BIODIVERSITY RESEARCH

Prospects for population expansion of the exotic aoudad (*Ammotragus lervia*; Bovidae) in the Iberian Peninsula: clues from habitat suitability modelling

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ABSTRACT

We studied the geographical distribution and habitat suitability of an introduced ungulate, the aoudad (*Ammotragus lervia*), that is currently expanding its range in south-eastern Iberian Peninsula. We assessed the niche of the species using Ecological Niche Factor Analysis (ENFA) on (1) environmental variables (climate and habitat type), and (2) potential aoudad landscape avoidance and human disturbance variables. We compared both niche descriptions to study the impact of human interference on niche selection of the species. ENFA models were calibrated using data on the population expanded from the original release location, in Sierra Espuña mountains, and validated using data from another free-ranging population, originated independently in the Alicante province. The habitat suitability model for the purely environmental niche predicts a potential distribution along a SW–NE axis in the study area, following the Cordillera Sub-Bética mountain range, being constrained by low winter precipitation, high altitude, high terrain slope, and the presence of forest. In addition to these ecological traits, roads and landscape use restricted the environmental range potentially available for the species. Since the aoudad is a potential competitor of native ungulates and a threat to endemic flora, prospects for its potential dispersion might be of great conservation value.

Keywords

Biological invasions, ENFA, exotic ungulates, habitat suitability modelling, Iberian Peninsula, realized niche.

INTRODUCTION

Both passive and active human actions have facilitated the transportation of species outside their original distribution range and habitats. Introduction of exotic species has become a serious issue in conservation ecology, resulting in the birth of a new discipline, the study of biological invasions (e.g. Hengeveld, 1989; Lodge, 1993; Ruesink *et al.*, 1995; Mooney & Hobbs, 2000; Sax *et al.*, 2005). It has been generally assumed that invasive alien species pose one of the greatest threats to biodiversity (Diamond, 1989; Wilcove *et al.*, 1998; but see also Sax & Brown, 2000; Brown & Sax, 2004; Gurevitch & Padilla, 2004; Didham *et al.*, 2005; Borges *et al.*, 2006). In this context, the interest in game species has played a major role in spreading many exotic mammals (e.g. Crosby, 1986; Macdonald *et al.*, 1988; Jaksic *et al.*, 2002; Richardson *et al.*, 2003). These introductions were often carried out without regard for their effects on the environment, for example, threats to native species and endemic flora (e.g. Mack & D'Antonio, 1998).

The aoudad, *Ammotragus lervia* Pallas 1777, is a North African caprid successfully introduced as a game species in mountainous desert regions of Texas, New Mexico, and California in USA (Ogren, 1965), and southern Spain (Cassinello, 2000). The aoudad has shown a formidable capacity to establish, spread, and extend its distribution (Gray, 1985; Cassinello *et al.*, 2004), characteristics typical of biological invasions (Williamson, 1996). During the phase of establishment of an invasive species, a series of factors that determine success operate in a stochastic manner primarily on mortality and sex ratios. Spread occurs when an established population grows in size and increases in distribution, thereby escaping stochastic extinction effects (Soulé, 1987).

Very few individuals are required for introduced ungulate populations to become established (Forsyth & Duncan, 2001). The aoudad, which is native to the Saharan Desert mountains where resources are scarce and sparsely distributed, encountered richer habitats where it was introduced in USA and Spain. Increased food availability, along with a scarcity of competitors

and predators, allowed high birth rates, and a swift spread of the population (see Wolf *et al.*, 1996). Following Colautti & MacIsaac's (2004) terminology, in this region the aoudad is in the process of changing from Stage III (localized and not dominant) to Stage IVa (widespread but not dominant). Here we analyse several environmental and anthropogenic factors (both human-ized landscape configuration and human degree or disturbance) that might be influencing the spread of the introduced aoudad population in south-eastern Spain. This knowledge may help to establish management procedures to prevent further range expansion, and reduce the potential negative effects of the aoudad on native fauna and flora.

The relationship between environmental variation (tempera-ture, precipitation, humidity) and the survival of a species can be used to model its potential response to environmental gradients (Austin *et al.*, 1990). These descriptions can be used to produce predictive maps of species distribution (see reviews at Guisan & Zimmermann, 2000; Ferrier *et al.*, 2002; Scott *et al.*, 2002; Guisan & Thuiller, 2005), as well as to describe the characteristics of the niche of the species (see, e.g. Peterson *et al.*, 1999; Robertson *et al.*, 2001; Soberón & Peterson, 2005; Araújo & Guisan, in press). In conjunction with the use of modern statistics, predictive models have become powerful tools to address relationships between species and their environment, being increasingly common in ecological literature. They gained importance as a research tool on conservation issues (see Araújo & Guisan, 2006; Guisan *et al.*, 2006), especially to assess the effect of climatic change on the distribution of organisms (e.g. Thuiller *et al.*, 2006), to study species niche (Guisan & Zimmermann, 2000) and the spatial patterns of biodiversity (e.g. Hortal *et al.*, 2004). A variety of methods have been used to analyse the ecological niche of the species from data on their presence (see Guisan & Zimmermann, 2000; Soberón & Peterson, 2005). Among others, there are methods based on presence-only data, such as BIOCLIM (Hortal *et al.*, 2005); methods that can handle with presence-only data, among others, such as Ecological Niche Factor Analysis (ENFA), GARP (e.g. Anderson *et al.*, 2002), or MAXENT (see, e.g. Guisan *et al.*, 2006); and methods based on both presence and absence (or pseudoabsence) data, such as GLM (Lobo *et al.*, 2006) (see a review of the performance of a number of methods at Elith *et al.*, 2006). In addition to these methods, others try to develop resource selection methods from data on the abundance of the species (e.g. Olivier & Wotherpoon, 2005; Boyce, 2006; Meyer & Thuiller, 2006).

