BIODIVERSITY RESEARCH

Invasive exotic aoudad (*Ammotragus lervia*) as a major threat to native Iberian ibex (*Capra pyrenaica*): a habitat suitability model approach

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ABSTRACT

The introduction of alien species to new environments is one of the main threats to the conservation of biodiversity. One particularly problematic example is that of wild ungulates which are increasingly being established in regions outside their natural distribution range due to human hunting interests. Unfortunately, we know little of the effects these large herbivores may have on the host ecosystems. This study deals with a first comparative analysis of the habitat requirements of two ungulate species that may be facing competition for resources in the south of Europe: the native Iberian ibex (*Capra pyrenaica*) and the exotic aoudad (*Ammotragus lervia*). The aoudad is a North African caprid introduced in 1970 as a game species in south-eastern Spain. It has adapted well, and populations have been freely expanding since then. Ecological Niche Factor Analysis is used to describe the realized niche of both species where their distribution ranges merge. Both species occupy marginal areas of rugged terrain in the region. Marginality is higher for the Iberian ibex, which also presents a higher tolerance of secondary environmental gradients than the aoudad. Highly suitable areas for each species are secondarily suitable for the other. Reclassified and cross-tabulated habitat suitability maps showing the areas of potential spatial coexistence and differences in ecological traits between both species are provided. The results obtained do not allow inferring resource competition between these species. However, current aoudad expansion could result in it invading the favoured habitats of the ibex. Inadequate hunting policy and monitoring, and increasing climatic resemblance of the study region to the native aoudad areas, due to a strong desertification process, are facilitating a high rate of expansion. We strongly recommend to eradicate or, at least, monitor these exotic populations, and promote active conservation practices, if one wants to preserve the unique natural resources present in this European region.

Keywords

Biological invasions, ENFA, habitat suitability modelling, Iberian Peninsula, resource competition, ungulates.

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INTRODUCTION

Alien invasive species are considered by the IUCN Species Survival Commission to be the second largest threat to indigenous species, following habitat destruction (Bergmans & Blom, 2001). The introduction of alien species in regions beyond their natural distribution ranges may alter the host ecosystems, thus affecting the viability of native fauna and flora (e.g. Diamond, 1989; Wilcove *et al.*, 1998). However, recent evidence postulates

that dominance of alien species over native ones is actually a consequence of degraded ecosystems which facilitate the spread of such aliens (see reviews in Gurevitch & Padilla, 2004; Didham *et al.*, 2005). Concerning ungulates, sport hunting is among the main driving forces behind the expansion of various species throughout the world (see, e.g. Macdonald *et al.*, 1988; Gortázar *et al.*, 2000; Jaksic *et al.*, 2002).

Rapid increases in the populations of large herbivores in the Iberian Peninsula are provoking their local overabundance

(Cassinello, 2000; Gortázar *et al.*, 2006). These high densities are resulting in a serious threat for plant communities due to overgrazing pressures (McNaughton, 1979; Mace, 1991; van de Koppel *et al.*, 1999). Thus, several non-native ungulates, including feral goats (*Capra hircus*), the European mouflon (*Ovis aries musimon*), and the aoudad (*Ammotragus lervia*), pose a serious risk and might be responsible for the rarefaction and extinction of endemic plants (Nogales *et al.*, 2006).

Uncontrolled exploitation and poaching along with habitat loss and fragmentation used to be the main threat to native European ungulate populations. However, current hunting regulations have led to their recovery and even expansion in most countries (e.g. Sidorovich *et al.*, 2003; Geisser & Reyer, 2004; Acevedo *et al.*, 2007b). Such expansion is noteworthy in areas where game activity is not allowed, i.e. protected lands and those close to urban zones (e.g. Whittaker *et al.*, 2001; Cahill *et al.*, 2003). In the Iberian Peninsula, the expansion of wild boar, *Sus scrofa*, has been recorded over several decades (Sáez-Royuela & Tellería, 1986; Gortázar *et al.*, 2000; Acevedo *et al.*, 2006). Other recent examples are roe deer, *Capreolus capreolus* (Acevedo *et al.*, 2005) and the Iberian ibex, *Capra pyrenaica* (Pérez *et al.*, 2002; Acevedo *et al.*, 2007b). Current distribution of the latter is a consequence of both natural and unnatural expansion processes, where most of translocations were carried out posterior to 1970, particularly during 1980s and 1990s (Pérez *et al.*, 2002). Also, such expansion may rely on recent habitat changes, i.e. abandonment of agricultural lands, game management translocations (Gortázar *et al.*, 2000), its recovery from past sarcoptic mange epizootics (Pérez *et al.*, 1997), and a decrease in hunting pressure on the species, probably caused by the incidence of this disease (see J.L. Garrido, unpublished data).

