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Contribution of habitat patches to network connectivity: Redundancy and uniqueness of topological indices

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ABSTRACT

In order to increase the efficiency of monitoring and conservation efforts, it is of key importance to develop sound quantitative methods that are able to indicate which key areas and landscape elements play prominent and crucial role in the functioning of habitat mosaics. In particular, network models are being widely used to evaluate the contribution of landscape elements to uphold connectivity and related ecological fluxes. However, monitoring programs and conservation practitioners are overwhelmed by a myriad of network indices without being fully aware of their differences for characterizing the importance of individual habitat patches in fragmented landscapes. We analysed a set of thirteen commonly used graph indices and the forest habitat network of goshawks living in NE Spain in order to (a) evaluate how the patch rank orders derived from these indices differ from each other and (b) identify which indices tend to quantify the same network characteristics and which others are quite unique in addressing topological characteristics that are not considered by the rest. We found that most of the variability in patch rankings can be captured by only three network indices. The largest group of redundant indices corresponded to those that intend to measure the amount of flux received by a given habitat patch. The connector fraction of the *integral index of connectivity* (IIC) and *probability of connectivity* (PC) indices and *betweenness centrality* (BC) stood out as quite unique by focusing on the way habitat patches act as connecting elements between other habitat areas. We discuss which indices can be most beneficial by clearly indicating and differentiating the value of the top patches compared to the others, so that conservation priorities can be established with lower uncertainties. We believe that our results can provide valuable guidelines by facilitating the selection of a few non-redundant and complementary indicators that quantify the important and distinctive roles of habitat patches in maintaining the connectivity of habitat networks.

1. Introduction

The combination of climate change and the fragmentation of natural habitats may be especially dangerous for native fauna and flora: the lack of habitat continuity may prevent organisms to escape from areas which are no longer inhabitable due to the new environmental conditions and the reduced size of the patches where they dwell. Connectivity ensures the possibility for dispersal and gene flow, both of which are crucial for avoiding population decline and extinction (Beier and Noss, 1998; Haddad et al., 2003). Thus, one key issue in landscape monitoring and conservation planning is related to the connectivity of the remaining natural habitats (Burel and Baudry, 2005; Vogt et al., 2007), which can be promoted through a more permeable landscape matrix or establishing new habitats and corridors in critical cases.

There is growing interest in the use of graph theoretical methods (network analysis) that allow delivering indicators for the identification of key elements of the landscape and the quantification of their contribution to overall connectivity. This approach is based on the patch/corridor model and assumes that complex landscapes can be described by a graph with nodes representing habitat patches and links representing the ability of a particular species to move or the possibility of an ecological flow to occur between two nodes in the graph. Links may correspond to ecological corridors that can be physically identified and distinguished in the landscape or to a more diffuse matrix that is permeable to movement and facilitates dispersal between relatively distant habitat areas. The quantification of important landscape elements (patches, stepping stones or corridors) and, consequently, the determination of conservation priorities are based mainly on topological indicators that reflect

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the relative importance of different elements in the habitat graph. The first, sporadic and intuitive graph theoretical studies (Cantwell and Forman, 1993; Urban and Keitt, 2001) are being replaced by a robust research trend of increasing predictivity and importance. Recently suggested methods include local (or mesoscale) indices to characterize the immediate neighborhood of graph nodes (habitat patches). Measures that have been used for this purpose are degree centrality (Jordán et al., 2003; Minor and Urban, 2007; Estrada and Bodin, 2008), closeness centrality (Jordán et al., 2003, 2007a; Estrada and Bodin, 2008), betweenness centrality (Minor and Urban, 2007; Bodin and Norberg, 2007; Estrada and Bodin, 2008; Dunn and Majer, 2009), eigenvalue centrality (Estrada and Bodin, 2008), subgraph centrality (Estrada and Bodin, 2008) and the Harary index (Ricotta et al., 2000).

Other authors prefer global indices in order to describe the macroscopic topology of the landscape. These include degree distribution (Rhodes et al., 2006; Minor and Urban, 2008), diameter (Minor and Urban, 2008; Ferrari et al., 2007), average path length (Rhodes et al., 2006; Minor and Urban, 2008) and the clustering coefficient (Jordán et al., 2003; Minor and Urban, 2008). There have been several attempts to apply methods borrowed from statistical physics (e.g. inferring vulnerability and resistance from degree distribution patterns) in landscape ecology (Rhodes et al., 2006; Minor and Urban, 2008).

Finally, some other studies also aimed to combine topological measures with patch quality and corridor permeability indicators (Jordán et al., 2003, 2007a; Minor and Urban, 2007). Beyond considering only binary topology, a promising approach is to study weighted landscape graphs in which link weights correspond to dispersal probabilities (Urban and Keitt, 2001; Saura and Pascual-Hortal, 2007; Saura et al., 2011). Indices quantifying macroscopic changes after deleting patches within this framework provide another link between methods utilizing local and global properties. These are based on either flux indices (Bunn et al., 2000; Urban and Keitt, 2001), graph diameter (Urban and Keitt, 2001), landscape or class coincidence probability (Pascual-Hortal and Saura, 2006), the integral index of connectivity (Pascual-Hortal and Saura, 2006; Neel, 2008; García-Feced et al., 2011; Laita et al., 2010; Erõs et al., 2011), or the probability of connectivity and related indices (Saura and Pascual-Hortal, 2007; Neel, 2008; Perotto-Baldivieso, 2009; Fu et al., 2010; Watts and Handley, 2010; Saura et al., 2011), among others. More recently, it has been shown how some of these latter indices (e.g. integral index of connectivity, probability of connectivity) can be partitioned into three separate fractions that quantify the different ways a particular habitat patch may contribute to habitat connectivity and availability in the landscape (Saura and Rubio, 2010). These three fractions are measured in the same units and allow for prioritizing the landscape elements and their different roles within an integrated analytical framework (Saura and Rubio, 2010).

Since all these methods aim to indicate and rank the relative contribution of landscape elements to the maintenance of connectivity, it is of outmost importance to fully understand their relationships and practical differences for the analysis of fragmented landscape networks. For this reason, our objectives were (a) to evaluate how the patch rank orders derived from these indices differ from each other and (b) to identify which indices tend to quantify the same network characteristics and which others are quite unique in addressing topological characteristics that are not considered by the rest. We consider a wide set of indices quantifying the importance of nodes as connectivity providers that have been used in recent landscape graph studies and focus on the analysis of the habitat network for the goshawk (*Accipiter gentilis*) in NE Spain. In this area, the role of connecting elements has been previously shown to be prominent and necessary for maintaining the habitat availability for this species. We quantify the patch rankings provided by these different indices and the relationships among them based on rank correlation and ordinal multivariate analysis.

