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Key connectors in protected forest area networks and the impact of highways: A transnational case study from the Cantabrian Range to the Western Alps (SW Europe)

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ABSTRACT

The connectivity of protected area networks depends on key elements located in strategic positions within the landscape, which uphold the ecological fluxes and sustain the diversity and longterm viability of native biota. Landscape planning requires objective and quantitative approaches to identify those key elements and reinforce the spatial coherence of protected area designs and related conservation schemes. With this objective, we apply for the first time recent methodological developments that, deriving from the probability of connectivity index, allow evaluating the role of both individual protected areas and links in the intermediate landscape matrix as providers of connectivity between the rest of the sites in the network. We focus on a case study covering the forest protected areas from the Cantabrian Range to the Western Alps (N Spain, S France and NW Italy), considering different dispersal distances and the impact of highways. We show how the proposed approach is useful to identify those protected areas and links that most contribute to uphold functional connectivity in this transnational network, as well as those road sectors where the defragmentation and barrier effect mitigation measures should be prioritized. We compare our results with other more qualitative and expert-based approaches that have been reported in the same area. The methodological approach could be easily adopted in a variety of other related landscape planning applications at different scales, with the required quantitative tools being available as free and open source software packages.

1. Introduction

The dispersal ability of organisms across changing landscapes is critical for long-term biodiversity conservation (Fahrig, 2007). Successful dispersal depends on landscape connectivity, which can be defined as the degree to which the landscape facilitates or impedes movement of species across the habitat resources existing in the landscape (modified from Taylor et al., 1993). Connectivity between protected areas is becoming an area of increasing international focus within the framework of nature conservation policies (Bennett and Mulongoy, 2006; Worboys et al., 2010). This is due to the importance given to avoiding the functional isolation of protected areas (Carroll et al., 2004), halting the loss of biodiversity (Bennett, 2004), and mitigating the effects of climate change in the native biota (Opdam and Wascher, 2004).

Connectivity is species-specific, because the response of each organism to the landscape's structure depends on the scale at which it perceives landscape heterogeneity and on its movement abilities through different land covers (Tischendorf and Fahrig, 2000). Therefore, ecological networks must be designed to integrate different spatial scales and different types of habitat (Bolck et al., 2004).

The majority of initiatives to develop coherent networks of protected areas, also known as ecological networks, are happening at a regional or national level (Jongman and Pungetti, 2004). However, administrative barriers in regions and countries must be overcome to increase the efficiency of ecological networks, in such a way that territories across borders are managed with an eco-regional focus (Bennett and Mulongoy, 2006). In this sense, there are increasingly more transnational initiatives being developed and promoted (Bennett and Mulongoy, 2006; Leibenath et al., 2010; Worboys et al., 2010).

Roads are one of the main elements within the landscape matrix (non-habitat areas in the landscape) responsible for losses of connectivity (Coffin, 2007; Forman et al., 2003). This is especially

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the case for high-volume roads (Alexander et al., 2005; Clevenger and Wierzchowski, 2006). Therefore, spatial configuration of the main transportation networks should be considered a basic criterion to preserve landscape connectivity not only to prevent their impacts (Thorne et al., 2009; Vasas et al., 2009) but also to restore permeability in critical areas (Bruinderink et al., 2003; Clevenger et al., 2002; Clevenger and Wierzchowski, 2006; van der Grift and Pouwels, 2006).

Mammals are frequently used as focal species for the design of ecological networks because (1) they are particularly sensitive to the barrier effect caused by roads, which inhibits the movement of organisms between habitat patches situated at both sides of these linear transport infrastructures, and because (2) the areas and linkages that they require can be also used by multiple other species and ecological fluxes (Beier et al., 2008a, 2008b; Bruinderink et al., 2003; Gurrutxaga et al., 2010a).

The coherence of a protected area network depends on the characteristics and spatial configuration of the reserves and of the non-protected intermediate landscapes through which potential functional connections for the biota are established. Different modeling methods have been used in order to calculate the contribution of the elements to the connectivity of a system or network. The most widespread approaches are those based on the analysis of metapopulations, defined as groups of spatially separated but interacting populations of the same species (Figueira and Crowder, 2006; Ovaskainen and Hanski, 2001), and graph structures, which represent a landscape as a set of nodes (habitat areas) functionally connected to some degree by links that join pairs of nodes (Bodin and Norberg, 2007; Fall et al., 2007; Fu et al., 2010; Jordán et al., 2007; Lookingbill et al., 2010; Minor and Urban, 2008; Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010; Urban and Keitt, 2001; Vasas et al., 2009).

Among the graph-based approaches for analyzing landscape connectivity, recent studies have developed metrics, based on the habitat availability concept, that quantify the amount of habitat that is available (reachable) in the landscape for a particular species or ecological flow: the habitat area existing within the patches themselves is integrated with the area that can be reached through the connections with other habitat patches or nodes, therefore accounting both for intrapatch and interpatch connectivity (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007). These habitat availability metrics, such as the probability of connectivity (PC), present a set of desirable properties for evaluating and prioritizing the contribution of landscape elements to the maintenance of landscape connectivity (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007). Despite being quite recent, the PC metric has already been used in a variety of functional connectivity and landscape planning applications. Among the various graph modeling possibilities foreseen in the original PC definition as proposed by Saura and Pascual-Hortal (2007), these functional connectivity studies have characterized the connections between nodes through Euclidean (straight-line) distances (García-Feced et al., 2011; Mitsova et al., 2011; Neel, 2008; Perotto-Baldivieso et al., 2009; Saura and Pascual-Hortal, 2007), through effective or least-cost distances that take into account the variable permeability and heterogeneity of the landscape matrix (D'Alessandro et al., 2009a, 2009b; Fu et al., 2010; Saura et al., 2011; Watts and Handley, 2010), through individual-based dispersal simulation (Morzillo et al., 2011), or through simple adjacency relationships in the case of river segments and aquatic connectivity (Erös et al., 2011).

