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A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study

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Abstract

Connectivity is a major concern for the maintenance of wildlife populations, ecological flows, and many other landscape functions. For these reasons many different connectivity indices have been used or proposed for landscape conservation planning; however, their properties and behaviour have not been sufficiently examined and may provide misleading or undesired results for these purposes. We here present a new index (probability of connectivity, PC) that is based on the habitat availability concept, dispersal probabilities between habitat patches and graph structures. We evaluate the performance of PC and compare it with other widespread indices through a set of 13 relevant properties that an index should ideally fulfil for adequately integrating connectivity in landscape planning applications. We found that PC is the only index that systematically accomplished all the requirements, overcoming some serious limitations of other available indices. We encourage the use of PC as a sound basis for planning decision-making. To demonstrate the use and potential of PC for practical landscape applications, we present an example of application to a case study for the goshawk (*Accipiter gentilis*) in Catalonia (NE Spain), where we identify those habitat areas that most contribute to overall landscape connectivity and evaluate the effectiveness and potential improvement of a protected areas network (Natura 2000) for conserving those critical habitat areas.

Keywords: Ecological networks; Landscape connectivity; Patches prioritization; Graphs; Reserve design; Connectivity metrics

1. Introduction

Landscape connectivity has been defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al., 1993). It is considered a key issue for biodiversity conservation and for the maintenance of natural ecosystems stability and integrity (Taylor et al., 1993; Clergeau and Burel, 1997; With et al., 1997; Collinge, 1998; Raison et al., 2001; Crist et al., 2005). As it facilitates animal dispersal, genetic flow and multiple other ecological functions of a landscape (Ricotta et al., 2000), connectivity is a major concern for wildlife population survival (Fahrig and Merriam, 1985) and reduction of extinction risk (Kramer-Schadt et al., 2004). It is therefore essential to consider connectivity as a basis for conservation planning and landscape change analysis (e.g. Nikolakaki, 2004; Noss and Daly, 2006; Pascual-Hortal and Saura, 2006). But before integrating it in operational decision-making it is extremely important to be aware of how connectivity should be measured in this respect (e.g. Calabrese and Fagan, 2004).

Several connectivity approaches and indices have been suggested so far for conservation applications substantially different in their definition and measurement (e.g. Schumaker, 1996; Keitt et al., 1997; Tischendorf and Fahrig, 2000a; Moilanen and Hanski, 2001; Goodwin, 2003; Calabrese and Fagan, 2004; Pascual-Hortal and Saura, 2006). Nevertheless, despite recent efforts in this respect (Tischendorf and Fahrig, 2001; Jordán et al., 2003; Pascual-Hortal and Saura, 2006), there is still a great need for research on the specific properties and measure-

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ment abilities of many connectivity metrics, which is essential to select the most appropriate indices with an objective and sound basis.

Two different types of outcomes are possible when analyzing present landscape connectivity. On one hand, a single index value may characterize the degree of connectivity of the whole landscape; this provides an idea of the current status of the landscape, but is simply descriptive and not particularly relevant for specific landscape planning purposes. On the other hand, an operational connectivity analysis would pursue identifying the most critical landscape elements for the maintenance of overall connectivity (Keitt et al., 1997; Jordán et al., 2003; Pascual-Hortal and Saura, 2006). Most critical landscape elements (typically habitat patches) would be those whose absence would cause a larger decrease in overall landscape connectivity. The relative ranking of landscape elements by their contribution to overall landscape connectivity according to a certain index (I) can be obtained by calculating the percentage of importance ($\mathrm{d}I$) of each individual element (Keitt et al., 1997; Urban and Keitt, 2001; Pascual-Hortal and Saura, 2006; Rae et al., 2007):

$$\mathrm{d}I(\%) = \frac{I - I'}{I} \times 100 \qquad (1)$$

where I is the index value when the landscape element is present in the landscape and I' is the index value after removal of that landscape element (e.g. after a certain habitat patch loss). Conservation efforts and reserve networks should therefore concentrate in protecting those sites (e.g. habitat patches) with a higher $\mathrm{d}I$. However, the results of this analysis may vary largely depending on the selected index. Therefore, using an adequate landscape-level connectivity index is critical for these purposes.

Indeed, many available connectivity-related indices may fail when addressing landscape connectivity for practical landscape conservation planning or change analysis, because they (i) indicate that landscape connectivity increases with increasing habitat fragmentation (Tischendorf and Fahrig, 2000a,b; Pascual-Hortal and Saura, 2006), (ii) predict zero connectivity in any landscape containing just one habitat patch, even if that habitat patch covers the whole landscape (Tischendorf and Fahrig, 2000a), (iii) are insensitive to the loss of (eventually big) isolated patches (Pascual-Hortal and Saura, 2006), or (iv) are unable to detect as more important those key stepping stone patches that when lost disconnect the remaining habitat in two or more isolated sets of patches (Pascual-Hortal and Saura, 2006), among others. Tischendorf and Fahrig (2000a,b) suggested that the measurement of connectivity should be based on immigration rates into equal-sized grid cells, instead of patch-based measures of connectivity, because the latter produced the counter-intuitive conclusion that habitat fragmentation increases connectivity. However, this has been criticized by Moilanen and Hanski (2001), who stated that patch-based measures of connectivity will not present the problem of increasing with fragmentation if they simply take into account the expected numbers of migrants (which may be for example assumed to scale linearly with patch area). Pascual-Hortal and Saura (2006) concluded that landscape connectivity should be considered within the wider concept of habitat availability in order to be successfully integrated in landscape conservation planning applications. Habitat availability is based in considering a patch itself as a space where connectivity occurs, integrating habitat patch area (or other patch attributes like habitat quality) and connections between different patches in a single measure. This approach recognizes that in many cases the connected habitat area existing within the patches themselves may be considerably larger than the one made available by the connections between habitat patches. For a habitat being easily available for an animal or population, it should be both abundant and well connected. Therefore, habitat availability for a species may be low if habitat patches are poorly connected, but also if the habitat is very connected but highly scarce (Pascual-Hortal and Saura, 2006).

