Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments

Örjan Bodin [a,b,*], Santiago Saura [c,1]

[a] Stockholm Resilience Centre, Stockholm University, 106 91 Stockholm, Sweden
[b] Department of Systems Ecology, Stockholm University, 106 91 Stockholm, Sweden
[c] E.T.S.I. Montes, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040, Madrid, Spain

ABSTRACT

Here we propose an integrated framework for modeling connectivity that can help ecologists, conservation planners and managers to identify patches that, more than others, contribute to uphold species dispersal and other ecological flows in a landscape context. We elaborate, extend and partly integrate recent network-based approaches for modeling and supporting the management of fragmented landscapes. In doing so, experimental patch removal techniques and network analytical approaches are merged into one integrated modeling framework for assessing the role of individual patches as connectivity providers. In particular, we focus the analyses on the habitat availability metrics *PC* and *IIC* and on the network metric *Betweenness Centrality*. The combination and extension of these metrics jointly assess both the immediate connectivity impacts of the loss of a particular patch and the resulting increased vulnerability of the network to subsequent disruptions. In using the framework to analyze the connectivity of two real landscapes in Madagascar and Catalonia (NE Spain), we suggest a procedure that can be used to rank individual habitat patches and show that the combined metrics reveal relevant and non-redundant information valuable to assert and quantify distinctive connectivity aspects of any given patch in the landscape. Hence, we argue that the proposed framework could facilitate more ecologically informed decision-making in managing fragmented landscapes. Finally, we discuss and highlight some of the advantages, limitations and key differences between the considered metrics.

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1. Introduction

Network-based modeling approaches are receiving increased interests in ecology (e.g. Bascompte, 2009; Bodin, 2009). Species interactions in food webs and plant-pollinator networks are two fields where network analysis is successfully applied (e.g. Bascompte et al., 2006; Pascual and Dunne, 2006). In landscape ecology and metapopulation studies network-based models (or graph theoretical as they are often called) are used to describe and analyze the possibilities for species movement among spatially separated patches of habitats in heterogeneous landscapes (Keitt et al., 1997; Urban and Keitt, 2001; Jordán et al., 2003; Pascual-Hortal and Saura, 2006; Bodin and Norberg, 2007; Fall et al., 2007; Estrada and Bodin, 2008; Urban et al., 2009; Saura and Rubio, 2010). Individual habitat patches are here modeled as nodes in a spatially explicit

landscape-wide network, and the links between the nodes represent possibilities for movement or dispersal between them (i.e. functional connectivity, see Taylor et al., 1993).

In general, network-based models and metrics have been suggested to possess a convenient benefit to effort ratio for conservation problems that require characterization of connectivity at relatively large scales (Calabrese and Fagan, 2004). They provide a spatially explicit representation of the landscape connectivity that is still usable even when the available information is relatively scarce, as is usually the case in real-world planning applications (Calabrese and Fagan, 2004). In addition, recent studies show that some network metrics are just as good as other more complex and biologically detailed metapopulation models in terms of their ability to, for example, identify habitat patches and linkages where conservation or restoration efforts could favorably be concentrated (Minor and Urban, 2007; Visconti and Elkin, 2009). Even though many of the adaptations of network science to the analysis of ecological connectivity are quite recent, there are already numerous examples of their application for landscape conservation planning purposes (e.g. Pascual-Hortal and Saura, 2008; Phillips et al., 2008; Perotto-Baldivieso et al., 2009; Vasas et al., 2009; Fu et al., 2010; Laita et al., 2010). In addition, recent empirical studies have also

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* Corresponding author at: Stockholm Resilience Centre, Stockholm University, 106 91 Stockholm, Sweden. Tel.: +46 703 410121; fax: +46 8 6747020.

E-mail addresses: orjan.bodin@stockholmresilience.su.se (Ö. Bodin), santiago.saura@upm.es (S. Saura).

[1] Tel.: +34 91 336 71 22; fax: +34 91 543 95 57.

demonstrated the capacity of the network approach to explain relevant ecological processes and patterns related to landscape connectivity (e.g. O'Brien et al., 2006; McRae and Beier, 2007; Neel, 2008; Andersson and Bodin, 2009).

Network-based modeling approaches currently applied in assessing and ranking habitat patch importance can, broadly, be classified into two different categories. The first category uses a two-stage process. First, a specific network metric developed to assess some aspect of the landscape's connectivity is chosen and calculated for a given landscape. Then, each individual patch (i.e. node) is removed, one at the time, and the resulting effect on the metric is recorded (e.g. Urban and Keitt, 2001; Saura and Pascual-Hortal, 2007). Patches are then ranked according to how much the connectivity metric decreased when they were removed. Hence, this category uses experiments (albeit theoretical) to assess patch importance. The second category uses properties or characteristics of the intact network to assess the importance of each and every individual patch. Here, network centrality is a key concept. Various variants of network centrality have been developed within the multidisciplinary field of network analysis (e.g. Wasserman and Faust, 1994). A common denominator for all these variants is that they assess different aspects of how *influential*, based on its topological position in the network, a specific node might be. Recently, a set of different centrality measures were tested and analyzed in terms of their potential in assessing individual patches' contribution to different aspects of landscape connectivity (Estrada and Bodin, 2008).

These two categories have different benefits and limitations. The category based on experiments delivers easily interpretable answers on what would be consequence of the removal of a particular patch (i.e. the importance of a patch equals the reduction of the connectivity metric following its removal). However, this approach is implicitly based on the assumption that the organisms that used to move through a particular patch are able to find the alternative dispersal pathways throughout the reduced network of patches, and that no competition among the dispersers for the use of the fewer remnant pathways limits the movement abilities of the species in the disturbed landscape.

Measures of a node's centrality, on the other hand, assess patch importance based on the network model of the intact landscape. In effect, they are aimed to assess how much (or in what way) a particular patch is involved in the *current* flows of organisms in the undisturbed landscape. Hence, they do not explicitly try to capture how the flows might change as a consequence of losing a particular patch. For this reason, centrality measures do not deliver easily interpretable estimates of the connectivity loss following a patch removal.

Furthermore, none of the methods in these categories are particularly good in predicting how vulnerable the remaining landscape would be, beyond the loss of a particular patch, to further patch removals. Using experimental approaches, such assessments are inherently difficult since they require the researcher to specify a non-arbitrarily chosen patch removal sequence beforehand. In contrast, assessments of patch importance using centrality measures do not require the researcher to specify a specific patch removal sequence. However, the centrality assessments are based on the intact network, and they will inevitably lose relevance as more and more patches are removed from the undisturbed landscape.

The discussion above shows that it would be desirable to (where relevant) bridge these different categories in such a way that their pros are preserved while their different cons are suppressed. Also, there is a need for new methods and metrics that help to assess the increases in landscape vulnerability following the removal of a certain patch. In this paper, we contribute to such development by undertaking integrated analytical investigations of the recently proposed habitat availability (reachability) metrics probability of

connectivity (*PC*) (Saura and Pascual-Hortal, 2007) and integral index of connectivity (*IIC*) (Pascual-Hortal and Saura, 2006), and the network centrality metric betweenness centrality (*BC*) (Freeman, 1977; Bodin and Norberg, 2007). The change in the *PC* and *IIC* metrics following experimental removals of individual patches can be partitioned in three different fractions which are relevant in assessing the different ways a habitat patch can contribute to habitat connectivity and availability in the landscape. In particular, one of these three fractions (the connector fraction described further down) evaluates a patch's contribution to connectivity between other patches by acting as a intermediate stepping stone patch (Saura and Rubio, 2010). As related to this fraction, *BC* measures how much a specific node sits between all other pairs of nodes in a network, i.e. it captures how many pairs of nodes are connected through that specific node (Freeman, 1977). A particular patch with a high score on *BC* may then experience comparative large flows of individuals that come not only from nearby patches, but also from patches which could be located quite far away in the landscape (Bodin and Norberg, 2007).

Based on the analyses of the *PC*, *IIC* and *BC* metrics, we suggest some extensions of the *BC* metric in order to more clearly link these metrics together in a common modeling framework. We show how this framework can be used to identify critical patches upholding dispersal processes in a fragmented landscape and to assess the distinctive contributions of individual habitat patches to connectivity. These analytical developments are tested and evaluated using data from two real-world landscapes in Madagascar and Catalonia (NE Spain). Based on these results, we suggest a procedure that could be used to rank patch importance. We conclude by discussing the scope of application and ecological relevance of each of these metrics in assessing various aspects of landscape connectivity.

2. Materials, methods and calculations

2.1. Habitat availability and network centrality

2.1.1. The habitat availability metrics PC and IIC

PC is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (see Table 1 for further details), and is given by (Saura and Pascual-Hortal, 2007):

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

where n is the number of habitat patches existing in the landscape, each with an habitat area a_i (a_i could instead represent some other relevant patch attribute such as habitat quality, although we, for the sake of simplicity, here only use it to represent area) and A_L is the total landscape area (both habitat and non habitat). p_{ij} is the probability of a species moving directly from patch i to j (without passing through any intermediate patch). Using network terminology, there is a link between patches i and j, and the weight of that link is set to the probability of direct dispersal between the two. Although there are several other possibilities, the probability p_{ij} is typically computed based on a negative exponential dispersal kernel (Hanski, 1994; Bunn et al., 2000; Hanski and Ovaskainen, 2000; Saura and Pascual-Hortal, 2007). In heterogeneous landscapes where the matrix is composed of several different types of land, the permeability of the matrix differs accordingly. In such cases, an appropriate option would be to apply a cost-distance approach to assess the probability of dispersal between patches i and j (e.g. Bunn et al., 2000; Fu et al., 2010). Irrespectively of which technique is used to assess the movement probabilities p_{ij}, all the analyses and models we apply throughout this paper, and all conclusions we draw from these analyses, are equally applicable. p_{ij}^* is

Table 1
Summary of the metrics used in developing the integrated modeling framework of connectivity presented here. Those metrics that are equivalent, i.e. the only difference is them being based on either the *PC* or *IIC* metrics (e.g. $dPCconnector_k$ and $dIICconnector_k$), are described as pairs.

