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How to fit the distribution of apex scavengers into land-abandonment scenarios? The Cinereous vulture in the Mediterranean biome

Isabel García-Barón[1,2] | Ainara Cortés-Avizanda[1,3,4] | Peter H. Verburg[5,6] | Tiago A. Marques[7,8] | Rubén Moreno-Opo[9] | Henrique M. Pereira[4,10,11,12] | José A. Donázar[1]

[1]Department of Conservation Biology, Estación Biológica de Doñana (CSIC), Sevilla, Spain

[2]AZTI, Pasaia, Spain

[3]Animal Ecology and Demography Group, IMEDEA (CSIC-UIB), Esporles, Spain

[4]Infraestruturas de Portugal Biodiversity Chair, InBio, Vairão, Portugal

[5]Environmental Geography Group, Institute for Environmental Studies, VU University Amsterdam, Amsterdam, The Netherlands

[6]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[7]Research Unit for Wildlife Population Assessment, Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, UK

[8]Centro de Estatística e Aplicações, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal

[9]Evolution and Conservation Biology Research Group, University Complutense of Madrid, Madrid, Spain

[10]CEABN/InBio, Centro de Ecologia Aplicada "Professor Baeta Neves", Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal

[11]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[12]Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Saale, Germany

Correspondence
Ainara Cortés-Avizanda, Department of Conservation Biology, Estación Biológica de Doñana (CSIC), Sevilla, Spain and Present address: Animal Ecology and Demography Group, IMEDEA (CSIC-UB), Esporles, Spain.
Email: ainara@ebd.csic.es

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Abstract

Aim: Farmland abandonment or "ecological rewilding" shapes species distribution and ecological process ultimately affecting the biodiversity and functionality of ecosystems. Land abandonment predictions based on alternative future socioeconomic scenarios allow foretell the future of biota in Europe. From here, we predict how these forecasts may affect large-scale distribution of the Cinereous vulture (*Aegypius monachus*), an apex scavenger closely linked to Mediterranean agro-grazing systems.

Location: Iberian Peninsula.

Methods: Firstly, we modelled nest-site and foraging habitat selection in relation to variables quantifying physiography, trophic resources and human disturbance. Secondly, we evaluate to what extent land abandonment may affect the life traits of the species and finally we determined how potential future distribution of the species would vary according to asymmetric socioeconomic land-abandonment predictions for year 2040.

Results: Cinereous vultures selected breeding areas with steep slopes and low human presence whereas foraging areas are characterized by high abundance of European rabbits (*Oryctolagus cuniculus*) and wild ungulates. Liberalization of the Common Agricultural Policy (CAP) could potentially transform positively 66% of the current nesting habitat, favouring the recovery of mature forest. Contrarily, land abandonment would negatively affect the 63% of the current foraging habitat reducing the availability of preferred food resources (wild European rabbit). On the other hand, the maintenance of the CAP would determine lower frequencies (24%–22%) of nesting and foraging habitat change.

Main conclusions: Land abandonment may result into opposite effects on the focal species because of the increase in nesting habitats and wild ungulates populations and, on the other hand, lower availability of open areas with poorer densities of European rabbits. Land-abandonment models' scenarios are still coarse-grained; the apparition of new human uses in natural areas may take place at small-sized and medium-sized scales, ultimately adding complexity to the prediction on the future of biota and ecosystems.

KEYWORDS

Aegypius monachus, ecological rewilding, European Union, farmland, land abandonment, socioeconomies

1 | INTRODUCTION

Human activities have historically lead to wide-ranging impacts on ecosystems functioning on the services provided and ultimately on biodiversity, but this trend is currently accelerating so understanding their consequences on wildlife viability is nowadays a key challenge in environmental sciences (Turner, Lambin, & Reenberg, 2007). European landscapes have supported historically larger numbers of human population and associated farming land exploitations which provoked wild large body-sized mammals and some bird species practically disappeared in most of the regions of the continent (Cardillo, Mace, & Jones, 2005; Gaston & Blackburn, 1995). After mid-20th century, however, the modernization of the agriculture lead to severe ecological and socioeconomic changes occurred in the European rural areas (Rounsevell, Ewert, Reginster, Leemans, & Carter, 2005; Stanners & Bourdeau, 1995) encompassing a sharp depopulation and land abandonment in some regions, and urbanization and agricultural intensification in others (Westhoek, van den Berg, & Bakkes, 2006).

The abandonment of the European farmland and pasture landscapes (−15% between 1970 and 2010, PBL, 2012, coined as ecological rewilding see Pereira & Navarro, 2015) has favoured the natural succession of vegetation towards scrubland and forests (Conti & Fagarazzi, 2005). This process of return to more natural states opens the opportunity for a new conservation strategy called "ecological rewilding" defined as the management of the first stages of ecological succession favouring the restoration of natural ecosystem processes and reducing human control of landscapes (Gillson, Ladle, & Araújo, 2011). The management of these abandoned areas has become a challenge for conservationists (Pereira & Navarro, 2015) being a prevailing issue in recent policy management discussions (MacDonald et al., 2000 see below). Several studies have attempted to model the impacts of certain policies (e.g., subsidies, laws on land uses and trade policies) on the evolution of land use systems (Lotze-Campen et al., 2014; Verburg, Tabeau, & Hatna, 2013). Based on different socioeconomic scenarios, these models provide future projections of the spatial dynamics of land use changes, which can be useful to understand ecosystem consequences of land abandonment (Pereira et al., 2010; Stürck et al., 2015; Verburg & Overmars, 2009).

Land-abandonment processes may have positive effects on ecosystem structure and functioning such as the stabilization of soils (Tasser, Mader, & Tappeiner, 2003), carbon sequestration (Houghton, Hackler, & Lawrence, 1999) and the temporary increase in the biodiversity (Laiolo, Dondero, Ciliento, & Rolando, 2004). Conversely, they may lead to undesirable loss of the landscape identity, including the irreversible loss of traditional farming forms (Antrop, 2005; Blondel, Aronson, Boudiou, & Boeuf, 2010). Regarding biodiversity, the consequences of these land-abandonment processes in Europe are controversial. Some studies have stated that land abandonment processes could reduce the human presence thus increasing the availability of suitable habitat for those species having been historically persecuted (Enserik & Vogel, 2006) but may have negative consequences on species of interest in conservation and very dependent of traditional agro-grazing practices (Fuller, 1987; Labaune & Magnin, 2002; Overmars, Schulp, & Alkemade, 2014). Within this context, it is of prime interest to predict the consequences of these processes according to different future socioeconomic scenarios and their consequences on populations viability and ecosystem functioning.

