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Natura 2000 sites, public forests and riparian corridors: The connectivity backbone of forest green infrastructure

Begoña de la Fuente[a,*], María C. Mateo-Sánchez[a], Gema Rodríguez[b], Aitor Gastón[a], Ramón Pérez de Ayala[b], Diana Colomina-Pérez[b], María Melero[b], Santiago Saura[a,1]

[a] Universidad Politécnica de Madrid. MONTES (ETSI Montes, Forestal y del Medio Natural). Ciudad Universitaria s/n, 28040, Madrid, Spain
[b] WWF-España, Gran Vía de San Francisco 8, 28005, Madrid, Spain

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A B S T R A C T

The connectivity of protected areas, such as the Natura 2000 network, is crucial for maintaining healthy ecosystems and for the delivery of ecosystem services into the wider landscapes in which they are embedded.

We here present a novel combination of methods for connectivity analysis across heterogeneous landscapes, integrating graph-based analyses, least-cost path modelling and the Probability of Connectivity metric, and apply these methods to the network of Natura 2000 woodland sites in mainland Spain. We deliver key insights on the connectors between Natura 2000 sites: their location and width (including transboundary ones), their prioritization in conservation and restoration scenarios involving different land uses, and the bottlenecks (weak points due to land use pressures) found along them. Based on these results, we characterize the landscapes traversed by the connectors within and outside the protected sites to inform related land management decisions.

We show that forests of public utility play a key role in sustaining Natura 2000 connectivity in Spain. They may qualify as an effective area-based conservation measure significantly contributing to the connectivity element of Aichi Target 11.

Riparian forests were part of the identified connectors much more frequently than expected by their area. They stand out as a crucial green infrastructure safeguarding the connectivity of Natura 2000 woodland habitats, particularly when forest species need to traverse landscapes dominated by agricultural and artificial land uses.

Natura 2000 sites have good connectivity conditions compared to unprotected lands. First, the identified woodland connectors preferentially traversed Natura 2000 lands. Second, the large majority of bottlenecks occurred outside Natura 2000. Natura 2000 sites cannot, however, be considered free from connectivity limitations; they still contained a significant number of bottlenecks that would need to be addressed in the site-level management plans.

The priority connectors for conservation were preferentially found in the well-forested and well-protected landscapes in the main mountain ranges of Spain. On the contrary, the priority connectors for restoration traversed much more frequently landscapes dominated by agriculture. In these landscapes, connectivity improvements largely depend on the restoration of riparian forests and on measures that mitigate the intensification of agriculture by promoting landscape complexity and natural vegetation remnants. The remarkable spatial segregation found between the priority landscapes for connectivity conservation and those of priority for restoration highlights the need for an integrated perspective for land use planning and for the management of the Natura 2000 network in Europe.

1. Introduction

The connectivity of protected areas (PAs) refers to the possibility of animal species, and of the genes, seeds and pollen they carry, to move from one protected site to another. The connectivity of PA networks is essential for the preservation of healthy ecosystems with a high species richness and genetic diversity, for the delivery of ecosystem services into the wider landscapes, and for allowing the adaptation of species to climate and land use changes (Krosby et al., 2010; Laurance et al., 2012; Thomas et al., 2012; De Oliveira et al., 2017). The importance of

* Corresponding author.
E-mail address: fuemarbego@hotmail.com (B. de la Fuente).
[1] Present address: European Commission, Joint Research Centre, Directorate D – Sustainable Resources, Via E. Fermi 2749, I-21027 Ispra, Italy.

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PA connectivity is recognized in the Strategic Plan for Biodiversity for 2011–2020 adopted in 2010 by the parties to the United Nations Convention on Biological Diversity (CBD), which includes twenty Aichi Biodiversity Targets. Under Aichi Target 11, the international community agreed to increase by 2020 the terrestrial area under protection to at least 17% in 'effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures´ (CBD, 2010). Recent global assessments have shown, however, that the connectivity element of Aichi Target 11 is far from being met; in 2016, only about one third of the world´s countries and ecoregions had 17% or more of their land covered by protected and connected areas (Saura et al., 2017, 2018). The main strategic priorities for sustaining or improving PA connectivity have been reported to considerably differ across countries (Saura et al., 2018). In many European countries, including Spain, ensuring the permeability of the unprotected landscapes in between PAs, rather than the designation of new PAs, has been highlighted as the main priority for well-connected PA systems (Saura et al., 2018). In this context, the role to be played by the wider (unprotected) landscapes and by other effective area-based conservation measures different from PAs (Jonas et al., 2014) stands out as crucial for sustaining and improving the connectivity of habitat networks.

One of the most important coordinated international actions for biodiversity conservation is the Natura 2000 network of protected areas in the European Union (EU). The aim of this network is to ensure the long-term persistence of Europe's most valuable and threatened species and habitats, listed under both the Birds Directive (79/409/EEC, amended as 2009/147/EC) and the Habitats Directive (92/43/EEC). Currently, the Natura 2000 network consists of more than 27,000 sites covering more than 18% of EU land (European Commission, 2016). This coverage is higher in some countries like Spain, where about 27% of the land is covered by Natura 2000 sites (European Commission, 2016). The importance of maintaining, or when possible improving, the connectivity of the Natura 2000 network is well recognized in the Habitats Directive: the EU member states are encouraged to conserve or restore the features of the landscape that increase the ecological coherence of the network and allow for the migration, dispersal and genetic exchange of wild species.

The amount of land that can be covered by fully-designated PAs is, however, limited (Bengtsson et al., 2003; Butchart et al., 2015), as well as the connectivity levels that can be achieved through PAs alone. For this reason, the functionality and long-term persistence of biodiversity relies on appropriate land use planning in the wider landscapes in which PAs are embedded; this includes the identification and management of key landscape elements in heterogeneous, multiple-use landscapes (Bengtsson et al., 2003; Garmendia et al., 2016; Tannier et al., 2016). In particular, sustainably managed forests and multifunctional forestry may play a key role in supporting the ability of species to move through unprotected lands (Laita et al., 2010; Bergsten et al., 2013), although such role has rarely been specifically evaluated in functional connectivity assessments. Riparian forests, on the other hand, are exceptionally rich in biodiversity, provide a wide range of ecosystem services, and can have a fundamental role in forest landscape functioning, acting as corridors between forest habitats and populations (Naiman et al., 1993; Gillies and StClair, 2008; Clerici and Vogt, 2013; Fremier et al., 2015). It is therefore advisable to consider the specific contribution of riparian forests in connectivity modelling and related landscape management recommendations. In this context, forests of different types should be conceived as part of the green infrastructure, which is defined as a strategically planned network of natural and semi-natural areas designed and managed to deliver a wide range of ecosystem services, including their ability to support connectivity (European Commission, 2013; Garmendia et al., 2016). In the EU, the Natura 2000 network constitutes the backbone of the green infrastructure, as explicitly recognized in the EU Green Infrastructure Strategy (European Commission, 2013). This strategy aims to ensure that the protection and restoration of green infrastructure become an integral part of land use planning and territorial development across multiple sectors.

Despite the importance of PA connectivity targets, there are very few comprehensive assessments that allow identifying which areas and landscape features, either within or outside protected lands, are most relevant to sustain the connectivity of protected forest sites and habitats over wide spatial scales. Many available studies have measured PA connectivity levels but have not mapped the functional connectors through which species movements and other ecological flows may be supported across the landscape (Laita et al., 2010; Minor and Lookingbill, 2010; Bergsten et al., 2013; Mazaris et al., 2013; Wegmann et al., 2014; Santini et al., 2016; Saura et al., 2017). Other studies that have mapped connectivity have not evaluated the specific contribution of forests or other specific green infrastructure elements to PA connectivity, but have rather considered other more generic landscape categories, such as wilderness areas, or the impacts of roads (Gurrutxaga et al., 2011; Gurrutxaga and Saura, 2014; Belote et al., 2016; Dickson et al., 2017). In addition, to our knowledge, none of these studies has assessed the connectivity performance of PAs compared to the unprotected landscapes, nor evaluated the degree to which connectivity restrictions may also be found within formally protected lands. Previous studies have either assumed PAs to be internally homogenous or have not separately disclosed the connectivity patterns within and outside PAs.

