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Predicting potential European bison habitat across its former range

Tobias Kuemmerle,[1,2,12] Volker C. Radeloff,[1] Kajetan Perzanowski,[3,4] Piotr Kozlo,[5] Taras Sipko,[6] Pavlo Khoyetskyy,[7] Andriy-Taras Bashta,[8] Evgenia Chikurova,[6] Ivan Parnikoza,[9] Leonid Baskin,[6] Per Angelstam,[10] and Donald M. Waller[11]

[1]*Department of Forest and Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, Wisconsin 53706 USA*
[2]*Earth System Analysis, Potsdam Institute for Climate Impact Research (PIK), P.O. Box 60 12 03, Telegraphenberg A62, D-14412 Potsdam, Germany*
[3]*Department of Applied Ecology, Catholic University of Lublin, Konstantynow 1H, 20708 Lublin, Poland*
[4]*Museum and Institute of Zoology, Polish Academy of Sciences, Ogrodowa 10, 38-700 Ustrzyki Dolne, Poland*
[5]*Scientific and Practical Centre for Bioresources, National Academy of Sciences of Belarus, 27 Akademicheskaya Street, 22070 Minsk, Belarus*
[6]*A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33, Leninsky Prospect, 119071 Moscow, Russia*
[7]*Ukrainian National University of Forest Technology, ul. O. Kobylanskoy 1, Lviv, Ukraine*
[8]*Institute of Ecology of the Carpathians, National Academy of Sciences of Ukraine, ul. Koselnytska, 79026 Lviv, Ukraine*
[9]*Institute of Molecular Biology and Genetics, National Academy of Sciences of Ukraine, ul Acad. Zabolotnogo 150, 03680 Kyiv, Ukraine*
[10]*Faculty of Forest Sciences, School for Forest Engineers, Swedish University of Agricultural Sciences, Box 43, 73921 Skinnskatteberg, Sweden*
[11]*Department of Botany, University of Wisconsin, 430 Lincoln Avenue, Madison, Wisconsin 53706 USA*

Abstract. Habitat loss threatens large mammals worldwide, and their survival will depend on habitat in human-dominated landscapes. Conservation planners thus face the challenge to identify areas of least conflict with land use, yet broadscale species distribution models rarely incorporate real landscape patterns nor do they identify potential conservation conflicts. An excellent example of such conservation challenges is provided by European bison (*Bison bonasus*). Almost extinct by the early 20th century, bison can only survive in the wild if large metapopulations are established, but it is unclear where new herds can be reintroduced. Using European bison as an example we conducted a continental-scale habitat assessment based on real landscape patterns. Our specific aims here were to (1) map European bison habitat throughout the species' former range, (2) examine whether broadscale habitat suitability factors differ from previously reported fine-scale factors, and (3) assess where suitable habitat occurs in areas with low potential for conflict with land use. We assessed habitat suitability using herd range maps for all 36 free-ranging European bison herds as habitat use data. Habitat suitability maps were compared with maps of land cover, livestock density, agricultural constraints, and protected areas to assess potential conservation conflicts. Our models had high goodness of fit (AUC = 0.941), and we found abundant potential bison habitat. European bison prefer mosaic-type landscapes, with a preference for broad-leaved and mixed forests. European bison metapopulations do not appear to be limited by habitat availability. However, most potential habitat occurred outside protected areas and has substantial potential for conservation conflicts. The most promising areas for establishing large bison metapopulations all occur in Eastern Europe (i.e., the Carpathians, the Belarus–Ukraine borderlands, and several regions in European Russia). The future of European bison and that of other large mammals in the wild thus clearly lies in Eastern Europe, because habitat there is most abundant and least fragmented, and because the potential for conflict with land use is lower. More generally we suggest that broadscale habitat assessments that incorporate land use can be powerful tools for conservation planning and will be key if large herbivore and carnivore conservation is to succeed in a human-dominated world.

Key words: Bison bonasus; *broadscale conservation planning; Eastern Europe and the former Soviet Union; habitat suitability; land use change; large herbivores; Maxent; species distribution modeling; wisent.*

Introduction

Humans have fundamentally transformed terrestrial ecosystems and global biodiversity patterns, mainly via land use change (Ceballos and Ehrlich 2002, Ellis and Ramankutty 2008). Large carnivores and herbivores require large areas of habitat, frequently conflict with land use, and are easy to poach (Woodroffe 2000, Gordon and Loison 2009). As a result, large-mammal populations worldwide have declined precipitously where land use has intensified (Ceballos and Ehrlich 2002, Morrison et al. 2007). Today, many large mammals only persist in fragmented populations, often

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[12] E-mail: kummerle@pik-potsdam.de

confined to protected areas that are increasingly isolated (DeFries et al. 2007) and bear extinction debt (Carroll et al. 2004).

The challenge is to ensure the survival of large carnivores and herbivores in human-dominated landscapes (Morrison et al. 2007, Gordon and Loison 2009). Conservation planning depends on information about the spatial distribution of available habitat, and we therefore need habitat assessments based on real landscapes (Schadt et al. 2002, Araujo et al. 2005, Fischer and Lindenmayer 2007). Although habitat suitability models are valuable tools for this task, they have most commonly been applied to small study regions. Such fine-scale habitat models often overly emphasize local conditions, and conservation efforts may not target the most promising areas when considering only a portion of a species' range (Mayer et al. 2005, Early et al. 2008). Most habitat assessments also fail to match the continental to global scales at which the underlying drivers of habitat loss operate (Bennett and Balvanera 2007). For example, land use change is increasingly influenced by global demand patterns that affect large regions (e.g., southeast Asian oil palm plantations [Koh et al. 2009] or Latin American soy bean expansion [Grau et al. 2005]). We thus need broadscale habitat assessments to complement fine-scale studies and to identify areas with the least conflict between wildlife and land use, especially for wide-ranging large mammals.

Europe's temperate forest zone is an archetype of a region where a long land use history fragmented large-mammal populations. Agricultural expansion drastically diminished forests until the 18th century, particularly in Western Europe, resulting in extirpations of many large mammals (Breitenmoser 1998, Schadt et al. 2002). Some areas in Eastern Europe, however, have remained strongholds for large mammals (Mikusinski and Angelstam 1998, Krasinska and Krasinski 2007). Today, European forests are again expanding (Kauppi et al. 2006), and the breakdown of the Soviet Union has resulted in decreasing human pressure in some rural areas (Ioffe and Nefedova 2004, Kuemmerle et al. 2008). Some large-mammal populations are recovering in response (Breitenmoser 1998, Enserink and Vogel 2006). However, identifying potential conservation opportunities requires continental-scale habitat assessments.

The European bison or wisent (*Bison bonasus*) is Europe's last surviving large grazer. Bison once roamed across the European temperate forest zone, with the species' historical range extending from the Pyrenees, to southern Sweden, and the Caucasus (Pucek et al. 2004). Habitat loss and overhunting drove European bison close to extinction. By the early 20th century only two isolated herds persisted, one in the Białowieza Forest in today's Polish–Belarusian borderlands and another in the Caucasus. The last wild bison was poached in 1927, but 54 animals survived in zoos (Krasinska and Krasinski 2007). Thanks to a breeding and reintroduction program, bison numbers have since increased to ~3000 animals, 1500 of which occur in ~30 free-ranging herds. These herds, scattered across Central and Eastern Europe, represent two genetic lines: the Lowland line (mainly in Poland, Belarus, and Lithuania) and the Lowland-Caucasian line (southern Poland, Russia, Ukraine, and Slovakia).

