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ORIGINAL PAPER

Integrating landscape connectivity in broad-scale forest planning through a new graph-based habitat availability methodology: application to capercaillie (*Tetrao urogallus*) in Catalonia (NE Spain)

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Abstract The loss of connectivity of forest landscapes is seriously hindering dispersal of many forest-dwelling species, which may be critical for their viability and conservation. In this context, explicitly incorporating connectivity considerations is an important challenge in current forest planning and management, but as yet there is a lack of operative methods for appropriate decision making in this respect. We describe a new methodology based on graph structures and a habitat availability index (integral index of connectivity) that integrates forest attributes (like habitat quality) and network connectivity in a single measure. We apply this methodology to examine the connectivity of the highly fragmented habitat of capercaillie (*Tetrao urogallus*) in Catalonia (NE Spain), where the threatened status of this forest bird species calls for landscape-level forest planning solutions. We analyse data on the distribution of capercaillie forest habitat at 1 km spatial resolution obtained from the recent Catalan Breeding Bird Atlas. We determine the functionally connected regions existing within its habitat distribution and identify the forest habitat areas that are more important for the maintenance of overall landscape connectivity for this species. Based on these results, we provide recommendations on certain critical public forests where management oriented to the conservation of capercaillie habitat is more necessary. These results highlight the potential and practical interest of the proposed methodology for successfully integrating landscape connectivity in broad scale forest planning.

Keywords Forest connectivity · Capercaillie · Forest planning · Habitat availability · Landscape ecology · Forest conservation · Graph theory · Ecologically based forest management · Multifunctional forestry

Introduction

The loss of connectivity of forested landscapes is one of the major threats for the conservation of the biodiversity and the ecological functions of forests (Taylor et al. 1993; Bunnell and Johnson 1998; Rochelle et al. 1999; Raison et al. 2001). Fragmentation and isolation of forest habitat patches lead to a spatially structured habitat pattern in which movements of dispersing individuals may be constrained, hampering the viability and conservation of forest-dwelling species (Fahrig and Merriam 1985; Saunders et al. 1991). This has led to an increasing interest in considering connectivity in current multifunctional forest planning and management. In this sense, the Improved Pan-European Indicators for Sustainable Forest Management by the Ministerial Conference on the Protection of Forests in Europe (MCPFE) include the indicator 4.7 "Landscape pattern" (landscape-level spatial pattern of forest cover) within the criteria on the "Maintenance, Conservation and Appropriate Enhancement of Biological Diversity in Forest Ecosystems". In addition, in the resolution 4 ("Conserving and enhancing forest biological diversity in Europe") of the Fourth MCPFE held at Vienna in

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2003, the Signatory States and the European Community commit themselves to ‘‘prevent and mitigate losses of forest biological diversity due to fragmentation and conversion to other land uses and maintain and establish ecological connectivity’’.

One of the forest-dwelling bird species most critically affected by the loss of habitat connectivity in Catalonia (NE Spain) is the capercaillie. The endemic subspecies of capercaillie (*Tetrao urogallus aquitanicus*) in Catalonia, which requires a strictly forested environment, is currently going through a delicate conservation status that has prompted the decision of considering it as endangered in this region (Estrada et al. 2004, Madroño et al. 2004), as appropriate for applications of the worldwide criteria (2001) of the International Union for Conservation of Nature (IUCN) and the regional correctors proposed by Gärdenfors et al. (2001). The current decreasing population trend lately observed for capercaillie in this region (Madroño et al. 2004) together with its poor breeding success both in Catalonia and in other regions of Europe (Canut et al. 1996; Moss et al. 2001), suggest that the current low-density capercaillie populations hardly guarantee long-term survival of this species (Storch 1995). Moreover, it is pointed out that the difficult situation of capercaillie will not improve unless the current limiting factors change (Estrada et al. 2004). Habitat loss and destruction, and consequently the loss of connectivity among the remaining forest fragments, are some of the main threats for capercaillie conservation. Although most common conservation measures are basically focused on the strict protection of its vital areas (leks, hibernating and breeding sites, etc.), this approach seems to be insufficient to meet the wide spatial requirements of capercaillie (Rolstad 1989; Angelstam 1990; Storch 1997; Canut 2001). To improve conservation status of this species it is necessary to conserve (and if possible, recover) functional connection among its populations, therefore facilitating dispersal of individuals and minimizing mortality risk. These species-specific considerations imply that forest planning and management should approach this problem by explicitly including connectivity considerations and, more specifically, by delimiting the most critical forest sites for the maintenance of capercaillie habitat connectivity.