Our results should provide valuable criteria (1) for the selection of non-redundant and complementary indicators for analysing the connectivity of landscape networks and (2) for identifying the important distinctive roles of habitat patches to be considered for indicator delivery. We believe that these guidelines are particularly important and necessary in a context where users (1) are increasingly overwhelmed by a myriad of indices related to connectivity and (2) face the need to base their conservation or monitoring programs only on one or a few indicators without being fully aware of their analytical and practical differences for landscape planning and change assessments, which have remained largely unreported in previous studies on the topic.

2. Methods

2.1. Study area and bird habitat data

We studied goshawk (*A. gentilis*) habitat in Catalonia (NE Spain), where this species dwells mainly in *Pinus nigra*, *Pinus halepensis*, *Pinus sylvestris* and *Quercus ilex* forests (Fig. 1). Bird occurrence and habitat distribution in Catalonia have been well-documented in the Catalan Breeding Bird Atlas (Estrada et al., 2004), with less than a thousand of goshawk pairs estimated in this region. Also, their conservation status is of concern, with the species suffering from a decreasing population trend and being currently considered as near threatened in Catalonia (Estrada et al., 2004). The preferred goshawk habitat is the old-growth, dense pine forest with large trees (Squires and Reynolds, 1997), while young individuals need large, non-fragmented forests (Bosakowski and Speiser, 1994). These habitats are threatened in Catalonia mostly by increased wildfire occurrence in the last decades, inadequate management of forests and other woodlands, and the urban sprawl in some localized areas.

Forest connectivity is of key importance because of the behavioral ecology of goshawks. The largest distance they can fly from their birth place is mostly determined by prey density (Byholm, 2003), especially for the younger individuals, while the adults are relatively faithful to their territories and typically competitively dominant around the nest. Thus, connectivity is mostly important for late-born young males, but large-distance dispersal is not typical for them either. One difficulty in studying the effect of fragmentation on bird survival is the possibility of extinction debts, i.e. a large time-lag between fragmentation processes and their impact on population persistence (Brooks et al., 1999). Land use and forest fragmentation have major effects not only on birds. We begin to understand the general effects on forest-dwelling species in larger geographical context (Wallenius et al., 2010).

2.2. Network construction

The study area was mapped by 1 km × 1 km UTM quadrats, and species occurrence probabilities were determined for each of them in the Catalan Breeding Bird Atlas (Estrada et al., 2004), based on field sampling and niche-based modeling (Guisan and Zimmermann, 2000). Based on this information, we identified 2352 goshawk habitat quadrats (those with a probability of species occurrence above 0.1) corresponding to a total of 397 patches (sets of neighbouring 1 km × 1 km UTM quadrats), as shown in Fig. 1. Each of these patches corresponds to one node in the graph, with nodes being weighted by an attribute corresponding to patch area multiplied by the probability of bird occurrence (as a proxy to habitat quality). We modeled this dataset through a complete weighted graph in which the estimated direct dispersal probabilities between

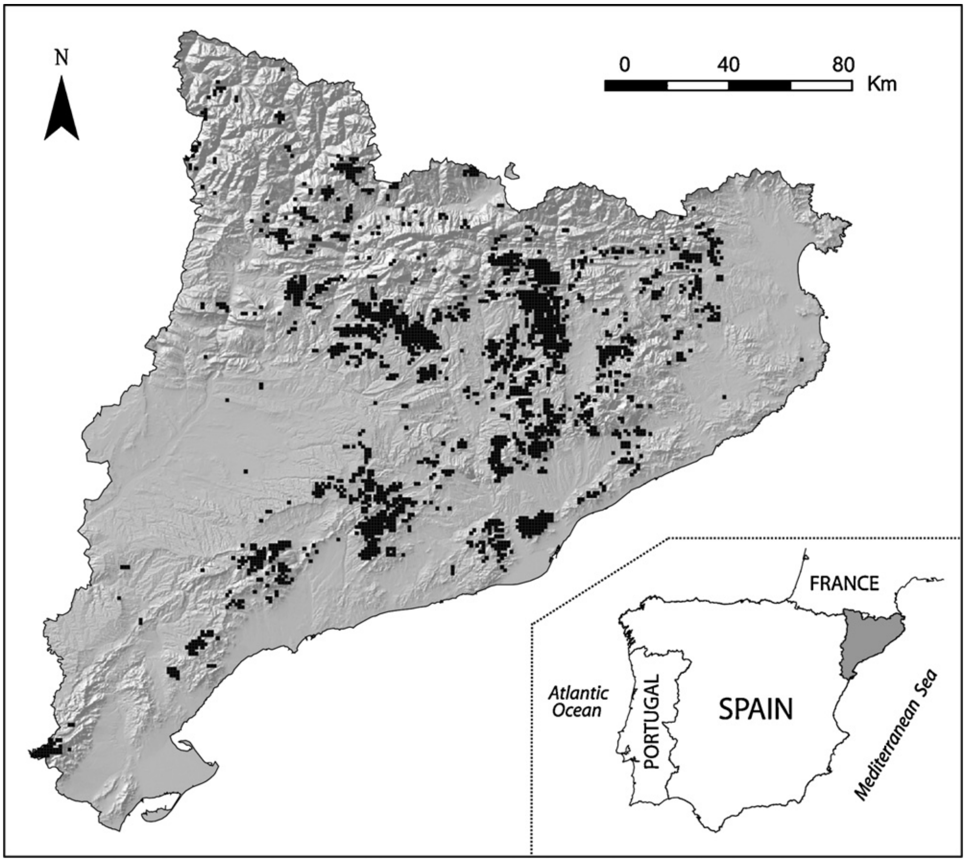

Fig. 1. Map of Catalonia with the quadrats corresponding to goshawk habitats marked by black dots. The location of Catalonia within the map of Spain is shown in the lower right map (based on Saura and Pascual-Hortal, 2007; with original data from Estrada et al., 2004).

each pair of habitat patches (p_{ij}) were used as the weights in the links (or edges) of the graph as follows:

$$p_{ij} = e^{-kd_{ij}} \quad (1)$$

where d_{ij} is the edge-to-edge distance between habitat patches i and j (in km, measured between the closest edge points) and k is a species-specific constant (here $k = 0.0462$) reflecting the dispersal behaviour of goshawks and their median natal dispersal distance ($p_{ij} = 0.5$) estimated at 15 km (Wiens et al., 2006; Saura and Pascual-Hortal, 2007). From this complete graph, we generated a unweighted graph by setting a dispersal probability (p_{ij}) threshold; a link between two patches existed only if the dispersal probability between them was higher than the specified threshold. In this unweighted graph, all the existing links were considered as equally effective for conducting movement, in contrast to the weighted graph where the link strength (weight) was modulated by the p_{ij} value. In all cases, we used undirected landscape graphs, since we have no information on source and sink patches, i.e. on asymmetric dispersal.

