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Habitat modeling for Hazel grouse – developing a management tool for the Parc régional Chasseral

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Abstract

Habitat suitability modeling (HSM) can be a powerful tool for conservation management provided that reliable and area-wide information of climate, landscape and habitat is available for the area of interest. Traditionally, mostly abiotic information about habitat distribution and composition was used in HSM. This was a particular limitation for forest inhabiting species such as the Hazel grouse (*Bonasa bonasia*) that strongly depend on the three-dimensional (3D) distribution and composition of forest elements and resources. To overcome this limitation, I developed a variable set of 3D vegetation structure that was derived from airborne Light Detection and Ranging (LiDAR) data. These variables were combined with other biotic and abiotic variables describing climate, topography and landscape (full model) aiming for spatially predicting habitat suitability for Hazel grouse (*Bonasa bonasia*) in the Parc régional Chasseral in the Swiss Jura mountains. Moreover, I developed a second HSM by using exclusively biotic variables of landscape composition and 3D vegetation structure (biotic model). Species presence data originated from a multi-year field survey in the park and from the Swiss Ornithological Institute. I applied an ensemble modeling approach consisting of seven standard species distribution model algorithms and evaluated their predictive performance using the cross-validated average of the area under the receiver operating characteristic curve (AUC). Both models performed excellent with an AUC of 0.959 for the full model and 0.914 for the biotic model. In the full model, climate performed best but appeared to be mainly indirectly related to habitat suitability via correlations to forest structure and composition. They still show influences of historical and current forest use with different strength along the altitudinal gradient. Average vegetation height and shrub cover were the best predictor variables in the biotic model with optimal values around 8 m and 30-35 %, respectively. The very good performance and accurate predictions of the biotic model indicated the excellent potential of 3D forest structure and composition data for modeling potential habitats of forest organisms that depend strongly on 3D niches. Patches with high suitability in the Parc régional Chasseral were predominantly concentrated at the southern slopes in the upper forest belt along the tree line in proximity to summer pastures on two spatially separate mountain ranges. The majority of the park perimeter was predicted with poor habitat suitability for Hazel grouses. Species conservation should target to increase the size of the regional Hazel grouse population by restoring the occupied habitat patches and by creating more suitable habitats next to them. In a second step, occupied habitat patches should be functionally connected by newly created stepping stone habitats.

Keywords

3D habitat structure, *Bonasa bonasia,* habitat suitability modeling, Hazel grouse, Jura mountains, LiDAR, mountain forest, species conservation, species distribution model

Zusammenfassung

Habitatmodelle können hilfreiche Instrumente für die Naturschutzplanung sein, wenn verlässliche und flächendeckende Informationen über das Klima, die Landschaft und die Lebensräume eines Gebietes vorhanden sind. In der Vergangenheit wurden meistens abiotische Informationen über die Verteilung und Zusammensetzung von Lebensräumen für Habitatmodelle verwendet. Dies schränkte deren Nützlichkeit für Waldorganismen wie beispielsweise das Haselhuhn (*Bonasa bonasia*) ein, weil sie stark von der drei dimensionale (3D) Verteilung und Zusammensetzung von Waldstrukturen und -ressourcen abhängig sind. Informationen über den 3D Aufbau von Waldbeständen standen bislang meistens nur für kleine Untersuchungsflächen zur Verfügung, für grossflächige Analysen auf Landschaftsebene fehlen solche Daten normalerweise gänzlich. Um diese Einschränkung zu überwinden, habe ich ein Set von 3D Vegetationsstrukturvariablen entwickelt, das ich aus LiDAR-Daten (airborne Light Dedection and Ranging) abgeleitet habe. Diese Variablen habe ich mit abiotischen und biotischen Variablen zu Klima, Topographie und Landschaft kombiniert (Vollmodell) mit dem Ziel, ein räumlich explizites Habitatmodell für das Haselhuhn (*Bonasa bonasia*) im Parc régional Chasseral im Schweizer Jura zu entwickeln. Um das Potenzial von LiDAR-Daten für Habitatmodelle von Waldvögel zu evaluieren, habe ich ein zweites Modell (biotisches Modell) erstellt, das ausschliesslich mit biotischen Variablen zur Landschaftszusammensetzung und Vegetationsstruktur kalibriert wurde. Die Artdaten zur Verbreitung des Haselhuhns stammen von einem mehrjährigen Haselhuhnmonitoring im Park und von der Schweizerischen Vogelwarte Sempach. Um das Habitatpotenzial herzuleiten, verwendete ich einen *ensemble model* Ansatz, bestehend aus sieben Standardalgorithmen. Die Modellgüte wurde anhand von kreuzvalidierten Mittelwerte des AUC (area under the receiver operating characteristic curve) ermittelt. Beide Modelle zeigten eine exzellente Genauigkeit mit AUC-Werten von 0.959 für das Vollmodell und 0.914 für das biotische Modell. Im Vollmodell hatte die Temperatur den grössten Einfluss auf die Habitatqualität der Haselhühner. Der Einfluss scheint hauptsächlich indirekt zu sein über die Zusammensetzung und Struktur der Wälder. Diese zeigen heute abhängig von der Höhenlage unterschiedlich starke Spuren der historischen Landnutzung. Durchschnittliche Vegetationshöhe und Strauchschichtdeckungsgrad waren die besten Prädiktoren im biotischen Modell mit Optimalwerten von 8 m respektive 30-35 %. Die hohe Genauigkeit des biotischen Modells zeigt das grosse Potenzial von 3D Vegetationsstrukturvariablen für die Modellierung des Habitatpotenzials von Waldorganismen. Im Parc régional Chasseral gibt es zwei Waldgebiete mit hoher Habitateignung für das Haselhuhn. Sie befinden sich an den Südhängen von zwei räumlich voneinander getrennten Bergrücken im Bereich der oberen Waldgrenze neben den Sömmerungsweiden. Der grösste Teil des Untersuchungsgebietes wies eine schlechte bis geringe Habitatqualität für das Haselhuhn auf. Um die regionale Haselhuhnpopulation im Park régional Chasseral zu fördern, sollten folgende Massnahmen mit abnehmender Priorität ergriffen werden: (i) bereits besiedelte, qualitativ hochwertige Waldstandorte erhalten oder restaurieren, (ii) neue Lebensräume in unmittelbarer Umgebung mit forstlichen Massnahmen oder durch Beweidung schaffen und (iii) Lebensraumfragmentierung durch die funktionelle Vernetzung der beiden Hauptverbreitungsgebiete mittels Trittsteinhabitaten verringern.

Schlüsselwörter

3D Habitatstruktur, Artenschutz, Art-Lebensraum Modell, Bergwälder, *Bonasa bonasia,*
Habitatmodell, Haselhuhn, Jura, LiDAR

Introduction

To understand how plants and animals are distributed in space and time and which factors determine the species-environment relationship is a central issue in ecology (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Elith & Leathwick 2009). According to Guisan and Thuiller (2005) there are three main factors that influence the distribution of a species: (i) limiting factors or regulators; such as factors controlling a species eco-physiology, e.g., temperature, water, soil composition, (ii) disturbances; such as all natural and human perturbations of the environment, and (iii) resources, defined as all compounds that are used by an organism for survival and reproduction (e.g., energy, water, nest site). The specification of such species-environment relationships represent the core of predictive geographical modeling in ecology (Guisan & Zimmermann 2000). During the last 15 years, species distribution modeling (SDM) has become an increasingly important tool to understand the ecology, occurrence and conservation of species (Guisan & Thuiller 2005). SDMs are used to assess the effect of environmental and land use changes on the distribution of species (e.g. Antoine *et al.* 1998; Kienast *et al.* 1998; Araújo & New 2007; Jeschke & Strayer 2008; Braunisch *et al.* 2014), to model the biogeographic envelop of species (e.g. Mourelle & Ezcurra 1996; Leathwick 1998; Zaniewski *et al.* 2002; Breiner *et al.* 2015), to investigate specific habitat requirements of species (e.g. Mathys *et al.* 2006; Graf *et al.* 2007; Braunisch *et al.* 2008; Müller *et al.* 2009b; Vierling *et al.* 2011; Farrell *et al.* 2013; Zellweger *et al.* 2013) or as basis for priority site selection in species conservation management (e.g. Schadt *et al.* 2002; Loiselle *et al.* 2003; Guisan & Thuiller 2005; Tole 2006; Phillips *et al.* 2006; Bergen *et al.* 2009; Müller *et al.* 2009b; Bässler *et al.* 2011; Bollmann *et al.* 2011; Farrell *et al.* 2013; Flaherty *et al.* 2014). For instance, Schadt et al. (2002) used SDM to model habitat suitability of Eurasian lynx (*Lynx lynx*) in Germany. Bollmann et al. (2011) predicted the occupancy of habitat patches by Capercaillie (*Tetrao urogallus*) in a fragmented landscape in Switzerland. Vierling et al. (2011) used SDM to examine spider community characteristics and single species distribution at scales ranging from stands to landscapes. Triggered by recent technical developments, many SDM tend to focus on modeling fine-grained habitat conditions (see Farrell *et al.* 2013; Zellweger *et al.* 2014). Zellweger et al. (2014) used SDM to model species occurrence probability of Hazel grouse (*Bonasa bonasia*) in Swiss mountain forests with small-scale resolved data on vegetation structure and composition.

