

# Assessing habitat quality for conservation using an integrated occurrence-mortality model

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## Summary

1. Habitat suitability models are usually produced using species presence or habitat selection, without taking into account the demographic performance of the population considered. These models cannot distinguish between sink and source habitats, causing problems especially for species with low reproductive rates and high susceptibility to low levels of mortality as in the case of the critically endangered Apennine brown bear *Ursus arctos marsicanus*.

2. We developed a spatial model based on bear presence (2544 locations) and mortality data (37 locations) used as proxies for demographic performance. We integrated an occurrence and a mortality-risk Ecological Niche Factor Analysis model into a final two-dimensional model that can be used to distinguish between attractive sink-like and source-like habitat.

3. Our integrated model indicates that a traditional habitat suitability model can provide misleading management and conservation indications, as 43% of the area suitable for the occurrence model is associated with high mortality risk. Areas of source-like habitat for the Apennine bears (highly elevated areas rich in beech forests, far from roads, and with low human density and cultivated fields) are still present, including outside the currently occupied range. However, attractive sink-like habitat (associated with high levels of pasture, low extent of mountain meadows, low steepness, low elevation, and closeness to secondary and urban roads) are present even inside protected areas.

4. *Synthesis and applications.* Identifying attractive sink-like habitat is crucial to prevent inappropriate management and to effectively address conservation issues: whereas existing source-like habitats should be preserved to halt habitat loss and degradation, attractive sink-like habitat should be managed to mitigate mortality risks or to decrease their attractiveness. In particular, area-specific management interventions and proactive actions (increased patrolling, road closure, human activity management, threat monitoring, etc.) aimed at reducing human-caused mortality are critical for the Apennine brown bear.

**Key-words:** ENFA, Apennine brown bear, Italy, Abruzzo, mortality-risk model, habitat model, sink habitat, source habitat, carnivore conservation, *Ursus arctos*

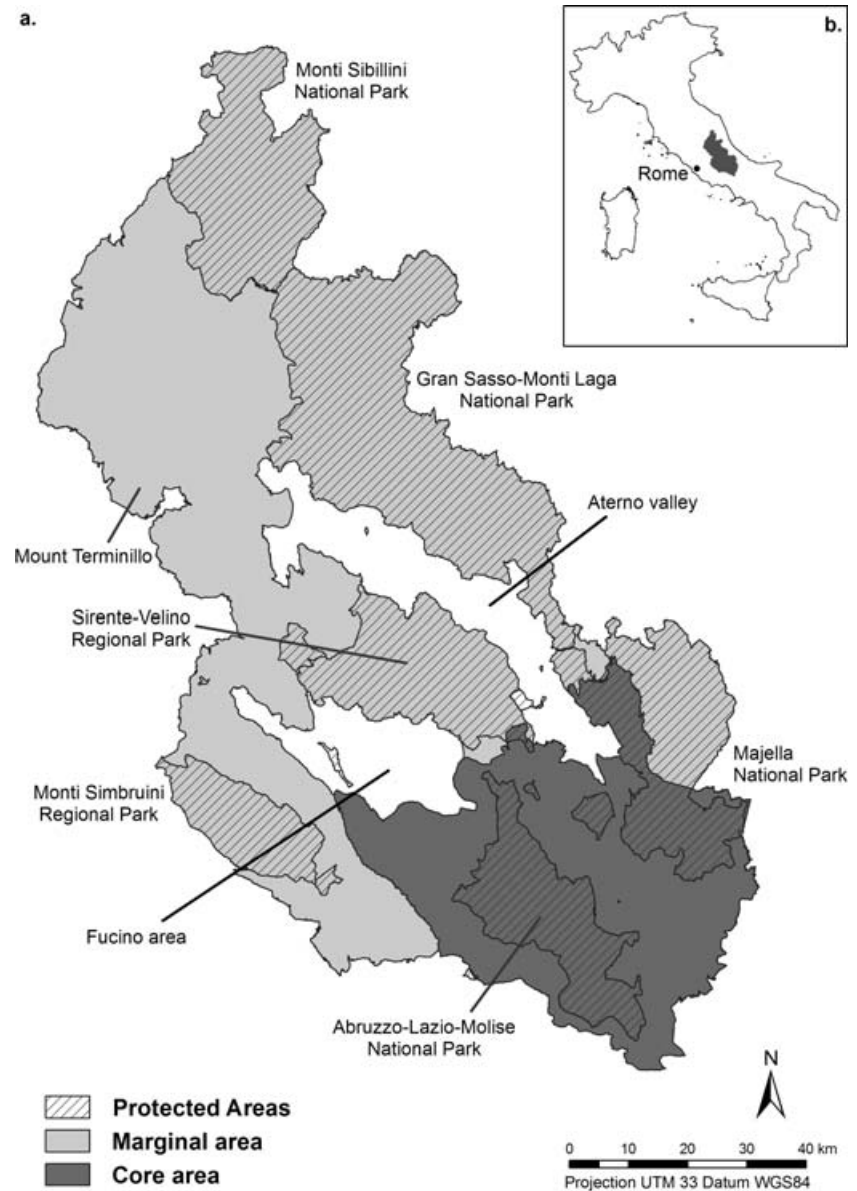
## Introduction

Habitat suitability models (HSM) are usually produced using species presence or habitat selection to infer habitat quality (Guisan & Thuiller 2005). However, this approach does not consider demographic performance at the population level, leading to erroneous conclusions if species occurrence does not correspond to positive reproductive and survival rates (Van Horne 1983; Garshelis 2000). High quality habitats identified using species occurrence alone might actually be located in ecological sinks, areas where reproductive and/or survival rates are too low to sustain a viable population (Pulliam 1988). 'Attractive sinks' represent a particular case

of ecological sink, with individual animals perceiving an area as good habitat even when human-related habitat conditions will ultimately reduce demographic performance (Delibes, Gaona & Ferreras 2001).

