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Research article

Characterizing the importance of habitat patches and corridors in maintaining the landscape connectivity of a *Pholidoptera transsylvanica* (Orthoptera) metapopulation

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Abstract

Since the fragmentation of natural habitats is one of the most serious problems for many endangered species, it is highly interesting to study the properties of fragmented landscapes. As a basic property, landscape connectivity and its effects on various ecological processes are frequently in focus. First, we discuss the relevance of some graph properties in quantifying connectivity. Then, we propose a method how to quantify the relative importance of habitat patches and corridors in maintaining landscape connectivity. Our combined index explicitly considers pure topological properties and topographical measures, like the quality of both patches (local population size) and corridors (permeability). Finally, for illustration, we analyze the landscape graph of the endangered, brachypterous bush-cricket *Pholidoptera transsylvanica*. The landscape contains 11 patches and 13 corridors and is situated on the Aggtelek Karst, NE-Hungary. We characterize the importance of each node and link of the graph by local and global network indices. We show how different measures of connectivity may suggest different conservation preferences. We conclude, accordingly to our present index, by identifying one specific habitat patch and one specific corridor being in the most critical positions in maintaining connectivity.

Introduction

The area loss of natural habitats and the fragmentation of the remaining ones lead to important questions concerning structural landscape properties (Wiens et al. 1993) and metapopulation dynamics (Hanski 1998, 1999). Recent studies indicate that fragmentation has several consequences: it selectively affects different species (Kruess and Tscharntke 1994; Zabel and Tscharntke 1998), it can affect sex-ratio (van Apeldoorn et al. 1992), influence community control (Crooks and Soulé 1999), and post-fragmentation extinction dynamics (Burkey 1989, 1999; Tilman et al. 1994). Studying the role of corridors in maintaining diversity (Gilbert et al. 1998; Beier and Noss 1998) and analysing their relation to percolation properties (Turner et al. 1989; Metzger and Décamps 1997) also contribute to better knowing ecological landscapes. However, we still face very important technical problems, for example, how to measure landscape connectivity (O'Neill et al. 1988; Turner 1989; Schumaker 1996; Tischendorf and Fahrig 2000a; Urban and Keitt 2001). There are many properties possibly useful in characterising landscape graphs, and we believe that the relevance of these network indices depends on the actual question (e.g., one is sensitive to the *fact* of connectivity, the other reflects better the *level* of connectivity, i.e., topological distances). Thus, there is no single solution of how to measure landscape connectivity. Graph theory has been proposed as a useful tool for landscape ecology (Keitt et al. 1997; Urban and Keitt 2001) suggesting the relevance of, for example, the minimum spanning tree in determining critical patches. We address the same question of how to measure connectivity, and the methods proposed below are believed to be of complementary nature, sometimes they may be biologically more sensible. For instance, the identification of corridors is not based on the distance of patches but on biology (i.e., the movement of individuals). Further, we compare the importance of patches and corridors in the same rank, which emphasises that they are inseparable in a network context.

Small, isolated populations generally live on the brink of extinction (Shaffer 1981), for example, because of inbreeding (Meglécz et al. 1998; Saccheri et al. 1998). In fragmented areas, intensive genetic exchange may compensate for the small size of local populations, and in a number of species it has been suggested that migration between local subpopulations is the only key for survival (at least, it decreases extinction risk, Fahrig and Merriam (1985) and Taylor et al. (1993), Tiebout and Anderson (1997); see also Thomas (2000)). Especially for some rare species, the balance between local extinctions and recolonization events may also help survival (Spiller and Schoener 1998; Carlson and Edenhamn 2000). In order to help conservation efforts, it would be of outstanding importance to have sensible measures of landscape connectivity and methods for evaluating the importance of spatial elements (patches, corridors) in maintaining connectivity (see Tischendorf and Fahrig (2000a, 2000b)). To quantify how subsystems (e.g., a particular patch) are related to the whole system (the landscape) is basically a topological problem and calls for a network perspective (cf. Higashi and Burns (1991)). This is to emphasise that the properties of landscape elements are understood in a network context, and this can be explicitly analysed by quantifying positionality in the network (here we note that our study is based on a descriptive, structural approach: we are interested only in migration *possibilities* and not in the migration process itself and its dynamical consequences, cf. Hanski (1998)). Nevertheless, we also acknowledge the importance of also topography, i.e., some consideration of the quality of graph points and links.