Although the European bison population has grown during the 20th century, the species faces an uncertain future. Effective population size (N_e) is much smaller than total population numbers due to the genetic bottleneck (only 12 founders), resulting in low genetic diversity (Olech and Perzanowski 2002, Pucek et al. 2004). Poaching and trophy hunting increased after the breakdown of the Soviet Union, extirpating some herds (Pucek et al. 2004, Parnikoza et al. 2009). Most importantly, all existing herds remain small and isolated (Perzanowski et al. 2004, Pucek et al. 2004). The minimum viable size of a bison population is estimated at 1000 animals but no herd is close to this threshold (Pucek et al. 2004). The species' survival in the wild now depends on establishing functioning metapopulations by enlarging existing herds and additional reintroductions (Perzanowski et al. 2004, Pucek et al. 2004), and this raises the question of where viable metapopulations could exist.

A few previous studies have assessed fine-scale European bison habitat selection, most notably in the Polish Białowieza and Borecka forests as well as the Bieszczady Mountains (Krasinski and Krasinska 1992, Krasinska and Krasinski 2007, Perzanowski et al. 2008). While these studies found bison to prefer broad-leaved or mixed forests in mosaic-type landscapes, habitat selection of most bison herds has never been assessed and no study has analyzed bison habitat across larger areas or for multiple herds. Moreover, most prior studies have focused on Lowland-line herds only, and no study has assessed habitat differences among the two genetic lines. Although European bison are generally assumed to be a woodland species (Pucek et al. 2004), empirical evidence suggests their niche may be fairly broad. For example, some bison herds are thriving in more open landscapes (Balciauskas 1999), and European bison may be adapted to grassland habitats (Mendoza and Palmqvist 2008). Overall, habitat selection of European bison populations as a whole remains unclear, and better knowledge on what characterizes suitable bison habitat at broad spatial scales is needed (Pucek et al. 2004).

Much of the historical range of the European bison remains dominated by agricultural land use, and there are several potential areas of conflict between bison herds and farming. Bison and livestock may compete for pasture and bison herds can inflict substantial crop damage (Krasinska and Krasinski 2007, Gordon and Loison 2009). Moreover, diseases transmitted between livestock and wildlife can be a major obstacle for conservation success (Bienen and Tabor 2006, Krasinska and Krasinski 2007). If viable European

TABLE 1. Herd range maps used in our European bison (*Bison bonasus*) habitat suitability analyses.

Genetic line	Herd
Lowland	Białowieza (PL), Belovezhskaya (B), Borecka (PL), Nadelsnictwo Walcz (PL), Knyszynska (PL), Lopatynska (UA),† Lyaskovichskaya (B), Naydianskaya (B), Osipovichskaya (B), Ozeranskaya (B), Ozerskaya (B), Berezinsky (B), Panevezys-Pasiliustum (L), Polesskyy (B) Volozhynskaya (B)
Lowland-Caucasian	Bieszczady (east and west, PL), Bukovynska (UA), Ceisky (RU), Cumanska (UA), Danivska‡ (UA), Kaluzhskiye (RU), Kavkazky§ (RU), Khmelnytska‡ (UA), Kliazmynsko-Luhskiy (RU), Konotopska (UA), Nadvirnjanska‡ (UA), Orlovskoe Polese (RU), Poloniny (SK), Rivnenska‡ (UA), Skole (UA), Teberdinsky (RU), Uladivska (UA), Ust Kobenskoe (RU), Zalisska (UA)

Note: Key to abbreviations: B, Belarus; L, Lithuania; PL, Poland; RU, Russia; S, Slovakia; UA, Ukraine.
† Now a Lowland-Caucasian line herd after additional reintroductions in 2008.
‡ Extinct herds.
§ Mountain bison (contain some blood from American bison; Pucek et al. 2004).

bison metapopulations are the goal, we need better information on which conflicts are more likely to occur, and we must identify candidate areas for metapopulations that have less potential for conflict than others.

Our goal was thus to conduct the first range-wide assessment of European bison habitat, based on a comprehensive data set of bison habitat use, and to assess potential conflicts between bison conservation and land use. Our main questions were: (1) What is the spatial distribution of potential European bison habitat throughout the species' former range? (2) What are the broadscale factors characterizing European bison habitat suitability, do they differ from previously reported fine-scale factors, and does habitat use differ among the two genetic bison lines? (3) What potential conflicts exist between European bison conservation and land use and where are areas with suitable habitat and low conflict potential that could be candidate areas for viable European bison metapopulations?

Data Sets Used

European bison occurrence data

We acquired range maps for all free-ranging herds registered in the European Bison Pedigree Book and the IUCN European Bison species conservation plan (Pucek et al. 2004), as well as for some additional herds (Table 1). We only considered herds with at least 10 animals and excluded failed reintroductions (e.g., Crimea, Bryansky Les). However, we included available range maps from recently extirpated herds (e.g., in Ukraine or the Caucasus). Some herd range maps were available from the literature (Krasinski and Krasinska 1992, Balciauskas 1999, Trepet 2005, Krasinska and Krasinski 2007, Perzanowski et al. 2008). For the other herds, wildlife biologists or game wardens familiar with the herds outlined herd range maps on topographic maps or satellite images. Seasonal habitat use maps were only available for two herds, and we used summer range maps, when herd ranges are less constricted, in all cases. All our herd range maps thus included winter habitat, which is critical for European bison survival (Krasinska and Krasinski 2007, Mysterud et al. 2007). In total, we obtained 36 herd range maps (Fig. 1) that covered a total area of ~9100 km^2 (median 106 km^2, SD 446 km^2). To parameterize our habitat models, we randomly selected 40 locations per herd with a 1-km minimum distance between points to minimize spatial autocorrelation and pseudo-replication. In total, we used 1329 locations (six herd ranges were too small to support 40 independent points).

Predictor variables

To capture land cover, we obtained the Moderate Resolution Imaging Spectroradiometer (MODIS) land cover map (version 5). This land cover map is derived from annual time series of reflectance images, vegetation indices, and land surface temperature from the MODIS satellites at a spatial resolution of 500 m (*available online*).[13] We acquired the 2004 map with the International Biosphere–Geosphere Programme legend that comprises 16 classes (10 natural vegetation classes plus three developed and mosaic land classes and three non-vegetated land classes). As additional continuous measures of land cover we include grids of percent tree, herbaceous, and bare ground cover from the MODIS Vegetation Continuous Fields product (version 4, 2001; *available online*).[14] We also derived land cover diversity grids by calculating Shannon's diversity index (Shannon 1948) within a 10 km radius (i.e., roughly representing the maximum home range of individual bison; Krasinska and Krasinski 2007, Perzanowski et al. 2008).

Forest fragmentation maps were derived using morphological image segmentation (Vogt et al. 2007). We categorized each forest pixel 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), or islet forests (patches too small to contain core forest; Vogt et al. 2007). We used an eight-neighbor rule and an edge width of 500 m (one pixel). We also calculated the distances of each pixel to the closest forest and core forest pixel.

