Available online at:

http://www.italian-journal-of-mammalogy.it/article/view/11695/pdf

Online first – 2016



doi:10.4404/hystrix-27.1-11695

Research Article

Combining multiple tools to provide realistic potential distributions for the mouflon in Sardinia: species distribution models, spatial pattern analysis and circuit theory

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Keywords: species distribution models (SDMs) MaxEnt morphological spatial pattern analysis (MSPA) GUIDOS toolbox CircuitScape Sardinia mouflon species management

Article history: Received: 18 January 2016 Accepted: 24 June 2016

Abstract

Species distribution models (SDMs) are commonly used to predict potential species distribution in ecology, biogeography, and conservation. However, the lack of consideration for many different aspects of the species' ecology often result in maps of limited practical value. Yet the wealth of information that is often available (especially for larger vertebrates) could help improve these models. Here, considering the mouflon (*Ovis aries*) in Sardinia as a case study, we propose a new integrated approach based on different aspects of the species ecology. In particular, we combined an SDM calibrated with an ensemble modelling approach with a morphological spatial pattern analysis and a model of structural connectivity. With this approach it was possible to map at the same time the distribution of potentially suitable habitat patches (and particularly of those being able to host a pregnant females) and of the structural corridors connecting these patches. Overall, while the SDM predicted that 14.5% (3480 km^2) of Sardinia was suitable for the presence of the mouflon, with our new integrated approach the percentage of areas suitable dropped to a much lower and more realistic 6.6% (1584 km^2). Our results have potentially important consequences for the practical conservation and management of the species in Sardinia.

Introduction

Species distribution models (SDMs) represent one of the most widely used tools in ecology, conservation biology, and global change biology (Guisan et al., 2013) to answer a range of questions going from evaluation and proposal of management strategies (Maiorano et al., 2015a), to species and community responses to global changes (Maiorano et al., 2011, 2013; Thuiller et al., 2015), to impact of climate change on ecosystem services (Civantos et al., 2012), to models of the potential species distribution (Falcucci et al., 2009, 2013; Puddu et al., 2009).

SDMs are empirical models relating known occurrences of species to environmental predictor variables using statistically derived response curves that aim to best reflect the species' ecological preferences (Guisan and Zimmermann, 2000). From a theoretical point of view, they are rooted in the concept of realized and fundamental niche as defined by Hutchinson (Guisan and Thuiller, 2005). Their utility clearly depends on their ability to accurately predict species potential occupancy in a given study area (Loiselle et al., 2003; Hernandez et al., 2006), but a number of studies have demonstrated that different SDM algorithms can produce different species distributions for the same species in the same study area (Araujo and New, 2007). Furthermore, the statistical technique considered to model species distribution is not the only source of uncertainty in the output maps (Buisson et al., 2010). A common problem with SDMs, in fact, is related to the lack of consideration (or better a limited consideration) for what is known about the ecology of the species considered at different spatial scales (e.g., Mortelliti and Boitani, 2008; Wisz et al., 2013). For example, when modeling the potential distribution of a species with large area requirements, areas of high habitat suitability can actually represent sinks (Falcucci

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Hystrix, the Italian Journal of Mammalogy ISSN 1825-5272 ©© ©©2016 Associazione Teriologica Italiana

doi:10.4404/hystrix-27.1-11695

et al., 2013) therefore providing misleading results (Mortelliti et al., 2011).

Here we propose an approach aimed at providing a more realistic picture of a species' potential distribution integrating different aspects of its ecology, going from the simple probability of presence as obtained from an SDM, to a spatially explicit definition of potential habitat patches resulting from a morphological spatial pattern analysis (which allows for the identification of habitat patches large and contiguous; Soille and Vogt, 2009) and a measure of structural connectivity (based on the spatial distribution of habitat patches and providing a proxy for functional connectivity). We applied our proposal to the case of the mouflon (*Ovis aries*) in Sardinia.

