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Distribution of large carnivores (*Ursus arctos*, *Lynx lynx*, *Canis lupus*) in relation to spatial and temporal changes in forests: the case of Albania (Carnivora)

Výskyt velkých šelem, medvěda hnědého (*Ursus arctos*), rysa ostrovida (*Lynx lynx*) a vlka (*Canis lupus*), ve vztahu k prostorovým a časovým změnám lesů: případ Albanie (Carnivora)

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Abstract. Forests represent the main terrestrial habitat for the protection of endangered large carnivores in Europe. Spatial and temporal changes in the forests may critically influence the survival of large carnivore species. Aiming at modelling the distribution of the critically endangered species – Eurasian lynx (*Lynx lynx*) and the protected species – brown bear (*Ursus arctos*) and grey wolf (*Canis lupus*) in relation to the changes in forest cover in Albania, specifically, I (1) tested different hypotheses on the drivers of the probability of the species occurrence; (2) assessed potential changes in the probability of the species occurrence between 2001 and 2011 in relation to the forest cover change; and (3) analysed the probability of the species occurrence with respect to protected areas. Hypotheses based on natural habitat factors produced models with high prediction accuracy of above 76% for all large carnivore species, and the probability of their occurrence showed a negative relationship with forest cover change. The area with suitable habitat for at least one of the three large carnivore species made up 38% of the study area, and 11.7% of this area were protected.

Key words. Albania, Balkan lynx, brown bear, grey wolf, forest cover change; large carnivore species conservation, protected areas

INTRODUCTION

Wild brown bear, European lynx and grey wolf populations in forests are to be conserved in southern Europe. The distribution of a species population is a key element in determining its conservation status (IUCN 2001). To conserve bear, lynx and wolf populations, there is a need for evaluation of their distribution in relation to forests to be able to properly design forest management practices at a large scale.

Regions with high habitat heterogeneity are important targets for conservation as they host relatively high numbers of plant and animal species. For example, Estavillo et al. (2013) have shown that landscapes with forest cover above 30% show a peak of species richness, e.g., of small mammal species, and this 30% forest cover may be considered as a biodiversity threshold.

A conservation measure is the expansion of protected areas (Rodrigues et al. 2004) that can be especially effective when embedded within a regional approach (Iojă et al. 2010), for example by expanding cross-border (forested) protected areas for the conservation of large-bodied animal species.

Species distribution models (SDMs) use statistical techniques to relate species distribution data (occurrence or abundances at given locations) to the environmental and spatial characteristics of these locations (Elith & Leathwick 2009). SDMs results can bring insight into the main factors that determine the observed species distribution and the extrapolation of the statistical relationships provides predictions on the spatial variation of habitat suitability in the entire study area. The information obtained by SDMs can be especially useful to develop effective management actions for the species (Guisan & Zimmermann 2000). SDMs provide information on how animals or plants selectively use resources, as characterized by the main environmental factors identified by the model, and show how the habitats of large carnivore species change in space, which is essential for designing management strategies for wildlife and for natural resources such as forests.

In this study, I focused on three protected large carnivore species – the brown bear (*Ursus arctos arctos*), grey wolf (*Canis lupus lupus*) and Balkan lynx (*Lynx lynx balcanicus*) in Albania. Populations of the bear, lynx and wolf are protected by national law and the Bern Convention, and the lynx is considered a critically endangered large carnivore species. Yet, these large carnivore species populations have declined in Albania to the current numbers of approximately 180 to 200 bear individuals, 5 to 10 lynx individuals and 200 to 250 wolf individuals (Kaczensky et al. 2012a). Large carnivore species populations in Albania are important for the connection of populations in Europe or those in the Balkan Peninsula. The Balkan lynx (*Lynx lynx balcanicus*) is a critically endangered large carnivore (IUCN 2015a) and its occurrence is concentrated between Albania and North Macedonia. The bear populations in Albania are a part of a larger brown bear population ranging from Slovenia to Greece; wolf populations are spread all over the Balkan peninsula (Kaczensky et al. 2012a).

I estimated the probability of occurrence of bear, lynx and wolf in Albania to understand how these large carnivore species use forests, and how forest cover changes after 2000 (Hansen et al. 2013) may have affected the distribution of these species. I developed species distribution models based on hypotheses on the spatial scales where animals perceived their environment, and on hypotheses on the driving mechanism. The "natural conditions and resources" model hypothesized that natural factors drive the large carnivore species distribution, whereas the "human disturbance" model hypothesized that anthropological factors limited the large carnivore species distribution.

Specifically, I aimed to understand: (1) the factors that determine the probability of occurrence of the bear, lynx and wolf in Albania and (2) how forest cover changes after 2000 may have impacted the occurrence of the large carnivore species. Firstly, I used large carnivore species occurrence data from the year 2001 and forest and land use data from the year 2001 to determine the most parsimonious models for each large carnivore species. Secondly, I updated the most parsimonious models using the large carnivore species data from the year 2011 (Kaczensky et al. 2012a), forest data from the year 2010 (Broxton et al. 2014), and forest cover change data from 2000 to 2014 (Hansen et al. 2013). Forest cover change between 2000 and 2014 was used as an approximation of the changes in forests up to the year 2011. Finally, I analysed the maps with the estimated probability of the species occurrence with respect to protected areas identifying new areas for the conservation of bear, lynx and wolf in Albania.

MATERIAL AND METHODS

Study area

The study area covered the entire country of Albania. Albania is situated in the Mediterranean Sea basin, which is the biodiversity hotspot (Mittermeier et al. 2011, Noss et al. 2015) and a global priority for conservation (IUCN 2017). The study area is locally enriched by a high number of wild plants and trees (Sanctis et al. 2018). Albania and its neighbouring countries of North Macedonia, Montenegro and Greece have a comparable total number of threatened mammal species (Temple & Cuttelod 2009). Yet, there is a higher total number of threatened species of plants and trees in Albania than in North Macedonia and Montenegro (IUCN 2017).

Forests, farmland and pastureland are the main land use types in Albania. Forest habitat destruction between 2001 and 2011 was highlighted as the common major threat for the three large carnivore species (Kaczensky et al. 2012a) (see Appendix).

Large carnivore species data

The bear, wolf and lynx data from the year 2001 were collected within the EMERALD I and II projects (CE & MEFWA 2006), Lynx Survey Europe 2001 – Balkan population conducted by KORA (a non-governmental organisation based in Switzerland) (von Arx et al. 2004) and the International Union for Nature Conservation (IUCN), IUCN/SSC Cat Specialist Group (IUCN/SSC CSG 2012).

The lynx data were collected in 2001, aiming at the development of conservation plans in the particular European countries (von Arx et al. 2004), see Appendix. The data were based on: (1) sightings, signs, snow tracking, inquiry (hunters and foresters), dead lynx findings (von Arx et al. 2004) and (2) a questionnaire among local wildlife experts about the species distribution, legal situation, level of predation on livestock, major threats to the lynx population, conservation measures (protected areas), judgment of the lynx status, and further information on the status of the lynx (von Arx et al. 2004).

A grid cell of 10×10 km was used to prepare lynx distribution maps following the standards of the Species Information Services (SIS) (von Arx et al. 2004). The population density of the lynx in Albania was estimated to range between 0.65 and 1.09 individuals per 100 km^2 cells (see Appendix) and was categorized into two classes. First, areas with a 'single confirmed record' consisted of one or more direct observations, tracks or dead lynx findings in the latest year (von Arx et al. 2004). Here, the lynx population density was less than 0.65/100 km^2. Second, cells were classified as 'permanently occupied areas' if more than 50% of the cell was occupied by the lynx. Here, the lynx population density was estimated to be higher than 0.65 (von Arx et al. 2004). The overall lynx distribution area ('single confirmed record' and 'permanent occupied areas') was 3,800 km^2.

For the bear and wolf, the occurrence records for 2001 were compiled at a resolution of 10×10 km grid cells by local wildlife experts similarly to the lynx data (personal communication with the staff of Ministry of Environment in the year 2008) and provided by the EMERALD I and II projects (CE & MEFWAd 2006). Grid cells were classified either as 'temporary presence' or 'permanent presence'.

The species data on the bear, lynx and wolf as of 2011 were collected from an online publication prepared by IUCN/SSC Large Carnivore Initiative for Europe for the European Commission (Kaczensky et al. 2012a, b). The resulting species distribution maps with the resolution 10×10 km were composed of 'sporadic occurrence' and 'permanent presence' grid cells.

To take advantage of finer resolution environmental variables, I downscaled the coarse large carnivore species occurrence records to a finer scale. To this end, I placed a nested 1×1 km grid cell within the original 100 km^2 grid cell. Using the Spatial Join function of the Analysis Tool in ArcGIS, for each 100 km^2 grid cell with a large carnivore species presence I randomly assigned one 1 km^2 grid cell as presence (Fig. 1). The argument for this downscaling is that the large carnivore species may be present anywhere within a 100 km^2 grid cell.

