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European Bison habitat in the Carpathian Mountains

Tobias Kuemmerle [a,*], Kajetan Perzanowski [b,c], Oleh Chaskovskyy [d], Katarzyna Ostapowicz [e], Lubos Halada [f], Andriy-Taras Bashta [g], Ivan Kruhlov [h], Patrick Hostert [i], Donald M. Waller [j], Volker C. Radeloff [a]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA
[b] Chair of Applied Ecology, Catholic University of Lublin, Konstantynow 1H, 20-708 Lublin, Poland
[c] Museum and Institute of Zoology, Polish Academy of Sciences, Ogrodowa 10, 38-700 Ustrzyki Dolne, Poland
[d] Ukrainian National Forestry University, vul. Gen. Chuprynky, 103, 79031 Lviv, Ukraine
[e] Department of GIS, Cartography and Remote Sensing, Jagiellonian University, ul. Gronostajowa 7, 30-387 Kraków, Poland
[f] Institute of Landscape Ecology, Slovak Academy of Sciences, Branch Nitra, Akademicka 2, P.O. Box 23B, 949 01 Nitra, Slovakia
[g] Institute of Ecology of the Carpathians, National Academy of Sciences of Ukraine, Koselnytska St. 4, 79026 Lviv, Ukraine
[h] Geographical Faculty, Ivan Franko University of Lviv, vul. Doroshenka, 41, 79000 Lviv, Ukraine
[i] Department of Geography, Humboldt-University Berlin, Unter den Linden 6, 10099 Berlin, Germany
[j] Department of Botany, University of Wisconsin-Madison, 430 Lincoln Avenue, Madison, WI 53706, USA

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A B S T R A C T

European Bison (*Bison bonasus*) barely escaped extinction in the early 20th century and now only occur in small isolated herds scattered across Central and Eastern Europe. The species' survival in the wild depends on identifying suitable habitat for establishing bison metapopulations via reintroductions of new herds. We assessed European Bison habitat across the Carpathian Mountains, a stronghold of European Bison and one of the only places where a viable bison metapopulation may be possible. We used maximum entropy models to analyze herd range maps and habitat use data from radio-collared bison to identify key habitat variables and map European Bison habitat across the entire Carpathian ecoregion (210,000 km^2). Forest cover (primarily core and perforated forests) and variables linked to human disturbance best predict bison habitat suitability. Bison show no clear preference for particular forest types but prefer managed grasslands over fallow and abandoned fields. Several large, suitable, but currently unoccupied habitat patches exist, particularly in the eastern Carpathians. This available suitable habitat suggests that European Bison have an opportunity to establish a viable Carpathian metapopulation, especially if recent trends of declining human pressure and reforestation of abandoned farmland continue. Our results also confirm the suitability of a proposed Romanian reintroduction site. Establishing the first European Bison metapopulation would be a milestone in efforts to conserve this species in the wild and demonstrate a significant and hopeful step towards conserving large grazers and their ecological roles in human-dominated landscapes across the globe.

1. Introduction

Land use, particularly habitat loss, degradation, and fragmentation, is the primary driver of global biodiversity declines (Ceballos and Ehrlich, 2002; Fischer and Lindenmayer, 2007; Foley et al., 2005). Large carnivores and herbivores are particularly at risk as they require large tracts of intact habitat, often conflict with people and land use, and are susceptible to poaching (Enserink and Vogel, 2006; Gordon and Loison, 2009). As a consequence, many large mammals are now limited to small, clustered populations or have been extirpated. Large mammals, however, play key roles in ecosystem functioning, meaning their absence may trigger ecological meltdown (Dobson et al., 2006; Pringle et al., 2007). Ensuring the long-term persistence of large mammals and restoring their ecological roles are therefore top conservation priorities (Ceballos et al., 2005; Gordon and Loison, 2009; Vera et al., 2006).

The European Bison or wisent (*Bison bonasus*) is a prime example of a large herbivore that nearly became extinct due to habitat loss and overhunting (Krasinska and Krasinski, 2007; Pucek et al., 2004). Only two sub-populations survived by the early 20th century. The last wild bison was poached in 1927 and only 54 animals survived in zoos (Pucek et al., 2004). Thanks to a systematic breeding program, there are now about 3000 European Bison, 1600 of

* Corresponding author. Tel.: +1 608 261 1050; fax: +1 608 262 9922.
E-mail addresses: kummerle@wisc.edu (T. Kuemmerle), StacjaKarpacka@miiz.waw.pl (K. Perzanowski), oleh.chaskov@googlemail.com (O. Chaskovskyy), kostapowicz@gis.geo.uj.edu.pl (K. Ostapowicz), lubos.halada@savba.sk (L. Halada), atbashta@ukr.net (A.-T. Bashta), ikruhlov@gmail.com (I. Kruhlov), patrick.hostert@geo.hu-berlin.de (P. Hostert), dmwaller@wisc.edu (D.M. Waller), radeloff@wisc.edu (V.C. Radeloff).

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which occur in about 30 reintroduced herds throughout Eastern Europe (Daleszczyk and Bunevich, 2009; Krasinska and Krasinski, 2007; Pucek et al., 2004). The European Bison is the last surviving species of Europe's large grazers.

