

*Schlussbericht des Projekts*

# **Predicted effects of climate change on indicator species of structural and biological diversity in mountain forests: towards adaptive forest management in the face of environmental uncertainty**

*im BAFU/WSL-Forschungsprogramm Wald und Klimawandel*



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Januar, 2014

Eidg. Forschungsanstalt für Wald, Schnee und Landschaft WSL, CH-8903 Birmensdorf



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Ein Projekt-Schlussbericht aus dem Forschungsprogramm «Wald und Klimawandel» von BAFU und WSL ([www.wsl.ch/wald\\_klima](http://www.wsl.ch/wald_klima))

Projektlaufzeit: 1.7.2010 – 30.6.2013

## Zitierung

Bollmann, K; Braunisch, V; Arlettaz, R. 2014. Predicted effects of climate change on indicator species of structural and biological diversity in mountain forests: towards adaptive forest management in the face of environmental uncertainty. Birmensdorf, Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL; Bern, Universität Bern; Freiburg, Forstliche Versuchs- und Forschungsanstalt BW. 35 S.

## Dank

Wir danken allen Personen, die zur Entstehung dieses Berichts beigetragen haben. Zuerst möchten wir der Leitung des Forschungsprogramms Wald und Klimawandel für den Zuspruch und die Finanzierung des Projekts danken, sowie Peter Brang (WSL), Julia Born (WSL) und Sabine Augustin (BAFU) für die operative Begleitung. Ein besonderer Dank gehört Nino Maag, der als wissenschaftlicher Assistent die Vorbereitung und Durchführung der Feldarbeiten stark unterstützt hat sowie allen Masterstudierenden und technischen Feldassistenten, die mit ihrem Einsatz einen erheblichen Teil zum Gelingen des Projekt beigetragen haben. Namentlich sind dies: Lisa Bitterlin, Joy Coppes, Karin Feller, Lucretia Deplazes, Lea Hofstetter, Maria Rusche, Jan Sadowski, Sarah Spille, Florian Zellweger. Speziell danken möchten wir Rudi Suchant, der bei der Konzeption des Projekts beteiligt war sowie Joy Coppes und Florian Zellweger für ihre inhaltliche und fachliche Unterstützung in der zweiten Phase des Projekts. Niklaus Zimmermann und Achilleas Psomas (alle WSL) haben die Klimadaten für unser Projekt zur Verfügung gestellt. Die Schweizer Vogelgedaten stammen zum grössten Teil aus der Datenbank der Schweizerischen Vogelwarte Sempach, Hans Schmid hat sie aufbereitet – vielen Dank. Ergänzende Daten für die Schweiz wurden der Raufusshuhndatenbank der WSL entnommen und im Jura haben François Mathey, Pierre Walder und Laurent Willenegger Daten zur Verbreitung des Dreizehenspechts beigesteuert. Die Vogelgedaten Baden-Württembergs stammen aus der Wildtiermonitoring-Datenbank der FVA. Felix Morsdorf hat uns bei den LiDAR-Daten beraten und die Algorithmen zu deren Prozessierung überlassen. Ergänzende Unterstützung haben wir erhalten durch Andi Baltensweiler, Christian Ginzler (beide WSL) und Pierrick Buri, Jean-Yves Humbert und Olivier Roth von der Uni Bern.

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## Zusammenfassung

Das Ziel der Studie war, den Einfluss des prognostizierten Klimawandels auf die Verbreitung und die realisierte Nische von vier ausgewählten Vogelarten des Gebirgswaldes zu untersuchen. Zudem quantifizierten wir, wieweit sich mit forstlichen Lebensraummaßnahmen negative Auswirkungen des Klimawandels kompensieren lassen. Als Modellarten wählten wir vier kälteadaptierte Vogelarten mit unterschiedlichen Habitatsprüchen, nämlich Haselhuhn (*Bonasa bonasia*), Auerhuhn (*Tetrao urogallus*), Sperlingskauz (*Glaucidium passerinum*) und Dreizehenspecht (*Picoides tridactylus*) und stellten folgende Fragen: (1) Inwieweit erklären Klima, Landschaftsstruktur und Vegetation das Vorkommen der Modellarten? (2) Wie wird sich der Klimawandel auf Habitatqualität und Artvorkommen auswirken? (3) Können diese Auswirkungen durch Habitatmanagement kompensiert oder abgeschwächt werden? Wir analysierten die Lebensräume der Modellarten auf 300 1km<sup>2</sup> grossen Testflächen entlang eines Höhengradienten in vier biogeographischen Regionen, namentlich Schwarzwald, Schweizer Jura, Nördliche Voralpen und Innere Alpen Graubündens. Die Feldarbeiten wurden von vier Feldteams durchgeführt, die aus einem wissenschaftlichen Assistenten (Koordinator), vier Masterstudierenden, einer Bachelorstudentin und zwei Feldassistentinnen bestanden. Basierend auf den terrestrisch erhobenen Vegetationsdaten und GIS-basierten Landschaftsdaten für die Testflächen wurde das Vorkommen der Arten unter aktuellen Klimabedingungen modelliert und ins Jahr 2050 extrapoliert, wobei das moderate IPCC-Szenario A1B angenommen wurde. Wir unterschieden zwei Modellansätze: der erste untersuchte das grossräumige Vorkommen auf Landschaftsebene (d.h. im gesamten Untersuchungsgebiet Baden-Württemberg und Schweiz), der zweite die lokale Habitatnutzung innerhalb der klimatischen Nische unter Berücksichtigung der vegetationspezifischen Habitatstrukturen.

Die Ergebnisse zeigen, dass das Klima nicht nur auf der Landschaftsebene sondern auch innerhalb der ökoklimatischen Nische der Arten einen bedeutenden Teil des Vorkommens erklärt. Mit dem Klimawandel wird für alle vier Arten ein Verbreitungsrückgang vorhergesagt (Durchschnitt: Dreizehenspecht –22%, Sperlingskauz –26%, Haselhuhn –30%, Auerhuhn –41%). Dieser Rückgang ist nur zum Teil auf Veränderungen in der Vegetation zurückzuführen. Die negativen Auswirkungen können teilweise kompensiert werden durch eine waldbauliche Anreicherung von einzelnen, artspezifischen Strukturelementen. Eine vollständige Kompensation ist jedoch nur mit kombinierten Massnahmen, d.h. der Förderung verschiedener Strukturelemente möglich. Für den Dreizehenspecht bedeutet dies beispielsweise, dass in Gebieten mit natürlicher Zunahme der Buche das stehende Totholzangebot erhöht und ein minimaler Anteil an Fichte in Beständen mit über 15 m Höhe im Aktionsraum der Art vorhanden sein muss.

Unsere Ergebnisse deuten darauf hin, dass das häufig vereinfacht dargestellte Wirkungsgefüge zwischen Klimawandel und Artvorkommen differenzierter betrachtet werden muss. Die Vorhersagen grossräumiger Art-Verbreitungsmodelle sind keine geeigneten Grundlagen für strategische Entscheide bei Zielkonflikten zwischen Artenschutz und Klimawandel, da sie kleinräumige Interaktionen zwischen Klima, Artvorkommen und Vegetationsstrukturen sowie sich daraus ergebende Handlungsspielräume für adaptives Management nicht berücksichtigen. Grossräumige Klimahüllenmodelle können daher dazu verleiten, laufende Artenförderungsprogramme vorschnell aufzugeben. Eine angepasste Waldbewirtschaftung, die gezielt Schlüsselstrukturen für unsere Modellarten in das

Waldmanagement integriert, kann negative Auswirkungen des Klimawandels auf die Lebensraumqualität abpuffern. Allerdings zeigen unsere Resultate auch, dass dies bei manchen Strukturvariablen ein Arbeiten gegen die natürliche Dynamik im Wald erfordert, wie sie unter Klimawandel vorhergesagt wird.

Die untersuchten Modellarten sind Indikatoren für unterschiedliche, komplementäre Strukturelemente in Bergmischwäldern sowie Schirmarten für die assoziierten Lebensgemeinschaften. Adaptive Massnahmen für diese Arten könnten somit auch die Resilienz des Ökosystems Bergwald verbessern.

Im beschriebenen Projekt wurden bisher vier isi-Publikationen veröffentlicht und ein Manuskript ist in Begutachtung. Das Projekt wurde im Hotspot (2/2013) vorgestellt und die Ergebnisse an zahlreichen Tagungen und Seminaren präsentiert. Fünf Studierende aus der Schweiz und Deutschland haben die Möglichkeit erhalten, im Rahmen des Projekts ihre Studienabschlussarbeiten durchzuführen.