Here, our aims are: (1) to discuss some relevant structural properties of landscape graphs that we feel are most useful in approaching the problem of relative importance of landscape elements (cf. Jordán (2000)), (2) to suggest a method of quantifying the importance of patches and corridors in maintaining landscape connectivity, (3) to propose a combined index explicitly referring to topological network properties, patch quality (local population size) and corridor quality (permeability), and (4) to illustrate our method with a field example.

We analyze how predictions based on either topology or topography differ and are related to each other. We also discuss how various connectivity measures differ in predicting critical landscape elements. We will finish by discussing conservation aspects and the possibility of setting preferences.

Study area and species

Orthopterans are excellent objects for landscape studies due to their stable taxonomy, easy identification, characteristic habitat use, communication behavior, and ecological importance in grasslands. Some papers on their spatial distribution are available (e.g., Nagy et al. (1999)). Here, for illustrating the proposed methods, we present the semi-quantitative landscape graph of the brachypterous bush-cricket *Pholidoptera transsylvanica* (Orthoptera) metapopulation living on the Aggtelek Karst (NE-Hungary, Central Europe). We identify the habitat patches and corridors and evaluate their positional importance from both topological and topographical viewpoints (our landscape graph seems to belong to the 'mesh' type, describing a more or less homogeneous network, with no patch of outstanding connectedness, see Cantwell and Forman (1993)).

The studied metapopulation is isolated from the two other existing Hungarian populations of *P. transsylvanica*, a biogeographically essential, highly characteristic, Eastern Carpathian ('Dacian') element of this fauna (Varga 1997; Rácz et al. 1997; Varga et al. 2000). This species prefers the skirt habitats of tall-grass, semi-dry swards (in the matrix of xerothermic mixed oak forest habitat, *Corno-Quercetum pubescentis-petraeae*, Varga-Sipos and Varga (1997)). Thus, a slight patchiness can be advantageous for the species (as the fraction of skirt habitats increases). However, if local populations become isolated because of strong fragmentation (caused by secondary succession leading from semi-dry swards to forest), or landscape connectivity dramatically decreases for

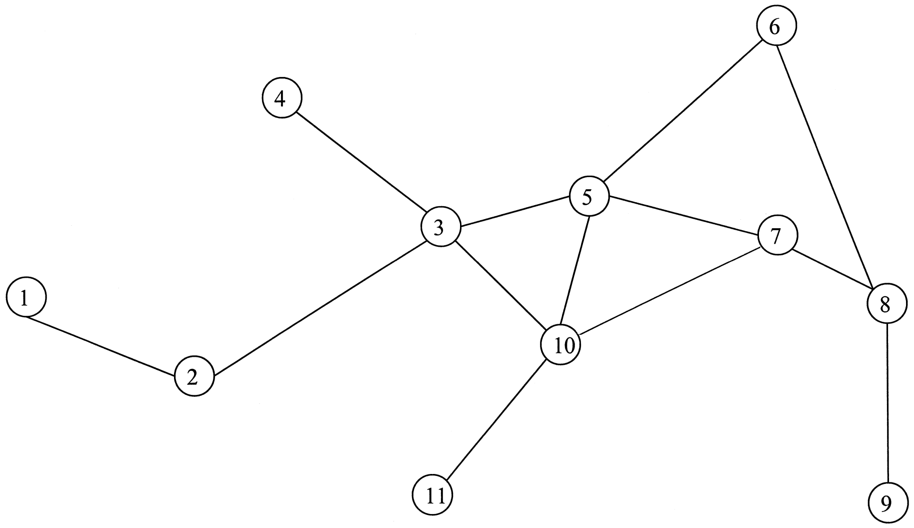

Figure 1. The landscape graph showing the topology of habitat patches (nodes) and corridors (links) of the studied P. *transsylvanica* metapopulation. Numbers identify the following patches (given in Hungarian): (1) Huszas tövör, (2) Kis tisztások, (3) Szilicei kaszálók, (4) U-alaká töbör, (5) 'Nagy-Nyilas, (6) Mogyorós-rét és tisztás, (7) Árvalányhajas, (8) Dénes töbör, (9) Nagyoldal mögötti tisztások, (10) Gyertyánsarjas, (11) Lófej-forrás alatti tisztás.

some reason, the metapopulation can be in danger of local extinction events. Thus, analyzing the landscape connectivity of this metapopulation is of high conservation value.

