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Brief note

Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation

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Abstract

The loss of connectivity of natural areas is a major threat for wildlife dispersal and survival and for the conservation of biodiversity in general. Thus, there is an increasing interest in considering connectivity in landscape planning and habitat conservation. In this context, graph structures have been shown to be a powerful and effective way of both representing the landscape pattern as a network and performing complex analysis regarding landscape connectivity. Many indices have been used for connectivity analyses so far but comparatively very little efforts have been made to understand their behaviour and sensitivity to spatial changes, which seriously undermines their adequate interpretation and usefulness. We systematically compare a set of ten graph-based connectivity indices, evaluating their reaction to different types of change that can occur in the landscape (habitat patches loss, corridors loss, etc.) and their effectiveness for identifying which landscape elements are more critical for habitat conservation. Many of the available indices were found to present serious limitations that make them inadequate as a basis for conservation planning. We present a new index (IIC) that achieves all the properties of an ideal index according to our analysis. We suggest that the connectivity problem should be considered within the wider concept of habitat availability, which considers a habitat patch itself as a space where connectivity exists, integrating habitat amount and connectivity between habitat patches in a single measure.

Introduction

Connectivity loss is a major threat for the conservation of biodiversity and the maintenance of the ecological functions of the landscape. Animal dispersal, and consequently population persistence, is one of the most critical processes highly dependent on the degree of landscape connectivity (Johnson et al. 1992; Schippers et al. 1996; Schumaker 1996; Grashof-Bokdam 1997). This has led to an increasing interest in considering connectivity for landscape management and conservation planning purposes.

In this context, graph structures have been shown to be a powerful and effective way of both representing the landscape pattern and performing complex analysis regarding landscape connectivity. Different ecological applications of graph theory focusing especially on connectivity analysis of heterogeneous landscapes for conservation have been recently reported (Keitt et al. 1997; Bunn et al. 2000; Ricotta et al. 2000; Urban and Keitt 2001; Jordan et al. 2003). Several authors (Bunn et al. 2000; Ricotta et al. 2000; Urban and Keitt 2001) suggest graph theory as a computationally powerful adjunct to other approaches that is able to overcome computational limitations that appear when dealing with large data sets (large number of patches). This is indeed the most frequent case when studying a landscape characteristic (connectivity) that has functional significance, and therefore needs to be measured, at broad scales.

A graph is a set of *nodes* (or vertices) and *links* (or edges) such that each link connects two nodes; it may be used for quantitatively describing a landscape as a set of interconnected patches (Ricotta et al. 2000; Urban and Keitt 2001; Jordan et al. 2003). Nodes represent patches of suitable habitat surrounded by inhospitable habitat (non-habitat) (Urban and Keitt 2001). The existence of a link between each pair of patches implies the potential ability of an organism to directly disperse between these two patches, which are considered connected. Links may have a physical correspondence on the landscape in the form of a corridor (e.g. hedgerows). In other cases links may just represent the functional connection between a pair of nodes (patches), and are typically obtained as a function of distance. Distances between patches can be defined as Euclidean distances or, preferably, as minimum cost distances that take into account the variable movement preferences and abilities of the species through different land cover types (Verbeylen et al. 2003; Stevens et al. 2004). The distance between patches is compared with dispersal distances for the animal or plant species under analysis to assign or not a link between those patches. In this study we will consider the existence of connections (links) as symmetric (undirected graphs), although other approaches taking into consideration source/sink dynamics (e.g. Pulliam 1988) could be as well implemented through directed graphs. In the graph theory terminology a *path* is a route along connected nodes (nodes connected by links) in which no node is visited more than once. The length of a path can be measured in terms of either distance units or number of links (topological distance). A *component* (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). 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. If a component can be disconnected by the removal of a single node, this node is a *cutnode* or *cutpatch*. If it is a link removal what causes the disconnection, then this link is called *cutlink*.

