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Modelling the ecological niche of an endangered population of *Puma concolor*: First application of the GNESFA method to an elusive carnivore

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ABSTRACT

Throughout central Argentina the distribution of puma (*Puma concolor*) has substantially contracted and appears to be restricted to relatively pristine areas. We identified factors affecting puma habitat use at a landscape scale to produce a habitat suitability map in a grassland/scrubland ecoregion in central Argentina. Additionally, we examined the advantages of the general niche-environment system factor analysis (GNESFA) to determine the use of space of this carnivore. To determine the presence of the carnivore, we used the following methods of observation: (1) photographs via camera trapping surveys. (2) Semi-structured interviews of local people. (3) Direct observation by way of sightings of live animals. (4) Indirect sightings by way of tracks. (5) Opportunistically recordings of dead individuals. We used GNESFA to study the factors affecting the use of space by the puma considering environmental, biological, anthropogenic factors, and MADIFA (Mahalanobis distance factor analysis) to create a habitat suitability map. Most suitable locations for puma were away from cropland or urban areas and from roads. Distances to roads and to scrubland patches were the limiting variables that influenced the narrowness of the niche of this felid. Pumas in this region preferred an environment of patchy scrubland which is typically created by selective logging. They did not limit their environmental preferences to closed habitats. This paper reports the first analysis of the factors determining the distribution of pumas in a grassland/shrubland ecoregion in the southernmost part of its distribution. This suggests that pumas may use human-modified habitats and withstand some degree of deforestation and fragmentation. Our results confirm the usefulness of this integral approach to identify the factors affecting the ecological niche of a cryptic, highly-vagile species.

1. Introduction

Mammalian carnivores play an important role both in the natural dynamics and the conservation strategies of many ecosystems (Sergio et al., 2008) but also are threatened by habitat loss and fragmentation globally (Crooks et al., 2011). The puma (*Puma concolor*) is the top predator of most Latin American ecosystems. This felid, globally and nationally categorized as "Least Concern" (Caso et al., 2008; Ojeda et al., 2012), has an extensive distribution, spanning from Canada to the southern part of Latin America and is found in a wide range of habitats, from deserts to tropical forests (Nowell and Jackson, 1996). Historically, pumas occupied almost all the territory of Argentina including densely populated regions like the province of Buenos Aires (Cabrera and Yepes, 1940). However, with the development of agriculture and livestock activities, the distribution range of this species has suffered a severe contraction. Consequently, the puma is currently concentrated only in the southern part of this province, where its presence appears to be associated with relatively pristine habitats (De Lucca, 2010).

Similar to most large carnivores, pumas require large home ranges and viable puma populations are dependent on extensive

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areas of suitable habitat. Abundant prey populations, dense vegetation cover, and rugged terrain are typically present in the habitats preferred by this felid (Logan and Sweanor, 2001).

Puma populations are constantly threatened by human persecution (De Angelo et al., 2011) as well as habitat loss and fragmentation (Crooks, 2002). The alteration of natural habitats is a process common in those regions where agriculture and ranching are the prevalent activities (Baker et al., 2008; Saunders et al., 1991). This development creates highly altered landscapes where patches of natural habitats are separated by areas with high anthropogenic pressure and carnivore populations are increasingly isolated with fragmented distributions.

Such populations are expected to present decreased genetic and demographic variability (Santos and Tellería, 2006) leading to consequent declines in numbers. For this reason, habitat fragmentation is one of the principal causes of species extinction worldwide (Schipper et al., 2008; Wilcove and Chen, 1998), especially for mammalian carnivores (Riley et al., 2003).

The southern part of Buenos Aires Province is a highly altered area (Fernández and Busso, 1999) and has been identified as a potential fragmentation hotspot by a global analysis of fragmentation processes (Crooks et al., 2011). Nevertheless, this region has been recognized as an area of priority for wildlife conservation, because it still hosts most of the components of its original vertebrate communities (Morello et al., 2012). However, the joint effects of some years of severe droughts and changes in land use policies have led to an increase in livestock (especially sheep) production recently. Increased logging of natural scrubland and augmented sheep availability have exacerbated puma-livestock conflicts that caused an apparent intensification in puma retaliatory killing (Lucherini et al., 2008). This human persecution may have jeopardized the viability of the puma population within this region. In the context of these land-use changes and anthropogenic threats, it is fundamental to understand the patterns of distribution and habitat suitability of pumas at a landscape scale to understand how these processes could affect their population.

In recent decades, the combination of presence-only records and distribution models has been frequently used to study the occurrence and distribution range of species, an especially challenging objective for highly mobile and secretive populations (Guisan and Zimmermann, 2000; Papeş and Gaubert, 2007). However, the utility of predictive distribution models to provide a reliable representation of population distribution has been seriously questioned, especially in the case of species with few confirmed localities (Gil and Lobo, 2012; Shcheglovitova and Anderson, 2013). To address the limitations of these previous methodologies, Calenge and Basille (2008) proposed a novel general exploratory framework for the statistical study of the space of a given species (called general niche-environment system factor analysis, GNESFA) that is based on the multidimensional Hutchinsonian niche concept (Hutchinson, 1957). This analytical tool associates the species occurrence with different environmental factors and identifies the direction in the ecological space where the distribution of the species differs the most from the area available for that species (Calenge et al., 2008). One of the advantages of this approach is that it uses presence-only data avoiding the need for absence data which is very difficult to obtain and often inaccurate for elusive species, like the puma.