P. transsylvanica can hardly be trapped. Mark-recapture techniques do not work for this species, due to its predatory way of life, sheltering and moving in the dense herbaceous vegetation. Nevertheless, its conservation value is so high (listed in the Hungarian Red Data Book, Orci (1997); and see Nagy et al. (1999)), that we decided to study its landscape structure, based on data by three independent estimations of topology (the arrangement of patches and corridors) and topography (local population sizes and corridor permeability). Estimations were based on acoustic field observations: three independent field observers made a preliminary census of the distribution of individuals, based mostly on the number of stridulating males; continuous observations were made during five subsequent years (Orci, *unpublished results*). We consider our estimated data semi-quantitative, regarding that the quality of patches (local population size) and corridors (permeability) are quantified by integers between 1 and 4. The 'consensus graph' (containing 11 patches and 13 corridors) was analyzed (Figure 1).

Terminology and model assumptions

In this paper, let metapopulation mean (*sensu* Pickett and Cadenasso (1995)) a set of connected *local populations* of a species, independently of their genetic and population dynamical differences, among which individuals are able to migrate regularly. Let *landscape* mean the patchwork of *habitat* patches (inhabited by local populations) connected by *corridors* (making migration possible). In the undirected *landscape graph*, patches and corridors are represented by *nodes* and *links*, respectively. In the topographical analysis, patch quality is characterized by the estimated *local population size* (estimated by LPS = {1, 2, 3, 4}), and the quality of corridors is characterized by an estimated *permeability* value (estimated by P = {1, 2, 3, 4}). Later, *the topographical distance* (d_{tgr}) of two neighbor patches will be defined as $d_{tgr} = 5\text{-}P$. Thus, a higher permeability value means smaller distance in a topographical sense. If a node or a link is removed from the landscape graph, then it can be divided into multiple components (isolation occurs between groups of individuals). Let the *maximal connected local population size* (LPS^{c}_{max}) mean the largest sum of local population size values of connected patches, in case of isolation follows the deletion of a landscape element from the graph (the number of individuals in the largest graph component). In the intact network, LPS^{c}_{max} equals 23 (i.e., the sum of

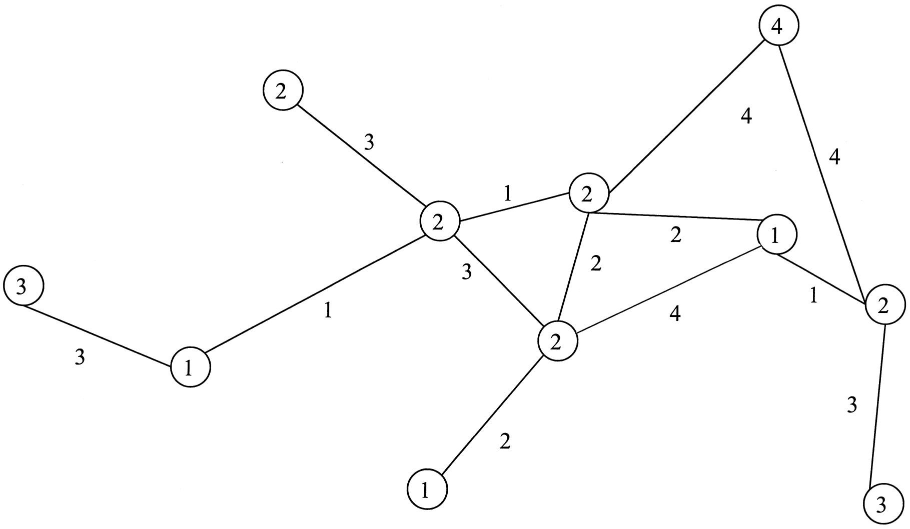

Figure 2. The landscape graph presenting the estimated local population sizes (LPS = {1, 2, 3, 4,}, shown within nodes) and the estimated topographical distance values (1-P (estimated permeability) = {1, 2, 3, 4}, shown on the links).

LPS_i estimated local population sizes). If, for example, we delete node N3 ('Szilicei kaszálók'), three fragments will appear (containing nodes [1, 2], [4], and [5, 6, 7, 8, 9, 10, 11]). In this case, the sums of local population sizes for these three fragments are 4, 2, and 15, respectively. Thus, LPS^c_{max} for N3 equals 15 (Table 1., cf. Figure 2).

We assume that migration does not depend on genetic and demographic factors (but see Lande (1988)), i.e., only topological and topographical factors influence migration patterns. Let permeability (P), as the single estimated index for graph links, perfectly describe corridor quality; and similarly, let local population size (LPS), as the single estimated index for graph nodes, perfectly describe patch quality. Source-sink dynamics (Pulliam 1988; Dias 1996) were not incorporated into our model; the landscape graph is undirected. Further, it is assumed that there is no difference between potential and actual permeability. This assumption is quite realistic, since (1) the individuals of this species are very mobile, following intraspecific acoustic signals, and (2) their predatory behavior also depends strongly on mobility (i.e., random walk). Finally, even if we take into account both pure topology (i.e., physiognomic effects, Dunning et al. (1992)) and topography, our analysis does not take into account landscape dynamics (for spatiotemporal connectivity analyses, see Johnson (2000) and Keymer et al. (2000)).