Despite this conservation success, Europe's largest terrestrial mammal remains at risk from extinction. The European Bison population has low genetic diversity due to its genetic bottleneck (only 12 founders), reducing reproduction rates and disease resistance (Olech and Perzanowski, 2002; Pucek et al., 2004). Thus, the effective bison population size (N_e) is far smaller than its census numbers. Moreover, most free-ranging bison herds remain small (<50 animals) and isolated. Minimum viable population size is estimated at ~1000 animals, much larger than any current herd (Perzanowski et al., 2004; Pucek et al., 2004). The challenge is thus to create viable bison metapopulations capable of ensuring genetic exchange among herds. Connecting herds will require both enlarging existing herds and additional reintroductions (Perzanowski et al., 2004; Pucek et al., 2004).

To accomplish this, we need a better understanding of existing suitable European Bison habitat and maps of where such habitat exists. Habitat preferences for a few herds have been studied in depth, primarily in the Polish and Belarusian Bialowieza forest (Krasinska et al., 1987, 2000; Krasinska and Krasinski, 2007). However, little is known about habitat selection in other bison herds or the species as a whole (Pucek et al., 2004). For example, although bison are generally considered a deciduous forest species preferring landscape mosaics, they also thrive both in coniferous forest (Krasinska et al., 2000; Pucek et al., 2004) and more open landscapes (Balciauskas, 1999). Moreover, most habitat studies to date were conducted at fine spatial scales in small areas (e.g., individual forest districts, Daleszczyk et al., 2007; Krasinska et al., 1987; Perzanowski et al., 2008). Broad-scale assessments are thus needed to guide conservation efforts.

The Carpathian Mountains in Central Europe have been a stronghold for reintroduced wild European Bison populations. Furthermore, human pressure has decreased considerably in the Carpathians after the breakdown of socialism, large farmland areas were abandoned (Kuemmerle et al., 2008; Turnock, 2002), and large carnivore and herbivore populations are increasing (Enserink and Vogel, 2006). This may offer opportunities to establish the first viable, free-ranging metapopulation of European Bison, which would be a milestone for conserving this species in the wild (Olech and Perzanowski, 2002; Perzanowski and Olech, 2007; Perzanowski et al., 2004).

An obstacle to achieving this optimistic scenario is our current lack of knowledge regarding bison habitat preferences and the availability of such suitable habitat in the Carpathians (Perzanowski et al., 2008; Pucek et al., 2004). Addressing this information gap was identified as a top research need in the species' conservation action plan (Pucek et al., 2004). One factor precluding an area-wide assessments of bison habitat in the Carpathians has been the lack of comprehensive bison presence/absence data, as required by traditional statistical habitat suitability models (Guisan and Zimmermann, 2000). Fortunately, recent approaches allow modeling habitat based on presence-only data, even when occurrence data are sparse (Elith et al., 2006; Wisz et al., 2008).

Our goal was to assess habitat suitability for Carpathian bison and to map potential European Bison habitat for the entire Carpathian ecoregion, thus assuming that the species currently does not realize its full potential distribution and that areas occupied by bison herds constitute suitable habitat. Our aim was not to quantify habitat connectivity or population viability. Specifically, we ask:

1. What determines suitable European Bison habitat in the Carpathians at the landscape scale?
2. What is the distribution of suitable European Bison habitat in the Carpathians?

2. The Carpathians

The Carpathians, Europe's largest mountain range, encompass an area of about 210,000 km^2 (~44.0–50.0N, 17.5–27.5E) in eight central European countries (Austria, Czech Republic, Poland, Slovakia, Hungary, Ukraine, Romania, and Serbia). Elevation ranges from 100 to 2665 m and topography is dominated by gentle slopes. Climate is temperate-continental with strong altitudinal gradients in mean annual temperature (9 °C in the plains to below 0 °C on mountain peaks) and precipitation (<500 mm to >2000 mm). Natural vegetation occurs in four altitudinal zones: foothills (<600 m) dominated by beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), and oaks (*Quercus* spp.), montane mixed forests with beech and fir (*Abies alba*) (600 to 1100 m in the north/1400 m in the south), subalpine coniferous forests (up to 1500 m/1800 m) with Norway spruce (*Picea abies*), pine (*Pinus cembra*), and alpine above treeline (UNEP, 2007; Webster et al., 2001).

The Carpathian region has exceptional conservation value. It harbors substantial old growth and semi-natural forests as well as valuable cultural landscapes, is rich in endemic biodiversity, and retains viable populations of all native large carnivores (brown bear, wolf, lynx, UNEP, 2007; Webster et al., 2001). The Carpathians are also one of the few places where European Bison roam freely. Six free-ranging bison herds currently exist: two in the Polish Bieszczady Mountains (western herd: about 150 animals, eastern herd: about 140 animals), one in northeast Slovakia (9 animals), and three herds in Ukraine (Skole District: 14 animals; Bukovina Mountains: two herds, together 80 animals). A seventh herd of 22 animals is being reintroduced in 2009/2010 in the Vanatori Neamt Nature Park in Romania.

Genetic diversity of the Carpathian bison population is low (e.g., 90% of the combined gene pool was provided by seven founders, Olech and Perzanowski, 2002; Perzanowski and Olech, 2007). The current effective population size also remains too small to ensure long-term viability. Moreover, the Ukrainian herds are isolated. Conservation of wild European Bison depends on substantially enlarging the Carpathian bison population as a whole and on establishing a free-ranging bison metapopulation (Perzanowski and Kozak, 2000; Perzanowski and Olech, 2007; Perzanowski et al., 2004). This goal, however, requires habitat maps across the Carpathians to identify suitable areas for reintroductions, range extension, and where we might best link existing herds. For our analyses, we adopted the ecoregion definition of the Carpathian Ecoregion Initiative (Webster et al., 2001), buffered by 30 km to include adjacent forests. We excluded the Serbian Carpathians as no bison exist there and the Danube River prevents dispersal.