2.3. Network indices and analyses

Although global, large-scale topological analysis of landscape graphs has a long history, the use of local measures to characterize the relative importance of landscape elements (patches and corridors) is quite recent (e.g. Jordán et al., 2003). Here we focus on 13 connectivity indices, as described in Table 1 and the references therein. In addition, we consider in the analysis the proportion of the total habitat attribute value in the landscape (sum of attributes for all patches) that corresponds to a particular analysed patch (*dA*). Although *dA* is not a connectivity index, it will be included to allow analyzing to what degree the rankings provided by the different topological indices differ from the prioritization obtained simply by considering the intrinsic patch characteristics (e.g. based only on attributes such as habitat area or quality). The third fraction of the *dIIC* and *dPC* indices (*dPCintra* and *dPCintra*, respectively) as described by Saura and Rubio (2010) is not included in the analysis because it is basically a squared function of the considered node attribute, and hence it will obviously provide the same ranking of habitat patches as *dA*. Based on *BC* (Table 1), a global index characterizing network centralization can be constructed (NCI_{BC}), as described in Wasserman and Faust (1994). We calculated this index for the whole network and different p_{ij} thresholds (determining which links existed in the graphs with unweighted links); this index was not used to rank habitat patches (as for those described in Table 1) but to evaluate the degree of structural heterogeneity at the p_{ij} threshold that was finally chosen.

2.4. Comparison of the patch rankings derived from the different indices

The agreement among different indices was evaluated by multivariate methods that are most suitable to ordinal data. To calculate the starting dissimilarity matrix, first the importance values were ranked for each index, and then the actual values were replaced by their ranks. A new matrix $R_{n,m}$ was thus obtained in which the number of rows (n) is the number of nodes in the network ($n = 397$) and the number of columns (m) is the number of indices ($m = 14$, the 13 connectivity indices plus *dA*). The next step was the calculation of the $m \times m$ dissimilarity matrix among these landscape network

Table 1
Description and references for the 13 connectivity indices analysed in this study. Higher values of all these indices indicate higher node importance in maintaining landscape connectivity.

Index name	Description and references	Graph type	Calculation
Normalised degree (*D*)	Number of other habitat patches linked to the analysed patch (divided by the total number of patches). It is equivalente to the NL (number of links) index in Conefor Sensinode. See Wasserman and Faust (1994).	U	I
Weighted degree (*wD*)	Sum of weights (here p_{ij} values) on the links fitting to the analysed patch. It is equivalent to the flux index (F) in Conefor Sensinode. See Wasserman and Faust (1994).	W	I
Closeness centrality (*CC*)	Number of nodes divided by the sum of the topological distances (number of links in the shortest path) between the analysed patch and every other reachable patch in the landscape. See Wasserman and Faust (1994).	U	I
Betweenness centrality (*BC*)	Number of shortest paths between all pair of patches that go through the analysed patch, divided by the total number of shortest paths between each pair of patches (Freeman, 1977). It assesses the frequency of mediating shortest paths through a particular patch, i.e. how much that patch is involved in the current flows of organisms in the undisturbed landscape. See Wasserman and Faust (1994).	U	I
Harary index (*dH*)	Sum of the inverse values of the topological distance between every two patches. If two patches belong to different components, their topological distance is infinity (a component is defined as a set of patches that can be reached from each other through existing links). See Ricotta et al. (2000).	U	R
Landscape coincidence probability (*dLCP*)	Probability that two points randomly located within the landscape belong to the same habitat component. It is a generalization of the Simpson's diversity index and the related degree of coherence (Bogaert et al., 2005). It is equivalent and conveys the same information as the C index proposed by Matisziw and Murray (2009) in undirected graphs (Saura, 2010). See Pascual-Hortal and Saura (2006).	U	R
Area-weighted flux (*dAWF*)	Sum of the products of the direct dispersal probability (p_{ij}) between each pair of nodes and the attributes of those nodes *i* and *j*. See Bunn et al. (2000), Urban and Keitt (2001) and Saura and Pascual-Hortal (2007).	W	R
Integral index of connectivity (*dIIC*)	Index calculated from the attributes of the patches and the topological distances between them. It takes into account the connected area existing within the patches, the estimated dispersal flux between different patches, and their contribution as stepping stones or connecting elements that uphold the connectivity between other patches. See Pascual-Hortal and Saura (2006).	U	R
dIICflux	One of the three *dIIC* fractions estimating the amount of dispersal fluxes between a particular patch (as the origin or destination of those fluxes) and the rest of the patches in the landscape (Saura and Rubio, 2010).	U	R
dIICconn	One of the three fractions of *dIIC* measuring the contribution of the analysed patch to the connectivity between other patches, as a connecting element or stepping stone between them (Saura and Rubio, 2010).	U	R
Probability of connectivity (*dPC*)	It is conceptually similar to *dIIC* but for weigthed graphs. It uses the maximum product probability instead of the topological distance between patches. See Saura and Pascual-Hortal (2007).	W	R
dPCflux	Analogous to *dIICflux* but for the *dPC* index in weighted graphs (Saura and Rubio, 2010).	W	R
dPCconn	Analogous to *dIICconn* but for the *dPC* index in weighted graphs (Saura and Rubio, 2010).	W	R

The last two columns indicate, respectively whether the index is (1) defined and computed in unweigthed (U) or weighted (W) graphs and (2) calculated by considering topological properties of the intact landscape network (I) or as the relative variation in the landscape-level connectivity index after the removal of a particular individual patch from the landscape (R). The first indices (I) were calculated by Ucinet 6.0 (Borgatti et al., 2002) and the others (R) through a new version of the Conefor Sensinode software package (Saura and Torné, 2009) available at http://www.conefor.org.

indices, in which δ_{jk} was defined by:

$$\delta jk = \sum_{i=1}^{n} \frac{|r_{ij} - r_{ik}|}{\max\{r_{ij}, r_{ik}\}} \qquad (2)$$

In words, the absolute rank difference between indices *j* and *k* for node *i* is divided by the maximum of the two rank scores, and these values are summed over all nodes. Thus, in calculating the dissimilarity, more weight was given to differences between more important nodes with lower rank scores (i.e. a given difference between important nodes matters more than the same difference in case of nodes that are near the end of the rank order). The structure in this matrix was evaluated by clustering and ordination as well, using the ordinal clustering algorithm suggested by Podani (2005) and non-metric multidimensional scaling (NMDS, see e.g., Legendre and Legendre, 1998), respectively. The hierarchical levels in the resulting dendrogram do not reflect dissimilarities, they are only the ranks of fusions themselves, from 1 to *m*-1. NMDS was run with two output dimensions required, and the analysis was repeated from random initial coordinates twenty times to select the best result. Ordination success in NMDS was measured numerically by the stress value, and graphically by the Shepard-diagram. Similar analyses of topological indices have been done for food webs as well (Jordán et al., 2007b). Compu-

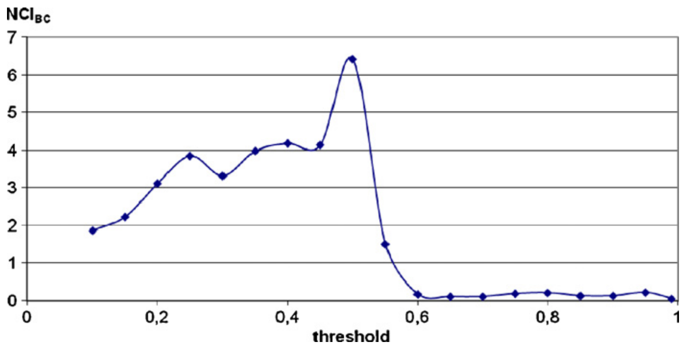

Fig. 2. Values of NCI_{BC} for the whole network as a function of the dispersal probability (p_{ij}) threshold.

tations were performed by the SYN-TAX 2000 software (Podani, 2001).