The modern mouflons represent the feral descendants of ancient domestic sheep stocks, brought by farmers to the islands of Corsica (France) and Sardinia (Italy), western Mediterranean. The species was apparently not present in either island before the Neolithic (Massetti, 1998; Gippoliti and Amori, 2002, 2006), but it has always been considered as direct part of the natural fauna in the two islands and it is currently listed in Annex II of the European Union Habitats Directive (Dir. 92/43/CEE). Largely present in Sardinia during the 19th century, already at the beginning of 1900s numbers were declining strongly as a response to heavy hunting regimes (both legal and illegal; Ghigi, 1911), linked also to international hunting expeditions traditionally targeting the species (e.g., Wagner, 1905). From the minimum of less than 400 individuals counted in 1969, the number of animals has been increasing up to the approximate 1500 animals estimated in 1985 (Apollonio and Meneguz, 2003) and the 7500 after 2000 (Apollonio et al., 2005, 2011). The current species distribution is however limited to eastern Sardinia (Ogliastra, Gennargentu, Supramonte) plus a few managed and protected areas were the species has been reintroduced, covering only a limited part of the original species distribution (Beccu, 1993) shown in Fig. 1.

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Figure 1 – Historical (source Beccu, 1993) and current distribution of the mouflon in Sardinia. Forest service corrals highlights the location of the corrals where captive mouflon are present.

With our approach, we model the species' potential distribution for the entire island of Sardinia considering at the same time habitat suitability, habitat distribution patterns and habitat connectivity. Our proposal can be easily translated into spatially explicit management and conservation options, with a particular focus on the potential recolonization of the species' historical distribution range.

Methods

We performed our analyses considering the entire island of Sardinia, the second largest island in the Mediterranean (roughly 24000 km²). The island fosters more than 1600000 inhabitants, 43% of which concentrated in two main urban areas located into the main lowland agricultural areas. The island has a complex topography, with more than 80% of the region occupied by hilly and mountainous areas (>300 m a.s.l.), and with a maximum elevation of 1834 m a.s.l. The mountainous areas are almost completely covered with evergreen sclerophyllous forests/bushes, and to a lesser extent with pastures. The main anthropogenic impacts on the island are related to the huge presence of free ranging sheep (almost 2.7 million animals) and goats (almost 240000 animals), accounting respectively for 43.3% of all sheep and 24.7% all goats officially registered in Italy.

Predictor variables

We considered different classes of variables potentially important in determining mouflon distribution: land use, water, anthropogenic factors, competitors, and topography (Tab. 1).

Data on land-use was obtained from the Sardinia regional geographic information system (www.sardegnageoportale.it) updated at 2008 and with a minimum mapping unit of 0.75 hectares (corresponding roughly to a scale 1:25000). The original database fostered more than 70 land-

Table 1 - Environmental variables used to model mouflon distribution.

Classes of variables	Environmental variables
Land cover	Agricultural lands
	Forests and woodlands
	Pastures and other natural areas
Water	Distance to water
Anthropogenic factors	Human population density
	Distance to roads
Biotic interactions	Loads of domestic sheep/goats
Topography	Terrain roughness index

use classes that we reclassified into 3 land-cover variables following the mouflon ecological requirements (Ciuti et al., 2009): agricultural lands, forests and woodlands, pastures and natural open areas (full details on thematic aggregations are available in Tab. S1). From the same regional geographic information system, we obtained data on water resources (temporary and permanent water courses and bodies) in vector format (shape-files) with a scale 1:25000. We used the database to produce a layer of distance to water.

The main competitors for space and resource use for the mouflon in Sardinia are represented by free ranging domestic sheep and goats, which can compete for food or can strongly increase the level of disturbance due to the presence of guarding dogs. To obtain a spatially explicit layer of domestic animal loads in Sardinia we used the statistics available at the township level from ISTAT (2013).

Following Motroni et al. (2004), and assuming that the spatial distribution of free ranging domestic animals follow the availability of food in the field, we partitioned the numbers of animals (sheep and goats) reported for each township proportionally to the area of each land-use class inside the same township and to the potential amount of food obtainable from each particular land-use class (Tab. 2). The final layer reported number of free ranging domestic sheep and goats per pixel over the entire study area.

The Italian Institute of Statistics provided the data on human population density at the subtownship level (updated at 2001; www.istat.it), while the road network was provided by a combination of the De Agostini, GeoNext, and TeleAtlas databases (updated to 2003). We used the first to calculate a layer of human population density, while the latter was used to calculate distance to roads.

