Connectivity or isolation? Identifying reintroduction sites for multiple conservation objectives for wisents in Poland

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Abstract

Large herbivores and carnivores today often only occupy small fractions of their former ranges, and restoring them is a conservation priority. Reintroductions may serve two critical goals in this context: (1) to expand and connect existing populations, or (2) to increase the number of separate populations as insurance in case individual populations are lost, for example, to disease. We developed an approach to identify reintroduction sites for both purposes, using an applied example of European bison or wisent (*Bison bonasus*) in Poland. Using a large occurrence dataset from all extant herds in Poland, we mapped suitable wisent habitats throughout Poland using a species distribution modelling approach. We identified 47 patches of suitable habitat, together covering 20,710 km^2, and used graph theory tools to identify the top candidate reintroduction sites for (1) connecting existing herds into larger metapopulations or (2) establishing 'reservoir' herds that could serve as a backup in case of mass die-offs. The most well-connected habitat patches ranged between 203 and 728 km^2 and occurred mainly in north-western and south-eastern Poland, in close vicinity to other free-ranging herds. In contrast, candidate sites for reservoir herds were smaller (204–410 km^2) and occurred mainly in central Poland. Our approach provides a possible blueprint for wisent reintroductions in Poland. More broadly, our work also highlights how jointly planning for multiple conservation goals for wide-ranging species that depend on reintroductions or translocations can be achieved at the regional scale.

Introduction

Large mammals around the world are under increasing pressure from habitat loss and overhunting, with many species holding out only in small, fragmented populations (Dirzo *et al.*, 2014; Ripple *et al.*, 2015). Preventing local extirpations and restoring populations across their historical ranges are central conservation goals, given the critical importance of large mammals in food webs and for ecosystem functioning (Gordon & Loison, 2009; Owen-Smith, 2014; Ripple *et al.*, 2014). While some large mammal populations have recently rebounded (Chapron *et al.*, 2014), many species still urgently depend on conservation management to restore them across their historical ranges.

Reintroductions are a key tool for broad-scale population restoration (Seddon *et al.*, 2014; Corlett, 2016). New populations make an important conservation contribution by increasing the total number of individuals of threatened species. In addition, reintroductions increasingly take place within wider strategies to increase connectivity and genetic exchange among populations, and thus to establish larger metapopulations

(Halsey *et al.*, 2015; Peters *et al.*, 2015). This requires identifying places where new populations would maximally contribute to linking existing but currently isolated herds (Kuemmerle *et al.*, 2011*a*2011a). However, managing towards metapopulations can backfire in case of wildlife disease outbreaks, which are an increasing threat to species of conservation concern globally (Daszak *et al.*, 2000; Aguirre & Tabor, 2008). For instance, the rinderpest has triggered mass die-offs of African ungulates (Holdo *et al.*, 2009), Ebola outbreaks pose a major threat to Africa's great apes (Leenderz *et al.*, 2017) and facial tumour disease extirpates Tasmanian devil populations throughout their range (McCallum, 2008). Effective reintroduction strategies must therefore increasingly manage the trade-off between establishing larger metapopulations on the one hand, and maintaining reservoir populations to fall-back in the case of disease outbreaks.

Wisents or European bison (*Bison bonasus*) are an example of a species where managers face this trade-off. Once roaming over large parts of Central and Eastern Europe, habitat loss and hunting have decimated wisent herds for

centuries (Kuemmerle *et al.*, 2012), leading to their extinction in the wild in the early 20th century. Fortunately, some animals survived in zoos, and an organized breeding and reintroduction program was quickly initiated. The recovery of wisents from the brink of extinction is now one of the greatest success stories of conservation globally: today over 4500 individuals roam in about 40 free-ranging herds, mainly in Eastern Europe (Krasińska *et al.*, 2014; Raczyński, 2017).

Despite these numbers, the species remains vulnerable as a result of the extremely low genetic diversity, as all extant wisents trace back to only 12 founder individuals (Krasińska & Krasiński, 2013). Current herds are small, and occur in isolation from each other, in Poland and elsewhere (Kuemmerle *et al.*, 2011*b*2011b). In order to safeguard European bison in the future, larger and more connected herds are needed (Kuemmerle *et al.*, 2011*a*2011a; Bleyhl *et al.*, 2015). This requires identifying places where new herds could help to link existing but currently isolated herds (Schnell *et al.*, 2013; Perzanowski & Januszczak, 2016).