Based on this approach, Pascual-Hortal and Saura (2006) proposed a new graph connectivity index (the integral index of connectivity), based on patches rather than cells. This index showed improved properties compared to other analyzed indices by adequately reacting to different relevant changes that can occur in the landscape (including indicating lower connectivity for increased habitat fragmentation) and by effectively identifying the most critical landscape elements (e.g. patches or corridors) for the maintenance of overall landscape connectivity. However, the indices considered by Pascual-Hortal and Saura (2006) were all based on a binary connections model, in which each two habitat patches are either connected or not, with no intermediate modulation of the connection strength or dispersal feasibility (Cantwell and Forman, 1993; Fagan, 2002; Jordán et al., 2003). This binary approach may be considered oversimplified; see for example the drawbacks of considering all patches within a given distance equally weighted in buffer connectivity measures in Moilanen and Nieminen (2002). The connections between habitat patches are best characterized through a probabilistic model, in which there is a certain probability of dispersal among habitat patches, typically modeled as a decreasing function of interpatch Euclidean or effective distance (Urban and Keitt, 2001; Adriaensen et al., 2003).

In this study we present a new landscape-level index, the probability of connectivity (PC), which is based on the habitat availability concept, interpatch dispersal probabilities and graph structures. We compare PC with other available landscape-level connectivity indices from a spatial analysis point of view, evaluating a wide set of desirable properties that an index would ideally fulfill for being adequate for landscape conservation planning and change analysis applications. Finally, to illustrate the use and potential of PC for landscape conservation planning purposes, we present an example of application of this index to a case study for the goshawk (*Accipiter gentilis*) in Catalonia (NE Spain). We analyze the connectivity of the goshawk habitat and identify those areas that most contribute to overall landscape connectivity for this species, evaluating the effectiveness of the Natura 2000 protected areas Network for conserving those critical habitat areas.

2. Methods

2.1. The probability of connectivity index

This new index is based on a probabilistic connections model, in which the dispersal probability p_{ij} characterizes the feasibility of a step between patches i and j, where a step is defined as a direct movement of a disperser between two habitat patches without passing by any other intermediate habitat patches. The p_{ij} for each pair of patches may be obtained in different ways, typically as a decreasing function of edge-to-edge interpatch distance (e.g. exponential function in Briers, 2002; Bunn et al., 2000; Hanski, 1994; Urban and Keitt, 2001, although other functions are also possible), and eventually being $p_{ij}=0$ for patches that are not connected in any way. Edge-to-edge interpatch distances may be computed as Euclidean or, preferably, as effective (minimum cost) distances by considering the variable movement abilities and mortality risk of a species through different land cover types (Tischendorf and Fahrig, 2000b; Ray et al., 2002; Adriaensen et al., 2003; Chardon et al., 2003; Nikolakaki, 2004; Revilla et al., 2004; Marull and Mallarach, 2005; Theobald, 2006). In other cases, p_{ij} may correspond to probabilities directly derived from specific actual movement patterns monitoring or mark-release-recapture methods, but these methods are generally limited to small study areas (Calabrese and Fagan, 2004) where data-intensive measurements can be carried out. Dispersal probabilities (p_{ij}) may also take into account the preference of certain dispersers to move to patches with higher habitat quality, even if they are located further (e.g. Bowne et al., 2006). Landscape level connectivity applications generally consider symmetric dispersal probabilities (the probability of dispersal from patch i to patch j being the same than from patch j to patch i), but asymmetrical probabilities may also be implemented in this model.

The probability of connectivity index (PC) is defined as the probability that two animals randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the connections (p_{ij}) among them. It is given by the following expression:

$$\mathrm{PC} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^{*}}{A_{\mathrm{L}}^{2}} \tag{2}$$

where a_i and a_j are the areas of the habitat patches i and j, and A_{L} is the total landscape area (area of the study region, comprising both habitat and non-habitat patches). These variables can also refer to other attributes different from patch area such as habitat quality or some other patch characteristic that may be considered relevant for the analysis (area-weighted quality, carrying capacity, recruitment-mortality ratio, population size, habitat suitability, core area, etc.). The product probability of a path (where a path is made up of a set of steps in which no patch is visited more than once) is the product of all the p_{ij} belonging to each step in that path. p_{ij}^{*} is defined as the maximum product probability of all possible paths between patches i and j (including single-step paths). If patches i and j are close enough, the maximum probability path will simply be the step (direct movement) between patches i and j ($p_{ij}^{*}=p_{ij}$). If patches i and j are more distant, the "best" (maximum probability) path would probably comprise several steps through intermediate stepping stone patches yielding $p_{ij}^{*}>p_{ij}$. In the particular case that the dispersal probabilities p_{ij} are given by a negative exponential as a function of interpatch edge-to-edge distance (Bunn et al., 2000; Urban and Keitt, 2001), the maximum probability path would be equal to the shortest path in terms of distance units. When two patches are completely isolated from each other, either by being too distant or by the existence of a land cover impeding the movement between both patches (e.g. a road), then $p_{ij}^{*}=0$. When $i=j$ then $p_{ij}^{*}=1$ (it is sure that a patch can be reached from itself); this relates to the habitat availability concept that applies for PC, in which a patch itself is considered as a space where connectivity exists. PC increases with improved connectivity and has a bounded range of variation from 0 to 1. PC equals 0 when no habitat patches are present in the study area, and equals 1 when $\sum_{i=1}^{n} a_i = A_{\mathrm{L}}$ (e.g. when all the landscape is occupied by habitat).

The definition of PC as a probability is equivalent to that for the degree of coherence (Jaeger, 2000), although the indices by Jaeger (2000) do not measure connectivity and do not consider the possibility of dispersal among habitat patches. Moreover, it should be noted that, as long as PC is used for the prioritization of landscape elements for conservation (as quantified by dI, Eq. (1)), it is unnecessary (for dI calculations) to compute or estimate the value of A_{L} (which renders PC interpretable as a probability), since that value will remain constant before and after any landscape change or element removal (A_{L} only depends on the extent of the study area). PC measures connectivity at the landscape level rather than at the patch level (see Moilanen and Hanski, 2001; Tischendorf and Fahrig, 2001). The computation of the PC index benefits from the application of graph-based algorithms for determining the maximum probability paths (p_{ij}^{*}, Eq. (2)). These graph algorithms are computationally powerful and efficient; they have been widely developed in other fields and more recently successfully applied within ecological connectivity studies (e.g. Ricotta et al., 2000; Urban and Keitt, 2001; Jordán et al., 2003; Brooks, 2006; O'Brien et al., 2006; Rae et al., 2007; Theobald, 2006). This is especially useful when it comes to calculate individual importances (dI) for a large number of landscape elements, as is the most typical case when dealing with this type of landscape-level analysis at broad scales. The computation of the PC index and the resultant dI values have been implemented in the new Conefor Sensinode 2.2 software, developed in the University of Lleida by modifying, reprogramming and including new features in the source codes developed by Dean Urban (Duke University) in the LandGraphs package (Sensinode 1.0). A free copy of this software can be obtained by contacting the authors.