We examine here how the spatial distribution of an apex scavenger may be affected by different socioeconomic scenarios including macroeconomic projections at global scale and land use models that translate these changes into spatial patterns of land abandonment at the European scale (Stürck et al., 2015). Vultures have a millenary link with human agro-grazing systems (Donázar, Naveso, Tella, &

Campión, 1997; Moreno-Opo, Arredondo, & Guil, 2010) with well-recognized roles as providers of regulatory and cultural ecosystem services (Cortés-Avizanda, Donázar, & Pereira, 2015; DeVault et al., 2015; Haines-Young & Potschin, 2013; Maes, Teller, Erhard, Liquete, & Braat, 2013). We took the Cinereous vulture (*Aegypius monachus*) as our study model because this species is known to be closely linked to the traditional agro-grazing systems in Mediterranean landscapes. Specifically, we aim (1) to model the Cinereous vulture's nest-site and foraging habitat selection. (2) On the basis of these mentioned models, to predict the potential habitat available for the species in peninsular Spain. Finally, (3) due to the land-abandonment patterns are governed by socioeconomic scenarios, we examined how future projections of abandonment in Europe could shape the persistence and expansion of the species. We focused on how the land-abandonment projections for 2040 may affect the availability of nesting and foraging suitable areas and the potential future expansion of this species.

2 | METHODS

2.1 | Focal species and study area

The Cinereous vulture is the largest bird of prey living in the Palaearctic (up to 12 kg) (Cramp & Simmons, 1980; del Hoyo, Elliot, & Sargatal, 1994). The Eurasian population is estimated on 7,200–10,000 pairs with around 2,068 breeding pairs in Spain (Moreno-Opo & Margalida, 2013), thus becoming the most important area for the species in Europe (BirdLife International, 2015). Because of the long-term population decline suffered across the entire distribution range, the species is globally listed as "near threatened" (Birdlife International, 2015). The species breeds in loose colonies reaching up to hundreds of pairs (45–312) with nests separated by distances from a few metres to several kilometres apart. It usually nests on the top of large trees (Cramp & Simmons, 1980; Dobado & Arenas, 2012; Moreno-Opo & Guil, 2007) avoiding areas with high human disturbance (Donázar, Hiraldo, & Bustamante, 1993; Fernández-Bellon, Cortés-Avizanda, Arenas, & Donázar, 2016; Morán-López, Sánchez Guzmán, Borrego, & Sánchez, 2006; Poirazidis, Goutner, Skartsi, & Stamou, 2004). The Cinereous vulture feeds on small-sized and medium-sized carcasses being the European rabbits (*Oryctolagus cuniculus*) the most important item (3%–60% of diet) in Mediterranean regions (Corbacho, Costillo, & Perales, 2007; Hiraldo, 1977). The species forages preferentially in open areas (Carrete & Donázar, 2005; Donázar et al., 1993; Moreno-Opo & Guil, 2007) mainly during the breeding season and independently of the distance to the breeding colony (Carrete & Donázar, 2005).

Our study was conducted in the peninsular Spain (492,173 km^2 of total surface, INE, 2006) where the complex orography and geographical characteristics determine that temperatures decrease northwards and precipitation south-eastward (Tullot, 2000). Accordingly, vegetation communities reflect this climate range. Thus, Atlantic vegetation occupies the north and north-west and Mediterranean biomes (woodland and scrubland) most of the centre and south of the peninsula. Where traditional agro-grazing systems dominate, the Mediterranean biome has been transformed into open habitats with scarce trees also called "*Dehesas* or *Montado*" (Peinado & Rivas-Martínez, 1987) occupying almost 5,000,000 ha in southern and south-western Iberia (Joffre & Rambal, 1993).

2.2 | Analytical procedures

2.2.1 | Modelling current nest-site and foraging habitat selection

We modelled the Cinereous vulture breeding sites based on the Spanish Breeding Bird Atlas (Figure 1a; Martí & del Moral, 2003). One hundred and fifty-six cells of 5,571 UTM of 10 × 10 km presented at least one breeding pair of Cinereous vulture. We removed cells with area <100 km^2 from the analysis, keeping 4,547 cells of UTM 10 × 10 km, 144 of which (3.2%) held breeding vultures. The potential foraging areas were estimated according to radio-tracking studies (Carrete & Donázar, 2005; Moreno-Opo et al., 2010). Consequently, for each of the 144 occupied squares, an area of 30 km diameter was established covering 2,500 km^2 (we created a buffer of 25 cells of 10 × 10 km, with the centre cell being the one used by vultures for breeding, Figure 1b).

Based on previous studies (Donázar et al., 2002; Carrete & Donázar, 2005; Costillo, 2005; Morán-López et al., 2006), we chose a primary set of 30 explanatory variables to characterize nest-sites and foraging habitats. For modelling the nesting sites, these variables were grouped into two categories: (a) environmental: describing physiography, climate and vegetation, and (b) human disturbance: describing the presence of human settlements and infrastructures. For modelling the foraging habitat, the variables were grouped in the same two above-mentioned categories (a, and b), joined by another category, (c) describing trophic resource availability (European rabbit, wild ungulates and livestock). To avoid co-linearity and the non-independence of the variables selected, we calculated the Spearman correlation coefficients for all the potential pairs of variables; those exceeding $|r| > .7$ were considered redundant, and then, the least biologically meaningful variable was consequently excluded from further analyses (Dormann, Elith, & Bacher, 2013). After this procedure, 8 and 12 explanatory variables were finally chosen respectively for nest-site and foraging habitat selection analyses (see Table 1).

We used generalized linear models (GLMs) to evaluate the presence/absence of Cinereous vulture (1/0; binomial response with a logit function). The data set was dominated by absences (144 and 742 presences, 4,403 and 3,805 absences for nesting and foraging, respectively). Thus, to balance the number of presences and absences, 1,000 independent samples of 144 and 742 absences were selected for nesting and foraging, respectively, and the model fit for each sample. Models were fitted using backward and forward stepwise procedures, using Akaike's Information Criterion (AIC) to select the best model of each trial. Models were built within the R environment (version 3.1.1, R Development Core Team 2014) using the function *glm* in the "stats" package.

