

# Up-scaling local-habitat models for large-scale conservation: Assessing suitable areas for the brown bear comeback in Europe

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## Abstract

**Aim:** Large carnivore populations in Europe are expanding into new areas. This generates opportunities to improve their conservation status, but also creates a need to address new conflicts with humans. Species management units are constrained by administrative boundaries, but effective conservation and conflict management require a continental-scale perspective on the opportunities and limitations for expanding populations. We assessed the conservation applicability and the uncertainties of transferring and up-scaling local habitat suitability models from multiple populations in support of large-scale, transboundary species conservation.

**Location:** Europe.

**Methods:** We evaluated the accuracy of local population models to predict European brown bear (*Ursus arctos*) distribution patterns in other populations and at the continental scale. We also assessed the benefits of combining predictions from multiple local population models, and we evaluated the limitations of transferring models among populations and environmental settings. Last, we estimated the availability of unoccupied suitable habitats in Europe for colonization by expanding populations.

**Results:** We found that integrating habitat predictions from multiple populations outperformed predictions from most individual populations. Results showed that about 37% of potentially suitable brown bear habitat in Europe remains unoccupied. As a synthesis of our results, we provide a set of predictive maps for the expansion of brown bears at the continental scale, including predictions from individual habitat models and a multimodel predictive map.

**Main conclusions:** We show that integrating habitat models from multiple populations provides richer and more reliable information on the distribution of suitable habitats in data deficient areas. This integration yields more reliable predictions compared to those based on individual populations and has important implications to manage species expansions and the associated conflicts. We also identified major limitations in transferring predictions among habitats; therefore, it is critical to enhance the reproducibility of habitat suitability models to apply local-scale habitat studies to broader-scale conservation practice.

## KEYWORDS

habitat suitability models, human–wildlife conflicts, model transferability, species recovery, transboundary conservation, *Ursus arctos*

## 1 | INTRODUCTION

Large carnivore species are experiencing population expansions in Europe as a result of conservation policy efforts and changes in public attitudes towards wildlife (Chapron et al., 2014). This recovery process provides novel opportunities to reduce conservation threats to these species, as well as restoring the critical role that large predators play on ecosystem functions (Fernández, Navarro, & Pereira, 2017; Ripple et al., 2014). One challenge is that as the conservation status of populations improves, new conflicts arise with humans, such as those which result from wildlife damages to human property (Bautista et al., 2016). Both natural recovery and assisted recovery of large carnivore populations require precise information on the availability and the connectivity of potential areas for the expansion of populations, as well as designing management practices and policies to prevent emerging conflicts.

Predictive habitat suitability models describing empirical correlations between the probability of species presence and environmental variables (Elith & Leathwick, 2009) have become key to evaluate the availability of habitats for species conservation, to assess the fragmentation of these habitats and to identify potential corridors. Furthermore, habitat models have demonstrated their utility for many different goals such as selecting reintroduction areas, assessing limiting factors for populations and considering species-specific requirements in reserve design and management (Bulluck, Fleishman, Betrus, & Blair, 2006; Danks & Klein, 2002; Fernández, Delibes, Palomares, & Mladenoff, 2003; Klar et al., 2008; Larson, Dijak, Thompson, & Millsbaugh, 2003; Vanreusel, Maes, & Van Dyck, 2007). Predictive models are also critical to identify areas where conflicts between species and human interests are more likely to occur, as well as to design management strategies aimed to reduce these conservation conflicts (Bautista et al., 2016; Kissling, Fernández, & Paruelo, 2009).

Predictive habitat suitability models are often developed for the area where the conservation or management actions are expected to be taken. However, in those areas where there are no species data available, it is a common practice to transfer predictions from other populations assuming that the limiting factors are similar in different areas (Hebblewhite, Miquelle, Murzin, Aramilev, & Pikunov, 2011; Mladenoff, Sickley, Haight, & Wydeven, 1995; Schadt et al., 2002). This practice may be compromised by factors that have misleading—if not disastrous—consequences for conservation planning. First, habitat limitation in newly evaluated areas may be determined by novel environmental conditions not assessed before (Barbosa, Real, & Vargas, 2009; Fernandez, Delibes, & Palomares, 2006). Second, certain populations may develop unique adaptations to their environment, and thus, habitat associations may not be representative

of other populations (Peterson & Holt, 2003). Therefore, it is not surprising that studies which evaluate the transference of models to new areas have found inconsistent results. For example, McAlpine et al. (2008) found predictions of koala habitat to be inaccurate when transferring predictive models to areas differing in biogeographical and land use characteristics. Likewise, Seoane, Bustamante, and Diaz-Delgado (2005) obtained poor predictive results for different bird species in nearby study areas with relatively similar topography, climatology and landscape characteristics. In contrast, a number of studies on different taxa have shown good predictive performance for model transference to both nearby (Vanreusel et al., 2007) and geographically distant areas (Acevedo et al., 2014; Whittingham et al., 2007). In other words, there are no general rules for determining a priori the reliability of transferring model predictions to address conservation problems in new areas.