Methods of analysis

We analyze the positional importance of landscape elements by measuring (1) the local network indices of nodes and links in the intact landscape graph, and (2) the global indices of the whole network both in its intact form and after deleting each node and link, one at a time. We perform each analysis on both *topological* and *topographical* grounds. Thus, each landscape element (node and link) is characterized by its (1) local topology, (2) deletion effect on landscape topology, (3) local topography, and (4) deletion effect on landscape topography. We will try to give a realistic quantification of patch and corridor importance by offering a combined index reflecting the most basic network properties (see Figure 3 later for some considerations).

The most fundamental properties of landscape graphs (and any network) are the number of nodes (N) and links (L). Each node can be characterized by the number of its neighbors (D = degree; the vector of D_i – values is called elsewhere the β – index). Typical network properties are the average and the standard deviation of D_i values for each node (D_{av} and D_{std}). D_{av} characterizes the density of corridors in the patchwork (similarly to the connectance, $C = 2L / N \times (N-1)$, and to the γ -index, $\gamma = L / 3(N-2)$, as standard network indices in ecology). D_{std} measures network homogeneity (with random disturbance, homogeneous networks seem to be less safe, Albert et al. (2000)). The clustering coefficient of

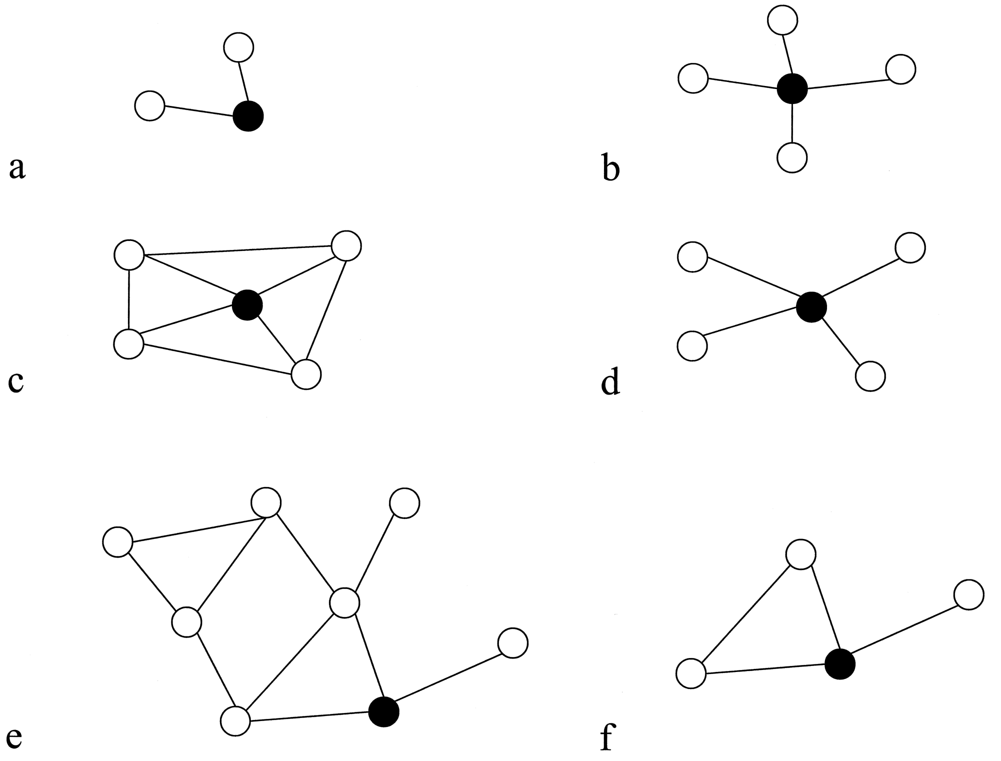

Figure 3. These six simple, hypothetical landscape graphs demonstrate how certain local indices may reflect positional importance. The habitat patch represented by the full circle is always in focus. Evidently, it is in more important position (1) in *b* than in *a*, because it is connected to more neighbor patches ($D_{(b)} = 4 > D_{(a)} = 2$); (2) in *d* than in *c*, because its neighbors are less connected ($CC_{(d)} = 0 < CC_{(c)} = 0.66$); and (3) in *f* than in *e*, because it is in less periferial position ($d_{av(f)} = 1 < d_{av(e)} = 1.71$).

