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

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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 socio-economic 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 modeled nest-site and foraging habitat selection in relation to variables quantifying physiography, trophic resources and human disturbance. Secondly, we evaluate 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 socio-economic land-abandonment predictions for year 2040.

Results: Cinereous vultures selected breeding areas with steep slopes and low human presence whereas foraging areas 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, favoring 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 of 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 and medium-sized scales, ultimately adding complexity to the prediction on the future of biota and ecosystems.

Keywords: *Aegypius monachus*, socio-economies, European Union, farmland, land abandonment, ecological rewilding.

(A) 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 et al., 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 (Gaston & Blackburn, 1995; Cardillo et al., 2005). After mid XXth century, however, the modernization of the agriculture lead to severe ecological and socioeconomic changes occurred in the European rural areas (Stanners & Bourdeau, 1995; Rounsevell et al., 2005) encompassing a sharp depopulation and land abandonment in some regions, and urbanization and agricultural intensification in others (Westhoek et al., 2006).

The abandonment of the European farmland and pasture landscapes (-15% between 1970-2010, PBL, 2012, coined as ecological rewilding see Pereira and Navarro 2015) has favored 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 the first stages of ecological succession favoring the restoration of natural ecosystem processes and reducing human control of landscapes (Gillson et al., 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, trade policies) on the evolution of land-use systems (Verburg et al., 2013; Lotze-Campen et al., 2014). 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 (Verburg and Overmars 2009, Pereira et al. 2010, Stürck et al. 2015).

Land abandonment processes may have positive effects on ecosystem structure and functioning such as the stabilization of soils (Tasser et al., 2003), carbon sequestration (Houghton et al., 1999) and the temporary increase of the biodiversity (Laiolo et al., 2004). Conversely, they may lead to undesirable loss of the landscape identity, including the irreversible loss of traditional farming forms (Antrop, 2005; Blondel et al., 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 et al., 2014). Within this context, it is of prime interest to predict the consequences of these processes according with different future socio-economic scenarios and their consequences on populations viability and ecosystem functioning.

We examine here how the spatial distribution of apex scavenger may be affected by different socio-economic scenarios including macro-economic 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 et al., 1997; Moreno-Opo et al., 2010) with well recognized roles as providers of regulatory and cultural ecosystem services (Haines-Young & Potschin, 2013; Maes et al., 2013; Cortés-Avizanda et al., 2015; DeVault et al., 2015). 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: i) to model the Cinereous vulture's nest-site and foraging habitat selection. ii) On the basis of these mentioned models, to predict the potential habitat available for the species in peninsular Spain. Finally, iii) due to the land abandonment patterns are governed by socio-economic 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.

(A) METHODS

(B) Focal Species and Study Area

The Cinereous vulture is the largest bird of prey living in the Palearctic (up to 12 kg) (Cramp & Simmons, 1980; del Hoyo et al., 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 meters to several kilometres apart. It usually nests on the top of large trees (Cramp & Simmons, 1980; Moreno-Opo et al., 2007; Dobado & Arenas, 2012) avoiding areas with high human disturbance (Donázar et al., 1993; Poirazidis et al., 2004; Morán-López et al., 2006; Fernández-Bellón et al., 2015). The Cinereous vulture feeds on small and medium-sized carcasses being the European rabbits (*Oryctolagus cuniculus*) the most important item (3-60% of diet) in Mediterranean regions (Hiraldo, 1977; Corbacho et al., 2007). The species forages preferentially in open areas (Donázar et al., 1993; Carrete & Donázar, 2005; 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 southeastward (Tullot, 2000). Accordingly, vegetation communities reflect this climate range. Thus, Atlantic vegetation occupies the north and northwest and Mediterranean biomes (woodland and scrubland) most of the center 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).

(B) Analytical procedures

(C) Modelling current nest-site and foraging habitat selection

We modelled the Cinereous vulture breeding sites based on the Spanish Breeding Bird Atlas (Fig. 1, a) (Martí & Moral, 2003). One hundred fifty-six cells of 5571 UTM of 10 x 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 x 10 km, 144 of which (3.2%) held breeding vultures. The potential foraging areas were estimated according to radio-tracking studies (Carrete & Donazar, 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 10x10 km, with the center cell being the one used by vultures for breeding, Fig. 1, b).

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 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 $|r| > 0.7$ were considered redundant and then the least biologically meaningful variable was consequently excluded from further analyses (Dormann et al., 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, 4403 and 3805 absences for nesting and foraging respectively). Thus, to balance the number of presences and absences, 1000 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 Core Team 2014) using the function glm in the 'stats' package.

According with Legendre & 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 et al., 2006) to evaluate the sensitivity (true positive rate) and specificity (true negative rate) for the all dataset. 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 (Pearce & Ferrier, 2000; Fawcett, 2006). All the analyses were performed with R 3.1.1 (R Core Team 2014) in the R package ROCR (Sing et al., 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 the 1000 nesting and foraging habitat models. Consequently, the map categorized all the UTM 10x10 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 1000 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 maximised (i.e. where the total amount of misclassification is minimised). 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.

