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Studiengang Diplom-Geoökologie

Modelling the spatial distribution of Blackbird  
(*Turdus Merula*) and Ring Ouzel (*Turdus Torquatus*) in  
Switzerland



## Diplomarbeit

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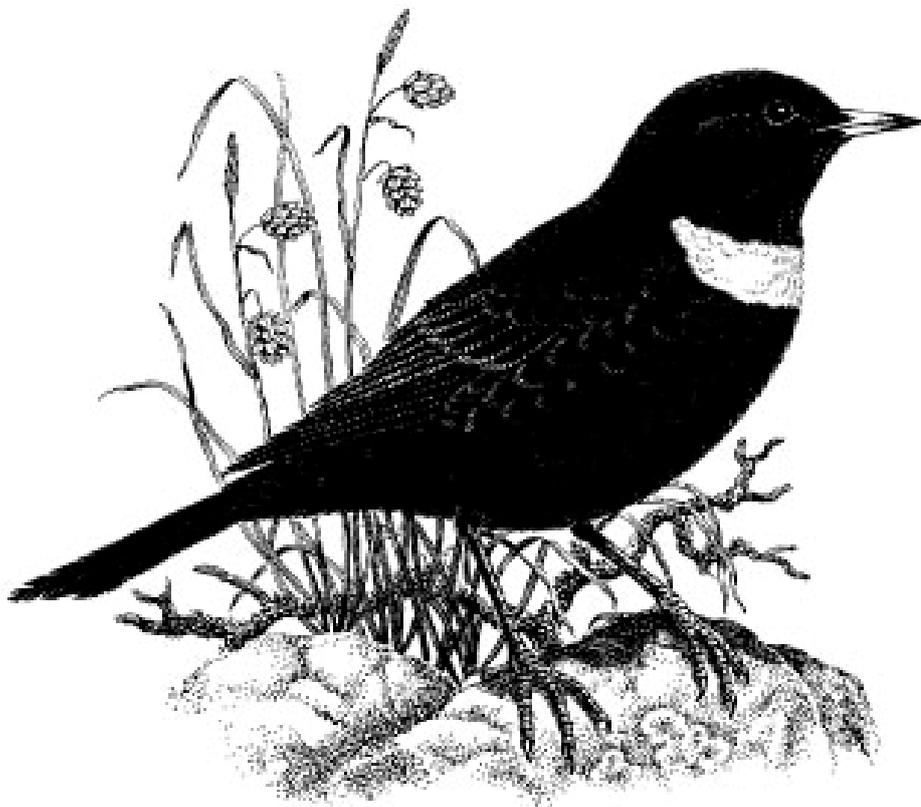
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## Das Samenkorn

Ein Samenkorn lag auf dem Rücken,  
die Amsel wollte es zerpicken.  
Aus Mitleid hat sie es verschont  
und wurde dafür reich belohnt.  
Das Korn, das auf der Erde lag,  
das wuchs und wuchs von Tag zu Tag.  
Jetzt ist es schon ein hoher Baum  
und trägt ein Nest aus weichem Flaum.  
Die Amsel hat das Nest gebaut,  
dort sitzt sie nun und zwitschert laut.

Joachim Ringelnatz



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## II Zusammenfassung

Unter Verwendung von Habitatmodellen beschreiben wir die Habitatpräferenz von Amsel (*Turdus merula*) und Ringdrossel (*T. torquatus*) in der Schweiz. Mit Hilfe verschiedener Klimaszenarien prognostizieren wir zudem die künftige potentielle Verbreitung beider Arten. Zur Beschreibung eines eventuell auftretenden Skalensprungs, d.h. einer Änderung in der Beschreibungskraft der Variablen auf verschiedenen räumlichen Ebenen, erstellten wir Modelle auf zwei unterschiedlichen Skalen. Während das Modell auf Makroskala mit einer Maschenweite von einem Quadratkilometer die gesamte Schweiz abdeckt, erstellten wir zudem eine Auswahl an Untersuchungsgebieten auf Revierebene.

Ringdrosseln zeigen ihren Verbreitungsschwerpunkt in der subalpinen Lage, während Amseln vornehmlich das Tiefland und die Tallagen besiedeln und nur vereinzelt in hohe Lagen vordringen. In einem Gürtel von ungefähr 400 Höhenmetern siedeln beide Arten parallel.

Trotz dieses auf der Makroskala erkennbaren Überschneidungsbereiches konnten wir in unserer Untersuchung auf Revierebene, von einer Ausnahme abgesehen, keine Koexistenz beobachten. Kleinräumige Unterschiede in der Habitatstruktur, insbesondere in der Vegetationsbedeckung scheinen demnach für die Habitatselektion von maßgeblicher Bedeutung zu sein. Auf Makroebene hingegen wurde der Einfluss klimatischer Variablen deutlich, die neben der Höhenlage auch dort typische Vegetationsstrukturen widerspiegeln.

Wie die Klimaszenarien zeigen, nehmen geeignete Ringdrosselhabitate bei steigenden Temperaturen ab und die Art weicht im Mittel um 440 m in höhere Lagen zurück. Für Amseln scheint sich eine zunehmende Erwärmung jedoch positiv auszuwirken, während das Verbreitungsgebiet im Tiefland beibehalten wird, dringt sie von den Tälern ausgehend zunehmend in höhere Lagen vor.

# 1. Research area

## 1.1 Geology

Switzerland covers an area of 41 239km<sup>2</sup> and essentially consists of two mountain chains with west-east orientation. The Jura in the northern part with altitudes up to 1607 m above sea level (asl) and the Alps in the south with the highest peak at 4634 m asl. These two ranges are separated by a lowland corridor, 50-100 km wide, generally referred to as the Swiss Midlands, ranging from about 360 to 900 m asl (Engler et al. 2004). Approximately 60% of Switzerland are covered by the Alps, followed by the Midlands with 30% and the Jura with 10% (Nigg 1975).

The Alps are a young mountain range, originating from tectonic upfolding during the Tertiary. Processes responsible for the great variety of different rocks found today are however far older. Several phases of marine sedimentation, subsequent uplifting, subsidence, plate movements and volcanic activity contributed to the lithology of the Alps. The geomorphology is largely the product of denudation, fluvial erosion and scouring during late Pleistocene glaciations (GBA).

The lakes of Thun and Vierwaldstadt are surrounded by the Northern Limestone Alps. These areas are partly overlain by helvetic nappes, consisting largely of marine sediments such as limestone and flysch. The higher central regions of the Alps consist of crystalline basement rocks, such as granite and gneiss (Nigg 1975).

## 1.2 Climate

Switzerland is influenced by oceanic as well as by continental climate. The western slopes of the Jura, the Black Forest in the north and the northern ranges of the Alps act as a meteorological barrier which results in more arid climate in the Western Midlands and the north-east of the country (BfS 2002). The local climate however is highly influenced by topographic features. Orographically induced rainfalls cause precipitation rates up to 4000 mm per year in the Bernese Highlands. Great differences exist between the wind-exposed luv and the protected lee sides of mountain ranges. Inneralpine areas, such as the Rhone valley can be very dry with precipitation rates below 600 mm per year (Nigg 1975). In addition, temperatures are a function of altitude. On average, mean temperatures drop by 0.7° C with every 100m of increasing altitude. Slope

exposure is another important microclimatic factor. Sun-exposed slopes are both warmer and drier than north-exposed slopes (Nigg 1975).

### 1.3 Vegetation

The vegetation of Switzerland belongs to the Holarctic flora, which characterises the temperate and cold climates of the northern hemisphere. Typical species are Pinaceae, Juncaceae, Salicaceae, Betulaceae, Ranunculaceae, Saxifragaceae and Aceraceae. Arctic, boreal and Atlantic-Mediterranean flora elements occur in altitudes above 1500 m asl (Hörsch 2001)

The biodiversity of Switzerland's natural vegetation is due to variations in relief, climate and soil. Plants range from subtropical in the southern valleys to sub-arctic species on high elevation sites.

Pristine forests covered most of the area before man first settled in what now is Switzerland. Beech trees (*Fagus sylvatica*) dominated the area up to 1000 m asl and the silver fir (*Abies alba*) was abundant in higher altitudes (Nigg 1975). Today highly modified forests cover 30 % of the countries' area, with fir (*Picea abies*) as the dominating species (Brassel and Brändli 1999).

The vegetation of Switzerland is generally classified in following altitudinal belts (cf. Nigg 1975; cf. BFS 2002):

1. Colline level (up to 600 m asl): In these areas pristine deciduous forests have been widely deforested and. They are now dominated by settlements, industries and transport routes, farmlands and orchards. Only 18% of forests remain.
2. Montan level (600-1200 m asl): Forests in this altitude mostly consists of beech, elm, maple, linden and willow trees, and are partly mixed with silver firs and pines. Timbered areas account for about 50% of the montan level and alternate with meadows and pastures.
3. Subalpine level (1200- approx. 2000 m asl): Coniferous forests with spruce and silver firs, larch trees, pines and yew trees are predominant in this area. The upper border of this level is identical with the timberline, which is ranging from 1800 m asl in the north and 2400 m asl in the inner alps.
3. The Alpine layer (above 2000 m asl) is located above the timberline. Trees only occur in small stands of pioneers such as the Swiss stone pine (*Pinus cembra*), dwarf pines (*Pinus mugo*) or

mountain alder (*Alnus viridis*). Alpine grasslands are used as mountain pastures (Alps) during summer. In its upper parts, only mosses and lichens are growing, bordered by the nival level, where rocks, ice and snow prevail (Nigg 1975; Brassel and Brändli 1999; Huovinen-Hufschmid 2001). Fig. 1 gives an overview of land use in Switzerland.

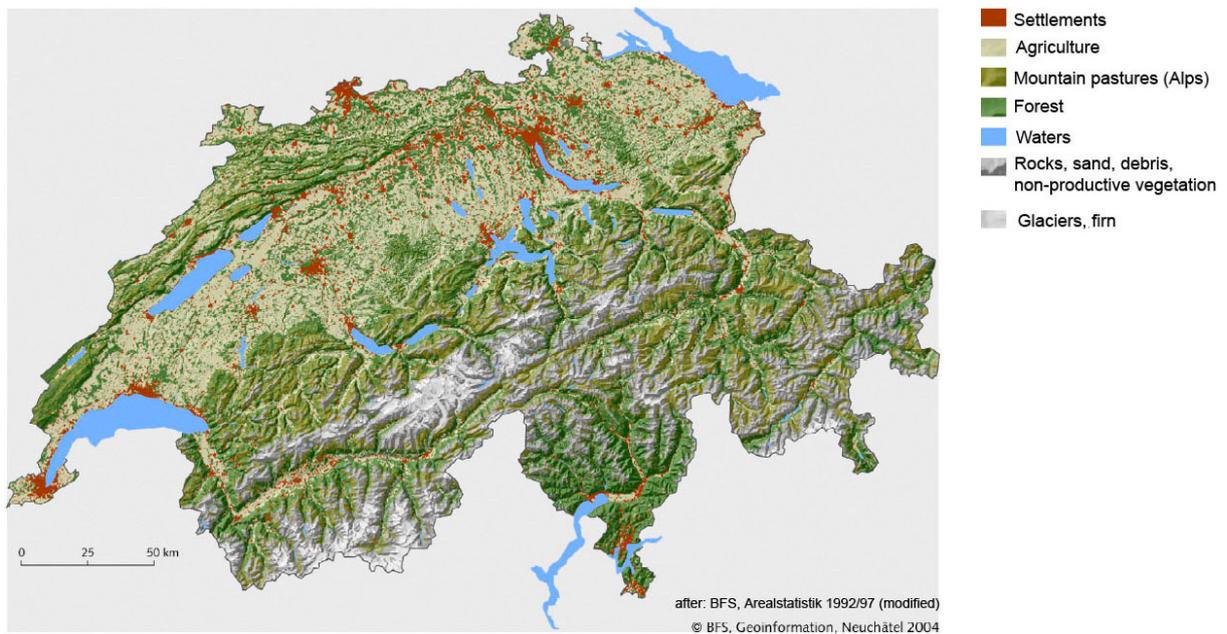


Fig.1: Land use in Switzerland, based on the Areal Statistics 1992/97 (cf. [www.bfs.admin.ch](http://www.bfs.admin.ch))

#### 1.4 Sampling sites for species distribution models on territory scale

All in all, we sampled fifteen square kilometre plots (Fig. 2). Two in the Napf upland (Luthern and Entlebuch), nine in the Bernese Oberland (Sigriswil, Brienz, Reichenbach, Kiental, Därstetten, Saanen, Lenk and Kandersteg) and two above Grindelwald, and two in the Valais (Visp and Vièrnamege).

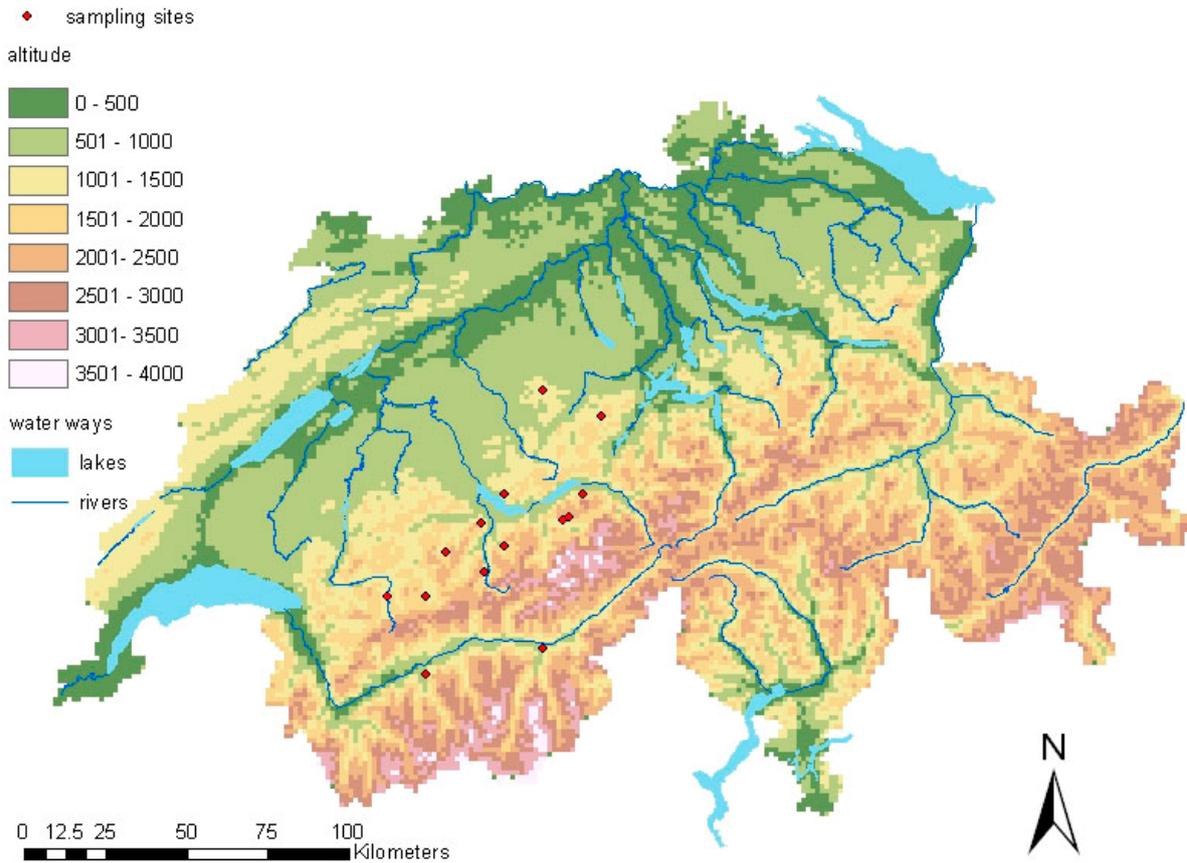


Fig.2: Switzerland: altitudinal range and sampling sites on territory scale

### 1.4.1 The Napf uplands

Located between Bern and Luzern the Napf-uplands form a barrier within the Swiss midlands with altitudes of more than 1400m. The Napf is mainly comprised of Miocene fluvial deposits from the ancient course of the Aare river. At present they crop out as resistant layers of conglomerates (the so called “Nagelfluh”) alternating with less resistant layers of sandstone and



clay which form terraces. During the last ice age, the Napf was not glaciated and thus the valleys, running radial from the centre are the result of mostly fluvial erosion processes.

With an annual precipitation rate of 1600 mm, the Napf is one of the most humid area sin the Swiss Midlands.

Fig.3: The Napf uplands above Entlebuch

Due to its impassability, the Napf area was first colonised through the valleys at the end of the 11<sup>th</sup> century. While the gentle sandstone and clay slopes have been cleared for farmland, the steeper Nagelfluh-sections are still covered with forest. Meadows are alternating with woodlands up to an altitude of 1000 m (e.g. Fig. 3). Higher areas were primarily used as mountain pastures (alps) resulting in a shift of the natural timberline. In the last decades however many pastures were left open and a natural spread of trees in abandoned grasslands took place in large areas of the Napf (Gutersohn 1950; Wiesli 1986).

#### 1.4.2 The Bernese Oberland (Bernese highlands)

The higher part of the Canton Bern is known as the Bernese Oberland, covering the northern central part of the Swiss Alps. Most mountains in this area belong to the main ridge of the Alps, forming a natural border to the south. The northern side is marked by steep slopes towards the Aare-river-system. Sedimentary rocks, but also autochthonous crystalline rocks characterise this area. The mountain ranges north of the Aare lakes, Lake Brienz and Lake Thun consist partly of limestone, partly of “Flysch”. The mountains Niesen and Stockhorn on the other hand belong to the “Préalpes Romandes”, which consists of cliffs and breccia. While pine forests cover parts of the slopes, arable areas of the Bernese Oberland are used traditionally as farm- and meadowland. (Wiesli 1986).



Fig. 4: Bernese highlands above Brienz

#### 1.4.3 The Valais

The canton of Valais belongs to the Pennine Alps, a mountain range in the western part of the Alps, covering parts of Switzerland, Italy and France.

Since basement rocks in this area consists mostly of silicate rocks, silicate plants prevail (Hörsch 2001). Due to the shelter of the surrounding mountains the main valley-system of the upper Valais and the lower Visp-valley are the driest areas in Switzerland (Braun-Blanquet 1964). Thus, especially at the south exposed slopes of the



Fig.5: Visp

Rhone valley, steppe vegetation grows (Hörsch 2001). While in the higher areas of our investigation sites pine (*Pinus cembra*) forest shows a predominance, oaks (*Quercus pubescens*) dominate the lower forests, with a potential to spread to higher altitudes at rising temperatures (Bonfils et al. 2005).

## 2. Species under study

### 2.1 *Turdus merula* - blackbird

The blackbird *Turdus merula* (Fig 6) is a common breeding bird all over Europe (Fig 8) except for northern Scandinavia. Its distribution is reaching as far as North Africa and eastern China. Blackbirds populate nearly all parts of Switzerland and are only absent in altitudes above 2200 m asl. Non-urban populations prefer habitats in dense forests with multiple layers, but rely on marginal groundcover because they are feeding on soil organisms such as earthworms. Otherwise blackbirds easily adapt to different environments, showing no obvious preferences (Glutz von Blotzheim et al. 1988). Formerly known as a mere forest inhabitant, blackbirds are now frequent in bosks, hedges, parks on cemeteries and even along avenues (Schmid et al. 1998)

### 2.2. *Turdus torquatus* – ring ouzel

The ring ouzel *Turdus torquatus* (Fig. 7) shows a scattered distribution all over central Europe, with an occurrence from Fennoscandia and Great Britain in the north, to the Alps in the south and the Carpathians in the east. Half of the birds' European population is found in Austria and Romania. Other European countries with high numbers of the ring ouzel are Norway, Germany, Switzerland Italy and Ukraine (Fig. 9). The species is divided in two subspecies: *torquatus* living in the northern areas and *alpestris* inhabiting the south. While the northern subspecies prefers steep rocky slopes, gullies and moorland (Tucker and Heath 1994), the southern subspecies has its main abundance in semi-open landscapes around the timberline. In Switzerland, subspecies *alpestris* inhabits areas in altitudes between 1200 and 2200 m asl in the Alps and above 1100 m asl. in the Jura (Schmid et al. 1998).