## Summary

The general goal of the study was to predict the impact of climate change on the distribution and realized niches of four species of conservation concern and to assess the mitigation potential of adapted forestry measures. We used four cold-adapted mountain forest bird species with complementary habitat needs: Hazel grouse (*Bonasa bonasia*), Capercaillie (*Tetrao urogallus*), Pygmy owl (*Glaucidium passerinum*) and Three-toed woodpecker (*Picoides tridactylus*). In particular, we investigated the following questions: (1) How do climate, landscape and vegetation explain the distribution of the model species? (2) To what extent climate change and climate-induced vegetation changes will affect habitat quality? (3) Can these changes be compensated or mitigated by adaptive habitat management?

We analysed the presence of the model species in 300 grid cells of 1km<sup>2</sup> along an altitudinal gradient in four biogeographic regions, in particular Black Forest, Swiss Jura, Northern Pre-Alps, and Eastern Central Alps. Field work has been carried out by one scientific assistant (coordinator), four master students, one bachelor student, and two technical field assistants. They formed four field teams of two persons each. Species presence was modeled as a function of climate, landscape and vegetation information under current climate, and then extrapolated to 2050, assuming the moderate IPCC16 scenario A1B. We used two modelling approaches at two spatial scales: first, we predicted species occurrence at the landscape scale (comprising the whole study area of Switzerland and Baden-Württemberg, Germany) by considering only climate and landscape information. In the second approach, we analyzed species occurrence at the local scale by also integrating vegetation structure. Results indicate that climate explains a considerable part of the species' occurrences on both the landscape scale and within the eco-climatic niche of the species. Climate change predicts a decline in occurrence for all four species, ranging from -22% (Three-toed woodpecker) to -41% (Capercaillie). Respective figures for Pygmy owl and Hazel grouse are -26% and -30%. These declines are partly caused by climate-induced vegetation changes which decrease the occurrence probability of all four species, particularly at the low-altitudinal margins of their current distribution. Negative effects could be compensated only partly by modifying and improving single, species-specific vegetation factors with habitat management measures. However, a full compensation could only be achieved if several factors would be changed directionally and in concert. In the Three-toed woodpecker, for instance, such a compensation would include an increase of standing dead wood within the species home range, itself containing a minimal amount of Norway spruce (*Picea abies*) with heights of 15 m or more.

Our results illustrate that the often simplified cause-effect relationship between climate change and species occurrence has to be considered more specifically. The prediction of large-scale species distribution models is not a suitable basis for strategic decisions in cases of trade-offs between species conservation and climate change, since they neglect climate-induced vegetation changes. Our study shows that an adapted habitat management that focuses on a relatively small set of decisive vegetation variables can mitigate indirect negative effects of climate change on mountain forest species. However, it partly requires working against the climate change-induced dynamics of vegetation development, and is as such also in competition with other ecosystem services.

Our study species are considered to be indicators of complementary structural habitat portfolios of mountain forests as well as umbrella species of the associated species community. Measures aiming at preserving the model species' habitat suitability may therefore be beneficial to a wide range of species and to the resilience of mountain forests in general.

So far, three isi-publications have been published, and two manuscripts are in review. The project has been described in "Hotspot" (2/2013), and parts of the results were presented at conferences and seminars. Five students from Germany and Switzerland had the possibility to do their bachelor or master thesis within the project.

# 1 Einleitung/Introduction

## 1.1 Background, state of research and contribution to integrative forest management under climate change

With a predicted global temperature increase of 2.0–4.5°C until the end of the century (IPCC 2007), climate change is expected to affect habitat quality and species distribution all over the world (Parmesan & Yohe 2003; Leadley *et al.* 2010). The proportion of wild species impacted by the most recent global warming was estimated at 41%, with effects distributed over all continents and taxonomic groups (Parmesan & Yohe 2003). Geographically isolated species adapted to cold climatic conditions but with little tolerance to climatic variation (Hulme 2005) face a particularly high risk of range contractions, if not local extinction (Hughes 2000). In Central Europe, adverse effects are mainly predicted for boreo-Alpine forms of montane and subalpine ecosystems (e.g. Sergio 2003; Alo & Wang 2008). These organisms are often glacial relics which occur here at the margins of their ecoclimatic and eco-physiological niche (e.g. Wilson *et al.* 2005; Braunisch & Suchant 2008). In many animal species, climate-induced range contractions are rarely caused by direct physiological constraints (Arlettaz *et al.* 2000), but indirectly by changes in habitat quality, food availability or interspecific interactions (Parmesan 2006; Gilman *et al.* 2010; Walther 2010).

In montane and subalpine forest ecosystems, biodiversity largely depends on the diversity of forest composition and structure (e.g. variability in tree species composition, vertical and horizontal forest structure, age structure of stands, presence of gaps, clearings, snags and dead wood) (Lindenmayer *et al.*, 2000; Bollmann *et al.*, 2005). Next to the site conditions (Braunisch and Suchant, 2008), the natural pattern of structural diversity of montane and subalpine forests is mainly attributed to cold ambient temperatures which entail low forest productivity, long succession cycles and a high potential for snow-break or wind-throw with subsequent susceptibility for insect calamities (Braunisch and Suchant, 2007; Bollmann *et al.*, 2008a). Although natural stand dynamics are largely overruled by forestry practices in most areas, climate change is expected to affect the abundance and distribution of structural parameters in forests, and consequently, habitat suitability and distribution ranges of the associated species. Diverging developments for different structural elements and species may impact long-term ecosystem functions and resilience. Adverse effects may be additionally amplified by modifications in forestry practices (like the shortening of harvesting periods or changes in the tree species portfolio) proposed to cope with future scenarios of climate change.

Several endangered mountain bird species such as the Capercaillie (*Tetrao urogallus*) or the Three-toed woodpecker (*Picoides tridactylus*) have been proposed as indicators for structurally rich boreal or mountain forests, if not as umbrella species for the underlying ecological communities (Suter *et al.*, 2002; Roberge and Angelstam, 2006). These species are thus frequently employed as surrogates in biodiversity conservation and restoration programs. With climate change and associated forest conversion, there is an emergent risk that the benefits of these programs will soon be curtailed if not obliterated (Araújo *et al.*, 2004). A new essential task of conservation biologists and restoration ecologists is to (I) quantify species-habitat relationships over climatic gradients, (II) predict climate-induced changes in distribution and habitat suitability in a spatially-explicit way, and (III) develop

adaptive conservation management strategies to ensure the persistence of biodiversity in ecosystems subjected to different scenarios of climate change.

Forests provide essential habitat to a wide array of Central European flora and fauna (Bollmann et al., 2009). It is obvious that in this region forest composition and use will be the main drivers of future changes in species richness. A rich and diverse biodiversity guarantees essential ecosystem functions and services in the long term (Loreau et al., 2002). Sound policies for orienting future forest composition and use are thus essential societal tasks if we want to keep the integrity of these biocenoses. Hence, future forestry practices have to account for climate change that will inevitably impact on forest use, while maintaining its biodiversity. Any conflicts between the different forest functions like timber production, recreation and biodiversity preservation have to be anticipated. Our project focused on a primarily non-economic, but essential functional product of forest management. It adds a trans-sectoral objective to the BAFU/WSL-research program 'forest and climate'. The outcome of the project will complement the program by allowing an interdisciplinary evaluation of the program's results thus providing an important integrative dimension. This is in line with the necessity of developing innovative, integrative management solutions capable of balancing the interests of forestry and biodiversity conservation.

## 1.2 Objectives and research questions

The aim of the study was to infer how the distribution and realized niches of forest species of conservation concern will be affected by climate change. We assessed how climatic variation influences key structural and vegetational habitat components of Central European subalpine forests by focusing on an appropriate set of bird species indicative of structural diversity in boreal and/or mountain forests. Based on this information we developed concrete guidelines for future adaptive forest management capable of ensuring the persistence of an autochthonous subalpine biocoenosis under a scenario of climate change.

We operated at two spatial scales: at the landscape scale, we investigated the species' predicted distribution patterns as a function of climate and landscape characteristics focusing on different sources of uncertainty. At the local scale, within the models eco-climatic niche, we then investigated the relative effects of climate, landscape and vegetation characteristics and changes thereof on species occurrence.

In particular, we addressed the following questions:

- How does the occurrence of our model species' depend on climate, landscape and vegetation characteristics?
- How will the distribution and habitat suitability of the studied species change under different combinations of climate variables?
- How does species' presence relate to forest composition and structure variables at the local scale; what are optimal habitat profiles and thresholds thereof?
- How climate change and associated vegetation changes will affect overall habitat suitability?
- Can decisive habitat features be modified by adaptive management in a way that negative effects of climate change could be mitigated or compensated?