Of special concern is the aoudad, an African generalist ungulate, which has been successfully introduced outside its African range as a game species in USA and Spain. There, it has adapted formidably to Mediterranean-like regions, where food resources are abundant, in contrast with the desert lands occupied in its native African range. In these areas, the abundance of resources, along with the scarcity of competitors and predators, results in high birth rates and a quick spread of the population (see Wolf *et al.*, 1996). Due to this, the aoudad has rapidly adapted to southern Iberian habitats, presenting elevated population growth rates (Cassinello, 2000; Cassinello *et al.*, 2004). The effects that this alien species may cause on native flora and fauna are yet uncertain, although its potential as a competitor of native ungulates has already been postulated, mainly based on diet overlap between the aoudad and desert bighorn, *Ovis canadensis nelsoni* (Simpson *et al.*, 1978), and mule deer, *Odocoileus hemionus* (Krysl *et al.*, 1980).

The relationships between environmental gradients and the adequacy for the survival of the populations of a species can be used to model the potential response of the species to these gradients (Austin *et al.*, 1990). Such description can be used to produce predictive maps of species distribution (Guisan & Zimmermann, 2000; Araújo & Guisan, 2006), and to describe the characteristics of the niche of the species (e.g. Chefaoui *et al.*, 2005; Soberón & Peterson, 2005; Araújo & Guisan, 2006;

Acevedo *et al.*, 2007a). Two kinds of predictive maps can be obtained for a species, describing (1) current distribution or (2) habitat suitability (i.e. potential distribution). The latter could serve as a tool for the study and threat assessment of biological invasions, as habitat suitability can be used as an indicator of the risk for a particular territory to be invaded by the alien species (e.g. Cassinello *et al.*, 2006).

The Ecological Niche Factor Analysis (ENFA, Hirzel *et al.*, 2002) models habitat suitability by comparing the environmental response of the species to the environmental characteristics of the entire study area. This methodology can be used to develop habitat suitability maps from raw presence data. Therefore, ENFA is recommended when absence data are not available (most data bases), unreliable (most cryptic and rare species), or meaningless (invaders) (Hirzel *et al.*, 2001). Recently, it has been proposed that a species niche can be described using ENFA results (Chefaoui *et al.*, 2005; Acevedo *et al.*, 2007a). Given that the factors identified by ENFA represent the main environmental gradients that are shaping the spatial response of the species in the study region, it can be assumed that the response of a species to these gradients constitutes its realized niche. Therefore, the distribution of habitat suitability scores through these factors could be used to describe and study the characteristics of the realized niche of species, as well as niche differentiation among several related species (Chefaoui *et al.*, 2005; Hortal *et al.*, 2005; Acevedo *et al.*, 2007a). Here, the realized niche is intended as the portion of the fundamental niche where the species is currently present, rather than where is competitively dominant (the original definition of Hutchinson, 1957; see discussion in Soberón & Peterson, 2005; Araújo & Guisan, 2006).

In this study, we compare habitat requirements and habitat suitability for native Iberian ibex and exotic aoudad inhabiting the south-eastern Iberian Peninsula, according to their current distribution (Pérez *et al.*, 2002; Cassinello *et al.*, 2004; Acevedo *et al.*, 2007b). Our goal is to compare the environmental requirements of both species to identify differences and similarities (see Acevedo *et al.*, 2007a), and advance whether competition for resources and threats to the Iberian ibex could be expected. To do this, we use ENFA and the niche description proposed by Chefaoui *et al.* (2005) to characterize the response of both ungulate species to the main environmental variations in the study area, as well as to predict their potential distribution. This is the first attempt to compare ecological traits between aoudads and Iberian ibexes, as to date no field study whatsoever has been carried out in the regions where both species coexist. The results are used to assess the potential impacts of current aoudad expansion in the conservation of ibex populations.

A recent study by Cassinello *et al.* (2006) used a similar methodology to assess the ecological niche of the aoudad in south-eastern Spain, discriminating between environmental and anthropogenic variables. The present study goes a step forward, exploring potential niche overlap between the aoudad and its close relative of the native Iberian fauna, namely, the Iberian ibex.
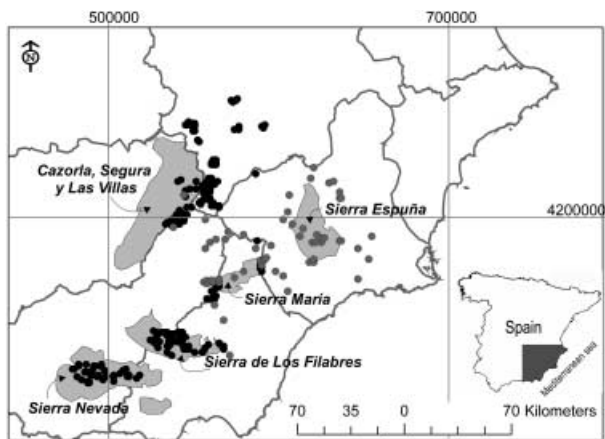
Figure 1 Presence data of the Iberian ibex (black dots) and the aoudad (grey dots), and location of the study area. Province borders are shown along with the main mountain ranges where the species can be found.

METHODS

The study area

We have chosen a geographical extent that hosts the environmental extremes present in the SE Iberian Peninsula (i.e. from coast to mountain), the current area of expansion of the aoudad (Cassinello *et al.*, 2004). This encompasses an area 340 km wide and 270 km long (61,961 km^2 of land area; UTM 29N geographical 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.), the 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, such as the Sierra Espuña (the site where the introduced aoudad population first became established), the Sierra María, the Sierra de Los Filabres, and the Cazorla, Segura y Las Villas Natural Park.

