Potential European bison (*Bison bonasus*) habitat in Germany

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INTRODUCTION

European bison or wisent (*Bison bonasus*) is Europe's largest land mammal and Europe's largest remaining grazer. The species has experienced turbulent times during the last 100 years. Bison populations in Europe had been in decline for centuries, mainly due to habitat loss and overhunting. By the end of the 19th century, European bison were confined to two isolated populations – one in the Białowieska Forest in what is today the border region of Poland and Belarus, another one in the Russian Caucasus mountains. Both of these populations were exterminated during and after World War I, rendering the species extinct in the wild.

Fortunately, a handful of European bison survived in reserves and zoos, and a quickly initiated restitution program saved the species from the brink of extinction. European bison herds were reintroduced back into the wild after World War II, starting in Poland, but quickly expanding into many other countries in Central and Eastern Europe. The global European bison population has been increasing since, with the exception of a 10-year period of population declines after the breakdown of the Soviet Union, when poaching became widespread. Today, 3,225 European bison roam freely in 40 wild (i.e., unfenced) herds across 8 countries – doubtless one of the greatest success stories of large mammal conservation worldwide.

Nevertheless, the species is far from being safe due to a number of reasons. First, existing herds are small (only a handful of herds exceed 100 animals) and occur in isolation from each other. This is particularly worrisome considering the extremely low genetic variability in the global bison population – most European bison herds would likely not survive in the long run. To safeguard bison in the future, a number of urgent conservation actions have been identified, including **establishing more European bison herds**, **substantially increasing existing herds**, and **connecting these herds** to establish European bison meta-populations. All of these conservation measures hinge on identifying suitable European bison habitat.

Germany once contained much of the heartland of European bison, and has recently seen the return of this species by the reintroduction of Germany's first free-ranging herd in the Rothaargebirge in Central Germany. However, Germany is one of Europe's most densely settled regions, with intensive land use in many areas. This begets the question whether, and if so where, there could be more free-ranging European bison populations. We here assess this question by mapping potentially suitable European bison habitat using species distribution modeling, and a huge dataset of European bison occurrence data, based on which we outline potential candidate sites for reintroduction projects. We also provide a guideline for follow-up, site-level assessments including local habitat characteristics, population viability, human dimensions issues, and bison management options. This will be complemented with a review of the historic European bison range, and habitat use to back up arguments for reintroducing this species in Germany. We would like to stress that such detailed site-level assessments (not part of this project), are essential for further evaluating the suitability of individual regions to host a free-ranging European bison population.

HISTORIC DISTRIBUTION OF EUROPEAN BISON IN EUROPE

Executive summary: *There is ample and well-documented evidence for the historic occurrence of European bison in Germany. While there is some uncertainty regarding the Eastern European and Western European limits of the historic range of European bison, large parts of Germany were doubtless containing bison populations in the past.*

Where European bison occurred during the Holocene is still a matter of substantial scientific debate, partly due to uncertainties about when and where European bison evolved from the Pleistocene Steppe bison (Pucek, Belousova et al. 2004, Kerley, Kowalczyk et al. 2011, Cromsigt, Kerley et al. 2012, Kuemmerle, Hickler et al. 2012). A number of expert-based delineations of the historic European bison ranges have been proposed (Pucek, Belousova et al. 2004, Sipko 2009, Tokarska, Pertoldi et al. 2011), generally covering large portions of the temperate zone and all of them including Germany within the historic distribution of European bison.

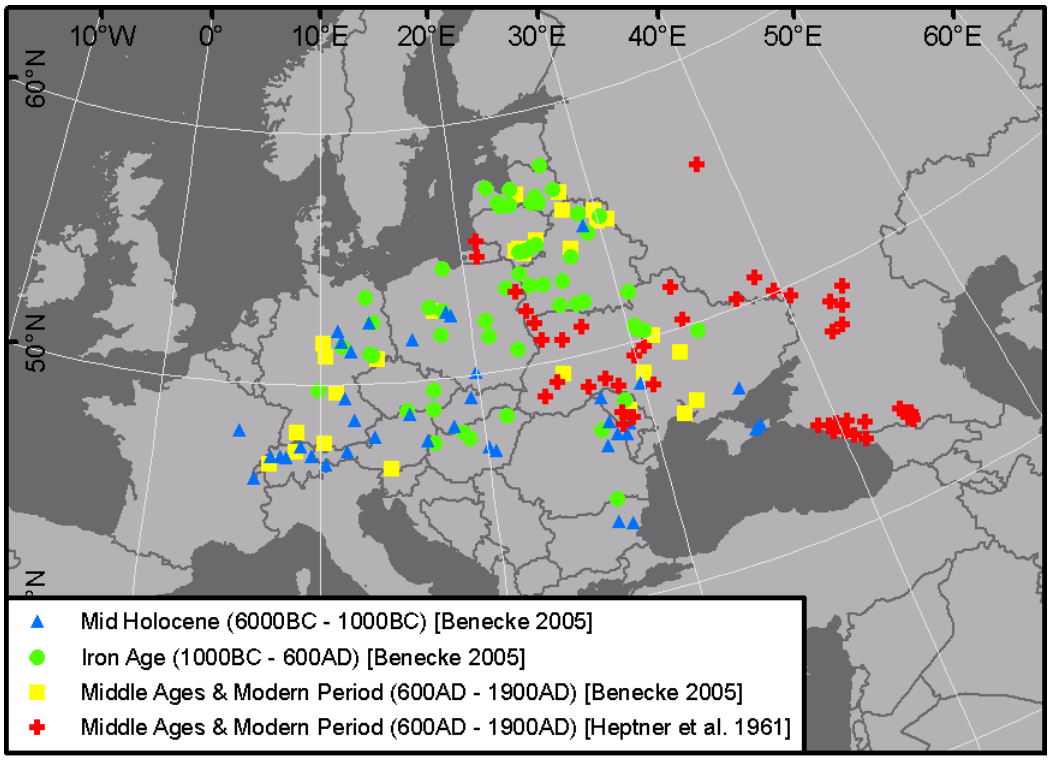


Figure 1: Historic European bison findings from archeozoological excavations (Benecke et al., 2005) and historic records (Heptner et al., 1961).

In the most comprehensive collection of historic bison occurrence data, Benecke et al. (2005) gathered archeozoological records from more than 7,000 excavations from 30 countries in Europe, showing numerous findings of bison remains (e.g., bones) in Germany, particularly in its East and South (Figure 1). Benecke et al.'s database did not extend into European Russia, but an

extensive compilation of European bison records (both bone findings and written records) exists for Europe's East (Heptner, Nasimovich et al. 1961).

In an alternative approach to reconstruct the historic distribution of European bison, Kuemmerle et al. (2012), used all available locations of historic bison occurrence together with historic climate and a vegetation data in a species distribution modeling framework. Their reconstructions provide further evidence for large tracts of Germany being an essential part of the historic range of European bison in the mid and late Holocene, until the large-scale transformation of landscapes starting in the middle ages (Figure 2).

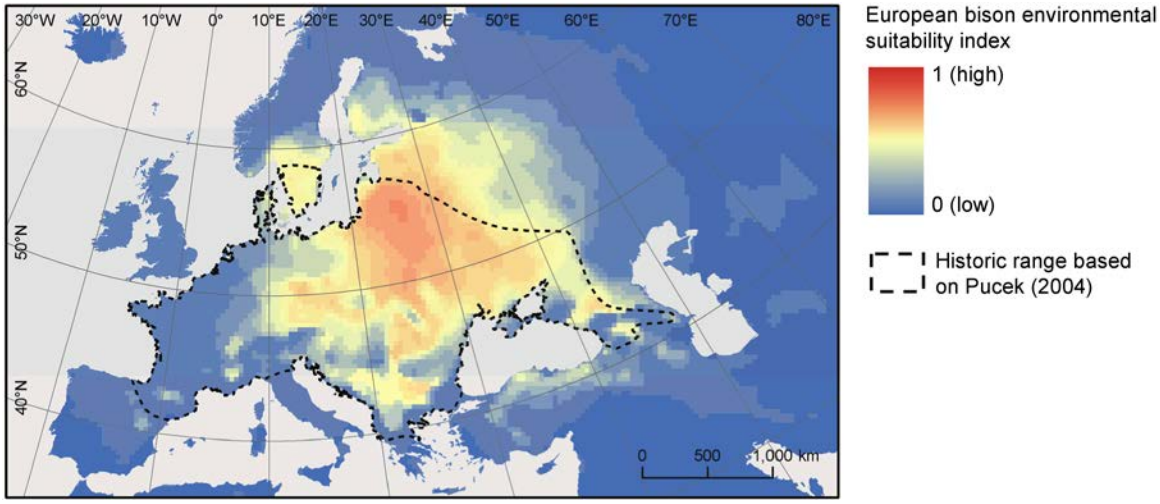


Figure 2: Range reconstruction using species distribution models which relate occurrence locations to environmental variables to predict species' distribution (see Kuemmerle et al. (2012) for details). This range reconstruction suggests that large parts of Germany were historically inhabited by European bison, but also that Germany may have constituted the western range limit of bison in Europe.

Taken together, all available information on the historic distribution of European bison suggests that Germany has been an important part of the species historical range since the last ice age. Given that environmental conditions in Europe have been fairly stable since the mid-Holocene, with similar climate conditions and potential natural vegetation (climax) communities than today, Germany would likely still be a stronghold of European bison in Europe without large scale human impact in the form of habitat loss via agricultural expansion and overhunting, that extirpated bison from the territory of Germany in the past. Potential releases of European bison herds in Germany should thus be seen as reintroduction projects.

EUROPEAN BISON HABITAT PREFERENCES

***Executive summary**: Existing knowledge on the feeding ecology of European bison shows that bison predominately feed on grasses and herbs, but their diet can include substantial shares of browse (i.e., twigs and leaves). Although European bison are clearly associated with forests, suitable European bison habitat should therefore contain substantial open areas. Habitat use in winter and summer can differ substantially, and where bison populations occur next to agricultural areas, conflicts with agriculture are common.*

The question what constitutes suitable European bison habitat has been in the focus of much scientific inquire. Insights about European bison habitat use can principally be drawn from two data sources: (1) studying habitat use of existing, free-ranging bison herds and (2) exploring paleo-ecological evidence.

Habitat use of contemporary European bison populations

Existing knowledge suggests that European bison, being a typical ruminant, are predominantly grazers. This is why European bison heavily depend on access to palatable herbs and grasses, which can be found both on the forest floor and in grasslands within or outside forests. Browse (i.e., twigs and leaves of woody species) contributes a minor, but nevertheless important part of European bison's diet (usually less than 20%). Habitat selection, including the use of open areas (e.g., clear-cuts, young plantations, forest glades, meadows and pastures) varies substantially between summer and winter and is directly connected with foraging patterns of the species. Where forest borders agricultural fields, bison will prefer fields over foraging in forests during winter (Korochkina 1969, Gebczynska and Krasinska 1972, Falińska 1973, Dzieciolowski, Kossak et al. 1975, Hofmann 1989, Krasińska and Krasiński 2007, Jaroszewicz and Piroznikow 2008, Kamiński, Hofman-Kamińska et al. 2010).

In terms of vegetation types preferred by bison, long-term studies from Białowieża Forest in Poland, showed that bison generally prefer sites dominated by deciduous or mixed forest over pure coniferous forests (Krasińska and Krasiński 2007). This preference is due to differences in the ground vegetation (herbaceous and gramineous species) in these forests, which provides the majority of bison forage. Therefore, sites with poor soil quality (e.g., podzoils), that do not support abundant ground vegetation, are not very suitable for bison. Preferences towards specific ground vegetation varies over the year. In deciduous forests, important feeding plants in spring and mid-summer are wood anemones (*Anemone nemorosa*), followed by ground-elder (*Aegopodium podagraria*), hedge woundwort (*Stachys silvatica*), wolly buttercup (*Ranunculus lanuginosus*) and common nettle (*Urtica dioica*). In late summer and early autumn, bison mainly feed on yellow archangel (*Galeobdolon luteum*) and wood sorrel (*Oxalis acetosella*). In mixed forests, reed grass (*Calamagrostis arundinacea*) is another important plant (Borowski and Kossak 1972, Krasinska, Cabonraczynska et al. 1987). In winter, bison diet contains more woody tissues (twigs and tree bark). However, bison can forage on whatever green plants are available under the

snow. In mountain areas, the most preferred food in winter are brambles (*Rubus hirtus*). If winter rape, cereals, or haystacks are available in the vicinity of forests, bison prefer feeding at open fields (Perzanowski and Marszałek 2012). Access to clean drinking water, preferably at watercourses, is another important habitat element throughout the whole year, although bison in winter may survive a number of days obtaining water from snow (Krasinska, Krasinski et al. 2014, Perzanowski and Olech 2014).

Winter feeding has a long tradition for many contemporary European bison populations on the one hand to supply animals with supplementary feed during the difficult winter period, and on the other hand to mitigate potential conflicts by keeping animals from damaging forests and crops during autumn and winter. Prolonged feeding at permanent sites causes an aggregation of animals around such sites which may be harmful for their health (transmission of diseases and parasites), and may change natural foraging behaviour and habitat use. Also, damages to trees (mostly debarking) are more widespread close to feeding sites (Bunevich 1999, Dackiewicz 1999, Krasińska and Krasiński 2007, Anusz, Kita et al. 2010). Wherever possible, winter feeding should be minimized, and reintroduction projects in areas where winter feeding will be necessary to sustain European bison populations or to minimize conflict with land use, should be avoided.

Existing studies on European bison habitat selection highlight that habitat selection can differ substantially among herds. We therefore here provide a brief summary of insights on European bison habitat use for some main populations that have been studied extensively. Generally, European bison populations were introduced to both lowland and mountainous areas, and we will first highlight insights from lowland herds, then proceed to populations living in mountain areas.

Most knowledge on European bison ecology derives from the Białowieska Primeval Forest (Brincken 1826, Jarocki 1830, Kulagin 1919, Sztolcman 1920, Wróblewski 1927, Borowski and Kossak 1972, Gebczynska, Gebczynski et al. 1991, Krasińska and Krasiński 2007). This site represents a typical European lowland forest, with substantial areas of primeval forest. After World War II, the Białowieska Forest was divided between Poland and Belarus, differing considerably regarding their management and protection status. In the Polish part of the Białowieska Forest, bison are most frequently observed in deciduous forest stands (mixed, fresh and moist deciduous forests (79% of observations) and alder woods (17%), although they periodically also make use of mixed-coniferous stands (Daleszczyk, Krasinska et al. 2007, Krasińska and Krasiński 2007). There are also distinct differences in habitat use among seasons. In spring (April – May) bison tend to concentrate in deciduous forest (51% of observations), while in June – July over 70% of observations come from mixed-coniferous forest. Alder stands are visited by the animals mostly during droughts in summer and in the autumn (up to 15% of records). Much feeding time (up to 40%) is spend in open areas (meadows, deforested glades, fields bordering the forest). In the Byelorussian part, coniferous tree stands are much more common (69% of the forested area), while deciduous stands account for 12% and alder woods for 19% (Kozul'ko and Zhukov 1999, Bunevich 2003). The most intensively frequented forests were fresh and wet coniferous forests, as well as fresh mixed stands (about 70% of observations), with

deciduous forests being much less frequently used in this part of Białowieska Forest (Bunevich 1989). Winter supplemental feeding is carried out in both parts of the Białowieska Forest.

The lowland population of European bison of the Borecka Forest (north-eastern Poland) almost exclusively utilizes fresh deciduous forests, and in the vegetative season, animals were more often observed in the forest (63% of records) than in the open (37%). Among open areas, meadows (75% of observations), clear-cuts and young plantations (15%), and agricultural fields (10%, rape, winter crops) were used intensively. Interestingly, after a storm and blowdown in 2002 that increased the proportion of open areas considerably, the home range of this population decreased, and movements outside of the forest in the summer have been reduced markedly (Żoch 2007). In Knyszyńska Forest (also north-eastern Poland), coniferous stands dominate and the herd frequently leaves the forest, and moves into cultivated fields between late autumn and the early spring (Krasinski, Bunevich et al. 1994, Krasińska and Krasiński 2007). The lowland population in West-Pomerania (north-west Poland), a region which resembles northern Germany, occurs in a mixed forest-agricultural landscape with about 40% forest cover. Cultivated fields, mostly large-scale monocultures, are the main foraging ground for this population (Janicka, Hołubczat et al. 2008, Karnecki 2008, Tracz, Olech et al. 2008). Generally, all these populations are supplied with supplementary feeding during winter (Krasinski and Krasinska 1992, Żoch 2007, Hofman-Kamińska and Kowalczyk 2010).

Although less well-studied, available information from other herds, also highlights the importance of open areas, and especially agricultural fields for E. bison populations. In Lithuania, bison inhabit a mixed forest-agricultural landscape, with a majority of feeding occurring on agricultural fields and managed meadows (Balciauskas 1999). Similarly, the Belarusian population “Volozhinskaya” (western Byelorussia) is foraging mostly in meadows close to the forests during spring and summer, while in autumn and winter the herd tends to remain inside the forest.

Concerning European bison populations inhabiting mountainous areas, most data on habitat use comes from the Carpathians, which extend over six countries in Central and South-Eastern Europe (Webster, Holt et al. 2001, Perzanowski and Marszałek 2012). The dominating habitat there is mixed beech – fir forest, i.e., the Carpathian beechwood (*Fagetum Carpaticum*), which resembles forest habitats that can be found in many parts of Germany (e.g., Rothaargebirge). European bison in the Carpathians generally prefer forest-dominated habitat with a mosaic of grassland patches in areas with low human disturbance (Kuemmerle, Perzanowski et al. 2010). The most detailed assessments in the Carpathians have been done for the Bieszczady Mountains (south-eastern Poland) where bison were first reintroduced (1963). Human population density there is very low (between 5 – 15 people per sq. km), and the majority of open areas consists of meadows or pastures in various stages of secondary succession (Augustyn and Kozak 1997, Winnicki and Zemanek 2009). In both winter and summer, European bison are mostly using the forest (>90% of the observations), with other used habitat types including meadows, pastures, fallow land, and glades (Perzanowski, Januszczak et al. 2011). The most heavily used forest

stands were dominated by beech (*Fagus sylvatica*) or spruce (*Picea abies*) in summer and beech, Scots pine (*Pinus sylvestris*) (23%), and alder (*Alnus incana*) in winter. European bison were also found to prefer more open canopies in summer (68% of records), while in winter closed canopy stands were preferred (Perzanowski, Wołoszyn-Gałęza et al. 2008).

Analysis of the use of the terrain of Bieszczady revealed that bison in summer were mostly present at elevations between 550-850 m above sea level (92.9%), while in winter between 450–750 m (98.0%). There are no records of the species' presence from elevations below 450 m in summer and from above 950 m in winter. Such distinct seasonal differences are connected mostly with the snow depth (sometimes exceeding 1 m), which in higher elevations (above 700 – 800 m) may occur from late October to early April. In spring, bison tend to follow the development of new vegetation, while in fall they shift towards lower elevations, usually synchronically with the appearance of the first snow. Further, bison tend to prefer slopes over valleys and mountain ridges (Perzanowski, Januszczak et al. 2011, Perzanowski and Marszałek 2012).

It has to be mentioned that the habitat preferences of European bison may vary even across short distances. In the Polish Bieszczady Mountains 93.0–96.6% of bison occurrences where located in forest whereas in the closeby Poloniny National Park (Slovakia) this was true for only 51.5%–72.6% of occurrence locations and animals made an extensive use of abandoned meadows and orchards (respectively 43.6% and 21.8%) (Adamec, Perdiková et al. 2006, Pčola, Adamec et al. 2006, Pčola and Gurecka 2008). This free ranging herd was most frequently observed within the range of 50 –700 m (Pčola, Adamec et al. 2006). In both those neighbouring Carpathian populations, bison are not truly dependent on supplemental winter feeding, however during severe winters they tend to use haystacks or hay-silage, which is provided there by forest service as supplemental forage for deer.

In sum, existing knowledge on contemporary European bison habitat use suggests that optimal habitats for lowland European bison in central and eastern Europe are forest complexes dominated by mixed/deciduous stands, with an admixture of alder woods with an ash, fresh mixed coniferous forest and some proportion of open areas (e.g., meadows and glades). Coniferous forests require larger proportions of open grazing grounds where bison may find additional forage. Generally, the heterogeneity of the environment is a key factor for assuring the suitability of an area for bison, because it allows them to find adequate food in all seasons of the year. However, bison populations that inhabit small forest plots surrounded by agricultural fields tend to leave the forest frequently and graze on the fields. The survival of such populations depends on their social acceptance, which is related to the level of crop damages (Krasinska, Cabonraczynska et al. 1987, Hofman 2008, Kowalczyk 2010, Krasińska, Krasiński et al. 2010, Krasinski 2010).

Paleo-ecological data on European bison habitat use

All contemporary free-ranging European bison populations have been reintroduced by people, because both population numbers and their habitat had been decimated in the past and European bison were pushed back into 'refuges' for centuries. It therefore remains to some extent unclear whether there is a potential bias in the current distribution of European bison towards less-then-optimal habitat for the species, and to what extent the species is connected to dense forest cover (i.e., as is currently the case for most herds) (Kerley, Kowalczyk et al. 2011, Cromsigt, Kowalczyk et al. 2012, Kuemmerle, Hickler et al. 2012).