Although there is a wide variety of connectivity indices in the literature (Hanski 1994; Bunn et al. 2000; Ricotta et al. 2000; Urban and Keitt 2001; Moilanen and Nieminen 2002; Jordan et al. 2003; Calabrese and Fagan 2004), many of them have been found to present serious limitations that make them inadequate for effectively integrating connectivity in forest conservation planning (Pascual-Hortal and Saura 2006). Also, the spatial scales traditionally considered in forest management should be broaden to adequately characterize connectivity, which occurs at a landscape scale (Merriam 1984; Wiens et al. 1997; Tischendorf and Fahring 2000; Raison et al. 2001). The wider geographical perspective (landscape level analysis of forests) significantly increases the computational complexity of the analysis by enlarging the amount of spatial data to be analysed, with the spatial relationships between the different landscape elements becoming more intricate.

In this context, a new methodology has recently been proposed, successfully enabling both the capture of fundamental landscape changes affecting connectivity and the detection of the most critical landscape elements for the maintenance of overall landscape connectivity (Pascual-Hortal and Saura 2006). This methodology is based on the use of graph structures and habitat availability indices for the analysis of forest connectivity. Graph structures may be used for quantitatively describing a forest landscape as a set of spatially or functionally interconnected patches; then, by adequately applying graph-algorithms, it is possible to overcome the computational limitations that appear when dealing with large data sets and thus perform complex analyses regarding forest landscape connectivity. The consideration of habitat availability (habitat amount and connectivity integrated in a single measure, Pascual-Hortal and Saura 2006) yields the possibility of innovatively applying a proper connectivity method for specific forest conservation planning problems.

In this study, we apply this new methodology to the analysis of capercaillie forest habitat in the region of Catalonia (Spain). Specifically, we base our quantitative analysis on the integral index of connectivity (IIC), which has been recently proposed and has been shown to present improved performance and characteristics in comparison with other available connectivity indices (Pascual-Hortal and Saura 2006). The objectives of this study and quantitative analysis of Catalan forest landscapes are (1) presenting the characteristics and potential of the proposed methodology for a wide range of broad-scale forest planning applications, (2) determining the forest habitat areas (at the resolution of 1 × 1 km) that are more critical for the maintenance of forest landscape connectivity for capercaillie in Catalonia, and (3) identifying the Catalan public forests in which an adequate management oriented towards the conservation of capercaillie habitat and its connectivity is more necessary, providing recommendations in this respect.