We here present a detailed analysis of the connectivity of the Natura 2000 sites covered by woodland habitats (forests and shrublands) in mainland Spain (≈ 500,000 km^2) by applying a novel combination of methods and tools for functional connectivity modelling in heterogeneous landscapes. We first mapped the connectors between the central points of the Natura 2000 sites, thereby also accounting for potential connectivity limitations that might be imposed by the land uses within these sites. Second, we characterized the width of the permeable land strips along these connectors. Third, we prioritized the key connectors in which to concentrate conservation and restoration efforts. Fourth, we identified the bottlenecks (weak sectors) along these priority connectors. Fifth, and importantly, we assessed the degree to which different land cover and tenure types are a key part of the green infrastructure supporting the connectivity of the PA system. In this assessment, we payed particular attention to the role of riparian forests and of the public forest lands officially declared as of Public Utility in Spain. By doing so, we provide recommendations for the management and restoration of ecological functionality at wide planning scales, considering both protected sites and multiple-use landscapes, and demonstrate the considerable added value of a set of methods that also has potential of application in other countries in Europe or elsewhere.

2. Materials and methods

2.1. Woodland habitats: definition and spatial distribution

We defined three woodland habitat types with different forest canopy cover (FCC) and stage of development of the tree layer: (i) closed mature forest, with FCC ≥ 60% and tree diameter at breast height above 20 cm, (ii) open forest, with 10% ≤ FCC < 60%, and (iii) shrublands, defined as areas covered by shrubs only or with a sparse tree layer (FCC < 10%). These habitat types were considered for three reasons. First, they allowed evaluating how the results of the connectivity analyses may vary for species with different requirements on woodland habitat structure. Second, they were sufficiently broad to be of interest to wider landscape planning and green infrastructure reinforcement strategies, which are unlikely to be attached to the details of particular species. Third, they had a wide distribution and representativeness in Spain, since they were present in the large majority of Natura 2000 sites (see below), which hence allowed providing insights that are relevant throughout all the study area.

The distribution of these woodland habitats in the Natura 2000 sites was obtained from the Forest Map of Spain (FMS) at a scale 1:50,000, developed by the Spanish Ministry of Environment in coordination with the Third Spanish National Forest Inventory. FMS has a minimum mapping unit of 2.5 ha for forests and of 6.25 ha for other cover types, and provides information on the FCC and stage of development of each forest patch.

All the analyses described below were performed separately for each of these three habitat types.

2.2. Natura 2000 sites

The focal areas to connect were the Natura 2000 sites covered by the abovementioned woodland habitats in mainland Spain. To identify the focal sites, we used the official Natura 2000 layer provided by the Spanish Ministry of Environment, and considered a different set of sites for each of the three habitats. We selected those sites that, according to FMS, contained an area of at least 3500 ha of habitat or had at least 20% of the site area covered by the considered habitat. Defining the focal sites also in terms of the percentage of area covered by the habitat, rather than only using a total area threshold, allowed to retain in the analysis sites that were small in size but that could host unique conditions or valuable ecosystems, such as riparian sites.

The selected Natura 2000 sites covered more than 90% of the total area of each of the habitats in all the Natura 2000 network of mainland Spain (94% for closed mature forest, 95% for open forest and 91% for shrublands). It was necessary to consider that the same location could be covered by more than one Natura 2000 site; i.e. areas designated both as a Special Area of Conservation under the Habitats Directive and as a Special Protection Area under the Birds Directive. To avoid these overlaps and associated double counting for the same habitat, we dissolved the layer with the selected Natura 2000 sites to obtain a set of non-overlapping Natura 2000 polygons. For brevity, we hereafter refer to these polygons simply as the selected Natura 2000 sites, which were 524, 547 and 345 sites for closed forests, open forests and shrublands, respectively.

The area of habitat in each of the selected sites was taken into account in the prioritization analysis described later in Section 2.4. Woodlands outside the selected Natura 2000 sites were taken into account as potential facilitators of movement between the selected sites, as given by the resistance surface described in Section 2.3.

2.3. Resistance surface and least-cost path modelling

We used a resistance surface with a spatial resolution of 100 m to characterize the difficulty for woodland species movement through different land cover types. We used a resistance surface with values parameterized for forest mammals that was used and described in previous studies (Gurrutxaga et al., 2011; Ministerio de Agricultura, Alimentación y Medio Ambiente, 2013; Gurrutxaga and Saura, 2014). This resistance surface was built based on expert knowledge (Gurrutxaga et al., 2010) and validated with landscape genetic data for the European pine marten (Ruiz-González et al., 2014). The resistance surface values were adjusted for the three woodland habitats so that the minimum resistance value (equal to 1) was found when the landscape was covered by the considered habitat. Resistance values increased when movement had to occur outside the considered habitat and particularly outside woodlands (e.g. agricultural lands), up to a value of 1000 for urban areas and transport infrastructure, as in previous studies (Gurrutxaga et al., 2011; Gurrutxaga and Saura, 2014; Clauzel et al., 2015a). Resistance values were assigned to the land cover types differentiated in the SIOSE (Sistema de Información sobre Ocupación del Suelo de España) land cover map of Spain for year 2005, which has a scale of 1:25,000 and a minimum mapped unit of 2 ha, and allowed a fine-scale mapping of landscape heterogeneity. The resistance values for transport infrastructure were given to those cells in the resistance surface that contained motorways, trunks and primary roads as mapped in OpenStreetMap (www.openstreetmap.org). Finally, to consider potential patterns of transboundary connectivity (i.e. connectors between Spanish sites traversing neighboring countries), we assigned the resistance values to Portugal and France based on CORINE Land Cover for year 2006 with a spatial resolution of 100 m, and to Andorra based on the land cover map for this country available at http://www.iea.ad/mapa-de-cobertes-del-sol-d-andorra-1995. In these neighboring countries, we considered transport infrastructure resistance using also OpenStreetMap, in the same way as for Spain. Further details on the resistance values for the SIOSE and CORINE land cover classes are provided in Table A.1 (Appendix A in Supplementary data).

In our analyses, we took into account (i) the potential limitations to connectivity due to the land covers existing within Natura 2000 sites and (ii) the spatial distribution of the woodland habitat within the sites. For this purpose, we calculated (see below) the least cost paths (LCPs) between the central points of the Natura 2000 sites, rather than between their edges, and assigned resistance values to all lands within and outside Natura 2000 as given by the land covers actually found in each case. We calculated the central point as the centroid of each of the individual woodland habitat patches within the Natura 2000 site that was closest to the centroid of all the woodland habitat patches in the site; see an example in Fig. A.1 (Appendix A in Supplementary data). This procedure ensured that LCPs started or ended in a central point that was actually located within the considered habitat. Determining the LCPs between the central points of the Natura 2000 sites, rather than between their edges, also allowed delineating fully continuous corridor pathways that were not interrupted in the lands within Natura 2000 sites (note that Natura 2000 covers as much as 27% of Spain).

We applied least-cost path modelling between the central points of all adjacent Natura 2000 sites, using Linkage Mapper 1.0.9 (McRae and Kavanagh, 2011) in ArcGIS 10 and the resistance surface with 100 m of spatial resolution described above, which gave a total of 1845, 1951 and 1187 LCPs for closed forests, open forests and shrublands, respectively. The concatenation of LCPs between consecutive adjacent sites formed the favorable pathways that could be followed in the movement between more distant, non-adjacent Natura 2000 sites. We obtained three results from this analysis. First, the effective distances between the sites, i.e. the difficulty of movement between them as quantified through the accumulated cost along the LCP. Second, the LCPs as the lines following the 100 m cells that minimized the accumulated cost between each pair of sites (between their central points). Third, a connector map showing the width of the permeable land swaths to the sides of the LCP lines (McRae and Kavanagh, 2011).