Paleo-ecological studies exploring the habitat use and diets of European bison long before the species was extirpated from its range therefore provide further evidence into European bison habitat selection that should not be neglected. For example, differences in the content of C^{13} isotope in plants growing under forest canopy and those from open areas are interesting to study the habitat selection of European bison in the past. Generally, the level of C^{13} in bones of European bison from the late Pleistocene and the early Holocene (40K – 9K years ago) indicate that those animals were grazing mostly at open areas. However, this tendency changed towards intensified use of forest habitats about 5,000 years ago, which could be connected with forest expansion after the last glaciation. Available evidence now points to European bison being mixed feeders (grazing and browsing) during the last millennia, before their extirpation in the wild (Hofman-Kamińska, Kamiński et al. 2011, Hofman-Kamińska, Bocherens et al. 2012, Bocherens, Hofman-Kamińska et al. 2015). Overall, current evidence points to a clear association of European bison to forested landscapes for at least the last 4,000–5,000 years.

MAPPING EUROPEAN BISON HABITAT IN GERMANY

***Executive summary**: To map European bison habitat in Germany, we gathered the most comprehensive dataset of bison occurrence points (telemetry data and field-tracked signs of habitat use) from all Polish European bison herds. These free-ranging herds exist in environmental conditions broadly similar to those of Germany, and the Polish herds generally are among the oldest wild bison herds existing. We model European bison habitat using a range of regional-scale environmental and human-pressure variables for the territory of Poland, Germany, Slovakia and the Czech Republic.*

Our results show widespread potentially suitable habitat, that is, habitat similar to those areas currently inhabited by free-ranging bison herds. Habitat was more widespread in Poland and Slovakia compared to Germany, mainly because of more human pressure in German landscapes. In Germany, potentially suitable bison habitat was predominantly found in heavily forested areas. Overlying our bison habitat map with maps of roads, settlements, and protected areas suggested that a number of sites could be particularly interesting for on-site assessments to investigate the potential for free-ranging European bison populations. These were, ordered from North to South: (1) Müritz-Schorfheide, (2) the area around

Celle/Hermannsburg, (3) the area between Spreewald, Cottbus, and Guben, (4) the Harz Mountains, (5) Thüringer Wald, (6) Spessart, (7) Pfälzer Wald, (8) Bayerischer Wald, (9) Schwarzwald, and (10) the Bavarian Alps. Among these, four sites - Müritz-Schorfheide, the Spreewald-Cottbus-Guben area, the Harz Mountains, and the Pfälzer Wald – were the most promising sites.

Approach

To identify areas of potentially suitable habitat for European bison populations in Germany, we used species distribution models. Generally, these models quantitatively describe species' habitat requirements, by analyzing environmental conditions at locations where the species occurs (i.e., occurrence locations), and contrasting these locations to sites where the species does not occur (i.e., absence locations). For many species, reliable absence data do not exist or are challenging to gather – especially for species like the European bison that have been extirpated from large parts of their range. A common solution in such cases is to contrast occurrences with a random sample of sites (i.e., background locations), describing the general distribution of environmental conditions in an area. For a more detailed and technical introduction to species distribution modeling we refer to Elith and Leathwick (2009) or Franklin (2010).

As our species distribution algorithm to map European bison habitat, we used maximum entropy modeling (Phillips, Anderson et al. 2006, Phillips, Dudik et al. 2009), which works well with small sample sizes and is among the highest performing approaches (Elith, Graham et al. 2006). Maximum entropy modeling has been used in a wide range of studies assessing species habitats and ranges, including for assessing European bison habitat at eco-regional to continental scales (Kuemmerle, Perzanowski et al. 2010, Kuemmerle, Perzanowski et al. 2011, Kuemmerle, Radeloff et al. 2011, Kuemmerle, Hickler et al. 2012, Bleyhl, Sipko et al. 2015). A detailed mathematical description of maximum entropy modeling is provided in Phillips *et al.* (2006, 2009) and Elith *et al.* (2011).

To fit maximum entropy models, we used Maxent (version 3.3.3, http://www.cs.princeton.edu/~schapire/maxent/). All model runs used default regularization parameters, a maximum of 2,500 iterations, and 10,000 random background points (Phillips and Dudik 2008). To prevent overfitting, we used only quadratic and hinge features. We validated our models by calculating the area under the curve (AUC) of the receiver operating characteristics (ROC) curve, based on ten-fold cross-validation. In addition, we carried out a cross-validation at the herd level (leaving out all occurrence points from one herd for validating the model parameterized using all other herds). Final habitat suitability maps were calculated as the average of the ten replicate runs, and we used a logistic link function to yield a relative habitat suitability index (HSI) between zero and one (Phillips and Dudik 2008). Because our sample of European bison occurrence data was not a random sample, the HSI index should be interpreted as a relative measure of habitat suitability, not a probability of occurrence. Likewise, because all contemporary European bison herds are reintroduced, and European bison only occur in low numbers relative to their historic population

sizes, our analyses cannot provide insights into the fundamental niche of European bison. Rather, our analyses identify those habitats that are similar to the areas where European bison populations are thriving today (i.e., habitat that are suitable for this species given current knowledge about European bison habitat selection).

Detailed European bison occurrence data were available from all free-ranging herds in Poland (see below), where herds have existed for relatively long time periods (i.e., many decades). As predictor variables to describe habitat conditions we used environmental variables (e.g., land cover, forest fragmentation, topography), and human disturbance variables (e.g., distance to roads, distance to settlements) at a scale of about 1:100,000 (see below), based on our experience from earlier work on mapping bison habitat elsewhere in Europe (Kuemmerle, Perzanowski et al. 2010, Kuemmerle, Radeloff et al. 2011). Based on these data, we parameterized a habitat model, resulting in a habitat suitability map highlighting areas, which are potentially suitable, and may have lower conflict potential with land use and people. We also used a jackknife procedure to assess variable importance. A few of our predictor variables were collinear ($r > 0.7$), and we fitted alternative models in such cases, retaining the variable yielding higher goodness-of-fit. As a robustness test, we compared our model based on telemetry data from all individuals to a model using only data from female bison. To test the influence of each herd on our final map, we also ran alternative models leaving out occurrence locations from one herd at the time.

To identify larger patches (or groups of patches) of suitable European bison habitat that could serve as candidate sites for future reintroductions, we overlaid our habitat suitability maps with maps of protected areas, roads, and settlements. Assuming that reintroduction projects will mainly take place in areas that contain suitable ample habitat inside protected areas, that are not heavily fragmented by roads, and that are not densely settled, this analysis allowed to identify regions for in-depth, ground-level feasibility studies.

Datasets used

European bison occurrence data

We gathered a comprehensive dataset of European bison occurrences for all five Polish herds (Western Pomerania, Bieszczady, Knyszyńska, Borecka, and Białowieska Forests). These herds together occupy an area of about 5,350 km² (minimum convex polygon) in a range of different environments, including lowland and mountainous areas. In total, our dataset included about 340,000 locations (Table 1), which to our knowledge by far constitutes the most comprehensive dataset of this kind ever collected.

Table 1: Summary of E. bison occurrence data used in this study.

Herd	*Telemetry sampling*		*Sampling years*	*Herd range size*
	Number of sampled animals	*total number of locations*		
Western Pomerania	7 m / 13 f	157,000	2011–2013	1,800 km²
Białowieska	3 m / 4 f	62,700	2012–2013	740 km²
Knyszyńska	4 m / 1 f	35,500	2012–2013	1050 km²
Borecka	3 m / 4 f	57,000	2012–2013	160 km²
Bieszczady	4 m / 2 f	29,400 *	2001–2010	1,600 km²

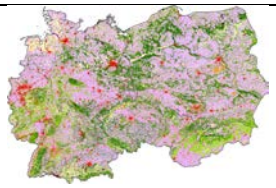
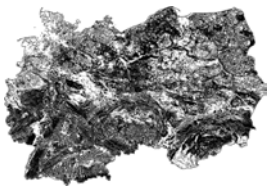
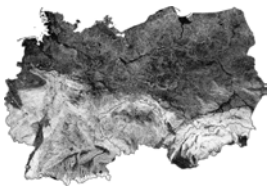
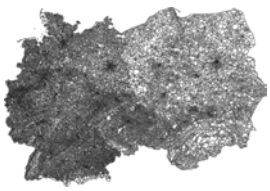
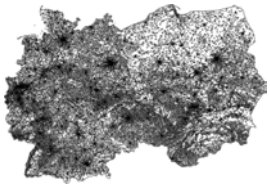
* Note that the data from this herd contain both telemetry data and other signs of bison presence mapped in the field (e.g., tracks, dung, feedings marks).

To parameterize our maximum entropy models, we randomly selected 500 points per herd, treating the closeby Białowieska and Knyszyńska herds as one herd. The area occupied by the Borecka herd was too small to allow for selecting 500 points, and we therefore used less points there. Background data for the maximum entropy modeling were taken from the area surrounding all known herds, using a buffer of 50 km (i.e., the largest distance cows and mixed bison groups have been observed to disperse). Using only background points from these buffer areas accounts for possible selection bias in the set of occurrence points (because bison locations were not sampled randomly across our study region).

Environmental layers

Based on previous experience in modeling European bison habitat at broad geographic extents in Europe (Kuemmerle, Perzanowski et al. 2010, Kuemmerle, Radeloff et al. 2011), we used six predictor variables (Table 2). All predictor variables were resampled to a 100-m resolution.

Table 2: Predictor variables used in the E. bison habitat suitability models.

Predictor		*Data source*	*Data type*	*Processing steps*
Land cover		CORINE 2006	Categorical	Aggregated to nine land cover classes
Forest fragmentation		CORINE 2006	Categorical	Morphological image segmentation
Distance to the forest		CORINE 2006	Continuous	Euclidean distance to nearest forest pixel
Slope		SRTM	Continuous	
Distance to roads		Open street map and Bundesamt für Kartographie und Geodäsie (Germany)	Continuous	Euclidean distance to nearest road
Distance to settlements		CORINE 2006	Continuous	Euclidean distance to nearest settlement

Habitat mapping

Our habitat model revealed substantial areas of potentially suitable habitat across the entire region that we investigated (i.e., Poland, Slovakia, Czech Republic and Germany). Habitat was more widespread in Poland, especially in southeast Poland (Carpathians), in Poland's northeast, and in Poland's northwest (Pomerania). Substantial areas of suitable habitat also occurred in Slovakia (mainly inside the Carpathians). The Czech Republic had less and smaller patches of potentially

suitable habitat, especially in the Carpathians bordering Slovakia, and in the Bohemian Forest bordering Germany.

In Germany, a number of larger patches of potentially suitable bison habitat were identified by our model. These patches tended to occur in the forested lower mountain ranges in Germany (e.g., Schwarzwald, Harz, Bayerischer Wald, Thüringer Wald, Pfälzer Wald), as well as in the Bavarian Alps. Two distinct larger patches of suitable habitat occurred in northern Germany, one in the Müritz-Mecklenburg Lake District and Schorfheide area, and one in the lowland region between Lüneburg and Celle. A detailed assessment of these regions is provided below.

Cross-validating our final maximum entropy model showed that our model was robust, with a cross-validated AUC value of 0.769 (standard deviation of 0.016). The most important variable in our model was distance to settlements, followed by land cover, distance to forest, distance to road and forest fragmentation. All variables contributed substantially to the model, with the exception of slope, which had only a minor influence in the model.

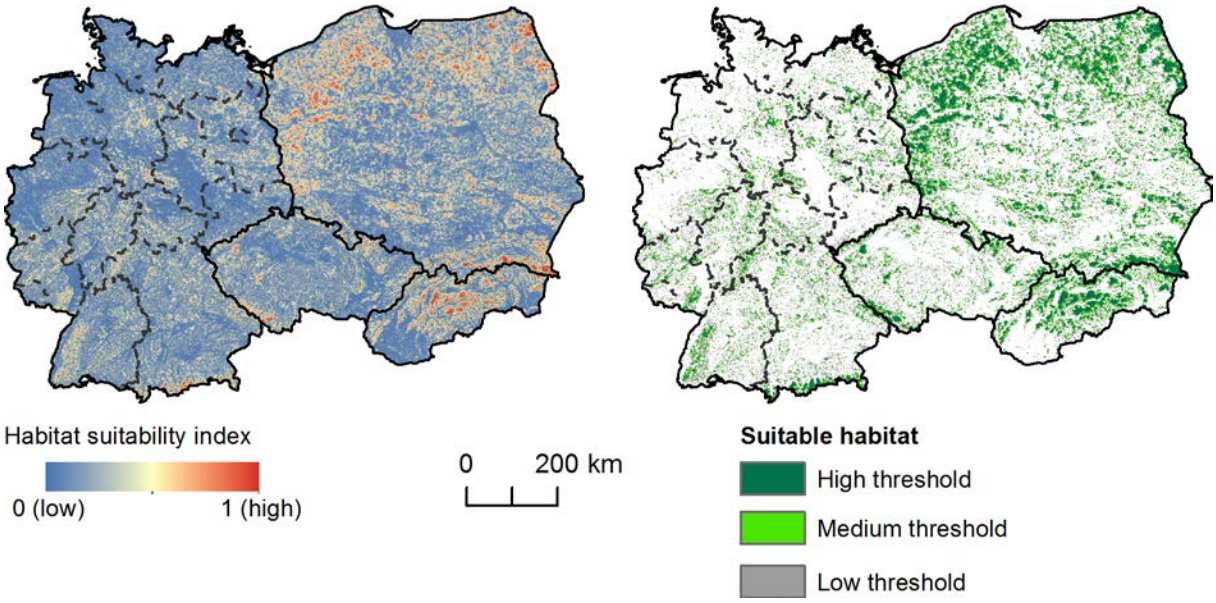


Figure 3: Final habitat suitability map. Left: continuous habitat suitability index between 0 (lowest suitability) and 1 (highest suitability). Right: Example of a categorization into suitable and unsuitable habitat, using the 10th percentile (low threshold), the 20th percentile (medium threshold), and the 30th percentile (high threshold) of the distribution of suitability values at the occurrence locations as a threshold.

The various robustness tests we carried out unanimously suggest that our final map was fairly robust against changes to model parameterization, and the selection of occurrence locations as input data for the model training. The habitat suitability map derived from a model parameterized using only occurrences from female bison was highly similar, and strongly correlated to our map using all occurrence data (r = 0.94, based on 10,000 random locations). Similarly, the mean

habitat suitability map derived from the models parameterized on input datasets that omitted one herd at the time also showed high correlation to our final map using all data (r = 0.99). Two herds had a particularly strong influence on the final map: leaving out the Bieszczady herd resulted in substantially less habitat being predicted in small/medium mountain ranges in the study area, including in Germany. Likewise, leaving out the Western Pomeranian herd resulted in less suitable habitat being identified in the northern part of our study region (e.g., northern Germany). These analyses highlight the value of gathering data from all currently free-ranging herds in the region – as was done for our study.

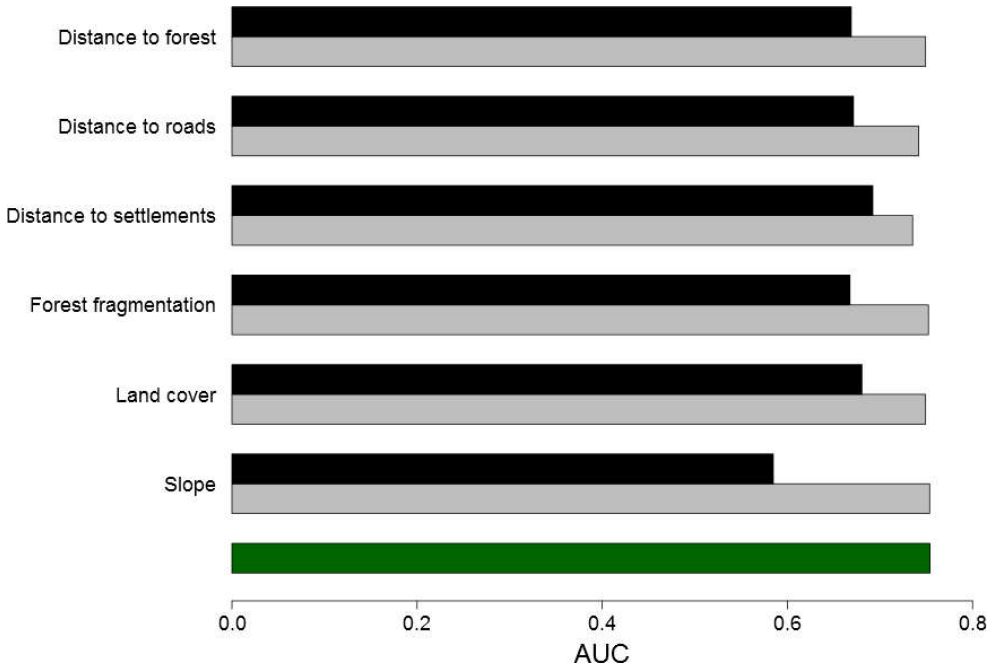


Figure 4: Results from the jackknife test of variable importance. Grey bars depict model fits when excluding a certain variable, whereas black bars depict model fits when building a model using this variable only. For comparison, the green bar denotes the model performance for the full model (all variables). The predictor variable with the highest black bar is distance to settlements, which therefore seems to have the most useful information by itself. The variable that decreases the total model fit (green bar) the most is also distance to settlements, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over 10 replicate runs.

European bison habitat map for Germany and location of potential candidate sites

Discussing potential candidate sites on a workshop among project partners and WWF-Germany in Berlin in July 2014 led to a list of ten candidate sites based on the availability of potentially suitable habitat identified, the existence of protected areas in the regions as a nucleus for reintroduction projects, the level of fragmentation of the landscapes by roads and settlements, and knowledge on the local conditions in terms of nature conservation infrastructure. The ten candidate sites identified in this study were (ordered from north to south): (1) Müritz-

Schorfheide, (2) the area around Celle/Hermannsburg, (3) the area between Spreewald, Cottbus, and Guben, (4) the Harz Mountains, (5) Thüringer Wald, (6) Spessart, (7) Pfälzer Wald, (8) Bayerischer Wald, (9) Schwarzwald, and (10) the Bavarian Alps. A detailed map and description of these sites is provided in the below. While these ten sites emerged from our analyses as particularly interesting, on-site assessments (e.g. of human-dimensions issues and habitat quality) are needed to evaluate the suitability and feasibility of reintroduction projects in these regions.