Table 1. List of predictor variables (excluding neighbourhood variables) used for the spatial models. The resolution of the data is 1 km^2. Mean elevation was calculated from the original data of 15×15 m resolution; NC – natural conditions, HD – human disturbance

Tab. 1. Přehled ukazatelových proměnných (vyjma sousedských proměnných) použitých pro prostorové modely. Rozlišení údajů je 1 km^2. Průměrná nadmořská výška byla spočtena pro původní údaje v rozlišení 15×15 m; NC – přirozené podmínky, HD – narušení člověkem

variable proměnná	definition of the variable popis proměnné	models modely
	land cover 2001 / půdní pokryv 2001	
1	pure beech and beech mixed with coniferous forests / bučina čistá či smíšená s jehličnatým lesem (%, km^2)	NC
2	mixed broadleaved forests / smíšený listnatý les (%, km^2)	NC
3	coniferous forests / jehličnaté lesy (%, km^2)	NC
4	cultivated land / obdělávaná půda (%, km^2)	NC
5	Mediterranean macchia / středomořská makchie (%, km^2)	NC
6	bare rocks and soil / skaliska a obnažená půda (%, km^2)	NC
7	urban and industrial areas / sídla a průmyslová plocha (%, km^2)	NC
8	oak forests / dubové lesy (%, km^2)	NC
	land cover 2010 / půdní pokryv 2010	
9	deciduous broadleaved forest as a proxy of pure beech and beech mixed with coniferous forests of 2001 / opadavý listnatý les jako náhrada bučiny čisté či smíšené s jehličnatým lesem (km^2)	NC
10	mixed forests / smíšené lesy (km^2)	NC
11	evergreen coniferous forest as a proxy of coniferous forests of 2001 / vždyzelený jehličnatý les jako náhrada jehličnatých lesů 2001 (km^2)	NC
12	woody savannas used as a proxy of Mediterranean macchia of 2001 / lesní savana jako náhrada Středomořské makchie (km^2)	NC
	forest cover / lesní pokryv	
13	forest cover connectivity / spojitost lesního pokryvu (km^2)	NC
14	forest cover 2000 / lesní pokryv 2000 (%)	NC
15	scaled forest cover 2010 / škálovaný lesní pokryv 2010	NC
16	forest cover change 2000–2014 / změna lesního pokryvu 2000–2014 (%)	NC
17	forest cover loss 2000–2012 / ztráta lesního pokryvu 2000–2012 (%)	NC
18	forest cover gain 2000–2014 / nárůst lesního pokryvu 2000–2014 (%)	NC
	natural environment / přírodní prostředí	
19	elevation / nadmořská výška (m)	NC
20	Terrain ruggedness index / index členitosti krajiny	NC
	anthropogenic variables / anthropogenické proměnné	
21	distance to nearest asphalted road / vzdálenost od nejbližší silnice (m)	HD
22	distance to nearest well-kept road / vzdálenost od nejbližší udržované cesty (m)	HD
23	distance to nearest seasonal road / vzdálenost od nejbližší dočasné cesty (m)	HD
24	distance to nearest dwelling road / vzdálenost od nejbližší cesty v sídle (m)	HD
25	distance to nearest village / vzdálenost nejbližšího sídla (m)	HD
26	village density 2001 / hustota sídel 2001 (number / počet)	HD
27	population diffusion 2001 / rozptyl obyvatelstva 2001	HD

variable proměnná	definition of the variable popis proměnné	models modely
28	asphalt road density / hustota silnic (km)	HD
29	well-kept road density / hustota udržovaných cest (km)	HD
30	seasonal road density / hustota dočasných cest (km)	HD
31	dwelling road density / hustota cest v sídlech (km)	HD
32	road density / hustota cest (km)	HD

The large carnivore species occurrence records of 2001 consisted of 24 permanent occurrences for the lynx, 41 for the bear, and 93 for the wolf, and those of 2011 consisted of 12, 66, and 125 occurrences, respectively (Fig. 1). Although the 2011 lynx data represented only sporadic occurrences in Albania, I assumed 12 locations (red dots in Fig. 1) being permanent occurrences, because they were connected to permanent occurrences on the border with North Macedonia (Kaczensky et al. 2012a). I used permanent occurrences to estimate the probability of occurrence for the bear, lynx and wolf.

Forest and environmental variable derivation

For species distribution modelling, I compiled data on topography, land cover in 2001 and 2010, forest cover in 2000 and 2010, forest cover change to 2014, and proximity and density of human infrastructures such as villages or roads (Table 1).

For the year 2001, I used land use and land cover data from the Albanian National Forest Inventory (ASAC 2004a) that has an original resolution of 15 m. This data set was derived from satellite images of Landsat 5 TM and Landsat 7 ETM+ (see Appendix). The accuracy of the land use and land cover maps was 67% for thicket and shrub lands and 85% for broadleaved, coniferous and crown coverage (ASAC 2004b). From this dataset I extracted eight classes that were hypothesized to be important for the occurrence of three focal large carnivore species: (1) beech, (2) oak, (3) broadleaved deciduous forests, (4) coniferous forests, (5) cultivated areas, (6) Mediterranean shrub areas, (7) bare and rock areas, (8) urban and industrial areas. For technical details of land classification see Appendix.

For 2011, I obtained data on the cover of deciduous broadleaved forest, evergreen coniferous forest, and shrublands provided by Broxton et al. (2014), see Appendix. These data were derived from 10 years (2001–2010) of MODIS-based Global Land Cover Climatology (Collection 5.1 MCD12Q1) with a resolution of 245 m. For each 1 km^2 pixel I selected the corresponding land cover class with the highest overall confidence. To approximate forest cover change between 2001 and 2011, I used the data on percentage forest cover change between 2000 and 2014 with the resolution of approximately 900 m^2 provided by Hansen et al. (2013). Forest cover change was the sum of forest cover gain (positive sign) and forest cover loss (negative sign) and 'trees were defined as vegetation taller than 5 m height' (Hansen et al. 2013). Forest cover loss was defined as a change from forest to non-forest during 2000–2014, and forest cover gain as a change from non-forest to forest (Hansen et al. 2013).

I used AsterDEM, a product of METI and NASA (METI & NASA 2011) with a resolution of 15 m to derive elevation and a terrain ruggedness index at the resolution of 1 km^2 (Naves et al. 2003). The vector layers of roads and villages were provided by the Environmental Legislation and Planning Albania. Road types considered were asphalted, well-kept, seasonal and dwelling roads. I quantified the impact of human population and roads in two ways, as density and distance variables. The density variables are the densities of each road type and villages per 1 km^2 cell. The distance variables are the minimum Euclidean distances of the 1 km^2 cell to the nearest road type and village.

I used the data on nationally designated areas (administrative protected areas) from the European inventory for Albania for 2013 and data on (administrative) protected areas from 2006 that were received by the Institute for Nature Conservation Albania. These data included boundaries of six protected area categories (strictly protected areas, national parks, natural monuments, habitat or species management areas, protected landscapes, protected areas with sustainable use of natural resources of International Union for Conservation of Nature (IUCN 2015b). All variables were transformed to a resolution of a 1 km^2 grid and calculated using the extensions available in ArcGIS 9.3 and ArcGIS 10.3 (ESRI, Redlands, California USA). For a list of variables used in the analysis see Appendix.

Forest neighbourhood variables

Species respond to habitat heterogeneity at multiple spatial scales (Morris 1987, Orians & Wittenberger 1991, Wiens 1976, 1989). The spatial scales are related to the perception of environment, e.g. forests, by large carnivore species individuals and the scale at which forest resources must be available. Yet, forest and environmental variables are not necessarily related to the spatial scales at which large carnivore species perceive the landscape in this study and at which a natural resources must be available. I therefore transformed the environmental variables into a set of neighbourhood variables (Naves et al. 2003, Schadt et al. 2002, Wiegand et al. 2008) defined as the mean value of the original variable within a specified neighbourhood radius around the target cell. I used five different radii (3, 4, 5, 10, and 15 km) representing areas of 28.3 km², 50.2 km², 78.5 km², 314 km², and 706.5 km², respectively for the lynx and 7 radii (3, 4, 5, 10, 15, 20 and 25 km) representing areas of 28.3 km², 50.2 km², 78.5 km², 314 km², 706.5 km², 1256 km², and 1962.5 km², respectively for the bear and wolf (a radius of 1 km representing an area of 3.14 km^2 was also used for the three large carnivore species).

Model types and forest cover change

I developed two sets of large carnivore species distribution models, one based on the permanent occurrence data collected in 2001 and land cover data for 2001, and one based on occurrence data of 2011 together with 2010, land use and forest cover data and data on forest cover change after 2000. The latter helped to assess the potential impact of land cover change on the probability of large carnivore species occurrence. The period after 2000 is the second decade after the political change from the socialist regime to a market based economy in 1990 that induced important changes in the quality and use of land and forests. I therefore expect that the changes in forest cover after 2000 would have impacts on the distribution of three large carnivore species in 2011.

Model selection and mapping

Species distribution models (SDMs) are increasingly used to quantify the relationships between species occurrence and the environment (Guisan & Zimmermann 2000, Guisan & Thuiller 2005, Guisan et al. 2013). SDMs provide information on how animals or plants selectively use natural resources, which are then incorporated as the main environmental factors into species models.

I developed large carnivore species models based on an information-theoretic approach, which focused on the search for a parsimonious model as the primary philosophy of statistical inference (Burnham & Anderson 2002, Fernández et al. 2006). *A priori* hypotheses were identified on groups of variables driving the occurrences of three large carnivore species based on environmental conditions and resources required for reproduction and survival (Table 2).