Fig.6: blackbird



Fig.7: ring ouzel

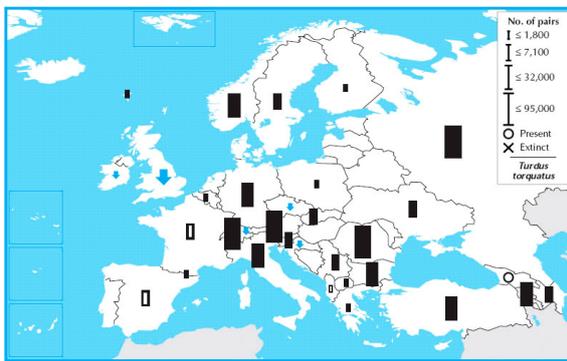


Fig.8: European Population size of blackbird (cf. [www.birdlife.org](http://www.birdlife.org))

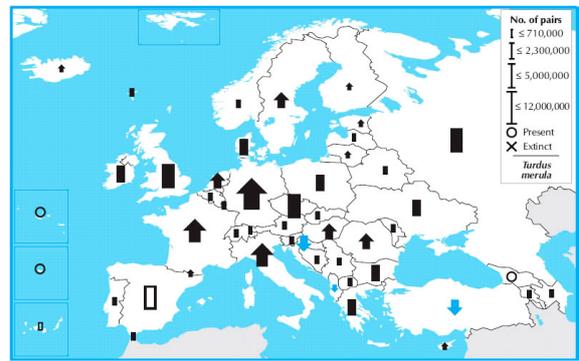


Fig.9: European Population size of ring ouzel

### 3. Paper

#### Modelling the spatial distribution of ring ouzel

#### *(Turdus torquatus)* and blackbird (*T. merula*) in Switzerland

To be submitted as:

Jens von dem Bussche<sup>1</sup>; Reto Spaar<sup>2</sup>; Hans Schmid<sup>2</sup> and Boris Schröder<sup>1</sup>. Modelling the spatial distribution of ring ouzel (*Turdus torquatus*) and blackbird (*T. merula*) in Switzerland. Journal of Ornithology.

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#### 3.1 Abstract

In order to characterise the habitat selection of ring ouzel (*Turdus torquatus*) and blackbird (*T. merula*) in Switzerland, we employed species distribution modelling and predicted the species' potential future distribution for climate change scenarios. To discover in how far downscaling leads to a difference in variables describing the realised habitat best, we modelled on two different scales. While the models on macroscale (grid of one square kilometre) cover the whole country, we selected a set of smaller plots for modelling on territory scale. Our research demonstrates that Ring ouzels occur in high altitudes only, whereas blackbirds occur from the lowlands up to high elevation sites. This leads to a range overlap of approximately 400 m in elevation. Despite both species coexisting on macroscale, a direct niche overlap on territory scale is rare. Small-scale differences in the vegetation cover seem to be predominant for habitat selection. On macroscale however, we observed a high dependency on climatic variables mainly representing the altitudinal range and thus preferred structural variables of the two species. Along with climate change, we predict a decline of suitable habitats for ring ouzels going along with a median altitudinal shift of 440 m. In contrast, blackbirds obviously benefit from higher temperatures and show a range expansion to higher elevations.

**Key words:** *Turdus torquatus*, *Turdus merula*, species distribution modelling, climate change scenario

## 3.2 Introduction

Within the last decade it became apparent that species distributions respond to the changing climate (Hughes 2000; Parmesan and Yohe 2003) and will do so exceedingly in the future (Theurillat and Guisan 2001; Huntley et al. 2006). Highest impacts are predicted to occur in high mountain systems like the Alps (Beniston et al. 1997; Hughes 2000; Theurillat and Guisan 2001; Sergio 2003).

In this study we address two common bird species in Switzerland: the ring ouzel (*Turdus torquatus alpestris*), which is restricted to high altitudes exceeding 1000 m asl (above sea level) and the blackbird (*T. merula merula*) occurring all over the country, except for high mountainous areas. The overlapping area is limited to a range of maximum 400 meters in altitude (Schmid et al. 1998).

While blackbirds preferably inhabit dense forests or shrubland with bare soils (Hatchwell et al. 1996; Stephan 1999), ring ouzels show their core distribution in open forests, often in close proximity to open landscape elements like alpine meadows (Glutz von Blotzheim et al. 1988; Schmid et al. 1998).

In the last century, European blackbirds expanded to the North as well as to higher altitudes (Glutz von Blotzheim et al. 1988). However, for ring ouzels a negative population trend is documented from 1990 onwards, coming along with a local retreat to higher altitudes (Kronshage 2003; Mattes et al. 2005).

Several authors presume that the proceeding displacement of the ring ouzel by the blackbird is at least partly caused by interspecific competition (Berg-Schlosser 1980; Oberwalder et al. 2002; Kronshage 2003). Structural differences in the habitats occupied by ring ouzels and those by the blackbird suggest diverging habitat requirements and therefore lead to a different explanation of the species' distribution. Coexistence in a limited altitudinal range and a lack of obvious evidences for direct competition (Glutz von Blotzheim et al. 1988) indicate that also factors other than interspecific competition may influence the habitat segregation of the two species.

To evaluate our hypothesis of differences in habitat requirements, we performed species distribution modelling, a method to examine the relevance of various environmental characteristics to explain species' spatial distribution (Guisan and Zimmermann 2000; Guisan and Thuiller 2005b). The objectives of this study were:

- (1) to analyse and to compare the habitat selection of both species on territory scale at selected sites,
- (2) to find out important explanatory variables controlling species distribution on macroscale,
- (3) to predict the spatial distribution of blackbird and ring ouzel for entire Switzerland based on predictive species distribution models, as well as
- (4) to predict the species distributions applying the same model for a set of several climate change scenarios.

Factors describing species' distribution at different spatial and temporal levels might vary in their explanatory value on different scales (Mackey and Lindenmayer 2001). In order to answer the question, in how far suitable habitats are described differently by comparable predictor variables, modelling is applied on two scales. Areas where both species live in sympatry, thus areas where both species are able to inhabit the same habitats are of special interest. Analysing the prevailing habitat characteristics in these areas leads to a better understanding of the realised niche and might reveal processes such as interspecific competition and habitat selection.

Using the most important variables of the species distribution models, we predict future distributions at different climate change scenarios (Frei 2004) for the years 2030, 2050, and 2070. Based on tendencies discovered most recently, our main hypothesis is a shift of the ring ouzel to higher altitudes accompanied by a spatiotemporal upward expansion of the blackbird.

### **3.3 Methods**

#### **3.3.1 Analysis on territory scale**

##### *3.3.1.1 Research areas*

We obtained species incidence data from the so-called MHB-program (monitoring of frequent breeding birds run by the Swiss Ornithological Institute in Sempach. During this monitoring program, 250 areas of one square kilometre, distributed all over Switzerland have been surveyed annually with respect to their breeding bird populations. If permitted by altitude and thus snow

cover, all sites were inspected at least twice, but mostly three times a year. The program started in 1999 and provides reliable information about the approximate location of bird territories and thus species occurrences. If a species has not been recorded in a square within the last 5 years, it is considered as absent.

Based on these mappings, we selected 14 suitable MHB-sites to record habitat data for blackbird and ring ouzel during our fieldwork from April to June 2005. We chose six sites where both species were present, four sites with only blackbird and four sites with only ring ouzel present. Twelve out of the fourteen sites were located in the Berner Oberland (Bernese Highlands); the remaining two in the Valais, where a large anthropogenically almost unaffected blackbird population remains in altitudes above 1000 m above sea level (a.s.l.). Altogether we sampled 176 territory plots, sized  $25 \times 25 \text{ m}^2$  in these sites: 94 plots of blackbirds (prevalence = 0.53); and 85 of ring ouzels (prevalence = 0.48). In one case only, a blackbird and ring ouzel plot showed a direct habitat overlap.

### *3.3.1.2 Sampling design, predictor variables, species data*

It is necessary to base a sampling design on the gradients hypothesised to determine the distribution of a species, and consider them primarily to stratify the sampling (cf. Guisan and Zimmermann 2000; cf. Hirzel and Guisan 2002). As an uncertainty about the actual territory of a bird prevails, the preferable method to choose plots randomly has to be applied carefully.

Due to the danger of misclassifying a species incidence, we deliberately chose occupied territories in which we randomly set up a  $25 \times 25 \text{ m}$  plot. Furthermore, we restricted the measured altitudinal range to sites located above 1000 m asl as no ring ouzels occur below and blackbirds are highly anthropogenic influenced in the lowlands.

For each independent sighting of a blackbird or ring ouzel, we recorded several predictor variables (Tab 1) reflecting the species' autecology. We selected variables suited to describe the habitat's location according to climatic effects, as well as structural variables.

Besides variables characterising the plot-inherent structure, we also included parameters describing the surrounding landscape, as this might influence a species' presence (Binzenhöfer et

al. 2005). Definitions for shape and composition of the forest edge, as well as the height of the different forest layers follow Stierlin (cf. Stierlin et al. 1994).

Tab.1: Overview of the variables recorded on territory scale, including median  $\pm$  MAD (Median Absolute Deviation) for ring ouzel and blackbird presence.

<i>Variable</i>	<i>Description</i>	<i>Median <math>\pm</math> MAD</i> <i>(count0/1 for binary data)</i>	
		<i>ring ouzel</i> <i>present</i>	<i>blackbird</i> <i>present</i>
<i>Topographic parameters</i>			
Altitude [m]	meters above sea level	1640 $\pm$ 120	1320 $\pm$ 100
Slope angle [°]	terrain inclination	48 $\pm$ 16	48 $\pm$ 12
Exposition [°]	later transformed to sine and cosine of the radian as well as to Beers' index (1966)	200 $\pm$ 80	250 $\pm$ 40
Profile curvature [ordinal]	vertical shape of terrain (1-concave, 2-convex, 3-convex-concave, 4-flat)		
<i>Vegetation parameters</i>			
all referring to the entire plot			
Forest ratio in plot [%]	total coverage by trees in plot	20 $\pm$ 5	85 $\pm$ 5
Coverage of herbaceous and mossy ground vegetation [%]	including ferns, grasses, herbs and mosses	45 $\pm$ 35	0 $\pm$ 0
Coverage of berry bush [%]	in particular <i>Rubus</i> and <i>Vaccinium</i> species	5 $\pm$ 5	0 $\pm$ 0
Under storey [%]	<1/3 main height	30 $\pm$ 10	80 $\pm$ 10
Intermediate forest layer [%]	1/3– 2/3 of main height	25 $\pm$ 10	70 $\pm$ 10
Upper forest layer [%]	>2/3 of main height	20 $\pm$ 10	60 $\pm$ 15
Tallest tree [%]	Median Height of the four tallest trees	20 $\pm$ 5	22 $\pm$ 5
Forest edge present/absent [binary]	no (0); yes(1)	28/57	10/84
Shape of the forest edge [ordinal]	no forest edge (0); straight (1); curved (2); sinuated (3); highly sinuated (4); loose (5)		
Composition of the forest edge [ordinal]	8 categories, according to Stierlin et al. 1994		
<i>Territory</i>			
Forest in territory [binary]	no (0); yes(1)	20/65	0/94
Territory centre in forest [binary]	no (0); yes(1)	34/51	11/83

Tab. 1 continued

<i>Variable</i>	<i>Description</i>	<i>Median ± MAD</i>	
		<i>ring ouzel present</i>	<i>blackbird present</i>
<i>Edaphic parameter</i>			
Soil moisture [binary]	dry (0); wet (1) determined by vegetation	38/47	22/72
<i>Other structural elements</i>			
rocks/ root bales/ tree stubs [%]	as perch for singing males	50 ± 25	0 ± 0
<i>Neighbourhood relationship parameters</i>			
	taken up to a distance of 400 m		
Distance to clearings [m]		0 ± 0	0 ± 0
Distance to meadows/pastures [m]		0 ± 0	0 ± 0
Distance to waters and wetlands [m]		180 ± 120	160 ± 140
Distance to settlements [m]	including huts and barns	190 ± 90	100 ± 50
Distance to roads, farm and forest tracks [m]		40 ± 40	40 ± 30

### 3.3.2 Analysis on macroscale

To model large-scale distribution (grid of 1 km<sup>2</sup>), i.e. the entire of Switzerland, we used several Swiss databases. Presence-absence data of blackbird and ring ouzel were derived from the Swiss Breeding Bird Atlas (Schmid et al. 1998). Data on climate and terrain were compiled from the databases BIOCLIM (Swiss Federal Research Institute WSL), GEOSTAT (Swiss Federal Statistical Office) and the Atlas on Vegetation Types (Hegg et al. 1993) for data on vegetation. Data on bird incidences are available to a maximum altitude of 2500 m asl. Ring ouzels indeed breed on high elevation sites up to 2600 m asl (Schmid et al. 1998). Thus, we could not depict the whole altitudinal range of ring ouzel occurrences. Latter is probably described better by a unimodal, than by a linear function, running the risk of predicting presences incorrectly at sites located above the mapped range. Therefore, we randomly generated 50 pseudo-absence plots in altitudes above 2800 m asl where we did not expect any ring ouzel incidences (cf. Beers et al. 1966; Hirzel et al. 2001; cf. Engler et al. 2004). We visualised occurrence probabilities at a grid size of 1km<sup>2</sup> for entire Switzerland using ArcGIS (ESRI™).

### 3.3.2.1 *Species distribution modelling*

Species distribution modelling aims to describe the distribution of blackbird and ring ouzel depending on the prevailing environmental factors. We used a GLM (Generalised Linear Model)-approach that allows the modelling of differently scaled variables within a single theoretical frame (Yee and Mitchell 1991). Logistic regression models are most suitable for binary response variables, as they are robust against overfitting and act highly parsimoniously (Hosmer and Lemeshow 2000; Schröder and Reineking 2004a). We performed all statistical modelling in R version 2.1.0 (R Core Development Team, 2006) using the packages “Hmisc” and “Design” provided by F. Harrell, Jr.

We employed Nagelkerke’s  $R^2_N$  (Nagelkerke 1991) for model calibration, as well as the AUC-value (area under the receiver operating characteristic curve) as a threshold-independent criterion (Fielding and Bell 1997; Harrell 2001) for model discrimination. While an AUC-value of 0.5 equals a random prediction,  $AUC > 0.8$  reflects an excellent and  $AUC > 0.9$  an outstanding model discrimination (Hosmer and Lemeshow 2000). For multiple models, we additionally calculated the correct classification rate, using a cut-off value  $P_{crit} = 0.5$  according to Schröder (2004).

### 3.3.2.2 *Variable selection*

We considered all linear and quadratic terms as well as all two-way interactions as potential predictors, excluding all variables with  $p > 0.05$  by a likelihood-ratio test on significance in a preliminary univariate analyses (Hosmer and Lemeshow 2000; Binzenhöfer et al. 2005). Furthermore, we excluded variables with  $AUC < 0.7$  after univariate modelling due to their poor performance. To avoid multicollinearity, we applied a two-sided rank-correlation-test after Spearman ( $r_s$ ) on the selected set of predictor variables setting a limit for considering both correlated variables of  $r_s = |0.7|$  according to Fielding and Haworth (1995).

Due to the high level of correlation of important variables on territory scale, we combined five predictors to a principal component using principal component analysis (PCA) (cf. Legendre and Legendre 1998; Hirzel et al. 2004). On macroscale however, we excluded the variables with the less explanatory value from a set of correlated predictors derived from a hierarchical partitioning analysis. This method allows the ranking of predictor variables according to their independent explanatory power (Chevan and Sutherland 1991; Mac Nally 2002; Mac Nally and Walsh 2004). A

shortcoming of hierarchical partitioning however is its inapplicability on polynomial terms (Heikkinen et al. 2005).

When applying non-spatial regression approaches such as logistic regression an important assumption for species distribution modelling is the independency of the underlying data (Hosmer and Lemeshow 2000). In case of spatial autocorrelation a value sampled at one plot can partly be predicted by the values sampled at surrounding plots (Legendre 1993) and therefore is not independent stochastically. In case of positive autocorrelation the probability of occurrence in a neighbouring region increases (Smith 1994). Using the R-libraries `spdep` (Bivand and Gebhardt 2000), `ncf` (Bjørnstad and Falck 2001) and modified functions created by Dormann (Dormann et al. 2006), we checked for residual spatial autocorrelation by calculating Moran's I (Moran 1950) and if necessary estimated an autologistic model. Moran's I is a weighted correlation coefficient used to detect deviations from spatial randomness testing for spatial autocorrelation in group-level data (Legendre and Legendre 1998; Lichstein et al. 2002).

To select the most parsimonious model that offers the highest degree of accuracy with the least amount of variables, we used Akaike's Information Criterion (AIC) (Akaike 1974; Opperl et al. 2004). Using stepwise backward selection, only variables with a high explanatory value remained in the final model.

We internally validated our final model by performing a bootstrap analysis (Verbyla and Litvaitis 1989; Efron and Tibshirani 1993) with 2000 iterations, to correct over-optimistic estimates of performance criteria that result from assessing model performance on training data (Schröder and Reineking 2004b; Opperl et al. 2004).

### 3.3.3 Sympatric occurrences

Besides modelling the distribution for blackbird and ring ouzel separately, we focused on the area of coexistence. While on territory scale ring ouzel and blackbird habitats overlapped once only, on macroscale, 13 % of the kilometre squares with blackbird presence and even 64% of those with ring ouzel presence showed an overlap. To analyse the most important variables characterizing sympatric localities, we computed two separate models with a binary response variable. We hereby differentiated kilometre squares where both species were present (overlapping =1) and those where blackbird or ring ouzel only were present (no overlap = 0).

Thus, one model reflects the realised niche overlap in comparison to an occurrence of solely ring ouzels and the second one in comparison to blackbird presence areas.

### 3.3.4 Climate change scenarios

To predict the future distribution of blackbird and ring ouzel in Switzerland, we applied a probabilistic climate projection on temperature and precipitation rates for Switzerland after Frei et al. (2004). The underlying assumptions for his projection derive from simulations developed within the European research project PRUDENCE (Christensen et al. 2002). Those simulations calculated from 16 model strings on climate represent different combinations of an emission scenario, a global climate model (GCM) and a regional climate model (RCM). While Frei et al. (2004) originally proposed two projections, one for northern and one for southern Switzerland, we merged them into a single projection since the related errors exceeded the differences between the two projections.

Using the variables “July temperature” and “annual precipitation rate”, as part of our final species distribution models, we generated nine scenarios for the spatial distribution of blackbird and ring ouzel. For the years 2030, 2050 and 2070, we calculated predictions with the lowest, the median and the highest value of the predicted changes.

## 3.4 Results

### 3.4.1 Territory scale

The final models for both species are based on three variables out of 29 potential predictors, including a principal component. Latter covers all structural variables, except the coverage of the berry bush layer. Surprisingly, the remaining three variables describe the habitat preferences of both species best. (Tab. 2). The coefficients show a clear contrast between the two species. The structural variables representing the coverage of the forest layers and the overall amount of forest in the plot show a positive relationship with blackbird incidences. However, a negative correlation can be found for the variable “ground vegetation”. On the contrary, ring ouzel habitats correlate negatively to the cover of the upper forest layers and forest ratio in the plot.

Ring ouzels seem to prefer dense moss, herb and berry bush layers. The altitudinal distribution likewise illustrates a clear trend: blackbirds rather occur in low, ring ouzels in high altitudes.

After internal validation, both models showed a high explanatory and predictive power. The model for the ring ouzel displays a corrected AUC of 0.988 and a corrected  $R^2_N$  of 0.892. The model for the blackbird performs similarly well with  $AUC_{corrected} = 0.99$  and  $R^2_{Ncorrected} = 0.87$ . Applying a critical threshold probability of  $P_{crit} = 0.5$ , the overall correct classification rate is 94.9 % for the ring ouzel and 95.5 % for the blackbird.

Tab.2: Regression coefficients, standard errors and p-values as well as performance criteria of the multiple territory scale models for blackbird and ring ouzel.  $R^2_N$  and AUC-values are given before and after internal validation with 2000 bootstrap replicates.

	<b>blackbird</b> (prevalence = 53.41 %)				<b>ring ouzel</b> (prevalence = 48.3 %)			
	Coef.	S.E.	p	Ind.eff. [%]	Coef.	S.E.	p	Ind.eff. [%]
Intercept	15.251	4.727	0.001		-14.82	5.019	0.003	
principal comp. <sup>1</sup>	-1.807	0.379	< 0.001	55.79	2.247	0.503	< 0.001	58.23
Altitude	-0.010	0.003	0.002	31.1	0.010	0.003	0.003	29.02
cov. berry bush	-6.033	1.950	0.002	13.1	6.266	2.176	0.004	12.75
	$R^2_N$   corr.		AUC   corr.		$R^2_N$   corr.		AUC   corr.	
	0.913   0.87		0.99   0.986		0.903   0.892		0.988   0.988	

### 3.4.2 Macroscale

#### 3.4.2.1 Ring ouzel

Due to insignificancies, low predictive performances or high correlations to other predictors we excluded several predictor variables during the modelling process. The final model comprised ten variables, of which five were derived from vegetation data after Hegg (1993) and one interaction term. Additionally, two quadratic terms were included in the model (cf. Tab. 3). According to its independent effect, the most important variable for characterising the ring ouzel's habitat on macro scale is the subalpine forest. Areas with a median ratio of these loose forests, consisting of spruce (*Picea abies*), stone-pine (*Pinus cembra*) and larch (*Larix deciduas*) feature a main ring

<sup>1</sup> First principal component of a PCA, containing following variables (loadings): cover upper layer (-0.503), coverage understorey (-0.519), forest ratio in plot (-0.542), cover moss/herb layer (0.425), explaining 50.7 % of the overall variance.

ouzel occurrence. At the forests' upper fringe, stands of dwarf-pines (*Pinus mugo*) even stretch out into the alpine region. Nutrient poor grasslands forbs and coppice of the high elevation site further characterise the preferred habitats on the macroscale,

Nutrient rich valley grassland, farmlands and meadows, mostly situated in the lowlands however correlate negatively to the ring ouzel's habitat as well as high amounts of rocks, debris and settlements. The July temperature proved to be an important variable as well, predicting most suitable ring ouzel habitats in the subalpine temperature range. The remaining interaction term reflects a presence of ring ouzels in areas with low to median temperatures and low to median precipitation rates. No ring ouzels occur in areas with high precipitation rates and high temperatures.