## 2 Material und Methoden/Material and methods

### 2.1 Methodological approach

The rationale of our project was as follows. At the landscape level, climate is one of the major natural determinants of mountain forest composition and structure, and associated biocoenoses. However, local vegetation conditions vary strongly between forest stands within the potentially suitable climate envelope and are strongly influenced by forestry practices. Focusing on a set of model species indicative of different aspects of structural and compositional diversity will be one of the most appropriate ways to identify and predict the areas supplying suitable conditions for mountain forest communities under changing climate circumstances. Investigating species' relevant habitat components over a comprehensive climate gradient and over a variety of management regimes will thus not only allow quantifying the amount of variance that is purely determined by climate, but it will also enable determining the necessary type and needed magnitude of habitat improvement measures for maintaining suitable habitats under predicted future conditions. Our project will single out climate change effects on vegetation conditions and species distributions by keeping the other environmental factors constant. Changes potentially induced by altered interspecific interactions (e.g. increased predation risk due to spreading of generalist predators into high mountain forests) were not considered in this context.

#### Model species

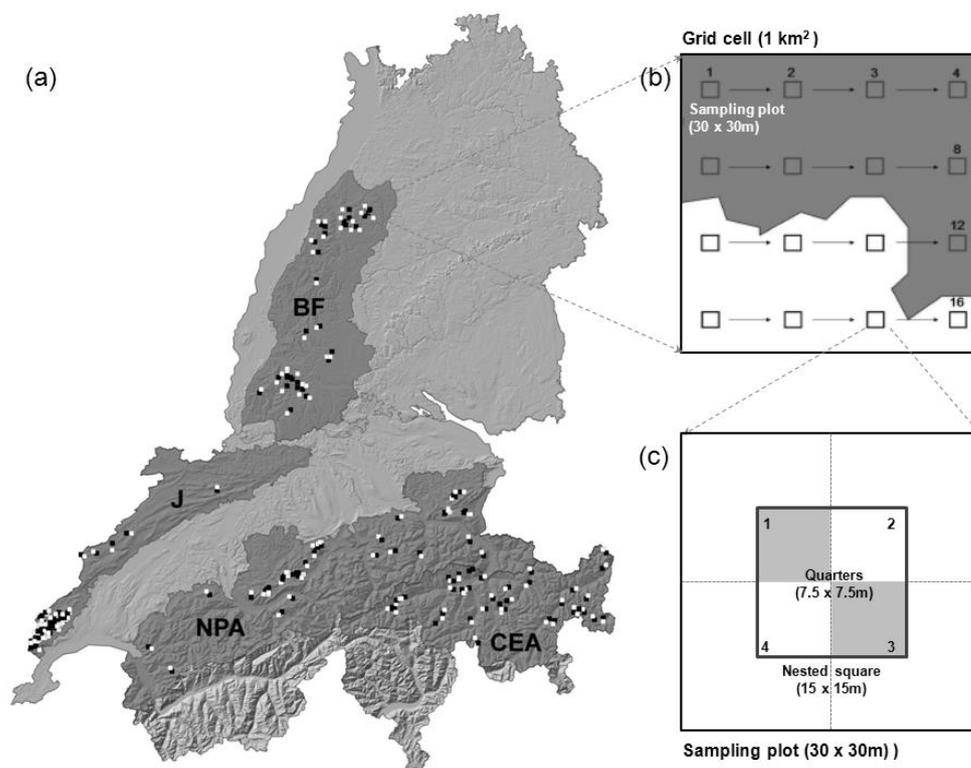
Our set of model species included: Capercaillie (*Tetrao urogallus*), Three-toed woodpecker (*Picoides tridactylus*), Pygmy owl (*Glaucidium passerinum*) and Hazel grouse (*Bonasa bonasia*). The species were selected according to the following criteria:

- (i) Specialisation to different structural elements and vegetation successional stages, and thus, in combination, considered as good surrogates of overall structural diversity,
- (ii) Umbrella species for autochthonous montane/subalpine forest species communities,
- (iii) Species-habitat relationships operating at a similar spatial scale,
- (iv) Species of conservation concern at the European scale,
- (v) Extant species distribution data for all study regions.

### 2.2 Study area

The study area encompassed Switzerland and Southern Germany with sympatric occurrence of the four model species in four mountain regions, representing a broad gradient as regards climatic, vegetation and land-use conditions. The Black Forest, expanding over 7'000 km<sup>2</sup> in Southwestern Germany, is a lower forest mountain range with elevations ranging from 120 to 1'493 m a.s.l (mean: 663). The Swiss Jura, 4'200 km<sup>2</sup> in size, is located in Western Switzerland and covers an altitudinal range between 500 – 1'718 m a.s.l (mean: 817). The Swiss Alps are here represented by two climatically and geographically distinct study regions: the "Northern Prealps", defined by the biogeographic regions Prealps and

Northern Alps with altitudes between 370 – 4'227 m a.s.l. (mean 1'391), and the Eastern Central Alps, with altitudes from 560 – 4'010 m a.s.l. (mean: 2'112) (Gonseth et al. 2001) (Figure 1). In the Black Forest and the Swiss Jura where elevations do not reach the tree line, the forests form semi-continuous habitats interspersed by pasture land, while in the Northern Prealps forests surround isolated treeless mountain tops. Finally, in the Eastern Central Alps, forests form distinct belts around continuous high elevation peaks. Forest composition also varies along the altitudinal and climatic gradient, with decreasing proportions of European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) giving way to a predominance of Norway spruce (*Picea abies*) when moving from the montane to the subalpine belt. Moreover, larger proportions of larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) can be found towards the Eastern Central Alps, where a continental climate prevails, in contrast to the other three regions, which are characterized by more oceanic climate conditions.



**Figure 1:** Study area (a) with the four mountain ranges [Black Forest (BF), Swiss Jura (J), Northern Prealps (NPA) and Central Eastern Alps (CEA)] and the spatial distribution of 1 km<sup>2</sup> grid cells with species' presence (white) and absence (black). Within each grid cell, environmental variables were recorded at or in the surrounding of maximum 16 regularly distributed sampling plots (b), with only plots located in the forest (dark grey) considered in the analysis. At each plot, vegetation variables were recorded in the field at different reference areas (c), either across the whole plot (30 x 30 m), within a nested square (15 x 15 m), or within the two external quarters thereof (7.5 x 7.5 m). (From: Braunisch *et al.* in review)

## 2.3 Species data

Data of species presence were adopted from two databases hosted by the Swiss Ornithological Institute, Sempach, Switzerland ([www.ornitho.ch](http://www.ornitho.ch); amended with grouse data from WSL and casual observations of Three-toed woodpecker from birdwatchers in the Jura

region) and the Forest Research Institute of Baden-Württemberg (FVA), Germany ([www.wildtiermonitoring.de](http://www.wildtiermonitoring.de)). Both databases contain long-term collections of observational data from ornithologists, foresters, hunters, birdwatchers as well as research personnel at a minimum resolution of 1 km<sup>2</sup>. Since data were not sampled systematically, no proven absence data were available. For the analyses at the landscape scale, all presence data were used.

For the local-scale analyses we selected at least ten 1 km<sup>2</sup> grid cells in each of the four study regions and for each of the model species. Selected grid cells are characterized by species observations in at least three years between 2006 and 2010 (Table 1, Figure 1). Presence cells were selected by a stratified random process so as to represent the extent of the species distribution and its climatic gradient in the respective study region, thereby preferring cells with repeated observations from multiple years. For each presence grid cell a corresponding cell, in the following referred to as “absence cell”, was selected, with “absence” defined as cells with no recorded species proof within the preceding 11 years (2000 – 2010). Absence cells were selected within a maximum of 5 km distance to the presence cell by randomly choosing one of the surrounding cells with at least 50% forest cover, while excluding all cells directly adjacent to the presence cell.

**Table 1:** Number of grid cell pairs (1 km<sup>2</sup>) with species presence and absence selected in each of the mountain regions across the study area (BF: Black Forest, J: Swiss Jura, NPA: Northern Prealps, CEA: Central Alps).

Species	BF	J	NPA	CEA	Total
Capercaillie	23	21	16	11	71
Hazel grouse	0	28	27	13	68
Three-toed woodpecker	11	12	30	15	68
Pygmy owl	15	22	21	13	71

## 2.4 Environmental data

### Sampling scheme

Environmental predictors were sampled area-wide (landscape-scale analysis) and at 16 sampling plots (local scale analysis), regularly distributed within each grid cell, with only plots located in the forest considered for the analysis (Figure 1). Our predictor set included variables of three main topics: climate (both scales), landscape (both scales) and vegetation (local scale), measured at different reference areas around each sampling plot (Appendix 1).