2.2. Properties of the PC index and comparison with other connectivity indices

To evaluate the characteristics and performance of PC and compare it with other available indices, we considered a set of 13 desirable properties that any connectivity index that is used for landscape conservation planning applications should ideally fulfill. We are aware that other additional properties may also be evaluated, but we included those considered more relevant according to previous literature in this topic (see references below) and also useful to highlight the differences between the available connectivity indices. The first three properties are desirable for landscape pattern metrics in general (Li and Wu, 2004; Saura, 2004; Garcia-Gigorro and Saura, 2005), while the rest refer to the sensitivity and adequate response of the indices to relevant spatial changes that may affect the landscape (properties 4–9) or to their prioritization abilities when detecting the most relevant landscape elements or changes (properties 10–12), as pointed out in previous researches for these properties (Keitt et al., 1997; Tischendorf and Fahrig, 2000a,b; Jaeger, 2000; Jordán et al., 2003; Pascual-Hortal and Saura, 2006). Only property 13 is considered here for the first time to our knowledge, for the reasons described below. Ideally, a desirable index would accomplish the following properties, providing an affirmative answer to each of the next questions:

(1) Does it have a predefined and bounded range of variation? (independent of the particular analyzed landscape). This is a desirable property of landscape indices in general, which makes them much easier to interpret, especially if the index is relative, ranging from 0 to 1 or from −1 to 1 (Li and Wu, 2004).
(2) Can it be computed both on vector and raster data? Landscape data for the analysis of connectivity are either available as raster data (e.g. per-pixel classifications of satellite images) or vector data (e.g. interpretation or segmentation of remotely sensed images) (Saura, 2002). An ideal index should not be limited by the type of available landscape data, in order to be widely applicable without need of data transformation (e.g. vector to raster), since those transformations may produce considerable distortions in landscape pattern characteristics (Bettinger et al., 1996; Congalton, 1997) and in the outcome of the connectivity analysis.
(3) Is it insensitive to subpixel resampling of landscape pattern? When an index is computed in raster data, it should be sensitive only to the underlying spatial pattern and not to a change in the pixel size if that change does not affect landscape composition or configuration. Some indices may be largely affected by spurious subpixel resampling, which is a serious limitation for their reliable use (Saura, 2004; Garcia-Gigorro and Saura, 2005).
(4) Does it indicate lower connectivity when the distance between patches increases? (while the rest of pattern and patches characteristics remain equal). In more general terms, this property should be understood as proper sensitivity of the index to a change in the interpatch dispersal feasibility, either quantified through distance (Euclidean or effective) or through other functional parameters directly related to the probability of successfully reaching to new habitat (e.g. mortality risk or immigration rates) (i.e. Keitt et al., 1997; Tischendorf and Fahrig, 2000a; Kramer-Schadt et al., 2004).
(5) Does it attain its maximum value when a single habitat patch covers the whole landscape? Some indices suffer from the problem that predict connectivity to be zero in any landscape containing only one habitat patch, even if that habitat patch covers the whole landscape. This is counter to our intuitive understanding of connectivity, which would associate a landscape completely covered with habitat with maximum connectivity and therefore with the highest possible index value for the analyzed landscape (Tischendorf and Fahrig, 2000a,b).
(6) Does it indicate lower connectivity as the habitat is progressively more fragmented? (assuming that it is divided in a larger number of patches but with the same total habitat area). Connectivity metrics should indicate low connectivity as habitat fragmentation increases; otherwise they would provide misleading results for conservation planning applications (Tischendorf and Fahrig, 2000a,b).
(7) Does it consider negative the loss of a connected patch? The loss of a habitat patch will not be in general positive for habitat conservation nor for overall connectivity, no matter if the patch is connected to some degree to other patches (in the sense that the patch presents $p_{ij} > 0$ with at least another habitat patch, property 7) or completely isolated ($p_{ij} = 0$ with every other habitat patch, property 8) (Fig. 1). We here exclude (as well as in property 9) those sink patches that may be having a negative effect for population conservation, which may occur in some circumstances if dispersing animals are not able to differentiate connected sink habitat where mortality exceeds recruitment (e.g. due to hunting or pesticides) from good-condition habitat (Delibes et al., 2001).
(8) Does it consider negative the loss of an isolated patch? (for the same reasons than for the previous property, and assuming that there are other habitat patches in the landscape) (Fig. 1). Note than in some cases a single big isolated patch

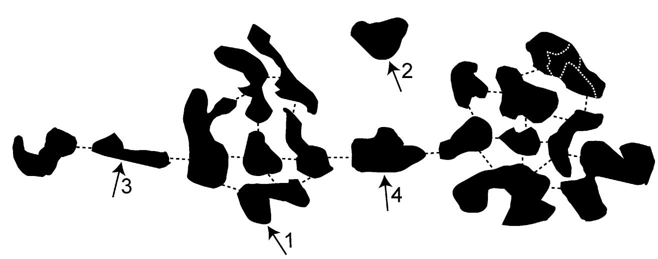

Fig. 1. A simple landscape to illustrate different types of habitat patches (as indicated by the numbered arrows) in terms of their relevance for evaluating the behavior and desirable properties of connectivity indices. Habitat patches are represented in black, and dashed black lines indicate those patches that are interconnected to some degree ($p_{ij} > 0$), while the rest are not directly connected ($p_{ij} = 0$). The different types of habitat patches shown here are: connected but not key stepping stone (patch 1, corresponding to property 7), isolated (patch 2, corresponding to property 8), key stepping stone (patches 3 and 4, corresponding to property 11), and a key stepping stone patch that when lost leaves most of the remaining habitat area still connected (patch 3) in comparison with a key stepping-stone patch that when lost separates the habitat in two disconnected halves (patch 4) (corresponding to property 12). One of the connected habitat areas (upper left) is divided into four different adjacent patches (as indicated by the white dotted lines), as they differ in their habitat quality or belong to different ownerships or administrative units (property 13).

may provide much more available habitat area than all the rest of (small) habitat patches together, even if these small patches are strongly interconnected (Pascual-Hortal and Saura, 2006).

(9) Does it consider negative the loss of a part of a patch? (with no variation in the rest of landscape pattern characteristics, such as number of patches, edge-to-edge interpatch distances, etc.). In the same conditions as for property 7, habitat loss cannot be interpreted in general as positive for habitat conservation or connectivity, no matter if it affects an entire patch or just a portion of it (Pascual-Hortal and Saura, 2006).

(10) Does it detect as more important the loss of bigger patches? (the rest of patches characteristics being equal). A loss of a patch is more relevant the more habitat area that patch comprises, as long as the consequences in terms of interpatch connectivity are identical (Keitt et al., 1997; Pascual-Hortal and Saura, 2006).