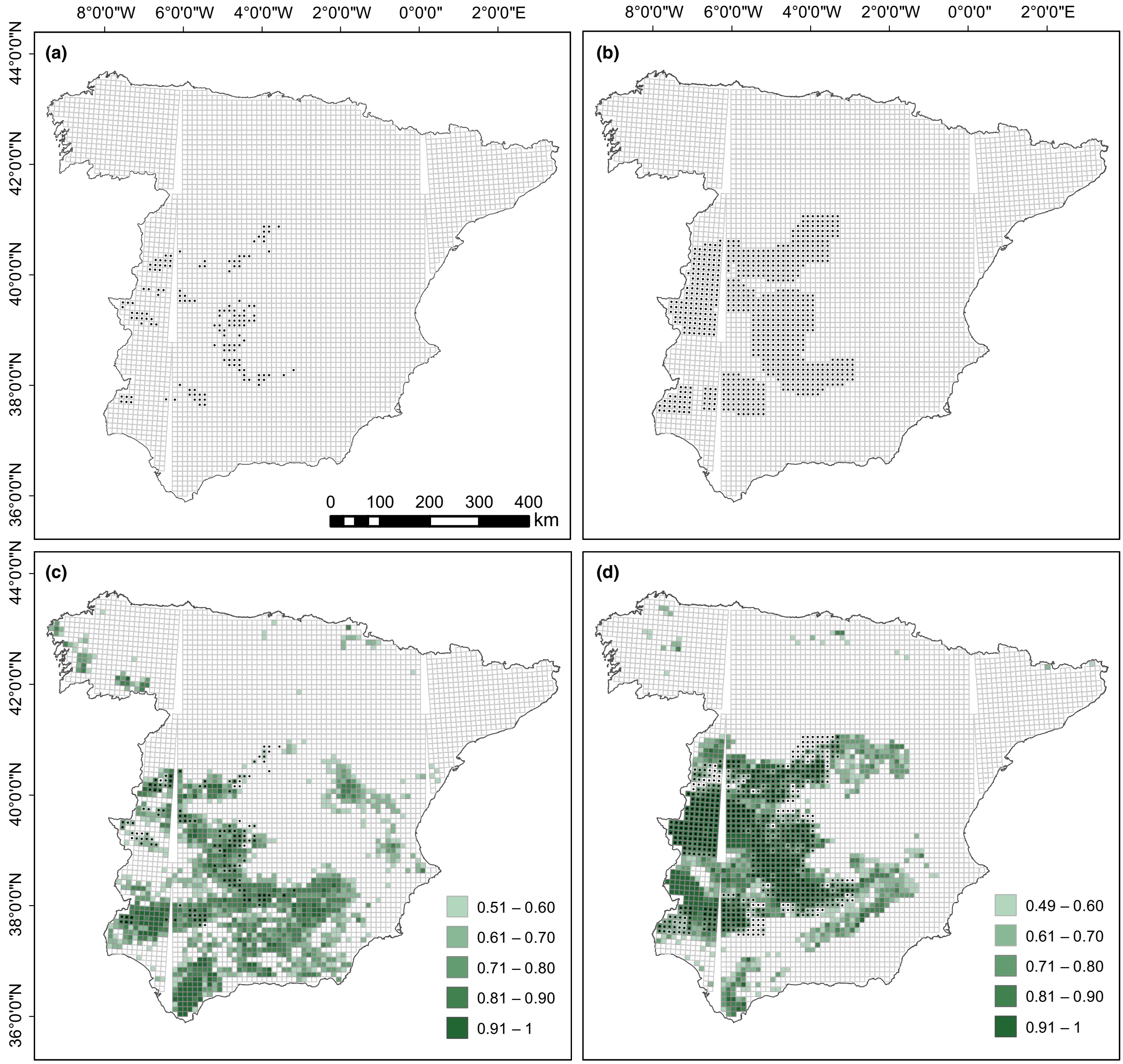

FIGURE 1 Distribution of Cinereous vultures in Peninsular Spain (a) nesting (based on Martí & del Moral, 2003); and (b) foraging (created according to inference from radio-tracking studies (Carrete & Donázar, 2005; Moreno-Opo et al., 2010). The last two maps represent the average prediction of the 1,000 final models showing each UTM 10 × 10 km cells predicted as suitable according to the cut-off value, (>0.51 for nest-site habitat and >0.49 for foraging habitat): (c) nest-site habitat; and (d) foraging habitat

According to Legendre and Legendre (1998), prior to analysis, slope and elevation were centred on their respective means to reduce co-linearity with higher order terms and standardized to unit variance. We also performed preliminary univariate analyses to examine the existence of potential nonlinear responses; then if required, we added quadratic terms into the models (Donázar et al., 1993).

To assess the models' performance, we used receiver operating characteristic (ROC) analyses (Hirzel, Lay, Le Helfer, Randin, & Guisan, 2006) to evaluate the sensitivity (true positive rate) and specificity (true negative rate) for all data set. Each point on the ROC curve represents the trade-off between making a true positive prediction versus a false-positive prediction with increasing prediction threshold. The result produces an area under the curve (AUC) that measures how well the model predicts point occurrences. The theoretically perfect result is AUC = 1.0, whereas a test performing no better than random yields AUC = 0.5 (Fawcett, 2006; Pearce & Ferrier, 2000). All the analyses were performed with R 3.1.1 (R Core Team 2014) in the R package ROCR (Sing, Sander, Beerenwinkel, & Lengauer, 2005) that calculates the ROC curves, the AUC and the threshold values.

Finally, the breeding-site and foraging habitat suitability maps were created as the average probability of presence obtained from

TABLE 1 Explanatory variables used in the analyses of Cinereous vulture nest-site and foraging habitat selection in Iberian Peninsula modelling

Category	Code	Description
Physiography	*Slope*	*†Mean slope (°)[a]
	Elev	*Mean elevation (m)[a]
Climatic	*Prec*	*†Mean annual precipitation (mm)[b]
	Temp	*Mean annual temperature (°C)[b]
Vegetation	*Forest*	*†Percentage coverage classified as native forest (Height > 7 m)[c]
	Reforest	*†Percentage coverage classified as reforestation (*Pinus* spp y *Eucalyptus* spp)[c]
	Scrubland	†Percentage coverage classified as scrubland from low to high height (<5 cm–3 m)[c]
	Shrubland	†Percentage coverage classified as shrubland from low to high height (5 cm–7 m)[c]
	Dehesa	†Percentage coverage classified as dehesa[c]
Human-related activities	*Build_use*	*Percentage coverage classified as use buildings (industrial, religious and residential)[d]
	Roads	*†Total length of roads (motorways, highways, country roads, paths and tracks) (km)[e]
	Inhabit	†Area of inhabited areas (m^2)[e]
Trophic	*Rabbit*	†Rabbit abundance (calculated by assigning each Spanish province an abundance value between 1 and 4)[f]
	Wild_ung	†Wild ungulates abundance (sum of richness values in the 50 × 50 km buffer)[g]
	Livestock	†Amount of biomass (kg/year). The weighted sum of the amount of biomass of livestock existing in all the municipalities included in the 50 × 50 km buffer[h]

