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RESEARCH ARTICLE

Past, present and future of wild ungulates in relation to changes in land use

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Abstract In recent decades, Mediterranean landscapes have been experiencing more rapid changes in land use than usual, which have affected the ecology of the species inhabiting this biodiversity hotspot. Some studies have assessed the effect of such changes on biodiversity, but most of these were diachronic studies of population dynamics, or synchronic studies of species habitat selection, whereas few studies have simultaneously taken into account temporal changes in habitat composition and changes in species distribution. This study analysed the effects of land-use changes on the distribution of wild ungulates (*Capreolus capreolus*, *Capra pyrenaica*, *Cervus elaphus* and *Sus scrofa*). Using favourability function and Markov chain analysis combined with cellular automata, we addressed the following objectives: (i) to examine the environmental determinants of ungulate distribution in the past (1960s) and present (1990s), (ii) to model land use for 2040 to forecast future species distributions and (iii) to assess the biogeographical differences between the above-mentioned study periods (past–present and present–future). Species favourability was predicted to be more widely distributed in the present than in the past, but this increase varied across species. Areas predicted to be favourable in the present should remain stable in the future, but in addition there will be more new favourable areas not previously occupied by these species. The results are discussed from the perspective of the socio-economic relevance of wild ungulates in relation to some unfavourable areas of Mediterranean regions.

Keywords Bovidae · Cervidae · Favourability function · Global change · Markov analysis · Predictive models · Suidae

Introduction

We are currently experiencing more rapid changes than usual in the global environment driven by human activities. One of the main concerns is the transformations in land use that have occurred within—in a historical context—a relatively short period (Vitousek et al. 1997). Land-use change has greatly altered a large proportion of the earth's land surface to satisfy mankind's immediate demands for

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natural resources (Lambin et al. 2001). These have resulted in substantial ecological consequences, such as a decline in biodiversity (e.g. Zhao et al. 2006). Agriculture is the most widespread type of land use in Europe, so any change in this can produce environmental changes that affect species diversity and distributions (e.g. Moreira and Russo 2007).

Land-use changes appear to have had a substantial impact on biodiversity in Mediterranean landscapes, as shown by a large number of studies (e.g. Suarez-Seoane et al. 2002; Falcucci et al. 2007). Further, most of these examples are diachronic studies of population dynamics or synchronic studies of species habitat selection. Few studies simultaneously take into account temporal changes in habitat distribution and changes in species spatial distribution (but see Sirami et al. 2009) to assess the effects of land-use changes on wildlife. On the other hand, most of the examples of the effects of land-use changes on vertebrate populations come from bird studies (e.g. Gil-Tena et al. 2009). However, few studies have analysed the effects of land-use changes on the past, present and/or future distribution of mammals in Europe.

Human land use is affected by several factors related to private and public choices (e.g. Lambin et al. 2001). The complex nature of human decisions makes it difficult to predict future land uses with any degree of confidence. To address the difficulties in modelling land-use change, a range of scenarios can be produced (e.g. Araújo et al. 2007). These scenarios are consistent simulations based on plausible but necessarily simplified assumptions of how the future may develop—for example those according to the Intergovernmental Panel on Climate Change (Nakicenovic et al. 2000)—and they are the only opportunity to evaluate the expected effects of land-use changes on vertebrate populations.

It is widely known that land-use changes have affected the distribution and abundance of game species in the recent past (see Gordon 2009). Agricultural intensification and landscape diversity have been shown to be relevant in modulating ungulate population dynamics (Acevedo et al. 2005, 2006). Thus, according to the landscape transformations described by Bouma et al. (1998), we expect that the current distribution of wild ungulates has increased compared to the past in those regions where agriculture was considered uneconomical and land abandonment and renaturalization have occurred, but have decreased in places where human activity has increased (see Hewison et al. 2001). Certain peculiarities increase the interest of game species as a study model. Useful data on game species are available from hunting records, and thus species population trends can be monitored in the long-term (e.g. Milner et al. 2006). Due to the high socio-economic importance of these species, studies focussing on how land-use changes and future land use will affect their distributions are of special interest for management purposes and could be used for hunting planning (see Acevedo and Cassinello 2009a).

The development of predictive habitat distribution models has recently gained importance as a relevant tool to assess the impact of global change on species' distributions (e.g. Thuiller et al. 2008). However, although many studies have explored the dynamics of land-use change (see Agarwal et al. 2002), only a few have used habitat distribution models to address the impact of land-use changes on animal populations (but see Lütolf et al. 2009). A variety of statistical models can be used to evaluate the impact of land-use changes on ecosystems as well as to predict the potential ecological consequences of future changes in land use (e.g. Millington et al. 2007). Amongst them, the favourability function (Real et al. 2006) is highly recommended to compare models of different species (see Acevedo et al. 2010). In addition, fuzzy logic can be applied to favourabilities—but not to probabilities or suitability values obtained with other methods—to compare the effect of land-use changes on the distribution of areas favourable to species in the future (Real et al. 2010). This makes favourability functions useful for biogeography conservation since it enables the assessment of geographical relationships not only between species, but also for the same species in different study periods, as in this study.