Model fitting is usually based on pattern-recognition approaches, whereby the relationship between a realized geographic distribution of a species and a set of predictor variables are examined to investigate the main determining factors of the species distribution (Guisan & Zimmermann 2000; Araújo & Guisan 2006). The underlying ecological concept is a pseudo-equilibrium relationship between the recorded environmental patterns and the observed species (Lischke *et al.* 1998). A matter of primary interest is the relative importance between abiotic and biotic factors and the significance of data resolution and scale (Guisan & Zimmermann 2000). Abiotic factors limit the distribution of a species due to its ecophysiology. For example climate controls the thermal and moisture regimes in a certain study area and limits the latitudinal and altitudinal range of a species. Other abiotic factors like topography or soil affect terrain attributes and therefore more regional and local aspects of species distribution. Otherwise, biotic factors such as vegetation composition and structure provide essential nutritional resources (Franklin 2009). Spatial scale is important for both environmental and species data (Levin 1992) and comprises both grain (resolution) and extent. The extent usually reflects the purpose of the analysis (Elith & Leathwick 2009). For instance, modeling approaches that aim to examine changes in species ranges under climate change tend to use broad spatial extents that are continental to global in scope (e.g., Araújo & New 2007; Cunze *et al.* 2013; Porretta *et al.* 2013; Crickenberger 2016), whereas models targeting to asses influences of habitat suitability as a basis for conservation management tend to focus on local to regional extents (e.g. (Flaherty *et al.* 2014; Vogeler *et al.* 2014; Zellweger *et al.* 2014). Grain size describes the spatial resolution of the data such as the grid cell size of predictor variables or the spatial accuracy of species data (Elith & Leathwick 2009). Environmental variables should comprise both, broad-scaled climate variables and finer-scaled variables that capture variation in energy and resource availability (Franklin 2009), because species distributions are likely driven in part by local, fine-grained habitat conditions (Farrell *et al.* 2013).

Traditionally, SDM mostly rely on abiotic variables such as climate and topography to describe the correlation between environment and species distribution (Franklin 1995; Guisan & Zimmermann 2000; Elith & Leathwick 2009). However recent developments in remote sensing technologies, particular in Light detection and ranging (LiDAR) opened the possibility to directly measure three-dimensional (3D) ecosystem and habitat structure across large areas (Vierling *et al.* 2008; Davies & Asner 2014; Zellweger *et al.* 2014). Therefore, this technology offers the opportunity to combine broad scale habitat models based on conventional GIS data with new developments in remote sensing techniques for developing resource selection models at local and regional scales (Zellweger *et al.* 2014).

In particular, species inhabiting forest ecosystems largely depend on the 3D distribution, composition and abundance of forest elements and resources (Franklin *et al.* 2002; Davies & Asner 2014; Zellweger *et al.* 2014). Structure encompasses both the variability of individual structural elements such as trees, shrubs and logs and the spatial arrangement of these elements, such as whether forests are single- or multi-layered, or whether the trees are uniformly spaced or clumped. Composition refers to the identity of plant species and their variability and proportion in a certain area (Franklin *et al.* 2002). Information on forest structure is traditionally measured by labor-intensive field surveys, and thus, is often only available across relatively small spatial extents (Davies

& Asner 2014). Remote sensing techniques in the past could only provide coarse grained information and were not able to percolate the upper-most portion of the canopy to measure structural characteristics below (Lefsky *et al.* 2002; Vierling *et al.* 2008). However, recent development in remote sensing techniques, such as Light detection and ranging (LiDAR) opens new possibilities to quantify accurate and contiguous measurements of the complete 3D forest structure at a high level of detail, across spatial scales from fine-scaled plots to an entire landscape (Lefsky *et al.* 2002; Hyyppä *et al.* 2008; Vierling *et al.* 2008; Davies & Asner 2014; Zellweger *et al.* 2014). LiDAR directly quantifies forest structure and provides metrics of vegetation height, density or volume as well as information based on single tree crowns (Goetz *et al.* 2007). LiDAR has thus spurred interest in modeling habitat suitability for forest dependent species (Ackers *et al.* 2015) and provides an excellent opportunity to assess how species are affected by vegetation and topographic structure (Davies & Asner 2014; Zellweger *et al.* 2014). Including LiDAR-related variables in SDM by describing small-scaled environmental factors can increase the accuracy of such models, especially in regions with low climatic and/or topographic variation (Camathias *et al.* 2013). LiDAR-based habitat variables of forest 3D structure represent gradients of biotic habitat characteristics which can be influenced in forest management by silvicultural measures. This allows for an improved integration of biodiversity conservation in forest planning (Zellweger *et al.* 2014).

Hazel grouse, a forest grouse and member of the family of *Phasianidae*, is a highly sensitive bird species with regard to small scaled forest structure and composition (Bergmann *et al.* 1996; Mathys *et al.* 2006; Müller *et al.* 2009b; Schäublin & Bollmann 2011). It mainly inhabits coniferous and mixed deciduous forest of the Eurasian boreal forest, but also mountain forests of central and eastern Europe (Bergmann *et al.* 1996). Hazel grouse is a highly sedentary bird and therefore has to meet its annual requirements within the inhabited forest stands. Territories range from 10 to 20 ha depending on habitat suitability (Zbinden 1979; Swenson 1991; Bergmann *et al.* 1996; Maumary *et al.* 2007). Three main resources have to be available in a territory: (1) food access during the whole year, (2) hiding and sleeping options and (3) breeding prospects. Due to seasonality in temperate and boreal regions, the abundance and distribution of these resources change across the distribution range of the species during the year. During winter Hazel grouse use the buds and catkins of light-demanding trees from the genera *Sorbus*, *Salix, Betula, Alnus, Sambucus, Corylus*, and *Populus*. After the snowmelt, food is mainly composed by saplings and herbs and in summer by berries, which are collected from the ground vegetation layer. Chicks mainly feed on insects during their first weeks of life (Zbinden 1979; Bergmann *et al.* 1996; Maumary *et al.* 2007). To provide a minimum of light demanding resource trees and shrubs, forest stands must include areas with low canopy cover and interspersed gaps. In contrast, Hazel grouse depend on relatively dense (coniferous) stands for breeding and hiding options to avoid predators. Both aspects must be given within the territories.

Therefore, Hazel grouse strongly depends on multi-layered forests with structurally diverse stands, including different successional stages and forest edges (Bergmann *et al.* 1996; Åberg *et al.* 2003; Mathys *et al.* 2006; Maumary *et al.* 2007; Müller *et al.* 2009a; Schäublin & Bollmann 2011; Zellweger *et al.* 2013). Between 1970 and 1990, a strong decline and range contraction of Hazel grouse occurred in central Europe. Regional populations decreased between 20 and 50% (Maumary *et al.* 2007). In Switzerland, Hazel grouse is now restricted to mountain forests in the Alps and partly in the Jura mountains. Especially in lower elevated areas, Hazel grouse disappeared (Blattner 1998; Maumary *et al.* 2007). Habitat deterioration and loss due changes in silvicultural practices is considered to be the main factor for the decline. During the past century, silvicultural practices have focused on the production of wood for economic reasons and therefore often converted structurally diverse and multi-layered stands into more uniform, structurally poor stands (Bergmann *et al.* 1996; Blattner 1998; Mulhauser 2003; Storch 2007). In many managed forests in cultural landscapes, there is a dominance of high forests (uniform single layer structure) and a lack of young successional stages (Bollmann *et al.* 2009). Therefore, structurally complex forests are often restricted to mountain regions, where small-scale changes in site conditions and natural disturbances support forest structural complexity (Čada *et al.* 2016). Switzerland has a high responsibility for the maintenance of Hazel grouse populations because of their vulnerability, the overall population size and the relative high species abundance in relation to the international situation (Keller & Bollmann 2001). Therefore Hazel grouse is listed as a priority breeding bird species for conservation action plans in Switzerland (Bollmann *et al.* 2002). Modifications in forest management that promote young successional stages and an adequate shrub layer with light-demanding trees and shrubs, such as *Sorbus*, *Corylus* or *Salix* spp. can support the Hazel grouse conservation and population viability at the local scale (Bergmann *et al.* 1996; Blattner 1998; Maumary *et al.* 2007).

Since 2007, the Federal Office for the Environment support regions in Switzerland which intend to establish regional nature parks (Regionaler Naturpark) as an instrument for sustainable development (Bundesversammlung der Schweizerischen Eidgenossenschaft 2014). Regional nature parks are characterized by high nature and landscape values and a low degree of human habitat deterioration. Local communities that participate with an initiative for the establishment of a park are encouraged to protect and promote local biotopes and their diversity and rarity of indigenous animals and plants and their habitats (Der Schweizerische Bundesrat 2014). In 2011, the region around the Jura mountain range of the Chasseral has been delineated as regional nature park. Being part of the regional distribution range of Hazel grouse, the park management decided to support Hazel grouse conservation by active habitat management (A. Gerber personal communication, March, 2016). Hence, a systematic multi-year field survey was performed with the goal to localize Hazel grouse occurrence within the park perimeter and to evaluate the occupied forest areas in term of habitat suitability. Since resources were restricted, the field survey focused on a limited extent to areas of the park which had been reported to be inhabited by Hazel grouse in the last 10 years. To overcome this limitation, the Parc régional Chasseral proposed a request to develop a SDM for Hazel grouse for the entire park perimeter. The SDM and the predicted habitat suitability map will be used as management tool to define priority areas for species conservation and to establish spatially explicit habitat management based on habitat potentials and deficits. This request of the park management constitutes the key motivation for this study with the aim to (1) test the potential of habitat suitability modeling for Hazel grouse conservation based on a combination of abiotic environmental variables describing climate, topographic and landscape features, and biotic variables describing 3D forest vegetation structure derived from airborne LiDAR, (2) to evaluate the potential of LiDAR to asses important structural habitat elements and resources for the forest specie and (3), to assess the predicted habitat suitability for conservation management.

Depending on the numerous ecological questions and modeling goals, there is currently a broad and sometimes confusing use of the term species distribution modeling (SDM) (Bradley *et al.* 2012; Guisan *et al.* 2013). In this study, I restricted my analysis to predictors that describe aspects of habitat suitability for Hazel grouse. Biotic interactions such as competition or predation or demographic data were not considered due to the lack of respective data. Hence, I use the more explicit term habitat suitability model (HSM) (see Bradley *et al.* 2012) for my purpose (Van Horne & Horne 1983; Bradley *et al.* 2012) instead of SDM to investigate the species–environment relationship of Hazel grouse in the Parc régional Chasseral.