3. Datasets used

3.1. Bison occurrence data

We used two types of European Bison occurrence data: (1) radio-telemetry points and GPS-locations of bison presence (direct observations, tracks, etc.) from the two Polish herds, and (2) range maps from all Carpathian herds. Telemetry data were collected from 2002 to 2006. Six bison were fitted with radio collars (one female, five males); positions were determined every 2–3 days using ground triangulation and a GPS. Records on bison presence have been collected weekly by State Forest and Polish Academy of Sciences staff since 2001. In total, 9922 bison locations were available within a minimum convex polygon of 1200 km^2.

Telemetry data were not available for the Slovak and Ukrainian herds. We instead acquired herd range maps for all Carpathian bison herds. These maps were digitized based on topographic maps (1:100,000) by local bison experts with detailed field knowledge about the specific herd. We cross-checked all herd range maps with recent high-resolution satellite images available in GoogleEarth to exclude all areas inaccessible to bison (e.g., settlements, water bodies, etc.). The herd range maps together covered an area of about 793 km^2.

3.2. Predictor variables

We derived fine-scale land cover maps for all six herds by classifying Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) satellite images (30-m resolution). Five Landsat footprints contained all six Carpathian bison herds plus the entire Ukrainian Carpathians not covered by the land cover map we used for the pan-Carpathian assessment (see below). We used two Landsat images (from 2000 to 2002) per footprint and Support Vector Machines (Huang et al., 2002; Kuemmerle et al., 2008) to classify nine land cover categories: 'coniferous forest', 'mixed forest', 'deciduous forest', 'unmanaged grasslands', 'managed grasslands', 'cropland', 'open settlements', 'dense settlements', and 'water bodies'. Unmanaged grasslands included permanent grasslands (e.g., riparian meadows, alpine grasslands, etc.), fallow farmland, and successional shrublands. A random sample of ground truth points ($\sim$2000 per footprint), collected from high-resolution images available in GoogleEarth, provided training and validation data. We used a minimum mapping unit of $\sim$0.3 ha and assessed the accuracy of the land cover maps using 10-fold cross-validation (Kuemmerle et al., 2009). All footprints had overall accuracies exceeding 90%.

To analyze the entire Carpathians, we used the CORINE 2000 land cover map (CLC2000, http://dataservice.eea.europa.eu). The CLC2000 has a grain of 100 m and a minimum mapping unit of 25 ha. As Ukraine is not covered by CLC2000, we resampled the fine-scale land cover maps to the spatial resolution of the CLC2000 map. The CLC2000 map does not include detailed information on grassland management and we therefore merged the two grassland classes (managed and unmanaged) of our fine-scale land cover maps into a single category. We also aggregated the CLC2000 class catalog encompassing 44 categories to match our eight land cover classes.

To assess forest fragmentation, we used morphological image segmentation (Vogt et al., 2007). Each forest pixel was categorized as either 'core forest' (no non-forest neighbors), 'edge forest' (at the outside of larger forest patches), 'perforated forest' (edges along openings inside larger forest patches), and 'islet forests' (patches too small to contain core forest, Vogt et al., 2007). To assess the effect of different edge definitions, we derived seven fragmentation maps using edge widths from 30 to 210 m, based on the fine-scale (30-m grain) land cover maps. For the CLC2000 map (100-m grain), we derived a fragmentation map with a 100-m edge width. We also calculated the Euclidian distance of each pixel to the closest forest pixel and to the closest core forest pixel at both scales.

We used the Shuttle Radar Topography Mission (SRTM) elevation model (http://srtm.csi.cgiar.org) to calculate slope (in degrees), aspect (the direction that a slope faces, measured in degrees), and ruggedness (Sappington et al., 2007) at 30-m and 100-m resolution. Two predictors measured human disturbance: (1) distance to roads and railways, and (2) distance to human settlements. We used official digital road data (1:50,000–1:200,000) for the Hungarian, Polish, Romanian, Slovak, and Ukrainian regions of our study area. For the Czech Republic and Austria, we used OpenStreetmap data (www.openstreetmap.org). We obtained railroad data for the entire study region from the Environmental Systems Research Institute (ESRI) Data and Maps Kit Europe 2008, allowing us to calculate the distance of each pixel to infrastructure (roads and railroads). We similarly calculated distances to the closest settlements based on the CLC2000 and digital topographic maps for Ukraine. A protected area layer was available from the Carpathian Environment Outlook database (UNEP, 2007).

4. Habitat mapping

4.1. Maximum entropy modeling

Maximum entropy modeling is a machine learning approach that has been adapted to model species distributions (Phillips et al., 2006). The assumption is that the true, but unknown distribution of a species is a probability distribution π over a set of locations X (i.e., all cells in the study area). This distribution π is approximated by deriving a probability distribution $\hat{\pi}$, that respects constraints inferred from environmental variables associated with the occurrence data. The maximum entropy principle (Jaynes, 1957) suggests that the distribution that approximates π best is the distribution $\hat{\pi}$ with maximum entropy, thereby ensuring that all available information is used while avoiding unjustified constraints on $\hat{\pi}$. To prevent overly complex models, regularization parameters are used (Phillips et al., 2006; Phillips and Dudik, 2008). Maximum entropy modeling is well-suited for mapping European Bison habitat in the Carpathians as it is relatively robust against false negatives. Such approaches are crucial for species occupying only a portion of their potential habitat (Engler et al., 2004). Moreover, maximum entropy models perform well with small sample sizes (Wisz et al., 2008), frequently outperforming traditional approaches (Elith et al., 2006).