Following an approach developed for the bear in Spain, I developed “natural” and “human” models (Naves et al. 2003, Martin et al. 2012; Table 2). The “natural conditions and resources” hypothesis included variables describing topography (i.e. elevation and terrain ruggedness index), forest cover and environmental variables. The latter were related with food abundance of the large carnivore species, with the degree of connectivity of forest, and forest cover change after 2000 (Table 2). The “human disturbance” hypothesis assumed that the absence of human activity would increase the probability of large carnivore species occurrence (Table 2).

Table 2. Model hypotheses based on the literature data on bear, lynx, and wolf biology
Tab. 2. Modelové hypothesy založené na znalosti biologie medvěda, rysa a vlka z literatury

hypothesis hypothesa	description popis	references and other sources literatura a další zdroje
natural conditions	large carnivores require dense, high, stable and undisturbed forests and high elevation to hide, breed and search for food. The bear relies on oak and beech forests for food, and the lynx on bare rocks for breeding.	BLSG (2008), Fernández et al. (2006), Fernández et al. (2003), May et al. (2008), Naves et al. (2003), Signer et al. (2019), Wiegand et al. (2008)
přirozené podmínky	velké šelmy potřebují husté, vysoké a nenarušené lesy a vysokou nadmořskou výšku pro úkryt, rozmnožování a lov potravy, medvěd je závislý na dubinách a bučinách, rys na skalách k rozmnožování.	
human disturbance	large carnivores stay away from human settlements, roads, and areas with low forest cover, because they cause higher mortality, higher disturbance and lower habitat quality for breeding, refuge and food	Grilo et al. (2019), Kramer-Schadt et al. (2005), Naves et al. (2003), Ordiz et al. (2013), Zimmermann et al. (2014)
narušení člověkem	velké šelmy se straní lidských sídel, cest a území s malým pokrytím lesy, neboť zvyšují úmrtnost, rušení a snižují biotopovou kvalitu pro úkryt, rozmnožování a lov potravy	

I randomly selected coordinates of pseudo-absence locations from the entire study area using Hawth's Tools (www.spatialecology.com) extension in ArcGIS 9.3 that satisfied three conditions: (1) the number of pseudo-absences of a large carnivore species was the same as the number of permanent occurrences, (2) not more than one pseudo-absence location was selected for a given grid cell, and (3) pseudo-absences were located in forest areas and preferably within the large carnivore species-specific habitats, because generating pseudo-absences further away from the optimum established by the occurrence data may increase over-prediction of the model (Chefaoui & Lobo 2008, Kanagaraj et al. 2011).

Prior to regression analysis, I excluded all independent variables that did not show significant differences between occurrence and pseudo-absence locations (Kruskal-Wallis test; $p>0.05$; see Appendix). I also removed explanatory variables that were highly correlated (Pearson correlation test; $r>0.7$). I checked the spatial autocorrelation of the dependent variables using the software Geoda095i (https://geodacenter.asu.edu) for the spatial dependency (similarity between occurrence record data of large carnivore species; see Appendix).

I used generalized linear models (GLM) with logit-link to relate the occurrence and pseudo-absence data to sets of landscape-scale explanatory variables to predict the probability of occurrence of a given large carnivore species. GLMs are an extension of classic linear regression models (McCullagh & Nelder 1989). I used binomial error structure (logistic regression) for the data. A logistic regression model predicts the probability of occurrence of a given large carnivore species at a given location within the study area. All logistic regression models were fitted with the program R 2.9.0 (R DCT 2009).

For 2001, I fitted in total 44 candidate GLM models that resulted from combining the two hypotheses ("natural conditions and resources" and "human disturbance" hypotheses; Table 2) with six neighbourhood scales for the lynx and eight neighbourhood scales for the bear and wolf. I selected the most parsimonious

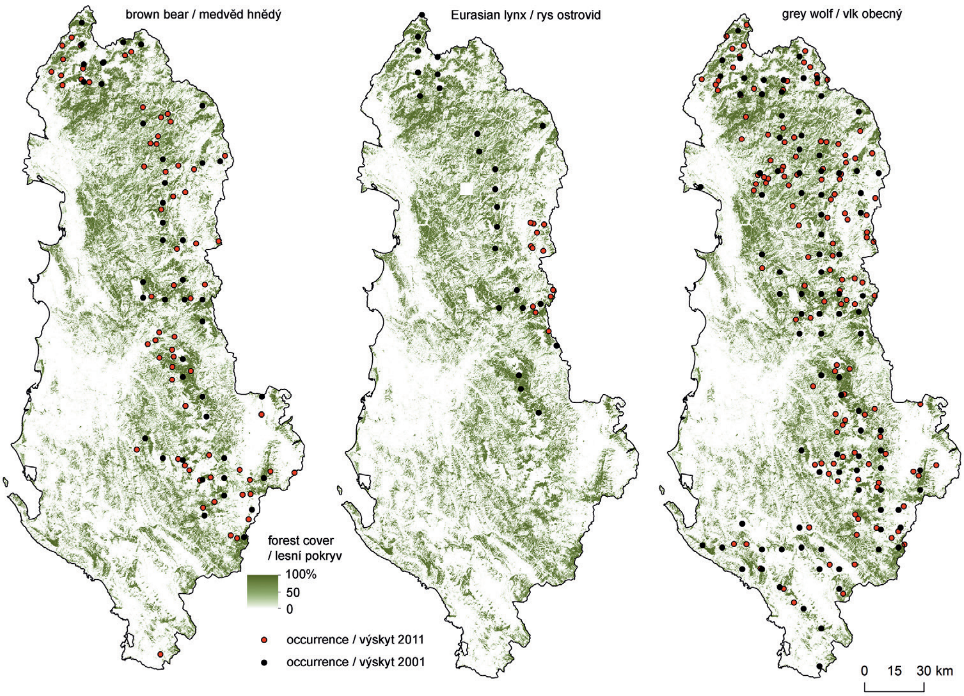

Fig. 1. Permanent occurrence of the bear, lynx, and wolf in Albania. The data for 2001 were collected by KORA for the Eurasian Lynx Online Information System for Europe (von Arx et al. 2004), for 2011 were available from the Kaczensky et al. (2012a). Percentage forest cover for 2000 was provided by Hansen et al. (2013).
Obr. 1. Stálý výskyt medvěda, rysa a vlky v Albánii. Údaje z roku 2001 byly shromážděny projektem "KORA for Eurasian Lynx Online Information System for Europe" (von Arx et al. 2004), z roku 2011 Kaczenskym et al. (2012a). Procenta lesního pokryvu vůči roku 2000 byla poskytnuta Hansenem et al. (2013).

model for each large carnivore species among the 12 (for lynx) or 16 alternative models (for bear/wolf) using AIC (Akaike Information Criterion). Then, I estimated Akaike weights (w_i) (e.g., Fernández et al. 2006) that represent the relative likelihood of a model among all candidate models (see Appendix).

In a next step, I used the neighbourhood scale and the set of variables of the most parsimonious models, but used land and forest variables from the year 2010 and large carnivore species data from 2011 to rerun the model. In this step, I considered two model variants: one with and one without forest cover change variables.

I mapped the predictions of the selected models to identify areas with high probability values (suitable habitat) and with low probability values (marginal and non-suitable habitat). I defined unsuitable habitat to have probability values between 0.25 and 0.5, and identified a threshold *H* that separates marginal and suitable habitat. I calculated the average value for all cells located in areas predicted to be suitable (i.e. a value >0.5) (e.g., Liu et al. 2005). The values of *H* were expected to be different for the bear, lynx and wolf. Areas with probability values above the threshold *H* were identified as a large carnivore species conservation area.

Model evaluation

All models were evaluated for discrimination success by calculating the area under a receiver operating characteristic curve (AUC). The value of the AUC ranges from zero to one. AUC=0.5 indicates a random prediction, AUC<0.7 is considered poor and AUC>0.8 indicates high model ability to discriminate between high probability of large carnivore species occurrences (occurrences) and low probability of large carnivore species occurrences (pseudo-absences in this study) (Hosmer & Lemeshow 2000). I also evaluated models using the True Skill Statistic (TSS), which is independent of prevalence (Allouche et al. 2006). TSS has values between 0 and 1, where between 0 and 0.4 is a poor prediction, between 0.4 and 0.5 is fair, between 0.5 and 0.7 is good, between 0.7 and 0.85 is very good, between 0.85 and 0.9 is excellent and between 0.9 and 1 is perfect (Nüchel et al. 2018). I ran Random Forests (RF) (Liaw & Wiener 2002) with the most parsimonious (GLM) models to calculate TSS. I used bootstrap test (10000× for a higher accuracy (Hesterberg 2015) and alpha level =0.05) for GLM models. I estimated the predictive accuracy of the most parsimonious models using the deviance explained in percentage (D^2) (this was also calculated by Random Forest) and assessed their predictive accuracy using a cross-validation approach. I calculated 100-fold cross-validation for logistic regression with a binary dependent variable (using species data from 2001) for every large carnivore species because I had one dataset for each species to check if there was over-fitting in the fitted models (Fernández et al. 2003, Kanagaraj et al. 2011). The dataset of a particular large carnivore species was divided into 100 parts (folds) where ninety folds were used for model fitting and the hundredth fold was used for testing the most parsimonious model. This was repeated 100×. Each fold was used for (most parsimonious) model testing.