2.4. Prioritizing connectors for conservation and restoration

We quantified the importance of each connector for the conservation and restoration of Natura 2000 connectivity through a graph-based approach based on the Probability of Connectivity (PC) metric (Saura and Pascual-Hortal, 2007; Saura, 2015; Saura and de la Fuente, 2017). We calculated PC using the Conefor software package (Saura and Torné, 2009), available and updated at www.conefor.org. PC has been used in previous studies on the conservation or restoration of habitat patches for connectivity (Saura and Pascual-Hortal, 2007; Clauzel et al., 2015a, 2015b), but here was applied to focus on the potential effects of changes in the connections between Natura 2000 sites. Specifically, we performed the following two analyses for each habitat (see further details in Appendix B in Supplementary data):

- The conservation importance of a connector was quantified as the decrease in the connectivity of the network of Natura 2000 sites that would occur if the current conditions in the connector were degraded or deteriorated up to a complete blocking of their connecting capacity. This conservation importance was quantified as the percent decrease in the PC value for the Natura 2000 sites (dPC) after the removal of the connector (link) from the graph.
- The restoration importance of a connector was quantified as the increase in the connectivity of the network of Natura 2000 sites that would occur if the current conditions in the connector were improved so that the connector was fully composed of the most favorable land cover for species movements (woodland habitat). This restoration importance was quantified as the percent increase in the PC value for the Natura 2000 network (dPC) after replacing the current effective distance (link weight) along the connector by a value equal to the length of the connector (effective distance that would be obtained if each cell along the connector had a resistance equal 1).

We selected the priority connectors for conservation and restoration for each habitat as the 10% of the connectors with the highest overall importance values in the conservation and restoration scenarios, respectively. In some cases, the same connector can be within both the conservation and restoration priority connectors. This occurs when such connector is already crucial, in its current state, to sustain the connectivity of some Natura 2000 sites but still could increase connectivity to remarkably higher levels if its conditions were further improved through restoration.

2.5. Identifying bottlenecks (weak points) along the priority connectors

We quantified the connectivity bottlenecks as the sectors of the priority connectors that were more fragile or restrictive to species movements because they were surrounded by hostile land uses in their immediate vicinity. To do so, we used one of the outputs of Linkage Mapper, which provided, for each 100 m cell to the sides of the LCP, the difference between the effective distance that would result if the path would need to go through that cell outside the LCP and the effective distance along the LCP. We calculated the average of that difference in a radius of 1 km (geographical distance) around each cell in the LCP, and identified as bottlenecks the 10% of the cells of the LCPs along the priority connectors that had the highest values of that average. These bottlenecks were therefore the sectors of the connectors in which their permeability decreased more sharply in the surroundings.

2.6. Characterizing the areas traversed by the connectors: Natura 2000 sites, public forests, riparian forests and other land covers

We characterized the land cover composition or tenure types of the areas traversed by all connectors, by the priority connectors and by the bottlenecks along priority connectors.

First, we quantified the percentage of the length of the connectors found inside Natura 2000 lands. Since the connectors were determined between the centers of the Natura 2000 sites, the connectors start and end within those sites and hence must traverse some distance within Natura 2000. For this reason, we also calculated, for the three habitats, the same connectors (LCPs) for the same Natura 2000 sites but in an hypothetical situation of homogenous landscapes, as given by a resistance surface with the same resistance value (equal to 1) in all mainland Spain (for all protected and unprotected lands). In these homogeneous landscapes, the connectors have no preference for, nor tendency to avoid, the Natura 2000 lands. A positive selection of Natura 2000 lands by the identified connectors therefore happens when their actual percentage inside Natura 2000 is, in the real landscapes, higher than the percentage of connectors inside Natura 2000 in the hypothetical homogeneous landscapes. All the Natura 2000 sites (and not just those with presence of a particular woodland habitat type) were considered in this assessment.

Second, we quantified the percentage of the connector length that was found inside Public Utility Forests (hereafter often referred to as public forests for brevity). The declaration of a forest as of Public Utility is the highest protection classification for public forests in Spain, as established by the Spanish Forest Law (both current and previous laws). Many of these forests were declared as of Public Utility already in the 19th century, with the main aim of halting the deforestation that was occurring, or was expected to occur, in forests lands lacking any form of legal protection (Mangas-Navas, 1999; Pérez-Soba, 2013). Public Utility Forests represent 86% of all public forest area in Spain, and are managed by the national or regional Spanish Forest Services. The Spanish Ministry of Environment provided the layer in which these Public Utility Forests are mapped. These public forest lands are predominantly covered by forests or woodlands, although they may contain some significant portions of other land covers such as grasslands, pastures or non-vegetated areas such as rocky outcrops.

Third, we paid particular attention to riparian forests by quantifying how much of the length of the connectors was found along riparian forests (including both natural and planted riparian forests next to rivers and streams), as mapped in the FMS.

Finally, we evaluated the percentage of all the different land cover types in the areas traversed by the connectors, using the FMS, as given in Table A.2 (Appendix A in Supplementary data).

3. Results

3.1. Connectors between Natura 2000 sites

We identified an extensive network of connectors between the Natura 2000 woodland sites in mainland Spain, as shown by the central axes (LCP lines) of the connectors (Fig. 1 and A.2 in Supplementary data). There were noticeable differences in the spatial distribution of connectors, from areas with a remarkable connector density, mainly within or nearby the main mountain ranges, to others that, in contrast, had none or very few connectors, as in certain parts of the southern plateau or the northern plateau (Meseta Central) and in some relatively large coastal areas (Fig. 1 and A.2 in Supplementary data).

There was a large variability in the conditions and width of these connectors (Fig. 2, A.3 and A.4 in Supplementary data). Some of the connectors spanned over wide swaths of land, so that movement could be distributed over relatively large areas in a quite unrestricted manner; i.e. with little increase in the difficulty of movement (accumulated cost) even at relatively large distances from the central axis of the connector (LCP line). These wide connectors are those shown as “connectors through a wide area with low resistance” in Fig. 2, A.3 and A.4 (in Supplementary data). On the contrary, some connectors were restricted to a very narrow band, covering little or no more land than that in the LCP line, and with large permeability decreases for any movement that