(11) Is it able to detect the higher importance of key stepping-stone patches? (the rest of patches characteristics being equal). Key stepping stone patches are more important than the rest of the patches for the maintenance of connectivity (Fig. 1), because their loss causes remnant parts of habitat to be isolated from each other ($p_{ij} = 0$ between the habitat patches belonging to different parts of the landscape) (Keitt et al., 1997; Jordán et al., 2003; Pascual-Hortal and Saura, 2006).

(12) Is it able to detect as less critical those key stepping-stones patches that when lost leave most of the remaining habitat area still connected? (the rest of patches characteristics being equal). A loss of a key stepping-stone patch is less important if it disconnects only a minor part of the total habitat existing in the landscape, while it is more critical if it separates the habitat in two disconnected halves (Fig. 1). This has been noted as important for connectivity indices by Pascual-Hortal and Saura (2006) and is consistent with a desirable structural property previously presented by Jaeger (2000) in the context of fragmentation indices.

(13) Is it unaffected by the presence of adjacent habitat patches? Adjacent (contiguous) habitat patches may be discriminated from each other by having different habitat quality, or as imposed by ownership, administrative or management limits (e.g. protected areas boundaries, forest management blocks or compartments, etc.) (Fig. 1). In many cases the conservation decisions may only be in practice implemented in a part of a habitat area (e.g. in the public but not in the privately owned part). In that case it would be more interesting to prioritize and analyze separately the importance of each of those individual adjacent parts (patches), rather than of the entire habitat area. Ideally, the overall value of an index (and the prioritization and planning decisions derived from it) would not be affected by the division of a habitat area into several adjacent patches for the analysis. This property was considered relevant in this study because the practical application of the indices will require in many cases dealing with this type of adjacent patches (as in the example of application we present later), which is usually dismissed despite its potential importance in the final outcome of the analysis.

We did not include every available connectivity-related index for comparison with PC, since we found it unnecessary and not possible due to space limitations, but we considered those landscape-level indices that (1) are most widespread and have been recommended for measuring connectivity after resulting the best ones in previous comparative analyses of landscape indices (Schumaker, 1996; Tischendorf and Fahrig, 2000a; Pascual-Hortal and Saura, 2006), (2) that are most similar to PC (Bunn et al., 2000; Urban and Keitt, 2001), or that (3) have been specifically developed for landscape conservation planning purposes (e.g. prioritization of habitat patches by their importance for maintaining overall connectivity) (Keitt et al., 1997; Urban and Keitt, 2001). For example, Pascual-Hortal and Saura (2006) compared a set of 10 graph-based connectivity indices in relation to their usefulness and effectiveness for landscape conservation planning and concluded that the integral index of connectivity (IIC) was the one with the best performance; therefore here we will only compare PC with IIC, skipping comparison with the other nine less competitive indices in that study. The eight connectivity indices that are here analyzed and compared with PC are:

- Flux (F) and area-weighted flux (AWF) by Bunn et al. (2000) and Urban and Keitt (2001), which are as well equivalent to a landscape-level version of the incidence function model (IFM) measures (Hanski, 1994; Moilanen and Hanski, 2001; Verheyen et al., 2004) obtained by summing the IFM values for all habitat patches in the landscape:

$$F = \sum_{i=1}^{n} \sum_{j=1, i \neq j}^{n} p_{ij} \quad (3)$$

$$\mathrm{AWF} = \sum_{i=1}^{n} \sum_{j=1, i \neq j}^{n} p_{ij} a_i a_j \quad (4)$$

- Patch cohesion (COH) index (Schumaker, 1996), given by

$$\mathrm{COH} = \left[1 - \frac{\sum_{i=1}^{n} p_i}{\sum_{i=1}^{n} p_i \sqrt{a_i}}\right] \left[1 - \frac{1}{\sqrt{N}}\right]^{-1} \quad (5)$$

where p_i and a_i are, respectively, the perimeter and the area of each of the n habitat patches, and N is the total number of pixels in the landscape. a_i and p_i are expressed respectively as the number of pixels and pixel edges of a patch. In this way, when all habitat patches are confined to single isolated pixels, COH attains its minimum value (COH = 0), while the maximum value (COH = 1) is reached when a single habitat patch fills the whole landscape.

- Integral index of connectivity (IIC) (Pascual-Hortal and Saura, 2006), based on a binary connections model in which two patches are linked (directly connected) if the distance between them is below a certain threshold dispersal distance:

$$\mathrm{IIC} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j/(1+\mathrm{nl}_{ij})}{A_\mathrm{L}^2} \quad (6)$$

where nl_{ij} is the number of links in the shortest path (topological distance) between patches i and j. For patches that cannot be reached from each other (no path exists between them) the numerator in the sum of Eq. (6) equals zero ($\mathrm{nl}_{ij} = \infty$). When $i = j$ then $\mathrm{nl}_{ij} = 0$ (no links needed to reach a certain patch from itself). IIC ranges from 0 to 1 and increases with improved connectivity. IIC = 1 in the hypothetical case that all the landscape is occupied by habitat.

- Correlation length (C) (Keitt et al., 1997; Rae et al., 2007), based on the binary connections model and on the identification of habitat components, where a component is defined as a set of interconnected (linked) patches for a given threshold distance (a path existing between every two patches in a component). It is a raster-based index given by

$$R_s = \frac{1}{n_s}\sum_{i=1}^{n_s}\sqrt{(x_i - x)^2 + (y_i - y)^2} \quad (7)$$

$$C = \frac{\sum_{s=1}^{m} n_s R_s}{\sum_{s=1}^{m} n_s} \quad (8)$$

where R_s is the radius of gyration of component s (as a measure of component size), x and y the mean coordinates of all the habitat cells in that component, x_i and y_i the coordinates of each habitat cell in that component, n_s the number of habitat cells in that component, and m is the number of components in the landscape.

- Dispersal success as quantified by Tischendorf and Fahrig (2000a) and Tischendorf (2001), defined as the total number of immigration events of all individuals into all habitat patches, where an immigration event is the first entry of an individual into a habitat patch not previously visited by that individual. In the dispersal simulation, individuals are first randomly located within a certain habitat patch (Tischendorf, 2001), and this initial patch is not counted as an immigration event (Tischendorf and Fahrig, 2000a). Individuals are allowed to return into previously visited habitat patches throughout dispersal simulation, but this does not contribute to incrementing dispersal success (Tischendorf, 2001).
- Search time, defined as the average number of movement steps that individuals, in the simulated dispersal, need to move to find a new habitat patch (not previously immigrated) from the former patch; only the number of steps taken by individuals who successfully dispersed to a new habitat patch are considered for the average (Tischendorf and Fahrig, 2000a; Tischendorf, 2001).
- Cell immigration (Tischendorf and Fahrig, 2000a; Tischendorf, 2001), which quantifies the rate of immigration into equal-sized habitat grid cells instead of immigration into entire habitat patches (e.g. differently sized territories), being in the rest equivalent to dispersal success (i.e. only the first entry of an individual into a habitat grid cell is counted as immigration event for that individual; individuals are initially located in a habitat cell that is not considered as an immigration event).