For an increasing number of species, habitat studies are available from different populations and geographical locations. This is advantageous as it allows comparing predictions generated from different populations and areas. Furthermore, local habitat studies may be integrated to produce combined predictions across a wider range of environmental conditions, which would eventually facilitate broader assessments of habitat distribution and uncertainties. Concordant habitat predictions obtained from different study populations would increase the confidence of assessments in new populations, guaranteeing more reliable conservation planning, while the inconsistent results would reveal potentially misleading management planning.

The brown bear (*Ursus arctos*, Linnaeus 1758) is a conservation flagship species in Europe that exemplifies the conservation conflicts associated with large carnivores. Rural land abandonment, reduced direct persecution and protection have resulted in the halt of the overall population decline and the recovery of most populations. At the same time, emotions associated with damages to livestock and human property on the one side (Bautista et al., 2016), and with rare events of direct attacks on humans on the other (Penteriani et al., 2016), decrease the willingness of some sectors of the society to coexist with bears. At present, brown bears are managed based on assessments of the population status at national to subnational levels and not at a population level. This can lead to the species being strictly protected on one side of an administrative boundary but hunted on the other side, as occurs between Poland and Slovakia (Kaczensky et al., 2012). The vast majority of the brown bear populations in Europe are transboundary (eight of ten), raising an urgent need to reconcile transboundary conservation policies from a continental-wide perspective on the distribution of brown bear habitats (Linnell, Steuer, Odden, Kaczensky, & Swenson, 2002; Swenson, Gerstl, Dahle, & Zedrosser, 2000). It is consequent that continental-scale

habitat assessments are needed to address pressing conservation problems and new conflicts arising from the fact that both threatened and expanding populations occur in different areas of Europe (Chapron et al., 2014; Kaczensky et al., 2012). Both conservation demands and a relatively broad availability of information on the species make the brown bear in Europe an ideal study system for assessing the consistency and the conservation implications of transferring and up-scaling predictions from different populations at the continental scale.

We analysed the accuracy of transferring local habitat predictions in support of European brown bear conservation on a continental scale. Using previous studies from different European populations, we also analysed aspects such as the influence of the geographical location and environmental differences when evaluating the accuracy of predictions. Furthermore, we tested whether a multimodel prediction that combines models fitted at different populations would reduce habitat prediction uncertainty as compared to single-model predictions. Last, we produced maps estimating the distribution of suitable habitat available for brown bears in mainland Europe by up-scaling multimodel predictions at the continental extent in support of transboundary conservation and conflict assessments.

## 2 | METHODS

### 2.1 | Study species

Brown bears are the most abundant large carnivore in Europe, with a total population estimate of 17,000 individuals in 2012 (Kaczensky et al., 2012). Despite this, some populations are small, isolated and subject to demographic and genetic threats of stochastic extinction (Swenson et al., 2000). The conservation of bears is especially challenging in most areas of Europe as large wilderness areas suitable for the species are scarce (Linnell et al., 2002).

The species is distributed in ten different populations, four of which contain more than 1,000 individuals. The Carpathian is the largest population with 7,200 individuals, whereas three populations contain fewer than 60 individuals, namely the Central Apennine, Pyrenean and Alpine (Kaczensky et al., 2012). The brown bear occurs across 22 European countries with contrasting conservation policies and regulations, making the management of the species particularly challenging (Linnell et al., 2002).

### 2.2 | Habitat assessment approach: overview

Our analyses followed four major steps:

1. Literature review in search of all studies evaluating the habitat selection by the brown bear in Europe and the identification of models potentially transferable to other populations.
2. Assessment of the transferability of predictions from each population-level study to other populations and of the accuracy of up-scaling predictions to the European extent.

3. Evaluation of the influence of geographical distance and biogeographical similarity on prediction accuracy.
4. Calculation of an assembled predictive map comparing the amount and the distribution of suitable habitats and the accuracy of predictions among all models as a new means to assess the habitat availability at the European scale.

