

Article

Landscape Connectivity and Suitable Habitat Analysis for Wolves (*Canis lupus* L.) in the Eastern Pyrenees

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Abstract: Over the last few decades, much of the mountain area in European countries has turned into potential habitat for species of medium- and large-sized mammals. Some of the occurrences that explain this trend are biodiversity protection, the creation of natural protected areas, and the abandonment of traditional agricultural activities. In recent years, wolves have once again been seen in forests in the eastern sector of the Pyrenees and the Pre-Pyrenees. The success or failure of their permanent settlement will depend on several factors, including conservation measures for the species, habitat availability, and the state of landscape connectivity. The aim of this study is to analyze the state of landscape connectivity for fragments of potential wolf habitat in Catalonia, Andorra, and on the French side of the Eastern Pyrenees. The results show that a third of the area studied constitutes potential wolf habitat and almost 90% of these spaces are of sufficient size to host stable packs. The set of potential wolf habitat fragments was also assessed using the probability of connectivity index (dPC), which analyses landscape connectivity based on graph structures. According to the graph theory, the results confirm that all the nodes or habitat fragments are directly or indirectly interconnected, thus forming a single component. Given the large availability of suitable habitat and the current state of landscape connectivity for the species, the dispersal of the wolf would be favorable if stable packs are formed. A new established population in the Pyrenees could lead to more genetic exchange between the Iberian wolf population and the rest of Europe's wolf populations.

Keywords: wolf (*Canis lupus*); Pyrenees; habitat suitability; ecological connectivity; landscape fragmentation; probability of connectivity (PC)

1. Introduction

Policies aimed at conserving threatened species and ecosystems have been key in preventing their further loss, resulting in the reversal of a trend that was leading to their extinction [1]. Nevertheless, biodiversity has continued to decline on a global scale over recent decades [2]. Prior to the decline in its populations, the wolf was widespread throughout Europe, especially where the presence of wild ungulates allowed its survival [3]. Wolf attacks on livestock, and in some cases humans, were the catalyst for its persecution, leading to the indiscriminate hunting of the species from at least the sixteenth century onwards [4,5]. By the nineteenth and twentieth centuries, the species had been drastically reduced in number and numerous local populations had been exterminated [6]. In France, breeding populations of the wolf disappeared around 1940 [7] and in Catalonia the last wolf was killed in the Eastern Pyrenees in 1945 [8]. However, the large carnivores still existing in Europe today—the brown bear (*Ursus arctos*), the lynx (*Lynx spp.*), the wolverine (*Gulo gulo*), and the wolf

(*Canis lupus*)—all enjoy some form of protection in countries in the European Union. Chapron et al. [9] consider the present coexistence of humans and large carnivores to be the outcome of joint conservation efforts among several countries over the past three decades.

The establishment of networks of protected natural areas and environmental and socio-economic changes in rural areas in recent decades has led to improvement in the quality of wildlife habitats. The current dense forests in mountain locations and the wolf's ability to colonize a diverse range of anthropogenically modified habitats has favored the recovery of wolf populations in areas of Europe where it had disappeared [10–12].

Chapron et al. [9] estimate that the current number of wolves in Europe exceeds 12,000 individuals, excluding populations in Russia, Belarus, and the Ukraine. These populations are distributed in nine different groups: Scandinavia (Norway and Sweden), the Karelian region (Finland), the central European lowlands (Western Poland, Eastern Germany, and the Baltic regions), the Carpathians (Slovakia, Czech Republic, Poland, Romania, Hungary, and Serbia), the Dinaric-Balkan region (Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Albania, Serbia, Greece, and Bulgaria), the Alps (Italy, France, Switzerland, Austria, and Slovenia), the Italian Peninsula (Italy), North-West Iberia (Spain and Portugal), and the Sierra Morena (Spain). However, the number of individuals in the Sierra Morena population has been seriously reduced in the last few years and is consequently now gravely threatened [13].

In the early twenty-first century, the presence of wolves was discovered on the Catalan side of the Eastern Pyrenees, an area where the species had disappeared almost a century earlier. The first scat samples were collected in Cadí-Moixeró Natural Park in 2000, although it was not until 2004 that they were analyzed and the presence of the wolf confirmed [13,14]. According to Lampreave et al. [14], the samples analyzed in the Catalan Pyrenees (Figure 1) up to 2011 confirm the presence of up to thirteen different wolves, twelve males and one female. Samples collected on the French side showed the presence of four different individuals in the Madres, Carlit-Peric, and Canigó Massifs, including one female [15].

Contrary to expectation, the wolves that have reached the Eastern Pyrenees have not come from existing populations on the Iberian Peninsula, but from the Italian Peninsula. Since the mid-seventies, when the Italian government started to protect the species, the wolf has gradually dispersed from Abruzzo National Park, situated in the central Apennines, to Mercantour Natural Park in the French Alps (Figure 1), where it arrived in the early nineties [16] and was rapidly protected nationwide according to French legislation. These populations quickly dispersed until reaching the Madres Massif in the French Eastern Pyrenees in 1999, where months later they crossed to the Catalan side (Figure 1) [14,17].

In recent years, the flow of lone wolves in the Eastern Pyrenees has been significantly reduced to two or three individuals distributed in two areas with a permanent wolf presence (Figure 1) [13,18,19]. The Madres Massif and the Cadí Massif (Figure 1) are areas with temporary wolf presence, while in March 2018 another lone wolf was killed on the road in the Catalan Coastal Mountain Range (Figure 1), Les Gavarres massif, where there had been no sightings since its reappearance. According to these data, nearly twenty different wolves in the Eastern Pyrenees, including two females, have been detected since their arrival in 2000. Despite being considered a protected species, the French National Action Plan for the Wolf (2013–2017) allows wolf hunting under some circumstances that, among other ecological processes, may have contributed to the reduction of wolf flux over the last few years. In Spain, the National Catalogue of Threatened Species (Catálogo Nacional de Especies Amenazadas) considers the wolf to be a huntable species to the north of the Duero river, whereas it is strictly protected to the south of it. In the case of Catalonia, the species does not have a protection status because it was not present there when the Spanish protection law was enacted. In accordance with the European Habitats Directive (Council Directive 92/43/EEC), the wolf is a species of priority community interest in the whole of Europe, except for the local Spanish populations north of the Duero, those in the north of Greece, and those all over Finland.

Loss of connectivity is the greatest threat to conserving biodiversity and maintaining ecological functions in the landscape. Landscape connectivity facilitates the movement of species, genetic exchange, and other ecological flows key to the survival of species and biodiversity conservation [21,22]. These functions acquire special relevance in the context of global environmental change, as species can be forced to change their natural ranges.

