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A spatial planning approach for the identification of critical habitat for threatened species

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Abstract
The designation of critical habitat for the conservation of threatened species has long been recognized in the environmental legislation of different countries. However, translating vague legislation about critical habitat into practical real-world designation remains challenging because of its sensitivity to many context- and species-specific criteria and assumptions. We explored how spatial prioritization tools can help navigate such challenges and explicitly address sensitivities. Using a case study on the endangered little bustard (*Tetrax tetrax*) in Spain and the spatial prioritization tool Marxan, we tested and compared different critical habitat spatial designs across a series of scenarios for the little bustard at the national level. The scenarios accounted for habitat availability requirements over the species' annual cycle, the species' representativeness across the territory, the spatial connectivity of its habitat and populations, and potential cost constraints. This approach allowed us to quantify the sensitivity of critical habitat designations to how these criteria are quantified and integrated. Considering unoccupied habitat as critical habitat for the species generated larger, more spatially aggregated solutions that would likely be harder to implement than scenarios focusing conservation efforts on currently occupied habitat only. Considering the species' extirpation risks at individual planning units as a constraint to management success generated completely different solutions than scenarios assuming homogeneous extirpation risk across the landscape. The overall connectivity of identified critical habitats across the entire study area was double in scenarios that accounted for extirpation risk in individual planning units than that in scenarios that held extirpation risk

constant across all units. Our approach, based on freely available software, can help guide conservation efforts by identifying new critical areas that maximize the effectiveness of conservation actions and can be used to assess the sensitivity and uncertainty of critical habitat designation to different criteria.

KEYWORDS
conservation planning, protected areas, species distribution models, stakeholder involvement, threatened species

INTRODUCTION

Protected areas are a fundamental tool for conservation worldwide (Geldmann et al., 2013; Watson et al., 2014). If adequately managed, they slow down land-use change, reducing habitat loss (Figueroa & Sánchez-Cordero, 2008; Geldmann et al., 2013; Hermoso et al., 2018), preventing local extinctions (Gillingham et al., 2015), and allowing populations to persist or increase in abundance and range (Lehikoinen et al., 2019). National and international agendas seek to further expand protected areas to stop the ongoing biodiversity crisis (IPBES, 2019). For example, the post-2020 Global Biodiversity Framework (CBD/WG2020/3/3) and the recently updated European Biodiversity Strategy for 2030 envision 30% of land and sea areas being conserved and effectively and equitably managed by 2030. However, this expansion faces many challenges, such as social conflict (e.g., governance by local communities that already play a key role in conservation [IPBES, 2022]) and competition with other land uses (Watson et al., 2014). Furthermore, protected areas do not always guarantee effective protection of target species (Hermoso et al., 2019). Therefore, it is increasingly recognized that "other effective area-based conservation measures," beyond static protected areas, must be developed and implemented (CBD/COP/DEC/14/8) to provide de facto protection to species of conservation concern.

Identification and designation of critical habitat is one example of such other effective area-based conservation measures. These were pioneered in the United States under the *Endangered Species Act* and are now included in the environmental legislation of many countries, such as Australia (*Environment Protection and Biodiversity Conservation Act 1999* - EPBC Act), Canada (*Species Risk ACT 2002, c.29*), Mexico (*Ley General de Vida Silvestre - 2000*), and Peru (*Estrategia Nacional de Diversidad Biológica al 2021*). In these instances, critical habitat for threatened species is defined not only as a series of physical or biological features but also as the physical area of occurrence of those features essential for the survival of the species, or more generally "essential to the conservation of the species and which require special management consideration and protection" (Endangered Species Act of 1973 - ESA, pp. 2 Sec 3). As a conservation tool, relative to protected areas, critical habitat designation allows greater management and geographic flexibility (e.g., its boundaries can be revisited under adaptive management) in that it addresses species' adaptive capacity and accounts for its ecological traits (e.g., dispersal), population dynamics (e.g., seasonal movements), and the dynamics of species' habitats (a sort of dynamic or floating protected areas as defined by Rayfield et al. [2008]).

The value and the difficulty of defining *critical habitat* lies in how generally this concept can be captured in environmental legislation and in how to translate such definitions into operational area designations (Miret-Minard et al., 2024). *Critical habitat* must be defined specifically for each species (i.e., it is not generalizable) in its recovery plan, although some legislation, such as *Spanish Law 42/2007 of Natural Heritage and Biodiversity*, anticipates the possibility of designating critical habitat for multiple species that share ecological requirements and threats. The scientific consensus is that the definition of *critical habitat* should follow population viability criteria (Camaclang et al., 2015; Rosenfeld & Hatfield, 2006). However, in practice, implementation is mostly influenced by other criteria, such as data availability or avoidance of socioeconomic conflict (Bird & Hodges, 2017; Martin et al., 2017). For example, an unoccupied habitat is usually important for threatened species recovery, but it is seldom counted as critical habitat, not even when recovery depends on translocation to or recolonization in a currently unoccupied habitat (Camaclang et al., 2015). The consideration of unfavorable habitats within the historical range of the species distribution that could be subject to restoration is even rarer (Seddon, 2010; Sovada et al., 2009).

Irrespective of how *critical habitat* is formally defined, and despite its proven effectiveness for conservation (Taylor et al., 2005), its documented implementation is still scarce, hindering the effective protection of threatened species. Bird and Hodges (2017) showed that 63% of species listed under the 2002 *Canadian Species at Risk Act* lack critical habitat designation 13 years after the act was fully implemented. Among species listed under the 1973 *US Endangered Species Act*, by 2002 only 36% had been attributed critical habitat (Taylor et al., 2005). Reasons for such poor implementation include insufficient funding, biases in the development of recovery plans, unclear legislation (often leading to court challenges), lack of knowledge on the species' ecology, and difficulty in translating available scientific knowledge into critical habitat designation (Bird & Hodges, 2017; García-Macía et al., 2021; Hagen & Hodges, 2006; Miret-Minard et al., 2024; Taylor & Pinkus, 2013; Walsh et al., 2013).

We explored how multiple-objective spatial prioritization can help navigate the challenges of defining critical habitat for threatened species and evaluated the sensitivity of the definition to different biological and nonbiological criteria (e.g., unoccupied habitat, historical range, potential recovery costs). Although spatial planning tools have been applied to support the designation of critical habitat (e.g., Dunk et al., 2019), their application remains scarce in practice. We focused on the little bustard (*Tetrax tetrax*) in Spain, a steppe and farmland bird species recently classified nationally as endangered after a population decline of >50% in the last 2 decades (García de la Morena et al., 2018). Such listing dictates the urgent development of a recovery plan (in <3 years), including the designation of critical habitat (*áreas críticas*) for the species, following *Spanish Law 42/2007 of Natural Heritage and Biodiversity*. Although the designation of critical habitat is not mandatory in recovery plans, in areas designed as such it is possible to prohibit or limit many threatening activities, such as hunting, forestry, agriculture, and mining. In Spain, autonomous regions (the first subnational administration level) are responsible for species and habitat protection, including the development of recovery plans and designation of critical habitat. However, the concept of critical area is defined very generally in national legislation, meaning that each autonomous region can interpret it differently. For example, some might decide to designate only breeding areas as critical habitats and ignore other areas important for other parts of a species' life cycle. Interpretation of the critical habitat concept also varies across experts involved in the conservation of the little bustard in Spain (Miret-Minard et al., 2024); scientists and managers have diverging perspectives on the key criteria to adopt.

The little bustard represents a particularly interesting case study with which to explore the complexity of critical habitat designation because its remaining habitat is primarily in areas of human use (extensive agriculture), which poses challenges regarding habitat management and land-use conflict. Moreover, the little bustard is an umbrella species for part of the steppe bird community, mostly specialist species linked to cereal and grassland-dominated landscapes (Morales et al., 2023). Therefore, the designation of critical habitat for the little bustard could benefit a range of other species associated with extensive cereal farmland, species that are experiencing similarly alarming declining trends across the Iberian Peninsula and Europe (Rigal et al., 2023).