Our main objective was to assess the effect of changes in land use on species distribution in an area where there has been a large reduction in landscape diversity in recent decades (Fernández-Alés et al. 1992). Specifically, we (i) describe environmental favourability for wild ungulates in the past and present, (ii) model land use for 2040 to forecast wild ungulate distribution in the future, and (iii) assess the biogeographical differences between past–present and present–future periods quantifying rates of increase, overlap, maintenance and shift of the favourability functions.

Materials and methods

Study area

This study was conducted in Andalusia, which covers 87268 km^2 in the southernmost part of mainland Spain. It is administratively divided into 771 municipalities, which were the territorial units used in the analyses (Fig. 1). The average area per municipality was 114.92 ± (SD) 147.18 km^2 (range 1.77–1247.14 km^2). The main mountain ranges are the Sierra Morena, along the northern fringe of the region, and the Baetic System, sub-divided into two ranges, Sub-baetic and Penibaetic (Fig. 1). The dominant vegetation in mountain ranges comprises pine forests, evergreen oak forests and scrubland. The most important plain is the Guadalquivir valley, which is longitudinally oriented. The valley bottom is covered by dry-farming herbaceous crops and river terraces, and the hill slopes by dry-farming woody crops. For additional details on the study area see Vargas et al. (2007) and Farfán et al. (2009).

Species data

To evaluate the associations between wild ungulates and land uses we modelled the abundances of the Iberian wild goat (*Capra pyrenaica*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), which are the most relevant big-game species in Andalusia (Vargas et al. 2007). For each species we distinguished the municipalities with high abundances from those with low abundances in the present (1990s) and in the past (1960s), using information from current hunting yields and from game species abundance maps available from the Mainland Spanish Fish, Game and National Parks Service, respectively (for details see Delibes-Mateos et al. 2009). Our response variable was a binomial index of abundance (IA) for each species in the Andalusian municipalities in which one and zero were assigned to high and low abundance data, respectively (Delibes-Mateos et al. 2009; Farfán et al. 2009). This was done by reclassifying logarithmic transformed hunting yields (for present) or abundance data (for past) into a six equal interval classes. The three highest classes were assigned an IA value of one, and the three lowest classes received a zero. Abundance and hunting yields are not always equivalent measures (Lucio 1991), as they are not the same quantitative variable. However, hunting yields provide a coarse but realistic picture of good and poor areas at broad spatial scales when absolute abundance values are lacking (Vargas et al. 2006).

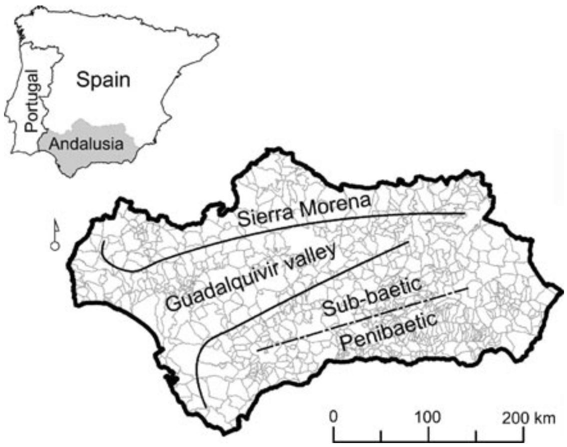

Fig. 1 Study area. Schematic representation of the main mountain ranges (the Sierra Morena, and the Baetic System sub-divided into two ranges, Sub-baetic and Penibaetic) and the largest plain (the Guadalquivir valley). Municipalities' boundaries are also shown

Environmental predictors

Spatial factor and topography

We obtained IAs for each game species and study period and related them to six predictor variables that provide information on the spatial location (latitude and longitude; Legendre 1993) and topography (four variables) in the Andalusian municipalities (Table 1). Altitude was obtained as a digital coverage by the Land Processes Distributed Active Archive Center with 100 m spatial resolution. Slope was calculated based on altitude using Idrisi (Eastman 2004). Exposures to the south and west were derived from GlobDEM50 high-resolution digital elevation data, based on raw data from the Shuttle Radar Topography Mission (Farr and Kobrick 2000) with the same spatial resolution of the previous coverage.

