Universität für Bodenkultur Wien
University of Natural Resources and Life Sciences, Vienna

Department für Integrative Biologie und Biodiversitätsforschung

Institut für Wildbiologie und Jagdwirtschaft

Habitat modeling of the Alpine ibex – *Capra ibex* – in the Swiss National Park and the National Park Hohe Tauern – a comparison

Masterarbeit
zur Erlangung des akademischen Grades

Master of Science
in
Wildlife Ecology & Wildlife Management

eingereicht von:

Plank Michael, Bakk. MSc

Matrikelnummer 0520980

Betreuer: Prof. Dr. Klaus Hackländer[1], Dr. Flurin Filli[2], Dr. Alfred Frey-Roos[1]

[1] Universität für Bodenkultur Wien, Institut für Wildbiologie und Jagdwirtschaft
[2] Schweizerischer Nationalpark, Bereich Betrieb und Monitoring

Februar 2013

Table of Contents

Abstract

The habitat preference of *Capra ibex* was modeled by applying generalized linear models (GLMs) and ecological niche factor analyses (ENFA). To get an insight into the differences in habitat preferences in the Western and Eastern Alps, two study areas with GPS collared individuals were selected and the summer and winter season was modeled. Both areas show very similar habitat preferences during the winter season and it was also possible to successfully predict the winter habitat in the Eastern Alps using the GLM of the Western Alps. By contrast, in summer the habitat preferences of *Capra ibex* varied widely between the study areas. A comparison of the two modeling techniques showed that the overall results are highly comparable. Due to the big influence of the validation method used, it was not possible to make a general recommendation for one modeling method or the other. A new approach to validate habitat models without absence data is presented, using the correlation of Local Convex Hulls with HSI values of the models.

Keywords

Capra ibex, Alpine ibex, habitat, GLM, ENFA, Swiss National Park, Hohe Tauern National Park, fragmentation, summer, winter

Zusammenfassung

Die Habitatbedürfnisse des Alpensteinbocks (*Capra ibex)* wurden mit Hilfe von zwei unterschiedlichen Modellierungsmethoden genau analysiert. Um einen Vergleich zwischen den westlichen und den östlichen Alpen zu bekommen, wurden zwei Untersuchungsgebiete ausgewählt, in denen Daten für GPS-besenderte Tiere zur Verfügung standen. Zusätzlich zum Gebietsvergleich wurden auch noch die jeweiligen Sommer- und Winterhabitate getrennt analysiert. Es zeigte sich, dass in beiden Gebieten die Habitatpräferenzen während des Winters sehr ähnlich sind, und es war weiters möglich, das Modell aus dem westlichen Untersuchungsgebiet für das östliche Gebiet zu übernehmen und damit akkurate Vorhersagen zu machen. Im Gegensatz dazu zeigte sich für die Sommereinstände von Steinwild eine große Variation zwischen den Gebieten. Der Vergleich zwischen den beiden Modellierungsmethoden ergab, dass die generellen Ergebnisse sehr gut vergleichbar sind. Jedoch konnten keinen allgemeinen Empfehlungen für eine bestimmte Methode gegeben werden, da sie sehr unterschiedliche Vor- und Nachteile besitzen und je nach verwendeter Validierungsmethode verschiedene Modellqualitäten aufweisen. Zusätzlich wurde eine neue Methode zur Validierung von Habitatmodellen, bei denen keine gesicherten Absenzdaten vorhanden sind, entwickelt und implementiert.

Schlagwörter

Capra ibex, Alpensteinbock, Habitat, GLM, ENFA, Schweizerischer Nationalpark, Nationalpark Hohe Tauern, Fragmentierung, Sommer, Winter

Introduction

The Alpine ibex (*Capra ibex*, LINNAEUS 1758) has an eventful history. In the 19th Century, the species became nearly extinct in the Alps, and during the early 20th century, it was reintroduced successfully to distinct areas (Ausserer 1946, Stuwe & Nievergelt 1991, Deutz & Greßmann 2001, Filli 2001, Giacometti 2006). Ausserer (1946) describes the importance of reintroducing *Capra ibex* based on historical evidence into areas where the needs regarding habitat quality, habitat size and reproduction are fulfilled. Modern techniques are now available to determine suitable habitats where a potential introduction of *Capra ibex* is possible. Habitat modeling is one of these methods using geographic information systems (GIS) in combination with a statistical approach.

Essential for habitat modeling is the knowledge about the species and the most important parameters which determine their occurrence. If these factors are well known, the suitability of a given habitat can be evaluated. Various studies showed that *Capra ibex* has varying demands on its environment during summer and winter. Therefore it is important to analyze the habitat suitability separately for different seasons. The habitat preferences of *Capra ibex* was focused in a variety of previous studies. Nievergelt (1966) describes the winter habitat to be in altitudes around 2.300 m, with a high slope of 30 - 45° and an exposition of south to west. This exposition provides higher amount of sun duration, lower snow height, a better thermoregulation (Nievergelt 1966, Singer et al. 2011). Only if the slope exceeds 45° also areas with northwest exposition will become suitable, with regard to the study area (Nievergelt 1966). Most important during the winter season are patches without snow cover and with an adequate food resource. Since snow cover is one of the mayor limiter for *Capra ibex*, areas with an annual precipitation of 700 - 1.700 mm are considered as optimal (Meile 2003). During summer season, alpine meadows are positively selected as important food reserve (Grignoli et al. 2003). Whereas rock and stone ravines are negatively selected due to low trophic resources. During the summer season *Capra ibex* is sensitive to higher temperatures, therefore they move to higher altitudes and search for sites with shade or good wind exposition (Nievergelt 1966). It is also also important for them to move to higher areas to utilize new food resources, and during the winter season they move to lower altitudes (Nievergelt 1966, Kofler 1981). The home range in winter is much smaller compared to the summer (Parrini et. al 2003) and the population densitiy rises from 2.6 Individuals per km² to 11.8 per km² in winter (Meile 2003). Therefore the winter habitat is the most limiting factor for a *Capra ibex* population. Forest and valley below the forest boundary are reported to be unsuitable and only single individuals cross these areas from time to time (Nievergelt 1966). In addition to this, Abderhalden (2004) point out that observations made during spring and fall have very high random effects. Hence it is important for habitat preference analyses to use only data from summer (July – September) and winter (January – March).

Females are reported to avoid areas with higher predation risk while they are giving birth and when they are lactating the fawn. Therefore they avoid flat, open pastures, have smaller home ranges and prefer steeper, more structured areas during summer compared to the males (Nievergelt 1966, Abderhalden 2004, Grignolio et al. 2007). Both sexes prefer south exposition, whereas the males are more tolerant to suboptimal exposures. Furthermore, the males usually use higher elevations during the summer season but some colonies could show a different pattern (Abderhalden 2004, Gupta 2008). In the winter season, the sexual segregation is lower compared to the summer season and the habitat requirements of both sexes do not differ greatly (Abderhalden 2004). Other factors which can alter habitat use is natural predation by large carnivors like *Ursus arctors*, *Canis lupus* and *Lynx lynx* (Nievergelt 1966), interspecific competition with *Rupicapra rupicapra* and *Cervus elaphus* (Meile 2003) or human disturbances like hunting and recreation.

Since a lot of the studies presented before differ in the detail of how *Capra ibex* uses the special areas, it is the aim to study two populations with new methods in very different areas. None of the previous studies examined the habitat use of *Capra ibex* in a small scale approach with modern modeling techniques. Therefore it is expected to get an deeper insight into the habitat dependencies and the interactions between various habitat variables. Assumptions about the overall needs of the study species and what amount of the habitat use is depending on the local availability are presented. One study area is located in its central part of the historic distribution of *Capra ibex* (Ausserer 1946), the Swiss National Park (SNP), where the conditions can be considered as optimal. A large population of *Capra ibex* lives in a protected area, where no hunting is performed and during the winter season no tourism is allowed (Filli, 2001). The second area, the Hohe Tauern National Park (HTNP), is located in the eastern part of the historical distribution (Ausserer 1946), and here human disturbances due to hunting and winter tourism are still present. In the SNP a very good dataset of *Capra ibex* observations from a long-term monitoring project (August 1992 to April 2011) is available and the area which can be used by the ibex colony is well known. Whereas observation data in the HTNP are available from January 2006 to December 2010. The results of habitat models usually depend a lot on the method which was used, due to this, two modeling techniques are performed in this study. It will also give an advice which method is more suitable for modeling this species with certain data. One method used are Generalized Linear Models (GLM), which are very common and have proven to be reliable in a wide range of studies. Since GLM depend also on absence data, which are in this case unreliable and not proven, the second method chosen was the Environmental Niche Factor Analyses (ENFA). This method was presented by Hirzel (2001), does not depend on absence data and was already used in a variety of studies to determine the habitat preferences (e.g. Acevedo et al. 2007). Furthermore it seems obvious that habitat fragmentation is also an important predictor for the distribution of a species. This parameter has not been discussed in previous studies on ibex habitat in this context, therefore also a habitat fragmentation analyses is performed to estimate the suitability of the study areas.

To make reliable statements about the differences and the similarity about the populations in the two study areas, this study was divided into following objectives:

1. *Which parameters contribute differently to the occurrence of Capra ibex in the two study areas?*

   Habitat parameters, which are distributed in the study areas unequally, are expected to be used different in the study areas. But habitat parameters like slope, northing, easting and curvature, which are likely to be available in the same amount in both areas are expected to be used in the same amount.

2. *Which modeling approach suites best to predict the actual occurrence (GLM vs. ENFA)?*

   It can be assumed, that GLM are more suitable in the SNP, because the available habitat for Alp Trupchun colony is very distinct and it is divided to the other colonies by large valleys and forest stands. In contrast to this, in the HTNP data for several individuals are available, which are distributed over a large area and no distinct area of possible movement can be defined. As a consequence, the absence data in the SNP is more reliable and the GLM performs better (Chefaoui et al. 2008).

3. *Is it possible to predict the habitat quality of the HTNP by applying the habitat model of the SNP?*

   Due to the knowledge about Capra ibex, it is expected, that the winter habitat is very distinct and requires special habitat characteristics to survive under such harsh conditions. Whereas the summer habitat is very variable, depending on the habitat availability, human disturbances, sex of the species and so on. So it is expected, that the winter habitat in both areas is very comparable whereas the summer habitat differs greatly (e.g. Nievergelt 1966, Meile 2003).

4. *How does the degree of habitat fragmentation vary between the summer and winter season, and between the two study areas?*

   Since the HTNP lies on edge of the historical distribution of Capra ibex in the European alps, the precipitation is higher, human disturbances are more common and so on, it is expected that the SNP provides a better habitat (Ausserer 1946). Therefore the habitat fragmentation will be lower in the SNP.

Based on the four different questions, following hypotheses were tested:

1. The requirements regarding slope, northing, easting and curvature do not differ significantly between the two study areas.

2. GLMs are more suitable to predict the actual occurrence of *Capra ibex* in the SNP, due to the reliability of the pseudo absence data (Brotons et al. 2004).

3. The winter habitat is more distinct than the summer habitat and it shows the same requirements in both study areas.

4. The SNP provides a better habitat for Capra ibex and therefore the degree of habitat fragmentation is lower than in the eastern part of its historical distribution.

Methods

Study area

In both study areas, *Capra ibex* was reintroduced in the 20th century (Buchli and Abderhalden 1998). Data of GPS collared individuals and similar field mapping information are available. Beside this accurate information about ibex presence, a very intense and long lasting monitoring of *Capra ibex* has created a large amount of additional presence data (Filli 2001, Greßmann & Pichler 2005). The SNP (survey area = 370.7 km²) is located in the Western Alps, showing a relative low amount of precipitation. In the valley areas of the SNP e.g. Zernez (1.474 m) a monthly precipitation of 106 mm in summer season and 38 mm during winter season is expected (Hijmans et al. 2005). On the highest peaks of the SNP the precipitation ranges to 172 mm in summer and to 135 mm in winter. In the SNP hunting is not allowed, all visitors have to use the available paths and roads (Filli 2001). In addition to this dogs are also not allowed and any kind of winter sport is forbidden. Therefore the habitat selection of *Capra ibex* is not driven by enemy-avoidance due to visitors. The visual observation points as well as data from GPS tagged individuals from the Alp Trupchun colony (46.5975° N, 10.0734° E) were used as presence data for *Capra ibex*. The HTNP is located in the Eastern Alps (Austria). In the valley area e.g. Matrei in Osttirol (975 m) a monthly precipitation of 117 mm in summer season and 45 mm during winter season is expected (Hijmans et al. 2005). On the highest peaks of the HTNP the precipitation ranges to 149 mm in summer and to 160 mm in winter. So the precipitation in the winter season is 18 - 19 % greater than in the SNP. In the HTNP (survey area = 1890.3 km², 47.0008° N, 12.5389° E) only GPS data of male individuals were available.

Habitat modeling

The following procedure for modeling habitat suitability is based on the 12 recommendations presented in Hirzel and Le Lay (2008). In a first step, habitat models for summer and winter were created for both areas. A series of ecogeographical variables were extracted from the digital elevation model (DEM), the dataset Habitalp (2007) and the WorldCLIM database (Hijmans et al. 2005). To reduce the number of variables, the whole dataset was reduced to the ecogeographical variables which are listed in Table 1, and the areas which were described to be unsuitable for *Capra ibex* were summed up in one variable.

All datasets were converted into 100 x 100 m cell size raster datasets. Due to the combination of two sampling techniques for the presence data of *Capra ibex* in SNP, a binomial distribution (0 = absence, 1 = presence) was used for the observation data. The observation dataset and the GPS dataset for summer and winter in the SNP were randomly split into one modeling dataset and one verification dataset (50% of the individuals each). Due to the low amount of presence data in the HTNP in respect of the extent of the area, no verification dataset was created here (Table 2).