Many different connectivity indices have been proposed and used in this context (Keitt et al. 1997; Bunn et al. 2000; Ricotta et al. 2000; Tischendorf and Fahring 2000b; Urban and Keitt 2001; Moilanen and Nieminen 2002; Jordan et al. 2003; Calabrese and Fagan 2004), but there is a lack of comprehensive understanding of their sensitivity to pattern structure and their behaviour to different spatial changes, which seriously limits their proper interpretation and usefulness. As remarked by Jordan et al. (2003) 'in order to help conservation efforts, it would be of outstanding importance to have sensible measures of landscape connectivity and methods for evaluating the importance of spatial elements (patches, corridors) in maintaining connectivity'. Also, Tischendorf and Fahrig (2000a) conclude that 'the response of connectivity measures to habitat fragmentation should be understood before deriving conclusions for conservation management'. In a more general context Li and Wu (2004) state that 'after two decades of extensive research, interpreting indices remains difficult because the merits and caveats of landscape metrics remain poorly understood. What an index really measures is uncertain even when the analytical aspects of most indices are quite clear'.

This study intends to provide further insights in this respect by performing a systematic analysis of the behaviour, characteristics and limitations of the different graph-based connectivity indices. We describe how indices react to the different types of change that can occur in the landscape and how indices differ in predicting which landscape elements (patches, corridors) are more important for the maintenance of overall habitat condition. We present new connectivity indices that show an improved performance in this respect and therefore might be applied more appropriately for the priorization of habitat patches for conservation. Finally we discuss how habitat patches area and the degree of connectivity between habitat patches may be integrated in a single habitat availability measure for an adequate decision making in conservation planning.

Methods

Connectivity indices

We will consider here indices that have been previously described in the literature, as well as new indices proposed by us to improve the properties and characteristics of already available ones. All the indices considered must meet the following requirements, which make them applicable in a wide range of situations for graph-based connectivity analysis: (1) can be calculated on a graph representation of the habitat, that is, as a set of nodes (habitat patches) and links (Boolean connections, each pair of patches being either connected or not connected), (2) can be calculated no matter if the graph has only one component or not, (3) can be used to assign an importance value for overall habitat connectivity to any type of graph elements (nodes, links, components, etc.) or combinations of elements, (4) can be calculated both on vector and raster landscape data. The following 10 indices were analyzed, with higher values of all these indices indicating increased habitat connectivity with the only exception of the number of components:

- *Total number of links* (L) in the habitat.
- *Number of components* (NC) in the habitat.
- *Mean size of the components* (MSC), where the size of a component is the sum of the areas of all the patches belonging to that component.
- *Size of the largest component* (SLC), where the largest component is the one with largest sum of patch areas belonging to that component.
- *Harary index* (H) (Ricotta et al. 2000; Jordan et al. 2003), defined as:

$$H = \frac{1}{2} \sum_{i=1}^{n} \sum_{j=1, i \neq j}^{n} \frac{1}{\mathrm{nl}_{ij}} \tag{1}$$

where n is the total number of habitat patches (nodes), and nl_{ij} is the shortest path between patches i and j in terms of topological distance (number of links). For patches that are not connected (belong to different components) $\mathrm{nl}_{ij} = \infty$.

- *Normalized Harary index* (NH), as described by Ricotta et al. (2000), developed to allow the comparison of habitats with different number of patches:

$$\mathrm{NH} = \frac{\mathrm{H} - \mathrm{H}_{\mathrm{chain}}}{\mathrm{H}_{\mathrm{planar}} - \mathrm{H}_{\mathrm{chain}}} \tag{2}$$

$$\mathrm{H}_{\mathrm{chain}} = (n-1) + (n-2)/2 + (n-3)/3 + \cdots + 1/(n-1) \tag{3}$$

$$\mathrm{H}_{\mathrm{planar}} = \frac{n(n+5)}{4} - 3 \tag{4}$$

- *Graph diameter* (GD), as considered in Urban and Keitt (2001), where the diameter is the maximum length of all shortest paths between any two nodes in the graph. Unlike the shortest path in terms of number of links used in H, NH and IIC indices, the shortest path in GD is computed in distance units. Graph diameter, as defined in Urban and Keitt (2001), is only computed for what they define as the largest component, which corresponds to the component with the largest number of nodes.
- Coincidence probability, with two different versions: *class coincidence probability* (CCP) and *landscape coincidence probability* (LCP). The expressions for these new connectivity indices are:

