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Sedentary but not dispersing wolves *Canis lupus* recolonizing western Poland (2001–2016) conform to the predictions of a habitat suitability model

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Abstract

Aim: To compare predictions of the habitat suitability model (HSM) for wolves *Canis lupus* in Poland with actual wolf distribution in western Poland after 15 years of recolonization.

Location: Western Poland (WPL, *ca.* 136,000 km^2), west of the 18°48′E meridian.

Methods: Data on wolf occurrence (8,057 records) were gathered in 2001–2016. Wolf presence in 10 × 10 km cells was classified as follows: (1) permanent occurrence with reproduction, (2) permanent occurrence with no reproduction and (3) sporadic occurrence (interpreted as dispersing individuals). These cells were compared to all 10 × 10 km cells in WPL with respect to the probability of wolf occurrence as predicted by the HSM and habitat variables important for wolves. For temporal analysis, data were divided into two 8-year subsets: the initial and later phases of wolf recovery.

Results: Wolves were recorded in 259 cells (19.8% of the study area). The pairs and packs settled in areas predicted by the HSM to have good and very good habitat, in cells characterized by high forest cover and low densities of roads. Wolf groups that reproduced were found in the best-quality habitats characterized by denser forest cover and markedly lower shares of anthropogenic structures. Dispersing individuals were mostly recorded in unsuitable and suboptimal habitats, and they avoided both the poorest and the best habitats. In the initial phase of wolf recovery, cells selected by wolves for settling down and those used by dispersing wolves did not differ in their habitat parameters. However, in the later phase, as WPL became more saturated with wolf packs, dispersing individuals were recorded in less suitable habitats.

Main conclusions: The HSM for Polish wolves predicted with high accuracy the areas later occupied by wolf groups in the western part of the country. A similar approach may also be useful to predict the future distribution of wolves in the lowlands of central and western Europe where environmental conditions are comparable and recolonizing wolves originate from the same source population.

KEYWORDS
Central Europe, dispersing wolves, forest cover, habitat modelling, habitat selection, model validation, reproducing wolves, road density, wolf population recovery

1 | INTRODUCTION

Although habitat suitability models (hereinafter HSMs) have been widely proposed as conservation and management tools, especially for rare and endangered taxa (Acevado, Cassinello, Hortal, & Gortázar, 2007; Brotons, Thuiller, Araújo, & Hirzel, 2004; Rondinini, Stuart, & Boitani, 2005; Zeigenfuss, Singer, & Gudorf, 2000), their predictive power for recovering populations has rarely been tested (Cianfrani, Lay, Hirzel, & Loy, 2010). Instead, researchers have rather focused on the validation of models using sets of independent data on species presence from the same or neighbouring populations (Lauver, Busby, & Whistler, 2002; Leblond, Dussault, & St-Laurent, 2014), which may have led to poor fit of models to data from different seasons or environments (Kirk & Zielinski, 2009).

Among predators, the most frequent habitat suitability assessments are for the wolf (*Canis lupus*), both in Eurasia (Blanco, Cortés, & Virgós, 2005; Corsi, Duprè, & Boitani, 1999; Falcucci, Maiorano, Tempio, Boitani, & Ciucci, 2013; Glenz, Massolo, Duonen, & Schlaepfer, 2001; Huck et al., 2010; Karlsson, Brøseth, Sand, & Andrén, 2007; Massolo & Meriggi, 1998) and in North America (Gehring & Potter, 2005; Haight, Mladenoff, & Wydeven, 1997; Mladenoff, Clayton, Pratt, Sickley, & Wydeven, 2009; Mladenoff & Sickley, 1998; Mladenoff, Sickley, Haight, & Wydeven, 1995; Mladenoff, Sickley, & Wydeven, 1999; Oakleaf et al., 2006; Potvin et al., 2005). This is a rather unique phenomenon because generalist species are unlikely to be modelled with great accuracy (Seoane, Carrascal, Alonso, & Palomino, 2005). Across their geographic range, wolves inhabit different environments: tundra, boreal and temperate forests, steppes and semi-deserts, and habitats transformed by humans to varying degrees (Mech & Boitani, 2003). Therefore, the predictive power of HSMs for wolves has been hotly debated (Fechter & Storch, 2014; Mech, 2006a,b; Mladenoff, Clayton, Sickley, & Wydeven, 2006). However, while some authors doubt the predictive power of HSMs for wolves (Cayuela, 2004; Mech, 2006a), others have revealed environmental factors that support or hamper wolf occurrence (Kaartinen, Kojola, & Colpaert, 2005; Llaneza, López-Bao, & Sazatornil, 2012; Thiel, 1985; Thurber, Peterson, Drummer, & Thomasma, 1994; Wydeven et al., 2001).

Nowadays, the validation of HSMs for wolves is essential, as wolves have been returning to areas from which they were extirpated decades or even centuries ago. This has been happening both by natural recolonization (Chapron et al., 2014; Fabbri et al., 2007; Hayes & Harestad, 2000; Kojola et al., 2006; Wabakken et al., 2007; Wydeven, Schultz, & Thiel, 1995; Wydeven et al., 2009) and by reintroductions (Fritts et al., 1997). This process has also been occurring in Poland, where wolves became strictly protected across the majority of the country in 1995 and in the whole country in 1998 (Mysłajek & Nowak, 2015). Due to protection, the population of wolves inhabiting eastern Poland grew in number and began to expand towards the western regions, from which they had been previously extirpated (Nowak & Mysłajek, 2017). Animals originating from Poland have also founded a growing population in Germany (Czarnomska et al., 2013), and this German-western Polish (the so-called Central European—see Reinhardt, Kluth, Nowak, & Mysłajek, 2013 for further details) wolf

population is critically endangered according to IUCN criteria (Linnell, Salvatori, & Boitani, 2008). The rapid recovery of the wolf population in western Poland (hereinafter WPL) observed in the last decade (Nowak & Mysłajek, 2016) has created an excellent opportunity for the validation of the previously proposed HSM, which was based on wolf presence data from the eastern part of the country (Jędrzejewski et al., 2008).