The adaptation of niche theory to species distribution modelling is currently under debate (Soberón & Peterson, 2005; Araújo & Guisan in press). Since, current terminology is rather ambiguous, and therefore could be misleading for the develop-ment of a general framework (Araújo & Guisan in press), a clear definition of the niche concepts used is needed when studying the geographical response of a species. To clarify the two different expressions of the geographical response of the aoudad, we use two different definitions of aoudad's geographical response based on Soberón & Peterson's (2005) and Araújo & Guisan's (2006) recent works: *Environmental Niche* (similar to Soberón & Peterson's *Fundamental Niche*), which is merely the response of

the species to abiotic factors, and *Observed Niche* (following Araújo & Guisan in press), which includes its interactions with the biotic part of the studied systems, in our case landscape configuration and human disturbance. In fact, following Araújo & Guisan (2006), the Environmental Niche could be better described as the Observed Environmental Niche, but we have preferred the term Environmental Niche throughout the text for the sake of clarity.

The Ecological Niche Factor Analysis (ENFA; Hirzel, 2001; Hirzel *et al.*, 2001, 2002) provides a good tool to describe the geo-graphical expression of the niche of a species. This ordination technique identifies the main gradients that a species responds to in an area. ENFA uses presence-only, presence/absence, or abun-dance data to compute a number of orthogonal factors from sev-eral predictors. Since these factors are built to maximize the discrimination between the areas where the species is present, compared to the rest of the region, they might be seen as the most important gradients the species is responding to in the study area (Hirzel *et al.*, 2002; see also Chefaoui *et al.*, 2005). It is then assumed that the response of a species along the principal axes constitutes a description of its observed niche (i.e. the spatial expression of its niche with regard to habitat conditions included within the predictors). ENFA methodology has been successfully used to model the environmental response of other caprids in their native range (*Capra ibex*, Hirzel, 2001; *Capra pyrenaica*, Acevedo *et al.*, 2006) as well as of reintroduced populations (e.g. *Gypaetus barbatus* in Switzerland, Hirzel *et al.*, 2004a). Note that several other approaches are available to build spatial predictions from presence only data (Hortal *et al.*, 2005; see a comparison in Elith *et al.*, 2006).

We used ENFA, as well as the derived niche description method proposed by Chefaoui *et al.* (2005; see also Hortal *et al.*, 2005), to (1) model the potential distribution of the introduced aoudad in the south-eastern Iberian Peninsula; (2) study the environmental determinants underlying the aoudad's spatial response (i.e. its environmental niche); and (3) evaluate the effect of landscape structure and human disturbance on such response (i.e. its observed niche).

METHODS

The study area

To properly define the geographical niche of a species within a given region, the area used to investigate the species' relationship with environmental variables should encompass extreme condi-tions present in the region. Thus, to carry out ENFA analyses, we chose a study area that contains both the aoudad population nuclei and the coastal and mountain environments present in SE Iberian Peninsula. The study area was 340 km wide and 270 km long, and 61,961 km^2 corresponded to dry land (UTM 29N geo-graphical reference system; NW corner: 450,000, 4,330,000; SE corner: 790,000; 4,060,000; Fig. 1), including the Sierra Nevada mountain range in the SW (rising over 3400 m a.s.l.), Segura coastal basin in the east (with mean altitudes below 20 m a.s.l.), as well as several other mountain ranges and high-altitude plains.
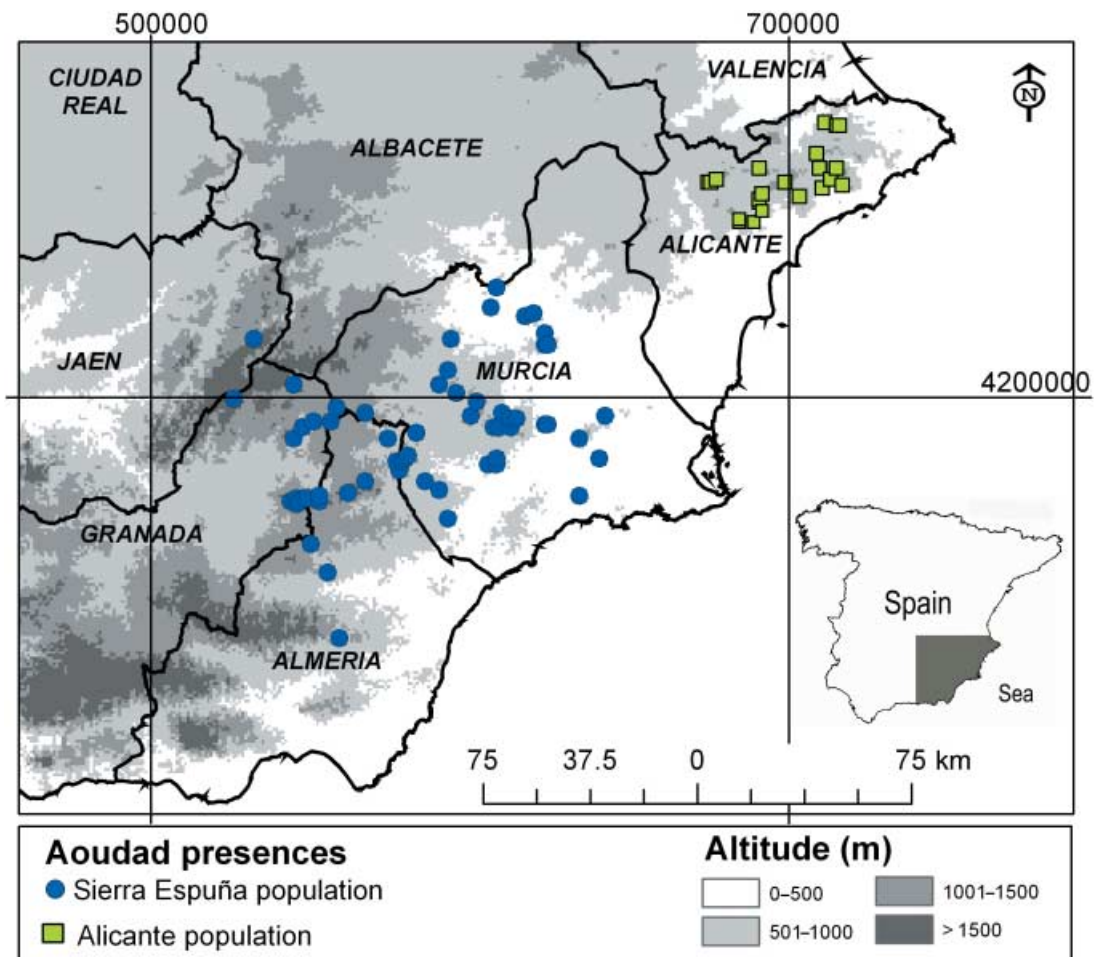
Figure 1 Location of the study area in south-eastern Spain. Province boundaries are shown. The records of the aoudad presence are depicted. The southernmost group (circles) corresponds to the dispersion of the Sierra Espuña nucleus, whereas the eastern ones (squares) are the nuclei in the Alicante province. The geographical coordinate system shown is the UTM.