Saura and Rubio (2010) have described more in depth the ingredients of the PC metric, and how the node importance values derived from this metric can be partitioned in three separate fractions (*dPCintra*, *dPCflux* and *dPCconnector*) that quantify the different ways in which nodes can promote habitat connectivity and reachability in the landscape. *dPCintra* corresponds to the connected area existing within the node (intrapatch connectivity). *dPCflux* quantifies the amount of dispersal flux that is estimated to occur between a particular focal node and the rest of the habitat areas in the landscape when that focal node is the origin or destination of those fluxes. *dPCconnector* quantifies the contribution of a node (or link) to the connectivity between other nodes, as a connecting element or stepping stone between them. All the landscape planning applications of PC reported so far (see previous references) have not separately evaluated the different roles of habitat nodes in the habitat network as provided by these three fractions. Therefore, the actual contribution of each of these roles remained mixed and potentially confused in the overall assessment of the importance of landscape elements for connectivity reported in those studies. Although this may be correct and interesting in some cases, in some others it may be too coarse and not so well suited to understand the spatial interactions and dependencies in the landscape network. Depending on the purposes of a specific application, the analyses should be focused on several or only on one of these three fractions. In particular, *dPCconnector* needs to be evaluated separately in order to effectively assess the role of individual landscape elements as irreplaceable providers of connectivity between other habitat areas. Unlike *dPCintra* and *dPCflux*, the computation of this fraction is independent of the area or other attributes of the habitat nodes, and only takes into account the topological position of the focal node in the landscape network and the characteristics of the rest of the habitat areas that are being connected through that node, in accordance with the habitat availability approach (Saura and Rubio, 2010). This avoids the tendency of some indices or fractions of just assigning a higher connectivity value to the biggest nodes in the landscape that has been reported for some network configurations and dispersal distances (Ferrari et al., 2007; Saura and Rubio, 2010). Indeed, *dPCconnector* has been shown to provide quite unique, useful and non-redundant information when compared to other widespread connectivity metrics (Baranyi et al., 2011). Finally, the *dPCconnector* fraction can be calculated both for nodes and links in the network, and their values are measured in the same units and can be directly compared in an integrated analytical framework (Saura and Rubio, 2010). This provides additional insights compared to previous related studies, which have focused only on the connectivity importance of the habitat areas and have not treated with the same analytical detail the role of links as connectivity providers in the intermediate landscape.

The objectives of this research are (i) to show how the *dPCconnector* fraction of the PC index can be used to identify those landscape elements that most contribute to uphold connectivity, and specifically those whose loss cannot be compensated by other elements in the remnant habitat network; (ii) to evaluate the role of nodes and links as connectivity providers in the European network of protected areas, Natura 2000, for dispersal movements of forest mammals with different dispersal capacities between the Cantabrian Range, the Pyrenees, the French Massif Central and the Western Alps; (iii) to detect at which points the highway network (where a highway is defined as a paved road with at least four lanes and a median strip) intersects with the most important connectivity elements, with the purpose of prioritizing the areas where defragmentation and permeability restoration measures for the fauna could be implemented; (iv) to identify at which dispersal distances the nodes and links play a more prominent role to sustain the habitat connectivity and availability in the entire network. The study area has been chosen for its crucial role in the ecological coherence of Southwestern Europe, which comprises important biodiversity reservoirs in the aforementioned mountain ranges (Worboys et al., 2010). The preservation and restoration of connectivity in the area requires adequate territorial planning, especially in transition areas between mountain ranges (IUCN, 2005). The approach here demonstrated should also be applicable in a variety of other landscape planning applications at different scales, which is facilitated by the free and open source Conefor Sensinode software package (Saura and Torné, 2009; available at http://www.conefor.org/).

2. Data and methods

2.1. Study area and spatial data

The study area comprises the North of the Iberian Peninsula, the Southern half of France and the North West of Italy, yielding a total of 68 provinces, corresponding to the third level of Nomenclature of Territorial Units for Statistics (NUTS, http://ec.europa.eu/eurostat/ramon/nuts/home_regions_en.html), the official framework for statistical purposes in Europe (40 in France, 22 in Spain, 5 in Italy and 1 in Andorra). The area covers part of the Atlantic, Mediterranean, alpine (Pyrenees and Alps) and continental (central area of France) biogeographical regions (EEA, 2009a). From West to East, the main mountainous areas where forest habitat concentrates are the Cantabrian Range, the Iberian System, the Pyrenees, the French Massif Central and the Western Alps (Jongman et al., 2006) (Fig. 1).

Forested areas (Fig. 1) comprise 30.2% of the study area. The rest of the land use areas are crops (32.6% of total area), bushes (11.7%), meadows (9.6%), agroforestry mosaics (5.4%), pastures (5%), urban areas (2.9%), rocks (1.5%) and water bodies (1.1%) (EEA, 2009b). The highway network has a density of 0.0357 km/km^2 and is quite evenly distributed within the study area. There are exceptions, such as in the transition area between the Pyrenees and the Cantabrian Range and towards the Northeast of the alpine region where there is a larger concentration of roads; in addition there are no highways across the Pyrenees (Fig. 1).

The protected areas' information corresponded to a vector map of the European Union's Natura 2000 network (EEA, 2009c). The national cartographical services provided the highway network in vector format at a 1:200,000 scale. Land use information was obtained from the European Union's Corine Land Cover 2000 map in raster format with a pixel resolution of 250 m (EEA, 2009b). Provincial administrative area delimiters, NUTS-3, which were used to define the study area were obtained in vector format (EEA, 2002).