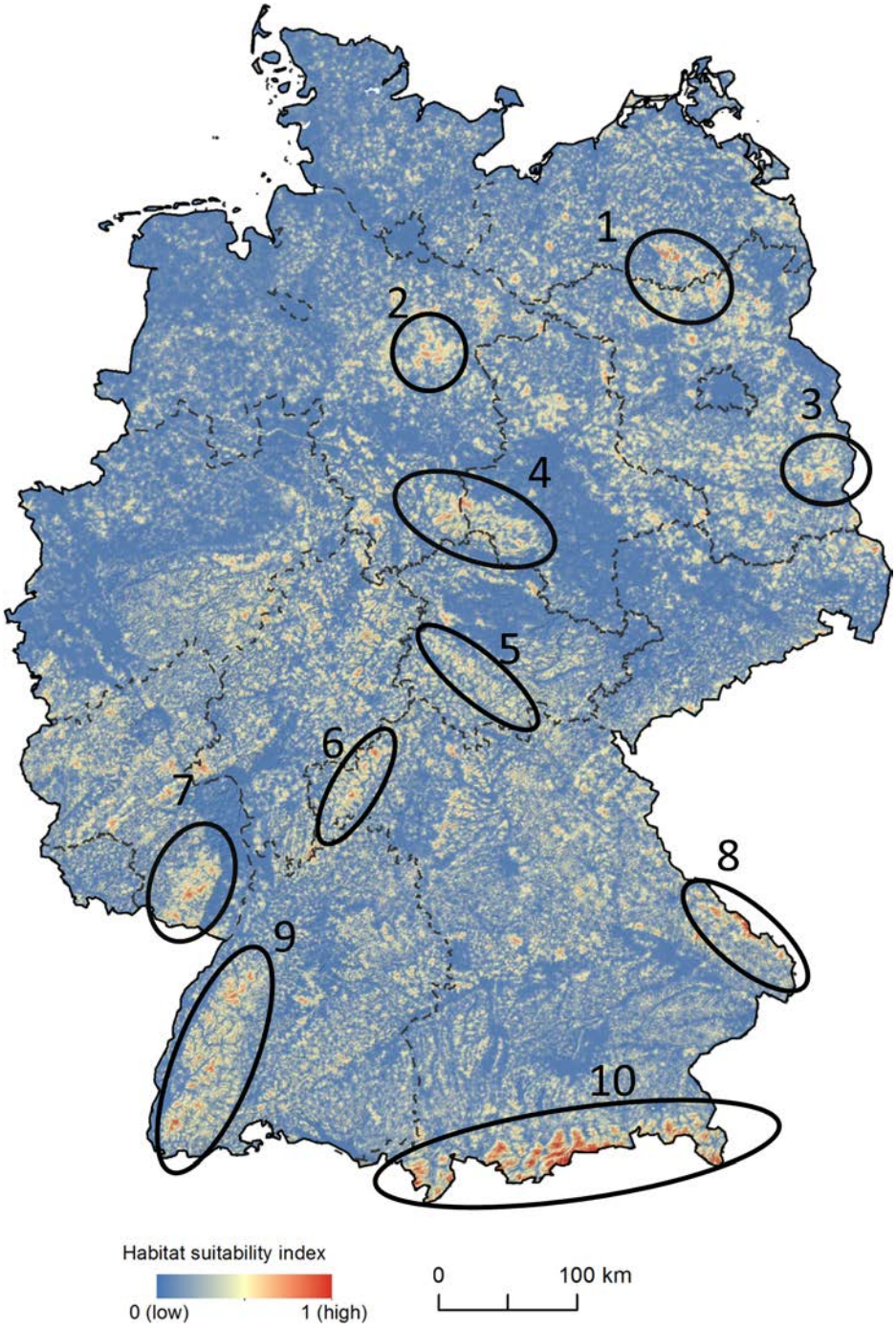
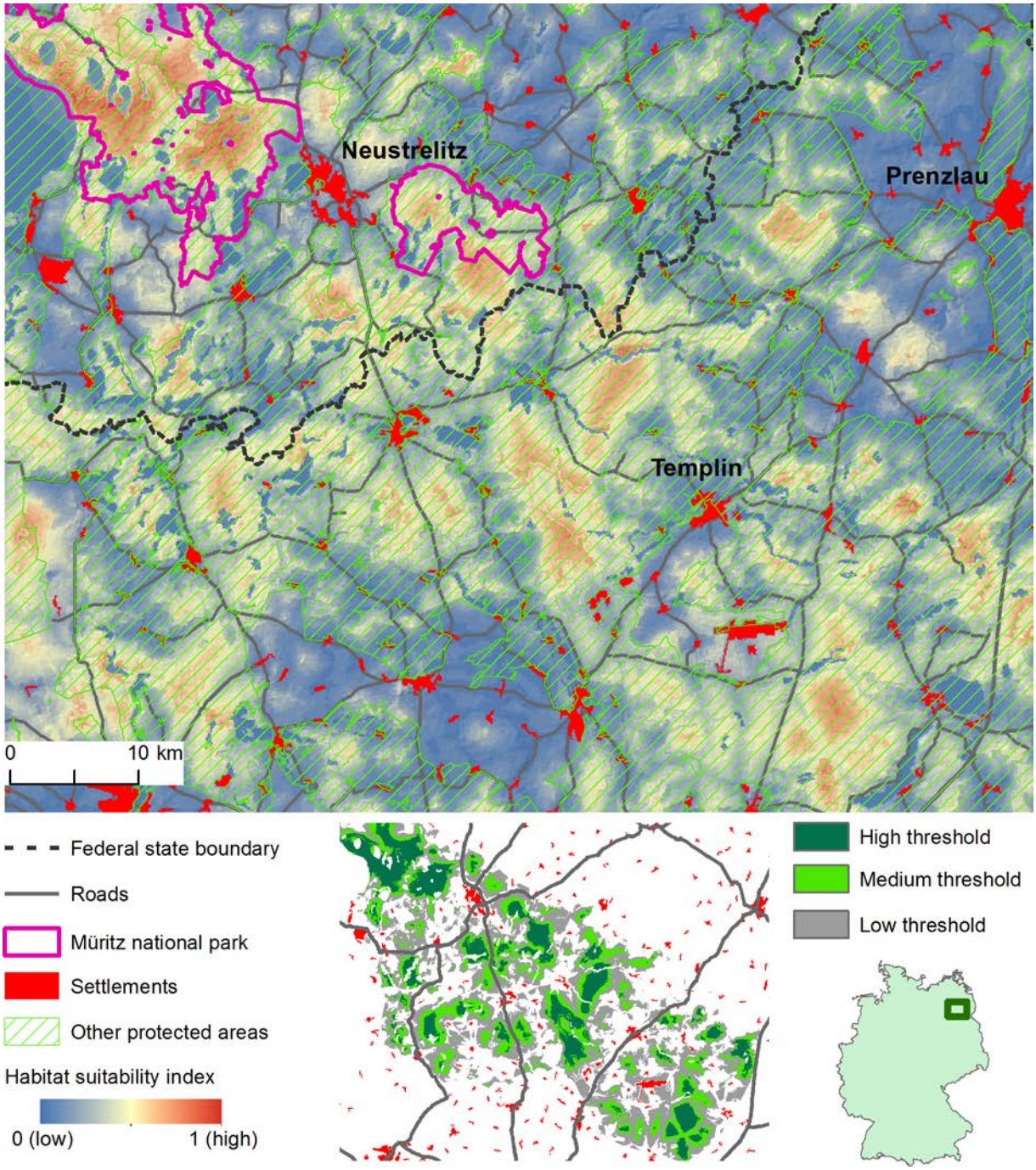


Figure 5: Overview of the 10 candidate sites in Germany (numbered from north to south without order of preference).

Note on the site descriptions: *The purpose of the site descriptions here is to summarize major characteristics of the regions identified of interest for further investigations, based on the broad-scale habitat suitability assessment carried out here. These descriptions do neither intend to provide a comprehensive assessment of site conditions nor do they replace local feasibility studies regarding a European bison reintroduction project. Both require more detailed, site-specific assessments (see section General Guidelines for Assessing Candidate Sites).*

Site 1: Müritz-Schorfheide



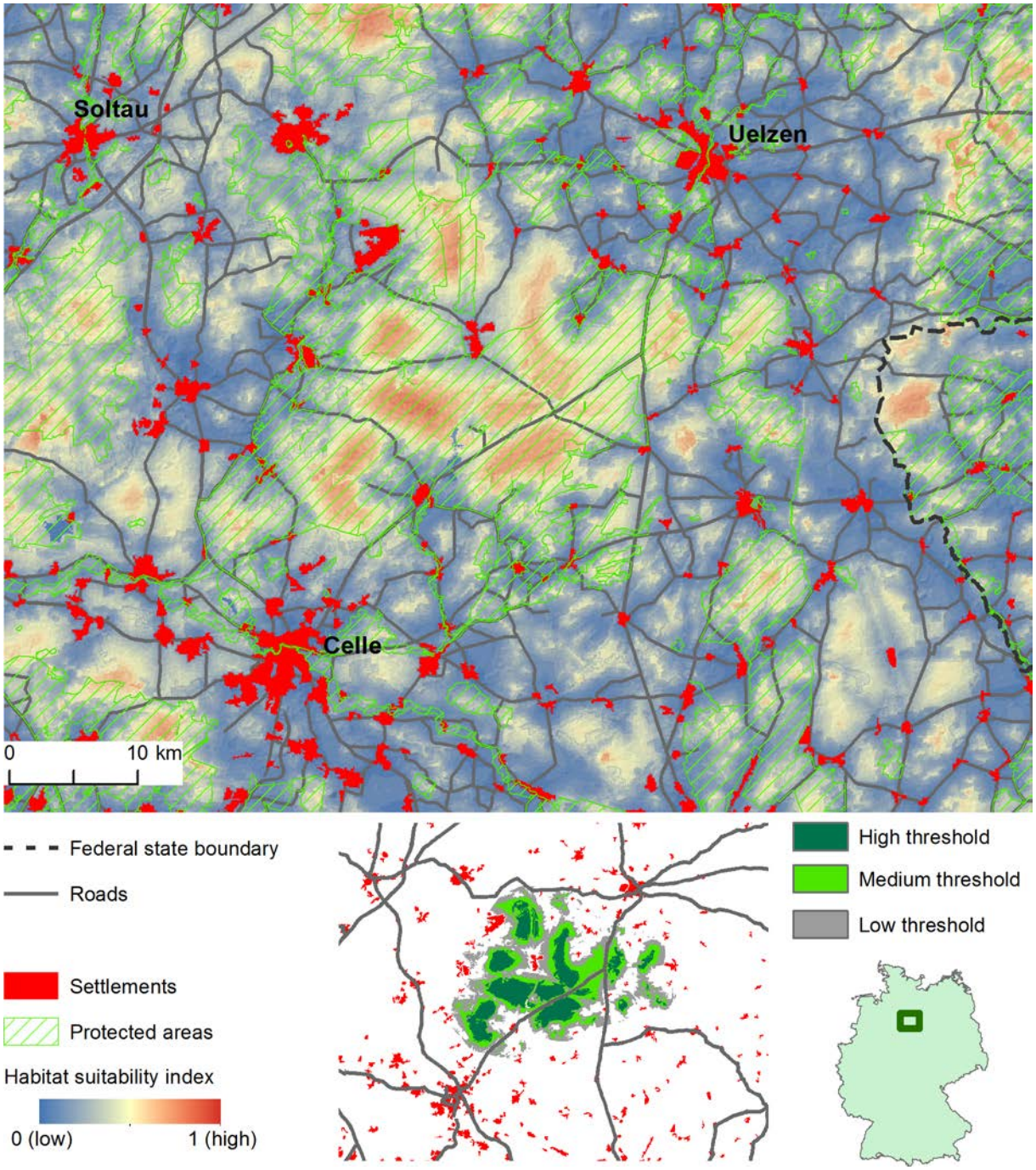
Müritz-Schorfheide was rated of outmost interest for further investigations based on our broad-scale habitat assessment. The region contained several large patches of highly suitable habitat, some of them comparable in size to those areas currently occupied by some free-ranging bison herds in Poland. The relatively high suitability of habitat found in this region was likely due to (a) similar environmental conditions than those found in the areas occupied by Polish lowland-herds, (b) a relatively low level of human pressure. For example, the area has a low density of roads and settlements, suggesting a low level of fragmentation of habitat. No highway (i.e., *Autobahn*) dissects the area and only two major roads (*Bundestrassen*), the B96 (in north-south direction) and the B198 (in east-west direction) divide the larger habitat network. Similarly, this area is characterized by a, for German standards, very low population density (e.g., 48 inhabits / km² in the Landkreis Mecklenburgische Seenplatte). In total, we found 330 to 1,550 km² of potentially suitable bison habitat, depending on the threshold chosen to separate suitable from unsuitable habitat (Table 3).

An additional strong advantage of Müritz-Schorfheide is that the majority of the potential bison habitat identified in the area is already under protection (90–96%) - to a large part thanks to the Müritz National Park, the largest terrestrial national park in Germany (320 km²). Furthermore, ample suitable habitat exists in the immediate surroundings of the Müritz-Schorfheide – habitat patches which also appear relatively well-connected and are partly protected (see Appendix C). Together, this suggests that a European bison population in Müritz-Schorfheide may have, in a visionary scenario, opportunities to expand their range toward other areas in the future. A final argument for this site is the fact that Müritz-Schorfheide is already a renowned destination for nature tourism in Germany and beyond.

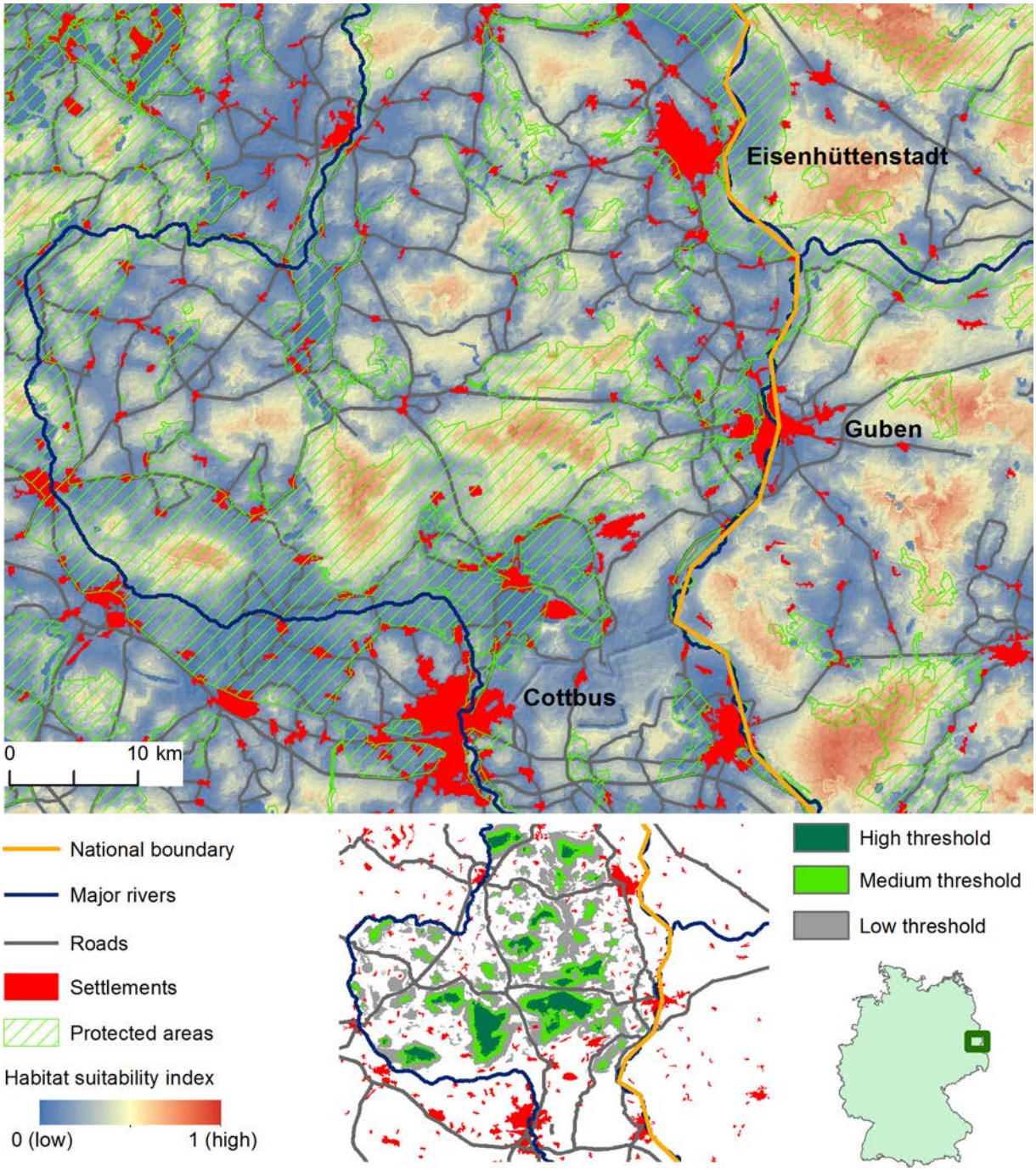
Site 2: Area around Celle/Hermannsburg

This area, roughly located between the cities of Celle, Soltau and Uelzen, harbors several larger areas of potentially suitable habitat. Much of this habitat occurs on an active military training ground (the Truppenübungsplatz Munster) and is characterized by a mixture of forest and open land, with a substantial share of heathland and wetlands. Most of the area is protected (70–80%, mainly through the Landschaftsschutzgebiet “Südheide”) and has recently become a haven for Germany’s expanding wolf population (e.g., in 2012 a pair of wolfs reproduced in the area). Large parts outside the military training ground are protected, with only a few roads crossing suitable habitat patches. In total, we found 170–600 km² suitable habitat (depending on the habitat threshold chosen, see Table 3).

Nevertheless, the larger habitat patches in the Northwest of the area appear separated from other larger patches of suitable habitat in the Southeast by the major road Bundesstrasse B191. Moreover, the site around Celle/Hermannsburg has also relatively few larger patches of suitable European bison habitat in its surrounding, and where such habitat patches exist, they are separated from Celle/Hemannsburg by strong barriers (e.g., Autobahn A7 in the West, Bundesstraße B4 in the East, Bundesstraße B171 in the North).


Soltau
Uelzen
Celle
0
10 km
Federal state boundary
Roads
Settlements
Protected areas
Habitat suitability index
0 (low)
1 (high)
High threshold
Medium threshold
Low threshold

Site 3: Area between Spreewald, Cottbus, and Guben



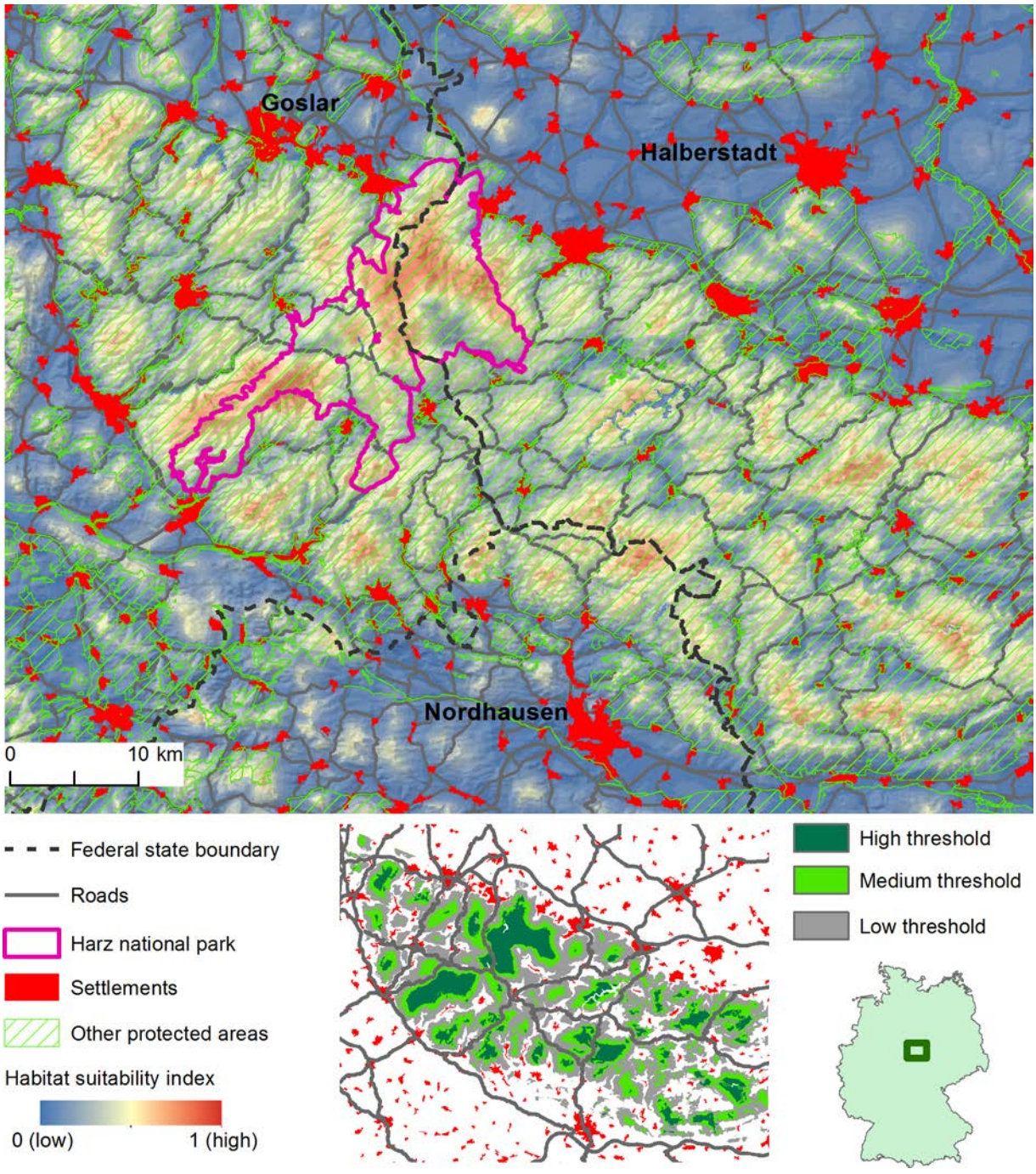
This area was rated high because it includes large patches of potentially suitable habitat between the Spreewald area and the cities of Eisenhüttenstadt and Guben. The area is characterized by, for German standards, low human settlement and road densities (71–78 inhabitants / km² in the three counties (*Landkreise*) of Dahme-Spreewald, Oder-Spree, and Spree-Neiße). Additionally, a relatively high proportion of suitable habitat is already found inside protected areas (30–45% of

the area, depending on the habitat threshold, see Table 4). Additionally, there are large potentially suitable habitat areas found inside former military training grounds. Few major roads dissect the area, with the exception of the B168 (north-south direction) and the B320 (east-west direction). Further advantages of the region are the river Spree, which would form a strong natural dispersal barrier to the west, beyond which more densely populated and more agriculturally dominated areas are found, and the close proximity to several larger patches of suitable habitat in Poland, which would in a visionary sense allow for future connectivity of a larger, transboundary European bison herd. Finally, the area is already known for having become a stronghold of other large mammals, including wolves and moose, in Germany after 1990. In total, we found 120–880 km² potential habitat (depending on the threshold chosen, see Table 3).