RESULTS

I did not detect significant spatial autocorrelations at the model grain of 1 km for the occurrence of the three large carnivore species in 2001 (i.e. autocorrelation values were <0.007 in absolute terms). For the three species, the models based on the “natural conditions and resources” hypothesis were selected as the most parsimonious model (hereafter ‘final model’). I obtained neighbourhood radii of 15 km for the bear, 3 km for the lynx and 1 km for the wolf (Table 3). The final models showed the highest accuracy for the lynx (AUC=0.95; TSS=0.80; RF TSS=0.80), followed by the bear (AUC=0.82; TSS=0.62; RF TSS=0.62) and the wolf (AUC=0.76; TSS=0.52; RF TSS=0.52). Overall, all models for the bear and lynx performed better than the models for the wolf in terms of model selection estimator and accuracy (Table 3a).

Bear models

The final model was selected from the “natural conditions and resources” hypothesis and obtained an Akaike weight of 50.7% and an AUC value of 0.82. The most significant variables of this model were elevation and forest cover at the 15 km neighbourhood scale, both with positive coefficients. Thus, the bear habitat comprised high elevation areas with a high proportion of forests within the 15 km neighbourhood (mainly pure beech and mixed beach coniferous forests) (sign and magnitude of coefficients and *p*-values are shown in Table 3b). The “human disturbance” hypothesis produced a reasonable fit of the data (with AUC=0.77; TSS=0.50; RF TSS=0.25) and included proximity of dwelling roads and the proportion of cultivated land within 20 km as significant variables. Rerunning the final model with data from 2010/2011 produced a poorer model with forest cover gain being marginally significant (Table 4a).

Table 3a. The summary of final (most parsimonious or the first ranked) natural and human logistic regression models for the bear, lynx and wolf distribution and model selection estimator for 2001; AUC = area under curve, RF = Random Forests, TSS = True Skill Statistics, D^2 = Deviance Explained, CV = cross validation, AIC W_i = Akaike weight, AIC = Akaike's Information Criterion. The large carnivore final models (ranked 1) are mapped and shown in Figs. 2 and 3

Tab. 3a. Přehled konečných (nejvíce parsimoniální anebo první v pořadí) regresních modelů hypothesy přirozeného a narušeného rozšíření medvěda, rysa a vlka a modelu selekčního odhadu pro rok 2001; AUC = oblast pod křivkou, RF = náhodný les, TSS = výsledek methody "True Skill Statistics", D^2 = vysvětlení odchylky, CV = potvrzení křížem, AIC W_i = Akaikova váha, AIC = Akaikovo informašní kriterium. Výsledné modely výskytu velkých šelem (ohodnoceny 1) jsou vymapovány na obr. 2 a 3

species druh	rank okruh	model	radii průměry (km)	AUC	TSS	RF TSS	D^2	RF D^2	CV (%)	AIC w_i (%)	AIC
bear / medvěd	1	1	15	0.82	0.62	0.62	0.17	0.12	64.6	50.7	91.2
	5	2	20	0.77	0.50	0.25	0.02	0.15	64.6	p<0.001	106.3
lynx / rys	1	1	3	0.95	0.80	0.80	0.51	0.51	75.0	98.5	39.2
	8	2	5	0.90	0.60	0.80	0.28	0.38	79.2	p<0.001	48.5
wolf / vlk	1	1	1	0.76	0.52	0.52	0.10	0.17	66.0	87	224.2
	12	2	15	0.72	0.42	0.36	0.01	0.07	62.9	p<0.001	244.3

Lynx models

The final model was selected from the "natural conditions and resources" hypothesis with a 3 km neighbourhood (Table 3a). It yielded an Akaike weight of 98.5% and predicts that the lynx occurrence tends to increase with elevation and forest cover, but tends to decrease with the proportion of the Mediterranean macchia within 3 km (Table 3b). The "human disturbance" hypothesis produced a reasonable fit of the data (with AUC=0.90; TSS=0.60; RF TSS=0.80) and was negatively related to the proximity of dwelling roads and proportion of cultivated land within 3 km (Table 2). The response curves from GLM and RF models indicated that the increase of cultivated land negatively affected the estimated lynx occurrence (Fig. 3). Rerunning the final model with data from 2010/2011 produced a reasonable model with forest cover loss being negatively related to the lynx occurrence (Table 4b). However, because of the few the lynx occurrence data from 2011, the explanatory variables were not significant.

Wolf models

The final model for the wolf was selected from the "natural conditions and resources" hypothesis with an approximate 3.14 km² neighbourhood. It yielded an Akaike weight of 87%, but a relatively low predictive power with AUC=0.76. This model predicted that the wolf presence was positively related to elevation and coniferous forests (Table 3b). The "human disturbance" hypothesis produced a poorer fit of the data (with AUC=0.72; TSS=0.42; RF TSS=0.36) and was related to the proximity of the nearest asphalt roads and proportion of cultivated land within 15 km (Table 3b). Rerunning the final model with data from 2010/2011 showed that forest cover change did not enter the model (sign, magnitude of coefficients and *p*-values are shown in Table 4b).

Table 3b. The summary of final (most parsimonious or the first ranked, see Table 3a) natural and human logistic regression models for the bear, lynx and wolf distribution. For explanation of variables see Table 1

Tab. 3b. Přehled konečných (nejvíce parsimoniální anebo první v pořadí, viz tab. 3a) regresních modelů hypothesy přirozeného a narušeného rozšíření medvěda, rysa a vlka. Vysvětlivky proměnných viz tab. 1

species druh	variables proměnné	coefficient koeficient	SE of coefficient SE koeficientu	*p-value* hodnota *p*	bootstrap *p-value* hodnota *p*	bootstrap CI α=0.05
bear / medvěd	19	0.001	0.0006	0.004	0.004	0.002
	14	–0.010	0.010	0.320	0.700	0.020
	1F	0.230	0.550	0.660	0.030	1.840
	14F	0.130	0.040	0.010	0.620	0.040
	intercept	–4.120	1.150	p<0.001	0.001	–0.880
	21	0.0001	0.00009	0.180	0.180	p<0.001
	24	0.0002	0.0001	0.030	0.060	p<0.001
	4F	0.820	0.580	0.150	0.140	1.850
	intercept	–2.530	1.040	0.010	0.010	–0.370
lynx / rys	19	0.001	0.001	0.090	0.050	0.003
	20	0.120	0.090	0.150	0.190	0.300
	14	0.040	0.020	0.030	0.400	0.020
	5F	–0.880	0.460	0.050	0.010	0.090
	2	0.008	0.010	0.580	0.010	–0.100
	6F	1.360	0.900	0.130	0.130	3.250
	intercept	–8.740	3.440	0.010	0.005	–2.640
	25	0.0004	0.0004	0.300	0.500	0.001
	24	0.0004	0.0002	0.060	0.020	p<0.001
	4	–0.007	0.020	0.710	0.420	0.006
	4F	–0.730	0.390	0.060	0.020	–0.020
	intercept	–1.460	0.950	0.120	0.150	0.380
wolf / vlk	19	0.001	0.0003	p<0.001	p<0.001	0.002
	14	–0.002	0.007	0.770	0.770	0.010
	3	0.010	0.009	0.030	0.020	0.030
	2	0.008	0.006	0.170	0.160	0.020
	intercept	–1.650	0.360	p<0.001	p<0.001	–0.990
	25	0.00005	0.0001	0.740	0.730	p<0.001
	24	0.00009	0.0001	0.370	0.370	p<0.001
	23	0.00001	0.0001	0.930	0.930	p<0.001
	21	0.0001	0.00007	0.040	0.040	p<0.001
	4	–0.001	0.006	0.100	0.060	p<0.001
	31	–0.110	0.750	0.870	0.860	1.200
	28	0.210	0.420	0.600	0.590	1.020
	27F	–0.0006	0.0005	0.260	0.210	p<0.001
	4F	0.630	0.350	0.070	0.090	1.370
	intercept	–1.490	0.810	0.060	0.070	0.130

Table 4a. The summary of the final (most parsimonious or the first ranked) natural logistic regression models with forest cover gain and forest cover loss for the bear, lynx and wolf distribution and model selection estimator for 2010/2011; for explanations see Table 3a
Tab. 4a. Přehled konečných (nejvíce parsimoniální anebo první v pořadí) regresních modelů hypothesy přirozeného lesního pokryvu a ztráty lesního pokryvu pro rozšíření medvěda, rysa a vlka a modelu selekčního odhadu pro roky 2010/2011; vysvětlivky viz tab. 3a

species druh	rank okruh	model	radii průměry (km)	AUC	TSS	RF TSS	D^2	RF D^2	CV (%)	AIC w_i (%)	AIC
bear	1	with 16	15	0.67	0.30	0.61	0.01	0.04	57.6	90.2	174.4
/ medvěd	2	without 16	15	0.63	0.38	0.38	–0.01	0.05	54.5	0.98	178.9
lynx	1	with 16	3	0.95	1.00	1.00	0.50	0.60	95.8	98.5	20.7
/ rys	2	without 16	3	0.87	1.00	1.00	0.25	0.47	87.5	1.5	25.9
wolf	1	with 16	1	0.64	0.52	0.40	–0.006	0.07	58.4	27.0	338.9
/ vlk	2	without 16	1	0.64	0.36	0.40	0.001	0.06	58.8	73.0	336.8

Identifying priority areas for conservation

The final models for three large carnivore species with data from 2001 were applied on 28,381 km² of the study area to map the probability of large carnivore species occurrence (Fig. 2). The bear, lynx and wolf showed similar distribution patterns of suitable areas in Albania. The thresholds *H* that separate marginal from suitable habitat were 0.79 for the bear, 0.75 for the lynx and 0.72 for the wolf, and the percentage of the study area covered by suitable habitat was 28%, 25% and 6.5%, respectively (Fig. 2). When merging all cells with suitable habitat for any of the three species, I obtained an area of 38% of the study area for large carnivore species conservation (Fig. 2a). Then, I merged all cells with suitable habitat of the bear and wolf predicted by the models with data from 2010/2011 with $H>0.61$ for the bear and $H>0.58$ for wolf. I obtained a conservation area comprising 23% of the total study area (Fig. 2b).