To fit maximum entropy models, we used the software Maxent (version 3.3, http://www.cs.princeton.edu/~schapire/maxent/). For all model runs we used a maximum number of 2500 iterations, 10,000 random background points, and default regularization parameters (Phillips and Dudik, 2008). Model validation was based on the area under the curve (AUC) of the receiver operating characteristics (ROC) curve (Fielding and Bell, 1997; Phillips et al., 2006; Wiley et al., 2003). We carried out 999 bootstrap AUC calculations to estimate confidence intervals. Maxent calculates several measures of variable importance: (1) relative gain contribution per variable (a goodness-of-fit measure similar to deviance, Phillips et al. (2006)), (2) variable response curves for single-variable models, and (3) a jackknife procedure to assess AUC/gain changes when excluding a variable. We also tested whether our models performed better than a random model using a one-tailed binomial test of omission (Phillips et al., 2006). Habitat suitability maps were calculated by applying Maxent models to all cells in the study region, using a logistic link function to yield a habitat suitability index (HSI) between zero and one (Phillips and Dudik, 2008).

4.2. Habitat suitability analyses

To assess European Bison habitat suitability, we conducted several analyses based on the fine-scale (30-m grain) set of input variables, and a 32,100 km^2 test area (one Landsat footprint; path/row 186/26). First, we compared two Maxent models based on different types of occurrence data: 500 random locations within mapped herd ranges or 500 randomly selected radio-telemetry points. We calculated AUCs for both models using a fourfold cross-validated strategy and assessed the map agreement by calculating Pearson's correlation coefficient (based on a stratified random sample of 10,000 locations). Predictions based on telemetry and herd range points were quite similar (see Section 5) allowing us to parameter-

Table 1
Predictors used for assessing European Bison habitat suitability in the Carpathians.

Variable	Source	Type	Acronym
Land cover	FS[a]: derived from landsat TM/ETM images BS: CORINE land cover map + landsat images for Ukraine	Categorical	LC
Forest fragmentation	Mapped from land cover maps based on image morphological processing (Vogt et al., 2007) FS: edge width 1–7 pixels BS: edge width 1 pixel	Categorical	FF
Distance to core forest	Calculated from FM	Continuous	D2CF
Distance to forest	Calculated from LC	Continuous	D2F
Slope	Calculated from SRTM Digital Elevation Model (DEM)	Continuous	SLOPE
Aspect	Calculated from SRTM DEM	Continuous	ASPECT
Terrain ruggedness	Calculated from SRTM DEM (Sappington et al., 2007)	Continuous	TR
Distance to settlements	Based on LC and topographic maps for Ukraine	Continuous	D2SETT
Distance to roads and railways	Road layer from various sources (details see Section 3.2)	Continuous	D2R
Protected areas	Map of protected areas (UNEP, 2007)	Categorical	PA
Distance to protected areas	Calculated from PA	Continuous	D2PA

[a] FS: fine-scale analyses (30-m grain of, carried out for a test region) BS: broad-scale analyses (100-m grain, carried out for the entire ecoregion).

ize Maxent models based on range map points from all existing Carpathian bison herds. We then used the more detailed telemetry to validate these models. For model training, we generated a random sample of 200 points within each of the six Carpathian herd ranges (1200 points in total). For model validation, we randomly selected 250 telemetry points. We used a minimum distance of 500 m between points to minimize autocorrelation and pseudo-replication.

Pairwise collinearity in our eleven predictor variables (Table 1) was measured with Pearson's correlation coefficient based on 10,000 random samples. Collinearity does not affect Maxent performance, but can hinder model interpretation. Only two variables pairs were collinear ($r > 0.65$): slope versus ruggedness, and distance to forest (D2F) versus distance to core forest. As slope and D2F yielded higher model performance we dropped the other two variables. For the collinearity analyses, we used the land cover map with a single grassland class (eight land cover categories in total) and the forest fragmentation map with an edge width of 30 m. We did not use elevation as a predictor because bison herds occur elsewhere at lower and higher elevations than the altitudinal range of the Carpathians.

Maxent offers a variety of features to constrain the maximum entropy distribution (Phillips and Dudik, 2008). Initial tests suggested that models overfitted the data when complex feature types were used (based on a comparison of AUC, variable response curves, and the resulting habitat suitability maps) and we therefore used only linear, product, and quadratic feature types. We also tested seven models with different edge widths (from 30 to 210 m) and retained the model with the highest AUC. To test how post-socialist land use change affected European Bison habitat, we substituted the land cover map with a single grassland category with the one including managed and unmanaged grassland categories. Finally, we assessed how protected areas influence a location's habitat suitability. We included the protected area variables (Table 1) in the best-performing model from the above tests and compared models based on performance measures and habitat suitability maps.

Once models were finalized, we projected our best-performing model to map bison habitat suitability for the entire Carpathians (100 m grain, Maxent is relatively robust towards changes in grain size, Guisan et al., 2007). To avoid extrapolation, we limited predictor variables to the ranges used for model fitting (Phillips et al., 2006). We summarized the amount of suitable habitat and the number of habitat patches >200 km^2 (a minimum area for a population of 50–70 bison, Pucek et al., 2004) for three suitability index thresholds (0.5, 0.6, and 0.7).

5. Results

European Bison in the Carpathians selected forest-dominated habitats with a preference for complex mosaics of forests and grassland patches in areas of low human disturbance. Our best model to predict European Bison habitat suitability based on herd range maps included seven predictors (aspect, distance to forest, distance to roads, distance to settlements, forest fragmentation with 120-m edge width (see below), land cover, and slope). This model had an AUC of 0.933 (95%-confidence interval 0.922–0.943) with a standard error of 0.0054. European Bison habitat selection was mainly determined by four predictors: forest fragmentation, distances to settlement, distance to forest, and land cover, accounting for relative gain contributions of 42%, 30%, 18%, 6%, respectively (combined, 95%).