The model performs well with a corrected  $R^2_N$  of 0.705 and  $AUC_{\text{bootstrapped}} = 0.950$  (Tab. 4) and correctly classifies 88.6 %, applying a critical threshold probability of  $P = 0.5$ . (cf. App.8).

Tab.3: Regression coefficients, standard errors, p-values, independent effect (determined by hierarchical partitioning), as well as performance criteria of the multiple macroscale models for ring ouzel.  $R^2_N$  and AUC-values are given before and after internal validation with 2000 bootstrap replicates.

ring ouzel (prevalence = 26.44 %)	Coef.	S.E.	P	Indep. eff. [%]
Intercept	-7.015	2.235	0.002	
subalpine forests	0.048	0.010	< 0.001	17.58
subalpine forests (quadratic term)	-0.001	< 0.001	0.003	-
nutrient-rich valley grasslands	-0.031	0.009	0.001	17.38
farmland and meadows	-0.029	0.005	< 0.001	15.54
forbs and coppice (upper montane, subalpine, alpine)	0.020	0.006	0.001	12.34
settlement areas	-0.063	0.021	0.003	11.74
July temperature	1.719	0.303	< 0.001	10.56
July temperature (quadratic term)	-0.095	0.011	< 0.001	-
nutrient poor grassland (upper montane/subalpine/alpine)	0.023	0.006	< 0.001	8.5
precipitation rates per year (divided by 100)	-0.262	0.110	0.017	3.64
rock / debris	-0.022	0.007	0.001	2.7
Interaction term precipitation rates* July temperature	0.026	0.009	0.004	-

Tab.4.:  $R^2_N$  and AUC-values before and after internal validation with 2000 bootstrap replicates for the final species distribution model for ring ouzel on macroscale.

AUC	AUC corr.	$R^2_N$	$R^2_N$ corr.
0.951	0.95	0.713	0.705

### 3.4.2.2 Blackbird

Due to high correlations, we excluded several variables such as altitude, radiation or annual temperature before starting model selection. The final model however comprises five predictor variables and one interaction term as shown in Tab. 5. As the hierarchical partitioning illustrates, the positive correlation to July temperatures is the most convincing variable with an independent effect of almost 45 %. As the model depicts entire Switzerland and thus includes urban areas, settlements are of great explanatory value, still featuring an independent effect of 20 %. Furthermore, blackbirds avoid uncovered areas and show a clear positive trend to inhabit dense forests. Latter show an interaction with the July temperatures: It seems that at high summer temperatures, blackbirds are completely independent of closed forests; in case of low temperatures however, there is a clear bond to dense forests. The model yields a performance of  $R^2_{N \text{ corrected}} = 0.66$  and  $AUC_{\text{bootstrapped}} = 0.95$  showing only very slight optimism (Tab. 6). At a cut-off value  $P_{\text{crit}} = 0.5$ , it correctly classifies 93.5 % of all observations (cf. App.8).

Tab.5: Regression coefficients, standard errors and p-values, independent effect (determined by hierarchical partitioning), as well as performance criteria of the multiple macroscale model for blackbird.  $R^2_N$  and AUC-values are given before and after internal validation with 2000 bootstrap replicates.

blackbird (prevalence = 84.13 %)	Coef	S.E.	P	Indep. eff. [%]
Intercept	-5.385	0.718	< 0.001	
Mean July temperature	0.597	0.057	< 0.001	44.65
Settlement areas	0.151	0.037	< 0.001	20.06
Unvegetated areas	-0.064	0.014	< 0.001	17.93
Dense forest	0.088	0.024	< 0.001	11.61
Precipitation rates per year	-0.001	< 0.001	0.001	5.74
July temperatures * closed forests	-0.005	0.002	0.005	

Tab.6:  $R^2_N$  and AUC-values before and after internal validation with 2000 bootstrap replicates for the final species distribution model blackbird ouzel on macroscale.

AUC	AUC corr.	$R^2_N$	$R^2_N$ corr.
0.951	0.950	0.671	0.664

### 3.4.3 Spatial autocorrelation

Both species' models showed a strong autocorrelation not only in the raw distribution data but also in the residuals after applying the non-spatial model. As illustrated in Fig. 10, the autocovariate considered in the spatial model removed most of the residual spatial autocorrelation. Since the autocovariate does not improve the performance of the final model, we did not include it as a separate variable for scenario analyses.

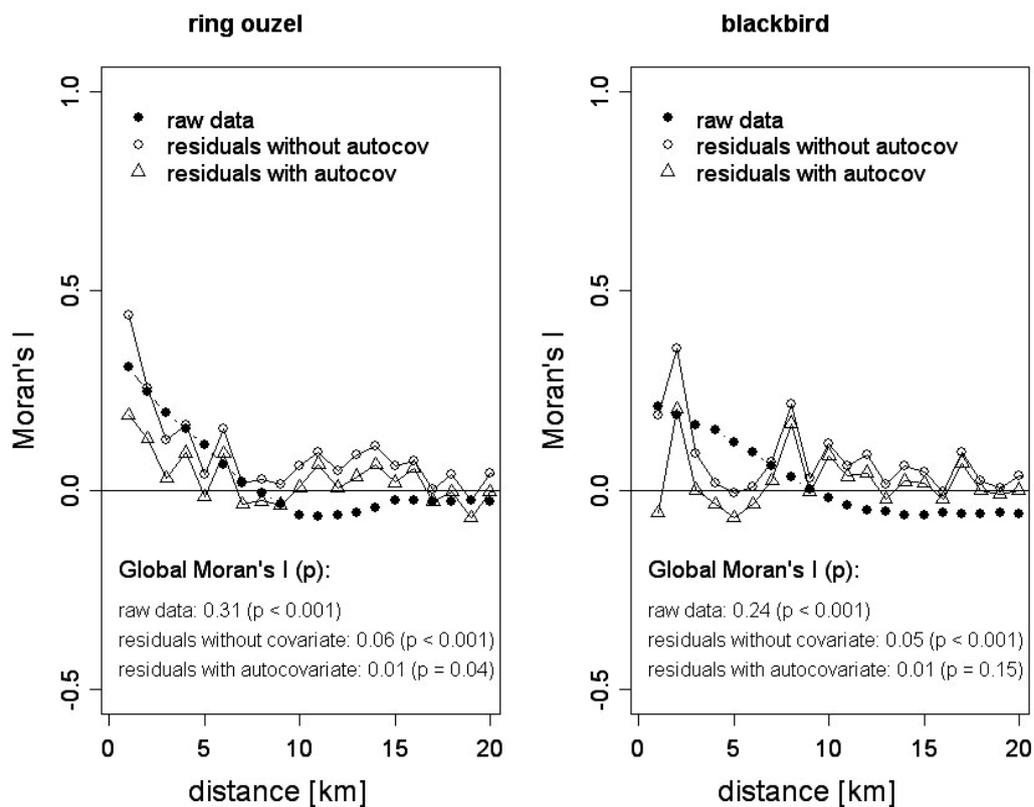


Fig.10: Correlograms, showing spatial autocorrelation for ring ouzel and blackbird, for raw data and data with and without a covariate, employing Moran's I

### 3.4.4 Climate change scenarios

Fig. 13 and 14 give an overview of the predicted distribution of blackbirds and ring ouzels throughout Switzerland. The first map illustrates the current situation followed by three scenarios for the years 2030, 2050 and 2070. As predicted climate change, shows a variance of the expected differences in temperature and precipitation rates. We therefore calculated three different scenarios for each year, reflecting the minimal, median and maximal expected values (cf. Tab. 7 and Tab. 8). The current distribution of blackbirds shows that this species populates the northern

lowlands. Blackbirds are likewise present in the major valley systems of the large rivers Rhone, Rhine, Ticino and Inn and adjacent valleys. Not later than 2030 at median temperature-rise and changes in precipitation rates, the blackbird will populate all areas in the Jura. In the inner Alps, we predict a range expansion to higher altitudes starting from the valleys. Current predictions for blackbirds show an occupation of 28585 km<sup>2</sup> applying a cut-off-value of  $P = 0.5$ . At median climate changes, we assume an expansion to 32297 km<sup>2</sup> in the year 2070 (Tab.9). Depending on local conditions, this spread matches an expansion of more than 130 m towards higher altitudes (Fig. 12). Ring ouzels on the opposite, are currently restricted to altitudes above 1000 m asl with a median distribution at 1760 m asl and show incidences in the Jura and Alps only. The climate change scenarios indicate a decline of suitable habitat for the ring ouzel, going along with a shift to higher altitudes. While ring ouzels currently occur on 12 248 km<sup>2</sup> with an occurrence probability exceeding 50%, in 2070 this counts for only 9960 km<sup>2</sup> at median changes and only 4061 km<sup>2</sup> left at maximal changes (cf. Tab. 9). We predict the median occupied altitude to rise for about 440 m up to 2200 m asl. (Fig 11).

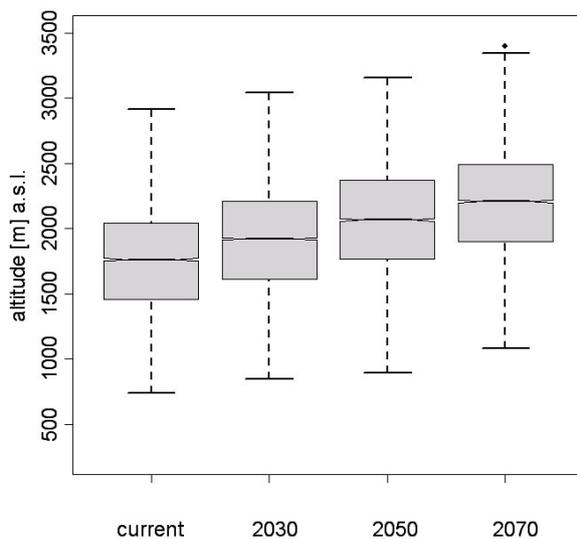


Fig.:11: Distribution of elevation of ring ouzel habitat for current distribution as well as climate change scenarios. Notches show the 95% confidence interval.

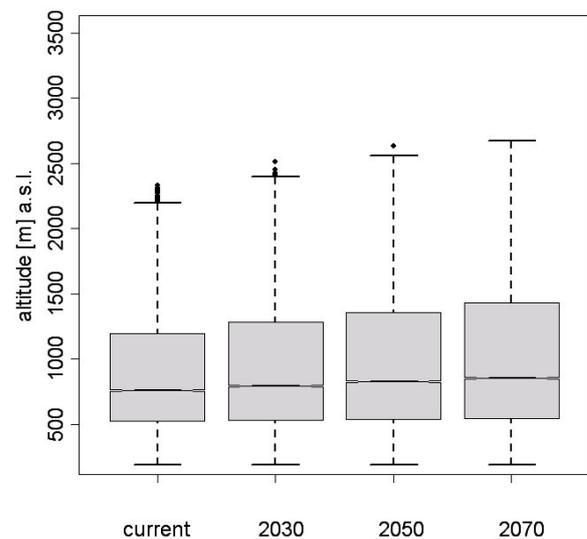


Fig.:12: Distribution of elevation of blackbird habitat for current distribution as well as climate change scenarios. Notches show the 95% confidence interval

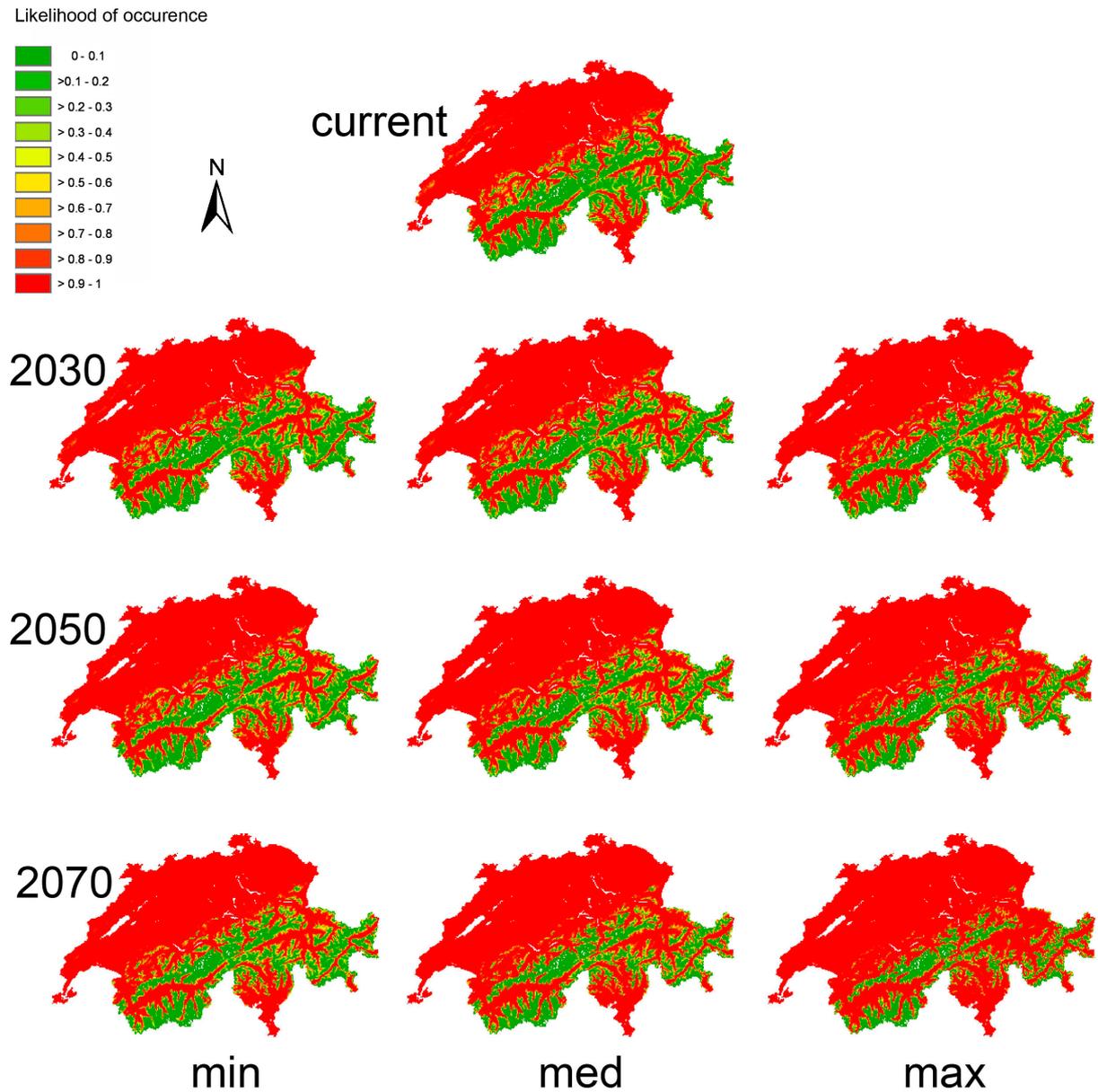


Fig.13: Predicted distribution of the blackbird for the present, 2030, 2050, 2070 at minimal, median and maximal changes in July temperatures and annual precipitation rates. For details on changing rates see Tab.7 and Tab. 8.

Tab.7: Changes in July temperature for 2030, 2050 and 2070 with minimal, median and maximal predicted changes. Values add to the current temperatures. (Frei 2004 modified)

Year	Min	Median	Max
2030	0.6	1.45	2.6
2050	1.4	2.75	4.9
2070	1.9	3.9	7.1

Tab.8: Changes in annual precipitation rates for 2030, 2050 and 2070 with minimal, median and maximal predicted changes. Values to be multiplied to the current precipitation rates. (Frei 2004 modified)

Year	Min	Median	Max
2030	0.905	0.98	1.04
2050	0.84	0.96	1.07
2070	0.78	0.95	1.12

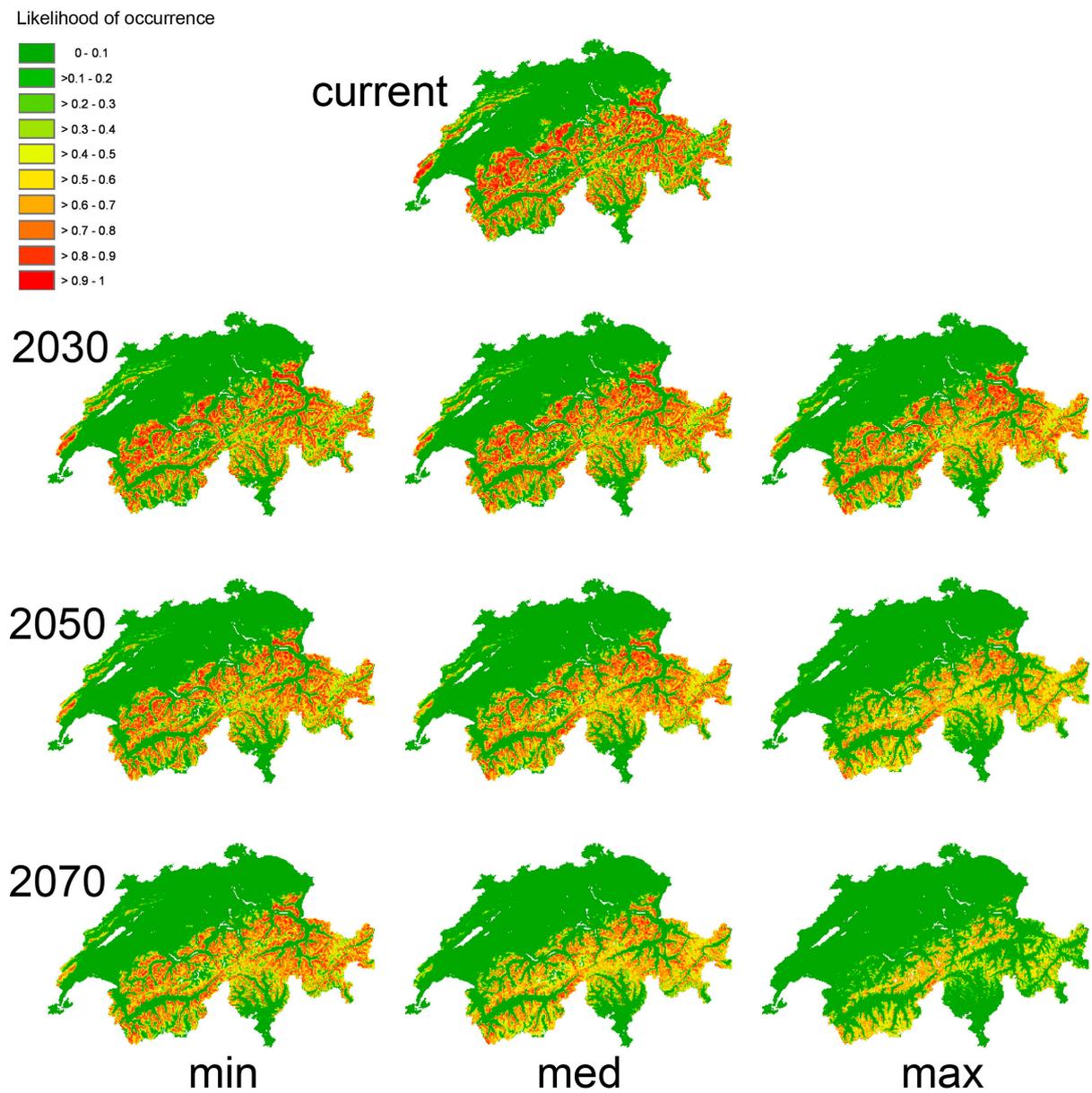


Fig.14: Predicted distribution of the ring ouzel for the present, 2030, 2050, 2070 at minimal, median and maximal changes in July temperatures and annual precipitation rates. For details on changing rates, see Tab.7 and Tab. 8.