Naves *et al.* (2003) originally proposed the identification of attractive sink-like habitats (areas of high habitat suitability and high human-caused mortality) and of source-like habitats (areas of high habitat suitability and low human-caused mortality) using a two-dimensional habitat model. Following Naves *et al.* (2003), sources and sinks are hereby referred to as sink-like and source-like habitats to indicate that these categories are based on habitat models without explicit consideration of demographic features. This framework can be used to develop two complementary strategies: conservation of source-like habitats, and management of attractive

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**Fig. 1.** Study area and location of the main protected areas: (a) subdivision of the study area in core area (Apennine brown bear core range) and marginal area; the Aterno valley and the Fucino area were excluded from the analyses; (b) location of the study area in Italy.

sink-like habitats to mitigate mortality risks (e.g. to control accessibility to humans) or to make these areas less attractive (i.e. to decrease habitat quality). The issue is particularly relevant for species with low reproductive rates and high susceptibility to low levels of mortality, especially in human-modified landscapes (Delibes *et al.* 2001). The Italian endemic Apennine brown bear *Ursus arctos marsicanus* Altobello, 1921, clearly represents such an example.

Following habitat loss and direct persecution (Ciucci & Boitani 2008), the Apennine brown bear is now restricted to a 5000–8000 km<sup>2</sup> area in central Italy (Fig. 1). The current population size does not exceed 40–50 individuals (Gervasi *et al.* 2008), corresponding to an effective population size of 4–10 bears (Ciucci & Boitani 2008), below what is usually considered a viable population (Wiegand *et al.* 1998).

The Apennine brown bear is protected by law and considered critically endangered by the International Union for the

Conservation of Nature (IUCN 2007). The core of the subspecies' distribution range covers 1500–2500 km<sup>2</sup> across the Abruzzo–Lazio–Molise National Park (PNALM) and surrounding areas (Fig. 1; Bologna & Vigna-Taglianti 1992; Posillico *et al.* 2004). Few indirect signs of bear presence or rare direct observations are recorded in other parts of the central Apennines (Terminillo mountains, Sirente–Velino Regional Park, Sibillini National Park, Fig. 1), most probably from dispersing individuals.

Recent HSMs suggest some 150–240 bears could theoretically live in the central Apennines (Posillico *et al.* 2004; Falcucci 2007). Moreover, Falcucci *et al.* (2008) projected that availability of suitable land-cover on a landscape scale should not be a relevant issue for bear conservation, at least up to 2020. These indications clearly support the idea that the subspecies can potentially recover in the future and occupy an area larger than the current range. However, the practical implications of

these analyses for conservation planning are limited because no consideration of human-related mortality has been included.

The importance of human-related mortality is indicated by 74 bears (L. Gentile and L. Sammarone, unpublished data) killed by humans in the last 30 years in areas considered to be good habitat inside the PNALM and its buffer zone. In this context, traditional HSMs cannot provide useful indications and habitat preservation does not represent *per se* a sufficient solution. Proactive conservation actions aimed at reducing human-caused mortality in the core population appear to be critical and extremely urgent in order to facilitate the natural expansion of the bear population in the long term (Ciucci & Boitani 2008).

Using both occurrence data and records of human-induced mortalities, we developed a habitat-based model for distinguishing attractive sink-like and source-like habitats for the bear in the central Apennines based on Ecological Niche Factor Analysis (ENFA; Hirzel *et al.* 2002), providing a tool that can effectively guide conservation planning and assist management intervention on a large scale.

## Materials and methods

### STUDY AREA

Our study area (9940 km<sup>2</sup>, Fig. 1) includes all protected areas ( $\geq 42\%$  of the study area) where bear occurrence has been recorded in the last 20 years (Febbo & Pellegrini 1990; Bologna & Vigna-Taglianti 1992; Boscagli *et al.* 1995; Posillico *et al.* 2004; Carpaneto & Boitani 2003; Ciucci & Boitani 2008). Outside of protected areas, we arbitrarily defined the boundaries of the study area following the main topographic features (ridges and rivers), or main roads and administrative boundaries in more densely populated areas.

The area is mainly mountainous and covered by deciduous forests (oak *Quercus* spp. below 1300 m elevation, beech *Fagus sylvatica* above 1400–1500 m) interspersed with pasture and cultivated fields at lower elevations. Human densities (higher at lower elevations) range from 0 to 369 inhabitants km<sup>-2</sup> at township level. We distinguished two zones within the study area (Fig. 1a): a core area (2402 km<sup>2</sup>), covering the core of the bear range and characterized by stable bear occurrence, and a marginal area (6381 km<sup>2</sup>), where records of individual bears are occasional and/or sporadic. The two areas are similar with respect to elevation, land-cover, human density, and road density (Supporting Information, Table S1).