Bison habitat suitability responded in different and characteristic ways to each predictor variable (Fig. 1). Habitat suitability increased with increasing distance from human settlements and roads, and declined with increasing distance from forest edges. Core forest, perforated forest, and to some extent forest edges all provided suitable habitat for bison. Bison preferred forests over other cover types but showed surprisingly little preference among forest types. Grasslands had moderate suitability values; all other land cover types were avoided. Habitat selection of European Bison in the Carpathians was only marginally affected by topographic variables (Fig. 1). Bison preferred to use managed grasslands over fallow fields (Fig. 2). Nevertheless, habitat suitability maps for models based on either one or two grassland categories were essentially identical (results not shown).

While forest fragmentation was the most important factor characterizing European Bison habitat selection (see below), varying edge width in the forest fragmentation maps did not affect model performance substantially (Fig. 3). Model performance peaked when using a 120-m edge width. As edge width increased, core forest and non-forest areas became less important and edge components became more important in the models, though changes in suitability values were overall small (HSI < 0.1).

Protected areas were important in determining a location's suitability for European Bison. While models with and without protected areas both performed well (AUC = 0.941 when including protected areas), the relative importance of variables and HSI maps changed markedly between models. When the protected area predictor was included, it had the highest gain contribution (40%, mostly at the expense of forest fragmentation and distance to settlements) and was the second most important variable in the jackknife analyses (after distance to settlements). Models with the

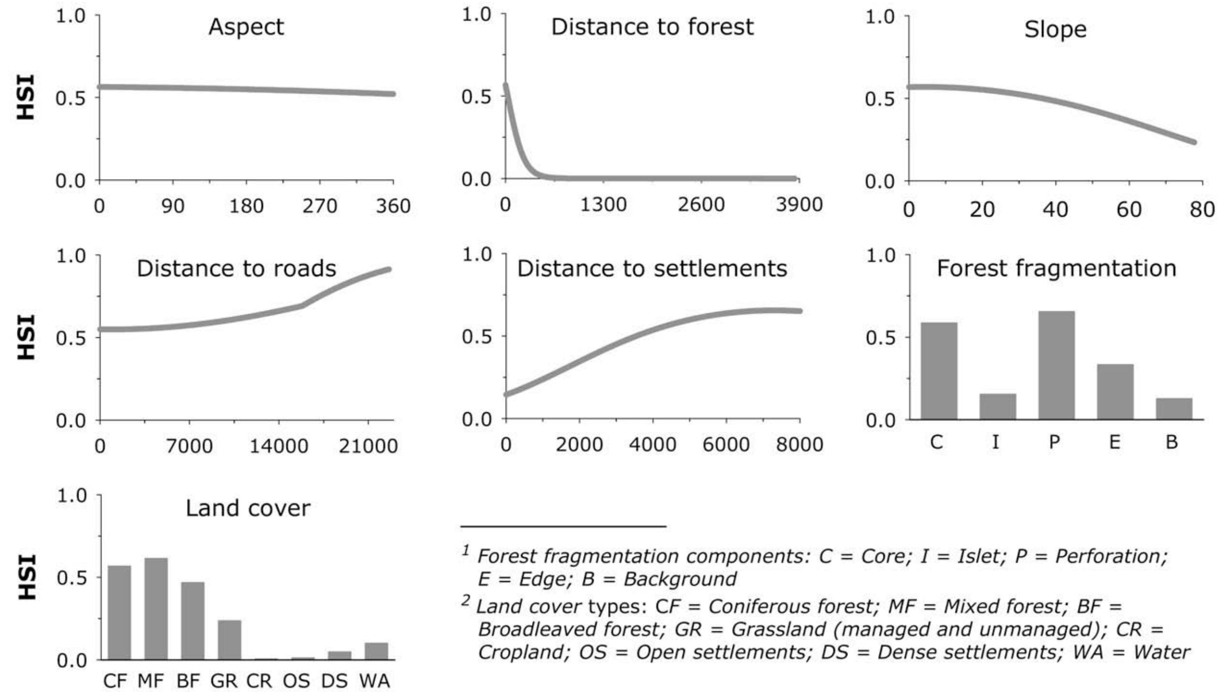

Fig. 1. Variable response curves for the seven predictors of the best-performing Maxent model (AUC = 0.933, standard error = 0.0054). Marginal response curves are shown for continuous predictors; single-variable response curves are shown for categorical predictors.

protected area variable predicted little suitable bison habitat outside protected areas (results not shown). We dropped the variable distance to protected areas as it decreased model performance.

Projecting the best-performing model to the entire Carpathian ecoregion revealed substantial areas of highly suitable, but currently unoccupied bison habitat (Fig. 4A). Most of these areas were, however, relatively fragmented and dispersed. Only a few large suitable habitat patches exist. In total, our map showed 46,400 km^2 of bison habitat for a suitability threshold of 0.5 (25,900 km^2 and 9300 km^2 for thresholds of 0.6 and 0.7, respectively).