Table 1: Ecogeographical variables used for the habitat modeling

Variable	Source	Details	Statistics	mean SNP (SE)	mean HTNP (SE)
elevation	DEM		mean	2214m (388)	2342m (429)
aspect	DEM	0-360°			
easting	aspect	sine of aspect; +1 east, -1 west	mean	-0.022 (0.634)	0.0356 (0.666)
northing	aspect	cosine of aspect; +1 north, -1 south	mean	0.018 (0.609)	0.014 (0.639)
slope	DEM		mean	30.7° (10.7)	31.2° (11.1)
curvature	DEM		mean	0.0 (0.7)	0.0 (0.8)
hillshade_summer	DEM	Date: 15.08 – 12:24; Location: Zernez 180° S - 57.37° altitude angle	mean	178.2 (49.0)	175.9 (53.8)
hillshade_winter	DEM	Date: 14.02 – 12:34; Location: Zernez 180° S - 30.25° altitude angle	mean	103.4 (70.2)	100.4 (74.3)
distance grassland	habitalp	Euclidian distance to nearest grassland	mean	154m (234)	231m (437)
distance waterbeds	habitalp	Euclidean distance to nearest waterbed	mean	499m (399)	466m (442)
distance unsuitable areas	habitalp	these are settlements, roads, forest stands, marshlands	mean	396m (590)	780m (764)
precipitation_summer	WorldCLIM	July, August, September	mean	131mm (16)	139mm (5)
precipitation_winter	WorldCLIM	January, February, March	mean	70mm (24)	88mm (17)
temperature_summer	WorldCLIM	July, August, September	mean	7.4°C (2.5)	6.1°C (2.6)
temperature_winter	WorldCLIM	January, February, March	mean	-6.0°C (1.8)	-7.8°C (1.9)

Table 2: Amount of presence points in the study area. k is the number of nearest neighbors which were used to construct the local convex hulls.

	summer	winter
Model_Trupchun	8793 (k = 40)	7310 (k = 40)
Verification_Trupchun	4571 (k = 40)	4342 (k = 40)
Hohe Tauern National Park	4867 (k = 25 - 40)	1316 (k = 25)

Generalized linear models (GLMs)

The following procedures were performed in ArcGIS 9.3 (ESRI, Redlands, USA): Since GLM depend on presence and absence data, random absence data were calculated. For the Alp Trupchun colony (SNP), the available habitat is well known and therefore it is possible to create suitable absence data. First, local convex hulls (LoCoHs) were created for all four datasets (Getz and Wilmers 2004). The k-values are presented in Table 2. As presence area, the 99% isopleths of the LoCoH was chosen. In the area of the Alp Trupchun colony and outside the LoCoHs the same amount of absence points like presence points were randomly created. In the HTNP, the available home ranges for the ibex colonies were unknown. Therefore, the absence points were generated in a 5 km radius around the LoCoHs.

Since GLMs are sensible to autocorrelations, a two-sided Spearman rank correlation test of all ecogeographical variables was performed and all correlations rS > 0.7 and $p < 0.05$ were assumed to be autocorrelated. The variable northing was strongly correlated with hillshade, and elevation with precipitation and temperature, therefore only northing and elevation were used for further analyses. Since it was assumed that some variables had an unimodal influence on habitat suitability, their square value was added as an additional variable (for elevation and slope). To achieve normality of habitat variables, these were transformed if necessary. All analyses above were conducted with the software Statistica 10 (StatSoft Europe GmbH, Hamburg, Germany).

The GLMs were calculated with the software R 2.14.1 (R Development Core Team 2011) using the package lme4 (Bates 2005). In each GLM the dependent variable was the presence (1) or absence (0) of *Capra ibex*. The R model with a full list of the independent variables and all interaction terms is presented in Appendix 1. As family function a binomial distribution and as link function logit was used. The presence and absence data were weighted following Maggini et al. (2006) to ensure a prevalence of 0.5. After the full GLM had been calculated for summer and winter, a stepwise backward reduction was performed, dropping the terms with the highest p value in each step. In the final model, only significant terms ($p < 0.5$) were included. All further analyses were carried out with the final model. In this model building approach, no Bonferroni correction was adopted (Moran 2003), so significance levels should not be interpreted like tests of a priori hypotheses (Forstmeier & Schielzeth 2011). The final models of the SNP were also projected to the HTNP to test if they can accurately predict the habitat preferences of *Capra ibex* in a different area. This is a very delicate step and the results of these predictions must be validated carefully since the resulting HSI maps can be misleading (Dormann 2007, Braunisch et al. 2010).

To compare the predicted distribution of *Capra ibex* in the two study areas, all predictor variables, which were not biased by differences in availability between the areas, were tested for a diverging mean value. Therefore, Bonferroni-corrected t-tests were performed.

Ecological Niche Factor Analyses (ENFA)

This approach is based on a comparison between those sites used, where species presence was proven, and the available habitat in the whole study area (Hirzel et al. 2002b). The ecological niche factor analysis (ENFA) is comparable to a principal component analysis that transforms all ecogeographical variables (EGVs, Table 1) into uncorrelated factors. Since EGVs are not independent and autocorrelations are problematic in different approaches like GLMs, the transformation of the variables during the ENFA is a major advantage. Therefore it was possible to use all the variables. The first factor of the ENFA output explains the species marginality, accounting for the difference between the species mean and the global mean regarding the applied EGVs. A high absolute value of marginality (range 0 to 1) indicates that the species lives in a very distinct habitat in relation to the global distribution. Positive coefficients indicate that the species selects values that are higher than the global mean and vice versa. An overall marginality value M can be calculated throughout all EGVs, so the marginalities can be compared between summer and winter. The other factors of the ENFA provide information about specialization. Higher absolute values of specialization indicate that the variance of the focal species is lower compared to the EGV. Also a global specialization index S can be calculated. To compute habitat suitability maps, it is important to select the most suitable algorithm (Hirzel & Arlettaz 2003, Braunisch et al. 2008). I calculated HSI maps with the median and the geometric mean algorithm, and the algorithm with the highest continuous Boyce index (window size = 20) in the 10-fold cross validation was selected (Hirzel et al. 2006). To create a bimodal HSI map with species presence and absence, presence was assigned to all habitat suitability values (HS) with the predicted to expected species presence (P/E) greater 1 (Appendix 2). All analyses above were performed in BIOMAPPER 4.0 (Hirzel et al. 2002a).

Model evaluation

The performance of the GLMs was calculated with Nagelkerke´s Pseudo R² (R^2_N; Nagelkerke 1991, Backhaus et al. 2008), the AUC value (Hosmer & Lemeshow 2000) and a confusion matrix (Fielding & Bell 1997, Hosmer & Lemeshow 2000). R^2_N values greater 0.2 indicate acceptable performance, values greater 0.4 good and values greater 0.5 very good performance (Backhaus 2006). AUC values between 0.7 and 0.8 indicate a good model, values between 0.8 and 0.9 a very good model and values greater than 0.9 an outstanding model for discriminating between presence and absence (Hosmer & Lemeshow 2000). Using the final model, predictions for the verification dataset in the SNP were calculated and the performance of the AUC value and a confusion matrix were compared to the model dataset. As a threshold value, the point where sensitivity equals specify was used (Figure 1; Hirzel 2002). To estimate if it is possible to predict the habitat suitability of the Eastern Alps with data from the Western Alps, the models of the SNP were applied to the HTNP. These predictions were compared to the native models of the Eastern Alps to estimate their performance.

The ENFA models were evaluated using the continuous Boyce index of the 10-fold cross validation (Hirzel et al. 2006). To compare the model performance directly to the GLMs, also the AUC value and the threshold dependent confusion matrix were calculated. The values of negative prediction power (NPP), positive prediction power (PPP) and correct classification rates (CCR) were compared (Fielding & Bell 1997, Hosmer & Lemeshow 2000). Since these methods depend on the pseudo-absences and a specific presence-absence threshold, they are not optimal to estimate the model performance. In addition to the confusion matrix, Spearman rank correlation tests of the presence point density (LOCOHs) to the HSI values of the GLM and ENFA maps were calculated. Therefore, the HSI maps were reclassified into 20 value ranges with equal width. Since areas with high density should be the most suitable areas for *Capra ibex*, HSI values are expected to be highest there and to decrease towards the areas with low point density. The presence point density was calculated for each of these 20 value ranges. Similar attempts are presented in Zaniewski et al. (2002) for native New Zealand ferns or Boyce et al. (2002) with two case studies for five boreal forest songbirds and for grizzly bears, respectively.

Habitat fragmentation

To contrast the habitat fragmentation of both areas, the presence-absence maps of the GLMs were compared. Therefore the patch cohesion index (COHESION) and the mean proximity index (PROX_MN) were calculated with Fragstats 4.1 (McGarigal et al. 2012). COHESION is a value for physical connectedness and provides information about the distribution of the raster cells which were classified as suitable (Gustafson 1998). PROX_MN is designed to measure the patch isolation in a complex of patches and can be standardized across different landscape extents. All maps must have the same resolution (100 m grid size) and the same search radius must be used (5 km; Gustafson & Parker 1992; Hargis et al. 1997).

Results

Generalized linear models

In most cases, the GLMs were able to predict the habitat quality very well. Due to the higher amount of presence data, the models of the SNP performed better than the model of the HTNP (Table 2, Table 3). The winter model of the SNP (R^2_N = 0.725, $AUC_{ver.}$ = 0.964, Figure 1) performed better than the summer model (R^2_N = 0.637, $AUC_{ver.}$ = 0.939). In the HTNP, the model of the summer habitat (R^2_N = 0.323, $AUC_{ver.}$ = 0.823) was more suitable than the winter model (R^2_N = 0.207, $AUC_{ver.}$ = 0.748) due to the lower amount of presence points in winter (Table 1).

GLM – SNP vs. HTNP

In Table 3, the results of the GLMs are presented. During winter the effects of elevation^2 (neg.), slope (pos.), northing (neg.), distance to unsuitable habitat (dis_unsuitable, pos.) or to water (dis_water, neg.) are very similar in both study areas. Major differences are attributable to easting (neg. in SNP) and various interactions. The interaction of northing with easting in the SNP shows that the east exposition becomes more suitable if the degree of south exposition reaches a maximum (Figure 2). Otherwise west exposition is more suitable. In the HTNP, the interactions of elevation and slope with dis_water indicate that lower elevations and lower degrees of slope are preferred, if the distance to water is shorter (Figure 3, Figure 4). Further interactions only account for a small amount of the final models (lower z-values). During the summer season, the effects of elevation (pos.), elevation^2 (neg.), slope (pos.), northing (neg.), dis_unsuitable (pos.), and the interaction of elevation with dis_grass are very similar (Figure 5, Figure 8). The interaction of elevation and dis_grass shows that higher altitudes are used if the distance to grass decreases. The main differences between the study areas relate to curvature (neg. in HTNP), easting (neg. in SNP), dis_water, dis_grass and a great amount of interactions. The interaction of slope with dis_grass in the SNP indicates that higher slopes are more suitable if the distance to grass is low (Figure 6). The interaction of easting with dis_water in the SNP (Figure 7) indicates that the west exposition is preferred if water supply is close, whereas the east exposition is preferred if water is less available. In HTNP four interactions can be considered as important ($p < 0.001$). The west exposition is preferred in low slope areas, whereas the east exposition is more suitable in high slope areas (Figure 9). The interaction of dis_unsuitable and dis_grass show that "unsuitable" areas are more attractive if the distance to grass feeding grounds increases (Figure 10). Furthermore, "unsuitable" areas are also more attractive if the distance to water is very high (Figure 11). All further interactions in the summer season contribute little to the final models.