#### 2.2.1 | Literature review

We carried out a systematic review in October 2017, by searching the databases ISI Web of Knowledge, Scopus and Google Scholar using different combinations of the key words “*Ursus arctos*,” “brown bear,” “habitat selection,” “habitat use,” “habitat preference,” “habitat model,” “resource selection” and “Europe” or “European.” We identified studies that provided the necessary information to replicate and transfer habitat probability calculations such as generalized linear models (GLMs; Appendix S1, Supporting Information). We could not reproduce predictions from other studies using MaxEnt (e.g., Almpnidou et al., 2014; Maiorano, Boitani, Monaco, Tosoni, & Ciucci, 2015), ecological niche factor analysis (e.g., Falcucci, Ciucci, Maiorano, Gentile, & Boitani, 2009; Mertzanis et al., 2008) and use-availability comparisons (e.g., Gavrilov, Zlatanova, Spasova, Valchev, & Dutsov, 2015; Kaczensky, 2000).

#### 2.2.2 | Up-scaling and transferring model predictions

We calculated all variables reported in the different local population habitat suitability GLMs using sources of data available at a European extent. Using these data, we calculated a map of predicted brown bear habitat in Europe from each of the published models. Because we required data to be available at a European extent, sources of our dataset differed from each original study (Appendix S2, Supporting Information). All calculations were performed at the same resolution as in the original studies. Then, maps were rescaled by averaging the prediction values of the finer grid within a coarser grid at a resolution of 25 km<sup>2</sup>. This was necessary to allow comparison among the different models (Appendix S3, Supporting Information).

We assessed the transferability of each model by testing the predictions against every other brown bear population. For this, we used a gridded dataset of the brown bear distribution in Europe in year 2012 at 100 km<sup>2</sup> resolution (Kaczensky et al., 2012). This dataset represents the most comprehensive and spatially consistent information of European brown bear distribution at the continental scale, although its resolution is coarser than the resolution of data used in local population habitat modelling studies ( $\leq 25$  km<sup>2</sup> in all cases). The dataset separates permanent from sporadic occurrences partly based on expert assessments. Permanent occurrences were those cells that were occupied at least 50% of the time over  $\geq 3$  years, or where reproduction or presence of resident adult females was confirmed. Sporadic occurrences were areas with occasional observations but no reproduction, such as observations of

dispersing individuals (Kaczensky et al., 2012). In our analyses, we only used permanent occurrences assuming that these would better reflect suitable habitats. Absence data were selected within a 50-km buffer around bear occurrences within each population, following Fernández, Selva, Yuste, Okarma, and Jakubiec (2012). These unoccupied areas are assumed to be accessible to potentially dispersing individuals. Ukraine, Belarus and Russia were excluded from our analyses as no comparable data on brown bear occurrence were available for these countries.

For the predictions of each local population model, we calculated the threshold separating suitable from unsuitable habitat. We determined the threshold as the value where the sensitivity (i.e., % of correctly classified occurrences) equals specificity (i.e., % of correctly classified absences) for the respective population where the model was fit. We used the AUC (area under the curve) to assess the capacity of model predictions to discriminate suitable from unsuitable habitat in each population (Fielding & Bell, 1997).

### 2.2.3 | Transferability and environmental similarity

We used the distance between populations and the biogeographical region where the population was located as proxies for environmental similarity between populations. We fitted a linear mixed model (LMM) to assess the correspondence between AUC values and the Euclidean distance in kilometres between the centroid of each model population and the centroids of all other populations, including the model nested within the respective population as a random factor. We also calculated the proportion of different biogeographical regions within the areas occupied by each population using the biogeographical regions' dataset for Europe (EEA, 2016). We calculated environmental similarity among populations according to the composition of biogeographical regions using the Sørensen similarity index (Wolda, 1981), which ranges from 0 (similar) to 1 (dissimilar), as a proxy of environmental similarity. We fitted a LMM assessing the correspondence between AUC values and the similarity index.

### 2.2.4 | Assembled predictions

In a final step, we aimed to provide a predictive map of suitable habitat distribution for the brown bear at the European extent. We calculated a multimodel concordance map combining the predictions of different models to assess agreement in the predicted distribution of suitable habitat. We assumed that an assembled prediction is more robust than single predictions, compensating for errors and uncertainties of each single model (Araújo & New, 2007). As different models were fitted on the same bear population, we only used the best predictive model for each population as indicated by AUC values.

Given that the different predictive models showed different optimal thresholds separating suitable from unsuitable habitat, we first needed to reclassify each map into a binary map of suitable vs. unsuitable habitat according to their respective thresholds. Then, we calculated the percentage of models that predicted a

given pixel as suitable or unsuitable. Last, we considered as suitable habitat only those areas predicted as suitable by at least 50% of the models.

All geospatial analyses were performed using ARCGIS 10.1 (ESRI, Redlands, California, USA), and statistical calculations were performed using the R v3.3.3 statistical package (R Core Team, 2017). The classification thresholds were calculated using the R package *PresenceAbsence* (Freeman & Moisen, 2008), the AUC value was calculated with the R package *SDMTools* (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014), the LMMs were fitted using the R package *nlme* (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017), the R square of each LMM was calculated with the R package *MuMIn* (Barton, 2018), and the Sørensen similarity index was calculated with the R package *vegan* (Oksanen et al., 2018).

