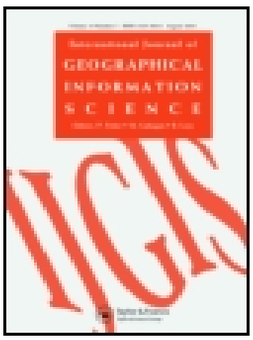


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Reintroduction of the European bison (*Bison bonasus*) in central-eastern Europe: a case study

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ABSTRACT

European bison (*Bison bonasus*), a flagship species for the burgeoning re-wildling movement, faced challenges common to large mammals globally. These include deforestation, land use conversion, poaching, and a lack of genetic diversity. Despite these limitations, organizations such as Rewilding Europe seek to reintroduce the species to its historic range. This study focused on finding suitable reintroduction locations for a population of at least 120 individuals. Through GIS-based multi-criteria decision-making using weighted linear combination and analytical hierarchy process, a model based on known bison habitat preferences, human-centered habitat constraints, and surface geography was used to identify regions large enough to accommodate a new herd. The study area included central-eastern Europe Union countries, specifically Germany, Poland, Lithuania, and Latvia. The model identified several highly suitable regions large enough to support a new herd, with the most optimal located in Poland. Highly suitable areas represented 2.7% of the study region. Relative isolation of suitable regions reinforced the challenges of promoting gene flow between reintroduced European bison herds. This model can be replicated in other conservation planning contexts, including reintroduction of large herbivores considering anthropogenic, ecological, and physical conditions.

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Multi-criteria analysis; European bison; conservation biology; reintroduction; rewilding

Introduction

Land use changes, habitat fragmentation, overhunting, invasive species, and pollution collectively threaten 25% of the world's mammal species (Maxwell *et al*. 2016). Of all species listed as threatened by the International Union for Conservation of Nature and Natural Resources (IUCN), 22.1% are mammals (Schmitz *et al*. 2015). Large mammals are three times more likely to be threatened than their small bodied counterparts and over 60% of the globe's large herbivores are considered threatened (Ripple *et al*. 2015). Large herbivores have what are considered 'high existence values,' as they exert positive influence over ecosystems by supporting trophic diversity and facilitating seed dispersal and nutrient cycling (Ramos *et al*. 2016,

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Ripple *et al*. 2015). Serving as ecosystem engineers, herbivores maintain and expand grasslands, thus increasing habitat diversity for plants and animals (Ripple *et al*. 2015). Conservation challenges exist because of complex conditions that threaten large herbivores.

Rewilding

Rewilding, as a restoration concept, remains a goal for many large mammal reintroductions. Jorgensen (2015) states that rewilding is a term researchers and environmentalists apply to many geographic and ecological contexts. Uses of 'rewilding' include: 'island taxon replacement, landscape restoration through species reintroduction, productive land abandonment, and releasing captive-bred animals into the wild' (Jorgensen 2015). European mammal rewilding studies commonly focus on one of two scenarios: 1) restoration of landscapes through species introduction, particularly for species extinct or endangered due to anthropogenic influence and 2) release of captive-bred animals. This form of rewilding promotes biodiversity with little or no need for active human management beyond initial reintroduction (Navarro and Pereira 2015, Svenning *et al*. 2016).

Geographic information systems: rewilding & reintroduction applications

As a discipline, conservation biogeography focuses on the distributional dynamics of species, individually and collectively. Degradation, extinction, habitat-suitability analysis, species-area relationships, and gap analysis form fundamental components of disciplinary research (Richardson and Whittaker 2010). In potential reintroductions of species, GIS (Geographic Information Systems) are employed to analyze relationships between environmental conditions and species distribution to gain information on habitat suitability across a landscape (Carrascal *et al*. 2017). In the case of rewilding by common European definition, or ecosystem restoration through reintroduction of apex predators or keystone species, applying geospatial analysis provides an opportunity to assess the utility of these methodologies and efforts.

Rewilding Europe is an organization founded in 2010 that promotes the reconstruction of functioning ecosystems. They currently manage nine areas across the European Union for large-scale rewilding programs (Rewilding Europe 2018) and are in the process of establishing a tenth site. European bison (*Bison bonasus*) remains a flagship species and considered for reintroduction (Rewilding Europe 2018). The work of Rewilding Europe serves as a case study for this research.

European bison overview

European bison are the largest herbivorous mammal in Europe with a historic range spanning much of the continent (including western, central, and southeastern Europe as well as the Caucasus mountains) (Ramos *et al*. 2016). The historic threats to this species include habitat loss and fragmentation, competition with livestock, low genetic diversity, disease, and poaching (Perzanowski *et al*. 2012, Balčiauskas and Kazlauskas 2014). At the end of the 19th century, two wild populations remained: one in the Białowieża Forest (located on the border of Poland and Belarus) and one on the western edge of the

Caucasus Mountains (Ramos *et al*. 2016). In 1927, the species was deemed extinct in the wild, and a new founder group of twelve captively-bred individuals became the genetic base for all living bison (Olech 2008, Schmitz *et al*. 2015). The species currently occupies less than 1% of its historic range (Kuemmerle *et al*. 2011b).

The IUCN status of European bison is 'vulnerable to extinction' (Olech 2008). After extinction in the wild a captive breeding program and reintroduction revived wild populations. By 2013, European Bison Pedigree Books noted 5,249 individuals worldwide (1,623 animals in captivity and 3,310 in free-ranging and semi-wild herds) (Raczyński 2017). The minimum viable population for bison is estimated to be 1,000, but no existing herd is close to 1,000 and no gene flow exists among current populations (Kuemmerle *et al*. 2011a, Bleyhl *et al*. 2015).

Several factors limit large population increases in free-ranging bison. There are two lineages: the Lowland line (Białowieża) and the Lowland-Caucasian Line (Caucasus Mountains), each now considered a subspecies (Olech 2008). Male bison commonly suffer from a disease impacting their reproductive organs known as balanoposthitis, particularly in the Lowland Line (Wolf *et al*. 2000). Despite existing challenges, efforts for reintroduction continue.