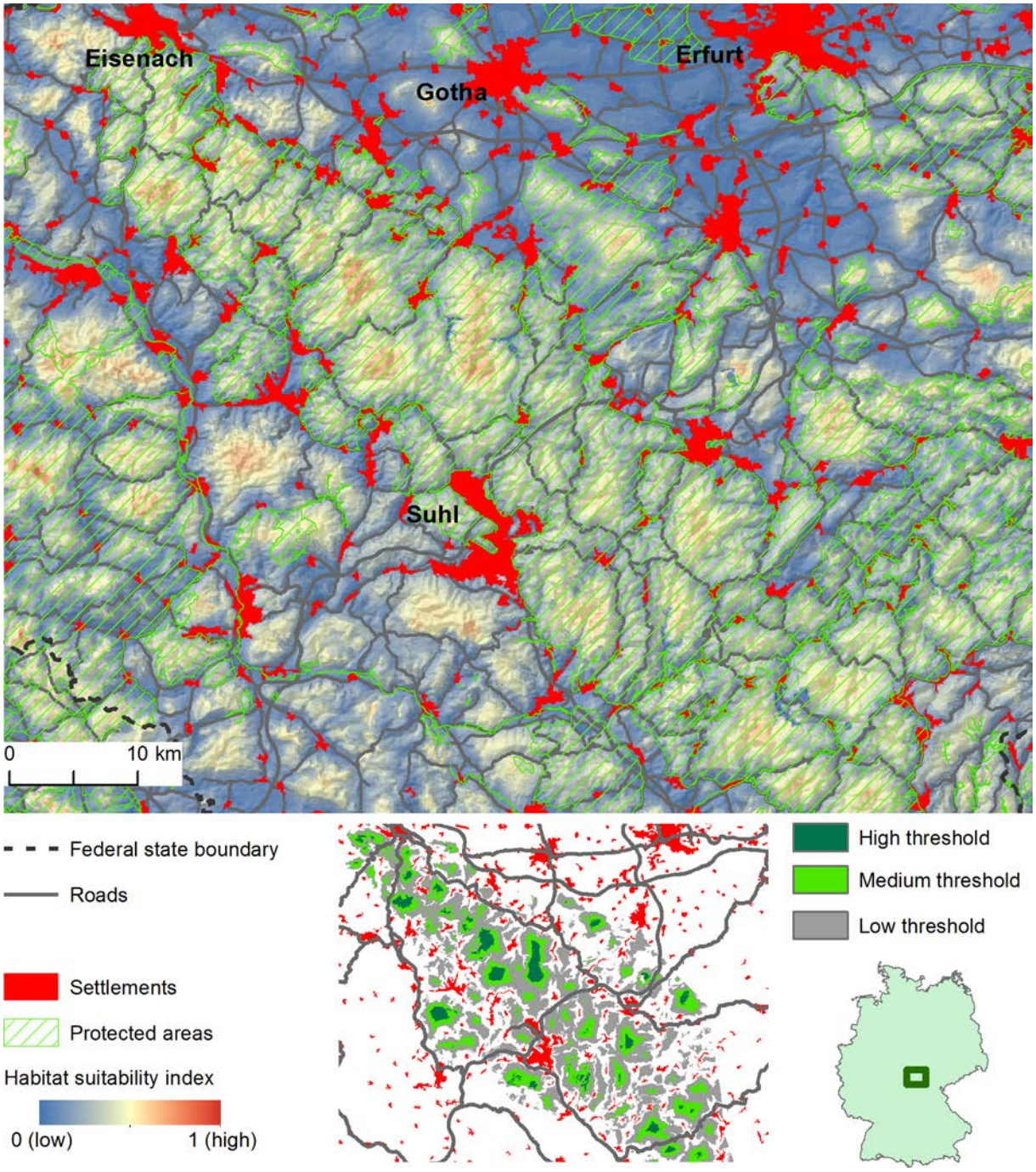
Site 4: Harz Mountains

The Harz mountain range was identified mainly because it contains, according to our assessment, one of the largest agglomerations of potentially suitable European bison habitat patches in Germany. The region hosts several large patches, some of which are equal in size to those occupied by contemporary European bison herds in Poland. Moreover, almost all areas identified as suitable are already under some form of protection (> 98% of the habitat identified in this region), with major parts of all suitable habitat within the boundaries of the Harz National Park (95–230 km² of the potential habitat, depending on the threshold chosen, see Table 4). The Harz region has also recently been the target of a lynx reintroduction program, and hosts large populations of other large mammals in Germany. Finally, the Harz Mountains are one of Germany's prime destinations for nature tourism, with several larger cities close-by (e.g., Göttingen, Hannover, Kassel, Leipzig). In total, we found 270–1600 km² of suitable habitat (depending on the habitat threshold, see Table 3).

Yet, the region is also divided by a number of major roads, some of which are relatively heavily trafficked (especially during tourist season) and that divide the larger habitat network in north–south direction (e.g., B241, B4) and east–west direction (e.g., B242). A potential disadvantage of this region in the long run may also be its relatively isolated location, as the Harz Mountains are surrounded by large stretches of intensively used agricultural land, relatively high rural population densities, and high densities of settlements and roads.


Goslar
Halberstadt
Nordhausen
0
10 km
Federal state boundary
Roads
Harz national park
Settlements
Other protected areas
Habitat suitability index
0 (low)
1 (high)
High threshold
Medium threshold
Low threshold

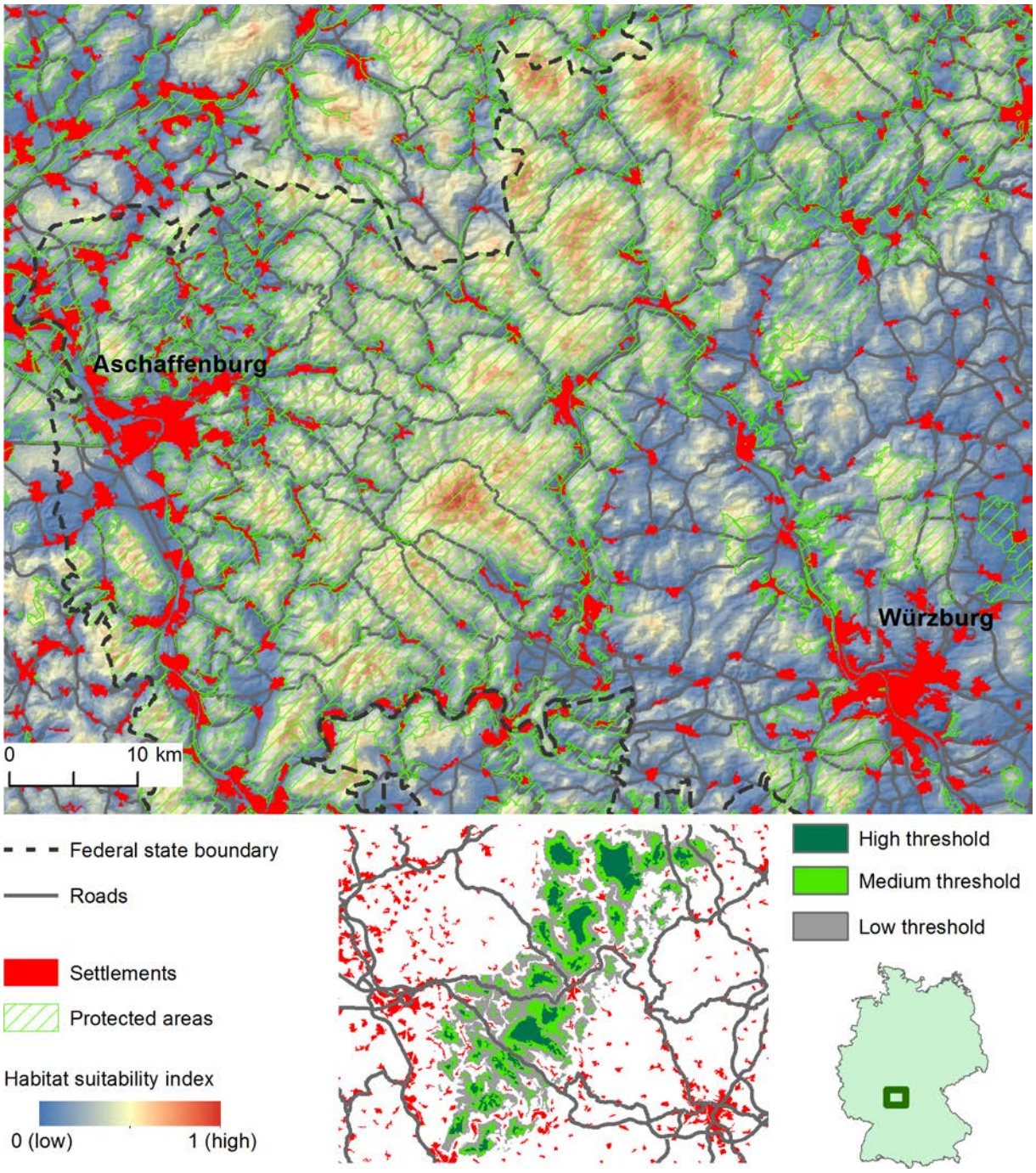
Site 5: Thüringer Wald



The Thüringer Wald emerged as a potential region with several larger tracts of suitable habitat, much of which is already protected to some extent (> 70% of the suitable area is protected, Table 4). While in some parts of the area low settlement and road density prevails (e.g., 69 inhabitants / km² in the Southeastern Landkreis Hildburghausen), many areas inside the Thüringer Wald are characterized by comparatively high human density and a high level of road fragmentation. The Thüringer Wald also contained relatively small areas of highly suitable

habitat according to our analyses (most conservative threshold chosen). In total, we found 70–1,200 km² suitable habitat, depending on the habitat threshold chosen (Table 3).

Site 6: **Spessart**

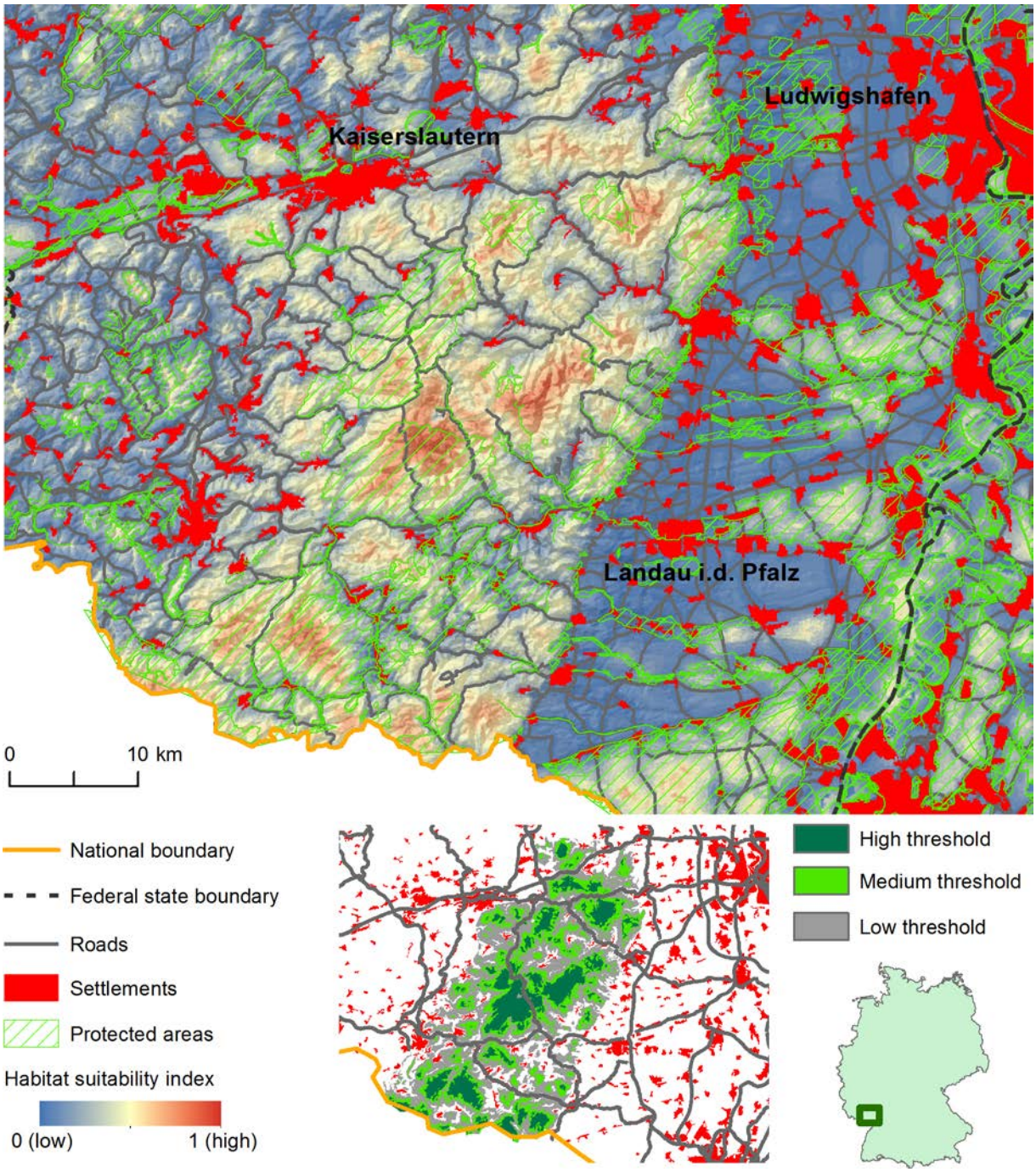


The Spessart region, one of Germany's most forested areas, was selected because it includes several larger potentially suitable habitat patches, most of which are already found inside protected areas (more than 90% of the suitable area for all thresholds we used to separate suitable and unsuitable habitat). The population density in the Spessart area itself is relatively low (e.g., 96 inhabitants / km² in the *Landkreis* Main-Spessart), however, the region is heavily fragmented by major roads, connecting major urban agglomerations in the vicinity and thus having temporarily high traffic volumes. For example, the larger potentially suitable habitat patches in the northern part of the Spessart region are separated from southern patches by the Bundesstrasse B26 and B276, and further South the Autobahn A3 constitutes a major and permanent barrier. Additionally, the northern patches are isolated towards potential additional habitat to the East due to the Autobahn A7, running in North-South direction. A potential disadvantage of this site also lies in the very heavily populated surroundings of the Spessart forests (e.g., greater Frankfurt area, Würzburg, Aschaffenburg). In total, we found 170–1000 km² suitable habitat (depending on the habitat threshold chosen, see Table 3).

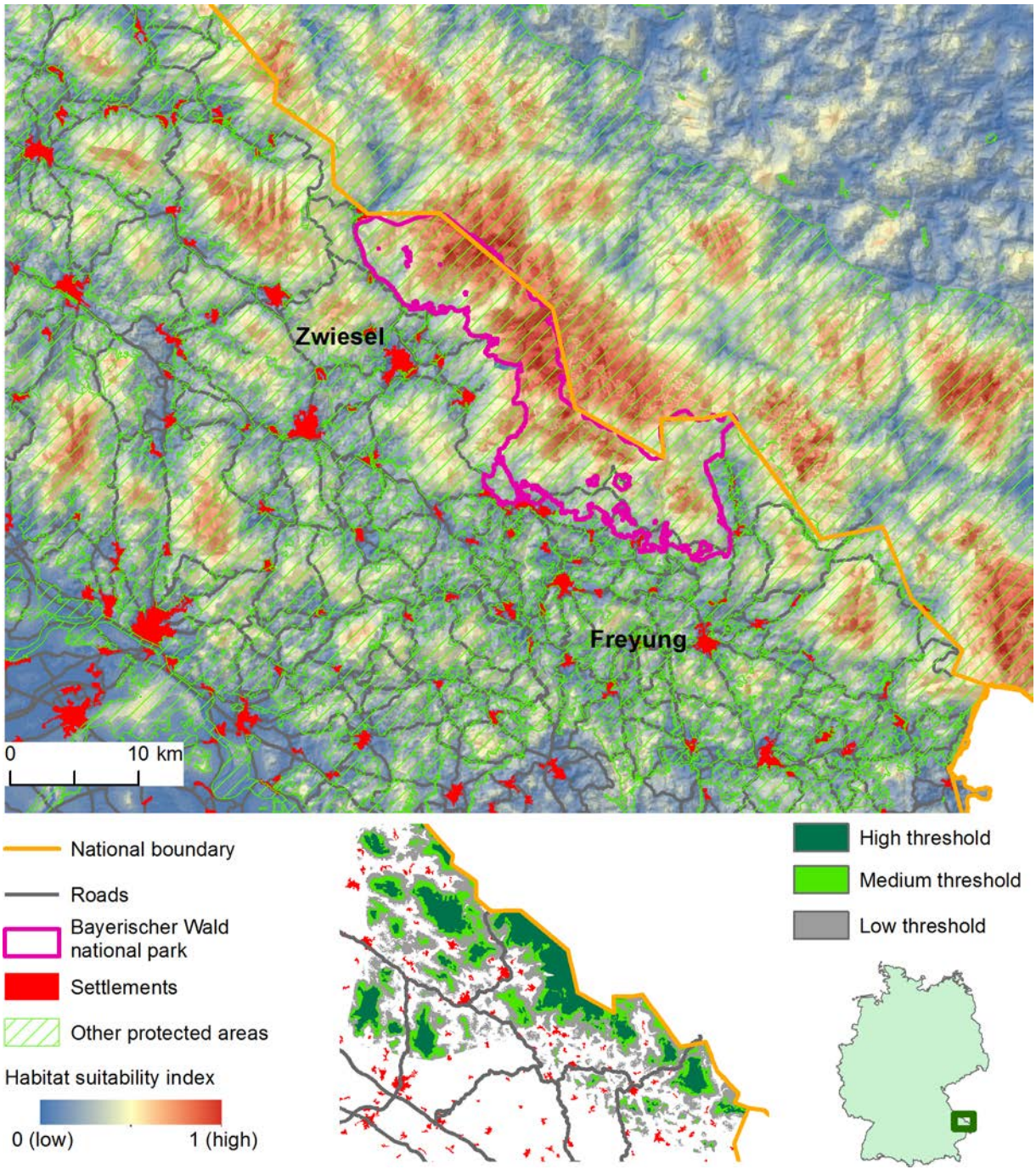
Site 7: Pfälzer Wald

The Pfälzer Wald emerged as one of the largest continuous patches of suitable European bison habitat in Germany in our analyses. The reason for this was the large and relatively unfragmented forest found in the area – constituting some of the largest forest patches in Germany. The region itself is also characterized by a very low population density (e.g., 101 inhabitants / km² in the Landkreis Südwestpfalz, which entails the majority of suitable habitat) and a comparatively low density of roads (only a few major roads such as the B10, dissecting the area in east-west direction, and the B48, dissecting the area in north-south direction). In total, we found 240–1170 km² suitable habitat (depending on the habitat threshold chosen, see Table 3).

Large parts of the Pfälzer Wald are managed with nature conservation goals in mind or are protected (e.g., a major part is included in the trans-boundary Palatine Forest-North Vosges Biosphere Reserve), and the designation of a new national park has been discussed for the region. An attractive feature of the region is also the possibility of joint German/French rewilding efforts, as in the case of the European lynx, as suitable European bison habitat presumably also exists in the French Vosges Mountains (although this was not assessed here). A potential disadvantage of the Pfälzer Wald region lies in its relatively close proximity to the Rhine valley, one of the most densely populated areas in Germany with intensive agriculture. Similarly, to the West and North the area is bordered by the densely populated Zweibrücken – Homburg – Kaiserslautern region.).


Kaiserslautern
Ludwigshafen
Landau i.d. Pfalz
0
10 km
National boundary
Federal state boundary
Roads
Settlements
Protected areas
Habitat suitability index
0 (low)
1 (high)
High threshold
Medium threshold
Low threshold

Site 8: Bayerischer Wald



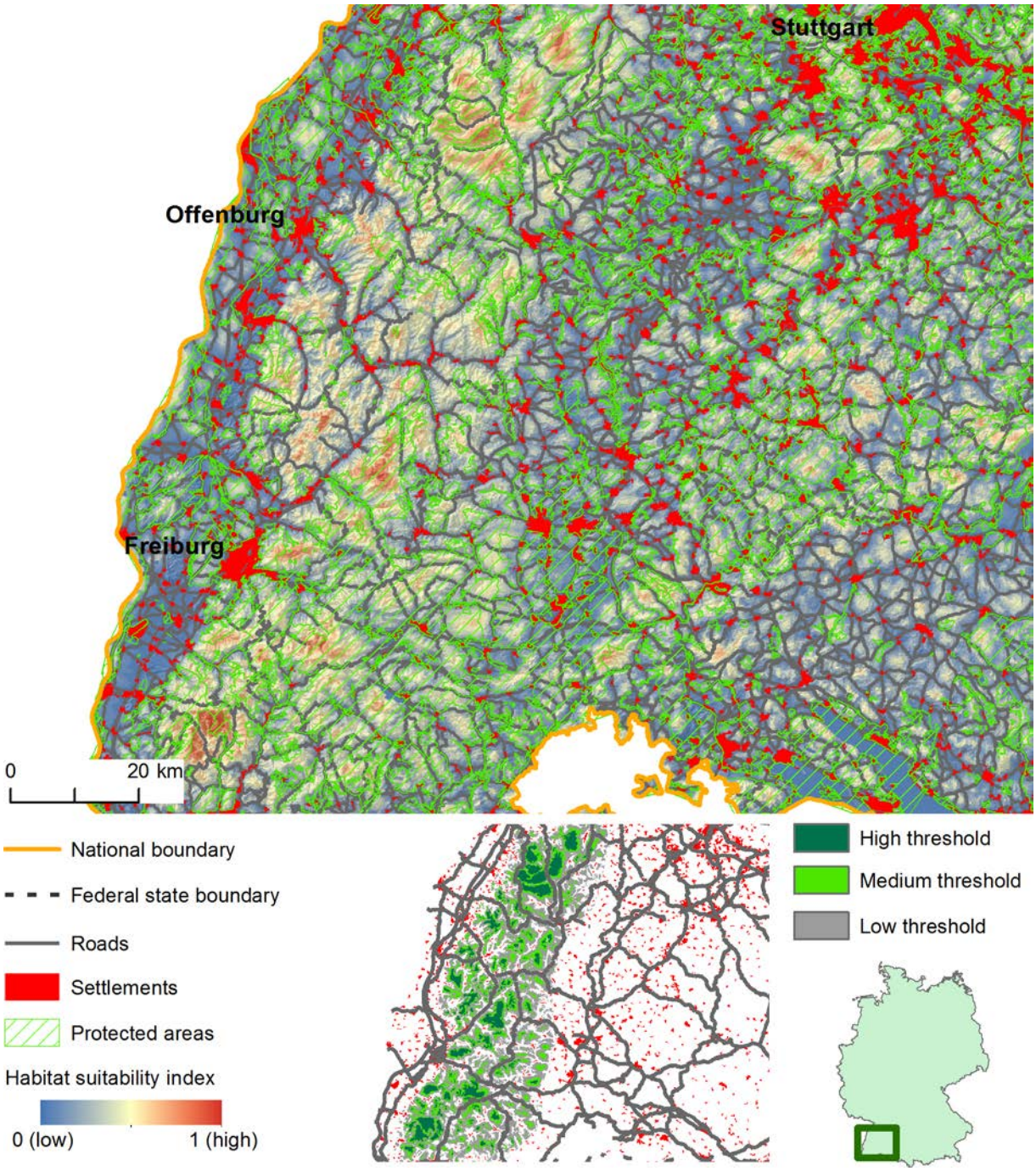
The area in and around the Bayerischer Wald National Park (which covers by itself an area of about 240 km²) entails a few larger suitable habitat patches, much of which is under some form of protection. Specifically, more than 95% of the area identified as suitable area for any threshold chosen is inside existing protected areas (Table 4). Human population density in the area is comparatively low (< 80 inhabitants / km² in the Landkreise Regen and Freyung-Grafenau).