To characterize human disturbance, we acquired four proximate variables. The Landscan 2007 map provided

13 ⟨http://modis-land.gsfc.nasa.gov/landcover.htm⟩
14 ⟨http://glcf.umiacs.umd.edu/data/vcf⟩

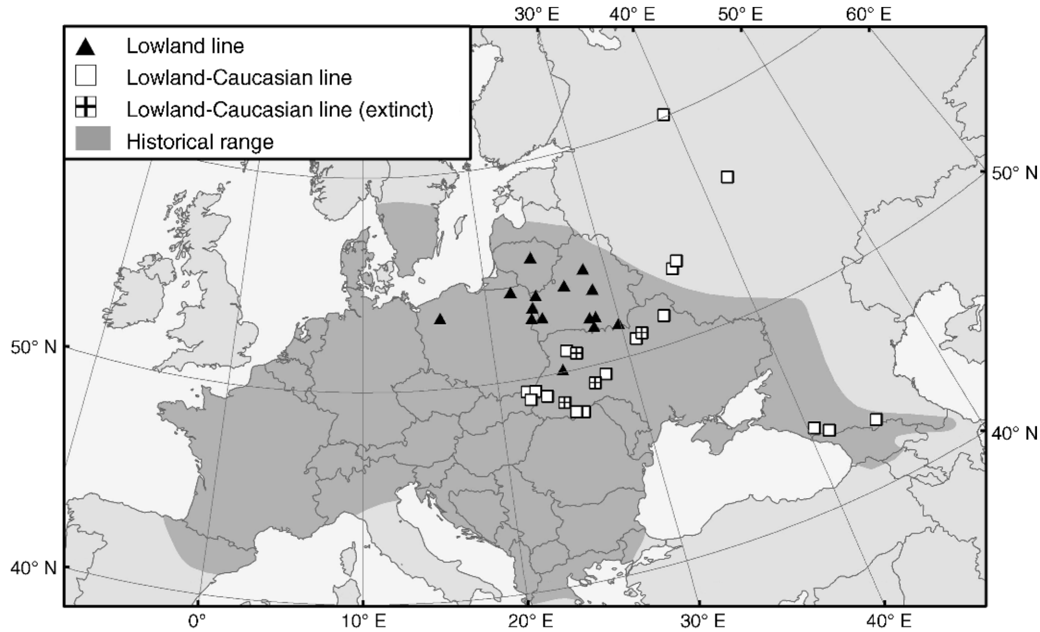

FIG. 1. Locations of European bison (*Bison bonasus*) herds in Central and Eastern Europe.

gridded population density (*available online*).[15] Second, we used a map of satellite-based nighttime lights (*available online*).[16] Third, we calculated road density within a 10 km radius based on a road layer from the Environmental Systems Research Institute (ESRI) Data and Maps Kit 2008 (ESRI 2008). And fourth, we calculated the distance of each pixel to the nearest settlement, using the ESRI Data and Maps Kit and urban areas from the MODIS land cover map. To avoid sampling bias (Phillips et al. 2009), we only calculated distances up to the maximum distance of a bison herd from a settlement (using the maximum value for all other locations).

As topographic data, we used the Shuttle Radar Topography Mission (SRTM) elevation model (*available online*).[17] Where SRTM data were unavailable (above 60° latitude), we used the Global 30 Arc Second Elevation Data (*available online*).[18] We then calculated-slope (in degrees) and a southernness index (north = 0; south = 1). We also included five bioclimatic variables from the WorldClim database (Hijmans et al. 2005): (1) mean annual temperature, (2) mean temperature of coldest quarter, (3) mean temperature of warmest quarter, (4) total precipitation, and (5) precipitation during coldest quarter. Finally, we included latitude as a proxy for climate influence. In total, we used 21 potential predictors that we projected to the Albers Equal Area Conic projection and resampled to a grain of 500 m.

15 ⟨www.ornl.gov/sci/landscan⟩
16 ⟨www.ngdc.noaa.gov/dmsp⟩
17 ⟨http://srtm.csi.cgiar.org⟩
18 ⟨http://eros.usgs.gov/Find_Data/Products_and_Data_Available/GTOPO30⟩

METHODS

Maximum entropy modeling

Maximum entropy modeling is a machine learning method for mapping habitat suitability (Phillips et al. 2006) and well suited for our habitat analyses. Maximum entropy modeling requires only occurrence data, performs well with small sample sizes (Wisz et al. 2008), is fairly robust against spatial autocorrelation (Segurado et al. 2006), and frequently outperforms traditional statistical approaches (Elith et al. 2006). Most importantly, the approach is robust against false negatives, a critical property when modeling species that do not realize their full niche (Engler et al. 2004).

The maximum entropy approach assumes that the potential, 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 $\hat{\pi}$, where constraints are inferred from environmental variables measured at each occurrence point. While many $\hat{\pi}$ exist that satisfy these constraints, the distribution $\hat{\pi}$ with maximum entropy approximates π best because it is least constrained (Phillips et al. 2006). Regularization parameters are used to prevent over-fitting. A detailed mathematical description of the approach is provided in Phillips et al. (2006).

Mapping European bison habitat

We used Maxent version 3.3.1 to fit maximum entropy models (R. Schapire, *unpublished software*). As occurrence data, we used the random sample of herd range points. Models were parameterized with a background sample of 10 000 points, default convergence thresholds, and automatic regularization (Phillips and Dudik 2008). We only used linear, quadratic, and product feature types, because initial tests suggested overfitting when using complex feature types. We predicted habitat suitability maps by applying the resulting Maxent models to all cells in the study region, using a logistic link function to yield a relative habitat suitability index (HSI) between zero and one (Phillips and Dudik 2008).

To validate our models, we used herd-level, fivefold cross-validation (i.e., retaining occurrence locations from six or seven herds per run) and calculated the area under the curve (AUC) of the receiver operating characteristics (ROC) curve. The ROC curve is a plot of the true positive rate (i.e., sensitivity) vs. the false positive rate (i.e., 1 − specificity) across all possible HSI thresholds that discriminate presence and absence. While originally developed for presence/absence data, ROC curves can be calculated from presence/background data sets too (Phillips et al. 2006). We also used a one-tailed binomial test of omission to test whether our models performed better than a random model (Phillips et al. 2006).

While Maxent is relatively robust against collinear variables, collinearity can impair the interpretation of variable influence. We calculated pairwise Pearson's correlation coefficients based on 10 000 random locations and included only one variable in cases of collinearity ($r > 0.65$). Distance to core forest and distance to forest were correlated ($r = 0.84$), and we dropped distance to forest because models that included distance to core forest had consistently higher AUC values. The five bioclimatic predictors were also highly correlated ($r > 0.9$), and we therefore only included one such predictor per model run.

To identify the best model for predicting range-wide European bison habitat suitability (question 1), we first parameterized a Maxent model that included only land cover, topography, and human disturbance variables. Second, we added climate variables by parameterizing one model that included latitude, and five models that included latitude and one of the bioclimatic variables. All models were compared based on cross-validated AUC values and the resulting HSI maps. To quantify the degree of similarity among habitat maps produced by two models, we used the I statistic (Warren et al. 2009) that measures niche overlap (0, no overlap; 1, identical niches). We also tested how substituting the five predictors based on the MODIS land cover map with predictors based on the GlobCover land cover map (*available online*)[19] affected our models and found no substantial difference among model performance, variable importance, and HSI maps.

Once habitat suitability maps were derived, we summarized the available habitat for each of 10 0.1-wide HSI bins and for three suitability thresholds (0.5, 0.6, and 0.7). We also assessed the number and spatial pattern of habitat patches larger than 200 km^2 (i.e., minimum habitat requirement for a herd of 50–60 bison; Pucek et al. 2004) and habitat availability within 50×50 km^2 grid cells.

To assess broadscale European habitat selection (question 2), we summarized the range of habitat conditions inside current bison herd ranges by calculating box plots (continuous predictors) and relative histograms (categorical predictors) for all herds, all Lowland-line herds, and all Lowland-Caucasian-line herds. We also assessed the importance of our predictors using a jackknife procedure that quantified AUC and gain changes when excluding a variable (Phillips et al. 2006). In addition, we calculated variable response curves for each predictor.