### Climate data (landscape and local scales)

Climate variables included the average temperature in the breeding season (May – July) and in winter (December – February), and the sum of precipitation in both periods (Appendix 1). Current climate (long-term averages from 1971 to 2000), was obtained from the worldclim-dataset (Hijmans *et al.* 2005) ([www.worldclim.org](http://www.worldclim.org)), which was downscaled from a 1 km<sup>2</sup> raster to a resolution of 100 x 100 m based on the SRTM-V4 digital elevation model and the method described in (Zimmermann & Roberts 2001).

For future climate conditions in the year 2050 (long-term averages from 2031 to 2050) we assumed the moderate IPCC emission scenario A1B. Variables derived from four different Global Circulation Models (GCM) in combination with four Regional Circulation Models (RCM) were used for the landscape-scale analyses; only one thereof, the GCM ECHAM5, downscaled using the CLM-RCM of the Max Planck Institute (<http://cera-www.dkrz.de>), was employed for the local-scale analyses. All climate data were processed and provided by the Research unit Landscape Dynamics of the Swiss Federal Research Institute WSL.

### **Landscape data (landscape and local scales)**

Landscape variables included information on topography, land cover and human infrastructure, obtained from different digital data sources (Appendix 1). Five topographical variables (slope, topographic position, eastness, northness and potential solar radiation) were derived from the digital elevation model (DEM) for each sampling plot. The topographic position index, calculated with the extension TPI 1.3a for ArcView 3.3 (Jenness 2006), qualifies a point's position relative to the surrounding terrain, with negative values indicating exposed sites such as hilltops or ridges, and positive values representing depressions. The potential solar radiation [ $W \cdot h / m^2$ ] in the breeding season was calculated according to (Fu & Rich 2002) using the function "area solar radiation" in ArcGIS 9.3 (ESRI 2008). Land cover variables encompassed the proportion of forest cover, intensively and extensively used agricultural land and wetland (mires and other habitat types on wet soils), as well as the density of outer forest edges within the surrounding area of  $1 \text{ km}^2$ . Human infrastructure was represented by the density of drivable roads per  $\text{km}^2$  and the distance to settlements.

### **Vegetation data (local scale)**

Vegetation variables included information on vegetation composition (tree species and ground vegetation), vegetation structure (related to stand structure and forest stand mosaic) and special habitat features or resources known to be essential to the focal species. Vegetation composition, stand structure and special resources were mapped in the field at the sampling plots, while information on the forest stand mosaic was derived from remote sensing data (Zellweger *et al.* 2013). For matter of precision, different variables were assessed at different reference areas around the sampling plot center: Tree species composition, successional stage, vertical and horizontal stand structure and selected habitat features (e.g. basal-branched trees or snags) were recorded within squares of  $30 \times 30 \text{ m}$ , whereas special resources like the number of rowans or lying dead wood were quantified within a nested square of  $15 \times 15 \text{ m}$ , two diagonal quarters of which ( $7.5 \times 7.5 \text{ m}$ ) were used to assess the ground vegetation (Figure 1, Appendix 1).

We derived variables describing the forest stand mosaic based on first and last return Light Detection and Ranging (LiDAR) data. For the cells in the Black Forest we used the revised point clouds for both terrain and surface models, as described in Schleyer (2001); for Switzerland, the corresponding data were provided by swisstopo (2011). MATLAB R2011a (Mathworks, Natick, Massachusetts, USA) routines (Morsdorf *et al.* 2010) were used to obtain terrain-corrected vegetation heights at a resolution of  $3 \times 3 \text{ m}$ , which resembles the crown projection of a small spruce tree. The normalized vegetation heights were interpolated to form a continuous canopy height model, which was classified into four

height classes, i.e. non-forested areas, shrub layer (<5 m), midstory (5-15 m) and canopy layer (>15 m) (processing details are provided in Zellweger *et al.* 2013). We used the height classes to calculate structural metrics describing the proportion of each height class per 1 km<sup>2</sup>, the number of gaps, the length of edges between different height classes representing different ecotone-types, as well as the total edge length between all height classes, which provided an index for overall canopy height heterogeneity (for details see Table 2). Stand mosaic metrics were calculated in FRAGSTATS 216 (McGarigal *et al.* 2002).

## Statistics

### Landscape scale analysis

For predicting species occurrence and climate-change induced changes thereof at the landscape scale, we chose a Maximum entropy modelling approach implemented in the software Maxent (Phillips *et al.* 2004; Phillips *et al.* 2006). Maxent is a machine-learning technique that contrasts the conditions at the species' locations with those prevailing throughout the study area and therefore does not need absence data. The environmental variables and functions thereof were used as predictors, including linear, quadratic and product terms, as well as hinge or threshold functions (Phillips *et al.* 2006). To best capture the complexity of species-habitat interactions we fitted the models with all predictor functions included ("auto-features"), with a random background sample of 10'000 cells (Barbet-Massin *et al.* 2012), a maximum of 500 iterations and a convergence threshold of 10<sup>-5</sup>. The models were evaluated using 10-fold cross-validation, measuring the accuracy by means of area under the receiver operating characteristics curve (AUC, Fielding & Bell 1997). With no absence data available, AUC-statistics were calculated on the random background cells instead (Wiley *et al.* 2003; Phillips *et al.* 2006), thus assessing the models' ability to discriminate between 'presence' and 'random' rather than between 'presence' and 'absence'. The resulting maps, showing the predicted probability of species presence for each raster cell of the study area, were converted into binary "presence-absence" maps, using the threshold at which the sum of sensitivity and specificity calculated on the test data was maximised (average over the 10 cross-validation replicates).

### Local scale analyses

Here, we describe the general statistical approach used for the local-scale analyses of the project modules. Deviations from that approach might have occurred, and are described in the resulting specific papers. In general, we modelled species presence as a function of the environmental variables recorded at the sampling plots using Mixed Effects Logistic Regression with the grid-cell pair, as our species sampling unit, treated as a random effect to account for spatial clustering. To identify the variables that best explained species presence we applied an information-theoretic approach (Burnham & Anderson 2002; Johnson & Omland 2004), using Akaike's Information Criterion (AIC) to identify the most parsimonious model.

We followed a hierarchical variable selection procedure: first, univariate models were run for each variable, testing also the quadratic term of variables for which we expected a unimodal response. Of pairs of correlated variables (Spearman's  $|r| \geq 0.6$ ) significantly contributing to explaining species presence in the univariate models we discarded the least

performing one. The retained predictors were then grouped into ecologically meaningful variable subsets. For each subset a model was calibrated by testing all possible variable combinations and identifying the most parsimonious model using the R-package MuMIN. The variables that significantly contributed to this “best” subset-model were used for calibrating the model at the next hierarchy-level. This way the variable set was stepwisely refined until a final model was obtained, potentially containing variables of all variable classes. The models’ fit was evaluated using the area under the receiver operating characteristics (ROC) curve (AUC).

Procedures to quantify climate-related changes in habitat suitability and the compensation potential are provided by Braunisch *et al.* (in review).

## 2.5 Project progress

We refer to the four „Meilensteinberichte“ which illustrate the progress and products of the project in detail and have been previously submitted to the steering committee.

### 3 Ergebnisse/Results

We present the main results of the project in four parts. The species' range dynamics under climate change and their dependence on the choice of different climate predictor variables is described in 3.1. The suitability of LiDAR derived habitat variables and its complementarity to local field variables to predict species occurrence is presented in 3.2. The third chapter (3.3) shows species range contractions and changes in habitat suitability as well as the compensation potential of a structural habitat management under the climate change scenario A1B. The last chapter (3.4) lists the research questions of the proposal and provides concise and short answers to them.