The Italian Military Geographic Institute provided a digital elevation model (original resolution 400 m²) that was used to account for topographic variables. In particular, we calculated an index of terrain roughness (TRI) as defined by Nielsen et al. (2004) and considering a 180 m-radius circular moving window. The index TRI has the advantage of providing a clear measure of the topographical complexity of an area, considering at the same time the variance in aspect and the variance in slope (Nielsen et al., 2004). Using the same 180 m radius, we run a map-algebra focal function over the entire study area for each layer. For continuous variables (e.g., distance to roads), 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 (e.g., agricultural land), it assigned the proportion of all pixels belonging to the given category inside the moving window. This function has

Land use class	Tonne/hectare of available food
Non-irrigated arable land	7
Pastures	10
Land mainly occupied by agriculture with significant areas of natural vegetation	3
Agro-forestry areas	1
Natural grasslands	4

the advantage of allowing for a better approximation of the composition of the environment surrounding the species locations, compared to more traditional modeling approaches in which species presence is only function of the habitat characterising the single pixel (Falcucci et al., 2009). The 180 m radius was chosen considering the flight distance of females with lambs (mean=164 m, standard deviation=17 m, n=114; Ciuti et al., 2008). All variables were resampled to a common origin and resolution (40 m cell size; smallest cell size possible in relation to computing power of the available workstation) using ArcGIS 10.3.1 (ESRI, Redlands, California). The same software was used for all spatially explicit data manipulation and visualization.

To avoid problem of multicollinearity in model calibration, we examine pair-wise correlation among all variables considering $r \ge |0.6|$, a conservative threshold according to the |0.7| suggested by Dormann et al. (2013). We never found a pair-wise correlation higher than |0.5| and therefore all 8 variables were retained for further analyses.

Species data

We considered the most updated data on the current species distribution as obtained from the Regione Sardegna Wildlife Database (Apollonio et al., 2011). For further analyses, we considered only the areas of presence covering the Gennargentu massif and the Lula Mountains (for a total of 1183 km²), as both are included into the historical distribution of the species (Fig. 1). We excluded the area of presence west of the Gennargentu and the Asinara island because both are recent introductions outside of the historical distribution range (Beccu, 1993).

For the two areas of presence we are considering, we randomly draw 471 points. The number was chosen considering the point density obtained drawing 10000 random points (the number of background points routinely used by MaxEnt) over Sardinia to be used as background points in the modeling procedure (see below). The entire study area was considered in this procedure as contrast to the current species distribution as it is easily accessible to the species through dispersal (Merow et al., 2013). The process was repeated 100 times, obtaining 100 alternative samples to be used in model calibration.

Species distribution modeling

To model the probability of presence for the mouflon over Sardinia we considered the maximum entropy algorithm as developed in MaxEnt (Elith et al., 2011). MaxEnt is based on a machine learning response that is able to estimate the most uniform distribution (corresponding therefore to the maximum entropy distribution) of presence points compared to background locations given the constraints derived from the environmental data (Phillips et al., 2006). We calibrated our models using default settings (Phillips and Dudik, 2008) and considering each of the 100 calibration datasets. We explicitly considered all suggestions for choice of settings defined in Merow et al. (2013), but we opted for default settings as these are in any case more appropriate for our particular case study. For each MaxEnt run we used a repeated split-plot approach with 10 replicates, and for each replicate we randomly removed from the calibration procedure 20% of the points to be used for model evaluation through AUC (Swets, 1988). In the end we calibrated 1000 models, obtained through 100 calibration sets times 10 replicates for each set. All models with positive evaluation (i.e., AUC \ge 0.7) were projected over the entire study area, and the final potential distribution for the mouflon in Sardinia was obtained as the weighted average of all models (Marmion et al., 2009).

To evaluate the importance of each predictor variable in determining the potential distribution of the mouflon we considered the increase in regularized gain, which can be considered comparable to the goodness of fit commonly used for generalized linear and additive models (Elith et al., 2011). The algorithm in MaxEnt, starting from a uniform distribution, tries to repeatedly improve the fit to the data by generating a probability distribution for the species considered. The gain is defined as the average log probability of the presence samples, minus a constant that makes the uniform distribution have a zero gain. Therefore, the gain starts at 0 with the uniform distribution and increases towards an asymptote as far as the distribution predicted by MaxEnt approximate the presence of the species. At the end of the run the gain indicates how close the model is to the presence samples (Elith et al., 2011). During model training, the algorithm keeps track of the contribution of each environmental variable to model fitting, and in the end provides a value corresponding to the percent contribution of each variable to model gain. This percent contribution can be used as an index of the relative importance of each variable included in the distribution model. Given that different results for variable importance can be obtained in different settings (e.g., different calibration sets), we summarized variable importance considering the average percent contribution of each, calculated considering all models with positive evaluation.