The study area comprised a number of sub-areas defined by the vegetation succession series present, which identify plant communities and soil composition (Rivas-Martínez, 1987). Mediterranean bushlands, oak trees (*Quercus* spp.), and reforestations with *Pinus halepensis* and *Pinus pinaster* abound in the study area (see details in Cassinello *et al.*, 2004).

The study species

The aoudad, a North African caprid (subfamily Caprinae), is now a common inhabitant of south-eastern Spain having been introduced as a small population (16 males and 20 females) in Sierra Espuña Natural Park in 1970 (see details in Cassinello, 2000; Cassinello *et al.*, 2004). Since then the population has increased rapidly and by 1990 around 2000 individuals were estimated to inhabit the Sierra Espuña and surroundings mountains (ARMAN, 1991). A sarcoptic mange episode affected the aoudad population in 1991, during which time the numbers of aoudad decreased by over 90% (González-Candela & León-Vizcaíno, 1999). However, the aoudad population recovered very quickly

in the area, and is currently estimated to be over 1000 individuals (González-Candela *et al.*, 2001). Apart from the population that originated in the Sierra Espuña, since 1990 another free-ranging population of aoudads has established in the Alicante province, originating from escapes from two game estates in the area (Serrano *et al.*, 2002; Cassinello *et al.*, 2004).

Data origin

Distributional data

The aoudad presence data come from Cassinello *et al.* (2004), and were obtained by surveys conducted intermittently during 3 years (from 1999 to 2001), mainly during August, September, and October, the beginning of the mating season when animal visibility is enhanced (Solbert, 1980; Gray & Simpson, 1982, 1983; J. Cassinello, pers. obs.).

In geographically explicit analyses, the spatial resolution (grid cell size) constitutes a key decision for the accuracy and reliability of the results (see Chefaoui *et al.*, 2005). In this study,

Table 1 Variables used in the analyses (including abbreviations). See text for details and data sources

Climate		Geomorphology		Vegetation	
PW	Precipitation in winter (mm)	Alt	Mean altitude (m)	VHTr	Humid-leaved tree area (%)
PF	Precipitation in autumn (mm)	AltMx	Maximum altitude (m)	VXTr	Xeric-leaved tree area (%)
PSp	Precipitation in spring (mm)	AltMn	Minimum altitude (m)	VHBsh	Humid-leaved bush area (%)
PSm	Precipitation in summer (mm)	AltRn	Altitude range (m)	VXBsh	Xeric-leaved bush area (%)
TW	Mean temperature in winter (°C)	Slp	Mean slope (°)	VPTr	Pine tree area (%)
TF	Mean temperature in autumn (°C)	SlpMx	Maximum slope (°)		
TSp	Mean temperature in spring (°C)	SlpMn	Minimum slope (°)		
TSm	Mean temperature in summer (°C)	Slp30	Area with slope higher than 30° (%)		
TMxW	Maximum temperature in winter (°C)	AspDv	Aspect diversity (H′ index)		
TMxF	Maximum temperature in autumn (°C)				
TMxSp	Maximum temperature in spring (°C)	*Habitat structure*		*Landscape use*	
TMxSm	Maximum temperature in summer (°C)	HFr	Forest area (%)	WULAI	Landscape Avoidance Index
TMnW	Minimum temperature in winter (°C)	HCFr	Coniferous forest area (%)		
TMnF	Minimum temperature in autumn (°C)	HBFr	Broadleaved forest area (%)	*Human disturbance*	
TMnSp	Minimum temperature in spring (°C)	HBsh	Bushland area (%)	DUr	Distance to urban areas (km)
TMnSm	Minimum temperature in summer (°C)	HGrs	Grassland area (%)	DRoad	Distance to the nearest road (km)
TRn	Annual range of temperatures (°C)	HDC	Dryland crops (%)	DHw	Distance to the nearest highway (km)
		LUDv	Land use diversity (H′ index)	DSE	Distance to Sierra Espuña nucleus (km)

we transformed the available data on aoudad presence (Cassinello *et al*., 2004) from 100 × 100 m UTM grid cells to a 1 × 1 km UTM grid cells. This could create error and scale problems, but previous studies have shown a degree of correlation in species' distribution patterns across narrow ranges of scales (Hartley *et al*., 2004).

Since free-ranging aoudads in the study area have two independent population nuclei, we used one population to calibrate ENFA models (Sierra Espuña population nucleus, *n* = 60 records), and the other, as an independent set, for the empirical evaluation of the predictive maps (Alicante population nuclei, *n* = 22 records).