Table 3: Results and performance of the generalized linear models

	winter				**summer**			
	Swiss NP		**Hohe Tauern NP**		**Swiss NP**		**Hohe Tauern NP**	
variable	**z**	**P**	**z**	**P**	**z**	**P**	**z**	**P**
elevation	-2.73	0.006	-1.05	0.30	4.03	<0.001	3.77	<0.001
elevation^2	-3.91	<0.001	-4.03	<0.001	-4.84	<0.001	-5.97	<0.001
slope	5.15	<0.001	6.33	<0.001	4.05	<0.001	3.99	<0.001
curvature	-0.34	0.73					-2.96	0.003
northing	-6.59	<0.001	-2.23	0.026	-2.63	0.008	-6.67	<0.001
easting	-2.80	0.005			-3.76	<0.001	-0.74	0.46
dis_unsuitable	3.42	<0.001	2.86	0.004	6.36	<0.001	2.12	0.034
dis_water	-5.26	<0.001	-4.71	<0.001	-10.05	<0.001	2.17	0.030
dis_grass	-7.26	<0.001	-1.34	0.35	-12.39	<0.001	2.40	0.016
elevation*slope	2.33	0.020						
elevation*curvature	2.05	0.041					2.40	0.016
elevation*northing					-3.16	0.002	-2.67	0.007
elevation*easting							-2.39	0.017
elevation*dis_unsuitable			-2.57	0.010	3.65	<0.001	-2.40	0.016
elevation*dis_water			3.81	<0.001	-2.73	0.006	2.52	0.012
elevation*dis_grass					5.81	<0.001	-3.76	<0.001
slope*northing							2.61	0.009
slope*easting							3.68	<0.001
slope*dis_water			3.59	<0.001				
slope*dis_unsuitable	-2.62	0.009						
slope*grass					-5.11	<0.001		
northing*dis_water					2.89	0.004		
northing*dis_unsuitable					3.03	0.002		
northing*dis_grass					-2.25	0.024		
northing*easting	-3.19	0.001						
easting*dis_water					4.64	<0.001		
easting*dis_grass							-3.18	0.001
dis_water*dis_unsuitable					6.95	<0.001	-3.45	<0.001
dis_grass*dis_unsuitable	excluded		-2.76	**0.006**	-7.19	**<0.001**		
performance								
AIC full model	170.51		548.03		506.33		1268.5	
AIC final model	129.09		513.78		482.14		1245.0	
Nagelkerke's R²	0.726		0.207		0.637		0.323	

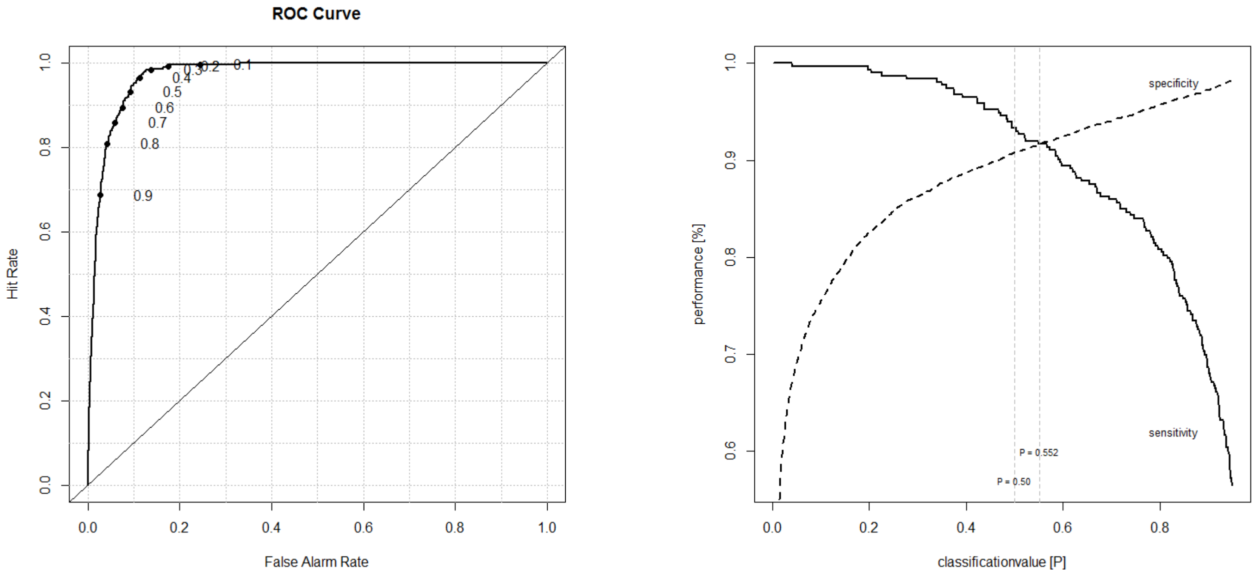


Figure 1: ROC Curve, evaluation of the cut value based on the sensitivity and specificity of the final winter model in the Swiss National Park

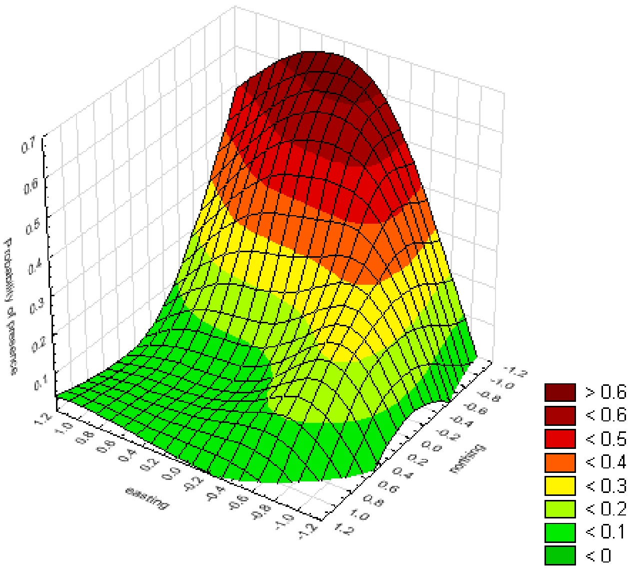


Figure 2: winter interaction of northing with easting in SNP

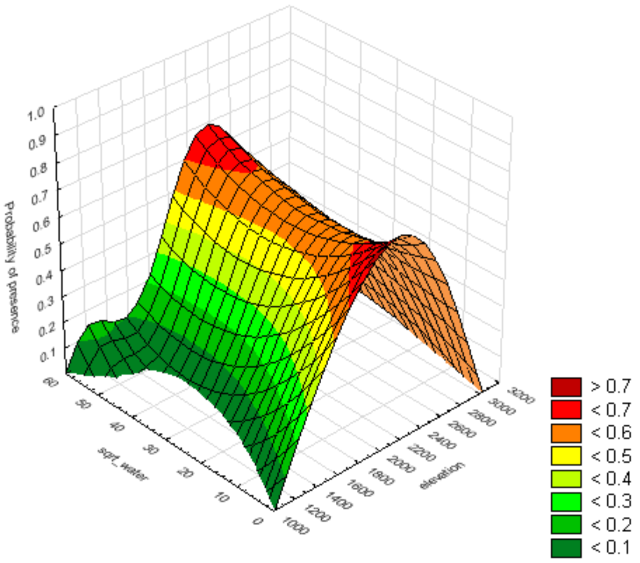


Figure 3: winter interaction of elevation with distance to water (dis_water) in HTNP

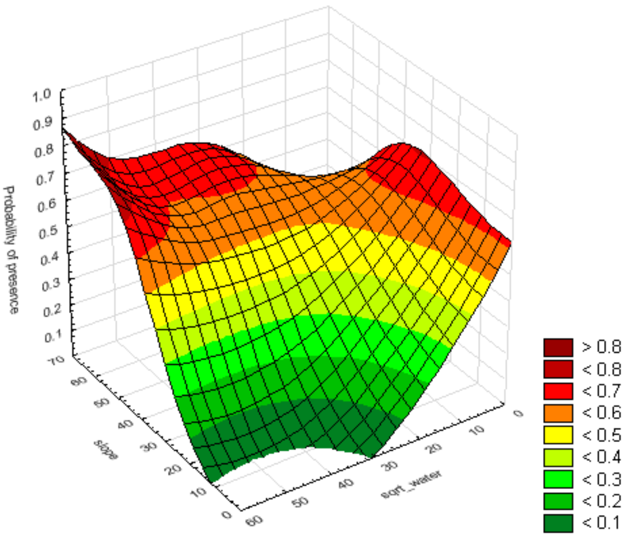


Figure 4: winter interaction of slope with distance to water (dis_water) in HTNP

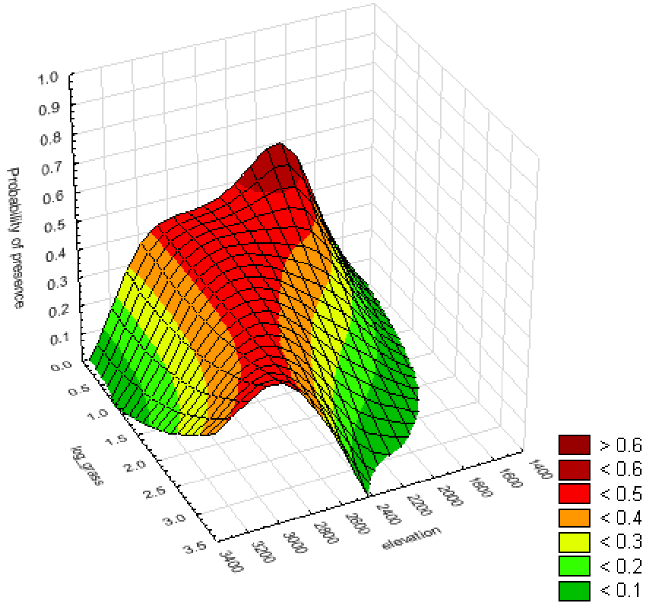


Figure 5: summer interaction of elevation with distance to grass (dis_grass) in SNP

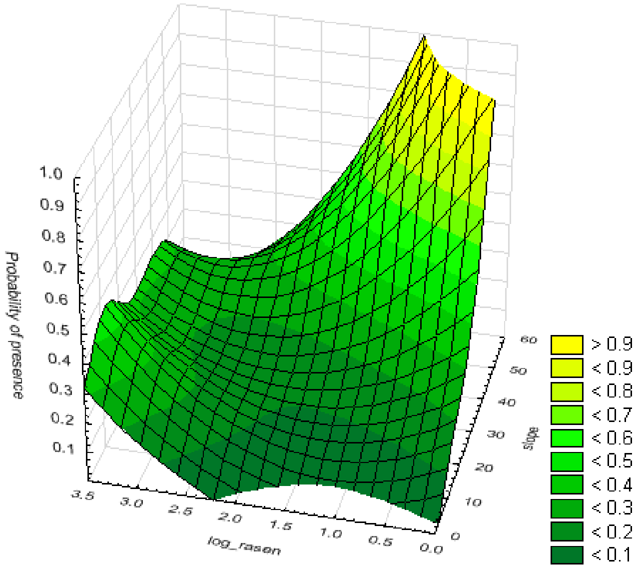


Figure 6: summer interaction of slope with distance to grass (dis_grass) in SNP

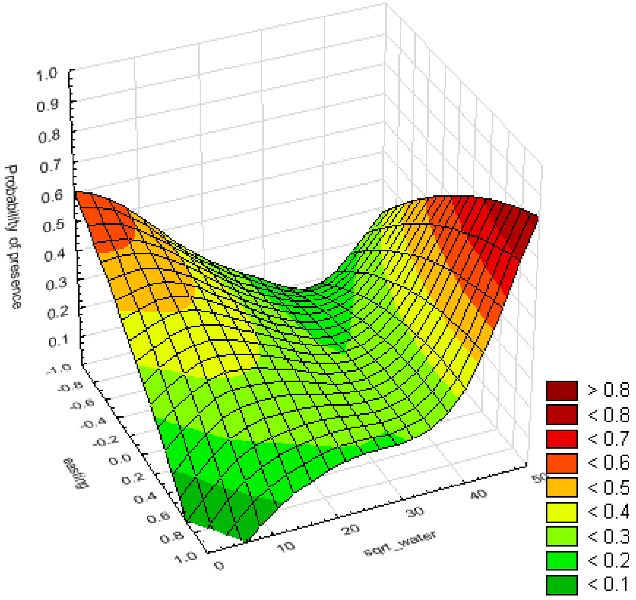


Figure 7: summer interaction of easting with distance to water (dis_water) in SNP

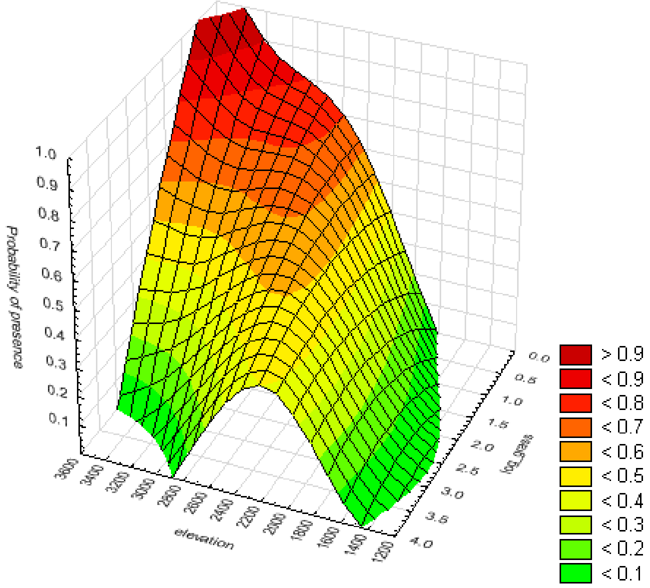


Figure 8: summer interaction of elevation with distance to grass (dis_grass) in HTNP

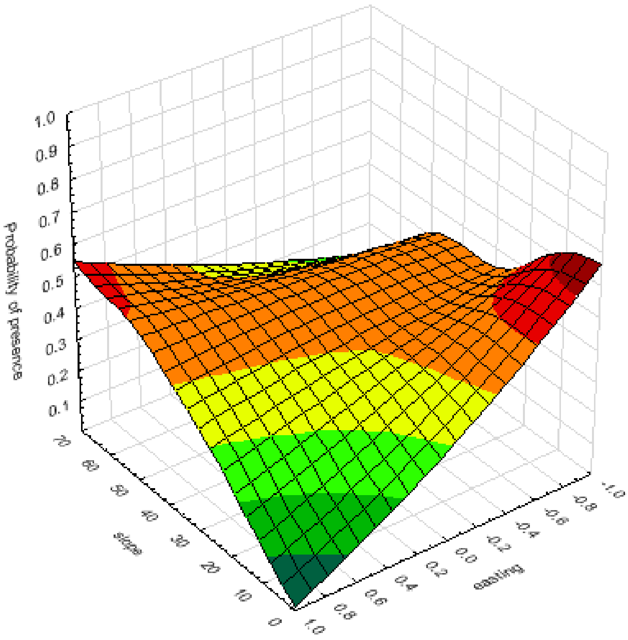


Figure 9: summer interaction of slope with easting in HTNP

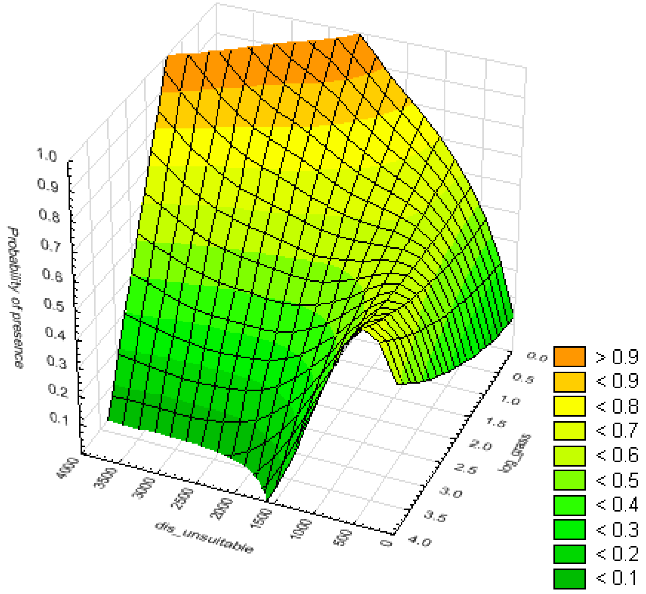


Figure 10: summer interaction of distance to unsuitable areas (dis_unsuitable) with distance to grass (dis_grass) in HTNP