(C) 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 like 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 macro-economic projections at the global scale and land-use models that translate macro-level 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 (Fig. 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 re-growth 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 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 10x10 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) RESULTS

Nest-site models showed that the presence of Cinereous vulture was related positively with terrain slope and negatively 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 "use buildings" (i.e. industrial, religious/cultural and residential) and the roads were scarce. Besides, the probability of presence of breeding vultures was positively associated to 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 a 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 (Supplementary Material, Fig. S2).

Suitability maps for nesting and foraging habitats (Fig. 1c and d) identified respectively 1210 and 1328 cells having >0.51 and >0.49 probability of presence of Cinereous vultures (27% and 23% of the peninsular Spain). These suitable areas are concentrated in the center and southern half of Iberia.

For both, current and suitable distributions, modeling 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 habitat) whereas under Localism and Eurosceptic the range was clearly lower (between 13.9/24.5% and 18.7/36.4% for current/suitable habitat) (Table 4, Fig.3). The potential impoverishing of foraging areas because the decrease of agro-grazing activities and the associated abundance of small and medium-sized carcasses show also a similar trend between scenarios (Table 4, Fig. 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 habitat) against Localism and Eurosceptic scenarios (12.3%/23.0% and 18.3/34.3%) (see also Figs. 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; Fig. 3).

Finally, the detailed results of the GLM analyses regarding the impact of land abandonment processes (Tables S2 and S3, Fig. S6) showed that higher probability of occupation by nesting vultures was positively related to higher probability of land abandonment in all the four socio-economic scenarios showing significant differences ($p<0.001$) 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 ($p=0.044$). With respect to the foraging habitat, higher probability of presence was negatively associated to land abandonment in all the scenarios reaching significant differences for Localism and Eurosceptic. Attending to those squares showing land-use changes significant differences ($p<0.001$) were found between Eurosceptic and both Libertarian and Social Democracy.

(A) DISCUSSION

We provide insight into the availability of suitable areas for the expansion of a prioritized species from a conservation and flagship 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 of 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 et al., 2016 and references therein), our results clearly shows 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 is high variation and uncertainty in the location and extent of these areas (Verburg et al., 2013; Renwick 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).

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 (Cortes-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 to habitat suitability for foraging vultures in all the four examined socio-economic 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 agro-forestry 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 and medium-sized prey (rodents) typical of open landscapes like 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 abandoning 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 socio-economic models of land abandonment: all of them highlighted association between abandonment and suitability for nesting vultures. In other words, the most favorable 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 et al., 2009) 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 favored individuals with shy behavior (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; Sánchez-Zapata & Calvo, 1999; Morán-López et al., 2006; Moreno-Opo et al., 2007).

Other positive effects of land abandonment may be linked to the increase food resources associated to the expansion of wild ungulate populations, underway since the middle 20th century (Breitenmoser, 1998; Gortázar et al., 2000; Apollonio et al., 2010). Wild ungulates appear also regularly in the diet of Cinereous vulture (Hiraldo, 1977, Corbacho et al., 2007). 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). Preference for wild ungulates and high humanization may also explain why large regions holding high extensive livestock densities (e.g. Ebro valley, Iberian Southeast) 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 since 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, 2011). It must be taken into account, however, that the long-distance foraging movements performed by large body-sized species like 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; Hernández-Matías 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. de la Puente et al. 2007, Moreno-Opo & Margalida, 2013). 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).

(B) 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 2010), 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 (Smallwood, 2007; Carrete et al., 2009). 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 et al., 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 et al., 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, Cortes-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 of the distribution range of different species would occur as well as changes in behavioral interspecific relationships, in the face of changes of the current environmental traits (Dawson et al., 2011). In a region such as the Iberian Peninsula, where a significant advance of desertification phenomena is expected (Schröter 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 (Araujo et al., 2011). Analyzing 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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BIOSKETCH

Isabel García-Barón (IGB) focuses her research on ecological spatial modelling, identification and study of anthropogenic threats and their applications in biodiversity and conservation management.

Author contributions: A.CA. and J.A.D. conceived the study; I.GB., T.A.M., A.CA. and J.A.D. compiled and analysed the data; P.H.V. prepared the land-use change scenarios; I.GB., A.CA., T.A.M. and J.A.D. wrote the paper; all authors commented on earlier versions of the manuscript.

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Table 1. Explanatory variables used in the analyses of Cinereous vulture nest-site and foraging habitat selection in Iberian Peninsula modelling. Note that all variables were calculated on a 10x10 km squares. Symbols preceding the description indicate the use of these variables in (*) nest-site and (†) foraging habitat models.