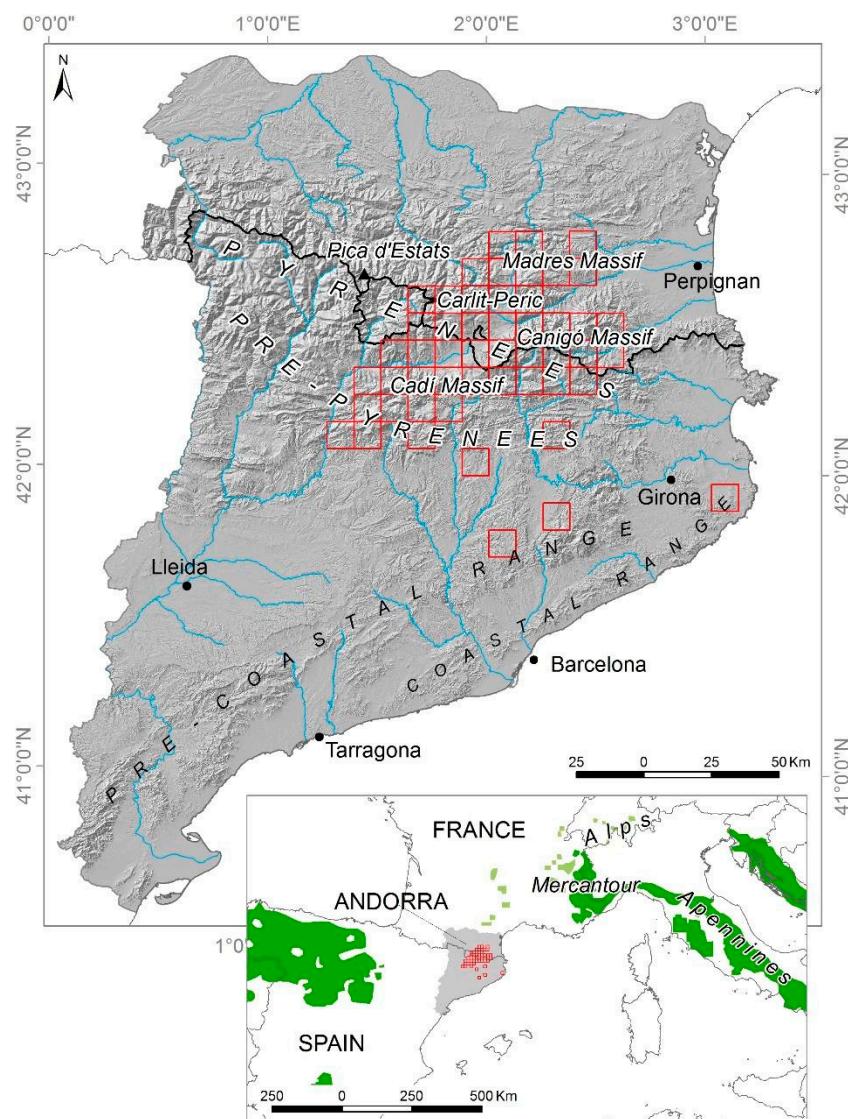


Figure 1. Location of the area of study in Catalonia, Andorra, and the south-east of France. The red squares indicate the presence of wolves at some time since 2000. Areas with permanent wolf presence are located around the Carlit-Peric region and the Canigó Massif. The small map shows the wolf distribution areas in southern Europe. The dark green cells indicate the permanent occurrence of the wolf, and the light green cells indicate its temporary occurrence. Source: Data taken from Lampreave et al. [14], Chapron et al. [9], and Bataille et al. [13,15,18].

The aim of this study is to identify the patches of habitat suitable for the wolf and to analyze their state of ecological connectivity. The landscape connectivity analysis performed here contributes to assessing the success or failure of the dispersal of the species if stable packs are formed in the future. The software Conefor 2.6 was used to analyze the overall connectivity of the network based on graph theory, generating a series of indicators on the availability of habitat.

2. Study Area

The area covered by this cross-border study comprises the entire territory of Catalonia, the French side of the Eastern Pyrenees (made up of the regions of Haute-Garonne, Ariège, Aude, and Pyrénées-Orientales), and the small state of Andorra (Figure 1), totaling an area of approximately 49,000 km². Although the average elevation of the area under study is not particularly high (over 75% of it is below 1000 m), the territory extends to the Eastern Pyrenees, which reaches a maximum altitude in the Pica d'Estats (3147 m). The great mountain range of the Pyrenees runs east to west along the northern edge of the area.

The study area has a notable variety of climates given the geographical shape and orientation of the landforms: coastal Mediterranean, Mediterranean with a continental tendency, sub-Mediterranean, Atlantic, and mountain. The vegetation of the area is thus characteristic of three distinct biogeographical regions: predominantly Mediterranean, but also an abundance of Eurosiberian and, to a lesser extent, Boreo-alpine vegetation [23]. This great variety in climate, vegetation, and altitude provides the necessary conditions for a huge diversity of fauna. There is an abundance of Pyrenean chamois (*Rupicapra pyrenaica*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), hare (*Lepus europaeus*) and, to a lesser extent, mouflon (*Ovis orientalis*) and red deer (*Cervus elaphus*), all potential prey for the wolf.

Regarding land cover in the study area, the predominant types are forests (40%) and arable lands (33%), followed by scrub and grassland (20%), while built-up areas occupy just 4% and pastures 3% [24–26]. Although pastures occupy a relatively low percentage of land in comparison with other types of use, extensive stockbreeding mainly of horses and cattle, but also to a lesser extent of sheep and goats, is particularly common in the Pyrenees. The areas occupied by forests, scrub, and grasslands, which together comprise more than 50% of the terrain, are mostly located at higher altitudes, where most of the protected areas of ecological and landscape value are also found. In total, more than 35% of the study area comes under some type of environmental protection.

From a demographic point of view, the area of study has a large human population imbalance with 85% of the Catalan population living in coastal areas [27], more than half of which are in the metropolitan area of Barcelona, where the density is between 1000 and 2000 inhabitants/km² [28]. The Pyrenees are the least densely populated region of the study area with 30 inhabitants/km² on the Catalan side of the mountain range [28] and 100 inhabitants/km² on the French side [29]. Andorra is the most populated area in the Pyrenees, with 165 inhabitants/km² [30].