METHODS

Little bustard current situation, trends, and conservation status

The little bustard is an iconic species of Palearctic grassland and extensive farmland ecosystems and is classified as near threatened worldwide and vulnerable in Europe by the International Union for Conservation of Nature (IUCN) (IUCN, 2022). It was historically distributed from northwestern Africa and Iberia to central Asia. Currently, only 2 subranges persist: western, encompassing Iberian, French, and Sardinian populations, and eastern, mostly in southern Russia and Kazakhstan (Morales & Bretagnolle, 2022). Although Spain harbors the bulk of the western population, Spanish little bustards have been declining over, at least, the last 2 decades (Morales & Bretagnolle, 2022), experiencing an overall regression of 50% between 2005 and 2016 (García de la Morena et al., 2018). This decline has led to its listing as endangered in the Spanish Red Data Book (López-Jiménez et al., 2021) and more recently to its listing as endangered in the *Spanish Threatened Species Act* (Real Decreto 139/2011). This population collapse is driven by agricultural intensification (Silva et al., 2022) and linked to the loss of certain grassland-like habitats, such as fallows and extensive pastures (Traba & Morales, 2019). The core of the Spanish population lies in the Iberian southern plateau, although other regions, such as the Iberian northern plateau, the Ebro Valley, Extremadura, and Andalusia, have also held historically relevant populations that are currently in steep decline (García de la Morena et al., 2018). Both habitat requirements and distribution of the species change over a year. Their migration within the Iberian Peninsula is of varying magnitudes, depending on the population of origin (García de la Morena et al., 2015). Conservation-oriented land-use management for the species (e.g., promotion of fallow fields via agroenvironmental schemes) has effectively boosted little bustard populations locally, given the rapid response of the species to improvements in habitat quality (increase in species survival and productivity) (Bretagnolle et al., 2011; Devoucoux et al., 2019; González del Portillo et al., 2024). Therefore, the designation of critical habitat where such management could be implemented represents a powerful conservation tool for the recovery of the species, even in areas currently hosting small populations (Traba et al., 2020).

Objectives of and main criteria for the identification of critical habitat

In May 2021, we held a 2-day workshop with farmland bird researchers, environmental nongovernmental organization consultants, stakeholders, technicians, and national and subnational managers responsible for the species' conservation. The aim of this workshop, and of the overall project leading to this study, was to precisely assess the potential for designating critical habitat as a management tool for this endangered species (workshop details in Appendix S1).

We selected workshop participants to ensure the representation of as many autonomous regions as possible and of competencies in little bustard ecology and steppe bird conservation. Participants (35 out of an initial list of 65 invitees) discussed the primary objectives and criteria of critical habitat for the little bustard, starting from the general definition set out in the *Spanish Law of Natural Heritage and Biodiversity* (*Ley 42/2007)*. Participants agreed on 3 fundamental objectives: assist the persistence and growth of the species' populations through the conservation of its preferred habitat throughout the species' annual cycle (breeding, postbreeding, and wintering); ensure representativeness of critical habitat (i.e., that critical habitat is identified and designated in all autonomous regions with the presence of the little bustard so that conservation efforts are well distributed across the Spanish territory); and promote habitat and populations' connectivity. We quantified these 3 objectives (viability, representativeness, and connectivity) in a spatially explicit way so we could integrate them into a spatial prioritization approach (Figure 1).

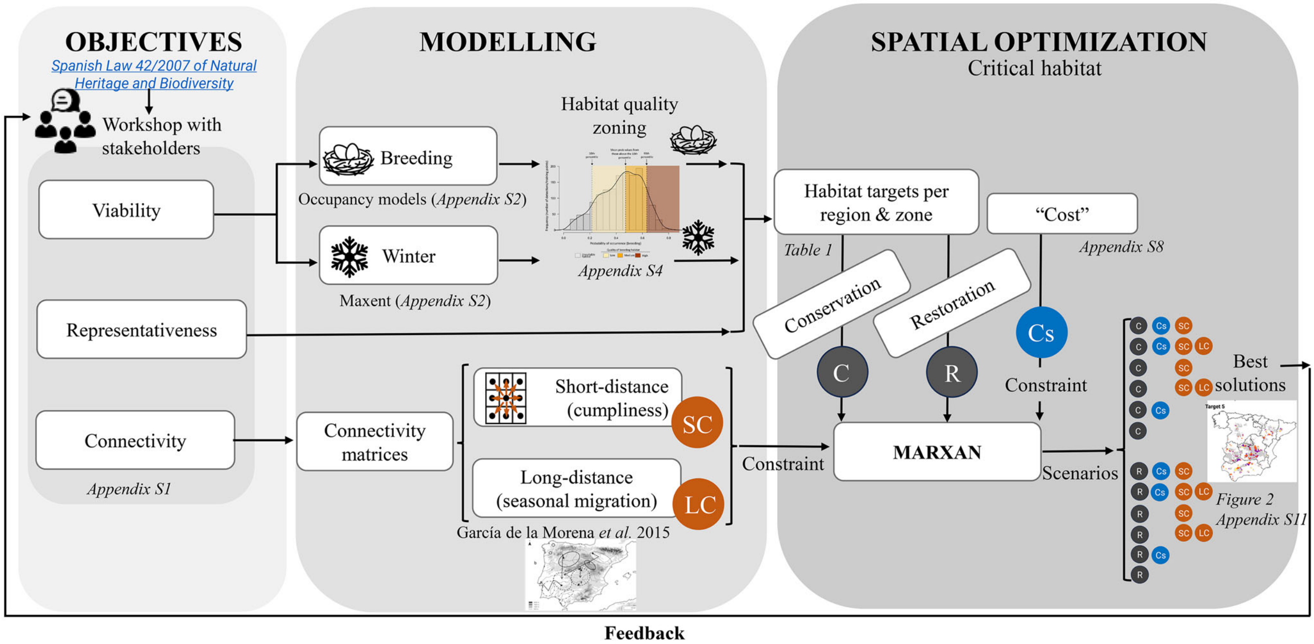

FIGURE 1 Workflow in the identification of critical habitat for the little bustard in Spain.

Habitat availability mapping (viability objective)

Ideally, population viability should be assessed through population models (Dunning et al., 1995), but available demographic data for the little bustard in Spain are aggregated by autonomous region (Traba et al., 2020), complicating inference at the higher resolution required for critical habitat designation. Therefore, we used models of occupancy (MacKenzie et al., 2002) and species distribution (Maxent; Phillips & Dudík, 2008; Phillips et al., 2006) to estimate little bustard habitat suitability across Spain throughout its annual cycle (breeding and wintering grounds). We fit models to data from the two national breeding and winter censuses available for the species (2005 [García de la Morena et al., 2006] and 2016 [García de la Morena et al., 2018]) and obtained habitat suitability predictions for the breeding and winter season that we used as a proxy for species population viability. Details of the modeling workflow are in Appendices S2 and S3, the latter following the overview, data, model, assessment, and prediction protocol (Zurell et al., 2020).

From the models, we obtained maps of the probability of occurrence (breeding season) and habitat suitability (winter season) for 2005 and 2016, which we then used to delimit zones of very good, medium, low, and null habitat quality for the little bustard across Spain. We used these zones as proxies of abundance and viability. Although this correlation is often weak (Jiménez-Valverde et al., 2021), for the little bustard our data and results supported our choice; mean abundance (males per km^2 in the breeding season) was significantly higher in areas of high-quality habitat than in areas of medium- and low-quality habitat (Appendix S4).

To delimit these zones, we followed a methodology proposed for the identification of priority intervention areas for the European turtle dove (*Streptopelia turtur*) (Herrando et al., 2018). This methodology combines model predictions (i.e., estimates of the probability of species' occurrence and habitat suitability) with the species detections used for model training to set a series of numerical thresholds that separate habitat into 4 zones according to their quality (Appendix S4a). While applying a threshold to model predictions degrades information, identifying critical habitat is a case where its application can be useful (Guillera-Arroita et al., 2015). In our case, discretization allowed us to define conservation targets (total area or extent of critical habitat per zone) in the spatial prioritization analyses (next section). Because thresholds are model dependent and zoning based on different models cannot be compared, for the breeding season, we projected the 2005 occupancy model to 2016 and zoned both with the 2005 thresholds (validation of model projections in Appendix S5). We made this choice because the 2005 model was built on the best baseline information of occurrence data of the little bustard at the national level (before the large population decline); therefore, we considered that it better captured the environmental preferences of the species. This was not necessary for the winter model, where we fitted a single model to aggregate data from both years (Appendices S2 & S3).