Research objectives: site suitability analysis as a solution

Bison herds require substantial portions of land. It is probable that the successful reintroduction will require individuals to live within human-dominated landscapes, which can result in human-bison interactions and with domesticated cattle. Siting a reintroduction of a new population requires the consideration of spatially explicit environmental factors related to bison ecology, rancher and farmer presence, and land use designations, among others. Spatial factors vary in relative importance to site suitability analysis. The methodological framework involved in site suitability analysis should integrate tools and procedures that make the decision process as unbiased and logically consistent as possible. Results are a selection of areas minimizing negative effects of bison on other organisms (i.e. domestic cattle) and systems (i.e. agriculture).

Our study aims to find suitable reintroduction sites for European bison in Central Eastern Europe, namely Germany, Poland, Lithuania, and Latvia. The goal of Rewilding Europe, to create 'the possibility for large herds of bison to once again roam the continent' (Rewilding Europe 2018), provided the inspiration for this research. We utilized a multi-criteria decision-making approach (MCDM) based on known habitat criteria, human-related spatial constraints, and surface geography to identify suitable regions to accommodate new herds. MCDM techniques are an important geospatial analysis method (Malczewski 2006). When used together, geospatial and MCDM analyses have synergistic capabilities. Their integration enables the analyst to identify and explore resulting spatial compromise alternatives based on evaluation criteria and constraints (Malczewski 2006). Analytical hierarchy process (AHP) can then be used to derive criteria weights and weighted linear combination (WLC) to overlay ranked and weighted criteria and reveal feasible spatial options (Carver 1991, Malczewski 2000, 2006). MCDM-GIS is commonly used in site suitability analysis, including for a range of ecological and environmental applications (Malczewski 2000, 2006). These methods have been used in other studies (see Malczewski 2006) and can be considered a replicable case study in large-herbivore reintroduction via MCDA site suitability analysis.

Methods

All spatial analysis was performed using ArcGIS Pro 2.3.1 (ESRI, 2019). All input layers were resampled to a resolution of 100 m × 100 m and projected to the European Terrestrial Reference System (ETRS) 1989 Lambert Azimuthal Equal-Area (LAEA) projection with meters as the linear unit of measurement.

Study region

A prior continent-scale habitat assessment found that portions of Eastern Europe provide the best conditions for large-scale bison reintroduction (Kuemmerle *et al*. 2011b). These landscapes are minimally fragmented and less likely to impose land use-related conflicts compared to the more developed areas of Western Europe (Kuemmerle *et al*. 2011b). The post-Socialist era in Eastern Europe was characterized by agricultural abandonment and growing environmentalist support (Kuemmerle *et al*. 2012). This region is where almost all free-roaming bison herds currently exist (Kuemmerle *et al*. 2011b), however, our study utilized a guiding framework related to Rewilding Europe, which focuses its efforts on EU-member countries. Therefore, the Eastern European countries of Ukraine, Belarus, and European Russian Territory were not considered for this project. The study region extent included Germany, Poland, Lithuania, and Latvia (Figure 1).



Figure 1. Study region including the countries of Germany, Poland, Lithuania, and Lat via. The historic bison range included these countries as far back as 1000 BCE (Kuemmerle *et al*. 2012).

Input variables

Almost all regions on the European continent face direct anthropogenic influence. Therefore, considerations for reintroduction sites encompassed the human-imposed constraints, natural resource features, and species preferences that impact reintroductions as opposed to species observational data. Locations of existing herds may not be the best indicator for suitable sites due to their anthropogenic placement origins. This study considered eight input variables to identify suitable reintroduction sites for bison (Table 1). These are described below.

Cultural factors

Land protection status

Current bison populations occur largely on protected lands but no standalone protected area is large enough to support the growth of an already-existing herd to 1,000 individuals (based on the World Database of Protected Areas, version 2009). Natura 2000 extends across 18% of the EU's land area and is the largest coordinated network of protected areas in the world (European Commission 2017). It is divided into three levels of protection: A denotes excellent, B is good, and C represents significant value. Values are based on restoration possibilities, habitat availability for concerned species, and isolation of focal species compared to wild populations (European Commission 2017).

Europe is also home to networks of state- and EU-based publicly protected lands outside the Natura 2000 program. These additional lands combine to bring the total European protected lands to approximately 22% (European Commission 2017). The land protection input criterion layer was comprised of a combination of Natura 2000 and general (state- and EU-level) protected land patches. Areas where these two sources of protection overlapped received higher ranks than those protected by only one of the two protection types.

Table 1. Data sources for input criteria.

Criteria	Originator	Dataset	Currentness	Extent
Distance to Agriculture	EEA	Corine Land Cover 2012	2012	33 countries in Europe
Distance to Development	EEA	Corine Land Cover 2012	2012	33 countries in Europe
Distance to Herds	Krasińska, M., & Krasiński, Z. A. Vlasakker van de 2014	n/a (Fig 23.1 from originator)	2007, updated 2010 2014	Contiguous Europe, confined mostly to northeast
Distance to Roads	DeLorme, ESRI Data & Maps	Roads	2008	World
Elevation	NASA JPL, ESRI Data & Maps	SRTM Elevation	2008	Europe and North Africa
Landcover	EEA	Corine Land Cover 2012	2012	33 countries in Europe
Land Protection Status	EC/EEA Natura 2000 Sites EEA	Natura 2000 Dataset Common Database on Designated Areas	2016 2017	Europe
Slope	NASA JPL SRTM	ESRI Elevation Data	2008	Europe and North Africa

Distance to development

A public survey conducted in Central Lithuania found that negative public perceptions of bison persist (Balčiauskas and Kazlauskas 2014). However, there is evidence that bison are relatively tolerant of nearby settlements (Wołoszyn-Gałęza *et al*. 2016). Distance to development was ranked such that closer vicinities were considered unfavorable, while farther ones were considered highly favorable using an equal interval classification scheme.