Despite its advantages, the framework proposed by Calenge and Basille (2008) is still poorly represented in the literature. No other articles, except the original, have used GNESFA to explore the factors affecting the use of the space. In fact, even after the publication of this work, several papers continued using the ecological niche factor analysis (ENFA, one of GNESFA's variants) not as an exploratory tool but to construct habitat suitability maps. (De Angelo et al., 2011; Galparsoro et al., 2009; Valle et al., 2011). This contradicts the recommendation that ENFA not be utilized for mapping (Calenge and Basille, 2008). Other authors have utilized only Mahalanobis distance factor analysis (MADIFA, another variant of GNESFA) to describe species distributions (Halstead et al., 2010; Hemery et al., 2011; Thiebot et al., 2011) and thus neglected to take full advantage of the benefits offered by the comparative approach described by Calenge and Basille (2008).

In this work, we identified biological and anthropogenic factors affecting puma habitat use at a landscape scale to produce the first habitat suitability map for the puma in the Argentine Espinal. This ecoregion is located in central Argentina and represents an ecotone between the Pampas grasslands and the Monte dry woodlands (Crooks et al., 2011; Fernández and Busso, 1999). Additionally, we examined the advantages of the novel approach proposed by Calenge and Basille (2008) to study the spatial ecology of this elusive and wide-ranging carnivore. Although the puma is a relatively adaptable species, at a regional scale it tends to show strong habitat associations (Dickson et al., 2013; Logan and Sweanor, 2001). Consequently, in the southern region of Espinal which has been highly altered by human activities (Fernández and Busso, 1999), we expected that the use of habitat by pumas would differ significantly from the available habitat. More specifically, pumas tend to prefer habitats that offer a certain degree of protection, typically because of their high vegetation cover (Dickson and Beier, 2002; Foster et al., 2010). We predicted that the ecological niche of pumas in the Espinal would be positively associated to the proportion of and/or distance to scrubland, because it provides effective cover and represents one of the most dense vegetation types in this region. In contrast, a negative correlation was predicted for open cropland. Finally, based on the previous studies which suggests this felid avoids human dominated areas (Burdett et al., 2010; Dickson and Beier, 2002), we expected that puma presence would be negatively associated with proximity to road and urban areas.

2. Materials and methods

2.1. Study area

Fieldwork was conducted in an area of 27,300 km^2 located in the southernmost part of Buenos Aires province in central Argentina and corresponding to Villarino and Patagones counties (Fig. 1). The study area belongs to the ecoregion known as Argentine Espinal and is characterized by a template, semiarid climate, where aridity increases toward the west and the south (Busso, 1997; Fernández et al., 2009; Fernández and Busso, 1999). The mean annual temperature is 15.3 °C. The annual precipitation varies from 350 to 550 mm and concentrates in spring and autumn. The topography is mostly flat and the natural vegetation is characterized by xerophytic deciduous woodland, prairies dominated by grassland, and prairies intermixed with extensive scrubland (henceforward, grassland with scrub). This region has experienced a marked transformation during the last decades due to the increase of agriculture and ranching activities, which are the most important regional sources of income (Fernández and Busso, 1999). From 1975 to 2002 logging decreased the percentage of woodland areas from 65% to 37% and this trend continues (Pezzola et al., 2004). This habitat alteration and fragmentation process has converted the original landscape into a mosaic of cropland and pastures with residual patches of original vegetation (Fig. 1).

2.2. Data collection and analysis

We used present data obtained from April 2008 to October 2013 from three sources of information. First, a systematic camera