$$\mathrm{CCP} = \sum_{i=1}^{\mathrm{NC}} \left(\frac{c_i}{A_{\mathrm{C}}} \right)^2 \tag{5}$$

$$\mathrm{LCP} = \sum_{i=1}^{\mathrm{NC}} \left(\frac{c_i}{A_{\mathrm{L}}} \right)^2 \tag{6}$$

where NC is the number of components, c_i is the total area of each component (sum of the areas of the patches belonging to that component), A_{C} is total habitat area (all habitat patches) and A_{L} is the total landscape area (area of the analyzed region, comprising both habitat and non-habitat patches). CCP is defined as the probability that two randomly chosen points within the habitat (class) belong to the same component; alternatively, it can be defined as the probability that two animals randomly placed within the habitat are able to find each other given the set of habitat patches and links. LCP is defined in a similar way as the probability that two randomly points (or animals) located within the landscape (i.e., points can lie either in habitat or non habitat areas) belong to the same habitat component (for which both points should lie in habitat patches and also a path trough links connecting both patches should exist). This index is a generalization of the degree of coherence (Jaeger 2000) by considering components instead of individual patches. As probabilities, both CCP and LCP range from 0 to 1.

– *Integral index of connectivity* (IIC), a new index first presented in this study that ranges from 0 to 1 and increases with improved connectivity. IIC = 1 in the hypothetical case that all the landscape is occupied by habitat. It is given by:

$$IIC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{a_i \cdot a_j}{1+\mathrm{nl}_{ij}}}{A_{\mathrm{L}}^2} \qquad (7)$$

where a_i is the area of each habitat patch and nl_{ij} is the number of links in the shortest path (topological distance) between patches i and j. For patches that are not connected (belong to different components) the numerator in the sum of Eq. (7) equals zero ($\mathrm{nl}_{ij} = \infty$). When $i = j$ then $\mathrm{nl}_{ij} = 0$ (no links needed to reach a certain patch from itself).

Desirable indices properties

The habitat as a connected system comprises both patches and links. Any loss in the elements that make up this system (Figure 1) can be considered negative to preserve the integrity of the habitat and the species that dwell in it, either as a consequence of habitat loss, connectivity loss, or both. Therefore, an ideal index should be sensitive to all these types of landscape changes that can occur (Figure 1) and should do it in a consistent way, i.e. always indicating a worsening in this respect.

On the other hand, among the different changes that can occur in a landscape, some of them may be more critical than others (for different reasons) in terms of their effects on overall habitat condition (Figure 2). An ideal index would be able to discriminate which of those changes are more relevant (Figure 2). Therefore that index would result adequate as a quantitative basis for priorizing the conservation of those landscape elements (patches, links, etc.) that are more critical for the maintenance of overall habitat connectivity. Jordan et al. (2003) also discussed how various connectivity measures differ in predicting critical landscape elements, although here we considerably broaden and improve this type of analysis.

Despite the fact that all indices provide an estimation of the current landscape 'degree of connectivity', this specific number little helps planners in the comparison of alternative management actions or conservation plans. The relative ranking of patches by their contribution to overall landscape connectivity is most useful in the decision process (Keitt et al. 1997; Urban and Keitt 2001). For calculating the importance of each particular landscape element (or change), comparisons need to be made with the *delta* values for each index (*dI*):

$$dI = 100 \cdot \frac{I - I'}{I} \qquad (8)$$

where I is the index value before the change and I' the value of the same index after the change (e.g. after a certain patch loss). Thus, *dI* may be either positive or negative depending on the type of change and on the definition and behaviour of each index. The importance of each landscape element would be the *dI* value resulting from the removal of that element from the landscape (with a higher *dI* indicating higher element importance for all the indices but NC, which should be interpreted in the opposite way). These *dI* are therefore considered more relevant for conservation planning (landscape elements priorization) and have been taken into account for further discussion. We developed a new version of the Sensinode software (by modifying the version 1.0 of the LandGraphs package developed by Urban and Keitt (2001))