2.2. The habitat network model

Nodes in the network corresponded to the protected areas which contained forest, the focal habitat of the analysis. Two or more contiguous protected areas with forests were considered as a unique node. The portions of the nodes which were intersected by highways were divided into different nodes so as to adequately estimate the impact of the infrastructures. To allow for a feasible processing of the large study area here considered and to focus the analysis on those protected areas that were more relevant at this wide transnational scale, we selected as nodes only those reserves with an area of at least 5000 ha. A total of 176 nodes were obtained. This accounted for 91.4% of the total area within the transnational protected forest area network. The case study focused on the connectivity model of the Natura 2000 protected area network for a generic functional group of forest mammals. They are suitable focal species due to their sensitivity to the most important and recent fragmentation and homogenization dynamics in the European landscape, such as road construction, urbanization and agrarian intensification and abandonment (Jongman, 2002). Measuring the accessibility between nodes using Euclidean distance is not recommended for non-flying species because it is necessary to take into account the heterogeneity and friction effect of the landscape matrix (corresponding to the non-habitat areas that might need to be crossed in order to move between nodes). The resistance of the landscape matrix for the functional group of focal species was parameterized into a generic friction surface (Table 1) through bibliographical review (Beier et al., 2008a; Epps et al., 2007; Fu et al., 2010; Saura et al., 2011; Schadt et al., 2002; Shirk et al., 2010; Verbeylen et al., 2003) and consultation with five experts on mammal ecology. Lower levels of impedance were not assigned to highway pixels with potential crossings (viaducts, drainage systems, tunnels). Thus, the highways' impact on the actual distances is homogeneous and the links pass through optimum areas for the installation of road-crossing structures (Beier et al., 2008a). Several authors have highlighted the importance of an adequate raster representation of linear elements (such as highways) in these friction surfaces in order to avoid artificial discontinuities (breaks or cracks) that lead to an underestimation of their actual barrier effect and related effective distances (Adriaensen et al., 2003; Rothley, 2005). Here we avoided raster breaks in linear barriers by reinforcing the width of the highways as recommended in previous studies (Adriaensen et al., 2003). In order to assess the impact of highways

Table 1
Resistance values of the friction surface.

Land use	Resistance
Forests	1
Bushes	5
Agroforestry mosaics	15
Pastures	30
Meadows	40
Rocks	40
Crops	60
Water bodies	100
Urban areas and highways	1000

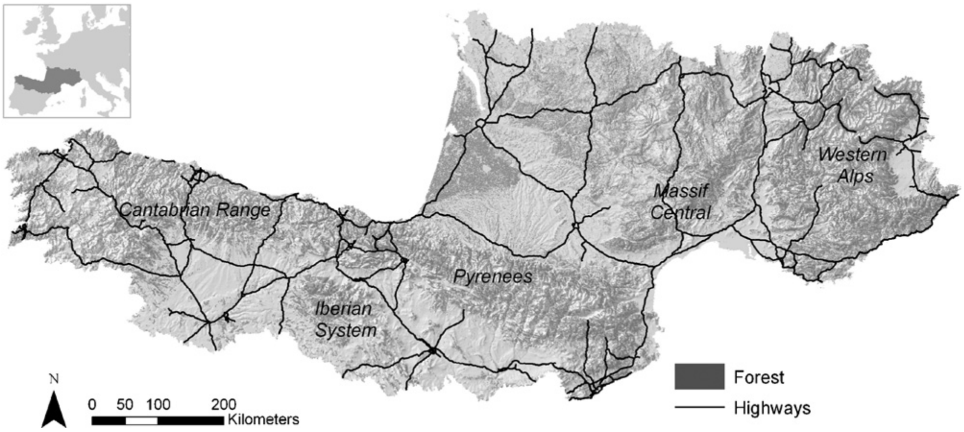

Fig. 1. Location of the study area and distribution of forested areas and highways within it.