Metric	Description and ecological interpretation
Probability of connectivity (PC)	A habitat availability (reachability) index taking into account varying probabilities of direct dispersal (p_{ij}) between different pairs of patches. It measures the probability that two animals randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected). This requires that both points fall into habitat areas and, in addition, that both points either fall (1) within the same habitat patch or (2) into different but connected patches so that it is possible to move between them through the links in the network.
Integral index of connectivity (IIC)	A habitat availability (reachability) index based on a binary network (unweighted links) as the underlying model of the fragmented landscape. It is similar to PC but, instead of assessing the *probabilities* for dispersal between all pair of patches, this metric uses estimates of *possibilities* for dispersals between all pairs of patches. Hence, if direct dispersal between any two patches in the landscape is assessed as being possible, the link strength is set to unity. Otherwise, it is set to 0 (i.e. no link is assigned between the two patches).
$dPC_k/dIIC_k$	The loss of habitat availability caused by the removal of patch k, evaluated as the relative decrease (%) in the PC or IIC value following the removal. It takes into account the area of habitat patch k, the estimated dispersal fluxes that start or end in patch k, and the contribution of patch k as a stepping stone or connecting element that upholds the connectivity between other habitat areas (see $dPCconnector_k/dIICconnector_k$ below).
$dPCconnector_k/dIICconnector_k$	The fraction of $dPC_k/dIIC_k$ corresponding to how much patch k contributes to connectivity between *other* patches by serving as an intermediate stepping stone (connecting element) that cannot be fully replaced by other patches in the network. This contribution depends only on the spatial (topological) position of patch k in the landscape. A high value implies that the loss of k would severely reduce the connectivity between other habitat patches.
Betweenness centrality (BC_k)	The sum of all shortest pathways between all pair of patches that go through patch k. Captures how much patch k sits between all other pairs of patches in a landscape, i.e. how much patch k is involved in movements between other pairs of patches by serving as an intermediate stepping stone patch. Patches with high scores on BC_k have been suggested as making up the backbone of the landscape since a disproportional high number of the shortest pathways throughout the whole landscapes go through these patches.
BC_k^{PC*}/BC_k^{IIC*}	A generalization of the BC_k metric that takes into account patch areas and maximum product probabilities (PC-based version) or topological distances (IIC-based version) between patches instead of only the number of shortest paths. In this way, this generalized metric assigns more weight to the paths that are expected to carry larger flows of organisms and that connect bigger and therefore likely more ecologically important patches. These adjustments add more ecological relevance to the BC_k metric when used in assessing connectivity in fragmented landscapes.
$C(50)_k^{PC*}/C(50)_k^{IIC*}$	Minimum number of patches that are able to compensate and (partially) replace >50% of the connectivity (as measured by BC_k^{PC}/BC_k^{IIC}) that is lost following the removal of patch k. A high value implies a less vulnerable network in terms of further patch removals since there are, by definition, many patches that will significantly contribute in compensating for the loss of patch k. If, on the other hand, only one patch by itself stands for all compensation (i.e. $C(50)_k^{PC}$ or $C(50)_k^{IIC} = 1$), the landscape network would likely be very vulnerable to the loss of that particular patch.

[*] Metrics developed in this work.

the maximum product probability, i.e. the maximum value of the product of the link weights (p_{ij}) of all the possible paths connecting patches i and j. Note that one or several intermediate links might be included in computing p_{ij}^*, representing all intermediate steps that an organism would have to pass along when following the 'optimal' path (in terms of probability) from i to j. When $i=j$ then $p_{ij}^* = 1$ (a patch can always be reached from itself); this relates to the habitat availability concept that applies to *PC* (and *IIC*), in which a patch itself is considered as a space where connectivity exists.

The *IIC* metric is similar to the *PC* metric but based on networks with unweighted links (see Table 1). *ICC* takes into account the topological distance (d_{ij}) between patches i and j (minimum number of links that have to be passed to move from i to j). When $i=j$ then $d_{ij} = 0$. *IIC* is given by:

$$IIC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \cdot a_j \cdot (1/(1 + d_{ij}))}{A_L^2} \qquad (2)$$

The importance of each individual patch k using either of these two metrics can be assessed by computing the metric before and after the removal of patch k (Eq. (3)) (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007):

$$dPC_k = 100 \times \frac{PC - PC_{remove}}{PC} \qquad (3A)$$

$$dIIC_k = 100 \times \frac{IIC - IIC_{remove}}{IIC} \qquad (3B)$$

dPC_k and $dIIC_k$ thus represent the relative decrease (in percentage) of PC and IIC following the removal of patch k. Both dPC_k and $dIIC_k$ can be partitioned in three fractions considering the different ways in which a habitat patch can contribute to habitat connectivity and availability in the landscape (Eq. (4)) (Saura and Rubio, 2010).

$$dPC_k = dPCintra_k + dPCflux_k + dPCconnector_k \qquad (4A)$$

$$dIIC_k = dIICintra_k + dIICflux_k + dIICconnector_k \qquad (4B)$$

$dPCintra_k$ and $dPCflux_k$ correspond, respectively, to patch k's contributions in form of its area (intrapatch connectivity) and the flux of dispersing organism that moves to or from it. The same applies to $dIICintra_k$ and $dIICflux_k$. Here, our interest is primarily the third fraction, which corresponds to the extent to which patch k acts as a connecting element or stepping stone between other habitat patches, i.e. to what extent it contributes to uphold functional connectivity between other patches in the landscape (Table 1) (Saura and Rubio, 2010). In the next sections we limit the details of our analysis to the PC-based metric $dPCconnector_k$ and how it relates to BC; an identical analysis of the $dIICconnector_k$ metric is however presented in Appendix A.

2.1.2. Betweenness centrality (BC)

BC was originally defined for binary networks, i.e. where all links are assigned either zero or unit value. BC for node k (BC_k) is defined, as proposed by Freeman (1977) and further described in Table 1, as the sum of all separate shortest paths ($g_{ij}(k)$) between all pair of patches ($i, j \neq k$) that go through k, divided by the total number of shortest paths (g_{ij}) between each pair of patches ($i, j \neq k$):

$$BC_k = \sum_i \sum_j \frac{g_{ij}(k)}{g_{ij}} \tag{5}$$

2.2. Assessing patch importance through the integration of network analysis and patch removal experiments

Here we investigate how the PC metric relates, analytically, to the network centrality metric BC. A similar analysis of the $dIICconnector_k$ metric is presented in Appendix A.

2.2.1. Integrating $dPCconnector_k$ and betweenness centrality

The $dPCconnector_k$ metric can be expressed as the sum of two different terms (Eq. (6)):

$$dPCconnector_k = \frac{100}{PC} \sum_i \sum_j a_i a_j p_{ij}^{*k}\{i, j \neq k \ and \ ij \in nm^*\}$$
$$- \frac{100}{PC} \sum_i \sum_i a_i a_j p_{ij, k \, removed}^{*}\{i, j \neq k \ and \ ij \in nm^*\} \tag{6}$$

where nm^* represents the list of combinations of i and j ($i \neq j$) where k is included in the shortest path between i and j in the initial/intact landscape (before removing k). That is, those pairs of nodes whose connection is favored by the presence of k (as a stepping stone facilitating the dispersal between i and j). p_{ij}^{*k} is the maximum product probability between those nodes i and j (belonging to nm^*) in the intact landscape. For the sake of simplicity, here we assume that a single shortest path (which is the path that maximizes the product probability) exists between i and j. Implications of multiple shortest paths are discussed in Appendix B. $p_{ij, k \, removed}^{*}$ represents the maximum product probability of the path between i and j after removing patch k (where i and j belong to nm^* in the intact landscape). It is apparent that $p_{ij}^{*} \geq p_{ij, k \, removed}^{*} \geq 0$ for every pair of patches i and j. None, some, or all of the new maximum product probability paths ($p_{ij, k \, removed}^{*}$) will include new nodes as a result of the removal of node k (which, by definition, was included in p_{ij}^{*k} in the intact landscape).

