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Key structural forest connectors can be identified by combining landscape spatial pattern and network analyses

Santiago Saura [a,*], Peter Vogt [b], Javier Velázquez [c], Ana Hernando [a], Rosario Tejera [a]

[a] Department of Forest Management and Economics, ETSI Montes, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040 Madrid, Spain
[b] Joint Research Centre of the European Commission, Institute for Environment and Sustainability, Land Management and Natural Hazards Unit, T.P. 261, Via E. Fermi, 2749, I-21027 Ispra (VA), Italy
[c] Department of Projects and Rural Planning, ETSI Montes, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040 Madrid, Spain

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ABSTRACT

Conservation and enhancement of ecological connectivity is widely recognized as one of the key objectives of forest landscape management. However, practical difficulties still exist due to the lack of pragmatic and operational methodologies that can be efficiently applied for these purposes within the scope of a forest management plan. Here we present the novel integration of two recent approaches for analyzing forest structural connectivity that offers considerable synergies and potential relevant benefits for forest planning at a variety of scales. We combine the morphological analysis of forest spatial patterns with recent indices for the analysis of landscape network connectivity based on the concept of measuring habitat availability (reachability) at the landscape scale. The combination of these approaches in a single integrated workflow embraces from (1) the diagnosis and characterization at the pixel level of the forest spatial patterns and their individual constituents, which are mainly the core habitat areas and the structural connectors (bridges) between them, to (2) the assessment of their individual importance to uphold ecological fluxes as irreplaceable providers of structural connectivity. We present and show different analytical possibilities within the integrated workflow from where the manager can choose depending on the planning targets and on the characteristics of the ecological processes of interest. We illustrate the application of the combined approach in two forested areas in Central Spain with different scales and management contexts, in which the structural connectivity between forest habitat areas needs to be sustained. Our assessment was able to discriminate and highlight a concise subset of cores and bridges that concentrated most of the contribution to the overall connectivity and functioning of the forest habitat network. This provides clear guidelines on where the conservation management efforts should be targeted, allowing for many alternative areas where the rest of the management objectives and activities can be accommodated as required by the multifunctionality of forest resources. The proposed integrated approach can equally serve to identify (a) those forest areas that play a crucial role to sustain ecological fluxes that are to be promoted by management, such as the dispersal of native biota or (b) those sites where the spread of wildfires or invasive species can be halted more effectively. The potential of the proposed methodology to inform and guide forestry decisions is reinforced by the availability of the required analytical tools (Guidos and Conefor Sensinode) as freeware software packages.

1. Introduction

Forest management is nowadays required to focus on the integrity and diversity of forest ecosystems and on the variety of environmental services they provide. A management plan is no longer considered successful if it only achieves the desired targets in one or a few forest functions, such as the productive values that for many decades dominated the design and implementation of management plans. At the same time, the shift from the traditional stand scale as the management unit to the wider landscape scale is being increasingly demanded and adopted by forest managers (e.g. Lafortezza et al., 2008). The focus is now on the spatial and temporal interactions between the different forest stands and tracts, rather than just on their individual (local) characteristics as if they could be considered as isolated resources and pieces of land.

Within this context, the need for conserving or promoting forest landscape connectivity is gaining increased acceptance as a key management objective due to its capacity to sustain many relevant

* Corresponding author. Tel.: +34 913367122; fax: +34 915439557.
E-mail addresses: santiago.saura@upm.es (S. Saura), peter.vogt@jrc.ec.europa.eu (P. Vogt), javier.velazquez@upm.es (J. Velázquez), ana.hernando@upm.es (A. Hernando), rosario.tejera@upm.es (R. Tejera).

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ecological fluxes and interactions in forest ecosystems (Forman, 1995; Crooks and Sanjayan, 2006; Bailey, 2007). Species dispersal, pollination, and genetic interchanges are some examples of key processes that are dependent on the degree of connectivity in the forest landscape (e.g. Bailey, 2007; Rosenvald and Lõhmus, 2008; Wang et al., 2010). In addition, maintaining or increasing landscape connectivity may be one of the best strategies to mitigate the potentially harmful effects of forest habitat fragmentation and climate change. However, in other cases an excessive connectivity may promote the spread of pests, diseases or wildfires; therefore managers are also interested in ways to halt or reduce the expansion of these undesired processes in what refers to the spatial pattern and configuration of forests within the landscape.

While these trends and needs are widely recognized and supported from many international and regional initiatives and regulations, considerable practical difficulties still exist because the methods for accounting for some of these ecosystem or landscape characteristics (e.g. connectivity) are not yet well established or even not really developed in such a way that can be operationally applied by forest managers. In addition, concerns on the quality and scarcity of the data needed to characterize and model some of these spatially and temporally complex processes introduce uncertainty on whether they can be really accounted for effectively in a particular management plan (e.g. Hodgson et al., 2009), given the usually limited resources that can be allocated for its development. Within the context of landscape connectivity, management decisions are complicated by the fact that connectivity is functional and species-specific; that is, the degree to which a landscape is perceived as connected or not depends on the species that makes use of the existing habitats and even varies within the same species depending on the sex, age and stage of development of the dispersing individuals, on population density and on the temporal scale of the movements being considered, among other factors (e.g. Dubois et al., 1994; Matthysen, 2005). Managers are usually overwhelmed by this multiplicity and variability of functional perceptions and responses among the numerous species dwelling in a particular forest landscape; in some cases this may even induce them to not take into account any connectivity consideration in their final forest plans. Therefore, an alternative for operational forest planning is focusing on enhancing or maintaining structural connectivity, as a simplified approach that only considers the spatial arrangement of forest habitats without explicit consideration of species-specific traits. This does not mean that the variable dispersal abilities of the different species through the landscape matrix are neglected, but rather that it is assumed that ensuring the physical continuity of the habitat will guarantee connectivity for the less mobile and more fragmentation-sensitive species, and by proxy also for the rest of the species with greater dispersal abilities. While a structural connection does not imply a functional connection (Tischendorf and Fahrig, 2000), different types of dispersers indeed require a structural corridor or are benefited by it (King and With, 2002). In addition, the planning guidelines derived from such structural connectivity approach may also be easier to link to forest and landscape units (e.g. corridors) that can be physically identified in the landscape (in which the management decisions are in fact implemented) and more simply communicated to stakeholders, policy-makers and to the society in general.