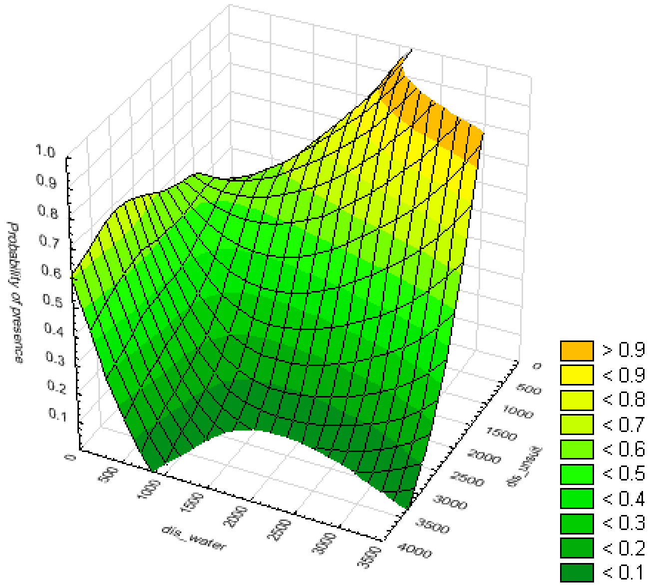


Figure 11: summer interaction of distance to water (dis_water) with distance to unsuitable areas (dis_unsuitable) in HTNP

The predicted areas of the SNP and the HTNP were compared using Bonferroni-corrected t-tests ($p < 0.0125$). Due to the different availability of habitats in the two study areas, only slope, curvature, northing and easting were tested. These variables could be assumed to be available to the same degree in both areas (Table 1). During the summer season, all variables differ significantly between the two areas. In winter, slope and curvature showed no significant difference, whereas northing and easting differed significantly (Table 4). The mean values of the EGVs determined as suitable area by the GLMs are presented in Table 5.

Table 4: t-test for the used habitat patches in the SNP and the HTNP

variable	winter		summer	
	t	**p**	**t**	**p**
slope	**-0.62**	0.53	**16.33**	< 0.001
curvature	**0.18**	0.86	**-7.41**	< 0.001
northing	**-33.86**	< 0.001	**-4.26**	< 0.001
easting	**-21.41**	< 0.001	**-16.44**	< 0.001

Table 5: Mean values of the ecogeographical variables which were determined as suitable area by the GLMs.

	HTNP_summer		**HTNP_winter**		**SNP_summer**		**SNP_winter**	
	mean	std	mean	std	mean	std	mean	std
elevation [m]	2468.4	189.3	2315.1	231.3	2463.9	254.1	2306	204.3
aspect [°]	176.4	81.1	171.7	95.3	193.4	90.9	196.1	72.4
slope [°]	33.3	12.3	36.2	12.3	33.2	11.4	35.3	11.2
hillshade	193	61.6	112.4	85.7	188.9	54.3	148.3	76.4
curvature	-0.1	3.4	0	4.5	-0.2	20.1	-0.4	21.2
grass [m]	95.3	198.5	49.4	117.1	115.4	256.6	23.9	40.8
water [m]	473.2	382.4	319.3	339.8	363.6	342.9	309.8	266.5
unsuitable [m]	844.3	508.2	724.3	554.6	783.6	722.2	322.7	413.1

ENFA – SNP vs. HTNP

The results of the ENFA are not statistically comparable between different study areas, since the marginality and the specialization are compared to the global mean of each study area (Table 1). But comparisons between winter and summer habitats in the same study area are suitable. In both study areas, the overall marginality is higher in the summer season (Table 6). Thus, more extreme habitats are used, e. g. higher elevations, greater distances to unsuitable areas and so on. In both study areas, the overall specialization is greater in winter than in summer (Table 6). Accordingly, the variance of habitats used is lower in winter than in summer. Since the study area in the SNP also contains the valley areas and the settlements, the overall marginality and specialization is higher than in the HTNP. During winter dis_grass, hillshade_w, northing and slope were most important (marginality > 0.3) in the SNP, whereas specialization was greatest for dis_grass, hillshade_w, northing and temp_w. In HTNP the marginality for dis_grass, northing and slope were most important, and the specialization was mostly dominated by dis_grass, precipitation_w and temp_w (Table 7). So both areas show a similar pattern of habitat selection, but easting for example shows a contrary influence.

Table 6: ENFA

	M	***S***	**c. Boyce (20)**
SNP, winter	0.86	3.77	0.881 +- 0.07679
SNP, summer	0.89	2.45	0.295 +- 0.4997
HTNP, winter	0.31	1.65	0.258 +- 0.4796
HTNP, summer	0.53	1.41	0.923 +- 0.04781

Table 7: Result of the ENFA for the winter season with the marginality and the specialization factors for both study areas.

	Swiss NP - winter			**Hohe Tauern NP - winter**		
	marg. 65.1%	spec. 1 14.8%	spec. 2 7.6%	marg. 33.9%	spec. 1 31.1%	spec. 2 7.8%
curvature	0.036	-0.009	-0.025	-0.18	-0.003	0.023
dis_grass	-0.348	-0.579	-0.121	-0.619	-0.196	0.034
dis_unsuitable	0.004	0.124	-0.266	0.064	-0.01	-0.05
dis_water	-0.330	0.141	-0.047	-0.078	-0.023	0.132
easting	-0.178	0.012	0.004	0.033	-0.014	0.017
elevation	0.099	-0.185	0.578	0.051	0.087	-0.098
hillshade_w	0.372	0.349	-0.09	0.25	-0.004	0.091
northing	-0.385	0.461	-0.107	-0.354	0.009	0.039
precipitation_w	0.182	0.295	-0.423	-0.006	0.654	-0.797
slope	0.608	-0.104	-0.248	0.596	0.000	-0.105
temp_w	-0.192	0.403	-0.564	-0.165	0.725	-0.559

During the summer season dis_unsuitable, elevation, precipitation_s, slope and temp_s are most important in the SNP (Table 8). The specialization is mostly correlated with precipitation_s and temp_s, and to a low amount dominated by hillshade_s and northing. In the HTNP dis_water, elevation, hillshade_s and northing are strongly correlated with marginality, whereas specialization is mainly correlated with elevation, precipitation_s, temp_s and dis_grass. The two areas show a very different pattern of habitat selection.

Table 8: Result of the ENFA for the summer season with the marginality and the specialization factors for both study areas.

	Swiss NP - summer			**Hohe Tauern NP - summer**			
	marg. 44.1%	spec. 1 34.7%	spec. 2 6.5%	marg. 8.4%	spec. 1 31.3%	spec. 2 18.0%	spec. 4 10.2%
curvature	-0.029	0.003	0	-0.046	0.024	0.013	-0.005
dis_grass	-0.001	0.007	-0.039	-0.100	0.083	0.403	-0.239
dis_unsuitable	0.506	0.015	0.066	0.016	0.033	0.075	-0.048
dis_water	-0.120	0.007	-0.040	0.457	0.089	-0.095	-0.016
easting	-0.170	-0.004	0.050	-0.254	0.009	0.205	0.044
elevation	0.348	-0.012	0.011	0.367	-0.337	0.197	0.198
hillshade_s	-0.053	-0.031	-0.642	0.351	-0.072	0.306	0.659
northing	-0.069	-0.033	-0.688	-0.433	-0.176	0.278	0.679
precipitation_s	0.497	0.669	-0.043	0.254	-0.752	-0.569	-0.053
slope	0.357	-0.031	-0.316	-0.051	-0.019	0.041	0.027
temp_s	-0.443	0.741	-0.044	-0.450	-0.518	-0.495	-0.001

ENFA – winter vs. summer

Comparisons between winter and summer habitats in the same study area are suitable and the values are statistically interpretable. In both areas, the change of habitat selection between winter and summer shows similar responses (Table 7, Table 8). In winter, the used area is characterized by lower dis_grass, lower dis_water, lower elevation, lower precipitation, greater slopes and higher temperatures compared to the global mean. In the SNP the winter area is also more exposed (curvature), has higher sun duration (hillshade) and a higher degree of south exposition. In the HTNP the winter area has a lower degree of west exposition, lower sun duration and a lower degree of south exposition compared to the summer habitat.

Performance of GLM vs. ENFA

The prediction performance of the different habitat models was compared using a confusion matrix, the AUC value and a density correlation. Based on the results of the confusion matrix and the AUC value, the GLMs outperformed the ENFA models. The results of the density correlation also prefer the GLMs in the HTNP in winter and in the SNP in summer, whereas the ENFA models are more suitable in the SNP in winter and in the HTNP in summer. The GLMs of the SNP were also projected to the HTNP. It appears that the winter habitat of *Capra ibex* in the HTNP is well predicted (AUC = 0.683; r = 0.68, p < 0.001), but the GLM of the SNP fails completely to predict the summer habitat in the HTNP (AUC = 0.508; r = 0.33, p = 0.16).

Table 9: Model comparison of GLM & ENFA. Confusion matrix, AUC values and Spearman rank correlations (r_S) of the presence point density to HSI values. The highest value of each group is highlighted (excl. model dataset).

				Confusion matrix				Density correlation	
Season	**Area**	**Algorithm**	**Cut point**	**NPP [%]**	**PPP [%]**	**CCR [%}**	**AUC**	**r_S**	***P***
winter	SNP	GLM, modeldata	0.552	91.70	91.69	91.70	0.972		
		GLM, verificationdata	**0.552**	**91.80**	**91.99**	**91.81**	**0.964**	0.50	0.024
		ENFA, verificationdata	18	84.42	86.32	84.51	0.926	**0.83**	**<0.001**
	HTNP	GLM, pred. SNP	0.552	74.11	47.82	67.50	0.683	0.68	<0.001
		GLM	**0.546**	**68.93**	**68.74**	**68.88**	**0.748**	**0.75**	**<0.001**
		ENFA	37	66.88	61.88	65.63	0.693	0.68	<0.001
summer	SNP	GLM, modeldata	0.546	87.78	87.79	87.78	0.949		
		GLM, verficationdata	**0.546**	**86.38**	**86.69**	**86.42**	**0.939**	**0.73**	**<0.001**
		ENFA, verficationdata	15	50.32	93.93	52.51	0.757	0.55	0.012
	HTNP	GLM, pred. SNP	0.546	49.32	53.58	50.20	0.508	0.33	0.16
		GLM	**0.537**	**74.01**	**74.05**	**74.02**	**0.823**	0.67	0.001
		ENFA	45	70.75	53.76	67.27	0.668	**0.88**	**<0.001**

Habitat fragmentation

The results of the calculations show that the suitable area during the winter season is more fragmented (lower values) in the SNP (Table 10), whereas the suitable areas are larger and better connected in the summer season. Contrary to the results in the SNP, habitat fragmentation in the HTNP is greater during the summer season. If both study areas are compared, the Mean Proximity Index states that the summer habitat of the HTNP is more fragmented than in the SNP, whereas the relations are completely different during the winter season.

Table 10: Habitat fragmentation values for the habitat suitability maps created by the GLMs.

	Mean Proximity Index	Patch Cohesion Index [%]
SNP, winter	24.1	91.9
SNP, summer	213.8	98.1
HTNP, winter	261.3	97.5
HTNP, summer	139.1	96.5

Discussion

Generalized linear models

The results of the GLMs show that the winter habitat is quite similar in the two study areas and that the effects of the main predictors are comparable. The main difference in the areas' winter habitats is attributable to various interactions. The differences in interactions may result from the fact that the two areas have a different habitat distribution. The suitable habitat can be described to be in intermediate altitudes, high slope areas, south exposition, higher distance to unsuitable areas (e.g. forest, settlement) and low distance to waterbeds. The model of the SNP indicates that also west exposition and low distance to grass areas are advantageous. These habitat preferences are in good concordance with published data about the habitat dependencies during the winter season (e.g. Nievergelt 1966, Kofler 1981, Meile et al. 2003). Due to the similar habitat use of *Capra ibex* in both study areas, it was possible to project the model of the SNP to the HTNP (AUC = 0.683). During the summer season, habitat use is more variable (lower AUC values) and it varies greatly between the study areas due to a lot of interactions. The overall dependencies of *Capra ibex* during summer are determined by high altitudes, high amount of slope areas and high distance to unsuitable areas. It would have been interesting see if the distance to paths and roads would have a different effect in both study areas, due to different protection laws on hunting, leading dogs, staying on trails and winter sports. It would be expected that the negative effect of human disturbance (if there is one) would be lower in the SNP than in the HTNP. But no data about the trails in the HTNP could be provided to examine this factor. Because of the differences in the other variables, it was not possible to project the model of the SNP to the HTNP (AUC = 0.508). This indicates that the requirements can only be generalized for the winter season, whereas *Capra ibex* is very flexible during the summer season. Therefore the habitat use depends mainly on the global habitat distribution of the available area. The overall habitat dependencies for summer and winter are in good concordance with Kofler (1981), Nievergelt (1966), Wiersema (1982) and Abderhalden (2004).