Methods

Study area and capercaillie distribution

The region of Catalonia (Northeast Spain, Fig. 1) has an extent of 32,000 km^2, comprises the provinces of Lleida, Girona, Barcelona and Tarragona, and has about 38% of its area covered by forests. Habitat distribution of capercaillie (*Tetrao urogallus aquitanicus*) in Catalonia (Fig. 1) was obtained from the Catalan Breeding Bird Atlas 1999–2002 (Estrada et al. 2004), which shows that the preferred habitat of this species basically corresponds to upper montane and subalpine forests in the Pyrenees and Pre-Pyrenees (N Catalonia), composed mainly of mountain pine (*Pinus uncinata*), European silver fir (*Abies alba*) and mixed fir-beech (*Abies alba-Fagus sylvatica*) forests. In this atlas, the species distribution map depicting evidence of breeding in the period 1999–2002 was obtained by analysing field data (species occupancy) collected in each UTM 10 × 10 km square lying completely within the territory of Catalonia. Then, presence-absence data gathered within a significant sample of UTM 1 × 1 km squares that fell within the known 10 × 10 km distribution of the species was the basis for estimating its probability of occurrence (from 0 to 1), which is assumed to be a surrogate for species abundance, as supported by additional analysis and validation with independent bird abundance data (Robertson et al. 1995; Estrada et al. 2004). The presence of the species in unsampled areas (non-surveyed UTM 1 × 1 km squares) was predicted through niche-based models, which are based on modelling the species' response to a set of environmental variables (i.e. forest types, land use, climate, relief, human influence, etc.) and on the subsequent prediction of their presence in unsampled areas based on those environmental variables (Guisan and Zimmermann 2000); see Estrada et al. (2004) for further details in the specific modelling within this atlas. As a result, occurrence probability maps for the whole of the study region were available at a 1 × 1 km resolution. In this study, we used this probability of occurrence as a measure of habitat quality (incorporated through a_i factor in Eq. 1), indicating that patches with higher probability of occurrence are more suitable for the capercaillie. Only 1 × 1 km squares that presented a significant probability of capercaillie occurrence (at least 0.2) were considered as ''habitat'' squares, resulting in a total of 522 squares (hereafter referred to as forest habitat areas, Fig. 1).

To adequately describe habitat structure as perceived by capercaillie (therefore assessing functional connectivity) it is essential to include the species movement pattern in the connectivity analysis (Tischendorf and Fahrig 2000). Capercaillie average dispersal distance, obtained as a result of a spring-summer

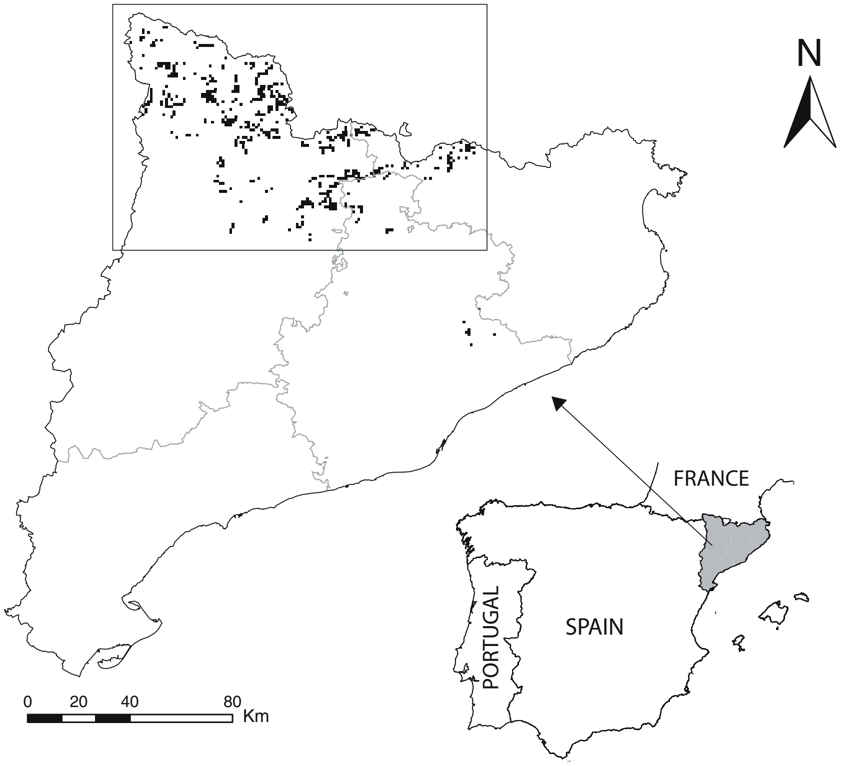

Fig. 1 Location of Catalonia in the map of Spain and distribution of capercaillie habitat in the map of Catalonia. *Black squares* correspond to capercaillie forest habitat areas (UTM 1 × 1 km squares with probability of occurrence ≥0.2 in the Catalan Breeding Bird Atlas 1999–2002, Estrada et al. 2004)

movements study with 52 radio-collared males (Hjeljord et al. 2000), was found to be 2.3 km (±0.37).