Past and present land use

We related the IAs to 23 land-use predictor variables in the Andalusian municipalities (Table 1). Variables

Table 1 Variables used to model favourability for big-game species in Andalusia

Code	Crop variables
IHER	Irrigated herbaceous crops (% area)[a]
IWC	Irrigated woody crops (% area)[a]
DHER	Dry herbaceous crops (% area)[a]
DHET	Dry heterogeneous crops (% area)[a]
IHET	Irrigated heterogeneous crops (% area)[a]
DWC	Dry wood crops (% area)[a]
MCNV	Mosaic of crops and natural vegetation (% area)[a]
HCWO	Herbaceous crops with oaks (% area)[a]
	Natural vegetation variables
BL	Built land (% area)[a]
WETL	Wetlands (% area)[a]
PAST	Pasture (% area)[a]
OAKW	Oak wood (% area)[a]
PWO	Pasture with oaks (% area)[a]
PWC	Pasture with conifers (% area)[a]
DSWO	Dense scrub with oaks (% area)[a]
SS	Sparse scrub (% area)[a]
SSWO	Sparse scrub with oaks (% area)[a]
DSWC	Dense scrub with conifers (% area)[a]
SSWC	Sparse scrub with conifers (% area)[a]
SSWD	Sparse scrub with diverse trees (% area)[a]
DSWD	Dense scrub with diverse trees (% area)[a]
CW	Conifer wood (% area)[a]
DS	Dense scrub (% area)[a]
	Topographical variables
ALTI	Altitude (m)[b]
SLOP	Slope (%)[b]
SE	Exposure to the south[c]
WE	Exposure to the west[c]
	Spatial variables
LONG	Longitude of the municipality's centroid
LAT	Latitude of the municipality's centroid

Sources: [a] Junta de Andalucía (2009)

[b] US Geological Survey (1996)

[c] derived from GlobDEM50 (Farr and Kobrick 2000)

related to land use were obtained for 1960s, 1990s and also for 2003 (Junta de Andalucía 2009). Variables for 2003 were not used for distribution modelling purposes; they were used only to validate predictions on changes in land use (see below). All these variables were obtained by transforming the corresponding digital polygons into raster images, and each pixel (1 pixel = 1 km^2) was assigned to the dominant land use. Finally, we extracted the proportion of each type of land use for each municipality.

Forecasting land-use maps (future): CA–Markov

To simulate how land use in future may develop, we assumed that transition rates observed in the past decades will remain similar in the next ones (e.g. Peterson et al. 2009). Markov chain analysis was used to model future land use on the basis of the preceding states; that is, a matrix of observed transition probabilities between states was used to project future changes in the landscape from current patterns. As spatially proximate objects are often more likely to exhibit similar attributes (Miller and Franklin 2002), we used a Markov and cellular automata (CA–Markov) approach to incorporate neighbouring states and improve model predictions of complex natural patterns (Deadman and Brown 1993). Transition matrices, representing the probability of change between individual land-use classes, were calculated for two periods, 1960–1990s and 1990s–2003, using the corresponding land-use maps (see above). A 5 × 5 contiguity filter was applied to define the neighbourhood of each cell and used to weight the suitability of areas near each existing cover type, thus defining the probability of establishment of each cover type (see Peterson et al. 2009). Three maps were generated: (i) the 2003 land-use map was predicted from the 1990s map and the 1960–1990s transition rates and compared to the data observed for 2003; (ii) the future (2040) land-use map was predicted from the 1990s data using the 1960–1990s transition rates and (iii) the future land-use map was also predicted from data for 2003 based on the 1990s–2003 transition rates. We obtained two maps for 2040 with different transition matrices to assess the consistency of our estimates at the municipality level.

We compared the observed and predicted percentages for 2003 and also both predicted percentages for 2040 using Pearson correlations. We also calculated the observed increase rate per land use (difference between percentages observed for the 2003 and 1990s maps) and the expected increase rate (difference between predicted percentages in land use for the 2003 map and observed percentages for the 1990s map). Both rates were correlated to assess if the municipalities with greater observed changes were also those where higher rates were predicted. Similarly, we compared the increase rates predicted for 2040 to our two transition matrices.

Favourability

For each species, we performed stepwise logistic regression (Hosmer and Lemeshow 1989) for IA on the predictor variables, for 1990s and 1960s data, to select a subset of significant predictor variables of wild ungulate distribution. We then used the favourability function described by Real et al. (2006) to eliminate from the model the effect of sample prevalence. The favourability for IA in each municipality is obtained from the formula:

$$F = \frac{P/(1-P)}{(n_1/n_0) + (P/(1-P))}$$

where P is the probability value given by logistic regression, and n_1 and n_0 are the number of municipalities with IA equal to 1 and 0, respectively. Residuals of the logistic functions were examined and tested for autocorrelation using the Moran's I spatial autocorrelation statistic (see Diniz-Filho et al. 2003). Moran's I test was checked for significance with the Bonferroni-corrected significance level.