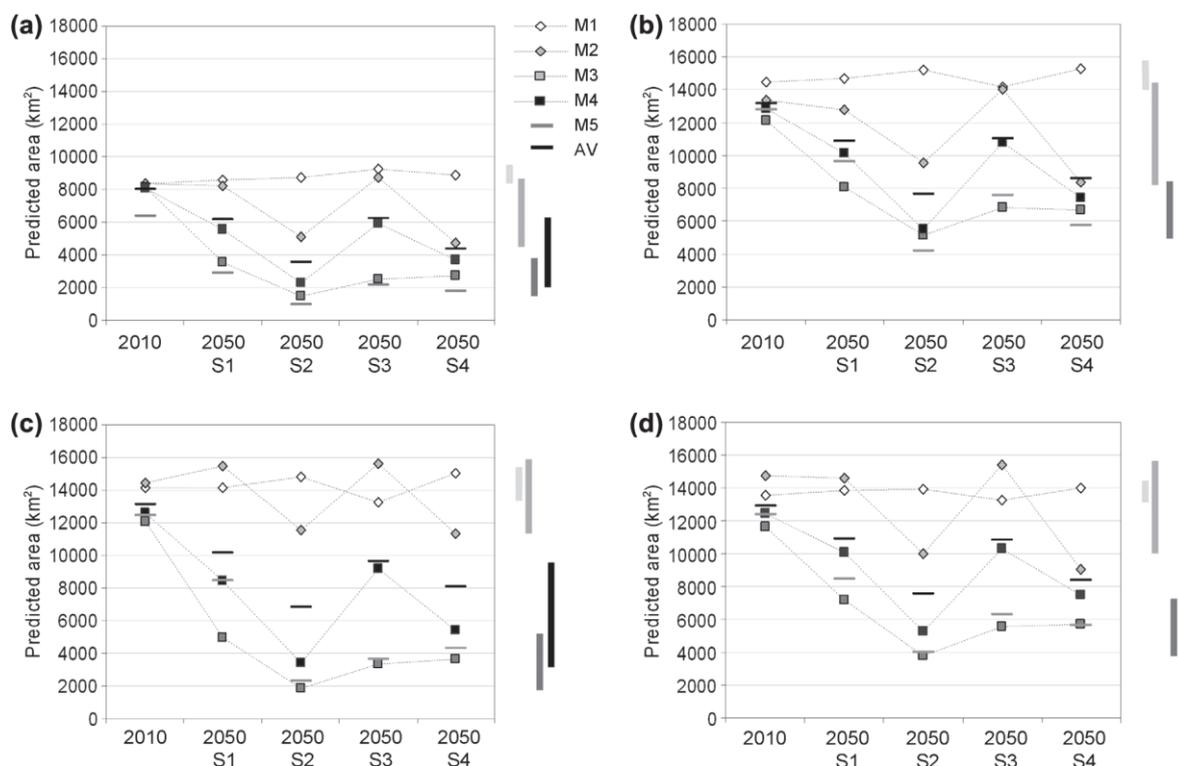
#### 3.1 Climate variables and uncertainty in species' range predictions (Braunisch *et al.* 2013)

Correlative species distribution models are usually employed to predict species range shifts under climate change. However, climate variables often show high collinearity and most statistical approaches require the selection of one among strongly correlated variables. When causal relationships between species presence and climate parameters are unknown, variable selection is often arbitrary, or based on predictive performance under current conditions. While this should only marginally affect current range predictions, future distributions may vary considerably when climate parameters do not change in concert. We investigated this source of uncertainty with regard to our model species using four highly correlated climate variables together with a constant set of landscape variables in order to predict current (2010) and future (2050) distributions. Simulating different parameterization decisions, we generated (a) four models including each of the climate variables singly, (b) a model taking advantage of all variables simultaneously and (c) an un-weighted average of the predictions of (a). We compared model accuracy under current conditions, predicted distributions under four scenarios of climate change, and – for one species – evaluated back-projections using historical occurrence data.

Strong collinearity ( $|r_s| > 0.7$ ) between temperature and precipitation variables was recorded across the study area, and overall correlation patterns did not, or only marginally, differ between current and future conditions and between different scenarios (ECHAM5, HadCM3, Arpège, CCSM3). However, the predicted changes of the climate variables (both within and between scenarios) were not correlated in a similar way, indicating non-linear changes with regionally diverging developments. Differences were recorded for both the strength of the correlations as well as for their directions, with even opposite changes predicted for the same climate variable in different seasons (e.g. summer temperature was predicted to rise locally in places where winter temperature was predicted to decrease).

All models performed well in predicting current species distributions. Accuracy was highest for the models of Capercaillie (mean AUC: 0.937 – 0.945) and lowest for those of Hazel grouse (mean AUC: 0.868 – 0.882). No significant differences in accuracy were found between models including the different climate variables singly or simultaneously, although the latter models tended to perform best in all species. Whereas predicted current distribution areas differed only marginally between the models with regard to both area size

and location, great differences were recorded for future forecasts. This finding was consistent over modelling approaches and applied to all climate scenarios. In addition, in the case of capercaillie, the uncertainty in range-forecasts attributable to variable selection was substantially larger than the uncertainty introduced by selecting different modelling methods, with a 14.8 times greater variance and a 15.7 greater maximum difference between range-changes. Most models predicted a reduction of the study species' distribution ranges, a finding that was particularly pronounced when including only winter temperature (Figure 3). On the other hand, range-expansions were also predicted, mainly by models focusing only on precipitation. The areas expected to be lost as habitat for the model species by 2050 were mainly situated at lower altitudes in the lower mountain ranges of Black Forest and Jura. The surface of lost areas was generally greater than the area predicted to be gained in higher altitudes in the Alps.



**Figure 3:** Distribution area of (a) Capercaillie, (b) Hazel grouse, (c) Pygmy owl and (d) Three-toed woodpecker, predicted by models based on different correlated climate variables (M1 – M4) under current (2010) and future (2050) climate conditions, as predicted by four scenarios of climate change (S1: ECHAM5, S2: HadCM3, S3: Arpège, S4: CCSM3). The lines show the averaged predictions of M1 – M4 (black) and a model (M5) including all four climate variables together (grey). The bars on the right indicate the differences between the scenarios for each model (M1: light grey, M2: grey, M3: dark grey, M4: black). Climate change scenarios (S1 – S4) and models (M1 – M5) are described in Braunisch *et al.* (2013). (From Braunisch *et al.* 2013)

### 3.2 Predicting current species' occurrence by remotely sensed forest structure-variables (Zellweger *et al.* 2013)

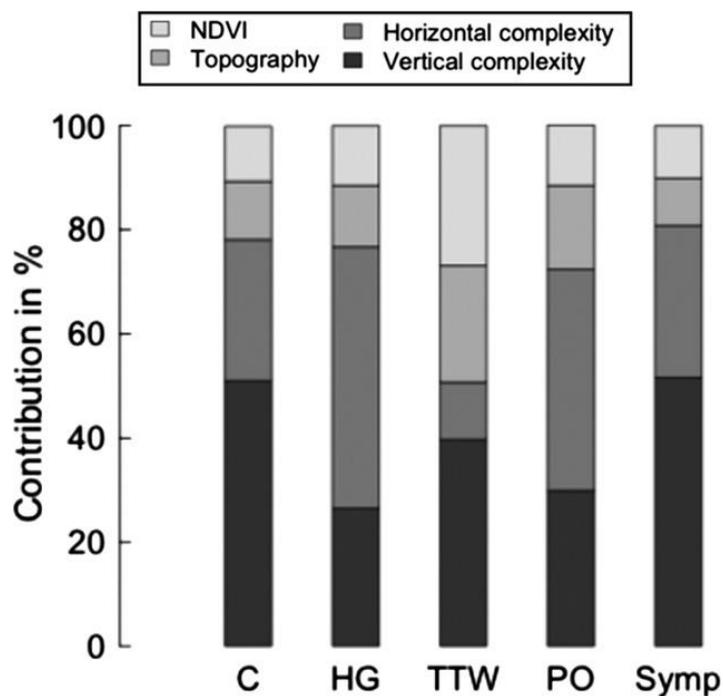
To assess the validity of the remotely sensed forest structural variables to predict species presence, with a particular focus on the metrics obtained from LiDAR, we developed BRT models for all four species individually, as well as for the sympatric occurrence of at least three species. Model predictive performance based on AUC values ranged from outstanding (sympatric occurrence, Capercaillie) to excellent (Hazel grouse, Three-toed woodpecker), and acceptable (Pygmy owl). The range of the explained predictive deviance varied considerably among the five models, with highest values for sympatric occurrence and Capercaillie, supporting the outstanding predictive power of these two models. All the five models showed a high robustness, as interpreted from the standard errors.

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

Half of the explained variance in the Hazel grouse model stems from CHM-derived variables, whereby such variables only marginally contributed to the Three-toed woodpecker model. Both, the Capercaillie and sympatric occurrence models show similar patterns of variable group contributions, with vertical complexity accounting for half of the explained deviance. Partial responses of the most important predictor variables are reported as fitted response curves for the sympatric occurrence model by Zellweger *et al.* (2013).