Note that all variables were calculated on a 10 × 10 km squares. Symbols preceding the description indicate the use of these variables in (*) nest-site and (†) foraging habitat models.
[a]ASTER Global DEM spatial resolution 30 m (ASTER GDEM Validation Team, 2011).
[b]Iberian Peninsula Digital Climatic Atlas (Ninyerola et al., 2005).
[c]Forest Map of Spain 1:200,000 (Ruiz de la Torre, 1990).
[d]Numerical Cartographic Base 1:25,000 (BCN25 © National Geographic Institute of Spain).
[e]Numerical Cartographic Base 1:200,000 (BCN200 © National Geographic Institute of Spain).
[f]Based on Virgós, Cabezas-Díaz, & Lozano, 2007.
[g]Based on Blázquez-Álvarez & Sánchez-Zapata, 2009.
[h]Based on Margalida, Colomer, and Sanuy 2011.

the 1,000 nesting and foraging habitat models. Consequently, the map categorized all the UTM 10 × 10 km cells of the peninsular Spain with a range of values from 0 to 1 (i.e., 0 for not suitable habitat and 1 for perfect suitable habitat). The threshold value above which each cell was characterized as suitable was estimated as the average of the 1,000 cut-off values for each cross-validation replicate and type of habitat. The cut-off value corresponded to the point on the ROC curve where specificity and sensitivity were maximized (i.e., where the total amount of misclassification is minimized). Thus, the cells characterized as suitable for nest-site habitat were those that had values higher than 0.51 and for foraging habitat those that had values higher than 0.49.

2.2.2 | Modelling future nest-site and foraging habitat selection

We built land-abandonment maps from simulations for a set of socio-economic scenarios. They accounted for changes in a broad range of topics such as human population growth, international trade policies, endogenous bioenergy demand, land use regulation and subsidies, forest protection and uptake of agro-environmental schemes, nature conservation policies, forest management, long-term climate change mitigation and climate impacts (Stürck et al., 2015). These scenarios (Libertarian Europe, Eurosceptic Europe, Social Democracy Europe and European Localism, hereinafter referred to as Libertarian, Eurosceptic, Social Democracy and Localism, respectively. Table S1) were developed within the VOLANTE project (Visions of Land Use Transitions in Europe, Lotze-Campen et al., 2014). They were simulated by a series of models that include macroeconomic projections at the global scale and land use models that translate macrolevel changes into spatial patterns of land abandonment at the European scale (Stürck et al., 2015), resulting in land change maps at a resolution of 1 km^2 (Figure 2).

Impacts of land abandonment may be predicted based on the well-known life-history traits of the species and results of the above-mentioned analyses. Thus, nesting habitat is limited by the existence of buildings or forest areas, which in turn will be affected by land abandonment. Thus, the drawdown of farmlands uses as livelihood by the migration of the countryside population to cities along with regrowth of forest and scrublands would convert currently unoccupied areas into new suitable breeding grounds. Foraging habitat is, on its part, mostly limited by the availability of wild prey (ungulates and wild rabbits). Presumably, land abandonment and the ecological succession resulting there from (i.e., pasture to scrubland or scrubland to forest) would reduce the abundance of the European wild rabbit due to the