We here present the novel integration of two recent approaches for analyzing the connectivity of forest habitat mosaics that offers considerable synergies and potential relevant benefits for forest planning at a variety of scales, contributing to address some of the concerns and limitations that forest managers face when intending to identify key structural connecting elements. These two approaches are (1) the morphological spatial pattern analysis (MSPA) of forest habitats (Vogt et al., 2007a,b; Soille and Vogt, 2009) and (2) recently developed indices for the analysis of landscape network connectivity based on the concept of measuring habitat availability (reachability) at the landscape scale, such as the integral index of connectivity (IIC) and the probability of connectivity (PC) (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010). MSPA allows classifying the forest landscape at the pixel level and the automated mapping of structural corridors (connecting elements) and other spatial pattern categories, with a feasible processing even at continental scales. MSPA has been used in different parts of the world including the analysis of forest landscape patterns and their changes by the European Commission (http://forest.jrc.ec.europa.eu/forest-pattern, http://forest.jrc.ec.europa.eu/download/data) and the United States Department of Agriculture Forest Service (http://forestthreats.org/tools/landcover-maps/mspa). The IIC and PC indices have been developed and are particularly suited to evaluate the contribution of each node (habitat patch) and link (corridor) to the maintenance of network connectivity; that is, they adequately quantify the impact that the removal of a particular forest patch or corridor would have in terms of forest landscape connectivity, as it may result from land use changes or management decisions. IIC and PC have been so far used in a wide array of applications related to connectivity in different parts of the world (see http://www.conefor.org/applications.html).

We illustrate the combined approach by applying it in two forested areas in Central Spain with different scales and management contexts, from the strategic planning of an entire province comprising almost 7000 km^2 to a management plan for an individual forest land of a few hundred hectares. We present and show the different analytical possibilities within the integrated workflow depending on the characteristics of the ecological fluxes of interest and the management targets and discuss the relevance of such an approach and its variants to inform forest planning. The potential of the proposed methodology to guide forestry decisions is reinforced by the availability of the required analytical tools as freeware software packages, Guidos and Conefor Sensinode, which can be downloaded from http://forest.jrc.ec.europa.eu/download/software/guidos and http://www.conefor.org, respectively.

2. Methods

2.1. Morphological analysis of forest spatial patterns

Morphological spatial pattern analysis (MSPA) can be used to segment a raster forest binary map (i.e. forest vs. non-forest areas) into different and mutually exclusive landscape pattern categories (Soille and Vogt, 2009). It allows an automated per pixel classification and description of the geometry, pattern, and connectivity of the forest landscape. This improves the pattern analysis from previous approaches, based on standard landscape configuration metrics that just provide an overall statistic over the entire study area without further indicating at which locations the different types of pattern and fragmentation occur. Moreover, it reliably detects connecting structures, a key feature for the quantification of the importance of the individual forest map elements in a network analysis. The seven basic forest pattern classes provided by MSPA are the following (Soille and Vogt, 2009), with a single edge width parameter (s) governing the entire classification process (Fig. 1):

- *Core*: core pixels are defined as those forest pixels whose distance to the non-forested areas is greater than the given edge width. Cores will be hereafter considered as the focal habitat area for subsequent analysis. All other forest pixels not corresponding to the core (habitat) areas are assigned to one of the six following remaining pattern classes.

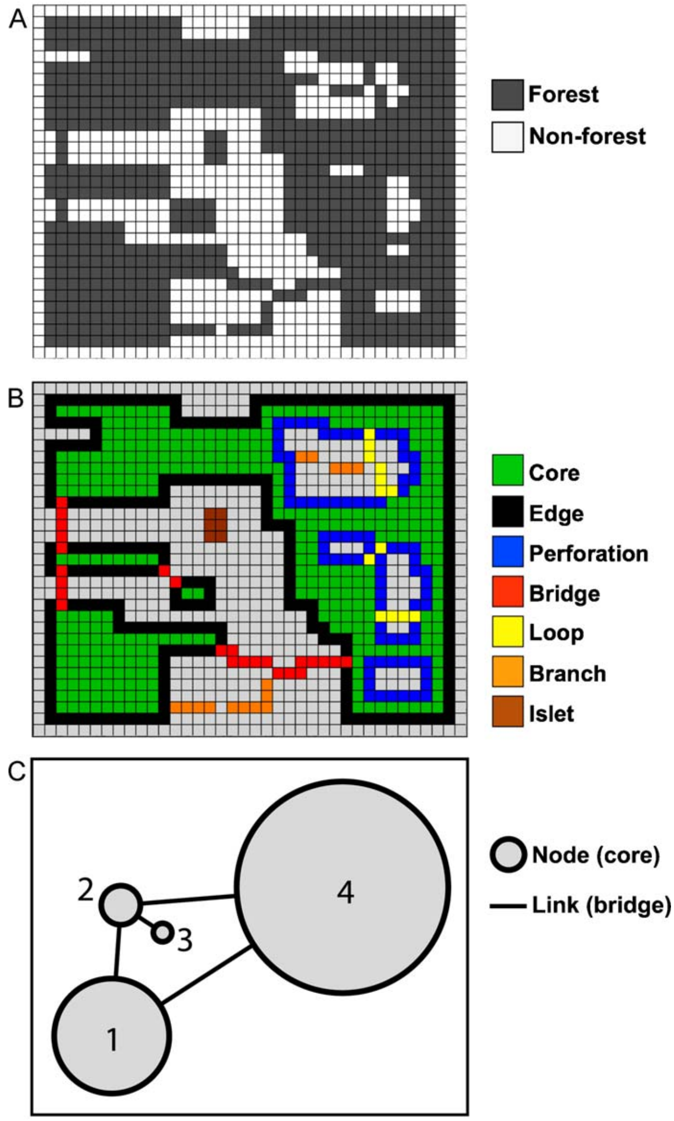

Fig. 1. A simple example to illustrate the process of the proposed forest structural connectivity analysis, from the forest map depicting the distribution of forest areas (A) to the MSPA classes resulting for an edge width of one pixel (B) and the graph representing the structural network as a set of nodes and links (C). The size of the four nodes in (C) is proportional to the amount of core area (attribute) in each node, and their numbers refer to each of the four MSPA identified cores. All the bridges are here assumed to be able to conduct movement between the cores at their ends independently of their length (l), as related to the IIC-steps and PC-infinite scenarios (see Section 2). In this example, only core 2 and bridge 2–3 play a key role as irreplaceable connectivity providers (connector >0) according to the PC-infinite scenario, while in the IIC-steps scenario, in addition to those elements, the other three bridges (1–2, 1–4 and 2–4) also have an important contribution through a positive value of the connector fraction.

- *Islet*: isolated forest patches that are too small to contain core pixels.
- *Bridge*: sets of contiguous non-core forest pixels that connect at least two different core areas at their ends. They correspond to structural connectors or corridors that link different forest core habitat areas. Therefore bridges make reachable a higher amount of habitat for those organisms that dwell in any of the two linked cores and that can effectively disperse through these corridors.
- *Loop*: similar to bridges but with the ends of the element connecting to different parts of the same core area. Therefore their presence does not increase the amount of core habitat that can be reached by a particular organism.
- *Edge*: a set of forest pixels whose distance to the patch edge is lower than or equal to the given edge width and corresponds to the outer boundary of a core area.
- *Perforation*: similar to edge but corresponding to the inner boundary of a core area.
- *Branch*: pixels that do not correspond to any of the previous six categories are classified as branch pixels. They typically correspond to elongated sets of contiguous forest pixels that emanate from a forest area and that do not reach any other forest area at the other end.