The HSM predicted that habitats suitable for this species cover *ca.* 24% of Poland and could support a population of 1220–1720 individuals, with the most probable population size about 1,500 wolves: a number nearly threefold larger than estimates of Polish wolf population size at the time the model was proposed. The original HSM, during its preparation, was initially validated with historical (1950–2006) qualitative data on wolf occurrence in Poland. This validation revealed that areas indicated by the HSM as suitable for wolves and those inhabited by wolves for at least one decade overlapped in 81%–86% cases. Also, the number of decades wolves inhabited an area positively correlated with habitat quality as suggested by the HSM (Jędrzejewski et al., 2008).

In this study, we compared the predictions of the HSM for wolves in WPL (from Jędrzejewski et al., 2008) with the present distribution of the species after 15 years of spontaneous recolonization (Nowak & Mysłajek, 2016; Nowak, Mysłajek, Kłosińska, & Gabryś, 2011). Our null hypothesis was that wolves would settle in the very good and good habitats indicated by the HSM. As wolves choose areas rather peaceful and distant to humans for breeding (Theuerkauf, Rouys, & Jędrzejewski, 2003), we also expected that wolves in WPL would rear pups in the best-quality plots. Following Mladenoff et al. (2009), we also anticipated that in the later phase of population recovery, wolves would settle in cells with worse parameters than in the early phase of the recolonization.

2 | METHODS

2.1 | Study area

The study area (Figure 1) covers the western part of Poland (*ca.* 136,000 km^2), between the meridian 18°48′E located in the central part of the country and the state border with Germany (14°07′E) in the west. The meridian 18°48′E separates the eastern part of Poland, where wolves occurred permanently before 2006 (i.e., when the HSM was developed), from the western part, where only a few wolves occurred at that time. Western Poland has a transitional continental–Atlantic climate, with mean temperatures from –1.1 to 0.6°C in January and from 18.1 to 19.5°C in July. Mean precipitation ranges from 504 to 766 mm. Snow cover persists for 50–60 days in the central part of the country, down to 40 days in WPL. The vegetation season lasts 220–240 days (Central Statistical Office, 2015b).

The landscape of the region, shaped mainly by Pleistocene glaciations (Marks, 2011), is mostly lowland (up to 200 m a.s.l.) with frontal and moraine hills. At the Polish–Czech state border, a range of the Sudetes Mountains extends with the highest summit being Mt. Śnieżka (1,602 m a.s.l.). Human population density averages 109

inhabitants/km^2 and varies from 73 in Lubuskie Province to 146 in the Lower Silesian Province (Central Statistical Office, 2015b). The majority of the area (57%) is agricultural land, with a predominance of arable fields. The average forest cover is 32%, but in the north-western and western provinces, for example, Western-Pomeranian, Pomeranian and Lubuskie, it reaches 35%, 36% and 49%, respectively. Forests are dominated by coniferous species (70%), mostly Scots pine *Pinus sylvestris*. Among deciduous species, oaks (*Quercus* sp.), birches (*Betula* sp.), black alder (*Alnus glutinosa*), beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) prevail. Forests are mostly (94%) owned by the state and managed by the Polish State Forests. Most of them are commercial stands, and only 1.5% is protected as national parks or reserves (Central Statistical Office, 2015a).

Three species of large carnivores occur in Poland—the wolf, Eurasian lynx *Lynx lynx* and brown bear *Ursus arctos* (Fernández, Selva, Yuste, Okarma, & Jakubiec, 2012; Jędrzejewski et al., 2008; Niedziałkowska et al., 2006)—but currently only the wolf has a stable population in WPL (Nowak & Mysłajek, 2016; Figure 1). The lynx is recorded here occasionally (Niedziałkowska et al., 2006; Nowak, Kasprzak, Mysłajek, & Tomczak, 2013). Wolves in WPL prey mostly on red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*; Jędrzejewski et al., 2012; Nowak et al., 2011); in this region, the densities of these prey are among the highest in the country (Borowik, Cornulier, & Jędrzejewska, 2013). In the north-western part, there is a small introduced population of European bison (*Bison bonasus*). WPL is sporadically visited by dispersing moose (*Alces alces*). There are also isolated populations of alien species such as fallow deer (*Dama dama*) and mouflon (*Ovis musimon*), which have been introduced to some locations for recreational hunting (Wawrzyniak, Jędrzejewski, Jędrzejewska, & Borowik, 2010).