We applied variation partitioning procedures to the final models (Borcard et al. 1992; Legendre 1993) using the four factors described in Table 1 (crops, natural vegetation, topography and spatial factor) to enhance their explanatory power and improve the reliability and interpretation of multiple regression in the presence of multicollinearity (Graham 2003). We estimated the variation independently explained by each factor (pure effects) and the variation simultaneously explained by two or more factors (overlaid effects) following subtraction techniques similar to previous studies (e.g. Real et al. 2003).

To make comparisons between observed and predicted data, the continuous favourability variable generated by logistic regression had to be converted to a binary one (presence–absence). For this purpose, a threshold—cut-off point used to reclassify model outputs as presence (over the threshold) or absence (under the threshold)—should be set at 0.5 for the favourability function (see Real et al. 2006). Parameters for models evaluation, sensitivity (ratio of correctly predicted presences to total number of presences), specificity (ratio of correctly predicted absences to total number of absences) and correct classification rate (ratio of correctly predicted presences and absences to total number of sampling sites) values were estimated from a confusion matrix to assess the agreement between the observed and predicted distributions. We also assessed the agreement between the model and the distribution data with Cohen's kappa coefficient (Fielding and Bell 1997). Values of kappa are between 0 and 1 (values close to 1 show a high level of agreement). Finally, the AUC was obtained to complete the characterization of the species distributions since it provides information about the generalist or restricted distribution in the study area (see Lobo et al. 2008).

Projections

Models created for one study period ('date 1') were projected onto another study period ('date 2') to predict the distribution of the areas favourable to the species in 2040 land-use scenario. Thus, areas favourable to each species at 'date 1' were projected to 'date 2' by replacing the date 1 land-use variables in the favourability models by those for date 2 (see Real et al. 2010). Values of the spatial and topographical variables were considered constant between periods.

Multicollinearity amongst predictors presents problems when a model is projected spatially or temporally outside the range of its calibration (see Barbosa et al. 2009). Consequently, we used each predictor's variance inflation factor (VIF) to quantify collinearity amongst predictors in the models for the present. VIFs were calculated for each predictor as the inverse of the coefficient of non-determination for a regression of that predictor on all others (see Zuur et al. 2010). VIF is a positive value representing the overall correlation of each predictor with all others in a model. Values >3 indicate 'moderate or high' collinearity.

Deconstructing favourability in the future: fuzzy logic

Favourability values can be regarded as the degree of membership of each area in the fuzzy set of sites which environmental conditions are favourable to the species, and which enables applying some fuzzy logic operations to distribution modelling (e.g. Real et al. 2006). The favourability function and the fuzzy indices derived from it are valuable tools to study biogeographical relationships between ecologically related species (Acevedo et al. 2010), as well as to assess for differences in the favourability patterns between scenarios such as those derived from climate (Real et al. 2010) or land-use changes. Thus, we used fuzzy logic indices described by Real et al. (2010) to calculate for each pair of past–present and present–future periods (1960–1990s and 1990s–2040, date1–date2, respectively) the increases in favourability (I), the favourability overlap (O), favourability maintenance (M) and the predicted shift in favourability (S):

$$I = \frac{cF_{\mathrm{date2}} - cF_{\mathrm{date1}}}{cF_{\mathrm{date1}}} \quad O = \frac{c(F_{\mathrm{date2}} \cap F_{\mathrm{date1}})}{c(F_{\mathrm{date2}} \cup F_{\mathrm{date1}})}$$

$$M = \frac{c(F_{\mathrm{date2}} \cap F_{\mathrm{date1}})}{cF_{\mathrm{date1}}}$$

$$S = \frac{Min[cF_{\mathrm{date1}} - c(F_{\mathrm{date2}} \cap F_{\mathrm{date1}}), cF_{\mathrm{date2}} - c(F_{\mathrm{date2}} \cap F_{\mathrm{date1}})]}{cF_{\mathrm{date1}}}$$

where, cX is the cardinality of the X fuzzy set (i.e. the sum of all the squares' favourability and Min is the minimum value). Fuzzy intersection is the minimum value between the favourability of two periods and fuzzy union the maximum value between them (Zadeh 1965).