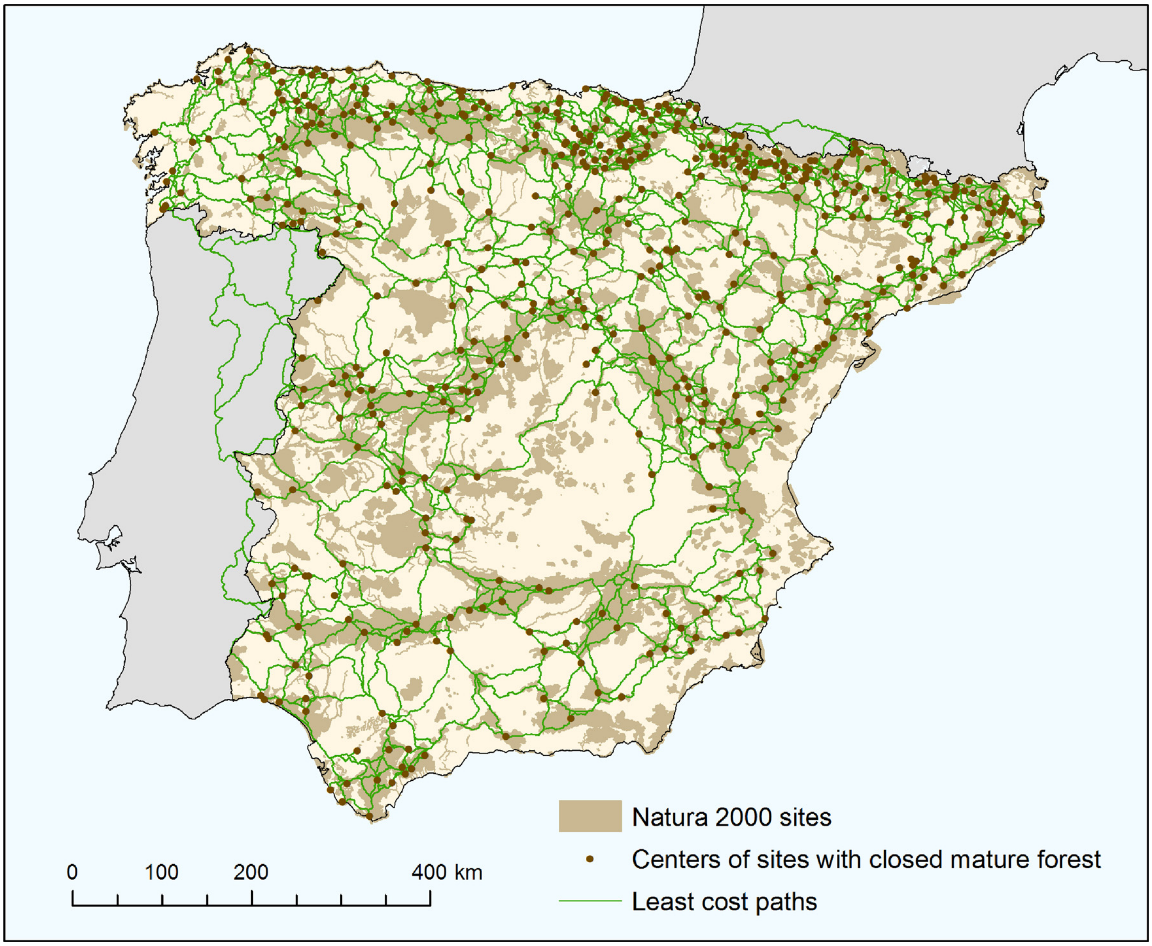

Fig. 1. Least cost paths linking the central points of the Natura 2000 sites with closed mature forest habitat in mainland Spain. The paths and central points for this habitat are overlaid on the Natura 2000 network (all sites shown, with or without the considered habitat). See Fig. A.2 in Appendix A in Supplementary data for a similar figure for the other two habitat types (open forest and shrubland).

needed to traverse the lands immediately adjacent to the central axis of the connector. These narrow connectors traversed mostly hostile landscapes dominated by high resistance areas, and funneled through the relatively sparse and thin strips with suitable vegetation, since these were the only available movement pathways to reach certain Natura 2000 sites. These narrow connectors are those shown as "connectors through a narrow band in a high-resistance area" in Fig. 2, A.3 and A.4 (in Supplementary data). Some low resistance areas were not traversed by any connector, either because they were peripheral areas that did not give access to any Spanish site, or because they were surrounded by other areas with high-resistance land uses (Fig. 2, A.3 and A.4 in Supplementary data).

The priority connectors for conservation tended to concentrate along the main mountain ranges of mainland Spain, with some exceptions (Fig. 3). The priority connectors for restoration, however, tended to traverse, more frequently than the conservation connectors, heterogeneous landscapes not dominated by woodlands but with an important presence of agricultural land uses and other human-made land covers, such as across the Guadalquivir Valley or some areas in the southern plateau (Fig. 3). This tendency was even more pronounced in the bottlenecks (weakest parts) of the restoration connectors; these bottlenecks were frequently found where the linkages traversed plain lands and agricultural landscapes to connect different Natura 2000 forest cores (Fig. 4). In comparison, the bottlenecks in the priority conservation corridors were more commonly found in relatively small discontinuities of the woodland-dominated areas within or nearby the main mountain ranges, as well as in shorter sections across non-forested landscapes of connectors linking relatively closer Natura 2000 sites (Fig. 4). There were, however, some sectors that were highlighted as bottlenecks both in the conservation and restoration scenarios (Fig. 4); these represented 9.8% of the total length of the conservation and restoration bottlenecks.

Some of the connectors between the Spanish Natura 2000 sites, including some of the priority connectors, traversed lands outside Spain, through the French side of the Pyrenees and particularly through Portugal (Figs. 1, 2 and 3), highlighting the importance and benefits of a transboundary perspective in connectivity and landscape planning in Europe.

3.2. *Characterization of the areas traversed by the connectors: Natura 2000 sites, public forests, riparian forests and other land cover types*

3.2.1. *Connectors and Natura 2000 sites*

A large proportion of all the connectors (44–46% of their total length) traversed landscapes within the Natura 2000 sites, and this happened considerably more frequently than what would be obtained in a case of no particular preference for Natura 2000 lands (35–37%), as

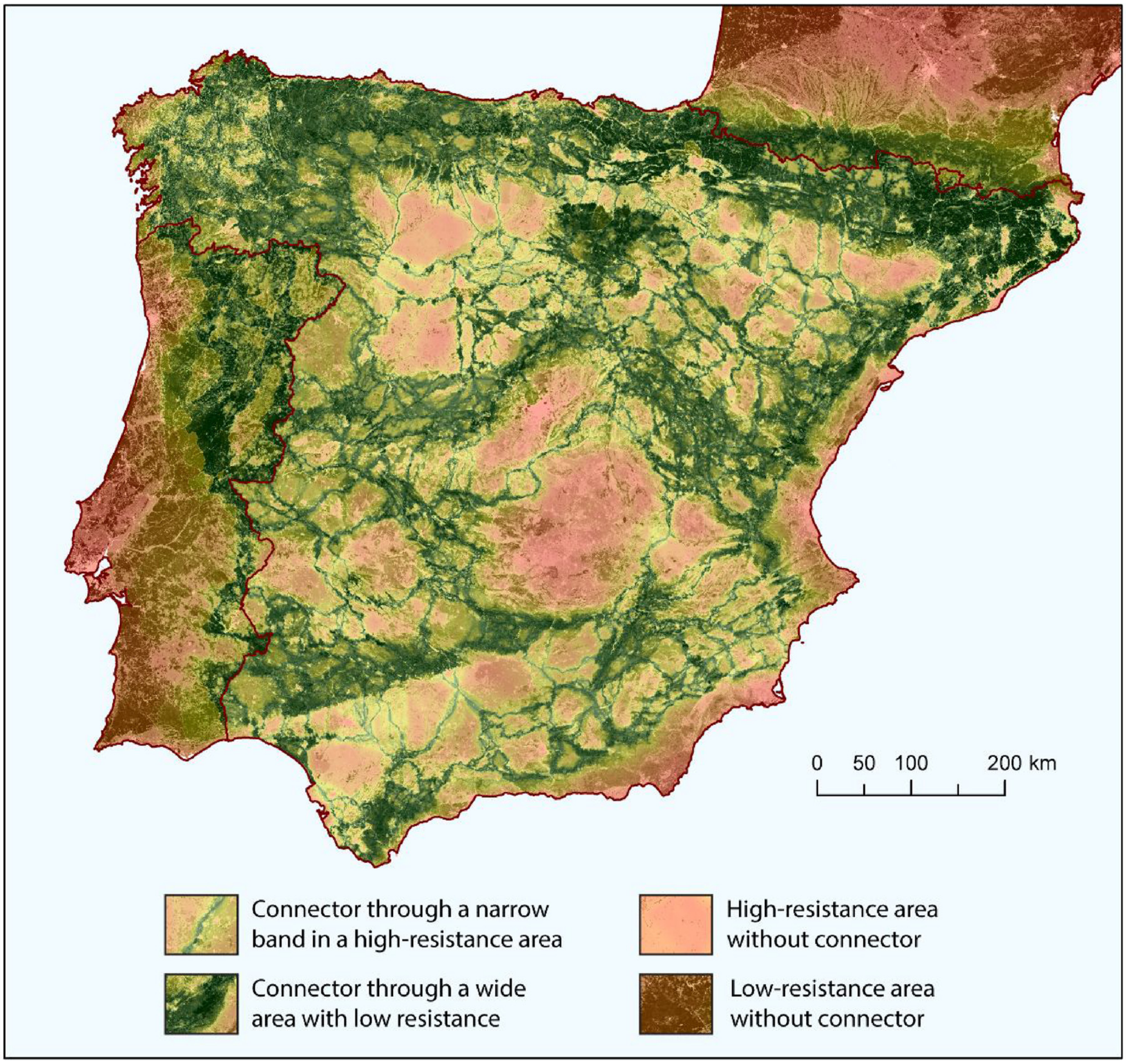

Fig. 2. Map of the connectors of variable width between the Natura 2000 sites with closed mature forest habitat, depicting four categories of land regarding connectivity (as indicated in the graphical legend) and intermediate cases between them. The map has been produced by overlaying, with some transparency, the connector map obtained from Linkage Mapper with the resistance surface. See Fig. A.3 in Supplementary data for the connectors and their width for the other two habitats (open forests, shrublands) and Fig. A.4 in Supplementary data for a similar representation with all the three habitats combined in a single map.

shown in Table 1. This result indicates that the connectors preferentially selected Natura 2000 lands, since they generally had lower-intensity land uses and better permeability conditions than the unprotected lands.