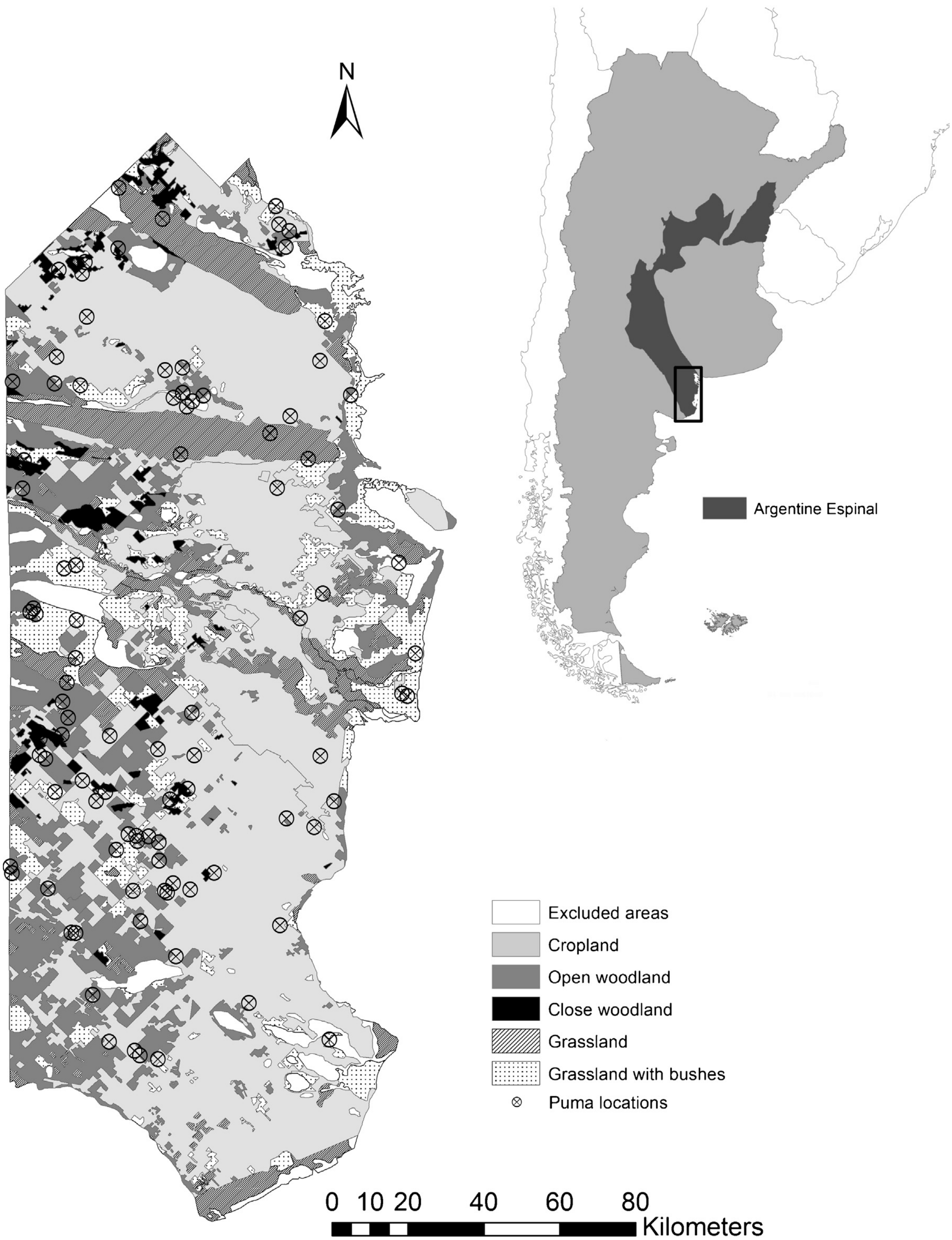

Fig. 1. Location of the study area in Argentina and with respect to the distribution of the Espinal ecoregion (small map). Habitat composition of the study area and the puma location records (large map).

trapping survey was conducted between January and May in 2011, 2012, and 2013 (Supplementary Fig. 1). We defined as puma "presence" each camera station with at least one photo of the species. To randomize the spatial arrangement of the sampling station and thus to survey a representative sample, we used a geographic information system (GIS) layer of the entire study area to create 100 random points with a distance among them of at least 6 km. Then we deployed cameras in 49 of those points and adjusted the survey design to the number of cameras available. Each survey lasted 35 days and all cameras were operational 24 h per day. Sampling effort was calculated as the product of the total number of stations by the number of effective days of sampling and totaled 7054 camera trap days. Second, semi-structured interviews to local ranchers were conducted from 2008 to 2013. The protocol specifically targeted the most knowledgeable persons about wildlife in the area, i.e., farmers and ranchers. Interviews were distributed across the whole study area and stratified by habitat. To avoid data auto-correlation we selected interview sites located at a minimum distance of 5 km from one another. The interview aimed at collecting a range of data; however, for the scope of this work, we used exclusively the information on the presence of puma. To be conservative and not overestimate puma occurrence, "presence" corresponded to all those interviews in which the answer to the question "How common is the puma in your farm?" was "common" (possible answers: "common", "rare" and "very rare"). Third, we used direct (sightings and dead individuals) and indirect (tracks) signs of puma presence that were opportunistically documented and recorded while traveling extensively across the study area to reach the interview and camera trap sites.

We characterized the study area using eight variables related to human perturbation and landscape composition (Table 1). For this purpose we used a land use vector map provided by the Argentina National Institute for Agriculture and Ranching Technologies (INTA) that identifies, through supervised classification, seven mutually exclusive land use categories (waterbodies, cropland, closed woodland, open woodland, urban areas, grassland, grassland with scrub and salty marshland). Since computational analysis required numerical variables, we converted the categorical (i.e., habitat) variables into a raster map with a final pixel size of 450 m^2. Because the perception of the landscape by carnivores is often related to the size of their home range (Kanagaraj et al., 2011; Naves et al., 2003), we used a radius of 4.5 km to draw a circle around each location point and calculated the proportion of each habitat category through the neighborhood analysis of ArcGIS 10.1®. This is the radius needed to create a circle equal to the size of the mean home range estimate for puma (65 km^2; Franklin et al., 1999).