## 3 | RESULTS

### 3.1 | Literature review

We found 36 habitat studies for the European brown bear in 8 of 10 populations in Europe. Habitat suitability has been studied for fractions of the Scandinavian, the Dinaric-Pindos, the Carpathian and the Eastern Balkan population, and most smaller populations, the Cantabrian, Pyrenean, Alpine and Central Apennine. In contrast, we did not find any habitat modelling study in the Karelian and Baltic populations (Appendix S1, Supporting Information).

The methods and scales applied across all studies were highly diverse. We were able to reproduce six of 14 studies that developed habitat models using GLMs, as the remaining studies included variables in their models that were not available at a European scale (e.g., number of buildings, distance to feeding stations or forest species composition). The six selected studies provided a total of 12 models developed on four different populations (Table 1, Appendix S4, Supporting Information). The variables included in these 12 models were available at a European scale, although the data sources we used sometimes differed from the original ones, as some original datasets were restricted to one specific study region (Appendix S2, Supporting Information). A harmonized dataset was available for human population density in Europe excluding Norway, Switzerland, Bosnia and Herzegovina, Montenegro, Albania, Macedonia and Serbia. Likewise, the roads' database did not include Bosnia and Herzegovina, Montenegro and Albania. Therefore, models including these variables could not be transferred to these areas.

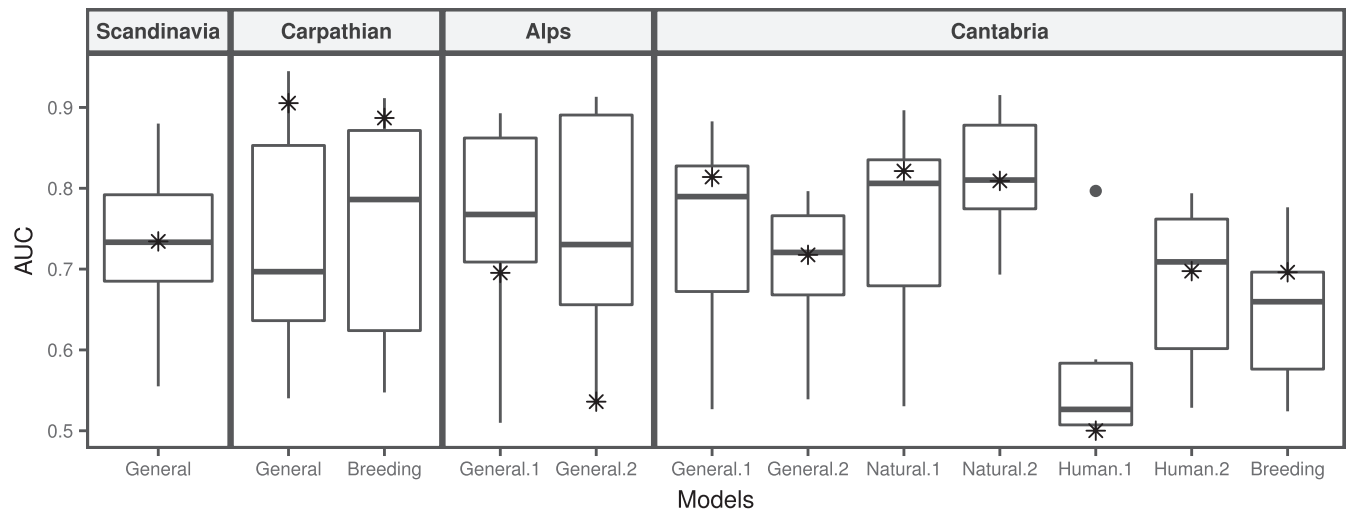
### 3.2 | Up-scaling and transferring model predictions

We found great variability in the performance of individual habitat models for predicting bear distribution in populations different to those where they were fitted (Figure 1). AUC values for transferred models ranged between 0.50 and 0.94. Although some model predictions were not better than random (AUC = 0.5), the overall AUC mean was 0.72, indicating that, on average, model predictions were moderately accurate. Variability in the predictive performance was

**TABLE 1** Models selected from the literature review for transferring and up-scaling habitat suitability predictions to a European extent