However, managing towards more connected wisent herds carries a substantial risk of catastrophic loss. Disease outbreaks pose a real threat to the species, because of weak resistance to infectious diseases. For instance, the entire herd at Pszczyna in Poland was lost due to foot and mouth disease in 1953/1954, about 30% of all wisents in the German breeding centre Hardehausen died from blue-tongue disease in 2007 and a bovine tuberculosis outbreak in the Bieszczady Mountains in 2012/2013 resulted in the elimination of this herd (Kita & Anusz, 2006; Perzanowski *et al.*, 2010; Pigan & Wojtowicz, 2015). Given the low effective population size of the global wisent population, such mass die-offs can be very detrimental for the conservation status of the species as a whole (Krasińska *et al.*, 2014). Thus, as an insurance against outbreaks spreading through larger wisent herds, it would be beneficial to maintain smaller, geographically separated 'reservoir' herds from which to restore herds after disease outbreaks. An effective bison reintroduction strategy should thus identify both areas where larger metapopulations of wisents could be established, as well as isolated habitat patches where reservoir herds could be reintroduced.

In Poland, establishing new wisent herds is furthermore timely, as some herds are apparently reaching 'socially acceptable' carrying capacities. Wisent presence can conflict with land use and forestry, as well as impact people directly (e.g. via vehicle collisions). As these conflict will increase as wisent herds grow, social acceptance of wisents in the landscape is likely to decline, potentially undermining long-term conservation success. To manage wisent herds, substantial culling of individuals is therefore increasingly applied to prevent conflicts to escalate. Culling in the case of a threatened species with an extremely low genetic variability, however, is highly questionable from both a moral and ecological perspective. Moving excess animals into suitable habitats elsewhere in Poland would therefore be a win-win situation for wisent conservation (Perzanowski & Olech, 2014).

Here, we developed an approach to identify reintroduction sites for multiple conservation goals, specifically, for increasing connectivity of existing herds and for establishing reservoir or insurance herds. Our overarching aim was to identify areas that provide suitable habitat for new wisent herds in Poland, and thus help restore the species across its historical range. Specifically, our objectives were to

1 Map suitable wisent habitat across Poland based on occurrence data from all extant herds.
2 Identify patches of suitable habitat that could host larger wisent herds.
3 Analyse the connectivity among these patches to identify (i) well-connected patch networks that could host wisent metapopulations, as well as (ii) isolated habitat patches that could function as reservoir herds.

Materials and methods

Study area

Our study area was the entire 312,000-km^2 territory of Poland. About half of the territory consists of agricultural lands, mainly cropland, but also major shares of meadows and pastures. In northern and north-western Poland, large scale monocultures dominate (e.g. cereals, rape seed), while in the south-eastern part of the country a majority of farms consist of small plots with a variety of crops (Statistical Yearbook for Poland, 2017). About a third of the study region consists of forestland (about 920,000 km^2), which is mostly owned and managed by the state. Forests in Poland are typically associated with poor soils, with habitat structure determined by soil type. The majority of forested area is coniferous, dominated by Scots pine, and smaller shares of oak, birch, spruce, beech and alder. Stand ages are relatively evenly distributed, with only a few stands older than 100 years (<10% of the total forested area; Milewski, 2016; Statistical Yearbook for Poland, 2017). Various forms of nature protection affect about two thirds of the Polish territory, however, only about 1% of the country is strictly protected (Statistical Yearbook for Poland, 2017).

Human population density in Poland varies greatly, from <60 people per km^2 in Podlaskie Province to >350 people per km^2 in Silesia. Generally, the lowest population densities are found along Poland's eastern border and in the north-western provinces (Statistical Yearbook for Poland, 2017). Only a few major highways exist, with most traffic occurring on provincial roads (Statistical Yearbook for Poland, 2017). Fences are currently planned or under construction along the main motorways, and will likely enforce the barrier function such highways constitute (Ziółkowska *et al.*, 2016*b*).