Environmental data

Data from an Iberian GIS database compiled and managed by J. M. Lobo, A. Jiménez-Valverde, R. M. Chefaoui, and J. Hortal (for details contact J. Hortal, or see http://www.biogeografia.com for additional information) were imported and processed into the raster-based Idrisi GIS System (Clark Laboratories, 2001, 2004). A set of GIS maps for the study area was produced, including a number of continuous variables that were thought to determine the aoudad distribution (see below). All of the variables were extracted at a 1-km² resolution, corresponding to the chosen resolution of aoudad presence data. This grain size chosen for the analyses is a consensus between the spatial accuracy of biological data, the mobility of the aoudad, and the large spatial extent used (see another example at Chefaoui *et al*., 2005).

Many climatic and ecological factors have been used to explain the variations in population abundance and distribution of ungulate species in the Iberian Peninsula (e.g. Acevedo *et al*., 2005, 2006). Here, we selected 42 variables that could act as

determinants of current aoudad distribution in SE Iberian Peninsula; 38 accounting for environmental variation (climate, habitat structure, vegetation characteristics, and geomorphology), one index of the adequacy of landscape to aoudads, and four for direct human disturbance (Table 1):

1 Seventeen climate variables were obtained from the monthly values of the digital version of the Spanish National Climate Atlas (provided by the Instituto Nacional de Meteorología; freely available at http://www.inm.es/); four accounting for seasonal precipitations (mm), 12 accounting for the mean, maximum, and minimum temperature at each season (°C); and one accounting for the annual range of temperatures (°C).

2 Nine geomorphology variables were extracted for each 1 km² pixel from an Iberian Digital Elevation Model of 100 m pixel width extracted from a global DEM (Clark Laboratories, 2000): mean, maximum, and minimum altitude (m a.s.l.); altitude range (metres); mean, maximum, and minimum slope (degrees); percentage of area with slopes greater than 30°; and mean aspect diversity, using a 7 × 7 pixel kernel on a nine-category reclassified aspect map (see Clark Laboratories, 2001, 2004 for the method; and Chefaoui *et al*., 2005 for an example of the use of this variable).

3 Habitat structure variables were obtained from the 250-m pixel width land use information of the CORINE NATLAN European project (EEA, 2000); six variables accounting for land cover (Table 1) were extracted as percentages of each land category per 1 km² pixel, whereas mean land use diversity was obtained with the same technique as aspect diversity.

4 Five variables account for the type of vegetation available, according to its nutritional value; the information on vegetation composition coming from the digital version of the Spanish National Forest Map (Ruiz de la Torre, 2002) was rasterized to a 100-m pixel width resolution, and reclassified to obtain the

surface of each 1 km^2 pixel occupied by pine trees (*Pinus* sp.), xeric-leaved trees (e.g. *Quercus ilex*, *Juniperus* sp.), humid-leaved trees (e.g. *Quercus pyrenaica*, *Fraxinus* sp.), xeric-leaved bushes (e.g. *Cistus* sp.), and humid-leaved bushes (e.g. *Pistacia* sp.).

5 A landscape avoidance index was created by combining available land use map and the degree of alteration made by human activity in comparison to natural habitats. This index was based on potential land avoidance by the aoudad rather than landscape preference or use, and could be applicable to most Mediterranean wild ungulates. We have denominated it Wild Ungulates Land Avoidance Index (WULAI). Land use variables receive a score proportional to the rareness of encountering aoudads in these landscapes, i.e. the further to the original habitat, the higher the score (up to 100). Thus, in the original CORINE NATLAN map (100 × 100 m pixel resolution; EEA, 2000) we assigned 100 to urban and other constructed areas; 50 to irrigated croplands; 30 to fruit orchards and patchy crops; 20 to vineyards; 10 to dry crops, olive groves, managed grasslands and mosaic of crops and natural vegetation; and finally 0 landscape avoidance to forest, bare rock, bushlands, and natural grasslands. WULAI scores were averaged across each square kilometre, ranging from 0 (minimum avoidance, maximum use) to 100 (maximum avoidance, minimum use).

6 Finally, four distance variables account for potential human disturbance (see, e.g. Osborne *et al.*, 2001; Schadt *et al.*, 2002): the distance to urban areas, roads, and first order roads (highways and national level roads), calculated with the Distance Operator tool of IDRISI 32 software. In addition, the distance to the Sierra Espuña population nucleus (DSE), that is, the original release location (Cassinello, 2000), was used in several analyses, to account for the recent dispersion of the species (see Acevedo *et al.*, 2005).

All variables were Box–Cox normalized prior to their use in the ENFA analyses.

Statistical analyses

Niche modelling

ENFA analyses were conducted using BIOMAPPER (Hirzel *et al.*, 2004b; freely available at http://www.unil.ch/biomapper/). This software uses the ENFA methodology to produce predictive maps of habitat suitability (i.e. potential distribution) from GIS information (see applications at Hirzel, 2001; Hirzel *et al.*, 2001, 2002, 2004a; Hirzel & Arlettaz, 2003; Gallego *et al.*, 2004; Chefaoui *et al.*, 2005; Hortal *et al.*, 2005; Acevedo *et al.*, 2006). We developed two different ENFA analyses, one to describe the Environmental Niche (herein, environmental niche model) using the variables in the first four of the above-mentioned groups and another one using all variables present in the six groups above to describe the likely Observed Niche. These analyses, and the resulting habitat suitability maps, are produced in two steps:

1 ENFA was used to characterize the response of the aoudad to the main variations of the used predictors in the study area. ENFA analysis identifies two key components of species environmental niches: *marginality* and *tolerance*, that is, how rare are the conditions selected by the species within the context of the studied region, and how tolerant is the species to modifications of these conditions produced by secondary gradients (see Hirzel, 2001 and Hirzel *et al.*, 2002). Computationally, *marginality* is a measure of the distance between the central trend of the species environmental selection and the mean environmental conditions of the region in the most important environmental gradient (i.e. the higher the marginality, the more extreme the conditions with regard to the area studied), and *tolerance* measures the range width with regard to all gradients present in the study area (see below), that is, how the species tolerates environmental variations (varying from 0 to 1, i.e. the closer to 0, the more specialist the species). In this context, the *specialization* of a species is defined as the inverse of its *tolerance*. In our study, aoudad presence data were used to identify a number of orthogonal factors in the predictors, accounting for the maximum differentiation between mean conditions for the study area, and mean conditions where the aoudad was found. The first factor (marginality factor) accounts for the marginality of the species, whereas the other factors (specialization factors) account for the species' response to other secondary environmental gradients.