Nevertheless, severely major roads fragment the area (e.g., Bundesstrasse B11, B12, B85) and depending on the habitat threshold chosen, the Bayerischer Wald contains lower levels of suitable habitat than other candidate sites (as low as 310 km²). However, what makes the region particularly interesting are the large patches of suitable habitat on the Czech side, where also human pressure is lower, offering possibilities for a transboundary European bison population.

Site 9: Schwarzwald

The Schwarzwald emerged as a region dominated by a large number of potentially suitable patches, most of them however relatively small in size. Many of these patches are having some form of protection status (38–40% of the suitable habitat patches are protected, Table 4) and the settlement and human population density in the Schwarzwald is relatively low compared to its surroundings. Since 2014, there is also a national park in the northern part of the Schwarzwald (with an area of about ~100 km²). In total, we found 530–3410 km² suitable habitat (depending on the habitat threshold chosen, Table 3).

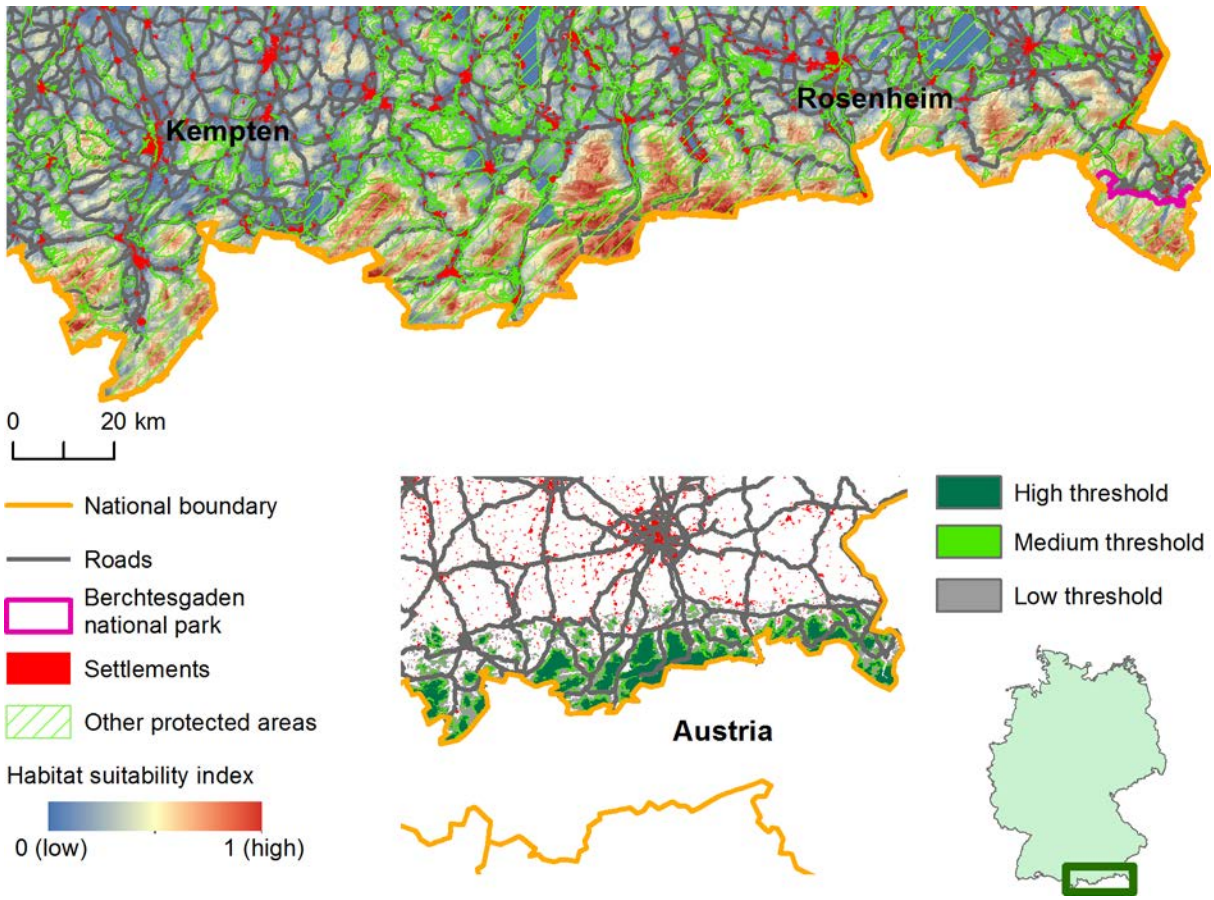
A disadvantage of this region lies in the relatively high degree of fragmentation of the Schwarzwald by roads, and the strong isolation of the Schwarzwald from the Vosges Mountains in France (separated by the river Rhine and several major roads). Major roads that fragment the area are for example the Bundesstraße B500 that is a popular touristic road through the Schwarzwald. Further, many major roads fragment the Schwarzwald in east west direction, most of which are highly frequented by tourists (e.g., the B 462 and the B33). Compared to the other candidate sites, human population density is also higher (> 130 inhabitants / km²). Due to the widespread management of pastures for milk production and livestock breeding, conflicts between European bison and livestock are to be expected in this area.



Note that this map is shown with a different scale than the maps of sites 1-8 (sites 9 and 10 cover a larger area).

Site 10: Bayerische Alpen

The final area highlighted as being potentially of interest in our assessment were the Bavarian Alps, which entail a number of large, continuous patches of potentially highly suitable habitat. This area is generally not fragmented by roads, but the few roads in mountain valleys can form strong barriers. In total, we found 1600–4350 km² suitable habitat (depending on the habitat threshold). Around 50% of the potential habitat is currently protected (Table 4). High suitability values there arise mainly from the low levels of settlement and road densities in the area. As in the case of the Schwarzwald (and also to some extent the Bayerischer Wald) a disadvantage of this site is the potential for conflict with livestock grazing in this region, rendering this site not of highest priority. Furthermore, much of the area is dominated by alpine conditions, in which European bison may thrive as the case of the Caucasian bison herds show, but that would require habitat to be available in every season (summer and winter habitat may not overlap in mountain regions – our assessment did not consider seasonal habitat differences).



Note that this map is shown with a different scale than the maps of sites 1-8 (sites 9 and 10 cover a larger area).

Table 3: Suitable habitat per site.

Site	Suitable habitat [km²] Threshold		
	Low	Medium	High
Müritz-Schorfheide	1550	760	330
Celle Hermannsburg	600	350	170
Spreewald, Cottbus, Guben	880	350	120
Harz	1680	730	270
Thüringer Wald	1200	360	70
Spessart	1000	480	180
Pfälzer Wald	1170	590	240
Bayerischer Wald	1140	590	310
Schwarzwald	3410	1400	530
Bayerische Alpen	4350	2560	1600

Table 4: The area of suitable habitat that is nationally protected (IUCN categories I–V) according to the three habitat thresholds.

Site	IUCN category*	Protected suitable habitat [km²]** Threshold		
		Low	Medium	High
Müritz-Schorfheide	II	270 (17%)	190 (25%)	120 (36%)
	IV	310 (20%)	180 (23%)	80 (23%)
	V	820 (53%)	350 (46%)	120 (36%)
	Total	1400 (90%)	710 (94%)	320 (96%)
Celle Hermannsburg	IV	40 (7%)	20 (6%)	10 (6%)
	V	400 (67%)	250 (71%)	130 (76%)
	Total	440 (73%)	270 (77%)	140 (82%)
Spreewald, Cottbus, Guben	IV	180 (20%)	100 (29%)	50 (42%)
	V	100 (11%)	20 (6%)	2 (2%)
	Total	280 (32%)	120 (34%)	52 (43%)
Harz	II	230 (14%)	160 (22%)	100 (37%)
	IV	100 (6%)	40 (5%)	10 (4%)
	V	1320 (79%)	530 (73%)	160 (59%)
	Total	1650 (98%)	730 (100%)	270 (100%)

Thüringer Wald	IV	50 (4%)	20 (6%)	5 (7%)
	V	830 (69%)	250 (69%)	50 (71%)
	Total	880 (73%)	270 (75%)	55 (79%)
Spessart	IV	10 (1%)	7 (1%)	3 (2%)
	V	920 (92%)	450 (94%)	160 (89%)
	Total	930 (93%)	457 (95%)	163 (91%)
Pfälzer Wald	Biosphere Reserve	320 (27%)	210 (36%)	110 (46%)
Bayerischer Wald	II	220 (19%)	170 (29%)	120 (39%)
	IV	9 (1%)	8 (1%)	6 (2%)
	V	860 (75%)	400 (68%)	170 (55%)
	Total	1089 (96%)	578 (98%)	296 (95%)
Schwarzwald	IV	180 (5%)	100 (5%)	50 (6%)
	V	1120 (33%)	450 (32%)	160 (30%)
	Total	1300 (38%)	550 (39%)	210 (40%)
Bayerische Alpen	II	200 (5%)	140 (5%)	90 (6%)
	IV	900 (21%)	650 (25%)	470 (29%)
	V	890 (20%)	540 (21%)	340 (21%)
	Total	1990 (46%)	1330 (52%)	900 (56%)

* Protected area calculations include the Biosphere Reserve "Pfälzerwald" and do not include the national park "Schwarzwald" since the exact boundaries were not available at the time of this report.

** Numbers in brackets show the relative amount of protected suitable habitat for each threshold.

GENERAL GUIDELINES FOR ASSESSING CANDIDATE SITES

***Executive summary**: Our regional-scale habitat suitability analysis provides an overview of the distribution of potential European bison habitat in Germany, and is a useful tool to identify candidate sites for further, ground-based analyses to decide whether candidate sites could host free-ranging European bison populations. These local-scale feasibility studies should entail five critical components: (1) fine-scale habitat assessment, (2) assessment of habitat fragmentation and connectivity, (3) assessment of carrying capacity and possible population structure, (4) human-dimensions assessment, (5) financial assessment*

Following our mapping of European bison habitat suitability and the identification of candidate sites, detailed ground-based assessments should analyze local site conditions to determine the feasibility of establishing free-ranging bison herds in these candidate sites. In this section, we

outline five key elements that should be covered by such site-specific feasibility studies. This section is meant to give an overview of the elements that should be considered for on-site feasibility studies – it is not meant to be a comprehensive guideline for such an assessment.

Fine-scale habitat quality assessments

Our regional-scale habitat assessment represents, to our knowledge, the most detailed habitat assessment carried out in central Europe, relying on the most comprehensive European bison occurrence dataset ever compiled. Yet, as any regional-scale analysis, our analysis relied on proxy variables that are available across the entire study region, and more detailed, ground-based assessments of habitat quality are needed to complement our regional-scale assessment.

Such local-scale assessments of habitat quality should include an assessment of the following, habitat-relevant factors:

- Forest cover and composition (i.e., stand composition, age structure). This should include and assessment of the availability of young, dense, and preferably coniferous stands providing shelter from wind and refuge conditions for cows during calving, as well as the availability of mature stands with closed canopy providing protection from heavy precipitation. Assessments should be based on ground visits and forest inventory data
- Composition and quantity of herbaceous cover inside forests, with special attention to species preferred by European bison (via forest inventory maps)
- Presence and character (e.g., productivity) of openings in the forest, with a special focus on glades, meadows, and clearcuts that could provide grazing grounds
- Year-round availability of drinking water, via, for example, water bodies (which may be susceptible to freezing in winter) and running water (i.e., creeks, rivers). Water quality and potential water pollution should also be considered

For candidate sites that remain a priority after on-site assessments, spatially-detailed data on the habitat elements identified in our regional-scale assessment, as well as in the local site visits should be gathered, and a fine-scale habitat suitability assessment should be carried out.

Assessment of habitat fragmentation and potential connectivity among herds

An assessment of habitat fragmentation should include the identification of movement barriers, within the prospective range of the new European bison herd, including for example fences, communication lines, power lines, cliffs, deep and wide rivers, major roads, and settlements. Regarding infrastructure it would be desirable to obtain traffic information for already existing roads in order to categorize roads. Also, information on planned infrastructure development projects should be obtained.

In addition, a landscape-scale connectivity analysis should be carried out, using tools such as movement selection models, cost-surface analyses, or circuit flow analyses, in order to (a) assess the connectivity among habitat patches in the region, (b) identify possible corridors linking these patches, (c) explore possible movement corridors out of the priority site, and (d) assess whether,

in a visionary sense, opportunities exist for linking the potential bison herd at the candidate site with other herds (or candidate sites) elsewhere.

Assessment of carrying capacity and possible population structure

Once on-site habitat quality assessments have been carried out, the environmental carrying capacity of the site can be estimated. An important consideration is whether European bison should be fed (or will have access to feeding sites) in winter, for example, at feeding stations established for red deer or wild boar, or at hay meadows or pastures to which bison may have access. Data on the volume, composition and seasonal availability of supplemental food can often be obtained from relevant forest districts or hunting managers.

It is important to note that the environmental carrying capacity (i.e., the maximum number of European bison that could survive in a given region) is almost always substantially higher than the socially-acceptable carrying capacity (i.e., the number of European bison that can co-exist without substantial conflicts with people, agriculture, or forestry, or substantial competition with other large ungulates). The socially-acceptable carrying capacity will depend on constraints to be identified in the human-dimensions assessment (see below).

It is advisable to develop a spatially detailed demographic model that allows for population viability analyses (for an example for European bison see Kuemmerle, Perzanowski et al. 2011). Such a model can, for example, be used to assess environmental carrying capacity, explore the likely spatial population structure of the new European bison herd, assess management options to influence the spatial population structure (e.g., foster or inhibit movement to certain areas), or to maintain a socially-acceptable carrying capacity (e.g., culling, sales, exchange). Based on these explorations, a population development plan for at last the first 10 years of the new herd should be developed. This plan must identify possible herd demography based on different initial group compositions and management interventions. This plan should be revised frequently once the reintroduction is underway.

An important consideration is the potential composition of the group of bison to be released, in consideration of local habitat conditions and carrying capacity. European bison experienced a drastic genetic bottleneck and the entire current gene pool of the species consists of only 12 genotypes, with very uneven distribution (Olech 2003, Pucek, Belousova et al. 2004). As a result, inbreeding levels among E. bison are high. The species is currently considered to be divided into two genetic lines: the Lowland Line (LL: 7 founders) and the Lowland-Caucasian Line (LC: 12 founder). Both lines are currently bred in separation. Because of those aspects, it is necessary to carefully plan the initial group of European bison to be released at a reintroduction site. In Germany, it would be preferable to rely on animals from the Lowland-Caucasian line (unless connectivity to a Polish LL herd may exist), because of the structure of the candidate sites, the availability of European bison bred in captivity, and the global strategy outlined by the European bison conservation center (EBCC).

The genetic structure of the initial European bison group should be as variable as possible. Wherever possible, animals should be obtained from different breeders, but at the minimum females and males should come from different herds. The choice of animals should be based on pedigree data and, if available, DNA analyses. European bison with a larger percentage of unique founders in their gene pool, for example with mtDNA of rare female-founders and males with the Y chromosome of *Kaukasus* or *Begrunder* (male founder individuals of the two existent breeding-lines), should be favored. All animals used for reintroduction should be genotyped, and their DNA should be stored in the GeneBank of EBCC. After about 5 years the herd should be monitored genetically via collecting and analyzing biological material in the form of hair or skin samples (e.g., with darts).

An important consideration is also the decision about the size of an initial European bison group. The minimum group size should be at least 5-7, but preferably >10 animals. The size of a founder group will ultimately also depend on the planned size of the herd once it is fully established. For example, in the Polish Białowieska forest 38 (14 males and 24 females) animals were released over a period of 20 years, and in Borecka forest 15 (7m, 8f) animals were released during 2 years (Grzegrzółka, Olech et al. 2004). The smaller the number of initially released animals, the larger the management effort at the beginning of the project. The sex ratio should be in favor of females (i.e., 1:1.5 to 1:2 in smaller groups), and the group should contain at least 2-3 males of different age. To establish a social hierarchy in the founder group, the animals to be released should be of different age, including at least one older female.

Human dimensions assessment

No reintroduction project should be initiated without a thorough human-dimensions assessment. Such an assessment should include:

- Assessment of potential conflicts with forest management (e.g., potential damages to forests due to browsing in rejuvenation plots, debarking of trees, etc.) as well as possible mitigation actions (e.g., fencing of young stands of the forest). Assessment of ongoing and planned forest management activities.
- Assessment of the potential of conflict with agriculture, including potential damages to crops and pastures, and risk of harmful interactions with livestock (e.g., injuries, transmission of diseases). This should also include the development of mitigation strategies (e.g., fencing of sensitive areas, compensation schemes).
- Assessment of nature conservation areas in the region. This should include an exploration of the possibility to use an already existing protected area as the release site, which would require an assessment of possible congruence between conservation goals in the area and the requirements of a free ranging European bison population.

- Assessment of the possibility to construct a temporary acclimatisation enclosure with a perspective of converting this infrastructure into a breeding enclosure. If a show enclosure is considered, it should be planned at the edge of the planned bison range.
- Assessment of the possibility for bison-related traffic accidents and conflict due to dispersing bison (e.g., into settlements).
- Exploration of the potential undesired interactions between European bison and people connected to forestry activities, hunting, or recreational activities (e.g., hikers, mountain bikers, cross-country skiers). This should include an assessment of the potential threats to European bison from people (e.g., poaching).
- An assessment of local attitudes of people towards the reintroduction of European bison.

Many of these aspects can be, at least partly, studied using a targeted survey instrument and semi-structured interviews with key stakeholders (forest managers, national park managers, key farmers, key landowners, mayors, etc.). The result of such an assessment should be to suggest, conservatively, a socially-acceptable carrying capacity of European bison for the candidate site, to develop an outreach strategy to create awareness and support for the reintroduction project, to develop a strategy to deal with potential conflicts that may arise, and to explore income opportunities related to the potential reintroduction. If the initial plan for the reintroduction project will be pursued further, this needs to be done in close cooperation with all relevant stakeholders and the public at large.

Considering the potentially broad extent of a European bison project, the potential impact of a bison population on ecosystems and land use, and the low number of European bison available worldwide, every reintroduction project should be based on a thorough legal assessment. Such an assessment clarifying the legal status of European bison regarding its occurrence in free-ranging herds has been conducted by WWF in 2014.

Financial assessment

Finally, a budget plan and timeline for the potential reintroduction project should be developed, considering (a) steps and budget needed for initiating the reintroduction project, (b) budget breakdown of the initial costs of the introduction (purchase of animals, transportation, medical care, construction of an enclosure), and (c) annual budget estimates for the annual long-term support of the reintroduction project and the management of the new European bison herd. Each item should identify clearly funding sources, and the institutions that would be responsible for executing the budgets.

Next steps

A number of concrete next steps can be recommended:

1. Ad-hoc on-site assessments of candidate sites

On-site assessments will be necessary to provide an ad-hoc assessment of the items listed in the section ‘General guidelines for assessing candidate sites’. These field visits should take 1-2 days, and include surveys of habitat quality, landscape composition, potential conflicts with land use or people at the candidate site, and potential carrying capacity. This should be complemented by gathering land-use plans, forest management plans, etc. It is essential to directly involve local stakeholders, and to assess their attitude towards a potential new European bison herd in their area. Ideally, contacts would be made with local forest managers, nature reserves, and local authorities etc. Such visits may also facilitate future planning for the localization of infrastructure (e.g., acclimatization enclosure, feeders etc.) necessary for the reintroduction.