Wisent habitat and occurrence data

Poland has been instrumental in wisent conservation for centuries. Wisents in Central Europe survived for a long time only in the Białowieska Forest, a royal hunting ground, and after they were extirpated from there, Poland carried out ex situ conservation in breeding centres and zoos. The first

reintroduction of wisents back to the wild also occurred in Poland, in 1952, when the first animals were released in the Białowieska Forest. A second major milestone in restoring wisents was the creation of a free-ranging herd in the Bieszczady Mountains in the Carpathians in 1963. Subsequently, free-ranging herds were established at Knyszyńska and Borecka Forests in north-eastern Poland, and in Western Pomerania (Fig. 1). These five herds utilize lowland and mountainous areas with a varying degree of open land and different forest types (Kuemmerle *et al.*, 2018) (see Supporting Information for detailed descriptions of the five herds). Today, the Polish population of wild wisents is the largest in the world, with about 1640 free-ranging individuals (Balciauskas, 2000; Perzanowski & Marszałek, 2012; Krasińska *et al.*, 2014; Raczyński, 2017).

We gathered a comprehensive dataset of bison occurrence points (telemetry data and field-tracked signs of habitat use) from all five free-ranging Polish European bison herds totalling 286,810 individual locations (Kuemmerle *et al.*, 2018). These data came from both radio/satellite collaring (97% of all points) and direct observations in the field (only Bieszczady, 3% of all points). Data from collars came from a total of 45 individuals (20 male, 25 female) with monitoring periods per individual ranging from 128 to 658 days (Table 1). To reduce spatial clumping of occurrence data, we randomly selected 500 points per herd with a minimum distance of 500 m (Kramer-Schadt *et al.*, 2013), treating the neighbouring Białowieska and Knyszyńska herds as one herd. This resulted in a final dataset comprising 1747 points (not all herds were large enough to contain 500 points with 500 m minimum distance).

Habitat suitability mapping

For mapping suitable European bison habitat throughout Poland, we used maximum entropy modelling (Maxent) (Elith *et al.*, 2006; Phillips *et al.*, 2006). Maxent is a machine-learning technique that estimates habitat suitability by contrasting the predictor variable values at presence locations to the overall distribution of the predictor variable values drawn at random locations (Merow *et al.*, 2013). We parameterized the models with 100,000 background points, a maximum of 2500 iterations and default settings for convergence thresholds and regularization (Phillips & Dudik, 2008). Furthermore, we used only quadratic and hinge features to limit model complexity and to prevent over-fitting (Elith *et al.*, 2011; Merow *et al.*, 2013). Because sampling background points from too broad areas might result in overly simplistic models (VanDerWal *et al.*, 2009), we took background points only in the minimum convex polygons of
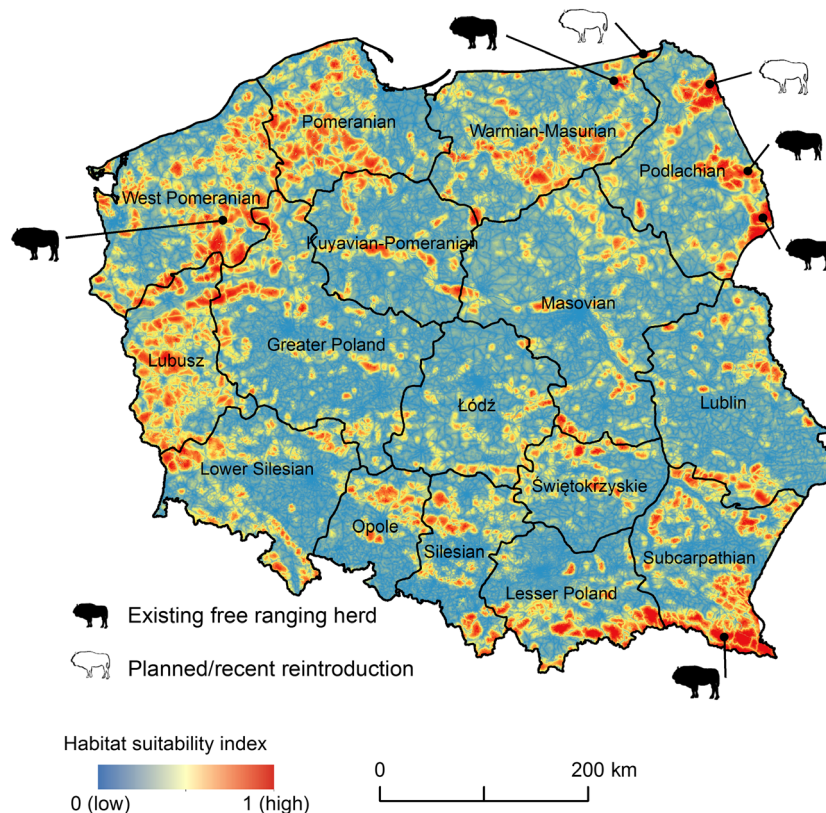
Figure 1 Wisent habitat suitability across Poland. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.onlinelibrary.wiley.com.]