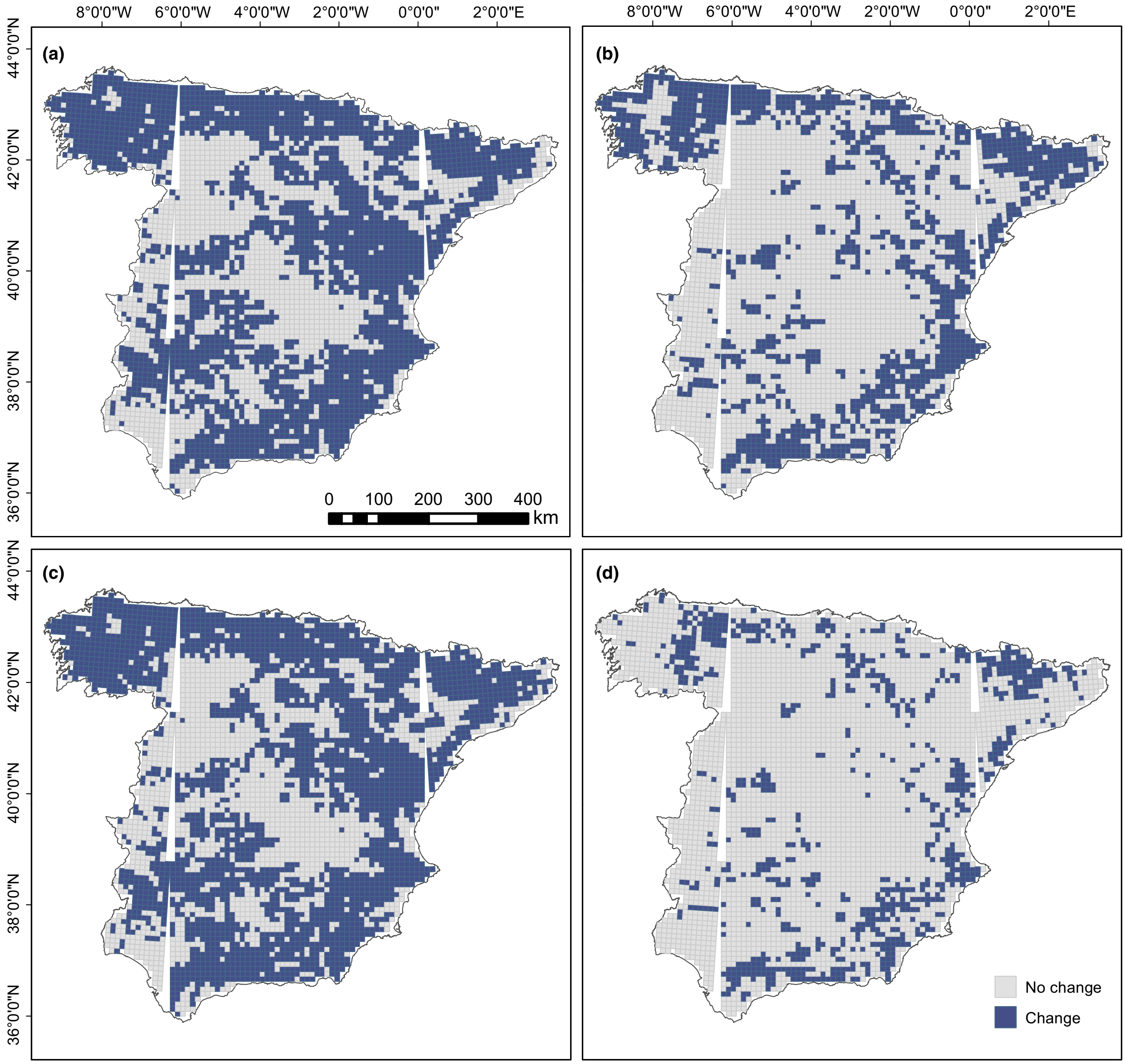

FIGURE 2 Peninsular Spain rewilding scenarios predicted for year 2040 (Stürck et al., 2015): (a) Libertarian Europe, (b) Eurosceptic Europe, (c) Social Democracy Europe, and (d) European Localism. Dark blue coloured 10 × 10 km cells show areas with the fraction of the area affected by land abandonment (change), and light blue coloured 10 × 10 km cells show areas without land abandonment (no change)

disappearance of mosaics of pastures, crops and scrubs which provide high-quality resources and refuge against predators (Cortés-Avizanda et al., 2015 and references therein). On this basis, we focused on the evaluation of how the land-abandonment processes can change the habitats of the Cinereous vultures. We first deal with a descriptive approach analysing in what extent land abandonment has positive or negative effects on the current nesting and foraging habitats. We specifically overlap the land use scenarios maps for 2040 (with cells characterized as either positive or negative probability of land abandonment) with the suitability maps for nest-site and foraging habitat (cut points respectively 0.51 and 0.49). In addition, we performed two GLM analyses (binomial errors and logit-link functions) examining how the probability of occupation by nesting and foraging Cinereous vultures was related to the land abandonment predicted by each land use scenario in each 10 × 10 km square. Thus, the response variable (probability of use) was confronted with a factor variable with eight levels. Post hoc Tukey tests were then applied. A schematic workflow of the entire analytical process is described in Figure S1.

3 | RESULTS

Nest-site models showed that the presence of Cinereous vulture was related positively with terrain slope and negatively

TABLE 2 Results of the best GLMs developed to the nesting habitat at a 10 × 10 km square scale

Variables	Est ± *SE*	*SD* Est	*SD SE*	Significant	D^2	*SD* D^2	AUC	*SD* AUC
Intercept	−22.859 ± 4.173	4.342	0.432	1,000	37.42	4.34	0.88	0.02
Build_use	−2.290 ± 0.707	0.493	0.053	972				
Roads	−0.003 ± 0.001	0.002	<0.001	783				
Prec	0.060 ± 0.014	0.017	0.002	998				
Temp	1.212 ± 0.204	0.211	0.021	1,000				
Slope	0.125 ± 0.052	0.077	0.028	777				
Slope^2	−0.026 ± 0.007	0.007	0.001	990				
Elev	0.006 ± 0.001	0.001	<0.001	997				
Elev^2	<0.0001 ± <0.001	<0.001	<0.001	919				
Forest	0.001 ± 0.002	0.009	0.004	910				
Reforest	−0.003 ± 0.003	0.014	0.007	913				

For each variable, it is represented the average estimate and the average standard error of the 1,000 models (Est ± *SE*), the standard deviation for the estimates (*SD* Est) and standard errors (*SD SE*), the number of models where each variable is significant ($p < .05$, "Significant"), the average deviance explained (D^2), the range of the AUC (Area Under the Curve) across the 1,000 models and their standard deviations (*SD* D^2 and *SD* AUC).

with variables describing humanization: buildings and roads (see Table 2). Accordingly, the species selected cells with intermediate rough lower or mean values of slope and where the "used buildings" (i.e., industrial, religious/cultural and residential) and the roads were scarce. Besides, the probability of the presence of breeding vultures was positively associated with higher average of temperatures and average of precipitation (Table 2). Almost no relationship was found between the presence of breeding vultures and the amount of forest or reforestation coverage. Regarding foraging models, the presence of species was positively associated with terrain slope, scrubland and open areas called "*dehesa/montado*" (see details Table 3). Contrary to nesting habitat selection models, the precipitation was not included in the models. The average deviance explained by the nest-site models was 37.4 ± 4.3% (Table 2) whereas for foraging habitat models was 47.2 ± 1.6% (Table 3). The respective corresponding average AUC values were 0.88 ± 0.02 and 0.92 ± 0.005 indicating a good and excellent classification performed, respectively (Figure S2).

Suitability maps for nesting and foraging habitats (Figure 1c,d) identified respectively 1,210 and 1,328 cells having >.51 and >.49 probability of the presence of Cinereous vultures (27% and 23% of the peninsular Spain). These suitable areas are concentrated in the centre and southern half of Iberia.

For both, current and suitable distributions, modelling predicted higher percentage of cells subject to land abandonment (and therefore, being susceptible of improving the quality of currently occupied and potentially suitable breeding areas). The impact was higher under the Libertarian and Social Democracy scenarios (between 48.6%/66.0% and 47.2%/66.4% for current/suitable nesting habitat), whereas under Localism and Eurosceptic, the range was clearly lower (between 13.9%/24.5% and 18.7%/36.4% for current/suitable nesting habitat; Table 4, Figure 3). The potential impoverishing of foraging areas because of the decrease in agro-grazing activities and the associated abundance of small-sized and medium-sized carcasses shows also a similar trend between scenarios (Table 4, Figure 3). Higher frequencies of cells would be affected under the Libertarian and Social Democracy (50.5%/62.6% and 49.5%/63.2% of current/suitable foraging habitat) against Localism and Eurosceptic scenarios (12.3%/23.0% and 18.3%/34.3%; see also Figures S3, S4 and S5). Departing from these data and considering simultaneously appropriate conditions for nesting and foraging, only 9.3% (Social Democracy), 9.4% (Libertarian), 8.1% (Eurosceptic) and 10.6% (Localism) of the land-abandonment forecasts in Iberia met simultaneous conditions as appropriate areas for nesting and foraging of Cinereous vultures. These areas were located in the eastern and southern border of the current distribution range (Central System and the Baetic mountains; Figure 3).