Environmental niche factor analyses

The ENFA shows that the winter habitat of *Capra ibex* in both areas lays in more moderate (lower marginality) and more specialized habitats. The winter habitat based on these results can be described to be in intermediate altitudes (low M), high slope areas, south exposition, low distance to grass and waterbeds, low precipitation and high sun duration. West exposition is also important for the SNP. These dependencies are comparable to the results of the GLMs. During summer more extreme habitats are used with lower degree of specialization. Marginality and specialization of the ecogeographical variables differ greatly between the two study areas during the summer season and results show a high flexibility in habitat use by *Capra ibex*.

Selecting the best model

Depending on the method used to evaluate the performance of the models, different recommendations would result. It was expected that in the SNP the GLMs perform better than the ENFA models, whereas the ENFA models perform better in the HTNP due to the uncertainty of the pseudo absences (Brotons et al. 2004). All models showed at least a good performance based on the confusion matrix, the AUC value and the density correlation (excl. the projected GLM of the SNP in the HTNP in summer). The confusion matrix and the AUC value both depend on pseudo absence data and both methods always prefer the GLMs (Table 9), which were calculated using the pseudo absences. Therefore they are more suitable to discriminate between presence and pseudo absence. Due to this bias, the main evaluation of the predictive performance should be based on the presence only related density correlation. The density correlation showed a varying performance of both model types. Due to these results, the hypothesis that GLMs are more suitable for the SNP and that ENFA models perform better in the HTNP cannot be confirmed. The two methods are too different and their performance was strongly based on the evaluation method. A similar attempt to compare GLM and ENFA by using presence only data is presented in Brotons et al. (2004) with breeding forest birds in Catalonia. In this attempt, GLM fitted best with the evaluation data, but the model selection was based on presence / pseudo-absence data. Similar to this is the study of Praca et al. (2009) which also highlights a better performance of GLM. Overall they showed, that model quality is generally better for species with more restricted requirement, like the winter habitat of *Capra ibex* in this study. In Zaniewski et al. (2002) the performance of weighted generalized additive models (GAM), which are similar to the weighted GLM in this study, are compared with ENFA based on a presence / absence dataset of ferns. Zaniewski et al. (2002) show that weighted GAM are more suitable to predict actual occurrence of the target species, but ENFA is more suitable to detect areas with high biodiversity. In contrast to this Cianfrani et al. (2010) provides a recomendation for modeling threatendend species or species which are expanding into new areas without absence data, since the can leave furture important habitat unrevealed. Overall no general recommendation can be given, but it seems that weighted GLM have a high potential of predicting species presence probability accurately and with randomly generated absence data (Zaniewski et al. 2002, Chefaoui & Lobo 2008). Some studies go further und use ENFA models in a first step to create pseudo-absences and in a second step GLM to calculate habitat models (Engler et al. 2004, Wisz & Guisan 2009). One further advantage of GLM is the possiblity to account for interactions betweens variables and, as it is shown in this study, it can provide additional information about the species behavior depending on various habitat parameters.

Projecting the model of the Eastern to the Western Alps

It was expected that *Capra ibex* uses similar habitats in both study areas during the winter season. The native models of both study areas show a good accordance between the models. In addition to this, it was possible to transfer the GLM winter model of the SNP to the HTNP with good performance values. The model quality was quite similar to the ENFA model, but the native GLM performed better. If there are no presence data available in the study area, it is feasible to predict the species distribution by using the data of another area with good data quality. This is only suitable for species with a low degree of variation or for seasons where the habitat demands can be expected to be very strict and limiting. As the summer season shows, the high variability of *Capra ibex* makes it impossible to predict the summer habitat accurately in the HTNP. Another explanation of the great differences during the summer season could be that in the SNP both males and females were collared. For the HTNP only data of male individuals were available. Abderhalden (2004) pointed out that the sexual segregation is greatest during the summer season. As discussed before, another large difference between the study areas are diverging protection laws regarding human disturbance like hunting and tourism, and these could also lead to a different habitat usage especially in summer, when a lot of tourists are visiting both national parks. During the winter season, no winter sports are allowed in the SNP. It can also be expected, that the winter habitat in the HTNP has also a low amount of disturbances based on the slope, exposition, altitude and the lower amount of visitors.

A recommendation for finding and establishing new colonies of *Capra ibex* would be to concentrate on the winter habitat, since this is the most limiting factor (Wiersema 1989). The mean distance between summer habitat and winter habitat is 4.7 km for males and 2.5 km for females (Abderhalden 2004). Therefore a suitable summer habitat should be available in the specified radius around the suitable winter habitat. *Capra ibex* can be very variable in the summer season and it is also a good competitor with other species (Kofler 1981). As this study shows, the winter habitat is very similar between study areas, which differ greatly in their global distribution of habitat parameters.

Comparing habitat fragmentation between the study areas

The results of calculations in the SNP are in good concordance with the expected variation of habitat suitability. During the winter season, fewer habitat patches are suitable and therefore fragmentation increases. In summer the habitat fragmentation in the HTNP is higher compared to the SNP. This indicates that suitable habitat patches are more fragmented across the study area and therefore the overall habitat quality is lower. The results of habitat fragmentation during the winter season in the HTNP are difficult to interpret. One explanation for the unexpected variation would be that the data quality (Table 2) was not good enough to build a reliable model (Table 9) and therefore these results should not be overinterpreted.

Conclusion

This study shows that both modeling methods can produce very good predictions, although with big differences in terms of how to interpret them. It is important to use the most suitable method to validate the habitat models. Depending on this decision the performance will be interpreted differently. Furthermore the study shows that it is possible to predict the habitat quality of a study area using data from another area if some requirements are fulfilled. Besides the technical needs, it is important to study species with a small ecological niche such as *Capra ibex* during the winter season which is also the most limiting time for this species (Wiersema 1989, Grotan et al. 2008). With special adoptions to behavior and metabolism they are able survive under these harsh conditions (Singer et al. 2011). For further studies, which will try to predict suitable habitats throughout the Eastern Alps, it is advisable to focus on the winter season.

Acknowledgments

I want to thank the team of the Swiss National Park, especially F. Filli, and the Hohe Tauern National Park, for the accommodation and provision of the modeling data. Furthermore I thank C. Purtscher, A. Frey-Roos, F. Filli, K. Hackländer and H. Edelhoff for helpfull and usefull comments on earlier drafts of this thesis. Last but not least I want to thank my familiy and Susanne for all their support and guidance during the last years.

Literature

ABDERHALDEN, W. D. 2004. *Raumnutzung und sexuelle Segregation beim Alpensteinbock Capra ibex ibex*. Dissertation, Albert-Ludwigs-Universität Freiburg i. Brsg.

ACEVEDO, P., CASSINELLO, J., HORTAL, J. & GORTAZAR, C. 2007. Invasive exotic aoudad (Ammotragus lervia) as a major threat to native Iberian ibex (Capra pyrenaica): a habitat suitability model approach. *Diversity and Distributions,* 13**,** 587-597.

AUBLET, J. F., FESTA-BIANCHET, M., BERGERO, D. & BASSANO, B. 2009. Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia*, 159**,** 237-247.

AUSSERER, C. 1946. *Der Alpensteinbock - Geschichte, Verbreitung, Brauch- und Heiltum, Sage, Wappen, Aussterben und Versuche zu seiner Wiedereinbürgerung*, Wien, Universum Verlagsges.m.b.H.

BACKHAUS, K. 2006. *Multivariate Analysemethoden. Eine anwendungsorientierte Einführung*. 11. Auflage, Berlin, Springer.

BACKHAUS, K., ERICHSON, B., PLINKE, W. & WEIBER, R. 2008. *Multivariate Analysemethoden - Eine anwendungsorientierte Einführung*. 12. Auflage, Berlin, Springer.

BATES, D. 2005. Fitting linear mixed models in R. *R News*, 5**,** 27-39.

BOYCE, M. S., VERNIER, P. R., NIELSEN, S. E. & SCHMIEGELOW, F. K. A. 2002. Evaluating resource selection functions. *Ecological Modelling*, 157**,** 281-300.

BRAUNISCH, V., BOLLMANN, K., GRAF, R. F. & HIRZEL, A. H. 2008. Living on the edge - Modelling habitat suitability for species at the edge of their fundamental niche. *Ecological Modelling*, 214**,** 153-167.

BRAUNISCH, V., SEGELBACHER, G. & HIRZEL, A. H. 2010. Modelling functional landscape connectivity from genetic population structure: a new spatially explicit approach. *Molecular Ecology*, 19**,** 3664-78.

BROTONS, L., THUILLER, W., ARAUJO, M. B. & HIRZEL, A. H. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, 27**,** 437-448.

BUCHLI, C. & ABDERHALDEN, W. 1998. The Alpine Ibex Project Albris Swiss National Park (SNP). *Zeitschrift für Jagdwissenschaft*, 44**,** 102-107.

CHEFAOUI, R. M. & LOBO, J. M. 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling,* 210**,** 478-486.

CIANFRANI, C., LE LAY, G., HIRZEL, A. H. & LOY, A. 2010. Do habitat suitability models reliably predict the recovery areas of threatened species? *Journal of Applied Ecology,* 47**,** 421-430.

DEUTZ, A. & GREßMANN, G. 2001. *Gams- & Steinwild. Biologie - Krankheiten - Jagdpraxis,* Graz, Leopold Stocker Verlag.

DORMANN, C. F. 2007. Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, 8**,** 387-397.

ENGLER, R., GUISAN, A. & RECHSTEINER, L. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology,* 41**,** 263-274.

FIELDING, A. H. & BELL, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24**,** 38-49.

FILLI, F. 2001. *Die Wiederbesiedlung des Steinbocks im Spiegel von Theorie und Management*. Dissertation, Technische Universität München.

FORSTMEIER, W. & SCHIELZETH, H. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65**,** 47-55.

GETZ, W. M. & WILMERS, C. C. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography*, 27**,** 489-505.

GIACOMETTI 2006. *Von Königen und Wilderern - Die Rettung und Wiederansiedlung des Alpensteinbocks*. Bern, Salm Verlag.

GREßMANN, G. & PICHLER, H. 2005. *Alpensteinwild um den Großglockner*, Matrei, Journal Verlag GmbH.

GRIGNOLIO, S., PARRINI, F., BASSANO, B., LUCCARINI, S. & APOLLONIO, M. 2003. Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. *Folia Zoologica*, 52**,** 113-120.

GRIGNOLIO, S., ROSSI, I., BASSANO, B., PARRINI, F. & APOLLONIO, M. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. *Ethology Ecology & Evolution*, 16**,** 255-264.

GROTAN, V., SAETHER, B. E., FILLI, F. & ENGEN, S. 2008. Effects of climate on population fluctuations of ibex. *Global Change Biology*, 14, 218-228.

GUPTA, S. 2008. *Habiat preference and seasonal distribution of Alpine Ibex (Capra ibex ibex) in Austria (Vorarlberg) and Swiss National Park (Val Trupchun).* Master thesis, University of Natural Resources and Life Sciences, Vienna.

GUSTAFSON, E. J. 1998. Quantifying landscape spatial pattern: What is the state of the art. *Ecosystems*, 1**,** 143-156.

GUSTAFSON, E. J. & PARKER, G. R. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecology*, 7**,** 101-110.

HABITALP 2007. *Alpine Habitat Diversity [Online]*. Berchtesgarden. Available: http://www.habitalp.de/englisch/seiten/homeenglish.htm [Accessed 16.03. 2012].

HARGIS, C. D., BISSONETTE, J. A. & DAVID, J. L. 1997. Understanding Measures of Landscape Pattern. In: BISSONETTE, J. A. (ed.) *Wildlife and landscape ecology: effects of pattern and scale*. Berlin, Springer-Verlag.

HIJMANS, R. J., CAMERON, S. E., PARRA, J. L., P.G., J. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25**,** 1965-1978.

HIRZEL, A. 2001. *When GIS come to life. Linking landscape- and population ecology for large population management modelling: the case of Ibex (Capra ibex) in Switzerland*. PhD thesis, Université de Lausanne.

HIRZEL, A. H. & ARLETTAZ, R. 2003. Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. *Environmental Management*, 32**,** 614-23.

HIRZEL, A. H. & LE LAY, G. 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, 45**,** 1372-1381.

HIRZEL, A. H., HAUSSER, J., CHESSEL, D. & PERRIN, N. 2002b. Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology*, 83**,** 2027-2036.

HIRZEL, A. H., LE LAY, G., HELFER, V., RANDIN, C. & GUISAN, A. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, 199**,** 142-152.

HIRZEL, A., HAUSSER, J. & PERRIN, N. 2002a. *Biomapper 4.0 [Online]*. Lausanne: Lab. for Conservation Biology. Available: http://www.unil.ch/biomapper [Accessed 08.11.2012].

HOSMER, D. W. & LEMESHOW, S. 2000. Applied logistic regression. 2nd Edition, New York, Wiley-Interscience.

KOFLER, H. 1981. *Ökologisch-vegetationskundliche Untersuchungen zur Nahrungswahl und Konkurrenz von Gams und Steinbock im Hochlantschstock/Stmk*. Dissertation, University of Graz.