The MSPA classification can be conducted with a 4- or 8-neighbourhood rule. In our study we apply the default 8-neighbourhood rule, i.e. two pixels of the same class belong to the same landscape element if they share either one of their sides or vertices.

2.2. Connecting elements in the forest landscape network: the connector fraction of the habitat availability (reachability) metrics

From the seven pattern classes provided by MSPA only two of them (cores and bridges) can provide some contribution to the connectivity between the forest habitat areas in the landscape (Fig. 1). The loss of either of these elements can have deleterious effects on forest connectivity, either by affecting (a) structural corridors (bridges) that link two or more core areas or (b) core habitat areas that themselves act as stepping stones between other forest habitat patches that would be otherwise disconnected by the lack of physical continuity of the forest in the landscape in between those patches. The rest of the MSPA classes correspond by definition to elements that are either fully isolated (islets) or that do not allow reaching a new core habitat area different from that from where the potential movement can originate (loops, edges, perforations, branches).

Therefore, the core and bridge classes resulting from the MSPA can be used to build a graph in which cores correspond to the nodes and bridges to the links between those nodes (Fig. 1). This MSPA-based graph allows evaluating how important each of the individual landscape elements is for maintaining structural connectivity in the forest landscape. This can be adequately assessed through metrics of habitat availability (reachability) at the landscape scale, such as IIC and PC. These metrics are based on considering a habitat patch itself (here core area) as a space where connectivity exists (with more connected area the bigger the patch is) and on integrating the connected area existing within the patches (intrapatch connectivity) with the area made available by (reachable through) the connections (here bridges) with other habitat patches in the landscape (interpatch connectivity) (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010). The main difference between IIC and PC is that the first metric is based on a binary connection model (unweighted graphs), where two particular patches are either directly connected or not (there is no intermediate modulation of the strength, quality or frequency of use of that connection), while PC relies on a more detailed probabilistic connection model (weighted graphs) where a certain probability of direct dispersal (p_{ij}) characterizes the links between nodes i and j in the graph. The overall degree of connectivity of a forest landscape can be evaluated through the IIC or PC values or through the related Equivalent Connected Area (ECA) index. ECA is defined as the size that a single forest habitat patch (maximally connected) should have in order to provide the same value of IIC or PC than the actual forest habitat pattern in the landscape (Saura et al., 2011). ECA is simply calculated as the square root of the numerator of IIC or PC. ECA is in general preferable to IIC or PC as a summary of overall connectivity because it has area units, it is easier to interpret and has a more usable range of variation (Saura et al., 2011). The importance of a particular core area or bridge for the maintenance of forest structural connectivity can be quantified as the relative decrease (%) in the overall connectivity index value caused by the removal of that element from the landscape (dIIC or dPC, depending on the selected metric). As shown by Saura and Rubio (2010) the dIIC or dPC importance values for each landscape element can be partitioned into three fractions that quantify the different ways in which that landscape can contribute to habitat connectivity and availability in the landscape:

$$dIIC = dIICintra + dIICflux + dIICconnector$$

$$dPC = dPCintra + dPCflux + dPCconnector$$

The intra fraction corresponds to the amount of connected area within the patch (intrapatch connectivity) and the flux fraction estimates the potential amount of dispersal flux expected to depart or to arrive to a particular habitat patch (i.e. it measures how well connected is a particular habitat patch to the rest of the habitat areas in the landscape). In this study we will hereafter focus on the connector fraction, which quantifies the degree to which a particular landscape element acts as a connecting element or stepping stone between other forest habitat areas in the landscape (Saura and Rubio, 2010). The computation of the connector fraction for a particular element is independent of the area or other attributes of that element; it only takes into account its topological position in the landscape network and the characteristics of the rest of the forest habitat areas that are being connected through that element, in accordance with the habitat availability concept (Saura and Rubio, 2010). This avoids the tendency of some indices or fractions of just assigning a higher connectivity value to the biggest habitat patches in the landscape, as has been reported for some network configurations and dispersal distances (Ferrari et al., 2007; Saura and Rubio, 2010). While habitat patches (here core areas) can contribute to the total dIIC or dPC through any of these three fractions, the structural corridors (here bridges) can only uphold habitat connectivity and availability through the connector fraction. dIICconnector or dPCconnector measure in the same way and with the same units the value of habitat patches and linkages (cores and bridges) as connectivity providers, which can be directly compared within an integrated analytical framework (Saura and Rubio, 2010).

2.3. Building a graph from the MSPA results and analyzing network connectivity: four variants with a common analytical background

We used two different network models of the forest landscape, unweighted and weighted graphs, as related respectively to the IIC and PC metrics and particular cases of them. From these models we evaluated connectivity according to four different scenarios regarding the movement abilities and dispersal behavior of the analyzed focal species or ecological processes and related assumptions. In all the cases, the total amount of core area in each node was used as the attribute of the nodes when computing the overall indices values and the corresponding connector fraction. In all the cases, the species movements or ecological flows were only considered possible to occur through forest areas. Therefore we focused our analyses on a structural connectivity perspective and the physical continuity of the forest areas. The four different scenarios were the following:

(1) *IIC-distance*: Unweighted forest network with movement through bridges limited by distance and the importance of individual elements quantified through dIICconnector. In this case, the focal species or ecological flows are considered only able to move a certain distance d outside the core areas through existing bridges. That is, if the length l that needs to be traversed to get directly from core i to core j (without passing by any other core area) through a particular bridge k (that contacts at its ends with i and j) is larger than d, then that structural corridor k will not be effective at conducting organisms or flows from i to j (although those flows might be possible through other pathways not involving k but passing through other intermediate bridges or core areas different from i and j). Whenever $l < d$, the direct movement between i and j is assessed as equally (and fully) possible (a link between i and j exists in the graph), while when $l > d$, no link or possibility for movement exists. This corresponds to a binary connection model as described earlier. In this scenario IIC will take into account the number of movement steps (links) needed to get from one core patch to the other through the shortest available pathway, with the degree of connectivity decreasing as that number gets larger (Pascual-Hortal and Saura, 2006).

(2) *IIC-steps*: Unweighted forest habitat network with all bridges being considered effective to conduct movement and with the importance of individual elements quantified through dIICconnector. This is similar to the previous scenario (can be thought of as a particular case of it) but where all the existing bridges are usable for direct movement between the two cores that they structurally connect at their ends. This will occur when the maximum length l that needs to be traversed through any of the bridges is smaller than the movement ability of the species or ecological flows (d) through these corridors. Here IIC will take into account the number of movement steps in the shortest path between cores in the same way than in the previous case, but now with all the MSPA bridges supporting successful movement. While IIC-distance requires calculating l for all bridges, IIC-steps is simpler to assess because it only requires identifying which cores are structurally connected by bridges.