2 Once ENFA factors are computed, habitat suitability scores for each pixel are calculated and mapped in accordance to the responses of the species to each factor. Partial suitability scores are computed for each factor as the percentage of distance to the median scores of observed presences, and habitat suitability is obtained as a weighted average of these partial suitabilities, according to the variability explained by each factor. These scores are then mapped using the ENFA factor maps (Hirzel *et al.*, 2002).

Model validation and accuracy

Two measures of how the resulting suitability model explains the observed data were used: *Explained Information*, which accounts for the total variability of the species distribution explained by the model, and *Explained Specialization*, which accounts for additional variability in the marginality and specialization factors that is not included in the Explained Information measure (Hirzel *et al.*, 2004b).

Since both Explained Information and Explained Specialization measures are derived from the observed data, no assessment of how the model can be extrapolated to the rest of the region is made. However, before using the ENFA results or habitat suitability maps (HSMs), we needed to evaluate their accuracy in describing the actual spatial response of the aoudad. A good way to assess the real accuracy of any spatial prediction is to use independent data to determine how model predictions perform outside the boundaries of the data used in developing the ENFA. We used two different validation strategies based in such assumption to determine (1) the predictive power of the ENFA model within the range of the population used to calibrate it (*within-data validation*, i.e. the accuracy to describe the distribution of the Sierra Espuña population), and (2) its ability to predict the geographical responses of other aoudad populations (*external validation*; i.e. placed outside of the bounds of the range

used to develop the model). While the former measures how the model fit into the data, the latter gives a measure of the generality of the niche description of the species. Within-data validation was made through the Jackknife cross-validation procedure implemented in BIOMAPPER 3.0 software (Hirzel *et al.*, 2001; Boyce *et al.*, 2002). Briefly, the data originally used for the ENFA analysis are partitioned in several spatially aggregated groups; each group is extracted once from the original data set, the models are recalibrated according to the new data set, and the prediction results are compared to the group of data plots extracted; this procedure is repeated as much times as groups defined (see Boyce *et al.*, 2002 for details). Model accuracy is measured as the agreement between independent and calibration data, using Spearman correlations. For the external validation, we used the presence data from Alicante population nuclei; the predictions of the Sierra Espuña model are compared with the presences in Alicante, and the degree of agreement between predictions and independent data is measured using Spearman correlations. This way, a truly empirical evaluation of the generality of the ENFA model in describing aoudad distribution is performed using an independent population.

Niche analysis

Following Chefaoui *et al.* (2005), we assume that the variation of habitat suitability scores across environmental gradients provides a description of the shape of the species' response to such gradients. To obtain a graphic representation of this response, we divided the marginality factor scores in 20 homogeneous intervals, and the average habitat suitability scores at each interval were represented for each habitat model (see Chefaoui *et al.*, 2005; Hortal *et al.*, 2005).

To evaluate the relationship between the habitat suitability maps obtained in the two models, they were reclassified to obtain suitable areas (HS scores between 50 and 75) and highly suitable areas (HS scores > 75) for each model, and then, we analysed the surface occupied by them.

RESULTS

Description of the environmental niche

Thirty-one environmental variables were used for the ENFA analysis, being reduced to four factors that explained 77.5% of the variance (Table 2). The marginality factor (first axis) explained a lowest percentage (0.73%) than specialization. The specialization factors (2, 3, and 4) explained 38.35, 26.61, and 11.81%, respectively. The maximum and mean slopes and altitude range were, in that order, the variables with the highest marginality coefficients, that is, the scores of these variables in the presence cells differed from their mean values in the study area (Table 2). The coefficients for these variables were positive, which showed that aoudads were associated to rough and craggy areas. Maximum and minimum altitude had the highest coefficients of the specialization factors, so that the aoudad distribution was specially restricted by these variables. The marginality factor

Table 2 Coefficients of the variables used in the environmental niche Ecological Niche Factor Analysis (ENFA). Variable codes as in Table 1

Variable	Marginality	Factor 2	Factor 3	Factor 4
1 HFr	0.324	0.000	0.000	0.000
2 HBsh	0.023	0.000	0.000	0.000
3 VXBsh	0.131	0.000	0.000	0.000
4 VPTr	0.205	0.000	0.000	0.000
5 HDc	−0.125	0.000	0.000	0.000
6 AltMx	0.231	0.702	0.707	0.731
7 AltMn	0.017	−0.636	−0.64	−0.662
8 AspDv	0.077	0.000	0.000	0.000
9 LUDv	−0.023	0.000	0.000	0.000
10 Alt	0.184	0.000	0.000	0.000
11 SlpMx	0.438	0.000	0.000	0.000
12 Slp	0.386	0.000	0.000	0.000
13 SlpMn	0.155	0.000	0.000	0.000
14 PW	−0.142	0.000	0.000	0.000
15 PF	−0.012	0.000	0.000	0.000
16 PSp	−0.086	0.000	0.000	0.000
17 PSm	−0.034	0.000	0.000	0.000
18 AltRn	0.361	−0.149	−0.15	−0.155
19 TRn	−0.052	0.128	0.116	0.025
20 TMxW	−0.016	0.000	0.000	0.000
21 TMxF	−0.083	0.000	0.000	0.000
22 TMxSp	−0.043	0.000	0.000	0.000
23 TMxSm	−0.101	0.000	0.000	0.000
24 TW	−0.122	0.206	0.187	0.04
25 TF	−0.171	0.000	0.000	0.000
26 TSp	−0.144	0.000	0.000	0.000
27 TSm	−0.213	−0.15	−0.136	−0.029
28 TMnW	−0.081	0.000	0.000	0.000
29 TMnF	−0.095	0.000	0.000	0.000
30 TMnSp	−0.095	0.000	0.000	0.000
31 TMnSm	−0.124	0.000	0.000	0.000

coefficient obtained for the aoudad was 1.29, which showed that there was an important separation of the species from the central part of the main environmental gradient shaping the aoudad distribution in the study area. In contrast, the global tolerance value was 0.31, which suggests a relatively small specialization (i.e. reduced tolerance to environments far from its optimum) of the species in this region.