Graph theory

The use of graph structures and algorithms has been shown to be a powerful and effective way of both representing the landscape pattern and performing complex connectivity analysis (Urban and Keitt 2001; Pascual-Hortal and Saura 2006). Although graph theory has been widely developed and applied in other fields (i.e. transport, communication and information networks, etc.) only some graph-based ecological applications tackling conservation problems have been recently reported (Keitt et al. 1997; Bunn et al. 2000; Ricotta et al. 2000; Urban and Keitt 2001; Jordan et al. 2003; Pascual-Hortal and Saura 2006).

In graph theory, a graph is a set of nodes (or vertices) and links (or edges) such that each link connects two nodes. In this study, a node corresponds to a UTM 1 × 1 km square defined as capercaillie habitat (a forest habitat area). Links, which may or may not have physical correspondence in the landscape (Pascual-Hortal and Saura 2006), represent in this case the functional connection between a pair of nodes (ability of direct movement of a certain species between two nodes). A route along connected nodes in which no node is visited more than once makes up a path. The topological distance corresponds to the length of a path measured in terms of number of links. A component (or connected region) is a set of nodes for which a path exists between every pair of nodes (an isolated patch makes up a component itself). Thus, there is no functional relation (no path) between patches belonging to different components. A graph component disconnects when a part of it, after a change in the landscape, becomes not reachable from some other part, causing an increase in the number of components in the landscape. In this study, links are considered symmetric and are obtained by comparing the edge-to-edge Euclidean distance between nodes (d_{ij}) with the 2.3 km average dispersal distance of capercaillie (Hjeljord et al. 2000). If $d_{ij} < 2.3$ km, a link was assigned between nodes i and j; otherwise, nodes i and j had no direct functional connection (no link).

Connectivity index and characterization of the importance of individual forest habitat areas

For the analysis of forest habitat connectivity we used the integral index of connectivity (IIC) (Pascual-Hortal and Saura 2006), which ranges from 0 to 1 and increases with improved connectivity. It is given by:

$$\mathrm{IIC} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{a_i \cdot a_j}{1+nl_{ij}}}{A_{\mathrm{L}}^2} \qquad (1)$$

where a_i is the descriptive variable of each forest habitat area (node) and nl_{ij} is the number of links in the shortest path (topological distance) between nodes i and j, calculated through the BFS (breadth-first search) graph algorithm (Cormen et al. 2001; Siek et al. 2001). For nodes that are not connected (belong to different habitat components) the numerator in the sum of Eq. 1 equals zero ($nl_{ij} = \infty$). When $i = j$ then $nl_{ij} = 0$ (no links needed to reach a certain node from itself). In this study, the node attribute considered as the a_i variable has been the capercaillie occurrence probability (as an indicator of habitat quality) in each 1 × 1 km square according to the Catalan Breeding Bird Atlas. A_{L} corresponds to the extent of the study area (Catalonia, 32,000 km^2).

IIC is considered a habitat availability index (Pascual-Hortal and Saura 2006) because it integrates topological properties (network connectivity) with forest habitat area attributes. A habitat availability index like IIC is able to identify as ‘more connected’ a landscape with two big (e.g. 1,000 ha) isolated forest patches than other landscapes with two connected but small (e.g. 10 ha) patches, since only one of the big patches provides more available forest habitat area than all the small patches put together (even if they are connected). Habitat availability for a species may be low if habitat patches are poorly connected, but also if the habitat is very connected but very scarce. Furthermore, IIC enables the detection of any type of negative change that might affect the forest landscape, whether it is connectivity loss, forest area loss or forest alteration (Pascual-Hortal and Saura 2006). Therefore, and also due to its adequate priorization abilities (as described below), index IIC is an appropriate metric for conservation planning problems (Pascual-Hortal and Saura 2006), such as the one tackled in this study.