2.2 | Collection of data on wolf occurrence

Our study was conducted from winter 2000/2001 to winter 2015/2016 during which a total of 8,057 independent wolf records were collected in WPL. Data on wolf occurrences were gathered mostly by staff of the Association for Nature "Wolf" as well as volunteers, who had been previously trained in wolf survey methods. From early winter, whenever snow cover was present, we conducted snow tracking, following wolves for distances up to 20 km and repeating tracking in the same territories several times. During the rest of the year, we hiked a dense net of transects along sandy forest roads and pathways to detect signs of wolf occurrence: tracks, prey remains, ground scratching, scent marks, and scats (see Nowak & Mysłajek,
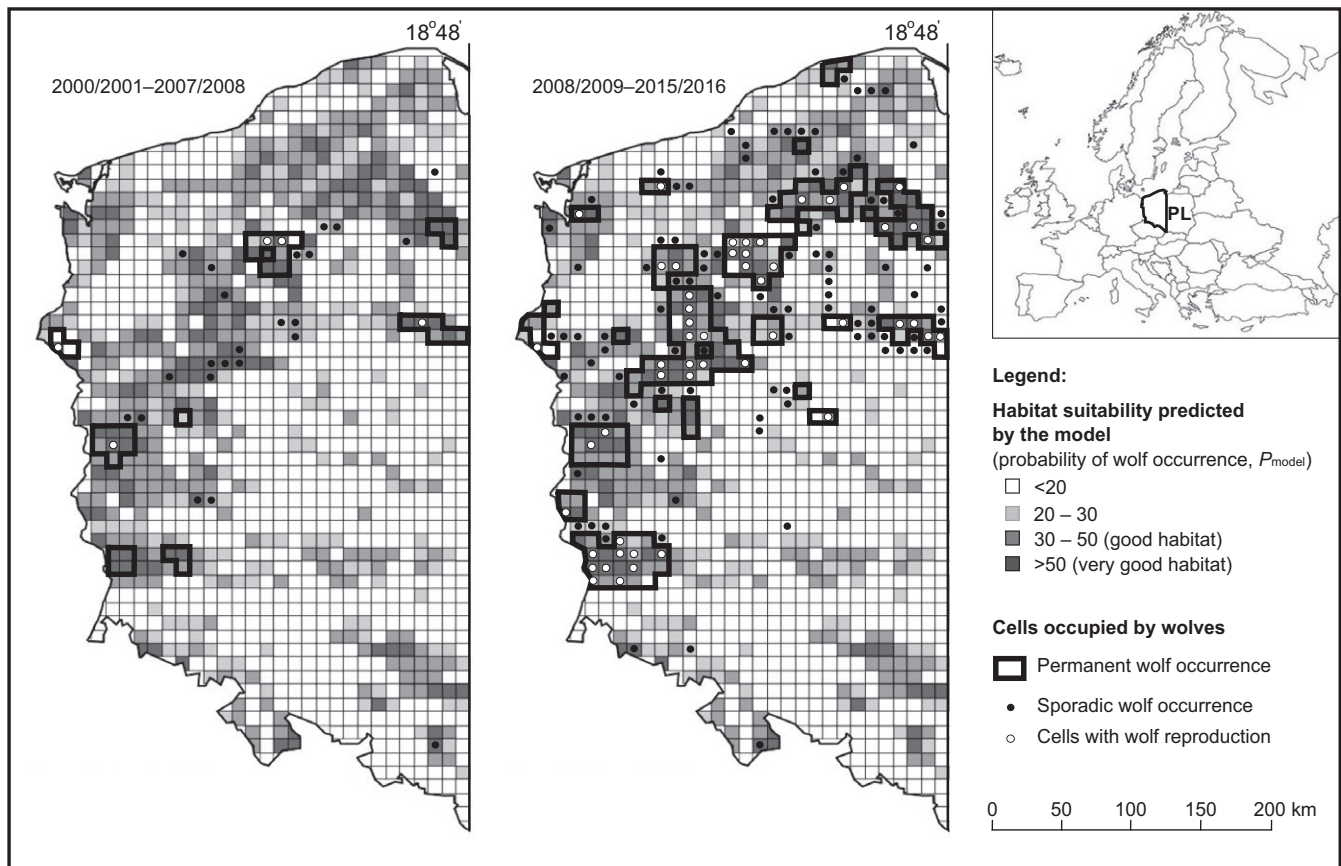

FIGURE 1 The study area (western Poland) divided into 10 × 10 km cells characterized by habitat suitability for wolves *Canis lupus* as predicted by the habitat suitability model (HSM; Jędrzejewski et al., 2008). The study area is located west of the 18°48′ meridian. The bold line denotes cells permanently inhabited by wolves for at least 1 year in 2000/2001–2007/2008 or 2008/2009–2015/2016, and open circles show cells where wolf reproduction was confirmed, while black circles denote sporadic wolf occurrence

2016 for details). Fresh faeces were also collected to assess wolf diet composition (Nowak et al., 2011), and since 2005 for DNA analyses (Czarnomska et al., 2013; S. Nowak & R.W. Mysłajek, unpublished data). The locations of all findings were recorded using a hand-held GPS device (60CSx, Garmin, USA). We also applied howling stimulation to detect wolves (see Llaneza, Ordiz, Palacios, & Uzal, 2005; Nowak et al., 2007; Nowak, Mysłajek, & Jędrzejewska, 2008 for details) as well as camera traps (Trophy Cam and Trophy Cam HD, Bushnell, USA)—see below for details.

Additional data were delivered by the State Forest Service and national parks and subsequently checked in the field by the authors or trained volunteers. Information about livestock killed by wolves was provided by the Regional Directorates for Environmental Protection (RDEP) operating in each province. Because wolf damages are compensated by the state, farmers report almost all incidents, which are later verified by the staff of RDEP. Incidental information about wolf presence was included in the analysis only if observers provided adequate pictures and videos of live or dead wolves.

2.3 | Validation of the HSM

The original HSM (Jędrzejewski et al., 2008) was based on data about the distribution and numbers of wolves in Poland from the National Wolf Census that was conducted in 2000–2006, and habitat variables taken from the CORINE land cover database for areas inhabited by wolves in the eastern part of the country (Jędrzejewski, Niedziałkowska, Mysłajek, Nowak, & Jędrzejewska, 2005; Jędrzejewski, Niedziałkowska, Nowak, & Jędrzejewska, 2004; Jędrzejewski, Nowak, Schmidt, & Jędrzejewska, 2002). Data on permanent wolf presence (over 15,000 records from eastern Poland) were analysed in a raster map of Poland with a grid of 10 × 10 km cells (Figure 1). Single records of wolves in central and western parts of the country were not included in the analyses as they represented dispersing individuals or few ephemeral recolonizing packs. The grid resolution was adopted according to the space requirements of wolves in the lowlands of eastern Poland, where home ranges of wolf packs, calculated as minimum convex polygons with 75% of annual locations, average 92 km^2 (Jędrzejewski, Schmidt, Theuerkauf, Jędrzejewska, & Kowalczyk, 2007). This is consistent with the recommendations of the European Commission for the assessment of species' conservation status under article 17 of the Habitats Directive 92/43 (European Commission, 2006). Cells divided by state borders or seashores were included in the analysis if >50% of their area was located in Poland.