We excluded from the study area the Aterno valley and the Fucino lowlands (considered as non-habitat for the bear; Fig. 1a), areas with highly intensive industrial, commercial and agricultural activities, and where no signs of bear presence have been historically recorded. A MANOVA performed over land-cover, distance to roads, elevation and human population density measured for 578 random points in the Fucino and Aterno areas and 3390 random points in the rest of the study area (1 point km<sup>-2</sup> for both), confirmed that the Aterno and the Fucino areas differ significantly from the study area (Wilks'  $\lambda = 0.635$ ,  $P < 0.0001$ ).

### PREDICTOR VARIABLES

We considered both environmental and anthropogenic factors (18 variables), all re-sampled using a common origin and 100 m<sup>2</sup> cell

size. We obtained land-cover data from the CORINE Land Cover (<http://dataservice.eea.europa.eu/dataservice/>). We aggregated the original 39 natural and semi-natural land-cover classes into 10 categories considered to be relevant for the ecology of bears in the Apennines (Carpaneto & Ciucci 2003). We also used the CORINE layer to calculate distance to forest edges (negative values inside the forest), considering all types of forests. To account for anthropogenic factors, we considered human population density at the sub-township level (Italian Institute of Statistics, updated to 2001) and distance to urban, primary, and secondary roads (De-Agostini-GeoNext and TeleAtlas road layers, updated to 2003).

We used a digital elevation model (Italian Military Geographic Institute) to account for elevation, slope (percentage), and a terrain ruggedness index (TRI, calculated within a 400-m circular moving windows; Nielsen *et al.* 2004). We chose the radius of the circular moving window performing a fractal analysis (Names 2006) on the movements of eight GPS radio-collared adult bears (see below). By combining the fractal dimension from all movement paths, we found a sharp discontinuity in the fractal curve (Names 2006) corresponding to 400 m, that we assumed as representative of the scale at which bears view their immediate surrounding area. According to the fractal dimensions of movement paths and to the ecological homogeneity of the core study area, analysis windows with larger radii were not expected to influence our results.

We used the same circular moving window to run a map-algebra focal function for each pixel within the study area and for each layer (except TRI). For continuous variables, the focal function assigned to the central pixel of the window the mean value calculated over all the pixels inside the window; for categorical variables it assigned the count of all pixels belonging to the given category. This function allowed for a better approximation of the bear's perception of the environment, and also for the transformation from categorical to continuous variables, as required by the modelling procedure (Hirzel *et al.* 2002).

We measured collinearity (here defined as  $r > |0.6|$ ) among the 18 variables using Pearson correlations as calculated in BioMapper (Hirzel *et al.* 2002). TRI was correlated both with elevation ( $r = 0.74$ ) and slope ( $r = 0.62$ ), and thus, it was excluded from further analyses.

### PRESENCE AND MORTALITY DATA

We obtained four presence-only data sets on bear occurrence inside the core distribution range. The first data set included direct or indirect signs of presence collected all year-round by the PNALM wardens from 1999 to 2003 (PNALM, unpublished data). The second included direct observations systematically and opportunistically obtained in 2006 inside the PNALM (P. Ciucci *et al.*, unpublished data). The third included locations of hair-sampled bear genotypes collected from 2000 to 2003 (Randi *et al.* 2004; Gervasi *et al.* 2008). The fourth data set included VHF- and GPS-locations on 11 radio-collared bears (seven adult females and four adult males) from March to December (2005–2006; P. Ciucci *et al.*, unpublished data). All data sets were censored for spatial accuracy and sub-sampled to increase spatio-temporal independence, selecting locations at least 400 m and 24 h apart from each other. The first two data sets (1310 and 89 bear locations) were pooled and used as input for the bear occurrence model; the other two (239 and 906 bear locations) were used for model evaluation. We assumed that potential annual variations in bear–habitat relationships over the period in which bear presence data were collected (1999–2006) were negligible in terms of their effects on model performance.

We obtained two data sets on bear mortality collected by the PNALM (L. Gentile, unpublished data) and the Italian Forest Service (Posillico, Petrella & Sammarone 2002; L. Sammarone, unpublished data) for a total of 74 cases of bears retrieved dead from 1980 to 2007. From these, we excluded 10 cases with inaccurate ( $\geq 0.5$  km) or missing coordinates and, to account for anthropogenic bear mortality only, additional 27 cases not attributable to human-caused mortality. We therefore considered 37 independent, human-caused bear mortality records.

#### ECOLOGICAL NICHE FACTOR ANALYSIS

We used ENFA to develop a bear occurrence model and a model of human-caused mortality risks. ENFA does not require absence data and it is relatively robust to different habitat-occupancy relationships, including those of unstable, exploited or expanding populations (Hirzel, Helfer & Métral 2001). ENFA extracts from a set of environmental variables all relevant ecological information, while minimizing multicollinearity and redundancy (Hirzel *et al.* 2002). To give an overall representation of a species' ecological niche, the ENFA algorithm calculates global marginality and global tolerance (Hirzel *et al.* 2004), both ranging from 0 to 1. Global marginality measures how much the species' habitat use is different from the mean habitat availability in the study area (the higher the value, the higher the difference). Global tolerance measures niche breadth (i.e., specialization), with low values indicating a specialist species and high values indicating a tolerant species. Moreover, ENFA calculates a set of new uncorrelated predictor factors from the available environmental variables. The first factor accounts for all the marginality, whereas the others refer to specialization (Hirzel *et al.* 2002). Further details on ENFA can be found in Hirzel *et al.* (2002, 2004). We implemented ENFA using Biomapper (<http://www2.unil.ch/biomapper/>).