The identified conservation areas are located in the cross-border area between (1) Albania and North Macedonia for the three large carnivore species, (2) Albania, Montenegro, and Kosovo for the bear and wolf, and (3) Albania and Greece for the wolf. It is very likely that the bear, lynx and wolf can pass country borders through conservation areas. These areas can ensure a potential connectivity of large carnivore species populations across country borders shown in Fig. 2. I found that 11.7% and 12.7% of the conservation areas of large carnivore species were protected in 2001 and 2011, respectively. For the model predictions of 2001, the percentage of suitable habitat within protected areas was 3.5% for the bear, 1.2% for the lynx and 3.2% for the wolf. For the year 2011, the percentage of suitable habitat within protected areas decreased (below 3%) for the bear, lynx and wolf (Fig. 4).

DISCUSSION

In this study, I combined coarse-scale data from species distribution maps provided for three large carnivore species, brown bear, Eurasian lynx and grey wolf in Albania, with data on forest cover, forest cover change, land use, and human infrastructures to gain insight into the main

Table 4b. The summary of the final (most parsimonious or the first ranked, see Table 4a) natural logistic regression models with forest cover gain and forest cover loss for the bear, lynx and wolf distribution for 2010/2011; for explanations see Table 1
Tab. 4b. Přehled konečných (nejvíce parsimoniální anebo první v pořadí, viz tab. 4a) regresních modelů hypothesy přirozeného lesního pokryvu a ztráty lesního pokryvu pro rozšíření medvěda, rysa a vlka a modelu selekčního odhadu pro roky 2010/2011; vysvětlivky viz tab. 1

species druh	variables proměnné	coefficient koeficient	SE of coefficient SE koeficientu	*p-value* hodnota *p*	bootstrap *p-value* hodnota *p*	bootstrap CI α=0.05
bear	19	0.0007	0.0004	0.080	0.070	0.001
/ medvěd	15	–0.700	0.400	0.080	0.060	0.020
	18	–44.500	23.40	0.050	0.020	–3.070
	intercept	–0.360	0.540	0.500	0.470	0.620
	19	0.0008	0.0004	0.050	0.040	0.001
	15	–0.680	0.400	0.080	0.070	0.050
	intercept	–0.650	0.520	0.210	0.200	0.340
lynx	2	–6.520	4.500	0.140	0.100	–2.150
/ rys	5F	–6.590	4.760	0.160	0.230	3.200
	17	–85.000	53.90	0.110	0.220	–24.700
	intercept	1.670	0.730	0.020	0.010	3.000
	2	–6.270	4.310	0.140	0.040	–2.330
	5F	–8.710	6.340	0.160	0.240	3.060
	intercept	0.960	0.550	0.080	0.030	1.920
wolf	19	0.0007	0.0003	0.010	0.009	0.001
/ vlk	15	0.130	0.320	0.680	0.670	0.730
	2	–1.620	0.620	0.009	0.008	–0.390
	17	–0.080	2.510	0.970	0.970	5.320
	intercept	–0.530	0.350	0.120	0.110	0.110
	19	0.0007	0.0003	0.010	0.007	0.001
	15	0.120	0.320	0.680	0.670	0.740
	2	–1.630	0.620	0.008	0.008	–0.380
	intercept	–0.530	0.350	0.120	0.110	0.140

factors that determine the distribution of the large carnivore species and to map the spatial variation of habitat suitability. I found that the "natural conditions and resources" hypothesis was favoured over the "human disturbance" hypothesis. This means that environmental conditions related to topography, food abundance and the degree of forest connectivity are more important in determining habitat suitability for the three large carnivore species than the negative effects of human activity. Areas with suitable habitat were mainly distributed in high elevation areas with rugged landscape and high forest cover (Fig. 2). However, descriptors of human activity such as the distance to the nearest dwelling road or proportion of cultivated land within a given neighbourhood yielded reasonable predictions of the bear and lynx occurrence and should therefore also play a role in constraining their distribution. Nevertheless, high elevation areas with rugged landscape and high forest cover tended to show lower human impact.

I estimated a neighbourhood where the large carnivore species may perceive their environment. For the bear I found a neighbourhood radius of 15 km, which coincides with the results

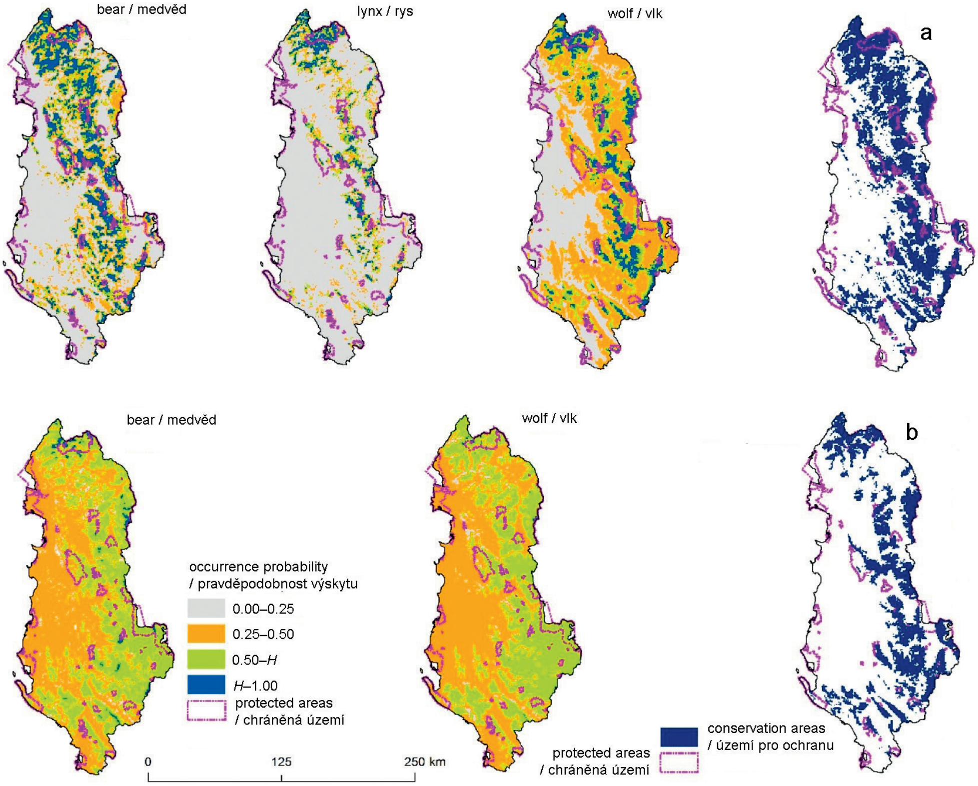

Fig. 2. Maps of estimated probability of occurrence of the bear, lynx and wolf in Albania based on the large carnivore GLM models (ranked 1) from Table 3. Maps of estimated probability of occurrence in 2001 for the bear, lynx and wolf and the conservation areas for the three species are in (a) (top-right). Maps of estimated probability of occurrence in 2011 for the bear and wolf and the conservation areas for the bear and wolf are in (b) (bottom-right). *H* is a threshold that separates marginal and suitable habitats for the large carnivores (Model selection and mapping). The lynx map of 2011 is in Fig. 3.
Obr. 2. Mapy odhadu pravděpopodobnosti výskytu medvěda, rysa a vlka v Albanii založeného na modelu GLM pro velké šelmy (ohodnoceném 1) v tab. 3. (a) mapy odhadu pravděpodobnosti výskytu medvěda, rysa a vlka v roce 2001 a chráněná území pro tři velké šelmy (nahoře vpravo). (b) mapy odhadu pravděpodobnosti výskytu v roce 2011 jsou pro medvěda a vlka a cráněná území pro medvěda a vlka (dole vpravo). *H* je hranice oddělující okrajové a vhodné biotopy pro velké šelmy ("Model selection and mapping"). Mapa výskytu rysa v roce 2011 je na obr. 3.

for the bear in northern Spain presented by Wiegand et al. (2008), for the lynx a neighbourhood radius of 3 km, which coincides with the results for the lynx published by Schadt et al. (2002) and for the wolf a neighbourhood radius of 1 km, which matches with the results for the wolf in the Iberian Peninsula presented by Grilo et al. (2019). The neighbourhood is of the order