Tab.9: Present number of occupied km<sup>2</sup> and likelihood for occupation at median scenarios in 2030, 2050 and 2070. Additionally the maximal scenario for 2070 is shown. Presented are the cut-off values  $P_{\text{krit}}=0.9, 0.8, 0.7$  and 0.5

$P_{\text{crit}}$	Ring ouzel				Blackbird			
	0.9	0.8	0.7	0.5	0.9	0.8	0.7	0.5
	occupied km <sup>2</sup>				occupied km <sup>2</sup>			
current prediction	1052	5439	8115	12 248	24 212	26 306	27 298	28 585
prediction for 2030 (median changes)	690	4306	7182	12 234	25 882	27 614	28 518	29 929
prediction for 2050 (median changes)	295	2687	5542	11 672	27 280	28 823	29 756	31 255
prediction for 2070 (median changes)	82	1330	3536	9960	28 455	30 010	31 010	32 297
prediction for 2070 (maximal changes)	8	121	638	4061	31 468	32 619	33 278	34 202

## 3.5 Discussion

### 3.5.1 Habitat selection of the ring ouzel

Glutz von Blotzheim, Bauer et al. (1988) and Schmid, Luder et al. (1998) describe the ring ouzel as a species that is strongly bound to coniferous mountain forests and preferring loose stands of trees interrupted by meadows, aisles, debris or ridges. Accordingly, our species distribution model on territory scale describes a predominance of open forests. Forest ratio and coverage of the intermediate and upper forest layer are negatively correlated to the species incidence. According to Kronshage (2003), the optimal ring ouzel habitat is located close to the timberline, in transition areas between forests and pastures. However, we did not find a significant dependency on surrounding landscape features like aisles or meadows on territory scale. On macroscale however, subalpine, mainly loose coniferous forests proved as a good predictor for ring ouzel incidences as long as forest coverage was neither too low nor too high. Furthermore, ring ouzel distributions correlated positively with grassland at high altitude. This would reinforce their preferred ecotone between forests and open grasslands, but surely cannot explain small-scale variations, as Kronshage (2003) describes. He describes a maximum ring ouzel occurrence on patchy areas with subalpine or alpine lawns and berry bush vegetation. Berg-Schlosser (1980) illustrates a clear

avoidance of dense forests with sparse or no ground vegetation. Our territory-scale model clearly supported this coherence, describing a positive correlation with the herb-, moss- and berry bush-layer. Ring ouzels seem to avoid areas with a high amount of debris and rocks on macroscale. On territory scale, however, we observed a positive correlation with exposed rocks and tree stubs, used as singing perches for male birds. The latter variable, however, was not part of the multiple model, but highly significant in the univariate case. Besides all mentioned structural variables, the July temperature has a high impact on the final model. Ring ouzels show a unimodal correlation with July temperatures, presumably reflecting the main occurrence in higher and thus colder altitudes, but avoiding areas where breeding becomes inefficient. Crucial factors are long snow cover, danger of late frosts, the absence of structures such as trees or shrubs as well as a lack of sufficient nutrition for the nestlings.

Concerning the avoidance of valley grasslands and deciduous forests, we surely have to consider the altitudinal effect besides structural differences. Kronshage (2003) describes nutrient rich valley meadows as an ideal feeding ground for thrushes, due to a great amount of earthworms. These are considered as the main nourishment for ring ouzels during the breeding time (Burfield 2002a in (Beale et al. 2006)). Still the distribution of ring ouzels correlates strongly negative to valley grasslands. Kronshage (2003) exemplarily illustrates this antagonism using the example of the ring ouzel population of the Oberengadin. There, ring ouzels tended to feed on valley meadows in former times but distances became too far as their breeding sites shifted up to the timberline.

Another aspect concerning food provisioning is the post-breeding dispersal to berry-rich dwarf-shrub areas, to which spatial proximity already during the breeding season might play an important role.

### **3.5.2 Habitat selection of the blackbird**

While ring ouzels prefer sparsely vegetated forests, blackbirds favour forests or shrub land with a dense understorey vegetation (Hatchwell et al. 1996; Stephan 1999). Glutz von Blotzheim, Bauer et al. (1988) describe the blackbird as extremely flexible except for a strong bond to bare ground with no or sparse vegetation. Furthermore, they show a distinctive need to stay close to coverage and to forage on unvegetated humus grounds in dense forests. Our model on territory scale shows this need quite well, since it reveals a negative relationship to ground vegetation and a

positive to the density of the upper layers and forest cover. We did not find a significant relation to surrounding open patches and thus, a relation ship to woodland edges. According to Marchant et al (1990) woodland edges are this species' ancestral habitat besides forests. Even though we tried to study blackbirds at the territory scale mostly unaffected by anthropogenic influences, we still found a highly significant positive relation to settlements, often to huts, barns or farmsteads. Latter variable however is not included in the final model. Nevertheless, the resulting model can only be transferred to "urbanised" blackbird populations to a very limited extend. The investigated areas highly differ from those in urban areas (e.g. Stephan 1999). Still some analogies are obvious : Landmann (1991) assumes a perpetuation of pristine patterns in habitat selection for blackbirds in urban areas and shows a positive relationship to dense bushes. Wysocki et al. (2004) describe the behaviour of a polish blackbird population in parkland. Territories with the most extensive shrubberies and the highest number of trees are occupied earliest in the year. Generally, a clear positive relationship between blackbirds and urban areas can be stated. (Glutz von Blotzheim et al. 1988; Stephan 1999).

The model on macroscale also clearly reflects this coherence, which shows a positive relationship between blackbird incidences and settlements in the square kilometre plots. Obviously, blackbirds benefit from rural settlements. These probably contribute to a warmer macroclimate and thus an extended breeding season (Glutz von Blotzheim et al. 1988; Mattes et al. 2005), as well as an increased food supply (Stephan 1999). Glutz von Blotzheim (1988) and Mattes, Maurizio et al. (2005) even describe local colonisation of the Alps via settlements, from where blackbirds spread into surrounding forests.

### 3.5.3 Comparison of the models on territory and macroscale

Due to different predictor variables, territory and macroscale results are comparable to a limited extent only. Nevertheless, a comparison of the most important variables on both scales shows some analogies and differences. Tables 2 , 3 and 5 provide an overview of the most important predictor variables in order of their explanatory value. On both scales, altitude showed a high effect on ring ouzel and blackbird distributions reflecting important climatic and structural factors. While on territory scale, the variable was included in the final model we had to exclude it on macroscale due to strategic considerations (keeping climatic variables for climate change scenarios in the modelling process). Nevertheless, highly important climatic variables such as July temperature and structural variables bound to specific elevation sites have the potential to

represent the altitudinal range on macroscale. While temperature and thus altitudinal conditions are of crucial importance in explaining blackbird incidences on the macroscale, for the ring ouzel structural elements are even more meaningful. This might be ascribable to the narrow altitudinal range at which ring ouzels occur. On territory scale however, structural variables are of highest importance. This could have been expected as structure plays a key role in bird's habitat selection. Blackbirds show a positive correlation to dense forests and avoid areas with no vegetation on both scales. They also prefer to inhabit areas in close proximity to settlements. Variables describing the habitat selection of ring ouzels do not show such a clear comparability, although several variables include structural elements. Therefore, we could state an accordance of open forests reflected by low forest coverage at territory scale and the preference of subalpine forests as well as alpine and subalpine lawns on macroscale. Although not included in the final model, alpine and subalpine pastures as well proofed as a significant variable in describing ring ouzel occurrence.

#### **3.5.4 Sympatric and parapatric localities**

Presumably, the most important conclusion that can be drawn from the comparison of the two scales is that niche overlaps are virtually non-existent on territory scale, except for the realised niches as modelled by the species distribution models. Small-scale differences in landscape structure determine the species' territories. Considering all sampled sites, we only found a direct niche overlap of blackbird and ring ouzel at one plot, both birds feeding on a meadow edged by deep forest as well as loose groups of trees.

By comparing the variables of the two multivariate models compiled for the overlapping area, (Tab. 10. and Tab.12), we can characterise the sites of coexistence on the macroscale. Areas with an overlap of both species show lower July temperatures and higher precipitation rates than the areas, with blackbird presence only. Furthermore, these areas show less farmland and meadows and less settlement areas than sites with a blackbird-presence only. On the other hand, they are characterised by a higher proportion of farmland meadows and settlements than areas were solely ring ouzels occur. The proportion of forbs, coppice and subalpine forest however is higher in the overlapping areas than for both single occurrences. Fig. 15 shows a response surface referring to an overlap in comparison to a ring ouzel only occurrence, Fig. 16 to a solely blackbird occurrence. Two explanatory variables, the July temperature and the proportion of subalpine forests are shown. In comparison to a solely ring ouzel presence, the species distribution overlaps

for almost the whole temperature and forest cover range. We however cannot observe any overlap at sites with lower temperatures and lower coverage of subalpine forests than at sites with ring ouzel presence only. In comparison, we observe that the occurrence of blackbirds only is highly dependent on the temperature. Only in areas, with temperatures lower than for blackbird-only occurrence, we observe an overlap.

Tab.10: Model comparing overlap areas with areas of blackbird presence only. Binary response: overlap =1; solely occurrence blackbird = 0. Variables sorted by explanatory value

	Coef	S.E.	P
Intercept	-13.800	3.402	< 0.001
July temperature	2.510	0.541	< 0.001
July temperature (quadratic term)	-0.114	0.021	< 0.001
nutrient-rich valley grasslands	-0.034	0.010	0.001
subalpine forests	0.022	0.008	0.009
farmland and meadows	-0.033	0.006	< 0.001
forbs and coppice (upper montane, subalpine, alpine)	0.021	0.009	0.019
settlement areas	-0.066	0.023	0.004
nutrient poor grassland (upper montane/subalpine/alpine)	0.027	0.008	0.001
precipitation rates per year	0.001	< 0.001	0.003
rock / debris	-0.023	0.009	0.008

Tab.11:  $R^2_N$  and AUC-values for the model comparing overlap areas with areas of blackbird presence only

AUC	$R^2_N$
0.969	0.754

Tab.12: Model comparing overlap areas with areas of ring ouzel presence only. Binary response: overlap =1; solely occurrence ring ouzel = 0. Variables sorted by explanatory value.

	Coef	S.E.	P
Intercept	1.927	3.343	0.564
July temperature	-0.267	0.305	0.381
dense forest	0.037	0.008	< 0.001
farmland and meadows	0.100	0.033	0.002
unvegetated areas	-0.023	0.015	0.128
rock / debris	-0.033	0.010	0.001
settlement areas	0.175	0.075	0.020
subalpine forests	0.066	0.015	< 0.001
subalpine forests (quadratic term)	-0.001	< 0.001	< 0.001
forbs and coppice (upper montane, subalpine, alpine)	0.019	0.010	0.049
precipitation rates per year (divided by 100)	-0.428	0.226	0.058
precipitation rates per year (divided by 100)* July temperature	0.039	0.020	0.052

Tab. 13:  $R^2_N$  and AUC-values for the model comparing overlap areas with areas of ring ouzel presence only

AUC	$R^2_N$
0.896	0.57

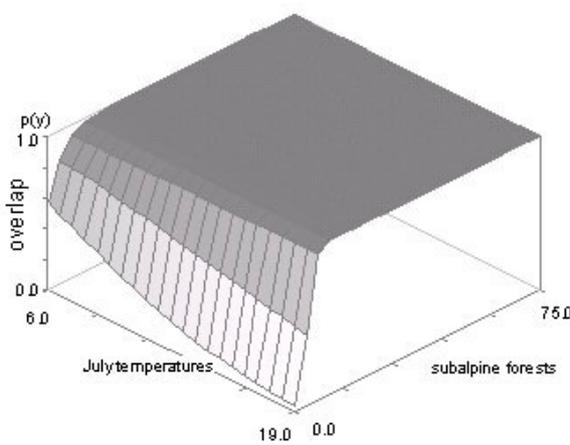


Fig.: 15: response surface: overlap blackbird and ring ouzel =1; only ring ouzel occurring = 0.

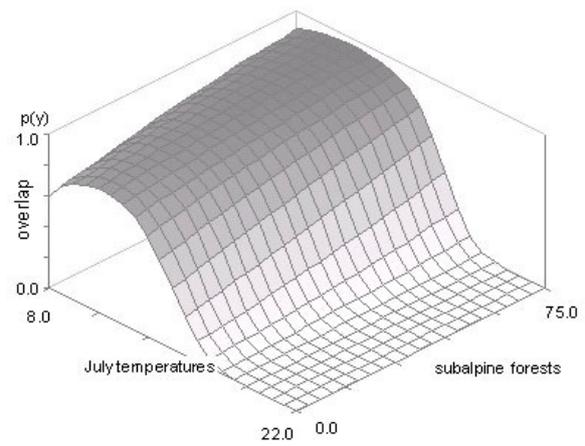


Fig.: 16: response surface: overlap blackbird and ring ouzel =1; only blackbird occurring = 0.

### 3.5.5 Climate change scenarios

The scenario assumptions are based on a change in temperature and precipitation rates, and do not consider naturally or anthropogenic induced changes in the composition and structure of vegetation. According to Theurillat and Guisan (2001) plant species and ecosystems in the European Alps have a natural inertia and tolerate an increase of 1-2 °C of mean air temperatures. Frei et al. (2004) however believe that this value will be exceeded by 2030 at maximal changes or latest in 2050 at a median climate change scenario. Furthermore, the scenarios probably underestimate changes at high altitudes, where the rise in temperature is expected to be considerably higher than in lowlands (Bolliger 2002). A shift of several species and re-composition of communities seems therefore inevitable. Models of changing forests ecosystems (Kienast et al. 1996; Bolliger et al. 2000; Bolliger 2002) predict a shift and re-arrangement of tree species over the altitudinal range. Rising temperatures lead to an uphill shift of the core areas for *Abies alba*, *Fagus sylvatica*, *Pinus sylvestris*, *Larix decidua* and *Picea abies*. Magnitudes of the shift are expected to range between 100 and 300 m for the scenarios ranging between a plus of 100 to 400 degree days (Bolliger et al. 2000). Especially in the montane and subalpine areas, conifer forests will decline in favour of deciduous forests (Bolliger 2002). Ecosystems, however, tend to react with a certain time lag (Magnusson 1990; Neilson et al. 2005). While Kienast (1991) simulates a change to new transitory forest types within 40 years following a rise in temperature of 1.5 °C, Bolliger, Kienast et al. (2000) do not mention an explicit period. Longevity of trees, lasting for several hundred years, and of clonal plants like the alpenrose (*Rhododendron ferrugineum*) prohibit a more detailed prognosis of the time scale for the expected changes (Theurillat and Guisan 2001). Especially in the now alpine areas the soil development rates remain uncertain due to complex interactions between vegetation and soil forming processes (Bolliger 2002). Equally controversially discussed is the question of a general shift of trees above the potential timberline, which however is artificially lowered by man through farming (Fischlin and Gyalistras 1997). While it remains uncertain, in how far current subalpine species will be able to shift to alpine areas, a fast forest expansion on abandoned pastures is most likely as this succession has already been in progress for the last decades (Bebi and Baur 2002; Baur et al. 2006). Between 1979 to 1985 and 1992 to 1997, the forests area in the Swiss Alps increased by 476 km<sup>2</sup>, of which 68% are located on abandoned mountain pastures, called “Sömmerungsgebiete” (Baur et al. 2006). A shift of deciduous forest to higher altitudes and the expansion of forests to areas formerly used as farmlands are likely to have a strong effect on the distribution of blackbirds and ring ouzels due to the severe change in forest structure. This will probably have a negative impact on the ring ouzel population as they avoid dense forests and

prefer the alteration between forests and open pastures. Negative effects of afforestation on ring ouzels have already been found in Scotland (Buchanan et al. 2003), as well as in Switzerland. For example in the Napf Mountains, where pastures have been abandoned some decades ago, the numbers of ring ouzels have declined since (Schmid pers. comm.). Mattes, Maurizio et al. (2005) mention that giving-up wood pastures lead to a further densification of the forests and therefore is a possible reason for shifts in ring ouzel habitats in the Upper Engadin's Bergell and Puschlav regions. Kronshage (2003) suggests that the replacement of former ring ouzel habitats by blackbirds is happening simultaneously to changes in forest structures. As blackbirds prefer a dense coverage, they will probably spread to higher altitudes. According to Bolliger (2000) there will be no significant uphill movement of the timberline, which would suggest that a shift of ring ouzels to higher altitudes is limited. Because of the presumable changes in the vegetation structure, we expect blackbirds to expand their range towards higher altitudes, while suitable ring ouzel habitats, are likely to decline in area. Nevertheless, ring ouzels will probably be able to expand their habitat even further above the timberline. Already today they inhabit areas with almost no trees (Schmid et al. 1998) and during our research have been found in rocky areas rich in structure, providing cover without any trees. We however do not expect high frequencies of breeding ring ouzels at sites above the timberline due to a thin soil cover and thus sparseness of earthworms, which are the main food resource during the breeding season.

### 3.5.6 Model criticism

Species distribution models are static and thus assume an equilibrium between the environment and the observed species patterns (Guisan and Zimmermann 2000). While they feature a high predictive ability in describing potential habitat suitability under given conditions, they cannot directly depict the underlying processes. Mechanisms such as biotic and abiotic interactions, genetic variability and thus evolutionary modifications, dispersal and fragmentation are not taken into consideration directly, even though they are of high importance. The modelled relationship of a species to the predictor variables however, can be understood as hypotheses tests regarding specific predictions of underlying processes.

Interactions, in-situ adaptations and differences in dispersal potentials can alter distributions markedly (Theurillat and Guisan 2001; cf. Pearson and Dawson 2003; Thuiller et al. 2005). An important criticism of the correlative approach is that species distribution as observed today may not be in equilibrium with the current climate. Future distribution might therefore show very different realised niches (Pearson and Dawson 2003). Guisan and Zimmermann (2000) state that

arctic and alpine species are relatively persistent or slow reacting to variability in environmental conditions. Assuming an equilibrium state is therefore less problematic. As this might be true for forest succession, human management in the Alps is a prime example for an ecosystem displaying a non-equilibrium state. Tree populations as well as grasslands are highly influenced by alpine farming. The potential timberline is artificially lowered by man (Theurillat and Guisan 2001), forests artificially interrupted by meadows. Changes in land use have already modified the natural environment of blackbird and ring ouzel as described earlier. Thus, a further change in land use might influence the species distribution even to a higher degree than predicted by changing climate only.

Static species distribution models are conceptually unable to cope with non-equilibrium situations, since they do not distinguish between the transient and equilibrium response of species to a stochastically and dynamically changing environment (Guisan and Zimmermann 2000). An alternative to these models are dynamic simulation models (e.g. Lischke et al. 1998). Linking population dynamics and thus factors like dispersal/migration, disturbance and abundance to simple presence/absence models (cf. Guisan and Thuiller 2005a) may highly improve the predictive power by including dynamic processes. A way of integrating biotic interactions into static distribution models could be the use of integrated systems of simultaneous regression equations or GLMs, described by Guisan and Zimmermann (2000) (see also Rudner et al. 2005; Schröder et al. 2006). Dynamic models however, require detailed data about species such as physiological parameters or interactions including competition and are thus applicable to a limited set of species only (Weng and Zhou 2006). We also have a limited mechanistic understanding of how biodiversity at species and population level responds to climate change. Thus bringing together static and mechanistic modelling is preferable. This would involve developing "hybrid" models with an explicit mechanistic and a correlative component (Araújo 2006).

### 3.5.7 Conclusion

To conclude, despite that species distribution models are lacking the consideration of dynamic processes, they still offer a powerful tool to predict future species distribution. Employing logistic regression, we characterised the realised niche of ring ouzel and blackbird on two spatial scales, revealing differences in explanatory variables. While structure (e.g. vegetation cover) is the most important factor in describing bird incidences on territory scale, climatic and topographical

variables play a key role on the macroscale. Examining species' coexistence within same plots we found significant differences between the two scales examined. On macroscale, the number of areas with blackbirds and ring ouzels coexisting exceeds the number of cells with ring ouzels occurring only. In contrast, we found an exclusive segregation on territory scale. The latter is highly determined by local differences in vegetation cover. Generally, blackbirds preferably inhabit lowland areas with a dense cover of forests and shrublands, whereas the territories of ring ouzels are characterised by a mosaic of open forests, pastures and meadows at higher elevations. The change of future species distribution under the climate change scenarios differ between the two species: While suitable ring ouzel habitats are likely to decline in numbers and this species will shift to higher elevation sites, blackbirds seems to profit from higher temperatures and supposedly expand their habitats to higher altitudes.

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We confirm that we have not performed any experiments that do not comply with Swiss laws.