Table 1. Overview of wisent occurrence data used in this study (see Kuemmerle *et al.*, 2018 for a detailed description of the occurrence data)

Herd	# of collared animals	Years	Total # of points	# of points after rarefying
Białowieska	3 m/5 f	2012–2013	58,807	245
Bieszczady	4 m/2 f	2001–2010	10,466[aa]	500
Borecka	2 m/4 f	2012–2013	57,188	261
Knyszyńska	4 m/1 f	2012–2013	43,659	241
West Pomerania	7 m/13 f	2011–2013	116,690	500

[a]Data from this herd contained 7502 points based on field-observed signs of wisent occurrence (e.g. tracks, dung, feeding marks). Because few telemetry data were available for Bieszczady, and because the herd roams across a fairly large territory, we used data from a wider time-period for this herd (see Kuemmerle *et al.*, 2018 for details).

each herd and 50 km buffers around these minimum convex polygons. This roughly represents the maximum dispersal of female wisents and cow/calf groups (Kuemmerle *et al.*, 2011*a*2011a; Krasińska & Krasiński, 2013).

To characterize habitat suitability, we used seven predictor variables (Table 2) found to be important in previous work on wisent habitat (Kuemmerle *et al.*, 2010; Bleyhl *et al.*, 2015). We obtained land-cover information from the CORINE Land Cover database (http://www.eea.europa.eu/data-and-maps/), and aggregated the original class catalogue into eight land-cover classes: coniferous forest, mixed forest, broadleaved forest, grassland, cropland, open settlements, dense settlements and water. To characterize forest fragmentation, we applied morphological image segmentation based on the combined forest classes, using an eight-neighbour rule and 100-m edge-width (Vogt *et al.*, 2007). This resulted in the five forest fragmentation categories: core forest (i.e. interior forest), edge forest, islet forest (i.e. forest patches too small to contain core forest), perforation (i.e. interior edges) and non-forest. As a second measure of forest fragmentation, we calculated forest neighbourhood variables, which capture the share of forests within a defined neighbourhood around a grid cell (Schadt *et al.*, 2002). We tested different neighbourhoods (100, 500,

1000, 2000, 4000 m), and used the neighbourhood distance resulting in the highest model area under the curve (AUC) (4000 m in our case). Finally, we calculated the Euclidean distance of every non-forest pixel to the nearest forest edge.

We derived information on slope based on the topography model from the Shuttle Radar Topography Mission (http://srtm.csi.cgiar.org). Human disturbance was measured as the Euclidean distances to roads and settlements. Roads were obtained from OpenStreetMap (www.openstreetmap.org) using categories: motorway, trunk, primary and secondary. Settlement data were based on the CORINE dense settlement class. We resampled all predictors to a 100-m resolution and a Lambert Equal Area projection. All model predictions were carried out at a resolution of 100 m.

To assess model fit, we used a 10-fold cross validation, using the AUC as a goodness-of-fit measure. To assess variable contributions, we build single-variable models, and used a jackknife test that compares models with and without a specific variable (Phillips & Dudik, 2008). While single-variable models give insight into the overall explanatory power of a variable, the drop in AUC when excluding a variable provides information on that variable's unique contribution to the overall model.

Identifying possible reintroduction sites

To delineate suitable habitat patches, we used the maximum training sensitivity plus specificity threshold (Liu *et al.*, 2013), calculated as the mean threshold across the 10 Maxent replicate runs. We converted patches to polygons and combined patches when they were closer than 500 m and not separated by a major road. To identify candidate sites for wisent populations, we selected aggregate patches larger than 200 km^2, an area required to sustain a herd of 50–60 animals (Pucek *et al.*, 2004).