The HSM of the environmental niche model (Fig. 2a) showed a high probability of appearance of the aoudad in the centre of the study area, following a south-west to north-east axis. Jackknife validations indicate that such potential map is reliable (within-data validation; mean Spearman $R = 0.92$), showing also a high predictive capacity when is extrapolated to the area where Alicante population is present to perform an empirical validation (external validation; mean Spearman $R = 0.60$).

Prospects on the observed niche

Thirty-seven environmental, landscape and human disturbance variables were included in the ENFA to develop the observed
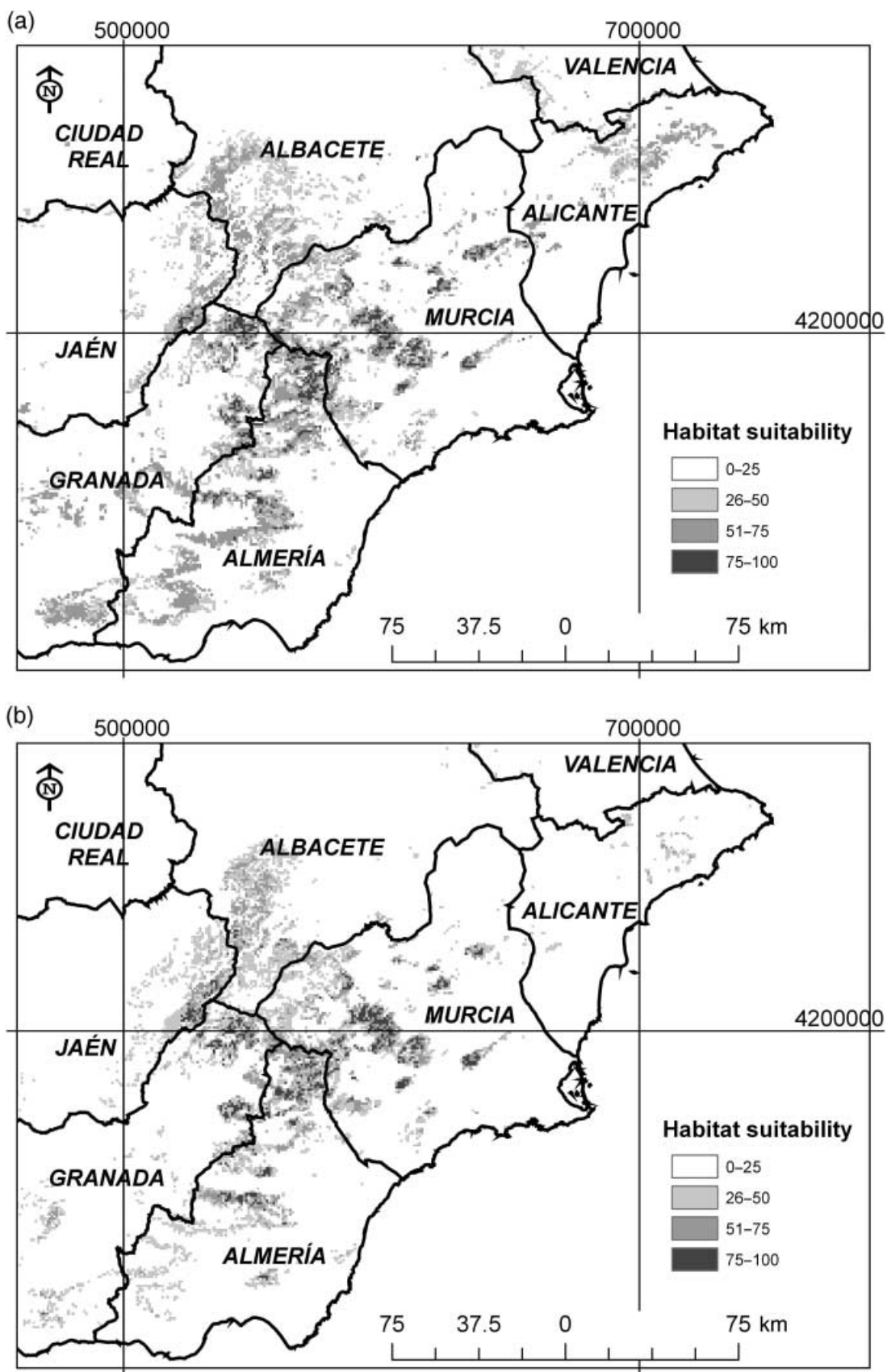
Figure 2 Habitat suitability maps for (a) the environmental niche model, and (b) the observed niche model. The scale on the right shows habitat suitability values (0 = low suitability; 100 = high suitability). The geographical coordinate system shown is the UTM.