Morphological Spatial Pattern Analysis

To operatively define the potential distribution of the mouflon in Sardinia, we divided the continuous probability map into 2 mutually exclusive classes corresponding to: (potentially) presence, and (potentially) absence. To distinguish among the two we choose a threshold corresponding the lower 10% of probability value as measured inside the polygons of presence. We obtained therefore a map in which each pixel was classified as either 0 (species potentially absent) or 1 (species potentially present). However, single and isolated pixels or small patches do not have a practical meaning for the management and conservation of the species or for its potential presence because they cannot host even a single animal. Therefore, we used the algorithms available in the software GUIDOS (Vogt, 2016) to perform a Morphological Spatial Pattern Analysis (MSPA) and to distinguish habitat patches (including cores, edges and perforations as defined in Soille and Vogt, 2009) vs matrix (all the rest) starting from our binary map. Moreover, considering habitat patches only, we also distinguished core areas vs simple habitat patches based on their size. In particular, core areas are defined as all habitat patches that have an area ≥ 1.74 km², a value determined considering the home range of pregnant females (mean=1.15 km²; SE=0.3 km²; Ciuti et al., 2009). In our analysis, core areas represent the strongholds of the potential species distribution, being large and continuous enough to host a female during reproduction.

Landscape scale structural connectivity

Considering all habitat patches identified through the MSPA as starting points, we used the circuit theory principles as implemented in the software CircuitScape (McRae et al., 2008) to model connectivity for the mouflon over Sardinia. Doyle and Snell (1984) have demonstrated that the intensity of current flow between two nodes (two habitat patches in our analyses) is proportional to the number of times an individual goes from one node to the other moving through the particular pixel being considered (McRae et al., 2008). Therefore, current flow can be used as a measure of the probability of movement between the two habitat patches, providing thus a continuous estimate of landscape structural connectivity for the species being considered. To get an estimate of current flow, a layer modelling resistance to movement is needed. For this purpose, following the most common approach available in the literature (e.g., Falcucci et al., 2008), we used the inverse of the continuous habitat suitability model, obtaining therefore a model of the structural connectivity for the mouflon in Sardinia.

Protected areas and conservation status

To evaluate the conservation status and identify areas of possible future reintroductions, we overlaid the core areas and the structural connectivity model with 4 datasets (Fig. 2), representing existing conservation areas (i.e., regional and national protected areas and public owned forests) and proposed conservation areas (i.e., the Natura 2000 network and the new protected areas proposed by the regional administration).

Less than 1% of Sardinia is covered by existing protected areas (Fig. 2a), most of which are limited to smaller islands, while public owned forests cover more than 9% of Sardinia (Fig. 2a). The protected areas proposed by the regional administration (Fig. 2b) would provide a huge increase, covering 17.1% of Sardinia, and the same is true for the proposed Natura 2000 network (terrestrial areas only; Fig. 2b), which when implemented, will cover 18.7% of the island. If all existing and



Figure 2 - Conservation areas in Sardinia: a) existing protected areas (PAs) and public owned forests; b) proposed protected areas Natura 2000 network.

proposed areas are considered together, almost 30% of Sardinia would be protected.

Results

All model evaluations provided an AUC value greater than 0.7, with a mean AUC=0.908 (min AUC=0.860, max AUC=0.939, standard deviation AUC=0.012). Considering the continuous species distribution model (Fig. 3a), areas of high suitability for the mouflon are distributed over the entire Sardinia, with small patches of medium suitability being present also in the main agricultural areas (see also Fig. S2 for an estimate of the variance in the suitability values). The 3 most important variables in determining species distribution were human population density, agriculture and terrain roughness, accounting all together for almost 93% of percent contribution (Tab. 3). In particular, the species probability of presence responded negatively and strongly to human population density and to agriculture (dropping quickly towards zero as soon as human population density and/or agriculture increase from 0) and positively to terrain roughness (increasing almost linearly for increasing values of TRI; Fig. S3).

Considering the 10% probability threshold (Fig. 3b), the areas of potential presence were reduced to 14.5% of Sardinia (3480 km²), basically limiting the areas suitable for the presence of the mouflon to the eastern part of the island and to mountainous areas. The MSPA further restricted the areas of potential presence to 6.6% of Sardinia (1584 km²), totally excluding all areas in the main agricultural plains (Fig. 3c). Considering also the spatial requirements of reproductive females, the core areas for the species presence are limited to 44 (Fig. 3c), corresponding to 6.1% of Sardinia (1458 km²).