To effectively address connectivity issues in conservation planning it is not enough to perform a merely descriptive habitat connectivity analysis; it is much more relevant to aim for decision support. Therefore, the identification of the most critical landscape elements in relation to its contribution to overall degree of connectivity, which is much more useful in the decision process (Keitt et al. 1997; Urban and Keitt 2001; Pascual-Hortal and Saura 2006), should be carried out for practical applications. To do this with a sound quantitative and objective basis, we first calculate the IIC index value for the whole landscape (overall degree of connectivity). We then remove systematically each forest habitat area (node) and recalculate the IIC when that node is not present in the landscape. The percentage of connectivity loss measures the individual contribution of each forest habitat area to the maintenance of capercaillie habitat connectivity (dIIC) as follows:

$$\mathrm{dIIC} = 100\frac{\mathrm{IIC} - \mathrm{IIC}'}{\mathrm{IIC}} \qquad (2)$$

where IIC and IIC′ correspond to the IIC value before and after (respectively) the loss of a certain node (forest habitat area). The importance of each node will be given by the dIIC value resulting from the removal of that node from the graph, with a higher dIIC indicating higher node importance. Although here we tackle a conservation planning problem focused on the maintenance of habitat connectivity, it is also possible to detect and prioritise positive changes that may occur in the landscape (like creation of new corridors or connections between habitat areas, improvements in habitat quality or increases in habitat area), by simply applying the same approach as quantified by Eq. 2. In the same way, it is also possible to assign individual importances to links (e.g. corridors) or combinations of nodes and links. In general, the dIIC might be either positive or negative depending on the improvement or decrease in overall habitat availability (including connectivity variations) produced by a certain change in the landscape. However, since loss of habitat area always involves a decrease of habitat availability for any species, and this has been the only landscape change approached here (in order to provide a prioritization of forest habitat areas to preserve), only positive values of dIIC are possible in this study ($\mathrm{IIC}' < \mathrm{IIC}$ after every node removal).

The dIIC values for each of the 522 nodes (capercaillie forest habitat areas) were computed through the new Conefor Sensinode 2.2 software, developed at the University of Lleida by modifying, reprogramming and implementing new indices in the Sensinode 1.0 version by Dean Urban (LandGraphs package, Duke University, Urban and Keitt 2001). A free copy of this new software can be obtained by contacting the authors.

Results and discussion

The graph connectivity analysis shows that there are 40 different habitat components (forest connected regions) for capercaillie within Catalonia, being isolated from each other as perceived by the capercaille. This means that, according to movement abilities of capercaillie (Hjeljord et al. 2000), dispersal of this species across the Catalan landscape appears to be seriously hindered due to the very low chances of effective connections between forest habitat components. However, 35% of the total habitat area corresponds to one single connected region (with 183 nodes out of 522), and the class coincidence probability (CCP) (Pascual-Hortal and Saura 2006) equals 0.18 for the capercaillie habitat, where CCP is defined as the probability that two individuals randomly placed within the habitat are able to find each other (Jaeger 2000; Pascual-Hortal and Saura 2006), which occurs if they are placed within the same component. This is a considerably better situation than if the capercaillie habitat was divided into 40 equally-sized components, in which case CCP would be as low as 0.025, with considerably lower chances for genetic interchange and population survival.

However, this diagnostic or descriptive analysis of forest landscape connectivity, although useful for evaluating the situation of the capercaillie in this respect, does not provide any objective or practical guidelines for forest planning or management that may be beneficial for forest connectivity or capercaillie conservation. This is provided by the quantification of the importance of each individual forest habitat area (1 × 1 km squares) for the maintenance of overall landscape connectivity (Fig. 2). By identifying most critical locations in the basis of the IIC index, it may be possible to focus conservation efforts directly on those forest habitat areas that, due to their attributes (e.g. habitat quality) and specific network situation, have a higher effect on the overall connectivity and habitat availability for this particular species. These results and their spatial resolution (1 km) are too coarse for directly determining in detail the forest management practices, which would require from finer forest inventory data. However, they are valuable in terms of forest planning and helpful for providing subsequent recommendations on the management goals, desirable stand structures, forest composition and silvicultural treatments that would better contribute to the conservation of capercaillie populations and their connectivity in this large region, as described below.