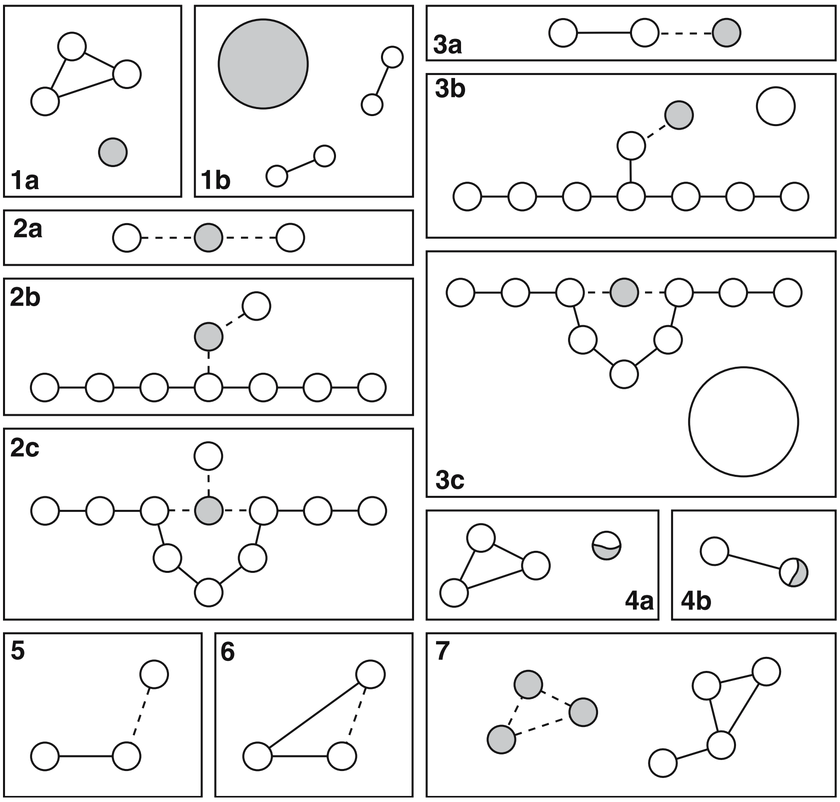

Figure 1. Different cases illustrating seven types of change corresponding to the loss of habitat patches (nodes, represented as circles of different areas), parts of patches, or connections between the patches (links, represented as lines). Patches (or parts of patches) that are lost are indicated in grey colour, and links that are lost are indicated by dashed lines. We assume that when a patch is lost also the links (functional connections) coming from it are lost. On the contrary, link loss does not imply the loss of the previously connected patches (cases 5 and 6 in Figure 1), and will be typically caused by the alteration of the land uses between the patches (e.g. construction of a road impeding the movement of certain species between those patches). The represented changes are: (1) loss of an unconnected patch (a patch with no links), (2) loss of a cutpatch, (3) loss of a connected patch but non-cutpatch, (4) loss of a part of a patch (with no link variation), (5) loss of a cutlink, (6) loss of a non-cutlink, (7) loss of an entire component (with more than one patch). In some cases more than one case per change type is included to illustrate some of the different reactions of certain indices depending on how that particular change occurs.

that computes the *dI* values for the ten connectivity indices and for each of the patches in a landscape graph.

Results and discussion

Indices sensitivity to landscape changes

IIC is the only ideal index in the sense of reacting to all types of change in a desirable and consistent way (Table 1). LCP also presented a good behaviour in this respect, being sensitive to all changes but to the loss of a non-cutlink (Table 1). The rest of the indices behave in an irregular and undesired way (according to our preferences) and therefore are less suitable, in more or less degree, for an analysis of this kind (Table 1). Especially inconsistent behaviour was found for indices like GD, CCP or NH (Table 1). This is what Li and Wu (2004) consider an inherent limitation of landscape indices, 'the variable and sometimes unpredictable responses to certain changes in spatial pattern' which 'may lead to misuse of landscape indices' because 'they cannot capture or distinguish some of the fundamental changes of landscapes in many situations'.