Analysis of environmental factors affecting the distribution of wolves in eastern Poland revealed that they selected habitats with high forest cover, low number of human settlements and low density of roads and railways (Jędrzejewski et al., 2004, 2005). Therefore, for HSM building, all 10 × 10 km cells were characterized in terms of their percentage area covered by the following: (1) forests, (2) wetlands and marshes, (3) meadows and pastures, (4) arable fields and (5) settlements and buildings, as well as (6) density of major roads (km/km^2) and (7) crude biomass of wild ungulates (kg/km^2 of forests; Jędrzejewski et al., 2008). Subsequently, a resource selection function was used

to estimate habitats suitable for wolves and potential population size in the whole country (Jędrzejewski et al., 2008). Probability of wolf occurrence in each cell was calculated based on wolf records (over 15,000) collected in 2000–2006 in eastern Poland (area with permanent occurrence of wolves). The number of wolf records (varying from 0 to 419 in a cell) was logarithmically transformed and expressed as percentage of the maximal log value of wolf records in any cell. Such a standardized wolf index was proportional to probability of wolf occurrence in the cells and was treated as a dependent variable in the multiple linear regression models. The set of all possible models with four most relevant habitat features (percentage area covered by forests, marshes, meadows, and density of roads) as explanatory variables was ranked by the Akaike information criterion. All four explanatory variables were retained in the most parsimonious model. Cells were divided into four groups according to their calculated probabilities of wolf occurrence (p_{model}): (1) very good (p_{model} > 50%), good (30%–50%), poor (20%–30%) and unsuitable habitats (<20%; Jędrzejewski et al., 2008). The HSM, during its preparation, was validated by comparing the predicted habitat patches with the historical distribution of wolves in Poland in the second half of the 20th century.

Our data on wolf occurrence in WPL in 2001–2016 were analysed in the same raster map with a grid of 10 × 10 km cells (1,311 cells) and the same set of habitat variables as the original HSM. We compared the habitat suitability as predicted by the HSM and quantitative measures of habitat variables in the following sets of cells: (1) cells where reproduction was confirmed, (2) cells with permanent wolf occurrence including those where reproduction was recorded, (3) cells with sporadic wolf occurrence and (4) all cells within the study area. For temporal analysis, we divided data of wolf occurrence into two subsets: (1) 2000/2001–2007/2008—early phase of recolonization and (2) 2008/2009–2015/2016—phase of intense recolonization (cf. Nowak & Mysłajek, 2016).

For HSM testing, we considered a grid cell to be permanently occupied by wolves in a given season (from the beginning of April of year n to the end of March in year n + 1), if at least two independent observations unambiguously confirming the presence of a pair or wolf group (≥2 adult individuals) were collected with an interval of at least 4 months between observations. Such evidences were as follows: tracks, scats, scent markings, remains of wolf prey, dens, direct observations, genetic proof and photo and video recordings. If there was only one sign of wolves in a cell in the second year and at least two evidences of ≥2 adult individuals in the third year, the cell was also considered continuously occupied in the second year.

Wolf reproduction in a cell was confirmed directly (by observations of pups—either personal or taken with photo and video cameras), through responses to howling stimulations, or indirectly (by observations of females with visible nipples during offspring milking, recordings of copulations during mating seasons, and freshly excavated dens at the end of winter or later). Whenever possible, in places where the activity of pups was most likely (e.g., near known dens or in the core areas of territories defined by the accumulation of scats—Zub et al., 2003 and Llaneza, García, & López-Bao, 2014), photo or video cameras were installed to confirm the presence of offspring.

Cells were considered as areas with sporadic wolf occurrence if the collected data confirmed only a short-term presence of lone individuals, and if only single observations of loners or groups, roadkill or single damage to livestock were recorded in a cell. Sporadic occurrence of wolves in cells could be records of dispersing individuals or extraterritorial forays of wolves occupying neighbouring areas (Ciucci, Reggioni, Maiorano, & Boitani, 2009; Ražen et al., 2016; Wabakken et al., 2007). In this study, we interpreted the cells with sporadic records of wolves as visits by dispersing individuals.

Data were tabulated and analysed in MapInfo Professional (MapInfo Corporation, USA). We assessed wolf selection of cells with various probabilities of their occurrence as predicted by the HSM, forest cover and road density using Ivlev's selectivity index, D (modified by Jacobs, 1974): $D = (r − p)/(r + p − 2pr)$, where r is the proportion of cells among cells inhabited by wolves with a given probability of wolf occurrence (p_{model}) and p is the proportion of these cells in the whole study area. D varies from −1 (the strongest negative selection) to +1 (the strongest positive selection), with 0 representing random utilization. Ivlev's selectivity index was calculated in Statistica (StatSoft, Poland).

Finally, based on our wolf records collected in 2001–2016, we performed a quantitative evaluation of the original HSM predictions for WPL. Firstly, in a generalized linear model, we related the binomial dependent variable (presence/absence of wolf in a given grid cell) to the HSM predictions (independent variable). Secondly, we run multinomial logistic regression with HSM predictions as an independent variable and wolf status in grid cells (absent, sporadic, permanent and permanent with reproduction) as a dependent variable (Agresti, 2002). Although the dependent variable (wolf status) had an ordinal character, we could not run ordered logistic regression because the proportional odds assumption was violated (likelihood ratio test, $\chi^2 = 32.2$, $p < 0.001$; ORDINAL package; Christensen, 2015). These statistical analyses were performed in R (R Development Core Team, 2015).

3 | RESULTS

From winter 2000/2001 to winter 2015/2016, wolves occurred in at least 259 cells (19.8%) in WPL, among which they permanently inhabited 154 (11.8%) for at least 1 year, and occurred sporadically in the remaining 105 (8.0%).

When compared to the general habitat variation in WPL, wolves settled down in areas with habitats predicted by the HSM to be good and very good (73% cells with $p_{model} > 40$%), in cells characterized by high forest cover and low density of roads (Figure 2). Indeed, their selectivity of a place to settle grew steadily with increasing habitat suitability and forest cover, and with declining density of roads (Figure 3). Sporadic occurrences of wolves, which most probably reflect dispersing individuals, were mostly recorded in unsuitable and suboptimal habitats (71% of cells in $p_{model} < 40$%): they clearly avoided both the poorest and the best habitats (Figure 3), with many of the latter already being occupied by wolf family groups.

The mean value for wolf habitat suitability predicted by the HSM was significantly higher ($p_{model} = 47.7$%) for cells actually settled by wolf packs than for all cells with sporadic records of wolves (29.1%; Table 1). Habitat characteristics that significantly differentiated cells with settled and cells with dispersing wolves included the following: forest cover, crude biomass of wild ungulates (both higher in permanently occupied cells), and arable fields, human settlements and road density (all with lower shares in permanently occupied cells; Table 1).