(3) *PC-distance*: Weighted forest habitat network with movement through bridges limited by distance and the importance of individual elements quantified through dPCconnector. This is similar to the IIC-distance case, but instead of sharply considering bridges as fully effective connectors or not depending on whether l is smaller or larger than d, each bridge contacting two cores i and j is characterized by a certain probability of direct dispersal between them (p_{ij}) that is used for the computation of the maximum product probability paths and the resultant PC and dPCconnector values (Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010). Therefore, we here adopt a probabilistic connection model where every bridge corresponds to a link in the graph and has an associated p_{ij} value (even if in some cases p_{ij} may be very close to zero for very long bridges and species with low mobility). The p_{ij} values were computed through a negative exponential function of the length l that needs to be traversed between i and j through existing bridges. To allow comparability of the PC-distance results with those of the IIC-distance scenario, the constant k that determines the decay rate of the negative exponential function was set to $k = 1/d$. In this way, the mean dispersal distance in the probabilistic model resulting from this negative exponential coincides with the threshold distance d used in the binary connection model.

(4) *PC-infinite*: Forest habitat network in which movement through bridges is considered as completely feasible with the maximum probability independent of the distance that needs to be traversed through those bridges to get from one core to another. The importance of individual elements is quantified through dPCconnector. This is a particular extreme case of the previous PC-distance scenario in which the movement abilities through bridges are so large (in a given temporal horizon) that the maximum direct dispersal probability $p_{ij} = 1$ is assigned to

all bridges (links). The difference with IIC-steps is that in this case, the number of required movement steps will not reduce the degree of connectivity assessed; a maximum degree of connectivity will be assigned when a pathway through bridges exists between any pair of core areas, no matter how long that available pathway might be or how many intermediate steps it might comprise (see the results for the IIC-steps and PC-infinite scenario in the example of Fig. 1). In other words, the maximum connectivity will be assigned by PC-infinite if all the core patches belong to the same (single) network component (where a component is defined as a set of patches that can be reached from each other through the available structural connectors; no movement is possible between patches belonging to different components). In this scenario, an individual link or core forest area will only have some value as a connectivity provider when its loss breaks up the forest network into a larger number of fully isolated structural components (Fig. 1). If the element loss causes an increase in the distance that needs to be traversed to get between some habitat areas, this will not have any impact in PC-infinite and that element will be regarded as unimportant for connectivity maintenance. In this case, the overall value of the PC index for a particular landscape would provide the same result as the landscape coincidence probability (LCP) and the related C index as discussed in Saura (2010).

For the IIC-distance and PC-distance scenarios, we considered the length l that needs to be traversed through existing structural connectors to move between each pair of cores. This l does not equal the bridge area or length or the Euclidean (straight line) distance between cores because bridges can have some width and sinuosity and because the same bridge can connect several cores, with only a section of it being used to get from one core to another. This length l was calculated as the effective (least-cost) distance between cores through a landscape matrix where bridges presented a resistance value of one unit and the rest of the landscape was treated as fully inhospitable for movement. Least cost calculations were performed through the PathMatrix extension (Ray, 2005) for ArcView 3.x. The results from PathMatrix can be directly used as an input for the Conefor Sensinode (connection file) when the format result option selected in PathMatrix is the Isolation by Distance (IDB) format. The only change required to that IDB file as produced by PathMatrix is to remove the first line of text ("geographical distance"). The IIC-distance and PC-distance scenarios were evaluated under different dispersal distance d values covering the range of bridge lengths in each of the study areas.

For each scenario, we evaluated the overall degree of forest structural connectivity (as measured by ECA for either IIC or PC), and the individual impact of losing each of the cores and of losing all the bridges connecting two particular cores (as evaluated through dIICconnector or dPCconnector). As complementary information, we also calculated the number of structural components in each of the networks and identified the cores and bridges belonging to each of them. All the calculations were performed through a new version (2.5) of the Conefor Sensinode software package (Saura and Torné, 2009).

3. Study areas and spatial data

3.1. Forests in the province of Segovia

The province of Segovia (6949 km^2) is located in Central Spain and belongs to the region of Castilla y Léon (Fig. 2). Most of the territory of Segovia is dominated by arable lands (61%), with 31% of the province covered by forests. The main forest tree species (ordered by the total area they cover in the province) are *Pinus pinaster*, *Quercus ilex*, *Pinus sylvestris*, *Quercus pyrenaica* and *Pinus pinea*. An important part of Segovia (26% of its territory) is included within the Natura 2000 European network of protected areas.

For this study, we considered the forest areas in Segovia as mapped in the raster version of the Corine Land Cover dataset for 2006 with a pixel size of 100 m. We jointly considered Corine classes 3.1, 3.2 and 3.3, respectively corresponding to broadleaved forest, coniferous forest and mixed forest, for the connectivity analyses. An edge width of 3 pixels (300 m) was used for the MSPA, which is the width being used in the fragmentation and spatial pattern analyses in the biodiversity assessments at the scale of the Spanish provinces within the Third Spanish National Forest inventory (Ministerio de Medio Ambiente, 1997–2007).

3.2. The public forested land Dehesa Boyal

Dehesa Boyal is a public forested land located in the Sierra de Gredos, within the Spanish region of Castilla y León (Fig. 2). This forest territory (hereafter shortened as Boyal) has a total area of 815 ha and is included in the Natura 2000 network as part of the Special Protected Area Pinares del bajo Alberche. The forest habitats present in Boyal are *Quercus pyrenaica* and *Quercus ilex* forests, as further described in Hernando et al. (2010a). These habitats are listed in Annex I of the Habitats Directive, by which European Member States are required to establish the necessary conservation measures and management plans that will ensure their favorable conservation status (Article 1.e).

A QuickBird scene covering the study area was used for mapping the *Quercus pyrenaica* and *Quercus ilex* forest habitats, which were later jointly considered as the focal forest area for the connectivity analyses. This scene was acquired on the 5th of August of 2005, with three visible and one near-infrared spectral bands, an 11-bit radiometric resolution and a spatial resolution of 2.44 m. The habitats were classified through the object-based image approach in the eCognition software. For this purpose, multi-scale levels, ancillary data, and class-related features were combined with the Quickbird imagery. The overall classification accuracy was 86.3%, and the Kappa statistic was 0.84. Further details are provided in Hernando et al. (2010b).

Both *Quercus pyrenaica* and *Quercus ilex* have traditionally been pruned and felled to provide firewood and cattle forage, with clear-cuts applied every 12–20 years. Nowadays firewood is more rarely extracted but the most common activity is livestock rearing with native pasture (silvopastoral system), as further described by Hernando et al. (2010a).

For the MSPA, an edge width of 4 pixels was set, corresponding to approximately 10 m. This width is adequate to capture the edge effect on the saproxylic stag beetle *Lucanus cervus*, which is an endangered species registered in the second appendix of the Habitats Directive of the European Union from 1992 and that in Boyal presents the southernmost part of its distribution in Europe (Ministerio de Medio Ambiente, 2006). Stag beetles have a limited colonization capacity and an excessive fragmentation of its natural habitats is considered among the major threats for its conservation (Ministerio de Medio Ambiente, 2006). However, this species is associated with cavities in trees, dead trunks, stumps, and decaying wood. It therefore needs from these structural elements both in the forest cores and in the connecting elements to make them usable and effective for conducting the dispersal movements.