Finally, the detailed results of the GLM analyses regarding the impact of land-abandonment processes (Tables S2 and S3, Figure S6) showed that higher probability of occupation by nesting vultures was positively related to higher probability of land abandonment in all the four socioeconomic scenarios showing significant differences ($p < .001$) in three of them (Libertarian, Localism and Social Democracy). Attending to those squares showing land use changes, slight significant differences were only found between the Eurosceptic and Localism scenarios ($p = .044$). With respect to the foraging habitat, higher probability of presence was negatively associated with land abandonment in all the scenarios reaching significant differences for Localism and Eurosceptic. Attending to those squares showing land use changes, significant differences ($p < .001$) were found between Eurosceptic and both Libertarian and Social Democracy.

4 | DISCUSSION

We provide insight into the availability of suitable areas for the expansion of a prioritized species from a conservation and flagship

TABLE 3 Results of the best GLMs developed to the foraging habitat at a 10 × 10 km square scale

Variables	Est ± *SE*	*SD* Est	*SD SE*	Significant	D^2	*SD* D^2	AUC	*SD* AUC
Intercept	−6.620 ± 0.433	0.303	0.039	1,000	47.20	1.63	0.920	0.005
Rabbit	0.325 ± 0.022	0.013	<0.001	1,000				
Wild_ung	0.083 ± 0.016	0.011	<0.001	1,000				
Livestock	<0.0001 ± <0.001	<0.001	<0.001	1,000				
Inhabit	<0.0001 ± <0.001	<0.001	<0.001	1,000				
Roads	<0.0001 ± <0.001	<0.001	<0.001	915				
Prec	0.002 ± <0.001	<0.001	<0.001	848				
Slope	0.083 ± 0.028	0.038	<0.001	891				
$Slope^2$	−0.013 ± 0.003	<0.001	<0.001	999				
Forest	−0.011 ± 0.004	<0.001	<0.001	802				
Reforest	0.005 ± 0.003	<0.001	<0.001	751				
Scrubland	0.028 ± 0.007	<0.001	<0.001	999				
Shrubland	0.007 ± 0.003	<0.001	<0.001	716				
Dehesa	0.020 ± 0.006	<0.001	<0.001	990				

For each variable, it is represented the average estimate and the average standard error of the 1,000 models (Est ± *SE*), the standard deviation for the estimates (*SD* Est) and standard errors (*SD SE*), the number of models where each variable is significant ($p < .05$, "Significant"), the average deviance explained (D^2), the range of the AUC (area under the curve) across the 1,000 models and their standard deviations (*SD* D^2 and *SD* AUC).

TABLE 4 Percentage of 10 × 10 km cells subject to land abandonment and its potential effects affecting the nesting and foraging habitat available for Cinereous vultures under the four future scenarios predicted for 2040 (European Localism "EurLoc", Eurosceptic Europe "Eurscep", Libertarian Europe "LibEur" and Social Democracy Europe "SocDem"; Stürck et al., 2015)

			Scenario			
Habitat	Effect	Vulture distribution	EurLoc	Eurscep	SocDem	LibEur
Nesting		Current	13.89	18.75	47.22	48.61
	Positive: Increase mature woodland	Suitable	24.46	36.45	66.45	66.03
Foraging		Current	12.26	18.33	49.46	50.54
	Negative: Reduce wild rabbit populations Positive: Increase wild ungulate populations	Suitable	22.97	34.26	63.18	62.65

We consider both the current vulture distribution and the suitable at distribution predicted by the modelling procedures (cut points: $p > .51$ for nesting habitat; $p > .49$ for foraging habitat). Colours highlight the effect in a 0–100 scale (from green to red). Credit photographs: Manuel de la Riva.

standpoint under different scenarios of land abandonment dependent of European policies. In all the cases, the availability of habitat for breeding and foraging not only would be maintained but also an increase in suitable areas is predicted. Although this result agrees with that found in the analysis of the effects of land abandonment on the distribution of other large body-sized vertebrates (see Milanesi, Breiner, Puopolo, & Holderegger, 2017; and references therein), our results clearly show profound differences between the considered scenarios. Particularly, we have found that in the case of a liberalization of the CAP (i.e., Libertarian and Social Democracy), the large-scale abandonment of marginal agricultural areas would lead to considerable expansion of potential habitats in comparison with the Eurosceptic and Localism scenarios. These results are consistent with other studies that have explored possible changes in agricultural area under parallel conditions, although there are high variation and uncertainty in the location and extent of these areas (Renwick, Jansson, & Verburg, 2013; Verburg et al., 2013). In general, it shows that maintaining the current land management policies (CAP and associated subsides) would reduce the long-term availability of abandoned (rewilded) lands by stopping (at least partially) rural exodus thus avoiding the loss of traditional agro-grazing practices in marginal areas, mainly mountains (Navarro & Pereira, 2012).