3. Materials and Methods

Conefor 2.6, a software based on ecological connectivity, was used to assess the landscape connectivity for wolf habitat [31]. This software uses availability, quality, and effective connectivity between habitat patches to develop a set of indicators that provide information on the probability of species dispersal and the probabilistic and topological relationships established between habitat fragments, according to graph theory [31,32].

A patch-based graph of landscape is defined using two basic elements: the spatial distribution of suitable habitat fragments (also called patches or nodes) and the set of connections (links) established between the nodes. A component is a set of nodes interconnected either directly or indirectly via stepping stones [33,34]. In this context, connectivity is conceived as the property of the landscape that determines the amount of reachable habitat in that landscape (intrapatch connectivity), via connections between different nodes (interpatch connectivity). Connectivity is often measured using a combination of interpatch and intrapatch connectivity [31]. Different studies in Europe quantify the suitable habitat for large mammals and then analyze the patch connectivity based on landscape graph-based models [35] or using cost-path analysis techniques [36]. The specific steps and processes that were carried out in this study are specified below.

3.1. Habitat Availability Map

A digital cartographic technique, known in Geographic Information System (GIS) language as “weighted overlay”, was used to obtain the habitat availability map for the wolf. This technique consists of superimposing the weighted variables that are considered to have the greatest influence on the wolf habitat (Table 1). The method used for this calculation is commonly applied to analyze both habitat availability [37–40] and movement of species through the landscape matrix [40–43]. The methodological process used is similar to developing a habitat suitability model based on environmental parameters [44].

The following methodology was applied to achieve fragments of potential wolf habitat: (i) computation of criteria weights using the Analytic Hierarchy Process (AHP), which has also been widely incorporated into different GIS applications to analyze suitability [45,46]; and (ii) the Ordered Weighted Averaging (OWA) method for producing suitability maps and running sensitivity analyses [47].

The AHP converts these evaluations into numerical values (weights or priorities), which are used to calculate a score for each alternative. A consistency index (CR) measures the extent to which the decision-maker has been consistent in its responses. Based on [45], if the $CR < 0.10$, the pairwise comparison matrix has an acceptable consistency and the weight values are valid and can be utilized. Otherwise, if the $CR \geq 0.10$, then the pairwise comparisons lack consistency and the matrix needs to be adjusted and the element values modified.

The OWA operator was first introduced to address the problem of aggregating a set of criteria functions to form an overall decision function [48]. OWA operators have been especially extensively used in Multiple Criteria Decision Analysis (MCDA) to provide support in complex decision-making situations, and they have notably been applied in GIS environments to produce land-use suitability maps with applications in land-use planning and management, such as landslide susceptibility mapping, wilderness mapping, ecological capability assessment, and so on. [49].

Cartographic analysis is known in GIS language as a “permeability matrix” or “friction map”, used in this study to quantify the habitat available to the wolf throughout the area of study. This analysis can be interpreted from a map depicting the cost or friction area, calculating the difficulty the wolf has to move in space, and demonstrating the degree of suitability of the habitat for a certain species (Figure 2A). This map differentiates between areas with a higher travel cost and those with the least accumulative travel cost, representing the least and most favorable areas, respectively. By selecting the most favorable locations, the most suitable areas for wolf settlement is obtained, constituting the wolf habitat availability map.

Table 1. Data source used for the elaboration of the wolf habitat suitability map.

State	Layer	Date	Source	Scale
Spain	Habitat typology	2005	DTES (Department of Territory and Sustainability) and University of Barcelona	1:50,000
	River network	2004	Catalan Water Agency (ACA)	1:50,000
	Rail network	2007	DTES	1:5000
	Road network	2013	DTES	1:5000
	Nature Network 2000	2013	DTES	1:50,000
	Urban areas	2005	Extracted by habitat typology layer	1:50,000
	Digital Elevation Model	2014	Catalan Institute of Cartography and Geology (ICGC)	15 m resolution
France	Habitat typology (CORINE Land Cover)	2006	European Environment Agency (EEA)	1:100,000
	River network	2014	Open Street Map (OSM)	-
	Rail network	2014	OSM	-
	Road network	2014	OSM	-
	Nature Network 2000	2011	EEA	1:100,000
	Natural Regional	-	Ministry of Ecology, Sustainable Development and Energy	-
	Urban areas	2006	Extracted by habitat typology layer	1:100,000
Andorra	Digital Elevation Model	2003	EEA	30 m resolution
	Habitat typology	2012	Institute of Andorran Studies	1:25,000
	River network	1995	Institute of Andorran Studies	1:5000
	Road network	1995	Department of Environment	1:5000
	Natural Parks	2013	Department of Environment	1:25,000
	Urban areas	2012	Extracted by habitat typology layer	1:25,000
	Digital Elevation Model	1995	Department of Environment	5 m resolution