GD and SLC present the problem of being insensitive to any change that affects a patch or link not belonging to the largest component, which may occur frequently in fragmented landscapes. In addition, GD will only react to changes affecting elements that are integrating part of the diameter

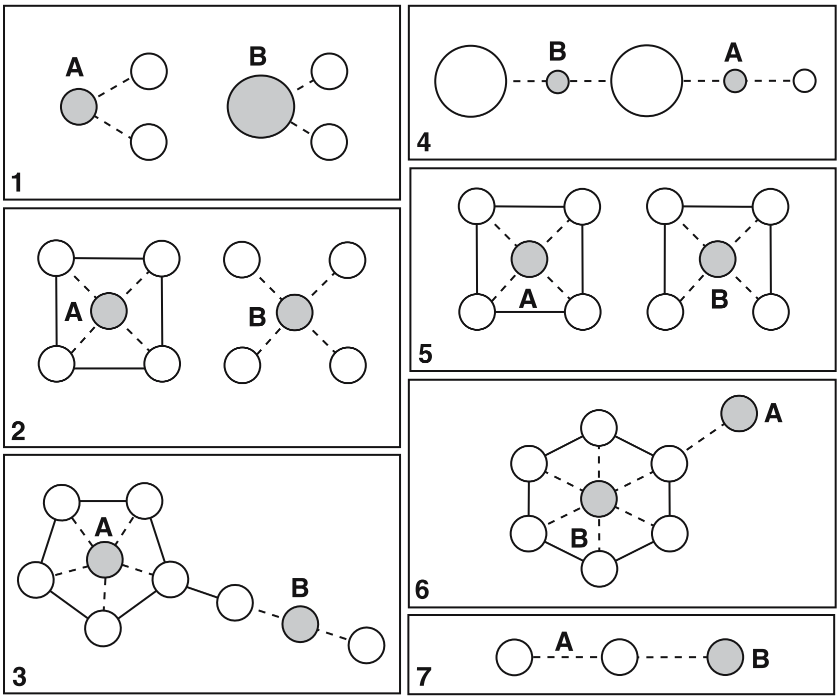

Figure 2. Seven cases to test the indices priorization skills, each showing a single landscape in which two changes (element losses) can occur (either A or B can be lost, but not both at the same time). Patches that are lost are indicated in grey colour, and links that are lost are indicated by dashed lines. We assume that when a patch is lost also the links (functional connections) coming from it are lost. In all the cases the change B is considered to be worse (more important) than A for the following reasons: bigger size of the patch lost (1), loss of a patch that disconnects the graph or component (cutpatch) (2 and 3), smaller size of the remaining largest component (4), increased topological distance between remaining patches (5 and 6), and habitat loss and link loss (patch B and the link coming from it) vs. only link loss (only link A) (7). We would therefore require from an ideal index to always assign a higher importance value (higher *dI*) to element B than to element A.

in that largest component: changes like 2b and 3b in Figure 1 would remain unnoticed (Table 1). Even if the affected elements do belong to the largest component and are part of the diameter, the reaction of GD to patches loss is variable, decreasing in some cases (changes 2a and 3a in

Table 1. Indices reaction to the different change types illustrated in Figure 1, indicating that: (−) the index decreases after that change, (+) the index increases after that change, (0) the index is not sensitive to that change.