These ad-hoc visits do not replace the local-sale feasibility studies outlined above. Rather, the ad-hoc site assessments should help to pick the 1-2 top choices in terms of candidate sites to implement more detailed feasibility studies.

2. Design and implement local feasibility studies in selected candidate sites

This should include the five main dimensions outlined in the ‘General guidelines for assessing candidate sites’:

a. Local habitat assessment
b. Local connectivity assessment
c. Population structure / carrying capacity assessment
d. Human dimensions assessment
e. Financial assessment and development of a reintroduction plan

SUMMARY & MAIN RESULTS

*European bison (*Bison bonasus*) were historically a part of the fauna of Germany, yet these charismatic animals and the role they played in ecosystems were lost until their recent reintroduction. The species is globally threatened, and is still recovering from a severe population decline and its subsequent extinction in the wild at the beginning of the 20th century. Identifying areas where additional European bison populations could be established within the former range of this species is therefore an important goal for the conservation of European bison.*

Here, we carried out what is to our knowledge the first regional, yet fine-scale habitat suitability analysis for European bison for Germany, Poland, the Czech Republic, and Slovakia. We chose this region because it allows using data on bison habitat use from some of the oldest and largest extant wild populations of European bison. We compiled the largest dataset of European bison occurrence points ever collected for this purpose, consisting of more than 340,000 points from radio-collars or field observations and included these data in a habitat suitability modeling framework based on state of the art, non-parametric modeling techniques.

Our results suggest that suitable European bison habitat is widespread in Germany, but mainly occurs in small, and often isolated patches. However, we identified a few promising candidate sites for larger populations of European bison. These areas were generally characterized by several larger patches of suitable habitat, low levels of human population and fragmentation due to roads, existing protected areas that entail large shares of the identified suitable European bison habitat, and a high potential for nature tourism.

The identified sites with such characteristics in our assessment were, ordered from North to South, (1) Müritz-Schorfheide, (2) the area around Celle/Hermannsburg, (3) the area between Spreewald, Cottbus, and Guben, (4) the Harz Mountains, (5) Thüringer Wald, (6) Spessart, (7) Pfälzer Wald, (8) Bayerischer Wald, (9) Schwarzwald, and (10) the Bavarian Alps. Among these, four sites - Müritz-Schorfheide, the Spreewald-Cottbus-Guben area, the Harz Mountains, and the Pfälzer Wald – were the most promising ones. Although the exact area of suitable habitat cannot be determined, our conservative estimation suggests that each of these sites harbors substantially more than 100 km² of suitable habitat. These sites should therefore be investigated, using more fine-scale habitat assessments sensitive to habitat quality and habitat connectivity. Should the potential of these sites be confirmed by such fine-scale, more local-scale assessments, a detailed feasibility study should complement the habitat assessment to assess in detail the human dimensions, population genetics and viability, budgetary, and legal components related to a potential reintroduction project in any of these sites.

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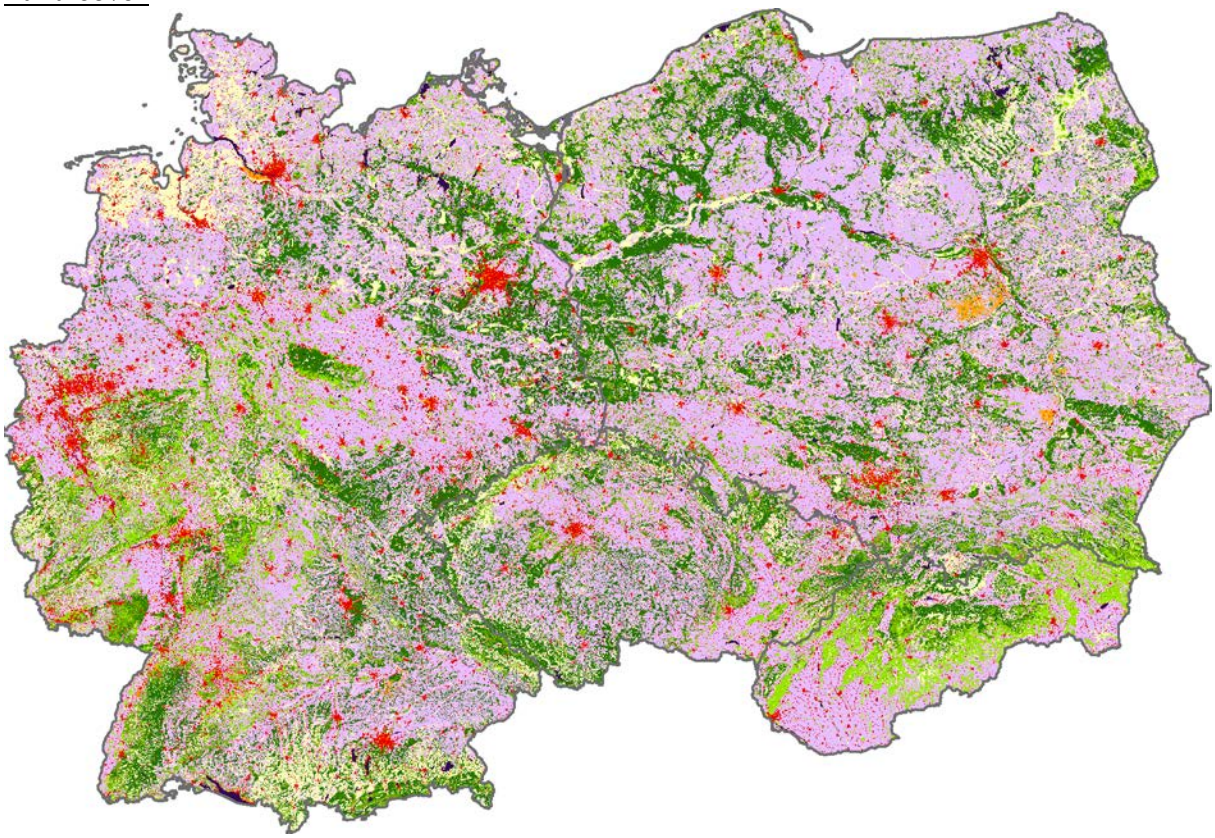
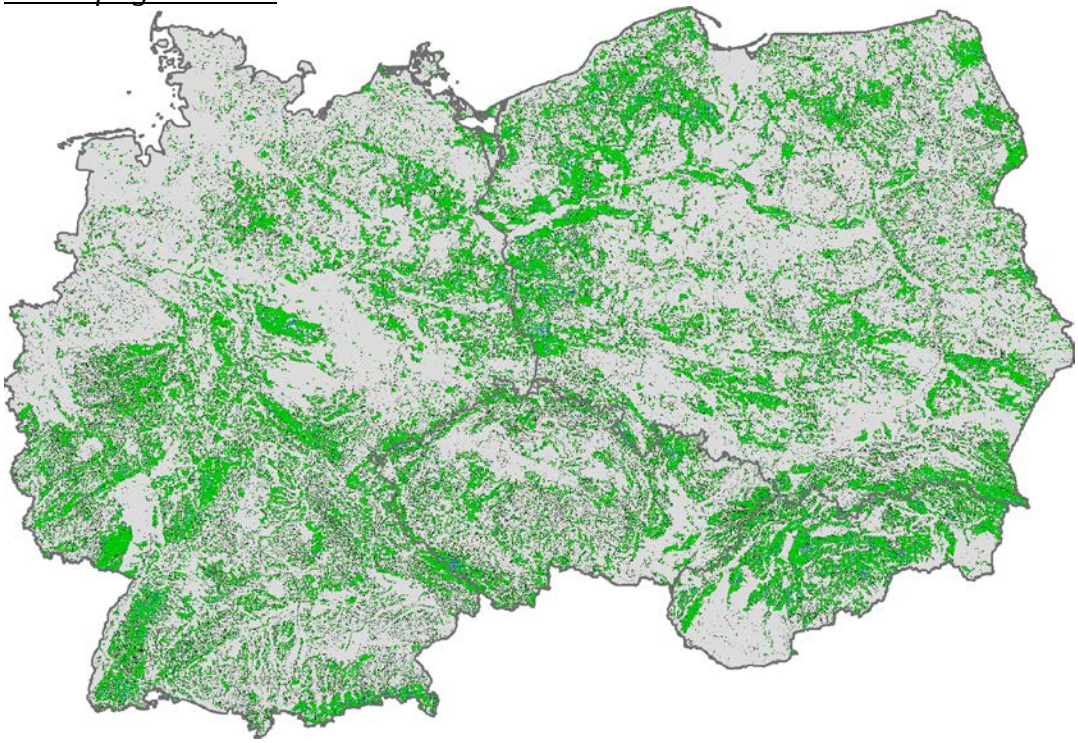
APPENDIX A: PREDICTOR VARIABLES