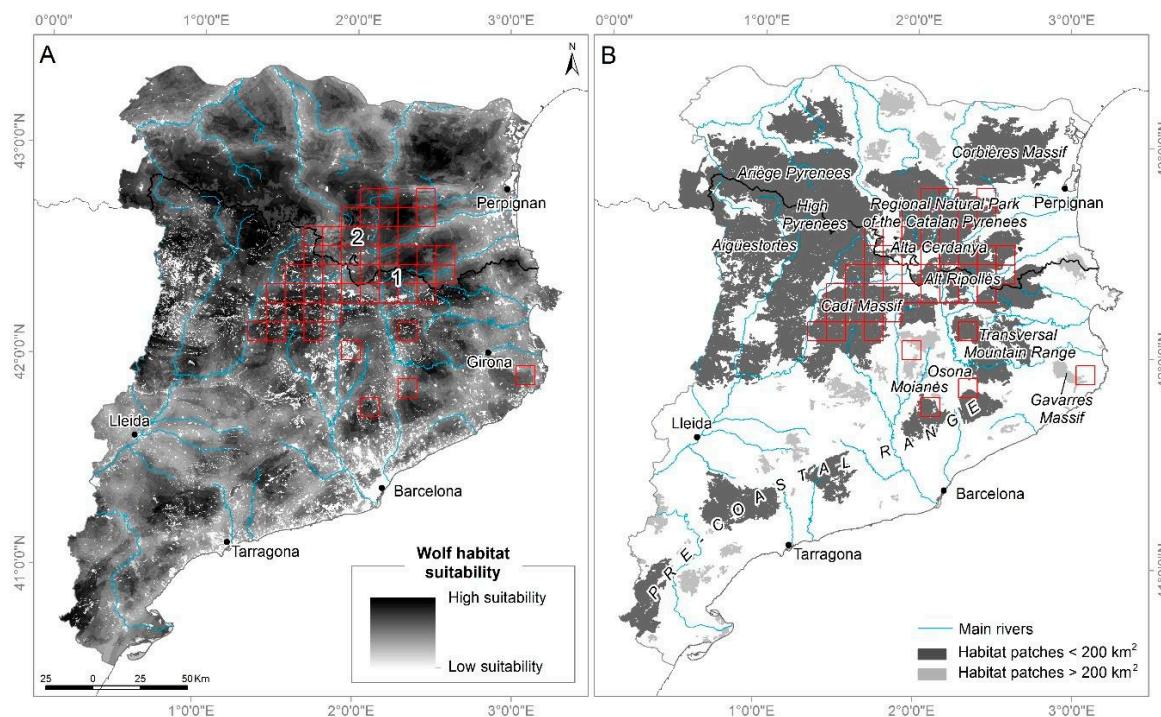


Figure 2. (A) Wolf friction map or degree of suitability for wolf habitat. (B) Optimal areas for wolf habitat classified according to size: only fragments above 200 km² are suitable for hosting stable packs of wolf populations. The red squares indicate the presence of wolves at some time since 2000. Areas with permanent wolf presence: 1—Alt Ripollès; 2—Alta Cerdanya. The most suitable fragments for wolf settlement (Figure 2B) are distributed along the main mountain ranges of the area of study and occupy almost one-third of the entire area.

Suitability Map Based on Wolf Ecology Criteria

Different published information [4,9,50–58] was considered to establish the ecological criteria and to create the wolf habitat suitability map. These studies consider some variables as key factors of wolf presence, such as roads, human settlements, altitude, protected areas, and type of habitats. However, no studies were found that deal with all the factors together to assess the influence of each variable for habitat suitability for the wolf. This paper, however, considers all the relevant environmental variables that could influence wolf survival according to the literature consulted: (i) type of habitat; (ii) proximity to watercourses; distances from (iii) urban areas, (iv) roads, and (v) railways; (vi) altitude; and (vii) protected natural areas.

Following processing using a combination of GIS tools (buffer, clip, merge, Euclidean distance, among others), the vector layers were rasterized using a pixel resolution of 30 m². The variables were then duly reclassified using a certain cost value of suitability for the wolf (Table 2). The values allotted to each variable and the weighted overlay of the layers were based on data on wolf habitats published in scientific journals. This methodological process based on the literature is frequently used as the basis for modelling connectivity for conservation initiatives [40]. Notably, however, the method used for the weighted overlapping of layers produces a few problems and limitations, among which the interpolation of the data should be highlighted [59].

One of the main variables that determine whether the wolf will settle in an area is the availability of prey, which depends largely on land cover, habitat type, and human activities, such as hunting management and grazing. The wolf adapts its diet to the environmental conditions of the territory in which it lives and the availability of prey, feeding on different kinds of prey depending on availability, with the composition of these species varying among the study areas. According to Zlatanova et al. [60], in Scandinavia the wolf feeds on wild ungulates such as elk (*Alces alces*) and reindeer (*Rangifer tarandus*);

on red deer, roe deer, and wild boar in Central Europe; and usually on wild boar and roe deer in Southern Europe. If there is a shortage of wild ungulates, however, the wolf will feed on livestock or even plant food, smaller prey, and garbage.

Table 2. Variables used in the wolf friction map. The permanent watercourses were selected for rivers and only the basic road network, consisting of highways, two-lane roads, and basic regional roads, were considered for roads.

Protected Natural Areas		Proximity to Urban Areas		Proximity to Roads		Proximity to Railway Lines	
Classification	Cost Value	km	Cost Value	km	Cost Value	km	Cost Value
Category I-II (IUCN)	1	0–0.5	10	0–0.5	10	0–0.25	10
Category III-IV	2	0.5–3	9	0.5–2	9	0–2	6
Category V-VI	3	3–6	7	2–4	8	2–4	4
Non-protected area	7	6–10	5	4–8	6	>4	2
		10–12	3	8–12	2		
		>12	1	>12	1		
Habitat Type		Proximity to Water Sources			Altitude (m)		
Classification	Cost Value	km	Cost Value	Threshold	Cost Value		
Small bodies of fresh water	3	0–0.10	10	0–500	6		
Bodies of saline water	9	0.10–3	1	500–1000	2		
Canals, reservoirs, and dams	9	3–5	2	1000–2000	1		
Sandy and silty coastal plains	7	5–12	3	>2000	3		
Saline scrublands and grasslands	7	>12	5				
Beaches	9						
Littoral cliffs	9						
Cliffs and rocky inlands	2						
Scrublands	2						
Grasslands and crops	2						
Forests	1						
Flooded habitats	6						
Peat lands	2						
Rocky screes	8						
Glaciers and areas with permanent snow	5						
Woody and arable crops	3						
Tree plantations	3						
Urban parks and gardens	10						
Cities, towns, and industrial areas	10						
Abandoned fields and ruderal areas	5						
Logged and burned areas	9						

Studies on wolf populations in human landscapes have determined that the density of wolves is directly related to the density of prey in the wild [58], and it is here that forest areas are especially valuable. Territory bordering on cropland is also sought by the wolf given that it is home to abundant prey such as wild boar, the numbers of which are currently increasing. Mountain crags are also used by wolves to hunt wild ungulates, where they establish their dens in natural holes in the ground [55]. Hence, in this study the land cover variable was given four times the weight of the other variables given that it is considered to exert a greater influence on habitat availability. This means that land cover was weighted 40%, while the other variables (Table 2) were each weighted 10%.

Forest cover was considered as the most favorable for wolf habitat, followed by scrub, moorland, meadows, and pastures, and to a lesser extent cropland (Table 2). Despite some studies determining that wolves avoid agricultural lands for breeding [61], there is evidence of stable packs of wolf populations in a northern-central Spanish agricultural area with a high human population density [62–64]. The highest friction cost value was assigned to built-up areas (Table 2).

Rivers do not constitute a barrier for the wolf as it can cross them with relative ease, depending on the flow and strength of the current, sometimes even entering them in pursuit of prey. The wolf only avoids extremely large bodies of water or deserts for both habitation and movements for dispersal [64,65]. Considering its daily need for water, especially during the denning period when breeding, it can be assumed not to stray too far from this resource.

Studies on the presence of the wolf in Galicia have also determined altitude to be a key factor in the distribution of this species [58], the probability of wolf presence in the territory progressively increasing with altitude. The wolf tends to avoid lower areas and medium-low altitudes where there are human settlements and human activities taking place, both of which decrease with increasing altitude [37]. According to Llaneza et al. [58], the maximum probability of wolf presence is located at an altitude of between 1000 and 2000 m, above which the likelihood of finding wolves once again decreases. This consideration was considered when allocating the friction cost values at different intervals of the altitude variable (Table 2).