Type of change	Index									
	L	NC	MSC	SLC	H	NH	GD	CCP	LCP	IIC
1. Loss of an unconnected patch (patch with no links)	0	−	+/0/−	0/−	0	+/0/−	0	+/0/−	−	−
2. Loss of a cutpatch	−	+	−	0/−	−	+/0/−	+/0/−	−	−	−
3. Loss of connected patch but non-cutpatch	−	0	−	0/−	−	+/0/−	+/0/−	+/0/−	−	−
4. Loss of part of a patch	0	0	−	0/−	0	0	0	+/0/−	−	−
5. Loss of a cutlink	−	+	−	0/−	−	−	0/−	−	−	−
6. Loss of a non-cutlink	−	0	0	0	−	−	+/0/−	0	0	−
7. Loss of an entire component (with more than one patch)	−	−	+/0/−	0/−	−	+/0/−	0/−	+/0/−	−	−

The indices reaction reported here considers all the different ways in which each type of change can occur, and not only the specific cases illustrated in Figure 1. Inconsistent behaviour of some indices, with their reaction depending on the particular way that type of change occurs, is indicated by combinations like (+/0/−) or (0/−).

Figure 1) but increasing in others (changes 2c and 3c in Figure 1). Another index with a considerably inconsistent behaviour is CCP: when a certain type of change occurs it may decrease (changes 1b and 3b in Figure 1), increase (changes 3c and 4a in Figure 1) or remain equal (changes 3a and 4b in Figure 1).

Ricotta et al. (2000) noted the limitations of H to compare the connectivity of landscapes with different number of patches and suggested the normalized expression of H (NH) as an effective index to quantify landscape connectivity in a meaningful way, allowing for comparison of landscape structures across space and time. However, NH reacts in an undesired and inconsistent way to many of the spatial changes considered (Table 1), being clearly worse than H in this respect.

Indices priorization skills

Most of the indices failed to detect the higher relevance of element B in some of the comparisons in Figure 2 (Table 2), and especially bad behaviour was found for indices like L, NC, NH or GD. IIC is the only index that showed adequate priorization skills in all the cases considered (Table 2). After IIC, LCP is the best performing index in this respect, but does not discriminate whether a certain patch loss produces or not an increase in the topological distance between remaining nodes (cases 5 and 6 in Figure 2), like many other indices (Table 2).

Nearly all the indices were unable to recognize as more important the loss of a patch than just the loss of the link that connects that patch to the rest of the habitat (case 7 in Figure 2). This is the case, among others, of those indices that do not explicitly consider patch area in their computation (L, NC, H, NH, GD). This is an intrinsic limitation for the use of these five indices for patches priorization, because being all the rest equal, any conservation plan would prefer to retain the biggest patches (like in case 1 in Figure 2).

Most of the indices were able to discriminate the situation where a patch (cutpatch) loss breaks up the habitat in two unconnected components (cases 2 and 3 in Figure 2 and Table 2). However, only SLC, CCP, LCP and IIC were able to detect if that change breaks up the system in two unconnected halves (in terms of habitat area) or if most of the habitat is still connected after that change and the part that gets disconnected is much smaller (case 4 in Figure 2 and Table 2).

From habitat connectivity to habitat availability

Many of the indices (L, NC, GD, CCP, H) identify as 'more connected' a landscape with two connected 1-ha habitat patches (a link existing between both patches, situation 1) than a landscape with two unconnected 100-ha habitat patches (situation 2). Although this may be consistent with a definition of connectivity as the degree to which the landscape facilitates or impedes movement *among habitat patches* (Taylor et al. 1993), situation 1 by no means can be considered better than situation 2. In fact the 1-ha patches in situation 1 may be the result of a huge fragmentation and habitat loss process in just one of the 100-ha pat-

Table 2. Priorization skills of the indices for the different specific cases shown in Figure 2, indicating which element loss (either A or B) is considered more important (worse) in terms of *dI* [relative variation of the index after that loss, Eq. (8)].