Methods

Study area

The study area is located in the north-western part of Switzerland (47° 8′ N, 7° 3′ E) and encompasses the perimeter of the Parc régional Chasseral including a buffer zone of 250 m (Fig. 1). The purpose of the buffer zone was to reduce edge effects for variables along the border. The park covers an area of 387 km^2 in the western Jura mountains of the Cantons of Bern and Neuchâtel. The elevation range starts at 429 m above sea level at the bank of Lake Biel up to 1607 m on top of the mountain Chasseral. The western Jura has an oceanic climate. The mean annual precipitation (period: 1981–2010) is 1289 mm, with a major part during summer and winter. The mean annual temperature is 6.3 °C with a maximum of 15.1° in July and a minimum of −1.4° in January (MeteoSchweiz, 2015). The landscape is characterized by a group of parallel mountain chains and a mosaic of forest, pastures, farmland and settlements. Forests are clustered as three forest belts in east-west direction. The natural timberline has been pushed down through pastoralism on the gentle areas in the higher zones of the mountain chains. On the north-facing slope of mount Chasseral, forest stands are more dense, compared to the south facing slope with dryer conditions. Forest composition changes from predominantly deciduous forest in low land areas to coniferous dominated forest at higher elevations.

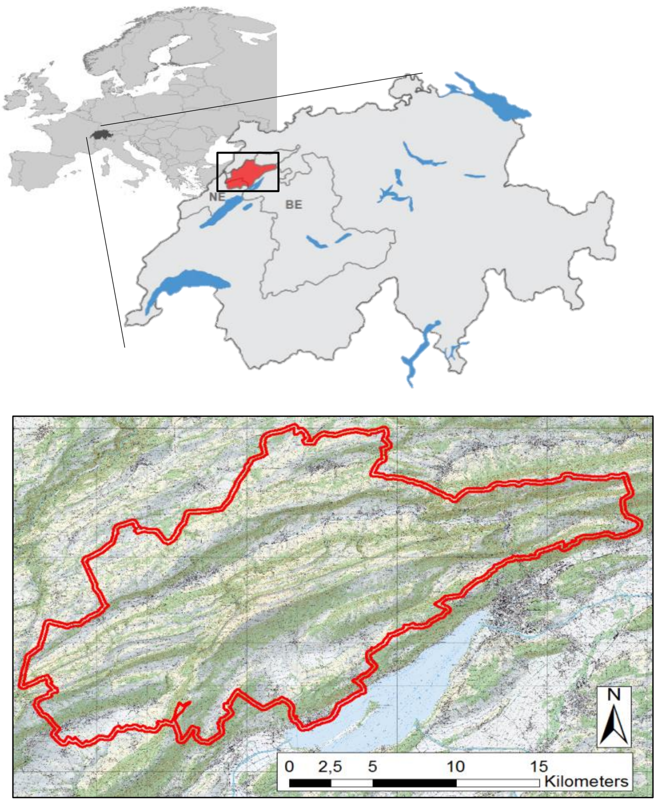


Fig. 1: Location of the Parc régional Chasseral in Switzerland. The study area included the perimeter of the Parc régional Chasseral with an additional buffer zone of 250 m. ©Netzwerke Schweizer Pärke 01/2012 EB - Swisstopo 5704002947

Study design

Because species respond differently to the same environmental parameter sampled at different resolutions (Guisan & Thuiller 2005), I analyzed the species-habitat relationship of Hazel grouse at different spatial resolutions. The study area was overlaid with three grids (rasters), using different cell sizes, i.e., 250 m, 125 m, and 50 m. Each grid cell was assessed individually and contained a minimum forest proportion of 20%, as delineated by the digital mapping product Vector25 (Swisstopo, 2014). Data analysis and modeling (see below) revealed that the model based on the raster with 125 m cell size was most informative, and represented an optimal trade-off between representing a substantial part of Hazel grouse territory and a level of detail required for a proactive forest and conservation management. Therefore, I focused on the model with a grid cell size of 125 m and provide the results based on the other spatial resolutions in the Appendix 3.

Presence-pseudo-absence approach

I predicted the habitat suitability of Hazel grouse in the Parc régional Chasseral based on a presence-pseudo-absence data approach (Guisan & Zimmermann 2000; Araújo & Guisan 2006; Soberón 2007); in other words, I compared habitats used by Hazel grouse with unused habitats (Jones 2001; Brotons *et al.* 2004; VanDerWal *et al.* 2009). Cells were defined as "presence" if they contained at least one Hazel grouse record, as described below.

Species presence data and pseudo-absence data

I used species presence data from the Parc régional Chasseral 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, which was launched after the park's establishment in 2001. Therefore, the park area was overlaid with a grid raster using a cell size of 250 m. Each grid cell was classified through visual interpretation of aerial photographs. Grid cells with low percentage of forests or high proportion of settlements were excluded. For the field survey, four grid cells were aggregated, which resulted in 632 aggregated grid cells. After a preselection of 83 aggregated grid cells that were classified as having the highest habitat suitability potential for Hazel grouse, 50 out of these 83 aggregated cells were randomly chosen and surveyed in the field. Data from the Swiss Ornithological Institute represent verified detection of Hazel grouse through experienced ornithologists. I only used species presence data recorded inside the buffered parc perimeter during the months of December to August. During autumn, juvenile birds disperse to find new territories and can therefore be observed in areas which are occupied only temporarily (Bergmann *et al.* 1996). Finally, 212 species presence point occurrences, 210 from the field survey and 2 from the database of the Swiss Ornithological Institute were used. They were assigned to 101 presence cells of 125 x 125 m.

To get pseudo-absence data, I randomly selected 10'000 background cells and weighted them equally with the presence data (see Barbet-Massin *et al.* 2012). Pseudo-absences were cells with no reported species evidence between winter 2011 and winter 2015 and assumed to be locations which could potentially be occupied and used by Hazel grouse.

Environmental variables

To record environmental conditions that influence habitat suitability for Hazel grouse, a large set of environmental parameters were used as independent variables (Table 1). LiDAR-derived variables were used to characterize small-scale structural characteristics of the vegetation and GIS-derived variables were used to describe forest composition and topography, climate and human influence.

Table 1: Description of environmental variables with sampling units and references squares. They describe the square size, for which the variables were processed. All variables were tested by pairwise correlation. If two variables had a correlation > 0.5, the variable with the higher ecological relevance was selected as a predictor. I selected two different predictor sets. The model approach "125_all" includes predictors describing forest structure or composition and topographic, climatic and human aspects. The model "125_biotic" consists only of biotic predictors.

Variable description	Unit	References squares (m)	Predictor selected in model	
			125_all	*125_biotic*
LiDAR-derived variables				
Average vegetation height	m	25	X	X
Standard deviation of successional stage	unit less	25	X	X
Shrub density	%	25	X	X
SD of shrub density	unit less	25		
Sum of small gaps	counter	5	X	X
Foliage height diversity	unit less	25		
GIS-derived variables				
Topographic position	unit less	25	X	
Roughness	unit less	25		
Slope	degrees	25	X	
Solar radiation in March	kJ/day	25	X	
Mean temperature	°C/month	100	X	
Mean precipitation	mm/month	100		
Distance to forest edge	m	25		
Length of forest edge	m	125	X	X
Proportion of forest	m^2	125		
Forest type	4 categories	125	X	X
Density of settlements	m^2	125		
Distance to settlements	m	25	X	
Distance to roads	m	25		
Length of roads	m	25	X	

LiDAR-derived environmental variables

LiDAR variables were derived by using discrete multiple return LiDAR data provided by the cantons of Bern and Neuchâtel. LiDAR data from the canton of Bern were recorded in April 2011 using the scanner Leica ALS60. The minimum point density was 4 points/m^2, with vertical position accuracy < ±0.3 m and a horizontal accuracy < ±1.0 m. The reported standard deviation of height accuracy was less than ±0.2 m in open areas and less than ±1.0 m in the forest. The cantonal data of Neuchâtel was acquired between May and June 2010 using the scanner Optech Gemini 166 KHz with a mean point density of 7 points/m^2. The mean vertical accuracy was 0.15 m and the mean horizontal accuracy 0.25 m. Raw data processing was performed using a suite of LAStools algorithms (Isenburg 2014). Following the classification of the raw data point cloud into ground and non-ground points and derivation of the normalized vegetation heights above ground, the *lascanopy* tool was used to describe the vertical distribution of vegetation points and related structural characteristics. I therefore gridded the data using different cell sizes (reference squares, Table 1) and upscale local-scale characteristics of forest structure and their spatial variation to the reference cell size of the species occurrence data (125 m). I excluded points below 0.5 m and above 55 m to reduce bias from both, potentially misclassified points, particularly towards the ground, and from bias through recorded objects other than the canopy.

I developed six LiDAR variables (Table 1) to describe spatial vegetation patterns that have been shown to represent essential aspects of Hazel grouse habitat (Bergmann et al. 1996; Åberg et al. 2003; Sachot et al. 2003; Mathys et al. 2006; Müller et al. 2009b; Schäublin & Bollmann 2011; Zellweger et al. 2013, 2014).

The first variable “average vegetation height” was developed with the lascanopy option “avg” and represents the average height of the vegetation points within the grid cell. Derived from the canopy height, defined as the height at which 90% of all points are below (lascanopy option “p90”), I defined the successional stage per reference square. For this purpose, I used the same vegetation height classes as the forestry department of the canton of Bern is using in practice. The classes were 0.5 m to 1.3 m for successional stage one, 1.3 to 10 m for successional stage two, 10 to 30 m for successional stage three and above 30 m for successional stage four. By calculating the SD of successional stages over all reference squares within a grid, I created the second variable termed “standard deviation of successional stages”. The variables “average vegetation height” and “standard deviation of successional stages” were selected because mean vegetation height and standard deviation of canopy height are known to represent important aspects of the physiognomy of the vegetation (Falkowski *et al.* 2009; Korpela *et al.* 2009; Müller *et al.* 2009). Bässler et al. (2011) distinguished standard deviation of canopy height as an indicator of the horizontal heterogeneity in the vertical structure of the canopy. A mosaic of different successional stages and a high vertical heterogeneity are expected to increase the habitat suitability for Hazel grouse (Bergmann *et al.* 1996; Mathys *et al.* 2006; Schäublin & Bollmann 2011).