The observation of good general conditions for connectivity within Natura 2000 was reinforced by the results for the priority connectors for conservation (Fig. 3), most of which ($\geq$66% for the three habitats) were found within Natura 2000, and in a much higher percentage than for all the connectors that included the non-priority ones (Table 1). Further reinforcing this observation, the bottlenecks along the connectors, i.e. the weakest parts of the connectors due to land use pressures, were predominantly found outside Natura 2000 (Table 1). In particular, the bottlenecks in the priority connectors for restoration were overwhelmingly located (78–86%) outside Natura 2000 (Table 1), indicating that most of the constraints for connectivity were found outside this system of PAs.

At the same time, however, the obtained results show that Natura 2000 sites cannot be considered as areas free of restrictions for connectivity and species movements. For instance, more than a third of the priority bottlenecks for conservation (33–41%) were found within Natura 2000 sites (Table 1).

3.2.2. Connectors and public forest lands

Public forest lands (those declared as of Public Utility in Spain) were part of the connectors much more frequently (about twice) than their availability in the landscape (Table 2). On the contrary, the bottlenecks in the priority restoration connectors were found within public forests less frequently than the 14.3% of the Spanish area they cover (Table 2); this did not happen when all forests, regardless of being private or public, were considered (Table A.2 in Supplementary data). For example, for the closed mature forest habitat, we found within public forests only 6.2% of the bottlenecks of the priority restoration connectors, compared to the 14.3% of area covered by public forests (Table 2); in comparison, 42.8% and 9.1% of such bottlenecks were

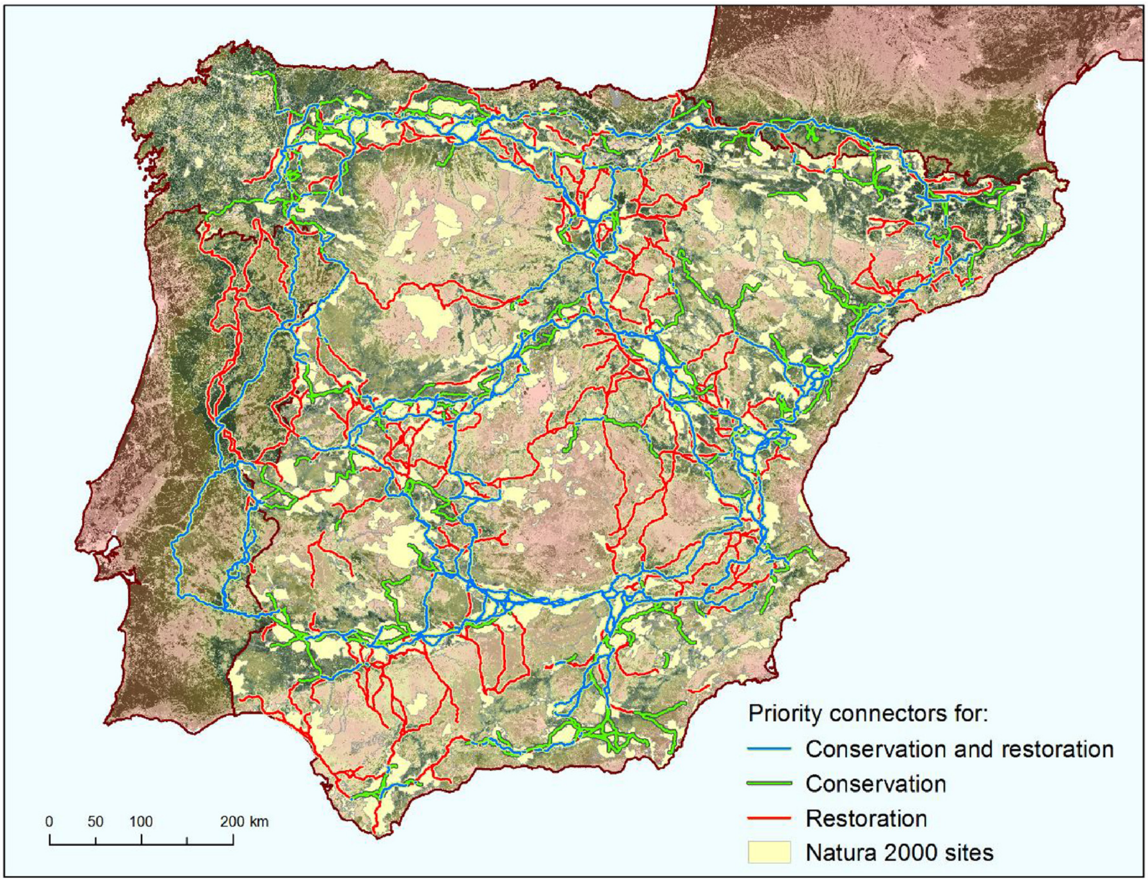

Fig. 3. Priority connectors for conservation and restoration for the network of Natura 2000 woodland sites in mainland Spain. The map shows the priority connectors for all the three woodland habitats together, overlaid on the Natura 2000 layer (all sites shown, with or without woodland habitat). The connectors that are a priority for both conservation and restoration are shown on top in blue color; they represent 24.1% of the total length of the priority connectors. Separate maps with the priority connectors for conservation and restoration are shown in Fig. A.5 in Supplementary data. Note that there might be some discontinuities in the pathways of these priority connectors because they are only the top 10% by importance (see methods); other connectors in between the priority ones may fall in the next importance class, e.g. the second decile by importance. The full set of connectors (represented by the LCPs) is shown in Fig. 1 and A.2 in Supplementary data. The background composition is as in Fig. 2 but with paler colors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

found within natural and planted forests respectively, above the 26.5% and 5.8% of the Spanish land covered by natural and planted forests respectively (Table A.2 in Supplementary data). Public forest lands also performed better than all forests in general (either natural or planted) in avoiding bottlenecks in priority conservation connectors; i.e. the ratio between the percentage of these bottlenecks and the percentage of the priority conservation connectors was, for all the three habitats, significantly lower when calculated for public forests (< 0.5) (Table 2) than when calculated for all forests (> 0.7) (Table A.2 in Supplementary data).

3.2.3. Connectors and riparian forests

The identified connectors showed a clear positive selection of riparian forests, i.e. connectors tended to funnel through riparian forests quite more frequently than the percentage of land covered by these forests (Table 3). For example, the connectors for closed mature forest habitat were found within riparian forests almost five times more often than the availability of these forests (3.36% vs. 0.68%, see Table 3). This selection frequency is much higher than the one found for all forests, which were only selected 2.5 times their availability in the landscape (Table A.2 in Supplementary data).

Regarding the priority connectors, riparian forests were much more frequent within the restoration connectors than within the conservation connectors (Table 3). The most noteworthy result was, however, that the bottlenecks in the priority connectors were found through riparian forests with a very high frequency; this was particularly the case for the bottlenecks in the priority restoration corridors (Table 3). For example, the priority connectors for restoration between closed mature forest and open forest sites funneled through riparian forests 26 and 18 times more frequently than the availability of these riparian forests in the landscape, respectively (Table 3).