Data origin

Aoudad and Iberian ibex distributional data

Aoudad distribution data (Cassinello *et al.*, 2004; Fig. 1) come from field observations and interviews with local shepherds, hunters, biologists, and park managers from regional environmental agencies, and were verified by visits to the areas where aoudads were reported. Iberian ibex distribution data were also obtained by means of field observations and interviews with forest rangers and staff from environmental agencies (Pérez *et al.*, 2002; Acevedo *et al.*, 2007b).

Environmental data

Many climatic and ecological factors have been described to affect the population abundance and distribution of ungulate species in the Iberian Peninsula (e.g. Acevedo *et al.*, 2005, 2006).

Table 1 Variables used in the analyses (and their measurement units). Average values are shown for the whole study region (global), and for the areas where the aoudad and the Iberian ibex are present.

Variables (unit)	Means		
	Global	Aoudad	Iberian ibex
Climate			
Winter rainfall (mm)	132.92	108.65	209.14
Summer rainfall (mm)	46.29	40.73	61.69
Mean summer temperature (°C)	22.95	21.9	19.28
Annual range of temperatures (°C)	15.33	15.21	15.58
Geomorphology			
Maximum altitude (m)	806.46	1066.77	1670.46
Altitude range (m)	101.14	187.37	204.59
Mean slope (degrees)	5.56	10.40	11.21
Maximum slope (degrees)	12.23	23.01	22.24
Habitat structure			
Forest area (%)	11.86	33.17	39.80
Shrubland area (%)	27.72	33.88	17.08
Human pressure			
Distance to urban areas (m)	3974.88	5714.69	7335.62
Distance to the nearest road (m)	2050.21	2915.65	3431.15

We selected 12 variables that could act as determinants of current aoudad and Iberian ibex distribution in SE Iberian Peninsula, also encompassing the range of climatic and ecological traits present in the study region (Table 1). Ten of these variables account for environmental variations (climate, habitat structure, vegetation characteristics, and geomorphology), and the other two do for human impact.

Data come from an Iberian GIS database compiled and managed by J. M. Lobo, A. Jiménez-Valverde, R. M. Chefaoui, and J. Hortal. 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; available at http://www.inm.es/). Geomorphology variables were calculated from an Iberian Digital Elevation Model of 100 m pixel width. Habitat structure variables were obtained from the 250 m pixel width land use information of the CORINE NATLAN European project (EEA, 2000). Finally, two variables accounting for human pressure on aoudad and ibex populations were obtained: distance to urban areas (i.e. to the urban and industrial categories following CORINE land cover map), and distance to the nearest road (including motorways and national and local roads, extracted from the Spanish National Digital Atlas, courtesy of the Instituto Geográfico Nacional; http://www.ign.es/).

We would like to point out that, although CORINE land cover maps are known to present low spatial accuracy and some spatial errors (see, e.g. Felicísimo & Sánchez-Gago, 2002), the CORINE 2000 version has largely improved these aspects (see the updated reports available at http://dataservice.eea.europa.eu/dataservice/). Also CORINE data have been qualified as well suited for distribution modelling, even for habitat-specific species such as marshland birds (Virkkala *et al.*, 2005). Therefore, it is doubtful

Table 2 Coefficients of the variables used in ENFA, and percentages explained by marginality (MF) and specialization factors (SF).

Variables	Aoudad model			Iberian ibex model		
	MF	SF 1 (43.49%)	SF 2 (17.53%)	MF	SF 1 (48.01%)	SF 2 (14.54%)
Forest area	0.36	0.00	0.01	0.26	0.07	–0.14
Shrubland area	0.03	0.15	0.03	0.02	0.11	–0.27
Maximum altitude	0.26	–0.28	0.26	0.47	–0.10	–0.37
Distance to the nearest road	0.25	0.07	0.02	0.22	0.01	–0.08
Distance to urban areas	0.25	0.09	–0.10	0.27	0.04	–0.15
Maximum slope	0.49	0.11	–0.15	0.25	0.20	–0.04
Mean slope	0.43	–0.07	–0.36	0.28	–0.09	–0.05
Winter rainfall	–0.16	0.58	–0.33	0.28	0.30	–0.40
Summer rainfall	–0.04	–0.51	0.41	0.21	0.09	0.40
Altitude range	0.40	–0.03	0.23	0.27	–0.01	0.13
Annual range of temperatures	–0.06	–0.44	–0.66	0.04	–0.89	–0.15
Mean summer temperature	–0.24	–0.27	–0.07	–0.49	0.15	–0.61

that these drawbacks in CORINE data result in misrepresentations of the relationship between the study species and habitat characteristics.

All variables were handled and processed in a GIS environment (Clark Laboratories, 2004). Information was extracted at 1 km² grain (1 × 1 km pixels). Such resolution has been chosen as a compromise between the spatial resolution of biological data (see discussion at Chefaoui *et al.*, 2005; see also Acevedo *et al.*, 2007a,b) and the scale at which the interaction between the two species might be important. Using a coarser grain we could have been able to find stronger relationships with the environmental predictors (see, e.g. Huettmann & Diamond, 2006), but our results would be less relevant for the assessment of potential interactions between populations of both species. All variables were Box–Cox normalized prior to their use in the ENFA analyses.