Distance to roadways

Past studies considered major roads, small roads, and forest roads as barriers to bison movement because small amounts of vehicular traffic can be hazardous (Bleyhl *et al*. 2015). However, given the great density of small roads in the study region, only larger, paved roads were considered in this study. Distance to major roads was ranked such that farther distances were considered more favorable, and vice-versa using a quantile classification scheme.

Physical factors

Land cover

A recent study utilizing multi-site habitat assessments showed bison exhibited generalist use patterns for both grasslands, croplands, and mixed forest mosaic landscapes. This research promoted the importance of these multi-site habitat assessments rather than population-specific studies to avoid assumptions about bison in other spatial and ecological contexts (Kuemmerle *et al*. 2018). Variability is often based on season, as bison tend to seek higher tree vegetation during snowpack and grasslands during warmer months (Bleyhl *et al*. 2015, Wołoszyn-Gałęza *et al*. 2016). Some land cover classes such as agriculture, infrastructure, sport facilities, urban development, and water were considered constraints. Thus, the land cover categories were converted to a binary (0,1) classification.

Distance to agriculture

Introduced bison may compete with livestock for pasture resources, threaten crops, and compromise the financial security of farmers (Hofman-Kamińska and Kowalczyk 2012). Disease transmission between bison and livestock poses a threat to successful population establishment (Kuemmerle *et al*. 2011b). Distance to agricultural land was ranked such that greater distances from agriculture were more favorable, and closer proximities deemed unfavorable using a quantile classification scheme.

Elevation

The upper elevation limit for bison is 2,100 m above mean sea level (AMSL; Olech 2008). Several studies have shown that bison rarely utilize habitats in regions above 1,000 m, though they have not shown a consistent range below this mark (Perzanowski *et al*. 2008, Deju 2011, Wołoszyn-Gałęza 2016). Despite this uncertainty, elevation was included because bison may use higher elevations as seasonal refugia and to retreat from human settlement (Wołoszyn-Gałęza *et al*. 2016). For ranking, areas of 2,100 to 2,500 m were excluded and regions of 1,000 to 2,100 m received the lowest suitability rank. The remaining regions were divided using an equal interval classification scheme and ranked accordingly.

Slope

While bison typically avoid steep slopes, relatively rugged terrain may be better for reintroduction because human development in these regions is constrained (Bleyhl *et al*. 2015). Prior studies on habitat suitability for bison found that herds did not exceed portions of habitat steeper than 28° (Bleyhl *et al*. 2015). For ranking, slopes of 28° and above were deemed restricted, and values between 0° and 20° were divided into equal intervals (5° each).

Biological factor

Distance to herds

The common size of today's bison groups is 30 to 60 individuals while populations or herds are typically doubled in number of individuals, but size and structure is largely environmentally dependent (Ramos *et al*. 2016). Annual movements for bison have been observed to rarely exceed 20 km. The data used here were created using the most recent bison herd status map that could be identified in the literature. (Krasińska & Krasińska 2014). The ranking classification for this variable excluded distances of 0 to 20 km from current bison herds to not directly overlap habitats. Distances from 20 to 506 km were ranked based on a quantile classification scheme, with distances closer to existing herds deemed more suitable.

Weighted overlay analysis

Eliminating constrained regions

Land cover was treated as a constraint variable, while all others were factor variables. A constraint scale consisting of −1 (restricted) and 1 (acceptable) was applied rather than 0 and 1, so as to avoid confusion with factor variables containing meaningful zero values (i.e. distance to roadways) (Table 2). Restricted areas were filtered out of each of factor by combining them with the constraint layer using a multiplication operation, resulting in a map of each factor variable containing positive and negative values. This step was performed before the standardized ranking of attribute values in the factor variables (Figure 2) because the feasibility of the final results is diminished if all values within a data layer are ranked relatively before the elimination of unfeasible portions of the data's extent

Table 2. Rankings and weights assigned to each factor variable.

	Distance from						
Rank	Development *(km)*	Agriculture *(km)*	Roads *(km)*	Bison Herds *(km)*	Land Protection Status	Elevation *(meters)*	Slope *(degrees)*
5	10.0–18.6	1.1–44.4	9.8–60.9	20–101	Natura A + CCDA	400–600	5–10
4	7.5–10.0	0.6–1.1	6.4–9.8	101–141	Natura A only; Natura B + CCDA	200–400; 600–800	0–5
3	5.0–7.5	0.3–0.6	4.3–6.4	141–190	Natura B only; Natura C + CCDA	0–200	10–15
2	2.5–5.0	0.1–0.3	1.2–4.3	190–263	Natura C only; CCDA only	800–1000	15–20
1	0.0–2.5	0.0–0.1	0.0–1.2	263–506	No protection	1000–2100	20–28
0			0.0	0–20		2100–2500	28–69
Weight	30.8%	28.5%	19.6%	9.8%	5.6%	3.3%	2.4%