Priorization skills comparisons	Index									
	L	NC	MSC	SLC	H	NH	GD	CCP	LCP	IIC
1. Bigger size of the patch lost	=	=	B	B	=	=	=	B	B	B
2. Loss of a cutpatch (first case)	=	B	B	B	B	B	B	B	B	B
3. Loss of a cutpatch (second case)	A	B	B	B	A	A	B	B	B	B
4. Smaller size of the remaining largest component	=	=	=	B	=	=	=	B	B	B
5. Increased topological distance (first case)	=	=	=	=	B	A	A	=	=	B
6. Increased topological distance (second case)	B	=	=	=	B	B	A	=	=	B
7. Habitat + link loss vs. only link loss	=	A	A	=	=	A	=	A	B	B

Certain indices assign the same importance to both changes (=). An ideal index should give always more importance to B in these specific comparisons.

ches of situation 2. A key point that we suggest in this respect is that a patch itself should be considered as a space where 'connectivity' occurs (or can occur). It is true that the two patches in situation 1 are connected but this yields only 2 ha of total connected habitat area, while in situation 2, even when the patches are not connected, each of them provides 100 ha of 'connected' habitat area. In many situations the connected area existing within the patches themselves may be much larger than the one existing due to the connections (links) between habitat patches. If an index only considers connectivity according to the strict definition of connection among patches (without considering the connectivity that occurs within habitat patches themselves) it will surely perform poorly as a guideline for conservation, and its use in this context should be avoided.

This gives rise to the concept of habitat availability, characteristic of the landscape that integrates both habitat area and habitat connectivity. 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. A habitat availability index will detect situation 2 as preferable to situation 1. The new developed indices IIC and LCP are habitat availability indices in this sense, integrating habitat patches area and connectivity between habitat patches in a single index. We suggest that a successful integration of connectivity considerations in the conservation decision making should be performed through these habitat availability concept and type of indices that we have presented in this study.

Patch attributes

Indices like IIC, CCP and LCP include in their expressions [Eqs. (5)–(7)] a descriptive variable for patches (a_i) that can be generalized to include other relevant patch attributes related to its composition and habitat quality (vegetation types and structures present in the patch, habitat suitability index, population sizes, carrying capacity, species rarity, etc.), and not only patch area. Therefore, any of the considerations about patch area reported before in this paper could be interpreted in more general terms as affecting some of the attributes of the node. This applies to the concept of habitat availability as well as to the different patches areas and habitat loss processes considered (Figures 1 and 2), with the performance of the indices being in this case the same to those already reported in Tables 1 and 2. This may improve the ecological realism of the analysis, and meet the need for the development of 'new "topoecological" indices that introduce qualitative differences among distinctive patches in the calculation of topological indices' (Ricotta et al. 2000).

Conclusions

Most of the indices that have been proposed and used for landscape connectivity analysis have not undergone a scrutiny of their behaviour and properties that should be tackled prior to the operational use of these indices. We performed a systematic analysis of the sensitivity to landscape changes and priorization skills of graph-based indices and showed that many of them present serious limitations that make them inadequate as a basis for conservation planning.

We suggest that the habitat availability approach is necessary to successfully incorporate landscape connectivity considerations in conservation planning. The habitat availability concept is based in considering a patch itself (even if it is isolated from the rest of the habitat) as a space where connectivity occurs (more the bigger the patch). IIC and LCP are habitat availability indices in this sense, integrating habitat patches area (and other patches attributes) and connectivity between habitat patches in a single measure.

The new IIC index achieves all the properties of an ideal index according to our preferences and to the set of analyzed cases, being both sensitive to all types of negative changes that can affect the habitat mosaic and effective detecting which of those changes are more critical for its conservation. IIC also has a defined and bounded range of variation (from 0 to 1), which is one of the desirable properties of landscape indices in general (Li and Wu 2004). The IIC index is general enough to be applicable to any landscape graph, either fully connected or not, and can evaluate the importance for maintaining overall connectivity of any landscape element or combination of landscape elements, which was not accomplished by several of the previously available connectivity indices. A good performance was also found for the LCP index, which can be directly interpreted as a probability. LCP shares many of the advantages described for IIC but is unable to discriminate whether a certain element loss produces or not an increase in the distance between the remaining connected patches.

Overall, we provide guidelines for a better understanding and a proper use and selection of connectivity-related indices, and we believe that our results may help planners to adequately incorporate connectivity considerations in the conservation decisions and in the analysis of landscape pattern change.

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