3. Results

The network structural heterogeneity was highest at the p_{ij} = 0.5 threshold, as indicated by the characteristic peak in the betweenness-based network centralization index (NCI_{BC}, see Fig. 2), followed by a sharp drop down to almost zero NCI_{BC} values for higher probability thresholds. Therefore, this p_{ij} threshold value was used for constructing the graph with unweigthed links and calculating the related indices.

Based on the rankings of the different indices at the level of individual nodes (Fig. 3), *BC*, *dH*, *dLCP*, *dIIC* and *dIICconn* are strongly skewed (with a few very critical patches and almost all the rest with low importance) while, for example, *D*, *wD* and *CC* are comparatively more uniformly distributed. In particular, most of the nodes had very similar *CC* values, close to the maximum attained value for this index (Fig. 3). *dA* was, together with *CC*, the index that assigned the highest comparative importance to the nodes near the end of the rank order (Fig. 3). Within the fractions of *dPC* and *dIIC*, the connector fraction (*dPCconn* and *dIICconn*, respectively) was the one with a more skewed distribution towards the most important nodes (Fig. 3). The IIC-based indices presented less uniform distributions than those of their *PC*-based counterparts (Fig. 3). The same, although to a lower extent, occurred for the equivalent *D* (graphs with unweighted links) and *wD* (weighted links) indices, with the former index presenting steeper slopes than *wD* in the distributions shown in Fig. 3.

Based on the ranking of nodes, *BC*, *dA*, the connector fraction of the habitat availability measures (*dIICconn*, *dPCconn*) and *D* are the atypical outliers (Fig. 4), while other indices provide more

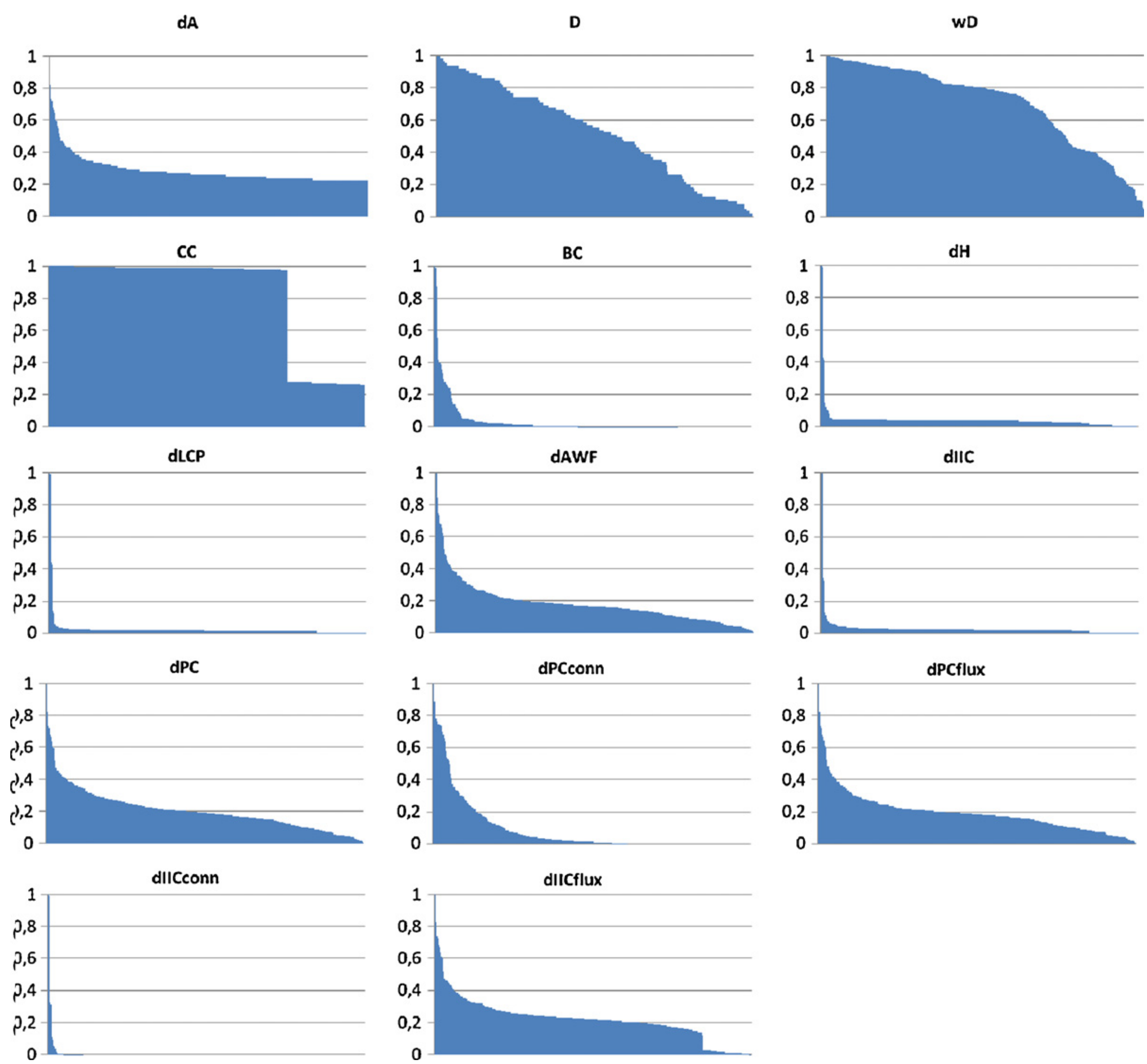

Fig. 3. Columns show the normalized (by maximum) values of the studied indices (*dA* in Fig. 3a plus 13 network indices in Fig. 3b–n), ranked for all the nodes. Some ranks show highly skewed distributions, like dIIC. Others are more evenly distributed, like D.

Table 2
The 20 most important nodes ranked according to the 14 indices studied. Node identities in bold (*N* = Node number), index values in normal settings.