Representativeness and connectivity in spatial optimization

We used the spatial prioritization software Marxan (Ball et al., 2009) to identify critical habitat for the little bustard across Spain and account for the 3 objectives agreed upon by stakeholders: habitat availability, representativeness, and connectivity (Figure 1). Marxan uses an optimization algorithm to select a subset of planning units that minimizes the following objective function (OF) (Equation 1) across I planning units and J habitat features:

$$\mathrm{OF} = \sum_{j}^{J} \mathrm{SPF} \times \text{feature penalty}_j + \sum_{i}^{I} \text{cost}_i + \mathrm{CSM} \sum_{i}^{I} \text{connectivity penalty}_{i1-i2}, \quad (1)$$

where the SPF is the species penalty factor, which is used to maximize the representativeness of habitat features; cost is the cost of each planning unit, which is used to minimize overall costs of spatial solutions; and CMS is the connectivity strength modifier, which is used to maximize connectivity across planning units and favors clumped solutions. The size of the planning units matched the resolution of the breeding and wintering models (1 km^2).

We defined habitat features as the low-, medium-, and high-quality habitat zones for breeding and wintering periods (3 habitat zones × 2 seasons = 6 habitat features). For each habitat feature, we set a range of targets representing how much area of each feature Marxan should try to include in the critical habitat solution (viability objective). This allowed us to evaluate the sensitivity of the best solutions in Marxan to target definition.

These targets were set independently for each autonomous region as a percentage of the total amount of each habitat feature available in each region (representativeness objective). However, because the total area and availability of habitat differed across regions, we applied a negative exponential correction factor to the target in relation to the size of the autonomous region. With this correction, in autonomous regions where there was very little habitat availability, targets represented all or almost all of the available habitat for the species, whereas in larger autonomous regions containing large areas of habitat (e.g., Castilla La Mancha, where winter grounds concentrate [Appendix S6]), the targets remained within a realistic range (Appendix S7). Therefore, the viability and representativeness objectives entered simultaneously the spatial prioritization algorithm through the definition of targets per habitat-quality zone and region via the SPF and feature penalties in the first term of Equation (1) (Figure 1).

We ran 2 different spatial prioritization scenarios that differed in whether critical habitat included areas where the little bustard populations recently disappeared. The *conservation scenario* set critical habitat targets over zones that had suitable habitat only in 2016 (Table 1). The *restoration scenario*, in addition to the above, set critical habitat targets over zones that went from medium-high habitat quality in 2005 to low habitat quality in 2016 (Table 1). This second scenario is based on the assumption that restoration measures could seek to increase habitat availability and promote recolonization of areas from which the species has recently disappeared. This will allow Marxan to select planning units where there is a greater probability of increasing habitat suitability through management interventions. It is easier to recover a population recently lost due to small losses of habitat quality than to recover an area where the habitat has been fully transformed (e.g., conversion of fallow land into a photovoltaic park or a woody crop such as a vineyard).

We ran both scenarios under 2 different spatial constraints associated with the risk of local extinction for each planning unit via the cost term in Equation (1) and the consideration of connectivity among planning units via the connectivity penalty term in Equation (1). Regarding the cost, in the null constraint scenario, cost was set equal to 1 across all planning units (i.e., constant across the study area), so there would not be spatial differences in the cost constraints to the selection of critical habitat. In the cost constraint scenario, we set cost as inversely proportional to the predicted extinction risk of the little bustard in each planning unit. This favored the identification of critical habitat in areas with low little bustard extinction risk, assuming these would better support populations in the midterm and, therefore, warrant a higher chance of success of management efforts. To estimate the probability of little bustard extinction risk and given the lack of spatially explicit data on population trends, we followed the approach by Franch et al. (2021) for atlas-type data. They estimated this probability as an interpolation at 1 km^2 of extinct (1) and nonextinct (0) cells with kriging (automap R package [Hiemstra et al., 2009]). Extinct cells were those 10 × 10-km grid cells in which the species was present in the 2005 census but absent in 2016. Nonextinct squares were those in which the species was present in both censuses (details in Appendix S8). In the absence of other cost measures that could be more relevant to the species' management (such as land acquisition and management costs or habitat restoration costs), this simple proxy allowed us to evaluate the sensitivity of the spatial optimization solutions to the cost constraint.

To address the connectivity objective, we sought to identify spatially aggregated critical habitat under the assumption that the persistence of a population requires a minimum habitat patch size and that it is easier to manage few, larger areas of critical habitat than many small, scattered ones. This was achieved using the connectivity penalty in Equation (1) (i.e., connectivity also entered the OF as a constraint [Figure 1]). We derived connectivity penalties from the geographic distance between each cell and the nearest 8 neighbors of each planning unit (d_{ij}, where i and j represent a pair of cells; penalty = d_{ij}^{-2}) (short-distance connectivity). The connectivity penalty was weighted in the OF by a CSM value. Higher CSM values in Equation (1) would result in solutions for which critical habitat was spatially clumped. Generally, this would lead to the selection of a larger number of planning units in Marxan solutions (higher costs). To ensure this relationship was reasonable, we calibrated the CSM value (Equation 1) for each scenario and target following Ardron et al. (2010) (details on CSM calibration in Appendix S9).

We also sought to incorporate in the connectivity matrix the existing knowledge on species movements that link populations across autonomous regions and to breeding and wintering grounds (García de la Morena et al., 2015) (i.e., to account for functional connectivity beyond the 8 neighbors described above). However, for the little bustard in Spain, the exact

TABLE 1 Range of target values (percentage of little bustard habitat identified as critical) tested in the Marxan spatial prioritization scenarios (conservation vs. restoration).

			Target[a]				
Scenario		Habitat quality	T1	T2	T3	T4	T5
Conservation	Breeding	High	33	50	75	85	100
	Breeding	Medium	15	33	50	65	75
	Breeding	Low	1	2	5	7	10
	Winter	High	5	12	25	33	50
	Winter	Medium	2	5	10	12	25
	Winter	Low	0	0	0	0	0
Restoration[b]	Breeding low → medium		5	12	25	33	50
	Breeding medium → high		15	33	50	65	75
	Breeding low→ high		0	0	0	5	10

[a]Target values were calculated as area-based percentages over the total habitat available for each habitat quality zone (breeding and wintering) in each autonomous region.
[b]The restoration scenario adds habitat recovery targets to those of the conservation scenario (a percentage of cells to be restored in relation to the total number of 1-km^2 cells that have lost habitat quality between the first and second national census of the little bustard [2005–2016]).

origin and destination of all individuals across all populations in their seasonal migrations are unknown. It would be unrealistic and too computationally demanding to assume that all breeding habitats in an autonomous region are potentially connected with all wintering habitats in the autonomous region of the wintering destination (connectivity matrix of ∼5 million connections). To at least partly account for the impact of such long-distance connectivity, we randomly selected a 1-km^2 cell within each of the 10-km^2 grid cells of the little bustard census in the origin and destination autonomous regions and assumed a potential long-distance connection among those. We added the connectivity penalties estimated from these long-distance connections to the connectivity penalties estimated on neighbor relationships (i.e., short-distance connectivity values). We ran all scenarios twice, once with the calibrated CSM value (Conn scenarios) and once with a CSM = 0 (NullConn scenarios), to assess the impact of connectivity constraints in spatial prioritization outputs (Figure 1). The Conn scenarios were run twice: once with only short-distance connectivity (clumpiness) and once with the additive effect of short- and long-distance connectivity (i.e., to account for the linkages among autonomous regions due to seasonal movements of the little bustard).

We, therefore, ran a total of 12 scenarios: conservation versus restoration, with and without cost constraints, with and without connectivity settings, and the latter further separated into short distance only and both short and long distances (Table 2; Figure 1). For each scenario, we ran Marxan 100 times with an adaptive annealing approach that allowed the algorithm to optimize the start temperature and cooling factor parameters and increased the number of iterations to 10 million to warrant convergence of solutions. We used standard values for the rest of the Marxan parameters. We selected the best solution out of the 100 independent runs (hereafter Marxan best solution). Table 2 provides a summary of all tested scenarios and the parameters considered in each, and Figure 1 is a summary of the modeling and spatial prioritization workflow.