Table 3 Coefficients of the variables used in the observed niche. Variable codes as in Table 1 DSE refers to the distance to the original release location in Sierra Espuña

Variable	Marginality	Factor 2	Factor 3	Factor 4
1. HFr	0.270	0.000	0.000	0.000
2 HBsh	0.019	0.000	0.000	0.000
3 VXBsh	0.109	0.000	0.000	0.000
4 VPTr	0.171	0.000	0.000	0.000
5 HDc	−0.104	0.000	0.000	0.000
6 AltMx	0.192	0.668	0.625	−0.694
7 AltMn	0.142	−0.605	−0.566	0.628
8 AspDv	0.064	0.000	0.000	0.000
9 LUDv	−0.019	0.000	0.000	0.000
10 Alt	0.153	0.000	0.000	0.000
11 SlpMx	0.364	0.000	0.000	0.000
12 Slp	0.321	0.000	0.000	0.000
13 SlpMn	0.129	0.000	0.000	0.000
14 PW	−0.118	0.000	0.000	0.000
15 PF	−0.010	0.000	0.000	0.000
16 PSp	−0.072	0.000	0.000	0.000
17 PSm	−0.029	0.000	0.000	0.000
18 AltRn	0.300	−0.141	−0.132	0.147
19 TRn	−0.043	0.184	−0.234	−0.144
20 TMxW	−0.013	0.000	0.000	0.000
21 TMxF	−0.069	0.000	0.000	0.000
22 TMxSp	−0.036	0.000	0.000	0.000
23 TMxSm	−0.084	0.000	0.000	0.000
24 TW	−0.101	0.296	−0.377	−0.232
25 TF	−0.143	0.000	0.000	0.000
26 TSp	−0.120	0.000	0.000	0.000
27 TSm	−0.177	−0.214	0.273	0.168
28 TMnW	−0.067	0.000	0.000	0.000
29 TMnF	−0.079	0.000	0.000	0.000
30 TMnSp	−0.079	0.000	0.000	0.000
31 TMnSm	−0.103	0.000	0.000	0.000
32 DSE	−0.473	0.000	0.000	0.000
33 DHw	0.107	0.000	0.000	0.000
34 DRoad	0.184	0.000	0.000	0.000
35 DUr	0.188	0.000	0.000	0.000
36 WULAI	−0.058	0.000	0.000	0.000

niche model (see Table 3). These variables were reduced to four factors explaining 75.6% of the variance (Table 3). Such reduction in explained variability from the environmental niche model comes from the higher complexity in the description of the region, provided by the new variables, which might be uncorrelated with the environmental ones used in the other model. Since ENFA is an ordination technique, based in the differences between the central trends of species and the whole region in the hyperspace formed by the descriptor variables used, the higher the number of uncorrelated variables, the more complex the description of variability, and thus the smaller the variability explained when these variables are incorporated to the analysis.

The marginality factor explained the lowest percentage (0.17%) of specialization in this model. The specialization factors (2, 3, and 4) explained 34.39, 22.60, and 18.43%, respectively. The

proximity to the original release location, followed by the maximum and mean slopes, and the altitude range were the variables with higher marginality coefficients, that is, the scores of these variables in the presence cells differed from their mean values in the study area (Table 3). As in the environmental niche model, this result indicates that aoudads show a preference for using rough and craggy areas. Similarly, maximum and minimum altitude had the highest coefficients among the specialization factors. The marginality coefficient obtained was 1.55, demonstrating an even higher separation of the species from the central part of the environmental gradient. The global tolerance value was 0.27, which suggests that the aoudad is relatively specialized in this region of southern Spain. The HSM (Fig. 2b) showed a high probability of appearance of the aoudad in the centre of the study area following a south-west to north-east axis, but this distribution was more patchily than in the environmental niche model. Again, Jackknife validation indicates that the predictive map of aoudad's observed niche is reliable (within-data validation; mean Spearman $R = 0.92$), also showing a high predictive capacity when is validated with the Alicante population (external validation; mean Spearman $R = 0.61$).

Changes in habitat suitability

The variation of mean habitat suitability scores of both environmental and observed niche models along the gradient identified by the marginality factors can be seen in Fig. 3. Both models showed similar environmental adaptations; however, the observed niche model was more restricted and had lower habitat suitability values than the environmental niche model. The suitable areas (HS > 50) in the environmental model covered 7.78% of the study area (4823 km^2), 34.77% of this area was suitable, and 12.32% was highly suitable (HS > 75) in the observed niche model (1677 and 594 km^2, respectively). On the other hand, the highly suitable areas in the introduced model covered 1.39% of the study area (861 km^2), being 76.07% suitable and 36.01% highly suitable in the observed niche model (655 and 310 km^2, respectively).

DISCUSSION

We performed an analysis of the factors determining habitat suitability (both in the environmental and in the observed niches) in the introduced aoudad population in south-eastern Spain. The species currently occupies several mountainous areas of the Cordillera Sub-Bética mountain range. Two main zones can be distinguished from the presence data, the one originating from the first release in Sierra Espuña Natural Park in 1970, which comprises a wide-ranging population; and a second one, further north, originating from escapes from a couple of hunting estates in Alicante (see Cassinello et al., 2004). Since data on habitat suitability in its native range in North Africa are not available, we have used nuclei from one of these zones (Alicante) as an independent test to determine the reliability of the geographical expression of both niche descriptions calculated from the other (Sierra Espuña nucleus).
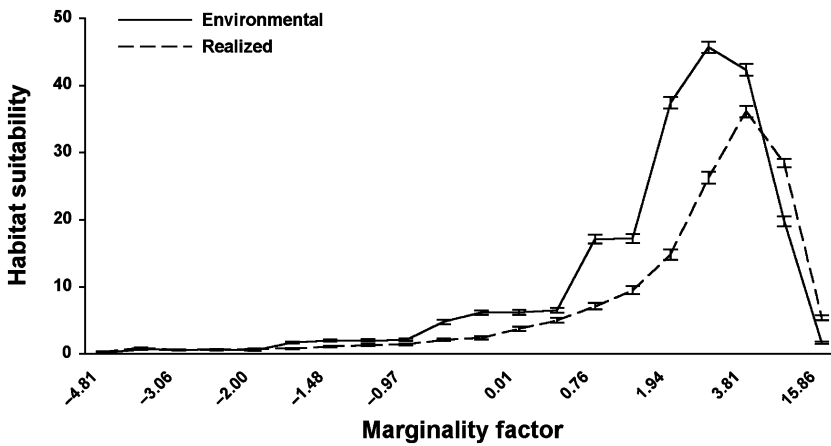
Figure 3 Variation of the mean habitat suitability scores along the gradient defined by the marginality factor. As the marginality factors for both models were highly correlated, we plotted them against the one from the environmental niche model. The marginality factor was divided into 20 intervals, and mean values per interval are shown.
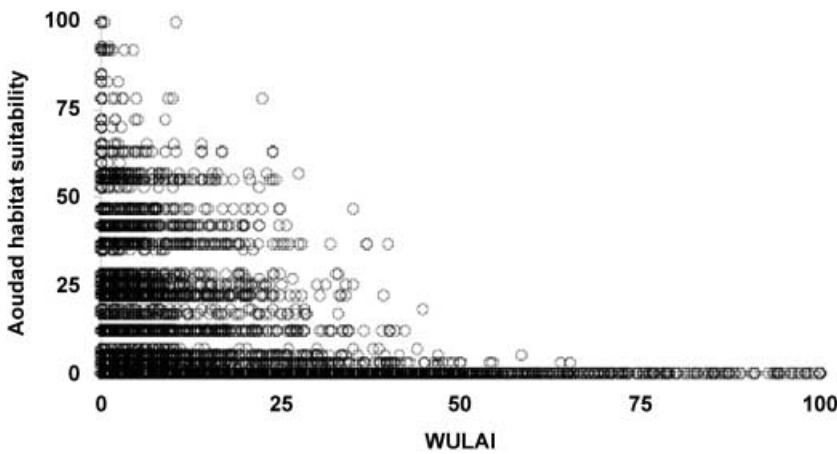