The first sum in Eq. (6) is conceptually similar to BC but takes into account areas and dispersal probabilities (weights of the links in the network), and uses the maximum product probabilities to define the shortest paths between nodes. From a landscape ecological perspective, including both the area product and the weighted links in a modified BC metric seems like a plausible and convenient generalization, making it conceptually compatible with the characteristics of the PC metric. We suggest the proposed generalization of the BC metric (denoted BC_k^{PC}, see Eq. (7)) as being particularly suitable for assessing the betweenness of a patch when the actual flows of organisms, and not just the possibilities for dispersals, are being considered.

$$BC_k^{PC} = \sum_i \sum_j a_i a_j p_{ij}^{*k}\{i, j \neq k \ and \ ij \in nm^*\} \tag{7}$$

The last sum in Eq. (6) represents all *rewired* maximum probability paths (i.e. shortest paths) that emerge following the removal of patch k. These are the alternative shortest paths that are available, after losing k, for connecting those pairs of patches whose

connection was favored by the presence of k in the intact landscape. Thus, the sum can be interpreted as a residual network where only paths between the pairs of patches that previously were connected through k are considered. We denote this residual network as $PC_k^{residual}$, and thus we can rewrite Eq. (6) as follows (Eq. (8)).

$$dPCconnector_k = 100 \frac{(BC_k^{PC} - PC_k^{residual})}{PC} \tag{8}$$

2.2.2. Using the proposed framework to assess different aspects of connectivity

By having linked $dPCconnector_k$ with the generalized BC metric, we can now use this integrated modeling framework of connectivity, that resembles the desired features from both these different types of metrics, to assess different connectivity aspects of individual habitat patches. First, it is clear that patches with high values of $dPCconnector_k$ are crucial because their removal would immediately reduce the connectivity, and therefore preserving these patches should clearly be of highest priority. This is shown in Fig. 1 where the removal of node 4 or 9, which are the ones with the highest $dPCconnector_k$, would lead to an immediate fragmentation of the network into isolated components.

However, a more complex question is how to rank patches that are no such obvious cut nodes. In Fig. 1, this is illustrated by the patches 2–3 and 5–8. None of these patches have $dPCconnector_k > 0$, because there are alternative paths between the remnant patches that are as good as the ones in the intact landscape. For example, after losing patch 2, patches 1 and 4 are still connected through a path with $p_{ij}^{*} = 0.25$ ($p_{14}^{*} = p_{13} \times p_{34} = 0.5 \times 0.5 = 0.25$), exactly as before, since patch 3 fully compensates for the loss of 2 as quantified by p_{ij}^{*}. However, having a low value of $dPCconnector_k$ does not guarantee that the removal of patch k does not severely affect the underlying dispersal pathways of the intact network as captured by the generalized BC (the dispersal backbone, see Bodin and Norberg, 2007; Urban et al., 2009). Furthermore, losing a patch with high BC_k^{PC} may also have implications for the vulnerability of the remaining network to further patch removals (e.g. after losing patch 2 the network would be severely affected by a subsequent loss of patch 3).

In order to address these issues, we start by recognizing that to attain a high $dPCconnector_k$ value, patch k would need to have a high BC_k^{PC} (see Eq. (8)). Also, $PC_k^{residual}$ needs to be low. The former means that a patch with a high $dPCconnector_k$ is also, by definition,
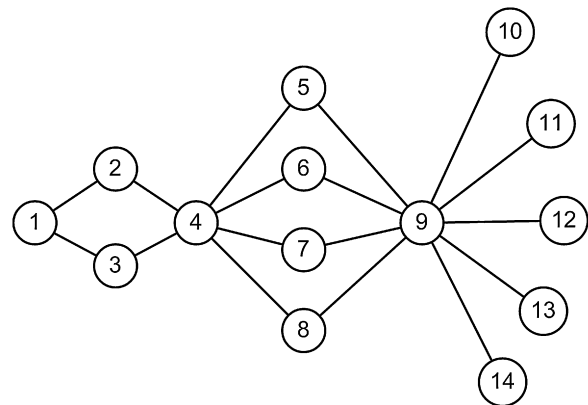

Fig. 1. A schematic illustrative network of 14 patches (represented as circles), each with an area = 1 and where $p_{ij} = 0.5$ for all links represented by black lines ($p_{ij} = 0$ for all the other pairs of patches). The $dPCconnector_k = 0$ for all patches except for nodes 9 and 4 (for which $dPCconnector_k$ equals 30.2% and 12.2%, respectively). The generalized betweenness centrality is 32.8% for patch 9, 15.2% for patch 4, 1.7% for patches 5–8, 1.6% for patches 2–3, 0.42% for patch 1 and 0.0% otherwise (all metric values expressed as percentage of the PC value in the intact landscape).

a patch with high BC_k^{PC}. Furthermore, the fact that $PC_k^{residual}$ must be low means that no other remaining patch in the residual network (pairs of patches for which the shortest path passed through k in the intact landscape) are able to fully compensate for the loss of patch k. That is, the alternative paths available after losing k are much fewer and/or weaker than those that were maintained by the presence of k. In other words, the connectivity of the residual network $PC_k^{residual}$ is low compared to that of the intact landscape.

In other cases, a certain patch k might score high in BC_k^{PC}, but other patches could be in place to compensate for the loss of k by providing opportunities for a rewired connectivity backbone. In such cases, $PC_k^{residual}$ would also be high, yielding a low $dPCconnector_k$. Hence, it seems important to distinguish between patches with high values of both $dPCconnector_k$ and BC_k^{PC}, and patches with high values of BC_k^{PC} but with a low value of $dPCconnector_k$ (Table 2).

The BC_k^{PC} of patches 2–3 and 5–8 in Fig. 1 are, respectively, 1.6% and 1.7%. This tells us that patches 5–8 are likely to be slightly more important in providing a backbone for long-range connectivity throughout the network. The remaining patches following the removal of any of the patches 2–3 or 5–8 will, however, be able to fully compensate for the loss of connectivity ($dPCconnector_k = 0$). The most remarkable difference between the patches 5–8 and 2–3 lies in how this compensation is distributed among the remaining patches. For example, if patch 2 is removed, patch 1 would be completely dependent on the remaining patch 3 to stay connected to the rest of the network. In other words, patch 3 alone will compensate for the loss of patch 2. On the other hand, if patch 5 is removed,

the compensation is shared equally among patches 6–8. Thus, in comparison with the removal of patch 2, losing patch 5 seems less critical in terms of the vulnerability of the remaining network.

This shows that the number of patches that compensate for the removal of a certain patch does have an impact on the vulnerability of the remaining network to further patch removals. However, the number, by itself, will not reveal anything about how the compensation is distributed among the remnant patches. If, for example, most of the compensation is done by just one patch even though several other patches also contribute, this information is not captured by just counting the number of compensating patches.

Thus, it would be desirable to measure to what extent each and every patch in the residual network $PC_k^{residual}$ will contribute to the compensation following the loss of patch k. In order to do so, we start by recognizing that the generalized BC of the patches in the residual network can also be calculated, although now only accounting for the pairs of patches where patch k was included in the shortest path in the intact landscape (we denote this $BC_{i,k\,removed}^{PC(k)}$ for all patches i in the residual network $PC_k^{residual}$).

This allows us calculating the *changes* in generalized BC ($\Delta BC_i^{PC(k)}$) of each and every node i in the residual network $PC_k^{residual}$ before ($BC_i^{PC(k)}$) and after ($BC_{i,k\,removed}^{PC(k)}$) the removal of patch k (Eq. (9)).

$$\Delta BC_i^{PC(k)} = BC_{i,k\,removed}^{PC(k)} - BC_i^{PC(k)} \{i \in nm^*\} \tag{9}$$

As said, of particular interest is whether these changes are distributed equally among the remnant patches, or if just one or a few

Table 2
Interpretation of the characteristics and role of the habitat patches as connectivity providers depending on the values of the three metrics considered in the integrated modeling framework. The table is equally applicable for the *IIC*-based metrics.

Metric value			What do the metric values indicate about the role of habitat patch k as a connectivity provider?
$dPCconnector_k$	BC_k^{PC}	$C(50)_k^{PC}$	
High	$BC_k^{PC} \gg dPCconnector_k$	Low	A central and irreplaceable patch being instrumental in upholding the strongest and most frequent paths throughout the landscape. Its loss cannot be fully compensated for by other patches in the network and will cause a significant decrease in landscape connectivity. Many important pathways constituting the dispersal backbone of the landscape network disappear and/or get significantly weakened. In addition, some of these losses will be compensated for by a small set of remaining patches. Therefore, the landscape will likely be very vulnerable to further removals affecting any of these few compensating patches.
		High	As above except that the compensation is shared among a larger set of remnant patches in the landscape. Therefore, the landscape is likely less vulnerable to further patch removals.
	$BC_k^{PC} \approx dPCconnector_k$	Low	If $BC_k^{PC} = dPCconnector_k$ there are no available pathways other than these that will be permanently destroyed. Therefore no compensation is possible, and $C(50)_k^{PC}$ equals 0. If BC_k^{PC} is only a little bit larger than $dPCconnector_k$, then only a minor part of the connectivity provided by k can be compensated for by other patches, and $C(50)_k^{PC}$ would remain being equal to 0.
		High	Not possible, for the reason described above.
Low	High	Low	Although many important pathways constituting the dispersal backbone of the landscape network disappear and/or get significantly weakened, most or all of these losses can be compensated for by a small set of remaining patches. Hence, if the dispersing species are able to change their movement patterns in line with the new spatial configuration of the remnant landscape, the net effect on connectivity remains low. However, the landscape will likely be very vulnerable to further removals affecting any of those compensating patches.
		High	As above except that the compensation is shared among a larger set of remnant patches in the landscape. Therefore, the landscape is less vulnerable to further patch removals.
	Low	Low	The patch does not significantly facilitate the connectivity between other habitat patches in the landscape, and is therefore of little interest in terms of its contribution as an intermediate stepping stone patch.
		High	Same as above.

patches alone will compensate for the loss of patch k. In order to measure this property, we define $C(50)_k^{PC}$ as the minimum number of patches for which the sum of their $\Delta BC_i^{PC(k)}$ exceeds 50% of the BC_k^{PC} (Table 1). If, for example, $C(50)_k^{PC}$ equals one, one remaining patch will alone compensate for more than 50% of the BC_k^{PC} of the removed patch k. Thus, a higher $C(50)_k^{PC}$ would imply a less vulnerable network following the removal of patch k since a fairly high number of nodes would be able to step in and (at least partly) compensate for the loss. If compensation of 50% of the BC_k^{PC} of the removed patch k is not possible, $C(50)_k^{PC}$ is 0 (or just undefined). The $C(50)_k^{PC}$ of the nodes 2–3 and 5–8 in Fig. 1 are, respectively, 1 and 2, which is in accordance with the discussion above. In Table 2 we summarize our discussions on all these metrics.