Although it is not a very shy animal, the wolf endeavors to avoid noisy and frequented places, such as the great urban areas and transport infrastructures [53,58,61,66]. The presence of inhabited areas is one of the main variables that determines wolf presence in a territory [67]. Studies conducted in the north-west of the Iberian Peninsula verify that wolf presence increases with decreased housing and population density [53,58]. The probability of wolf presence in humanized landscapes increases as the density of roads per square kilometer decreases and the distance from the main road network increases. This has been evidenced in the Iberian Peninsula [53,57,58], as well as in some places in Europe [61,68,69] and in the United States [50]. In fact, more than 50% of wolf casualties result from impact on roads [51,54]. According to Rodríguez-Freire and Crecente-Maseda [56], highway AP-9 may have divided the existing population of wolves in the north-west of the Iberian Peninsula into two groups all along the road.

In a study of wolf populations in the north-west of the Iberian Peninsula, Vilà et al. [51] determine their daily movements to range between 10 km and 12 km. Hence, a threshold of 12 km was used for the friction cost value in relation to distance from waterbodies, urban areas, and roads. The use of distance thresholds for certain landscape elements to assess their impact on the distribution of species is common in this type of research [41,42]. These studies also analyze different landscape elements and weigh them to assess the habitat suitability of species.

Protected natural areas were weighted positively. Human activities that can disturb wolf presence, such as hunting and access for motor-driven vehicles, are forbidden or regulated in protected areas. To this effect, the different categories of the IUCN (International Union for Conservation of Nature) classification were considered (Appendix A). The more protected the area, the more positively the variable was weighted (Table 2). Nevertheless, in the study area, most of the natural protected areas correspond to categories V and VI of the IUCN classification.

Using the suitability map, places of less value on the map were selected (with pixel values < 3), thus producing the availability map or optimal areas for the wolf. The areas where the wolf could form stable packs were then differentiated from those where it could only make sporadic incursions. The territory used by the packs is considered as the space required for lone wolves to form stable populations or packs if the requisite conditions for reproduction are met. Recent studies have shown that for Iberian wolves this area is on average around 200 km^2 [52]. The packs of Italian wolves that have recently arrived in Mercantour similarly use an area of approximately 200 km^2 to this end [55]. In line with these data, only patches larger than 200 km^2 were selected to analyze the ecological connectivity of the landscape by means of a set of indices presented in the following section.

All the cartographic information was processed using the ESRI ArcMap program. A UTM (Universal Transverse Mercator) map projection was employed to work on the maps using the reference system ETRS89 (European Terrestrial Reference System 1989), UTM zone 31N. The original scale of the different information layers used for this analysis should be considered since this determines the degree of detail in the resulting mapping. To this effect, the type of habitat map in France was made on a large-scale (1:100,000), while the habitat map in Catalonia was on a scale of 1:50,000, and the habitat map in Andorra was on a scale of 1:25,000 (Table 1).

3.2. Assessing Habitat Availability and Connectivity

Conefor, a management support tool that quantifies the importance of each habitat by fragmenting, functionally maintaining, or increasing landscape connectivity, was used to assess the landscape connectivity of the wolf. The probability of connectivity (PC) indicator, one of the most recommended indexes for planning and decision-making, also used for assessing the state of connectivity of different species [70,71], was employed. This index quantifies functional connectivity between a set of interconnected nodes and is obtained by weighting the attributes given to each habitat fragment (in this case, the surface area occupied by each fragment) and the dispersal probability of each node with the remaining nodes. It is given by the following expression [72]:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}{A_L^2} \quad (1)$$

where a_i and a_j are the area of the habitat patches i and j , n is the number of habitat patches in the landscape, A_L is the total landscape area (habitat and non-habitat patches), and p_{ij} is the product probability of an animal moving directly from patch i to j over the shortest path. p_{ij}^* is the maximum product probability of all possible paths between patches i and j (including single-step paths).

The contribution to overall habitat availability and connectivity is calculated by the relative ranking of each patch:

$$dPC_k (\%) = \frac{PC - PC'}{PC} \quad (2)$$

where dPC_k is the importance of node k to overall habitat availability in the landscape. PC' is the PC value after removing k from the analysis. The dPC_k [73] can be divided into three fractions according to the different ways each path can contribute to habitat connectivity and availability in the landscape:

$$dPC_k (\%) = dPC_{intra_k} + dPC_{flux_k} + dPC_{connector_k} \quad (3)$$

where dPC_{intra_k} corresponds to the available habitat area provided by patch k in terms of intrapatch connectivity. The topological relationships (the position of each node within the landscape network) between each patch do not affect the calculation of this metric; only local features (area) do. dPC_{flux_k} is the flux through connections of patch k to or from all the other patches in the graph structure when k is the start or end node of that flux. In this case, the local characteristics of the patch and its position within the landscape network affect the computation of this fraction and a patch with a higher attribute value produces more flux if the rest of the factors are equal. $dPC_{connector_k}$ is the contribution of k to the connectivity between other habitat patches as a connecting element (or stepping stone) between them. The calculation of this metric only depends on the topological relationships; any other attribute considered does not affect this fraction.

Corridors or links established between nodes are determined by the wolf's ability to move from one node to another through an unfavorable area. In this study, it was considered that there is a 50% probability of the species moving between different habitat fragments if the distance between them in a straight line was 75 km or less. The same dispersal distance was established for both males and females, although males tend to disperse at higher rates than females [74,75]. Saura and Pascual-Hortal [72] recommend a probability value of 0.5 as the distance corresponding to the median dispersal distance of the species under analysis.

The threshold distance of 75 km is equal to the average annual number of kilometers travelled by the wolf on its journey from the French Alps to the Eastern Pyrenees [17]. It is also equivalent to the Euclidean distance of some wolves' intrusions from the Cadí-Moixeró (the place most frequented by wolves in Catalonia) to outlying areas such as the regions of Moianès and Osona [14], or more recently the Gavarres Massif (Figure 2B). The fact that wolves adapt well to different environmental

conditions [3,62,76] means that they can travel great distances through fairly unfavorable habitat (as demonstrated by the dispersal of the Italian wolf from the central Apennines to the Eastern Pyrenees).