Packs or pairs that reproduced were found in 52 cells (4.0% of all cells and 33.8% of permanently occupied cells) characterized by significantly higher values of habitat suitability predicted by the HSM (mean $p_{model} = 55.7$%), denser forest cover and markedly lower shares of anthropogenic habitats (arable fields, built-up area, roads; Table 1). Among 52 cells where wolves reproduced, 15 (28.8%) were located in active or disused military training areas and four (7.7%) in national parks. Among 10 cells with reproduction where the forest cover was lower than 50%, six included military training areas (four active, two disused).

In the early phase of recolonization (from 2000/2001 to 2007/2008), cells selected by wolves for settling down and those used by dispersing wolves did not differ in their habitat parameters (Tables S1 and S2). New cells that became occupied by wolf packs or pairs in the latter phase of population recovery (2008/2009–2015/2016) showed only slightly (and not significantly) lower values in habitat quality compared to the early phase. However, in 2008/2009–2015/2016, cells with sporadic occurrences of wolves showed markedly lower habitat suitability indices (mean $p_{model} = 27.7$) compared to both permanently settled cells in the same years (46.9%) and cells used sporadically in the earlier phase (45.8%); they also declined greatly in 3–5 parameters of habitat quality (Table S1). As WPL became more saturated with wolf packs, dispersing individuals had to travel through suboptimal or even pessimal habitats.

In general, our empirical data on wolf occurrence showed that the original HSM predicted habitat suitability for wolves with good accuracy. The probability of grid cell to be assigned as occupied by wolves increased significantly with growing HSM predictions (slope = 6.77 ± 0.44, $Z = 15.3$, $p < 0.001$; Figure 4). An increase in the HSM predictions was associated with the significant growth in likelihoods of grid cells to be found as hosting sporadic, permanent and permanent-with-reproduction occurrence of wolves compared to cell with no wolf records (Table 2, Figure 4). Each class reached its maximal probability at different values of HSM predictions—wolves absent at low values, sporadic occurrence at moderate values and permanent occurrence without or with reproduction at high values of HSM predictions (Figure 4).

4 | DISCUSSION

Our study is one of the very few (Cianfrani et al., 2010; Mladenoff et al., 1999) that cross-validates a HSM built upon pre-colonization data obtained from a neighbouring area of continuous wolf range with a post-colonization dataset. We revealed that the HSM for wolves in
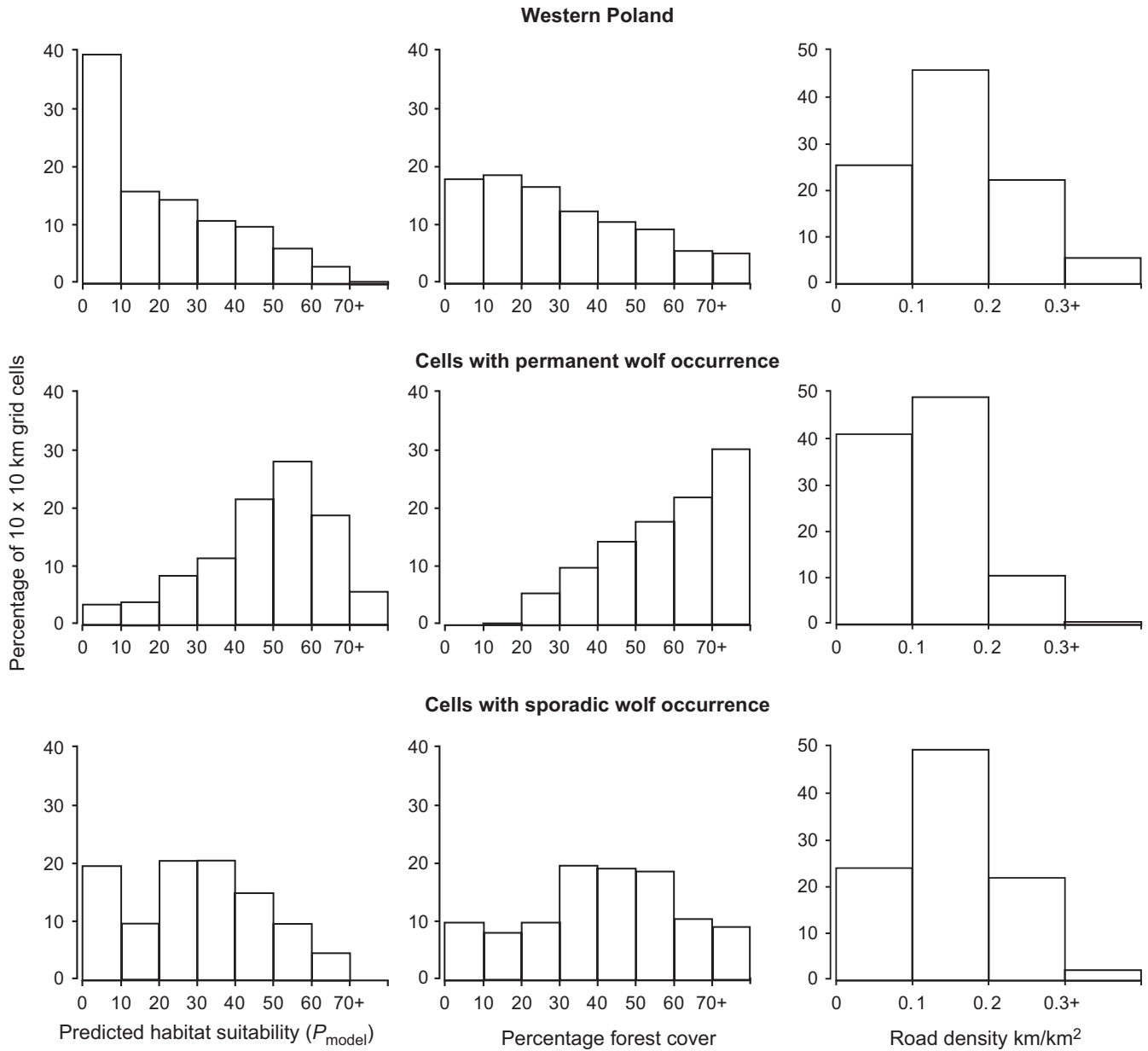
Western Poland

Cells with permanent wolf occurrence

Cells with sporadic wolf occurrence

FIGURE 2 Frequency distribution (%) of all 10 × 10 km cells in western Poland (n = 1311 cells, upper row), cells with permanent occurrence of wolves (n = 154, middle) and cells with sporadic occurrence of wolves (n = 105, lower row) with respect to general habitat suitability as predicted by the model (left column) and two essential features of habitat: percentage forest cover (middle column) and road density (right column) within cells. See text for definitions of permanent and sporadic wolf occurrence

Poland (Jędrzejewski et al., 2008) predicted with high accuracy the areas where these predators ended up settling in WPL. Moreover, in concordance with our hypotheses, wolves selected the best-quality patches for reproduction, and in the second phase of recolonization, when some of the high-quality habitats were saturated, wolves—especially dispersing individuals—were recorded in less optimal habitats than in the early phase of population recovery.