2.3. Case study for the goshawk in Catalonia

To illustrate the use and effectiveness of PC for landscape conservation planning applications, we studied the habitat connectivity of a forest-dwelling raptor, the goshawk (*Accipiter gentilis*), in the region of Catalonia, located in the Northeast of Spain (Fig. 2). Catalonia is a heterogeneous region comprising the provinces of Barcelona, Girona, Lleida and Tarragona and with a total extension of 32,107 km^2, including mountainous areas like the Pyrenees (with an altitude up to 3143 m) and a long coastline along the Mediterranean Sea. The climate is, according to Papadakis classification, mostly Mediterranean temperate, with presence also of maritime temperate climate in the coast and temperate cold climate in the Pyrenees. According to the Third Spanish National Forest Inventory, about half of the total area of Catalonia are forests with a canopy cover above 20%, with *Pinus halepensis*, *Pinus sylvestris*, *Quercus ilex* and *Pinus nigra* as the most abundant forest tree species (Ministerio de Medio Ambiente, 2005). The forest-specialist goshawk is a sedentary dispersal-dependent species that is currently considered as near threatened in Catalonia (Estrada et al., 2004) by following the worldwide International Union for Conservation of Nature criteria (IUCN, 2001) and the regional correctors proposed by Gärdenfors et al. (2001). Less than 1000 goshawk-breeding pairs are estimated in Catalonia (Estrada et al., 2004), and this species is suffering from a decreasing population trend mainly associated to the degradation of its forest habitats. Large forest fires and an inadequate management of forest fragments and woodland areas have contributed to the decline of breeding pairs due to the difficulties in finding sufficient wooded areas in a good conservation condition for providing proper breeding sites (Estrada et al., 2004). Since food availability is the primary factor limiting juvenile survival (Wiens et al., 2006a), the preservation of this raptor needs of large and connected forest cover that may allow holding great prey densities and thus, large and permanent goshawk populations (Estrada et al., 2004).

Habitat distribution data were obtained from the Catalan Breeding Bird Atlas (Estrada et al., 2004), which provides the estimated probability of occurrence of the goshawk in 1 km × 1 km UTM squares covering all Catalonia, as a result of field sampling and niche-based modeling (Estrada et al., 2004). Evidence of breeding in the period 1999–2002 was obtained in that atlas by analyzing field data (species occupancy) collected in each UTM 10 km × 10 km square lying completely within the territory of Catalonia. Then, presence-absence data gathered within a large sample of UTM 1 km × 1 km squares that fell within the known 10 km × 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 km × 1 km squares) was predicted through niche-based models, which are based on modeling the species'