3.2.4. Connectors and other land cover types

Connectors tended to clearly avoid agricultural areas (Table A.2 in Supplementary data), and avoided even more prominently urban areas (Table A.2 in Supplementary data), in accordance with the preference for forest and woodland covers for the type of species, habitats and resistance surfaces here considered. Agricultural areas were much more abundant, and hence more determinant for Natura 2000 connectivity, than urban areas; more than 40% of the territory of mainland Spain is covered by agriculture (Table A.2 in Supplementary data), which implies that the connectors that link Natura 2000 woodland sites must,

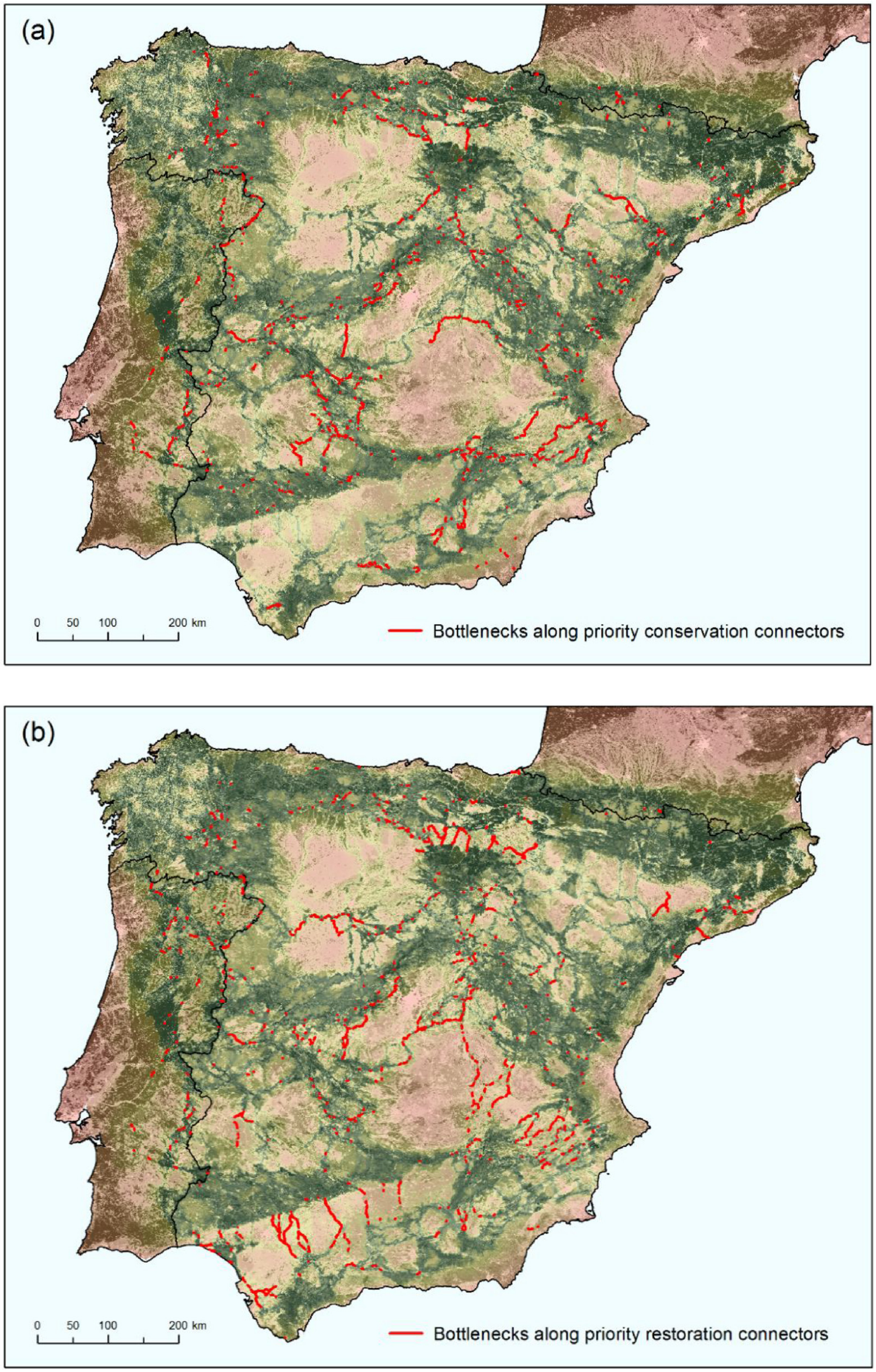

Fig. 4. Bottlenecks along the priority connectors for conservation (a) and restoration (b) between Natura 2000 woodland sites in mainland Spain. The maps show the bottlenecks along the priority connectors of all the three woodland habitats together. The background composition is as in Fig. 2 but with paler colors.

with some frequency, pass through these agricultural areas. However, only between 6.5% and 8.5% of all connectors traversed crops (Table A.2 in Supplementary data). Especially rare were the priority connectors for conservation traversing agricultural areas (only about 3%) and urban areas (0.2% or less), at least ten times less than the availability of these areas in the landscape (Table A.2 in Supplementary data). This finding indicates that the corridors with best conditions for the forest species and habitats were also those less affected by intensive agriculture and urban land use. Agricultural lands were considerably more common in the restoration than in the conservation priority

Table 1
Percentage of the connectors traversing Natura 2000 sites, for the three woodland habitats and different categories of connectors (all connectors, priority connectors and bottlenecks in priority connectors). The connector percentage has been calculated considering the total length of the connectors between the central points of the Natura 2000 sites, which hence necessarily traverse at least the portion of Natura 2000 land from the center to the edge of the sites. A positive selection of Natura 2000 lands by the connectors occurs when such percentage (as obtained in the real landscape setting) is higher than the percentage that would be obtained if the connectors were delineated in an hypothetical situation in which all lands (protected or unprotected) have the same resistance (homogeneous landscape setting). The homogeneous landscape corresponds to the case of no preference for, nor avoidance of, Natura 2000 lands. The last row gives the percentage of mainland Spain covered by the Natura 2000 network (this percentage is independent of the connectivity analyses).

		Woodland habitat to connect		
		Closed mature forests	Open forests	Shrublands
All connectors	Real landscape setting	45.0	43.9	46.2
	Homogeneous landscape setting	35.8	35.3	36.8
Priority connectors	Conservation	66.3	67.6	66.0
	Restoration	54.9	51.8	48.1
Bottlenecks in priority connectors	Conservation	33.0	40.6	36.3
	Restoration	13.9	16.4	21.9
Natura 2000 coverage in mainland Spain		27.0		

Table 2
Percentage of the connectors found inside public forests (those declared as of Public Utility), for the three woodland habitats and different categories of connectors (all connectors, priority connectors and bottlenecks in priority connectors). These values can be compared, as a reference, with the percentage of mainland Spain covered by these public utility forests, as given in the last row (this percentage is independent of the connectivity analyses).

		Woodland habitat to connect		
		Closed mature forests	Open forests	Shrublands
All connectors		31.2	25.7	26.2
Priority connectors	Conservation	39.3	26.7	38.3
	Restoration	33.2	17.4	34.1
Bottlenecks in priority connectors	Conservation	17.6	9.7	18.9
	Restoration	6.2	3.1	13.3
Percentage of mainland Spain covered by public utility forests		14.3		

Table 3
Percentage of the connectors found along riparian forests, for the three woodland habitats and different categories of connectors (all connectors, priority connectors and bottlenecks in priority connectors). These values can be compared, as a reference, with the percentage of mainland Spain covered by riparian forests, as given in the last row (this percentage is independent of the connectivity analyses).

		Woodland habitat to connect		
		Closed mature forests	Open forests	Shrublands
All connectors		3.36	2.40	1.39
Priority connectors	Conservation	1.31	1.04	0.76
	Restoration	2.42	2.31	1.27
Bottlenecks in priority connectors	Conservation	8.28	4.50	4.10
	Restoration	18.02	12.22	5.86
Percentage of mainland Spain covered by riparian forests		0.68		

connectors (Table A.2 in Supplementary data). In addition, bottlenecks along the priority restoration connectors were very frequently found immersed in the agricultural matrix (between 25% and 40% of these bottlenecks, depending on the habitat). Such findings indicate that it is through these agricultural landscapes where restoration and land use planning measures may be given a high priority to enhance the likelihood of successful movement of woodland species between Natura 2000 sites.

By contrast, and as expected, the connectors between the woodland sites were preferably concentrated through forests (Table A.2 in Supplementary data), particularly for the connectors between the sites with mature or open forest. Similarly, the highest frequency of shrubs was found in the connectors between Natura 2000 shrubland sites (Table A.2 in Supplementary data).

Dehesas, as related to the low tree canopy cover of these multifunctional agro-sylvo-pastoral systems, were selected by the priority connectors more frequently than their availability in the landscape only for open forests (Table A.2 in Supplementary data). Even for open forests, the connectivity role of dehesas was not found to be as prominent as for other land covers or landscape elements (Natura 2000 sites, public forests, riparian forests, forests in general).