Metrics of comparison across scenarios

After obtaining the best solution from each scenario, we compared scenarios with different summary metrics: number of planning units required by the best solution (identified as critical habitat); spatial structure of the identified critical habitat in each scenario, represented by 4 landscape metrics computed using the *landscapemetrics* package (Hesselbarth et al., 2019) in R (number of patches, where a patch is an aggregation of 2 or more contiguous planning units identified as critical habitat; average size of patches; coefficient of variation among patches; and a clumpiness index that measured the degree of spatial aggregation of critical habitat planning units [range −1 to 1; −1, maximum disaggregation; 0, aggregation of cells within categories not different from random; 1, maximum aggregation, that is, all selected planning units form a single patch]); and overall critical habitat connectivity achieved, calculated using a connectivity index that measures the relative connectivity achieved in the solution compared with the maximum connectivity that could have been achieved if all planning units in the solution were fully connected (the index is independent of the number of planning units in the solution and, therefore, comparable across scenarios and targets [Hermoso et al., 2020]).

We also evaluated the percent overlap between the critical habitat identified by Marxan scenarios and the current network of protected areas (special protected areas declared under the European Birds Directive 2009/147/EC). We considered only those special protected areas where the little bustard is declared among the species of conservation interest for that site.

Finally, we estimated the proportion of the total population size across the autonomous regions that could be theoretically covered by the critical areas identified across the different scenarios. First, we estimated the species density per 1-km grid cell in each of the breeding habitat quality zones (low, medium, and high quality; see "Habitat availability map-

TABLE 2 Scenario combinations considered in the identification of critical habitat for the little bustard across Spain.[a]

Scenario acronym	Approach	Cost	CSM	Connectivity matrix
Conserv_Cost_Conn[b]	Conservation	Proportional to extinction risk	Yes	Short distance
Conserv_Cost_Conn	Conservation	Proportional to extinction risk	Yes	Short + long distance
Conserv_NullCost_Conn	Conservation	Equal across planning units	Yes	Short distance
Conserv_NullCost_Conn	Conservation	Equal across planning units	Yes	Short + long distance
Conserv_Cost_NullConn	Conservation	Proportional to extinction risk	No	–
Conserv_NullCost_NullConn	Conservation	Equal across planning units	No	–
Rest_Cost_Conn[b]	Restoration	Proportional to extinction risk	Yes	Short distance
Rest_Cost_Conn	Restoration	Proportional to extinction risk	Yes	Short + long distance
Rest_NullCost_Conn	Restoration	Equal across planning units	Yes	Short distance
Rest_NullCost_Conn	Restoration	Equal across planning units	Yes	Short + long distance
Rest_Cost_NullConn	Restoration	Proportional to extinction risk	No	–
Rest_NullCost_NullConn	Restoration	Equal across planning units	No	–

[a]Scenarios resulted from the combination of the the intended goal pursued with the definition of *critical habitat* (conservation vs. restoration), the costs assumed for the planning units, and the application or non application of the connectivity strength modifier (CSM) penalty (Equation 1).
[b]The scenarios, including the connectivity penalty (Conn), were run twice: once considering short-distance connectivity only (i.e., clumpiness) and second considering the joint effect of short- plus long-distance connectivity (i.e., to promote spatially aggregated solutions that account for the potential seasonal movements of the little bustard among autonomous regions).

ping") by overlapping species observations in the 2016 census with the projected quality zones for that year (mean density of individuals per square kilometer and zone). This was estimated separately per autonomous region, given the large variations in population sizes among them. Then, knowing how many planning units were identified as critical habitat in each autonomous region, scenario, and zone (i.e., in each Marxan best solution), we estimated the theoretical density of individuals that could be covered by these planning units and the proportion these represented in relation to the total available planning units in a given quality zone. We used this measure as a proxy of the percentage of the total theoretical population size that could be covered by the critical habitat identified in each solution.

RESULTS

Critical area targets were achieved for all habitat quality zones and across all autonomous regions, scenarios, and targets tested (Appendix S10). Marxan solutions approached optimality in all cases, as indicated by the simulated annealing algorithm convergence across all scenarios tested and by the low deviation in the OF's score across each set of 100 runs. Critical areas for the conservation of the little bustard were mostly identified in central and southwestern Spain (Figure 2). However, because targets were set individually for each autonomous region, Marxan best solutions identified critical habitats across all regions where the species was present. While there were large overlaps between the solutions of the conservation and the restoration scenarios, the latter generated more aggregated solutions, with larger patches generally connecting disjointed patches or enlarging small patches that had already been identified as critical in the conservation scenario (Cost_Conn scenarios) (Figure 2; Table 3), leading to a larger total number of units (i.e., more total area identified as critical for the species) (Table 3). These results were consistent across all tested targets. The results presented in this section refer to scenarios considering both long- and short-term connectivity as constraints because the differences in landscape metrics and overall configuration of spatial solutions were small between the 2 connectivity alternatives tested. Comparative results of solutions run with short-distance connectivity only when comparison was needed are in online appendices.

When the extinction risk of planning units was assumed homogenous across the study area (NullCost_Conn scenarios), the critical areas identified were smaller in size and more scattered through the study area than in scenarios where extinction risks were heterogeneous (Cost-Conn) (Figure 2; Table 3). Overall, solutions for the NullCost_Conn scenario selected a smaller number of restoration units (total square kilometers) (Table 3) but were more expensive than solutions of scenarios focused on areas where extinction risk was lower (Cost_Conn scenarios) (Figure 3). The spatial allocation of critical habitat differed substantially between the Cost_Conn and the NullCost_Conn approaches, both in the conservation and restoration scenarios, particularly in the largest autonomous regions where there were more planning units available for selection and extinction risk was highly variable across the territory (Figure 2; Appendices S8 & S12). For a given overall cost, scenarios with heterogenous extinction risks (Cost_Conn) had lower overall connectivity of critical habitats than those with spatially homoogeneous extinction risks, regardless of connectivity penalty (NullCost_Conn, NullCost_NullConn) (Figure 4).

Across all scenarios, on average, <25% of the areas identified as critical habitat were covered by special protection areas designated for the little bustard. This percentage was lower in the conservation and restoration Cost_Conn heterogeneous extinc-

TABLE 3 Summary statistics of the spatial structure of critical habitat for the little bustard in Spain identified in the Marxan best solutions for each combination of scenario and target and considering long-distance habitat connectivity.[a]