As a proxy for shrub cover, I calculated the variable "shrub density" using the ratio of all vegetation points between 0.5 m and 5 m in relation to the total point cloud. In addition, I computed the "SD of the shrub density" within each 125 m grid cell to represent the spatial heterogeneity of the shrub layer. Shrub layer and its composition are key factors influencing habitat suitability for the Hazel grouse (Sachot *et al.* 2003; Mathys *et al.* 2006; Müller *et al.* 2009b; Schäublin & Bollmann 2011; Zellweger *et al.* 2014).

To identify forest gaps, I generated the variable "sum of small gaps". It represents the sum of all reference squares of 5 m whose canopy height was below 1.3 m. The relatively small resolution of 5 m for the reference squares was necessary to identify even very small forest gaps, which still could have an ecological effect on habitat suitability of Hazel grouse. Forest gaps were reported in many studies as an import aspect for Hazel grouse occurrence (Saari *et al.* 1998; Mulhauser 2003; Sachot *et al.* 2003; Müller *et al.* 2009b). In addition, the height cutoff of 1.3 m allowed for examining the lower part of forest structure, which includes important food resources, like berry bushes (Mulhauser 2003).

The lascanopy option "dns" was used to produce relative height density raster for calculating the variable "foliage height diversity" (FHD). FHD is defined as the Shannon Index *H'* following MacArthur & Macarthur (1961). We generated four height density rasters according to the following height intervals: 0 to 1.3 m, 1.3 to 10 m, 10 to 30 m and >30m. FHD is a common index to assess the vertical complexity among the forest vegetation layers, which is expected to be positively related to Hazel grouse habitat quality (e.g., Bergen *et al.* 2009; Zellweger *et al.* 2013; Bae *et al.* 2014).

GIS-derived environmental variables

I used the mean and standard deviation of topographic position, topographic roughness and slope to represent different aspects of the terrain (Table 1). Topographic position is a variable that indicates the exposure of a location in space compared to the surrounding terrain. Positive values express ridges, hilltops and exposed sites. Negative values stand for sinks, gullies, valleys or toe slopes. The measure summarizes various micro- to meso-climatic and edaphic features. The topographic position was calculated in GIS by applying circular moving-windows with increasing radii to a digital elevation model (Swisstopo 2015b; Zimmermann & Roberts 2001). Topography, topographic roughness and slope are supposed to influence the habitat quality of Hazel grouse indirectly by influencing forest structure through changes in exposure, steepness and soil condition (Schäublin & Bollmann 2011). I further considered solar radiation (potential shortwave radiation in March) as another environmental variable, because it also influences soil characteristics and light conditions and therefore plant development and forest structure (Kimmins 2004; Wermelinger 2004). To calculate this variable by using the DEM, the method developed by KUMAR et al. (1997) was used, which incorporates topographic shading effects.

To represent climate, I used long-term monthly means of average temperature (°C) and precipitation (mm) in June during the period of 1960–2006 (Table 1). Temperature and precipitation were spatially interpolated using a DEM as described in Zimmermann & Kienast (1999). The local climate influences the reproduction of Hazel grouse by reducing chick mortality in dry and warm weather in early summer (Bergmann *et al.* 1996).

To measure supplementary aspects of spatial vegetation patterns in addition to the LiDAR variables, four GIS-related variables describing forest edges, the proportion of forest and the forest type were developed (Table 1). For forest edge I used two variables: "Distance to forest edge" and "length of forest edge". The former describes the accumulated distance to forest edges within a grid cell. It was constructed by subdividing each cell into the smaller scaled reference squares and calculating the sum of distances of all reference squares within a grid cell, which had no forest cover, to the nearest reference square with forest. The second variable "length of forest edge" counts the total length of forest edge within a grid cell. The variable "proportion of forest" represented the percentage of the area covered with forest within the final grid cell. The forest cover layer used for these calculations is based on the Vector 25 dataset provided by swisstopo (Swisstopo 2015a) in which "shrub forest" (Cat. 6), "forest" (Cat. 12) and "open forest" (Cat. 13) were summarized as forest cover. The variable "forest type" was derived from satellite images (Landsat-5, Thematic Mapper, WMG25, BFS GEOSTAT) by an automated maximum likelihood classification. Forest type was available in four different categories: conifer forest, conifer-dominated mixed forest, deciduous-dominated mixed forest, and deciduous forest. Graf et al. (2005) confirmed the high accuracy of this classification.

To represent human disturbance, I used the variables "density of settlement" and "distance to settlements" (Table 1). Single buildings were represented by their footprint in m^2, the dataset SwissTLM3D_1.2_Gebäudefootprint_2014 provided by swisstopo (Swisstopo 2015c). Density of settlement represented the sum of all footprints of buildings within a grid cell, while distance to settlements was calculated the same way as distance to forest edge. Settlements with a footprint below 80 m^2 were suggest as not permanently inhabited and excluded from the analysis. Human activities affect habitat suitability of Hazel grouse negatively, though Hazel grouse is not as sensitive as other grouse species such as Capercaillie (Blattner 1998).

I assumed a positive effect of certain roads on habitat suitability, because they can represent open, linear ecotones within forests, with light-demanding woody plants providing important winter food resources for the Hazel grouse (cp. Bergmann *et al.* 1996). As indicators for this effect, I generated the variables "distance to roads" and "length of roads" (Table 1). Both variables were processed from the dataset SwissTLM3D_Strassen (2014) provided by swisstopo (Swisstopo 2015c), which comprises different categories of roads. I only used the categories 15 to 18 and combined them into less frequented roads, because of their maximum width of 2.80 m.

Predictor selection

For all variables, bivariate correlations were assessed. From variable pairs showing a Spearman's rank correlation coefficient higher than 0.5, only the variable considered to be ecologically more meaningful was selected as a predictor (cp. Appendix 1 and 2). Finally, I selected two different predictor sets to model habitat suitability of Hazel grouse (Table 1). One predictor set included 4 LiDAR and 8 GIS-related predictors describing forest structure or composition, topographic, climatic and human aspects. I chose the variable temperature, instead of precipitation. I expected that temperature is ecologically more relevant in the study area than precipitation, because of the temperature gradient along elevation. It affects forest composition more than disparity in precipitation in the study area. The second predictor set included 4 LiDAR and 2 GIS-related predictors, describing only biotic aspects of forest structure and composition. It was termed "125_biotic" model.

Statistical modeling

Model calibration, evaluation and validation

For the statistical analysis, I calculated an ensemble prediction using seven standard species distribution model algorithms. To consider model variability and to improve reliability of the model predictions, I averaged the outcomes of the single modeling methods on the area under the receiver operating characteristic curve (AUC) (see Segurado & Araujo 2004; Araújo & New 2007; Elith & Graham 2009; Jones-Farrand *et al.* 2011). I 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). This number of alternative modeling algorithms have been used to classify the probability of species' presence (and absence) as a function of a set of environmental predictors. The task is to identify potentially complex, non-linear relationships in multi-dimensional environmental space (Pearson 2007). To calibrate the models of the individual modeling algorithm and to generate the ensemble prediction of habitat suitability, I used BIOMOD (Thuiller *et al.* 2009) with the R package "BIOMOD2" (R package version 3.3-3/r713) (Thuiller *et al.* 2015) and additionally integrated the BIOMOD_tuning function to tune single model parameters.

The predictive performance of the ensemble models was assessed using a 5-fold cross validation procedure which was repeated five times. I thus used 80% of the data as training data and tested its predictive performance on the remaining 20% of the data. Model accuracy was evaluated based on AUC which provides a single measure of overall accuracy and is not dependent upon a particular threshold (Fielding & Bell 1997; Boyce *et al.* 2002). AUC tests both, presence and absence records (Pearson 2007). However, AUC can be applied using pseudo-absence data instead of absence records (cp. Phillips *et al.* 2006). AUC values >0.7 represent acceptable, 0.8–0.9 excellent, and >0.9 outstanding model discrimination (Hosmer & Lemeshow 2000). In addition, I used sensitivity and specificity for the evaluation process. Sensitivity describes the proportion of recorded presence plots, which are predicted correctly as presence in relation to the total of recorded presences (including recorded presence plots which were predicted wrongly as absences). Hence, specificity defines the proportion of correct predicted absence plots in relation to the total of absences (including absence data, which were predicted wrongly as presence) (Pearson 2007). To interpret 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). To infer the direction and shape of the effect of each predictor on the Hazel grouse habitat suitability, I calculated response curves (Thuiller *et al.* 2009).

Results

Model performance

The model “125_all”, in which all predictors were used, fitted excellently (Results for the models based on grid cell sizes of 250m and 50m, see Appendix 3). The model achieved a median AUC value of 0.959 (Table 2). The marginal standard deviation of 0.021 for the AUC rejected an overfit of the model due the calibration process. Values higher than 90.00 for both specificity and specificity confirm the high accuracy of this model. Four predictors had a median predictor contribution higher than 0.1 and explained together 1.0 of the shared variable importance. The two GIS-derived predictors “temperature” and “solar radiation” were the most important predictors affecting habitat suitability of Hazel grouse, the former with a contribution of 0.598 and the latter with 0.246. The predictors “Shrub density” and “average vegetation height”, the most influential LiDAR-derived variables, had a median predictor contribution of 0.161 and 0.139, respectively. All other predictors made a marginal contribution to the model with mean variable importance below 0.05.

Also the model “125_biotic”, in which only biotic (structural) predictors are used, had an excellent predictive power with an AUC from 5-fold cross-validation of 0.914 (Table 2). With sensitivity and specificity median values of 90.00 and 84.38, specificity was lower compared to the model that used all predictors. In addition, standard deviation of all evaluation values of model “125_biotic” were higher compared to the model “125_all”. The two most important predictor variables “average vegetation height” and “shrub density” had a median variable importance of 0.693 and 0.228, respectively. In comparison to the “125_all”, the predictor contribution of “average vegetation height” was much higher and the importance of the other predictors (≥ 0.1), with the exception of “forest type”.