4. Discussion

4.1. Public forests: an effective area-based connectivity conservation measure compatible with sustainable use

Our findings suggest that the public forest lands declared as of Public Utility in mainland Spain may meet all the requirements to be considered as effective area-based conservation measures contributing to the functional connectivity of PA systems and the related Aichi Target 11 connectivity element. They are frequently part of the identified connectors (much more frequently than what expected by the area they cover in the landscape) and tend to be free of connectivity constraints (they have less bottlenecks than other types of forests or landscapes), therefore playing a key role in maintaining connectivity between Natura 2000 woodland sites in mainland Spain.

These positive outcomes regarding the connectivity role of these public forest lands are because of two reasons. First, these public forests were declared in locations that are now found strategic for connecting the forest habitat sites distributed throughout mainland Spain. Second, the sustainable forest management practices generally applied in these public forest lands, which frequently include production objectives and which in most cases were in place many decades before the Natura 2000 network was created, have been successful in maintaining or restoring forest cover and the functionality of these key connectivity areas. Many of these forests were declared as of Public Utility in the 19th century or early in the 20th century to halt deforestation in many parts of Spain, providing them with full legal support to preserve the forest cover and avoid land use changes, and have a long history of protection and management by the Spanish Forest Services (Mangas-Navas, 1999; Pérez-Soba, 2013). More than 100 years after, it becomes apparent that their designation and management has had benefits for objectives that were not at the forefront of the planning concerns by then, but that are now central to the objectives of land use policies, of the Natura 2000 network of protected sites and of the strategies for green infrastructure support and reinforcement.

Our findings are in agreement with other analyses that have highlighted, even if in more local study areas within Spain focusing in a particular forest species (the capercaillie, *Tetrao urogallus*), the importance of public forest lands for connectivity (Pascual-Hortal and Saura, 2008; Velázquez et al., 2017). The extent to which the key role we have underlined here for public forests in mainland Spain is generalizable to other countries in Europe or elsewhere would need from further research. There are evidences, however, showing a remarkable connectivity contribution of certain types of forests under sustainable management practices. For instance, Bergsten et al. (2013) found, in an analysis for northern Sweden, that non-formally protected sites such as those classified as Woodland Key Habitats, which are located within managed forests, were able to significantly increase the connectivity levels for mature pine forests compared to what was provided by fully designated PAs alone. Similarly, Laita et al. (2010) concluded that, in Finland, Woodland Key Habitats could be a valuable and efficient addition to the connectivity of the reserve network.

4.2. Riparian forests as key elements of the green infrastructure sustaining protected area connectivity

Our results show that riparian forests have an outstanding importance in upholding the connectivity of woodland habitats in the Natura 2000 network. This key connectivity role is evidenced by riparian forests being part of the identified connectors between Natura 2000 forest sites much more frequently than expected by the area covered by riparian forests in the landscape. Our finding is in line with several studies that examined the movement or distribution of forest animal species, such as mesocarnivores or seed-dispersing birds, and concluded that functional connectivity is favored by the presence of riparian areas, particularly when they can be used as corridors across open agricultural lands (Machtans et al., 1996; Gillies and StClair, 2008; Balestrieri et al., 2015; Şekercioğlu et al., 2015; Carvalho et al., 2016; Santos et al., 2016).

Clerici and Vogt (2013) examined the spatial continuity of riparian zones in Europe. They showed that some areas in mainland Spain, and some Spanish rivers like Guadiana, Tajo or Ebro, face a medium to high pressure from agricultural and urban land uses, suggesting a relatively critical situation for the conservation of riparian ecosystems. Weissteiner et al. (2016) reported that significant parts of Spain, and of other European countries, have riparian deficiencies, defined as a low ratio between the actual area and potential riparian zones along rivers, mostly because of agricultural land use pressures and related conversion of natural vegetation to crops. These results are further reinforced by those we obtained in this study by focusing on a functional connectivity perspective. Riparian forests were disproportionally found, far more than their percent land cover, in the bottlenecks of the priority connectors. These bottlenecks are the weakest and narrowest parts of the connectors that are most important to sustain Natura 2000 connectivity. Any local land cover or land use change in these key connectors may hamper or even completely block their functionality.

The riparian bottlenecks were much more frequent in the priority corridors for restoration, i.e. those in which an improvement of the current quality of the connector would translate in a more prominent enhancement of the connectivity of the Natura 2000 woodland sites. This finding clearly highlights the need to concentrate considerable efforts in the restoration of the riparian vegetation belts, increasing their width and their continuity along the key corridors, if the Natura 2000 connectivity is to be significantly improved beyond current levels. These restoration actions could also mitigate other important land use impacts on riverine ecosystems such as those related to water and soil quality (Vale Junior et al., 2015), hence matching well with the green infrastructure aim of enhancing multiple benefits simultaneously (Garmendia et al., 2016).

4.3. How well do protected areas conserve connectivity?

Management effectiveness of protected areas (PAs) can be defined as how well PAs are being managed for protecting their values and achieving their conservation goals (Hockings et al., 2006). Even when an area is designated as protected, this does not necessarily imply that the adequate management actions are taken to meet the conservation goals for which such area is declared. Insufficient financial resources, lack of governmental support, or conflict with other sectors, land uses or landowners may undermine the actual effectiveness of PAs, which would eventually lead, in the extreme case, to 'paper parks' with no measurable benefits for forest biodiversity or ecosystem health. Several studies have shown that the world´s PAs are able to reduce, although not to stop, deforestation, land use change and other pressures on species richness and population abundance as compared to unprotected sites (Joppa and Pfaff, 2011; Geldmann et al., 2013; Gray et al., 2016; De Oliveira et al., 2017). In Europe, the available research indicates that, as in other continents, PAs are having positive conservation outcomes, as evidenced by their comparison with other unprotected areas or with the same areas before the protection was in place (Geldmann et al., 2013).

Despite the above-mentioned assessments, no studies had, to our knowledge, specifically evaluated through functional connectivity analyses the effectiveness of PAs in conserving the permeability and quality of the land to support species movements. We here show that the Natura 2000 sites in mainland Spain have considerably better conditions for forest connectivity than the non-protected landscapes. A positive condition of the Natura 2000 sites regarding connectivity was evidenced mainly by two results. First, the priority conservation connectors for forest habitats preferentially traversed Natura 2000 lands. Second, the connectivity bottlenecks, particularly those in the connectors to be restored, were found much less frequently within the Natura 2000 sites than what expected from the percentage of priority connectors found within the Natura 2000 network. Our finding on the positive outcomes of the Natura 2000 network should however be considered with two caveats. First, in those Natura 2000 sites that have been recently designated, or in which management plans have only recently started to be implemented, the connectivity conditions may be more related to the conditions of the area before the Natura 2000 designation than to the actual protection or effective management brought in by such designation. In these cases, longer term monitoring of the trends in functional connectivity patterns through time may provide a more informative and comprehensive assessment of the actual contribution of the Natura 2000 designation and implementation in those sites. Second, our conclusion is basically based on comparing the landscapes within and outside the PAs, with connectivity conditions being clearly better within the Natura 2000 network. However, having higher connectivity than in the unprotected lands does not necessarily mean that connectivity levels are enough to support the movement and persistence of all species of conservation value, particularly in the currently changing environmental conditions, which would need to be evaluated in specific assessments outside of the scope of this study.

At the same time, our findings indicate that Natura 2000 sites cannot be considered as areas free of limitations for connectivity, given that, even if to a clearly lower degree than in the unprotected landscapes, we still found within Natura 2000 a notable proportion of bottlenecks. Therefore, the management plans for the Natura 2000 sites, and the land use regulations therein, should also include specific actions to promote connectivity in order to better meet the conservation goals of this network of protected areas.

4.4. Conserving or restoring the connectivity of Natura 2000 forest sites? Two different answers for two different land use contexts

Given that the connectivity of PA systems, and of the Natura 2000 network in Europe, is a key objective of the biodiversity policies, two main efforts would be required on this matter. First, the appropriate conservation of those connectors that, in the current situation, most contribute to sustain the connectivity of the PA system. Second, the restoration of those linkages that, if improved in their conditions and permeability, would allow for the most significant enhancement of the current connectivity levels of the entire PA system. Our approach allowed to identify the priority connectors both for conservation and restoration in mainland Spain, and showed that these two sets of connectors are found in quite different locations and that they involve considerably different landscapes, land uses and management contexts.