MAGGINI, R., LEHMANN, A., ZIMMERMANN, N. E. & GUISAN, A. 2006. Improving generalized regression analysis for the spatial prediction of forest communities. *Journal of Biogeography*, 33, 1729-1749.

MCGARIGAL, K., CUSHMAN, S. & ENE, E. 2012. FRAGSTATS v4: *Spatial Pattern Analysis Program for Categorical and Continuous Maps [Online]*. Amherst: University of Massachusetts. Available: www.umass.edu/landeco/research/fragstats/fragstats.html [Accessed 12.11.2012].

MEILE, P., GIACOMETTI, M. & RATTI, P. 2003. *Der Steinbock - Biologie und Jagd*, Bern, Salm Verlag.

MORAN, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, 100, 403-405.

NAGELKERKE, N. J. D. 1991. A Note on a General Definition of the Coefficient of Determination. *Biometrika*, 78, 691-692.

NIEVERGELT, B. (ed.) 1966. *Der Alpensteinbock (Capra ibex L.) in seinem Lebensraum - Ein oekologischer Vergleich*, Hamburg: Paul Parey.

PRACA, E., GANNIER, A., DAS, K. & LARAN, S. 2009. Modelling the habitat suitability of cetaceans: Example of the sperm whale in the northwestern Mediterranean Sea. *Deep-Sea Research Part I-Oceanographic Research Papers,* 56, 648-657.

R DEVELOPMENT CORE TEAM 2011. *R: A language and environment for statistical computing*. 2.14.1 ed. Vienna: R Foundation for Statistical Computing.

SINGER, C., RUF, T. & ARNOLD, W. 2011. Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. *Fuctional Ecology*, 25, 537-547.

STUWE, M. & NIEVERGELT, B. 1991. Recovery of Alpine Ibex from near Extinction - the Result of Effective Protection, Captive Breeding, and Reintroductions. *Applied Animal Behaviour Science,* 29, 379-387.

WIERSEMA, G. 1989. Climate and Vegetation Characteristics of Ibex Habitats in the European Alps. *Mountain Research and Development*, 9, 119-128.

WISZ, M. S. & GUISAN, A. 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecol,* 9, 8.

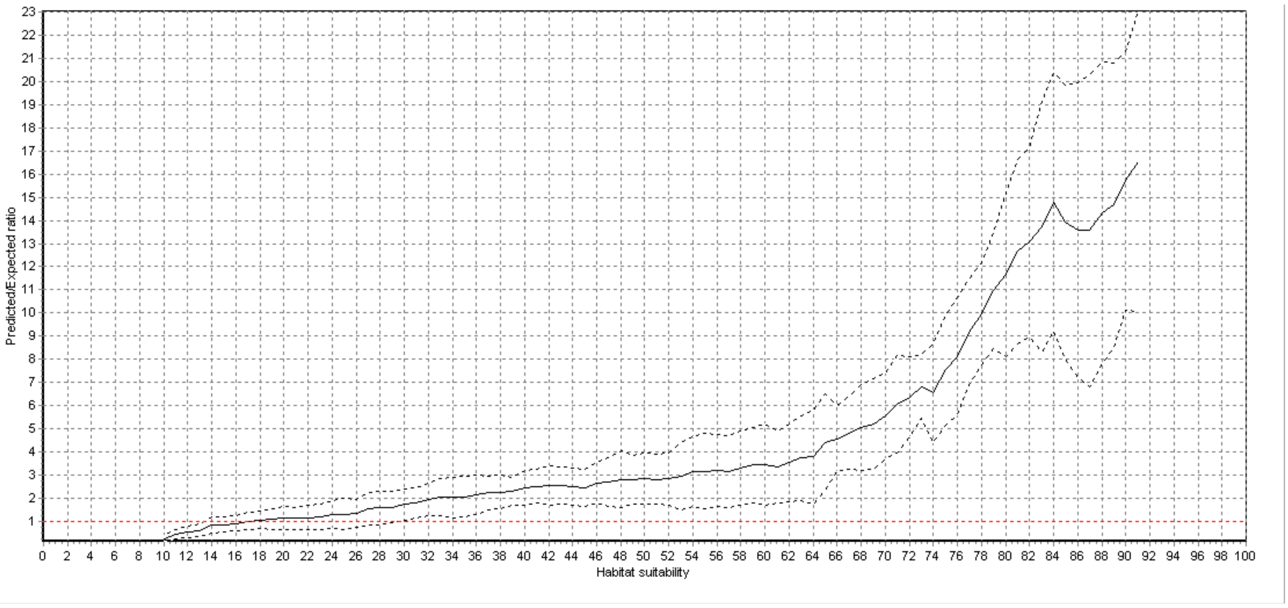
ZANIEWSKI, A. E., LEHMANN, A. & OVERTON, J. M. C. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, 157, 261-280.

Appendixes

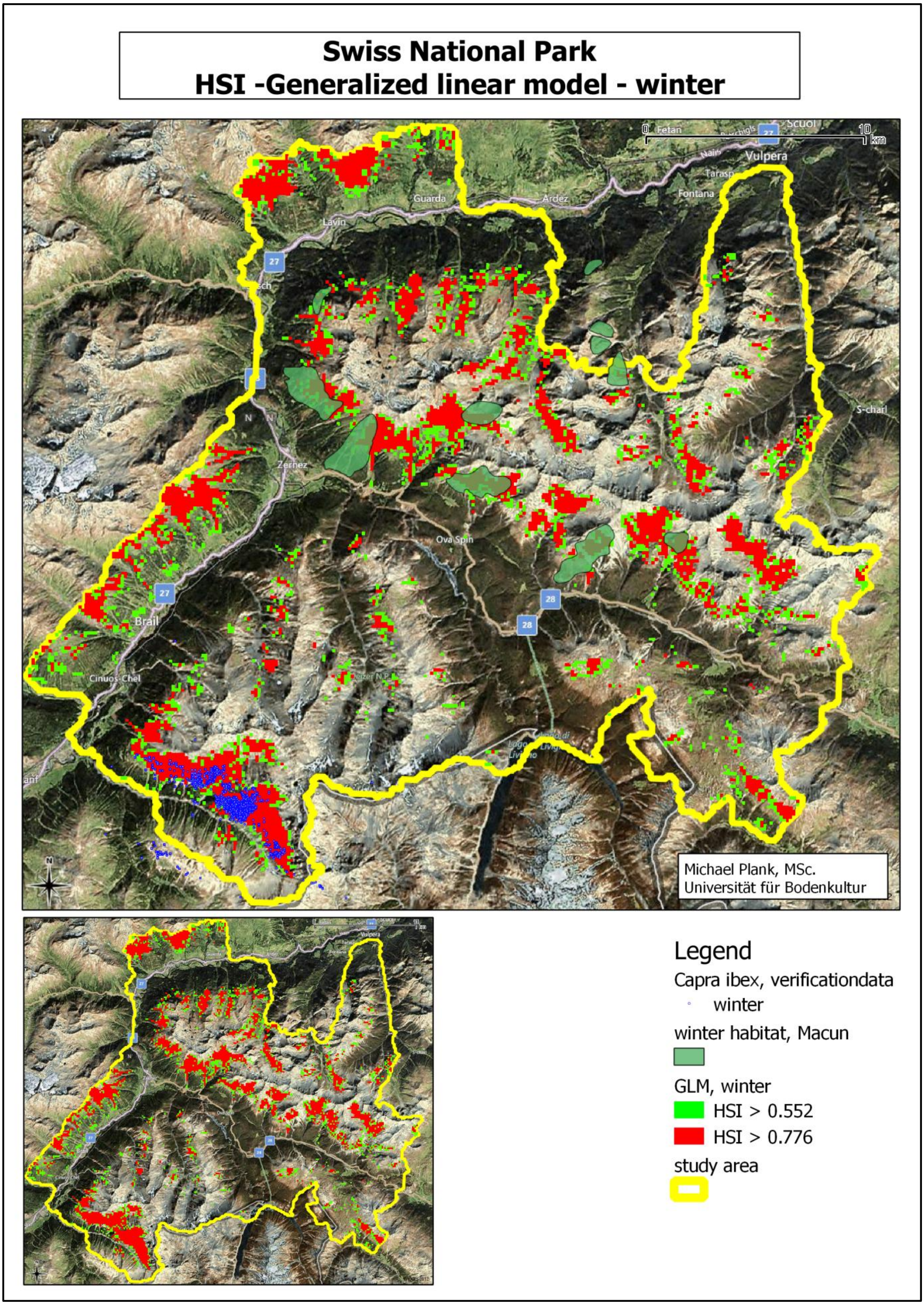
Appendix 1: Full R code for the GLM model

```
full_model=glm(presence_absence~
elevation+
I(elevation^2)+
slope+
I(slope^2)+
curvature+
northing+
easting+
sqrt_gewaes+
dis_unsuit+
log_rasen+
elevation:slope+
elevation:curvature+
elevation:northing+
elevation:easting+
elevation:sqrt_gewaes+
elevation:dis_unsuit+
elevation:log_rasen+
slope:curvature+
slope:northing+
slope:easting+
slope:sqrt_gewaes+
slope:dis_unsuit+
slope:log_rasen+
curvature:northing+
curvature:easting+
curvature:sqrt_gewaes+
curvature:dis_unsuit+
curvature:log_rasen+
northing:sqrt_gewaes+
northing:dis_unsuit+
northing:log_rasen+
northing:easting+
easting:sqrt_gewaes+
easting:dis_unsuit+
easting:log_rasen+
sqrt_gewaes:dis_unsuit+
sqrt_gewaes:log_rasen+
dis_unsuit:log_rasen,
family=binomial (link="logit"),
weights=weigths_presence_absence,
data=data_full_model)
```

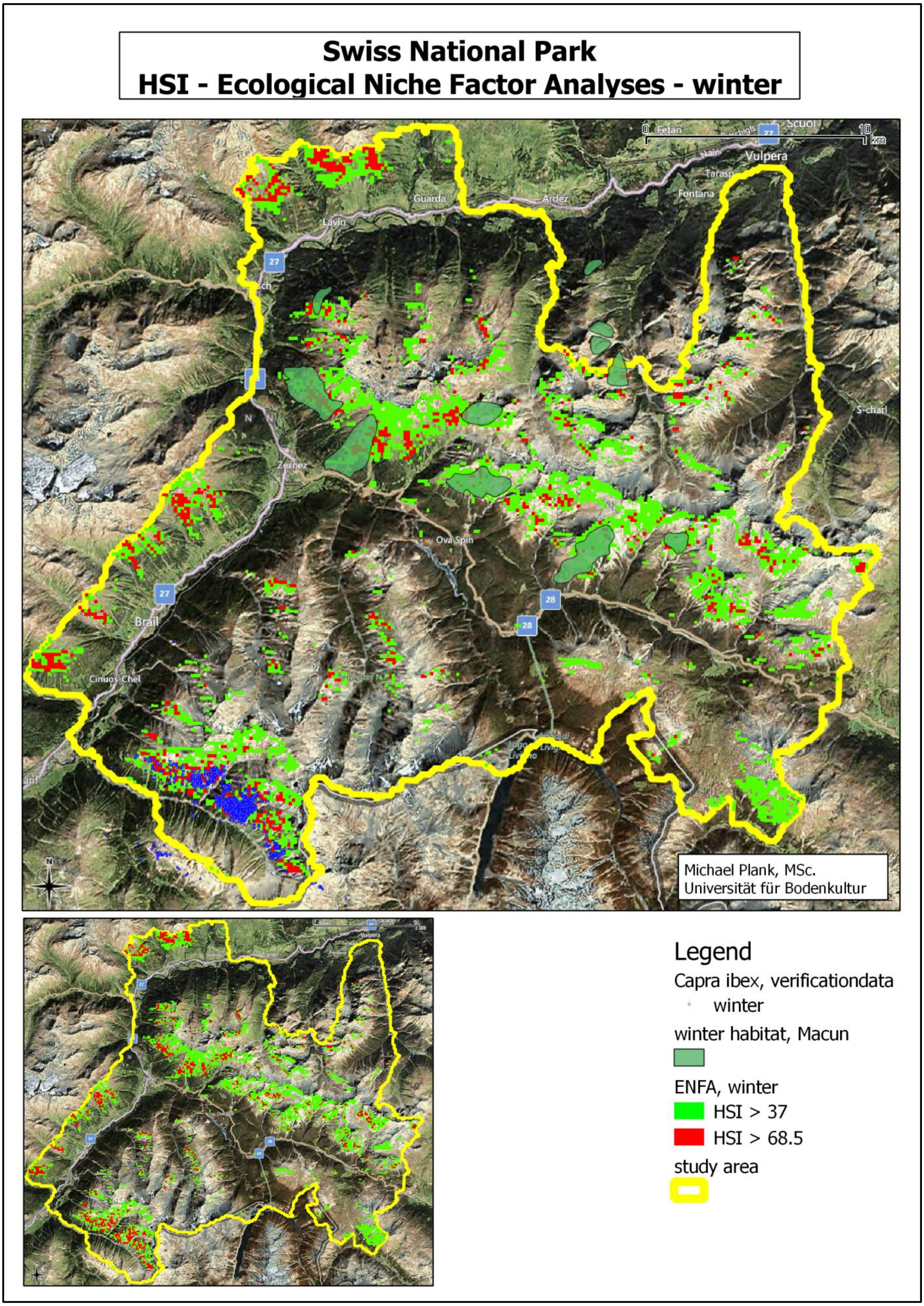
Appendix 2: Curve of the predicted to expected species presence (P/E)