			Critical habitat summary metric[b]					
	Scenario[c]	Target[d]	Npatch	PatcAr	PatcArCV	Clumpiness	Total km^2	SPA (%)
Conservation	Cost_Conn	1	394	2364.21	498.7	0.93	9315	5.80
	Cost_Conn	2	438	2484.25	412.72	0.92	10881	9.70
	Cost_Conn	3	581	2368.67	471.27	0.91	13762	10.85
	Cost_Conn	4	656	2242.68	441.68	0.9	14712	12.84
	Cost_Conn	5	774	2160.72	481.48	0.89	16724	13.27
	NullCost_Conn	1	454	212.11	195.86	0.37	963	34.27
	NullCost_Conn	2	651	265.59	287.46	0.46	1729	34.24
	NullCost_Conn	3	896	350.22	316.32	0.56	3138	33.62
	NullCost_Conn	4	1053	376.26	388	0.58	3962	31.55
	NullCost_Conn	5	1153	474.76	357.34	0.62	5474	28.17
	Cost_NullConn	1	492	195.93	133.89	0.23	964	26.14
	Cost_NullConn	2	720	241.25	184.28	0.28	1737	26.37
	Cost_NullConn	3	1075	288.28	215.4	0.33	3099	29.40
	Cost_NullConn	4	1163	331.38	242.82	0.35	3854	30.07
	Cost_NullConn	5	1368	389.55	383.12	0.4	5329	28.43
	NullCost_NullConn	1	720	133.06	68.16	0.08	958	32.36
	NullCost_NullConn	2	1088	155.33	115.11	0.12	1690	32.25
	NullCost_NullConn	3	1701	176.78	166.67	0.16	3007	29.63
	NullCost_NullConn	4	1914	196.45	199.62	0.18	3760	29.15
	NullCost_NullConn	5	2368	217.36	220.27	0.2	5147	29.03
Restoration	Cost_Conn	1	395	2920.25	318.19	0.94	11535	5.79
	Cost_Conn	2	466	2645.92	349.69	0.92	12330	12.06
	Cost_Conn	3	488	3427.87	406.88	0.93	16728	13.56
	Cost_Conn	4	534	3937.08	519.78	0.93	21024	11.91
	Cost_Conn	5	588	3631.97	492.22	0.92	21356	14.34
	NullCost_Conn	1	567	185.36	180.94	0.25	1051	35.59
	NullCost_Conn	2	787	244.35	245.08	0.36	1923	34.48
	NullCost_Conn	3	1079	309.55	284.32	0.45	3340	29.58
	NullCost_Conn	4	1293	327.3	348.2	0.46	4232	29.77
	NullCost_Conn	5	1393	412.13	363.63	0.51	5741	26.67
	Cost_NullConn	1	519	205.78	235.41	0.26	1068	24.63
	Cost_NullConn	2	795	244.53	247.42	0.3	1944	24.74
	Cost_NullConn	3	1103	311.6	237.61	0.34	3437	27.35
	Cost_NullConn	4	1229	349.63	269.5	0.36	4297	29.07
	Cost_NullConn	5	1475	397.02	370.82	0.39	5856	26.49
	NullCost_NullConn	1	789	132.45	66.15	0.07	1045	31.00
	NullCost_NullConn	2	1133	167.34	108.05	0.13	1896	29.69
	NullCost_NullConn	3	1715	192.19	169.48	0.17	3296	29.04
	NullCost_NullConn	4	1990	210.25	199.29	0.18	4184	28.08
	NullCost_NullConn	5	2359	238.41	258.11	0.22	5624	27.17

[a] Appendix S12 contains scenario solutions under short distance connectivity.
[b] Critical habitat metrics: Npatch, number of patches of critical habitat; PatcAr, mean patch area; PatcArCV, mean patch area coefficient of variation; clumpiness, measure of aggregation; total km^2, total area identified as critical habitat; SPA, percentage of the total area protected under the figure of spatial protected area.
[c] See Table 2 for a full description of scenarios and meaning of scenario acronyms.
[d] See Table 1 for a description of targets and their values.

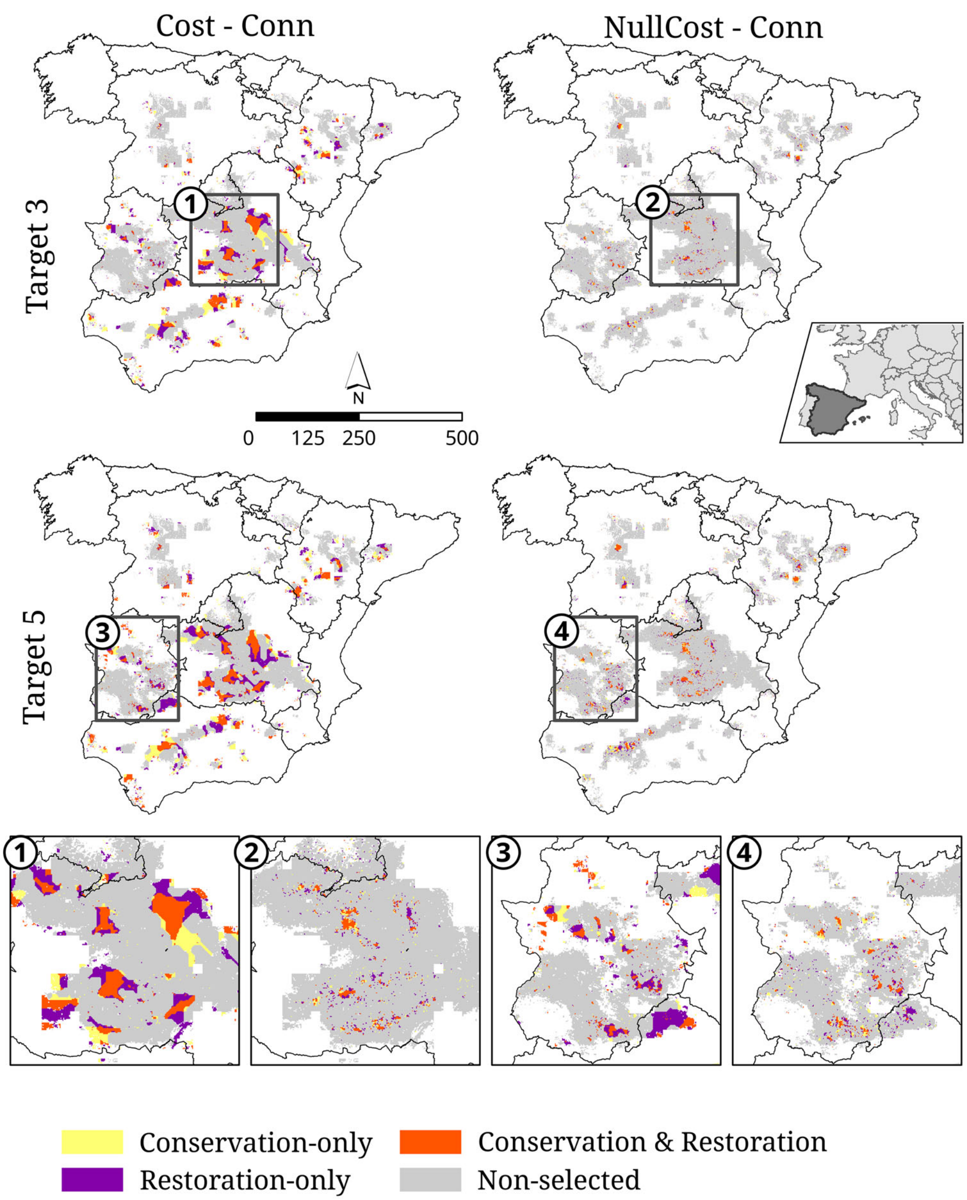

FIGURE 2 Comparison of Marxan best solutions for scenarios for conservation and restoration of critical habitat when the risk of extirpation cost (left panels) and null cost (NullCost) (right panels) was considered and for 2 of the tested targets (see Table 1 for a description of targets and their values). All scenarios applied connectivity strength modifier (CSM) penalties to short- and long-distance connectivity (Conn) (yellow, critical habitat in conservation scenarios; purple, critical habitat in restoration scenarios; orange, critical habitat in both scenarios; gray shading, planning units not selected as critical habitats; numbered squares, details on differences in selected planning units between scenarios for Castilla la Mancha [1 and 2] and Extremadura [3 and 4]). Solutions across all scenarios and targets in Appendix S11.

tion risk scenarios than in the other scenarios (NullCost_Conn, NullCost_NullConn, Cost_NullConn) (Table 3). Critical habitat identified under the conservation and restoration Cost_Conn scenarios covered around 21% of the total population that could be supported by the habitat available in 2016 (average across all targets) (Table 4). This value was substantially smaller under the other scenario combinations (<10% even under Target 5; NullCost_Conn, Cost_NullConn, and NullCost_NullConn). When these values were broken down by habitat quality zones, the identified critical habitat covered up to 77% (target 5) of the theoretical population that could be supported by high-quality habitat zones (Appendix S13).