The basic principle of GNESFA analysis consists of the choice of one of two distributions, the utilization units (in our case, the cloud of pixels with presence of puma) as the "Focus Distribution", or the environmental units (the set of pixels on which each environmental variable was measured) as the "Reference Distribution". The cloud of points is then "distorted" so that the reference distribution takes a standard spherical shape in the multidimensional space. Then the GNESFA searches for the direction where the focus distribution shows the greatest difference from this standard spherical shape. The analysis has properties that depend on the distribution chosen as a reference and uses two important concepts to describe the niche of the species: marginality and specialization. The marginality is a measure of the eccentricity of the niche relative to the distribution of available points in the ecological space (a large marginality means that the species lives in a very particular habitat), whereas the specialization is a measure of the niche restriction relative to the distribution of available points (the more specialized is the specie, the less tolerance to the variation of a particular condition it is expected to show). When the main interest of the analysis is related to the identification of the variables affecting the shape (unimodal vs. multimodal niches) and of the marginality and specialization of the species, the availability should be chosen as the reference and the utilization distribution as the focus. This is the case of the factor analysis of the niche taking the environment as the reference (FANTER), which can thus be considered a special case of GNESFA. However, sometimes we are mainly interested in whether the species "considers" the proposed environment as suitable (within the niche) or not (far from the niche). In those cases the utilization distribution should be chosen as the reference and the suitability of the available pixels can be measured by the distance between them and the utilization distribution as a whole (Clark et al., 1993). The distribution of used pixel will then take a standard shape, and the GNESFA will indicate the direction of the ecological space in which the available space differs the most from this distribution. This is the approach used by the MADIFA. Another consideration is possible, for which each of the two distributions are both the reference and the focus distribution. This symmetrical point of view has the advantage of avoiding the need of choosing one distribution as the reference. This special case is the basis of the ENFA. The first factor extracted by ENFA gives the marginality coefficient, which ranges from −1 to +1 and indicates the rarity of the conditions selected by the study animals within the study area.

The fact that this approach allows researchers to have three different points of view creates a theoretical framework to analyze different aspects of the ecology of a species that otherwise would involve the use of several techniques.

Three main steps are involved in GNESFA analyses. First, it centers the matrix of environmental units choosing the centroid of the reference distribution (i.e., availability or utilization depending on the chosen approach). This is the 'point of zero information' and anything that is at this point is trivial and uninformative, whereas anything that deviates from it is relevant. The second step of GNESFA consists of a principal component analysis (PCA) of the data, which implies a rotation of the cloud of points so that: (i) the reference variance of the environmental units on the first component is maximized, and (ii) the correlation between the coordinates of the environmental units on different components are equal to 0 (Legendre and Legendre, 1998). The last step of the GNESFA is the analysis of the focus distribution in the distorted ecological space created in the previous step by performing a non-centered PCA. The cloud of points selected as the focus distribution should be spherical only if it is identical to the reference distribution. In other words, all the eigenvalues of this PCA should be equal, which would indicate that: (i) the centroid of the focus distribution is the same as the centroid of the availability distribution and (ii) the variance of the focus distribution is the same in all the directions of the ecological space.

Finally, factorial maps of the niche in the ecological space can be obtained by plotting the coordinates of the environmental units on a restricted number of principal components. The biological meaning of the principal components can be derived from the strength and direction of the correlation between them and

Table 1
Description of the environmental variables used in the GNESFA analysis for pumas in the Argentine Espinal (Argentina).

Name	Description
Distance to urban areas (DU)	Straight line distance to the closest urban area
Distance to scrubland (DB)	Straight line distance to the closest pixel corresponding to the scrubland class
Distance to cropland (DC)	Straight line distance to the closest pixel corresponding to the cropland class
Distance to road (DR)	Straight line distance to the closest road
Distance to water (WD)	Straight line distance to the closest pixel corresponding to the water body class
Proportion of grassland with scrubland (PGB)	Frequency of pixels occupied by the grassland with scrub class in a circle with a radius of 4.5 km centered in the location point
Proportion of grassland (PG)	Frequency of pixels occupied by the class grassland in a circle with a radius of 4.5 km centered in the location point
Proportion of scrubland (PB)	Frequency of pixels occupied by the class scrubland in a circle with a radius of 4.5 km centered in the location point

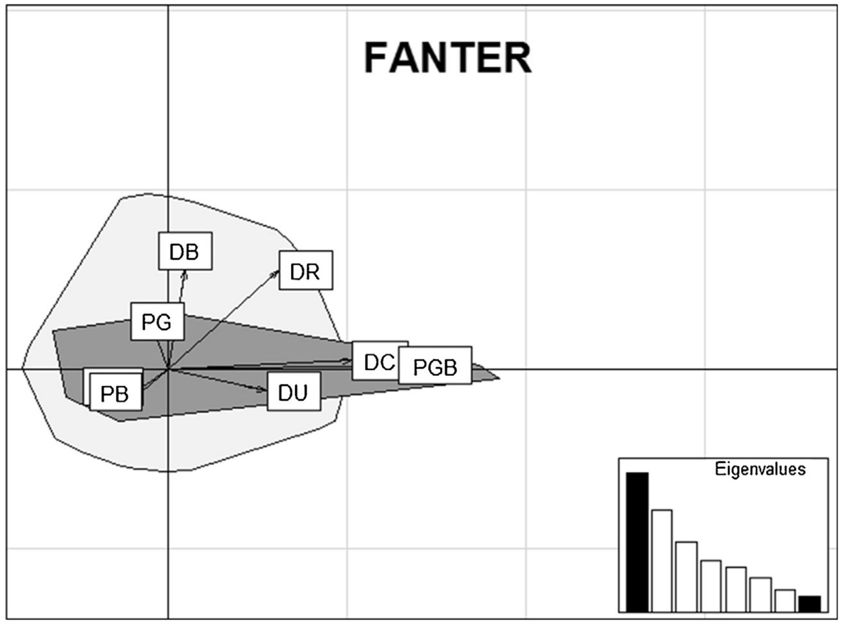

Fig. 2. Biplot of the factor analysis of the niche taking the environment as the reference (FANTER) for pumas in the Argentine Espinal. The horizontal axis represents the first component taken, the vertical axis the last component taken and the bottom panel is a barplot of eigenvalues of the axes. DU, distance to urban areas; DB, distance to scrubland; DC, distance to cropland; DR, distance to road; WD, distance to water; PGB, proportion of grassland with scrubland; PG, proportion of grassland; PB, proportion of scrubland.

the environmental variables used in the analysis. To choose the number of components to keep for the interpretation, we can look for a break in the decrease of the eigenvalues (broken-stick method; Barton and David, 1956; Frontier, 1976).