Quantification of the individual importance of every single habitat area in terms of percentage variation in the total degree of connectivity enables a further decision-support analysis, which consists of the identification of the public-managed forests holding a higher amount of connectivity importance (Fig. 3). As shown in Table 1, there are few public forests that concentrate high values of accumulated connectivity importance (sum of dIIC for all the 1 × 1 km squares falling within

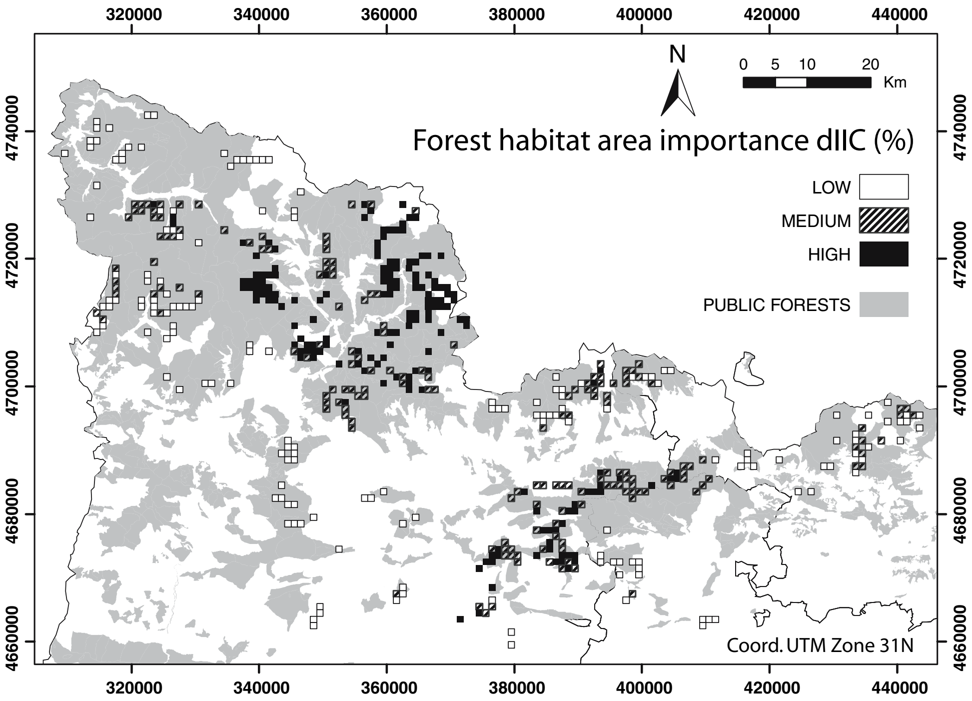

Fig. 2 Characterization of the importance (dIIC, Eq. 2) of individual forest habitat areas for capercaillie connectivity by applying the integral index of connectivity. The three importance classes have been set so that each one contains one third of total capercaillie forest habitat area. High, medium and low importance classes correspond respectively to dIIC values ranging from 14.45 to 0.45%, 0.45 to 0.19% and 0.19 to 0.03%. Public forests represented in a *grey shade* correspond to those managed by the Catalan Department of the Environment. The geographical extent of this figure corresponds to the *rectangle* over Catalonia indicated in Fig. 1

that forest) and that this value rapidly decreases for the subsequent forests in the importance ranking (Table 1). As it may be observed, there is one single forest (Muntanya (Espot)) with nearly a 30% of importance for overall degree of connectivity. This forest comprises only 4% of total capercaillie habitat area, but it is a high quality habitat all belonging to the same largest component; thus, the conservation of this forest habitat is critical to maintain connectivity in this key largest component. For similar reasons, there is also a public forest (Selva de Noarre (Tavescan), Table 1) that concentrates one of the highest accumulated connectivity importances (nearly a 6% of importance) although representing <0.1% of total capercaillie habitat area. Thus, the individual dIIC values obtained for these UTM squares and public forests (Figs. 2, 3; Table 1) are the result of its large amount of habitat area, good topological conditions and high habitat quality, which is, in short, the concept of habitat availability intended to be measured by the IIC index. This result highlights the potential of the method for detecting those forests that, although having little percentage of habitat area in relation to the total habitat area of the study region (and even in comparison with other forests), are classified as very important for the conservation of forest landscape connectivity for the capercaillie.