The level of structural connectivity allow for the identification of one main distributional area for the mouflon in Sardinia (Fig. 4), corresponding roughly to the historical distribution range and limited to the eastern side of the island. A total of 33 core areas, all extremely well connected from a structural point of view, represent the potential distribution of the species, having the Gennargentu massif as the core of the distribution and going with a few areas towards north (up to the Monti di Lula and the Goceano massif) and especially towards south up to the Sarrabus-Gerrei. The remnant 11 areas are all disconnected, outside of the historical distribution, and relatively small. The two core areas identified in the Asinara island correspond to the actual presence of the species (introduced in Asinara in 1952), and the same is true for the core area north of Oristano where a local population of mouflon is present since 1990s following an escape from corrals.

Among the existing protected areas (Fig. 2a), only the Asinara National Park covers an existing population of mouflon corresponding to a core area identified by our model (although introduced and not part of the historical distribution). Public owned forests (Fig. 2a) cover slightly more than 35% of the mouflon core areas, with a particularly good coverage for the Sarrabus-Gerrei and the Gennargentu areas. The protected areas proposed by the regional administration (Fig. 2b) would represent an extremely important addition for the conservation of the mouflon, covering 44.3% of the core areas and increasing substantially the level of protection for the Gennargentu massif, while covering totally the areas in the Sarrabus-Gerrei. The proposed Natura 2000 network (terrestrial areas only; Fig. 2b), if implemented, would further increase the percentage of core areas being protected (55.6%). Finally, considering all existing and proposed areas together, the system would cover 74.5% of the core areas for the mouflon.

Discussion

Our analyses clearly demonstrate the importance of integrating multiple tools (such as SDMs, MSPA, and CircuitScape) to improve the ecological realism of models predicting potential species distribution. With our approach we were able to clearly define the potential distribution of the mouflon in Sardinia, identifying explicitly: 1) core areas,

Table 3 - Variable contribution as measured in MaxEnt.

Environmental variable	Variable importance
Agricultural lands	27.89% (±3.42%)
Forests and woodlands	0.82% (±0.52%)
Pastures and other natural areas	1.06% (±0.45%)
Distance to water	1.75% (±0.59%)
Human population density	53.11% (±2.68%)
Distance to roads	1.77% (±0.69%)
Loads of domestic sheep/goats	1.68% (±0.83%)
Terrain roughness index	11.92% (±3.14%)



Figure 3 – a) continuous species distribution model for the mouflon in Sardinia; b) binary species distribution model obtained applying a 10% threshold over the continuous SDM; c) core areas obtained through a morphological spatial pattern analysis with outlined in green all areas that are big enough to host at least a single reproductive female mouflon.

theoretically able to support groups of animals for their entire life cicle, 2) habitat areas, theoretically able to support single animals or smaller groups, and 3) potential corridors connecting one or more core area. The richness and detail of information we are providing has potentially important implication for the management and conservation of the species, much more than what would be available with the simple probability of presence that more traditional approaches propose (e.g., Puddu et al., 2009).

Obviously, our analyses have a number of limitations. The direct identification of core habitat areas would require in the ideal setting a good knowledge of parameters like habitat specific (or even better patch specific) population growth rates, something that however is extremely difficult to have for the current distribution and basically impossible if the aim is that of modeling the potential species distribution. Along the same line of reasoning, to really model connectivity among core habitat patches, data on movement patterns of dispersing animals would represent the ideal target together with analyses like step selection functions (Thurfjell et al., 2014), Brownian bridges (Horne et al., 2007), and similar (e.g., Squires et al., 2013; Zeller et al., 2014). In the absence of these types of data, at least the knowledge of behavioural states (LaPoint et al., 2013) would represent a minimum requirement to be able to move from structural connectivity (what we have been able to model) towards functional connectivity, which would represent the ideal target of any connectivity analyses. The most important drawback in our model is not linked to the approach but to the data available. We were not able to obtain reliable point data on species presence, and we therefore used a resampling approach as it has been proposed in other modelling exercise (e.g., Alsos et al., 2012). However, in support of the reliability of our results, we repeated the sampling procedure of presence data-points for 100 times, obtaining a direct idea of the variance in our results linked to our modelling approach. All areas with the highest variance in probability of presence are outside of the core

areas (Fig. S2), while inside core areas the variance never exceeded a value of 0.05. Furthermore, even considering all inherent limitations of our analyses, the results of model evaluation were extremely good, although limited to an internal evaluation only with a repeated split-plot approach. Moreover, the core habitat areas that we identified correspond with the two areas where the species has been introduced and is now present with stable and independent population, providing therefore a further and independent confirmation of the reliability of our model. A last note of caution is granted considering the subjective threshold that we choose to distinguish between areas of potential presence and areas of potential absence. In fact not biological and/or ecological reason can justify the 10% threshold that we used. However, the threshold was set on purpose on a very conservative value, even excluding areas inside the known current presence. In this way it was possible to clearly identify only area with high potential suitability for the species presence.