#### BEAR OCCURRENCE MODEL

By pooling the first two data sets on bear locations (see above), we obtained 1399 occurrence points (64% from spring to early hyperphagia, March–August; 30% from late hyperphagia to denning, September–December) that we used in the ENFA analysis to build a bear occurrence model (BO model) for the entire study area. Although ENFA should prove robust to unstable or expanding populations (Hirzel *et al.* 2001), we tested for the possibility of bias due to the absence of bear locations outside the core area. Specifically, using the same occurrence points, we built a second BO model considering as the area of available habitat the core area only. We measured the convergence between the two BO models (entire study area vs. core area only) by calculating the spatial correlation between their suitability scores (Goodchild 1986). We also compared the two ENFA analyses considering global marginality, global tolerance, and the relative importance of the different environmental variables. Based on the distribution of the original suitability values (ranging 0–100), we reclassified the BO model into four discrete suitability classes: unsuitable (first quartile), low (second quartile), medium (third quartile), and high suitability (fourth quartile).

#### MODEL OF HUMAN-CAUSED MORTALITY RISK

Using the bear mortality data set, we followed the same procedure described above to build a model of human-caused mortality risk (BM model) for the bear covering the entire study area. We also

measured the convergence between the BM model for the entire study area and a BM model covering the core area only obtained using the same mortality data set. We then calculated the spatial correlation between the two models (Goodchild 1986), and compared global marginality, global tolerance, and the relative importance of the different environmental variables. We reclassified the BM model into four classes of human-induced mortality risk using the same procedure described for the BO model.

The limited sample size of human-caused mortalities may affect accuracy and stability of the final BM model. However, the accumulation of a larger data set of bear human-induced mortalities is unrealistic, and thus, we quantified the model's stability by comparing the BM model with alternative models obtained using progressively rarefied data sets of mortality events. Starting from the original data set ( $n = 37$  mortality records), we randomly excluded  $i$  records at a time ( $1 \leq i \leq 19$ ). We thus obtained sub-samples of size  $n_i$  ranging from 36 to 18 records, and for each sub-sample we built a new BM model. We repeated the process based on  $j$  random replicates (without replacement) for each sub-sample of size  $n_i$ , and we built  $\sum_{i=1}^{19} j_i$  BM models for each rarefied data set. As the number of all possible random replicates for a given sub-sample size ( $n_i$ ) increases rapidly with increasing  $i$  ( $j = n!/(n - n_i)! n_i!$ ), we randomly selected 100 replicates for values of  $i \geq 2$ , obtaining 1837 BM models (37 for  $n_i = 36$ , plus 1800 for  $18 \leq n_i \leq 35$ ). We set the minimum sub-sample size at  $n_{19} = 18$  mortality events, one more than the number of variables used to build the model. For each of the 1837 alternative models, we calculated the spatial correlation with the original BM model suitability scores (Goodchild 1986).

#### MODEL EVALUATION

We evaluated the predictive power of the BO model using two independent data sets (239 hair-sample locations, and 906 radio-locations of collared bears) and calculating the Boyce index (Boyce *et al.* 2002; Hirzel *et al.* 2006). The Boyce index offers a measure of how much model predictions differ from a random expectation, by calculating the ratio between two frequencies for each suitability class: the frequency predicted by the model (proportion of evaluation points falling in a given suitability class) and the frequency expected (proportion of the study area belonging to a given suitability class). The Boyce index (ranging from  $-1$  to  $+1$ ) is a Spearman rank correlation between the predicted-to-expected ratios and the mean value of each habitat suitability class. Positive values close to 1 indicate a high predictive value for the model (i.e. model predictions consistent with the evaluation data).