Table 2: Median predictive performance and median predictor contribution of model ensembles for the Parc régional Chasseral. The model “125_all” is based on a combination of environmental variable describing climate, topographic and landscape and LiDAR-derived small scale structural vegetation patterns. In the model “125_biotic”, only biotic (structural) predictors were used. In addition to median values of AUC, sensitivity and specificity and the standard deviation (parenthesized) were calculated. The median predictor contribution is given in percent. All evaluation values are based on a 5-fold-cross-validation with 5 repetitions.

	Model 125_all	125_biotic
Median predictive performance		
AUC	0.959 (0.021)	0.914 (0.036)
Sensitivity	90.00 (6.415)	90.00 (7.576)
Specificity	92.55 (3.886)	84.38 (5.403)
Median predictor contribution		
LiDAR-derived predictors		
Average vegetation height	0.139	0.693
Standard deviation of successional stages	0.016	0.153
Shrub density	0.161	0.228
Sum of small gaps	0.029	0.122
GIS-derived predictors		
Topographic position	0.004	
Slope	0.044	
Solar radiation in June	0.246	
Mean temperature	0.598	
Forest type	0.027	0.073
Length of forest edge	0.017	0.151
Distance to settlements	0.005	
Length of roads	0.003	

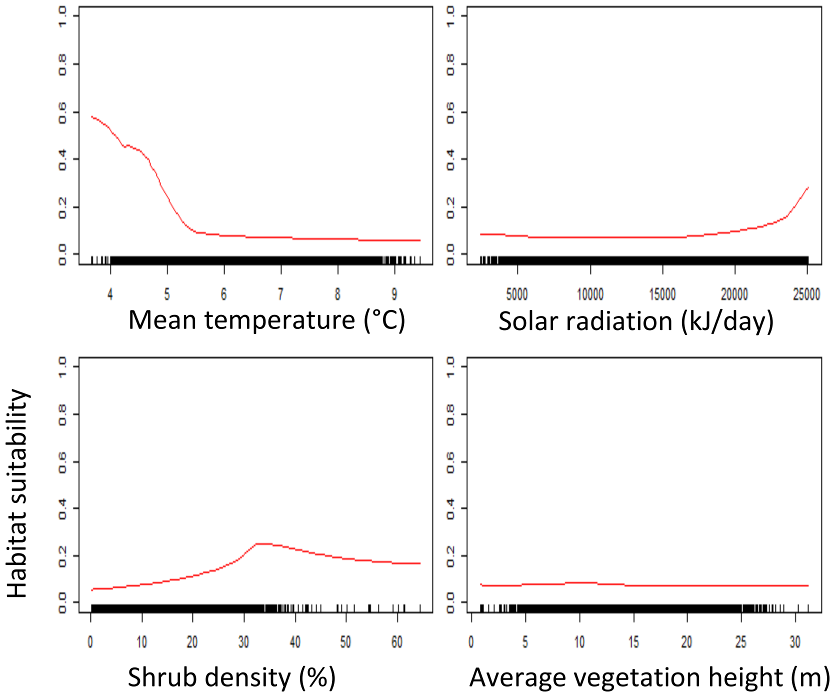
Predictor response curve

I focused my examination of the response curve on the best predictors. For further results see Appendix 4.

“Temperature” as the most influential predictor in the model “125_all”, was negatively correlated with Hazel grouse occurrence: The response curve in Fig. 2a shows a decreasing habitat suitability by increasing temperature. Mean temperatures above 5°C strongly reduced habitat suitability. Contrary, a rising solar radiation promotes habitat suitability for Hazel grouse, especially in the range of the highest values. The response curve of shrub density indicates an optimum density between 30 and 35 %. In contrast, the response curve of “average vegetation height” depicted no trend for the effect of vegetation height on habitat suitability.

However, in the model “125_biotic”, “average vegetation height” as the most influential predictor, showed an optimum height of around 8 m (Fig. 2b). The declining function of vegetation heights above 8 m depicted a decreasing habitat quality with increasing heights. “Shrub density”, the second most importance predictor showed a unimodal response with an optimum between 25 and 30 %.

(a)



(b)

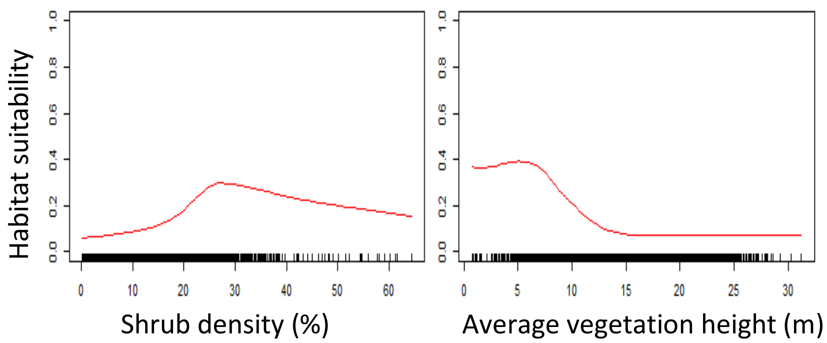


Fig. 2: Response curves of the most influential predictor variables of the ensemble model “125_all” (a) and of the ensemble model “125_biotic” (b). The graphs show the effect of a particular predictor: increasing values on the y- axis indicate that the probability of Hazel grouse presence responded positively, decreasing values the opposite. The x-axis shows the data range of predictor variable measurements in the study area.

Model predictions

The map of habitat availability of the model "125_all" depicted habitat suitability values >600 in two linear patches along the upper forest line (Fig. 3). In the center of the park around the mountain Chasseral, high suitable areas were arranged as a band with a concentration on the southern slope of the mountain range. A few small patches with high suitability were spread close by. Besides, high suitability areas could be identified in the south-west of the park area along the Mont d'Amin, close to the border of the park. These two patches of high suitability were completely segregated. Across the remaining perimeter only very small suitable patches for Hazel grouse could be identified.

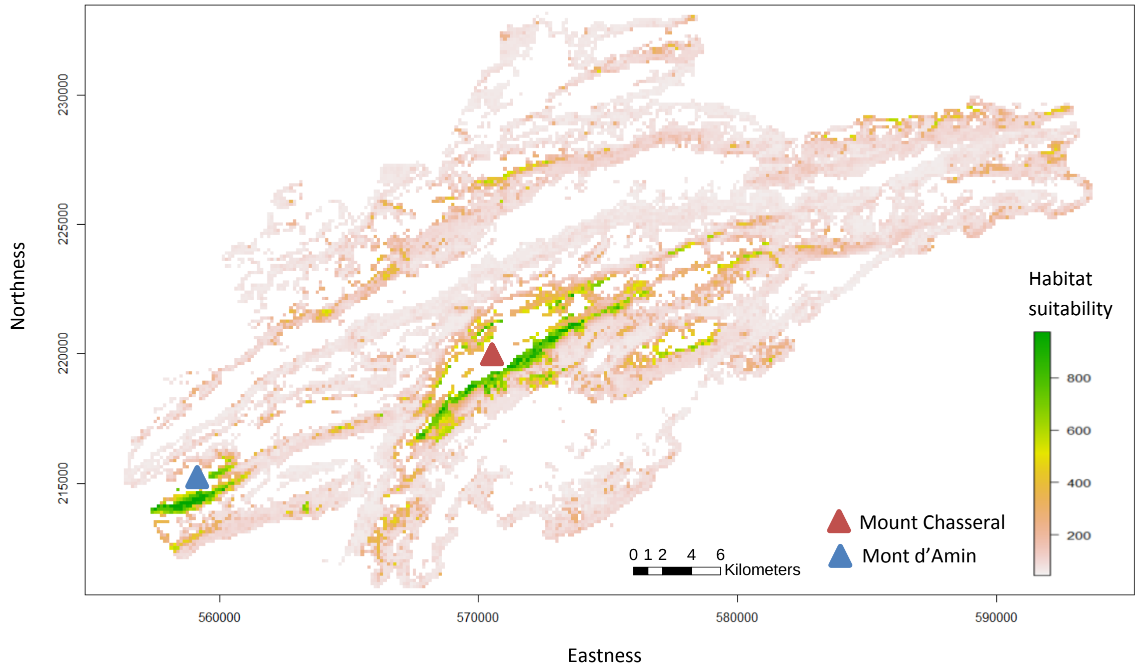


Fig. 3: Predicted habitat suitability in the Parc régional Chasseral illustrated with values from 0 to 1000. The predictions are based on the model ensemble "125_all". Cells with green or greenish colors implied areas with high suitability for Hazel grouse. Intermediate habitat suitability is indicated in yellow and areas with low suitability in reddish. The x- and y-axis represent the Swiss coordinate System (CH1903_LV03).

The already mentioned patches with pixels of high suitability (Chasseral, Mont d'Amin) were also predicted in the model "125_biotic" (Fig. 4). However, the extent was smaller and suitable patches, in general, were more dispersed over the study area. Just as in the model "125_all", the majority of the park perimeter was predicted with poor habitat suitability for Hazel grouses.