node i (CC_i) gives the connectance of the subgraph containing the neighbors of node i and the links between them. The average clustering coefficient (CC_{av}) characterizes the whole network, weighted by the number of neighbors for each node (D). The minimal number of links forming a path connecting nodes i and j is their distance (d_{ij}), the average distance of node i from all other nodes is d_{av}. If nodes i and j are unconnected (belong to different components of the graph), $d_{ij} = \infty$. As the topographical distance, we defined above d_{tgr}, from which d_{avtgr} gives the average topographical distance. For taking the quality of nodes into account, we estimated another index: LPS is the estimated local population size. The positional importance of links has been characterized by the averaged D, CC, d_{av} and d_{avtgr} values of their endpoints.

While the distance matrix (**D**) of a landscape graph contains d_{ij} elements, the reciprocal distance matrix (**R**) has d_{ij}^{-1} values (Ivanciuc et al. 1993; Ricotta et al. 2000). From this, the Harary-index (H) is the half of the sum of d_{ij}^{-1} values (Plavsic et al. 1993; Ricotta et al. 2000). The normalized Harary-index ($\hat{H}$) is given by $(H-H_{chain})/(H_{planar}-H_{chain})$ for connected, and by H/H_{planar} for unconnected graphs (anonymous reviewer, pers. comm.). Here, $H_{chain} = N-1+(N-2)/2+(N-3)/3+...+1/(N-1)$, and $H_{planar}=N(N+5)/4$. (Instead of **R** and H, **D** and W (the Wiener-index) can also be used for measuring connectivity, but only for connected graphs.) In our case, **R** and H are preferred since unconnected graphs also appear after analyzing the deletion of either nodes or links.

As a derived graph, we also constructed and present the intersection multigraph of the original landscape graph. Here, nodes are joined by a link not if the patches represented are connected by a corridor, but if they have a common neighbor node in the original landscape graph (Harary (1969); cf. Sugihara (1984)). Intersection multigraphs (i.e., graphs with multiple edges) are useful in identifying the dominant cliques of mostly important nodes (a clique, as a complete subgraph, represents the neighbors of a node in the original landscape graph, see Figure 4 and cf. Figure 1). The positional importance of node i is larger if (1) the clique representing its neighbors is of

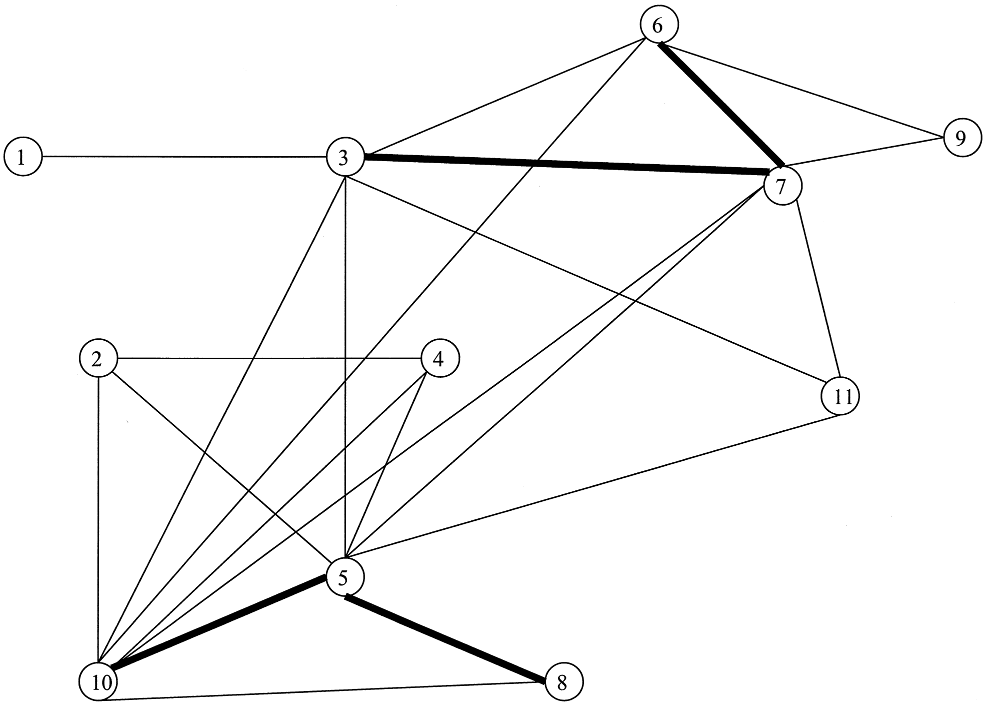

Figure 4. The intersection multigraph of the landscape graph presented in Figure 1. Multiple links are thick: they reflect parallel pathways of length 2. Each dominant clique contains four nodes: [2, 4, 5, 10], [3, 5, 7, 11], and [3, 6, 7, 10], representing the four neighbors of nodes N3, N10, and N5, respectively. See further explanation in text.