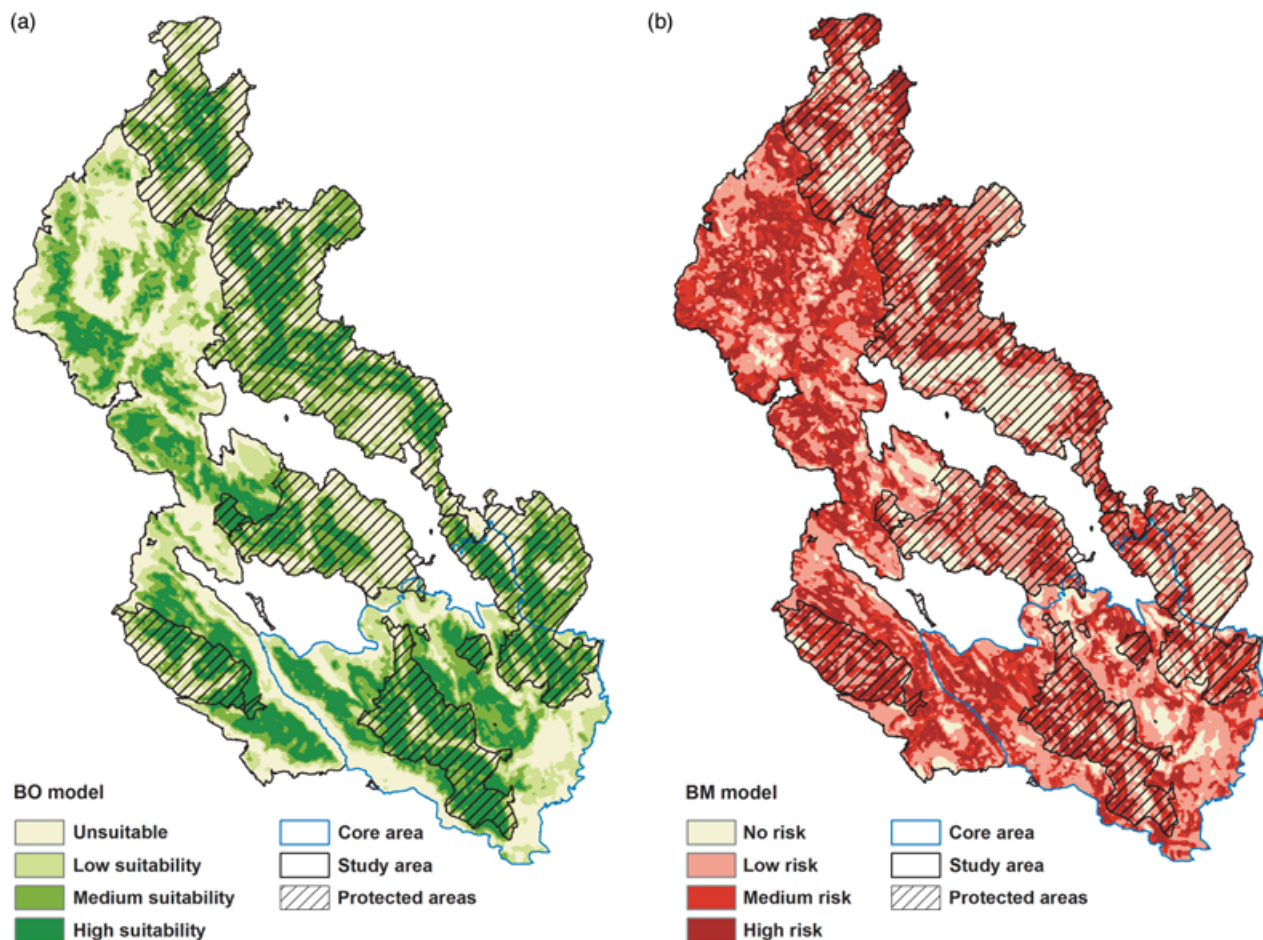
In the absence of an evaluation data set for the BM model, we used a jackknife procedure (Efron & Tibshirani 1993) over the 37 human-caused mortality records to calculate the Boyce index for the BM model. The predicted frequencies were obtained by assigning, at each of the 37 points, the mortality-risk class calculated with a model built using the 36 jackknife locations, whereas the expected frequencies were calculated using the BM built with all the 37 mortality locations.

#### TWO-DIMENSIONAL HABITAT MODEL

To obtain the final two-dimensional model, we integrated the reclassified BO and BM models for the study area. We defined seven habitat states (Fig. 2) based on the interactions between suitability and mortality risk categories: unsuitable habitat (unsuitable class in the BO model and all mortality risk values); attractive sink-like habitat states (medium and high mortality risk); source-like habitat states

BM model	high	unsuitable	3rd level attractive sink-like	2nd level attractive sink-like	1st level attractive sink-like
	medium		3rd level source-like	2nd level source-like	1st level source-like
	low	unsuitable	3rd level source-like	2nd level source-like	1st level source-like
	no risk		3rd level source-like	2nd level source-like	1st level source-like
		unsuitable	low	medium	high
BO model					

**Fig. 2.** Subdivision into the seven habitat categories of the two-dimensional model based on the bear occurrence (BO) and the bear mortality (BM) models.



**Fig. 3.** (a) Bear occurrence (BO) model; (b) Bear mortality (BM) model.

(no and low mortality risk). The three suitability classes in the BO models were used to define three possible levels (of attractive sink-like or source-like habitat): third level corresponding to low suitability, second level corresponding to medium suitability, and first level corresponding to high suitability (Fig. 2). Although no claim is made about the correspondence among these categories and specific positive or negative growth rates for the bear population, we assume that they do represent reliable rankings for attractive sink-like and source-like habitats.

## Results

### BEAR OCCURRENCE MODEL

The BO models covering the entire study area and the one covering the core area only were highly correlated in their

suitability scores ( $r = 0.96$ ;  $P < 0.0001$ ), indicating low bias from this source. Moreover, the two ENFA analyses gave comparable results for global marginality, global tolerance, and for the relative importance of the different predictor variables. The Boyce index for the BO model was 1 ( $P < 0.0001$ ) for both the evaluation data sets.

In the BO model (Fig. 3a), we maintained the first nine factors (marginality plus the first eight specialization factors) for 93.4% of the total information (100% of the marginality and 86.9% of the specialization). ENFA results showed that the Apennine brown bear habitat differs considerably from the mean conditions found over the entire study area (global marginality = 0.76), although the species' ecological requirements do not seem to be restricted considering the range of conditions found in the study area (global tolerance = 0.52).