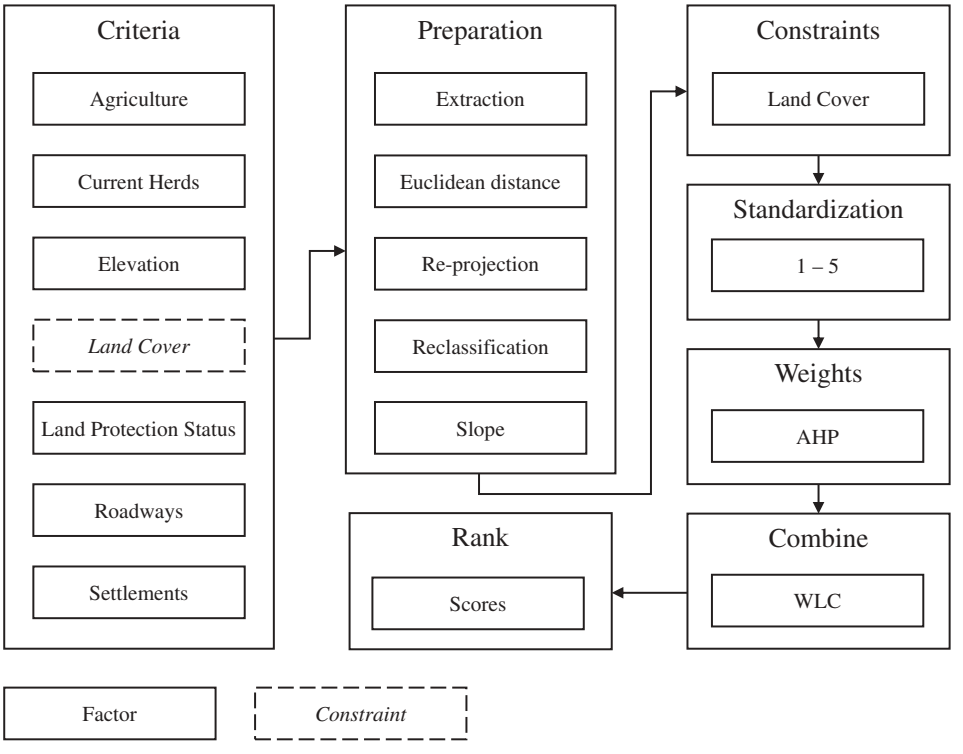


Figure 2. Workflow for a reintroduction suitability analysis for Bison in central eastern Europe.

(Malczewski 2000, 2004). This is especially true when ranking factor variables by considering the distribution of values (e.g. employing percentiles to scale continuous data).

Factor ranking

Real-life conditions can rarely be divided into binary categories, and so it is beneficial to employ a method that generates outputs that are ranked on a scale of suitability, more closely resembling natural conditions. Each factor criterion's values were standardized to a scale of 1 (least suitable) through 5 (most suitable), with the ranking 0 given to values that were unsuitable or restricted (Table 2). The zeros were transformed to Nodata since the method of combining these factors involved the addition operator rather than multiplication. This ensured that areas deemed unsuitable in any of the input layers persisted through to the final output. Thresholds were chosen based on known preferences and ecology of bison (e.g. grazing preferences), known risks and limitations posed by humans (e.g. interactions with domesticated cattle), and common practices in conservation (e.g. avoiding sites near roads to include core habitat).

Factor weighting

Analytical hierarchy process (Saaty 1994) was used to determine weights, representing relative importance, for the factor criteria (Table 3). Using AHP limits inconsistency and bias when determining the importance of criteria compared to attempting to weigh all considerations against each other at once (Carver 1991, Malczewski 2006, Romano *et al.*

Table 3. Comparison matrix used in determining relative weights for input criteria. (A) Proximity to development, (B) proximity to agriculture, (C) proximity to roads, (D) proximity to current herds, (E) land protection status, (F) elevation, and (G) slope.

Criteria	A	B	C	D	E	F	G
A	1.00	1.00	2.00	6.00	7.00	8.00	9.00
B	1.00	1.00	2.00	5.00	6.00	7.00	8.00
C	0.50	0.50	1.00	4.00	6.00	6.00	7.00
D	0.17	0.20	0.25	1.00	4.00	4.00	6.00
E	0.14	0.17	0.17	0.25	1.00	3.00	4.00
F	0.13	0.14	0.17	0.25	0.33	1.00	2.00
G	0.11	0.13	0.14	0.17	0.25	0.5	1.00

Consistency ratio: 0.070

2015). A pairwise comparison matrix was used to rank the relative importance of each factor against the rest, one at a time. A consistency ratio of 0.07 was obtained, indicating that these comparisons were consistent in a logical string (i.e. A > B > C; so, consistently, A > C).

The criteria distance to development, agriculture, and roads were given the highest weights (30.8%, 28.5%, and 19.6%, respectively) because these disturbance factors for bison are most important in the context of human interactions (Table 2) (Ziółkowska *et al*. 2012, Balčiauskas and Kazlauskas 2014, Bleyhl *et al*. 2015). Distance to herds received the next highest weight (9.8%) since effective metapopulation dynamics would help to ensure a new herd persists long-term (Akçakaya *et al*. 2007). Land protection status followed in importance (5.6%) since it has been suggested that the most suitable habitat lies outside of protected lands, though more protected lands exist now (Kuemmerle *et al*. 2011b). Finally, slope and elevation received the lowest weights (3.3% and 2.4%, respectively) since little is known about the preferences of bison with regards to these landscape characteristics (but see Wołoszyn-Gałęza *et al*. 2016), and since the study region is highly homogeneous in elevation and slope, variability in these criteria likely has little impact on bison habitat use compared to bison in more mountainous regions, such as the Carpathians.

Weighted linear combination

Once all factor criteria were ranked and all weights determined, the weighted sum of layers was calculated (Figure 3). The final suitability values (Figure 4) followed a Gaussian distribution (mean = 2.5, SD = 0.6). As a result, the values of 1 through 5 were ranked based on an equal interval classification.