higher dimension, and (2) node i is less joined to its clique. For example, node N5 is connected to nodes N3, N6, N7, and N10 in the *landscape graph*, thus, these four nodes form a complete subgraph in the *intersection multigraph*, so that N5 joins at three points: N3, N7, and N10, reflecting the fact that there are links in the *landscape graph* between N3 and N10, and between N10 and N7. Here, the dimension of the clique reflects D = 4 and these joining points reflect CC = 0.33 (2 links out of a possible 6). Thus, dominant clique analysis is a helpful tool in analyzing the positional importance of nodes in graphs, reflecting D and CC simultaneously.

All of these indices characterize some aspects of positional importance within a network. A patch is evidently more important in the landscape if it is connected to more neighbor patches (high D_i, see Figure 3). If these neighbors are less connected to each other (small CC_i), the key position is more evident (Figure 3). With similar D_i and CC_i, centrally positioned patches (small d_{av}) can be thought to be in more important positions (Figure 3). A part of these topological indices and topographical quantities (d_{tgr}, LPS), characterizing the quality of landscape elements, can add valuable information about the role of patches and corridors in maintaining connectivity.

However it is not easy to compare and synthesize different measures of positional importance, we suggest a combined index (I) reflecting the major topological and topographical properties. Let the importance (I) of the ith landscape element (either patch or corridor) be $I_i = (D_i - CC_i) / (d_{avtgr(i)} + LPS^c_{max(i)}$, where D_i is its degree, CC_i is its clustering coefficient, $d_{avtgr(i)}$ is its average topographical distance, and $LPS^c_{max(i)}$ is the maximal connected local population size after its deletion. Of course, this combined index is invited to be developed and refined. Its merit is reflecting both topological and topographical properties, as well as both function and structure. So, even in its present form, it may help in considering conservation preferences.

Results

Table 1 shows all of the calculated local and global network indices for each node and link. Different indices predict different patches and corridors to have primary importance, especially if topography is also considered. For example, D suggests N3, N5, and N10 to be the most important nodes. Among them, CC suggests that N3 is more important than the others. d_{av} suggests, conversely, the higher importance of N5 and N10, and if topography is taken into account, d_{avtgr} predicts that N5 is the key patch. The intersection multigraph suggests again the key position of N3 (all three nodes have a four dimension clique but N3 is less joint to its clique). Apart from the topological and topographical local indices of landscape elements, we also can cast a glance at the network properties after their deletion. N5 seems to be the most important, if d_{av}, D_{std}, CC_{av} or $\hat{H}$ are considered. N10 also looks to be of primary importance (for d_{av} and CC_{av}) but N3 is always in the middle. Further, importantly, as topography is taken into account again, N3 turns out to be the key patch in the landscape (consider both LPS^{C}_{max} and H). Similar differences in ranking their importance also exist at links, of course.

Table 2 presents the ranking of landscape elements, according to their combined importance index (I). Habitat patches are both among the most and the least important parts of the landscape. Patch N3 ('Szilicei kaszálók') is the most critical patch, while patch N11 ('Lófej-forrás alatti tisztás') has the smallest value for connectivity. Among corridors (whose importance is less extreme), L3-5 (between 'Szilicei kaszálók' and 'Nagy-Nyilas') has the highest, while L1-2 (between 'Huszas töbör' and 'Kis tisztások') has the lowest importance.

Discussion

Even if our presented data are of semi-quantitative nature, the presented methods can contribute to site-selection decisions (Cabeza and Moilanen 2001), and, in general, setting conservation priorities (keeping in mind that priorities based on one species may be in conflict with priorities based on others). We also note that in cases where connectivity is disadvantageous (e.g., spreading disease, fire, or a 'Genghis Khan' invader, see Pimm (1991)), similar methods may be helpful with reversed sign (and slight modifications as appropriate), i.e., how to disconnect habitat patches easily.