Although 39 patches larger than 200 km^2 exist for HSI > 0.5 and 25 of these areas exceed a threshold of 0.6, only two exceed a threshold of 0.7 (Fig. 5). Several very large patches (>1500 km^2) occurred in Romania and Ukraine in relatively close proximity to each other, with the largest contiguous habitat patch occurring in southern Romania (4310 km^2, suitability threshold of 0.5). Romania also had by far the largest amount of suitable habitat (>24,800 km^2, suitability threshold of 0.5), especially in regard to the highest HSI values (Table 2). Whereas Poland, Slovakia and Ukraine also had large areas of suitable habitat, bison habitat in Austria, the Czech Republic and Hungary was scarce. Habitat suitability maps based on fine-scale and broad-scale predictors did not differ appreciably (Fig. 4B). We only projected the best model without protected area variables (suitable habitat outside protected areas could become the target for future protected areas).

Our comparison of the two different European Bison occurrence datasets (telemetry data versus herd ranges maps) suggested that our conclusions about bison habitat selection were not affected by the choice of occurrence data. Maxent models based on telemetry data and herd range maps performed similarly well (AUC of 0.985 and 0.977, respectively) and the relative importance of factors characterizing habitat selection was very similar for both datasets. Habitat suitability index (HSI) maps predicted by these two models showed similar spatial patterns and assigned high suitability to contemporary bison ranges (Fig. 6A). Their HSI values were also highly correlated (r = 0.97) with few differences between predic-

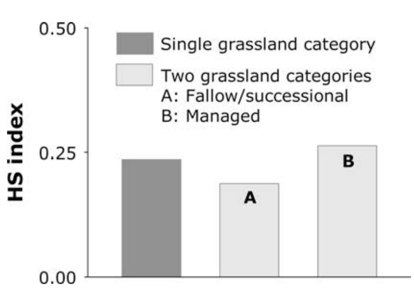

Fig. 2. Difference in habitat suitability index (HSI) scores when using Maxent models with a single or two (managed and unmanaged) grassland categories. HSI values of the other land cover categories were not affected by the choice of land cover map (see Fig. 3). Both models (with one or two grassland classes) had identical goodness of fit (AUC = 0.933, standard error = 0.0054).

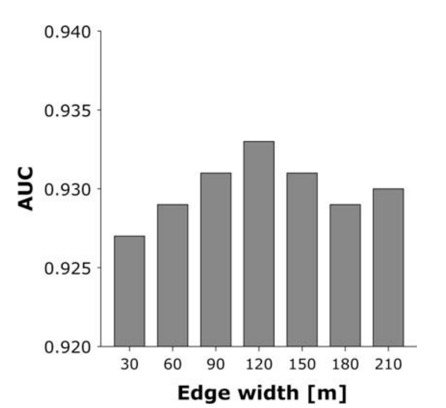

Fig. 3. Changes in Maxent model performance when varying edge width in the forest fragmentation variable.

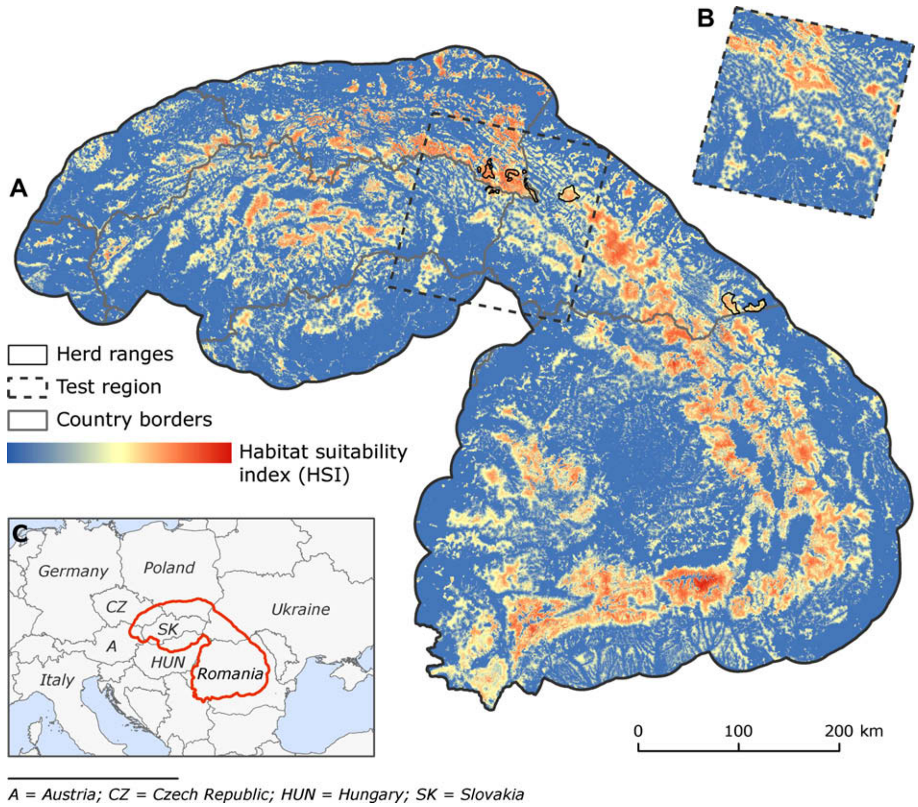

Fig. 4. European Bison habitat suitability index map for the entire Carpathians (A), habitat suitability map for the test region based on fine-scale predictors (B), and location of the study region in Central Europe (C).