4. Results

One-third of the study area can be considered as potential habitat for the wolf, and more than 90% of this space is suitable for hosting stable packs. The most suitable areas are the main mountain ranges and forests, coinciding with those inhabited by humans (Figure 2A). Specifically, these areas are located in the area of the High Catalan Pyrenees and the Cadí Massif on the Spanish side; and the Regional Natural Park of the Catalan Pyrenees, the Regional Natural Park of the Ariège Pyrenees, and the Corbières Massif on the French side.

Various scenarios were simulated to attribute different weights to the layers and to estimate the sensitivity of different schemes (Table 3). The seven variables were weighted differently according to three scenarios, supplying distinct availability maps with a diverse number of pixels with high suitability (<3).

Table 3. Sensibility analysis carried out for three scenarios where the variables were weighted differently depending on each variable. The raster layer is composed of nearly 9,000,000 pixels.

Variables	Scenario 1	Scenario 2	Scenario 3
Habitat type	70	15	40
Protected natural areas	5	15	10
Proximity to roads	5	14	10
Proximity to railway	5	14	10
Proximity to urban areas	5	14	10
Proximity to water sources	5	14	10
Altitude	5	14	10
Total weight (100%)	100	100	100
Consistency ratio	0.043	0.017	0.054
Count pixels high suitability (<3)	4,854,192	1,245,961	2,576,337
Patches > 200 km ²	1	9	12
Patches < 200 km ²	0	52	90

The data for the sensibility analysis provided in Table 3 shows that Scenario 3 is the best option in terms of connectivity analysis.

The main variables that determine whether the wolf will settle in an area is the availability of prey, which depends largely on land cover and human activities such as hunting management and grazing, explaining why the land cover variable must weigh more than the other variables given that it exerts a greater influence on habitat availability. The most consistent scenarios would therefore be Numbers 1 and 3. However, since the objective of this study was to assess the landscape connectivity of patches suitable for wolf settlement, Scenario 1 was discarded as it only contains a whole patch of habitat suitable for wolf packs. Scenario 3 thus presented as the most appropriate to apply the landscape connectivity analysis using Conefor software.

Of the 49,000 km² of countryside analyzed (A_L), 16,800 km² scored the highest in terms of suitability for wolf habitat, which is approximately equivalent to a third of the study area. The resulting landscape graph is dominated by one large component (or set of interconnected nodes) consisting of 126 nodes, either directly or indirectly connecting habitat fragments (using stepping stones). Only 12 of these nodes are larger than 200 km², the size needed for the establishment of wolf packs. These 12 nodes were used for the connectivity analysis.

The priority nodes for wolf connectivity coincide with the larger nodes and those better connected with adjacent nodes (Figure 3 and Table 4). According to the probability of connectivity (dPC), the node that contributes most to habitat availability and global connectivity is the largest patch in the west of the Catalan–French Pyrenees (Node 1 in Table 4), representing nearly half of the available habitat

in the countryside studied (7950 km^2) and with a dPC value of 75.3% (Table 4). This fragment also shows high values of intrapatch connectivity or dPCintra (24.3%), and of dPCflux (49.6%). Secondly, Node 2 is in the Alta Cerdanya, Alt Ripollès, and the Regional Natural Park of the Catalan Pyrenees, occupying 2500 km^2 and showing the highest contribution to connectivity among other habitat patches as a connecting element or stepping stone (dPCconnector = 2.8%). This node also contributes through connections from Node 2 to all the other patches in the graph structure or from all the other patches to this node (dPCflux = 26.16%).