Various network indices have different biological meanings and are useful in different situations. For example, the normalized Harary-index ($\hat{H}$) is very sensitive to the *fact* of connectivity, thus, it is more informative as metapopulation size is dangerously close to the minimal viable population size (MVP). In this case, connectedness itself is what is to be analyzed first, and then its quantitative value (because in case of a minimal isolation, metapopulation size may decrease below the MVP). But if the population is well above the MVP, the central question is not whether it is connected but how connected it is. Here, $\hat{H}$ can be useful again, but the relevance of other indices (e.g., d_{avtgr}) increases. Similarly, D_{std} may be particularly informative if we have some data on landscape dynamics: network heterogeneity seems to be very relevant in this case. Our proposed importance index (I) tries to combine the most fundamental and seemingly most useful characteristics making corridors and patches important – both topological and topographical, as well as both local and global indices have been incorporated.

We also demonstrate how topological and topographical predictions may differ (i.e., how important it is to add function to structure, cf. Tischendorf and Fahrig (2000a) and see Jordán (2001)). Consider the different importance ranks for d_{av} and d_{avtgr}. Topology predicts N2 to have the 17th or 18th place in the rank of all landscape elements, based on the former index, however, accordingly to the later one, N2 has the 9th largest importance. Or if one considers only the decrease of connected metapopulation size after a deletion (LPS^{c}_{max}), the importance of the corridor L3-5 or that of the patch N7 can be seriously underestimated (and misunderstood). But if we are not interested in population size, only in connectivity itself, we may fall in a very common trap: an artefact of connectivity measures is that they increase as fragmentation proceeds (e.g., fragmentation seems to be advantageous, cf. Tischendorf and Fahrig (2000b)). In this case, considering how large is the *still connected* population (LPS) is essential. So, we emphasize how important it is to take into account some quality measure of both corridors and patches.

As for this particular landscape, we suggest that the most important patch in maintaining landscape connectivity is N3 ('Szilicei kaszálók'), while the most critically positioned corridor is L3-5 (from 'Szilicei kaszálók' to 'Nagy-Nyilas'). We believe that the methods presented are worth further development and possibly will be helpful and applicable in conservation projects and landscape design. For example, a naïve view would suggest protecting the habitat patch where the most individuals live, however, topological and topographical considerations might help in realising the exceptional importance of a habitat patch

Table 1. Network indices characterizing landscape elements.

	LOCAL				GLOBAL					
	topology			topography	topology				topography	
	D	CC	d_{av}	d_{avtgr}	D_{av}	D_{std}	CC_{av}	$\hat{H}$	LPS^{c}_{max}	H
whole web	–	–	–	–	2,36	1,286	0,197	0,344	23	14,38
NODES										
N1	1	–	3,5	7	2,4	1,35	0,2165	0,38	20	12,73
N2	2	0	2,6	4,3	2,2	1,398	0,245	0,612	19	9,83
N3	4	0,17	1,9	3,6	1,8	1,135	0,214	0,423	15	6,29
N4	1	–	2,8	6,3	2,4	1,17	0,222	0,303	21	12,58
N5	4	0,33	1,8	3,3	1,8	0,92	0	0,123	21	9,13
N6	2	0	2,3	6,2	2,2	1,23	0,277	0,276	19	12,64
N7	3	0,33	2,1	4,2	2	1,054	0,168	0,204	22	10,08
N8	3	0	2,6	4,7	2	1,491	0,334	0,597	18	10,12
N9	1	–	3,5	7,4	2,4	1,265	0,207	0,372	20	12,81
N10	4	0,33	1,8	4,7	1,8	1,033	0	0,542	20	10,36
N11	1	–	2,7	6,5	2,4	1,174	0,238	0,333	22	12,49
LINKS										
L1/2	1,5	–	3,05	5,65	2,18	1,4025	0,2165	0,611	20	12,73
L2/3	3	0,085	2,25	3,95	2,18	1,192	0,245	0,54	19	10,16
L3/4	2,5	–	2,35	4,95	2,18	1,328	0,222	0,595	21	12,58
L3/5	4	0,255	1,85	3,45	2,18	1,03	0,1665	0,275	23	11,92
L3/10	4	0,255	1,85	4,15	2,18	1,029	0,1665	0,275	23	14,38
L5/10	4	0,33	1,8	4	2,18	1,029	0,084	0,2954	23	13,39
L5/6	3	0,17	2,05	4,75	2,18	1,192	0,263	0,263	23	13,99
L5/7	3,5	0,33	1,95	3,75	2,18	1,113	0,151	0,3175	23	12,9
L10/7	3,5	0,33	1,95	4,45	2,18	1,113	0,15	0,288	23	14,38
L10/11	2,5	–	2,25	5,6	2,18	1,266	0,238	0,5939	22	12,49
L6/8	2,5	0	2,45	5,45	2,18	1,266	0,228	0,296	23	14,2
L7/8	3	0,17	2,35	4,45	2,18	1,1923	0,267	0,275	23	12,25
L8/9	2	–	3,05	6,05	2,18	1,336	0,207	0,609	20	12,81