Figure 4 Relationship between the habitat suitability for the aoudad, and the Wild Ungulates Land Avoidance Index (WULAI) from the observed niche analysis (see Fig. 2b).

Habitat suitability of the aoudad in Spain

According to our characterization of its environmental niche (see Fig. 2a), the aoudad selected areas characterized by a low winter precipitation regime, high altitudes, and terrain slopes as well as with the presence of forest lands. These results agree with the habitat selection expected for a mountain ungulate such as the aoudad, where rocky and precipitous areas abound, from the sea level up to the extent of snow-free altitudes (see Shackleton, 1997). This niche characterization for the aoudad is highly reliable, as our maps showed a high predictive power when validated using the second population in Alicante. Therefore, we suggest a high potentiality for this exotic ungulate to conquer new areas around its current distribution range in southern Spain.

The description of aoudad's current habitat suitability varies when landscape avoidance and anthropogenic variables are included in the analysis to develop the observed niche model. When landscape avoidance and human disturbance effects are included in the ENFA model, it appeared that the aoudad was associated with less mountainous areas, with higher temperatures, and forest and dryland crop areas (see Table 3). Human land use data will also be more patchily distributed than environmental parameters, therefore contributing to a more

patchy distribution. This resulted in a narrower, more patchy suitability map (Fig. 2b), due to the landscape and human disturbance constraints added to ENFA calculations. The high coefficients obtained for the distance to the original release locality indicate that current aoudad distribution is clearly shaped by the location of the initial release. In addition, the observed niche was narrower than the environmental niche, and was also placed nearer to one of the extremes of the marginality factor axis (see Fig. 3).

There was an important relationship between habitat suitability for the aoudad and the intensity of human disturbance; humanized landscapes with moderate-to-high WULAI scores appear not to be suitable for the species. If WULAI scores are plotted against HSM scores, there is a progressive diminution of the maximum habitat suitability for the aoudad as its landscape avoidance increases, reaching 0 above intermediate levels of disturbance (Fig. 4). However, the current analysis does not allow us to separate the effects of different types of land use on the aoudad range expansion. These single effects could be even stronger than that measured by our landscape use index, so the exact effects of landscape modification by humans on aoudad dispersion remain untested. As an example, distance to roads presents more explanatory power than WULAI (see Table 3), an effect of using

a complex mixture of land use categories (EEA, 2000) within a single index (see Methods). Thus, further analyses are needed to unravel the individual effects of these human impacts on aoudad habitat selection.

Conservation concerns

Most ungulate species in Spain are currently expanding in range (e.g. the Iberian ibex; Pérez *et al.*, 2002; Acevedo *et al.*, 2006). Some species are occupying new habitats that may have not supported large herbivores for a long time; consequently, local plant species may have evolved without recovering high grazing pressure, so that they may not be tolerant to a more intensive herbivore presence. Furthermore, the increasing presence of allochthonous ungulates, such as the European mouflon (*Ovis aries musimon*) and the aoudad, makes things worse as they may particularly threaten local plant species (Rodríguez-Piñero & Rodríguez-Luengo, 1992). It has been seen that exotic species can substantially influence the composition and structure of plant and animal communities, alter nutrient and water cycles, and change disturbance regimes (e.g. Parker *et al.*, 1999; Mack *et al.*, 2000; Holmgren, M. 2002).

This work shows that the potentially high expansion capacity of the exotic aoudad in the south of Spain is resulting from the similarity of the host habitat to that of the region of origin, North Africa. In Spain, the aoudad has not yet reached suitable areas located at much higher altitudes (i.e. Sierra Nevada mountain range), which is the native land of the Iberian ibex. We hypothesize that if the aoudad reaches these areas, potential competition may arise with the ibex, given the biological similarities of these caprid species. In addition, the Sierra Nevada (a Spanish National Park) is known to be an important hotspot for Iberian plants, both in terms of richness and endemism (see Castro Parga *et al.*, 1996; Lobo *et al.*, 2001). Therefore, if the aoudad reached the region, many endangered endemic plants could be at a higher risk. Given this potential threat, it is important to develop strategies to prevent the aoudad dispersing through the suitable areas located in the western limits of its current distribution (see Fig. 2). Our analysis has identified several constraints to the dispersal of the aoudad associated with the intensity of human disturbance and land use. This suggests that further investigations on the individual effects (e.g. management of cultivated landscapes, grazing intensities and competition with livestock) could help to design land use strategies that are able to create a landscape matrix that offers a high frictional effect on aoudad dispersal.

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