We are aware of possible limitations of our data. The survey of wolves in a large study area is a demanding task, as these carnivores possess large territories (Jędrzejewski et al., 2007), the utilization of which varies in space and time (Jędrzejewski, Schmidt, Theuerkauf, Jędrzejewska, & Okarma, 2001; Kusak, Skrbinšek, & Huber, 2005;

Uboni, Smith, Mao, Stahler, & Vucetich, 2015). Territorial packs leave abundant traces of presence (Llaneza et al., 2014; Zub et al., 2003) that are easy to detect even in areas with low population density (Kojola et al., 2014). Camera traps and howling stimulations also helped with the discovery of both adult wolves and their pups (cf. Galaverni et al., 2012; Llaneza et al., 2005). Thus, we believe that the established packs were revealed with a good enough accuracy. However, dispersing individuals are difficult to detect (Ciucci et al., 2015; Ražen et al., 2016; Wabakken et al., 2007). Direct observations of such individuals are more likely in areas that are intensively used by people such as roads, the vicinity of villages and towns, than in deep forests. Furthermore, lone wolves, which possess neither mates nor

TABLE 1 Habitat characteristics (mean ± *SE*, range in parentheses) of 10 × 10 km cells with permanent wolf occurrence (all cells, n = 154), where reproduction was (n = 52) or was not recorded (n = 102), and cells with sporadic wolf occurrence (n = 105) in western Poland, in 2000/2001–2015/2016

Characteristics of 10 × 10 km cells	Cells with permanent wolf occurrence			Cells with sporadic wolf occurrence
	All	With reproduction	No reproduction	
Habitat suitability for wolves predicted by HSM	47.7 ± 1.3 (4.5–75.4)	55.7 ± 1.8**** (19.1–75.4)	43.6 ± 1.5 (4.5–71.0)	29.1 ± 1.7**** (0–66.6)
Crude biomass of ungulates (kg/km^2 of forest)	235.6 ± 5.9 (114.1–556.7)	243.3 ± 11.2 (123.2–556.7)	231.8 ± 6.9 (114.1–423.3)	206.9 ± 7.1** (64.0–503.9)
Forest cover (%)	59.6 ± 1.4 (19.7–94.4)	67.1 ± 2.4*** (24.9–94.4)	55.8 ± 1.6 (19.7–88.1)	41.6 ± 2.0**** (0.04–86.6)
Wetlands and marshes (%)	8.2 ± 0.4 (0–30.4)	7.9 ± 0.7 (0–19.1)	8.4 ± 0.5 (0–30.4)	6.5 ± 0.4* (0–22.0)
Meadows and pastures (%)	10.4 ± 0.8 (0.3–69.9)	11.9 ± 1.8 (0.3–69.9)	9.6 ± 0.7 (0.5–40.9)	9.1 ± 0.7 (0.8–37.0)
Arable fields (%)	19.0 ± 1.2 (0–64.7)	10.8 ± 1.6**** (0.1–48.2)	23.2 ± 1.5 (0–64.7)	37.5 ± 2.0**** (0.03–92.4)
Settlements and buildings (%)	2.8 ± 0.2 (0–13.6)	2.3 ± 0.3* (0–9.4)	3.0 ± 0.2 (0–13.6)	5.3 ± 0.6**** (0–47.3)
Density of roads (km/km^2)	0.10 ± 0.01 (0–0.32)	0.08 ± 0.01** (0–0.27)	0.11 ± 0.01 (0–0.32)	0.14 ± 0.01*** (0–0.39)

Habitat suitability for wolves is from the model in Jędrzejewski et al., (2008). Statistical significance of differences was tested between cells permanently inhabited by wolves with and without reproduction (statistical significance is denoted by asterisks in the column "with reproduction") and cells inhabited permanently and those inhabited sporadically by wolves (asterisks in the column "sporadic occurrence"), with a Mann–Whitney U test. *p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.0001.

territories, rarely defecate or urinate along roads and trails (Rothman & Mech, 1979). Therefore, in our study, the area of sporadic occurrence of wolves could have been underestimated and biased towards less suitable habitats.

In spite of the general agreement on the importance of biological (biomass of prey, availability of refuge areas, interspecific competition) and human-related factors (roads, settlements, human population density) influencing wolf occurrence across their range (Jędrzejewski et al., 2008; Mladenoff et al., 2009), there are still substantial differences among proposed HSMs that make their comparison and assessment difficult. Dispersing wolves can cross hostile environments, whereas the successful establishment of packs, dependent on the prior bonding of pairs (Hurford, Hebblewhite, & Lewis, 2006), takes place mainly in higher-quality habitats (Mladenoff et al., 2009). Consequently, during the construction of a HSM for wolves it is essential to distinguish between predictors of areas with just a general presence of the species, including floaters, and the permanent range of the species, where they can establish territories (Marucco & McIntire, 2010). Models based on observations of solitary wolves wandering in search of mates and free territories, especially if such data included, for example, media reports, may provide inconclusive results (Fechter & Storch, 2014). Also Cianfrani et al. (2010) highlighted that numerous technical aspects may limit a HSM's predictive power as data from recovering populations have to be gathered over vast areas, in all seasons and for several years.