In the forests carrying a high connectivity importance (Table 1) it is recommended that forest management focuses on the conservation of capercaillie's habitat. Thus, any forest management should consider aspects regarding composition and structure of tree canopy, wild berries presence and the spatial distribution of the forest mosaic (Canut 2001). According to capercaillie specific use of forests in the Catalan Pyrenees, this would mainly concern the conservation and adequate management of Mountain pine (*Pinus uncinata*) forests and, to a lesser extent, of Scots pine (*Pinus sylvestris*) forests. Structural pattern of capercaillie-dwelling forests should show high spatial heterogeneity, canopy cover of about 50% and uneven-aged stands. Additionally, the presence of blueberry shrubs (*Vaccinium myrtillus*) should be strengthened by avoiding repeated and frequent forest interventions that may hinder the natural regeneration of this species (as well as regeneration of *Pinus uncinata*). It is proposed (Canut 2001) to carry out time-spaced shelterwood cuttings that may allow acceptable regeneration of these species. In Scots pine (*Pinus sylvestris*) forests, shelterwood cuttings are likewise recommended in order to help natural regeneration of the shrub species typically accompanying Scots pine (*Arctostaphylos uva-ursi*, *Juniperus communis* and *Buxus sempervirens*), which are also important in the capercaillie's diet. Nevertheless, the application of this type of cutting is only advisable in considerably dense forests (more than 1.000 stems/ha) (Canut 2001); otherwise, ecotone creation by clear cuttings in extensions of 0.5 ha (never larger than 1 ha) may be a solution for the vegetation regeneration in compatibility with forest