4. Results and discussion

4.1. Pattern of core habitat areas and bridges and overall connectivity in the study areas

In Segovia, 35% of the forest area corresponded to core habitat (that covered a total of 53,070 ha) and 12% to bridges, with 282

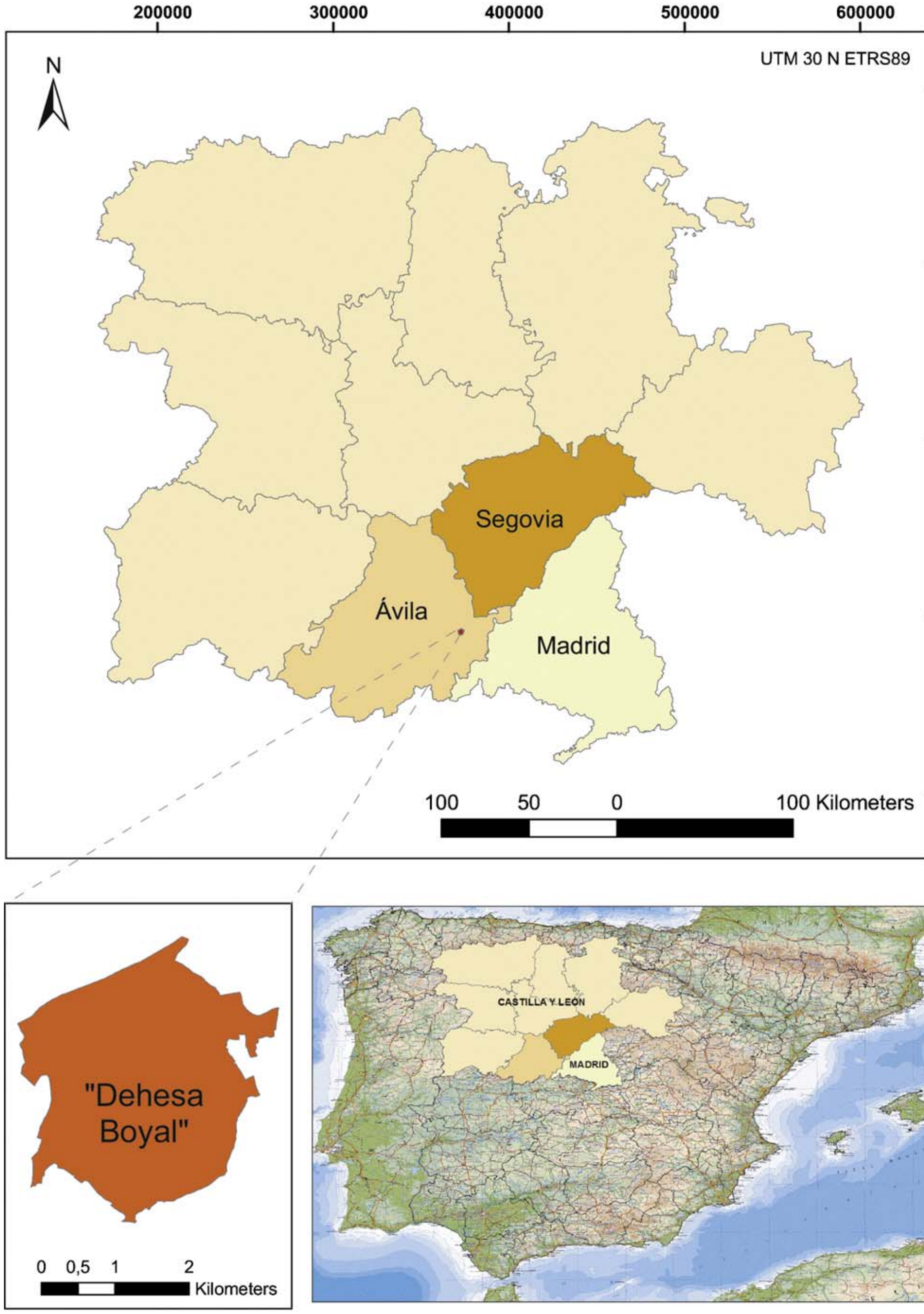

Fig. 2. Location of the two analyzed study areas in Central Spain, corresponding to the Province of Segovia and to the public forest land "Dehesal Boyal". Both provinces are within the region of Castilla y León and adjacent to the region of Madrid.

Table 1
Percentage of forest area and number of elements corresponding to each of the MSPA classes in Segovia and in Boyal.

MSPA class	Segovia		Boyal	
	Forest area (%)	Number of elements	Forest area (%)	Number of elements
Core	35.21	282	70.73	161
Islet	6.56	236	0.91	163
Bridge	12.45	149	3.44	131
Loop	2.81	60	1.71	124
Edge	28.95	512	13.96	664
Perforation	0.44	6	4.89	166
Branch	13.58	1808	4.36	3560

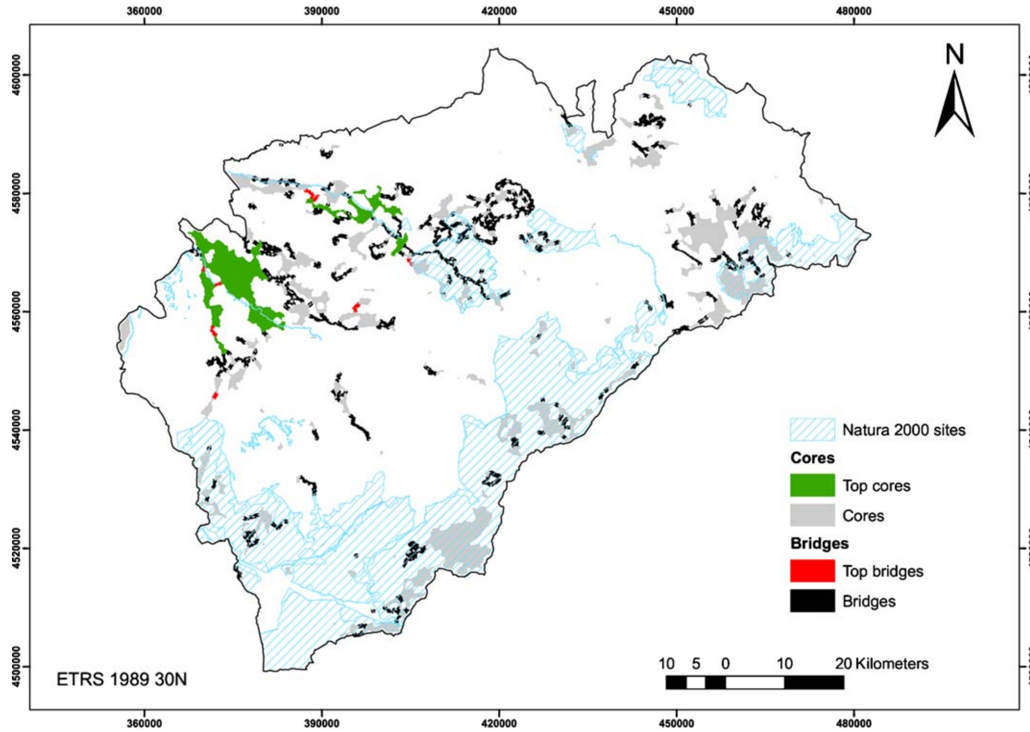

Fig. 3. Distribution of forest cores and bridges in the province of Segovia. The seven cores and seven bridges with the highest importance for maintaining structural forest connectivity (average value of the connector fraction for all the scenarios) are highlighted. The distribution of Natura 2000 sites is also shown.