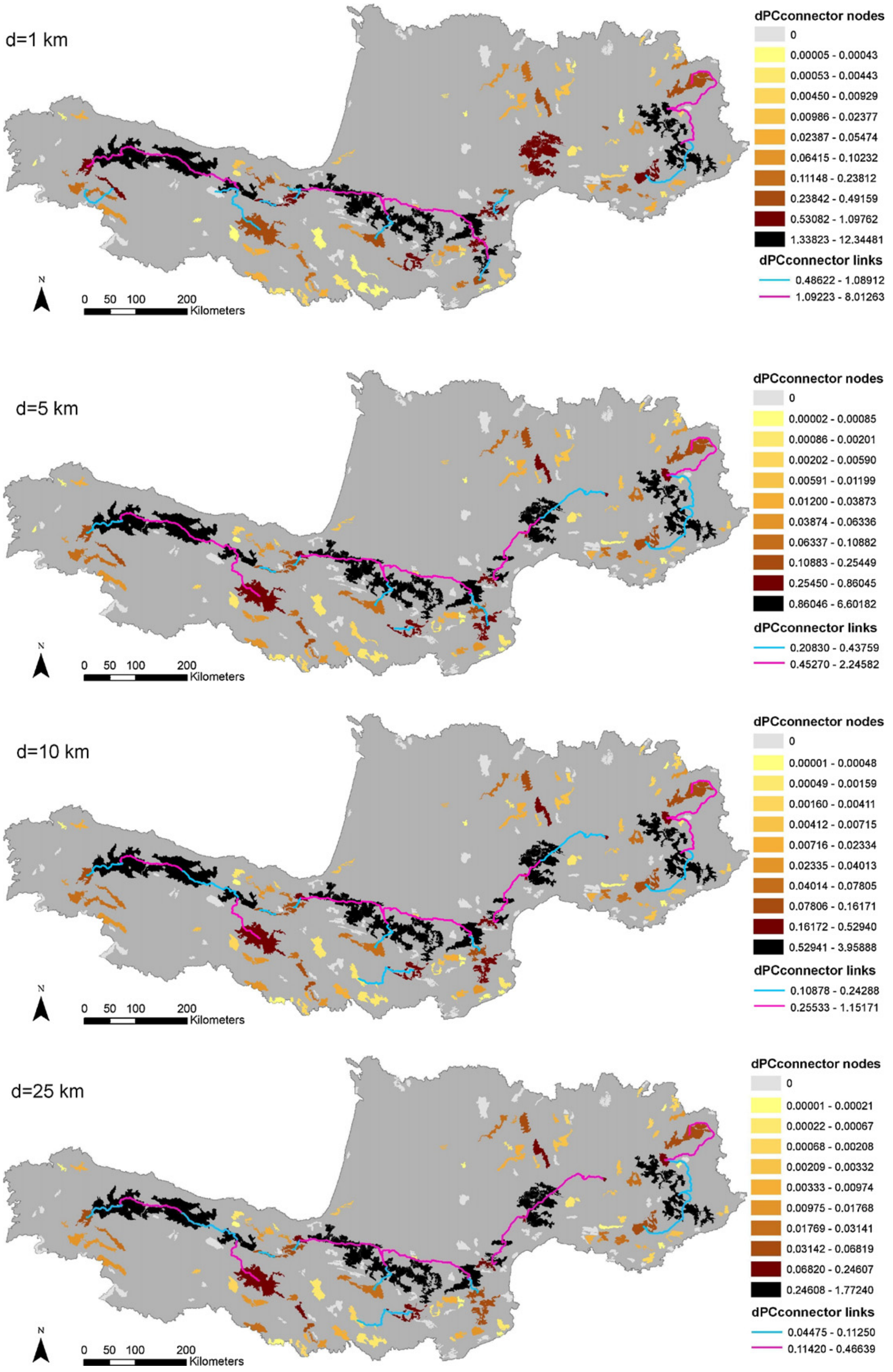

Fig. 2. Importance of nodes and links as connectivity providers (*dPCconnector*) in the scenarios without highways for different dispersal distances. Non-zero *dPCconnector* values for the nodes have been grouped into 10 classes, each one with an equal number of nodes. Nodes with *dPCconnector* = 0 are grouped in another class. The top 20 *dPCconnector* links are represented for each scenario, grouped into two classes with 10 links each.

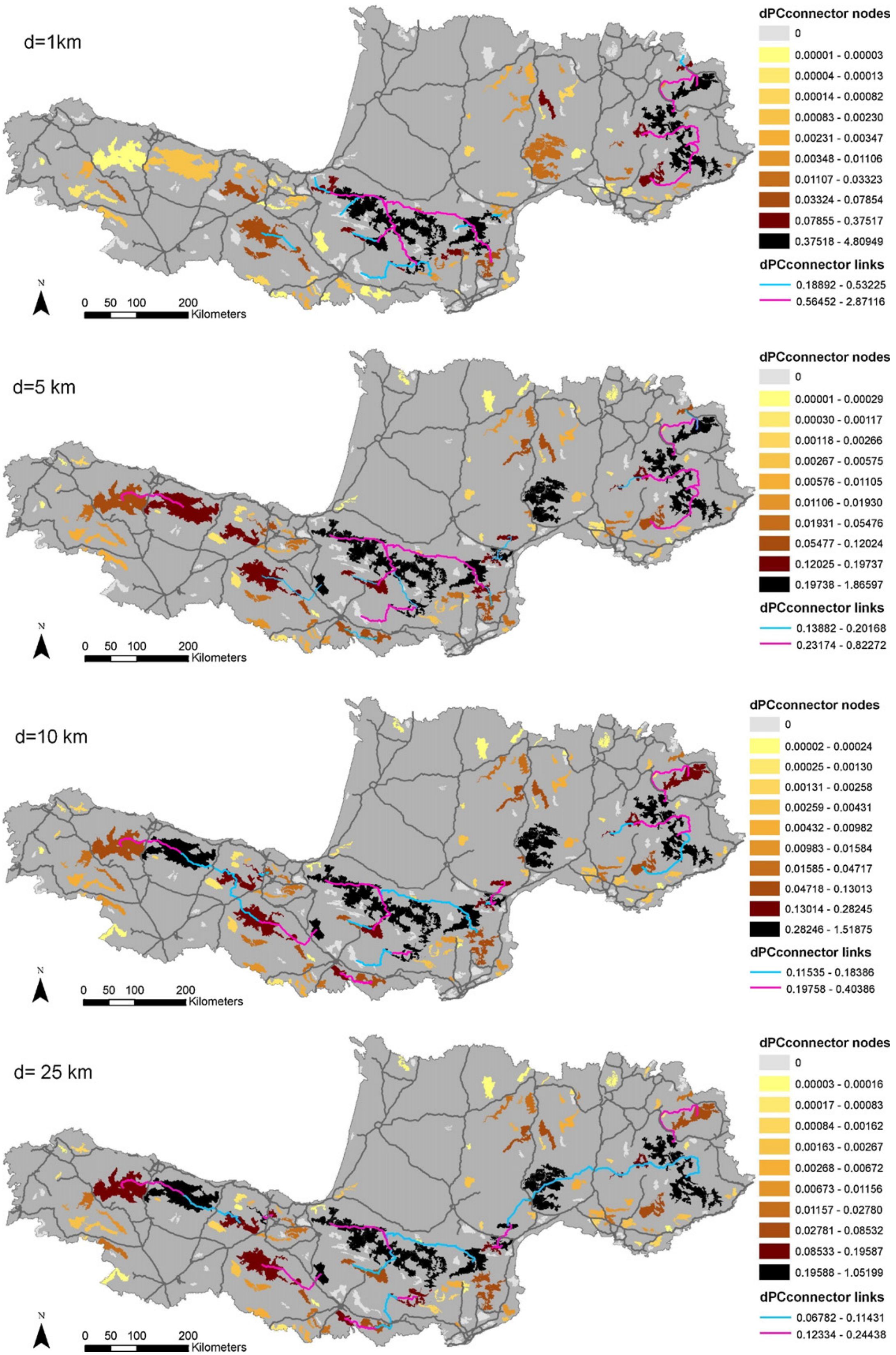

Fig. 3. Importance of nodes and links as connectivity providers (*dPCconnector*) in the scenarios with highways for different dispersal distances. Non-zero *dPCconnector* values for the nodes have been grouped into 10 classes, each one with an equal number of nodes. Nodes with *dPCconnector* = 0 are grouped in another class. The top 20 *dPCconnector* links are represented for each scenario, grouped into two classes with 10 links each.