Positive values of I indicate the species' expansion (denoted E), which is a gain in favourable areas, whereas negative values of I mean a net loss of favourability areas for the species (denoted L). The value L is considered an absolute value and if $L > 0$ then $E = 0$. Thus, date 2 favourability can be deconstructed by this expression:

$$cF_{\mathrm{date2}} = cF_{\mathrm{date1}} \times (M + S + E)$$

Results

Land-use scenarios

The transition matrices estimated for the 1960–1990s and 1990s–2003 models, representing the probability of each land-use class changing to another, are shown in Appendix 1. When predictions for 2003 using the 1960–1990s transition model were compared with observed land use in 2003, a close relationship was found (mean Pearson's coefficient ± SE, minimum–maximum, n: 0.981 ± 0.003, 0.947–0.999, 23). Consistent results were obtained when we compared the predictions for 2040 using the 1960–1990s and 1990s–2003 models (0.953 ± 0.007, 0.870–0.993, 23). Similarly, when the observed increase rate for 2003 (difference between percentages observed for the 2003 and 1990s maps) and the predicted increase rate (difference between predicted percentages in land use for the 2003 map and observed percentages for the 1990s map) were compared, highly significant correlations for all land-use classes were obtained (0.969 ± 0.005, 0.911–0.998, 23). The increase rates predicted for 2040 (calculated between 1990s and 2040) obtained from the 1960–1990s and 1990s–2003 models were also highly correlated (0.924 ± 0.011, 0.829–0.989, 23).

Favourability functions

We obtained significant models for each species and study period (past and present), excepting for roe deer in past, due to its reduced distribution. These models (see Table 2) were in agreement with the observed data according to the evaluation parameters, and all species showed restricted distributions in the study area according to AUC values (Table 3).

Two different spatial patterns in the favourable areas for IA in past were obtained, one for red deer and Iberian wild goat and another for wild boar (Fig. 2). The first two species were distributed outside of the Guadalquivir valley whereas the latter was mainly occupying that area. These spatial relationships amongst species were altered in the models for present in which wild boar shifted its distribution to the area occupied by red deer, and the Iberian wild goat and roe deer were restricted to the southern mountain areas (Fig. 2). Our results showed that species favourability was more widely distributed in the present model than it was in the past

Table 2 Logistic regression models and their corresponding statistics for wild ungulates in the past (a) and at present (b)

Variables	Models								
	Iberian wild goat			Red deer			Wild boar		
	B/SE	Wald	Sig.	*B*/SE	Wald	Sig.	*B*/SE	Wald	Sig.
(a)									
DHER	−3.17/5.93	0.286	0.593	−10.33/6.06	2.91	0.088			
DHET	5.79/1.91	9.21	0.002				−4.20/2.23	3.55	0.059
CW	9.90/2.60	14.52	<0.001						
SLOP	0.18/0.09	3.67	0.055				−0.17/0.05	12.99	<0.001
SSWO							2.74/1.59	2.95	0.086
DSWO							16.00/4.02	15.87	<0.001
DWC							1.31/0.52	6.30	0.012
MCNV							−13.74/4.67	8.64	<0.001
SSWC				6.93/2.10	10.89	0.001	13.72/4.25	10.43	0.001
HCWO							−26.46/12.42	4.54	0.033
LAT				0.04/0.01	8.21	0.004	0.01/0.01	7.33	0.007
LONG							0.01/0.002	27.88	<0.001
Constant	−7.51/1.62	21.34	<0.001	−89.70/30.03	8.92	0.003	−38.87/12.78	9.25	<0.001

Variables	Models											
	Iberian wild goat			Red deer			Roe deer			Wild boar		
	B/SE	Wald	Sig.	*B*/SE	Wald	Sig.	*B*/SE	Wald	Sig.	*B*/SE	Wald	Sig.
(b)												
DHER	2.81/0.74	14.50	<0.001	1.65/0.73	5.05	0.025						
IWC										−13.17/4.26	9.56	0.002
CW							8.61/3.26	6.98	0.008	5.70/1.62	12.37	<0.001
SSWO	7.98/1.68	22.54	<0.001									
DSWO				16.85/2.21	58.02	<0.001				9.23/2.12	18.85	<0.001
PWO				3.55/1.32	7.20	0.007				52.75/22.39	5.55	0.018
DSWC				11.10/3.38	10.78	0.001						
MCNV				−24.79/7.56	10.75	0.001						
HCWO							16.89/8.23	4.22	0.040			
SSWD	7.28/2.75	7.03	0.008							10.52/2.64	15.88	<0.001
PAST				11.80/2.97	15.77	<0.001	16.52/4.85	11.59	0.001	5.39/2.53	4.56	0.033
PWC				68.34/21.47	10.13	0.001						
DS										5.96/2.29	6.76	0.009
SS										2.37/0.49	23.41	<0.001
ALTI	$2*10^{-3}/3*10^{-4}$	23.86	<0.001									
OAKW										5.08/2.41	4.46	0.035
LATI	−0.04/0.01	34.17	<0.001	$0.01/5*10^{-3}$	5.62	0.018	−0.08/0.02	13.74	<0.001	$0.03/4*10^{-3}$	60.13	<0.001
Constant	90.21/16.06	31.56	<0.001	−30.33/11.35	7.14	0.008	170.79/47.25	13.07	<0.001	−64.24/8.09	63.00	<0.001