DISCUSSION

The identification and legal designation of critical habitats is key to the conservation of threatened species (IUCN, 2022; Taylor et al., 2005). Our results suggest that which areas should be designated as critical habitat depends on a series of specific

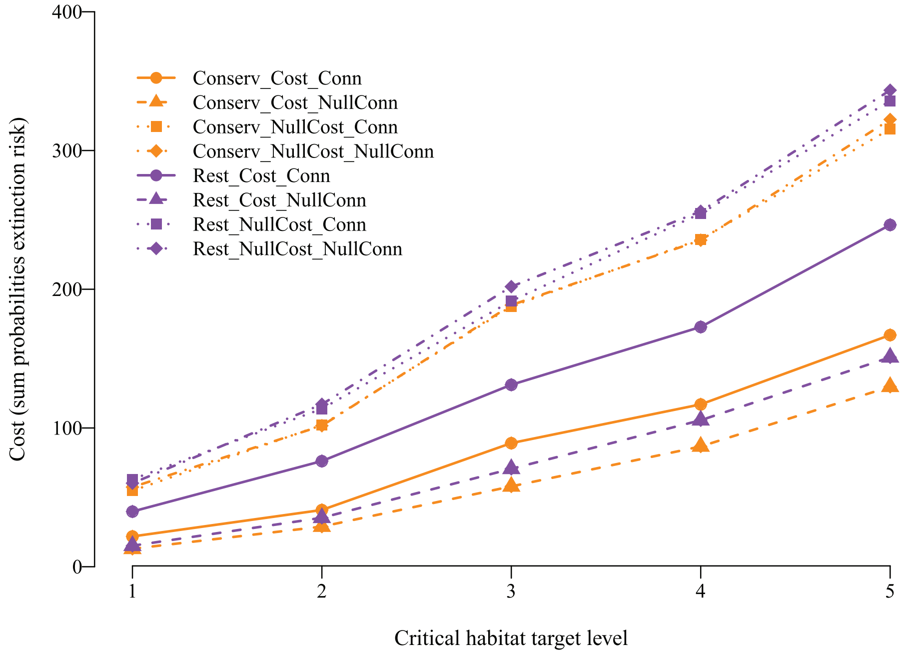

FIGURE 3 Estimated costs of critical habitat identified for the little bustard across conservation and restoration scenarios and targets based on the short- and long-distance connectivity matrix. To ease the comparison between scenarios, costs were calculated by summing up the probability of extinction risks of the planning units identified as critical habitats in Marxan's best solutions for each scenario and target. Scenario acronyms are defined in Table 2. Target levels range from 1 to 5. Target values represent different percentages of little bustard habitat sought to be identified as critical in Marxan solutions. Target values, detailed by habitat quality type, are defined in Table 1.

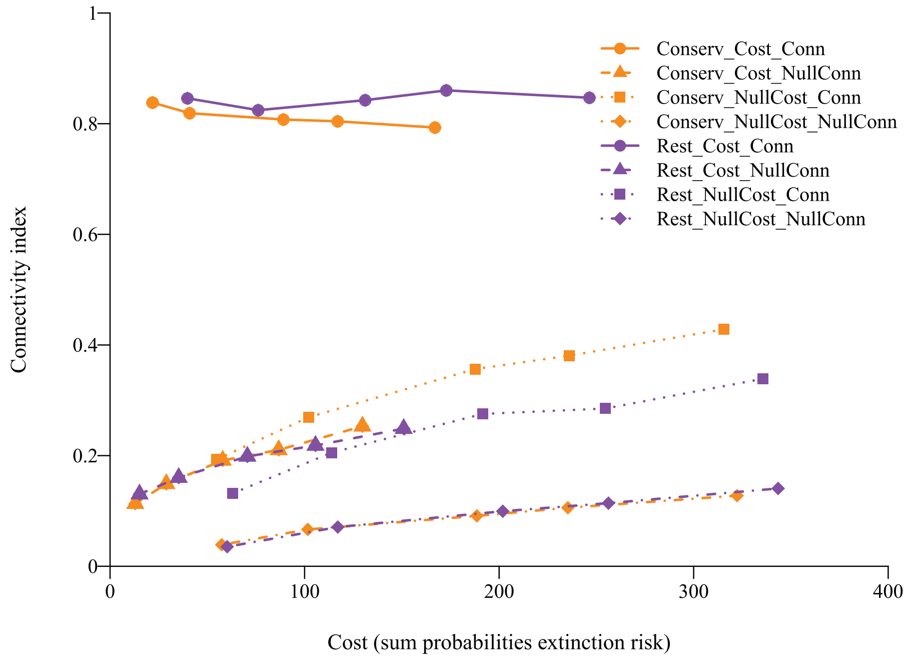

FIGURE 4 Overall connectivity of identified critical habitat achieved with Marxan best solutions across conservation and restoration scenarios for the little bustard based on short- and long-distance connectivity matrix and cost values. The connectivity index (unitless) is 0 when all planning units in Marxan best solutions are totally disjointed and 1 when they all belong to a single connected habitat patch. To ease the comparison between scenarios, costs were calculated by summing the probability of extinction risks of the planning units identified as critical habitats in Marxan's best solutions for each scenario and target. Scenario acronyms are defined in Table 2.

TABLE 4 Proportion of the Spanish little bustard theoretical population that could be covered by the identified critical habitats under each combination of scenarios (conservation vs. restoration with [cost] and without cost [NullCost] and with [Conn] and without connectivity [NullConn] constraints) and target values.[a]

		Theoretical population covered (%)	
Scenario[b]	Target[c]	Conservation	Restoration
Cost_Conn	1	11.45	13.08
Cost_Conn	2	13.29	15.03
Cost_Conn	3	18.02	21.38
Cost_Conn	4	19.57	27.58
Cost_Conn	5	21.90	28.60
NullCost_Conn	1	2.14	2.32
NullCost_Conn	2	3.58	3.96
NullCost_Conn	3	5.94	6.34
NullCost_Conn	4	7.20	7.72
NullCost_Conn	5	9.38	9.91
Cost_NullConn	1	2.13	2.34
Cost_NullConn	2	3.52	3.97
Cost_NullConn	3	5.70	6.38
Cost_NullConn	4	6.80	7.70
Cost_NullConn	5	8.75	9.81
NullCost_NullConn	1	2.13	2.31
NullCost_NullConn	2	3.51	3.93
NullCost_NullConn	3	5.68	6.26
NullCost_NullConn	4	6.78	7.62
NullCost_NullConn	5	8.74	9.66

[a]Appendix S13 contains results broken down by quality of habitat zones.
[b]See Table 2 for a full description of scenarios and meaning of scenario acronyms.
[c]See Table 1 for a description of targets and their values.

decisions that policy makers and managers must make: how much habitat to protect and of which quality, how to distribute efforts across the landscape, whether connectivity is relevant, whether extinction risk costs should be considered, and how the latter should be quantified. Such constraints are likely to always remain context and species specific, which represents an inherent challenge of critical habitat designation. Our spatial planning approach allowed us to explicitly and transparently assess this sensitivity to criteria, constraints, and targets.

The conservation scenario represented a minimum-requirements scenario, in which the priority was to conserve the last remnants of habitat for the little bustard at minimum cost. The restoration scenario also identified critical habitat areas where recent declines in habitat quality occurred—with consequent detrimental effects on local populations—but that still retained low- and medium-quality habitat that could be the target of restoration efforts. This unoccupied habitat could play a key role in population persistence, particularly for species for which habitat loss and degradation have been the main causes of their decline (Camaclang et al., 2015). This is the case for the little bustard, which has been affected by the loss of fallow land and the overall intensification of agricultural practices (Traba & Morales, 2019). Unoccupied habitats could serve as targets for translocations following restoration interventions (e.g., Seddon, 2010; Sovada et al., 2009). Both scenarios conveyed different trade-offs between the management target and the area needed. The conservation scenario represented an overall least-cost and containment solution (fewer selected planning units in the Marxan solution), but it further reduced the chances of recovering the species in unoccupied habitats and the maintenance of self-sustaining populations in some autonomous regions. The restoration scenario, in contrast, maximized the opportunities for recovery in unoccupied areas (slightly higher coverage of the theoretical population) (Table 4) but required a larger number of planning units, generating spatial solutions likely more difficult to implement. Large areas generally imply high management costs and more potential conflicts with other uses. In our case, the largest part of the identified critical habitat was beyond the limits of current protected areas.

When we gave all planning units the same cost (NullCost scenarios) (Table 2), critical habitats were more frequently located in zones that already experienced a strong population decline from 2005 to 2016. Allocating limited resources to unoccupied areas could pose a higher risk of unsuccessful management, particularly in a conservation scenario that seeks to keep the remaining populations stable. However, in practice, some stable populations might be small and isolated, and it might be suboptimal to prioritize them over populations that are declining but occur in areas with substantial amounts of habitat (e.g., opportunities for recovery and restoration might be missed). Finally, although we used extinction risk as a constraint to the selection of planning units (i.e., we assumed the cost penalties in Equation [1] to be inversely proportional to extinction risk), our analyses could be easily adapted to include other constraints more directly related to land management costs, such as subsidies to promote set-aside (fallow) land or to preempt habitat transformations harmful for the species (Traba & Morales, 2019), for example, for land-use change for woody crops, photovoltaic arrays, irrigation, power lines, and urbanization (Silva et al., 2022).