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The black and white drawing of the ring ouzel in the prefix, we took from:

[http://www.shropshire.gov.uk/sustainability.nsf/viewAttachments/DOC-1FCB6F683F75785480257085004E4FB1/\\$file/Birds%20-%20Ring%20Ouzel%20-%20Species%20Action%20Plan%20July%202003.pdf](http://www.shropshire.gov.uk/sustainability.nsf/viewAttachments/DOC-1FCB6F683F75785480257085004E4FB1/$file/Birds%20-%20Ring%20Ouzel%20-%20Species%20Action%20Plan%20July%202003.pdf)

## 5. Appendix

App.1: Categories, summarising the vegetation types after Hegg (cf. Hegg et al. 1993)

Category	Denotation	includes following vegetation types after Hegg
JB1	dwarf-shrub heathland	Loiseleurio-Vaccinion (alpine dwarf- shrub heathland, wind exposed), Rhododendro-Vaccinion (subalpine dwarf- shrub heathland, protected by snow cover), Juniperion nanae (subalpine dwarf- shrub heathland, warm-dry local climate), Rumicion alpine ("Lägergesellschaft")
JB2	subalpine forests	Erico-Mugion (mountain pine forests on limestone, subalpine), Vaccinio-Piceion (subalpine spruce forests), Melico-Piceion (spruce forest / wood melick spruce forest, dry), Rhododendro-Mugetum prostratae (dwarf pines), Rhododendro-Cembretum (stone pines), Rhododendro-Laricetum (larch forest), Spagno-Mugetum (upland moor forest)
JB3	coniferous forest (planted)	Larix-forest (larch forest), Picea-forest (spruce forest), Pinus-forest (pine forest)
JB4	coppice / shrub / grooves	Rubo-Prunion spinosae (atlantic shrublands), berberidion (thermophile shrublands, berberis-shrub), corylus-shrub (hazel), coppice, Fagus-coppice (beech-coppice), grooves
JB5	gardens / parks / growings	fruit orchard, parks, growings, vineyard, market gardening
JB6	rock / debris	Potentillion caulescentis (limestone rock vegetation), Androsacion vandellii (silicate rock vegetation), Thlaspion rotundifolii (lime stone debris), Petasition paradoxii (schist debris), Androsacion alpinae (silicate debris), Epilobion fleischeri (alluvions), Sedo-Scleranthion (gravel, sand, wall decks, belay)
JB7	meadows at springs / oligotrophic lake and pond shores	Littorellion (shallow oligotrophic lake and pond shore), Cardamino-Montion (meadow at spring, poor in lime), Cratoneurion (meadow at spring, rich in lime, tuff-forming)
JB8	moorland	Caricion canescenti-fusca (acetous fen), Caricion bicolori atrofuscae (alpine fen, limestone), Caricion davallinae (colline, montan, subalpine fens), Sphagnion fusci (upland moor)
JB9	colline and montan deciduous forests	Salicion albae (willow trees on alluvials), Alnion glutinosae (alder forest on swampland), Pino-Betuletum pubescentis (pine/birch forest on swampland), Quercion robori-petraeae (oak-birch-forest on acetous soils, poor in nutrients), Quercion pubesc.-petraeae (thermophile oak forests), Orno-Ostryon (hop-beech forest), Alnion incanae (alder forest), Fraxinon (hardwood forest), Aceri-Fraxinetum (ash forest along streams, maple forest at slope foot), Carpinion (demanding deciduous forests/ mixed forest), Luzulo-Fagion (beech forest, acetous soils, montane), Asperulo-Fagion (Braunerde beech forest submontane), Cardamino-Fagion (authentic beech forest, lime, submontane), Cephalanthero-Fagion (orchid beech forest), Seslerio-Fagion (beechforest on steep slopes, lime), Tilion (thermophile mixed linden forests), Lunario-Acerion (forest in gorge), birch groove, locust forests
JB10	colline/montane dry nutrient poor meadows	Xerobromion (dry nutrient poor meadows colline/montan), Mesobromion (semi dry nutrient poor meadows colline/montan), Andropogonetum gryllii (dry nutrient poor meadows at steep slopes), Festucion spadiccae (steep dry slopes, subalpine, poor in lime)
JB 11	upper montane/subalpine/alpine dry nutrient poor meadows	Seslerio-Bromion (semi dry meadows upper montan), Seslerion coeruleae (dry grasslands on limestone, alpine/ subalpine)
JB 12	littoral and free water	Nanocyperion (rushes), Convolvulion sepii (tall forbs beside cane), Potamogetonion (free water, submerged vegetation), Nymphaeion (free water, floating leaf vegetation), Phragmiton (cane), Magnocaricion (sedge reed)
JB 13	snow beds	Salicion herbaceae (snow beds on silicate), Arabidion coeruleae (snow beds on lime)

JB14	coniferous woods (montan)	Erico-Pinion (pine on lime, montan), Molinio-Pinion (pine on clayey soils), Ononido-Pinion (open spruce forest, very dry), Piceo-Abietion (montan spruce forest, acetous moist-wet), Calluno-Pinion (pine on silicate, montan)
JB15	alpine/subalpine lawns	Oxytropido-Elyinion ( lawns on ridges, naked rush swards), Caricion ferrugineae (moist lawns on lime, sedges “Rostseggen”), Caricion curvulae (sedges “Krummseggen”, alpine, climax), Festucetum halleri (fescue, alpine, steep slopes, silicate), Festucion variae (subalpine steep slopes, silicate), Laserpitio-Poion violaceae (subalpine steep slopes, silicate, deep soils), Caricion sempervirentis (sedges “Horstseggen”, deep soils, acetous, subalpine), Nardion (nutrient poor lawns, extreme acetous, smooth slopes)
JB16	heathland (montan)	Calluno-Genistion (Ericaceae, dwarf-shrub), Juniperetum sabiniae (heathland on rocky ground)
JB17	forbs and coppice (upper montan, subalpine, alpine)	Calamagrostion (arund.) (tall grass, subalpine), Adenostyilion alliariae (tall forbs), Salicetum helveticae (willow tree shrub on silicate), Salicion pentandrae (wet forests, subalpine)
JB18	nutrient-rich valley grasslands	Arrhenatherion
JB 19	mountain meadows	Polygono-Trisetion (nutrient rich mountain meadows), Poion alpinae (Alp meadow), larch meadows, “Wytweide”
JB 20	gravel- and sand-alluviums at rivers	Agropyro-Rumicion
JB 21	wet meadows	Calthion + Filipendulion (nutrient-rich wet meadows and forbs), Molinion (wet litter-poor meadow)
JB22	pastures	Cynosurion

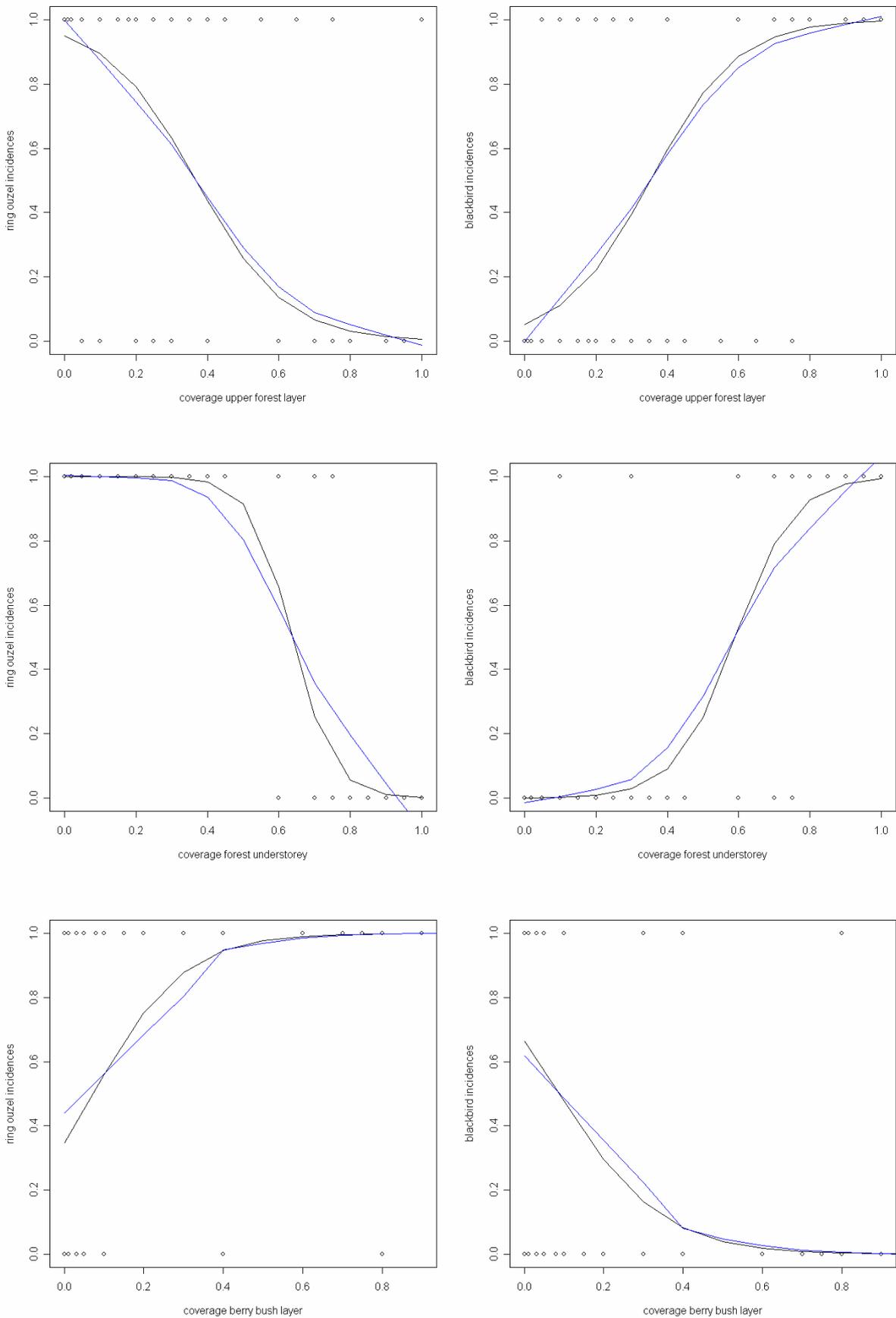
App.2: Categories of land use – derived from database GEOSTAT

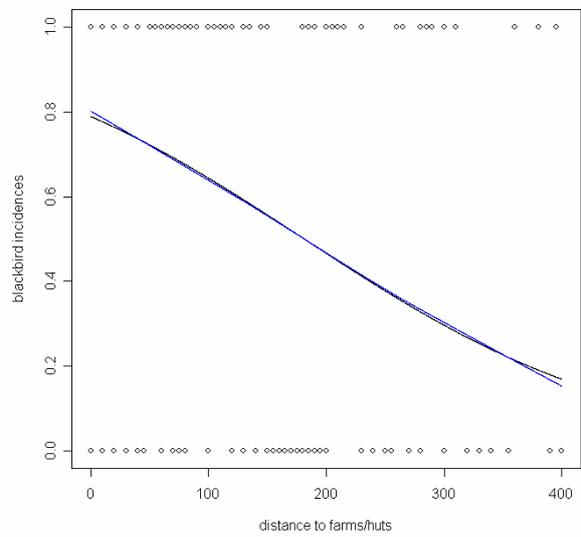
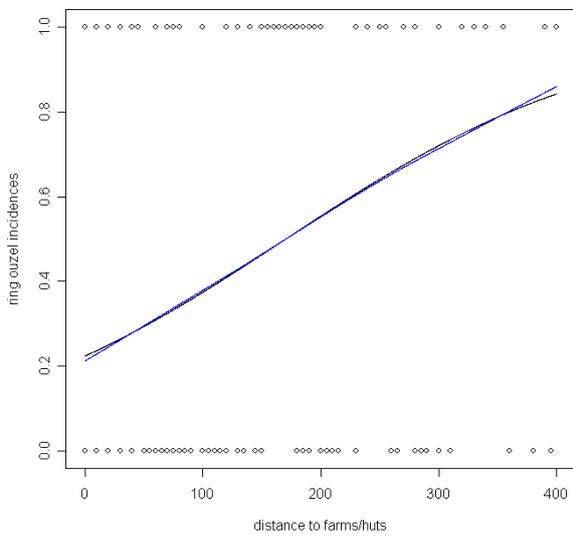
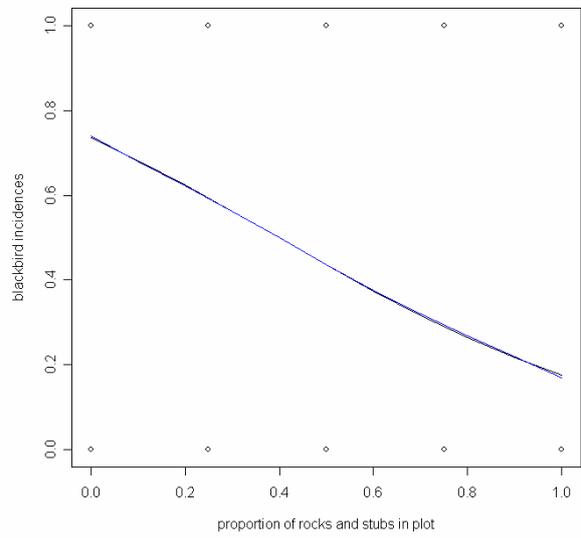
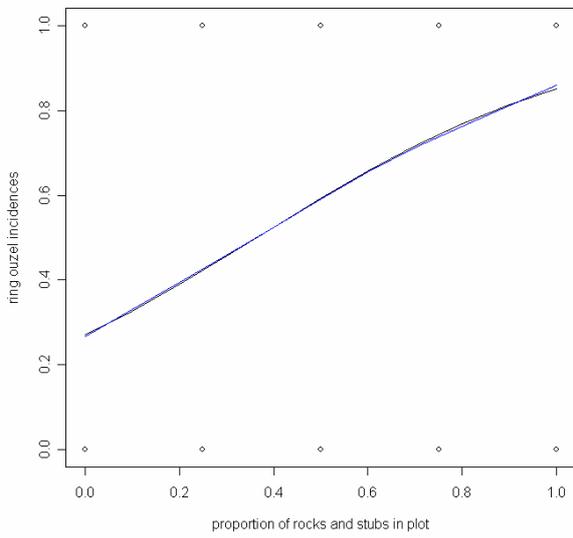
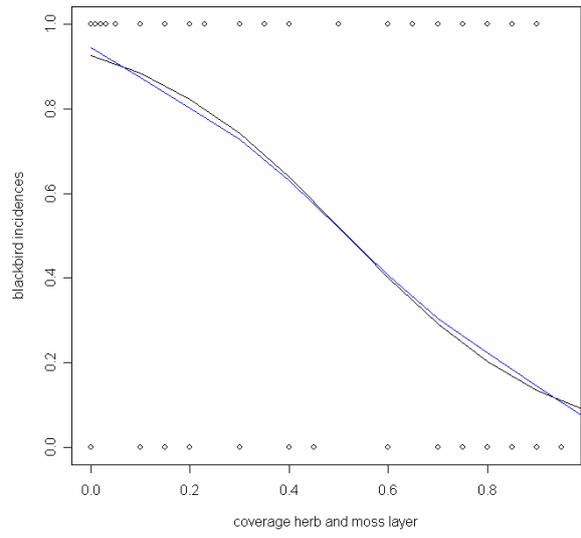
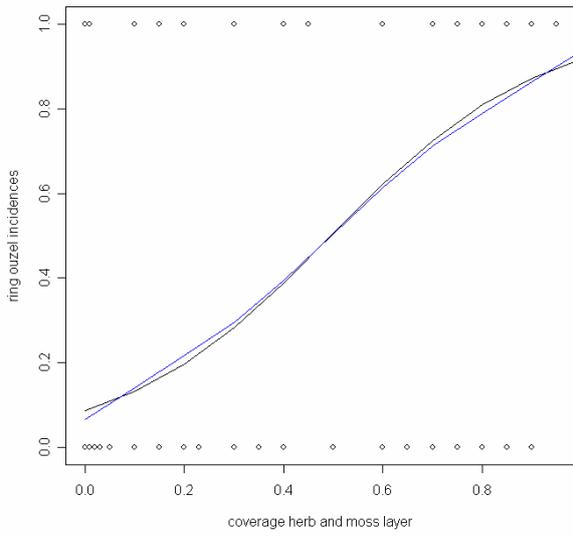
Category	Denotation
N1	closed forest
N2	loose forest
N3	low forest
N4	coppice
N5	vine yard
N6	orchard
N7	market garden
N8	meadows and farmland
N9	pasture in village (“Heimweide”)
N10	periodically cut mountain meadows (“Maiensaesse, Heualpen”)
N11	Alp- and Jura-pastures
N12	lakes
N13	rivers and streams
N14	non-productive vegetation
N15	unvegetated areas
N16-N24	settlements and traffic

for further details compare:

<http://www.bfs.admin.ch/bfs/portal/de/index/infotehk/nomenklaturen/blank/blank/arealstatistik/02.html>

App.3: Plots of the univariate models for ring ouzel and blackbird incidences, plotted against predictor variables on territory scale, with *lowess* smoothing function (blue line). Only Models with a p-value <0.05 and an AUC>0.7 a) ring ouzel b) blackbird

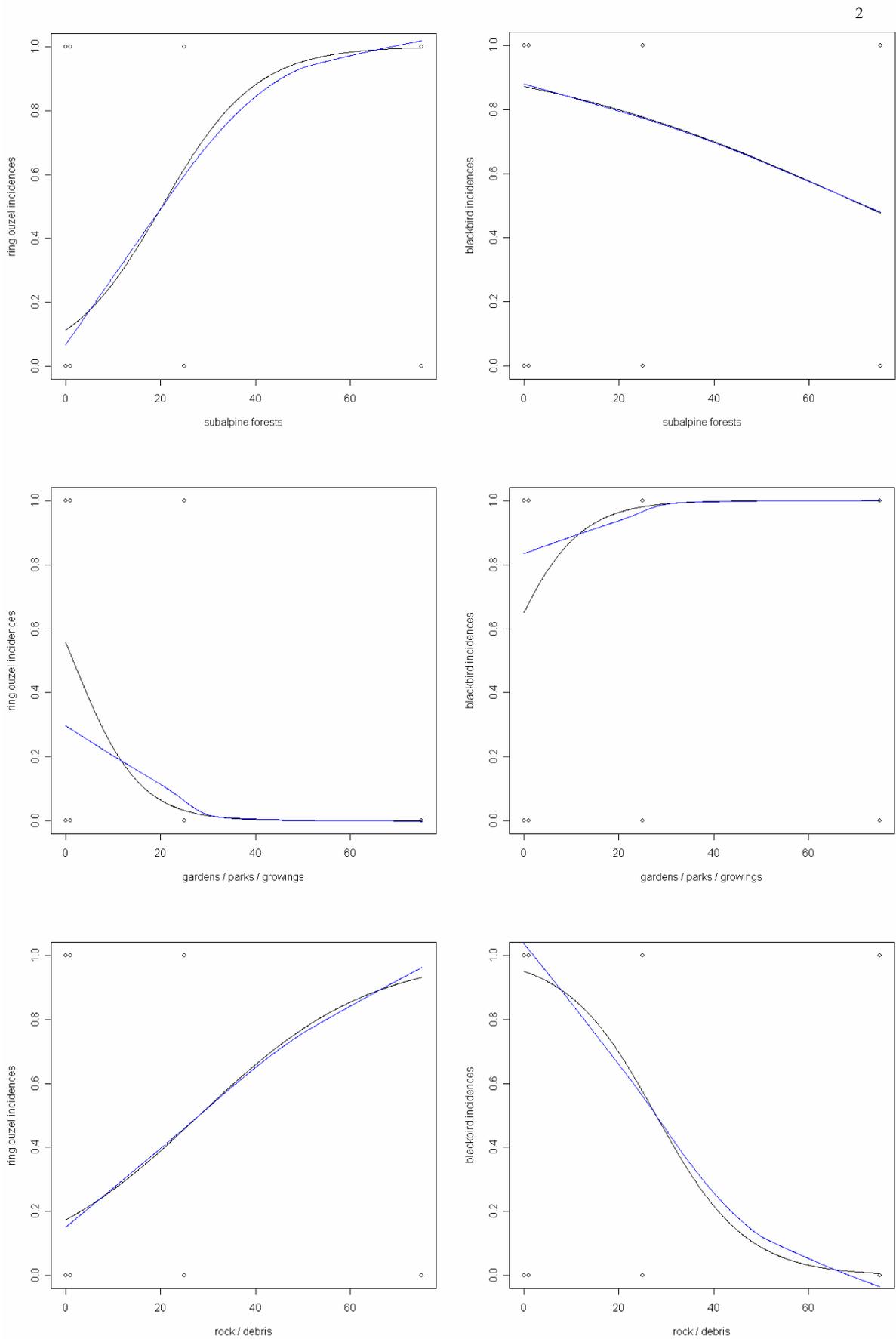


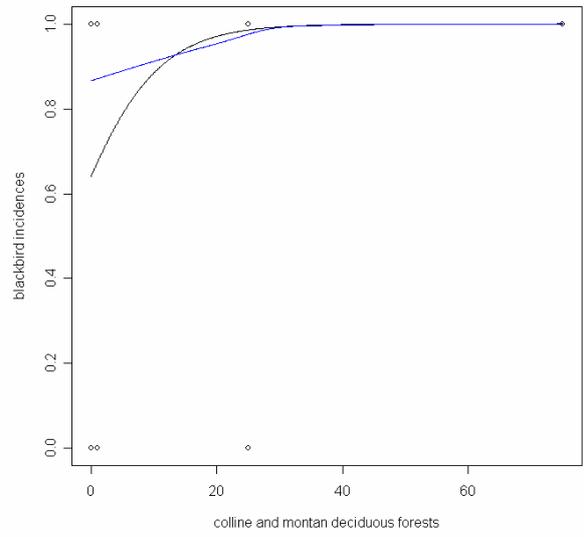
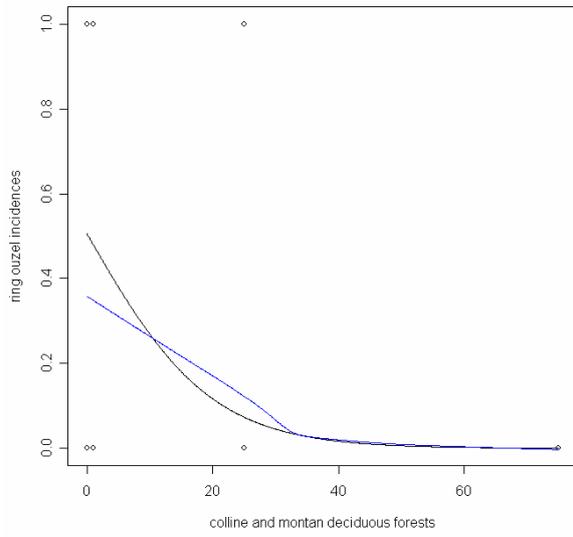


App.4: Plots of the univariate models of ring ouzel and blackbird incidences, plotted against predictor variables on atlas scale, with *lowess* smoothing function (blue line).