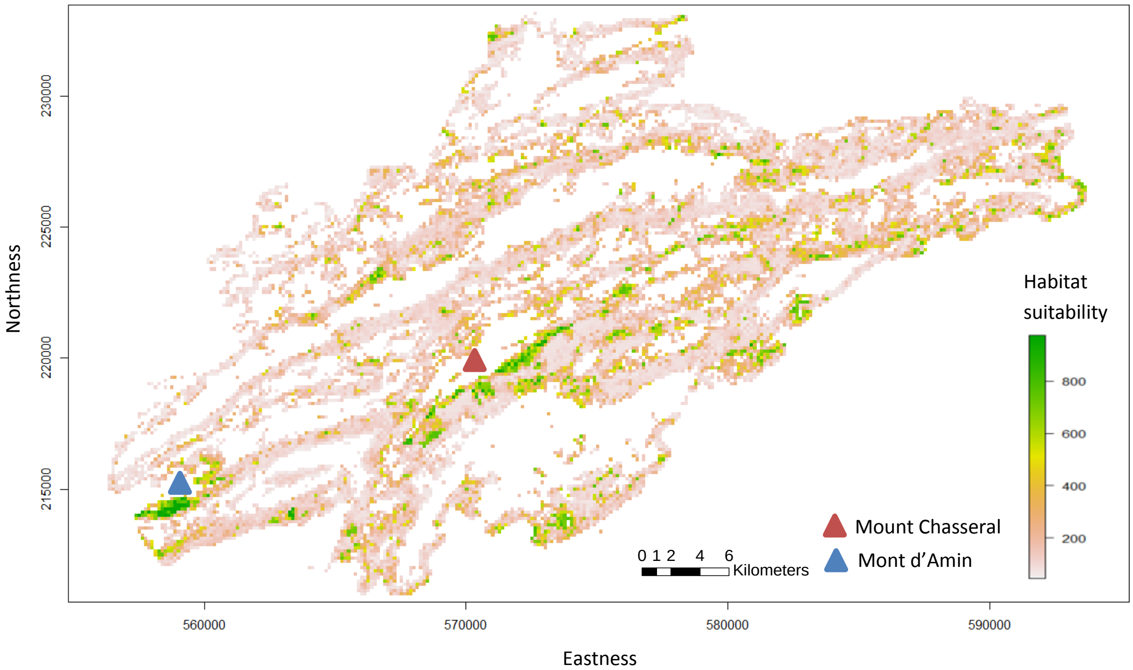


Fig. 4: Predicted habitat suitability in the Parc régional Chasseral illustrated with values from 0 to 1000. The predictions are based on the model ensemble "125_biotic". Cells with green or greenish colors indicate areas with high suitability for Hazel grouse. Intermediate habitat suitability is indicated in yellow and areas with low suitability in reddish. The x- and y-axis represent the Swiss coordinate System (CH1903_LV03).

Discussion

Potential of habitat suitability modeling for Hazel grouse

I assessed the potential of habitat suitability modeling for Hazel grouse in the Parc régional Chasseral based on a combination of environmental variables describing climate and topography, landscape composition and vegetation structure. The excellent performance of the model "125_all" shows the high applicability of habitat suitability modeling for the Hazel grouse at the landscape scale. Effects of overfitting can be rejected due the small standard deviation of the AUC in the model evaluation. Even though model accuracy was only the second best of the three tested resolutions (see Appendix 3), the model with a grid cell size of 125 m was chosen because the difference between model accuracy of all three models were marginal and 1 ha is a wide-spread and frequently used planning unit in silvicultural and conservation management (A. Gerber personal communication, March, 2016). The 125 m cell sizes allowed for assessing habitat conditions at a high spatial precision across the entire landscape. An effect of losing resolution of habitat features through averaging environmental patterns for each grid cell is much smaller compared to larger grain sizes (e.g., 1km^2) which are frequently applied in other studies (Gottschalk *et al.* 2011). The use of pseudo-absence due to the lack of verified absence information in the study area could have negatively affected the model (Brotons et al. 2004; Gu & Swihart 2004). However, Barbet-Massin et al. (2012) showed that selecting 10'000 cells from the background as pseudo-absences with equal weighting for presences appears to be a good alternative and is thus widely used in predictive distribution modeling (e.g., Ferrier et al. 2002a; Ackers et al. 2015; Breiner et al. 2015). I cannot exclude that the decision of the park management for a focus of the species field survey on the best suitable areas could have provoked a certain bias by missing exceptional occurrences in suboptimal habitats (see Brotons *et al.* 2004; Gu & Swihart 2004). However, the integration of random observation of the Swiss Ornithological Institute represents a certain balance.

Both, GIS-derived and LiDAR-derived predictors showed high median predictor contributions and recorded relevant aspects of habitat quality for Hazel grouse. However, the "model 125_all" revealed a strong influence of temperature and solar radiation on habitat suitability of Hazel grouse. The response curve of "temperature" indicates that the habitat suitability of Hazel grouse decreases with increasing temperature. Only a mean temperature in June below 5°C supports habitat suitability positively. This strong influence of temperature and its small suitable range raises the question of a direct or indirect effect of this variable on habitat suitability of Hazel grouse within the study area. Due to the mountainous conditions, temperature is negatively correlated with elevation, and thus, the model defined areas at low elevations as less suitable. However, historical records in this region prove former occurrence of the species at lower elevations than the topographically lowest point of the study area (Blattner 1998). Climate conditions of the study area are well nested within the climate envelope of the species' global range. In Siberia, Hazel grouse can withstand very low temperature of -45°C without problem, a situation that is exceptional in the Swiss Jura mountains (Mulhauser 2003). Hazel grouse also occurs in the deciduous forests of the canton of Tessin in the southern part of Switzerland (Maumary *et al.* 2007). In contrast to the predicted negative correlation of temperature and habitat suitability, annual variation in temperature influences the breeding success, whereby cold and wet weather conditions increase mortality of juveniles (Bergmann *et al.* 1996). In this study, it can thus be assumed that temperature is indirectly related to Hazel grouse habitat suitability by its effect on forest type, i.e. coniferous vs. deciduous. Also Zellweger et al. (2016) showed, that the effect of climate on species richness of butterflies in forest dominated landscapes appeared to be mainly indirect, via correlations with habitat type and structure. Moreover, other studies highlighted aspects of forest structure complexity and forest composition as key-factors for Hazel grouse habitat (Bergmann *et al.* 1996; Åberg *et al.* 2003; Mathys *et al.* 2006; Schäublin & Bollmann 2011; Zellweger *et al.* 2014) and hence temperature alone cannot limit habitat suitability in a restricted study area of this dimension.

The majority of grid cells with high habitat suitability occur at the southern slope of the Mount Chasseral and Mont d'Amin. They are concentrated as a band along the upper forest in proximity to the tree line and the above pastures on the mountain chain (see Fig. 3). Today, the natural treeline is still pushed down by pastoralism. However, the comparison of contemporary aerial photographs with historical maps, such as the Siegfriedkarte from the beginning of the 19th century, shows that the forest expanded up to 200 m into the pastures due to land use changes. This gradual and heterogeneous forest edge consisting of early successional stages and old growth stands provide suitable habitats for the Hazel grouse. Also Montadert & Klaus (2011) showed that forest edges in a forest-pasture mosaic were suitable habitats for Hazel grouse in a mountainous landscape. The long-term historical use of the upper grasslands and adjacent forests as wood pastures is considered to be an important indicator of contemporary habitat quality for Hazel grouse. In the Swiss Jura mountains, as well as within the park area, wood pastures were widespread at the beginning of the 19th century (Grossmann 1927). I suggest that grid cells with high habitat suitability close to grassland in my study area still comprise positive effects on forest structure and composition due to the former land use as forest pasture. This reasoning is in line with Montadert & Leonard (2003) who assumed that the expansion of Hazel grouse in a mountainous habitat consisting of forest-pasture mosaics is largely related to the abandonment of grazing activities and the subsequent spontaneous reforestation of pastures. The subsequent spontaneous forest succession in pastures and forest pastures has created an optimal habitat for Hazel grouse. Moreover, Mayer & Stöckli (2005) compared grazed and ungrazed subalpine forests and showed that grazing caused a multi-layered forest structure with a higher percentage of threes belonging to early successional stages compare to ungrazed forest with more dens and uniform stands. Furthermore, Mountford & Peterken (2003) showed, that species richness in the shrub cover increased due to grazing and that the impact of heavy grazing can be recognized for many decades after the abandonment. In contrast, forest stands next to open grassland on lower elevations were mostly predicted as less suitable in this study. The impact of contemporary forest management on low elevation areas is obviously negative and has replaced the effect of the historical land use. The higher proximity and accessibility of the forest could have triggered a more intensive use and may have resulted in a dominance of single-layered stands with lower structural diversity. Also, forest succession is faster in lower areas with milder climate and supports the transformation to high forest stands (DeLong & Meidinger 2003; Bolli *et al.* 2007). The combination of this forest transformation and a higher availability of anthropogenic food sources for generalist predators in lower areas (Storch 2007) could explain the loss of historically occupied stands in lower areas of the park. Based on my results, I suggest that temperature indirectly represents effects on forest structure and composition due to contrasting land use practices along the altitudinal gradient over time.

Solar radiation seems to influence habitat suitability strongly. An increased availability of light on the ground allows for developing a diverse shrub cover, including many light-demanding trees and shrubs that provide food resources. It prevents growing of only shade tolerant plants such as beech. Further, forest stands with a high solar radiation will exhibit warmer soil temperatures and a higher potential of drought stress and are thus more susceptible to disturbance agents that enhance forest structural complexity (Fischer *et al.* 2013). Natural disturbance (e.g., wind storm, drought, insect calamity) are important drivers for suitable Hazel grouse habitat in natural forests (Bollmann 2010). However, solar radiation can only be used as an indirect indicator for such physiological relationships.

The predictors „shrub density“ and „average vegetation height“ are variables describing biotic aspects of the 3D habitat profile and are therefore key-variables of habitat suitability for Hazel grouse (Bergmann *et al.* 1996). The summed predictor contribution of 0.3 confirms the importance of the 3D forest structure. The optimum proportion of shrub layer of 30 to 35% of the total vegetation (see Fig. 2b) reflects the tight preference of Hazel grouse for multi layered forests with abundant shrub cover. These results indicate that single layered high forest stands with low or absent shrub layers do not represent habitat for the species (see also Mathys *et al.* 2006; Zellweger *et al.* 2013, 2014).

The high accuracy of the model using the full predictor set showed the good applicability of this modeling approach for modeling habitat suitability of Hazel grouse. The use of abiotic predictors, in this case temperature, may buffer the signals of other predictors and have therefore a limited potential to represent the potential ecological niche in a restricted study area. The high predictor contributions of „shrub density" and „average vegetation height" confirmed the importance of 3D forest structure for the species.