Despite the intuitive importance of promoting functional connectivity of populations to foster species recovery (Hanski, 1999; Hilty et al., 2020), connectivity is not always explicitly acknowledged in legislation about critical habitat (*Spanish Law of Natural Heritage and Biodiversity* [Ley 42/2007]; MITECO, 2022). Managing fewer, more connected critical habitat areas is more cost-effective than managing the same total area distributed in a more scattered way (case of NullConn scenarios [Appendix S11]). We achieved this by penalizing solutions in which planning units were less spatially aggregated (via CSM [Equation 1]). We also integrated connectivity between breeding and wintering grounds (seasonal migration movements) by considering the potential for long-distance dispersal of individuals between autonomous regions (García de la Morena et al., 2015).

Although management responsibilities lie within autonomous regions, seasonal long-distance dispersal requires coordination in the identification of critical habitats among regions and in planning species management at the Iberian scale. For example, designation of critical habitats with the sole focus on breeding populations in northern and northeastern Spain could be in vain if the wintering grounds in Castilla La Mancha—hosting about 63% of the overall Spanish population between December and March (García de la Morena et al., 2018)—are not identified and managed as critical habitats as well. Postbreeding areas are also necessary for the population viability of the little bustard (García de la Morena et al., 2015; Morales et al., 2021) and should be considered when designating critical habitat. However, we could not include these in our analyses because postbreeding data are scarce and biased, a condition likely to be common to many threatened species.

The spatial planning process, involving close collaboration with managers, also helped bring to the surface issues related to the practical interpretation of legislation. Although the current Spanish legislation focuses the definition of *critical habitat* exclusively on the ecological needs of a species, our consultation with stakeholders involved in the conservation and management of the little bustard (Appendix S1) suggested this was not clear in practice. The ambiguity and generality of the definition of *critical habitat* in the Spanish legislation encourage managers to include socioeconomic criteria—especially the potential for land-use conflict—when identifying critical habitat, particularly for a species, such as the little bustard, that is strongly dependent on seminatural systems (Miret-Minard et al., 2024). However, socioeconomic criteria are not explicitly stated in the legislation, potentially resulting in implicit, ad hoc trade-offs and decisions that threaten transparent, rational decision-making (Game et al., 2013). Our spatial planning approach could reduce this threat by explicitly including socioeconomic constraints, such as the economic value of large solar photovoltaic projects over low-cost marginal soils, such as those of extensive cereal farmlands (main habitat of the little bustard in Spain [Serrano et al., 2020]).

Obviously, the results of any planning process, including ours, will be influenced by the type of data available. Ideally, extinction risk should be derived from a spatially explicit population model, but this is not available for the little bustard and is unlikely to be available or realistic to obtain for most threatened species, inevitably increasing uncertainty. Spatial planning helps evaluate this uncertainty explicitly, including that regarding costs (Carwardine et al., 2010; Naidoo et al., 2006). In our case, we communicated these uncertainties to stakeholders during a second workshop where we presented the results of the spatial optimization workflow leading to the identification of critical habitat (including those of intermediate results, such as the habitat suitability maps). Our discussion with stakeholders led to the development of methodological guidelines that can now be used as a reference by the autonomous regions to identify critical habitats for the little bustard and other threatened species in a transparent and consistent way.

The designation of critical habitat is a conservation tool with great potential, especially where the designation of protected areas is not feasible or necessary. Protection of critical habitats can help in the conservation of species, such as the little bustard, that have seasonal distributions of habitat needs that are not adequately covered under protected areas, especially in human-dominated landscapes. Critical habitats could be adapted to changes in conservation and management needs more easily than protected areas. The spatial planning approach we demonstrated here could help guide those efforts to maximize the efficiency of critical areas.

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REFERENCES

Andron, J. A., Possingham, H. P., & Klein, C. J. (2010). *Marxan good practices handbook, Version 2*. Pacific Marine Analysis and Research Association. www.pacmara.org

Ball, I. R., Possingham, H. P., & Watts, M. E. (2009). Marxan and relatives: Software for spatial conservation prioritization. In A. Moilanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritisation: Quantitative methods and computational tools* (pp. 185–195). Oxford University Press.

Bird, S. C., & Hodges, K. E. (2017). Critical habitat designation for Canadian listed species: Slow, biased, and incomplete. *Environmental Science & Policy*, *71*, 1–8.

Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P., & Badenhausser, I. (2011). Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. *Ibis*, *153*, 4–13.

Camaclang, A. E., Maron, M., Martin, T. G., & Possingham, H. P. (2015). Current practices in the identification of critical habitat for threatened species: Identifying critical habitat. *Conservation Biology*, *29*, 482–492.

Carwardine, J., Wilson, K. A., Hajkowicz, S. A., Smith, R. J., Klein, C. J., Watts, M., & Possingham, H. P. (2010). Conservation planning when costs are uncertain. *Conservation Biology*, *24*, 1529–1537.

Devoucoux, P., Besnard, A., & Bretagnolle, V. (2019). Sex-dependent habitat selection in a high-density Little Bustard *Tetrax tetrax* population in southern France, and the implications for conservation. *Ibis*, *161*, 310–324.

Dunk, J. R., Woodbridge, B., Schumaker, N., Glenn, E. M., White, B., LaPlante, D. W., Anthony, R. G., Davis, R. J., Halupka, K., Henson, P., Marcot, B. G., Merola-Zwartjes, M., Noon, B. R., Raphael, M. G., Caicco, J., Hansen, D. L., Mazurek, M. J., & Thrailkill, J. (2019). Conservation planning for species recovery under the Endangered Species Act: A case study with the Northern Spotted Owl. *PLoS ONE*, *14*, Article e0210643.

Dunning, J. B., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H., & Stevens, E. E. (1995). Spatially explicit population models: Current forms and future uses. *Ecological Applications*, *5*, 3–11.

Figueroa, F., & Sánchez-Cordero, V. (2008). Effectiveness of natural protected areas to prevent land use and land cover change in Mexico. *Biodiversity and Conservation*, *17*, 3223–3240.

Franch, M., Herrando, S., Anton, M., Villero, D., & Brotons, L. (2021). *Atles dels ocells nidificants de Catalunya: Distribució i abundància 2015–2018 i canvi des de 1980*. Institut Català d'Ornitologia/Cossetània Edicions.

Game, E. T., Kareiva, P., & Possingham, H. P. (2013). Six common mistakes in conservation priority setting. *Conservation Biology*, *27*, 480–485.

García de la Morena, E., Bota, G., Mañosa, S., & Morales, M. (2018). *El sisón común en España. II Censo Nacional (2016)*. SEO/BirdLife.

García de La Morena, E., Bota, G., Ponjoan, A., & Morales, M. (2006). *El sisón común en España. I censo Nacional (2005)*. Sociedad Española de Ornitología/BirdLife.

García de la Morena, E. L., Morales, M. B., Bota, G., Silva, J. P., Ponjoan, A., Suárez, F., Mañosa, S., & De Juana, E. (2015). Migration patterns of Iberian little bustards *Tetrax tetrax*. *Ardeola*, *62*, 95–112.

García-Macía, J., Pérez, I., & Rodríguez-Caro, R.-C. (2021). Biases in conservation: A regional analysis of Spanish vertebrates. *Journal for Nature Conservation*, *64*, Article 126094.

Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M., & Burgess, N. D. (2013). Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation*, *161*, 230–238.

Gillingham, P. K., Bradbury, R. B., Roy, D. B., Anderson, B. J., Baxter, J. M., Bourn, N. A., Crick, H. Q., Findon, R. A., Fox, R., & Franco, A. (2015). The effectiveness of protected areas in the conservation of species with changing geographical ranges. *Biological Journal of the Linnean Society*, *115*, 707–717.

González del Portillo, D., Morales, M. B., & Arroyo, B. (2024). Temporal trends of land-use favourability for the strongly declining little bustard: Assessing the role of protected areas. *PeerJ*, *12*, Article e16661.