2.3. Habitat suitability map

In addition, we constructed a habitat suitability map to predict areas favorable for the puma occurrence. We used MADIFA because it takes into account the environmental availability on the area where the niche was sampled and consequently may provide better predictive accuracy (Tsoar et al., 2007). This method is also convenient since it is easily available and implemented, runs on a free software, and more importantly has been recommended instead of the commonly used ENFA due to the mathematical proprieties of its components (marginality and specialization) (Calenge and Basille, 2008). We used 20% quantiles to break the range of values into five classes that we assumed correlated with increasing quality of habitats for puma (Johnson and Gillingham, 2005).

For each of the analysis we evaluated the significance of each of the axes chosen using a Monte Carlo procedure with 500 randomizations and we took as significant all p values lower than 5%. All statistical analyses were implemented R version 3.0.1 (R Development Core Team, 2013) using the packages adehabitatHS and adehabitatMA from R language (Calenge, 2006).

3. Results

We collected a total of 110 points of presence. 66 localities were from the interview process which represented 41.3% of the total interviews conducted. 21 locations were obtained by remote camera stations (8.4% of all the installed camera trap stations; Supplementary Fig. 1), and 16 positions were records of dead pumas. Lastly, 7 localities contain signs (tracks) of puma presence.

The eigenvalue diagram of the FANTER showed a clear, significant pattern for the first axis (eigenvalue = 2.79, $P < 0.03$), but not for the last one. The first component was mainly correlated with PGB (R = 86%) and DC (R = 69%). The factorial map of the niche (Fig. 2) showed the marginal position of the niche in relation to the first axis: pumas were located in sites with a higher than expected proportion of grassland with scrub (20% of the localizations were located in sites with more than 40% of proportion of grassland with scrub, while this class represented only the 7.9% of the study area) and located near cropland more rarely than expected (only the 32.7% of the location points where in sites less than 60 m away from cropland, while this class corresponded to the 45% of the study area).

The randomization test for the first eigenvalue of ENFA indicated a significant specialization on at least one component ($S_1 = 2.90$, $P < 0.02$). The marginality was also significant ($m^2 = 0.81$, $P < 0.002$). As expected and confirming the results of the first axis of FANTER, there was a correlation between the marginality component of the ENFA and the first component of the FANTER (R = 63%). Because the first component explained only 31.3% of the total specialization, we decided to include the second component, thus collectively explaining 54.2% of the specialization in the resulting interpretation. The biplot of the ENFA formed by the marginality axis and the first specialization axis showed that PGB is the main variable contributing to the marginality of the species, and to a lesser extent, DU, DR, and DC (Fig. 3a). The analysis of the correlations between variables and each component showed that DR was the variable that contributed the most to the first specialization axis. In addition, DB was the principal variable that explained the second axis of specialization (Fig. 3b). As a consequence, pumas seemed to be little tolerant to large variations in the distance to roads and the distance to scrubland (i.e., puma niche was restricted on a limited range for these variables), with a mean shift toward large distance to road and small distance to scrubland.

The tests of the first and the second axis of MADIFA were significant (eigenvalue$_1$ = 3.491, $P_1 = 0.029$; eigenvalue$_2$ = 2.312, $P_2 = 0.017$). The eigenvalue barplot indicated a break after the second eigenvalue (Fig. 4). Therefore, we focused our interpretation on the first two axes. The first component of the MADIFA was correlated with the first specialization component of the ENFA (R = 89%) and with the last component of the FANTER (R = 98%).