Size and shape filtering

The most highly suitable values (ranks 4 and 5) were converted to vector data and simplified so that contiguous areas of large sizes could be isolated. The resulting contiguous polygons were filtered for size. Initially, the threshold of 3,333 km^2 was used, since this area is likely to support approximately 1,000 individuals assuming 60 bison per 200 km^2 based on current surveys of bison group sizes (Ramos *et al*. 2016). However, there is no historical reference point related to the area occupied by bison herds of 1,000 or more individuals. No areas of 3,333 km^2 were identified, so instead

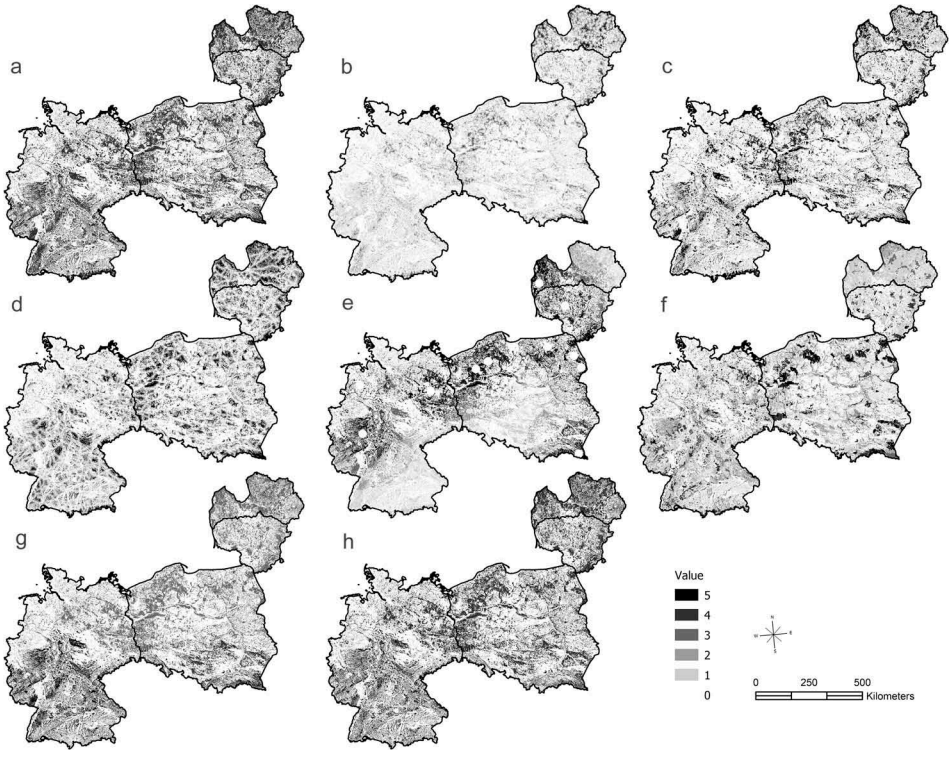


Figure 3. Ranked suitability indices for the land cover constraint (A) and each factor criterion: (B) Distance to development, (C) distance to agriculture, (D) distance to roads, (E) distance to herds, (F) land protection status, (G) elevation, and (H) slope.

a threshold of 400 km^2 was used, which, under the assumptions employed in this analysis is likely to support a 120-individual herd or population to support demographic security. Five highly suitable patches larger than 400 km^2 in size were isolated across the study region.

Sensitivity analysis

Three sensitivity analyses (Table 4) were performed to evaluate the impacts of input criteria exclusion and weight modification on the suitability results and prioritization of reintroduction sites (Nekhay *et al*. 2009); 1) all seven input criteria were considered equal in their importance and assigned weights of 14.3%, except for slope which received a weight of 14.2% to ensure that the sum was equal to 100%, 2) the AHP-derived weights were inverted so that slope was given a weight of 30.8% and distance to development a weight of 2.4% (due to the odd number of input criteria, the distance to herds criteria remained constant (9.8%) and 3) elevation and slope criteria were excluded from analysis. The remaining 5.7% weight was equally distributed to the other five criteria with the distance to development and distance to agriculture criteria receiving an additional 0.1%. A summary of the input criteria analyzed, and each iteration's weight distributions is given in Table 6.

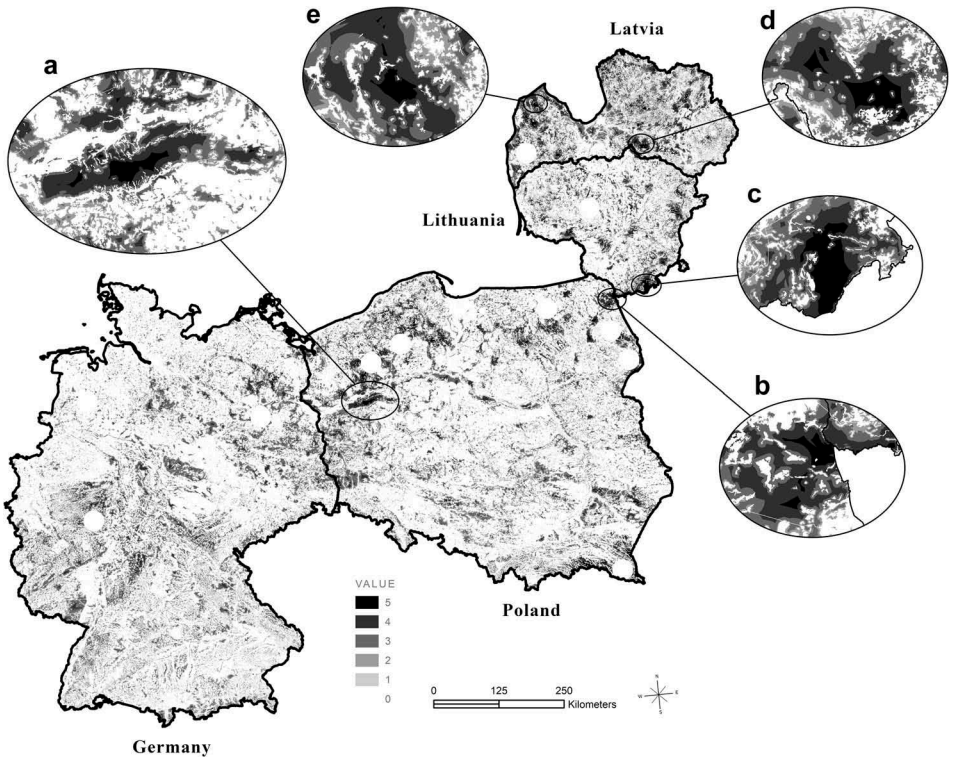


Figure 4. Composite map of all seven weighted input variables. Darkest shades denote most suitable areas for reintroduction.