Although HSMs can give valuable suggestions for species conservation (Bonn & Schröder, 2001; Buse, Schröder, & Assmann, 2007), they are often criticized for their poor performance (Anderson et al., 2016; Reiley, Bednarz, & Brown, 2014). Inconsistency between models and reality is mainly explained by inadequate sampling of species'

occurrences, limited range of habitat covariates, inadequate consideration of data variability, wrong estimations of wildlife–habitat relationships, misinterpretation of results and application of the model to inappropriate spatial scales (Barry & Elith, 2006; Roloff & Kernohan, 1999). We tested a HSM that was based on large, multi-year empirical data about permanent wolf presence, collected in areas with biogeographic features (topography of terrain, climate, vegetation, ungulate community and population densities, and forest management system), and human impact and attitude very similar to the region being recolonized by wolves. All this contributed to a high accuracy of the tested HSM in predicting areas recolonized by wolves in WPL. Additionally, the fact that the wolf population in the eastern part of the country was the main source of dispersers settling in WPL (Czarnomska et al., 2013) strengthened the predictive power of the HSM for wolves in WPL. Indirectly, our study also attested to the permeability of ecological corridors between eastern and WPL, as modelled by Huck et al., (2011).

Wolf homesites, that is, areas where they give birth and rear pups (dens and rendezvous sites), are mostly selected for various microhabitat features (Capitani et al., 2006; Kaartinen, Luoto, & Kojola, 2010; Norris, Theberge, & Theberge, 2002; Trapp, Beier, Mack, Parsons, & Paquet, 2008) and are located far from human settlements and main roads, roughly in the centre of their territories (Ballard & Dau, 1983; Theuerkauf et al., 2003; Unger, Keenlance, Kohn, & Anderson, 2009). Similarly, in WPL for the rearing of pups, wolves chose areas where forest cover was high, and the area of arable land and density of roads were low. Where wolves reproduced in habitats with lower forest cover (<50%), most of them (70%) were located in military training areas that were active, disused or undergoing spontaneous reforestation by pine and birch. These areas
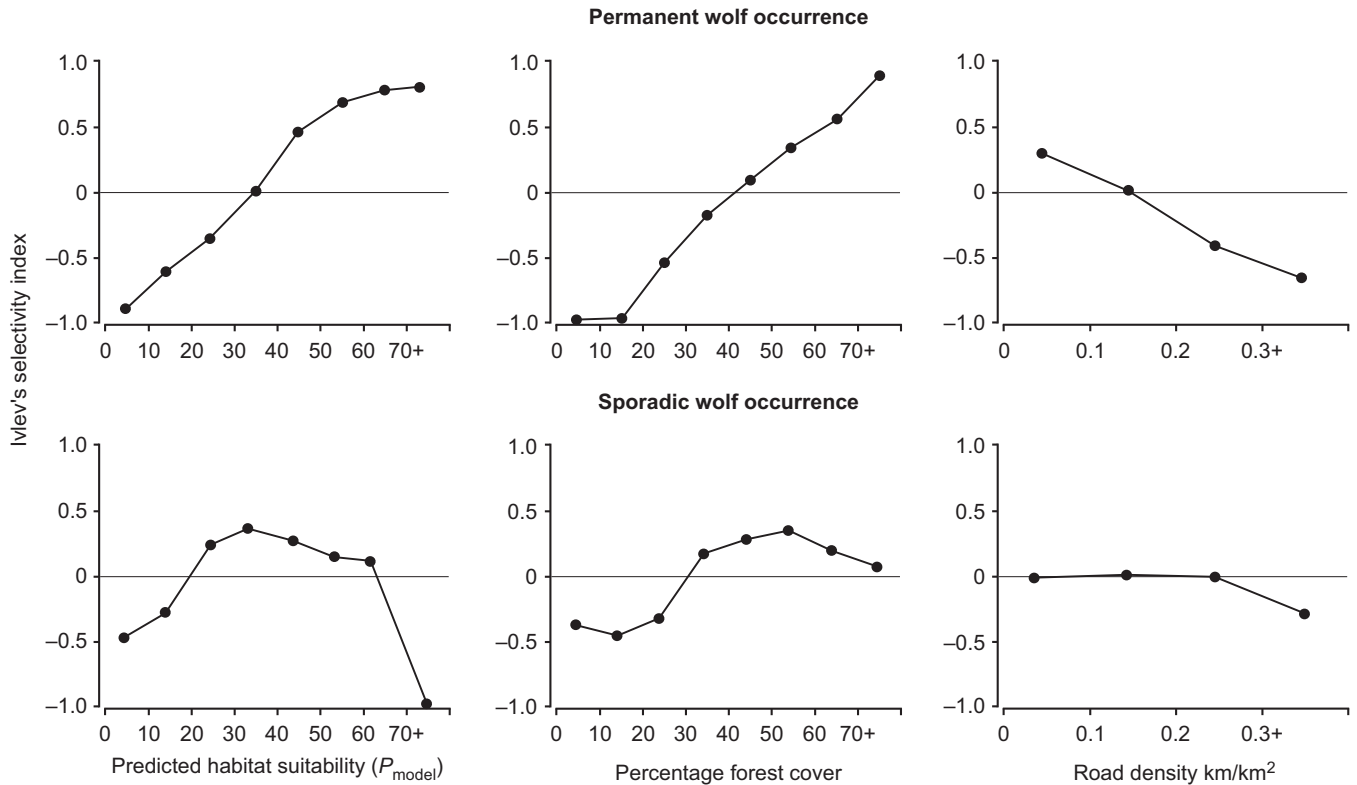
FIGURE 3 Wolf selection of cells with various probabilities of their occurrence as predicted by the HSM (left column), forest cover (middle column) and road density (right column) expressed using Ivlev's selectivity index, with *D* (modified by Jacobs, 1974) varying from −1 (complete avoidance) to 1 (the strongest positive selection). Calculation of *D*-values is based on data shown in Figure 2

were not described in the CORINE land cover database as forests; thus, the actual forest cover in such plots was higher. Additionally, public access to active military training areas is strictly limited for most of the year. In the unused training areas, logging activity was very low because of the young age of forest succession and the threat of misfires. Therefore, military training areas have an important complementary role to play in nature conservation, including that of large carnivores (Merrill, 2000; Warren et al., 2007; Zentelis & Lindenmayer, 2015).