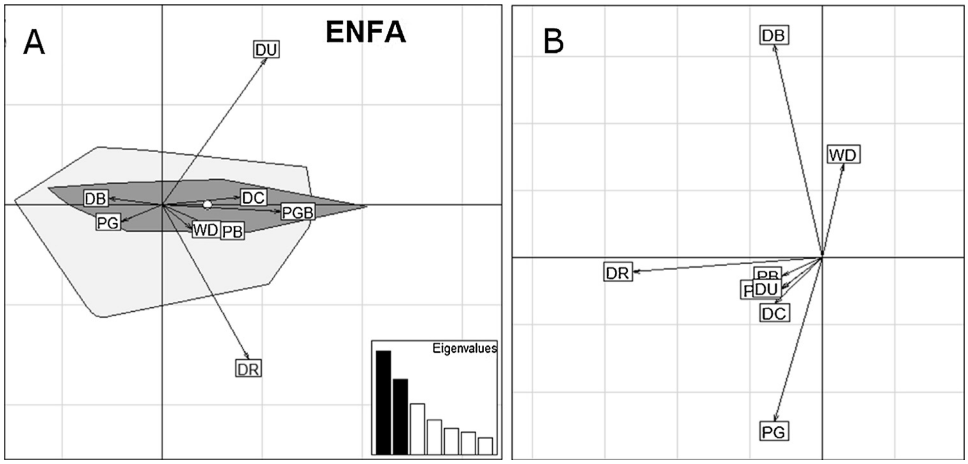

Fig. 3. (A) Biplot of the ecological niche factor (ENFA) for pumas in the Argentine Espinal. The horizontal axis represents the marginality component, the vertical axis the first specialization component and the bottom panel is a barplot of eigenvalues of the axes. (B) Correlations between the environmental variables and the first specialization (abscissa) and the second specialization (ordinate) component. DU, distance to urban areas; DB, distance to scrubland; DC, distance to cropland; DR, distance to road; WD, distance to water; PGB, proportion of grassland with scrubland; PG, proportion of grassland; PB, proportion of scrubland.

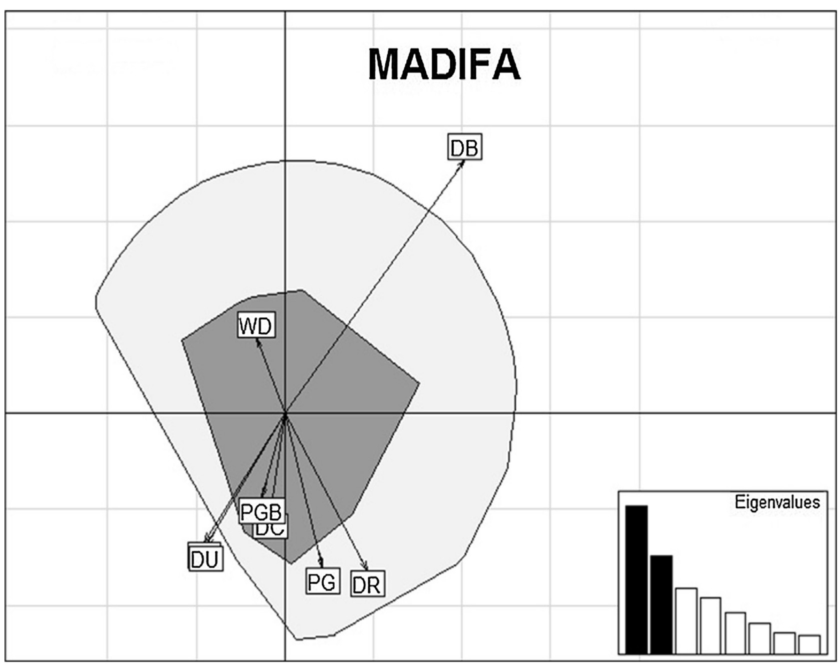

Fig. 4. Biplot of the Mahalanobis distance factor analysis (MADIFA) for pumas in the Argentine Espinal. The horizontal axis represents the first component taken, the vertical axis the second component taken and the bottom panel is a barplot of eigenvalues of the axes. DU, distance to urban areas; DB, distance to scrubland; DC, distance to cropland; DR, distance to road; WD, distance to water; PGB, proportion of grassland with scrubland; PG, proportion of grassland; PB, proportion of scrubland.

The second component of the MADIFA was strongly correlated with the second specialization axis of ENFA ($R = 87\%$), and although to a lesser extent was also correlated to the first specialization component and the marginality component of ENFA ($R_1 = 41\%$ and $R_2 = 43\%$) (Table 2). The DB was the main variable affecting the position of the availability niche in relation to the used niche for both the first and the second component. To a lesser extent, DC and PB contributed to the first component and PG to the second one.

The habitat suitability map was computed by using the first two axes of the MADIFA because they accounted for a large part of the variance (Fig. 5). The map shows that only 16.3% of the area was classified as "Highly Suitable", while the categories "Unsuitable" and "Moderately Unsuitable" collectively represented 37.5% of the total area.

4. Discussion

This paper reports the first analysis of the factors determining the distribution of the puma in the southernmost part of the

Table 2
Results of the GNESFA analysis for pumas in the Argentine Espinal. γf_1, first axis extracted by FANTER; γf_8, last axis extracted by FANTER; m^2, first axis extracted by ENFA corresponding to the marginality; S_1 and S_2, first and second specialization axes from ENFA; γm_1 and γm_2, first and second axes of MADIFA. *P*, result of the randomization test performed with 500 randomizations. Level of significance: 5%.

Analysis	Axes		
FANTER	$\gamma f_1 = 2.79$; $P = 0.029$	$\gamma f_8 = 0.31$; $P = 0.952$	–
ENFA	$m^2 = 0.81$; $P = 0.002$	$S_1 = 2.90$; $P = 0.026$	$S_2 = 2.12$; $P = 0.015$
MADIFA	$\gamma m_1 = 3.49$; $P = 0.019$	$\gamma m_2 = 2.31$; $P = 0.031$	–