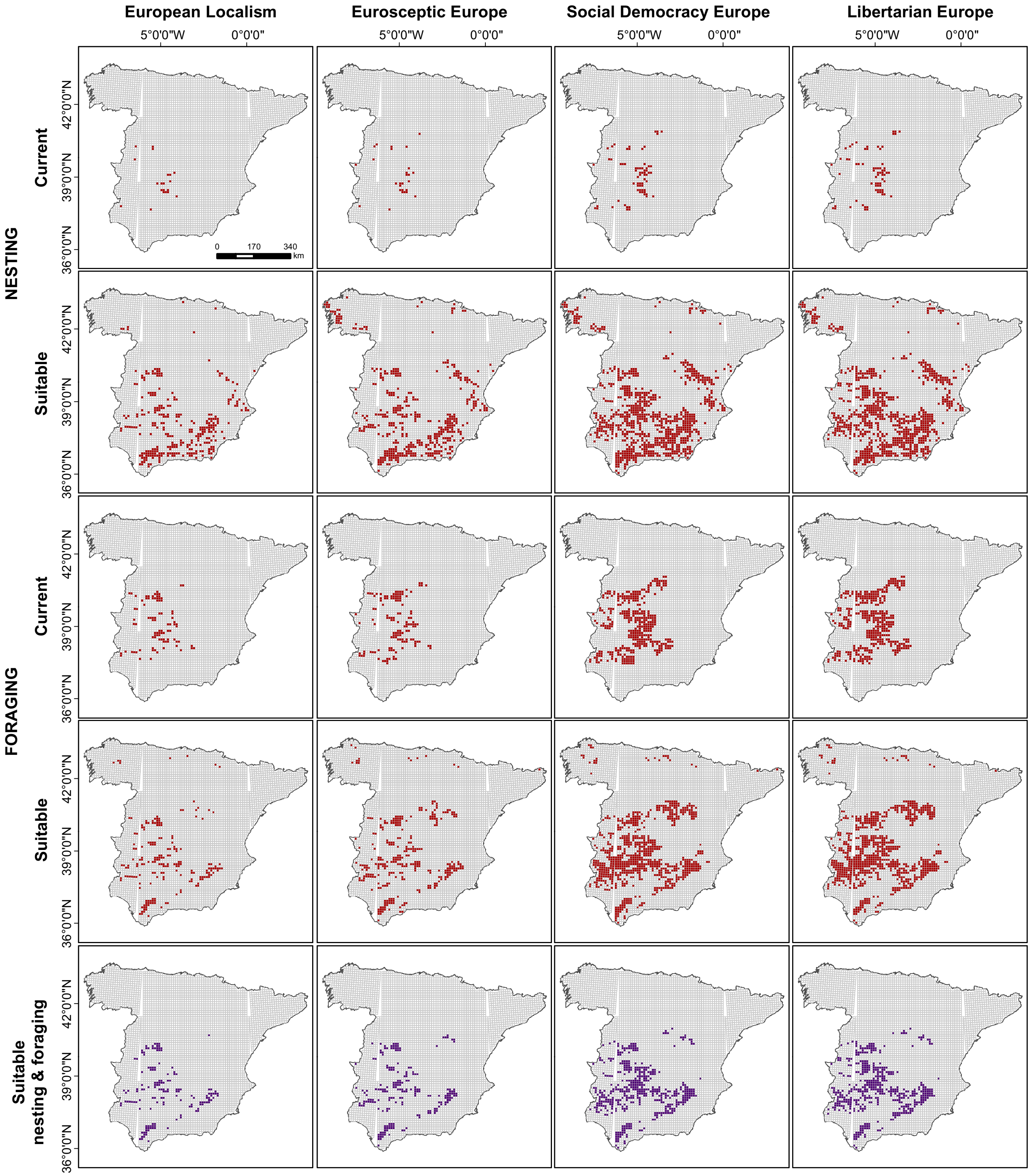

FIGURE 3 Result from the maps overlap showing the nest-site and foraging current and suitable habitat for the Cinereous vulture in Spain peninsular subject to land abandonment predicted by the future scenarios for 2040 (Stürck et al., 2015). The bottom panels (in purple) show the cells predicted simultaneously as suitable for both, nesting and foraging, according to the cut-off values, (>0.51 and >0.49, respectively). Maps with cells with simultaneously appropriate current nesting and foraging habitat are similar to the patterns shown in the upper row of panels

That land abandonment is beneficial or not for the maintenance of biodiversity is an open debate (see Navarro & Pereira, 2012 and references therein). In the case of the top scavengers, there are contradictory starting points (Cortés-Avizanda et al., 2015) and in any case, no attempt to quantify the effect of different land-abandonment scenarios. To be able to discern, we must deepen our results, particularly in relation to the nesting and foraging habitat. Starting with the later, our results show that land abandonment was negatively associated with habitat suitability for foraging vultures in all the four examined socioeconomic models, only slightly differing between them in the observed general trend. In consequence, the most favourable foraging areas seem to have no high probability of being abandoned in the next future. Cinereous vultures show a clear preference for open Mediterranean woodlands ("*dehesa/montado*") a traditional agroforestry system encompassing high biodiversity (Blondel et al., 2010) and relatively higher densities of wild prey (ungulates and wild rabbits; Carrete & Donázar, 2005) whose abundance was decisive in our predictive models. In fact, the Cinereous vulture depends heavily on lagomorphs (3%–60% of diet, Hiraldo, 1977; Corbacho et al., 2007), a pattern also found in the rest of their distribution area where the diet is based on small-sized and medium-sized prey (rodents) typical of open landscapes such as natural and semi-natural steppes (Dobado & Arenas, 2012 and reviews therein). In this scenario, and as was stated above, farmland abandonment and the subsequent ecological succession would negatively affect European wild rabbit abundances (Cortés-Avizanda et al., 2015).

Opposite impacts of land abandonment may be predicted for nesting habitat. The exodus of humans and the changes in professional tasks in rural areas would determine the expansion of woodland which would increase the availability of suitable breeding grounds (see above). In fact, detailed statistical analyses reinforce the consistency of the pattern regarding each of the four socioeconomic models of land abandonment: all of them highlighted the association between abandonment and suitability for nesting vultures. In other words, the most favourable areas to hold breeding Cinereous vultures would be more prone to be abandoned in the next decades. Our results interestingly have detected a stronger negative effect of the existence of buildings (active or in ruins) which would be therefore a proxy of historical human occupancy and harassment. This may explain why the Cinereous vultures and other large body-sized species (especially those nesting in trees particularly vulnerable to human persecution, Martínez-Abraín, Oro, Jiménez, Stewart, & Pullin, 2010) have been historically absent of many regions of the Mediterranean Basin (Donázar, 2013). Although direct persecution (hunting) of large birds of prey has currently almost disappeared from the Mediterranean regions (de Juana & de Juana, 1984; Donázar et al., 2016), the reluctance of these species towards humans still remains (Donázar, 2013), probably because the long-term selective processes imposed by the above-mentioned persecution would have favoured individuals with shy behaviour (Ciuti et al., 2012). This fact may also explain why we found a clear preference by steeper areas for breeding which is consistent with findings from previous studies (Donázar et al., 1993; Morán-López et al., 2006; Moreno-Opo & Guil, 2007; Sánchez-Zapata & Calvo, 1999).