Wolves recolonizing WPL first settled in the best habitats predicted by the HSM, while afterwards they were recorded in areas of worse quality. Intraspecific competition is important for wolf spatial structure (Rich, Mitchell, Gude, & Sime, 2012) and survival (Cubaynes et al., 2014). When there is a lack of competition, dispersers have the opportunity not only to choose habitats that best satisfy their needs, but also to adapt their territory size to the quality of local habitats (Kittle et al., 2015). Up to 2016, wolves in WPL had not yet saturated all suitable habitats. According to the HSM (Jędrzejewski et al., 2008), WPL (west of the meridian 18°48′E) has a total of 40,600 km^2 of good and very good habitats. Over the last 3 years of our study, wolves permanently inhabited 13,100 km^2, which is 32% of the potential habitat. Taking into consideration the observed population increase and good survival of pups (Nowak & Mysłajek, 2016), we predict that wolf numbers and range in WPL will grow, and within several years, the population may inhabit the majority of suitable

areas. This forecast is based on the premise that wolf protection in Poland will continue and the habitats will not deteriorate. However, the ongoing increase in built-up areas, rapid development of transport infrastructure and increase in traffic volume (Central Statistical Office, 2015b) may enhance the negative impact on wolf survival and forest integrity in WPL. Therefore, expected landscape changes may hamper the process of wolf population recovery (cf. Carroll, Phillips, Schumaker, & Smith, 2003) or force wolves to colonize less suitable habitats.

We believe that the high accuracy of the tested HSM in predicting areas recolonized by wolves in WPL may also be beneficial for modelling wolf occurrence in areas with biogeographic and social features similar to Polish conditions, for example, lowlands of central and western Europe that are being colonized by individuals originating from eastern and WPL (Andersen et al., 2015; Czarnomska et al., 2013). Although our analysis provides useful suggestions for scientists attempting to build HSMs for wolves in other parts of Europe, we urge to take into consideration only data from the most probable source populations; the environmental variables connected with specific areas, for example, terrain roughness and altitudes in mountains (Jędrzejewski et al., 2005; Llaneza et al., 2012); and the associations of habitat types and diet composition with population genetic structure, likely induced by the natal-habitat-biased dispersal observed in wolves (Carmichael et al., 2007; Pilot et al., 2006; Stronen et al., 2014).
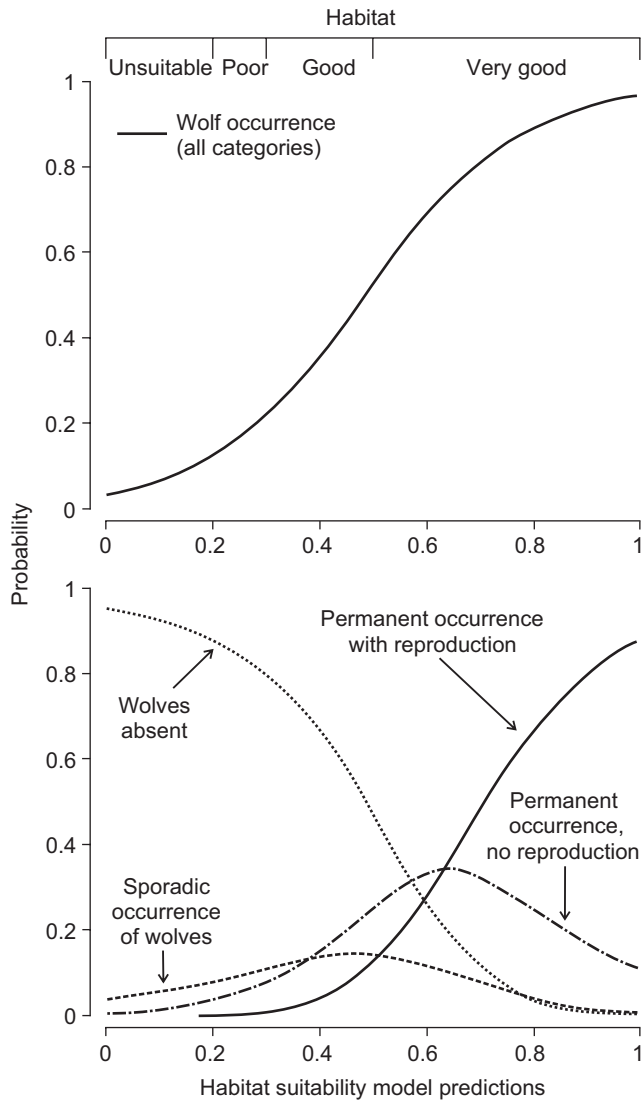
FIGURE 4 Upper panel: the probability of 10 × 10 km grid cell in western Poland to be found as occupied by wolves in 2001–2016 in relation to the original predictions of HSM. Lower panel: the probability of a cell to be found in each of the four empirical classes of wolf presence/absence (absent, sporadic occurrence, permanent and permanent-with-reproduction occurrence) in relation to HSM predictions. See text for statistical details

TABLE 2 Coefficients of multinomial logistic regression describing the concordance between the probability of 10 × 10 km cells to be found occupied by wolves in 2001–2016 (in three classes: sporadic, permanent and permanent with reproduction) with the original HSM predictions

Variable class	Intercept	Coefficient ± SE	z-Value	p-Value
Sporadic	−3.19	4.01 ± 0.56	7.14	<.001
Permanent	−4.87	8.51 ± 0.70	12.15	<.001
Permanent with reproduction	−8.36	14.07 ± 1.35	10.41	<.001

Cells with no wolf records were set as a reference level.

5 | CONCLUSIONS

Our study has shown that HSMs, if based on large sets of field data, are useful tools for predicting areas to be colonized by wolves. The results of such analyses may be used to foresee wolf population development and plan management decisions regarding, *for example*, livestock depredation, habitat connectivity and protection. Taking into account the good fit of the current distribution of the recovered wolf population in WPL to the HSM constructed for Polish wolves and because wolves recolonizing these areas mainly originate from the lowland part of Poland and the Polish–German borderland, we suggest using a similar approach to predict the future distribution of wolves in the lowlands of central and western Europe where environmental conditions are comparable. In widespread species that show large-scale differentiation into genetically and ecologically distinct subpopulations, HSMs will have the best predictive power within the same subpopulation.

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SUPPORTING INFORMATION

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