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Modeling the potential distribution for a range-expanding species: Wolf recolonization of the Alpine range

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ABSTRACT

The wolf is naturally recolonizing the Alpine range. Potentially, eight different countries are affected, clearly calling for transboundary management planning. In this framework, using the partitioned Mahalanobis distance, and considering environmental, anthropogenic, and biotic variables, we produced a model of the potential distribution of the wolf over the Alpine range, accounting for the ecological characteristics of the species and for the lack of equilibrium in the current distribution. Low human population density, increasing distance from infrastructures, intermediate elevations and high prey-species richness were the most important factors in predicting wolf presence, followed by the presence of natural land-covers. Based on the projections of our model, we predicted a large availability of high suitability areas across the entire alpine range, which promises great potential for wolf range expansion in the near future. Moreover, protected areas cover 47% of the high suitability areas, and many may act in the future as source habitat patches across the entire alpine region. Our model provides a useful planning tool to develop, evaluate and implement transboundary conservation and management interventions at a broad, biologically meaningful scale across the entire Alpine range. By depicting the potential species distribution in the Alps, our model will aid regional and local managers to design proactive approaches to wolf conservation, especially in areas that have not yet been colonized by the species.

1. Introduction

Species distribution models (SDMs) are rooted in the concept of realized and fundamental niche as defined by Hutchinson (Guisan and Thuiller, 2005). In order to transpose these ecological concepts into statistical models a number of assumptions should hold (Elith and Leathwick, 2009). Among these, the equilibrium postulate (Guisan and Theurillat, 2000) is particularly important, especially to project an SDM in space or time (Araujo and Pearson, 2005). However, for many taxa disequilibrium between species and their environments may be common (e.g. Svenning and Skov, 2004), especially when dealing with species that are undergoing range expansion (e.g. invasive species; Gallien et al., 2012). In this context, any SDM will be largely influenced by the definition of the area available for the expansion (Václavík and Meentemeyer, 2009), definition that is almost invariably subjective, with the exceptions of populations limited by geographical barriers (Puddu et al., 2009; see Gallien et al. (2012) for a recent advancement on the topic).

Large carnivores in Europe represent a clear example of this challenge, as many of them are expanding their distribution in response to direct conservation actions, changes in national and international legislations, and in response to a decreasing pressure of human activities on mountainous landscapes linked to a decreasing human population density, land abandonment and re-forestation, and increase of prey species (Boitani, 2003; Falcucci et al., 2008). In this framework, an SDM projecting species distribution in the near future across an entire region (e.g. the Alps) would be of paramount relevance allowing for large scale, transboundary, and biologically meaningful conservation plans (e.g. Rodrìguez-Soto et al., 2011).

In the case of large carnivores, the definition of the area available for their expansion (and consequently the identification of ecologically meaningful points of absence or pseudo-absence) is problematic because they have wide dispersal capacities (Vangen et al., 2001), and can also cross sub-optimal and unsuitable environments when dispersing (Ciucci et al., 2009). Thus, only modeling algorithms based on presence-only data should be considered. However, most techniques (e.g., ENFA, Hirzel et al., 2002; Maxent, Phillips et al., 2006) still require the definition of the area available for the species and, in order to correctly represent the species' niche, all require that the species presences cover the full range

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of habitat variation to which the species respond, basically representing the ecological optimum for a given species (Rotenberry et al., 2006).

The partitioned Mahalanobis distance proposed by Rotenberry et al. (2006) is a variation of the classical Mahalanobis distance (Clark et al., 1993), and it (1) identifies a minimum set of basic habitat requirements for a species, (2) does not require absence (or pseudo-absence) data, and thus (3) is independent from the selection of any area available for range expansion. Therefore, on a theoretical basis, it represents a better option to predict the potential distribution of a species undergoing range expansion.

Here we present an application of such an approach to predict the potential distribution of the wolf (*Canis lupus*) over the entire alpine range and across 8 different countries. Starting from the Apennines, the Italian wolf population is recolonizing the Alpine range after about a century of absence (Valière et al., 2003; Ciucci et al., 2009). A transboundary management plan is urgently needed to coordinate national and local policies and management interventions (Linnell and Boitani, 2012), and there is great potential for an SDM to guide proactive management in a timely manner.

We developed such a model considering environmental, anthropogenic, and biotic variables, and using data of wolf presence collected in the area currently occupied with stable populations. Our aim was to provide the first application of the partitioned Mahalanobis to a species that is going through a process of range expansion over a large area, and therefore to develop a SDM based on robust theoretical grounds that should complement previous efforts on the same species over the Alps (Marucco and McIntire, 2010; Marucco, 2011). We assessed both the calibration and the discrimination capacity of our model (sensu Pearce and Ferrier, 2000) using procedures that account for the lack of an independent data set. Moreover, we discussed the implications of the model projections across the entire Alpine range for wolf conservation, and we also provided practical examples of how our model can support management and conservation planning at a transboundary scale, with a particular focus on the efficacy of the existing network of national and international alpine protected areas.