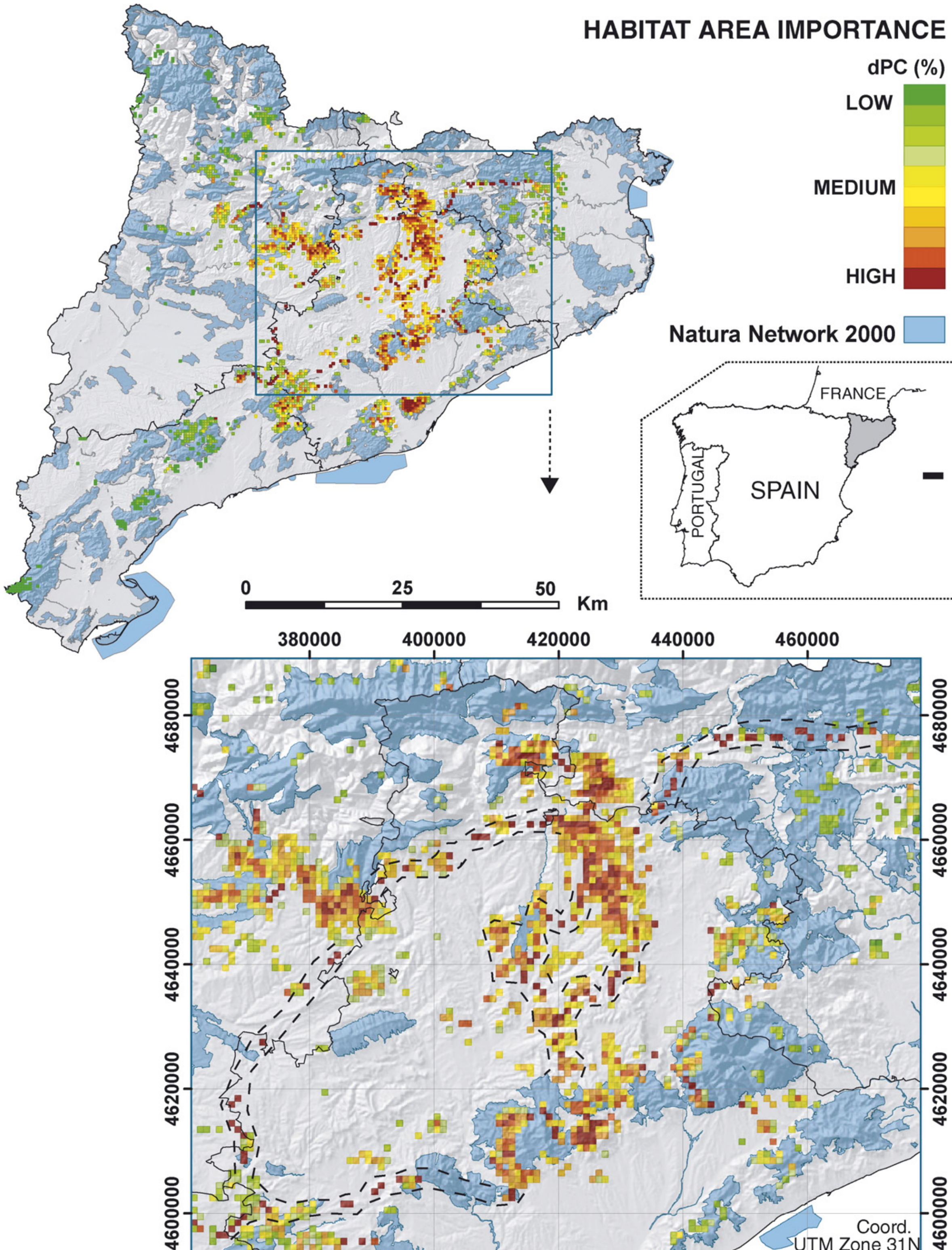

Fig. 2. Importance of each goshawk habitat patch in Catalonia in terms of its individual contribution to the maintenance of overall landscape connectivity as measured by dPC (Eq. (1)). The resultant dPC values are shown in 10 importance classes, each of them containing the same number of 1 km × 1 km habitat patches. The protected areas in the Natura 2000 Network in Catalonia (official version produced by the government of Catalonia on 29 September 2006) are shown in blue color. The dashed lines in the detailed view delineate some examples of corridors of key habitat areas connecting large clusters of goshawk habitat. The location of the study area (Catalonia) is indicated within the map of Spain.

response to a set of environmental variables (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 modeling within this atlas. As a result, goshawk occurrence probability maps for the whole study region were available at a 1 km × 1 km resolution. All squares with a probability of occurrence greater than 0.1 were selected in this study as habitat areas, making up a total of 2352 habitat patches (1 km × 1 km squares) to be analyzed (Fig. 2). The probability of occurrence in each square was considered as a measure of habitat quality and a relevant patch attribute for the analysis (a_i factor in PC index, see Eq. (2)), indicating that patches with higher probability of occurrence are more suitable for goshawks. Note that many of the habitat patches with different quality for the goshawks were adjacent to each other (Fig. 2), as related to property 13.

For the computation of PC index, we applied a decreasing exponential function of the interpatch distance (as in Keitt et al., 1997; Hanski, 1998a; Bunn et al., 2000; Briers, 2002; Urban and Keitt, 2001; Verheyen et al., 2004), from which all interpatch dispersal probabilities (p_{ij}) were calculated as

$$p_{ij} = \mathrm{e}^{-kd_{ij}} \tag{9}$$

where d_{ij} is the edge-to-edge interpatch distance (km) and k is a constant. We set $k = 0.0462$ to obtain a dispersal probability of 0.5 for the 15 km of median natal dispersal distance for the goshawk reported by Wiens et al. (2006b). This distance equals to about four times the diameter of the average breeding territory (3.8 km) in Wiens et al. (2006b), very similar to the corresponding figure in Catalonia, which is 3.6 km as derived from the average of six independent studies for the goshawk in this region (Estrada et al., 2004). This function is also consistent with the dispersal distance of 17 km for the goshawk used by D'Eon et al. (2002), or with the 4% of the goshawks dispersing further than 50 km reported by Glutz et al. (1971).

We evaluated the importance of each habitat patch (1 km × 1 km square) for the maintenance of overall landscape connectivity for the goshawk through the PC index and the Conefor Sensinode 2.2 software, by systematically removing each of the 2352 patches from the landscape and evaluating their individual impact in terms of dPC (Eq. (1) for the PC index).

3. Results and discussion

3.1. Performance of PC and other connectivity indices

Most of the indices failed to accomplish at least some of the properties that would be desirable for an index intended to measure connectivity for landscape planning and change analysis applications (Table 1). The most frequent limitations of the analyzed indices were those related to their performance when detecting the higher importance of certain stepping stone patches (properties 11 and 12), dealing with adjacent patches (property 13), responding to habitat fragmentation (property 5), and reacting to the loss of isolated patches or parts of habitat patches (properties 8 and 9) (Table 1). The probability of connectivity (PC) was the only index that systematically fulfilled all the requirements (Table 1), therefore improving several characteristics of other available indices in this respect.

Particularly bad performance was found for indices like flux, area-weighted flux, patch cohesion, correlation length, dispersal success and search time (Table 1), either by always reacting in the opposite way to that desired or by presenting inconsistent and variable responses for most of the analyzed properties; their use for integrating landscape connectivity in landscape planning applications is thus discouraged from this point of view. For example, the reaction of patch cohesion to some landscape changes was not systematic but dependent on the perimeter and area characteristics of the involved patches; in fact, this is the only information that determines the values of the patch cohesion, which is the only index fully independent on how the patches are distributed throughout the landscape (property 4). For the correlation length the reaction was also variable in some cases, because the loss of a patch can either increase or decrease the radius of gyration depending on the position of that patch within each particular component. The flux and area-weighted flux indices, despite being based on dispersal probabilities like PC, presented a considerably poor performance; this is mainly because they do not consider possible paths between patches that, moving through several intermediate stepping-stone patches, are more optimal than a direct interpatch movement (p^*_{ij} instead of p_{ij}) and because they do not incorporate the habitat availability concept (for instance, there is no interpatch flux when a single habitat patch fills all the landscape; note that the case $i = j$ is not included in Eqs. (3) and (4)). For this latter reason the loss of an isolated patch (property 8) or a part of an isolated patch (a particular case of property 9) are not considered negative by the flux or area-weighted flux indices.

Apart from PC, only two indices fulfilled most of the desired properties: the integral index of connectivity (IIC, not achieving only two of the properties) and the cell immigration (not achieving five of them). The limitations of IIC compared to PC are mostly due to the oversimplified representation of interpatch connections through the binary model, compared to the probabilistic one in which PC is based. Only in cases of data scarcity (in which p_{ij} cannot be estimated) or for simplicity of analysis and interpretation, the use of IIC instead of PC could be justified. However, it should be kept in mind that (1) IIC is not able to adequately deal with adjacent patches (Table 1), (2) IIC is, as any binary index, much more sensitive to uncertainties in the estimation of the threshold dispersal distance than PC, since patches become sharply connected or disconnected depending on that value, and (3) IIC does not modulate the strength of the connection or the dispersal feasibility between any two patches that are separated by a distance above or below the fixed threshold (Table 1). In any case, if the binary connections model is chosen for the analysis, the use of IIC instead of other available binary indices like correlation length should be clearly advocated.