**Table 2:** Performance of the final BRT models in terms of predictive deviance explained ( $D^2$ ) and area under the receiver operating characteristics curve (AUC) as well as the contribution of the predictor variables (in percent) to the total deviance explained. For  $D^2$  and AUC, means and standard errors (SE) calculated from ten cross-validation replicates are provided. (From: Zellweger *et al.* 2013)

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



**Figure 2:** Predictor variable group contributions to total deviance explained in the five final BRT models. C = Capercaillie, HG = Hazel grouse, TTW = Three-toed woodpecker, PO = Pygmy owl, Symp = Sympatric occurrence. (From: Zellweger *et al.* 2013)

### 3.3 Species occurrence, predicted changes in habitat suitability and management compensation potential under climate change (Braunisch *et al.* 2014)

Each final species' occurrence model contained variables from the climate, landscape and vegetation variable groups performed good to excellent. Model accuracy was highest for Pygmy owl (AUC: 0.947, SD: 0.005) and lowest for Three-toed woodpecker, but still showing a good fit (AUC: 0.877, SD: 0.010). All species had a unimodal response to winter temperature and a positive correlation with precipitation in early summer, in Pygmy owl also areas with higher winter precipitation were selected. As regards landscape characteristics, all species, except Hazel grouse, preferred mires and forests on wet soils and showed at least a trend to avoid forests with a high road density and located in the vicinity of settlements. A negative response was also found for Capercaillie towards a high density of outer forest edges, which can serve as an indicator of avoidance of forest fragmentation. The presence of Hazel grouse and Three-toed woodpecker was negatively affected by the proportion of intensively managed agricultural land in the surrounding, while Pygmy owl showed a positive correlation.

Except for the proportion of forest patches of the upper most height class, which showed a quadratic relationship for Capercaillie and was positively correlated with the presence of the three other species, the retained vegetation variables varied greatly between species' models. Capercaillie presence was mainly explained by the abundance of gaps per km<sup>2</sup>, a low to moderate proportion of beech in the canopy and high cover of *Vaccinium* spp., mainly bilberry (*Vaccinium myrtillus*) in the field layer, as well as by low canopy height heterogeneity. Hazel grouse presence was mainly related to the availability of food resources, i.e. the proportion of resource trees and a high cover of herbs and bilberry. Features providing cover, like basal-branched trees and a patchy ground vegetation distribution were preferred, while the vicinity of outer forest edges was avoided. Three-toed woodpecker occurrence was positively correlated with the presence of conifers and resource trees, and a high abundance of snags, while two- or multi-layered stands and stands with a high shrub cover were avoided. As in Capercaillie, woodpecker presence was also negatively correlated with the abundance of hard stumps, indicating recent harvesting activities. Finally, Pygmy owl habitat was characterized by a greater density of "sharp" forest edges, a greater abundance of basal-branched trees and a higher ground vegetation cover than in locations where the species was absent.

Climate change was predicted to negatively affect the probability of occurrence of all model species. When considering only climatic changes, the greatest impact was predicted for Hazel grouse, amounting to a reduction of presence probability of 29% in the currently occupied sites. The least-affected species was the Three-toed woodpecker with -22%, while Capercaillie (-27%) and Pygmy owl (-24%) were in intermediate positions (Table 3). Yet, when also considering climate related vegetation changes, a significant additional reduction of presence probability of 14% was recorded for Capercaillie while the conditions for the other three species remained more or less constant. Predicted climate change effects differed greatly between the four study regions, with the greatest impacts on all species recorded for the Black Forest. The Central Eastern Alps were least affected by climate-change related habitat alterations, except for Capercaillie, which was predicted to suffer least in the Swiss Jura and the Northern Prealps.

**Table 3:** Modelled probability of species presence ( $P_{\text{pres}}$ ) across the study area, as well as mean predicted changes ( $\Delta P$ ) between 2010 and 2050 under climate change. The first model considers only changes in climate variables (2050C), the second (2050CV) takes also predicted vegetation changes into account (CC: Capercaillie, HG: Hazel grouse, TTW: Three-toed woodpecker, PO: Pygmy owl). (From: Braunisch *et al.* in review)

Species	2010		Change 2050C		Change 2050CV	
	$\Delta P_{(\text{pres})}$	SD	$\Delta P_{(\text{pres})}$	SD	$\Delta P_{(\text{pres})}$	SD
CC	0.803	0.203	-0.265	0.148	-0.407	0.187
HG	0.795	0.220	-0.292	0.204	-0.302	0.208
TTW	0.717	0.201	-0.222	0.123	-0.215	0.129
PO	0.817	0.226	-0.237	0.333	-0.256	0.346

The mean compensation potential, defined as the maximum increase in presence probability ( $\Delta P(\text{presence})$ ) under the selected scenario of climate change, ranged between 0.02 (95% confidence interval CI: 0-0.05) for ground vegetation cover (GVCOV) and 0.72 (0.33 – 0.93) for the density of sharp edges (ED134), both in pygmy owl (Table 4). Adverse effects of climate change on Capercaillie could be compensated best by increasing the number of gaps (GAPINDEX) from zero to 28 per km<sup>2</sup>, while Hazel grouse availed most of an increase in bilberry (VAC) and resource trees (RESTREE). Increasing the number of snags (STANDDEAD) and the proportion of canopy heights >15 m (HEIGHT4) most benefitted the Tree-toed woodpecker. Yet, the comparison of the target species' response curves under current and future climate conditions also showed that it was difficult or even impossible to maintain the prevailing occurrence probability by modifying only one vegetation variable. A considerable increase could be achieved by changing more than one variable towards the species' optimum: For Capercaillie a  $\Delta P(\text{presence})$  of 0.65 could be achieved when both VAC and GAPINDEX were modified so as to reach their optimal values. The maximum compensation potential for Hazel grouse reached 0.73 with optimal proportions of RESTREE and VAC, while combining a maximum ED134 with a high number of basal-branched trees (BBTREE) increased  $\Delta P(\text{presence})$  for Pygmy owl to 0.82. The probability of Three-toed woodpecker presence could be increased by 0.65 when changing HEIGHT4 and STANDDEAD towards their recorded maximum and by 0.77 when the latter variable was in combination with no recent harvesting activities.

Further results are presented in the published papers (Braunisch *et al.* 2013; Zellweger *et al.* 2013; Zellweger *et al.* 2014), in the manuscripts in review (Braunisch *et al.* in review, Hofstetter *et al.* in review) and in the master theses (Deplazes 2012; Sadowski 2012; Zellweger 2012; Hofstetter 2013).

**Table 4:** Compensation potential, defined as the maximally achievable increase in predicted probability of species presence  $\Delta P_{(pres)}$  under altered climate conditions, which could be obtained when modifying the respective variable from its recorded minimum towards the species' optimum. The two variables that were modified in concert to show their combined compensation potential are highlighted in bold (CC: Capercaillie, HG: Hazel grouse, TTW: Three-toed woodpecker, PO: Pygmy owl). (From: Braunisch *et al.* in review)

Variable (unit)	Optimum	CC $\Delta P_{(pres)}$	HG $\Delta P_{(pres)}$	TTW $\Delta P_{(pres)}$	PO $\Delta P_{(pres)}$
	0->100				
CHEIGHT4 (%)	(0->70<-100)	0.22 (0.08-0.43)		<b>0.30 (0.12-0.47)</b>	0.09 (0.02-0.28)
GAPINDEX (n)	0 -> 28	<b>0.62 (0.28-0.82)</b>			
ED134 (m/ha)	0 -> 700				<b>0.72 (0.33-0.93)</b>
GVCOV (%)	0 ->100				0.02 (0.00-0.05)
SPR (%)	0->70<-100			0.37 (0.25-0.50)	
PIN (%)	0->100			0.35 (0.11-0.46)	
RESTREE (%)	0->100		<b>0.48 (0.10-0.68)</b>	0.29 (0.04-0.43)	
HERB (%)	0->100		0.31 (0.09-0.52)		
VAC (%)	0 -> 100	<b>0.27 (0.06-0.50)</b>	<b>0.61 (0.36-0.71)</b>		
BBTREE (n)	0 -> 18		0.44 (0.04-0.66)		<b>0.29 (0.03-0.78)</b>
STANDDEAD (n)	0 -> 42			<b>0.40 (0.12-0.49)</b>	
HSTUMP (n)	16 -> 0	0.19 (0.10-0.20)		0.41 (0.15-0.50)	

### 3.4 Concise answers to research questions

- How does the occurrence of our model species' depend on climate, landscape and vegetation characteristics? Climate variables made considerable contribution to explain future species occurrence. Greater divergence was found for the decisive landscape variables. All species, except hazel grouse, preferred mires and forests on wet soils and showed at least a trend to avoid forests with a high road density and located in the vicinity of settlements. Hazel grouse, together with Three-toed woodpecker, was negatively affected by the proportion of intensively managed agricultural land in the surrounding. The retained vegetation and forest structural variables differed remarkably among the model species.
- How will the distribution and habitat suitability of the studied species change under different combinations of climate variables? We found considerable differences in species' range predictions depending on the climate scenario used and the set of predictor variables applied. Predicting current distribution areas differed only marginally between the models, great differences were recorded for future forecasts. This finding was consistent over modelling approaches, and applied to all climate scenarios. Variable selection proved to be an important source of uncertainty for range predictions. Averaged models and models containing all climate variables simultaneously produced intermediate, and presumably, most reliable predictions.
- How does species' presence relate to forest composition and structure variables at the local scale; what are optimal habitat profiles and thresholds thereof? At the

local scale, variables describing horizontal and vertical complexity significantly contributed to sympatric species occurrence. Topography-related variables were far less important. Thresholds for crucial habitat variables were comparatively assessed for capercaillie and hazel grouse. We found that thresholds were quite similar for the two sympatric species and not clear-cut: different values applied for a particular variable depending on other habitat variables at the site.