To explore potential conflicts between free-ranging European bison populations and agriculture (question 3), we calculated the proportions of four HSI classes (0.4–0.5, 0.5–0.6, 0.6–0.7, and >0.7) occurring in cropland, cropland-natural mosaic, and seminatural areas. Similarly, we cross-tabulated these HSI classes against a map of climatic constraints for agriculture (three categories: no, moisture, or temperature constraints) as well as a map of soil constraints for agriculture (seven categories ranging from no constraints to unsuitable for agriculture; Fischer et al. 2002). We also cross-tabulated the HSI classes against maps of sheep and cattle density (Wint and Robinson 2007). To identify candidate areas for bison metapopulations, we excluded suitable habitat in cropland areas, in areas of high livestock density (>20 animals/km^2), and in areas without constraints for agriculture. Finally, we summarized the proportion of European bison habitat within protected areas based on the World Database of Protected Areas (version 2009; *available online*).[20]

Results

Our initial Maxent model, based on MODIS land cover, human disturbance, and topography predictors, had a high goodness of fit (AUC = 0.922). Adding latitude as a predictor controlled for the northern distribution of suitable habitat (Fig. 2A, C), increasing model fit markedly (AUC = 0.941). HSI maps were very similar when comparing model runs with and without bioclimatic variables (Fig. 2A, B; $I = 83$), although AUC values increased somewhat (e.g., AUC = 0.955 when including precipitation during coldest quarter). Habitat predictions within the region containing contemporary bison herds remained largely unchanged when adding bioclimatic variables. However, bioclimatic variables led

[19] ⟨http://ionia1.esrin.esa.int⟩

[20] ⟨www.wdpa.org⟩

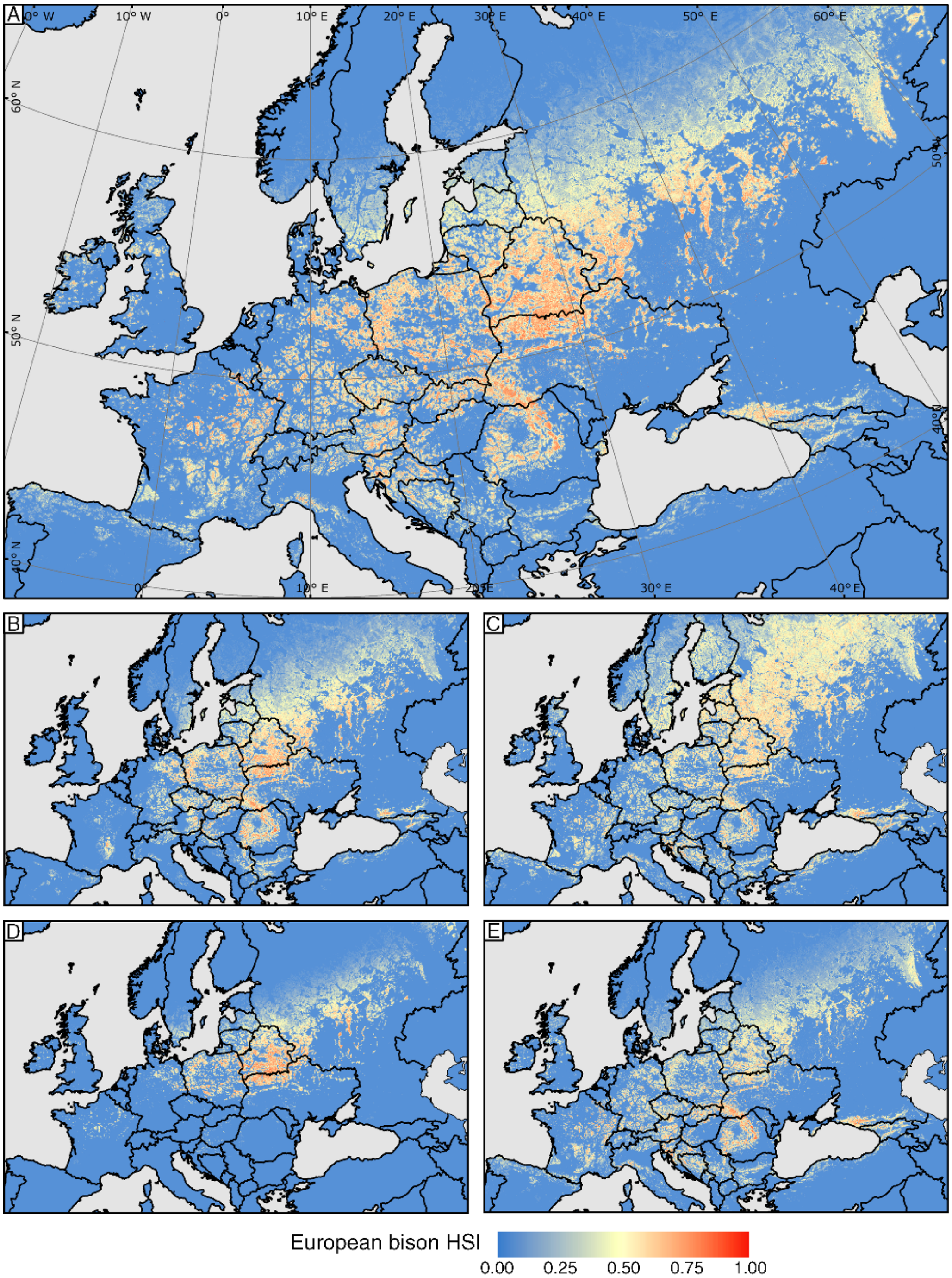

FIG. 2. (A) European habitat suitability index (HSI) map based on a model using occurrence data from all herds and land cover, forest fragmentation, human disturbance, latitude, and topography as predictors. (B) Same model as in panel (A), plus bioclimatic predictors. (C) Same model as in panel (A), but without the latitude predictor. (D) Same model as in panel (A), but using only occurrence data from Lowland line herds. (E) Same model as in panel (A), but using only occurrence data from Lowland-Caucasian line herds. Black lines indicate country borders.

to omissions of suitable habitat patches outside this region (but well within the species' historical range). We therefore did not include the bioclimatic variables in our final model, which used 14 predictors (land cover, forest fragmentation, distance to core forest, land cover diversity, road density, distance to settlements, population density, nighttime lights, elevation, slope, southernness, and latitude; AUC = 0.941, standard error = 0.006).

The HSI map predicted by the final model showed widespread potential European bison habitat within the

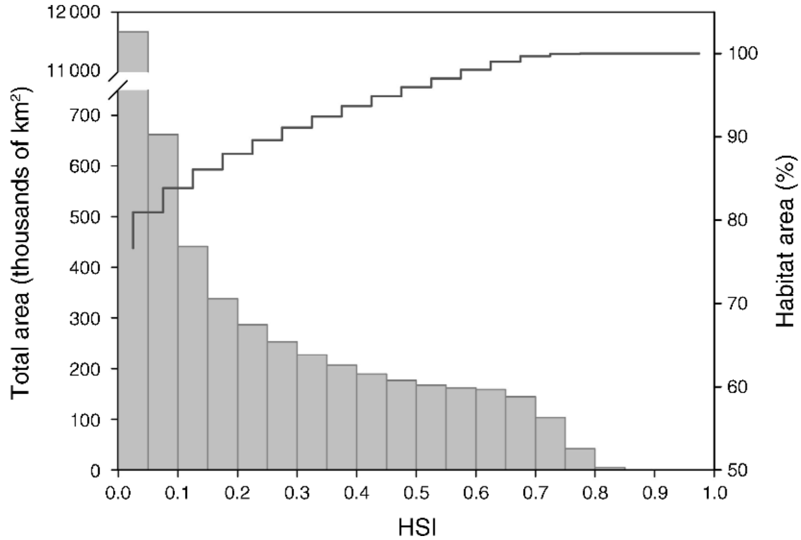

FIG. 3. Habitat suitability index (HSI) distribution for the final Maxent model (Fig. 2A). Bar graph: histogram of the total area in each 0.05-wide HSI bin (left vertical axis). Stepped line: cumulative relative distribution of habitat area (right vertical axis).

species' historical range (Fig. 2A). Large habitat patches were mainly clustered in the forest zone of Central Europe and European Russia, with a clear east–west trend (highest habitat suitability and more available habitat in the east). Our models also assigned high suitability values to European bison strongholds, such as the Białowieza forest, as well as several potential reintroduction sites (identified by independent assessments; Perzanowski and Olech 2007, Sipko 2009).