The priority connectors for conservation tend to largely concentrate along the main mountain ranges of Spain, which in general are better covered by Natura 2000 sites and are more forested. The conservation connectors are, therefore, predominantly found in those areas where classically the efforts for biodiversity conservation and PA designation have been concentrated, i.e. in relatively remote, comparatively less productive areas, in which there is less conflict with other land uses such as agriculture or urbanization (Joppa and Pfaff, 2009).

On the other hand, the priority connectors for restoration, and especially the bottlenecks along them, are found much more frequently across more human-modified landscapes, typically dominated by agricultural land use, within which some relatively scarce and narrow strips of natural remnant vegetation can be found. In these landscapes, therefore, the conditions for the movement of forest species are much more restrictive, and any significant improvement in the permeability of these key but limiting landscapes would translate in considerable benefits for the connectivity of the woodland habitats in the Natura 2000 network. The concentration of restoration efforts in these landscapes would however require a quite different strategy from that used in the more natural areas at higher elevations in the mountain ranges. In particular, the effective implementation of these restoration needs would be largely dependent on reinforcing the riparian forest belts and on the measures to mitigate the intensification of agriculture. The agri-environment schemes introduced by the European Common Agricultural Policy may be particularly suited for this purpose, especially when aimed at enhancing or maintaining landscape complexity (Concepción et al., 2008) and based on an integrated landscape-scale collaboration between farmers (Leventon et al., 2017). For instance, Gastón et al. (2016) highlighted the importance of agricultural landscape heterogeneity for an emblematic woodland species like the Iberian lynx, which selected with significant frequency, particularly during dispersal events, permanent tree crops (olive groves), agroforestry areas and other landscapes where crops are mixed with significant remnants of natural or seminatural vegetation.

The reported and projected future trends of land use polarization in Europe may negatively affect the heterogeneity and multifunctionality of many European landscapes (Stürck et al., 2018). These trends could lead to locally well-connected forest landscapes, such as those in mountain areas where rural land abandonment is leading to rewilding and woodland expansion. These landscapes may become, however, more isolated at wider spatial scales, if they are surrounded by increasingly intensified landscapes with poor and deteriorating permeability for woodland species movements. There is, therefore, a need of significant efforts for conserving and restoring key green infrastructure elements in agricultural or urban landscapes, from riparian forests to woodlots and other natural vegetation remnants scattered in these areas, in order to counteract these detrimental trends for the connectivity and ecological functionality of European landscapes. These efforts would benefit from an integrated perspective in the management of Natura 2000 connectivity that spans across sectors and is able to link different landscapes to deliver coherent and ecologically functional habitat networks at regional, national and continental scales.

4.5. Scope of application, limitations and further research

We have provided a detailed analysis of the connectors between Natura 2000 sites in mainland Spain, and of the green infrastructure elements that best support connectivity through the unprotected landscapes, for three different woodland habitats. Our analysis does not however exclude the need for more focused analyses on individual species of conservation concern, which may have particular habitat needs and movement preferences not exactly matching those we here considered, or that may be distributed either only in specific locations of the Spanish mainland or beyond the limits of our study area if they extend across several European countries. This is the case for instance of emblematic woodland species in Spain for which dedicated connectivity analyses have been reported, such as the Iberian lynx (Gastón et al., 2016; Blázquez-Cabrera et al., 2016), the brown bears (Mateo-Sánchez et al., 2014), or the capercaillie (Pascual-Hortal and Saura, 2008; Velázquez et al., 2017). Our assessment should be viewed as a more general assessment of the connectivity of the Natura 2000 woodland sites, and of the related green infrastructure, that covers the overarching preferences of a broad range of taxa associated to forests and shrublands, but not necessarily of each species in particular. On the other hand, we focused on woodland habitats because of their relevance for biodiversity and their remarkable importance in mainland Spain ($>$ 90% of the area covered by Natura 2000 was considered by focusing on the sites with a significant presence of woodlands). However, other habitat types, such as wetlands or extensive agricultural lands used by steppe birds, are also of interest for connectivity planning, and could be the focus of future studies extending and adapting this approach to these other habitats.

Although we used the more detailed land cover maps available for Spain, with a 1:25,000 scale and a minimum mapped unit of 2 ha, some finer-scale vegetation patterns and green infrastructure elements may not be captured or sufficiently well represented in the available maps. For example, scattered trees, hedgerows, small woodlots or other natural vegetation remnants interspersed in agricultural landscapes, which may be an important permeability factor for the dispersal or species such as the Iberian lynx (Gastón et al., 2016), may be omitted in the available maps. A more detailed characterization of vegetation structure in forest or agricultural landscapes using the information from LiDAR or other remote sensors can further improve the predictions of wildlife habitat use (Wilsey et al., 2012; Betbeder et al., 2017; Gastón et al., 2017). These remain avenues for additional research that, building on recent developments on remote sensing and geospatial technologies, may further enrich the insights from this type of assessments, either at a national scale or in smaller study areas, to support specific connectivity and land use planning measures.

Our identification of connectors between PAs was based on least cost path modelling, which is possibly the most widely adopted approach for related connectivity assessments (e.g., Rabinowitz and Zeller, 2010; Gurrutxaga et al., 2010, 2011; Mateo-Sánchez et al., 2014; Belote et al., 2016; Blázquez-Cabrera et al., 2016). Least cost paths rely however on the assumption of movement optimality and of identifying only the single best movement pathway between each pair of PAs. There are approaches, such as circuit theory (McRae et al., 2008) or the randomized shortest paths (Panzacchi et al., 2016), that relax these assumptions by incorporating some degree of randomness or exploration in species movements, and by highlighting multiple plausible pathways (and not just the best one) that may be used with some frequency by the considered species when moving between a particular pair of PAs. The usefulness of these approaches has been demonstrated in several related connectivity studies (e.g., Panzacchi et al., 2016; Dickson et al., 2017), although some of their results may need to be interpreted with caution (Mateo-Sánchez et al., 2015; Marrotte et al., 2017). For instance, Marrotte et al. (2017) found that a high current density from circuit theory was not associated to more connectivity (gene flow) but to areas with neighboring pixels with high resistance to movement (pinch points) that constricted gene flow. On the other hand, it may not be possible to focus connectivity-planning efforts in multiple pathways simultaneously, given the usually scarce resources for conservation and restoration as well as the multiple demands on land use. In such cases, focusing on a single highest quality (least cost) path may be a more practical approach. In any case, we acknowledge that the use of other species movement assumptions and modelling frameworks could provide complementary useful information that may be considered in future related assessments.

Finally, we have shown a positive connectivity performance of PAs: in particular, protected lands concentrate a clearly higher proportion of the connectors between the PA centers than what would be expected if unprotected and protected lands were equally good as connectivity providers. The connectivity role of PAs may be however evaluated in a wider set of cases involving not only the distribution of the connectors between PA centers, as done in this study, but also between other locations such as key habitat or biodiversity areas in the unprotected landscapes. Further research along this line would allow for a more comprehensive picture on the connectivity contribution of PAs that involves a wider set of habitat and population patches between which species movements may need to be promoted and managed.

4.6. Conclusions

We have applied a novel combination of methods to map, prioritize and characterize the corridors between protected areas (Natura 2000 sites), including transboundary linkages, and we have assessed which elements of the green infrastructure are more valuable, either in their current conditions or after restoration, to support the connectivity of Natura 2000 woodland sites in mainland Spain.

Our results provide a fundamental spatially-explicit information to guide the efforts for land use and green infrastructure planning aimed to enhance the connectivity of Natura 2000 woodland sites in Spain. They also provide the most detailed case study available so far on the performance of the landscapes within protected areas regarding the functional connectivity of woodland habitats.

Our approach has the potential to be applied to other habitat types, study areas and land use contexts different from the ones here considered, and, by doing so, to support and stimulate the design and implementation of land management measures able to promote the connectivity of functional landscape networks in Europe.

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Appendices A and B.

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