Table 4. Distribution of weights applied in sensitivity analysis.

Input Criteria	AHP Weights	Equal Weights	Inverted Weights	Minus Elevation and Slope Criteria
Distance to development	30.8%	14.3%	2.4%	32.0%
Distance to agriculture	28.5%	14.3%	3.3%	29.7%
Distance to roads	19.6%	14.3%	5.6%	20.7%
Distance to bison herds	9.8%	14.3%	9.8%	10.9%
Land protection status	5.6%	14.3%	19.6%	6.7%
Elevation	3.3%	14.3%	28.5%	–
Slope	2.4%	14.2%	30.8%	–
Total	100.0%	100.0%	100.0%	100.0%

Results

Composite index scores

The workflow used in this investigation identified areas of suitable land for the reintroduction of bison by creating a composite index map spanning the extent of the study region (Figure 4).

Due to a lack of knowledge regarding herd distributional ranges, each pre-existing bison herd was given a buffer with a total area of 200 km^2 (radius of approximately 8 km) to serve as generic herd areas which were designated as restricted. The total

Table 5. Total area and percentage of study region per final weighted suitability score class.

Suitability Rank *(Composite Score Range)*	Total Area within Study Region (km^2)	Percentage (%) of Study Region
5 *(4.2–5.0)*	1,493.6	0.2
4 *(3.4–4.2)*	19,805.8	2.5
3 *(2.6–3.4)*	79,137.8	9.9
2 *(1.8–2.6)*	123,396.9	15.4
1 *(1.0–1.8)*	37,199.1	4.7
0 *(0.0)*	538,320.2	67.3

Table 6. Sites consisting of at least 400 km^2 of contiguous land that is required to support 100–120 bison. Note that site #2 extends across the border between Poland and Lithuania (Figure 4), but the majority of it falls within Poland.

Site #	Country	Total Land Area *(km^2)*
1	Poland	614.4
2	Poland	504.8
3	Lithuania	483.7
4	Latvia	441.3
5	Latvia	412.7

suitable area of the output for all five classes (i.e. all areas not eliminated by restricted designations and therefore not entirely detrimental to bison success) equated to 32.7% of the study region. Additionally, the total area for the two most suitable categories (zones with a composite suitability score of 3.4 through 5.0) was 21,300 km^2, or 2.7% or of the entire study region (Table 5).

The largest patch of highly suitable area (Site 1) was found in the western part of Poland (614.4 km^2; 0.060). This site was characterized as rectangular in shape with a serrated edge, but highly intact core area. The site falls entirety within the Puszcza Notecka forest promotion complex, and its boundary closely models that of the protected forest land. The next two largest sites were located near the border of Poland and Lithuania. Site 2 was primarily in Poland with a small section extending into Lithuania, and measured 504.8 km^2. The site was almost entirely contained within the Augustowska Primeval Forest, although the section in Lithuania was mostly non-protected. Site 3 is completely within Lithuania (483.7 km^2; 0.072). The majority of that site was coincident with the Dainava Forest and the southeastern portion shared a common area with the Cepkeliu Marsh. Both portions of Site 3 exhibited highly irregular shapes, interior 'holes', and noticeably smaller core areas. Sites four and five were located in Latvia with a majority of land area remaining unprotected. Site four (441.3 km^2; 0.063) consisted of more core area and fewer holes, while site five (412.7 km^2; 0.054) varied more in its edge and interior holes. Site five included protected lands, namely the Ance and Glass swamps and forests and Rakupe Valley nature reserve. None of the five sites included contiguous areas of greater than 400 km^2.

Model sensitivity

The results of the sensitivity analysis confirm the stability of the model since the locations and distributions of each class of suitability and the largest, contiguous sites remained

relatively constant through each iteration. Locations receiving overall suitability scores of 3.4 to 5.0 and contiguous sites of greater than or equal to 400 km^2 are highlighted in Figure 5 and in Table 8. In all four iterations, the proportions of the study region receiving each degree of suitability did not fluctuate more than 14.6% (Table 7), ranging from 0.5% in the high scores (5.0–4.2) to 14.6% in the second lowest class. Overall, the AHP weighted and analysis performed without the elevation and slope criteria generated nearly identical