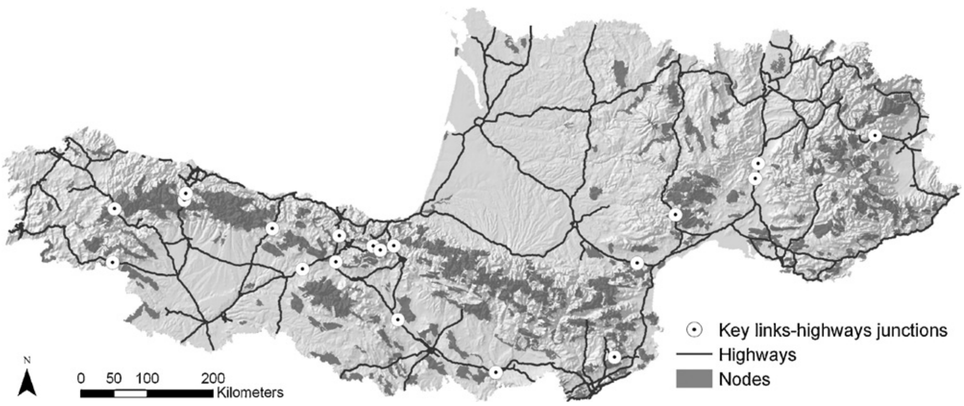

Fig. 4. Intersections between highways and key links (those 20 links with the highest *dPCconnector* in all the analyzed scenarios).

on network connectivity we built two resistance surfaces (with and without including the resistance values for highways) with a pixel size of 250 m and a total of 7,281,032 pixels covering the study area. The effective distances between each pair of nodes were calculated with Pathmatrix 1.1 (Ray, 2005) as the accumulated cost through the least cost paths throughout the friction surfaces (Adriaensen et al., 2003; Ray, 2005). Given the uncertainty that is usually associated to the friction values for different land cover types (Rayfield et al., 2010), we performed a sensitivity analysis in order to assess the robustness of our results to the friction value for highways (the least permeable element in which our study specifically focused). For this purpose, we used a highway friction value 50% below and above the 1000 value that finally resulted from expert knowledge and bibliographic research; that is, the least cost path calculations and subsequent analyses (see below) were also performed for two additional resistance surfaces with a friction value for highways of 500 and 1500 units (the rest as specified in Table 1).

The different species of mammals vary by degree of mobility (Bowman et al., 2002; Sutherland et al., 2000), and within each species the dispersal distance may vary due to changing characteristics such as population density (Matthysen, 2005) or the temporal scale used (Theobald, 2006). Thus, the connectivity analysis was carried out in the area of study (with and without highways) taking into account a wide range of median dispersal distances (d) representing medium to large mammals: $d = 1$ km, $d = 5$ km, $d = 10$ km and $d = 25$ km. Therefore, a total of eight landscape scenarios were analyzed (four without highways and four with highways). Given that the number of nodes (n) was 176, the number of links in the complete graph for each scenario was 15,400 ($(n^2 - n)/2$). The dispersal distance d in each scenario was multiplied by the median value of resistance in the friction surface, and the result determined the effective distance (accumulated cost) threshold corresponding to a 0.5 dispersal probability between nodes (p_{ij}) (Saura and Pascual-Hortal, 2007). Therefore the d values considered in subsequent analyses and results corresponded to the effective capacity of the species to move between protected areas expressed as an accumulated movement cost, i.e. after accounting for the variable permeability and heterogeneity of the landscape matrix. A particular species with a given d value will be able to move a larger geographical distance through permeable areas than through a matrix with abundance of highways or other land cover types with high friction values.

2.3. Identifying key connecting elements: the probability of connectivity index and the dPCconnector fraction

The probability of connectivity (PC) index has been described in detail in Saura and Pascual-Hortal (2007). PC is defined as the probability that two points (organisms) randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected), given a set of habitat areas and the links between them. This requires that both points fall into habitat areas and in addition that both points either fall (1) within the same habitat area or (2) into different but connected areas so that it is possible to move between them through the links in the network. For the computation of PC and its fractions, the links first need to be characterized through a probability of direct dispersal between two habitat areas i and j (p_{ij}), here calculated from a negative exponential function of the effective (minimum-cost) distance between protected areas (see above). From those p_{ij} values PC calculates the product probability of every possible path between i and j (where a path is a sequence of links in which no node is visited more than once). The path with the maximum product probability (p^*_{ij}) is considered as the best or more feasible one to conduct the movement of dispersing individuals from i to j through the landscape network. This takes into account that when dispersing from i to j a series of movements through other nodes may be more feasible than a direct movement between i and j without making use of any intermediate stepping stone or landscape element ($p^*_{ij} > p_{ij}$); see Saura and Pascual-Hortal (2007) and Saura and Rubio (2010) for further details. The importance of a particular protected area or link as a provider of connectivity between other protected areas is quantified through the *dPCconnector* fraction derived from the PC index (Saura and Rubio, 2010). A certain node or link will present a *dPCconnector* higher than zero only (1) when it is part of the best (maximum product probability) path used for dispersal between other nodes in the initial landscape and (2) when the alternative paths between the remnant patches that are available after losing that node or link cannot compensate for the connecting role played by that node or link in the intact landscape (Bodin and Saura, 2010; Saura and Rubio, 2010).