- How climate change and associated vegetation changes will affect overall habitat suitability? Climate variables and climate-induced vegetation trends contributed significantly to explaining species occurrence. Both variable types decreased the average probability of model species' presence for 2050: Capercaillie  $-0.41$ , Hazel grouse  $-0.30$ , Pygmy owl  $-0.26$ , and Tree-toed woodpecker  $-0.22$ . Changes in species presence were particularly distinct at the low-altitudinal margins of their distribution. However, range-expansions were also predicted, mainly by models focusing only on precipitation.
- Can decisive habitat features be modified by adaptive management in a way that negative effects of climate change could be mitigated or compensated? Although most study sites were located in managed forests, climate change was predicted to have a negative effect on most of the vegetation variables with regard to their impact on the model species. While the models suggested a reduction in coniferous tree species and resource trees, the proportion of beech was predicted to increase. A decrease was also predicted for the abundance of gaps and the density of inner forest edges, which would go along with a reduction in ground vegetation cover and basal-branched trees. Nevertheless, our data shows that negative effects of climate change on the species predicted occurrence can be partially compensated by habitat management measures. However, a considerable increase can only be achieved by changing more than one variable towards the species' optimum.

## 4 Diskussion/Discussion

So far, plenty of studies have been published that predict negative impacts of climate change on biodiversity in general (Malcolm *et al.* 2006; Pereira *et al.* 2010). Regarding the large scale effect of climate change, our study supports the common view and available evidence that cold-adapted species are experiencing a decline in distribution area. While the magnitude of range decline differed among our model species, all were more affected in the low altitudinal and peripheral regions of their eco-climatic envelopes. In contrast to most existing studies assessing climate change impact, our study is particularly innovative in providing quantitative guidance for evidence-based habitat management that can buffer against the negative impact of climate change and climate-induced changes in vegetation composition and structure. To our knowledge, this is the first study that (roughly) quantifies the impact of climate change on species occurrence at the small scale by means of empirical data for measuring its indirect effects on vegetation characteristics. Because habitat features can be modified by forestry practice, our analysis illustrates the mitigation and compensation potential of habitat management in face of predicted negative effects of climate change. We did not only predict declines in potential distribution area as many former studies did (e.g. Parmesan 2006; Tingley *et al.* 2012; Zimmermann *et al.* 2013), but also provide quantitative evidence for both, the expected changes in key habitat characteristics and the future abundance of these features. These are crucial key habitat thresholds for increasing future species occurrence probability under the scenario A1B. Results show that full compensation of climate-change effects is difficult (if not impossible) to achieve. Compensation moreover often requires the modification of more than one habitat feature. This study offers sound guidance for developing suitable adaptive management measures aiming at conserving emblematic target species, which – as they are considered as umbrella species and indicators for structural diversity – would also support a representative species community of mountain forests. Yet, since these measures require a certain effort to work against climate-change induced vegetation trends, the results also highlight the conflicts emerging from the multifunctional goals that modern forestry must achieve, pinpointing the difficulty to frame societal priority decisions among various ecosystem services (Bollmann & Braunisch 2013) that are likely to compete against each other in times of climate change (Bollmann *et al.* 2009; Bollmann 2011).

Heller & Zavaleta (2009) have reviewed 130 papers, spanning 22 publication years, that propose forestry management recommendations in the face of climate change. They conclude that most recommendations for adaptive management remain extremely general, lacking implementation specificity, which renders them impossible to implement in practice. These authors identified three main strategies and activity fields from that bench of studies, proposed to counteract the detrimental impacts of climate change: (i) anticipatory reserve selection to secure future biodiversity hotspots, (ii) improvement of landscape connectivity to allow species to track climate change, and (iii) on-site management to either increase the resilience or the resistance of populations or ecosystems to climate change.

The present study was designed to cover point (iii) and in addition, to provide specific recommendations for operational forestry measures. Although the possibility to preserve climate-vulnerable species in their current habitats is frequently questioned (Araujo *et al.* 2004; Araujo *et al.* 2011), we show here that an "intensive" management that has the potential to enhance species-relevant habitat features might compensate for adverse

effects of climate change. However, a full compensation is difficult to achieve and mostly requires the management and modification of more than one habitat feature. This is due to the fact that “optimal habitat values”, i.e. values needed to achieve maximum compensation, can rarely be reached under real world conditions. Especially in variables, such as the abundance of snags (Three-toed woodpecker), basal-branched trees (for Pygmy owl) or gaps (for Capercaillie), the optimum corresponded to the maximum is largely determined by extremely high values at the local scale. While patches with the observed maximum of 42 snags per 900 m<sup>2</sup> (dbh > 12cm) may be locally beneficial for the Three-toed woodpecker, these values must certainly not be achieved across the whole area (Bütler *et al.* 2004). Consequently, for defining reasonable target values for management, the spatial distribution and average abundance of key variables across the entire potential distribution area (*sensu* Braunisch & Suchant 2007) should be further considered. Moreover, some variables are characterized by a trade-off between feature recurrence and size: a high number of 28 gaps (<0.1 ha) per hectare may be possible if they are small, whereas fewer but larger gaps may also be sufficient for capercaillie. Suchant & Braunisch (2004, 2008) recommend a minimum of 10% of the forest area to be gaps, which might be a more appropriate management target.

To tap the full compensation potential, the combined effect of moderately modifying different variables has to be considered and measures must be flexibly adapted to local site conditions. While gaps or edges may be created in all situations, the abundance of bilberry, for example, can only be increased under suitable soil and light conditions (Broome *et al.* 2014). Yet, despite the high efforts and inherent limitations, habitat improvement may be the favorable option in an uncertain future. The study of Jeltsch *et al.* (2011) showed that habitat improvement led to higher species persistence under climate change than creating new habitats in prospectively suitable locations. Considering the high divergence between species range forecasts under climate change, enhancing structural complexity and improving local habitat quality in currently occupied areas represents a conservative “no regret” strategy – particularly in forest ecosystems which are well known for their buffer effect on local climate conditions compared to open habitats (Renaud *et al.* 2011). Especially given the high uncertainty constraining the possibilities to adequately predict species distribution dynamics and regional species survival under climate change (Braunisch *et al.* 2013), programs that actively aim to enhance habitat conditions and extend the total habitat area might be more effective to mitigate negative impacts of climate change than the widespread recommendation of establishing habitat corridors between current and future distribution areas (Rose & Burton 2009; Kostyack *et al.* 2011). Moreover, measures that enhance structural diversity and improve habitat quality might provide an important temporal advantage for species to adapt to future environments. In Capercaillie for instance, habitat area has been shown to be more important for patch occupancy than connectivity (Bollmann *et al.* 2011). Moreover, overall habitat quality increases the viability of local populations (Graf *et al.* 2007).

There is an obvious trade-off between a forest management that aims at strengthening ecosystem resilience and conservation programs for cold-adapted species in mountain forest. This in particular accounts for altitudinal zones with mixed-deciduous forest (i.e. high-montane zone) where climate change is expected to decrease the amount of naturally regenerating coniferous trees in favor of immigrating deciduous tree species, i.e. beech and oak *ssp.* In our study area, such development are mainly except to occur in the Black Forest,

Jura mountains and lower Pre-Alps (Zimmermann *et al.* 2013). In this zone, forest policy supports the transformation of spruce-dominated stands to stand with a tree species composition that accords with the potential natural vegetation (standortgerechte Baumartenzusammensetzung), i.e. stands with a higher proportion of beech. Such developments will contradict efforts to improve habitat quality for Capercaillie and Three-toed woodpecker in this altitudinal zone. However, such developments are not expected for the Inner Alps because dominant deciduous tree species are currently absent there and will not significantly invade subalpine forests within the next century (Zimmermann *et al.* 2013). Thus, there is a distinct need for defining area specific goals concerning the different forest services and functions. Overall, we recommend relaxing the “paradigm of potential natural vegetation” in regions with a high probability of sympatric occurrence of our model species.