2.3. Evaluation of the integrated framework in real landscapes

The theoretical investigations provided us with a modeling framework that seems applicable in valuing and prioritizing the importance of individual habitat patches in a fragmented landscape. However, in order to evaluate the performance of this framework in a real-world setting we tested it in two different landscapes. We modeled these landscapes using the network-based approach, and then we calculated all the metrics analyzed in this work, both on the node and the whole network level. We used the freely available software tools JMatrixNet (Bodin et al., 2006) and Conefor Sensinode (Saura and Torné, 2009) (www.conefor.org) to carry out the calculations (the latter slightly modified). MatLab was used to present the results graphically.

We run the analyses for different estimates of species dispersal abilities. For the binary networks models that we constructed to evaluate the *IIC*-based metrics, we defined a threshold distance D. All patches separated with a distance larger than D were considered as disconnected, and therefore no link was assigned between them in the network model. For the probabilistic networks used when calculating the *PC*-based metrics, we estimated the direct dispersal probability p_{ij} between patch i and j using the negative exponential function of the Euclidean interpatch distance (straight line edge-to-edge distance). This is expressed as $p_{ij} = \exp(-k \times d)$ where d is the distance between the patches (cf. Hanski, 1994) and k is a constant that is set to $k = 1/D$ in order to obtain the same overall level of connectivity as in the binary model where $p_{ij} = 1$ if $d < D$ and 0 otherwise. In this way, the integral from zero to infinity of the p_{ij} function equals D both in the binary and probabilistic models.

We varied the distance threshold D to get an overview on where $dPCconnector_k$, $dIICconnector_k$ and the corresponding generalized BC are of most significance (cf. Saura and Rubio, 2010). Then we calculated all metrics for those threshold distances. We selected the 20 patches with the highest scores of the *PC*- and *IIC*-based versions of the generalized BC metric for both study areas and presented these patches in more detail. We also calculated the Pearson correlation coefficient between relevant pair of metrics to evaluate to what extent they captured different aspects of the landscape connectivity. For all calculations, we accounted for the potential existence of multiple shortest paths (Appendix B).

2.3.1. Study areas description

The two landscapes we used for the evaluation were (1) a agricultural landscape in southern Madagascar (Bodin et al., 2006), and (2) a forested landscape covering the capercaillie (*Tetrao urogallus*) habitat in Catalonia (NE Spain) (Estrada et al., 2004; Pascual-Hortal and Saura, 2008). The Madagascar landscape is located in the Androy region in the very south of Madagascar. It contains hundreds of small forest patches that are scattered in an agricultural landscape and together only constitute approximately 3.5% of the

total geographical area (Bodin et al., 2006). The Spanish landscape comprises the areas of suitable habitat for the capercaillie in the region of Catalonia, which has a total extent of about 32,000 km². The capercaillie habitat is however concentrated in the upper mountain and subalpine forests in the Pyrenees and Pre-Pyrenees at the north of Catalonia, where it occurs at its southernmost part of its European distribution. Capercaillie is an endangered species in this region that is severely affected by the loss of habitat connectivity, among other conservation threats. Habitat distribution data for this species were obtained from the Catalan Breeding Bird Atlas 1999–2002, as a result of field surveys and niche-based modelling (Estrada et al., 2004). An estimate of the probability of capercaillie occurrence was obtained in that atlas for every 1 km × 1 km cell in Catalonia. Here, we considered as habitat those cells with a probability of capercaillie occurrence of at least 0.2, as in Pascual-Hortal and Saura (2008). This yielded a total of 522 1 km × 1 km cells confined in 131 geographically separated habitat patches (nodes).

3. Results

We started by varying the distance thresholds D, for both study areas, to estimate at which dispersal distances the intermediate connecting patches are most important for overall habitat
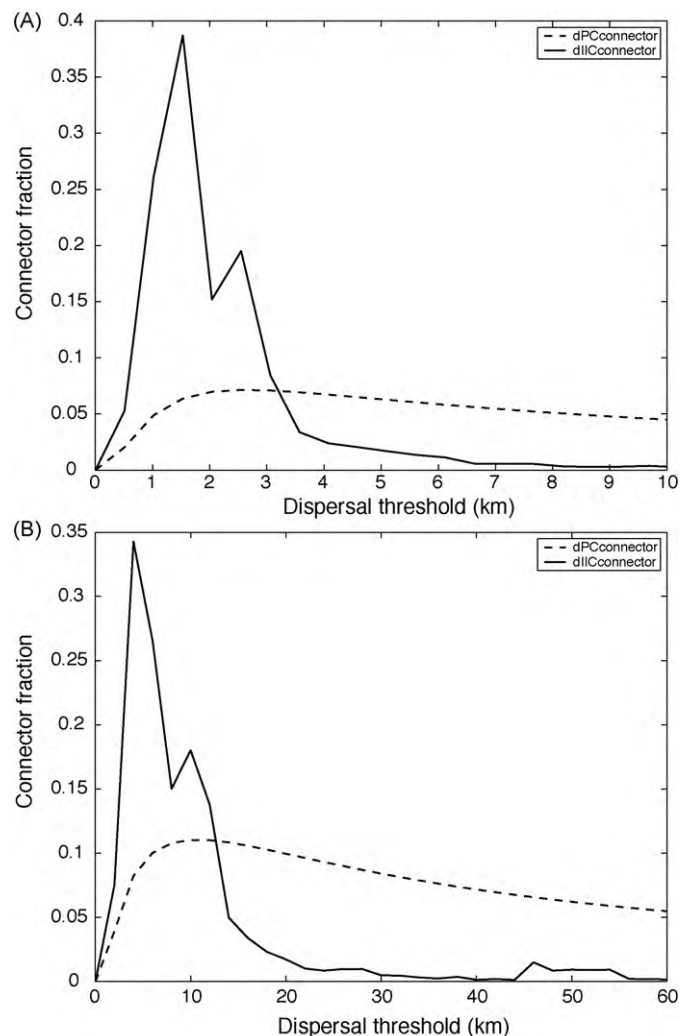

Fig. 2. (A and B where A corresponds to the Madagascar study area, and B to the Catalonian study area) Sum of $dPCconnector_k$ and $dIICconnector_k$ values for all patches k, expressed as their proportion of the total sum of all dPC_k and $dIIC_k$, respectively, for increasing threshold distances D (cf. Saura and Rubio, 2010).

connectivity and availability in the landscape as measured using $dIICconnector_k$ and $dPCconnector_k$ (Fig. 2A and B). The maximum contribution of $dIICconnector_k$ (as shown in Fig. 2) was considerably higher (peaks at about 40% and 35% for the Madagascar and Catalonian cases respectively) and was found at a lower dispersal distance than for $dPCconnector_k$ (which never exceeded 7% and 11% for the two study areas). For large dispersal distances, the contribution of $dPCconnector_k$ was on the other hand higher than that of $dIICconnector_k$ (Fig. 2). The contribution of $dIICconnector_k$ is almost zero for large distances, but $dPCconnector_k$ still makes some contribution at these distances.

At a threshold distance of 2.5 km, $dPCconnector_k$ is at its maximum for the Madagascar case, and the $dIICconnector_k$ is also fairly high (although it peaks for a slight lower value of d). The same occurred for a threshold distance of 6 km for the Catalonian case. This is actually close to the estimated 5 km of median dispersal distance for the capercaillie in the Pyrenees (Menoni, 1991). Thus, we used these threshold values for the rest of the analysis. The rational for using these threshold values is that those species having a dispersal distance of approximately D will experience the landscape as fragmented, but still fairly well connected since many intermediate stepping stone patches are within reach thus making movements throughout the landscape possible and feasible in successive steps through those intermediate patches. When the dispersal abilities are large enough (well above D), species can move directly from one patch to another without needing intermediate stepping-stones or connecting elements that facilitate this dispersal (Saura and Rubio, 2010). On the contrary, when dispersal is largely limited (dispersal distances below D), species cannot move to any other piece of habitat in the landscape, and virtually no habitat patch can be used as a stepping stone for further movement to other destination patches. Hence, the threshold distance D approximates the peak of a distinctive region of connectivity in between a fully fragmented landscape where dispersal is inherently limited, and a landscape where direct dispersals between any pair of patches are increasingly possible. Accordingly, it is mostly for species within this region of connectivity that our results are of immediate relevance since our focus is primarily on how different patches contribute as connectivity providers facilitating movements throughout the landscape. The results for the three metrics in the integrated framework (Table 2) calculated at these threshold distances are graphically presented in Figs. 3 and 4.