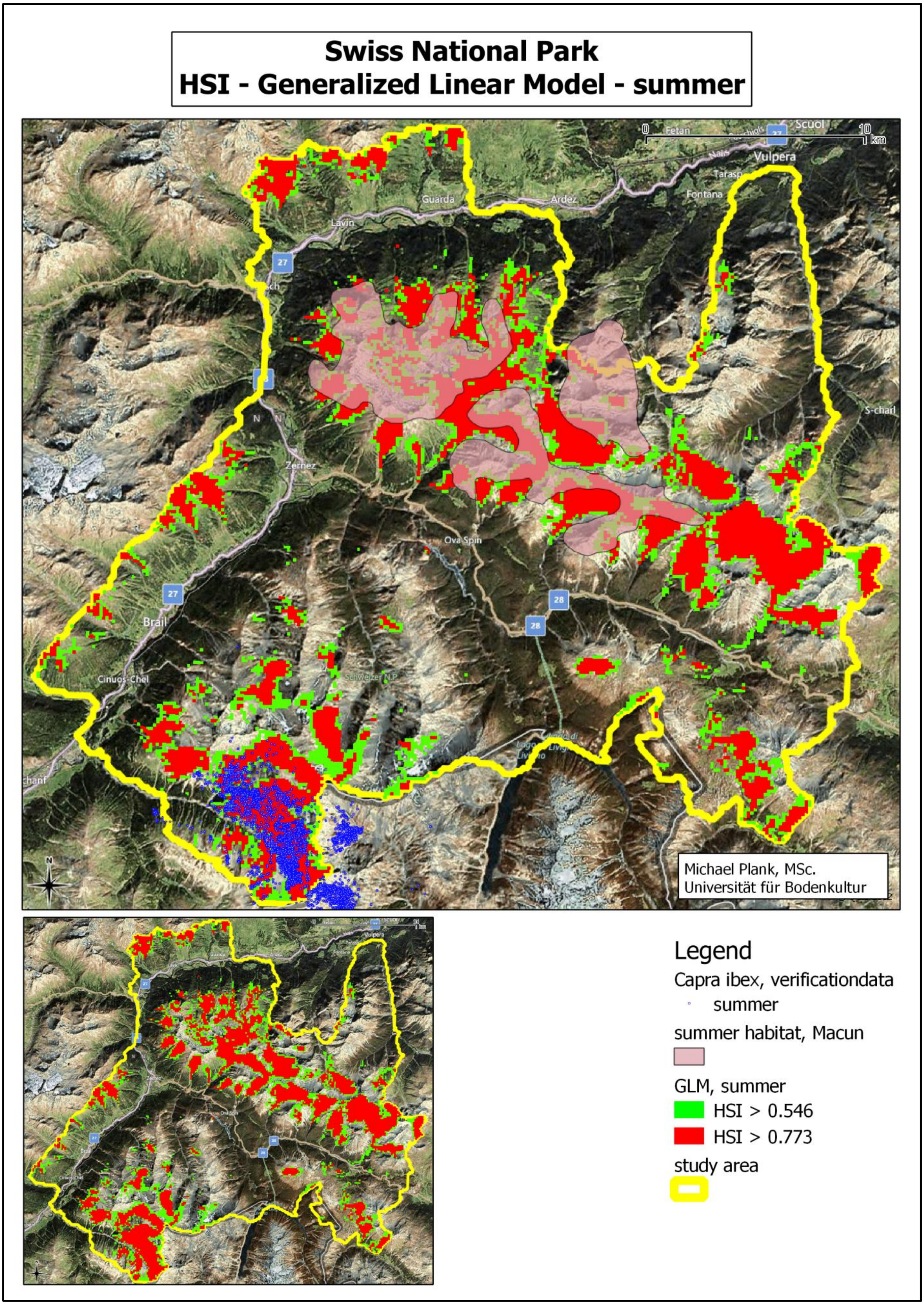
Appendix 3: Generalized liner model of the Swiss National Park in winter.



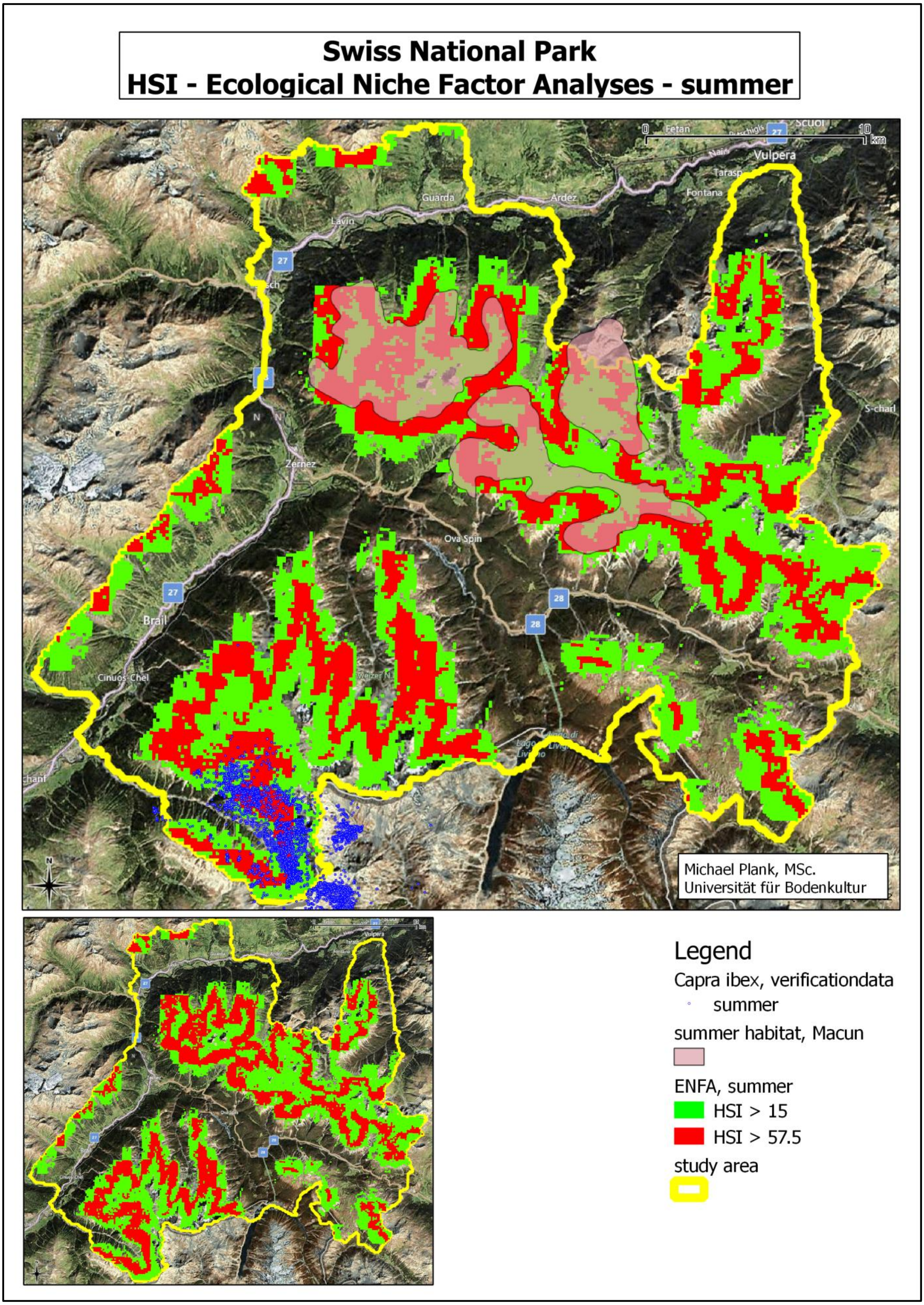
Appendix 4: ENFA model of the Swiss National Park in winter



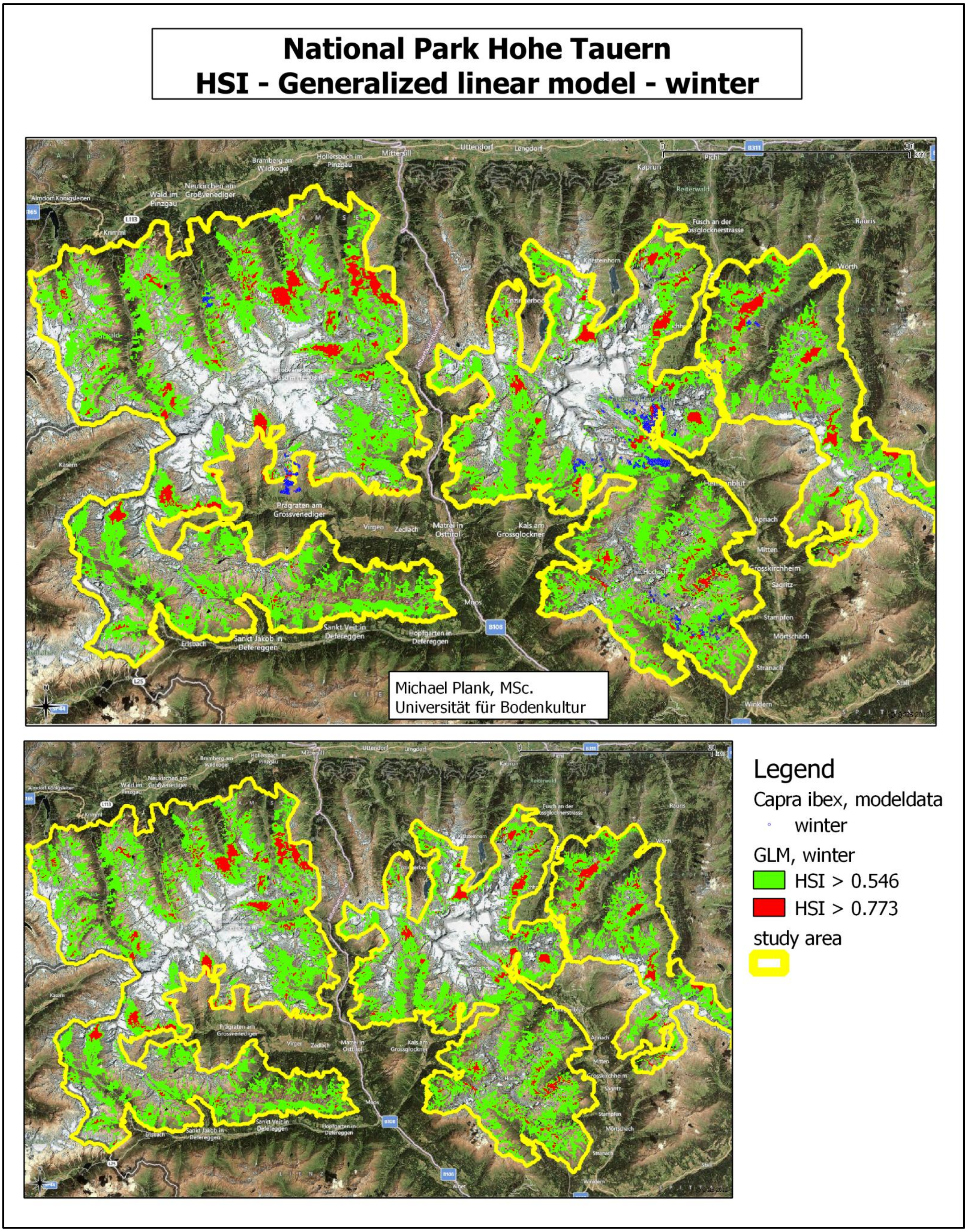
Appendix 5: Generalized liner model of the Swiss National Park in summer



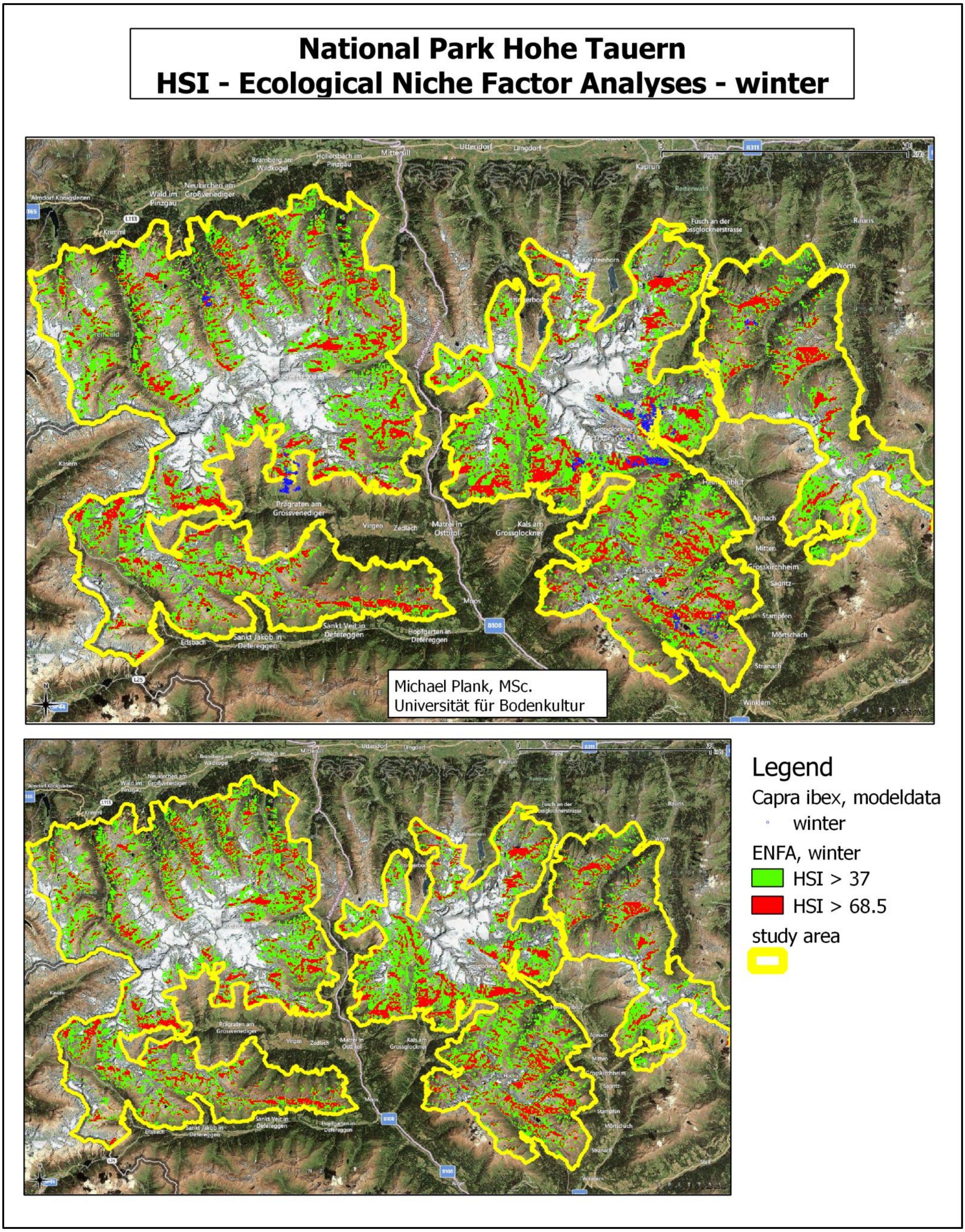
Appendix 6: ENFA model of the Swiss National Park in summer