Abbreviations of variables as in Table 1

B parameter coefficient and its standard error (*SE*), *Wald* Wald test statistics, *Sig.* significance

Table 3 Summary of the parameters estimated to characterize the comparisons between the models and the observed distributions

Species	Study period	Sensitivity	Specificity	CCR	Kappa	AUC
Wild boar	Past	0.87	0.74	0.76	0.38	0.88
Iberian wild goat		1.00	0.84	0.84	0.09	0.95
Red deer		0.93	0.84	0.85	0.15	0.93
Wild boar	Present	0.70	0.76	0.74	0.44	0.81
Iberian wild goat		0.74	0.76	0.76	0.22	0.85
Red deer		0.78	0.85	0.84	0.44	0.90
Roe deer		0.87	0.93	0.93	0.31	0.98

Sensitivity, specificity and correct classification rate (CCR) are reported as proportions

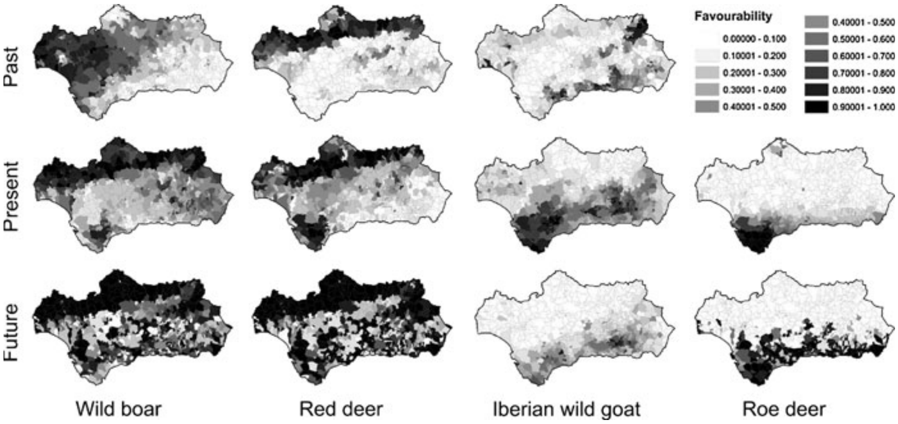

Fig. 2 Favourability and projections of favourability (for 2040) in each municipality of Andalusia for each big-game species and study period. Graduated colours from *black* (the most favourable areas) to *white* (the most unfavourable areas)

model, but this increase varied across species. According to obtained VIF values no effects of multicollinearity were expected in the projections (mean VIF value and range: 1.35, 1.10–1.59).

For all species, natural vegetation had relatively high weight in explaining species' favourability in the present models, but crops were particularly important past models (Fig. 3). Latitude and longitude were retained in most of the final models, mainly in those developed for present (Table 2), showing that IAs for that period were spatially structured. Moran's I of Pearson's residuals of each model indicated statistically significant spatial autocorrelation up to approximately 20 km. We did not considered this to be a problem with our modelling because the distance of spatial autocorrelation was small relative to the average size of the municipalities (Diniz-Filho et al. 2003).

Fuzzy indices

Fuzzy indices (I, O, M, S, E and L) were estimated for each species between past and present favourabilities, but also between the present models and those projected for the future (Table 4). Briefly, the highest I for the 1960–1990s period was obtained for red deer and Iberian wild goat (0.443 and 0.442, respectively). In the future scenario (1990s–2040 period), deer had the highest I (1.108 and 1.004 for roe deer and red deer, respectively). For the 1960–1990s and 1990s–2040 periods, we obtained high M (>0.666 and >0.529, respectively) for all species studied. For Iberian wild goat, we predicted a L (0.456) for its favourable areas in 2040. Areas that are currently favourable to wild ungulates are predicted to remain stable in the future. In addition, for all species except goats, there will be new favourable areas not previously occupied.

Discussion

On the methodological approach

The effect of land-use changes on species' distribution can be addressed using different approaches

Fig. 3 Variation partitioning of the final models. Values shown in the diagrams are the percentages of variation in high hunting yield in past (*in parenthesis*) and present explained exclusively by crops (CR), natural vegetation (NV), topography (TO) and spatial factor (SPA) and by the combined effect of these factors. Should be noted that the spatial factor was not retained modelling Iberian wild goat present abundance, but it was in the model for past; and, similarly the topography was not retained modelling wild boar past abundance, but it was in the model for present. See Table 2 for details about variables included in each of the above-mentioned factors