Statistical analyses

Niche modelling

BIOMAPPER 3.0 (Hirzel *et al.*, 2004; http://www.unil.ch/biomapper) was used to model the niche of the study species. This software uses ENFA to produce predictive maps of habitat suitability (i.e. potential distribution) from GIS variables (see applications at http://www2.unil.ch/biomapper/bibliography.html). How these maps are produced has already been explained in detail in former works (Hirzel *et al.*, 2002; Cassinello *et al.*, 2006).

Model validation and accuracy

Explained Information (ExI) and Explained Specialization (ExS) are used to measure how the resulting suitability model explains the observed data. The former accounts for the total variability of the species distribution explained by the model, whereas the latter accounts for additional variability on the marginality and

specialization factors not included in the ExI measure (Hirzel *et al.*, 2004). In addition, the robustness and predictive power of the habitat suitability models (HSMs) were assessed by means of the spatially explicit jackknife cross-validation procedure implemented in BIOMAPPER software (Boyce *et al.*, 2002; Hirzel *et al.*, 2002).

Niche description

ENFA analysis identifies two descriptors of species environmental niches: marginality and tolerance coefficients (see above). We also describe the shape of the environmental niche of the species as the variation in the habitat suitability scores throughout the environmental gradient defined by the Marginality Factor (see Chefaoui *et al.*, 2005; Hortal *et al.*, 2005; Acevedo *et al.*, 2007a). To do this, Marginality Factor scores were divided into a number of homogeneous intervals, and mean habitat suitability scores at each interval were represented for each species. In addition, the HSM map obtained for each species was reclassified (see Chefaoui *et al.*, 2005; Acevedo *et al.*, 2007a) in three categories according to HSM scores: low habitat suitability (0–33); medium habitat suitability (34–66); and high habitat suitability (66–100). These new maps were cross-tabulated in the GIS environment to pinpoint zones suitable for the two study species (high habitat suitability for the Iberian ibex and high habitat suitability for the aoudad), where coexistence and competition could occur. The environmental variables that characterize each zone were examined using Bonferroni corrected ANOVA analyses (Perneger, 1998).

RESULTS

The 12 environmental variables considered were reduced to three factors in both ENFA analyses (see Table 2), explaining 82.34% and 83.20% of the variance in the aoudad and Iberian ibex distributions, respectively. The first axes explained very low percentages of the specialization for both species (< 4%).
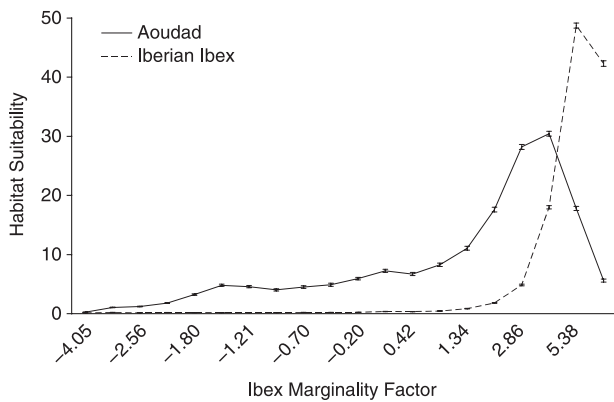
Figure 2 Variation of mean habitat suitability scores along the marginality factor. The factor was divided into 20 intervals, and mean habitat suitability modelling (HSM) values are shown. As marginality factors for both models were highly correlated, only one was used to plot the figure, the ibex model.

Maximum and mean slopes, altitude range, and presence of forests were the variables with higher scores in the marginality factor for the aoudad model, while low summer temperatures, maximum altitude, mean slope, and winter rainfall were so in the ibex model. Temperature range and winter rainfall presented the higher coefficients at the specialization factors for the two species, which thus show similar secondary restrictions (Table 2).

Both ungulate species occupy marginal areas in the study region (aoudad marginality coefficient = 1.15; ibex marginality coefficient = 2.08, see Fig. 2). However, although the Iberian ibex is more marginal than the aoudad in its environmental selection according to the main environmental gradient in the region, this species is quite tolerant to the secondary environmental gradients (tolerance coefficient = 0.84). Therefore, ibex distribution appears to be more in equilibrium with regional conditions than aoudad distribution, which is less tolerant of secondary gradients (tolerance coefficient = 0.68). Moreover, highly suitable areas for each species were secondarily suitable for the other one (Fig. 2).

The HSMs thus obtained are highly reliable, since our model validation produced the following outcome: ExI = 66%, ExS = 83%, and an average Spearman coefficient at jackknife validations of 0.97 for the ibex, and ExI = 65%, ExS = 82%, and Spearman coefficient = 0.95 for the aoudad.

Reclassified HSMs for both species are shown in Fig. 3, where areas of low, medium, and high habitat suitability are depicted. Cross-tabulated HSMs show the areas of spatial coexistence between both species (i.e. highly suitable for both species) as well as those areas highly suitable for each exclusively (Fig. 4). High suitability areas were significantly different in ecological traits for the two species (Table 3, Fig. 5), and were also different from the sites highly suitable for both species.