Figs. 3 and 4 illustrate that there are large variations among the patches in terms of their scores on the different metrics, which seems to reveal relevant and not necessarily self-evident information about the patches' contribution to different aspects of landscape connectivity. The abovementioned variability is clearly shown in Figs. 5 and 6 where the 20 patches with the highest scores of the PC- and IIC-based versions of the generalized BC metric are presented together with their scores of $dPCconnector_k$ and $dIICconnector_k$ (sorted based on their BC scores). In all, Figs. 3–6 indicate that it is not necessarily the case that if a patch scores high on BC_k^{PC}, it always scores high on $dPCconnector_k$ (and the same applies to the IIC-based metrics).

In the Madagascar landscape, the Pearson correlation coefficient between $dPCconnector_k$ and BC_k^{PC} for the *complete* set of patches is $r = 0.79$, and between $dIICconnector_k$ and BC_k^{IIC} $r = 0.47$. For the Catalonian case, the Pearson correlation coefficient between $dPCconnector_k$ and BC_k^{PC} is $r = 0.92$, and between $dIICconnector_k$ and BC_k^{IIC} $r = 0.69$.
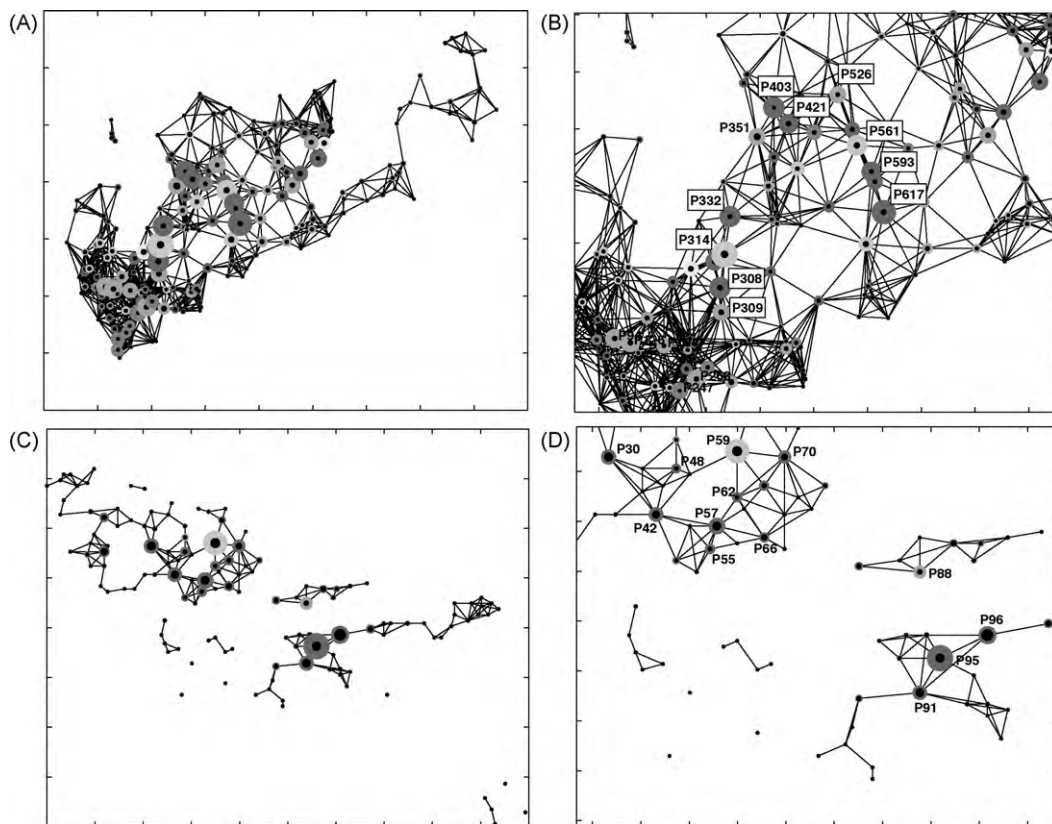

Fig. 3. (A) and (B) represent the Madagascar study area (B being a close-up of a portion of the network in A). (C) and (D) similarly represent the Catalonian study area. The nodes (patches) are represented by circles and the links by lines in all figures. The threshold distance D, used when constructing these network models, was set to 2.5 km for Madagascar and 6 km for Catalonia. The sizes of the nodes are proportional to BC_k^{PC} (gray circles) and $dPCconnector_k$ (black circles). The sizes are relative to the maximum value of these specific metrics for the networks. The grayness is approximately proportional to $C(50)_k^{PC}$ (darker = lower values). The labels in (B) and (D) refer to the patches in Figs. 5 and 6.
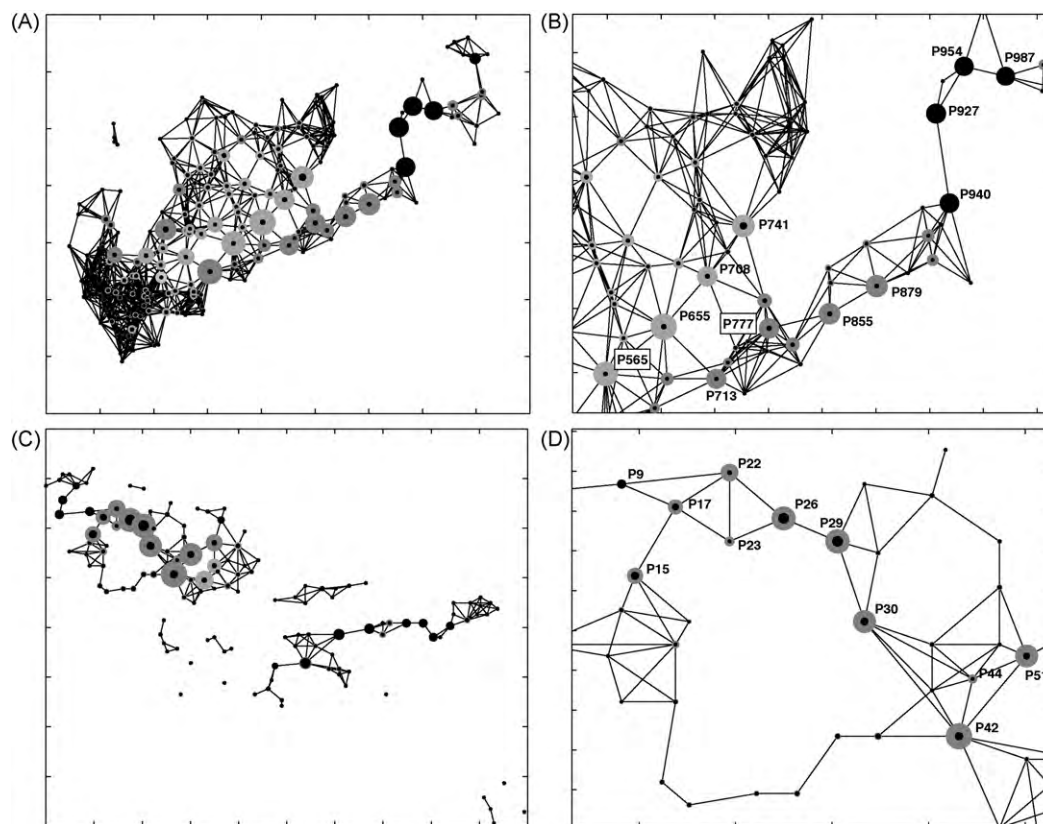
Fig. 4. (A) and (B) represent the Madagascar study area (B being a close-up of a portion of the network in A). (C) and (D) similarly represent the Catalonian study area. The nodes (patches) are represented by circles and the links by lines in all figures. The threshold distance D, used when constructing these network models, was set to 2.5 km for Madagascar and 6 km for Catalonia. The sizes of the nodes are proportional to BC^{IIC} (gray circles) and $dIICConnector_k$ (black circles). The sizes are relative to the maximum value of these specific metrics for the networks. The grayness is approximately proportional to $C(50)_k^{IIC}$ (darker = lower values). The labels in (B) and (D) refer to the patches in Figs. 5 and 6.

4. Discussion

4.1. An integrated modeling framework for PC, IIC and the generalized betweenness centrality

As shown by the analytical evaluation of these conceptually different metrics, it is clear that they are capturing different aspects of a patch's contribution to the connectivity of the landscape (Table 1). Furthermore, the evaluation also shows how these conceptually different metrics are analytically related to each other. This provided for an integration of the two conceptual different approaches typically applied when assessing patch importance using a network-based approach (i.e. patch removal experiments and network analysis) into a common modeling framework. The analytical linkages between these different conceptual approaches, as we have shown here, can help a researcher to assess different connectivity aspects of individual patches in an integrated way without being limited to either one of these conceptual approaches (Table 2). Finally, by adding patch area and varying dispersal possibility to the generalized BC metric (Eqs. (7), (A2); and Eqs. (B3) and (B6)), the metric will not only be more compatible with the PC and IIC metrics, but it will also better account for spatial characteristics of importance in assessing species dispersals in landscapes.