core patches and 149 structural connectors (Table 1 and Fig. 3). In Boyal 71% of the total forest area was classified by MSPA as core habitat (300.27 ha) and above 3% as structural corridors, with 161 cores and 131 bridges (Table 1 and Fig. 4). The rest of the forest in both areas corresponded to MSPA classes that do not contribute to structural connectivity as considered in this study. The length that needed to be traversed between two directly connected cores trough a bridge (l) ranged from 241 to 10,398 m (with an average of 2078 m) in Segovia and from 6 to 236 m (average 50 m) in Boyal.

The much higher core area proportion in Boyal was due to the smaller edge width (s) used in the MSPA analysis compared to Segovia (corresponding to 10 and 300 m, respectively) as related to the different scale and management context in each of the study areas. In addition, the forest pattern in the province of Segovia was more fragmented as this study area comprises a much larger extent and land cover heterogeneity (including non-wooded lands) than the Boyal forest land (Figs. 2–4).

This difference between the two study areas was very pronounced when structural connectivity was analyzed by considering the role of bridges as connectivity providers: in the most optimistic corridor dispersal scenario (PC-infinite) the ratio between the ECA (equivalent connected core area) and the total forest core habitat area was 99.4% for Boyal and only 37.5% for Segovia. These ratio values are different for the other scenarios but still much higher in Boyal than in Segovia (compare the ECA values in Tables 2 and 3 with the total core area in each study area as reported above). The bridges in Boyal allowed joining in a single component almost all the forest core habitat (there were 25 other components but these comprised only a tiny proportion of the total core area), while in Segovia the existing bridges still left the core habitat divided into 85 isolated components, with the largest one representing only 28% of the total core area.

Bridges were more numerous in Segovia than in Boyal (Table 1), but the number of connections (links) between different habitat patches is a bad indicator of the degree of connectivity, as noted by

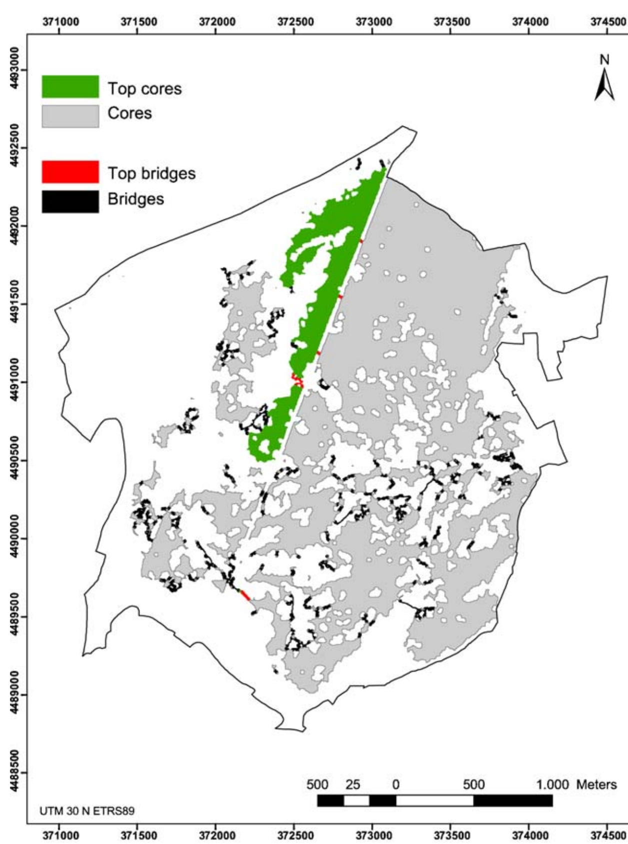

Fig. 4. Distribution of forest cores and bridges in the Dehesa Boyal forest land. The three cores and three bridges with the highest importance for maintaining structural forest connectivity (average value of the connector fraction for all the scenarios) are highlighted.

Table 2
Maximum and sum of the *dIICconnector* or *dPCconnector* values for all the cores and bridges and Equivalent Connected Core Area (ECA) values for the different forest network connectivity scenarios in the province of Segovia. For IIC-distance and PC-distance results are shown for different dispersal distances (d) representative of the range of variation in bridge length (l) and capturing the variability of the metric response in the province.

	ECA (ha)	Core importance (connector (%))		Bridge importance (connector (%))	
		Maximum	Sum	Maximum	Sum
IIC-distance d = 1000 m	12,786	0.60	1.13	6.06	10.83
IIC-distance d = 1500 m	13,582	7.22	15.77	7.23	25.58
IIC-distance d = 2000 m	14,411	6.90	25.82	8.14	38.49
IIC-distance d = 3000 m	14,954	2.85	15.05	8.14	29.40
IIC-distance d = 10,000 m	15,523	3.25	17.98	8.52	31.12
IIC-steps	15,532	3.24	17.73	8.51	30.29
PC-distance d = 1000 m	13,231	0.91	3.52	5.05	15.88
PC-distance d = 1500 m	13,945	1.31	6.93	6.68	22.72
PC-distance d = 2000 m	14,542	1.44	10.24	7.82	27.19
PC-distance d = 3000 m	15,451	2.33	15.80	9.45	32.45
PC-distance d = 10,000 m	17,872	6.08	31.79	13.63	40.69
PC-infinite	19,915	9.19	45.59	16.67	42.36

Pascual-Hortal and Saura (2006). Indeed, the fragmentation process has to progress considerably in order to produce a large number of separated patches and therefore allow for the possibility of more numerous bridges to exist between them. No bridges would exist in the maximum connectivity case where all the habitat is located in a single large core habitat patch.

4.2. Contribution of individual cores and bridges to structural forest connectivity: how many of them are really irreplaceable and crucial to uphold ecological fluxes?

Bridges had a considerably more prominent role as structural connectivity providers than cores in both study areas, as shown by the higher maximum and summed values of *dIICconnector* and *dPCconnector* (Tables 2 and 3). The number of elements with a positive value of the connector fraction was also higher for bridges (e.g. 43% and 32% respectively in Segovia and Boyal for the PC-infinite scenario) than for cores (17% and 11% for the same scenario, as reported above). While bridges are by definition centrally located in the sense that they contact with at least two different habitat areas at their ends, some of the cores may be situated in the periphery of the forest network and therefore be useless as stepping stones that allow gaining access to other core habitat areas.