Reference	Population	Model name	Variables <sup>a</sup>	Spatial resolution
Katajisto (2006)	Scandinavian	General model <sup>b</sup>	Land cover and human related	1,100 × 1,100 m
Fernández et al. (2012)	Carpathian	General model <sup>b</sup>	Land cover and human related	5 × 5 km
		Breeding model	Land cover and human related	5 × 5 km
Güthlin et al. (2011)	Alpine	General.1 model <sup>b</sup>	Land cover, human and topography related	250 × 250 m
Peters et al. (2015)	Alpine	General.2 model <sup>b</sup>	Land cover, human and topography related	25 × 25 m <sup>c</sup>
Naves et al. (2003)	Cantabrian	General.1 model	Land cover, human and topography related	5 × 5 km
		Natural.1 model	Land cover and topography related	5 × 5 km
		Human.1 model	Human related	5 × 5 km
		Breeding model	Land cover related	5 × 5 km
Martin et al. (2012)	Cantabrian	General.2 model	Land cover, human and topography related	5 × 5 km
		Natural.2 model <sup>b</sup>	Land cover and topography related	5 × 5 km
		Human.2 model	Land cover and human related	5 × 5 Km

<sup>a</sup>Details in Appendix S4, Supporting Information. <sup>b</sup>Models used to create the assembled predictive map. <sup>c</sup>We developed the model at 100 m as this was the minimum resolution at which we could obtain the variables included.



**FIGURE 1** Transferability of each evaluated model on all other populations. Asterisks represent the AUC values of the models predicting the model-fitting population

not attributable to the number of predictor variables used in the model or to the type of variables (i.e., natural vs. human predictors).

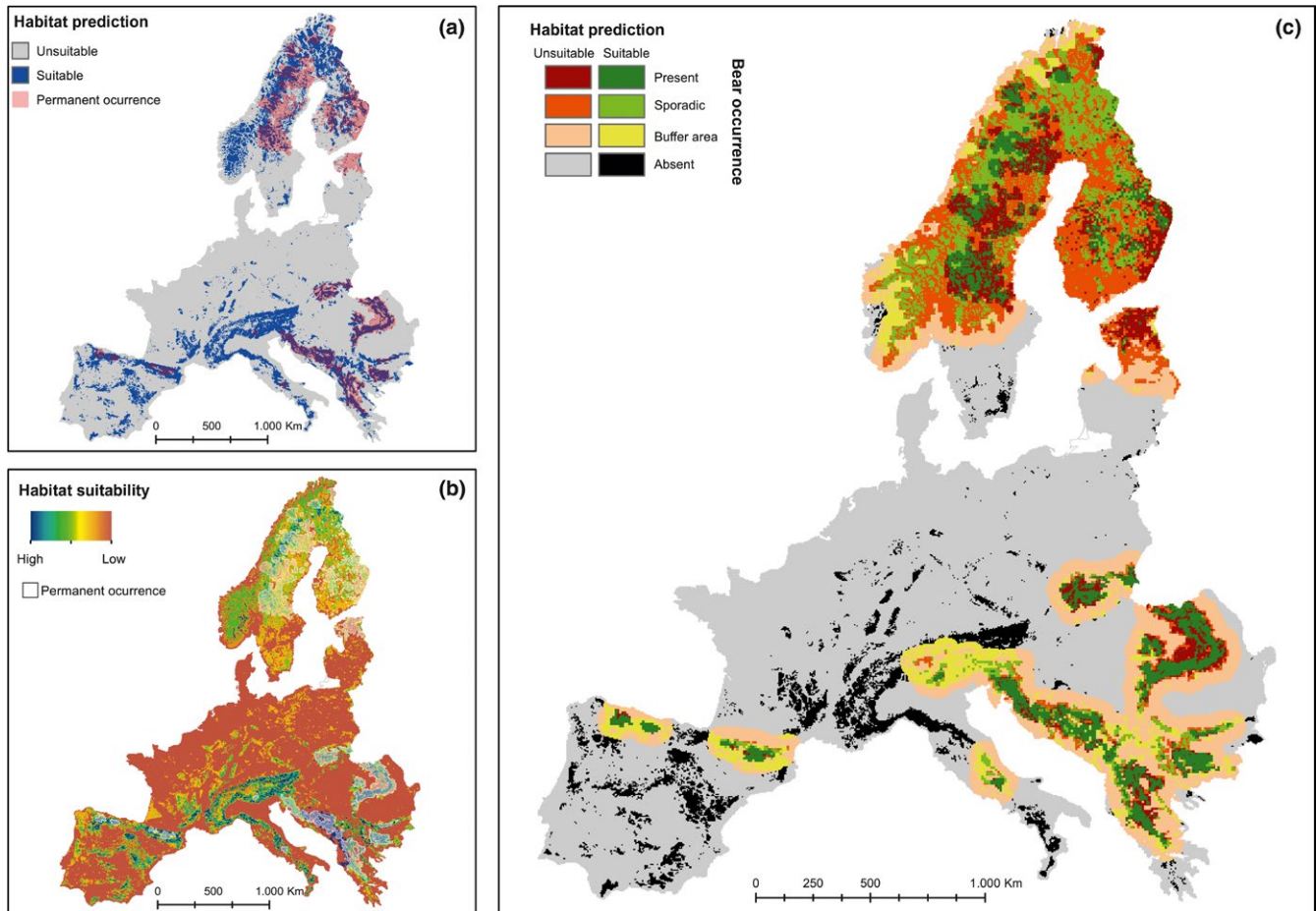
LMM (slope ± SE = -0.139 ± 0.045; *p* = 0.003; *R*<sup>2</sup> = 0.253), indicating that model predictions were less accurate when transferred to populations with dissimilar biogeographical characteristics.