4.2. Towards an integrated patch ranking procedure

As indicated in Figs. 5 and 6, neither $dIICconnector_k$ nor $dPCconnector_k$ seem to coincide with BC_k^{IIC} or BC_k^{PC} for the top 20 patches, and thus they apparently capture quite different connec-

tivity characteristics. If exactly the same set of patches would score high using any of these metrics, the presented modeling framework would naturally be of little practical value. Hence, although the levels of correlations for the complete set of patches are fairly high, the variability among individual patches is considerable, and we argue that taking these differences into account would lead to more ecologically well-informed decisions when prioritizing patches for conservation.

Note for example the patches P403 and P351 in Fig. 5A where the ratios of BC_k^{PC} to $dPCconnector_k$ are very different (see also Fig. 3B). Patch P403 has a high BC_k^{PC} whereas the $dPCconnector_k$ is very small, and patch 351 has a slightly lower BC_k^{PC} but a much higher $dPCconnector_k$. Hence, these patches are important since they both are significant components of the connectivity backbone (captured by their high scores on BC_k^{PC}). However, losing patch P403 will not necessarily induce any sharp reduction in connectivity (captured by $dPCconnector_k$) assuming that the dispersing organisms will quickly find new shortest paths through the landscape to compensate for the loss, whereas losing patch P351 actually has a notable impact as evaluated by $dPCConnector_k$. Furthermore, it is interesting to compare patch P308 with P561 (Fig. 5A and Fig. 3B). They score fairly equal on both $dPCconnector_k$ and BC_k^{PC}, but the $C(50)_k^{PC}$ is much higher for P561 (seen by the different levels of grayness in Fig. 3B). Hence, if patch P308 is lost, the following increase in BC_k^{PC} among remaining patches will be limited to very few or just one patch. Hence, the vulnerability of the connectivity backbone would increase significantly. On the other hand, losing patch P561 implies that a larger number of patches will compensate for the loss, leaving the network comparatively less vulnerable to fur-
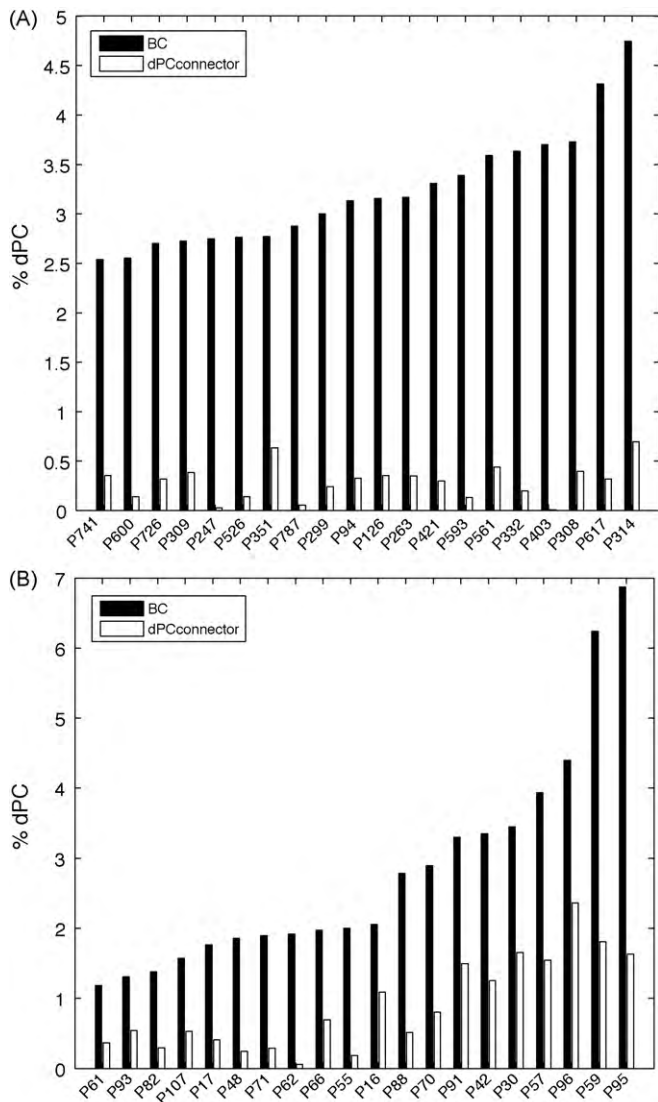
Fig. 5. Generalized betweenness centrality BC_k^{PC} and $dPCConnector_k$, ordered by BC_k^{PC} (top 20 patches) for the Madagascar case (A) and the Catalonian case (B).
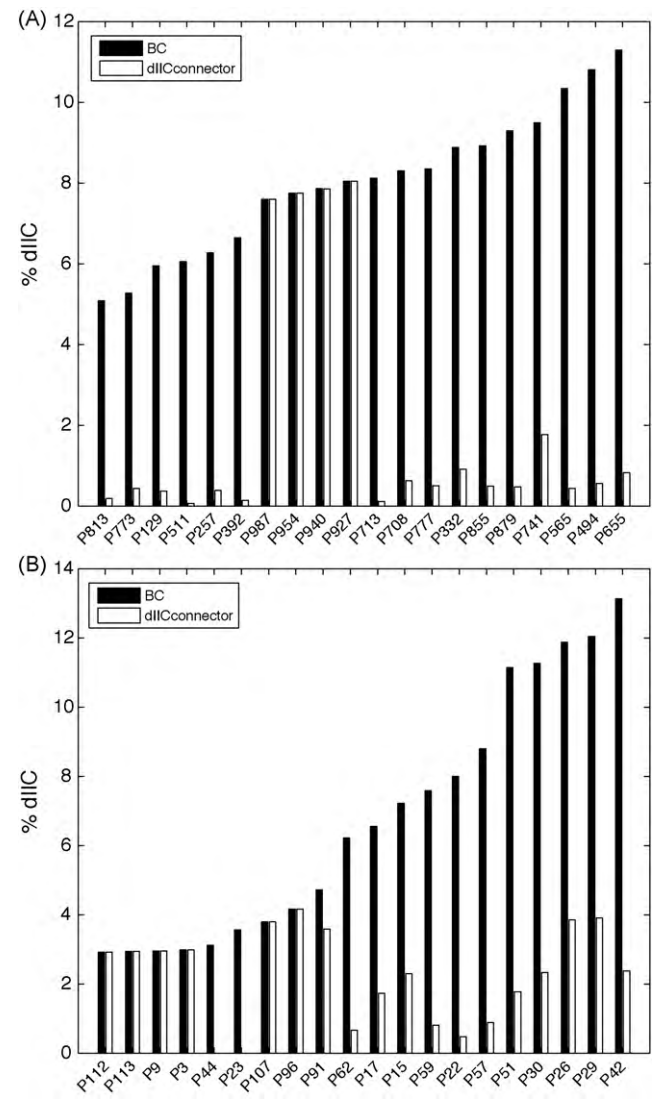
Fig. 6. Generalized betweenness centrality BC_k^{IIC} and $dIICConnector_k$, ordered by BC_k^{IIC} (top 20 patches) for the Madagascar case (A) and the Catalonian case (B).

ther removals. This shows the ability of the $C(50)_k^{PC}$ metric to assess individual patch importance for a set of patches with similar values of $dPCConnector_k$ and BC_k^{PC} (Table 2).

The same pattern applies for the IIC-based metrics. Note for example the patches P713 and P927 in Fig. 6A where the ratios of BC_k^{IIC} to $dIICconnector_k$ are very different (see also Fig. 4B). Removing patch P927 will immediately and significantly reduce the connectivity as quantified by $dIICconnector_k$, whereas removing P713 would not. The BC_k^{IIC} of P713 is, however, quite high. Hence, removing P713 would require a substantial rewiring of the dispersal pathways in the remaining network.

However, it is not always a trivial task to balance between the different connectivity aspects captured by the $dPCconnector_k$ metric, the BC_k^{PC} metric and the $C(50)_k^{PC}$ metric when assessing the importance of the different patches (Tables 1 and 2). Typically the generalized BC_k^{PC} and $C(50)_k^{PC}$ would complement the prioritization provided by $dPCconnector_k$ in those cases where $dPCconnector_k$ is zero (or low), or when two or more patches have the same (or rather similar) $dPCconnector_k$ values (the same applies for the IIC-based metrics). As illustrated above, there can be large variations of the BC_k^{PC} and $C(50)_k^{PC}$ metrics for patches with very similar $dPCconnector_k$ values (and vice versa). Hence, it seems reasonable

to group patches with similar scores on the $dPCconnector_k$ together, and then evaluate their contributions to the connectivity internally within the groups based on their scores on the BC_k^{PC} and $C(50)_k^{PC}$ metrics. In using this approach, small variations in $dPCconnector_k$ among patches within the same group are discarded as insignificant, and instead priority is given to the BC_k^{PC} and $C(50)_k^{PC}$ metrics. The groups themselves should, however, be ranked according to their mean $dPCconnector_k$ scores, and the ranking of the groups outweighs the internal ranking of the patches within the groups. To illustrate this, consider the following example: patches P59, P95 and P30 have very similar $dPCconnector_k$ scores (Fig. 5B), and could thus be ranked as approximately equally important if only considering the $dPCconnector_k$ metric. However, the BC_k^{PC} metric for P95 and P59 is nearly twice the value for P30, and these patches should therefore be considered more important. Furthermore, the $C(50)_k^{PC}$ is lower for P95, thus that patch would rank higher than P59 (P95 also has a slightly higher BC_k^{PC}). Hence, the large difference in BC_k^{PC} and to some extent $C(50)_k^{PC}$ would outweigh the small difference in $dPCconnector_k$ *within* that group. However, the value of the $dPCconnector_k$ metric for P96, which is not part of this group, is significantly higher (about 30%) than for any of the patches P59, P95 and P30, and should therefore be considered more important than

any of the patches within that group. In summary, based on these results and our previous elaboration of different aspects of individual patches' contribution to landscape connectivity (Table 2), we propose a generalized patch ranking procedure as follows (the procedure is equally applicable for IIC- as for PC-based metrics):

1. Assess $dPCconnector_k$, BC_k^{PC} and $C(50)_k^{PC}$ for all patches.
2. Group patches with similar values on $dPCconnector_k$.
3. Divide the patches in the groups above into subgroups based on them having similar scores of BC_k^{PC}.
4. Rank all patches according to the following criteria (with a descending order of priority):

a. Their group's average score of the $dPCconnector_k$.
b. Their subgroup's average score on BC_k^{PC}.
c. Their score of $C(50)_k^{PC}$ (the lower the more important).