Even with these differences, our results show that most of the cores and bridges did not play an effective role as irreplaceable connectivity providers in the study areas (as evaluated by dIICconnector or dPCconnector). Moreover, the distribution of the connector values among the forest elements that effectively contributed through this fraction was very uneven. In fact, most of the total connecting role (sum of the dIICconnector or dPCconnector values for all the elements of a particular type in each study area) was accounted for in just a few key cores or bridges in all the scenarios; for example, in the IIC-steps scenario only the two top cores and four top bridges accounted for more than the half of the total sum of connector values in Segovia for each of these two types of landscape elements, while the same was true for only two cores and the single most important bridge in Boyal (similar results were found for the other scenarios).

Indeed, a particular patch may have quite a central location in the landscape network (being located in between other core areas), but still be of low importance for the conservation of structural connectivity (as indicated by dIICconnector or dPCconnector) because many other cores or bridges may be able to compensate for its loss. If the rest of the available paths in the remnant network are almost as favorable for movement as those that were facilitated by the presence of a particular element in the intact habitat mosaic, such an element cannot be considered critical as an irreplaceable connectivity provider in the forest landscape (Bodin and Saura, 2010). In addition, even for those elements whose loss cannot be compensated by others, the final importance can vary largely depending on the size of the habitat units that get disconnected (either fully or partially) from the rest of the core forest; if only a minor habitat piece is affected, that core or bridge will be considered as well of low importance according to dIICconnector or dPCconnector even when it might be the only existing connector for that small amount of habitat.

The high discriminatory power of the connector fraction here reported can be considered as a desirable and useful feature that allows highlighting a concise subset of cores and bridges that can be regarded as particularly important for the functioning of the over-

Table 3
Maximum and sum of the *dIICconnector* or *dPCconnector* values for all the cores and bridges and Equivalent Connected core Area (ECA) values for the different forest network connectivity scenarios in the Boyal forest land. For IIC-distance and PC-distance results are shown for different dispersal distances (d) representative of the range of variation in bridge length (l) and capturing the variability of the metric response in the study area.

	ECA (ha)	Core importance (connector (%))		Bridge importance (connector (%))	
		Maximum	Sum	Maximum	Sum
IIC-distance d = 50 m	245.51	0.28	0.44	9.63	11.40
IIC-distance d = 75 m	254.53	4.13	18.08	13.26	28.33
IIC-distance d = 100 m	254.55	4.14	16.06	13.28	27.84
IIC-distance d = 200 m	256.13	4.14	12.42	13.23	24.37
IIC-distance d = 500 m	256.79	4.13	12.66	13.21	24.74
IIC-steps	256.79	4.13	12.66	13.21	24.74
PC-distance d = 50 m	252.46	1.28	2.52	13.51	18.08
PC-distance d = 75 m	258.18	2.69	5.59	16.11	23.09
PC-distance d = 100 m	262.51	3.92	8.67	17.86	27.00
PC-distance d = 200 m	273.44	6.88	17.67	21.31	36.06
PC-distance d = 500 m	285.59	9.53	27.72	23.93	44.20
PC-infinite	298.49	11.70	37.44	25.87	50.94

all forest habitat network. A forest manager can therefore get clear guidelines on where the management and conservation efforts should be concentrated and prioritized, while at the same time having many alternative areas where to accommodate the rest of the management objectives and activities as required by the multifunctionality of forest resources.

In the Boyal forested land, the main management measure to be implemented in the key connectors here determined (top bridges in Fig. 4) consists of fencing to reduce the impact of livestock. This is because continuous grazing and browsing by cattle represents a serious problem for the survival of the acorns which, together with the soil compaction by livestock (that hinders seedling establishment), is the main threat for *Quercus* forest habitat regeneration and persistence. In these key areas fencing should be accompanied by a series of pruning and thinning treatments to reduce stand density. This would promote the growth of a smaller number of selected stems and the transition to more developed and mature forest stages. The abundance of cavities and large pieces of dead and decaying wood would therefore increase, improving the habitat quality and hence supporting the capacity of the connecting elements to attract and conduct dispersal for the endangered stag beetle.

The planning implications in the province of Segovia, given its much wider extent and the variety of forests it comprises, would focus, rather than on specific management measures at the stand level, on the large-scale design of the network of protected areas and on elucidating where the connectivity conservation efforts should be concentrated (Fig. 3). Only 13% of the key cores and 6% of the key bridges were protected by the Natura 2000 network (average percentages for the different scenarios and distances listed in Table 2). This is because the Natura 2000 sites are concentrated in the SE of Segovia, along the highest altitudes in the Sierra de Guadarrama, failing to protect the key connecting core areas towards the North of the province (Fig. 3). On the other hand, the much weaker protection for key bridges than for key cores is a result of the criteria that have been used in the past for the selection of reserves not only in Segovia but in many other parts of the world. These were based basically in selecting for protection the largest blocks of forest habitat, while largely neglecting the same protection for corridors and other connectivity providers that made it possible to uphold the ecological fluxes and related ecosystem functioning between the protected areas. This paradigm is now shifting, and there is a large consensus in that the intermediate landscape elements need also to be taken into account in order to ensure the appropriateness and effectiveness of modern reserve designs (Williams et al., 2005).

4.3. Connectivity assessment for the different network scenarios: which one is more relevant to inform management decisions?

The maximum contribution of connecting elements to overall habitat availability was found in both study areas for the PC-infinite scenario, and both for cores and bridges (Tables 2 and 3). This is because when the species and fluxes are able to move freely throughout the network of cores and bridges irrespective of the distance to be traversed, the loss of a particular connecting element can have a larger impact on fluxes coming from further apart (eventually from any other site in the habitat network or component). However, when dispersal is limited by distance (IIC-distance or PC-distance) or by the number of movement steps (IIC-steps), the amount of fluxes and source areas that can use that element is comparatively lower, resulting in lower maximum and summed values of the connector fraction (Tables 2 and 3).

An important question that then remains is: which of the four scenarios is more relevant to inform forest management decisions as related to structural connectivity? It certainly depends on the management context and the type of ecological processes considered. For species able to disperse over very large distances through available connectors (i.e. very small bridge length compared to d), IIC-steps or PC-infinite are the less data demanding scenarios and hence seem most appropriate. PC-infinite can also be suitable for those cases in which the structural connectors are fully effective conducting the movement with no cost or mortality for the species or flows: e.g. no predation occurs when the individuals disperse through these bridges and enough foraging resources are available along the connecting element. However, whether these conditions are fulfilled or not depends largely on the spatial and temporal scale of the analysis. The dispersal of the same species could be analyzed through PC-infinite in a particular and relatively limited study area with accordingly small cores and bridges (e.g. Boyal) but would need to be better considered through other more detailed scenarios like IIC-distance or PC-distance when the same dispersal process is analyzed at a wider spatial scale (e.g. Segovia). In this latter case, the length of the bridges that extend through the study area may considerably exceed the typical dispersal range of the species. Therefore the degree of connectivity would most probably be overestimated if assessed through IIC-steps or PC-infinite in this case, with the consequent potential biases in the assessment of the key forest elements and their individual importance. Even within the same study area and species, depending on whether the focus is on daily movements that configure the home range of a species or on genetic transmission across generations, the very different time horizons and related range of movements will determine which of these scenarios can be considered more appropriate for the structural connectivity analysis.