We did not address and quantify the impact of nitrogen deposition on the vegetation within the distribution area of our model species. Eutrophication is still an area-wide problem and highest levels of nitrogen deposition are regularly measured in central Europe (Forest Europe 2011). Increases in N deposition have been shown to change ground vegetation composition by decreasing the abundance of dwarf shrubs in favor of fast growing grass species (i.e. *Deschampsia flexuosa*, Nordin *et al.* 2005). This development is also known from central Europe (own observation) and considered to impact habitat quality of forest grouse species negatively. Nitrogen deposition will further boost tree growth and thereby alter light conditions. Such developments reduce the future potential for open stands and are of disadvantage for our model species. However, the knowledge about the interaction of nitrogen deposition and habitat quality under climate change is still poor and should be given greater emphasis in future studies.

Difficult and rarely tackled is the effect of natural disturbance in forest ecosystems and their probable impact on forest transition and biodiversity conservation (Vanderwel & Purves 2014). It is generally considered that the majority of European forest species have evolved in forests that were repeatedly and significantly influenced by wind storms, fire and floods as well as browsing patterns of large ungulates, first by mega-herbivores and, in historic times, by domestic animals and meso-herbivores (Bengtsson *et al.* 2000). Climate change will fasten the periodicity of stochastic disturbance events (Jentsch & Beierkuhnlein 2008; Usbeck *et al.* 2010; Bellard *et al.* 2012) and thus, also influence the abundance and structural characteristics of mountain forests and their habitats (Bollmann 2010). In particular, species which are dependent on early seral stages (e.g. Hazel grouse) or dead wood (Three-toed woodpecker) will profit from such dynamics. This may be a reason why we consider the predicted decline of Hazel grouse occurrence to be considerably overestimated in our study (see also Zellweger *et al.* 2014). Thus, more sophisticated models that incorporate the interdependence of natural disturbances with climate change and interspecific relationships of the study species with food plants, competitors and predators (e.g. Yang & Rudolf 2010) would be desirable and increase the accuracy of model predictions to detect changes in community structure and ecosystem functions in the future.

In addition to the initially planned analyses, we studied the potential of remote sensing information for improving the habitat models for our model species (Zellweger *et al.* 2013). This approach revealed a high potential in predicting area-wide habitat suitability of the four species, in particular with regard to sympatric occurrence. Sympatric species occurrence reflecting overall forest structural complexity was predicted better than single species

occurrence. To support management and monitoring schemes we identified variable threshold effects based on partial dependence plots. Variables related to vertical foliage distributions were most important, followed by horizontal structural attributes such as canopy height variation, forest edges and gaps. Site factors represented by topographic position and vegetation productivity (NDVI) improved all models and were most important for the species depending on dead wood (Tree-toed woodpecker). We conclude that recent advances in remote sensing allow for large-scale determination of forest structural characteristics suitable for developing species and habitat distribution models of considerable generality, while keeping an unprecedented level of detail. Our approach allows forest managers to amend regional and countrywide management plans with reliable maps depicting areas of high forest structural complexity and habitat quality, which will facilitate the integration of conservation-relevant information into multifunctional forestry under climate change.

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## Bisherige Produkte aus Projekt/Publications and theses

### **ISI-publications**

Braunisch V., Coppes J., Schmid H., Suchant R., Arlettaz R. & Bollmann K. (2013). Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. *Ecography*, 36, 971–983.

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### **Non ISI-publications**

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### **Master theses**

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## 6 Anhang/Appendix

**Appendix 1:** Variables used as predictors to model species presence, their source and the reference area at which they were recorded.

Category	Variable	Description	Unit	Reference area	Source
<b>Climate</b>					
	T57	Average temperature May-July	°C	100x100m	Wordclim/WSL
	T122	Average temperature Dec.-Feb.	°C	100x100m	Wordclim/WSL
	P57	Precipitation sum May-July	mm	100x100m	Wordclim/WSL
	P122	Precipitation sum Dec.-Feb.	mm	100x100m	Wordclim/WSL
<b>Landscape</b>					
<b>Topography</b>					
	SLOPE	Slope	degree	30x30m	DEM
	TOPEX	Topographic position index	index	1km <sup>2</sup>	DEM
	EAST	Eastness (sine of aspect)	(-1) - 1	30x30m	DEM
	NORTH	Northness (cosine of aspect)	(-1) - 1	30x30m	DEM
	SOLAR57	Pot. solar radiation May-July	Wh/m <sup>2</sup>	30x30m	DEM
<b>Land cover</b>					
	FOREST	Forest	%	1km <sup>2</sup>	Vektor25/ATKIS
	FEDGEOUT	Density of outer forest edges	m/km <sup>2</sup>	1km <sup>2</sup>	Vektor25/ATKIS
	FEDGEIN	Density of inner forest edges	m/km <sup>2</sup>	1km <sup>2</sup>	Vektor25/ATKIS
	INTENSIVE	Intensive grassland and arable land	%	1km <sup>2</sup>	GEOSTAT / Landsat5 <sup>4</sup> /
	EXTENSIVE	Extensive grassland	%	1km <sup>2</sup>	GEOSTAT / Landsat5 <sup>4</sup> /
	WETSOIL	Proportion of mires and wet soils	%	1km <sup>2</sup>	Mire inventory BAFU, FVA Vektor25/ATKIS
<b>Infrastructure</b>					
	ROADDENS	Density of roads	m/km <sup>2</sup>	1km <sup>2</sup>	Vektor25/ATKIS
	SETTLEDIST	Distance to settlements	m	Plot center	Vektor25/ATKIS
<b>Vegetation</b>					
<b>Vegetation structure</b>					
<b>Stand mosaic</b>					
	CHEIGHT1 CHEIGHT2 CHEIGHT3 CHEIGHT4	Percentage of forest of height classes 1,2,3,4 respectively 1: <1.3m 2: 1.3 – 5m 3: 5-15m 4: >15 m	%	1km <sup>2</sup>	LiDAR
	GAPINDEX	Number of gaps of at least 0.1ha	n/ha	1km <sup>2</sup>	LiDAR
	CHH	Canopy height heterogeneity: total edge	m/ha	1km <sup>2</sup>	LiDAR

		length between all four height classes			
	ED134	Length of "sharp" edges (between ground vegetation and forest of > 5m)	m/ha	1km2	LiDAR
	ED12	Length of "soft edges" (between ground vegetation and forest <5m)	m/ha	1km2	LiDAR
<b>Stand structure</b>	SUCC	Age of the forest in 6 categories: 1 = regeneration (<1.3m height) 2 = thicket (<10cm DBH*) 3 = pole stage (<30cm DBH) 4 = tree stage (<60cm DBH) 5 = „old“ forest (≥ 3tr. >60cm DBH) 6 = multi-age	Category 1-6	30x30m	Fieldwork
	STANDSTRU	Vertical structure as number of layers: 1 = one, 2 = two 3 = multi layered	Category 1-3	30x30m	Fieldwork
	GVDIS	The pattern of ground vegetation was classified into 3 categories: 1=homogeneous, 2=patchy, 3=clumped	Category 1-3	30x30m	Fieldwork
	CANCOV	Canopy (≥5m) cover	%	30x30m	Fieldwork
	SHRUBCOV	Shrub (≥1.3m<5m) cover	%	30x30m	Fieldwork
	GVCOV	Ground vegetation (<1.3m) cover	%	30x30m	Fieldwork
<b>Vegetation composition</b>					
<b>Tree species</b>	BEE	Percent of beech	%	30x30m	Fieldwork
	SPR	Percent of spruce	%	30x30m	Fieldwork
	PIN	Percent of pine	%	30x30m	Fieldwork
	FIR	Percent of fir	%	30x30m	Fieldwork
	RESTREE	Percent of resource trees ( <i>Sorbus</i> sp., <i>Salix</i> sp., <i>Betula</i> sp., <i>Alnus</i> sp., <i>Corylus</i> sp. and <i>Sambucus</i> sp.)	%	30x30m	Fieldwork
<b>Ground vegetation</b>	HERB	Percent of herbs	%	7.5x7.5m	Fieldwork
	FERN	Percent of ferns	%	7.5x7.5m	Fieldwork
	GRASS	Percent of fir grass	%	7.5x7.5m	Fieldwork
	VAC	Percent of bilberry ( <i>Vaccinium</i> sp.)	%	7.5x7.5m	Fieldwork
	BERRY	Percent of berries (other than <i>Vaccinium</i> sp.)	%	7.5x7.5m	Fieldwork
<b>Special features</b>	ROW	Number of rowans >3m	n	15x15m	Fieldwork

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BBTREE	Number of basal branched trees	n	30x30m	Fieldwork
STANDDEAD	Number of standing dead trees >12cm	n	30x30m	Fieldwork
HSTUMP	Number of hard stumps >12cm	n	15x15m	Fieldwork
SSTUMP	Number of soft stumps >12cm	n	15x15m	Fieldwork
E1	Presence of inner forest edge	1/0	30x30m	Fieldwork
E2	Presence of outer forest edge	1/0	30x30m	Fieldwork

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