Other positive effects of land abandonment may be linked to the increase food resources associated with the expansion of wild ungulate populations, underway since the middle 20th century (Apollonio, Andersen, & Putman, 2010; Breitenmoser, 1998; Gortázar, Herrero, Villafuerte, & Marco, 2000). Wild ungulates appear also regularly in the diet of Cinereous vulture (Corbacho et al., 2007; Hiraldo, 1977). In Iberia, the Cinereous vulture consumes them in a higher proportion than other obligate scavenger species probably because the species prefer to forage in wilder habitats thus reducing competition with dominant and social griffon vultures (*Gyps fulvus*) which rely more frequently on farms and supplementary feeding stations (Hiraldo, 1977; Donázar, 2013; Cortés-Avizanda et al. 2012; Cortés-Avizanda, Carrete & Donázar, 2010). Preference for wild ungulates and high humanization may also explain why large regions holding high extensive livestock densities (e.g., Ebro valley and Iberian South-east) were not identified as suitable areas by our models.

In summary, the target species presents a clear duality in the expected effects of land abandonment as it needs forests to nest but relatively open areas to obtain the food. However, land abandonment seems likely to affect more potential nesting areas than foraging areas, so the overall effect can be positive. This picture nonetheless, may be far from being temporarily stable. The availability nesting and foraging habitats in rewilding landscapes may change radically because more dense and fewer used woodlands and scrublands are subjected to recurrent wildfire in the Mediterranean Basin (Kelly & Brotons, 2017; Moritz et al., 2014). This could lead to decrease these new available suitable nesting habitats, but on the contrary, burnings could also reduce the density of the shrubs thus creating new patchy areas benefiting the European wild rabbit (Rollan & Real, 2010). It must be taken into account, however, that the long-distance foraging movements performed by large body-sized species such as the Cinereous vulture would cushion these effects because breeding and foraging areas use to be clearly separated (Carrete & Donázar, 2005).

It must be also emphasized that, when future projections are made, the constraints derived not only from the adequacy of habitats but from the life-history traits of species themselves cannot be ignored. In this sense, our target species shares with the rest of obligate avian scavengers and other large body-sized birds of prey, a "conservative" strategy that includes high philopatry and low colonizing abilities (Forero et al., 2002; Hernandez-Matias et al., 2010). This means that, although in the coming decades, large areas of Mediterranean Iberia may be suitable for housing Cinereous vultures, this scavenger may not probably colonize these regions in a similar period. In fact, although the Iberian population of Cinereous vultures has increased almost ten-fold during the last four decades, its distribution area has remained almost unchanged (see e.g., Moreno-Opo & Margalida, 2013; de la Puente, Moreno-Opo, & del Moral, 2007). Within this context, active rewilding strategies (reintroduction projects) would be necessary to re-establish populations of large scavengers after land abandonment (Deinet et al., 2013).

4.1 | Perspectives

Land abandonment in the Mediterranean Basin may shape the provision of ecosystem processes, including functions and services that are scarcely recognized. Our study highlights that there are broad regions in the Iberian Peninsula that may be suitable for a top scavenger in the future. A substantial fraction of these areas may be subject to future transformations derived from land abandonment, and the outcomes of this process will largely determine the likelihood of colonization by these scavengers. Therefore, it is not only the exploration of the locations of likely land abandonment that are important, but also the processes of re-growth and landscape change following. While these have been included to some extent in the model projections used (Verburg & Overmars, 2009), there are still large knowledge gaps. It is expected that large-scale land-abandonment processes would not result in uniform outcomes, but rather in patchy landscapes of different wilderness patterns which ultimately add complexity to the prediction of the probability of presence (and abundance) of biota. The development of ecological succession depends not only on the end of traditional human uses but also on the management and processes such as fires or invasive species (Kelly & Brotons, 2017; Pereira & Navarro, 2015 and references therein).

From a species-specific point of view, it should not be forgotten that abandonment of traditional land uses might not imply necessarily lower pressures on wildlife. Large areas, mainly in mountain ranges, formerly devoted to traditional agro-grazing activities are currently suffering a conversion to new intensive uses (recreational activities, eco-tourism, intensive forestry) which may significantly reduce breeding habitats and affect the breeding success of diffident species (Donázar et al., 2002; Arroyo & Razin, 2006). Additionally, infrastructures such as wind turbines or power lines are increasingly built in remote areas thus becoming a new concern for the viability of the populations of the large gliding birds (Carrete, Sánchez-Zapata, Benítez, Lobón, & Donázar, 2009; Smallwood, 2007). Also, land abandonment (including active rewilding processes) imply primarily the rebuilding of complex ungulate–carnivore interactions which may trigger bottom-up and top-down regulation within ecosystems (Ripple et al., 2001) and spatiotemporal changes in the availability of food resources for vertebrate scavengers (Wilmers, Crabtree, Smith, Murphy, & Getz, 2003). At the end, however, the viability of populations of large body-sized mammals (ungulates and carnivores) will be strongly dependent of the interactions with humans and of how potential conflicts are solved (Bisi, Kurki, Svensberg, & Liukkonen, 2007). In fact, these conflicts, notably predation of carnivores on livestock, may lead to indirect persecution of vultures by poisoning which has virtually extirpate entire populations on large parts of the Mediterranean Europe during the last centuries (Bijleveld, 1974; Donázar et al., 2009, Cortés-Avizanda et al., 2015).

From a more global perspective, the effects of land use changes on biodiversity will interact with impacts caused by global change, especially derived from global warming in coming decades in the Mediterranean basin (Hampe & Petit, 2005; Giorgi & Lionello, 2008). Specifically, synergic or antagonistic effects in the expansion or reduction in the distribution range of different species would occur as well as changes in behavioural interspecific relationships, in the face of changes of the current environmental traits (Dawson, Jackson, House, Prentice, & Mace, 2011). In a region such as the Iberian Peninsula, where a significant advance of desertification phenomena is expected (Schroter et al., 2005), the results of our study may be modulated in an opposed way, by reducing the extent and quality of mature forests selected by the Cinereous vultures to breed. This would be certain especially in the southernmost of the distribution area and foreseeing an expansion of the species to northern latitudes (Araújo, Alagador, & Cabeza, 2011). Analysing the interactions between land use change, climate change, ecological succession and its effects on the habitat of target species requires more complex approaches than those used on our study. However, our study indicates an order of magnitude of the potential changes in available area under land abandonment, which is a starting point for further investigation.

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ORCID

Isabel García-Barón http://orcid.org/0000-0001-5962-0819

Ainara Cortés-Avizanda http://orcid.org/0000-0002-9674-6434

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BIOSKETCH

Isabel García-Barón (I.G.-B.) focuses her research on ecological spatial modelling, identification and study of anthropogenic threats and their applications in biodiversity and conservation management in both, marine and terrestrial ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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