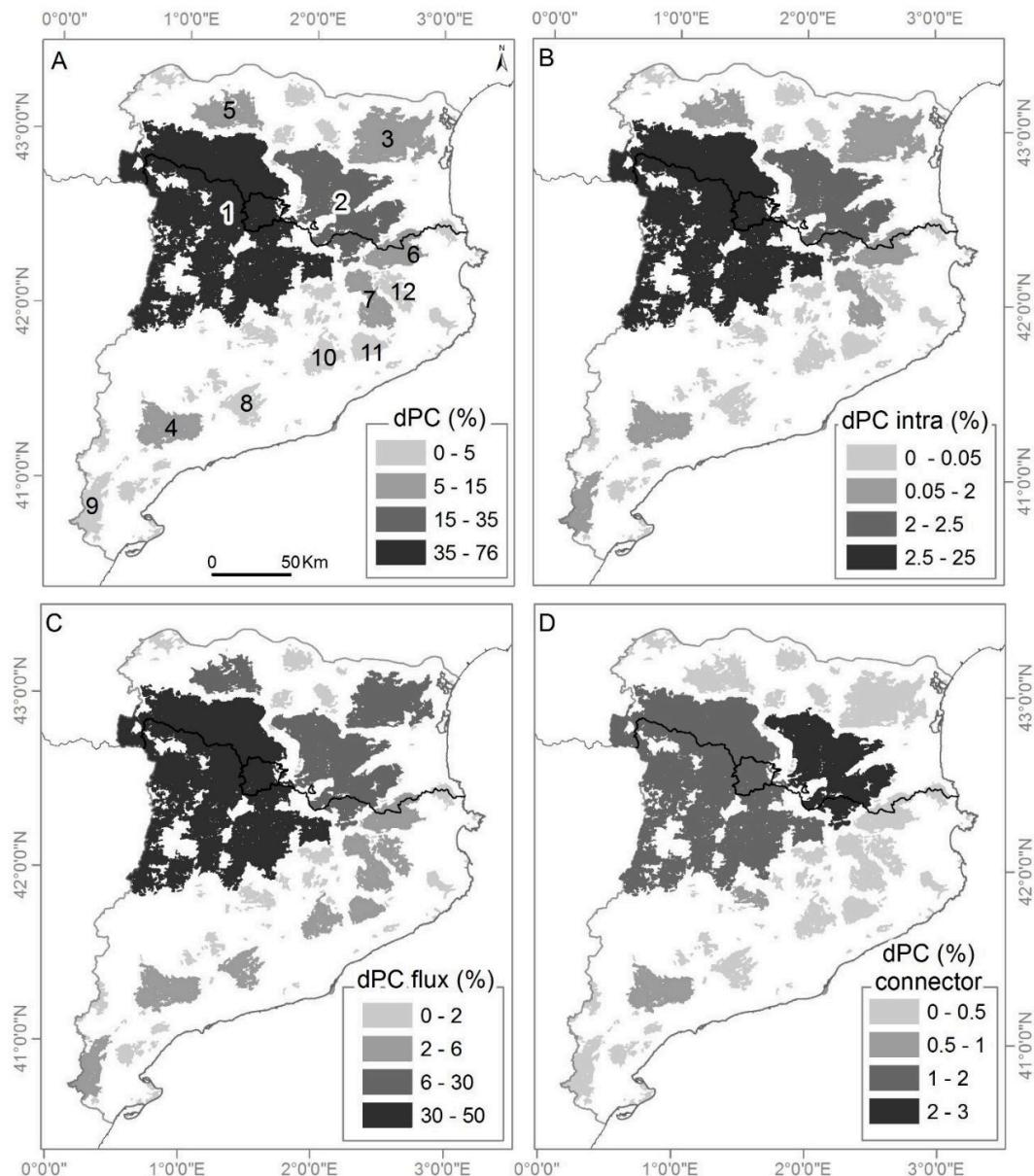


Figure 3. Importance of wolf habitat fragments according to the dPC (A) probability of connectivity and the three fractions of dPC: dPCintra (B) the available habitat area provided by a patch itself in terms of intrapatch connectivity; dPCflux (C) the flux through connections of a patch to or from all the other patches in the graph structure when this patch is the start or end node of that flux; and dPCconnector (D) the connectivity between other habitat patches as a connecting element or stepping stone between them). Nodes $> 200 \text{ km}^2$ are numbered from 1 to 12.

Table 4. Importance of wolf habitat fragments $> 200 \text{ km}^2$ according to the dPC (probability of connectivity) and the three fractions of dPC: dPCintra (the available habitat area provided by a patch itself in terms of intrapatch connectivity); dPCflux (the flux through connections of a patch to or from all the other patches in the graph structure when this patch is the start or end node of that flux); and dPCconnector (the connectivity between other habitat patches as a connecting element or stepping stone between them).

Node	dPC	dPCintra	dPCflux	dPCconnect	km^2
1	75.32	24.36	49.67	1.29	7951.60
2	31.38	2.42	26.15	2.81	2505.50
3	14.24	0.59	13.64	0.01	1234.08
4	6.80	0.15	5.67	0.98	625.46
5	6.64	0.12	6.51	0.01	562.31
6	6.22	0.10	5.93	0.20	502.42
7	5.73	0.09	5.49	0.16	470.54
8	3.45	0.03	2.97	0.45	291.75
9	3.37	0.07	3.28	0.02	412.76
10	3.02	0.03	2.99	0.00	265.75
11	2.72	0.02	2.68	0.02	234.41
12	2.65	0.02	2.50	0.14	209.84

The rest of the nodes showing significant values are located on the edge of the two principal patches (Nodes 1 and 2), also especially contributing across the dPCflux which, on the one hand, takes the topological positions of the nodes within the entire network into account and, on the other hand, considers the attribute of the node (area). On the French side, the Corbières (Node 3) and an isolated fragment of the Pyrenean Ariège (Node 5) stand out. In Catalonia, secondary nodes can be found in the Alta Garrotxa (Node 6), the Transversal Mountain Range (Nodes 7 and 12), and the Pre-Coastal Mountain Range. In this mountain range, the Montsant–Prades Mountains (Node 4), the Ports de Beseit (Node 9), the Montmell–Ancosa sector (Node 8), Sant Llorenç del Munt (Node 10), and Montseny (Node 11) stand out.

5. Discussion

5.1. Large Expanse of Land Available for Movement and Settlement

The availability of a habitat and good connectivity between fragments make the presence of the wolf possible over a large part of Catalonia and the northern side of the French Pyrenees. However, Mech [77] shows that some models of area prediction for recovering the wolf fail. Thus, the patches suitable for the species can be understood as an indication of where wolves will probably settle first rather than the places where they will actually become established in the medium and long term.

The state of ecological connectivity between the patches studied reveals that the area is a single component where wolves can move anywhere. Each node is connected to the others either directly or via other nodes (stepping stones) given that in all cases the distance to another node is less than the considered dispersal distance of 75 km. Establishing a specific dispersal distance has proven difficult since wolves can successfully disperse through hostile, unsuitable areas [65,78] for various lengths of time and distance [12,79]. In Europe, some studies present dispersal rates similar to the one chosen in this study, as is the case with Finnish wolves who showed a dispersal distance of 98.5 km [80]. However, this number may be much higher, estimated at between 250 and about 400 km [81–83], and even reaching 800 km in the movements of the population of German wolves to Poland [12]. Ciucci et al. [83] determine the Italian grey wolf straight line dispersal distance (from the Northern Apennines to the Alps) as 240 km. Similar data were presented by Ražen et al. [84], who set the straight line dispersal distance between the Dinaric-Balkan and Alpine grey wolf populations at 230 km. Exceptionally, Blanco and Cortés [63] determine a low range of 31.5 km as the dispersal distance for male grey wolves in the north-central region of Spain.

Other studies show similar dispersal distances for male grey wolves in North America. Ballard et al. [85] studied the dispersal of the wolf in Southcentral Alaska, determining the dispersal distance for males as 84 km; Gese and Mech [86] determined the male grey wolf mean dispersal distance in north-east Minnesota as 88 km; Wydeven et al. [87] fixed the mean distance of 65 km for the dispersal of wolves in Wisconsin; and Jimenez et al. [75] recently set male grey wolves' dispersal distance in the Rocky Mountains (North West America) at 98.1 km.

In the area of study, the fragments that contribute most to habitat availability (via intrapatch or interpatch connectivity) are in the Pyrenees and the Pre-Pyrenees. The samples collected and observations of the species verify that the places most visited by the wolf in Catalonia during the period in question was the areas Cadí Massif, Alt Ripollès, and Alta Cerdanya, while in France it was the Eastern Pyrenees (Figure 1). These areas are not only the largest and best connected with the rest according to the results obtained (Figures 2 and 3), but they also have a wide variety of potential prey for the wolf, such as the hare, the wild boar, the roe deer, the mouflon, and the Pyrenean chamois [14,15,19].

5.2. *The Pyrenees, a Strategic Location for Wolf Conservation in Europe*

Conservation of regional habitat connectivity has the potential to facilitate the recovery of the wolf, which is currently recolonizing portions of its historic range of distribution. The geographical situation of Catalonia makes it a suitable meeting point between the Iberian Peninsula's own wolf population and the population originating in the Italian Apennines. The differences between the two populations make wolf colonization of the Pyrenees a conservation goal itself, with the aim of increasing the gene flow between populations. A new established population in the Pyrenees could lead to more genetic exchange between the Iberian population and those in the rest of Europe, which would be a further step in re-establishing natural gene flow. Increasing the number of habitat fragments suitable for the wolf all across Europe to act as stepping stones would be a good strategy to conserve regional habitat connectivity and to maximize species protection at a minimum cost, in addition to being a step further in re-establishing natural gene flow between the wolf populations in Spain and the rest of Europe.