DISCUSSION

One of the possible adverse consequences of the presence of the exotic aoudad in the south of Europe is its effect on other taxonomically related native ungulates, or on ecologically convergent species. Here we present the first study on habitat similarities between the aoudad and the Iberian ibex, according to data on the distribution of both species in the south-east of the Iberian Peninsula.

Table 3 Environmental differentiation between the areas of potential coexistence of the aoudad and the Iberian ibex, and the areas suitable to each one of these species (HS > 66 in both models). Results of the analyses of variance are shown; ANOVA test coefficient (F), Bonferroni-corrected *P*-value (ns = no significant, ***$P \leq 0.0001$); the areas with significantly higher values for a given dependent variable in each comparison are indicated (A = aoudad, C = potential coexistence, and I = Iberian ibex).

| Variables	Aoudad vs. potential coexistence			Aoudad vs. Iberian ibex			Iberian ibex vs. potential coexistence		
	F	*P*-value	Area with a higher mean value	*F*	*P*-value	Area with a higher mean value	*F*	*P*-value	Area with a higher mean value
Forest area	56.52	***	C	72.13	***	I	8.34	ns	—
Shrubland area	19.28	***	A	0.82	ns	—	14.75	***	I
Maximum altitude	612.68	***	C	3212.16	***	I	27.82	***	I
Distance to the nearest road	48.89	***	A	43.11	***	I	95.35	***	I
Distance to urban areas	30.23	***	C	94.01	***	I	0.12	ns	—
Maximum slope	0.30	ns	—	70.04	***	I	13.84	***	I
Mean slope	0.52	ns	—	225.10	***	I	57.60	***	I
Winter rainfall	814.17	***	C	1046.59	***	I	65.42	***	C
Summer rainfall	1168.11	***	C	941.18	***	I	84.14	***	C
Altitude range	2.89	ns	—	209.29	***	I	64.14	***	I
Annual range of temperatures	193.29	***	C	150.00	***	I	96.73	***	C
Mean summer temperature	498.62	***	A	2222.7	***	A	15.61	***	C
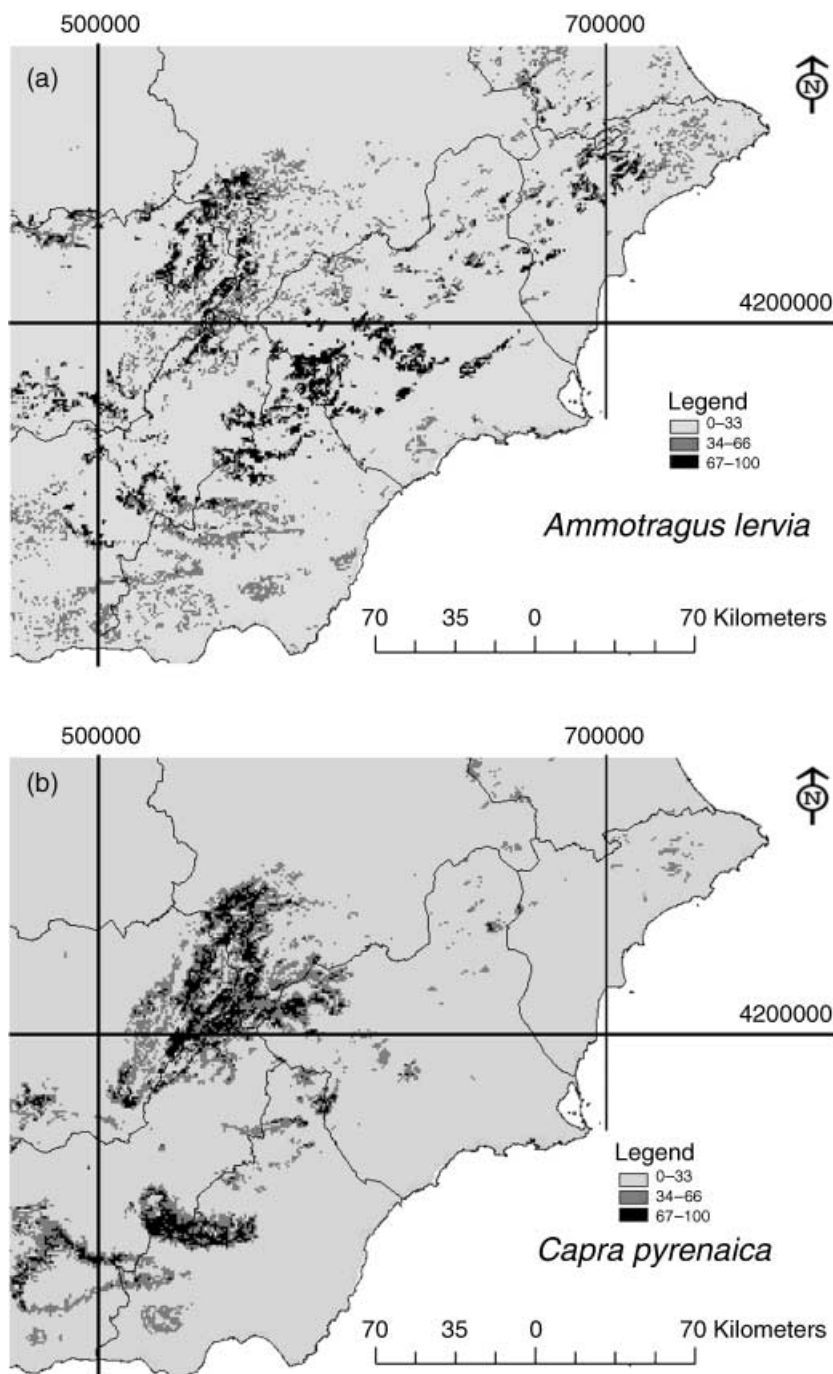
Figure 3 Habitat suitability maps for the study species: (a) the aoudad and (b) the Iberian ibex. Habitat suitability scores have been reclassified in three categories (0–33 = low suitability, 34–66 = medium suitability, and 67–100 = high suitability).