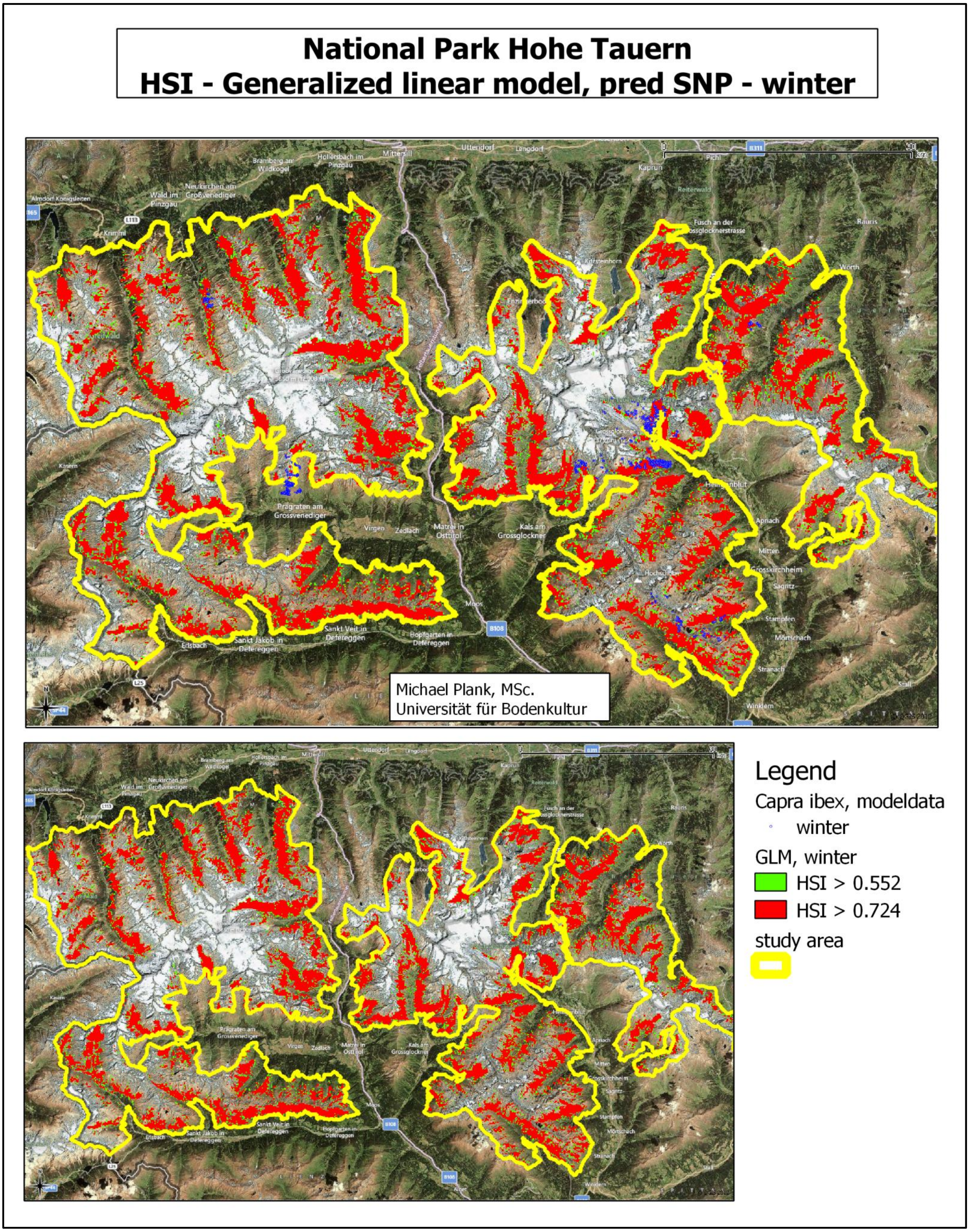
Appendix 7: Generalized liner model of the Hohe Tauern National Park in winter



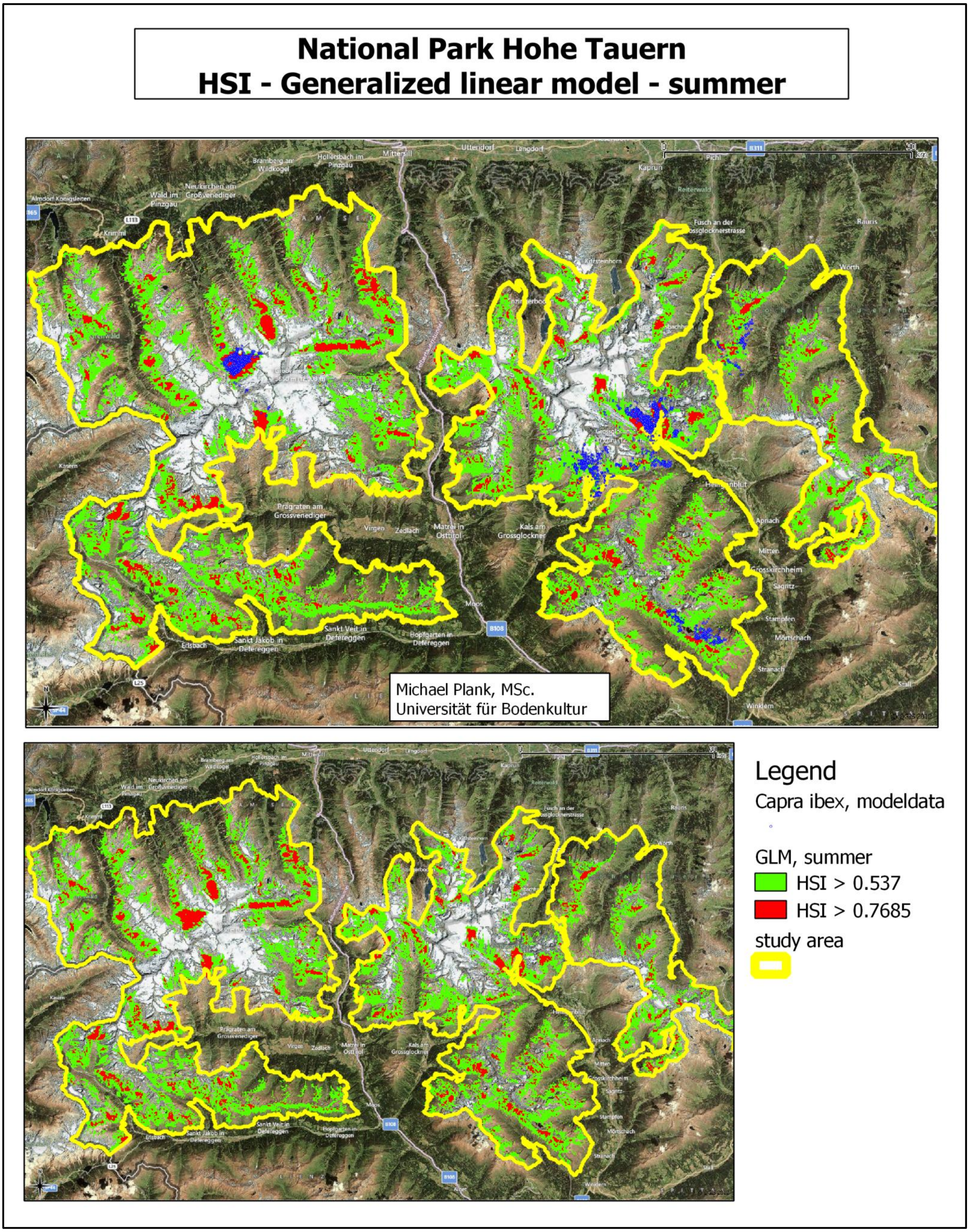
Appendix 8: ENFA model of the Hohe Tauern National Park in winter



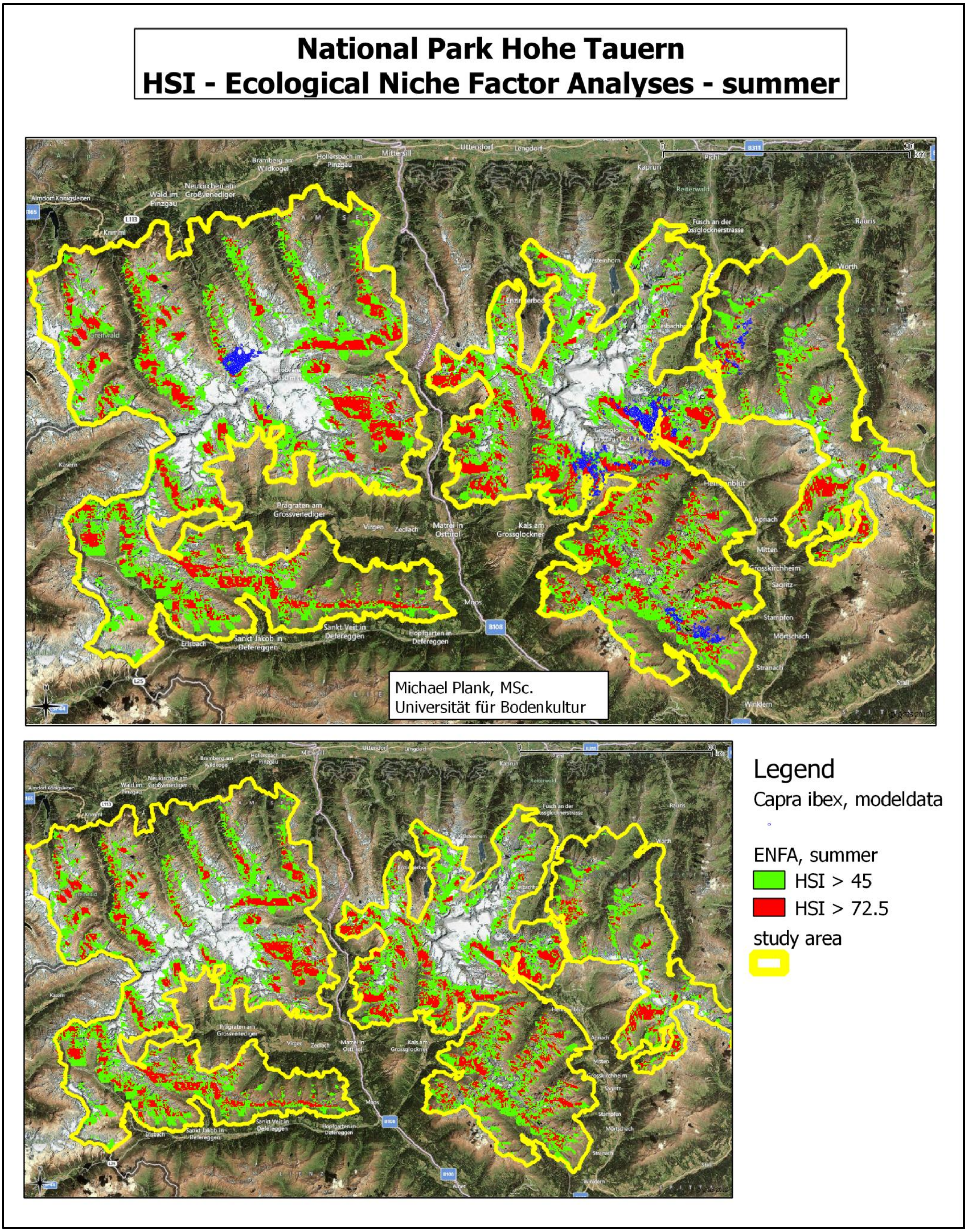
Appendix 9: Projected Generalized linear model from the Swiss National Park to the Hohe Tauern National Park in winter



Appendix 10: Generalized liner model of the Hohe Tauern National Park in summer



Appendix 11: ENFA model of the Hohe Tauern National Park in summer



Appendix 12: Projected Generalized linear model from the Swiss National Park to the Hohe Tauern National Park in summer