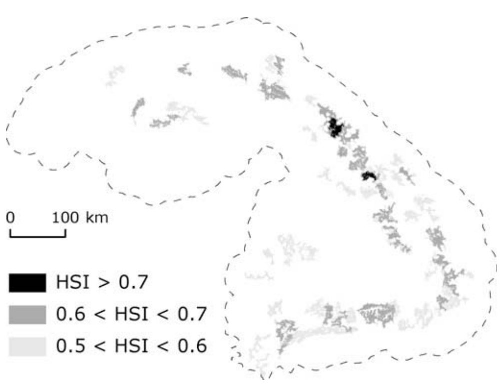

Fig. 5. Patches of suitable bison habitat larger than 200 km^2 for habitat suitability index thresholds of 0.5, 0.6, and 0.7.

tions, especially for HSI values >0.6 (Fig. 6B). All models in our analyses differed significantly ($p < 0.0001$) from a random model.

6. Discussion

If wild European Bison are to survive, they will need functioning metapopulations of >1000 individuals as existing herds are small and isolated (Pucek et al., 2004). The Carpathians are among the few places where such a metapopulation could become reality. Gaps in knowledge about suitable bison habitat characteristics and locations in the Carpathians have been major obstacles for conservation planning. Our analysis suggests that European Bison are relatively flexible in their use of habitats at the landscape scale and we identified several large, currently unoccupied patches of suitable habitat. If bison are not limited by habitat availability, we may be able to enlarge and connect existing herds and reintroduce new ones to create a viable bison metapopulation.

Bison habitat suitability in the Carpathians was mainly characterized by forest fragmentation and human disturbance. Bison preferred mosaic-type landscapes with interior forest openings and grassland/forest edges, thus confirming studies elsewhere (Krasinska et al., 1987; Krasinska and Krasinski, 2007; Pucek et al., 2004). We were surprised to find no clear preference for a particular forest type. Although fine-scale habitat analyses showed that bison prefer broadleaved and mixed forests (Pucek et al., 2004), our results suggest that coniferous forest may be as suitable at the landscape scale. Frequent clear-cutting in coniferous forests (e.g., in Ukraine, Kuemmerle et al. (2009)) may account for this result as it creates forest openings and bison forage. Moreover, coniferous

Table 2
Area currently occupied by free-ranging European Bison herds and area of suitable bison habitat in each Carpathian country (considering only the area inside our study region).

	Area currently occupied by wild European Bison herds (km^2)	Available suitable habitat (km^2)		
		0.5 > HSI > 0.6	0.6 > HSI > 0.7	HSI > 0.7
Austria	0	94	26	3
Czech Republic	0	726	324	91
Hungary	0	683	251	18
Poland	255	2217	2628	2002
Romania	0	10,670	9021	5131
Slovakia	27	3157	1932	735
Ukraine	510	2965	2422	1280
Entire Carpathians	793	20,511	16,603	9259

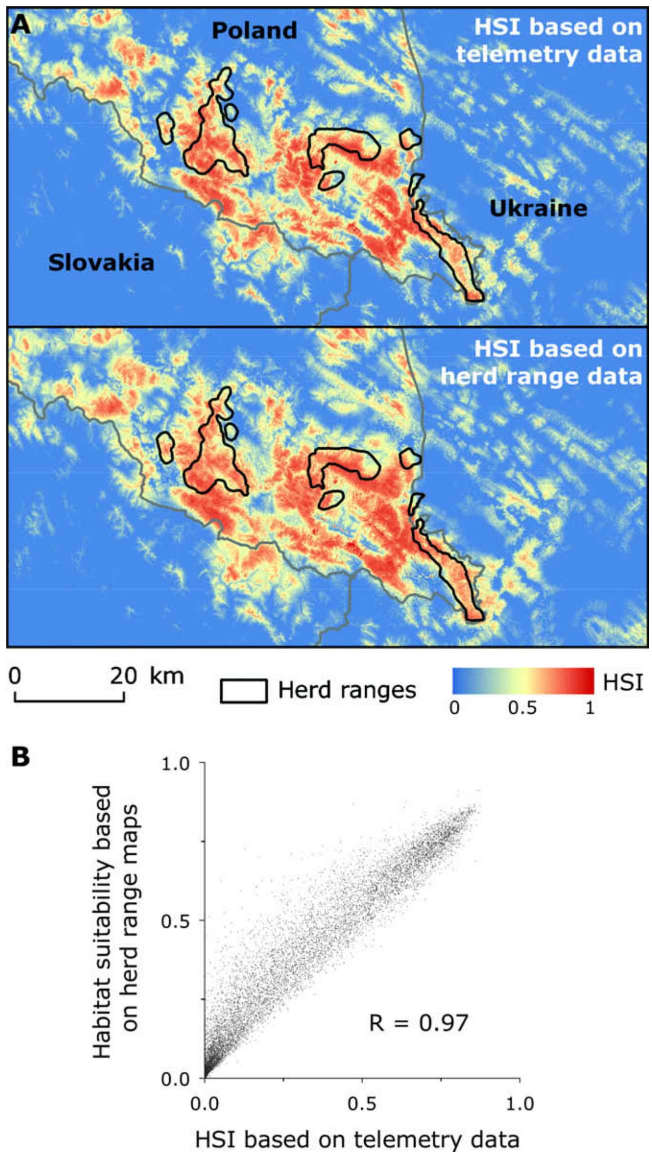

Fig. 6. Habitat suitability index (HSI) maps based on radio telemetry data (A, top) and herd range maps (A, bottom), and comparative scatterplot for 10,000 random locations (B).

forests in the Carpathians often form mosaics with other forest types and grasslands where bison can graze (Perzanowski et al., 2008), suggesting European Bison thrive in many forest types as long as openings are available (Daleszczyk et al., 2007; Krasinska et al., 2000; Perzanowski et al., 2008; Pucek et al., 2004). It is important to note that seasonal forest type preference may exist, for example in winter when bison herds use only a fraction of their summer range (Krasinska and Krasinski, 2007; Perzanowski et al., 2008). The spatial distribution of European Bison in the Carpathians prior to human influence remains uncertain. The Carpathians are, however, fully contained within the species historic range (Pucek et al., 2004) and the relative flexibility of bison to use different forest habitats suggests bison most likely occupied the majority of the ecoregion. In contrast, bison today occupy substantially less than 1% of their former range in the Carpathians, similar to the American plains bison (Sanderson et al., 2008).