On the methodological approach

The ENFA-based methodological approach used here (based on Chefaoui *et al.*, 2005) could be of great utility for the study of the realized niches of most species, as well as for monitoring the potential spread of invasive species (Cassinello *et al.*, 2006). Since the seminal works of Austin *et al.* (1990), Nicholls (1989), and Margules *et al.* (1987), Generalized Linear and Generalized Additive Models (GLM and GAM, respectively), linked to GIS applications, have become very popular in species distribution predictions (e.g. Guisan *et al.*, 2002; Nogués-Bravo & Martínez-Rica,

2004). When absence or pseudo-absence data are available, more robust habitat models can be built from these techniques (e.g. Engler *et al.*, 2004; but see Hirzel *et al.*, 2001). However, in the specific case of invading species, sometimes these species are not yet occupying all their potential habitats in the landscape, and ENFA could produce better results than GLM, as 'absence data' of this species would not be reliable (Hirzel *et al.*, 2001).

Given that both the Iberian ibex and the aoudad are under remarkable expansion processes in the study region (Cassinello, 2000; Pérez *et al.*, 2002; Cassinello *et al.*, 2004; Acevedo *et al.*, 2007b), we used ENFA analyses to implement maps of the
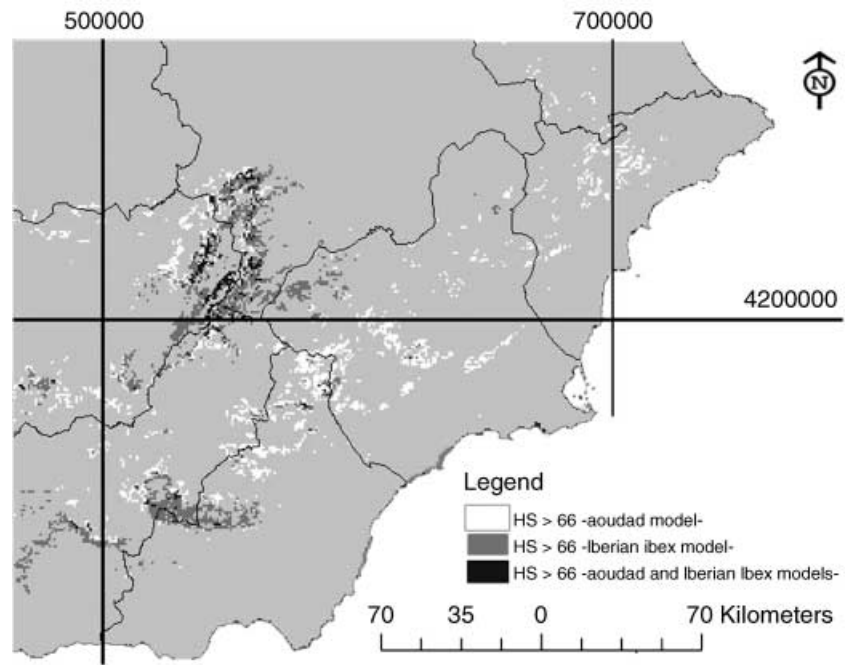
Figure 4 Map showing the highly suitable areas (habitat suitability > 66) for each one of the study species, as well as the areas of potential coexistence.
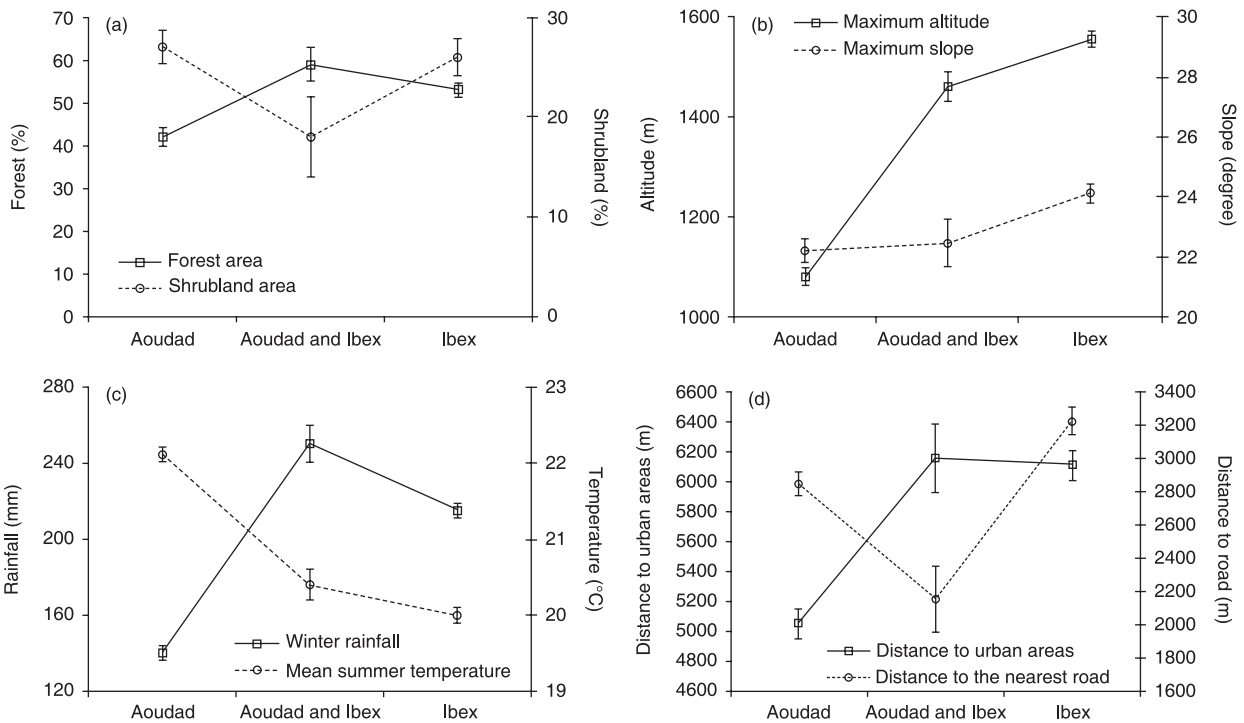