Category	Code	Description
Physiography	*Slope*	*† Mean slope (^{0}) [1]
	Elev	* Mean elevation (m) [1]
Climatic	*Prec*	*† Mean annual precipitation (mm) [2]
	Temp	* Mean annual temperature (^{0}C) [2]
Vegetation	*Forest*	*† Percent coverage classified as native forest (Height > 7 m) [3]
	Reforest	*† Percent coverage classified as reforestation (*Pinus* spp y *Eucalyptus* spp) [3]
	Scrubland	† Percent coverage classified as scrubland from low to high height (< 5 cm - 3 m) [3]
	Shrubland	† Percent coverage classified as shrubland from low to high height (5 cm - 7 m) [3]
	Dehesa	† Percent coverage classified as dehesa[3]
Human-related activities	*Build_use*	* Percent coverage classified as use buildings (industrial, religious and residential) [4]
	Roads	*† Total length of roads (motorways, highways, country roads, paths and tracks) (km) [5]
	Inhabit	† Area of inhabited areas (m^2) [5]
Trophic	*Rabbit*	† Rabbit abundance (Calculated by assigning each Spanish province an abundance value between 1 and 4) [6]
	Wild_ung	† Wild ungulates abundance (sum of richness values in the 50x50 km buffer) [7]
	Livestock	† Amount of biomass (kg per year). The weighted sum of the amount of biomass of livestock existing in all the municipalities included in the 50x50 buffer [8]

1. *ASTER Global DEM spatial resolution 30m (ASTER Global DEM Validation Team, 2009)*
2. *Iberian Peninsula Digital Climatic Atlas (Ninyerola et al., 2005)*
3. *Forest Map of Spain 1:200000 (Torre, 1990)*
4. *Numerical Cartographic Base 1:25000 (BCN25 © National Geographic Institute of Spain)*
5. *Numerical Cartographic Base 1:200000 (BCN200 © National Geographic Institute of Spain)*
6. *Based on Virgós et al. 2007*
7. *Based on Blázquez-Álvarez and Sánchez-Zapata 2009*
8. *Based on Margalida et al. 2011*

Table 2. Results of the best GLMs developed to the nesting habitat at a 10x10 km square scale. For each variable it is represented the average estimate and the average standard error of the 1000 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 ($p < 0.05$, 'Significant'), the average deviance explained (D^2), the range of the AUC (Area Under the Curve) across the 1000 models and their standard deviations (SD D^2 and SD AUC).

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	1000				
Build_use	-2.290 ± 0.707	0.493	0.053	972				
Roads	-0.003 ± 0.001	0.002	< .001	783				
Prec	0.060 ± 0.014	0.017	0.002	998				
Temp	1.212 ± 0.204	0.211	0.021	7000				
Slope	0.125 ± 0.052	0.077	0.028	777	37.42	4.34	0.88	0.02
$Slope^2$	-0.026 ± 0.007	0.007	0.001	990				
Elev	0.006 ± 0.001	0.001	< .001	997				
$Elev^2$	< .0001 ± < .001	< .001	< .001	919				
Forest	0.001 ± 0.002	0.009	0.004	910				
Reforest	-0.003 ± 0.003	0.014	0.007	913				

Table 3. Results of the best GLMs developed to the foraging habitat at a 10x10 km square scale. For each variable it is represented the average estimate and the average standard error of the 1000 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< 0.05, 'Significant'), the average deviance explained (D2), the range of the AUC (Area Under the Curve) across the 1000 models and their standard deviations (SD D2 and SD AUC).

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	1000	47.20	1.63	0.920	0.005
Rabbit	0.325 ± 0.022	0.013	< .001	1000				
Wild_ung	0.083 ± 0.016	0.011	< .001	1000				
Livestock	< .0001 ± < .001	< .001	< .001	1000				
Inhabit	< .0001 ± < .001	< .001	< .001	1000				
Roads	< .0001 ± < .001	< .001	< .001	915				
Prec	0.002 ± < .001	< .001	< .001	848				
Slope	0.083 ± 0.028	0.038	< .001	891				
Slope^2	-0.013 ± 0.003	< .001	< .001	999				
Forest	-0.011 ± 0.004	< .001	< .001	802				
Reforest	0.005 ± 0.003	< .001	< .001	751				
Scrubland	0.028 ± 0.007	< .001	< .001	999				
Shrubland	0.007 ± 0.003	< .001	< .001	716				
Dehesa	0.020 ± 0.006	< .001	< .001	990				

Table 4. Percentage of 10x10 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"; Stuerck et al. 2014). We consider both the current vulture distribution and the suitable at distribution predicted by the modeling procedures (cut points: p > 0.51 for nesting habitat; p> 0.49 for foraging habitat). Colors highlight the effect in a 0-100 scale (from green to red). Credit photos: Manuel de la Riva.

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

FIGURE LEGENDS:

Figure 1. Distribution of Cinereous vultures in Peninsular Spain a) nesting (based on Martí and Del Moral, 2003); b) foraging (created according to inference from radio-tracking studies (Carrete and Donazar, 2005, Moreno-Opo et al., 2010). The last two maps represent the average prediction of the 1000 final models showing each UTM 10x10 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; d) foraging habitat.

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 colored 10x10 km cells show areas with the fraction of the area affected by land abandonment (change) and light blue colored 10x10 km cells show areas without land abandonment (no change).

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.