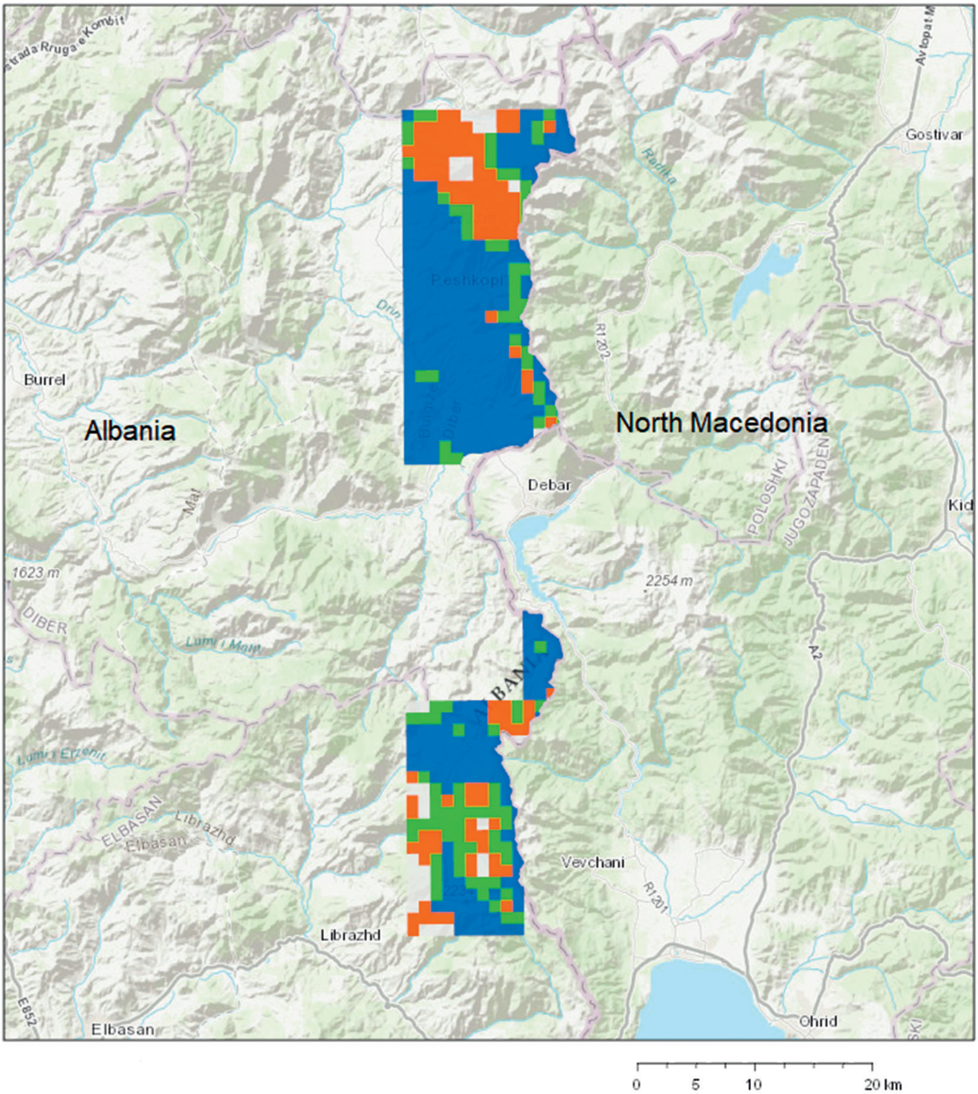

Fig. 3. The map of estimated probability of the lynx occurrence in 2011. The estimated probability between 0.50 and *H* (0.75) is in green colour and between *H* and 1.00 is in blue colour displayed in grid cells of 10×10 km. *H* is a threshold that separates marginal and suitable habitats for the lynx (Model selection and mapping).

Obr. 3. Mapy odhadu pravděpopodobnosti výskytu rysa v roce 2011. Odhadovaná pravděpodobnost mezi 0.50 a *H* (0.75) je zeleně, mezi *H* a 1.00 je modře v síti 10×10 km. *H* je hranice oddělující okrajové a vhodné biotopy pro rysa (“Model selection and mapping”).

of magnitude of female home ranges for the bear and lynx, and of refuge (and breeding) areas for wolf.

Forest-drivers of distribution

The bear tended to select areas with higher forest cover in the neighbourhood, the lynx selected areas with higher forest cover, and the wolf selected areas with broadleaved and coniferous forests. Forests determined the distribution of large carnivore species supporting the "natural conditions and resources" hypothesis. Previous studies have demonstrated the importance of forest cover (BLSG 2008, Martin et al. 2012, Müller et al. 2014) and of bare rock forests (Fernández et al. 2003, Signer et al. 2019) for the lynx, of forest cover for the bear and wolf (May et al. 2008, Martin et al. 2012). The results showed that forest cover and its changes influenced the occurrence of the bear and lynx.

The change in forest cover could likely affect the availability of forests for the three large carnivore species, forcing them to search for new areas for food. I found that the changes in forest cover after 2000 influenced the distribution of the bear, lynx and wolf. Areas with forest gain were potentially avoided by the bear whereas areas with forest loss tended to be avoided by the lynx and wolf. I note here that forest cover loss would mean the loss of dense forest cover, available food resources and refuge areas for the large carnivore species. Although forest cover gain would mean increased forest resources, young forests or low trees would be avoided by the bear because they are not dense enough and not attractive for the bear in terms of food and refuge availability. The bear behaviour against forest cover gain can be interpreted as 'a trade-off' between forest food and security (see Martin et al. 2012) (forest cover gain occurred near villages with a distance varying between 200 m and 3 km showing a strong inverse linear correlation with the distance to the nearest villages with a R^2 of 0.93%). The bear generally avoids people by changing its movement patterns after facing a (human) disturbance (Ordiz et al. 2013).

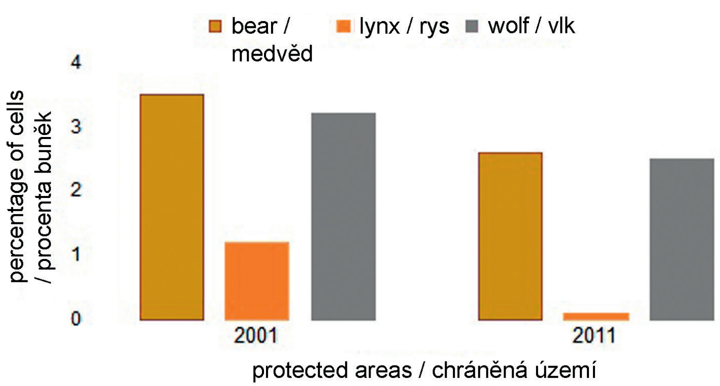

Fig. 4. The percentage of the study area with suitable habitats within protected areas for three large carnivores as predicted for 2001 and 2011.
Obr. 4. Procentuální zastoupení studovaného území s biotopy v chráněných územích vyhovujícími třem druhům velkých šelem jak předpovězeno pro roky 2001 a 2011.

The change of suitable habitat of the lynx could be linked with the loss of forests, of food and with the reduced lynx populations. The habitat suitable for the lynx in Albania as of 2011 was reduced compared to 2007. The suitable habitat was concentrated in the vicinity of the North Macedonian border where most of the vital lynx population is reproducing (BLSG 2008).

Forest and large carnivore data issues

I had to deal with differences in data collection for the large carnivore species, forest and land cover changes. To address these limitations, I used the most relevant data collected approximately in 2001 and 2011. The large carnivore species data were collected using the local ecological knowledge, which is yet important for species distribution modelling and conservation of poor data species (see Zhang & Vincent 2017). To increase data availability for predicting the occurrence and conservation areas of large carnivore species, there is a need for a frequent, seasonal and standardized monitoring of the species data and a regular collection of forest and land data in the future. A continuous monitoring of forest practices would be also beneficial to reveal a detailed response of large carnivore species to the changes in forest cover. This could help to better understand the complex relationship between forest cover changes and large carnivore species occurrence, and to reveal in details the complex interactions among large carnivore species that search for food and refuge in the same forested areas.

CONCLUSIONS

I conclude that a possible management option is to expand the already existing protected areas for the brown bear, grey wolf and Eurasian lynx conservation in the trans-boundary areas between Albania and North Macedonia, indicating that a regional approach may be required for conservation of the species (Iojă et al. 2010) and conservation of landscape connectivity at the regional and local scale (see Horváth et al. 2019). Another major conclusion is that the bear, lynx and wolf need a landscape-level protection of forests to meet their requirements for refuge, food and breeding. The importance of particular landscape and forest characteristics (e.g., tree height) is decisive not only for the large carnivore species, but also for a number of sympatric smaller carnivores and their coexistence (Soto & Palomares 2015). I highlight that the protection of large carnivores would mean maintaining the functioning ecosystem and protection of species associations that are possibly less resilient to environmental change (Smith et al. 2016) as well as to forests (Barnosky et al. 2016). Today, protection of the three large-bodied animals presents a unique opportunity for Albania and its neighbouring country of North Macedonia (see Kojola et al. 2018) in Europe. The results of this study highlight that large carnivore conservation requires the maintaining of the heterogeneous landscape of Albania through a strong cooperation between national and international organisations, which is ongoing now (Kaczensky et al. 2012a). I finally conclude that there is a need to regularly collect seasonal large carnivore species data and conduct an intensive research on forest habitats.