N	*dA*	*N*	*dH*	*N*	*dLCP*	*N*	*dIIC*	*N*	*dIICflux*	*N*	*dIICconn*	*N*	*dAWF*
327	0.880	**244**	18.214	**244**	37.359	**275**	26.597	**327**	2.272	**244**	25.994	**327**	2.778
297	0.722	**275**	18.077	**275**	37.183	**244**	26.545	**297**	1.867	**275**	25.745	**297**	2.347
314	0.643	**155**	7.802	**155**	16.435	**155**	9.076	**314**	1.669	**155**	8.489	**314**	2.090
313	0.633	**156**	7.522	**156**	15.860	**156**	8.666	**313**	1.644	**156**	8.200	**313**	2.045
328	0.593	**245**	2.650	**245**	5.142	**245**	3.364	**328**	1.543	**245**	2.879	**328**	1.907
296	0.584	**249**	2.159	**249**	4.642	**249**	2.937	**296**	1.518	**249**	2.464	**296**	1.895
299	0.564	**100**	1.847	**327**	2.028	**327**	2.323	**299**	1.454	**241**	1.370	**299**	1.828
315	0.534	**241**	1.833	**297**	1.665	**241**	1.945	**315**	1.381	**243**	1.344	**315**	1.741
329	0.524	**177**	1.712	**314**	1.483	**297**	1.902	**329**	1.359	**177**	1.028	**329**	1.686
298	0.504	**243**	1.697	**313**	1.460	**243**	1.856	**298**	1.305	**100**	0.925	**298**	1.653
321	0.495	**153**	1.399	**328**	1.369	**314**	1.697	**300**	1.177	**153**	0.498	**300**	1.461
322	0.485	**197**	0.925	**296**	1.347	**313**	1.671	**286**	1.078	**197**	0.221	**286**	1.361
300	0.455	**176**	0.889	**299**	1.301	**328**	1.566	**330**	1.076	**176**	0.180	**330**	1.330
308	0.435	**122**	0.790	**315**	1.233	**296**	1.540	**321**	1.055	**202**	0.141	**285**	1.258
286	0.415	**201**	0.748	**329**	1.210	**177**	1.509	**347**	1.052	**122**	0.107	**287**	1.233
293	0.415	**101**	0.742	**298**	1.165	**299**	1.475	**322**	1.034	**184**	0.086	**336**	1.193
330	0.415	**85**	0.738	**321**	1.142	**315**	1.400	**303**	1.020	**190**	0.083	**303**	1.182
347	0.405	**88**	0.738	**322**	1.119	**100**	1.394	**285**	1.008	**199**	0.076	**318**	1.148
303	0.396	**94**	0.738	**300**	1.051	**329**	1.378	**336**	0.983	**208**	0.074	**347**	1.102
252	0.386	**95**	0.738	**308**	1.005	**298**	1.322	**287**	0.974	**201**	0.063	**290**	1.100

N	*dPC*	*N*	*dPCflux*	*N*	*dPCconn*	*N*	*wD*	*N*	*D*	*N*	*CC*	*N*	*BC*
327	2.611	**327**	2.573	**101**	0.464	**286**	78.113	**74**	16.414	**191**	0.972	**244**	18.55
297	2.147	**297**	2.121	**88**	0.413	**297**	78.028	**75**	16.414	**192**	0.972	**275**	18.334
314	1.914	**314**	1.894	**145**	0.364	**287**	78.005	**76**	16.414	**195**	0.972	**208**	16.223
313	1.885	**313**	1.865	**233**	0.363	**298**	77.947	**77**	16.414	**197**	0.972	**197**	10.337
328	1.768	**328**	1.751	**217**	0.355	**285**	77.851	**72**	16.162	**204**	0.972	**176**	7.765
296	1.739	**296**	1.722	**348**	0.346	**296**	77.735	**73**	16.162	**205**	0.972	**184**	7.314
299	1.681	**299**	1.665	**150**	0.345	**275**	77.643	**78**	16.162	**201**	0.971	**193**	7.298
315	1.593	**315**	1.578	**346**	0.343	**288**	77.564	**71**	15.909	**207**	0.971	**236**	7.28
329	1.563	**329**	1.550	**281**	0.343	**299**	77.479	**85**	15.909	**209**	0.971	**204**	6.647
298	1.505	**298**	1.492	**294**	0.342	**314**	77.454	**81**	15.657	**210**	0.971	**205**	6.647
300	1.358	**300**	1.348	**141**	0.341	**315**	77.366	**88**	15.657	**211**	0.971	**191**	6.265
286	1.241	**286**	1.232	**353**	0.326	**284**	77.299	**93**	15.657	**193**	0.97	**195**	5.507
330	1.241	**330**	1.232	**148**	0.316	**313**	77.166	**94**	15.657	**194**	0.97	**100**	5.21
303	1.182	**303**	1.174	**138**	0.306	**295**	77.111	**70**	15.404	**212**	0.97	**178**	5.165
88	1.177	**285**	1.145	**272**	0.296	**316**	76.886	**82**	15.404	**213**	0.97	**192**	4.936
348	1.154	**287**	1.116	**345**	0.269	**300**	76.664	**95**	15.404	**215**	0.97	**237**	4.832
285	1.153	**336**	1.116	**282**	0.248	**312**	76.546	**284**	15.404	**216**	0.97	**263**	4.689
287	1.123	**318**	1.087	**259**	0.245	**328**	76.376	**295**	15.404	**217**	0.97	**259**	4.53
336	1.123	**321**	1.074	**273**	0.240	**329**	76.252	**296**	15.404	**220**	0.97	**153**	4.528
322	1.117	**347**	1.059	**344**	0.231	**107**	76.248	**312**	15.404	**221**	0.97	**194**	4.104

similar rankings with some overlaps: *dA* and *dPC* both suggest node #327 and the following nine nodes with exactly the same ranks (Table 2). However, the fractions of the *dPC* index behave differently, while *dH*, *dLCP* and *BC* agree at the first (#244) and second (#275) priorities (Table 2). As shown in Fig. 4, *dIIC* and *dPC* tended to rank patches similarly to their flux fraction (*dIICflux* and *dPCflux*, respectively), while the most redundant priorities were those derived from *dPCflux* and *dAWF*. These latter two indices also tended to coincide, although to a lower degree, with *wD*. Table 2 presents the most important 20 nodes ranked for each studied index.

The NMDS diagram shows how the dissimilarity structure of different indices is portrayed by clustering and ordination (Fig. 5). The scatter of points corresponds very well the clustering result. That the 2D solution is a faithful summary of multidimensional point pattern is shown by the Shepard diagram (inset, Fig. 5) and the relatively low stress value (0.065). The *dA* index is the most unique (which might be expected since this index is the only one independent of the node location within the landscape), followed by the topological indices *dPCconn*, *dIICconn* and *BC*, which characterize distinctly different properties of the habitat network. Our analyses revealed similarities in the patch ranking provided by the rest of the analysed connectivity indices, which tended to be grouped relatively close in the multidimensional scaling (Fig. 5).