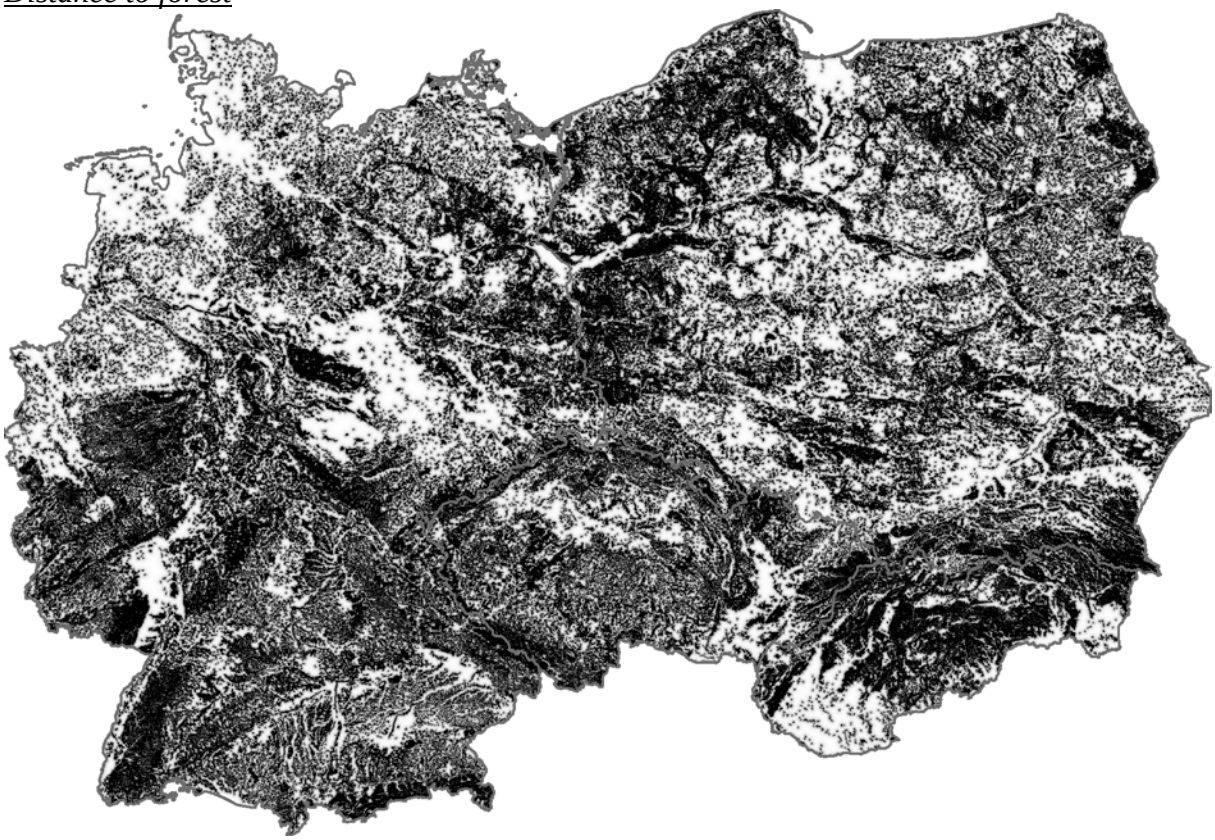
Land cover



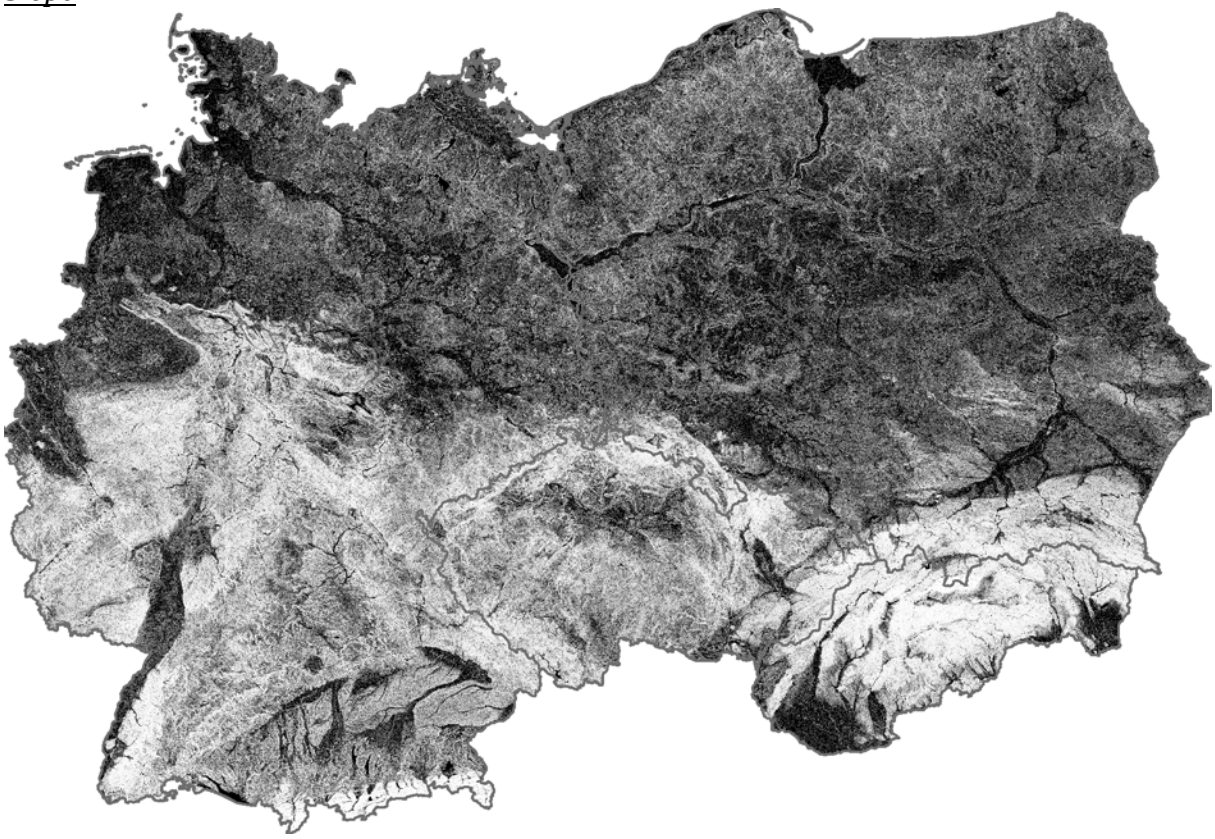
Forest fragmentation



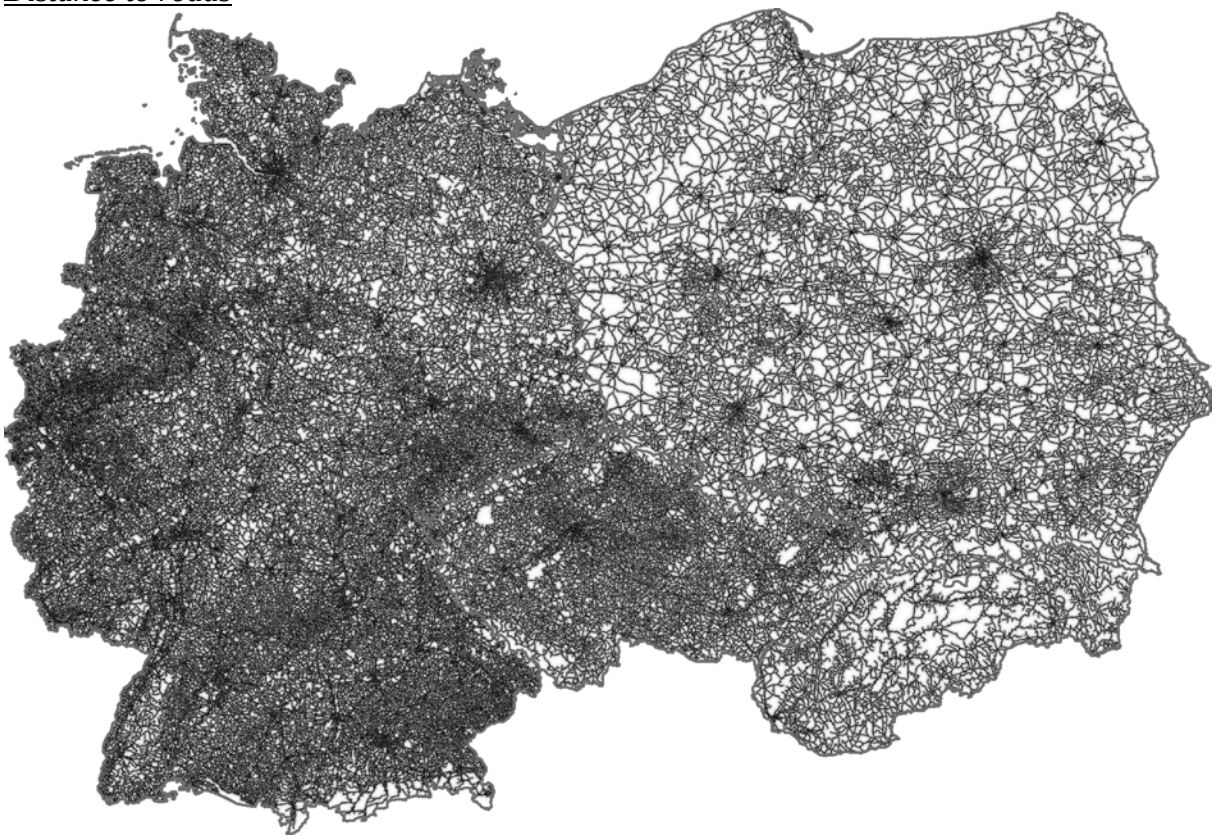
Distance to forest



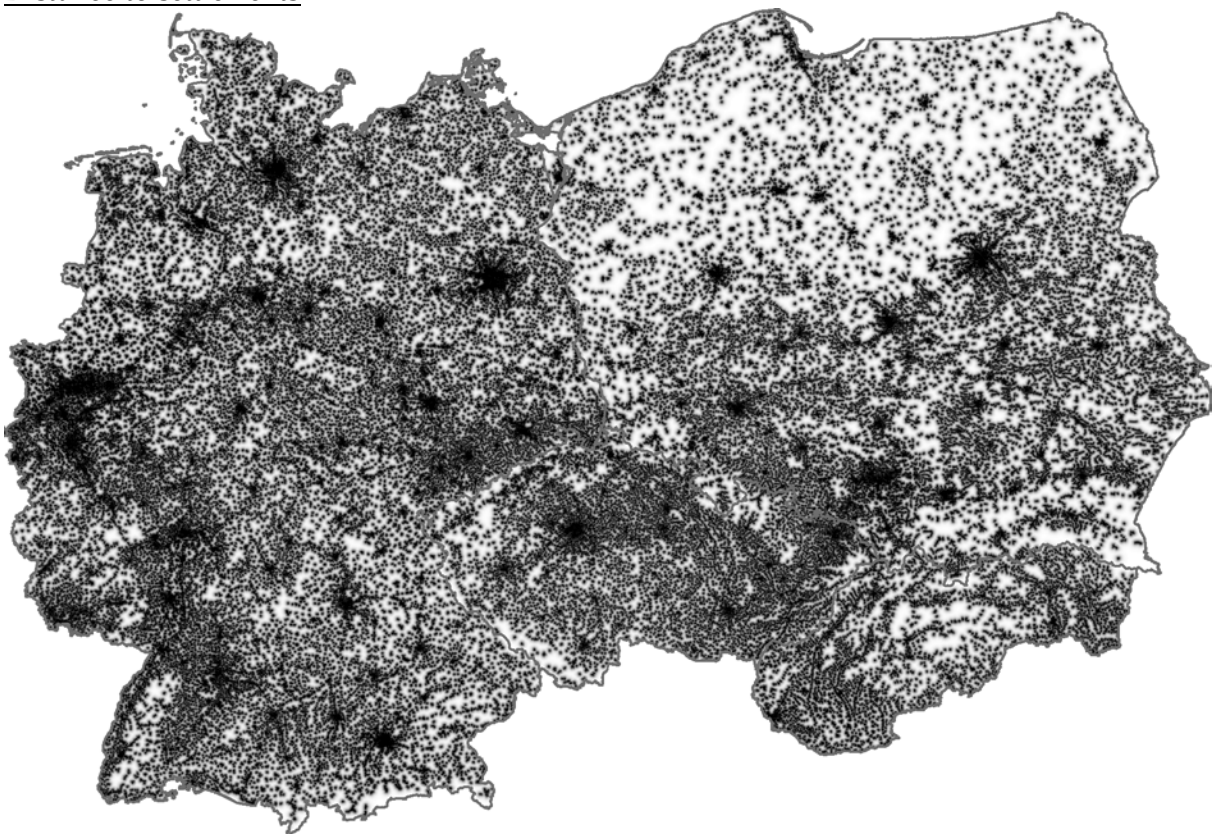
Slope



Distance to roads

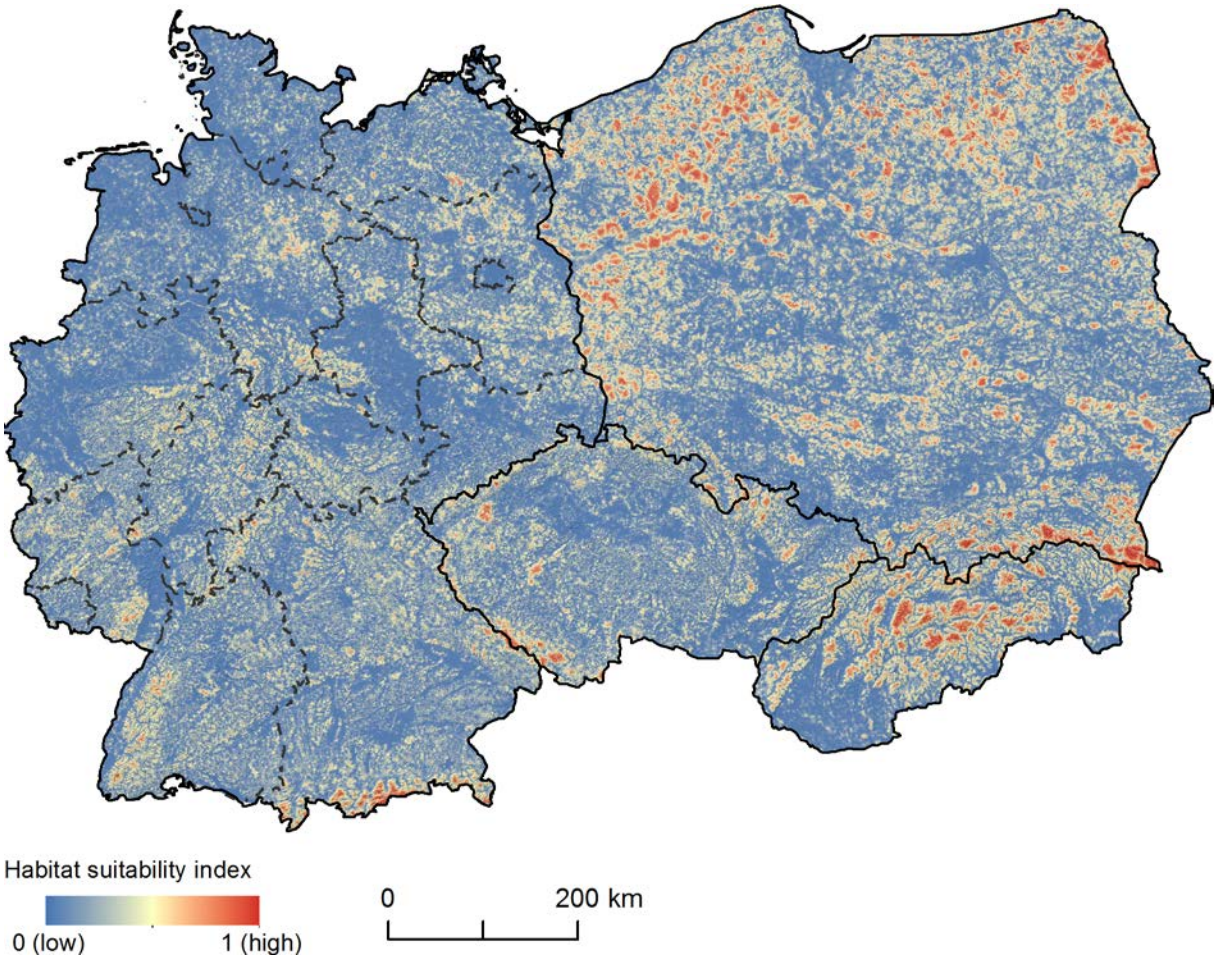


Distance to settlements

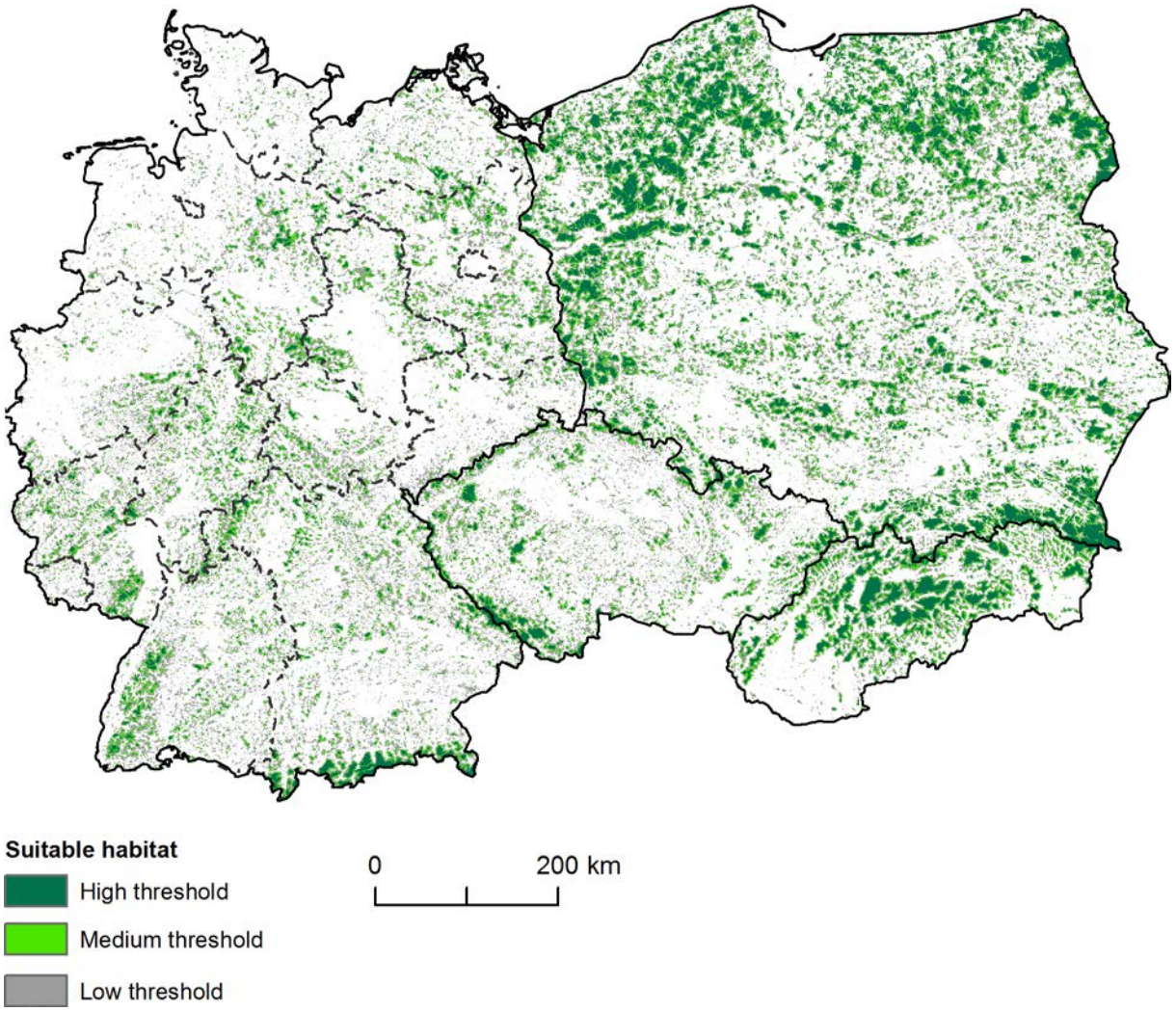


APPENDIX B: EUROPEAN BISON HABITAT MAP

Habitat suitability index

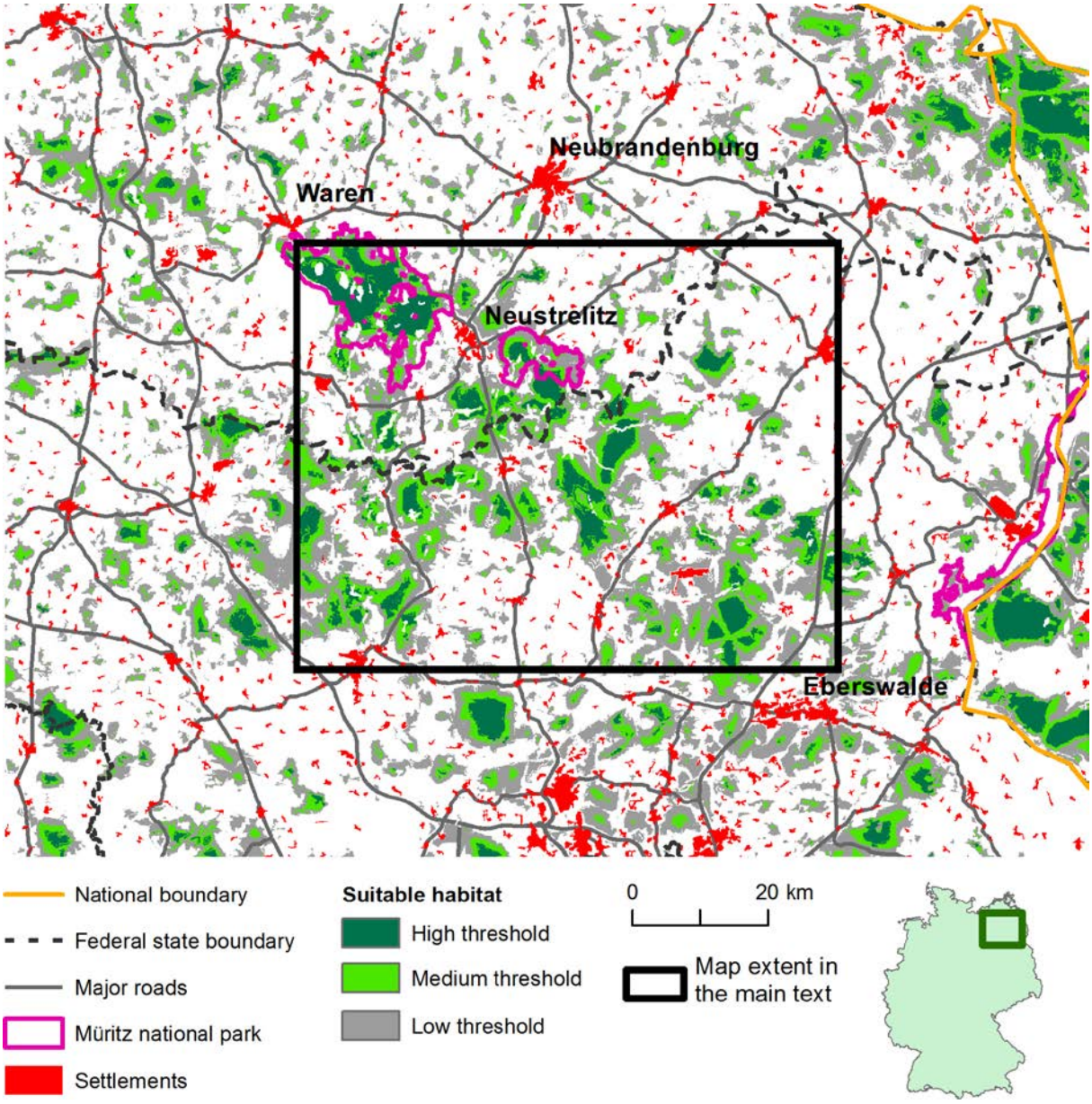


Suitable habitat according to thresholds

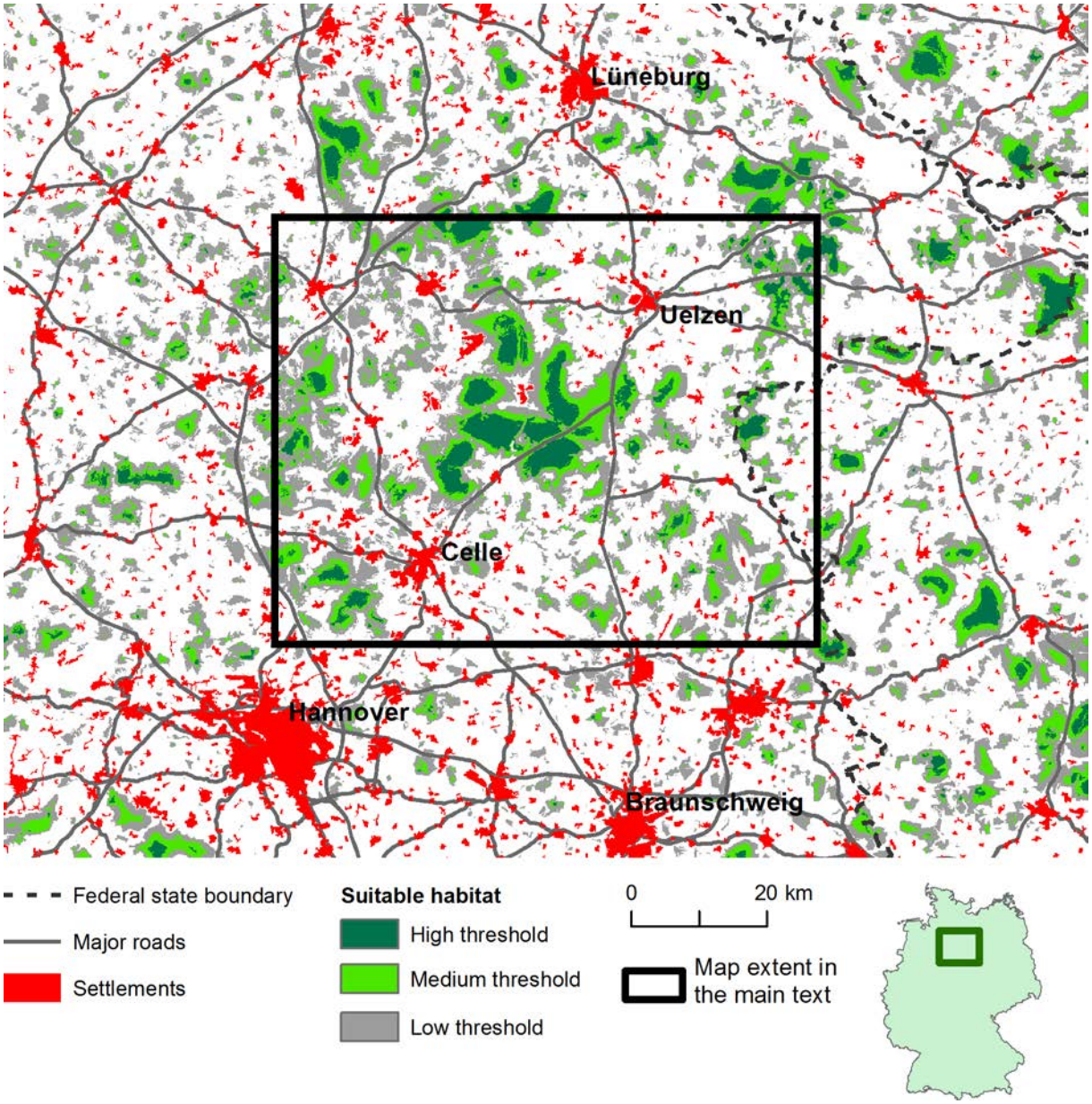


APPENDIX C : OVERVIEW OF THE CANDIDATE SITES