Figure 5 Plots showing mean ($\pm$ SE$_{95\%CI}$) values of some ecological variables present in highly suitable areas for the aoudad, aoudad and Iberian ibex, (potential coexistence areas) and Iberian ibex. Statistically significant differences are indicated in Table 3. (a) Percentage of forest and shrubland areas; (b) maximum altitude and slope; (c) winter rainfall and mean summer temperature; and (d) distances to urban areas and roads. We have added solid and dotted lines between the suitable areas in order to clarify the different trends.

potential distribution of both species. In addition, ENFA could also be more useful than a GLM when ecological interpretation is the aim of the study, even in situations where a GLM provides higher correlations to the observed data (Hirzel *et al.*, 2001).

The niche-description methodology derived by Chefaoui *et al.* (2005), based in such premises, is used here to describe the realized niches of both caprids in south-eastern Iberian Peninsula. However, ENFA results usually overestimate habitat suitability

(Zaniewski *et al.*, 2002; Engler *et al.*, 2004); therefore, such limitation should be considered when interpreting our results.

Niche description for the study species

The Iberian ibex and the aoudad occupy restricted habitats in the study area. However, the ibex presents a higher tolerance of secondary environmental gradients than the aoudad. This might suggest that the aoudad has as yet not reached all potentially suitable areas in the region, some of them being located at higher altitudes. According to the known biology and ecology of the aoudad (e.g. Ogren, 1965; Shackleton, 1997; Cassinello, 1998), and from our results (see Fig. 1 and Cassinello *et al.*, 2006), the species shows a strong potential to reach and settle in other mountainous regions native to the Iberian ibex, such as the Sierra Nevada mountain range (part of the Spanish National Parks network since 1999).

According to our analyses, the aoudad selects areas characterized by high slopes and altitude ranges, and an important presence of forests (see also Cassinello *et al.*, 2006). Such requirements agree with the habitat selection made by the aoudad both in its native North African range (Shackleton, 1997) and in the regions where it has been introduced (Johnston, 1980; Cassinello, 2000). On the contrary, although the Iberian ibex also selects mountainous areas, these are more marginal than those used by the aoudad, characterized by low summer temperatures and high altitudes, and, to a lesser extent, by high slopes (see also Acevedo *et al.*, 2007b) and high winter rainfall. In these areas, food availability according to its diet is expected to be higher (Martínez & Martínez, 1987; Martínez, 2000).

The results of this study defined a series of ecological traits that can be easily related to the mountain ranges where the two study species are predominantly found in the south-east of Spain (see Fig. 1). Thus, the aoudad ranges a wide variety of mountainous regions of very different altitudes and scattered throughout the study area (see Fig. 3a), whereas the ibex is found in spatially restricted areas, in the mountain ranges with higher elevations in the study area (Fig. 3b).

Cross-tabulated HSMs allowed the comparison between areas highly suitable for one of the study species (but not for the other) and areas highly suitable for both species (the areas of potential coexistence). Differences found between the ecological variables included in the analyses can be explained by the characteristics of the mountain ranges concerned. Basically, we appreciate higher marginality values and lower plasticity in the Iberian ibex than in the aoudad, which comparatively tends to act as a generalist in terms of habitat preference (e.g. Gray & Simpson, 1980; Escós & Alados, 1992). Also, areas of coexistence are more similar in terms of climate to highly suitable areas exclusively of the ibex, so that before a hypothetical competitive situation, the native caprid may be at an advantage. It is noticeable that the aoudad significantly selects areas with lower winter rainfall and higher mean summer temperatures, thus resembling its North African origin (Shackleton, 1997). Finally, the areas highly suitable for the aoudad are closer to urban areas and roads than are those of the Iberian ibex, probably because of the higher niche plasticity

of aoudads and the location of their release site, the Sierra Espuña and surrounding mountains (see Cassinello, 2000).

Implications for conservation

A competition conflict could arise in areas of potential coexistence between the Iberian ibex and the aoudad, due to the *a priori* biological similarities of both caprids (Schaller, 1977). Current distribution of the study species already overlaps (Fig. 1), and our HSMs indicate that this overlap might increase in time. If the aoudad reaches core native areas of the Iberian ibex (e.g. Sierra Nevada, Sierra de Cazorla), the viability of ibex populations might be compromised. But, would the aoudad actually be a threat to the Iberian ibex?

Given our results, currently the areas of coexistence of both species are potentially scarce (merely 14.8% of all the highly suitable areas for the ibex) and tend to be approaching to optimal conditions for the ibex. However, we are probably not witnessing yet all the competitive potential between both species, since the aoudad seems to have not yet reached its optimum. Nevertheless, as Putman (1996) highlights, it is problematic to extract the implications for competitive interactions from measures of niche overlap. High levels of overlap can imply competition, but only if resources are limited. In fact, observations of high overlap might equally well be indicative of a lack of competition (de Boer & Prins, 1990; Putman, 1996). On the other hand, species segregation can also be a result of competition. In our case, however, the aoudad has only recently reached the domain of the Iberian ibex, so that we would not expect that competition leading to segregation has already happened between both species. As far as we know, it would be then premature to indicate whether the aoudad will or will not be a threat to the native ibex and to which degree.

Despite this reasoning, recent evidence showed the displacement of the Iberian ibex to suboptimal habitats by extensive goat livestock presence in central Spain (Acevedo *et al.*, 2007b). This should alert us on possible similar effects in south-eastern Spain caused by the aoudad, a species strongly gregarious (Gray & Simpson, 1982; J. Cassinello, pers. obs.).

There is also another threat to be considered. Both study species are colonizing new habitats in the south of Spain and their expansive movements are noticeable (Pérez *et al.*, 2002; Cassinello *et al.*, 2004; Acevedo *et al.*, 2007b), although both have experienced similar population decreases due to sarcoptic mange episodes few years ago (Pérez *et al.*, 1997; González-Candela & León-Vizcaíno, 1999). Concerning to future sarcoptic episodes, as the current ibex distribution in the study region is characterized by isolated nuclei (see Fig. 1; Pérez *et al.*, 2002), contacts between them would be less probable than contacts with hypothetically infected aoudad populations, which may occupy larger extensions in the study area. Thus, if the aoudad acts as a vector of this disease, it would then represent a risk for the ibex.

The increasing presence of exotic ungulates in Spain, due to sport hunting introductions (i.e. the European mouflon and the aoudad), may particularly threaten local plant species (Rodríguez-Piñero & Rodríguez-Luengo, 1992). In the case of the aoudad, its expansion might put the threatened, highly

endemic flora of Sierra Nevada at serious risk. The critical importance of such a mountain range for the conservation of Iberian plant biodiversity (see, e.g. Castro Parga *et al.*, 1996; Blanca *et al.*, 1998; Lobo *et al.*, 2001) means that monitoring the aoudad grazing habits (both intensity and grazed species) in its expanding range should be a priority.

Finally, there is a series of factors that may determine the current degree of Iberian ibex and aoudad expansion and the effects caused by the latter on native fauna and flora. Recent climatic changes and the strong desertification that is taking place in the south-east of Spain (e.g. Puigdefábregas & Mendizábal, 2004), resulting in lower rainfall regimes and higher mean annual temperatures, may cause significant habitat changes that will favour the expansion of a desert caprid, such as the aoudad. On the other hand, the strong interest displayed in the aoudad by private game estates in the south of Spain, and the subsequent risk of animals escaping from badly maintained fences (Cassinello *et al.*, 2004; P. Acevedo, pers. obs.), may speed up this colonization process and therefore exacerbate their effects on the host ecosystem.

To sum up, when looking at cumulative effects, the presence of the exotic aoudad in the south-east of the Iberian Peninsula should be considered as a major problem for the ecosystem. Although current evidences do not yet show straight threats, we should start taking measures to prevent them to occur, as we are dealing with an invasive alien species that should be strictly controlled (see, e.g. Bergmans & Blom, 2001; Wittenberg & Cock, 2001; http://www.iucn.org/en/news/archive/2001_05/press/alien2001.html; Genovesi & Shine, 2003). One straightforward action to be taken should be the eradication of the species. This may confront with opposite interests by hunters and owners of game estates, and mainly with the difficulty of carrying out such an enormous task on a population of probably more than 2000 individuals spread out across an extremely large area (Cassinello, 2000; Cassinello *et al.*, 2004). But time is critical, and if no action is taken in the near future, the ongoing expansion of the species will reduce the possible management alternatives.

ACKNOWLEDGEMENTS

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