTE/SGRF/SITN/.../3dlaser_2010.pdf (accessed 20 July 2016).

Tattoni, C., R. Franco, and P. Paolo. 2012. Can LiDAR data improve bird habitat suitability models? *Ecol. Model.* **245**, 103–110.

Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *J. Anim. Ecol.* **68**, 647–657.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. BIOMOD - A platform for ensemble forecasting of species distributions. *Ecography* **32**, 369–373.

Thuiller, W., D. Georges, and F. Breiner. 2015. biomod2: Ensemble platform for species distribution modeling. http://R-Forge.R-project.org/projects/biomod/ (accessed 28 October 2015).

Vierling, K. T., L. A. Vierling, W. A. Gould, S. Martinuzzi, and R. M. Clawges. 2008. Lidar: shedding new light on habitat characterization and modeling. *Front. Ecol. Environ.* **6**, 90–98.

Vierling, K. T., C. Bässler, R. Brandl, L. A. Vierling, I. Weiß, and J. Müller. 2011. Spinning a laser web: predicting spider distributions using LiDAR. *Ecol. Appl.* **21**, 577–588.

Vogeler, J. C., A. T. Hudak, L. A. Vierling, J. Evans, P. Green, and K. T. Vierling. 2014. Terrain and vegetation structural influences on local avian species richness in two mixed-conifer forests. *Remote Sens. Environ.* **147**, 13–22.

Wiesner, J., H. Bergmann, S. Klaus, and F. Müller. 1977. Siedlungsdichte und Habitatstruktur des Haselhuhns (*Bonasa bonasia*) im Waldgebiet von Białowieża (Polen). *J. Ornithol.* **118**, 1–20.

Yao, W., P. Krzystek, and M. Heurich. 2012. Tree species classification and estimation of stem volume and DBH based on single tree extraction by exploiting airborne full-waveform LiDAR data. *Remote Sens. Environ.* **123**, 368–380.

Zaniewski, E., A. Lehmann, J. M. Overton, and J. Mcc. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecol. Model.* **157**, 261–280.

Zbinden, N. 1979. Zur Ökologie des Haselhuhns *Bonasa bonasia* in den Buchenwäldern des Chasseral, Faltenjura. *Ornithol. Beob.* **76**, 167–214.

Zellweger, F., V. Braunisch, A. Baltensweiler, and K. Bollmann. 2013. Remotely sensed forest structural complexity predicts multi species occurrence at the landscape scale. *For. Ecol. Manage.* **307**, 303–312.

Zellweger, F., F. Morsdorf, R. S. Purves, V. Braunisch, and K. Bollmann. 2014. Improved methods for measuring forest landscape structure: LiDAR complements field-based habitat assessment. *Biodivers. Conserv.* **23**, 289–307.

Zellweger, F., A. Baltensweiler, C. Ginzler, T. Roth, V. Braunisch, H. Bugmann, et al. 2016. Environmental predictors of species richness in forest landscapes: abiotic factors versus vegetation structure. *J. Biogeogr.* **43**, 1080–1090.