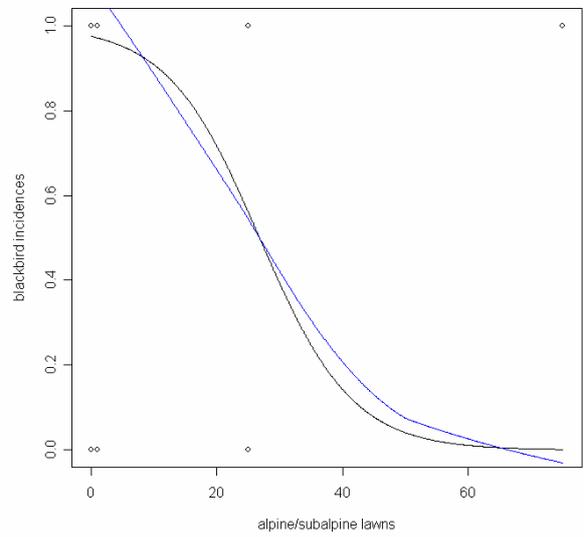
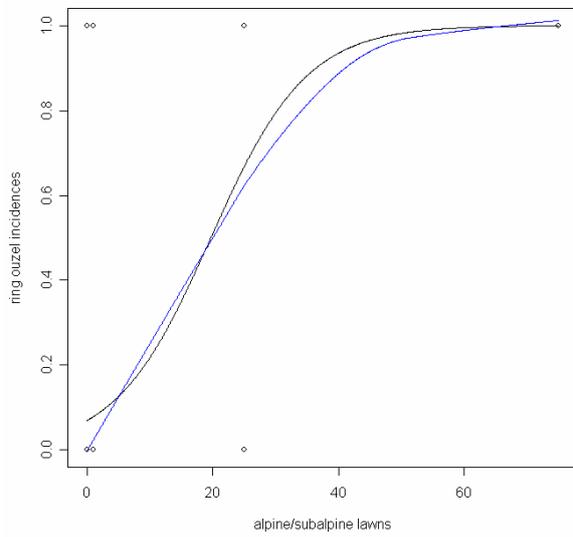
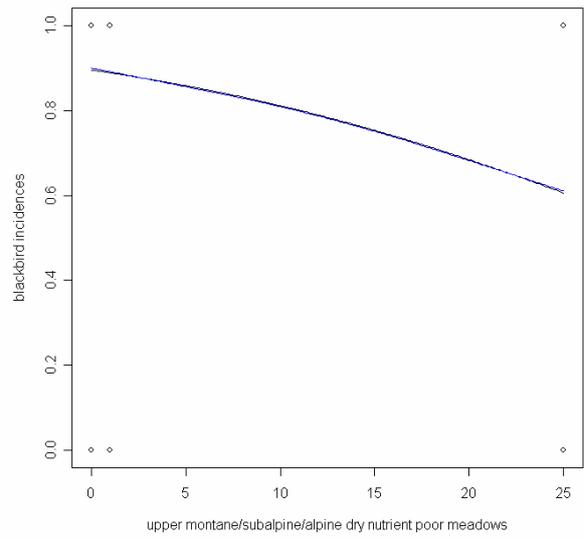
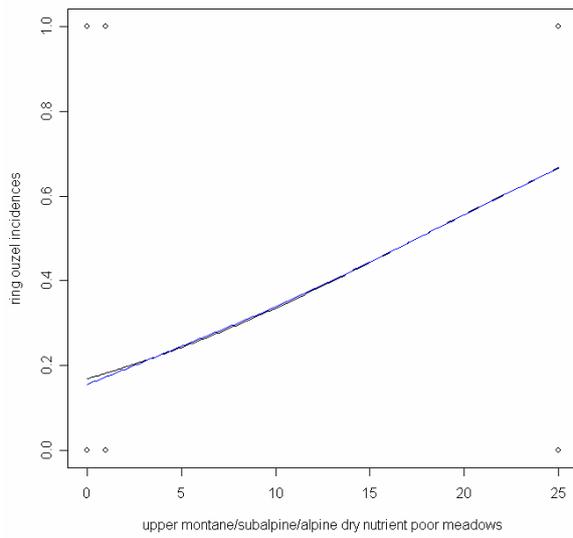
a) ring ouzel

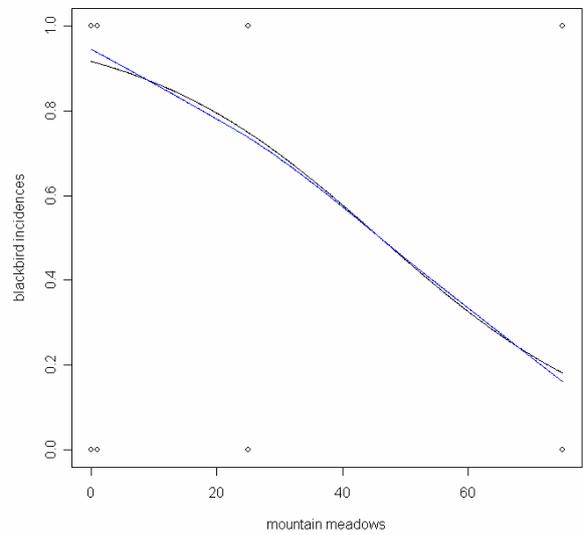
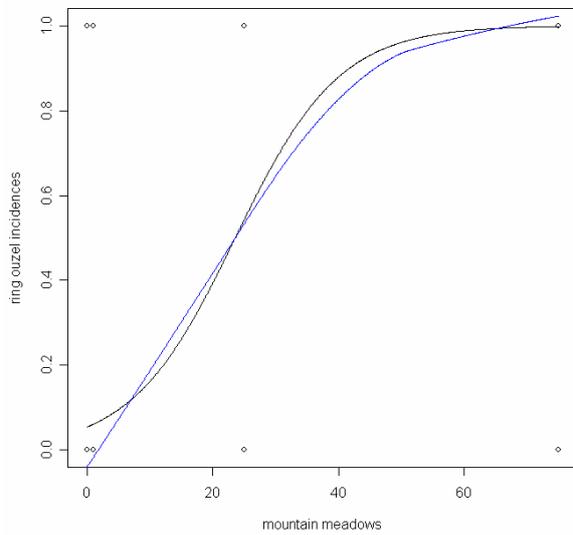
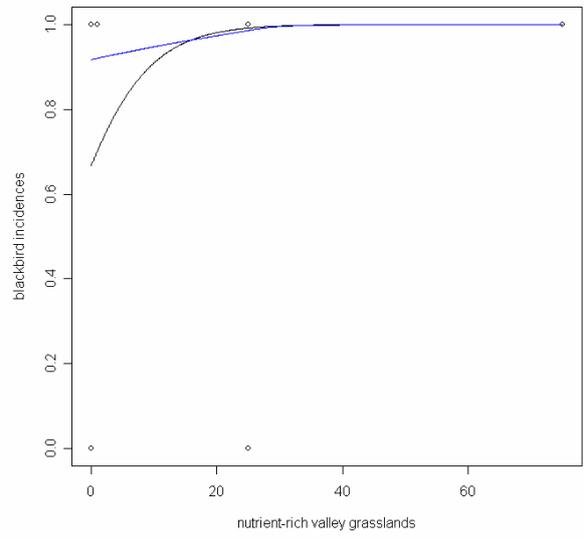
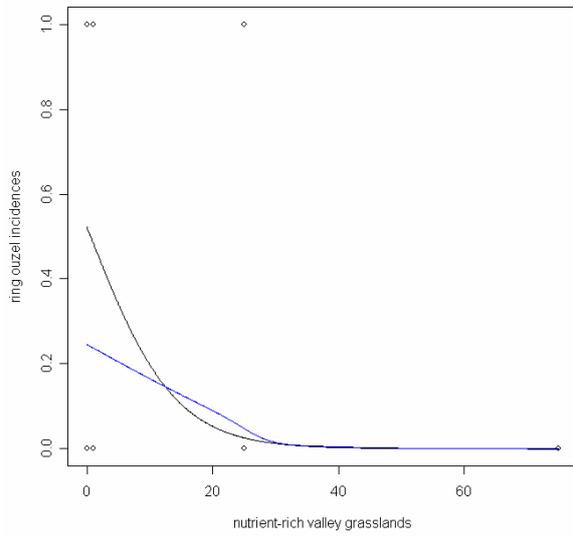
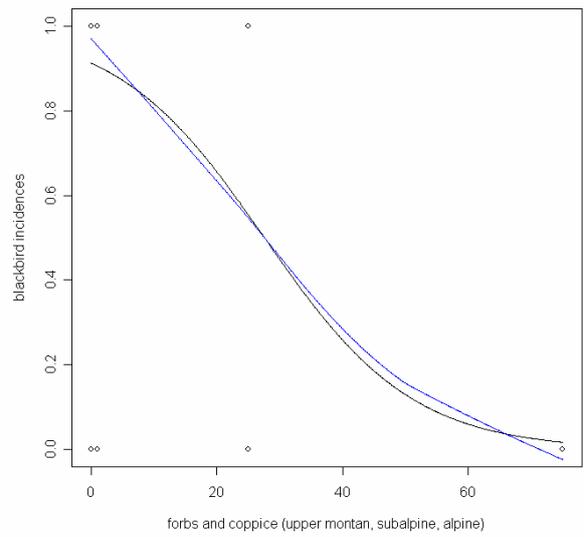
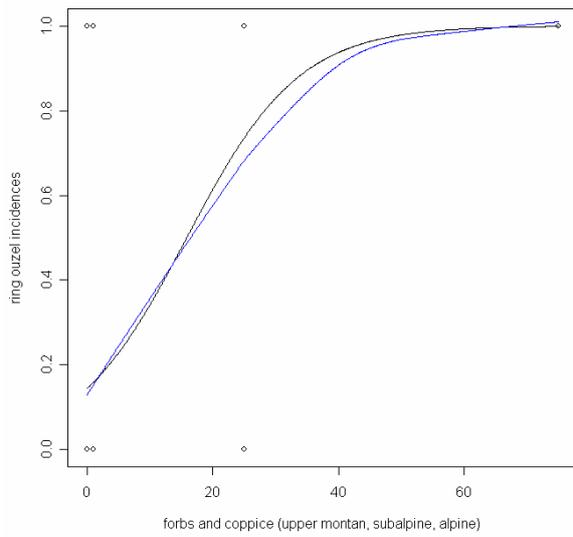
b) blackbird

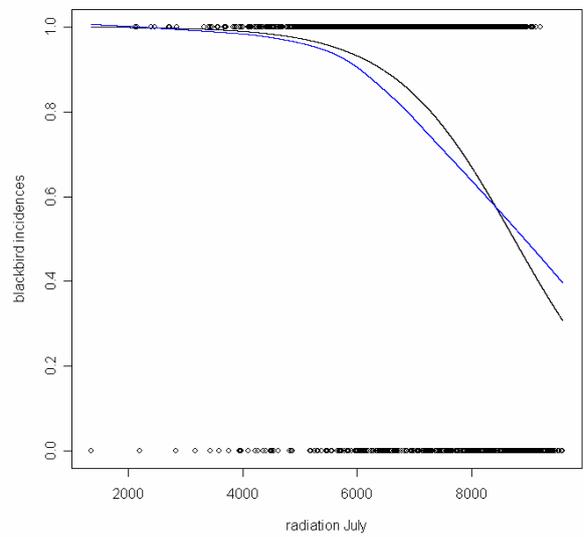
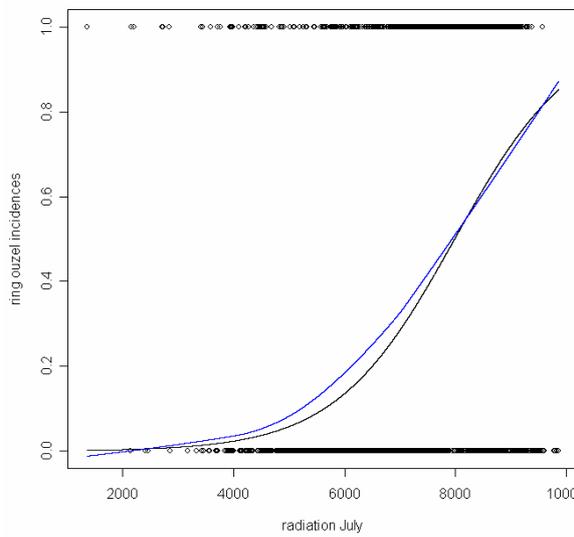
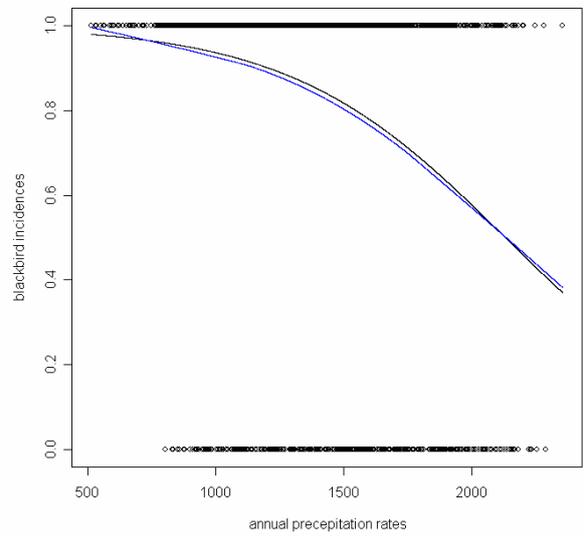
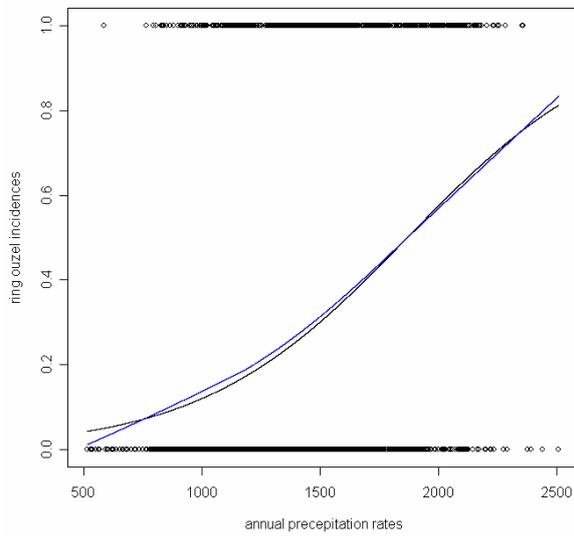
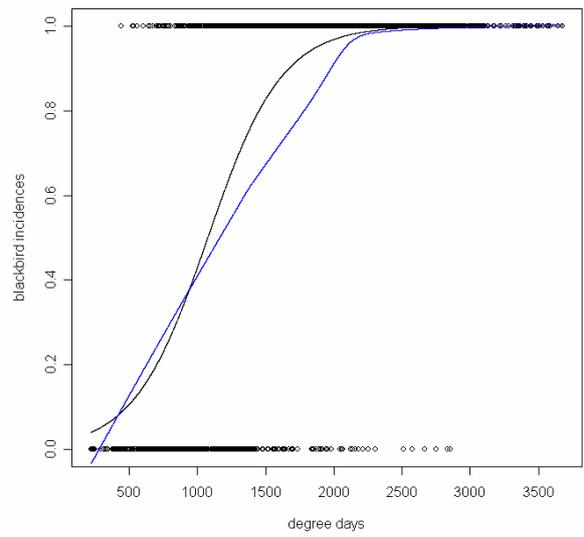
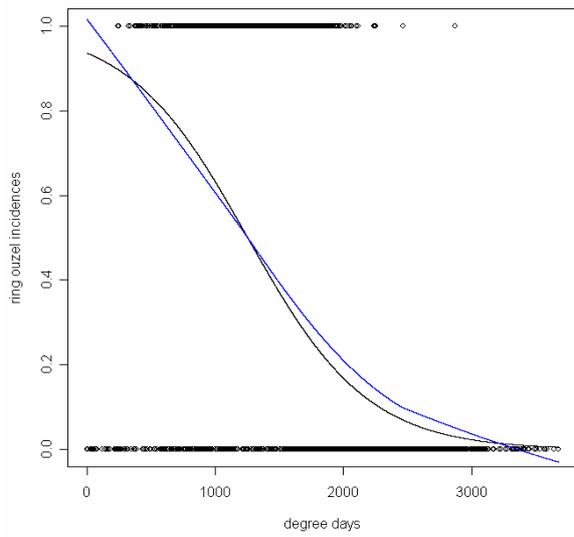


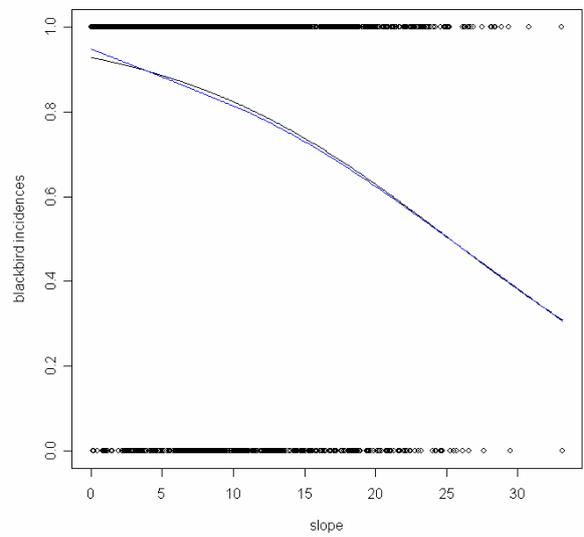
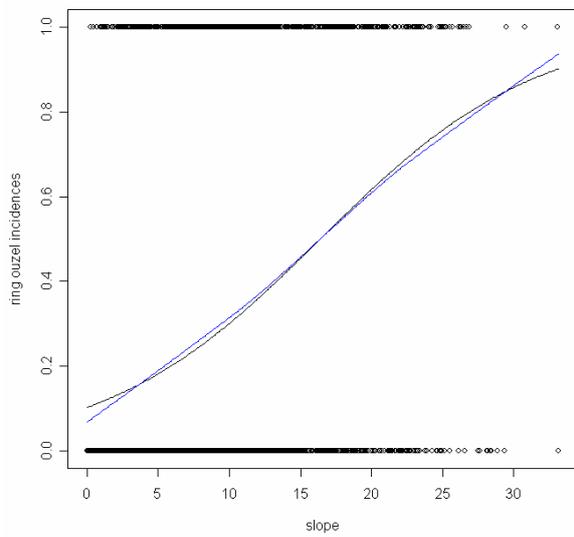
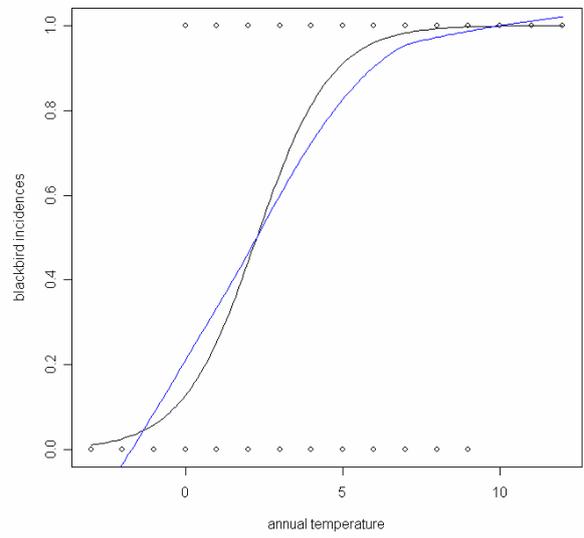
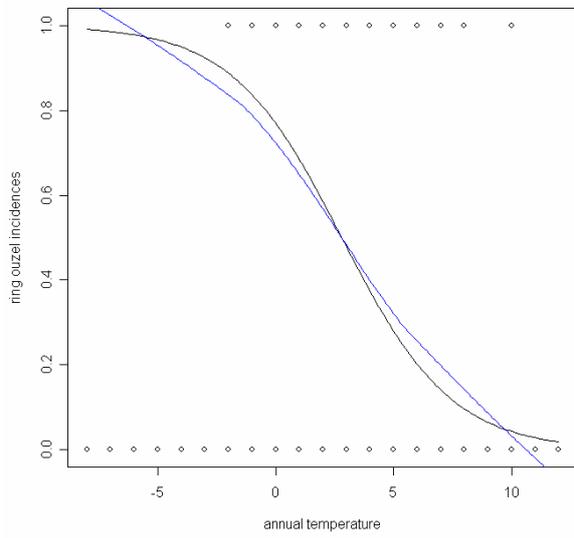
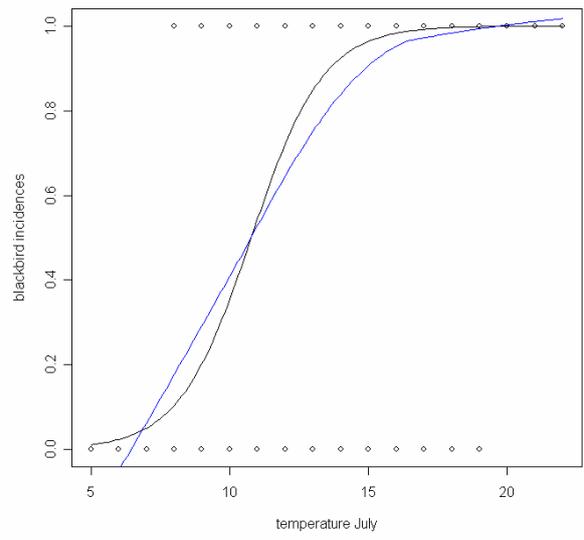
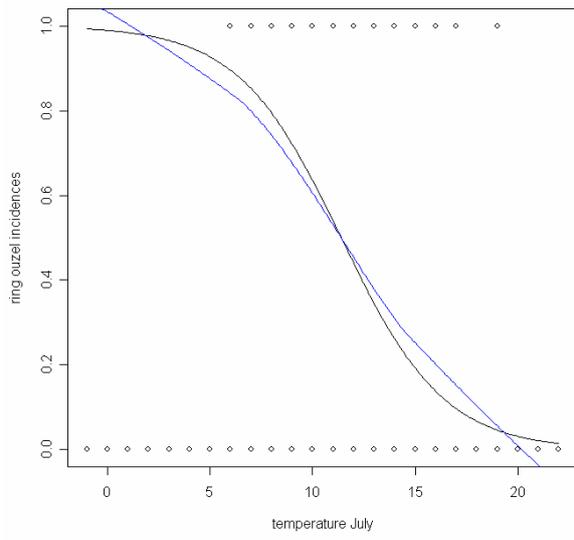