### 3.3 | Transferability and environmental similarity

In general, populations geographically closer to the model-fitting population showed a higher model-transfer AUC than more distant populations. This result was supported by the LMM, where we found that AUC was negatively correlated with the distance between the modelled population and the population where predictions were transferred (slope ± SE = -3.43e-05 ± 1.432e-05; *p* = 0.0186; *R*<sup>2</sup> = 0.205). We also found a negative relationship between the Sørensen similarity index and the AUC value shown by the fitted

### 3.4 | Assembled predictions

We calculated an assembled predictive map based on the proportion of models that predicted suitable habitat at each pixel (Figure 2). For this, we only included one model from each population, except the Alpine population where we included both models as they were fitted on different regions and datasets (Table 1). The assembled map showed that 56% of the area with permanent occurrences was predicted as suitable habitat by at least three of the five models,



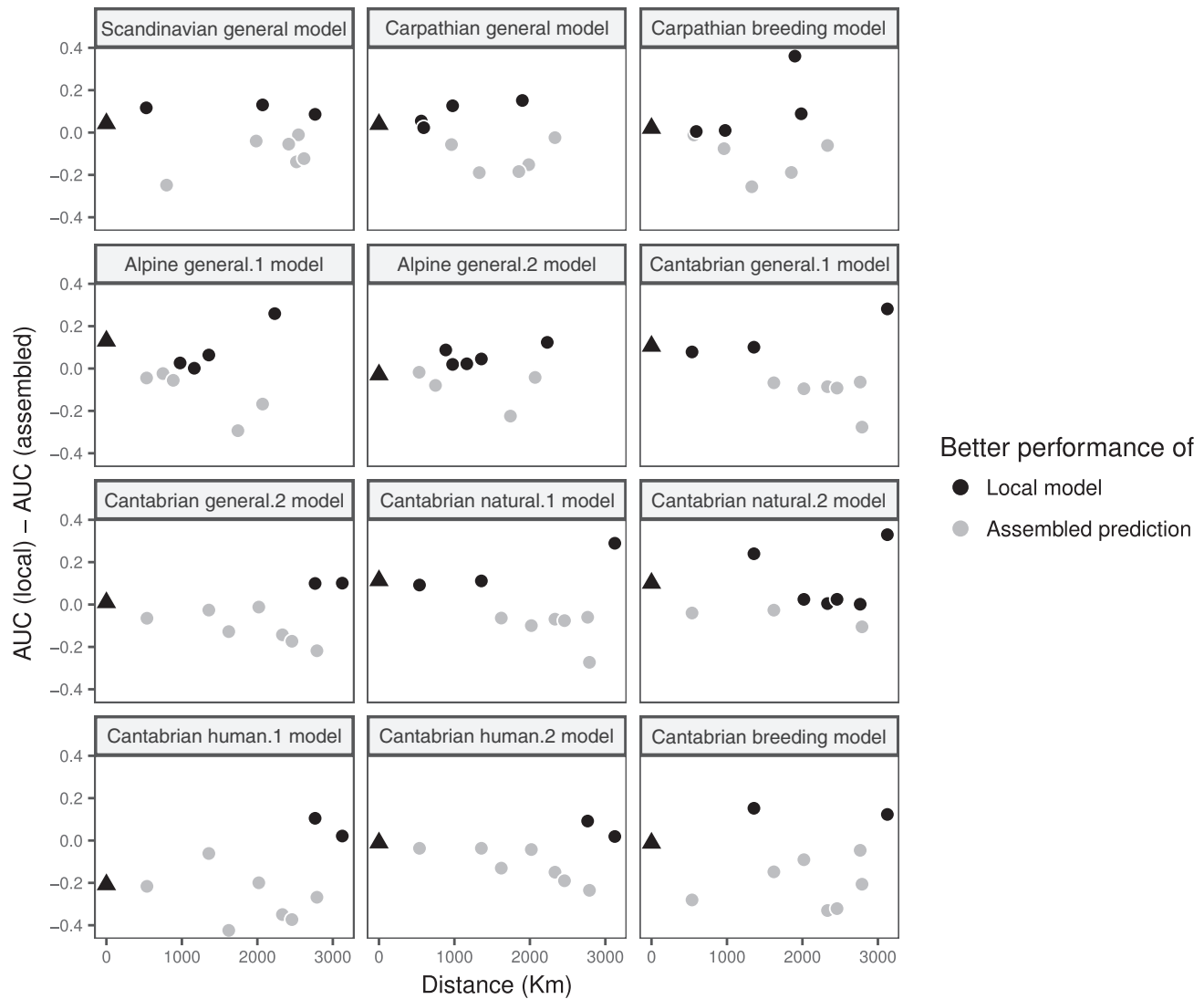
**FIGURE 2** Assembled predictive map. (a) *Suitable*: At least 50% of the models predict suitable habitat. *Unsuitable*: Less than 50% of the models predicted suitable habitat. (b) Continuous scale of habitat suitability. *High*: All models predicted suitable habitat. *Low*: All models predicted unsuitable habitat. (c) Overlaid with the areas of permanent occurrences, sporadic occurrence and the unoccupied 50-km buffer surrounding each population. The assembled predictive map was based on a total number of five models, but for the regions where human population density data was not available, the number of models was two, and for the regions where road data was not available, the number of models was one. *Permanent occurrence* and *sporadic occurrence* as provided by Kaczensky et al. (2012). Raw raster data in Appendix S7, Supporting Information [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