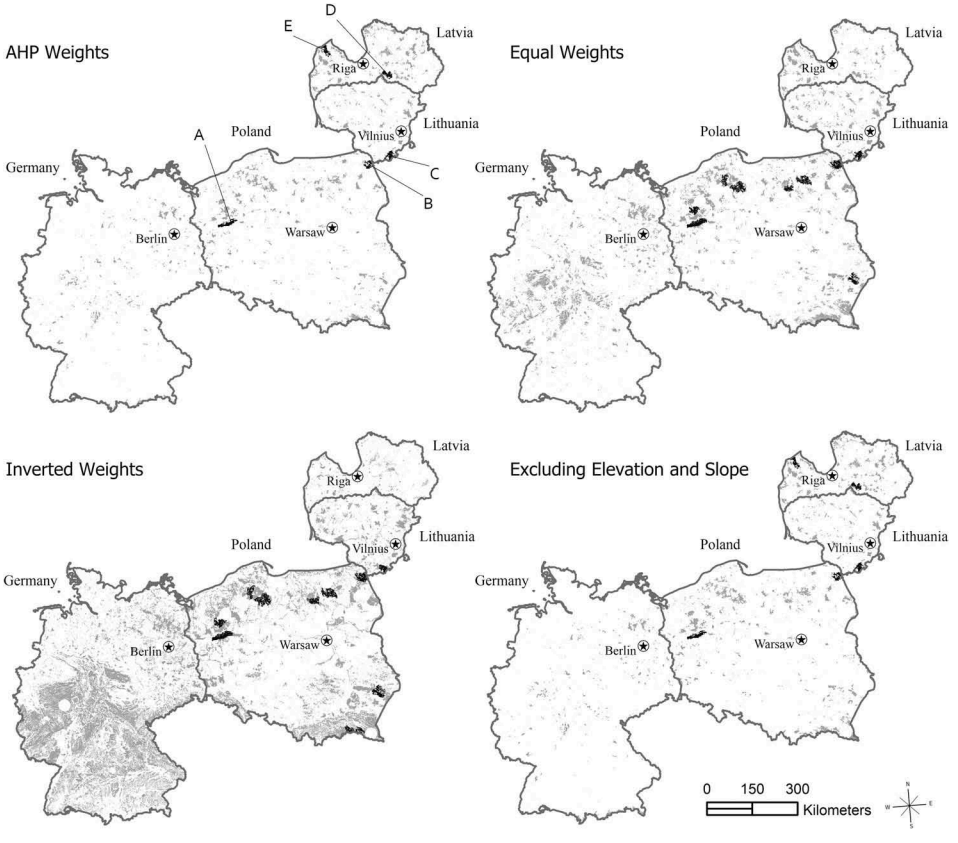


Figure 5. Comparison of location, distribution, and size of most suitable sites resulting from the original suitability analysis and three iterations of sensitivity analysis. Light gray areas depict the first and second highest suitability classes (3.4–5.0), while the black areas indicate large, contiguous regions over 400 km^2 in size. The letters indicate sites ranging from the largest (A) to smallest (E).

Table 7. Distribution of land area within the study region by suitability ranks.

	Percentage (%) of study region			
Suitability Rank *(Composite Score Range)*	AHP Weights	Equal Weights	Inverted Weights	Minus Elevation and Slope Criteria
5 *(4.2–5.0)*	0.2	0.1	0.6	0.2
4 *(3.4–4.2)*	2.5	4.8	10.0	2.6
3 *(2.6–3.4)*	9.9	16.5	21.2	9.2
2 *(1.8–2.6)*	15.4	11.2	0.8	15.1
1 *(1.0–1.8)*	4.7	0.1	0.1	6.4
0 *(0.0)*	67.3	67.3	67.3	66.5
Total	100.0	100.0	100.0	100.0

Table 8. Total number of sites, minimum and maximum land areas, and distribution of sites by country.

Sensitivity Analysis	Total number of Sites	Min/Max Total Area (km^2)	Distribution of Sites			
			Germany	Latvia	Lithuania	Poland
AHP weights	5	412.7/614.4	0	2	1	2
Equal weights	9	402.8/980.6	0	0	1	8
Inverted weights	11	415.6/1131.0	0	0	1	10
Minus elevation and slope	5	412.7/664.7	0	2	1	2

Table 9. Comparison of location, distribution, and size of largest (400 km^2) suitable sites in each iteration of sensitivity analysis. Numbers correspond to their ranking in terms of largest to smallest.

Sensitivity Analysis	Site ID				
	A	B	C	D	E
AHP weights	1	2	3	4	5
Equal weights	1	3	5	–	–
Inverted weights	2	4	9	–	–
Minus elevation and slope	1	2	3	4	5

results. Not surprisingly, however, the inverted weighted analysis resulted in the greatest differences.

The results in Poland were characterized by having the same or more suitable sites in each iteration of the analysis, while no sites were found within Germany in any of the four iterations. The total number of sites identified within Latvia and Lithuania ranged from zero to two. The inverted and AHP weighted interaction resulted in the largest sites of 1130.0 and 614.4 km^2, respectively.

Each analysis iteration generated a different number of suitable sites and it is important to note that many of the same locations were identified multiple times and with similar total land area rankings (Figure 5; Table 9). For example, site A was found to be the largest suitable site in three out of the four analysis iterations. Site B was found to be in the top three in terms of overall land size in all but one iteration, while sites D and E were not identified in either the equal or inverted weighted iterations. Site C was identified as being near the top in all but the inverted weights iteration. While the core for these sites remained generally the same, they increased or decreased their footprint based on the characteristics of the surrounding areas.

The most suitable sites were consistent across sensitivity analysis iterations. This provides further confidence that the original AHP weighting scheme is appropriate for identifying those areas that have the valid combination of physical and cultural factors needed to provide suitable habitat for bison.

Discussion

Interpretation of results

The small number of highly suitable reintroduction regions in the composite index (Figure 4) was expected because the weighted overlay included land cover as a constraint, which eliminated or fragmented much of the study region. Fortunately,

the data used for this variable had more than 30 categories of land-use and land cover types, so the elimination of restricted land cover types and preservation of desirable land cover types was highly refined. Consequently, areas surrounding suitable patches were lower in suitability, and this is consistent with the literature in that current herds maintain no genetic flow among them (Kuemmerle *et al*. 2011a, Bleyhl *et al*. 2015), the surrounding lands are barriers to movement, and isolated 'pockets' comprise the areas suitable for bison herds. Previous studies of the southern range of European bison in the Carpathian Mountains were more favorable in terms of number of potential reintroduction sites (Kuemmerle *et al*. 2011b, Ziółkowska *et al*. 2012), which were not included in this study

The size and structure of bison groups and populations is largely environmentally dependent (Ramos *et al*. 2016), so the size and shape of the reintroduction area has direct influence on herd size. This study did not yield any regions that could support 1,000 individuals in a contiguous area (assumed to be approximately 3,333 km^2) given the constraints of human development and transportation networks. The shortage of large tracts of land to support bison is a challenge for conservationists, but the Natura 2000 and other networks of publicly funded protected areas are actively working to increase connectivity between smaller herds (by protecting and restoring connective land tracts) and to use genetic analyses to promote diversity.