2. Methods

2.1. Study area

Our study area (≈300,000 km^2; Fig. 1) includes the entire Alpine range as defined by the Alps Convention (http://www.alpconv.org; Southern boundaries defined by Falcucci et al., 2007), spanning a total of eight countries: Italy, Monaco, France, Switzerland, Germany, Liechtenstein, Austria and Slovenia. The climate of the study area varies from temperate, to continental, to alpine, and the topography is mainly mountainous, with elevations ranging from sea level to 4810 m a.s.l. The landscape is characterized by large deciduous, mixed, and evergreen forests, with high elevation areas covered by sparse vegetation and/or glaciers (depending on elevation). Human influence is mostly limited to the main valleys, the coastal areas and the plains (Falcucci et al., 2007; Maiorano et al., 2008).

2.2. Eco-geographical variables

We considered four classes of variables potentially important in determining wolf distribution: land use, anthropogenic factors, trophic resources, and topography. All variables were resampled to a common origin and resolution (300 m cell size) using ArcGIS 9.3 (ESRI©, Redlands, California). The same software was used for all spatially explicit data manipulation and visualization.

We obtained land cover from GlobCover V2.2 (ESA Globcover Project), a global land use dataset with a spatial resolution of 300 m and a thematic resolution of 22 classes (http://www.esa.int/due/ionia/globcover). We reclassified the original 22 land cover classes into eight variables (Table 1) considered to be relevant for the ecology of the wolf in the Alps. We used GlobCover also to calculate a layer of distance to forest edges (negative values inside forests, positive outside).

To account for anthropogenic factors, we considered human population density and distance to infrastructures (roads and railways). We obtained from the European Environmental Agency a digital map of human population density in 2001 with a spatial resolution of 100 m for Italy, France, Germany, Austria, and Slovenia. For Switzerland, we considered a digital map produced by GEOSTAT (Swiss Federal Statistical Office) with the same spatial resolution but referring to a census taken in 2000. To obtain a complete picture of the transportation network over the alpine range we integrated three different datasets: the road network developed by DeAgostini Editore for Italy, OpenStreetMap (http://www.openstreetmap.org), a global open-source road network, and the Digital Chart of the World (http://www.maproom.psu.edu/dcw), which provided the railway network. From all these data sources, we generated four layers of Euclidean distance, considering three classes of roads (main roads, including highways and roads of national importance with $\geqslant 2$ lanes; secondary roads, including roads of regional importance generally with one lane only; other roads, including all remnant urban and extra-urban roads), and the railway network.

To account for the availability of prey species, we considered all wild ungulates preyed upon by wolves over the Alpine range (chamois, *Rupicapra rupicapra*, roe deer, *Capreolus capreolus*, red deer, wild boar, and fallow deer, *Dama dama*; Gazzola et al., 2005; Marucco, 2010). However, no abundance data for these species are available for the study area, and thus we considered prey species richness as calculated from fine-scale species-specific SDMs (Maiorano et al., accepted pending revisions). Furthermore, considering prey species richness we emphasized the additive value that more than one prey species exerts on wolf habitat suitability (Ciucci et al., 2003). We did not consider domestic prey and other food of anthropogenic origin because these data are not available over the entire study area with a resolution comparable to the other layers that we considered.

We obtained all topographic variables from the Digital Elevation Model (DEM) produced by the USGS/NASA Shuttle Radar Topographic Mission with a spatial resolution of 90 m (http://srtm.csi.cgiar.org/). In particular, we considered elevation, slope (percentage), and a terrain ruggedness index (TRI; Nielsen et al., 2004), calculated within a 1200-m circular moving window. We chose the radius of the moving window considering the wolf's perception of the environment at a landscape scale, as measured performing a fractal analysis (Nams, 2006; Falcucci et al., 2009) based on the Global Positioning System (GPS) locations of a dispersing wolf (Ciucci et al., 2009).

We used the same circular moving window to run a map–algebra focal function for each pixel within the study area over land use variables and human population density. For continuous variables (e.g., human population density), the focal function assigned to the central pixel of the window was the mean value calculated over all pixels inside the window itself; for categorical variables (e.g., land use categories), it assigned the count of all pixels belonging to the given category. This function, besides allowing for a better approximation of the wolf's perception of the environment at a landscape scale, allowed also for the transformation from categorical to continuous variables.

We measured collinearity ($r \geqslant |0.6|$) among the 18 variables using Pearson correlations. Artificial areas (correlated with human