SOUHRN

Lesy představují hlavní suchozemský biotop pro ochranu ohrožených druhů velkých šelem v Evropě. Prostorové a časové změny v lesích mohou kriticky ovlivňovat přežívání a přežití velkých druhů šelem. Ve snaze modelovat rozšíření kriticky ohroženého druhu – rysa ostrovida (*Lynx lynx*) a chráněných druhů – medvěda hnědého (*Ursus arctos*) a vlka obecného (*Canis lupus*) – ve vztahu ke změnám v lesním

pokryvu v Albanii, jsem (1) testoval různé hypothesy ukazatelů pravděpodobnosti výskytu těchto tří druhů; (2) hodnotil potenciální změny ve výskytu velkých šelem mezi lety 2001 a 2011 ve vztahu ke změnám v lesním pokryvu, a (3) analysoval pravděpodobnost výskytu těchto druhů ve vztahu k míře ochrany území. Hypothesy založené na faktorech přírozeného prostředí produkovaly modely s vysokou přesností pravděpodobnosti (více než 76 %) pro všechny druhy velkých šelem a pravděpodobnost jejich výskytu vykazovala záporný vztah se změnou lesního pokryvu. Území s vhodnými biotopy pro alespoň jeden ze dří druhů velkých šelem tvořilo 38 % studovaného území (tj. výměry Alabanie) a 11.7 % tohoto území bylo chráněno.

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APPENDIX

Study area

Albania has an administrative area of 28,748 km² (including an island) with a human population of 3.1 million. Altitude varies from 0 to 2,751 m a. s. l. Climate is Mediterranean in the west and continental in the east of the country. Albania has approximately 21,096 km of well-kept and seasonal roads including asphalt and 2,884 villages with the average population of 591 inhabitants per village (mean±SD = 591±663.26). Human population is scattered in villages, rural areas and high elevation areas, which have experienced outmigration since the 1990s. Density of village roads (mean) is the highest in the west (0.37 km/km^2), south (0.13 km/km^2) and east (0.14 km/km^2) and lowest in the north (0.07 km/km^2). Coastal and flat areas in the west are urbanized and densely populated. Highland rural regions have lower accessibility to infrastructure compared to lowlands; they have a very low level of arable land allocation per capita that is considered as one of the main causes of poverty in rural areas.

The dense forests and woodlands (i.e. above 30%) covered 23% of Albania's land area in 2000 (Hansen et al. 2013). The changes in forest cover of 13.3% in absolute terms between 2001 and 2014 is composed of forest cover gain (+2.2%) and forest cover loss (–11.1%) (Hansen et al. 2013). On average, the annual forest loss was 7% between 2001 and 2014 with the largest forest loss of 16% in 2008 and of 17% in 2012; 'Forest Loss Year' was a disaggregation of the total 'Forest Loss' to annual time scales' (Hansen et al. 2013). In Albania, wood collection for firewood is still important in rural areas (Laze 2014) contributing to forest disturbance. Private forests, which are introduced after the collapse of socialist regime in 1990, occupy roughly 2% of the study area. The agricultural land was more extensive in the west (54.5%) and south (18.6%) compared to the north in 1991 and expanded more in the south (by 6% in 2001) after the collapse of socialist regime (ASAC 2004a).

After the breakdown of socialism, protected areas were named according to the International Union for Conservation of Nature (see IUCN 2015b), and these areas have increased in size and network. The protected areas covered 10.6% of the country and national parks constituted 35% of these protected areas in 2013.

Large carnivore data

Large carnivore species data were collected in Europe, but not in Albania before 1990. Lynx data collection started between 1990 and 1995 and then again in 2000. Within the Lynx Survey Europe 2001 – Balkan population, data were collected by the means of a 'standardised questionnaire' which was compiled by wildlife experts to update the status report for the years 1996–2001 and to compare (new) large carnivore species data with those collected by previous surveys conducted in 1990–1995 (von Arx et al. 2004). A wildlife expert having information about the lynx (between 1996 and 2001) was asked to fill in a questionnaire (von Arx et al. 2004) for Albania and to provide raster maps of the 10×10 km resolution. The questionnaire required information on lynx status, distribution and development of the lynx population(s) within Albania, legal situation, losses of lynx, predation on livestock, major threats to the population(s), conservation measures. Judgement of the population, threats, conservation measures, and criteria for the judgement were adopted from the IUCN Species Information Service (SIS), and the IUCN Red List (von Arx et al. 2004). Raster maps (grid cells) of the 10×10 km resolution were used to describe the distribution of lynx because they were found to (1) be very simple and straightforward, (2) give a coherent picture of the cross-border lynx populations, (3) allow for a minimum differentiation within the occupied area (by species) (von Arx et al. 2004). Raster maps can help to produce habitat maps and potential distribution maps using the Geographical Information System (GIS). A grid cell of 10×10 km that was more than 50% constantly occupied by the lynx was assigned as 'a constantly occupied area'. A grid cell of 10×10 km that was less than 50% sporadically occupied by lynx was assigned 'a sporadically occupied area' (von Arx et al. 2004).

Large carnivore species population was assessed following the standards of the Species Information Services (SIS) for all countries in Europe (von Arx et al. 2004) including Albania. The Albanian lynx population was up to 25 individuals, covering an area of distribution of 3800 km^2 in the year 2001 (von Arx et al. 2004). Raster maps (grid cells) of 10×10 km were used to describe the distribution of the bear and wolf in Albania in 2001.

Land cover variables

The Albanian National Forest Inventory (ASAC 2004a) was used as a source of the data on land use/land cover. Ten classes of land cover of the Albanian National Forestry Inventory, resolution of 15 m (ASAC 2004a) were used as follows: beech, oak, broadleaved deciduous forests, coniferous forests, cultivated areas, Mediterranean shrub areas, bare and rock areas, urban and industrial areas, aquatic vegetation and perennial waters (Table 1). Landsat 5 TM and Landsat 7 ETM+ images have been processed for photo--interpretation purposes using the Landsat 7 ETM+ images from October as the basis for interpretation. The Brovey fusion procedure was applied to combine False Colour Composite (FCC) band combination 453 multi-spectral imagery at 30 m resolution with panchromatic imagery at 15 m resolution; the panchromatic pixel resolution of 15 m and the spectral resolution of the multi-spectral bands of the FCC were obtained; validation included ground truth data (ASAC 2004a). Position accuracy for the 2000/2001 images was approximately less than 34.5 m on the ground and position accuracy for the 1991 images was 15.8 m on the ground (ASAC 2004a).

Mixed broadleaved and coniferous forests were mostly middle-aged coppice management type forests representing 19.4% of all Albanian forests, and natural forests were mostly middle-aged and old high forest management type representing 80.4% of all Albanian forests (ASAC 2004c). High forests are a mostly semi-natural and natural forest type composed of pure + mixed coniferous forests (24.8%), pure + mixed broadleaved forests (63.2%), mix of broadleaved and coniferous forests (12%). High forests of the age between 21 and 120 years covered 81.7% of the area of all high forests. Coppice management type forests were composed of pure and mixed broadleaved forests (95.8%), pure and mixed coniferous forests (4%). Coppice forests of the age between 11 and 30 years presented 59.4% of all coppice forests. Shrub forests (0.3% of all forests) of the relatively small age between 6 and 25 years were 78.4% of all shrub forests in Albania (ASAC 2004c).

Results of Kruskal-Wallis test

Variables of the bear that remained after the Kruskal-Wallis test were as follows: 13, 22, 21, 19, 4, 2, 6, 7, 28, 20, 27F3, 27F5, 27F10, 27F15, 27F25, 26F20, 1F3–25, 10F10, 10F15, 10F20, 10F25, 4F10–25, 5F3, 6F4–25, 6F3, 2F3–5, 11, 3F3, 3F4, 3F5, 14F1–25. Forest and land cover data of 2010 that passed the test with the bear occurrence record data of the year 2001 were 19, 15, and 1F15. Forest and land cover data of 2010 that passed the test with the bear occurrence record data of 2010 were 19, 15 and 18.

Variables of the lynx that passed the Kruskal-Wallis test, for the the lynx occurrence data of 2001, were as follows: 19, 1, 4, 2, 24, 23, 14, 20, 27F5, 27F3, 27F1, 26F20, 1F4, 1F5, 1F3, 1F10, 10F3, 10F4, 10F5, 10F10, 10F15, 4F3, 4F4, 4F5, 5F3, 5F4, 5F5, 6F3, 6F4, 6F5, 6F10, 6F15, 14F4, 14F5, 14F10, 14F15. Forest and land cover data of 2010 that passed the test with the lynx occurrence record data of 2001 were 19, 13, 5, and 6. Forest and land cover data of 2010 that passed the test with the lynx occurrence record data of 2011 were 2, 5 and 17.

For the wolf models, variables that passed the Kruskal-Wallis test are as follows: 14, 19, 20, 14F10, 14F15, 14F20, 14F25, 2, 3, 4, 21, 23, 25, 28, 31, 27, 4F15, 6F10, 6F25, 1F25, 1F15, and 1F20. Forest and land cover of 2010 that passed the test with the wolf occurrence record data of 2001 were 19, 20, 2, and 3. Forest and land cover of the year 2010 that passed the test with the wolf occurrence record data of 2011 were 19, 2, and 17.

Spatial autocorrelation of dependent variable

Spatial autocorrelation of dependent variables should be checked to decide whether to use samples or not; samples could be used to reduce the spatial autocorrelation of the dependent variable. The autocorrelation of a dependent variable jeopardizes the results (Naves et al. 2003), for this reason spatial it was checked using Geoda095i in this study.

The uncertainty of results

I selected the best approximating fitted model from the complete set of candidate models using Akaike Information Criterion (AIC). Then, I assessed uncertainty on this selection by weighting all AIC scores by the score of the best model (w_i) (Fernández et al. 2006). Akaike weight scores were above 0.05 thus these models were acceptable. Akaike weights scores for best approximating models were above 0.05 for the three large carnivore species occurrences. The values of Akaike weights and validation showed that pseudo-absence random selection did not significantly affect the model results.