Our final model predicted a large area (783 000 km^2) of suitable European bison habitat across the study region for a HSI threshold of 0.5 (454 000 km^2 and 151 000 km^2 for thresholds of 0.6 and 0.7, respectively; Fig. 3). Although suitable habitat was relatively widespread (Fig. 4, left column), only a relatively small proportion of this habitat occurred in large patches ($>$200 km^2; Fig. 4, middle column). We found 418 large habitat patches for the 0.5-threshold (288 and 49 patches for thresholds of 0.6 and 0.7, respectively), almost all of which occurred in Eastern Europe (Poland, Belarus, European Russia, and the Carpathians; Fig. 4, middle column). Habitat connectivity, measured as the amount of available habitat within 50×50 km^2 grid cells, was also highest in these regions (Fig. 4, right column).

Concerning broadscale habitat selection of European bison, our comprehensive sample of herd range maps showed that European bison used a wide range of habitat conditions (Fig. 5). While most herd ranges were forest-dominated, some herd ranges also include substantial open areas. Human disturbance was generally low in the areas occupied by bison. The variables forest fragmentation, land cover type, fractional tree cover, distance to core forest, and latitude were most important in the habitat suitability models (individual gain contributions $>$10%, together accounting for $>$74%) and the jackknife analyses of AUC values. Variable response curves showed that European bison preferred deciduous and mixed forests in mosaic-type landscapes that contain areas of high herbaceous cover. Coniferous forest had intermediate suitability scores, whereas all other land covers were avoided. The relative importance of human disturbance and topography variables was low.

Lowland- and Lowland-Caucasian-line herds used relatively similar habitats (Fig. 5). Lowland-Caucasian lines, however, inhabited a broader range of elevation and slope conditions. Lowland-line herds used more open habitat (less forest cover, more mosaic landscapes, lower tree cover, and higher herbaceous cover) than Lowland-Caucasian-line herds (Fig. 5). The importance of most variables was highly similar for Lowland or Lowland-Caucasian models and variable response curves did not differ appreciably among the two genetic lines. The Lowland-line model had a higher goodness of fit than the Lowland-Caucasian-line model (AUC of 0.984 and 0.925, respectively).

The two HSI maps that we developed for the two genetic European bison lines were relatively similar in Central Europe, where both lines co-occur (Fig. 2D, E). The Lowland model predicted substantially less suitable habitat than the Lowland-Caucasian model, especially outside Eastern Europe, resulting in a relatively low overall similarity between the two maps ($I = 0.62$). The map predicted by the Lowland-Caucasian model was also more similar to the map based on a model using all herds (Fig. 2A) than the Lowland model ($I = 0.89$ and $I = 0.68$, respectively).

In regard to potential conflicts between European bison and agricultural land use, the majority of suitable bison habitat occurred in seminatural and natural areas.

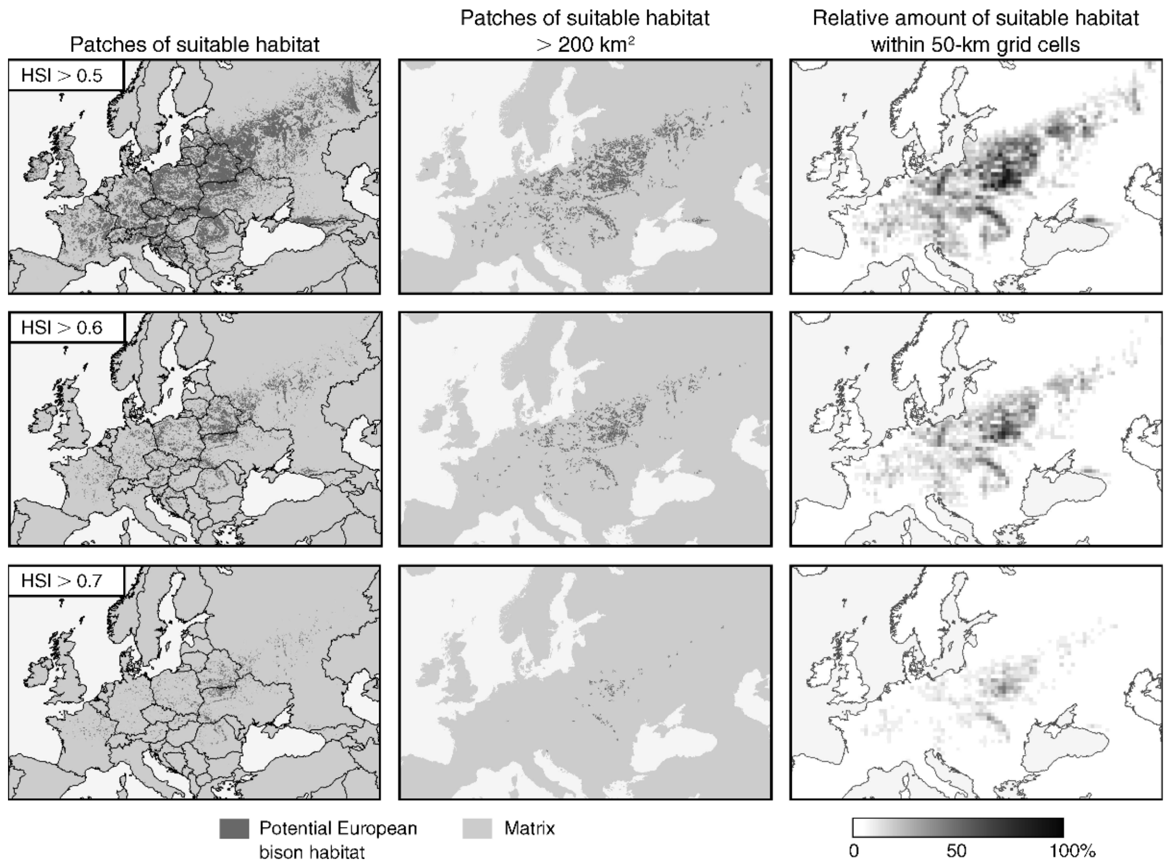

Fig. 4. Total patches of suitable habitat (left column), patches of suitable habitat larger than 200 km^2 (middle column), and relative percentage of available habitat within 50×50 km^2 grid cells (right column) for habitat suitability index (HSI) thresholds of 0.5, 0.6, and 0.7.

While we found some suitable habitat in natural-vegetation/cropland mosaics, relatively little high-quality habitat occurred in cropland-dominated areas (Fig. 6A). Protected areas harbored only a small fraction of all suitable bison habitat, although this share increased with increasing HSI scores (to 13%; Fig. 6B). Our maps also revealed substantial amounts of habitat in regions where poorer soils constrain agriculture (Fig. 6C). In contrast, almost all suitable habitats occurred in areas without climate constraints (Fig. 6D). Most high-quality habitat (HSI > 0.5) was located in areas of intermediate or high cattle density (Fig. 6E). Interestingly, cattle density increased in tandem with higher European bison habitat suitability values. Sheep were scarce in areas of high bison habitat suitability (Fig. 6F).