European Bison preferred managed over fallow grasslands. This preference is not surprising, since the region's unmanaged grasslands often contain pine, alder, or thorny shrubs (*Prunus* spp. *Crataegus* spp. etc.) and forage quality is lower. Extensive farmland abandonment following the breakdown of socialism has not resulted in a substantial increase in suitable bison habitat in the Carpathians. However, this could change in the future as abandoned fields become reforested, creating the complex mosaics of forests and grasslands preferred by bison. Farmers in countries now in the European Union (i.e., all except Ukraine) receive subsidies for maintaining meadows, which could also benefit European Bison if such meadows were relatively remote. In many areas in the Carpathians though, current abandonment trends will likely continue, causing managed grasslands close to forests to become scarce (Baur et al., 2006; Kuemmerle et al., 2008). Abandoned fields may become important for European Bison in such areas, because they provide more and better quality forage than the forest herb layer (Pucek et al., 2004).

European Bison preferred areas with low human pressure (i.e., away from roads and settlements, Fig. 1). Rural populations in many regions in the Carpathian have declined during post-socialism. While this threatens cultural landscapes that overlap with much of the Carpathian biodiversity, decreasing human pressure may provide opportunities for the conservation of top herbivores. Where land-use intensity decreases, range extension of bison herds and additional reintroductions may become possible, especially if there are socio-economic benefits (e.g., slowly increasing ecotourism in the Carpathians, UNEP, 2007). Moreover, restoring the role of large grazers such as European Bison may become crucial for maintaining semi-open landscapes (Perzanowski and Olech, 2007; Vera et al., 2006), and thus for conserving Carpathian biodiversity in the long run.

Our ecoregion-wide habitat map suggests that much suitable European Bison habitat exists in the Carpathians, much of which is currently not occupied because the species likely is well below carrying capacity. Even when counting only large patches (>200 km^2), suitable habitat (HSI > 0.5) exceeded the area currently occupied by almost 300 European Bison in the Polish Bieszczady Mountains (about 1200 km^2) more than 10-fold, with patches well connected by less suitable habitat (Figs. 4 and 5). Overall, this suggests that a bison metapopulation is not restricted by habitat availability. Our habitat map also showed high suitability for the release site of an ongoing World Wildlife Fund reintroduction project and for two other possible reintroduction sites selected by bison experts (all in Romania, Perzanowski and Olech, 2007). Our models' ability to reproduce these independent assessments highlights the value of broad-scale habitat modeling for conservation planning (Millspaugh et al., 2009).

The maximum entropy models ably predicted bison habitat as demonstrated by their high goodness of fit. It was also reassuring to find that models based on telemetry data matched those based on herd range maps, increasing our confidence in extending these results to areas where only one type of data exist and the region as a whole. Nevertheless, some uncertainty remains. To be conservative, we did not extrapolate our maps beyond the ranges of variable values used to train and validate the models. This only limited predictions for a few small areas, mostly far from roads and settlements where suitability should not decline. This should not bias our map.

Uncertainty in predictive habitat maps can also arise from coarse predictors or missing variables (Barry and Elith, 2006; Hampe, 2004). Although we predicted European Bison habitat across a large area, we relied on fine-scale predictors, several orders of magnitude finer than the home range of a bison herd (Krasinska and Krasinski, 2007; Perzanowski et al., 2008). While we cannot rule out that finer scale data would have resulted in better predictions, we note that maps based on finer-scale (30 m) models were highly similar to those based on coarser grain data (100 m), suggesting the grain change did not impair Maxent performance (Guisan et al., 2007). As is the case in any habitat analyses, we cannot fully rule out overprediction due to missing covariates (Barry and Elith, 2006). Our approach was based on actual vegetation maps, thereby avoiding some of the pitfalls of bioclimatic niche models (Pearson and Dawson, 2003). Moreover, we predicted a relative index of bison habitat suitability. Our maps should therefore not be interpreted as probabilities of occurrence and HSI threshold separating suitable and unsuitable habitat should be selected cautiously. Finally, our models do not capture biotic factors such as species interactions, social organization (e.g., single animals vs. herds), demographic variation, or behavior, that can all influence habitat selection (Hampe, 2004; Keith et al., 2008; Krasinska and Krasinski, 2007).

What are the implications of our Carpathian habitat analyses for the European Bison conservation? A good model leads to better decisions than could be made without it (Millspaugh et al., 2009). Our habitat maps serve to inform bison conservation in at least three ways. First, our results show that the Carpathians provide enough habitat for a viable European Bison metapopulations. Second, our map points to several potential reintroduction sites, most notably in Ukraine and Romania, and wildlife managers can now prioritize reintroductions sites in the context of all available bison habitat. Third, our analyses showed that substantial bison habitat exists outside protected areas. Our analyses showed that protected areas are important for bison conservation and our maps should help to inform efforts underway to extend the region's protected area network, like the NATURA 2000 program of the European Union. The European Bison is the last surviving species of Europe's large grazers. Our analyses provide hope for the long-term conservation of this species and other large herbivores in human-dominated landscapes and for restoring their important ecological functions in general.

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