Although the proposed framework and suggested ranking procedure provided by the integrated evaluation of these different metrics shows potential for ecologically informed multi-criteria connectivity analyses, we fully acknowledge that this procedure is just a general skeleton that would need to be calibrated for specific ecological processes and adjusted to the needs of particular conservation management applications. Although this is out of the scope of this paper, empirical data, spatial explicit population models and/or simulations would be required to validate and/or refine the general procedure outlined above. In the same way, the involvement of stakeholders and local expert knowledge would help to decide the final weight that should be given to each of these metrics, as suited to the management objectives and conservation context of specific cases. For example, this could be the case of deciding if patch 2 in Fig. 1 is to be considered more or less important than patch 5 for the purposes of a particular conservation plan. Both patches 2 and 5 have $dPCconnector_k = 0$, and patch 5 has a slightly higher BC_k^{PC} but also a higher value of $C(50)_k^{PC}$ (Fig. 1). If, for example, the risk for further removals is assessed as low, a manager might choose to overlook the lower value of $C(50)_k^{PC}$ for patch 2 and instead focus on the fact that patch 5 has a slightly higher value of BC_k^{PC} and thus assign a higher priority for preserving patch 5. On the other hand, if the risk for further removals is assessed as high, a manager might instead focus on the lower value of $C(50)_k^{PC}$ for patch 2 and hence assign a higher priority to that patch. This altogether shows that these different metrics should be evaluated together, and depending on the particularities and management needs in a given situation, more weight should be given to one or the other metric. In spite of this irreducible ambiguity, we still argue that by applying these different metrics, a manager would be given a set of relevant tools that would help to make these kinds of assessments less arbitrary and more transparent.

We conclude this discussion on patch ranking with some notes about the PC-based metrics. As said earlier, when using a negative exponential dispersal kernel based on the Euclidean distance between patches to assess dispersal probabilities, no p_{ij}'s would equal zero and hence, from a topological point of view, a link exists between every pair of patches. Hence, in order for a patch to have $dPCconnector_k$ greater than zero, it has either to: (1) be located quite close to the shortest possible straight line connecting a particular pair of patches, and/or (2) extend spatially in approximately the same order of magnitude, or higher, as the dispersal distance of the studies species. If none of these criteria are fulfilled, $dPCconnector_k$ would be zero, and the potential of a patch acting as a stepping stone is accordingly very low (BC_k^{PC} would be very low as well). On the other hand, if at least one of these criteria is fulfilled, it seems quite unlikely that $dPCconnector_k$ would be exactly zero for a given patch since that would require another patch to be situated in such a way in the landscape that its contribution as intermediate stepping stone, as expressed by the $dPCconnector_k$ metric, would be exactly the same as the first patch. This altogether suggests that if a patch has a $dPCconnector_k$ equal to zero, it is fairly unlikely that its BC_k^{PC} would be greater than zero. In fact, both case studies support this claim. In Madagascar, all patches with a $dPCconnector_k$ equal to zero also have a BC_k^{PC} equal to zero (not shown). In Catalonia, basically the same pattern applies. So it seems that BC_k^{PC} and $C(50)_k^{PC}$ do not provide much help for ranking those patches that have a $dPCconnector_k = 0$ and are therefore only of use for patches with a $dPCconnector_k$ greater than zero. It is, however, important to point out that this does not apply when using the IIC-based metrics. Most of the patches where the $dIICconnector_k$ equals zero still have a $C(50)_k^{IIC}$ and BC_k^{IIC} greater than zero (both in the Madagascar and Catalonia study areas). This difference is also captured by the lower correlations between the IIC-based metrics as compared to the PC-based metrics.

4.3. PC- and IIC-based metrics – which one to use?

It seems clear that PC- and IIC-based metrics are quite different in their practical outcomes since patches with high scores on the PC-based metrics do not necessarily score high on the IIC-based metrics. This is qualitatively shown in Fig. 3A and C where the patches with the highest scores of $dPCconnector_k$ are situated more at the core of the networks whereas patches with high scores on $dIICconnector_k$ tend to be situated comparatively more in the periphery and/or along single pathways (as seen in Fig. 4A and C). Furthermore, the $dIICconnector_k$ tends to represent a larger proportion of $dIIC$ as compared to $dPCconnector_k$ vs. dPC_k for short dispersal distances, whereas the opposite applies for long dispersal distances (Fig. 2). This means that, for the study areas presented here, intermediate patches seems to be more important (for short to intermediate dispersal distances) when representing the landscape as a binary network in comparison to the probabilistic network model that is used for the PC-based metrics. The probabilistic network model accounts for direct dispersal also between patches that are separated by comparatively large distances and hence weakly connected, whereas the binary network model completely disregards these links and instead fully relies on intermediate stepping stone patches for dispersals. This reduces the strong influence of intermediate stepping stone patches in probabilistic models for short to intermediate dispersal distances. However, in landscapes different from those studied here, where the spatial extent of the patches is in the same order of magnitude as the dispersal distances of the species, intermediate stepping stone patches would be of higher importance also when applying the PC metric for short to intermediate dispersal distances.

For our study areas, losing some of the most critical stepping stone patches in the binary network model can completely break the network into isolated network components which instantly reduces the IIC score. This kind of criticality is also reflected in Fig. 2 where the shapes of the $dIICconnector_k$ curves are more irregular compared to the $dPCconnector_k$ curves. When increasing the threshold dispersal distance D, patches that were previously isolated will become connected, and sometimes they also connect isolated groups of patches together. From that follows that the importance of intermediate stepping stone patches can vary very rapidly when changing the threshold distance for the IIC-based metrics.

On the other hand, losing a stepping stone patch in the probabilistic network used to construct the PC metric will only reduce the amount of flux, not fully break the network apart. This is an effect of the exponential dispersal kernel typically applied to calculate the dispersal probabilities. Since the probability p_{ij} is always >0 for finite distances, losing a patch may decrease the flows, but

never cut them down completely as in the binary case. Therefore $dPCconnector_k$ does not experience the sharp thresholds as seen for the $dIICconnector_k$ metric.

When the dispersal distance is high, eventually higher than the maximum distance separating any pair of habitat patches, then a link exists between any pair of patches. Therefore any habitat patch can be reached directly from any other patch without the need of any other stepping stone patch ($dIICconnector_k = 0$). However, in the probabilistic model that applies to PC, if the direct dispersal probabilities have been computed as a negative exponential of the edge-to-edge distance between patches, even if the dispersal distances are very high, the direct dispersal probabilities will never be as high as 1 (as long as the distance between patches is higher than zero). Therefore, the loss of intermediate habitat patches will always have some effect (even if it is weak) on the connectivity between the remnant patches as quantified by PC. This explains why the proportion of the connector fraction is higher for dPC than for $dIIC$ at large threshold distances (Fig. 2).

The key question is, therefore, when is the PC metric more appropriate, and when is the IIC metric the one to choose? As always, it depends on the question. The PC metric encapsulates the estimated magnitudes of the dispersal flows, and it does not rely on a, sometimes arbitrary, sharp fixation of an assessed threshold dispersal distance. Instead, it gives more weight to patches and links that potentially carry large flows of organisms, and much less weight to patches and links that carry fewer organisms. Furthermore, since the PC metric uses the product of the individual dispersal probabilities between pair of patches to assess the flows throughout the network, it follows that if these pair-wise probabilities p_{ij} are $\ll 1$, the product decreases very rapidly, and essentially vanishes for network distances (i.e. number of intermediate links) higher that just a few number of steps. Thus, the patches that are confined within relatively dense clusters, where the patches are situated fairly close to each other, are the ones that will score high on $dPCconnector_k$. This is seen, for example, by comparing the Figs. 3A and 4A. In Fig. 3A, many of the patches in the dense cluster in the western region of the study area reach high scores of the $dPCconnector_k$, whereas their scores on $dIICconnector_k$ are insignificant (Fig. 4A). Hence, if the main interest is to study flows of organisms irrespectively of their origin (i.e. if they are from neighboring patches, or if they originate from more long-distant patches), PC-based metrics are preferred. One typical situation where this approach is highly applicable is when assessing whether a certain set of patches would be suitable as a home range for a particular species. For a set of patches to be able to attract that species, the set should not be experienced as too scattered thus making it too hard for the species to fulfill its daily needs of finding food, shelter, etc. (e.g. Andersson and Bodin, 2009).