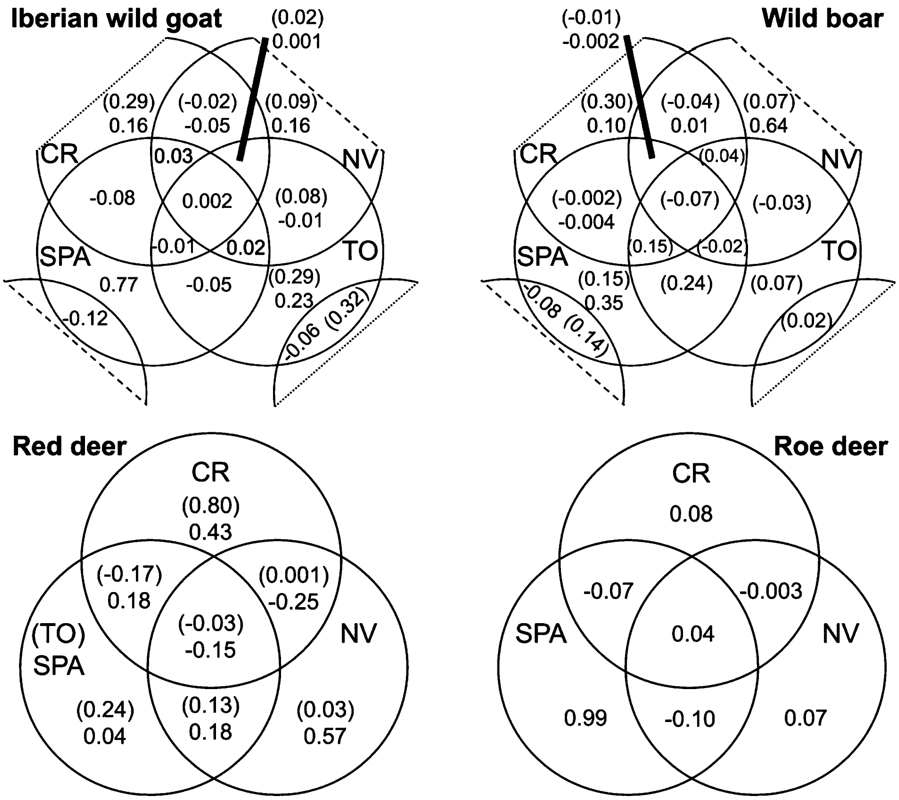

Table 4 Rates of overlap (*O*), maintenance (*M*), shifting (*S*) and increase (expansion [*E*] or net loss [*L*]) between the favourabilities obtained for each study period: past–present, and present–future (projection for 2040 based on the present model)

Species	Period	*O*	*M*	*S*	*E*	*L*
Wild boar	Past–present	0.411	0.666	0.334	0.286	0
Iberian wild goat		0.427	0.731	0.269	0.442	0
Red deer		0.431	0.736	0.264	0.443	0
Wild boar	Present–future	0.563	0.858	0.142	0.383	0
Iberian wild goat		0.521	0.529	0.015	0	−0.456
Red deer		0.413	0.877	0.123	1.004	0
Roe deer		0.344	0.796	0.204	1.108	0

(Lambin and Geist 2006). Many studies have used historical data to empirically derive transition matrices across landscapes (e.g. Conway and Lathrop 2005). Other studies have used landowner decision making (Pocewicz et al. 2008), and hypothetical scenarios considering different alternatives of land-use changes, such as various scenarios of agricultural intensification to assess the potential effect of these strategies on species' distributions (e.g. Lütolf et al. 2009). Even when the accuracy of the simulated scenarios is very difficult to assess, these approaches offer a way to think about alternative possibilities regarding change (Trees and Trees 2003).

Given the observed land-use changes between 1960 and 1990s, the future land-use scenarios we simulated were conservative and quite robust, as shown in the validation steps. Nevertheless, this should be interpreted within the context of the spatial resolution used in our study. At finer spatial scales, CA–Markov may not be a suitable procedure because it is able to correctly describe the change rate in land use, but is not able to accurately define the specific localities where the change will occur, as this procedure randomly converts pixels into new land-use categories within areas of highest probability of change (Deadman and Brown 1993). Future studies are needed to assess the limitations of CA–Markov in terms of spatial resolution.

On the other hand, fuzzy indices enhance the usefulness of the favourability function when, from a biogeographical perspective, the aim of the study is to compare models (Acevedo et al. 2010). There is a substantial body of literature describing and assessing the impact of various scenarios on species' distributions. Differences between scenarios are usually assessed using descriptive parameters of the species' distribution by scenario (e.g. Virkkala et al. 2008), and then they are directly compared or included in a simple change's index (e.g. Levinsky et al. 2007). 'Visual evaluation', not supported by any statistical analyses, has also been used to describe differences in the species distribution range predicted for different scenarios of change (Lütolf et al. 2009). The assessment conducted in this study, derived from Real et al. (2010), is a complete biogeographical description of change in species' distribution, since favourability in the future is deconstructed into the percentage that has increased, overlapped, maintained and shifted in relation to the current favourability.