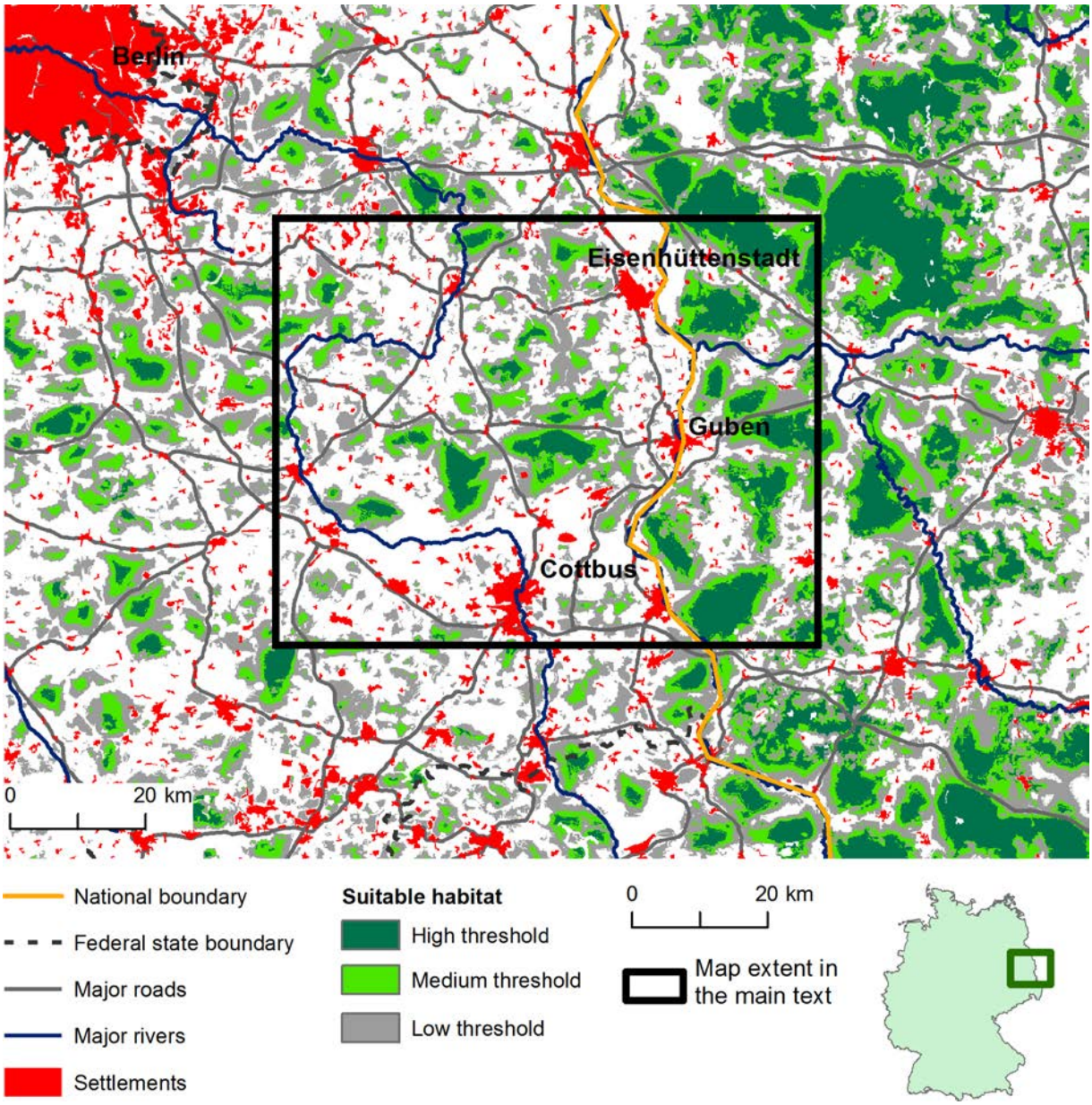
Site 1: Müritz-Schorfheide



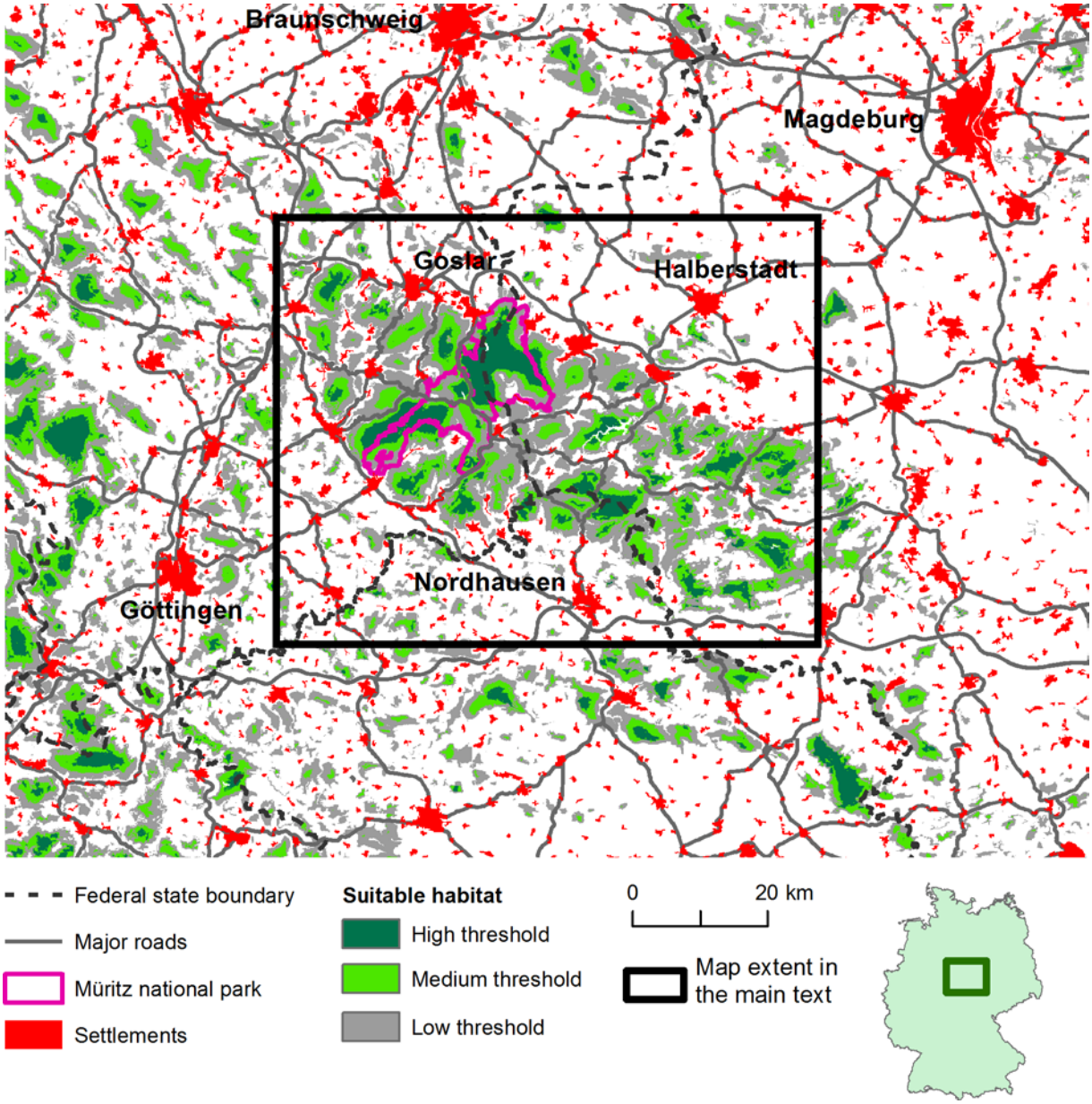
Site 2: Area around Celle/Hermannsburg



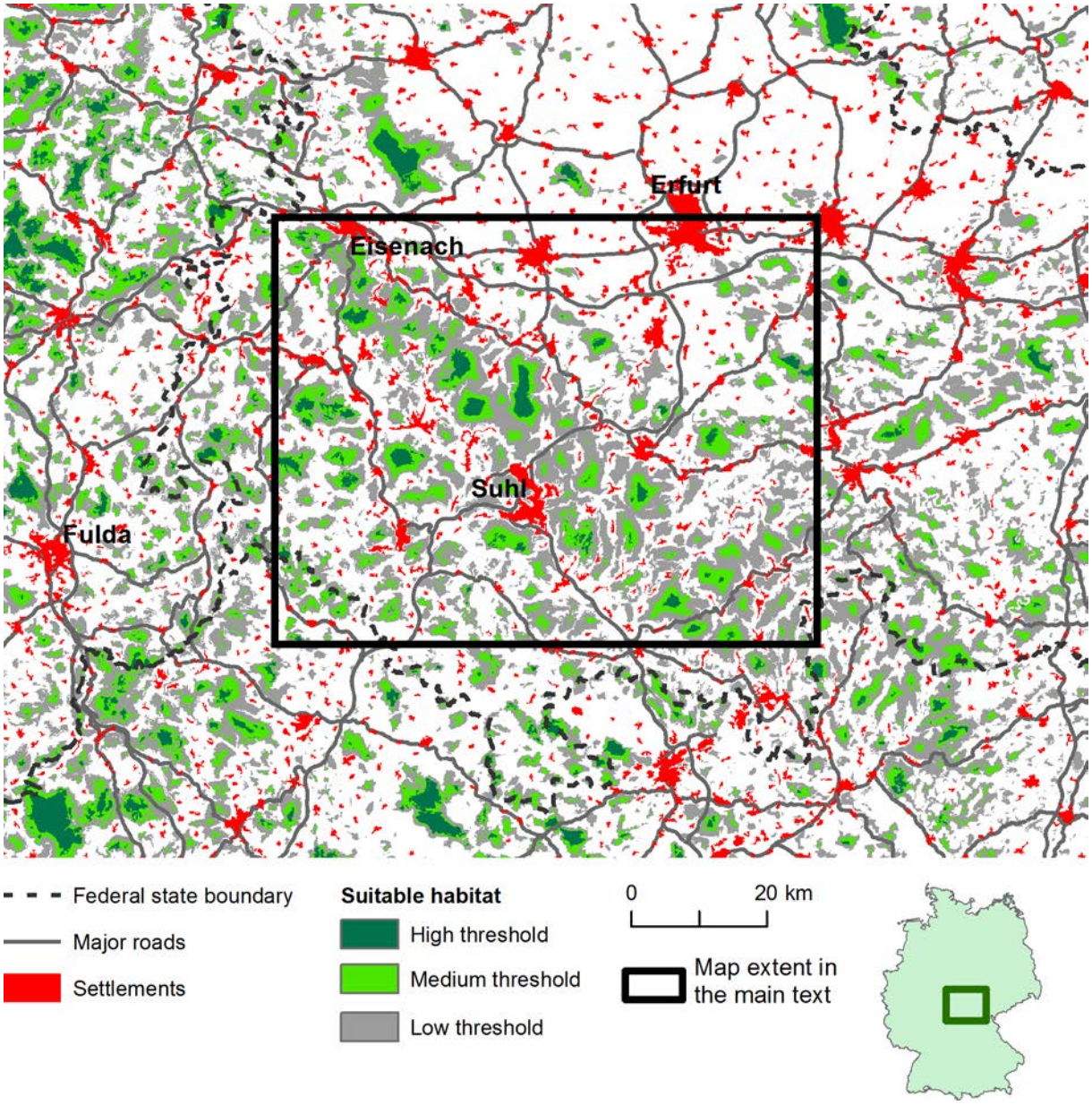
Site 3: Area between Spreewald, Cottbus, and Guben



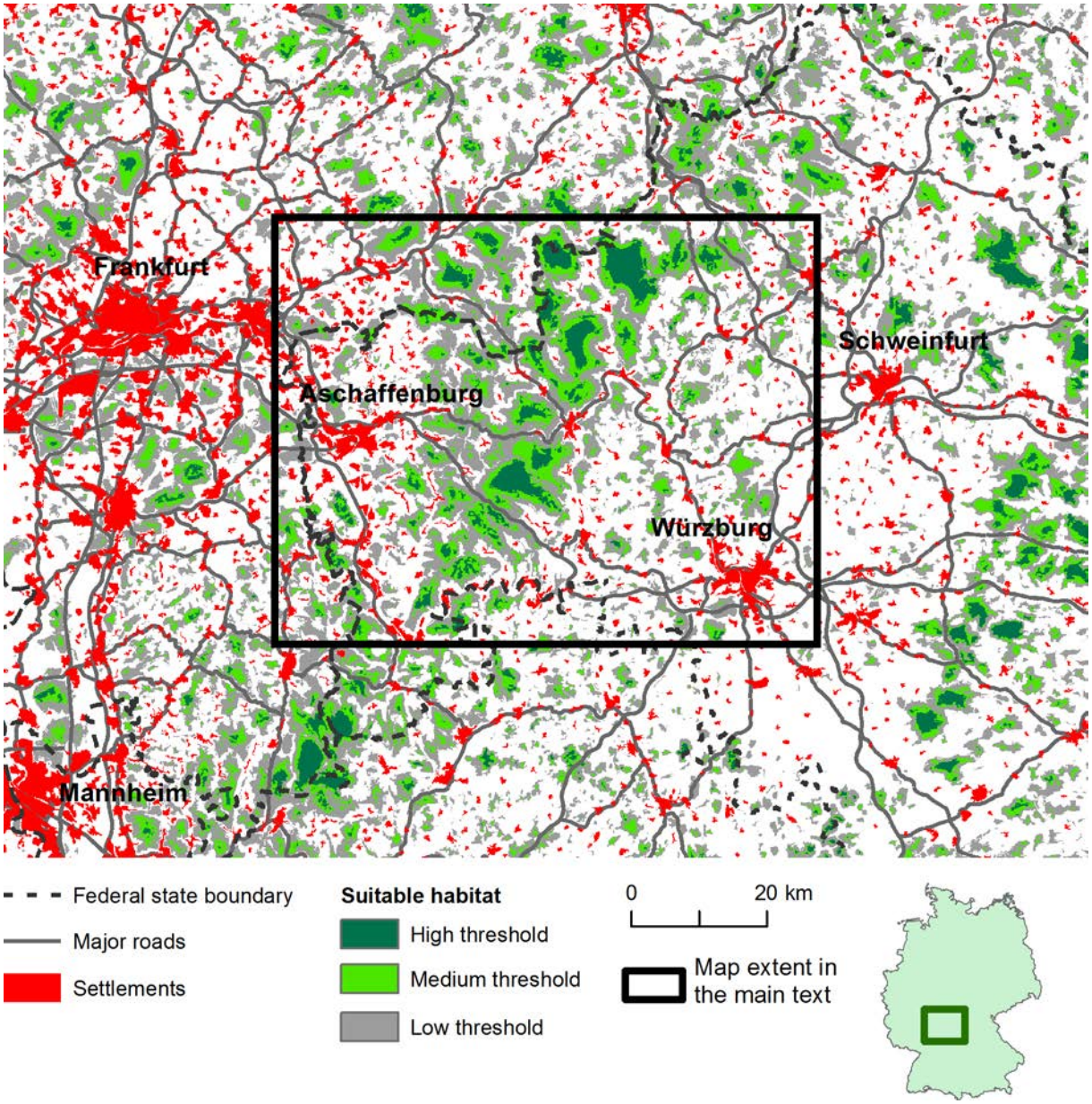
Site 4: Harz Mountains



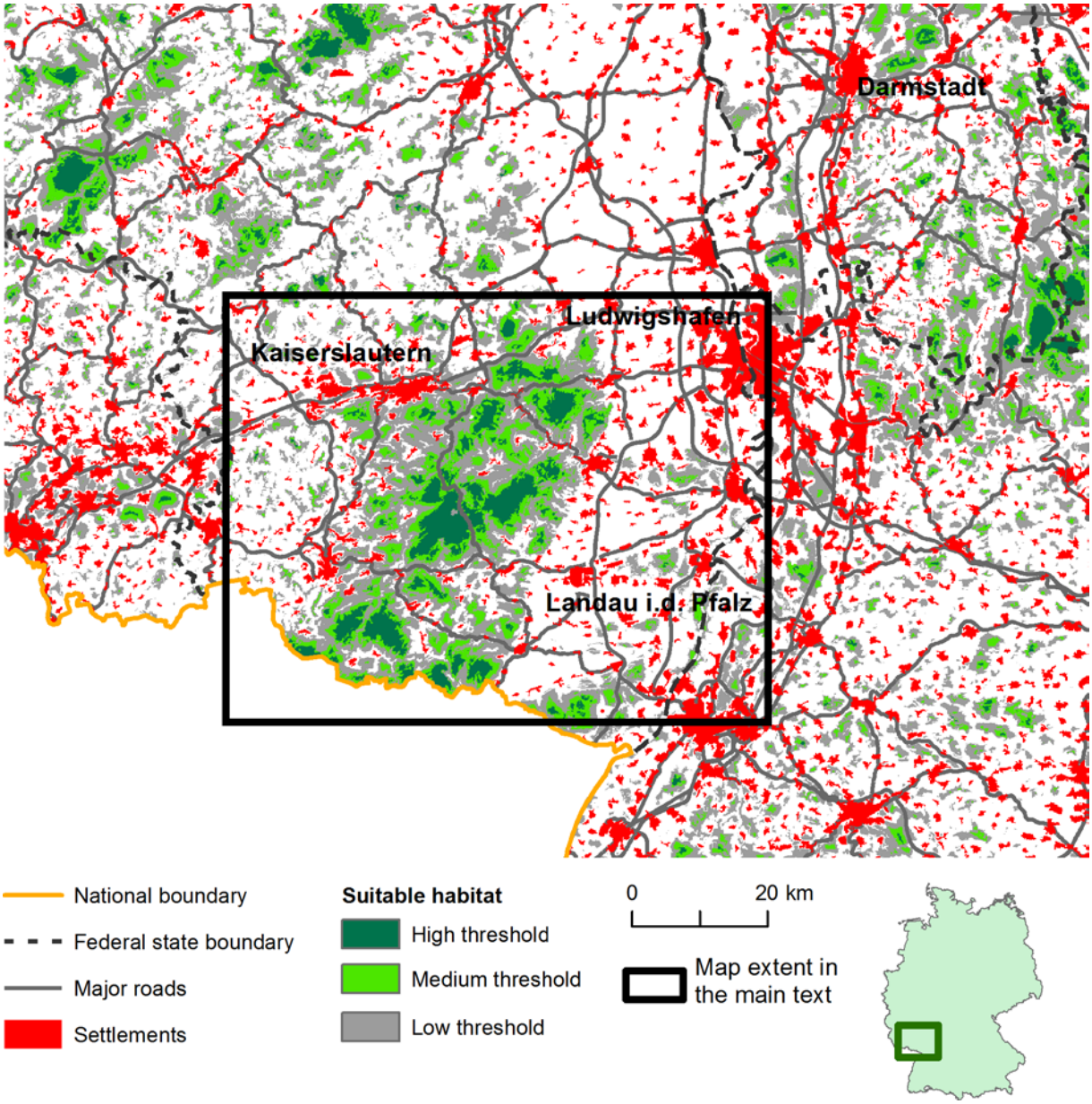
Site 5: Thüringer Wald



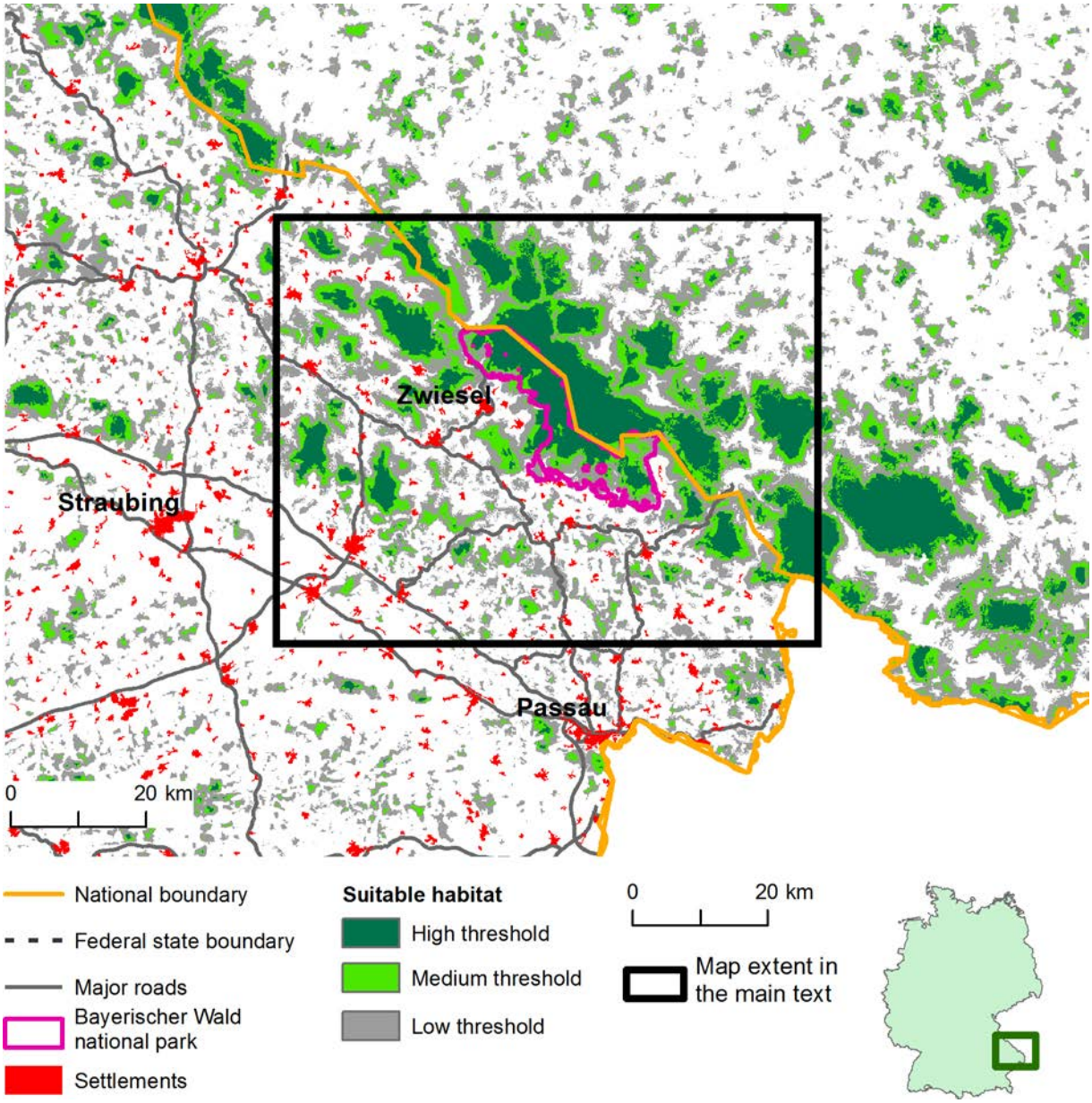
Site 6: Spessart



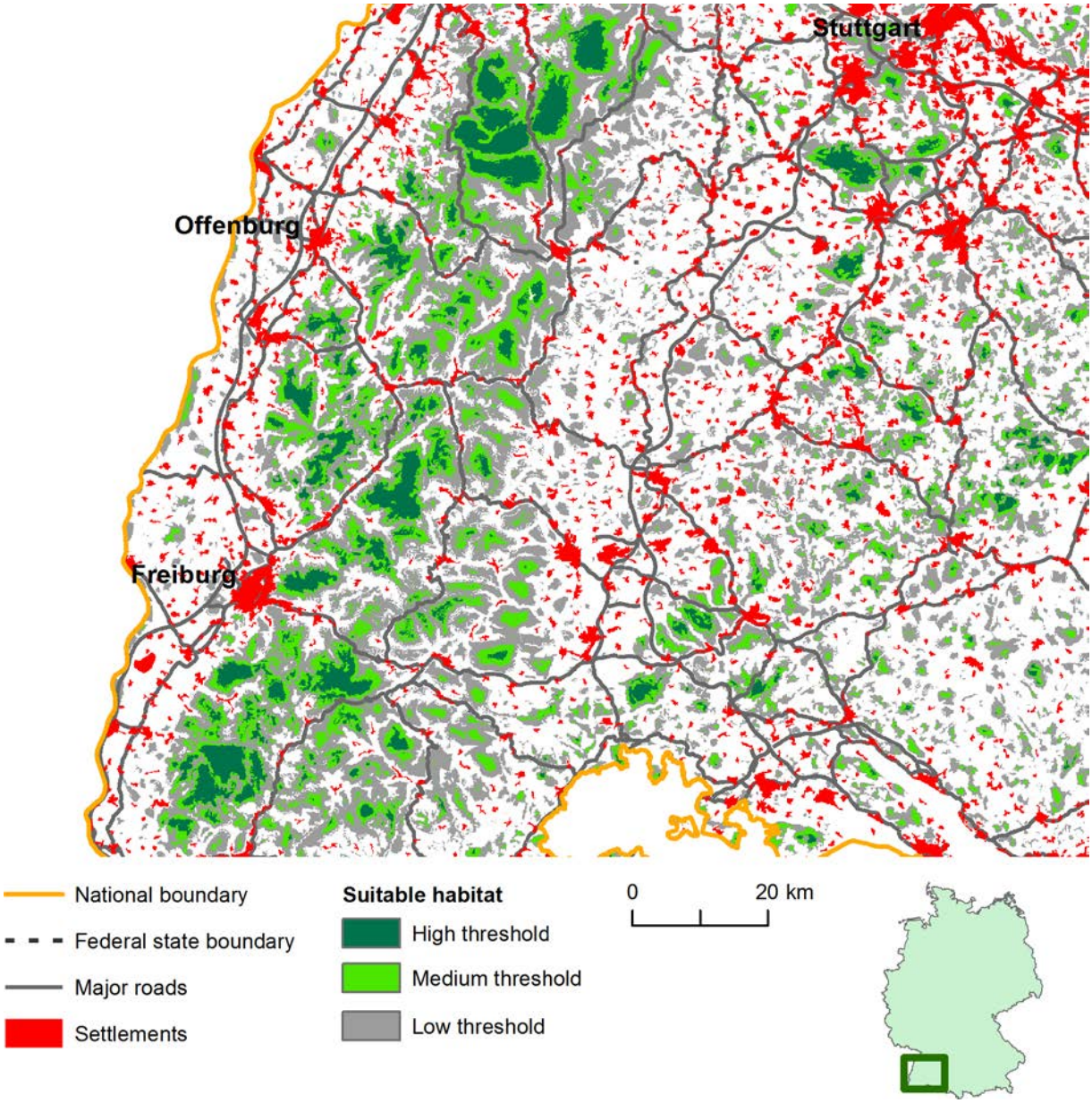
Site 7: Pfälzer Wald



Site 8: Bayerischer Wald



Site 9: Schwarzwald



Site 10: Bayerische Alpen