Most high-quality bison habitat occurred in areas with at least one potential for conflict between bison conservation and agricultural land use (Fig. 7). Removing habitat that occurred in areas with few agricultural constraints, high cattle density (>20 individuals/km^2), or in cropland areas removed most of the high-quality (HSI > 0.5) habitat patches in Western Europe. In Eastern Europe though several large habitat patches of low-conflict areas remained, most notably in the Carpathians (southeast Poland, Slovakia, Ukraine, and Romania), along the Belarusian–Ukrainian border, in Western Russia (Smolensk, Bryansk, and Kaluga regions), and in Central–European Russia (Tambov, Ryazan, and Mordovia region; Penza, Ulyanovsk, and Chuvash regions).

Russia had, by far, the largest amount of suitable European bison habitat in areas with low conservation conflict potential (Table 2), followed by Ukraine, Poland, Belarus, and Romania. These countries also had the largest number of contiguous patches larger than 200 km^2 of such habitat. Altogether, ~360 000 km^2 of suitable habitat occurred in low-conflict areas, including 208 patches larger than 200 km^2. Most of these patches are currently not occupied by free-ranging European bison herd.

Discussion

Maintaining large carnivore and herbivore populations in human-dominated landscapes is one of the biggest challenges for conservation planning (Carroll et al. 2004, Gordon and Loison 2009). European bison today occupy substantially <1% of their former range and wild European bison will only persist if we can

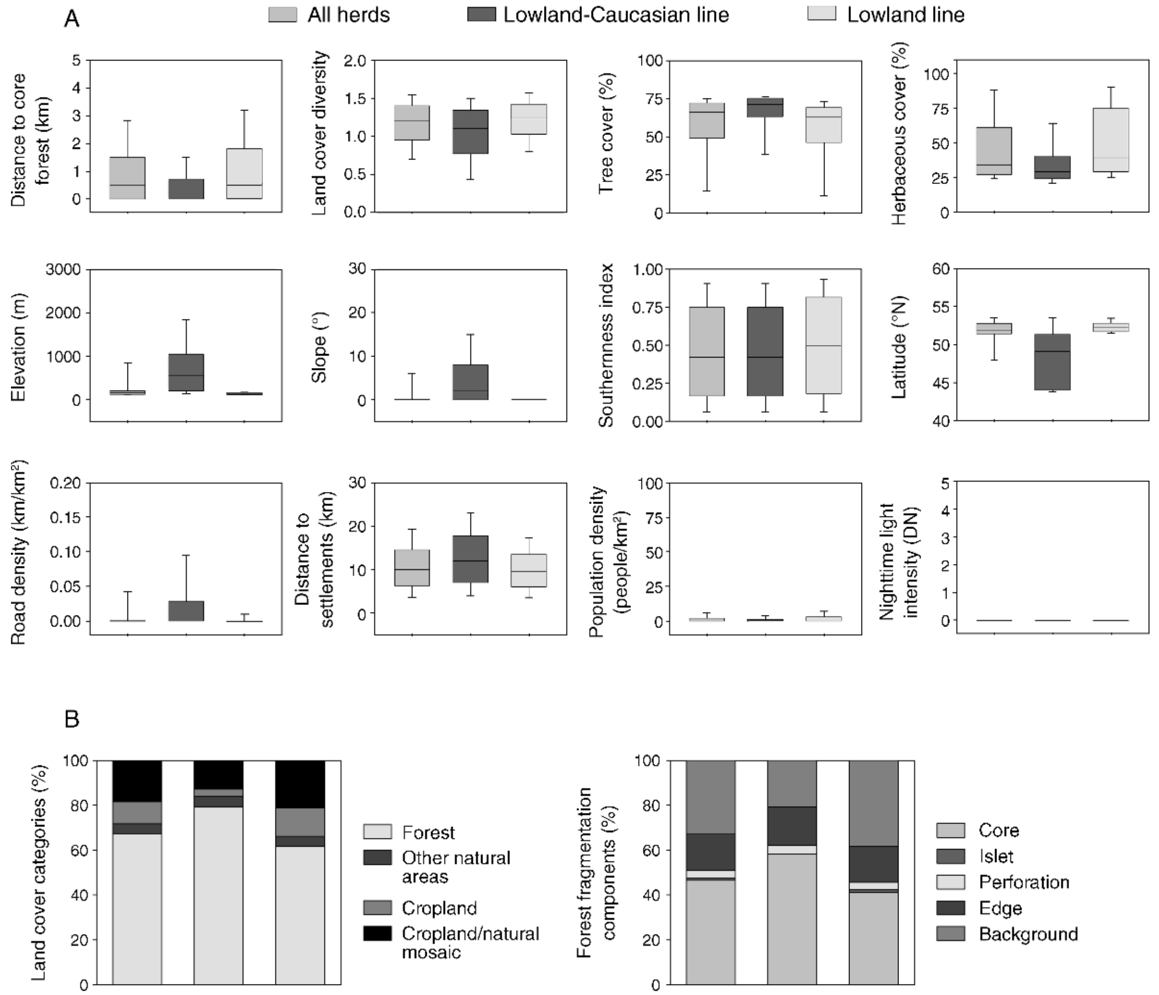

FIG. 5. Habitats used by contemporary European bison herds. (A) Box plots for all herds, Lowland-Caucasian herds, and Lowland herds for all continuous predictors (whiskers mark 10th and 90th percentiles; the line indicates the median). For the southernness index, 0 is north, and 1 is south. Nighttime light intensity is measured with a dimensionless index (DN, digital number; the maximum DN in the data set was 63). (B) Percentages of different land cover (left) and forest fragmentation components (right).

establish viable metapopulations and we need broadscale habitat assessments to select priority areas (Pucek et al. 2004). Our analysis spanned the historical range of European bison and identified widespread habitat. The most promising areas for large bison populations are all clustered in Central and Eastern Europe and are currently largely unoccupied. This suggests viable European bison populations in these regions are not limited by habitat availability.

The question whether European bison prefer closed woodlands or more open habitats has long been debated (Pucek et al. 2004, Krasinska and Krasinski 2007). There is increasing evidence that bison benefit from more open habitats (Balciauskas 1999, Mendoza and Palmqvist 2008). Our analyses of contemporary bison herd ranges (Fig. 5) and our models provide further support for this view. European bison clearly prefer mosaic-type landscapes of forests and herbaceous vegetation, thus confirming fine-scale assessments (Daleszczyk et al. 2007, Perzanowski et al. 2008). However, we found bison to prefer broad-leaved and mixed forests while some finer-scale studies suggest equal preference for coniferous stands (Perzanowski et al. 2008, Kuemmerle et al. 2010). Thus, the forest type that bison select may ultimately depend on scale with bison utilizing coniferous stands locally as shelter when these stands are close to other forest types or when coniferous stands are logged and early-succession vegetation provides forage, such as in the Carpathians (Kuemmerle et al. 2007, Perzanowski et al. 2008).