Potential of LiDAR to assess 3D forest structure and forest composition

To assess the potential that LiDAR data offers for habitat modeling, I developed the biotic model, which predicts habitats suitability of Hazel grouse in the Parc régional Chasseral solely based on biotic predictors. Four of the six predictors were derived from LiDAR, two from GIS-layers (Table 1). The high model accuracy with an AUC of 0.914 and the high values of specificity and sensitivity demonstrated the excellent applicability of LiDAR-derived predictor variables for modeling habitat suitability of Hazel grouse. These results are in line with previous studies which used LiDAR as a complementary source of habitat information (see Farrell *et al.* 2013; Flaherty *et al.* 2014; Vogeler *et al.* 2014; Zellweger *et al.* 2014; Ackers *et al.* 2015). In contrast to other studies, my results demonstrate that habitat suitability of Hazel grouse can be predicted exclusively on the basis of biotic forests variables. This highlights the importance of 3D forest structure for the Hazel grouse itself and confirms the high applicability of LiDAR for accurately recording 3D ecosystem structure. Modeling habitat suitability of a forest species only with biotic predictors integrate human habitat management. I used predictors that are at least partly controlled by silvicultural management and hence subject to practical implementation. The median predictor response curve of the two most influential predictors "average vegetation height" and "shrub density provided explicit information on how their combination affects habitat suitability of the Hazel grouse. The optimum contribution of "average vegetation height" around 8 m could indicate either a multi-storied forest with different successional stages, or a two-layered forest where the average of these layers is around 8 m. These results exclude one-layered high forest stands with marginal shrub density from suitable habitats and are consistent with the previous discussed results from the full model.

However, LiDAR is not able to record and define vegetation composition and single species directly (Bergen *et al.* 2009). Measurements of shrub density with LiDAR-derived predictors cannot distinguish between a species rich shrub layer and a pure beech shrub cover. This limitation is essential for Hazel grouse because the species is a food specialist and the incidence of specific food plants tend to be a crucial factor for Hazel grouse occurrence in mountain areas (e.g., Müller *et al.* 2009; Schäublin & Bollmann 2011). To reduce this methodological limitation, I selected predictor variables, which describe both, the complexity of forest structure itself and the light or temperature conditions in the lower stratum of the forest, as a proxy for the potential growth of light demanding woody species (see Müller & Brandl 2009). However, the accuracy of the model and the fine-scaled differentiation of suitable grid cells demonstrated the high potential of LiDAR-derived predictor variables to examine forest characteristics related to the structure and the understory vegetation and therefore for assessing habitat suitability of forest species across entire landscapes.

Management implications

Despite a surge in the development of HSM/SDMs in this decade, evidence of the application of these models in real-world conservation management remains sparse (Guisan *et al.* 2013). There is few literature that document the use of HSM/SDMs for conservation decision making (e.g., Soberon *et al.* 2001; Ferrier *et al.* 2002; Leathwick *et al.* 2008; Bässler *et al.* 2011; Bennetsen *et al.* 2016). Most of the studies only underlined the high potential of HSM/SDMs for conservation management without specific applications and adaptions. Therefore, only little guidance exists on how HSM/SDMs can support decision making for conservation purpose (Guisan *et al.* 2013). In this study, I attempted to inform the conservation management in the Parc régional Chasseral on the abundance and distribution of suitable Hazel grouse habitat. Conservation management should target for an increase in the size of the regional Hazel grouse population by conserving the occupied habitat patches and by creating more suitable habitats next to them. In a second step, occupied patches should be functionally connected by newly created stepping stone habitats.

To increase the suitability and connectivity of Hazel grouse habitat in the Parc régional Chasseral, I recommend the following measures:

Habitat area

(1) The two largest habitat patches with high suitability (Fig. 3) in the prediction of the model “125_all” define the core areas of the regional Hazel grouse population. A comparison of the predictions of the full and biotic models within these patches shows that many grid cells have low structural suitability. The structural improvement of these grid cells in matters of average vegetation height and shrub density in combination with a silvicultural promotion of food plants would restore the habitat and indirectly strengthens the Hazel grouse population itself. Only healthy populations produce enough emigrants that can colonize nearby habitat patches according to the source-sink metapopulation theory (Thomas & Kunin 1999).

(2) Second, increase habitat suitability of the adjacent areas to provide space for new territories. According to the size of a Hazel Grouse territory of 10 to 20 ha (Bergmann *et al.* 1996; Maumary *et al.* 2007), successful management depends on sufficiently large area.

(3) Third, improving the connectivity of the two core patches by silvicultural management in the less suitable forest between. Rueda et al. (2013) showed that Hazel grouse is very sensitive to habitat fragmentation. Hazel grouse as a highly sedentary and territorial bird does not cross open landscapes of more than 200 m (Bergmann *et al.* 1996). Even the effect of

isolation is less evident in a forest landscape, Åberg et al. (1995) supposed a maximum distance of around 2 km between suitable habitats.

Habitat quality

(1) Transformation of single-layered high forest stands to multi-storied stands with a well-developed shrub cover. This could be achieved by creating an irregular pattern of gaps with unevenly distributed mature trees. Alternatively to silvicultural measures, an extensive and temporal restricted pasturing could also improve habitat quality.

(2) Promotion of light-demanding shrub species e.g. *Sorbus, Salix, Betula, Alnus, Sambucus, Corylus*, and *Populus* as crucial food resources during winter. In particular, these species should be preserved during thinning actions. Rather, these resource plant can be encouraged by a clever silvicultural light management on the ground layer.

(3) Creating forest gaps with diameters of around 30 m (Müller *et al.* 2009b) to offer foraging and breeding sites in summer, but still small enough to provide shelter.

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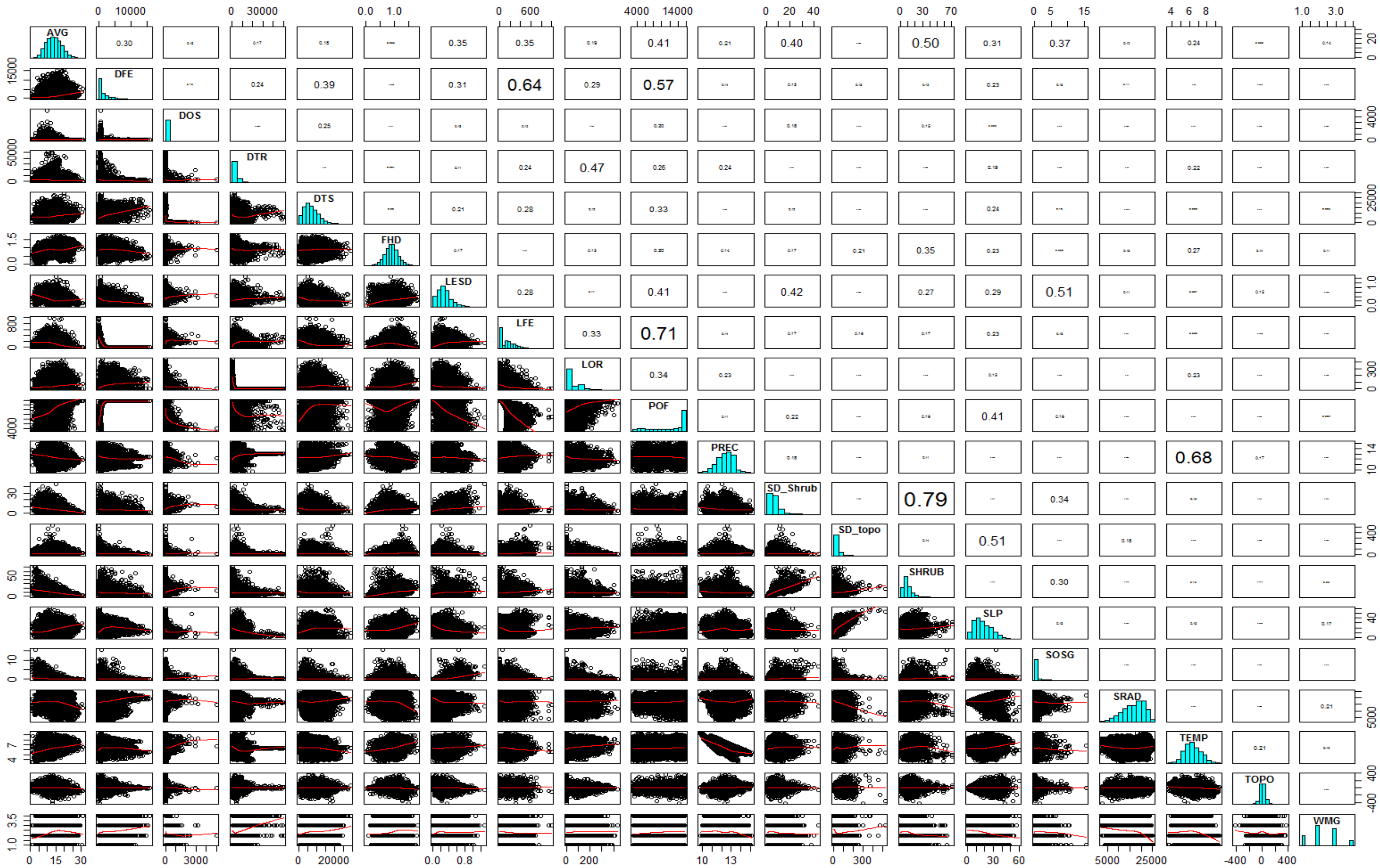
Appendix 1 – Description of the environmental variables and their assignment to different models. result of the pairwise correlation

Description of environmental variables, their units and abbreviation. The references squares describe the square size in meters, in which the variable processing based on. All variables were tested by pairwise correlation (Appendix 2). If two variables had a correlation > 0.5, the variable with the higher ecological relevance was selected as a predictor. I selected two different predictor sets. The model approach "model_all" includes predictors describing forest structure or composition and topographic, climatic and human aspects, which were tested for grain size of 250, 125 and 50 m. The model "125_biotic" consists only of biotic predictors and were used only for a grain size of 125 m.