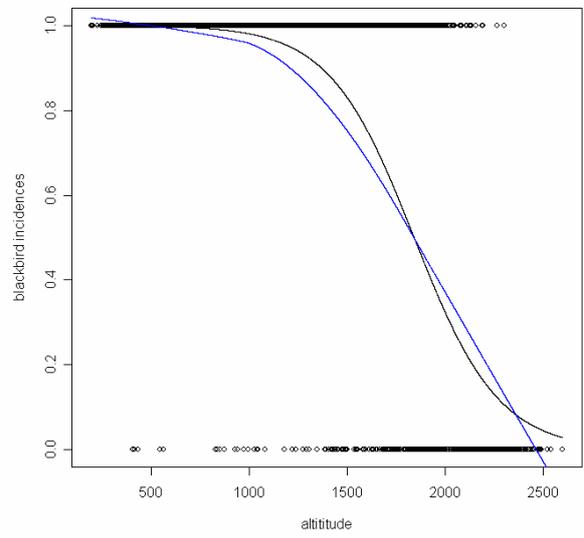
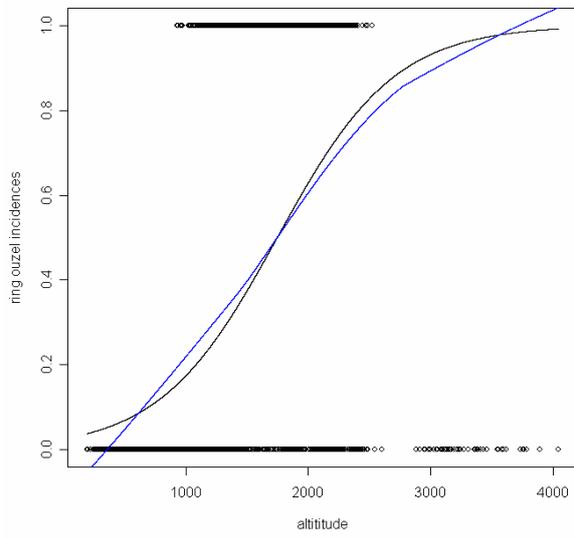
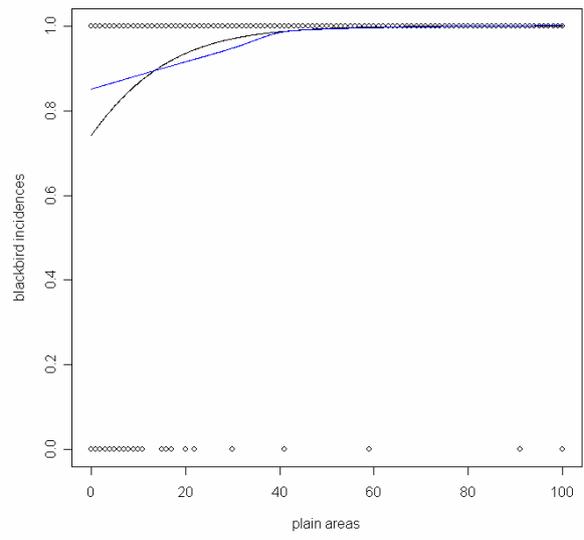
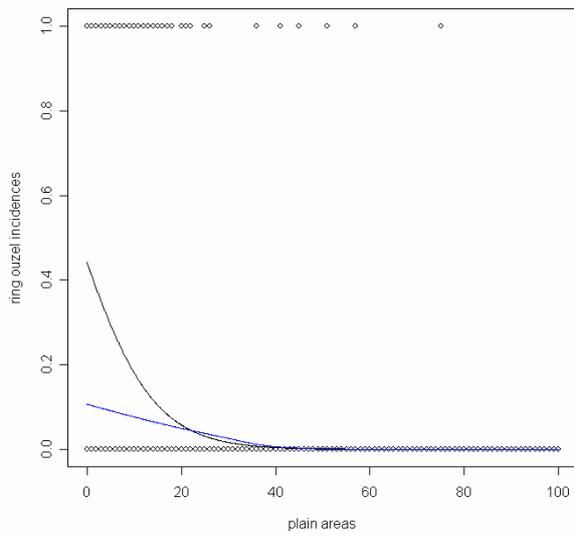
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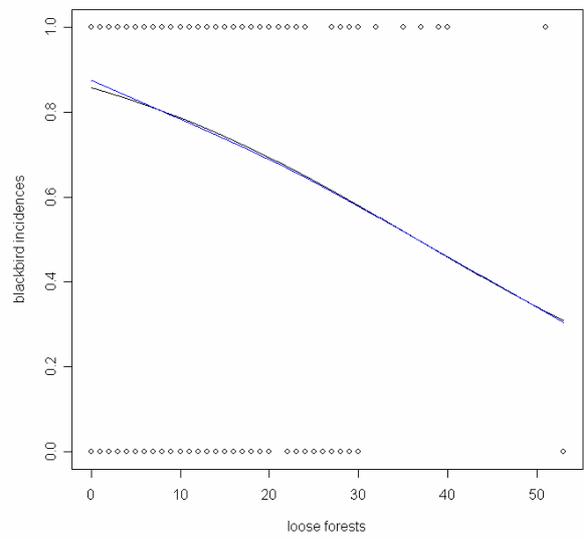
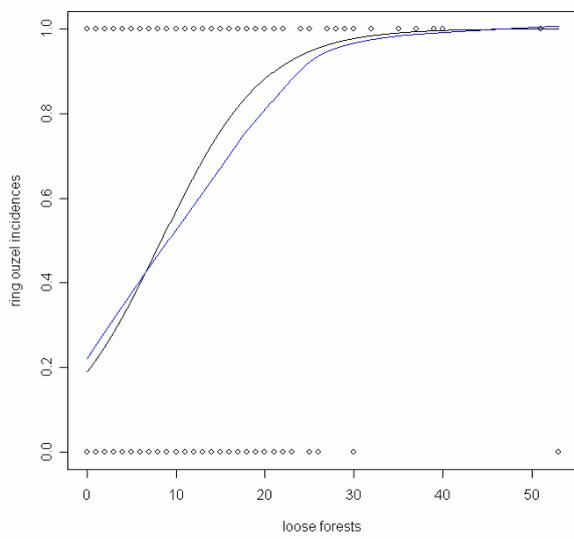


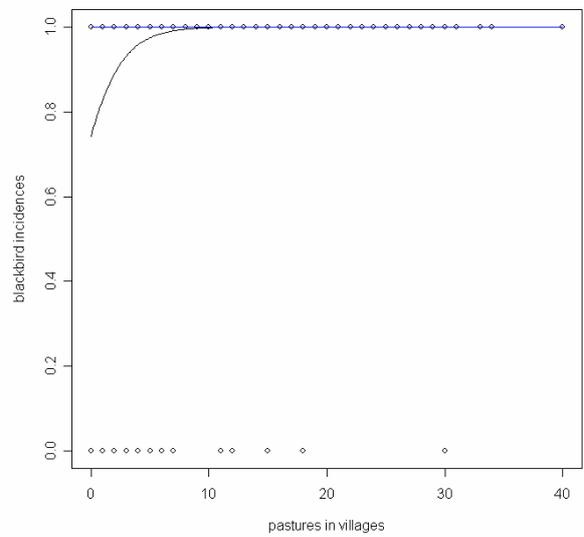
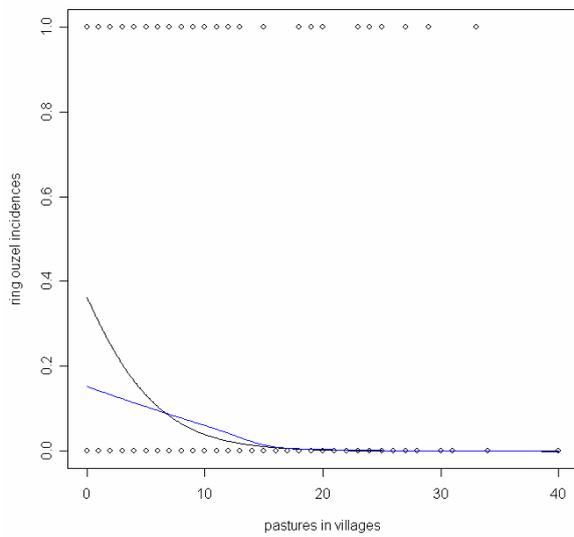
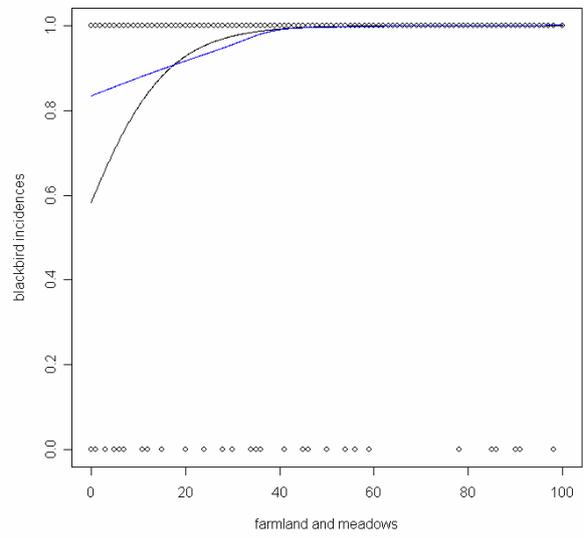
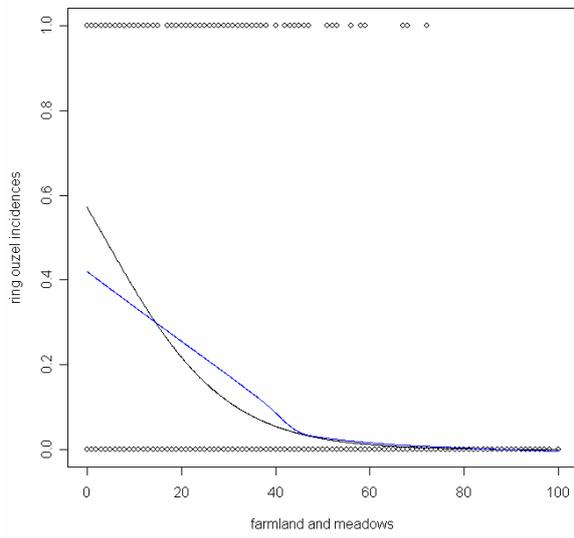
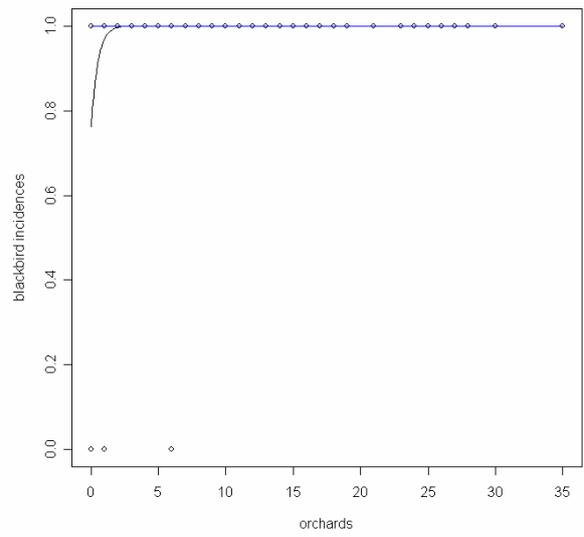
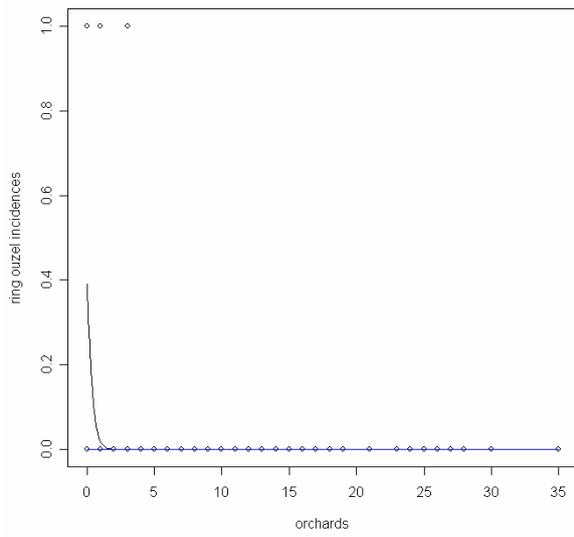


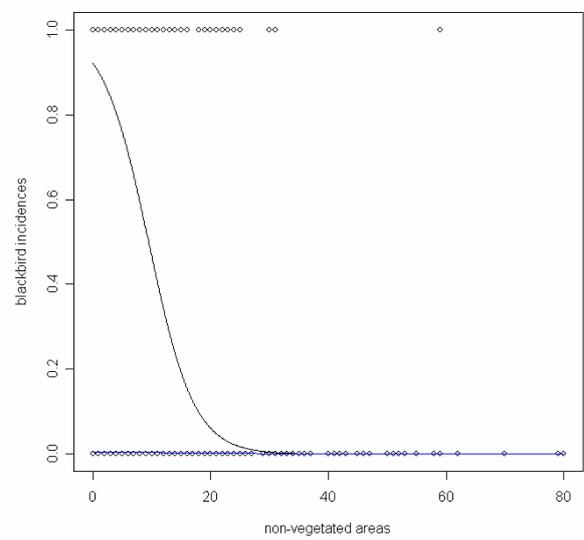
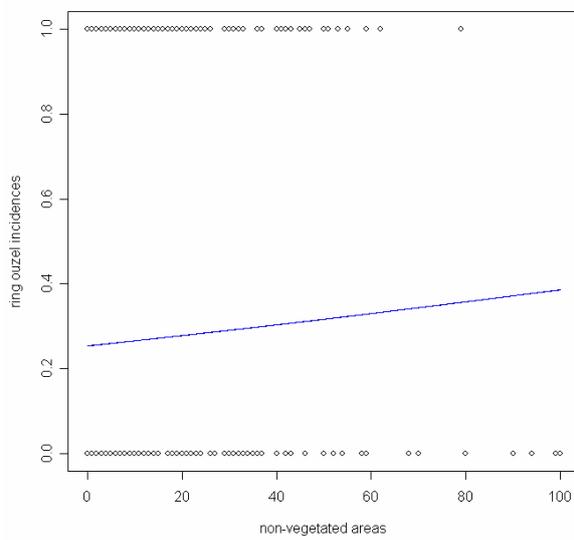
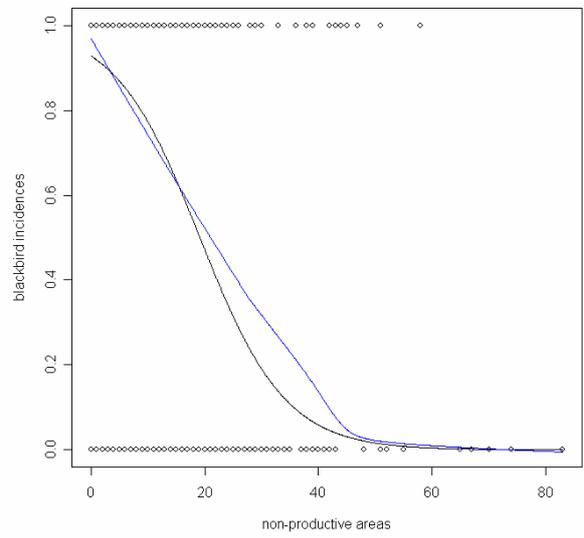
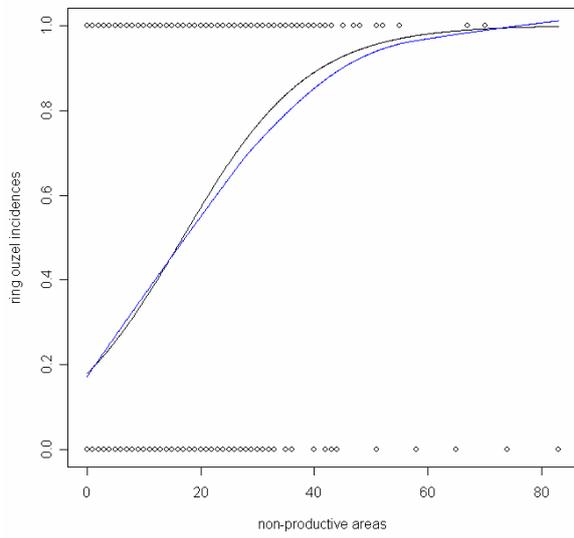
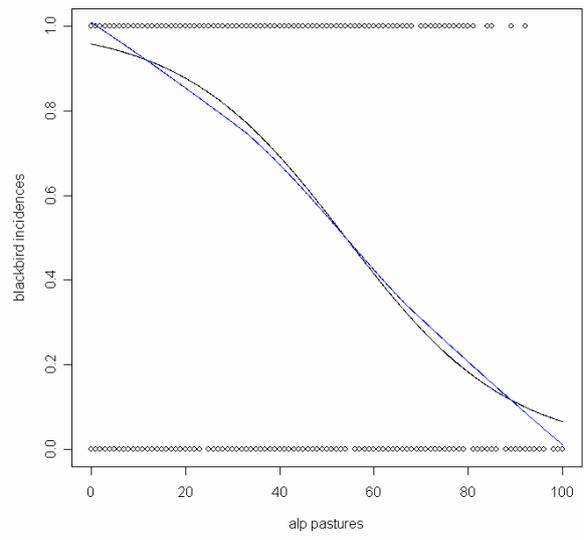
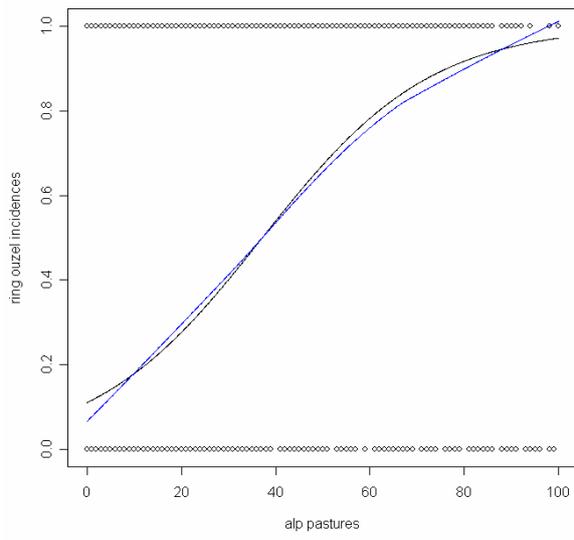