Although broadscale European bison habitat suitability is clearly linked to forest cover, it is important to note that our models were based on current bison occurrences and so characterize the species' realized niche. European bison may have been pushed back into forest-dominated

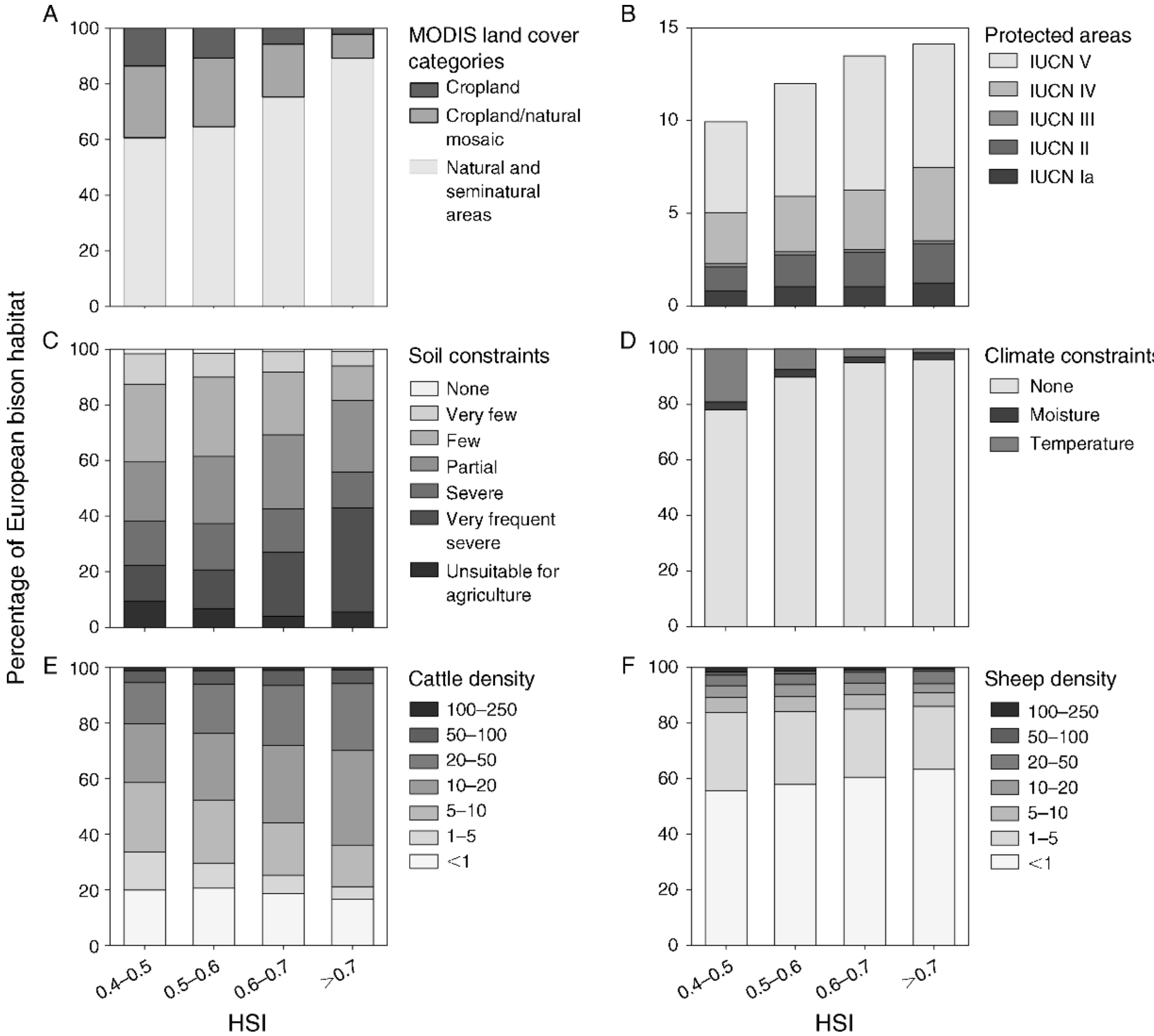

FIG. 6. Percentage of European bison habitat within (A) different MODIS land cover classes; (B) protected area categories; (C) areas with soil constraints for agriculture; (D) areas with climate constraints for agriculture; and different densities of (E) cattle and (F) sheep.

landscapes as human populations and agriculture expanded, allowing bison only to persist in parts of their fundamental niche (Pucek et al. 2004). Three factors support the view that contemporary bison habitat occupancy may largely be a legacy of past human pressure. First, we found that habitat conditions used by bison were much broader than previously reported (Fig. 5). Second, although the habitat maps of Lowland and Lowland-Caucasian lines differed (Fig. 2D, E), habitat selection of both genetic lines was overall similar (Fig. 5). The fact that Lowland-Caucasian herds inhabited a broader range of habitat conditions (e.g., regarding elevation and latitude) may be explained by past reintroduction programs, which sought to keep both lines geographically disjunct (Pucek et al. 2004). Third, bioclimatic variables, commonly used to characterize species' fundamental niches, were not useful in our case, and the strongest predictors of bison habitat suitability were all linked to land cover and land use.

Our herd range data set did not allow for modeling seasonal habitat dynamics, although winter habitat is important for ungulate survival (Gaillard et al. 2000). European bison winter habitat is typically a region within a herd's summer range (Krasinska and Krasinski 2007, Perzanowski et al. 2008). Our habitat suitability maps thus included winter habitat in most cases, but we cannot fully rule out overprediction in some areas where suitable summer habitat does not contain adequate winter habitat. We therefore recommend fine-scale, site-specific assessments of forage availability for candidate reintroduction areas.

Some bison herds are fed during winter, likely affecting their survival and carrying capacity (Pucek et

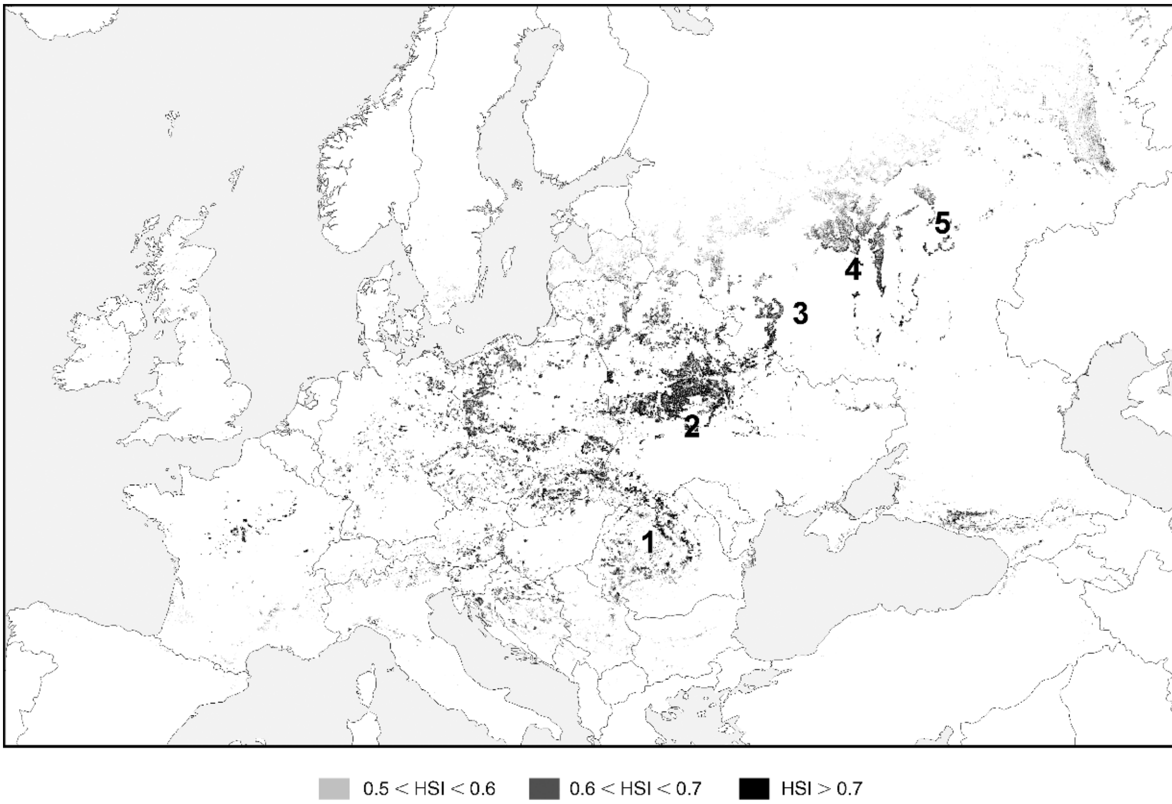

FIG. 7. Areas with suitable European bison habitat (HSI > 0.5) and relatively low conservation conflict potential: (1) Carpathian Mountains, (2) Belarusian–Ukrainian borderlands, (3) Bryansk and Kaluga regions, (4) Ryazan, Mordovia, Tambov, and Nizhni Novgorod regions, (5) Penza, Ulyanovsk, and Chuvash regions, all in Russia.