Variable description	Unit	Abbreviation	Predictor selected in model	
			model_all	*125_biotic*
LiDAR-derived variables				
Average vegetation height	m	AVG	X	X
Standard deviation of successional stage	unit less	LESD	X	X
Shrub density	%	SHRUB	X	X
SD of shrub density	unit less	SD_SHRUB		
Sum of small gaps	counter	SOSG	X	X
Foliage height diversity	unit less	FHD		
GIS-derived variables				
Topographic position	unit less	TOPO	X	
Roughness	unit less	SD_topo		
Slope	degrees	SLP	X	
Solar radiation in March	kJ/day	SRAD	X	
Mean temperature	°C/month	TEMO	X	
Mean precipitation	mm/month	PREC		
Distance to forest edge	m	DFE		
Length of forest edge	m	LFE	X	X
Proportion of forest	m^2	POF		
Forest type	4 categories	WMG	X	X
Density of settlements	m^2	DOS		
Distance to settlements	m	DTS	X	
Distance to roads	m	DTR		
Length of roads	m	LOR	X	

Appendix 2 – Bivariate correlation matrix for each pair of environmental variables. The squares with the figures show the distribution of values of each variable. The squares with the number show the correlation between the variable on the x-axis and the variable on the y-axis. Abbreviation are explained in Appendix 1.



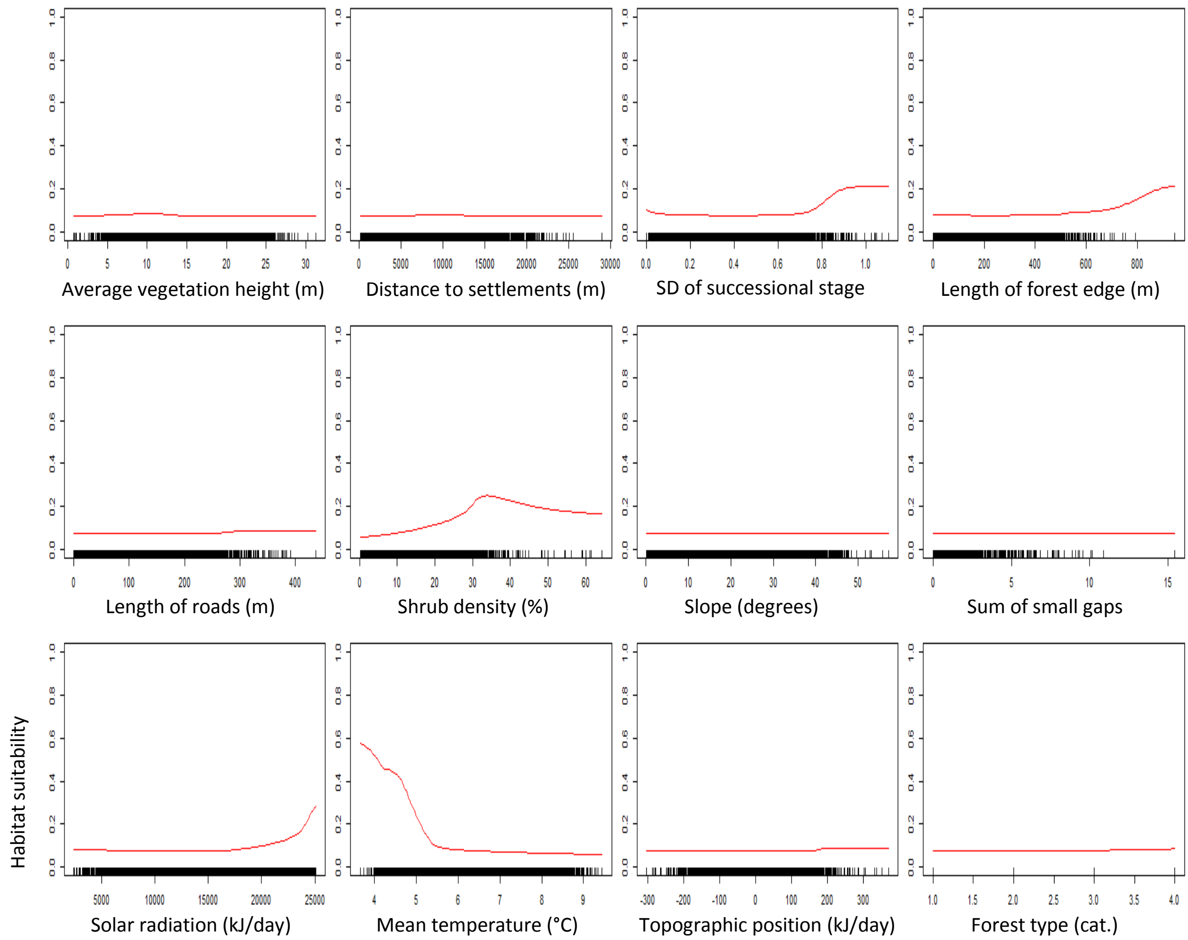
Appendix 3 – Results of the models "250_all", "125_all" and "50_all"

Model performance of model ensembles based on a combination of environmental variables describing climate, topography, landscape and LiDAR-derived small scale structural vegetation patterns with a spatial resolution of 250 m, 125 m, and 50 m (grain sizes). To measure the median predictive performance, AUC, sensitivity and specificity and the standard deviation (parenthesized) were calculated. The median predictor response is given in percent. All evaluation values are based on a 5-fold-cross-validation with 5 repetitions.

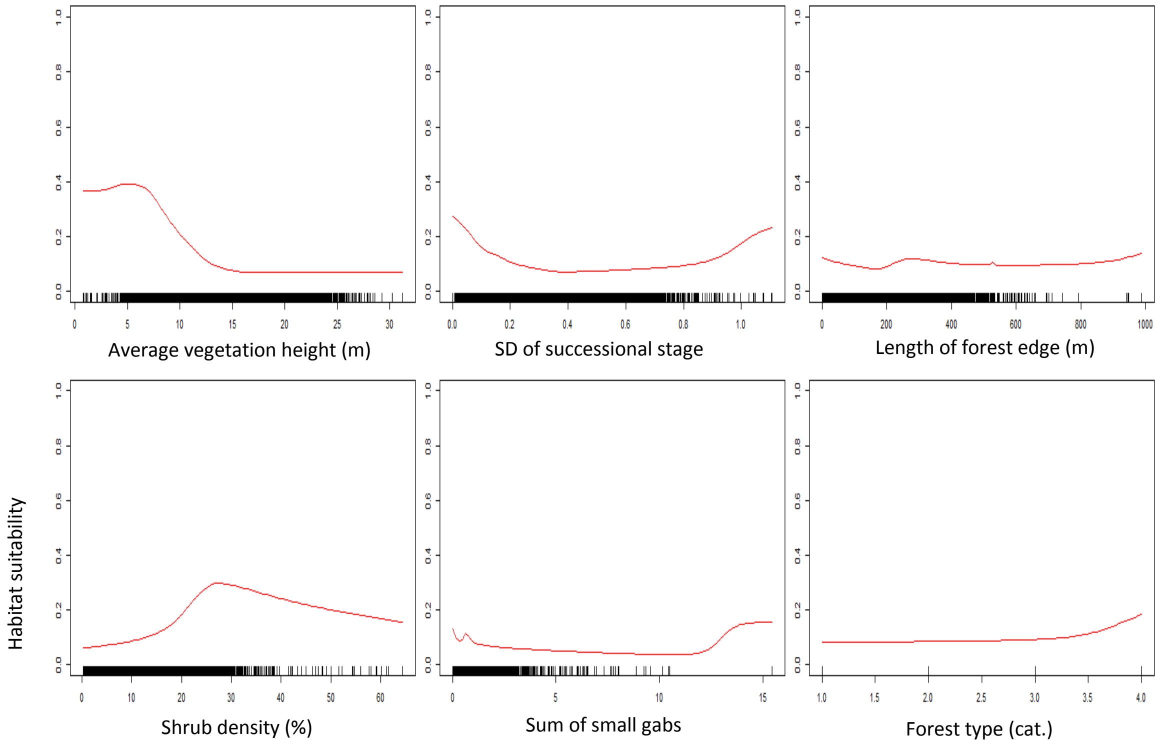
	Model name		
	250_all	125_all	50_all
Median predictive performance			
AUC	0.953 (0.029)	0.959 (0.021)	0.971 (0.021)
Sensitivity	92.86 (7.319)	90.00 (6.415)	92.00 (5.487)
Specificity	90.05 (5.807)	92.55 (3.886)	92.12 (4.806)
Median predictor contribution (%)			
LiDAR-related predictors			
AVG	0.032	0.139	0.183
LESD	0.049	0.016	0.009
SHRUB	0.170	0.161	0.055
SOSG	0.011	0.029	0.026
GIS-related predictors			
TOPO	0.019	0.004	0.009
SLP	0.033	0.044	0.052
SRAD	0.283	0.246	0.240
TEMP	0.677	0.598	0.584
WMG	0.072	0.027	0.055
LFE	0.010	0.017	0.023
DSETTL	0.009	0.005	0.010
LFROAD	0.006	0.003	0.007

Appendix 4 – Response curves of each predictor in the model "125_all" (a) and in the model "125_biotic" (b). Because of the higher predictive performance and the better resolution of data, only the model approach based on a grain size of 125 m was further investigated.

(a) Response curve of each predictor used in the ensemble model "125_all". The graphs show the effect of a particular predictor: 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 each predictor variable measured in the study area.



(b) Response curve of each predictor used in the ensemble model "125_biotic". The graphs show the effect of a particular predictor: 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 each predictor variable measured in the study area.



Eidesstattliche Erklärung

Ich erkläre eidesstattlich, dass ich die Arbeit selbständig angefertigt habe. Es wurden keine anderen als die angegebenen Hilfsmittel benutzt. Die aus fremden Quellen direkt oder indirekt übernommenen Formulierungen und Gedanken sind als solche kenntlich gemacht. Diese schriftliche Arbeit wurde noch an keiner Stelle vorgelegt.

Datum: Unterschrift: