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ORIGINAL PAPER

Ecological niche overlap between co-occurring native and exotic ungulates: insights for a conservation conflict

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Abstract Exploitative competition implies an indirect interaction in which a resource exploited by one species is not available for another; e.g., when species share diet or habitat. It plays a key role in community structure and dynamics. Here we evaluated the niche overlap between the exotic aoudad (*Ammotragus lervia*) and the native Iberian ibex (*Capra pyrenaica*) where the species coexist in the Iberian Peninsula, along two main dimensions, the trophic niche and the environmental niche. Then we assessed the spatial segregation of the species. We expected that if a niche overlap was high, competition could drive spatial segregation to allow co-existence. We analyzed their trophic niche overlap by using the content of stable isotopes δ^{15}N and δ^{13}C in the hair of both species. To establish environmental niche competition, we compared the similarity in their habitat, estimated by environmental niche models based on the fine-scale presence records of each species obtained from field surveys. To test if spatial segregation occurred, we analyzed both species' co-occurrence. Our results indicated that both species shared a similar trophic niche measured by stable isotopes, both species showed a similar distribution of suitable areas, and that both species' environmental niches were more similar than expected. Finally, a negative spatial association was found between the aoudad and Iberian ibex. These results reveal that both species are ecologically similar and suggest that fine-scale spatial segregation might have favoured their co-existence in semiarid Mediterranean mountains. Our results show that integrating information on trophic and environmental niche overlap with fine scale spatial distribution might improve the study of competitive interactions among wild ungulates.

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Introduction

Interspecific interactions such as competition play a key role in the ecosystem structure and dynamics (Barbosa and Castellanos 2005; Tilman 1987). For the competition process to happen, the following conditions must be met: (1) different species must share resources; (2) resources must be limited; (3) the joint exploitation of these resources must negatively affect both species' performance (Milne 1961; Prins 2000). Competition can be based on interference or exploitation among sympatric species (Begon et al. 2006). Interference competition happens when both species directly interact, preventing another species from exploiting resources (Begon et al. 2006; Linnell and Strand, 2000). Exploitative competition implies indirect interactions in which a resource consumed by one species is not available for another (Lang and Benbow 2013; de Boer and Prins 1990).

Studies that focus on competition between species that exploit the same resources (i.e. intraguild competition) usually encompass ecological processes with species that have co-evolved (Ballejo et al. 2018; Grassel et al. 2015; Wright 2002). Co-evolved competing species can co-exist because they differ in the realized niche; i.e. resources and conditions that a species exploits as a result of interactions with other species (Giller 1984). According to Hutchinson (1957), the niche concept is defined as an *n-hyperdimensional volume*, where n is the number of dimensions that compose the niche. Therefore, niche differentiation can occur along different dimensions, such as food or habitat. Among the mechanisms that facilitate co-existence and alleviate competition, predation (Chesson 2000) or spatial segregation on fine scales to exploit shared resources are highlighted processes (e.g. Barrio and Hik 2013).

Novel intraguild competition processes may appear when exotic species are introduced beyond their natural range and interact with the native species they share resources with (Mooney and Cleland 2001). These new interactions can reduce the abundance and richness of native species (Blackburn et al. 2004; Gaertner et al. 2009). Introduced invasive species are considered the second cause of biodiversity loss (Wilcove et al. 1998) and they are associated with alterations of ecosystem processes (Raizada et al. 2008) and the community structure (Hejda et al. 2009). It has also been detected that exotic species may affect the genetic diversity and the evolutionary pathway of native species (Mooney and Cleland 2001). This phenomenon has been evaluated in different areas of the world; e.g., introduced carnivores into Australia (Doherty et al. 2017) or Europe (Bonesi et al. 2004; Harrington et al. 2009), or between exotic and native deer in North America (Faas and Weckerly 2010).

In the case of wild ungulates, introductions usually respond to sport hunting interests (Spear and Chown 2009). Different studies on the competition between exotic and native ungulates have concluded that non native species impair native species (Stewart et al. 2002; Dolman and Wäber 2008). Other studies have also shown positive effects, such as facilitation processes between non native and native ungulates. For instance, Gordon (1988) found that during spring the native red deer (*Cervus elaphus*) from the Scottish island of Rum (Pérez-Espona et al. 2013) preferentially grazed in areas that had been grazed by cattle during the previous winter, because cattle improves forage availability for red deer. Another example of facilitation was described by Odadi et al. (2011). These authors detected that during the wet season in a savannah ecosystem, the zebras (*Equus* spp.) decreased cover of dead grass and the cattle got access to higher-quality food. So, the interactions between native and non native ungulates could vary among different systems.

Besides translocations, wild ungulates are currently in a process of recolonization in developed countries (Apollonio et al. 2010). This rewilding process leads to an increased spatial overlap among ungulates. Considering that current ecosystems are subject to intense human influence which includes the elimination of predators, the presence of livestock and the introduction of exotic species (Latham 1999) novel competition interactions may arise.

Both natural rewilding and introductions are commonplace in Europe, including Mediterranean ecosystems (Apollonio et al. 2010). The Iberian ibex, an endemic ungulate to the Iberian Peninsula, had disappeared in most of its range. Nevertheless, since the mid-twentieth century, its populations have increased and large areas from which it had disappeared have been recolonised (Acevedo and Cassinello 2009).

The aoudad is an ungulate native from North Africa, whose populations are decreasing in its native range due to habitat loss or degradation and human persecution (Durant et al. 2014). Currently the species is catalogued as vulnerable by IUCN in its native range (Cassinello et al. 2008). However, it has been introduced into several countries of Europe and America in the twentieth century. In southeastern Spain the aoudad was introduced in the 1970s motivated by hunting interests (Cassinello 1998; Valverde 2005) to protect the semiarid landscapes of Murcia through the presence of a hunting large herbivore adapted to the dry conditions (Valverde 2005) and probably also for conservation purpose (Valverde 2004). The individuals for the introduction came from different zoos and from unknown African origin. The fact of the introduction of an exotic species outside of its native range for conservation purpose is currently known as "assisted colonization" (Seddon 2010). Thus, the introduction of the aoudad in the Iberian peninsula for conservation purpose might be considered a pioneering example of an assisted colonization before this concept had been fully established. Moreover, animals from the Western Sahara (Spanish protectorate at that time) of several threaten ungulates (dama gazelle *Nanger dama*, dorcas gazelle *Gazella dorcas*, Cuvier's gazelle *Gazella cuvieri*, and aoudad) were brought to a captive breeding center created in Spain in 1971 for conservation purposes (currently called Experimental Station of Arid Zones, EEZA by its initials in Spanish; https://www.eeza.csic.es).

Since the 1990s, both the aoudad and Iberian ibex have co-existed in some mountains of the Region of Murcia (SE Spain), and the expansion of both species has been apparently influenced by habitat connectivity and interspecific competition (Anadón et al. 2018). Previous studies indicate that the introduced aoudad could compete with native ungulates, particularly with the Iberian ibex (Acevedo et al. 2007; but see Cassinello 2018). Besides the aoudad has been described as a potential hazard to threatened vegetation due to high population densities, although this deleterious effect could be caused by other overabundant large herbivores, even native species (Velamazán et al. 2017). Furthermore, crop damage has been also pointed out as another emergent issue leading to the application of management tools such as diversionary feeding to mitigate these impacts (Pascual-Rico et al. 2018). Due to these problems associated with the exotic species (see Mori et al. 2017), the aoudad was first included in the Spanish catalogue of invasive species in 2013 (Real Decreto 630/2013, Spanish Government) although the population in Murcia Region introduced legally before 2007 was excluded. However, in a sentence by the Spanish Supreme Court (sentence 637/2016) following a demand by conservationist, the aoudad was included as an invasive exotic in all its range within the Spanish territory, which spurred a heated debate among the main stakeholders (i.e. wildlife managers, hunters, ecologist, farmers and conservationists). The potential competition between the aoudad and the Iberian Ibex was one of the main arguments to consider the exotic aoudad as an invasive species. Nevertheless, after national Government approved a law (Law 7/2018) to return to the situation in which aoudad populations introduced legally before 2007 are not considered as invasive species. Given the changing legislative situation of a current conservation conflict among the stakeholders abovementioned, it is necessary to assess with scientific criteria the potential competition between the aoudad and the Iberian ibex.

Our main objective with the present study was to evaluate the potential competition between the Iberian ibex (native species) and the aoudad (exotic species) in the mountain ranges where they live in sympatry. Specifically, we evaluated the ecological niche overlap along two main dimensions, the environmental niche and the trophic niche, because they are the commonest partitioned dimensions (Schoener 1983; Toft 1985). Then we assessed the spatial co-occurrence of both species on the fine scale. We expected that if a niche overlap was high, competition could drive spatial segregation to allow co-existence.

Material and methods

Study area

The study was conducted in different areas in the Region of Murcia (SE Iberian Peninsula; see Fig. 1 and Table A.1) where both the Iberian ibex and aoudad (Artiodactyla order) co-exist. The study area includes mountain ranges with a mean of 116.7 ± 71.6 km^2

and 1239.6 ± 321.1 m.a.s.l. (see Table A.1for more detailed data on each mountain range included in the study). The climate is Mediterranean, the mean temperature range from 10 to 16 °C, and the mean rainfall of 375 mm per year.

Region of Murcia forms part of the Iberian ibex's historical range, which drastically declined in the first half of the twentieth century, followed by recovery over the last five decades (Anadón et al. 2018). The aoudad was introduced into the region in the 1970s for hunting purposes, specifically in the Sierra Espuña Regional Park (37°47′–37°56′N, 1°27′–1°40′W). Since then, this exotic species has spread to other mountains in the region (see Supplementary Material A.1 for more biological information about study species).

Trophic niche overlap

We, in collaboration with local hunters, collected hair samples of both ungulates (Iberian ibex n = 25, of which 10 males, 13 females and 2 indeterminate samples; aoudad n = 26, of which 13 males and 13 females) during different hunting seasons in 2013 and 2014 in the Region of Murcia (Fig. 1). In all cases, the frontal dorsal hair nearest the skin was collected and cut by stainless steel surgical scissors. All hair samples were immediately stored in a paper envelope tube until their isotopic analyses were conducted. All hair samples were cleaned and powdered, and 0.3–0.4 mg of each hair sample was packed into tin capsules. Isotopic analyses were performed at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana (www.ebd.csic.es/lie/index.html). Samples were combusted at 1020 °C using a continuous flow isotope-ratio mass spectrometry system (Thermo Electron) by means of a Flash HT Plus elemental analyzer interfaced with a Delta V Advantage mass spectrometer which applies international standards, run each 9 samples; LIE-CV and LIE-PA, previously normalized with the international standards IAEA-CH-3, IAEACH-6, IAEA-N-1 and IAEA-N-2. Stable isotope ratios were expressed in the standard δ-notation (‰) relative to Vienna Pee Dee Belemnite (δ^{13}C) and atmospheric N_2 (δ^{15}N). Based on laboratory standards, the measurement error (standard deviation) was ± 0.1 and ± 0.2 for δ^{13}C and δ^{15}N, respectively.

The trophic niche overlap was measured by comparing the degree of isotopic overlap between species (Jackson et al. 2011). As alternative to the isotopic metrics provided in SIBER procedures (Jackson et al. 2011), we examined the isotopic niche overlap between species adapting the framework proposed by Broennimann et al. (2012), which applies kernel smoothers to species occurrence in a two-dimensional gridded space. In our case, this space was defined for the respective overlap analysis by the δ^{15}N and δ^{13}C

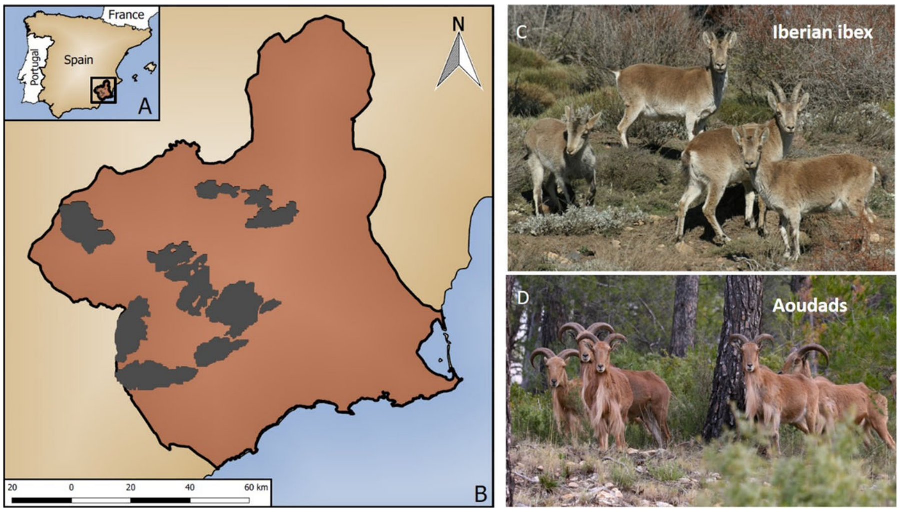


Fig. 1 **a** Position of the study area in the Iberian Peninsula. **b** Map of the study area (mountains in the Region of Murcia, SE Spain). Black areas indicate the mountains where the Iberian ibex and the aoudad co-exist. **c** and **d** are pictures of the study species in the study area

values of all the individuals (see Navarro et al. 2015). Specifically, the trophic overlap based on the isotopic values of both species was calculated using the D-metric, which ranges from 0 (no overlap) to 1 (complete overlap). We applied a permutation-based approach (100 permutations) to evaluate whether the overlap values were higher than expected at random according to the available isotopic space (similarity test, Warren et al. 2008). These analyses were conducted using the 'ecospat' library in R software. Interspecific differences in the δ^{15}N and δ^{13}C values were tested by using Student's t-tests. The significance level for all the tests was set at $p < 0.05$.

Environmental niche overlap

We developed an environmental niche model (ENM) for both species in the mountains that they share. Then we compared the similarity of the resulting models. We used the Maximum Entropy Software, Maxent 3.3.3 k (Phillips and Dudik 2008), to develop an ENM of the two species independently using presence-only data. We compiled presence records of each species using the observations obtained from the autumn censuses of target species. These censuses were made in 2012, 2014, 2015 and 2016 in the mountains where both species were present (Iberian ibex n = 174; aoudad n = 429). Species position data were transferred to a geographic information system. We assigned the presence records to a grid cell matrix of 200 × 200 m of the study area. We selected this grid size to obtain the highest resolution of the study area and to avoid the sampling error when assigning the field observations in the map. We used the area under the curve (AUC) that derived from the test data as a yardstick provided by Maxent to evaluate the model's efficacy. We considered test AUC values > 0.75 with sufficient discriminatory capacity (Elith 2000).

To predict the habitat suitability of both the Iberian ibex and aoudad, we used land cover and topography variables as environmental predictors (Table 1). Land cover variables represented the percentage cover of the habitat in the study area in a 200 × 200 m grid cell. Topography variables were obtained from a 5-m resolution digital elevation model, from which the elevation and slope variables were developed. The nature of our variables as well as the size of extent and grain of our models thus define niche overlap analysis related to landscape habitat use patterns, rather than distribution limiting factors, that would act at larger spatial scales.

We employed ENMToolsv.1.4.4 (Warren et al. 2010) to measure the similarity of the ENMs generated with MaxEnt. With this software, we calculated Schoener's (1968) D index to quantify niche similarity, which was estimated by comparing habitat suitability for each grid cell of the study area using ENMs.

To test whether ENMs were more similar than expected by chance, we ran a background test. To do so, the test generates a null distribution for the ENM difference expected between one species and the occurrence points placed at random within the range of the other species. The niche similarity hypothesis among species is rejected if Schoener's D is significantly higher or lower than those expected from the null distribution (Warren et al. 2010). In our case, significantly higher or lower values implies that D is over the 0.975 percentile or below the 0.025 percentile (the equivalent to $p = 0.025$) of the null distribution values (two-tailed comparison), respectively.

Spatial segregation

We tested if our study species more or less co-occurred spatially than expected by random on the 200 × 200 m grid scale. To calculate the number of cells occupied by at least one species, we used QGIS (2017). The obtained dataset consisted in a presence–absence matrix with rows taken as species (n = 2) and columns as occupied cells (n = 465). We used the "cooccur" package in R (Griffith et al. 2016), which

Table 1 Predictor variables used to assess habitat. All the variables were continuous

Variable	Source
Land cover	
Forest	CLC 2012 CC-BY 4.0 ign.es
Shrubland	
Grassland	
Rocky	
Croplands	
Artificial areas	
Topography	
Elevation	MDT5 2009 CC-BY 4.0 ign.es
Slope	Derived from MDT5 2009 CC-BY 4.0 ign.es

applies the probabilistic model of species' co-occurrence (Veech 2013) to assess if species co-occur positively or negatively.

Results

Trophic niche overlap

The $\delta^{15}N$ and $\delta^{13}C$ values did not differ statistically between species ($\delta^{15}N$, Iberian ibex = 3.68 ± 1.05 ‰, aoudad = 3.38 ± 095 ‰, $t = -1.08$, $p = 0.28$; $\delta^{13}C$, Iberian ibex = − 23.85 ± 0.66 ‰, aoudad = − 23.94 ± 0.87‰, $t = -0.42$, $p = 0.67$). Similarly to the isotopic values, the isotopic niche overlap was high between both species (D-index = 0.59, $p = 0.23$), the trophic niche of the aoudad overlapped 84.4% the trophic niche of the Iberian ibex, and conversely, the trophic niche of the Iberian ibex overlapped 77.6% the trophic niche of the aoudad (Fig. 2).

Environmental niche overlap

The AUC of the MaxEnt model for the Iberian ibex was 0.88, and the AUC for the aoudad was of 0.82. Both species showed a very similar distribution of suitable areas (Fig. 3). For the Iberian ibex, the model showed that this species correlated mainly with elevation and slope, and negatively with croplands. The other variables contributed less than 5% to the model. With the aoudad, croplands contributed the most and negatively to the model, as did slope, elevation and grassland (Fig. 4).

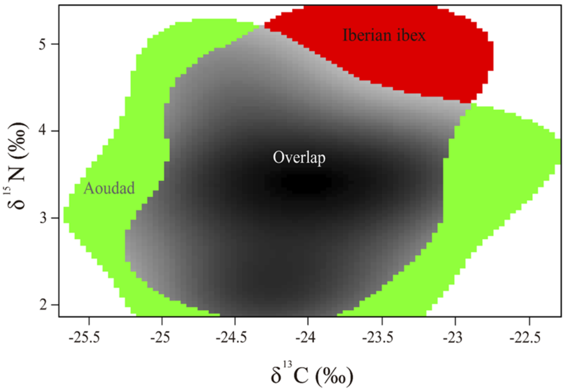


Fig. 2 Isotopic niche of both the Iberian ibex and the aoudad, and the overlap niche between them

The environmental niche overlap between the studied species was quantified using Schoener's D index, which was 0.71. The background test indicated that our study species were more similar than expected by chance (Schoener's D > 97.5% of the null distribution values; Fig. 5).

Spatial segregation

In the spatial segregation analysis on the fine scale, of the 465 cells of 200 × 200 m occupied by at least one of the two species, we found that only six were both co-occurred species. The spatial co-occurrence analysis showed a negative significant association between the Iberian ibex and the aoudad ($p < 0.001$).

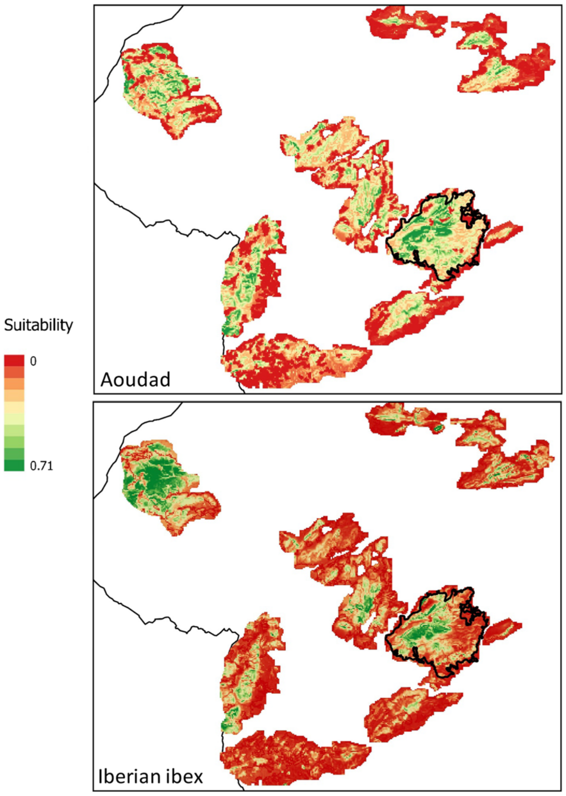


Fig. 3 Habitat suitability models for both the aoudad and Iberian ibex as assessed from MaxEnt. The province and the Sierra Espuña Regional Park limits (black lines) are shown for spatial reference

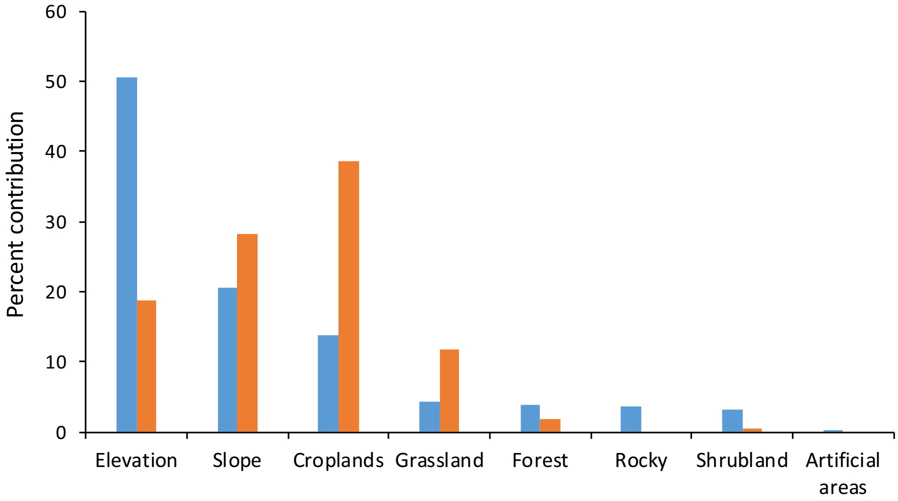
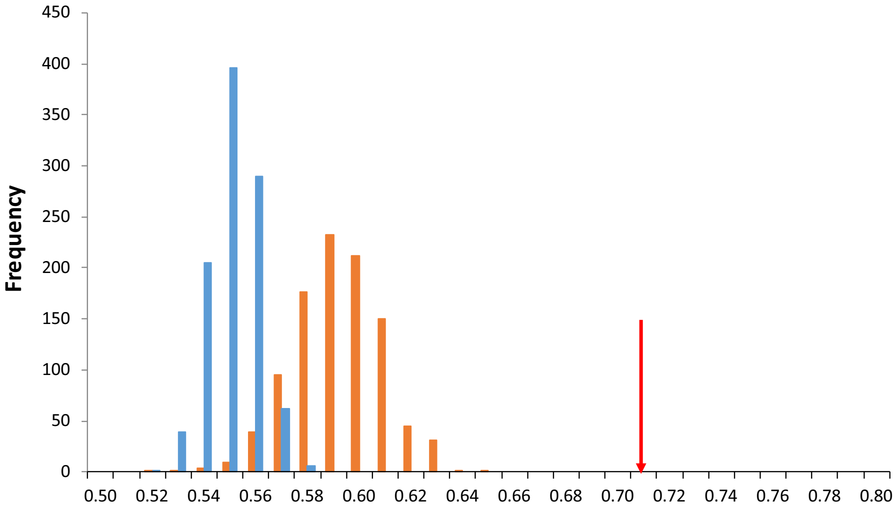


Fig. 4 Contribution of the environmental variables to construct the MaxEnt environmental niche models for both the Iberian ibex (blue bars) and aoudad (orange bars)

Fig. 5 Background test histograms for the Iberian ibex (blue bars) and the aoudad (orange bars). Schoener's D index (red arrow) was higher for the null distributions generated of both the aoudad and Iberian ibex. This indicates that the two species are more similar than expected based on available habitat



Discussion

Our study case provides us with the opportunity to evaluate, in several ways, the differences in the ecological niche between exotic and native species of the same ecological guild. According to the stable isotope analysis results, the Iberian ibex and the aoudad showed high trophic niche similarity. Regarding habitat selection based on environmental niche models, the study species showed a large overlap in habitat use, but with slight differences on the fine scale. In the co-occurrence test, as the studied species showed a negative association, they avoided co-occurring on the fine scale. These results indicate that both species potentially compete in the trophic and environmental niche dimensions, and that spatial segregation might be a key mechanism to allow for long-term co-existence.

Trophic niche overlap

Although stable isotope analyses do not provide definitive assessment of diet in the manner of stomach content analysis, feeding observations or faecal analysis (Layman et al 2012), it is a useful tool employed for reconstructing diets (Kelly 2000; Layman et al.

2012). The isotopic analysis of hair implies that the levels of nitrogen and carbon correspond to the plants eaten several months before. So, the results reflect the diet of the animals during the spring and early summer, when the plant productivity (NDVI) is maximum in the region (see Barbosa et al. 2019) and therefore the food available is greater than during the rest of the year. $\delta^{15}N$ is a proxy of a species' trophic level (Peterson and Fry 1987) and, although herbivores can consume vegetation with different $\delta^{15}N$ levels (Pacyna et al. 2018), no differences were found in our study species. Nevertheless, similar $\delta^{13}C$ values indicate that species feed on the same kind of vegetation, in our case C3 plants; i.e. they were mainly browsers in our study area. However, it must be considered that the feeding patterns of ungulates do not remain constant over time and some species show high feeding plasticity (Acevedo and Cassinello 2009; Lehmann et al. 2011). Studies about the Iberian ibex have demonstrated that browsing focuses on shrub or tree species. (Martínez 1989, 2002). The aoudad in the southeast of the Iberian Peninsula also showed preference for shrub species (Fernández-Olalla et al. 2016). Moreover, our study species also feed on grass and forb species (Martínez 1989, 2002; San Miguel et al. 2010). Therefore, the proportion of browse, grass and forb eaten by both the Iberian ibex and the aoudad might depend on vegetation availability, season and the weather conditions (Cassinello 1998; Wilson and Mittermeier 2011). For example in their natural distribution area, both species can habit from sea level up to about 3000–4000 m (Cassinello 1998; Granados et al. 2007), which indicates that they can occupy ecosystems with different plant communities. Moreover, the dietary plasticity of both ungulates allows them to feed on less palatable plants, such as *Rhamnus lycioides* bushes and *Pinus halepensis* trees (San Miguel et al. 2010). In our case, and according to the values established by Moreno-Gutiérrez et al. (2012) for $\delta^{13}C$ of leaf cellulose for several plant species, *S. tenacissima* forbs and *R. lycioides* bushes may form an important part of the diet of both the Iberian ibex and the aoudad in our study area.

The aoudad showed a higher standard deviation of the $\delta^{13}C$ levels than the Iberian ibex. Hence its trophic amplitude was wider. The trophic niche overlap of the aoudad on the Iberian ibex was higher than that of the Iberian ibex on the aoudad. These results may indicate that the aoudad feeds on a higher diversity of plants than the Iberian ibex, which could be interpreted as an advantage for the exotic species *versus* the native species. Nevertheless, native herbivores may have narrower trophic niches than sympatric exotic species because the diet of the former includes fewer items, but exploits better the resource by feeding on the most nutritious plants available (Jarman and Sinclair 1979; Reus et al. 2017).

Environmental niche overlap

The ecological niche models reveal that both the Iberian ibex and the aoudad similarly respond to habitat features, although the percentage contribution of each variable varied. The distribution of both species is positively linked to elevation and slope, and altered areas (i.e. croplands) appeared to be avoided. It is interesting that despite including only the mountain ranges where both species cohabit in this study, the ENMs slightly differed from one another. This means that the species in these restricted areas did not distribute in the same way. These results agree with previous studies conducted for both species (Acevedo et al. 2007; Anadón et al. 2018).

One of the ways to detect ecological niche differences is by comparing the ENMs developed by the MaxEnt software, which has been demonstrated as the most capable method for modelling distributions of mammals and other species (Hernandez et al. 2008; Phillips et al. 2006). According to de Boer and Prins (1990), a large overlap in habitat use could be a sign of non problematic co-existence between two species, while a small overlap might indicate segregation processes due to competition. The niche overlap found for our study species was large (Schoener's D index = 0.71), and the background test showed that the environmental niches for both species were more similar than expected. This may be related to the fact that both species (included in the Caprini tribe) present morphological, biological and behavioural similarities.

Spatial segregation

If the niche overlap was large, we expected competition possibly drive spatial segregation. Our results showed that spatial segregation could already be acting as a mechanism to allow for co-existence, despite the interaction noted between our study species being a result of recent human intervention (with no common evolutionary history). Therefore, if we consider that our results indicate that both species are ecologically similar in terms of the evaluated niche dimensions and the detected spatial segregation, then both species could compete, especially when resources are limited; e.g., when environmental perturbations occur, such as drought periods. Competition between both the Iberian ibex and the aoudad could lead to one species' displacement, and even to one of them eliminating the other through the principle of competitive exclusion; i.e. one competing species eliminating or excluding another species (Hardin 1960). To determine the output (i.e. competitive exclusion or co-existence), it will be necessary to estimate the competition coefficient of each species and the carrying capacity of the environment in future research.

In summary, in the given conditions, the strong similarity in the trophic and environmental niche of both the Iberian ibex and the aoudad indicates potential competition between them. However, the spatial segregation on the fine scale seems to act as a mechanism to facilitate the co-existence between the native and exotic ungulate species.

Currently the aoudad has been eliminated of the Spanish Catalogue of Invasive Exotic Species for some areas where it was introduced. However, Carboneras et al. (2017) created a prioritised list of invasive alien species where the species are ranked according to their potential threat to biodiversity in Europe. According to this list, the aoudad is considered in an invasion phase and it may be a major impact to biodiversity and ecosystems. This study sheds light on the research gap that exists on the interaction between the Iberian ibex and the exotic aoudad, which can be applied in the development of wildlife policies aimed at better management and conservation of the species.

The zoologist J. A. Valverde anticipated the future consequences of human activities on the Sahara's megafauna (see Durant et al. 2014; Brito et al. 2018) when he proposed the aoudad introduction in the Iberian Peninsula (Valverde 2004). However, this pioneering assisted colonization example, accomplished more than 40 years ago, failed to forecast the ongoing conflicts among different stakeholders and native species from a conservation perspective. Nowadays, assisted colonization is a controversial tool due to the possible consequences that may result (Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009), both short and long-term. Although it is rarely used (e.g. Kuussaari et al. 2015), there are several proposals for its application (e.g. https://theaustralianrhinoproject.org) that should be done with caution, if finally this tool is applied (Loss et al. 2011).

The situation of the aoudad in Spain is paradoxical, since it is catalogued as vulnerable in its native range. However, there are other similar cases around the world. The Philippine deer (*Rusa marianna*) and the banteng (*Bos javanicus*) are vulnerable and endangered, respectively, in their native range. However, these two species were introduced in other non-native areas where they established in the wild (Bradshaw et al. 2006; MacKinnon et al. 2015). Gibson and Yong (2017) proposed translocation of these introduced populations to their native ranges if threats to the species disappear. Thus, it is possible to mitigate conflicts and impacts in the non-native areas and contribute to the conservation of species in their native range.

Ungulates (Artiodactyla order) are the mammals with the highest proportion of successful introductions around the world (Clout and Russel 2007). In their natural ranges, their abundance and distribution are increasing, which also occurs in new colonised areas for introduced species (Apollonio et al. 2010). The consequences of herbivore ungulate introduction, whatever the reason, can alter biodiversity interactions (Vázquez and Simberloff 2003), and tend to strongly impact the new ecosystems that they occupy (Duffy 2003). One of the new processes that may appear is competition with native species, especially within the same guild (see Dolman and Wäber 2007). However, competition interactions are not easy to demonstrate in the field because manipulations to evaluate changes in carrying capacity and population dynamics in relation to the relative abundance of interacting species are difficult to perform in the wild (Hakkarainene and Korpimäki 1996). Nevertheless, our results show that integrating information on trophic and environmental niche overlap with fine scale spatial distribution might improve the study of competitive interactions among wild ungulates and support science-based management decisions.

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