In some cases it is, however, reasonable to disregard the exact assessments of the dispersal probabilities in the PC-based metrics and apply the IIC metrics instead. If focus is, for example, on genetic transmission, is does not matter that much if the flow of organisms is very high or low, as long as it is high enough to provide at least one or few immigrating individual organisms for each generation (Mills and Allendorf, 1996; Wang, 2004). Actually, this implies that the IIC metrics may be better suited to study long-term mixing of populations instead of the actual movement of individuals. As long as the movement probability for an individual situated in a certain patch to reach a neighboring patch is not too low, it is reasonably to assume that at least one individual can mix with the local population in the neighboring patch and thus create a new foothold from where further genetic transmission can take place. This means that all patches that are genetically connected would, over time, make up a single metapopulation. This suggesting discussion is supported by the findings from a recent study where more significant correlations were found between genetic diversity statistics and the $dIIC$

metric compared to the dPC metric (Neel, 2008). Furthermore, in applying this IIC-based perspective on dispersal, more focus is laid on the topology, or reachability, of the network, and less focus on assessing the actual quantities of organisms that flow throughout the landscape.

Acknowledgements

Appendix A. Extending the analysis and ranking procedure to the IIC metric

Similar as for the PC metric, IIC can be divided into three different fractions (Eq. (4B)). The last fraction (Eq. (4B)) can be expressed as follows (Eq. (A1)):

$$dIICconnector_k$$

$$= \frac{100}{IIC}\sum_i\sum_j a_i a_j (1/(1+d_{ij}))\{i, j \neq k \ \text{and} \ ij \in nm^*\}$$

$$- \frac{100}{IIC}\sum_i\sum_j a_i a_j (1/(1+d_{ij,k\,removed}))\{i, j \neq k \ \text{and} \ ij \in nm^*\}$$

$$(A1)$$

The first sum in Eq. (A1) is similar to the proposed BC_k^{PC} metric but instead of the maximum probability product, an inverse function of the topological distance is used to define and weight the shortest paths (Table 1). We denote this modified form of betweenness centrality BC_k^{IIC} (Eq. (A2)).

$$BC_k^{IIC} = \sum_i\sum_j a_i a_j \frac{1}{1+d_{ij}}\{i, j \neq k \ \text{and} \ ij \in nm^*\} \quad (A2)$$

As before, nm^* represents the list of combinations of i and j ($i \neq j$) where k is included in the shortest path between i and j in the initial/intact landscape (before removing k). Also, the second sum in Eq. (A1) represents the residual network $IIC_k^{residual}$ following the removal of patch k, where the residual network is made up of the patches that previously were connected through patch k. In comparing with the original definition of BC, BC_k^{IIC} is including the area product, and instead of accounting for the number of shortest paths, irrespectively how distant the pair of nodes are, BC_k^{IIC} gives less weight to the shortest paths connecting nodes that are more distant (i.e. the denominator in Eq. (A2) increases with the number of intermediate links). Thus, similarly to BC_k^{PC}, this metric weights the shortest paths depending on their assessed "strength", but BC_k^{IIC} is only accounting for the topological network distance and not an estimated potential flow of organisms.

Furthermore, we use the same approach as in Eq. (9) to define the changes in $\Delta BC_i^{IIC(k)}$ in the residual network $IIC_k^{residual}$ (Eq. (A3)).

$$\Delta BC_i^{IIC(k)} = BC_{i,k\,removed}^{IIC(k)} - BC_i^{IIC(k)}\{i \in nm^*\} \quad (A3)$$

$C(50)_k^{IIC}$ is then defined as the minimum number of $\Delta BC_i^{IIC(k)}$ that, summed up, exceed 50% of the BC_k^{IIC} (Table 1). $C(50)_k^{IIC}$ for patch 2 and patch 5 in Fig. 1 equal 1 and 2 respectively and are, in this case, the same as $C(50)_k^{PC}$. As discussed earlier, the removal of patch 2 leaves the remnant network more vulnerable to further

patch removals than what the removal of patch 5 would have done, and that property is accordingly captured by the $C(50)_k^{IIC}$ metric in the same way that for $C(50)_k^{PC}$. Thus we conclude that the patch ranking procedure presented earlier is equally applicable as when using these IIC-based metrics.

Appendix B. Accounting for multiple shortest paths

The analytical investigations of the different metrics suggests a generalization of the PC and IIC metrics to make them better suited to specifically deal with cases when multiple shortest paths between patches exist in the landscape (like in the originally defined BC metric). Here we present how to account for the potential presence of multiple shortest paths. It should be noted that this does not change the computations nor the interpretations of the PC and IIC metrics themselves, but it makes it explicit how the individual patches contribute to the metrics in those cases where multiple shortest paths exists. We first present how we generalized the PC metric to take into account possible existence of multiple shortest paths. Exactly the same procedure is then applied to the IIC metric.

We started by modifying the following in the definition of the PC metric (Eq. (B1)).

$$p_{ij}^* = \frac{1}{L}\sum_l^L p_{ij}^{*l} \tag{B1}$$

where p_{ij}^{*l} is one of the L shortest paths between node i and j. Obviously, $p_{ij}^* = p_{ij}^{*l}$ for all $l \in L$. Thus, this modification does not change the value of the computed PC metric, but it clearly shows that all possible shortest path can be accounted for by assuming that the total flow going through all shortest paths should be the same as if there was just one shortest path. BC_k^{PC}, as a result of applying Eq. (B1) for computing the p_{ij}s, will now include all pairs of i and j where k is included in at least one of the (possibly multiple) shortest paths. This also implies that there might be paths that do not include k (Eq. (B2)).

$$p_{ij}^* = \frac{1}{L}\sum_l^L p_{ij}^{*l} = \left(\sum_l^{L_k} \frac{p_{ij}^{*l(k)}}{L} + \sum_l^{L_{k'}} \frac{p_{ij}^{*l}}{L} \right) \quad \{L = (L_k + L_{k'})\} \tag{B2}$$

where L_k and $L_{k'}$, and $p_{ij}^{*l(k)}$ and p_{ij}^{*l}, represent the numbers, and maximum probability products, of the shortest paths including and excluding k, respectively. If there are shortest paths that do not include k, these paths will clearly remain the same following the removal of k.

Furthermore, we also make it explicit that the generalized version of the betwenness centrality (BC_k^{PC}, Eq. (6)) should, in line with the original definition of betweenness centrality, account for multiple shortest paths. Thus, we rewrite Eq. (6) into Eq. (B3):

$$BC_k^{PC} = \sum_i \sum_j a_i a_j \sum_l^{L_k} \frac{p_{ij}^{*l(k)}}{L} \quad \{i, j \neq k \ and \ ij \in nm^*\} \tag{B3}$$

Since the first sum in Eq. (B2) is included in the refined definition of BC_k^{PC} (Eq. (B3)), and the last sum in Eq. (B2) remains intact following the removal of node k, we need to add the last sum in Eq. (B2) to the right hand side of Eq. (6) which we then rewrite as Eq. (B4).

$$dPCconnector_k = \frac{100}{PC}\left(\frac{BC_k^{PC} - \sum_i \sum_i a_i a_j p_{ij,k\,removed}^* + \sum_i \sum_i a_i a_j \sum_l^{L_{k'}} p_{ij}^{*l}}{L} \right)$$
$$\{i, j \neq k \ and \ ij \in nm^*\} \tag{B4}$$

Hence, this last sum can be regarded as a correction term following the generalized definition of the betweennness centrality. The term compensates for the flows that arise from all shortest paths that are parallel to the ones where node k is involved, but which are not included in the definition of the BC_k^{PC}. This becomes apparent by rearranging the sums in Eq. (B4) where the value of the parallel shortest paths not including k should be subtracted from the new emerged paths p_{ij}^* in the residual network (see Eq. (B5)).

$$dPCconnector_k = \frac{100}{PC}\left(\frac{BC_k^{PC} - \left(\sum_i \sum_j a_i a_j p_{ij,k\,removed}^* - \sum_i \sum_j a_i a_j \sum_l^{L_{k'}} p_{ij}^{*l} \right)}{L} \right)$$

$$= \frac{100}{PC}\left(\frac{BC_k^{PC} - \sum_i \sum_j a_i a_j \left(p_{ij,k\,removed}^* - \sum_l^{L_{k'}} p_{ij}^{*l} \right)}{L} \right)$$
$$\{i, j \neq k \ and \ ij \in nm^*\} \tag{B5}$$

When a single shortest path exists then $L_{k'} = 0$ and $L_k = 1$, and Eq. (B5) simplifies to Eq. (6).

Following the same procedure as above, but for the IIC metric, gives Eqs. (B6) and (B7).

$$BC_k^{IIC} = \sum_i \sum_j a_i a_j \sum_l^{L_k} \frac{1/(1 + d_{ij}^{l(k)})}{L} \quad \{i, j \neq k \ and \ ij \in nm^*\} \tag{B6}$$

$dIICconnector_k$

$$= \frac{100}{ICC}\left(\frac{BC_k^{IIC} - \left(\sum_i \sum_j a_i a_j \left((1/(1 + d_{ij,k\,removed})) - \sum_l^{L_{k'}}(1/(1 + d_{ij}^l)) \right) \right)}{L} \right)$$
$$\{i, j \neq k \ and \ ij \in nm^*\} \tag{B7}$$

where $d_{ij}^{l(k)}$ and d_{ij}^l and represents the shortest topological paths between patch i and j that are, and are not, including patch k, respectively.

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