al. 2004, Krasinska and Krasinski 2007). However, those herds where winter severity is strongest (i.e., high latitudes, mountainous areas) survive and reproduce without supplemental winter feeding (Pucek et al. 2004, Krasinska and Krasinski 2007, Perzanowski et al. 2008, Sipko 2009). It is unlikely that winter feeding resulted in pseudo-presences (i.e., herds that would vanish without winter feeding), and we therefore suggest that winter feeding did not bias our presence-only model. Our models had high goodness of fit and reproduced well all areas currently occupied by European bison, as well as several potential reintroduction sites that were identified by independent assessments (Sipko and Mizin 2006, Perzanowski and Olech 2007), all of which strengthened our confidence in our results.

Including the latitude predictor prevented our model from extrapolating beyond the range of environmental conditions currently inhabited by European bison (Fig. 2A). Our habitat suitability map thus likely represents a conservative estimate of available habitat at the current range limits. This may be particularly the case for northern European Russia, where suitability scores were low in our base model, but higher in the model without the latitude predictor (Fig. 2A, C). One European bison herd (Ust Kobenskoe, ~60° latitude) survives and reproduces in this region since 1991 without additional winter feeding (Sipko 2009), attesting to the potential of this region to contribute to European bison conservation.

Protected areas have long been a stronghold of European bison populations and harbor most existing bison herds as well as unoccupied high-quality habitat (Fig. 6). However, many protected areas are isolated and no protected area is large enough for a viable bison population (>1000 animals). Although extending protected area networks will undoubtedly contribute to bison conservation, our results highlight that the key to functioning bison metapopulations lies outside strictly protected areas, because the vast majority of suitable habitat is currently not protected.

To expand and sustain a functional European bison meta-population, it will be necessary to address the potential conflicts between growing bison populations and agricultural land use. Our results showed that most bison habitat occurs in areas with considerable cattle densities. This is not surprising, as livestock husbandry and protected areas (that harbor most bison herds) concentrate in areas unsuitable areas for crop production (Asner et al. 2004, Joppa and Pfaff 2009). Potential hybridization between bison and cattle, direct competition, and disease transmission represent major challenges for bison conservation where cattle density is high

TABLE 2. Extent of suitable European bison habitat in areas of relatively low conservation conflict, and available and occupied areas >200 km^2 per country.

Country	Extent of suitable habitat in low-conflict areas (km^2)	No. areas >200 km^2	No. areas >200 km^2 with ≥1 free-ranging European bison herd
Austria	6041	5	
Belarus	40 099	23	8
Bosnia and Herzegovina	3300	2	
Croatia	6440	5	
Czech Republic	10 060	4	
Germany	14 132	6	
France	6863	3	
Georgia	3505		
Hungary	3255	3	
Ireland	438		
Italy	4196	1	
Kazakhstan	1190	2	
Latvia	6025	2	
Lithuania	8442	6	
Moldova	279		
Poland	45 664	34	4
Republic of Bulgaria	905		
Romania	25 765	26	
Russian Federation	107 076	49	3
Serbia	2343		
Slovakia	9966	10	
Slovenia	1443	1	
Sweden	1371		
Switzerland	419		
Turkey	429		
Ukraine	46 570	26	2

Notes: Suitable areas are defined as having a habitat suitability index (HSI) > 0.5. Only countries with at least 200 km^2 of suitable habitat in areas of low conservation conflict are shown.

(Krasinska and Krasinski 2007). A second potential conflict exists with small-scale farming, which remains widespread throughout Eastern Europe. This conflict potential may be larger than the conflict potential with intensive farming (little suitable habitat occurred in such areas; Fig. 6), particularly given the increasing importance of traditional farming for local livelihoods after the breakdown of socialism (Elbakidze and Angelstam 2007). Addressing both conflict potentials will require broadscale management of socio-ecological systems (Bienen and Tabor 2006, Gordon and Loison 2009).

Our analyses of potential conservation conflicts also showed great potential for extending the current range of European bison. The total amount of suitable habitat in areas of relatively low conservation conflict was about 40 times the area currently occupied by European bison (Table 2). The most promising candidate areas for European bison metapopulations (i.e., areas with much suitable habitat and low conflict with land use) lie in Eastern Europe (Fig. 7). Some of the candidate areas we identified already harbor small European bison herds in protected areas that may provide starting points for larger populations. Farmland abandonment, plummeting livestock numbers (e.g., −75% and −60% between 1992 and 2006 in Ukraine and Russia, respectively; *available online*),[21] and outmigration from rural areas, have reduced conservation conflict potentials, especially where intensified agriculture dominated during socialism.

Several of the candidate bison recovery areas occur in border regions, such as in the Carpathians or between Belarus and Ukraine, emphasizing the need for broadscale, trans-boundary conservation planning similar to the South African peace parks (van Aarde and Jackson 2007) or the Yellowstone-to-Yukon Conservation Initiative (*available online*).[22] The Natura 2000 Framework, which seeks to integrate nature conservation and land use, and which regards European bison as a focal species, could be an important tool for such cross-boundary conservation planning.

Poland, Belarus, and Russia all support relatively large bison populations with species management plans in place (Krasinska and Krasinski 2007, Sipko 2009). Besides Romania, which harbors large areas of unoccupied bison habitat, Ukraine emerges as another key country, because it harbors sizeable portions of several cross-border candidate areas (e.g., connecting the northern and southern Carpathians), and this habitat remains almost entirely unoccupied. Ukraine has arguably been the country where bison conservation has struggled the most after 1991 (>60% decline of animal numbers, extirpation of six out of 10 herds; Parnikoza et al. 2009), and new legislation and capacity building are

[21] ⟨http://faostat.fao.org⟩

[22] ⟨www.y2y.net⟩

urgently needed to realize the country's potential for contributing to European bison conservation. Interestingly, our habitat analyses also predicted substantial areas of suitable bison habitat outside the species historical range (Figs. 1 and 2), especially in Central European Russia. This bolsters views that this region may hold substantial conservation opportunities (Sipko 2009), particularly when considering projected warmer climate and vegetation transitions (Morales et al. 2007).

Only a few studies have modeled habitat of large carnivores and herbivores at continental scales. Our study suggests that continental-scale habitat models can give important insights into broadscale habitat selection and the spatial pattern of available habitat, thereby complementing site-specific assessment. We found widespread high-quality European bison habitat and identified several candidate sites for viable European bison populations in Eastern Europe where conflict potential with land use is relatively low. This provides hope for the conservation of large carnivores and herbivores, and for restoring their ecological roles in human-dominated landscapes. If conservation planning is to succeed in a world increasingly transformed by human activities, it has to account for real-world habitat patterns and the processes that change these patterns. Moving from bioclimatic niche models toward broadscale habitat models that incorporate patterns of land use represents a major step in this direction.

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