**Table 1.** Contribution of the 17 environmental variables to the marginality and specialization factors for the bear occurrence (BO) and mortality (BM) models

Predictor variables	BO model		BM model	
	Marginality	Specialization	Marginality	Specialization
Intensive agriculture	-0.128	13.571	0.06	6.912
Heterogeneous agriculture	-0.179	12.776	-0.006	6.218
Oak forest	-0.156	17.152	-0.152	6.85
Broadleaved forest	-0.171	11.7	0.205	6.251
Mixed forest	0.095	8.655	0.125	4.821
Beech forest	0.469	24.896	0.121	12.657
Pasture	-0.015	10.385	0.638	7.196
Mountain meadows	-0.112	20.611	-0.444	16.972
Moors	-0.12	14.829	-0.007	8.508
Barren	0.098	9.572	-0.017	10.023
Distance forest edge	-0.269	8.316	-0.197	11.915
Distance primary road	0.422	5.088	0.287	4.146
Distance secondary road	0.168	4.595	-0.197	7.805
Distance urban road	0.281	6.848	-0.126	5.908
Population density	-0.118	10.709	-0.059	6.219
Elevation	0.497	11.43	-0.197	10.048
Slope	0.121	5.186	-0.281	6.592

The marginality scores (Table 1) showed that bear presence is associated with high-elevation areas rich in beech forests, far from roads, and with low human density and few cultivated fields. Some specialization is apparent particularly for beech forests, mountain meadows, oak forests, agricultural areas, and moors (Table 1).

#### MODEL OF HUMAN-CAUSED MORTALITY RISK

The BM models for the entire study area and the one for the core area only were highly correlated in their mortality risk scores ( $r = 0.75$ ;  $P < 0.0001$ ). The two ENFA tests gave comparable results for global marginality, global tolerance, and for the relative importance of the different predictor variables. The jackknife Boyce index for the BM model was 0.8, indicating a good model performance, although it was not statistically significant ( $P = 0.2$ ) because of the low power of the test ( $1 - \beta = 0.42$ ,  $\alpha = 0.05$ ; Faul *et al.* 2007).

In the BM model (Fig. 3b), we considered the first seven factors (the marginality plus the first six specialization factors) accounting for 92.8% of the total information (100% of the marginality and 83.9% of the specialization). ENFA results showed that human-caused mortality risk for bears is associated with environmental conditions on average different from the mean values found in the study area (global marginality = 0.56), although risk of human-caused mortality is not particularly restricted considering the range of conditions that characterize the study area. The marginality coefficients (Table 1) showed that human-caused mortality risk for bears in our study area is associated with high levels of pasture, low extent of mountain meadows, low steepness, low elevation, and closeness to secondary and urban roads. Some specializations are evident for beech forest and mountain meadows, for elevation, and for distance to forest edge (Table 1).

Correlation among the study area BM model and the alternative 1837 BM models based on increasingly rarefied data sets indicated substantial stability of the model, with a mean correlation of  $r = 0.797$  ( $\pm 0.12$  SD), ranging from 0.649 (for data set with  $n = 18$ ) to 0.969 ( $n = 36$ ).

#### TWO-DIMENSIONAL HABITAT MODEL

The two-dimensional habitat model (Fig. 4) classified 26% of the study area as unsuitable, 32% as an attractive sink-like habitat, and 42% as a source-like habitat, with no particular difference among the core and the marginal area (with the exception of a higher share of attractive sink-like habitats in the core area and a higher share of unsuitable zones in the marginal area; Supporting Information, Table S2).

Unsuitable areas (Fig. 4; Supporting Information, Table S3) were mainly localized in low-elevation flat areas, where agriculture was the dominant land-cover and with high human population and road densities. Moving towards higher elevations, there was a mosaic of second- and third-level attractive sink-like and source-like habitats, followed by first-level attractive sink-like and source-like habitats. The first-level source-like habitats occurred mostly along the steeper slopes, away from urban and secondary roads, with beech forest and mountain meadows being the dominant land-covers. Beech forests are also important for first-level attractive sink-like habitats which, compared to first-level source-like habitats, were located closer to secondary roads and in areas with lower slopes (Supporting Information, Table S3). The third- and second-level attractive sink-like habitats were much more heterogeneous, with oak and mixed, broadleaf forests covering respectively 58% and 19% (Supporting Information, Table S3). Herbaceous and low vegetation are the predominant land-cover classes in the



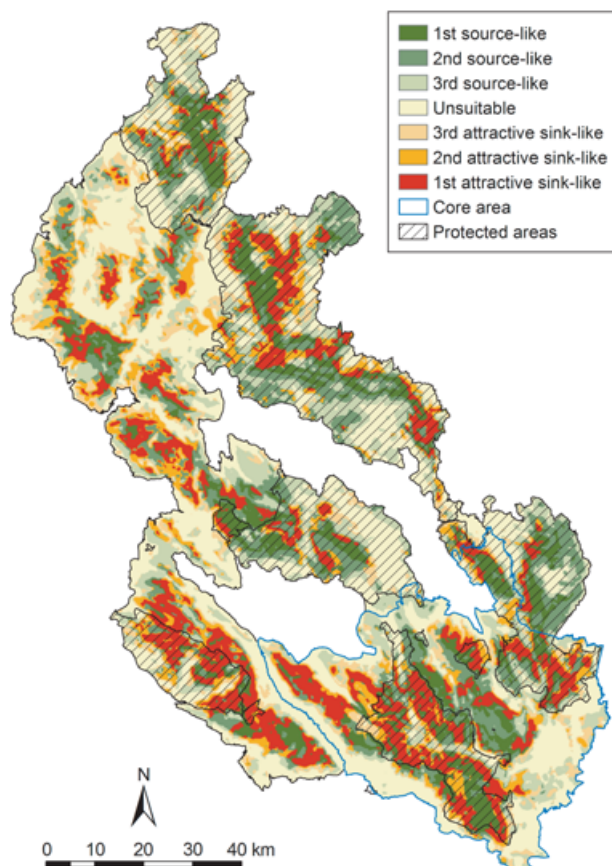


Fig. 4. Two-dimensional habitat model.