Distribution models

The wild ungulates modelled are not homogeneously distributed within the study area. In this Mediterranean region big-game species are currently constrained to woodlands, whereas small-game species mainly inhabit agricultural areas (Vargas et al. 2007). However, the same spatial pattern was not obtained in the models for the past when wild boar was distributed in agricultural land (Fig. 2). Delibes-Mateos et al. (2009) found that wild boar distribution was significantly associated with small-game species distributions in the 1960s, but is currently related to the distribution of big-game species. They hypothesized this was a consequence of landscape transformations that had occurred over the past few decades; however, specific analyses to determine the changes were not conducted.

Our models provide more detailed explanations regarding the ecogeographical determinants of past and present favourability for each species. In general, natural vegetation and spatial factors had more weight in relation to explaining species' favourability in the models for the present, but crops were more relevant in models of the past. This pattern was observed for all studied wild ungulates (Fig. 3). A plausible explanation is that crops and natural vegetation were traditionally combined, thereby shaping heterogeneous landscapes in mountain areas occupied by ungulates. However, the abandonment of traditional agricultural usage in these areas has led to the homogenization of the landscape as a consequence of renaturalization (Fernández-Alés et al. 1992), and hence wild ungulates are currently occupying similar areas even when land use has changed (Gortázar et al. 2000).

This pattern cannot be generalized to wild boar, which has drastically altered its distribution area between the study periods. Our results show that favourability for wild boar in the past was determined by low areas with crops but is currently determined mainly by scrubland. The same argument we have previously used for goats and deer (i.e. rural abandonment) can be used to explain the changes between study periods observed for wild boar. This species was probably displaced from mountainous regions by humans in the past, since boar disturbances caused significant losses for traditional users of this landscape (e.g. Calenge et al. 2004). Mountain areas formerly managed with traditional strategies are currently only devoted to game and recreational purposes in our study area and have been re-occupied by boar, even attaining high densities.

Finally, favourability for roe deer was determined by spatial factors. Model predictions suggest that current favourability for roe deer is strongly related to historical factors, such as the locations where populations were released or where existing native populations re-colonized the territory (e.g. Acevedo et al. 2005).

Observed and expected trends in wild ungulate distributions

Our results show that areas favourable to wild ungulates were more constrained in the past than at present, which is in agreement with a generalized expansion of these species reported not only in the Iberian Peninsula (Acevedo et al. 2005, 2006, 2007a) but also in other European countries (Ward 2005; Falcucci et al. 2007). The increase in favourable areas in this period was not uniform for all species. Thus, red deer have expanded their distribution compared to the past, this process having been accelerated by human intervention (see Acevedo and Cassinello 2009a). On the other hand, the net increase of favourability for wild boar was smaller, and their distribution range was shifted probably due to landscape alterations derived from rural abandonment (see above). Finally, the Iberian wild goat showed a high rate of increase in present but it was forecasted to reduce in the future. The expansion of this species in the past decades in Spain was related to governmental protection aimed at regulating hunting pressure (see Pérez et al. 2002) and, to a lesser extent, to human translocations (Acevedo and Cassinello 2009b). Currently one of the main Iberian wild goat populations in the study area—Sierra Morena—exists in a very fragmented landscape and is likely constrained by other ungulates (Pérez et al. 2002). Our results suggest that, in addition to competition with sympatric species, the viability of this population could be also determined by land-use changes. More efforts are needed to test this hypothesis.

Wild ungulate distributions are mediated not only by natural processes but also by human management strategies promoted by hunting interests. Many factors are involved in their population trends, and therefore, it is quite difficult to accurately predict distributions of these species in future scenarios. Two assumptions are needed: (i) transition rates amongst land uses and species–habitat relationships are constant over the study period and (ii) the effect of population management is negligible, at least in relation to other factors, on the future species' distribution. The former can be generalized to all species, but the latter is more relevant when working with intensively managed species (e.g. Acevedo et al. 2007b, 2008).

Our results suggest a positive effect of land-use change on future areas favourable to all species studied except for Iberian wild goat (Table 4; Fig. 2). In general terms, and again with the exception of goats, all species will maintain a high proportion of the current favourable areas in the future, but these will be more widely distributed and include habitat not previously occupied.

If wild ungulates continue to expand in the next decades, a number of primary studies should be undertaken to improve the knowledge of the species and assure both their conservation and the conservation of the environment by avoiding undesirable overabundance situations (see Gortázar et al. 2006). As we understand it, a crucial issue is that the available information on the species, although useful, should be centralized and monitored according to scientific criteria. It would be useful to promote periodic meetings of scientists and wildlife managers to share their views and establish appropriate approaches for conservation science and management.

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