Overall, our model outline that there is still a good level of habitat suitability for the mouflon inside the entire historical distribution range (Fig. 2), and the main core areas are all well connected, theoretically allowing for the establishment of active movements between different subpopulations (Fig. 3). Given the relatively lower level of anthropogenic impact on the landscape compared to the first half of the XXI century, our model provide a spatial explicit tool that can help management and conservation of the species in Sardinia. The potential expansion of the current distribution should be considered, facilitating the establishments of new subpopulation especially south of the Gennargentu massif. In particular, we would envision two main subpopulations corresponding to the Gennargentu massif, where the species is currently present, and to the Sarrabus-Gerrei areas, where the species could be reintroduced. All other core areas in between could be used as stepping stones to ensure connection among the two main nuclei.



Figure 4 - Structural connectivity for the mouflon in Sardinia.

An expansion of the population of muoflons also in other areas would potentially benefit also other species of conservation interest. This is the case particularly for the area between Oristano and Sassari, where the species accidentally escape in the 1990s and established a population. Although the core areas are only of marginal importance for the conservation of the mouflon, the presence of the species and an eventual increase in the number of animals would benefits species of high conservation interest such as vultures (Thibault et al., 1993) or the eagle (Seguin et al., 2001) for which the mouflon represent potentially an important source of food.

The regional wildlife management plan (Apollonio et al., 2011) also suggest as possible an introduction in the Monte Lattias, Monte Arcosu, and Monte Linas, and in the Sulcis-Iglesiente areas (south-west Sardinia). For both regions we identified existing core areas, but we do not consider these two regions as priorities for eventual reintroductions, as both areas host the endemic corsican red deer (*Cervus elaphus corsicanus*; Puddu et al., 2009). Given that there is no direct evidence to exclude the possible competition between the two species, and considering that the two areas are outside of the historical distribution range for the mouflon, we suggest avoiding any introduction of mouflon, at least not before a viable population is established in the main distributional area.

According to our model, the presence of free ranging domestic livestock is not an important factor in determining the distribution of the mouflon, which is driven mainly by human population, agriculture, and terrain roughness. However, the ongoing and progressive abandonment of mountain pastures by domestic animals (linked mainly to socioeconomic factors) can easily lead to an important growth in forests with a loss of open areas (Puddu et al., 2012), reducing de facto the areas suitable for the presence of the mouflon. At the same time, the presence of diseases such as the blue tongue which can be transmitted from domestic livestock to mouflon call for a cautionary approach. In this context, the presence of a totally isolated population on the island of Asinara represent an important backup in case of disease outbreaks.

From a conservation point of view, existing protected areas are basically marginal for the conservation of the species, with the only exception of the population on the Asinara island. The outlook is substantially improved if we consider also the public owned forests in which hunting is prohibited. However, these areas do not consider explicitly the conservation of the mouflon (or any other wildlife) in their management plans and can actually be detrimental for the mouflon by actively increasing the area covered by closed forests. A shift in their priorities would certainly favour the conservation of the species while avoiding any potential conflict with local stakeholders.

The proposed protected areas (Natura 2000 and proposed regional parks) would represent a tremendous addition for the conservation of the mouflon. Almost 75% of the core areas we identified would be totally covered by conservation areas, providing also a very good coverage for the most important connectivity corridors. However, a number of political and administrative problems are slowing the process (not only in Sardinia; Maiorano et al., 2015b), to the point that the true establishment of the entire system of areas is at the moment highly improbable (Puddu et al., 2009). In this context our integrated model can represent the proper input for a participatory management decision process, in which any of the different types of areas we identified can be considered explicitly. *[%*]

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Associate Editor: H. Rebelo

Supplemental information

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

- Table SI Thematic aggregation of the original land cover classes available in the regional land use database.
- Figure S2 Variance in probability of presence values obtained through the 1000 species distribution models.

Figure S3a Response curve for agriculture.

- Figure S3b Response curve (average for all models) for human population density.
- Figure S3c Response curve for terrain roughness index.