second and third level of source-like habitat (68% and 64%, respectively). In both cases, human population density was higher compared to the first level of source-like habitat (Supporting Information, Table S3).

## Discussion

Any evaluation of habitat quality should be explicitly linked with demographic features or vital statistics (Thomas & Kunin 1999), especially for slow-reproducing species living in human-dominated landscapes (Naves *et al.* 2003). Since survival can vary among habitats and landscapes, relying on animal occurrence alone for the assessment of habitat quality is questionable (Van Horne 1983; Battin 2004), with the risk that attractive sinks remain undetected. From a practical conservation perspective, therefore, traditional HSMs can produce incomplete or misleading indications when the model output is integrated into conservation and management planning. Notwithstanding habitat suitability (but see Mitchell & Powell 2003), survival and long-term population dynamics of a species can be substantially affected by human-caused mortality (Treves & Karanth 2003), which may eventually drive small populations to extinction (Swenson *et al.* 1995). This is particularly true in the case of large carnivores living in human-dominated landscape where factors

determining survival and reproduction are often unrelated or even negatively correlated (Naves *et al.* 2003).

Although habitat loss has often been indicated as one of the main factors potentially affecting the Apennine brown bear population (Boscagli 1999; Lorenzini *et al.* 2004), bear habitat availability at the landscape scale does not seem to represent a limiting factor (Posillico *et al.* 2004; Falcucci *et al.* 2008), and the same indication is given by our BO model. However, comparing our final two-dimensional model with those already available (Posillico *et al.* 2004; Falcucci *et al.* 2008; our BO model), it is clear that most of what is usually identified as suitable habitat for the bear the Apennines is actually composed of attractive sink-like habitats (43% of all the suitable in our BO model). Thus, effective control of human-related mortality should be regarded as high priority for the conservation of the bear population (Posillico *et al.* 2004; Ciucci & Boitani 2008). From this perspective, a habitat quality model based on demographic performance would represent a useful tool for the conservation and management of the Apennine brown bear population.

We used bear presence and mortality as a proxy of demographic performance in the absence of more detailed demographic data, assuming that human-caused bear mortalities can be used to model the effect of habitat and anthropogenic features on bear survival, and that bear presences can be used to model occurrence. The same approach, based on logistic regression functions, has already been used to identify attractive sink-like and source-like habitats for brown bears in Spain and Canada (Naves *et al.* 2003; Nielsen, Stenhouse & Boyce 2006). For the Apennine brown bear population, we preferred ENFA because Generalized Linear Models can be negatively affected if the modelled population has yet to reach its equilibrium density in the study area, or if its extent of occurrence is still limited compared to the available habitat (Hirzel *et al.* 2001). It is important to recognize, however, that a distribution model considering an area only marginally used by a species has a number of potential ecological and theoretical problems (Guisan & Thuiller 2005). In our case, no data sets on presence or mortality were available outside the core area due to the occasional and inconsistent presence of bears in the marginal area. Nevertheless, since we deemed it important to produce a model applicable to the entire bear range in the central Apennines, we performed our ENFA tests over the entire study area and we compared the BO and BM models with those developed for the core area only. In both cases, the relative importance of the predictor variables was the same, the suitability scores were highly correlated, and the values of global marginality and tolerance were very similar, clearly indicating that our core-area only models can be safely expanded to the entire study area.

Naves *et al.* (2003) built their two-dimensional model considering only variables related to natural resources for the model of habitat suitability and human-related variables for the mortality model. They argued that an occurrence model including both natural and human variables can potentially obscure the separation of effects on reproduction and survival. However, we followed the approach suggested by Nielsen,

Stenhouse & Boyce (2006), considering both types of variables in both models. In central Italy, the interspersed of resources among artificial and natural habitats is particularly widespread and well-established (Falcucci, Maiorano & Boitani 2007), and it would be misleading to distinguish 'pure' human-related effects from natural ones on survival and/or habitat suitability.

Evaluation of both models was positive, even if there was weaker evidence in support of the BM model due to the low power of our test. However, the BM model was extremely stable in its predictions for increasingly smaller sample sizes, further supporting our confidence in the model itself. As no data set on demographic statistics is yet available for this bear population, no formal evaluation was possible for the two-dimensional habitat model. We therefore adopted the simplest possible approach by selecting the suitability/mortality risk threshold values, with no direct indication that this is the optimal solution for the system we analysed (Liu *et al.* 2005; Jiménez-Valverde & Lobo 2007). As a consequence, the classification adopted for our two-dimensional model may be susceptible to some degree of arbitrariness and, although it does provide useful management indications, we cannot claim that it is representative of the unknown underlying demographic patterns. However, indirect support for the model comes from the Velino-Sirente Regional Park (Fig. 1), the only protected area outside PNALM that has hosted at least one reproducing female and other bears over the past 10 years (P. Morini, personal communication): this area has the highest share of first-level source-like and the lowest share of first-level attractive sink-like habitat.