Guillera-Arroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A., Kujala, H., Lentini, P. E., McCarthy, M. A., Tingley, R., & Wintle, B. A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography*, *24*, 276–292.

Hagen, A. N., & Hodges, K. E. (2006). Resolving critical habitat designation failures: Reconciling law, policy, and biology. *Conservation Biology*, *20*, 399–407.

Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press.

Hermoso, V., Morán-Ordóñez, A., & Brotons, L. (2018). Assessing the role of Natura 2000 at maintaining dynamic landscapes in Europe over the last two decades: Implications for conservation. *Landscape Ecology*, *33*, 1447–1460.

Hermoso, V., Morán-Ordóñez, A., Canessa, S., & Brotons, L. (2019). Realising the potential of Natura 2000 to achieve EU conservation goals as 2020 approaches. *Scientific Reports*, *9*, Article 16087.

Hermoso, V., Morán-Ordóñez, A., Lanzas, M., & Brotons, L. (2020). Designing a network of green infrastructure for the EU. *Landscape and Urban Planning*, *196*, Article 103732.

Herrando, S., Carboneras, C., Villero, D., Brotons, L., Milanesi, P., Arroyo, B., Bas-Defossez, F., Bota, G., Días, S., Moreno, L., Peach, W., Quillfeldt, P., & Tryjanowski, P. (2018). *Modelling large-scale spatial distribution and habitat associations of European Turtle-dove Streptopelia turtur during the breeding season* (Workshop report; Project LIFE14 PRE/UK/000002 EuroSAP). Forest Science Center of Catalonia.

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography*, *42*, 1648–1657.

Hiemstra, P. H., Pebesma, E. J., Twenhöfel, C. J. W., & Heuvelink, G. B. M. (2009). Real-time automatic interpolation of ambient gamma dose rates from the Dutch radioactivity monitoring network. *Computers & Geosciences*, *35*, 1711–1721.

Hilty, J., Worboys, G. L., Keeley, A., Woodley, S., Lausche, B., Locke, H., Carr, M., Pulsford, I., Pittock, J., White, J. W., Theobald, D. M., Levine, J., Reuling, M., Watson, J. E. M., Ament, R., & Tabor, G. M. (2020). *Guidelines for conserving connectivity through ecological networks and corridors*. International Union for Conservation of Nature. https://portals.iucn.org/library/node/49061

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)*. IPBES Secretariat.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). (2022). *Methodological assessment of the diverse values and valuation of nature of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)*. IPBES Secretariat.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IUCN). (2022). *The IUCN Red List of Threatened Species. Version 222-2*. International Union for Conservation of Nature. https://www.iucnredlist.org

Jiménez-Valverde, A., Aragón, P., & Lobo, J. M. (2021). Deconstructing the abundance–suitability relationship in species distribution modelling. *Global Ecology and Biogeography*, *30*, 327–338.

Lehikoinen, P., Santangeli, A., Jaatinen, K., Rajasärkkä, A., & Lehikoinen, A. (2019). Protected areas act as a buffer against detrimental effects of climate change—Evidence from large-scale, long-term abundance data. *Global Change Biology*, *25*, 304–313.

López-Jiménez, N., García de la Morena, E., Bota, G., Mañosa, S., Morales, M., & Traba, J. (2021). Sisón común, *Tetrax tetrax*. In N. López-Jiménez (Ed.), *Libro Rojo de las Aves de España* (pp. 125–136). SEO/BirdLife.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*, 2248–2255.

Martin, T. G., Camaclang, A. E., Possingham, H. P., Maguire, L. A., & Chadès, I. (2017). Timing of protection of critical habitat matters. *Conservation Letters*, *10*, 308–316.

Miret-Minard, G., Hermoso, V., Villero, D., Bota, G., Brotons, L., & Morán-Ordoñez, A. (2024). Navigating divergent perspectives on critical habitat designation: Insights from the little bustard (*Tetrax tetrax*) conservation in Spain. *Journal for Nature Conservation*, *80*, Article 126633.

Ministerio para la Transición Ecológica y el Reto Demográfico (MITECO). (2022). *Conservation Strategy for threatened birds linked to agro-steppe environments in Spain*. https://www.miteco.gob.es/es/biodiversidad/publicaciones/pbl_estrategia_aves_esteparias_tcm30-542262.pdf

Morales, M. B., & Bretagnolle, V. (2022). An update on the conservation status of the Little Bustard *Tetrax tetrax*: Global and local population estimates, trends, and threats. *Bird Conservation International*, *32*, 337–359.

Morales, M. B., Mañosa, S., Bretragnolle, A., Villiers, E., & García de la Morena, E. L. (2021). Migration, movements and non-breeding ecology. In V. Bretagnolle, J. Traba, & M. B. Morales (Eds.), *Little bustard ecology and conservation* (pp. 123–149). Springer.

Morales, M. B., Merencio, Á., & de la Morena, E. L. G. (2023). Evaluation of a potential umbrella species using favourability models: The case of the endangered little bustard (*Tetrax tetrax*) and steppe birds. *Biodiversity and Conservation*, *32*, 3307–3327.

Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H., & Rouget, M. (2006). Integrating economic costs into conservation planning. *Trends in Ecology & Evolution*, *21*, 681–687.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259.

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*, 161–175.

Rayfield, B., James, P. M., Fall, A., & Fortin, M.-J. (2008). Comparing static versus dynamic protected areas in the Quebec boreal forest. *Biological Conservation*, *141*, 438–449.

Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., Del Moral, J. C., Domşa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., … Ieronymidou, C. (2023). Farmland practices are driving bird population decline across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *120*, Article e2216573120.

Rosenfeld, J. S., & Hatfield, T. (2006). Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 683–698.

Seddon, P. J. (2010). From reintroduction to assisted colonization: Moving along the conservation translocation spectrum. *Restoration Ecology*, *18*, 796–802.

Serrano, D., Margalida, A., Pérez-García, J. M., Juste, J., Traba, J., Valera, F., Carrete, M., Aihartza, J., Real, J., Mañosa, S., Flaquer, C., Garin, I., Morales, M. B., Alcalde, J. T., Arroyo, B., Sánchez-Zapata, J. A., Blanco, G., Negro, J. J., Tella, J. L., … Donázar, J. A. (2020). Renewables in Spain threaten biodiversity. *Science*, *370*, 1282–1283.

Silva, J. P., Arroyo, B., Marques, A. T., Morales, M. B., Devoucoux, P., & Mougeot, F. (2022). Threats affecting little bustards: Human impacts. In V. Bretagnolle, J. Traba, & M. B. Morales (Eds.), *Little bustard: Ecology and conservation* (pp. 243–271). Springer.

Sovada, M. A., Woodward, R. O., & Igl, L. D. (2009). Historical range, current distribution, and conservation status of the swift fox, *Vulpes velox*, in North America. *The Canadian Field-Naturalist*, *123*, 346–367.

Taylor, E. B., & Pinkus, S. (2013). The effects of lead agency, nongovernmental organizations, and recovery team membership on the identification of critical habitat for species at risk: Insights from the Canadian experience. *Environmental Reviews*, *21*, 93–102.

Taylor, M. F. J., Suckling, K. F., & Rachlinski, J. J. (2005). The effectiveness of the Endangered Species Act: A quantitative analysis. *Bioscience*, *55*, 360–367.

Traba, J., Bota, G., Mañosa, S., García de la Morena, E. L., & Morales, M. B. (2020). *Análisis de viabilidad de la población de sisón común en España. Anexo de las bases científicas para la elaboración de la estrategia nacional de conservación del sisón común (Tetrax tetrax)*. Fundación Biodiversidad.

Traba, J., & Morales, M. B. (2019). The decline of farmland birds in Spain is strongly associated to the loss of fallowland. *Scientific Reports*, *9*, Article 9473.

Walsh, J. C., Watson, J. E. M., Bottrill, M. C., Joseph, L. N., & Possingham, H. P. (2013). Trends and biases in the listing and recovery planning for threatened species: An Australian case study. *Oryx*, *47*, 134–143.

Watson, J. E., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, *515*, 67–73.

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Townsen Peterson, A., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., Yates, K. L., … Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*, 1261–1277.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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