In this regard, it would be of great interest to quantify how the Pyrenees is contributing to the global landscape connectivity for wolves in Europe. A study similar to the present one could be performed to determine the *dPCconnector*, which is the contribution of each patch to the connectivity between other habitat patches as a connecting element or stepping stone between them [31].

5.3. *Management, the Key to Maximize Conservation and Minimize Conflicts*

To the north of the river Duero the wolf is a hunted species, meaning that individuals in these populations can be indiscriminately killed. On the other side of the Pyrenees, however, the environmental conservation and recovery policies undertaken in much of Europe, coupled with threatened species protection, has made it possible to promote a slow but steady recovery in certain areas of the continent, especially in Italy, Switzerland, and Eastern and Central France [88]. This may explain why the wolf coming from Italy arrived in the Pyrenees before the Iberian one. Nonetheless, the lack of legislation in Spain for protecting the wolf in the Pyrenees and the current hunting plan for wolves in France may have led to the drastic decrease in individuals detected prior to 2011. Recent hunting activity in France has reduced the flux of lone wolves, resulting in the Madres Massif being recently re-classified as an area of temporary wolf presence given that its presence has not been able to be confirmed during the last two winters [18]. The reduction of flux from France impedes new arrivals in the Eastern Pyrenees coming from the European continent. However, the wolf's high reproductive potential and long-distance dispersal ability are crucial for its resilience and quick recovery in areas where they have been exterminated by indiscriminate hunting by humans [78,89].

Sooner or later wolves will become established in the Pyrenees, so it is important to know where they will potentially settle to be able to foresee and mitigate potential human–wolf conflicts. The most suitable areas for the wolf revealed by this analysis are those where future conflicts with livestock

owners are expected. Hunting tourism will also be a source of conflict with ecologists, with the wolf hunted in accordance with the laws of each European country.

Mech [90] evinces various practices in different European countries (Germany, France, Sweden, or Finland) that flaunt legislation and go against the expansion of the species, including poaching and hunting. Nevertheless, culling of the wolf population by means of drives has failed in its goal of reducing depredations on livestock in Spain [91]. It is well known that uncontrolled dogs could be responsible for some of the attacks on livestock. Echegaray and Vilà [10] found that most of the wolf feces they analyzed contained the remains of wild prey, whereas the dog feces they examined mainly contained the remains of domestic animals. Imbert et al. [92] also indicates that wolves in Liguria consume mainly wild ungulates and, to a lesser extent, livestock. In the same region, Torretta et al. [93] show that the species most consumed by wolves are wild boar and roe deer. Llaneza and López-Bao [94] show how in the north-west of Spain changes in agricultural and environmental policies over the last three decades have shifted the wolf's diet, 95% of which was previously based on anthropogenic food sources.

Despite the numerous scientific arguments, the recovery of wolf populations in rural areas is not welcomed. People living far from wolf territories have more positive attitudes towards wolf conservation than those living within or close to wolf territories [95]. Conflicts between policies and biodiversity conservation are not always easy to manage. The interests of the agents involved are in conflict and it is difficult to design management policies that satisfy both visions. Therefore, it is hugely important to integrate policies into biodiversity conservation to anticipate future wolf–human conflicts. Mech [90] indicates the need to modify the Bern Convention (Council of Europe 82/72/CEE) and the European Habitat Directive (Council Directive 92/43/EEC), enacted to re-establish wolf populations, according to local situations, so that wolves are able to live alongside humans with only minimal conflict.

To this effect, the Finnish literature could be a reference for integrating efficient conservation policies. Karlsson and Sjöström [95] suggest that surveys of human perception towards wolf conservation should be done in territories where conservation and management initiatives are expected to be carried out. However, after studying citizens' perceptions using surveys, Bisi et al. [96] state that people living in areas where wolves occur feel that neither legislative bodies nor conservationists listen to their opinions. They report that their requests have not been heard, while concessions to these requests would create a universally supported policy or would at least increase tolerance of wolves.

6. Conclusions

This paper presents a method for identifying and assessing the availability and ecological connectivity of wolf habitat in the Eastern Pyrenees. It is a procedure that should be implemented from the Italian Peninsula to the Iberian Peninsula, via the French Mediterranean, to be able to analyze the capacity of the region to accommodate wolf dispersal flows in the coming years.

Protection of the species in Catalonia and France will play a key role if the flow of lone wolves reaches the levels of previous years. Wolf settlement and dispersal in certain parts of the area of study could consequently become a reality in the following decades. In the medium to long term, protection of the species may lead to the settlement of stable wolf packs in the Pyrenees, from where they would disperse into better connected adjacent areas (Pre-Pyrenees) and make occasional incursions to the better connected points (central Catalonia and the Coastal Mountain Range). The environmental conditions are even favorable enough for some individuals to disperse through the interior of the Iberian Peninsula via the Pyrenees and the Coastal Mountain Range. In the long run, the Pyrenees could become a meeting area between the wolves of the Iberian Peninsula and the populations in the Alps and the Apennines.

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Appendix A

Table A1. Protected area categories according to the International Union for the Conservation of Nature.

Categories	Main Features
Ia. Strict Nature Reserve	Protected areas that are strictly set aside to protect biodiversity and possibly geological/geomorphological features, where human visitation, use, and impacts are strictly controlled and limited to ensure protection of the conservation values.
Ib. Wilderness Area	Protected areas that are usually largely unmodified or slightly modified, retaining their natural character and influence, without permanent or significant human habitation.
II. National Park	Large natural or near natural areas set aside to protect large-scale ecological processes. They also provide a basis for environmentally and culturally compatible spiritual, scientific, educational, and recreational activities.
III. Natural Monument or Feature	Areas set aside to protect a specific natural monument. They are generally quite small protected areas and often have high visitor value.
IV. Habitat/Species Management Area	Protected areas aimed at protecting particular species or habitats, and their management reflects this priority. Regular and active interventions are needed, but this is not a requirement of the category.
V. Protected Landscapes/Seascape	A protected area where the interaction of people and nature over time has produced an area with a distinct character of significant ecological, biological, cultural, and scenic value.
VI. Protected area with sustainable uses of natural resources	Protected areas that conserve ecosystems and habitats, together with associated cultural values and traditional natural resource management systems. Low-level non-industrial use of natural resources compatible with nature conservation is seen as one of the main aims of the area.

IUCN protected area management categories classify protected areas according to their management objectives. The categories are recognized by international bodies such as the United Nations and by many national governments as the global standard for defining and recording protected areas and as such are increasingly being incorporated into government legislation.

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