Cell immigration is equivalent to the dispersal success index but considering habitat cells instead of habitat patches. It was proposed as a cell-based index by Tischendorf and Fahrig (2000a) to solve some of the problems presented by the patch-

Table 1
Response of the different indices to the 13 properties relevant for their use for quantifying connectivity in landscape conservation planning and change analysis applications

	Probability of connectivity	Flux	Area-weighted flux	Patch cohesion	Correlation length	Integral index of connectivity	Dispersal success	Search time	Cell immigration
(1) Does it have a predefined and bounded range of variation?	Yes	No	No	Yes	No	Yes	No	No	No
(2) Can it be computed both on vector and raster data?	Yes	Yes	Yes	No (*)	No	Yes	Yes	Yes	No
(3) Is it insensitive to subpixel resampling of landscape pattern?	Yes	Yes	Yes	No (*)	Yes	Yes	Yes	Yes	No
(4) Does it indicate lower connectivity when the distance between patches increases?	Yes	Yes	Yes	No	No (**)	No (**)	Yes	Yes	Yes
(5) Does it attain its maximum value when a single habitat patch covers the whole landscape?	Yes	No	No	Yes	Yes	Yes	No	No	Yes
(6) Does it indicate lower connectivity as the habitat is progressively more fragmented?	Yes	No	No	Yes	No	Yes	No	No	Yes
(7) Does it consider negative the loss of a connected patch?	Yes	Yes	Yes	No	No	Yes	Yes	No	Yes
(8) Does it consider negative the loss of an isolated patch?	Yes	No	No	No	No	Yes	No	No	No
(9) Does it consider negative the loss of a part of a patch?	Yes	No	No	No	No	Yes	No	No	Yes
(10) Does it detect as more important the loss of bigger patches?	Yes	No	Yes	Yes	No	Yes	No	No	Yes
(11) Is it able to detect the higher importance of key stepping-stone patches?	Yes	No	No	No	Yes	Yes	Yes	No	Yes
(12) Is it able to detect as less critical those key stepping-stones patches that when lost leave most of the remaining habitat area still connected?	Yes	No	No	No	No	Yes	No	No	No
(13) Is it unaffected by the presence of adjacent habitat patches?	Yes	No	No	No	Yes	No	No	No	Yes

An ideal index should systematically provide an affirmative answer to each of these questions. An affirmative answer here means that the index consistently achieves that property in every case (i.e., with no variable reaction depending on the particular way a certain type of spatial change occurs). The following special considerations apply when marked by the asterisks: (*) for the original version of the patch cohesion index by Schumaker (1996), but the modification of this index proposed by Saura (2004) may allow fulfilling these properties (**) only indicates lower connectivity if the distance increases from below to above the threshold distance.

based dispersal success, which were mostly related to properties 5 and 6 in this study. However, we show that a cell-based index is not necessary and neither convenient for successfully achieving those desirable properties. PC achieves these and other properties (some of them not fulfilled by cell immigration, see Table 1) while at the same time is a patch-based index. PC does not depend on raster data for its computation and it is therefore of wider applicability, avoiding the pattern distortions that arise when converting vector landscape data to a certain cell size (Bettinger et al., 1996; Congalton, 1997; Rae et al., 2007). More importantly, it should be noted that an arbitrarily high value of the cell immigration index can be obtained for a given landscape by simply fixing increasingly smaller pixel sizes through pattern resampling (property 3), which yields a larger number of cells that can be immigrated. This instability and cell-dependency problem arises when the indices measure immigration events into unitless cells; this may have a considerable impact for landscape analysis purposes, as has been previously noted for other indices like patch cohesion (Saura, 2004; Garcia-Gigorro and Saura, 2005). The solution to the problem that some patch-based indices like dispersal success may present is better solved by a habitat availability index like PC. Even if the analysis was based on equally sized cells, PC presents some advantages compared to cell immigration according to the set of properties considered (Table 1); e.g., cell immigration does not always fulfill property 8, since it is not sensitive to the loss of an isolated habitat patch comprising only one cell. There are additional differences between cell immigration and PC, apart from those shown in Table 1, related to the different approach and way of computing these indices. An overall landscape PC value is obtained in a single processing through graph algorithms, while for cell immigration that overall value is quantified through a large set of simulations of individuals dispersing throughout the landscape (Tischendorf and Fahrig, 2000a; Tischendorf, 2001); those simulations depend also on parameters such as the number of dispersing individuals in the landscape or the type of simulated movement (e.g. random walk), which is not the case for PC. Finally, it should be noted that the cell immigration index, by considering cells of equal characteristics, may not allow easily integrating in the analysis differences such as habitat quality when those may be considered relevant for the final outcome.

3.2. Important areas for the goshawk landscape connectivity

The application of the probability of connectivity index (PC) to the analysis of individual patches importances (1 km × 1 km habitat areas) allows identifying and prioritizing the goshawk habitat sites that most contribute to overall landscape connectivity for this species (Fig. 2), as evaluated by dPC (Eq. (1)). This outcome is particularly useful for landscape planning and reserve design decision-making, as it allows concentrating conservation efforts in those areas that are most important for connectivity maintenance, in which an eventual habitat loss would have more critical impact on the remnant habitat network and on the habitat availability for this species. In this sense the analysis highlights, among others, several examples of critical areas in the form of corridors composed of a series of stepping-stone patches (Fig. 2), such as that with a general SW–NE orientation connecting large clusters of goshawk habitat from the "Sistema Prelitoral Central" (SW) to the "Alta Garrotxa" (NE) through the surroundings of the "Serres de Queralt i els Tossals" protected areas.

The maximum dPC value (%) for a single habitat patch was 1.27% (corresponding to one of the stepping-stone patches in the abovementioned corridor). This is a remarkably high value considering that the goshawk habitat in the study area comprises 2352 1 km × 1 km habitat patches, with a single patch therefore covering only 0.04% of total habitat area. It should be noted that PC is a habitat availability index, as required for an adequate quantification of connectivity in landscape planning applications (Pascual-Hortal and Saura, 2006), therefore integrating both interpatch connectivity and habitat patches attributes (habitat quality in this case) in a single measure. Therefore, a high dPC value for a patch may in general correspond to its importance in terms of interpatch connectivity (e.g. key stepping stone patch), to its intrinsic high habitat quality, or to a combination of both factors. In this case study, the correlation between habitat patch quality and resultant dPC is significant but not high, with Pearson's and Spearman's (rank) correlation coefficients of $r = 0.252$ and 0.481, respectively. A regression between dPC (dependent variable) and habitat patch quality (independent variable) only explained 12% of the variation (as measured by R^2) in dPC values (when fitting a power law, as it resulted the best simple model in terms of R^2 for this regression). This indicates that most of the final importance of each patch for the overall goshawk habitat availability is determined by its topological position within the landscape network and the potentially negative effects of its loss on the mosaic of remnant patches. The contribution of intrinsic habitat characteristics not dependent on the configuration and spatial structure of the habitat in the landscape seems to be comparatively much lower in this case. These results support that connectivity is a critical issue to consider for conservation planning and for the viability of the goshawk populations in Catalonia, which cannot be fully accomplished without explicit reference to landscape-scale connectivity characteristics and related ecological processes.