The value of *dPCconnector* was calculated for every node and link in our network models for the transnational study area. The calculations were performed for the different dispersal distances and before and after taking into account the impact of highways on the permeability of the intermediate landscape matrix (see previous section). The comparison of the *dPCconnector* values for individual nodes and links with and without the effect of highways allowed assessing those key landscape elements that might be affected to a larger extent by the impacts of the transportation networks. This assessment was complemented by overlapping the 20 links with the highest *dPCconnector* values with the highway network, identifying those intersection points where the measures for mitigating the barrier effects might need to be concentrated. In addition, to evaluate the potential impact of the uncertainties that may be associated to the highway friction value in the prioritization of nodes

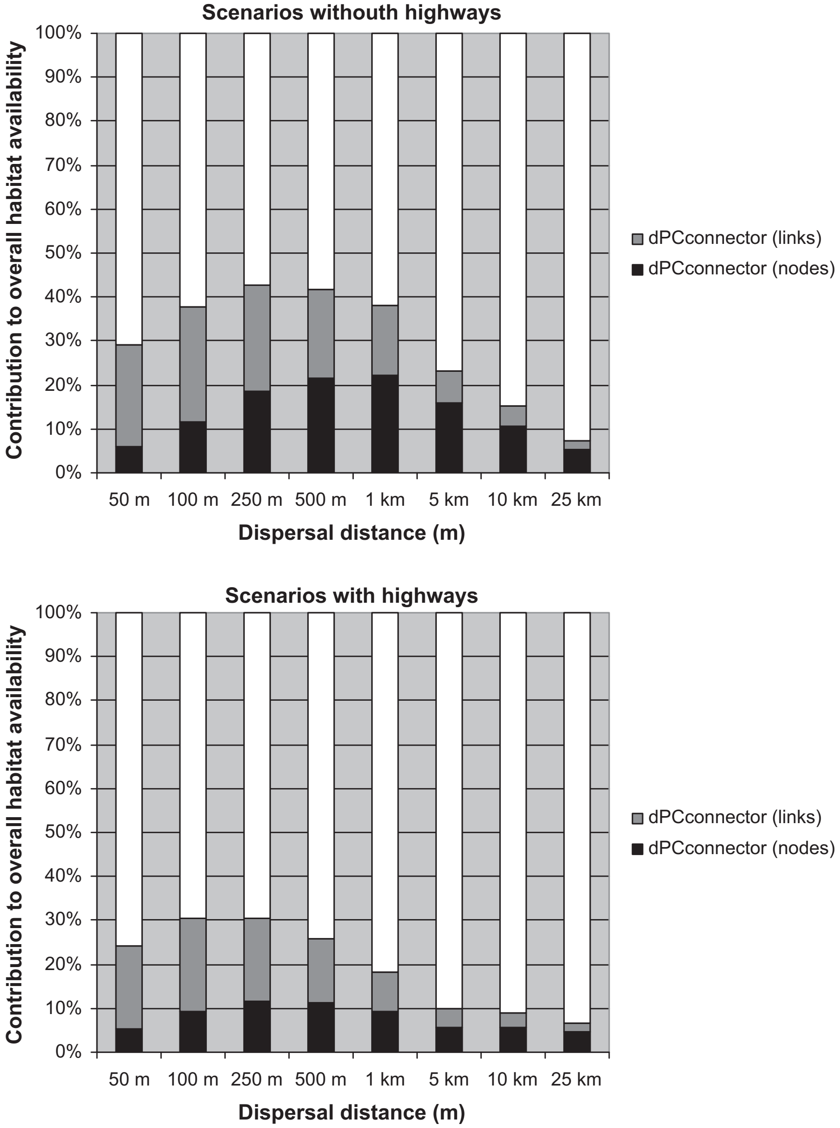

Fig. 5. Relative contribution of *dPCconnector* to the total importance of nodes and links for habitat availability and connectivity in the protected area network, as a function of the median dispersal distance.

and links as connectivity providers, we computed the Kendall's tau_b rank correlation coefficient between the *dPCconnector* values for every node and link resulting from a 1000 highway friction and the same *dPCconnector* values for a highway friction of 500 and 1500 units (this correlation was performed separately for nodes and links).

The relative contribution of the connecting elements (as measured by *dPCconnector*) to the overall habitat availability in a given network was calculated as the sum of the *dPCconnector* values for all nodes and links in the network divided by the sum of the *dPC* values for the same set of nodes and links (this ratio was multiplied by 100 to express it as a percentage), as in Saura and Rubio (2010). This contribution was also calculated for several other additional dispersal distances (500 m, 250 m, 100 m and 50 m) because the relative importance of *dPCconnector* can be particularly high for limited dispersal distances (Saura and Rubio, 2010).

All the calculations were performed through a new version (2.5) of the Conefor Sensinode software package (Saura and Torné, 2009), available at http://www.conefor.org/. All subsequent results related to the impact of highways refer to the resistance surface with the 1000 highway friction value unless otherwise explicitly stated.