4. Discussion

4.1. How redundant the indices are and how many unique topological roles can be differentiated?

The most differentiable and largest group of relatively redundant indices corresponded to those that, in some way or another, intend to capture the amount of flux or connections that a given patch receives from other habitat areas in the landscape (*D*, *wD*, *CC*, *dH*, *dAWF*, *dLCP*, *dIIC*, *dPC*, *dIICflux*, *dPCflux*). Either based on just the number of links (connections) a patch receives, on the topological distance to other patches, or on the amount of flux estimated to arrive through those connections, *D*, *wD*, *CC*, *dH*, *dAWF*, *dIICflux* and *dPCflux* all fall into this group. While *dIIC* and *dPC* are in fact influenced by three different components, as described above (intra, flux, connector), the *dIICflux* and *dPCflux* fractions are those that largely dominate the total *dICC* and *dPC* values for species with medium to large dispersal abilities relative to the habitat spatial pattern (Saura and Rubio, 2010), as is the case of the goshawk habitat analysed here. Although the definition of *dLCP* (Table 1) does not make explicit reference to the individual connections arriving at an individual patch as for the other indices in this group, the identification of graph components is actually based on determining the number of patches that are connected to a given node,

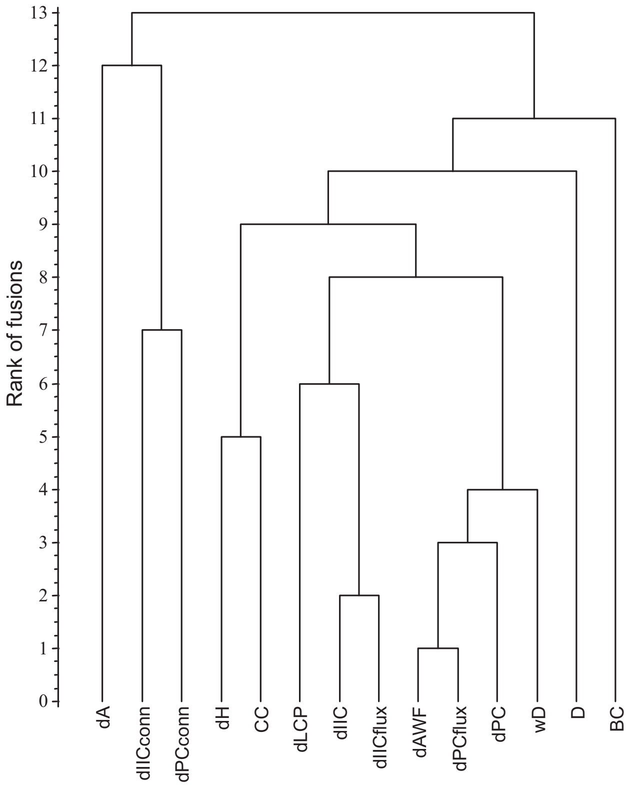

Fig. 4. Dendrogram illustrating dissimilarity structure between indices based on ordinal clustering. The units on *y* axis refer merely to the sequence of fusions and do not mean actual dissimilarities. Identical indices would be joined at level 0. Note the high closeness (but no identity) of indices *dAWF* and *dPCflux*.

either through a direct link or through a path comprising more than one step through other intermediate patches. Therefore *dLCP* ultimately performs quite similarly to the other indices in this group. The fact that some of these indices do not take into account node attributes (*D*, *CC*, *dH*, *wD*) while the rest include them explicitly in their formulae (*dAWF*, *dLCP*, *dIIC*, *dPC*, *dIICflux*, *dPCflux*) was reflected in our results, where these two subtypes of indices clustered in two well-separated subregions in the ordination space (Fig. 5), and also in the dissimilarities in the dendrogram (Fig. 4). However, despite this noticeable effect, the node weights (patch attributes) did not seem to have a paramount effect in the final overall rankings, compared to other factors and indices that are discussed below.

Indeed, some other indices like *BC*, *dPCconn* and *dIICconn* stood out as quite unique compared to the rest of the analysed topological indicators (Figs. 4 and 5). This is due to the intrinsically distinctive way in which these three indices quantify the topological importance of habitat patches in a landscape network. Unlike most of the other analysed indicators, they do not evaluate how well-connected a patch might be (in terms of the amount of connections or migrants expected to arrive or depart from a particular patch as the starting or ending point of those ecological fluxes), but how important that patch is for maintaining the connectivity or upholding the biological interchanges between the rest of the habitat areas. A particular patch may be well connected to other habitat patches (as indicated by most of the measures mentioned above) but it might not play a key role as a stepping stone that facilitates dispersal between other patches in the landscape network. The non-redundancy of these two roles is supported by our results and agrees with previous analytical studies for the *PC* index (Saura and Rubio, 2010). Different studies have applied the *PC* index for functional connectivity analyses that used minimum-cost (effective) distances for characterizing the p_{ij} values (D'Alessandro et al., 2009; Fu et al., 2010; Watts and Handley, 2010), as originally defined and foreseen for the *PC* index by Saura and Pascual-Hortal (2007). However, one of these studies (Watts and Handley, 2010) only considered the intra and flux fractions but not the connector one, by calculating *PC* directly from p_{ij} instead of from p_{ij}^* (the latter accounting for stepping stones). Therefore, when *PC* is calculated in such a way, it may in general miss the uniqueness provided by this last fraction and make the index more redundant with the other network indices described earlier.