One limitation of our approach is that the BM model may be affected by different sources of bias. In particular, we do not expect that our sample included all human-caused bear mortalities, but we do believe that most of the bears killed in these past three decades were reported. Accordingly, we assume that the spatial pattern of mortality events is representative of the true distribution of human-induced mortality risk for the Apennine bear population. In fact, given the estimated population size of 40–50 bears (Gervasi *et al.* 2008), we expect the unreported proportion of human-caused bear mortality to be limited and to reflect patterns similar to the known sample. In addition, given the high social appeal of the bear among local populations, and the high human activity within the bear range (park patrolling, livestock grazing, tourism, timber harvesting, hunting, etc.), it is unlikely that killed bears go unreported for long. Moreover, our simulations to test the BM model performance showed that the model was consistent and stable over increasingly smaller sample sizes, yielding confidence in its spatial predictions. As our main aim was to provide a tool to encourage a reduction in human-caused bear mortality, the effect of potential sources of bias in our bear mortality data should be minimal and, most importantly, should not affect the habitat-specific ranking in mortality risk.

Given the limited sample size of our bear mortality data, we could not distinguish among different human-related mortality causes within attractive sink-like habitats. Moreover,

we pooled all bear mortalities reported from 1980 onwards for sample size requirements, thereby equating patterns of mortality risk throughout the last 27 years. Although human-caused bear mortalities have fluctuated significantly over the past 20 years, management or control reactions to illegal mortality have not changed or intensified (Ciucci & Boitani 2008), and it can be reasonably assumed that today Apennine brown bears face similar mortality risks to those in the 1980s.

A similar problem was potentially introduced in our BO model (pooling fallacy: Schooley 1994), for which we used bear presence data collected from March to December, and for different age and sex classes. A higher resolution in our BO model could have been achieved by focusing on the most sensitive demographic vector (reproducing females) during the most critical biological season (late hyperphagia), but unfortunately no such data are yet available for our bear population. However, we are confident that the habitat quality description we achieved through the integrated BO/BM model is adequate enough to provide a meaningful improvement over previous habitat quality models.

In terms of overall habitat quality, our integrated model indicated that the core area still hosts important habitat for the Apennine brown bear, and that the marginal area comprises several unoccupied and potentially suitable areas where the population can be expected to expand in the future. However, areas of medium to high mortality risk are widespread throughout the study area (Fig. 3b), with attractive sink-like habitats being common inside and outside protected areas (Fig. 4).

We found that many areas characterized by high habitat suitability, as identified through traditional modelling (Posillico *et al.* 2004; Falcucci 2007; Falcucci *et al.* 2008; Fig. 3a), were highly interspersed with attractive sink-like habitats (Fig. 4), confirming that human-caused mortality should be regarded as the most important threat to the Apennine brown bear population (Ciucci & Boitani 2008). We consider the identification of first-level source-like and attractive sink-like habitats as an essential element of a renewed Apennine brown bear conservation strategy. Our model identifies first-level attractive sink-like habitats in the core area and along potential travel routes used by bears dispersing from the PNALM, and provides a first description of their environmental characteristics. Area-specific management interventions (patrolling, road closure, human-conflict management, threat monitoring, etc.) should be quickly implemented to prevent human-caused mortality. In this perspective, the authorities in charge will benefit from knowing the distribution of attractive sink-like habitats within their jurisdiction and the potential role they might play in maintaining large-scale habitat connectivity for the bear. On the other hand, management interventions aimed at increasing habitat attractiveness and suitability for bears (e.g. the long time feeding campaigns implemented in the PNALM; Ciucci & Boitani 2008), could obtain the opposite, unexpected result and increase susceptibility of bears to human-caused mortality if these interventions are not planned according to the distribution of mortality risk. If risk factors are not adequately mitigated, management



actions focused on a specific land-cover category should not be considered as priorities for conservation given that, based on our results, first-level sink-like and source-like habitats share similar environmental characteristics. In addition, landscape patterns should be explicitly considered when targeting restoration or management areas to avoid isolation of sites within a high mortality risk matrix.

Nielsen, Stenhouse & Boyce (2006) recognized that two-dimensional modelling allows different conservation and management goals. For instance, the 'no net loss' of source-like habitats: if a given land-use activity ends up turning a bear habitat area into an attractive sink-like habitat, an equivalent amount of attractive sink-like area should be restored towards source-like bear habitats (e.g. deactivation and revegetation of roads). However, given the current situation of the Apennine brown bear population and its range (Ciucci & Boitani 2008), we believe any efforts should rather be devoted at this stage to significantly reduce the extension of attractive sink-like habitats. Especially within established protected areas like the PNALM, a management goal of 'net loss' in first-level attractive sink-like habitats should be promoted through proactive management intervention and effective direct control of human access and activity.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Environmental characteristics of the study area

**Table S2.** Habitat states in the core and in the marginal area

**Table S3.** Contribution of the different predictor variables to habitat state

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