Data availability was temporally limited, and this may have impacted the size, shape, and isolation of the resulting habitat patches. A small number of the input data layers, such as elevation and slope, are constant, but other inputs are continuously changing. The study would have benefited from current data layers, however, a more recent data layer was not publicly available. Although the least-current non-static data layers used here were both published within the last decade (2010), both of these layers (roadways and current bison herd status) are likely to have changed in the eight years between publication and use in this analysis, especially given the highly dynamic anthropogenic landscapes shifting across Europe (Helmer, 2015, Navarro and Pereira 2015).

Distribution & characteristics of potential reintroduction sites

Following size filtration, the largest amount of suitable area for reintroduction (Table 6) and the top two potential sites were found in Poland. All five highly suitable sites were located outside of Germany. This is consistent with a previous study that found Eastern Europe to be minimally fragmented and more suitable for large-scale bison reintroduction (Kuemmerle *et al*. 2011b). Poland has moderate development but also a well-established network of protected lands. Poland also places cultural value on bison. The Białowieża Forest was the last stronghold of bison in the wild before their ultimate extinction and subsequent reintroduction (Bison Specialist Group 2015). Bison continue to be highly protected in the forest, which is the historic hub for much of the behavior and movement studies on which successful reintroductions occur today (Bison Specialist Group 2015). The largest potential sites (after filtering for size) from the weighted analyses were near to already-established populations, many of which lie in Poland or outside of the study region in eastern non-EU member countries. It is important to note areas surrounding current bison herds and potential future herds were restricted, not just areas of low suitability.

Further understanding of the ecosystems and protected areas underlying highly suitable sites can provide insight into more specific site selection. One consideration for

the most suitable site (Site 1), located within Notecka Forest in Northwestern Poland, relates to its forest ecosystems. While the habitat preferences of European bison are detailed differently across sources, some authors have noted that bison prefer mosaic landscapes, including mixed deciduous coniferous forest areas (Bleyhl *et al*. 2015). Notecka Forest, a large forest complex of approximately 137,000 hectares, is comprised of 97% coniferous and mixed coniferous forest including 95% pines based on past artificial plantings (Lesisz and Osińska-Skotak 2017). While portions of the forest are protected, free-roaming bison populations may be limited by habitat constraints.

The second most suitable site (Site 2), located within the Augustowska Primeval Forest network, is in a region with special protection status within Natura 2000 (Bialystok 2012). The forest is home to nearly 50 mammal species, including a natural bison predator, the wolf (Bialystock, 2012). While pines dominate the area, there are patches of mixed forest within (Bialystok 2012). The Augustowska region may provide habitat and trophic connections in support of bison reintroduction. In fact, in 2018 an introduction occurred (Vlasakker, 2014, Klich *et al*. 2018). This recent bison reintroduction work in the Augustowska region supports the results of our model in selecting suitable reintroduction locations for the species.

Site 3, located in southeastern Lithuania, was adjacent to several existing bison populations. Lithuania is one of the few countries currently home to free-roaming populations (Olech 2008). With some overlap with the Dainava Forest, the largest forest in Lithuania, this site is found in regions supporting wolf populations (Lithuanian Fund for Nature 2019). Highly suitable sites numbers 4 and 5 were in Latvia. Of all sites, these exhibited the smallest proportions of protected areas. Site 4 overlapped with the smallest amount of protection area. Small amounts of protection area could present challenges to enforce laws protecting bison in these regions. These examples provide some insight into the factors to be considered in more depth to assign priority to sites selected by the suitability model.

Calls for further study: greater understanding of bison preferences and distributions

Additional criteria such as snow cover and forest fragmentation could be considered, though doing so may further isolate potential reintroduction patches. The amount of snow cover throughout the region can have an effect on the amount of vegetation and food availability during the winter season, and herd movement has been observed in times of snowfall (Wołoszyn-Gałęza *et al*. 2016). Forest fragmentation was not considered in this study because, while recent research shows that bison are refugee species that prefer edge habitat, there are still those who describe bison as mostly forest-dwelling (Kuemmerle *et al*. 2011b). Because of this lack of consensus on bison preferences, this analysis considered general forest and meadow land cover types to be of equal, highly suitable ranking. Future research into the preferences of bison with regards to core or edge habitat may necessitate weighing either of these land cover types more heavily.

A more comprehensive understanding of the current bison population ranges is needed for future studies. Past studies have incorporated site-specific assessment opinion and tracking data to map specific range maps for herds (Kuemmerle *et al*. 2011b, Ziółkowska *et al*. 2012). In this study, the bison herd ranges were generalized to a standard range size of 200 km^2 (in circles buffering herd points) since the most current data that could be

identified on the status of bison herds existed as point data. This likely caused an inaccuracy in the data, with ranges either being over- or underestimated. A more refined understanding of herd range shapes could bolster our understanding of landscape preferences and barriers to metapopulation connectivity.

Implications for conservation success of bison

Bison remain threatened across the European landscape due to a variety of factors including human conflict and poaching, habitat loss, and lack of genetic diversity. Captive breeding programs and small herd size reintroductions within confined areas have been considered successful, but now the bison promotion project is in transition. Organizations such as Rewilding Europe and The Bison Specialist Group are striving to create conditions that will not require continuous human intervention. Conservation success for bison will be dependent on enlarging herds and ensuring connectivity and gene flow between reintroduced populations (Ziółkowska *et al*. 2012). Careful planning to avoid contact with disease-bearing livestock and to ensure suitable habitat is also required for additional reintroduction schemes. All of these considerations can be accounted for using spatial data and MCDM approaches such as weighted linear combination and analytical hierarchy process in a GIS (Carver 1991, Malczewski 2006). The methodological framework used here yielded potential reintroduction areas that met a strict and comprehensive set of criteria, and these findings can inform conservation and management decisions in the future, and specifically help with determining the minimum area as well as viable population sizes for reintroduced bison. The framework used in this study can be adapted to other species in need of reintroduction.

The vector and raster data and codes that support the findings of this study are available in Zenodo with the identifier doi: 10.5281/zenodo.3448825.

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No potential conflict of interest was reported by the authors.

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