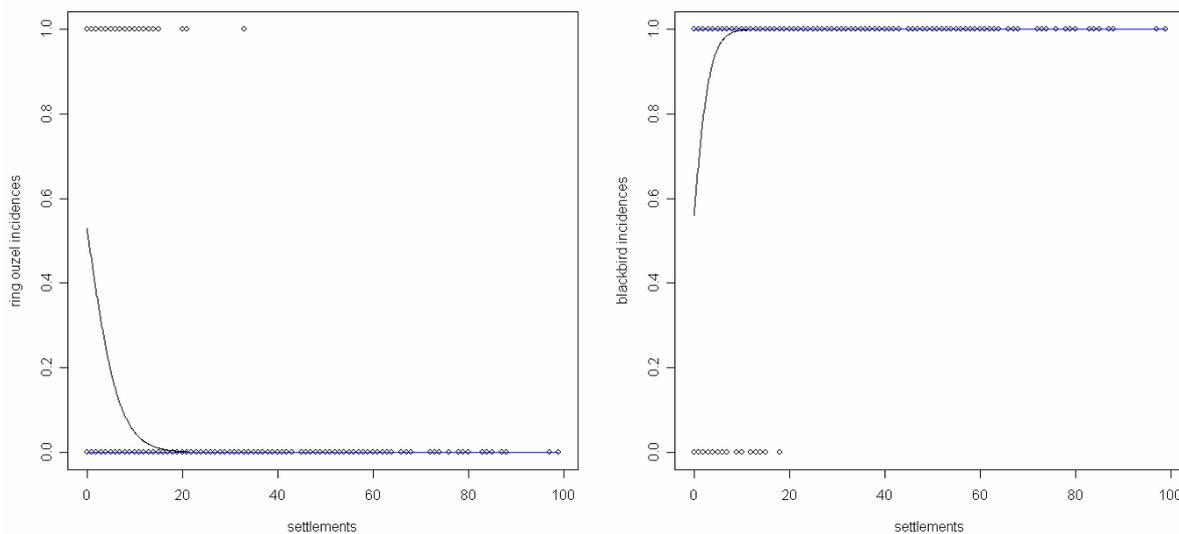


2









<sup>2</sup> Variables significant, but with AUC-values < 0.7

For data on the univariate models on territory-and macroscale, as well as models for quadratic- and interaction terms see the annexed CD-ROM

App.5: bivariate rank correlation coefficient after Spearman. Display of those variables of the model on territory scale, which show p-values < 0.05 and AUC-values > 0.7 at univariate analysis.

	altitude	forestratio plot	cov.upper. forest.lyr	cov.understo- rey	cov.berry- bush	cov.herb moss	rock.stubs cov.	farm.hut
altitude	1.000	-0.621	-0.577	-0.578	0.326	0.452	0.278	0.227
forestratio plot	-0.685	1.000	0.823	0.877	-0.478	-0.606	-0.465	-0.347
cov.upper forest.lyr	-0.571	0.823	1.000	0.712	-0.427	-0.521	-0.468	-0.243
cov.understo- rey	-0.623	0.877	0.712	1.000	-0.579	-0.553	-0.491	-0.436
cov.berry- bush	0.195	-0.478	-0.427	-0.579	1.000	0.255	0.563	0.389
cov.herb smoss	0.406	-0.606	-0.521	-0.553	0.255	1.000	0.226	0.157
rock.stubs cov.	0.327	-0.465	-0.468	-0.491	0.563	0.226	1.000	0.330
farm.hut	0.261	-0.347	-0.243	-0.436	0.389	0.157	0.330	1.000

$r_s > |0.7|$

App.6: Bivariate rank correlation coefficient after Spearman. Display of those variables of the atlas model, which show p-values < 0.05 and AUC-values > 0.7 at univariate analysis. Only variables which feature two-sided rank correlations > 0.7 are shown.

	DEGDAYS	PRECJAN*	PRECYEAR	RADJUL	TEMPJUL	TEMPYEAR	N8_97	N11_97	N15_97	N17_97	N22_97	N16BISN24
DEGDAYS	1.000	-0.412	-0.481	-0.748	0.965	0.965	0.578	-0.769	-0.606	0.525	0.504	0.619
PRECJAN*	-0.412	1.000	0.763	0.349	-0.425	-0.415	-0.250	0.451	0.151	-0.250	-0.271	-0.317
PRECYEAR	-0.481	0.763	1.000	0.389	-0.486	-0.478	-0.395	0.493	0.271	-0.301	-0.347	-0.397
RADJUL	-0.748	0.349	0.389	1.000	-0.756	-0.759	-0.424	0.640	0.378	-0.388	-0.403	-0.487
TEMPJUL	0.965	-0.425	-0.486	-0.756	1.000	0.981	0.602	-0.786	-0.614	0.537	0.514	0.632
TEMPYEAR	0.965	-0.415	-0.478	-0.759	0.981	1.000	0.603	-0.780	-0.617	0.530	0.517	0.631
N8_97	0.578	-0.250	-0.395	-0.424	0.602	0.603	1.000	-0.694	-0.615	0.442	0.423	0.515
N11_97	-0.769	0.451	0.493	0.640	-0.786	-0.780	-0.694	1.000	0.569	-0.521	-0.495	-0.613
N15_97	-0.606	0.151	0.271	0.378	-0.614	-0.617	-0.615	0.569	1.000	-0.431	-0.411	-0.496
N17_97	0.525	-0.250	-0.301	-0.388	0.537	0.530	0.442	-0.521	-0.431	1.000	0.603	0.823
N22_97	0.504	-0.271	-0.347	-0.403	0.514	0.517	0.423	-0.495	-0.411	0.603	1.000	0.840
N16BISN24	0.619	-0.317	-0.397	-0.487	0.632	0.631	0.515	-0.613	-0.496	0.823	0.840	1.000
JB1	-0.658	0.202	0.322	0.514	-0.672	-0.673	-0.626	0.675	0.632	-0.435	-0.426	-0.517
JB5	0.723	-0.359	-0.527	-0.577	0.743	0.744	0.756	-0.728	-0.578	0.513	0.504	0.600
JB6	-0.540	0.135	0.258	0.353	-0.552	-0.553	-0.611	0.530	0.706	-0.380	-0.365	-0.429
JB15	-0.755	0.263	0.404	0.595	-0.765	-0.766	-0.693	0.765	0.663	-0.506	-0.479	-0.589
JB16	0.121	-0.107	0.127	-0.100	0.124	0.115	-0.119	-0.059	0.116	0.040	-0.028	0.015
JB17	-0.643	0.215	0.333	0.484	-0.656	-0.656	-0.596	0.641	0.601	-0.437	-0.387	-0.495
JB18	0.633	-0.283	-0.367	-0.534	0.659	0.657	0.625	-0.674	-0.517	0.456	0.418	0.514
JB19	-0.749	0.393	0.448	0.629	-0.760	-0.758	-0.534	0.731	0.445	-0.424	-0.381	-0.480
MEDIAN_HE	-0.928	0.373	0.487	0.777	-0.939	-0.944	-0.645	0.784	0.654	-0.523	-0.531	-0.640
SLOPE_PERC	-0.536	0.215	0.354	0.436	-0.562	-0.558	-0.538	0.500	0.469	-0.271	-0.304	-0.362
SLOPE_DEGR	-0.536	0.215	0.354	0.436	-0.562	-0.558	-0.538	0.500	0.469	-0.271	-0.304	-0.362
FL	0.620	-0.293	-0.420	-0.516	0.643	0.642	0.578	-0.559	-0.466	0.348	0.371	0.461

$r_s > |0.7|$

App.7: (continued)

	JB1	JB5	JB6	JB15	JB16	JB17	JB18	JB19	MEDIAN_HE	SLOPE_PRC	SLOPE_DEGR	FL
DEGDAYS	-0.658	0.723	-0.540	-0.755	0.121	-0.643	0.633	-0.749	-0.928	-0.536	-0.536	0.620
PRECJAN*	0.202	-0.359	0.135	0.263	-0.107	0.215	-0.283	0.393	0.373	0.215	0.215	-0.293
PRECYEAR	0.322	-0.527	0.258	0.404	0.127	0.333	-0.367	0.448	0.487	0.354	0.354	-0.420
RADJUL	0.514	-0.577	0.353	0.595	-0.100	0.484	-0.534	0.629	0.777	0.436	0.436	-0.516
TEMPJUL	-0.672	0.743	-0.552	-0.765	0.124	-0.656	0.659	-0.760	-0.939	-0.562	-0.562	0.643
TEMPYEAR	-0.673	0.744	-0.553	-0.766	0.115	-0.656	0.657	-0.758	-0.944	-0.558	-0.558	0.642
N8_97	-0.626	0.756	-0.611	-0.693	-0.119	-0.596	0.625	-0.534	-0.645	-0.538	-0.538	0.578
N11_97	0.675	-0.728	0.530	0.765	-0.059	0.641	-0.674	0.731	0.784	0.500	0.500	-0.559
N15_97	0.632	-0.578	0.706	0.663	0.116	0.601	-0.517	0.445	0.654	0.469	0.469	-0.466
N17_97	-0.435	0.513	-0.380	-0.506	0.040	-0.437	0.456	-0.424	-0.523	-0.271	-0.271	0.348
N22_97	-0.426	0.504	-0.365	-0.479	-0.028	-0.387	0.418	-0.381	-0.531	-0.304	-0.304	0.371
N16BISN24	-0.517	0.600	-0.429	-0.589	0.015	-0.495	0.514	-0.480	-0.640	-0.362	-0.362	0.461
JB1	1.000	-0.592	0.561	0.743	0.018	0.725	-0.562	0.539	0.700	0.471	0.471	-0.486
JB5	-0.592	1.000	-0.550	-0.750	-0.091	-0.610	0.727	-0.698	-0.771	-0.553	-0.553	0.605
JB6	0.561	-0.550	1.000	0.596	0.183	0.551	-0.456	0.458	0.623	0.547	0.547	-0.532
JB15	0.743	-0.750	0.596	1.000	0.081	0.744	-0.720	0.671	0.795	0.524	0.524	-0.549
JB16	0.018	-0.091	0.183	0.081	1.000	0.013	0.015	-0.032	0.007	0.194	0.194	-0.153
JB17	0.725	-0.610	0.551	0.744	0.013	1.000	-0.590	0.563	0.671	0.463	0.463	-0.471
JB18	-0.562	0.727	-0.456	-0.720	0.015	-0.590	1.000	-0.656	-0.675	-0.423	-0.423	0.447
JB19	0.539	-0.698	0.458	0.671	-0.032	0.563	-0.656	1.000	0.765	0.558	0.558	-0.589
MEDIAN_HE	0.700	-0.771	0.623	0.795	0.007	0.671	-0.675	0.765	1.000	0.648	0.648	-0.724
SLOPE_PRC	0.471	-0.553	0.547	0.524	0.194	0.463	-0.423	0.558	0.648	1.000	1.000	-0.757
SLOPE_DEGR	0.471	-0.553	0.547	0.524	0.194	0.463	-0.423	0.558	0.648	1.000	1.000	-0.757
FL	-0.486	0.605	-0.532	-0.549	-0.153	-0.471	0.447	-0.589	-0.724	-0.757	-0.757	1.000

\* variable significant for ring ouzel only

$r_s > | 0.7 |$

App.8: Goodness criteria for the final models after bootstrapping: sensitivity (proportion of correct prognoses for correctly predicted presences), specificity (proportion of correct prognoses for correctly predicted absences), %correct (proportion of correct prognoses) and Cohen's kappa for P\_fair (equal values for sensitivity and specificity), P\_kappa (maximal value for kappa) as well as P=0.5 ( $P_{crit} = 0.5$ )

## a) blackbird on territory scale

	P_fair	P_kappa	P=0.5
P_crit	0.49	0.54	0.5
sensitivity	0.957	0.947	0.947
specificity	0.951	0.963	0.963
% correct	0.955	0.955	0.955
kappa	0.909	0.909	0.909
	excellent	excellent	excellent

## b) ring ouzel on territory scale

	P_fair	P_kappa	P=0.5
P_crit	0.62	0.578	0.5
sensitivity	0.93	0.953	0.953
specificity	0.989	0.9602	0.945
% correct	0.965	0.96	0.949
kappa	0.92	0.92	0.898
	excellent	excellent	excellent

## c) blackbird on macroscale

	P_fair	P_kappa	P=0.5
P_crit	0.478	0.498	0.5
sensitivity	0.968	0.9652	0.965
specificity	0.721	0.74	0.74
% correct	0.928	0.935	0.935
kappa	0.72	0.728	0.728
	very good	very good	very good

## d) ring ouzel on macroscale

	P_fair	P_kappa	P=0.5
P_crit	0.463	0.42	0.5
sensitivity	0.86	0.888	0.827
specificity	0.898	0.886	0.906
% correct	0.888	0.887	0.886
kappa	0.722	0.724	0.71
	very good	very good	very good

App. 9: Hierarchical partitioning for the final models of blackbird and ring ouzel on territory scale. I = Independent effect, I [%] = Independent effect in percent, J=Joined effect, Total = Total effect

## a) blackbird on territory scale

	I	I [%]	J	Total
Comp.1	53.293	55.795	27.480	80.774
Hoche	29.710	31.105	22.485	52.195
Deckung.Beerenstr.	12.513	13.101	6.073	18.586

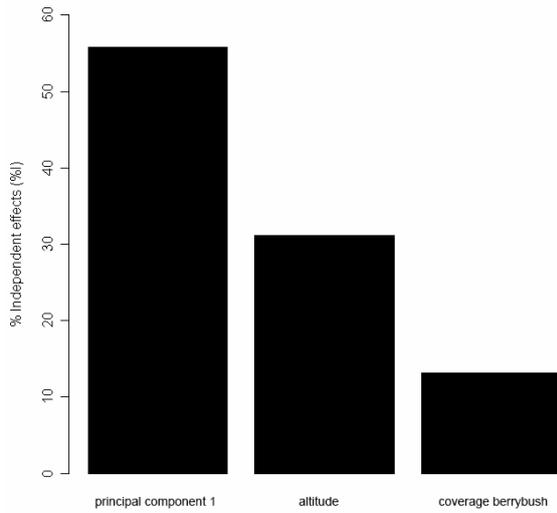
b) ring ouzel on territory scale

	I	I [%]	J	Total
Comp.1	57.960	58.23453	27.696	85.656
Hoehe	28.883	29.01992	22.384	51.268
Deckung.Beerenstr.	12.685	12.74555	6.779	19.465

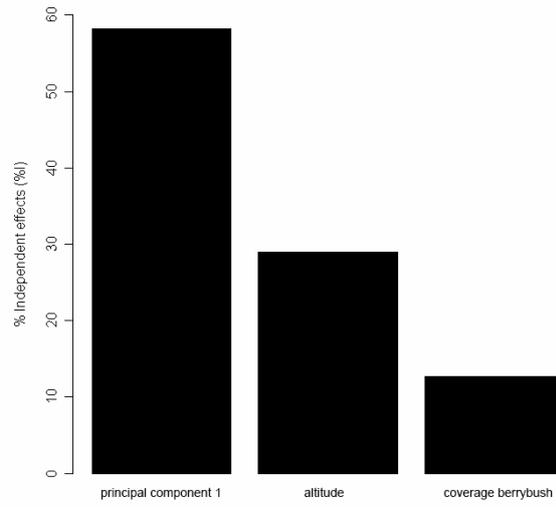
App.10: Variables of the final models on territory scale plotted against the independent effect (in percent)

a) blackbird, b) ring ouzel

a)



b)



App.11: Hierarchical partitioning for the final models of blackbird and ring ouzel on macroscale. I = Independent effect, I [%] = Independent effect in percent, J=Joined effect, Total = Total effect

a) blackbird

	I	I [%]	J	Total
TEMPJUL	293.656	44.654	298.211	591.868
N16BISN2	131.933	20.062	191.694	323.627
4				
N15_97	117.918	17.931	200.634	318.552
N1_97	76.382	11.615	90.958	167.340
PRECYEA	37.735	5.738	67.583	105.317
R				

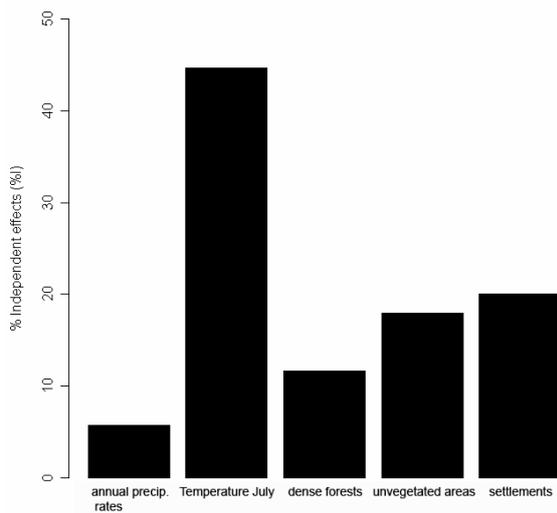
b) ring ouzel

	I	I [%]	J	Total
JB18	140.901	17.380	356.594	497.494
N8_97	125.956	15.537	333.735	459.690
TEMPJUL	85.642	10.564	316.953	402.595
JB2	142.492	17.577	226.657	369.148
N16BISN24	95.194	11.742	250.969	346.163
JB17	100.050	12.341	242.776	342.825
JB11	68.914	8.501	158.725	227.639
PRECYD100	29.540	3.644	112.564	142.104
JB6	22.007	2.715	93.230	115.238

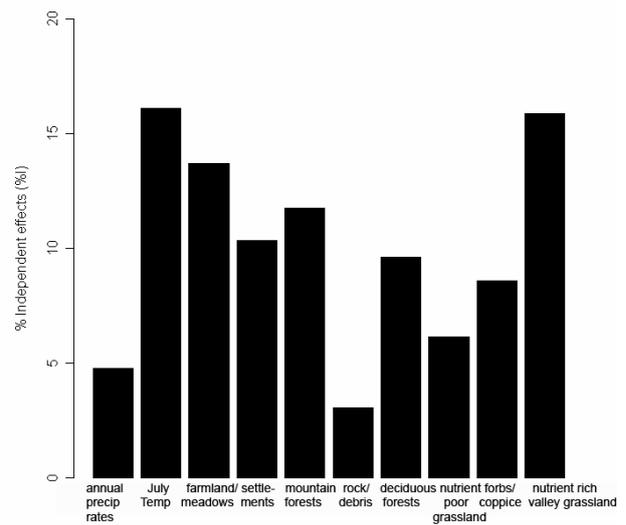
App.12: Variables of the final models on macroscale plotted against the independent effect (in percent)

a) Blackbird macroscale, b) Ring ouzel

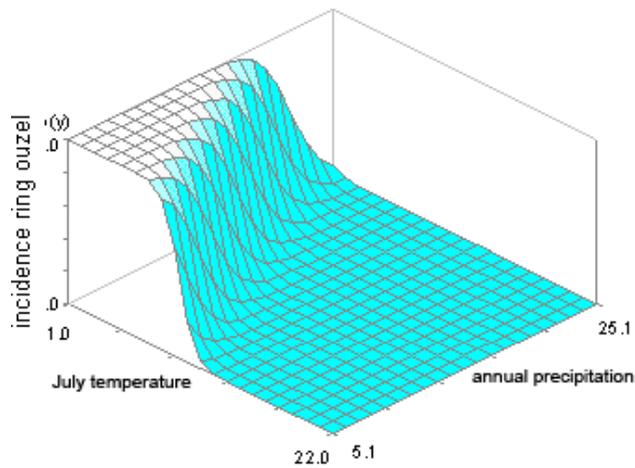
a)



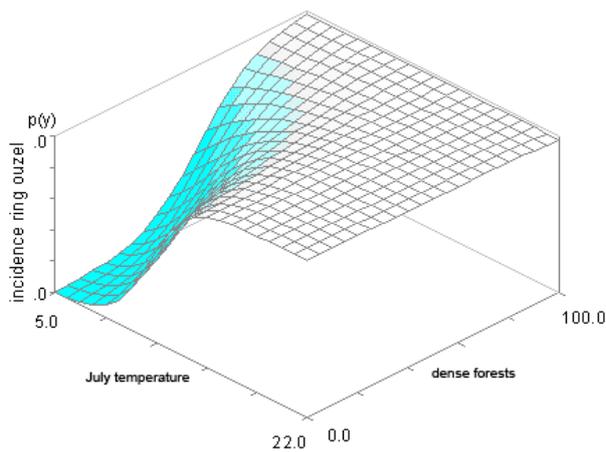
b)



App. 13: Interaction-term between July temperature and annual precipitation rates in the final model for ring ouzel on macroscale



App. 14: Interaction-term between July temperature and proportion of dense forests in the final model for blackbird on macroscale



For further data, results, R- codes and this manuscript as pdf-file please confer to the attached CD-ROM.

Hiermit versichere ich abschließend, diese Arbeit selbstständig verfasst zu haben und keine weiteren, als die angegebenen Hilfsmittel und Literaturquellen verwendet zu haben.

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Jens v.d. Bussche, Potsdam, den 29.08. 2006