However, there are still considerable differences in the rankings provided by *BC*, *dIICconn*, and *dPCconn*, particularly between *BC* and the other two, as reflected in the distance between them in the multidimensional scaling ordination (Fig. 5). These differences can be explained by the analytical and methodological differences between these indices and the way they quantify the role of habitat patches as connectivity providers (Bodin and Saura, 2010). *dIICconn* and *dPCconn* are based on removing a patch from the network and calculating the resultant decrease in the value of the connectivity index (*IIC* and *PC*, respectively); larger decreases are considered indicative of a more important role of the patch for maintaining network connectivity. However, *BC* is based on the topological properties of the intact network and indicates the degree to which a particular patch is involved in the current flows of organisms (shortest paths between habitat areas) in the undisturbed landscape. *BC* does not consider how the flows may change as a consequence of a particular habitat loss and does not take into account how adequate for movement the remnant available paths in the disturbed network might be. Therefore, a particular patch may have quite a central location in the landscape network as measured by *BC* and related centrality measures, but still be of low importance for the conservation of connectivity (as indicated by *dIICconn* or *dPCconn*) because many other patches may be able to compensate for its loss. Thus, the available paths in the disturbed network are (almost) as favorable for movement as those in the intact landscape (Bodin and Saura, 2010). Although it is therefore possible for a patch to have a low *dPCconn* or *dIICconn* together with a high *BC*, a patch first needs to be central (part of the best and most frequent paths among several other habitat areas) in order to score high in *dIICconn* or *dPCconn*, the latter indicating that the patch is not only central but irreplaceable as a connectivity provider (Bodin and Saura, 2010). For these reasons, since the correlation between the centrality of a patch and the amount of flux it receives (both measured in the intact landscape) is higher than between that flux and the degree of irreplaceability of the patch, *BC* tends to stay closer to the majority of the flux-related indices than *dIICconn* or *dPCconn* (Figs. 4 and 5). This shows that these two types of measures and approaches (*BC* and *dIICconn*/*dPCconn*) are complementary and indicative of different aspects and roles of the habitat patches in the landscape network, although in most of the cases a higher weight would be given to *dIICconn* or *dPCconn* compared to the centrality measures in a ranking procedure oriented to conservation planning (Bodin and Saura, 2010). The ranking discrepancies between *dIICconn* and *dPCconn* are due to the different connectivity model on which each of them relies (binary and probabilistic connections), which is the same reason that explains the dissimilarities between *D* and *wD* or between *dIIC* or *dPC* (Fig. 5). In fact, the indices based on these two different graph types (with weighted or unweighted links) were grouped in two easily differentiable and separated subregions in the ordination space, which was particularly noticeable for the cluster of ten measures related to the amount of flux received by a patch (see dashed lines in Fig. 5). However, using weighted or unweighted links to model the landscape network did not have again such a prominent effect as the conceptual differences and the different patch roles and connectivity aspects being evaluated by the different indices.

All the analysed connectivity indicators prioritized habitat patches in a considerably different way from that resulting from just considering the intrinsic habitat patch characteristics (*dA*, here corresponding to the product of habitat area and species probability of occurrence) with no reference to the landscape configuration or the spatial relationships between landscape elements. Although this may look natural, previous studies have shown that this result is not always guaranteed in connectivity analysis, and that in many cases the rankings derived from a connectivity analysis can coincide to a large extent with the simpler decision of conserving first those patches with larger habitat area or quality (Ferrari et al., 2007; Saura and Rubio, 2010). If the results of the connectivity indicators and *dA* do not differ much, it might even question the need to base the conservation decisions on a connectivity model that is more data-demanding and subjected to more uncertainty than other more classical approaches (Hodgson et al., 2009). However, our analysis was focused on a habitat network and species for which connecting elements and topological properties emerge as highly relevant both from a spatial network and ecological point of view (Saura and Pascual-Hortal, 2007), as further guided and confirmed by our analysis on the betweenness-based network centralization index (Fig. 2). If the same habitat configuration was used by other species with much larger or modest dispersal abilities, then the connectivity analysis itself, and the patch rankings and resultant redundancies would be of much less interest and many of the measures would tend to collapse with other non-topological criteria such as *dA* (Keitt et al., 1997; Saura and Rubio, 2010).

We have also found here that the threshold-dependence of topological indices gives non-trivial information about the landscape graph. For example, the value of NCI_{BC} (network centralization) depends strongly on the actual p_{ij} value chosen. This is especially important for connecting structure to function, as the critical dispersal threshold is very much like a biological property. The same network can be evaluated differently for two species of different dispersal behaviour. This means that landscape management must integrate spatial and behavioral aspects and priorities may differ depending on the combinations. The threshold-sensitivity also supports results of Dunn and Majer (2009).

4.2. How effective are the different topological indicators in highlighting and emphasizing the importance of key patches compared to the rest?

Some topological indices like *CC* tended to assign very similar values to most of the habitat patches, and therefore seem to have a quite limited capacity for discriminating a concise subset of patches that can be regarded as particularly important for the functioning of the overall habitat network. A manager would expect that an operational indicator is useful enough by being able to highlight only a few key patches where the conservation efforts should be first concentrated and prioritized, given that the conservation resources and the amount of land that can be allocated to protected networks are usually scarce. This does not mean that the conservation manager should be satisfied with protecting only a small subset of the total habitat area available for a particular endangered species, but that the actual planning would be clearly benefited from the outcomes of indices that clearly separate and differentiate the values of the top patches compared to the others, so that the conservation priorities can be established with lower uncertainties. Otherwise, if all the patches are valued very similarly as connectivity providers, it is doubtful whether a particular subset of patches would be significantly more effective for conservation than any other that can be selected following some other criterion (e.g. independently of network configuration). In this case, the uncertainties and potential errors in the input data required for connectivity analysis may outweight the very slightly higher relevance of the top topological patches compared to the others according to such indicator.

In general, using p_{ij}'s as weights in the graph links softened the distributions of index values at the patch level (e.g. compare *PC*-based with *IIC*-based indices, or *wD* with *D*). This is because the patches remain valuable (to some degree) as connectors for a larger range of distances to other habitat areas when dispersal probabilities are considered. In unweigthed graphs, all patches separated beyond the sharp distance or probability threshold are modeled as completely isolated from each other (through a direct link), while in weighted graphs those patches can still receive some direct flux and provide some stepping stone effect that allows further dispersal from one patch to the other. Therefore, a smaller subset of patches tends to be highlighted as critical in unweighted graphs (a part of those located below the threshold distance only) compared to weighted networks. Indeed, the indices with the most skewed distributions were all based on binary links (*dH*, *dLCP*, *dIIC*, *dIICconn*, *BC*), as shown in Fig. 3.

The results on the fractions of the *IIC* and *PC* indices suggest that although many patches can be connected to a reasonable degree and receive or produce a sufficient amount of flux (*dIICflux*, *dPCflux*), only very few patches are able to both (a) act as a stepping stone that sits in between the usual movement paths between other habitat areas and (b) be irreplaceable as a connectivity provider because the alternative movement pathways that would be available after their loss are much weaker than those that were facilitated by their presence in the intact network. Although the first type of patches (a) is already not abundant in the landscape network, as quantified by *BC* (Bodin and Norberg, 2007; Estrada and Bodin, 2008) and its skewed distribution shown in Fig. 3, this scarcity becomes much more prominent when the potential alternatives to compensate for the losses are considered (b), as quantified by *dIICconn* and its even more highly skewed distribution compared to *BC* (with both measures being based on graphs with unweigthed links). Therefore, these key connectors, in the way that they are quantified by *dIICconn* or *dPCconn*, seem to be comparatively the scarcest ones and therefore those in which the largest efforts should be concentrated both for their adequate identification (through appropriate analytical tools and high-quality input data) and effective conservation. This discussion is supported beyond the *IIC* and *PC* measures, since all the topological indices with the least skewed distributions (*dIICflux*, *dAWF*, *dPC*, *dPCflux*, *wD*, *D*, *CC*) corresponded to the group of flux-related indices (see Figs. 3 and 5). For these measures, the trade-offs that arise when confronting the network topology considerations with other planning objectives and constraints (e.g. land productivity, land tenure types, development of transport networks) result in less conflict because the next candidates for conservation available in the ranking may be almost as good as the top ones that may need to be discarded from the final reserve design. The opposite is the case for those other measures that, as described above, exacerbate the differences and critical role of some (few) selected patches, with the other alternative patches being much less effective for supporting the ecological flows and network functioning as measured by these indices.