Analysing connectivity and isolation among habitat patches

To assess connectivity among habitat patches, we calculated a resistance surface to wisent movements. We inverted and linearly rescaled the habitat suitability map to values from 1

Table 2. Predictor variables used to model and map wisent habitat suitability

Predictor	Data source	Data type	Unit	Description
Land cover	CORINE 2012	Categorical	–	Eight broad land-cover classes (coniferous forest, mixed forest, broadleaved forest, grassland, cropland, open settlements, dense settlements and water)
Forest fragmentation	CORINE 2012	Categorical	–	Five forest fragmentation components (core forest, edge forest, perforation forest, forest islets) derived using morphological image segmentation
Distance to forest	CORINE 2012	Continuous	m	Euclidean distance to the nearest forest pixel
Forest neighbourhood	CORINE 2012	Continuous	%	Share of forest within a 4000 m neighbourhood
Slope	SRTM	Continuous	deg.	Slope in degrees
Distance to roads	OpenStreetMap	Continuous	m	Euclidean distance to nearest road (classes: motorway, trunk, primary, secondary and tertiary)
Distance to settlements	CORINE 2012	Continuous	m	Euclidean distance to nearest settlement

CORINE = CoORdination of INformation on the Environment; SRTM = Shuttle Radar Topography Mission

(resistance for areas with highest habitat suitability) to 100 (resistance for areas with lowest habitat suitability). This assumes that habitat suitability is a reasonable proxy of the suitability of a movement (Ziółkowska *et al.*, 2016a). We used settlements and motorways as total barriers, primary roads as partial barriers with a resistance value of 1000 and secondary roads as partial barriers with a resistance value of 500. These values were adopted from a more fine-scale wisent connectivity analysis in southern Poland (Ziółkowska *et al.*, 2016b). We calculated the least-cost path for all patch pairs in cost-distance space using the Linkage Mapper Toolkit (McRae & Kavanagh, 2011). The most connected patches were those with lowest cost-weighted distance to already occupied patches. The most isolated patches were those with highest cost-weighted distance to any other patch. We ran the connectivity analysis at 300-m resolution because it was computationally demanding and tests on subsets suggested no substantial difference when comparing to runs based on the 100-m grid.

Results

Our habitat suitability model identified widespread wisent habitat, mostly in northern and north-western Poland (Fig. 1). Larger clusters of patches with high habitat suitability occurred particularly in south-eastern Poland (i.e. in the Carpathians), in north-eastern Poland (e.g. Warmia-Masuria, Podlaskie) and western Poland (e.g. West Pomerania, Lower Silesia). The threshold value used to separate habitat patches from the matrix (i.e. the maximum training sensitivity plus specificity threshold) was 0.39 in our case.

The variables that contributed most to determining wisent habitat suitability in Poland were forest neighbourhood (64% gain contribution) followed by forest fragmentation (13%) and distance to roads (12%). In general, wisent habitat suitability increased with increasing forest cover at the landscape scale. Wisent habitat was further characterized by larger areas of core forest and interior forest edges (indicating the importance of forest openings). With increasing distance to roads and settlements, wisent habitat suitability increased. Our Maxent model had an AUC value of 0.77.

We identified 47 habitat patches with an area >200 km^2, together covering 20,710 km^2 (Fig. 2). Patch sizes ranged from 203 to 1439 km^2 (mean: 441 km^2, SD: 282 km^2). The majority of these patches were located in the provinces of Western Pomerania and Pomerania, and the Lubusz and Subcarpathian Pprovinces. Forest was the main land cover within the habitat patches we identified (on average, forest covered 81% of these patches), but most patches contained substantial open areas as well (19% on average). Almost all patches (44 of the 47) were at least partly inside a protected area (i.e. IUCN categories II, IV or V), with five patches located at least partly inside a strictly protected area (i.e. IUCN category II). In total, 30% of the total patch area were protected. Three potential habitat patches were crossed by a motorway (Fig. 2).

Several suitable habitat patches were located in close proximity to each other (mean Euclidean distance among neighbouring patches was 18 km; Fig. 2). Least-cost path length between neighbouring patches ranged from 0.6 to 125 km (mean: 20 km, SD: 32 km). Spatially, three clusters of relatively well-connected patches occurred in (1) western, (2) north-western and (3) south-eastern Poland. The top five patches with lowest least-cost path distance to currently occupied patches were distributed close to these three clusters. On average, the top five connected patches were 374 km^2 in area (range: 203–728 km^2).