3. Results

The contribution of individual elements to the transnational network connectivity depended on the dispersal distance and on whether the impact of highways was considered (Fig. 3) or not (Fig. 2). Larger dispersal distances (from $d = 1$ up to $d = 25$ km) caused a decrease in the *dPCconnector* values for nodes and links (Figs. 2 and 3). For a given dispersal distance, accounting for the effect of highways also reduced the *dPCconnector* values (Fig. 3). The prioritization of nodes and links as connectivity providers was considerably robust to changes in the highway friction value as high as 50% from the 1000 friction that was selected for the transnational case study. The tau_b rank correlation coefficient between the *dPCconnector* values in the network for a 1000 highway friction and those corresponding to 500 and 1500 units for the highway friction were respectively as high as 0.950 and 0.923 for links and 0.853 and 1.000 for nodes. Therefore the identified intersections between the key links and the highway network were equally robust to these changes in the highway friction value as assessed in the sensitivity analysis. These intersections were concentrated mainly in the transition areas between mountain ranges, as shown in Fig. 4.

In the scenario with a dispersal capacity of 1 km and highways (Fig. 3), the Pyrenees and the Alps maintained their important role as connectors between protected areas in comparison with the scenarios without highways (Fig. 2), due to the fact that they were not fragmented by infrastructures. However, the Cantabrian Range, the transition area between the Cantabrian and the Pyrenees and the French Massif Central suffered a remarkable loss of their connecting role between the nearby nodes when the roads were considered (Fig. 3). The loss of connectivity in the protected areas of the transition areas between the Cantabrian and the Pyrenees and their links was particularly striking (Fig. 3). A high density of highways caused a considerable isolation of their protected areas, which in the absence of roads would have been estimated to be important connectivity providers by acting as stepping stones between other nodes. The latter also occurred, although to a lesser extent, in the scenarios with highways and a larger dispersal capability ($d = 5$, 10 and 25 km) (Fig. 3).

In the scenario corresponding to $d = 5$ km and without highways the axes of the Cantabrian Range/Iberian System and the Cantabrian Range/Pyrenees/Massif Central were highlighted as constituting an important ecological continuum (Fig. 2). The protected areas of the Western Alps, being relatively more distant than the Massif Central, form a unit which is functionally less linked to that continuum. When highways were considered for $d = 5$ km, the links between the main ranges lost some of their importance (Fig. 3). The key links for functional connectivity were limited to the area around the Pyrenees and the Alps. Due to a loss of connectivity in several other potential corridors, the links between the Iberian System and the protected areas located in its Southeastern region acquired a higher importance when the roads were considered. A similar effect was observed in nodes located in the Southeast of the study area.

The scenario for $d = 10$ km showed similar qualitative results that for $d = 5$ km (Fig. 2). However, there was a lower dependency on the link between the Western Cantabrian Range and the key node located to the East (Fig. 2), as a result of the larger dispersal capabilities. For the same reason, the impact of the infrastructures was lower for $d = 10$ km than for $d = 5$ km, particularly for the link between the Cantabrian Range and the Iberian System (Fig. 3). In $d = 25$ km with highways, the link between the Cantabrian Range and the Iberian System was not among the most important due to the increase in dispersal capability. However, the importance in connectivity between the transition area of the Pyrenees/Massif Central and the Western Alps increased for $d = 25$ km (Fig. 3). Thus, for a dispersal distance of 25 km with highways, the connector between the Pyrenees and Alps was more critical for the connectivity of the ecological network than the one between the Cantabrian Range and the Iberian System (Fig. 3).

On the other hand, the contribution of the $\Sigma dPCconnector$ of nodes and links to the total availability of habitat was greater in scenarios without highways than in those which accounted for their effect (Fig. 5). The threshold distance at which the *dPCconnector* contribution was greatest was 250 m for the scenarios without highways and 100 m for those with highways (Fig. 5).

4. Discussion and conclusions

The identification of key nodes and links providing connectivity in a network of protected areas such as the one studied here represents a significant contribution to decision making in territorial planning, allowing to incorporate spatially explicit preventive measures in the environmental assessment of plans and projects (Bennett, 2004). The results here obtained are usable for the application of Directive 92/43/EEC, which, within the framework of the European Union, regulates the development of the network of protected areas Natura 2000. In this sense, the Directive, in article 10, urges that all the elements of the landscape which are essential to guarantee the ecological coherence of the network should be properly managed, a requirement which is basic to its effectiveness (Kettunen et al., 2007).

The key links identified in this study confirm the location where other authors had situated, through expert-based approaches, the connecting zones between the great habitat nuclei within the mountain ranges in this study area (Jongman et al., 2006; Worboys et al., 2010). These previous studies had focused on the identification of the most relevant areas in the design of a coherent ecological network, by analyzing the distribution of the different habitats and land uses within the landscape. Our results, however, rely on a quantitative methodology and additionally highlight the importance of considering the link between the Cantabrian Range and the Iberian System, which had not previously been included in the framework of the transnational initiative of the Cantabric-Alps great mountain corridor (Worboys et al., 2010). Neither had it been included as a "search area for corridors" in the indicative map of the Pan-European ecological network for Western Europe (Jongman et al., 2006). This Cantabric-Iberian link, although apparently more distant than a more direct physical *E–W* axis, acts as a facilitator of fluxes between the Cantabrian Range and the Pyrenees (and beyond) due to the lower density of highways compared to other potential areas for target species movements. Around the identified key links an adequate urban planning is required, avoiding urban sprawl and the conversion of remaining natural or seminatural areas along the valley bottoms. Besides, it is necessary to integrate the existing urban nuclei into the landscape matrix with the design and implementation of green belts.

Our results show how important it is to ensure the permeability of the large infrastructures which communicate or cross the principal mountain ranges if the connectivity of the Natura 2000 network is to be maintained. The identification of junction sectors between the key links and the highway network (Fig. 4) allows us to point out areas in which it is critical to diagnose (with further analysis and field observations at finer scales) the permeability of the roadways (Clevenger and Wierzchowski, 2006). These junctions should contain a sufficient density of adequate crossings for fauna (Gurrutxaga et al., 2010b). Particularly for those highways that were constructed years ago with little consideration to their permeability for ecological fluxes, corrective defragmentation measures should be prioritized and implemented (Iuell et al., 2003; van der Grift and Pouwels, 2006). The number of key link-highway junctions detected in the Cantabrian–Pyrenean transition area is considerable, and agrees with previous studies carried out on this area at more detailed scales (Gurrutxaga et al., 2010a).