while 88% of the area without bears was predicted as non-suitable (Figure 2a,b). When comparing the predictive performance of each individual model with that of the assembled map, we found that the latter outperformed individual population models 70% of the times (shown as negative differences in AUC in Figure 3).

Across mainland Europe, the assembled map predicts 1.016.925 km<sup>2</sup> of potentially suitable habitat, of which 37% remains unoccupied (Figure 2c). When focusing on the 50-km buffer surrounding each population, on average 24% (*SD* 16%) contains suitable, unoccupied habitat. The population with the highest availability of unoccupied suitable habitat is the Alpine population with 58% of the buffer area being predicted as suitable. In contrast, the Baltic population contains only 4% of suitable habitat in the surroundings (Appendix S5, Supporting Information). Individual population models predicted a highly variable amount of potentially suitable habitat, ranging between 7% and 56% of entire Europe (Appendices S3 and S6, Supporting Information).

## 4 | DISCUSSION

Determining the transferability of ecological models for predicting habitat availability is critical to guide conservation management and policy. Model transferability to new areas may be affected by a diversity of factors such as the model characteristics (including the discriminatory capacity of predictors), similarities between the area where the model was fitted and area where predictions are transferred or species-specific adaptations to the local environment (Werkowska, Márquez, Real, & Acevedo, 2017). Our study illustrates that a comparative assessment of multiple models from different populations represents an important advantage for assessing the consistency and uncertainties of habitat predictions at the continental scale. It is important that this provides conservation managers with richer information for planning conservation opportunities and preventing conflicts derived from expanding populations. Our predictions provide novel insights on the availability of suitable habitat



**FIGURE 3** Differences in AUC that result from transferring predictions from each local population model (AUC local) versus the assembled predictive map (AUC assembled). Values are plotted against the distance of each population to the model-fitting population. Triangles represent the difference in predictions of the population where the local model was fitted

for brown bears at the European continental scale. We found that according to the concordance predictive map, on average 25% of the areas situated within the dispersal distance of brown bears were suitable for the species. This depicts promising opportunities for improving the conservation status of European populations.

In recent years, brown bear populations have expanded and recolonized areas where they historically occurred (Chapron et al., 2014; Milanesi, Breiner, Puopolo, & Holderegger, 2017). Our results suggest that they will continue to expand into unoccupied suitable habitats. We found a lower relative amount of suitable unoccupied habitat around brown bear populations that showed a stable population size in recent years (i.e., between years 2006 and 2011, Kaczensky et al., 2012). This was the case for the Carpathian and the Central Apennine populations (6% and 15% of predicted suitable habitat within the dispersal buffer zone, respectively). In contrast, the amount of unoccupied suitable habitat was high for growing and expanding populations such as the Cantabrian (36%) and the

Pyrenean (35%) populations. This was also true for the Alpine population which had the largest amount of unoccupied suitable habitat available in potential expansion areas (58%). It is remarkable that the subpopulation in the Italian Alps has doubled its population size between 2006 and 2011 (Kaczensky et al., 2012). These results indicate that our habitat assessment is in agreement with demographic assessments and suggest that non-expanding populations may be already limited by the availability of suitable habitat in the surroundings. Furthermore, we also found extensive, relatively well-connected areas of suitable unoccupied habitat far away from currently persisting populations where bears went extinct decades to centuries ago, including relatively large areas in the Iberian Peninsula, Italy and the Alps. The favourable habitat conditions detected in many unoccupied areas depict plausible candidate areas for improving the conservation status of the species through favouring potential expansions and/or planning reintroductions. However, the causes of bear absence in all these areas need to be analysed in

more detail, as other historical or persisting limiting factors may not be captured in the assembled habitat predictions (e.g., connectivity limitations and direct human pressures).