If we consider other ecological process such as wildfire spread, the temporal dimension gains even more importance for managing the forest landscape. When the objective is to reduce the amount of potential burnt forest land with a minimum cost in terms of forest habitat area loss, the key bridges here identified are in fact thin strips of forest land that might be able to effectively impede the fire spread over large areas. This would provide indications about where to concentrate extinction efforts once the fire has initiated, or about where to prioritize preventive measures such as forest thinning, cleaning, or firebreak construction. This applies to surface forest fires or to low intensity passive crown fires as long as fire whirls and spotting do not play a role in propagating the fire beyond the fire front without need for continuity in the forest fuel layer. When dealing with forest fire spread, the distance d should not be interpreted as a "static" distance that the fire is able to spread, but as the amount of advance in the fire front that can be expected in a given time horizon. This should be linked both to the predicted fire spread rates and to the time that a given fire source could be expected to burn before it is effectively suppressed or at least attacked by available extinction crews and equipment. The PC-infinite case corresponds to the non-extinction scenario, in which the fire will potentially burn all the vegetation fuel that is available and can be reached thanks to the bridges from a particular ignition point, which is unlikely to be the case in most of the situations. Similar considerations would apply for the spread of other disturbances, diseases, or invasive species.

5. Conclusions and further possibilities

We have presented the novel integration of two recent approaches for the analysis of forest landscape structural connectivity in a single workflow. The individual strengths and benefits provided by MSPA and the network habitat availability metrics naturally complement each other in an intuitive and effective manner. The proposed integration presents considerable synergies and added value to inform forest planning at a variety of scales, as has been illustrated in two study areas in Central Spain. Within this joint analytical framework, we have offered a variety of ways (scenarios) to model and analyze forest network connectivity from where the manager can choose, depending on the focal ecological processes and the management targets. All these scenarios can be assessed in any study area through the new and freely available versions of the Guidos (MSPA) and Conefor Sensinode (network connectivity analysis) software packages. The proposed integration of the two approaches has already gone beyond the conceptual developments by implementing some of the features of Conefor Sensinode directly within Guidos. In this way, Guidos is now able to present the different forest landscape elements identified from the MSPA together with their individual importance for maintaining forest structural connectivity as evaluated through the PC-infinite scenario. For the other three scenarios (or any other analytical variant the user might want to consider) Guidos is able to produce from the MSPA results the appropriate files (node file and connection file) in the format that can be directly used by Conefor Sensinode without need of any other intermediate processing step. We believe that these solid links between both packages reinforce the applicability and practical possibilities of the proposed methodology.

The methodology here presented focuses both on the forest habitat patches and on the structural connectors (corridors) as thin strips of forest that allow increasing the amount of habitat that can be reached by forest dwelling species. These structural connectors are indeed important physical entities for biological conservation and forest biodiversity assessment. From a planning perspective, they can be considered as bottlenecks and crucial areas for species movement and as fragile elements that are likely to be the first affected by landscape changes and management decisions, therefore making them of particular conservation planning concern. We fully recognize however that structural connectivity does not embrace the full spectrum of possibilities that can be considered in a landscape connectivity assessment. Indeed, a functional connectivity analysis would need to take into account the ability of the species or ecological flows to venture and move a certain distance through different non-forested land covers in the landscape matrix (Harrison and Bruna, 1999; Tischendorf and Fahrig, 2000). Connectivity may be ensured not only when the existing forest habitat units are physically contiguous but also when a permeable matrix, a series of stepping stones or other connecting elements allow for the movement of a particular organism between habitat areas that might be physically distant (With et al., 1997; Adriaensen et al., 2003; Manning et al., 2009; Rey Benayas et al., 2008). Even within the scope of structural connectivity, and besides the physical continuity of forest areas, an important factor to ensure movement of species is the quality of connectors, which also varies across species (Harrison and Bruna, 1999). In addition, the width of the edge effect is also likely to vary not only with species but with many other factors such as the type of land covers in the matrix surrounding the forest areas and the fragment age (Laurance et al., 2007). In general, we recognize that the approach here adopted would need to incorporate more detailed species-specific traits in order to provide fully solid management guidelines in particular case studies. Finally, it is important to note that maintaining or upholding forest connectivity is not the only conservation alternative (and not necessarily the most efficient one) to ensure species viability. In particular, other well established measures such as maintaining or improving the amount and quality of habitat within individual forest patches can make an important or even larger contribution to the conservation of multiple species and ecological processes (Hodgson et al., 2009).

Our focus here was on a methodological framework for structural connectivity analysis, conceived as an operational approach that is easy to relate to forest management units and decisions and that can serve as an initial proxy for more complicated and detailed functional connectivity assessments. Our approach does not intend to exclude these other possibilities outlined above but rather provides planning guidelines related to structural connectivity that can be complemented and refined where appropriate with further empirical support and specific studies oriented to individual taxa and their functional responses to the landscape structure. In particular, the combined approach here proposed could be also applied or adapted to incorporate other considerations and analytical possibilities, such as (a) a more restrictive and species-oriented definition and identification of the input forest habitat areas and usable corridors, rather than a generic analysis jointly considering all forested areas within the landscape, (b) accounting for variable edge widths for different forest types and land covers in the surrounding matrix, (c) combining habitat availability indices with graph centrality metrics to gain insights on the vulnerability of the remnant forest landscape network to additional habitat losses (Bodin and Saura, 2010), (d) evaluating the potential benefits and efficiency of adding new forest habitat areas in the landscape through forestation or restoration programs (García-Feced et al., 2011), (e) comparing the relative contribution to overall habitat connectivity and availability of investing efforts in protecting the structural connectors with the contribution resulting from other conservation management alternatives that might be more effective in some cases, as can be quantified by considering the three fractions of IIC or PC (Saura and Rubio, 2010), and (f) assessing the effect of route redundancy on network analysis and related ecological flows (Rayfield et al., 2011). Functional connectivity analyses can also be undertaken and have been previously been reported through both the MSPA (Vogt et al., 2009) and the IIC or PC metrics (Saura and Pascual-Hortal, 2007; Saura et al., 2011, and many other studies as described in http://www.conefor.org/applications.html). Here we have presented a novel and different type of use of these metrics for a structural connectivity analysis linked to the MSPA that is less data demanding than those previous functional applications, and therefore may better match with the typical amount of data that is available or can be acquired in the context of a particular forest management plan.

In summary, our approach provides a solid methodological background not only for mapping core habitat areas and the structural connectors that may be able to conduct ecological fluxes between them, but also for measuring their individual role as irreplaceable providers of structural connectivity with the same units of measurement. Such a role is likely to be concentrated in a few forest elements, which allows implementing management measures to ensure structural connectivity while making such objective compatible with other management targets in the forest landscape.

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