We also identified the five most isolated patches with highest least-cost path distance to other patches. These patches are potential priority sites for establishing reservoir herds (Fig. 2). Three of those patches were found in central Poland (Fig. 2). All of the top five isolated patches were relatively small (range: 204–410 km^2 and 278 km^2 on average, compared to 441 km^2 average patch size for all patches).

Discussion

Reintroductions and translocations are important tools to restore species throughout their former ranges. This is particularly relevant for large mammals, which play important ecological roles, yet have been extirpated from wide areas of their historical ranges. Where recent land-use and socio-economic changes have lowered human pressure in rural areas, such as in post-Soviet Eastern Europe, opportunities for large mammal restoration are emerging. Using the case of wisents in Poland, we highlight an approach to identify a set of potential reintroduction patches that serve two complementary conservation goals: connecting existing herds into larger metapopulations on the one hand, and establishing reservoir herds as an insurance against disease outbreaks on the other. By combining species distribution and connectivity modelling, we highlight that there is still ample unoccupied and fairly well-connected habitat for wisents in Poland (>20,000 km^2). Five patches in western, north-western and south-eastern Poland appear particularly promising for expanding herds and for linking existing herds into larger wisent metapopulations. Assuming a minimal required area of one individual per km^2, these patches could host around 500 additional animals (Krasińska *et al.*, 2014). In contrast, the five most isolated habitat patches, candidates for reservoir herds, occurred mainly in central Poland and may host at least 400 individuals. We caution that these numbers are conservative estimates and that actual carrying capacities of patches depend on a range of factors not considered here (e.g. forage quality). At a time when several wisent herds in Poland are reaching socially acceptable carrying capacities, resulting in a need to either cull or relocate individuals, our analysis provides a possible blueprint for translocations and reintroductions in Poland. More generally, we highlight how multiple conservation goals can be addressed through identifying a set of reintroduction sites for large mammals, and make full use of rewilding opportunities.
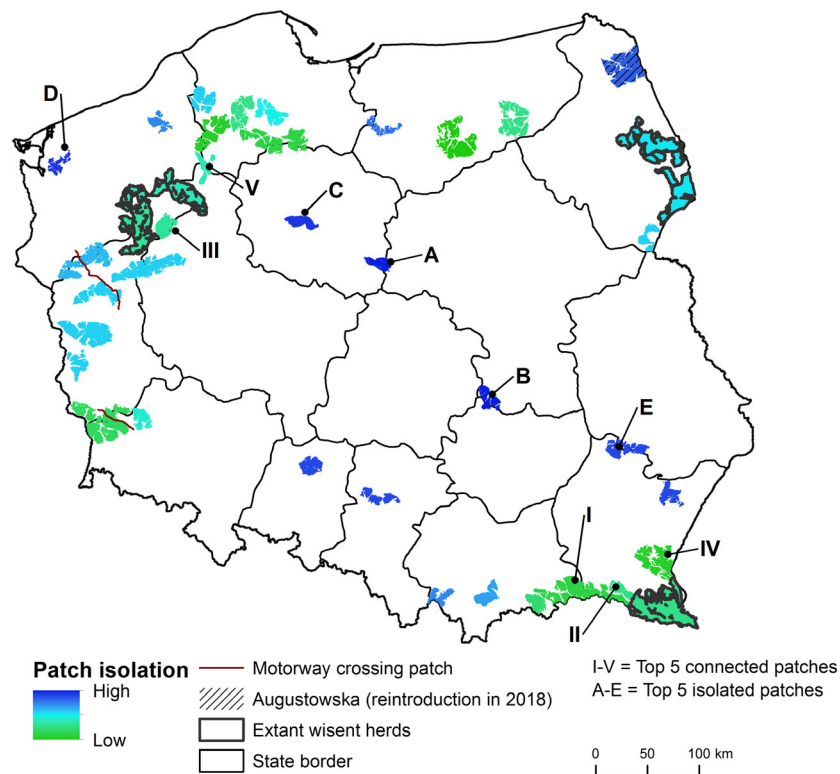
Figure 2 Potential wisent habitat patches throughout Poland and their level of isolation. Patch isolation was based on least-cost path distance to the closest neighbouring patch. The five most connected (ranked from I to V according to their level of connectedness) and the five most isolated patches (ranked from A to E according to their level of isolation) are highlighted. Most connected patches were those with lowest least-cost path distance to a currently occupied patch. Most isolated patches were those with highest least-cost path distance to any neighbouring patch. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.onlinelibrary.wiley.com.]