4.3. Conclusions and further research

Overall, our results show that the conservation priorities derived from different topological indices can be quite dissimilar. Indices classified together in the dendrogram provide more or less redundant information, while a selection of indices from different branches can provide a multi-sided, complementing view on the landscape mosaic. We argue that no particular landscape indicator used alone is able to single out the most important landscape elements and account for all the involved aspects that are relevant for a monitoring program. Instead, several measures, used simultane-

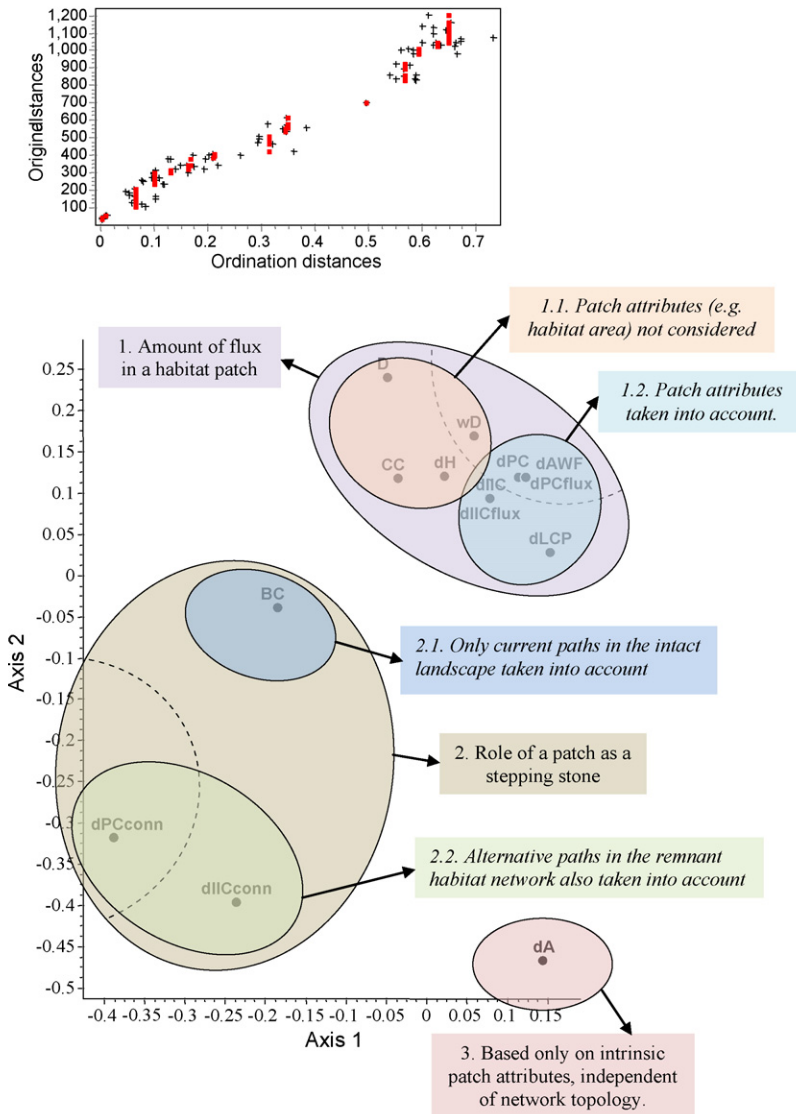

Fig. 5. Nonmetric multidimensional scaling of indices based on their dissimilarities calculated using Eq. (2). On the top, Shepard diagram shows that most discrepancy in the 2D solution comes from larger dissimilarity values. On the bottom, the best 2D solution (as represented by the two most important dimensions explaining similarity) with interpretation of groups overlaid. The dashed lines separate the indices based on weighted and unweighted graphs within the two groups of topological measures.

ously, may provide a more complete view on the role of landscape elements in maintaining landscape connectivity and in the functioning of ecological networks. A multiplicity of carefully selected indices may provide the most useful information by characterizing different aspects of positional importance of patches (see also Peng et al., 2010; for measures quantifying spatial patterns).

However, we suggest that most of the variability in the patch rankings provided by the wide set of indices here considered can be in fact captured by three different aspects as described above: the amount of flux a patch is estimated to receive, the degree to which a patch is valuable to uphold the connectivity between other habitat areas different from itself, and the intrinsic patch attributes (e.g. habitat area or quality) that capture the non-spatial and network independent importance of a patch, which is always a basic reference and an important ingredient of any final conservation plan or monitoring system. These three aspects revealed by cluster analysis and multidimensional scaling match very well with the three fractions (intra, flux, connector) of the measures of habitat availability (reachability) at the landscape scale (e.g. *dIIC*, *dPC*). These fractions are measured in the same units providing an integrated framework for network analysis (Saura and Rubio, 2010) that can be particularly valuable by guiding indicator delivery and related decision making. However, the differences between *BC* and *dICCconn*/*dPCconn* still suggest that, in addition to these three fractions, the classical network centrality measures (or modifications of them) also play a role and indicate additional interesting information on the network structure and on the patches positional importance. This behaviour of the betweenness centrality measure in our analysis partly reinforces the earlier study of Estrada and Bodin (2008), based on principal component analysis.

We recognize, however, that unique indices are not necessarily better, they just provide different, hopefully meaningful information. The same applies to the indices with a high discriminatory power that highlight landscape elements and roles that are particularly scarce in the habitat network. Although promising as candidate indicators that concentrate and exacerbate the non-linear responses of the network functioning to habitat losses, they cannot be directly assumed to mean biological relevance (e.g. for sustaining population viability or adaptation capacity). Further research and validation with multi-species data and simulated processes would be needed. In addition, we recognize that our results have been obtained by the analysis of a single habitat network, although there are analytical reasons and previous findings on indices behaviour that support our conclusions beyond the specific results on the goshawk case study. Thus, the most important future tasks include (1) performing simulations for metapopulation dynamics (cf. Ciocchetta and Jordán, 2010), (2) analysing similar data sets for other networks and species with different traits and habitat requirements, (3) extend these analyses towards interacting species (metacommunity dynamics), and (4) modeling a hierarchical system of social networks, food webs and landscape graphs (e.g. Ciocchetta and Jordán, 2010). The final aim is to set realistic and feasible, quantitative conservation priorities based on a sound combination of a few relevant indicators. The main goal is to prepare a "guide" that helps understanding the exact biological meaning of the presented indices and matching particular biological problems to suitable indicators and network analytical tools.

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