It should also be noted that the sum of all dPC (%) values (Eq. (1)) for each of the habitat patches in a landscape does not necessarily equal 100%. This sum will be, in most situations, greater than 100%; in this particular study for the goshawk it was 240%. This sum will be larger the more critical habitat areas for connectivity exists in the landscape. For example, if quite many key-stepping stone patches (see properties 11 and 12, Fig. 1) were present (e.g. along a corridor) so that the loss of any of them would disconnect the remaining habitat in two disconnected halves, each of those patches would cause a large decrease in habitat availability when lost (as measured by PC), and eventually their dPC values would, all together, sum up a percentage much larger than 100%. As in other complex systems and ecological networks, the presence of several elements may be necessary for the stability of the whole (e.g. Montoya et al., 2006), where the whole should be considered as more than just the sum of its separated parts.

We compared our results on the critical patches for goshawk connectivity with the European Natura 2000 Network in Catalonia (Fig. 2), which has a great impact in territorial planning in this region. The Natura 2000 Network is a European Union-wide protected areas system based on the Bird Protection Directive (1979) and the Habitat Directive (1992), aiming to create a network covering different habitat types and to promote the conservation of natural habitats and of wild fauna and flora while taking into account the economic, social and cultural requirements and specific regional and local characteristics of each Member State. Our analysis shows that 71% of the important areas for goshawk landscape connectivity fall outside this protected areas Network (as measured by the sum of dPC for all the 1 km × 1 km habitat squares or portions of them located outside this network), including most parts of the abovementioned corridors (Fig. 2). This suggests that the proposed Natura 2000 Network in Catalonia may not be able to protect most of the critical habitat areas for this nearly threatened species. Although enlarging the reserves network may be conflicting by having a considerable socio-economic impact, a remarkable improvement in the network effectiveness for the goshawk could be obtained with a relatively minor increase in protected area; more than the half of goshawk connectivity importance could be protected (51% instead of the current 29% falling inside Natura 2000) by just extending the Natura 2000 Network about 17,000 ha covering the most important corridors and clusters of key habitat areas (Fig. 2). This represents an increase of only 1.6% in the total area of that network.

It should be remarked that our goal was just to illustrate how the PC index can be employed in an example of a landscape planning application, as well as presenting what type of results can be obtained through this index and how they should be interpreted. Therefore, our analysis did not intend to consider all the details that may be of interest to analyze the goshawk connectivity in this region. Our results should be considered only as indicative and as a first planning step that should be refined further before being implemented in practice. This may involve, for instance, considering the effect of different land cover types (e.g. roads) in the goshawk movements, and collecting empirical data on actual connectivity and dispersal distances specific for Catalonia through radio tracking or mark-release-recapture techniques. All these considerations can be as well integrated into the analysis through the PC index. Finally, note that although here we analyzed equally sized squared patches (but with different habitat quality), due to the raster structure of the information in the Catalan Breeding Bird Atlas, the PC index is not restricted to this type of data but is able to handle any other spatial set comprising patches with different sizes, shapes and attributes when necessary.

3.3. Use of PC and other connectivity indices in landscape conservation planning

The rapid expansion of quantitative methods in landscape ecology and the increasing need of objective methods for measuring connectivity have stimulated the development of a wide set of connectivity-related indices that are now available for land managers. However, their properties, behavior and adequacy for landscape conservation planning have not been sufficiently evaluated and the risk of potential misuse is evident. Many of these available indices are often applied without further interrogation about what are they really measuring, in a context where land managers lack of solid and objective guidelines for selecting an appropriate index for their particular applications.

We have evaluated, from a spatial analysis point of view, the advantages and pitfalls of different landscape-level connectivity indices and their potential performance for landscape conservation planning and change analysis applications. We have shown that many of the analyzed connectivity indices that were available for these purposes present serious limitations that discourage their use as a basis for planning decision making (e.g. patches prioritization) according to the set of analyzed properties. On the contrary, the new probability of connectivity (PC) is the only index addressing all the desirable properties, improving some of the characteristics of other existing indices in this respect. PC is a habitat availability index by integrating habitat amount (or other attributes like habitat quality) and connectivity in a single measure. This, together with other features, allows PC being adequately sensitive to the different types of relevant changes that may affect the landscape mosaic, as well as properly identifying the most critical landscape elements for the maintenance of overall landscape connectivity from a habitat availability perspective. The probability of connectivity index is easy to interpret and can be applied in different landscape planning applications through the free Conefor Sensinode 2.2 software, which has been specifically developed for these purposes. For these reasons, we believe that PC is an appropriate and improved index for objective and practical decision making in landscape conservation planning and change analysis, where connectivity considerations should be integrated with a sound and quantitative basis.

However, in practice managers and scientists face the difficulty of getting suitable data to integrate connectivity in applied conservation planning, with different types of indices having different data requirements (Calabrese and Fagan, 2004). Some of the most data-demanding methods rely on direct field measurements of actual connectivity that are too labor intensive and are generally limited to small study areas. Some of the simplest indices that only measure structural connectivity (e.g. nearest neighbor measures) are too crude to be considered as ecologically realist. Analyzing the tradeoff between information content and data requirements, Calabrese and Fagan (2004) concluded that the indices based on the graph-theoretic approach (like PC) "possess the greatest benefit to effort ratio for conservation problems that require characterization of connectivity at relatively large scales. These measures provide a reasonably detailed picture of potential connectivity, but have relatively modest data requirements". In fact, PC is general enough to be adaptable to a wide range of situations with different levels of detail and data availability in the analysis of connectivity, both for characterizing interpatch connections (through Euclidean distances, minimum cost distances, radiotracking data, etc.) and patches attributes (patch area, habitat quality, etc.).

We recognize that PC is not necessarily the best index for every possible application regarding connectivity, but just for the type of landscape planning approach and the set of evaluated properties described in this study. We are aware that other analyses regarding connectivity may require a different approach in which an index different from PC would be more appropriate. For example, other analyses may focus on evaluating connectivity for an individual habitat patch, rather than for the entire landscape as quantified by PC (see Moilanen and Hanski, 2001; Calabrese and Fagan, 2004), or on measuring the capability of a population to rebound from a perturbation affecting a significant habitat proportion, through a long distance landscape rescue effect (Urban and Keitt, 2001). On the other hand, PC is not suited to predict population dynamics, which may be addressed where needed through different types of metapopulation models (e.g. Hanski, 1994, 1998b), assuming that empirical data are available to infer the required model parameters.

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