Saving the wisent from extinction and re-establishing it in the wild have been a spectacular conservation success. Starting with just 54 animals surviving in captivity, the global wisent population now counts more than 4500 free-ranging animals (Raczyński, 2017). However, no herd is currently large enough to persist indefinitely, and establishing larger wisent metapopulations is therefore important (Schnell *et al.*, 2013; Perzanowski & Januszczak, 2016). Our analyses identified three clusters of patches that appear particularly promising: (1) south-eastern Poland (i.e. Bieszczady National Park, Magurski National Park and their surroundings) where already three free-ranging herds exist, (2) north-eastern Poland, that hosts herds in Białowieża, Borecka and Knyszyńska, and where an additional reintroduction project in one of the patches we identified is already ongoing (i.e. Augustowska) and (3) western Poland, where several bison herds already occur, and that might be connected to potentially suitable habitat complexes in Eastern Germany. Importantly, while these patches can make a substantial contribution to connecting existing herds, they can by themselves foster larger wisent herds. Considering the generally positive attitude towards wisents in contemporary Polish society, the ample unused habitat for wisents should provide promising conditions for expanding wisent conservation efforts.

Although in Poland range expansions of extant herds into neighbouring territories have occurred, especially in Western Pomerania, colonization of unoccupied habitat patches has been unexpectedly slow (Tracz & Tracz, 2010). Two reasons possibly explain this. First, dispersal and range expansion might be density-dependent, and only occur as wisent herds reach or exceed densities at which resources (i.e. food) become limiting. Because substantial conflicts with agriculture, forestry and transport are likely to ensue at such high densities, the socially acceptable carrying capacity is likely much lower (Balciauskas & Kazlauskas, 2014). In addition, the practice of winter feeding in some herds, mainly used to prevent damages to agriculture and forestry, may discourage outmigration. Second, dispersal can be inhibited by barriers, especially more heavily trafficked roads, as highlighted for the Bieszczady herd that is currently not expanding westward despite the ample suitable habitat (Ziółkowska *et al.*, 2016b 2016b). Thus, although natural range expansion might occur, translocations of animals from existing herds to other suitable habitat patches, as well as exchange of individuals among herds, will likely be needed to achieve the long-term goal of larger, viable wisent metapopulations (Olech & Perzanowski, 2011; Perzanowski & Januszczak, 2016). The priority patches we highlight here

(Fig. 2) are good starting points for such efforts, especially when complemented with spatial population viability analyses that can estimate effective population sizes or overall population sizes that should be reached to lower extinction risk in the long-run (Hanski & Ovaskainen, 2003; Kuemmerle *et al.*, 2011*a*2011a).

The threat of wisent herds being extirpated by disease is high, given the evidence from several past incidents and the low genetic diversity that likely makes herds vulnerable to pandemics. Moreover, most free-ranging herds today occur at higher densities compared to the past, and winter feeding, which concentrates animals heavily during parts of the year, is still practiced in most free-ranging herds. The risk of epidemic spread of disease is therefore real if existing herds are connected into larger metapopulations. Establishing reservoir herds that can serve to restock larger herds in such cases is thus important and should occur in parallel to efforts to linking and expanding extant herds. Our work highlights the five most isolated patches that could be good candidate sites for such reservoir herds (four of which are located in central Poland). Wisent reintroductions into such patches (none of them particularly large) have so far not received attention, but establishing reservoir herds should become a priority for wisent conservation in Poland (and elsewhere).