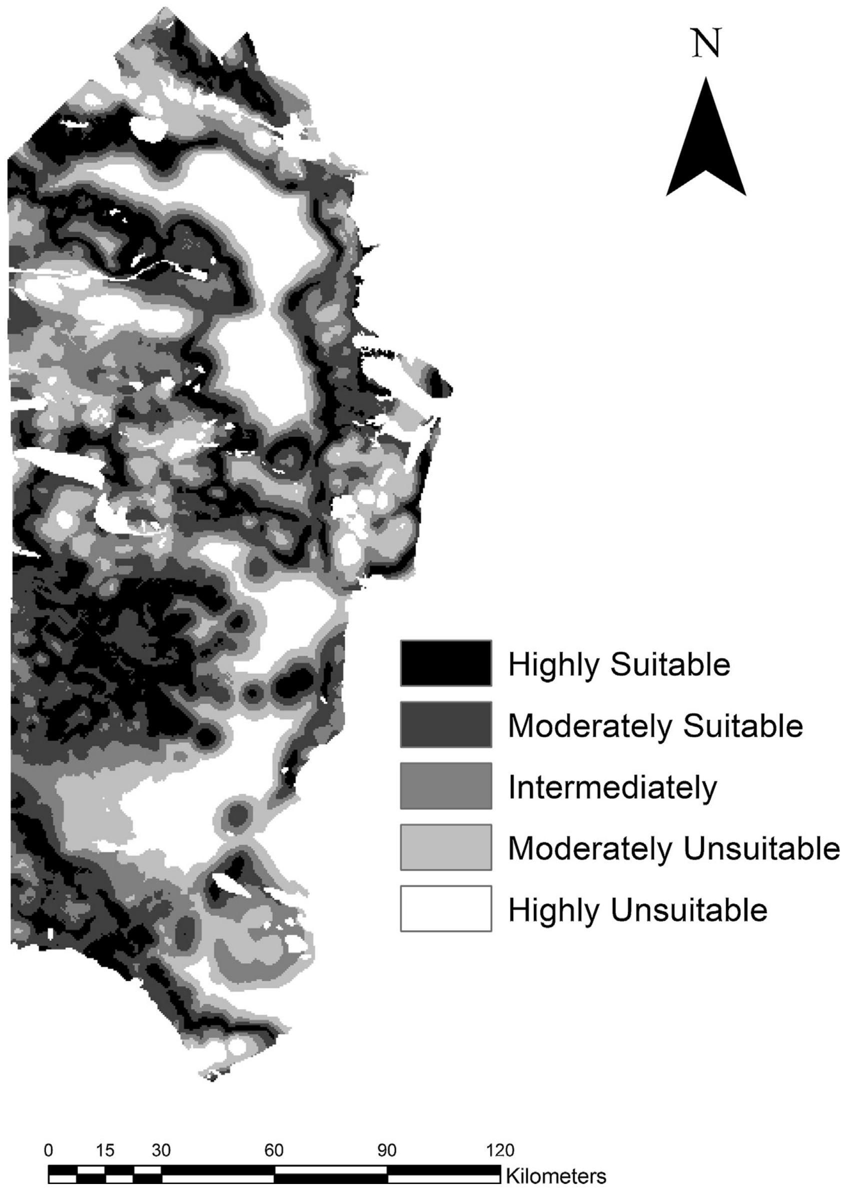

Fig. 5. Habitat suitability map for the puma in the Espinal of Argentina computed using the first two components of the MADIFA. We break the range of values into 5 categories using the 20% quantiles.

Espinal of south-central Argentina. Although they are based on a relatively small sample size, our results consistently show that the major environmental variables affecting this species' ecological niche (i.e., its marginality) were the proportion of grassland with scrub, distance to cropland, distance to urban areas, and distance to roads. Given the hunting pressure on pumas occurring in our study area, avoiding areas with relatively high anthropogenic activity is a strategy to reduce the likelihood of being hunted. Thus, as expected, the most suitable locations for the species were away from crops, urban areas, and roads. Additionally, distances to roads and to scrubland patches were the main variables that determined the narrowness (i.e., specialization component) of the niche of this felid, indicating that the puma would tolerate low levels of variation of those variables.

However, pumas in this region did not show the expected preference for closed habitats but rather for the relatively open grassland with some relict scrub. It cannot be ruled out that the fact that most of the occurrence locations we collected came from rancher interviews may have potentially introduced a certain bias toward puma use of grassland with scrubs. However, the habitat stratification we used as sampling design and the observation that cattle is not concentrated in grassland with scrub in our study area but rather distributed through different habitats (including cropland, closed woodland, open woodland, grassland, and grassland with scrub) suggests that this bias should not be strong. Grassland with scrubs are typically created by selective logging of the natural scrubland, thus confirming that pumas can make use of human-modified habitats (Burdett et al., 2010) and withstand some degree of deforestation and fragmentation (De Angelo et al., 2011). Because in our study this habitat type is usually found in proximity of scrubland and mostly used for extensive livestock ranching, we speculate that puma use of grassland with scrub represents a trade-off between the need for some degree of protective cover (as suggested for Southern Californian pumas by Dickson et al. (2005) and good prey availability including vizcachas (*Lagostomus maximus*), European hares (*Lepus europaeus*), Patagonian maras (*Dolichotis patagonum*), American rheas (*Rhea americana*), and domestic sheep, which appeared to be comparatively more abundant in open areas (N. Caruso unpubl. data). It is also possible that landscape-scale preference for a human-modified habitat recorded in this region is adjusted through a fine-scale habitat selection by individual pumas (Burdett et al., 2010) promoting accessibility to shelter.