Many local population models performed better for predicting the species distribution in the populations where they were fitted than when transferred to other European populations. This was expected as idiosyncratic conditions may play a major role in local species–habitat relationships. For example, human population density is an important determinant of habitat quality in both the North Carpathian and the Cantabrian populations (Fernández et al., 2012; Naves, Wiegand, Revilla, & Delibes, 2003), but mean human population density is two times higher in the North- Carpathian than in the Cantabrian, so the magnitude of its influence on the probability of bear presence is very different. One limitation that is difficult to account for is population-specific differences in the relationship in the models between surrogates of the human influence (e.g., human population and urban densities) and the type and the magnitude of human activities in those regions (e.g., land tenure systems, forest and natural resource use, or urban area configuration). These differences make it challenging to transfer predictions of the human impacts on species using simple surrogates of the human activity as is customary in habitat modelling.

A second limitation of transferring habitat predictions was the reduced availability of spatially consistent information for some environmental predictors. This information is critical for transferring predictions from previously published studies to new areas with different environmental settings. The number of human settlements, density of roads and human population density were calculated in local habitat studies at a higher spatial and thematic resolution than the datasets available at the continental scale. As an example, two predictive models showed that habitat probabilities in the Alpine population were associated with distance to roads. Transferring predictions of road effects to other areas requires that road datasets are produced at a similar level of detail and using consistent criteria on what elements are mapped. Thus, it cannot be guaranteed that continental-scale predictions captured the intensity of the effects of roads on the presence of bears in the same way in all populations. Differences in the spatial resolution of environmental datasets may also explain some inconsistencies in transferability results, such as the lower predictive capacity of the Alpine habitat models as compared to most other European populations. Last, some studies included habitat variables of high thematic detail not available at the European scale, for example describing forest age or species composition (e.g., Frączkowiak, Theuerkauf, Pirga, & Gula, 2014; Leclerc et al., 2015), distance to individual buildings (e.g., Steyaert et al., 2011) or distance to feeding stations (e.g., Ghoddousi, 2010).

A third limitation we encountered was that some studies could not be reproduced due to the type of model selected or to model reporting deficiencies. Models, such as ENFA or MaxEnt, were at critical disadvantage in this respect as they did not provide the necessary information to reproduce the predictions. Another example is studies that fail to provide all the necessary information, such as

an exact description of variables and their units, although they are based on models such as GLMs that are in principle easy to reproduce. It is important to note that all these aspects limit the utility of habitat suitability studies and illustrates the key importance of ensuring replicability of ecological models for conservation applications. Enhancing reproducibility is critical for expanding the application of habitat studies beyond local study populations and to aid further-reaching conservation goals. For this, the latest developments in scientific sharing practices should be promoted, including making the code of the analyses available (Mislán, Heer, & White, 2016), together with accurate descriptions of the information sources, well-documented protocols and, ideally, making all data open so that models can be refitted for new purposes.

We found that models performed better when transferred to populations that were geographically closer or biogeographically more similar to the population where the model was originally fit. However, an assemble approach combining the predictions from different populations was in most cases more robust than single models for continental-scale habitat assessments. Using this approach, we were able to provide maps depicting the potential expansion and new conflicts areas of a large carnivore species undergoing a recovery process. These maps inform different expansion scenarios, which allow for comprehensive assessments of consistencies and prediction uncertainties in transferring and up-scaling predictions for conservation planning.

In conclusion, integrating results of habitat suitability models developed at multiple populations has clear advantages for providing more accurate, transferable and informative predictions for conservation. This is especially important for up-scaling models from local populations to broader spatial scales, as well as for assessing the potential habitat distribution in less studied populations where applying models from other populations can be seriously misleading. However, better publishing and sharing practices need to be adopted by researchers to facilitate reuse of habitat models for wider conservation applications, as deficient model reporting and restricted access to datasets hinder their transferability.

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## DATA ACCESSIBILITY

The sources of the variables used in the models are listed in Appendix S2, Supporting Information. The variables included in each model and their estimates are detailed in Appendix S4, Supporting Information.



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## BIOSKETCHES

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## SUPPORTING INFORMATION

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

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