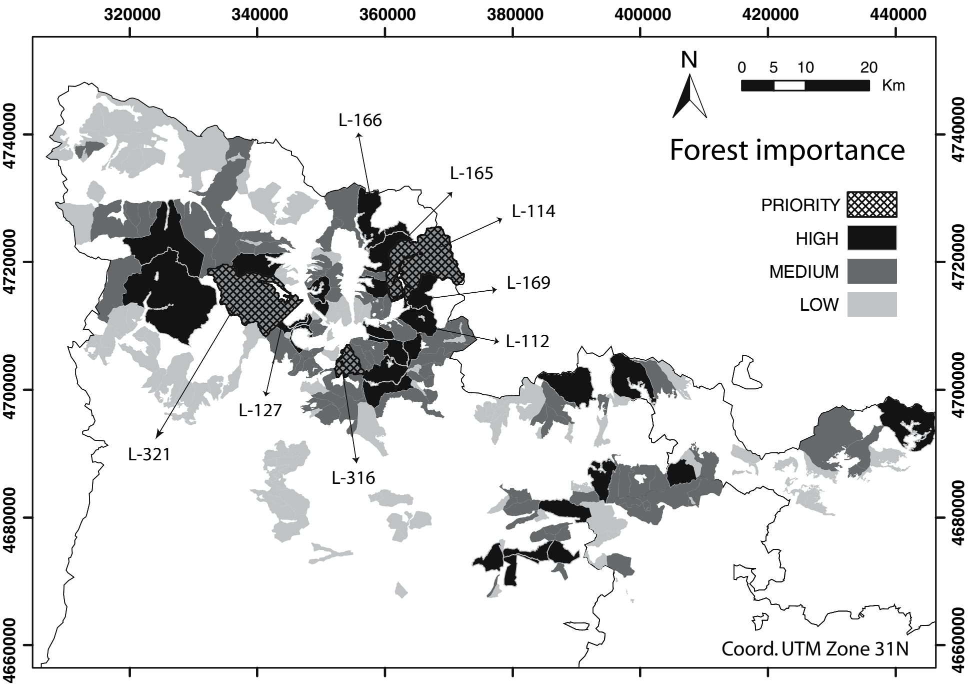

Fig. 3 Classification of public forests in terms of their contribution (accumulated dIIC) to overall capercaillie habitat connectivity, as measured through the integral index of connectivity. Accumulated dIIC for each public forest (forest importance) has been obtained as the sum of the individual importances (dIIC, Eq. 2) of the 1 × 1 km habitat areas (or portions of them) falling within each forest. The three most important public forests have been grouped in the "priority" class. The forests in the low, medium and high classes (including priority forests in this latter class) represent the same amount of total forest area. The *labels* and *arrows* identify the most important public forests listed in Table 1. Public forests with no presence of capercaillie habitat are not shown in this figure. The geographical extent of this figure corresponds to the *rectangle* over Catalonia indicated in Fig. 1

harvesting (Canut 2001; Valkeajärvi and Ijäs 1986). Controlling the number of predators, such as the wild boar (*Sus scrofa*) (Estrada et al. 2004) would most probably decrease capercaillie mortality. Finally, the authorization of forest treatments only outside of the most sensitive periods for capercaillie according to its biological annual cycle, together with the temporal access restriction on certain forest trails (that may entail human frequentation nearby capercaillie vital areas), may help avoid a decrease in the species' low reproductive rate.

Table 1 List of the most important public-managed forests in relation to their contribution to overall habitat connectivity for the capercaillie

Forest ID	Name of forest	Forest total area (ha)	Accumulated connectivity importance dIIC (%)
L-321	Muntanya (Espot)	8,020	29.54
L-316	Viuse (Llavorsi)	1,280	13.10
L-114	Obaga i Solana (Areu)	7,730	12.57
L-112	Obaga (Alins)	1,922	7.02
L-166	Selva de Noarre (Tavescan)	2,553	6.76
L-127	Sta Barbara - Bosc Negre (Escalo i Escart)	450	5.90
L-169	Muntanya (Noris)	1,579	5.82
L-165	Plans de Riberals (Boldis)	1,938	5.10

The accumulated connectivity importance value (dIIC) in each forest is obtained as the sum of the individual importances (dIIC, Eq. 2) of the forest habitat areas (or portions of them) falling within each forest. Only forests with an accumulated dIIC above 5% are listed. Forest total area includes both habitat and non-habitat areas within that forest

Conclusions

Considering the relevance of the connectivity issue in the conservation of many forest-dwelling species it is necessary to explicitly incorporate connectivity in current forest planning and management. The integral index of connectivity (IIC) and the analysis methodology proposed in this study enable the quantification of the individual contribution of every forest habitat area to overall landscape connectivity. By representing a forest habitat mosaic through graph structures and applying appropriate graph-based algorithms (as required by the index IIC) it is possible to obtain these results for large study areas and sets of forest patches, which is the usual situation when tackling conservation problems at the landscape scale.

The analysis of capercaillie habitat in the study region shows the low degree of connectivity existing within the current forest habitat areas, which appear to be clustered in many different and functionally isolated regions. Nevertheless, the amount of habitat area belonging to some of these regions and the evidence of capercaillie's presence in certain zones (Estrada et al. 2004) indicate that dispersal is still present within some regions of capercaillie distribution in Catalonia. The proposed methodology is valuable in order to maintain the current dispersal flux within each connected region, allowing the successful determination of the high-priority forest habitat areas in relation to their contribution to overall degree of connectivity. This analysis has been useful to identify the public forests in which capercaillie-friendly management schemes should be implemented to help guarantee long-term viability of this species. This demonstrates the potential of the methodology for analysing forest connectivity of other species and study areas and, generally, for the effective integration of connectivity considerations in broad-scale forest planning and forest-dwelling species conservation schemes.

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