Our assessment identifies potential habitat patches for wisent reintroductions using a top-down approach. A next useful step would be to complement this with a bottom-up assessment of habitat quality, particularly food availability, and social constraints, both of which would ultimately determine the size of new wisent herds. In our assessment, we identify habitat patches to be largely forested, in line with previous work (Kuemmerle *et al.*, 2010; Kuemmerle *et al.*, 2018). Importantly, wisents predominantly graze (up to 80% of their food consists of grass and herbs, only 20% of browse), and food availability varies with forest type and age, and the proportion of open areas in the landscape (e.g. forest glades). Wisents do require sufficient open habitat available, and even small openings in the forest (that might be omitted by our analyses) can be critical for wisents. Food availability is particularly limiting in winter, where biomass available to wisents in Polish forests can vary between 8.2 and 21.9 tons of dry matter per km^2, translating into plausible wisent densities between 0.3 and 0.6 individuals per km^2 (Bobek *et al.*, 1991; Bobek *et al.*, 1992; Krasińska & Krasiński, 2013; Krasińska *et al.*, 2014). A thorough assessment of local food availability is thus crucial to provide a useful estimate for local habitat suitability and the potential size of a new wisent herd – and such assessments should be an important criteria to choose among alternative candidate sites. Likewise, human population density, traffic volumes, proximity to settlements, land ownership, as well as the extent and mode of agriculture (wisents particularly come into conflict with cropland) are important human dimensions to consider to further evaluate possible reintroduction sites (Perzanowski & Olech, 2007; Perzanowski *et al.*, 2015).

Our analyses relied on the most comprehensive wisent occurrence dataset collected to date, spanning a wide range of environmental conditions, herd sizes and reintroduction histories. Our habitat models had high fits and yielded plausible results, consistent with prior, more fine-scale assessments (Daleszczyk *et al.*, 2007; Kuemmerle *et al.*, 2010; Krasińska & Krasiński, 2013; Bleyhl *et al.*, 2015; Kuemmerle *et al.*, 2018). Still, the number of sampled animals per herd was sometimes low (e.g. for the Bieszczady herd). Moreover, all data we used stem from reintroduced herds, and although most of these herds have existed for decades, we cannot fully rule out remaining bias due to herd placement. Wisents are also currently not in equilibrium with their environment, as herds are still small, suggesting our habitat suitability assessment is conservative. In addition, including additional environmental and socio-economic variables that were unavailable to use (e.g. forest understory productivity or snow depth) would improve our models further. As the extent of winter feeding is unknown, we could not include this in our habitat models, although this would be beneficial. The extent of forest association for some herds would likely be lower, especially during winter, without this supplementary feeding (Krasińska & Krasiński, 2013). We also used two types of occurrence points, telemetry data and field-validated occurrence points (only for the Bieszczady herd). It would have been preferable to rely on a standardized sampling scheme, yet the non-telemetry data we included do not bias the habitat assessment, as we have tested in prior research (Kuemmerle *et al.*, 2018). Furthermore, landscape suitability for movement is reasonably proxied by habitat suitability, but telemetry data from dispersing individuals and more fine-scale barrier information (e.g. road traffic) could improve our corridor assessment (Ziółkowska *et al.*, 2016a). We also did not consider wisent herds from neighbouring countries in our connectivity assessment, but these herds are either far away, or separated by border fences (e.g. Belarus). Finally, we chose a relatively large minimum patch size of 200 km^2, in line with current IUCN recommendations for herds of at least 50 individuals (Pucek *et al.*, 2004). Still, actual carrying capacity will depend on local habitat quality (see above) and larger patch sizes might be required, especially considering that herds might break up into smaller groups (Krasińska *et al.*, 2014) or relocate, as has happened for the Western Pomeranian herd, the Bieszczady herd or the herd in Briansky Les in Russia (Chistopolova *et al.*, 2014; Perzanowski & Januszczak, 2016; Yanuta *et al.*, 2016). Conversely, smaller patches could function as important stepping stones.

Connecting isolated and small populations of threatened species is an important conservation goal, but often discounts substantial risk of epidemic disease outbreaks in connected populations. Mitigating this risk requires shifting to a restoration strategy that complements establishing larger metapopulations of species of conservation concern, such as the wisent in our case, with reservoir herds that can serve as backup. We highlight how combining habitat suitability models and connectivity assessments can provide a blueprint for such a dual reintroduction and translocation strategy. Poland has been instrumental in the restitution of wisents in the past, and remains a central country for safeguarding the species in the future. Implementing a dual strategy of

metapopulations and reservoir populations can provide an example for other countries that contain ample habitat for large mammals in Europe (e.g. throughout Eastern Europe), and make an important contribution to rewilding by lifting large mammal numbers to functionally relevant population sizes.

Acknowledgements

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.