Natural candidate GLM model

Natural model defined the requirements of large carnivore species concerning food, refuge and reproducs tion. I investigated whether the estimated probability of the species occurrence changed in time and space, and checked if the forest cover change and forest cover change neighbourhood were explanatory to the estimated probability of the species occurrence for refuge and food. The natural candidate model helped to define spatial requirements of large carnivore species concerning food and refuge. Elevation, forest cover and terrain index neighbourhood variable was included in this model. Elevation, terrain index and forest cover defined the presence of large carnivore species for food, refuge and breeding (Naves et al. 2003, Kramer-Schadt et al. 2005, Fernández et al. 2006, Nielsen et al. 2006, May et al. 2008). Predictor variables were as follows: beech forest connectivity, oak forest connectivity, coniferous forest connectivity, broadleaved forest connectivity, Mediterranean macchia shrub connectivity, forest cover change connectivity, forest cover change connectivity in percentage, forest connectivity percentage of beech, oak, Mediterranean macchia shrubs, coniferous, broadleaved. The assumption was that forests determined largely the presences of large carnivore species for food. Forest cover change connectivity could define the changes of the estimated probability of large carnivore species occurrences for food.

Similarly, forests were very important for providing a refuge to large carnivore species. Bare rock neighbourhood, forest connectivity, distance to nearest forest edge, forest cover change, forest cover change connectivity were included. Bare rock neighbourhood and forest cover connectivity variables indicated the refuge sites of the lynx and bear (Fernández et al. 2003, 2006, Kramer-Schadt et al. 2005).

Human candidate GLM model

Human explanatory variables were as follows: distance to nearest asphalt road, distance to nearest well-kept road, distance to nearest seasonal road, distance to nearest dwelling road, density of asphalt roads, density of well-kept roads, density of seasonal roads, density of dwelling roads, neighbourhood density of villages, cultivated land diffusion 2001, population diffusion 2001. I assumed that population and village locations disturbed the large carnivore species habitats. Roads were assumed to negatively affect large carnivore species presence (Naves et al. 2003, Zimmermann et al. 2014). Village roads were checked if they negatively affected large carnivore species presence.

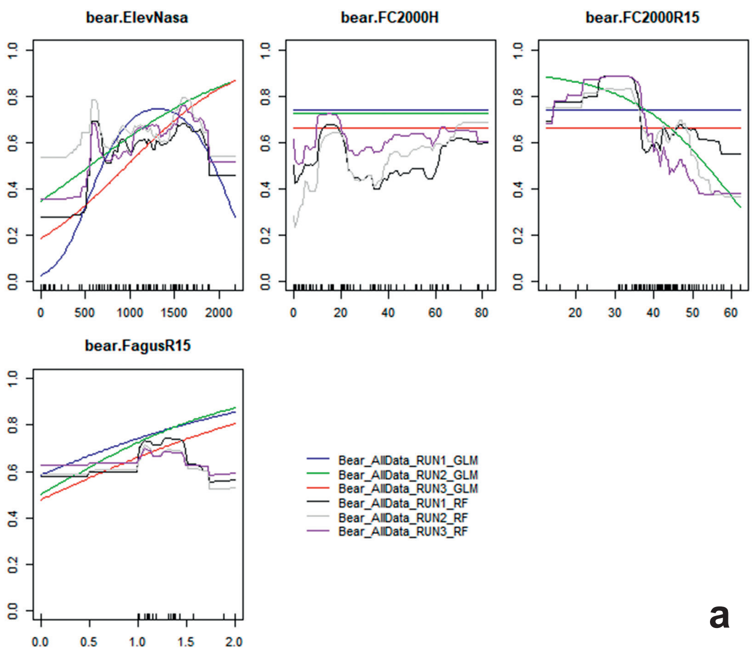
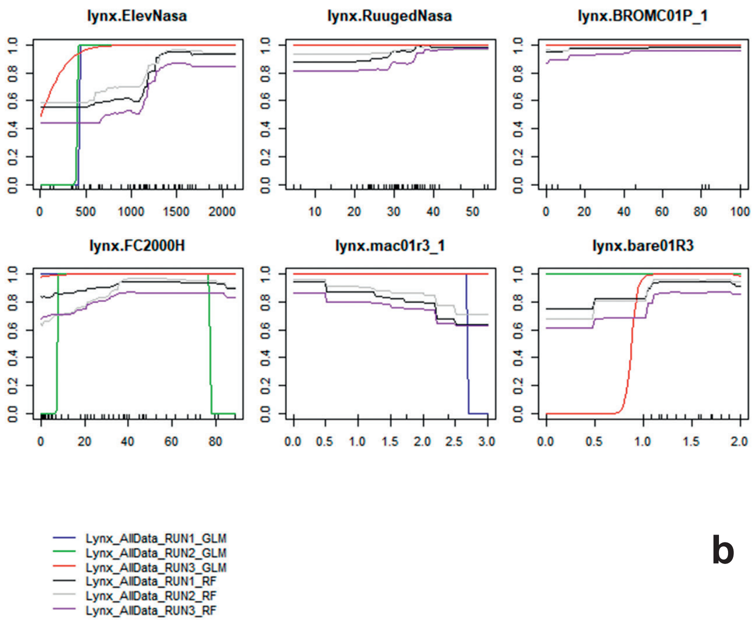
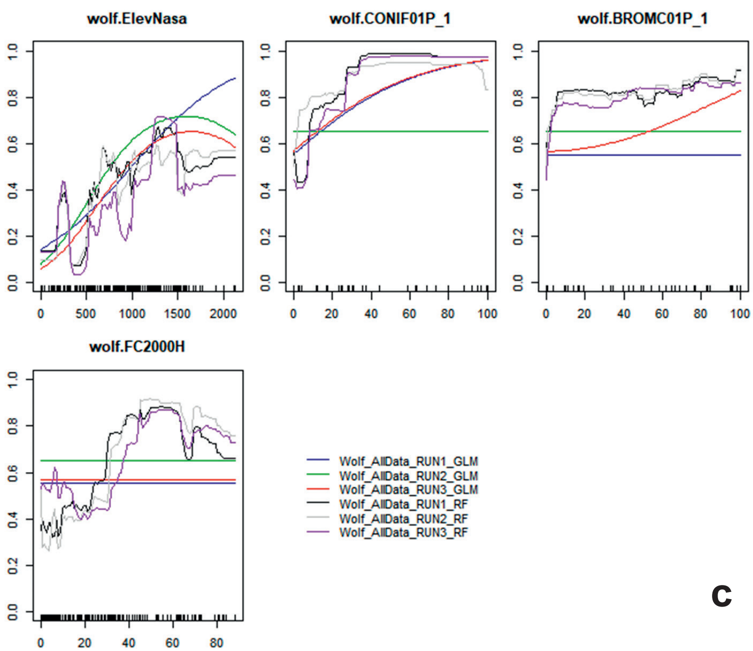


Fig. 5. Estimated response curves (logistic regression: probability presence) of GLM models for the first ranked one and RF models (RF TSS>0.50) for (a) bear, (b) lynx (c) wolf, (d) model ranked 8th for the lynx. Estimated response curves show how the logistic (regression) prediction changed. GLM and RF models are shown in Tables 3 and 4.
Obr. 5. Křivky odhadu odezvy (logistická regrese: pravděpodobnost přítomnosti) modelů GLM pro první v pořadí a pro modely RF (RF TSS>0.50) pro (a) medvěda, (b) rysa, (c) vlka, (d) model 8. v pořadí pro rysa. Křivky odhadu odezvy ukazují jak se logistická (regresní) předpověď změnila. Modely GLM a RF jsou ukázány v tab. 3 a 4.



b



c

Fig. 5. (continued).
Obr. 5. (pokračování).

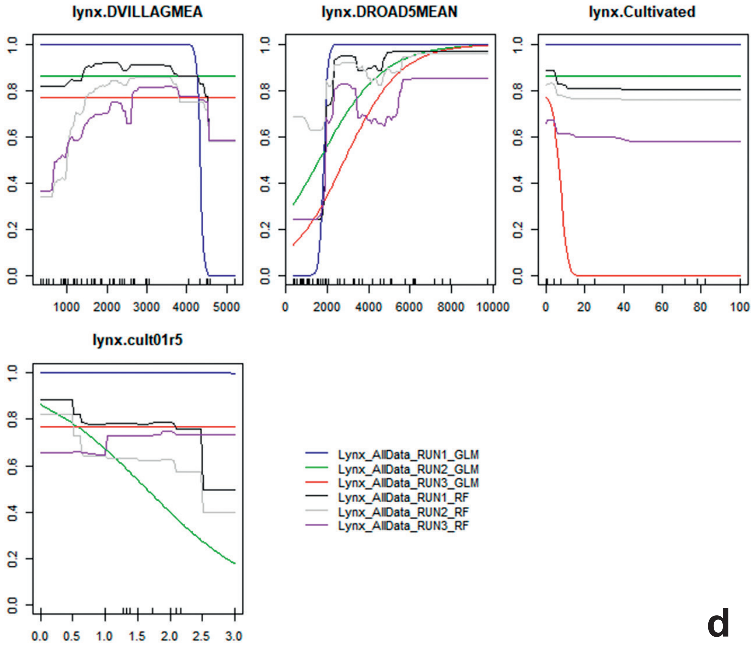


Fig. 5. (continued).
Obr. 5. (pokračování).