This acquires even greater importance when we take into account the distribution of the large future infrastructures which have been planned for the coming years. Depending on their design, high speed railway axes may have a similar fragmentation effect to that of highways, especially in stretches running over the surface, where they are bounded by fences. Several Trans-European transport network priority projects (European Commission, 2005) also cross the study area. The construction of these transport corridors is ongoing at the time of writing, though the commencement of certain stretches has been planned for the coming years (European Commission, 2010). As part of the high speed railway axis of southwest Europe, the Atlantic branch is to cross the key links between the Cantabrian Range and the Pyrenees and between the Cantabrian Range and the Iberian System. The Mediterranean branch will cross the key link between the Massif Central and the western Alps, as well as the central area of the Iberian system. Within the high speed rail interoperability in the Iberian Peninsula, it is planned that the North/Northwest corridor will cross the Cantabrian Range at three different places in addition to the already existing highway network. The railway axis project from Lyon to the Ukrainian border will cross the southwestern Alps from east to west. Stretches which cross the high areas of the Cantabrian Range, the Pyrenees and the Alps include the construction of long-distance tunnels, which will diminish their adverse effect on connectivity as compared with the effect at lower altitudes.

It should be noted however that not all the species and ecological processes are affected in the same way and depend to the same degree on the key connecting elements that have been identified here. In particular, for species with large dispersal abilities, the *dPCconnector* contribution to overall habitat availability decreases, with the minimum found for the largest considered distance of 25 km (Fig. 5). These vagile species are able to reach other protected areas with little constraints and without being largely affected by the connectivity bottlenecks that may be identified in the study area. On the other hand, species with large mobility limitations will not be particularly benefited by the presence of these connecting elements (or the efforts invested in their creation or restoration), since they are ultimately restricted to the habitat areas where they dwell and their persistence would be better promoted by focusing in the amount and quality of habitat inside the nodes (Hodgson et al., 2009; Saura and Rubio, 2010). This is indicated by the lower *dPCconnector* values for the shortest dispersal distances, particularly for nodes (Fig. 5). In between these two extremes, species with intermediate dispersal abilities of about 1 km or lower where here found to be those more dependent on the spatial configuration of the nodes (protected areas) in the reserve network and on the permeabilization measures in the intermediate landscape matrix. Indeed, the focus on connecting elements here adopted should not be viewed as the only management alternative in order to ensure species viability in the study area. In particular, other well established measures such as maintaining or improving the amount and quality of habitat within each protected area (Hodgson et al., 2009) can make a large contribution to the conservation of multiple species, as can be accounted for by the other two fractions of the PC metric (Saura and Rubio, 2010).

We acknowledge the limitations in our study regarding the ecology of specific species. In addition, the outline of protected areas gives no account of the variability of the forest habitat and protected areas are assumed to be homogeneous entities. For instance, Corine land cover data make no distinction between natural forests and forest plantations, nor does it contain data on the quality of habitats, even when it is the most detailed and consistent source of information regarding land use throughout all the study area. Finally, the friction surface was determined through bibliographic sources and consultation with experts, but no empirical data were considered regarding animal mobility, genetic distance, absence/presence or density of populations (Beier et al., 2008a). However, our results on the key nodes and links in this transnational network seemed to be considerably robust to changes in the friction values assigned to highways, at least within the range of a 50% variation as evaluated in our sensitivity analysis. Further guidelines on the impact of different friction values in the results of the least cost path approach and related sensitivity analysis are provided by Rayfield et al. (2010). In any case, least cost paths have been here taken as the network links and effective distances between nodes have been calculated as minimum cost distances. This approach underestimates, to a certain degree, the connectivity of the total landscape, given that there are other alternative links with relatively low cumulative resistances that could also contribute to dispersal and ecological fluxes (McRae et al., 2008; Pinto and Keitt, 2009; Theobald, 2006). The analysis we have carried out should also be complemented with studies focusing on species that are associated to other habitats such as grasslands, mountain pastures, aquatic or rocky areas, and that could be considerably impacted by the fragmentation of their networks. However, we believe that our eco-regional focus, taking protected areas and landscape structure as the starting point, is highly complementary with studies of connectivity based on specific species (Fischer and Lindenmayer, 2007). In addition, the methodological approach here presented could be easily applied and refined in other studies of connectivity at different spatial and temporal scales, taking into account most of the limitations and considerations outlined above, as well as other land use and climate change scenarios. For instance, in the study of specific species, the incorporation of empirically obtained data (such as displacement routes, dispersal capacity, habitat use, home range size, genetic differentiation, etc.) could be easily integrated in the same type of analysis.

We believe that the *dPCconnector* fraction, as one of the important ingredients of the PC index (Saura and Rubio, 2010), makes a significant contribution to the detection of key connecting areas, not necessarily extensive, and key ecological corridors in the landscape networks with a quantitative basis. Its value and potential for territorial and species conservation planning and for the design of networks of protected areas is supported by the following characteristics: (1) it is based on a solid methodological background as developed in recent studies on the measurement of habitat availability (reachability) and connectivity at wide landscape scales, (2) the *dPCconnector* value of a particular habitat site is independent of its area but takes into account the ecological characteristics of the rest of the protected areas in the ecological network, (3) it takes into consideration the adequacy and availability of alternative movement paths and the degree to which a particular landscape element is irreplaceable as a connectivity provider (Bodin and Saura, 2010) and (4) the approach here demonstrated is available for any other case study or planning application by being implemented in a freeware and open source package (Conefor Sensinode).

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