This is one of the first studies reporting the use of pumas of relatively open grassland/scrubland habitats. Similar habitat types might have been used by the puma populations occurring in the central parts of the North America and the Southern Cone of South America previous to their development by European settlers (Walker and Novaro, 2010). Little is known about the current habitat use of this species for Latin America. Pumas in the Venezuelan Llanos seem to select open dry pastures more than expected, but they were mostly found within 0–500 m of the edges of forest patches larger than 300 m (Scognamillo et al., 2003). In the Chilean Patagonia the use of grassland by pumas appeared to be limited to hunting (Elbroch and Wittmer, 2012). These results show a certain agreement with ours and strengthen our hypothesis of the trade-off between good prey availability and protective cover.

The GNESFA indicated that the species habitat niche differed considerably from the mean environmental conditions found across the study area (showed by both ENFA-marginality: 0.80 and FANTER). Additionally, pumas in this region were restrictive in the selection of the range of conditions in which they inhabit. Because pumas are affected by habitat loss, fragmentation, and hunting pressure (De Angelo et al., 2011; Laundré et al., 2009; Newby et al., 2013), this result is consistent with our prediction based on the observations that local puma populations have to withstand a high degree of habitat modification and the strong persecution by ranchers (Lucherini et al., 2008).

To our knowledge, this is the first paper using the technique proposed by Calenge and Basille (2008) and our results confirmed the usefulness of this comprehensive approach to identify the factors affecting the ecological niche of a cryptic, highly vagile species. Conservation planning and wildlife management increasingly rely on models of habitat association derived from regional surveys of species occurrence to improve understanding of a species' ecology (Carroll et al., 2010). The marginality metric captures the rarity of the conditions selected by the focal species with respect to those available in the study area and the specialization concept measures how tolerant a species is to modification in a given set of environmental variables. Thus, these metrics are relevant to managers because they enable the identification of the key habitats or factors limiting the distribution of a species in a given area. Although these metrics are not unique to GNESFA, in agreement with Calenge and Basille (2008), we found GNESFA an effective tool to analyze presence-only data that are the most frequent source of spatial information available for elusive species and obtain sound results. Because GNESFA is by its very nature exploratory, it does not rely on many constraining hypothesis (e.g., no minimum sample size required) and also allows researchers to use different sources of data in the analysis, contrary to other presence-only study methods which require fulfilling several limiting assumptions (Calenge and Basille, 2008). These characteristics make the GNESFA particularly attractive for wildlife researchers, especially those working with elusive species who usually manage scarce and multi-source data bases. GNESFA has the additional advantage of encompassing three consistent factor analyses (FANTER, MADIFA, and ENFA) allowing researchers to explore, from different points of view, diverse aspects of the niche-environmental system and to investigate them even when unusual situations exist (which is the case of FANTER that allows to study non-unimodal niches). Regarding this aspect, we agree with Calenge and Basille (2008) who mentioned the possibility of concurrently using more than one method with graphical displays of the niche within its environment as the most interesting aspect of the GNESFA. Particularly, we observed an extensive internal coherence in the results produced for our data by the different components of this analysis. This is demonstrated by the high levels of correlation between the first axis of FANTER and the marginality component of ENFA as well as between the first component of MADIFA, the first specialization axis of ENFA, and the last component of FANTER. Finally, the second component of MADIFA was also correlated with the second specialization component and with the marginality component of ENFA, suggesting that MADIFA captured mostly the specialization and a small proportion of the marginality in its analysis.

Most of the information available on pumas refers to Central and North America, whereas little is known about its natural history and conservation in the southernmost part of its distribution range. In Argentina the livestock industry is very widespread and has a relevant role in the country's economy. Thus, for the conservation of puma populations the comprehension of its ecological requirements in ranchlands is essential. To understand the habitat types that pumas successfully use and which land cover features represent a danger or adversely affect their survivorship, it is fundamental for the managers to develop conservation measures. The status of puma populations in Buenos Aires province has declined over recent decades due to the increase of hunting and the lack of protected areas. Our habitat suitability map shows that the most unsuitable areas corresponded to those of greater anthropic development (i.e., the areas in proximity of roads crossing the region). It also indicates that areas with high habitat suitability for pumas were scarce (16.3% of the whole study area, corresponding to ca. 3860 km^2), very fragmented, and tended to match the parts of the region that have been modified by human activities in the recent years. The fact that these high quality areas are fragmented suggests that the matrix of moderately suitable or neutral areas in which they are immersed is of great conservation relevance.

Metapopulation dynamics caused by differential habitat quality have been reported for pumas in different parts of its distribution range (Andreasen et al., 2012; McRae et al., 2005). Given the important effect of grassland with scrub on puma occurrence in the Espinal of central Argentina, future research should aim to identify the habitat specific mortality rates in order to evaluate if source-sink population dynamics are playing an important role in the regional conservation of the species. Based on our results pumas could survive in the areas where the natural woodlands have been selectively logged to create more pastures for livestock provided the local ranchers are ready to tolerate the presence of this potential predator.

We conclude that our results suggest that successful puma conservation in the southern Espinal of Argentina will hinge on land management practices that conserve the integrity of critical habitat patches. Moreover, it will also require the permeability of puma dispersal through areas with low habitat quality to enable the maintenance of genetic flow throughout this region.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2014.11.004.

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