Topological and topographical indices for both habitat patches (i.e., nodes in the landscape graph, N) and corridors (i.e., links in the landscape graph, L), characterizing their local position and the global effect of their deletion. Local indices (D, CC, d_{av}, and d_{avtgr}) quantify the position of landscape elements (i.e., nodes and links) in the intact (i.e., static) network. Global indices (D_{av}, D_{std}, CC_{av}, $\hat{H}$, LPS^{c}_{max}, and H) characterize the properties of the whole network both in intact form (first row) and after the deletion of each landscape element (one at a time). Topological indices quantify the landscape graph shown in Figure 1., while topographical indices take into account the estimated qualities of patches and corridors, presented in Figure 2. Note that according to different indices, the importance rank of landscape elements differ. For example, considering d_{avtgr}, node N5 is in the most important position (3.3 is the lowest value, meaning the highest 'centrality'), however, looking at a dynamical index, LPS^{c}_{max}, we may see that deleting this habitat patch does not decrease seriously the size of the connected (i.e., non-isolated) metapopulation. (The values suggesting maximal importance are: D = 4, CC = 0, $d_{av} = 1.8$, $d_{avtgr} = 3.3$, $D_{av} = 1.8$, $D_{std} = 0.9$, $CC_{av} = 0$, $\hat{H} = 0.123$, $LPS^{c}_{max} = 15$, and H = 6.29.)

with not so many individuals but being in a critical position within the whole landscape. The loss of more individuals may occasionally be less dramatic if gene flow between the survivors remain much more intensive. This is to say that the conservation value of both habitat patches and corridors should be assessed in a network context.

Table 2. The rank of landscape elements, according to the suggested importance index.

node/link	importance (I)
N3	0,2059
N5	0,151
N10	0,1486
L3-5	0,1416
L3-10	0,1379
L5-10	0,1359
N8	0,1322
L2-3	0,127
L5-7	0,1185
L7-10	0,1154
L7-8	0,1031
L5-6	0,102
N7	0,1019
L3-4	0,089
L6-8	0,0879
N2	0,0858
L10-11	0,0837
N6	0,0794
L8-9	0,0695
L1-2	0,0511
N1	0,03
N4	0,0297
N9	0,0296
N11	0,0284

The overall importance (I) of patches and corridors in maintaining the connectivity of the studied landscape. The habitat patch coded by N3 is the most important element for connectivity, while the deletion of patch N11 has the less dramatic effect. The importance of links is less variable, however, note that the loss of the corridor L3-5 is more disadvantageous than the loss of 8 patches out of 11.

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References

Albert R., Jeong H. and Barabási A.-L. 2000. Error and attack tolerance of complex networks. Nature 406: 378–381.

van Apeldoorn R.C., Oostenbrink W.T., van Winden A. and van der Zee F.F. 1992. Effects of habitat fragmentation on the bank vole, Clethrionomys glareolus, in an agricultural landscape. Oikos 65: 265–274.

Báldi A. and Kisbenedek T. 1999. Orthopterans in small steppe patches: an investigation for the best-fit model of the species-area curve and evidences for their non-random distribution in the patches. Acta Oecologica 20: 125–132.

Beier P. and Noss R.F. 1998. Do habitat corridors provide connectivity? Conservation Biology 12: 1241–1252.

Burkey T.V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. Oikos 55: 75–81.

Burkey T.V. 1999. Extinction in fragmented habitats predicted from stochastic birth-death processes with density dependence. Journal of Theoretical Biology 199: 395–406.

Cabeza M. and Moilanen A. 2001. Design of reserve networks and the persistence of biodiversity. Trends in Ecology and Evolution 16: 242–248.

Cantwell M.D. and Forman T.T. 1993. Landscape graphs: Ecological modeling with graph theory to detect configurations common to diverse landscapes. Landscape Ecology 8: 239–255.

Carlson A. and Edenhamn P. 2000. Extinction dynamics and the regional persistence of a tree frog metapopulation. Proceedings of the Royal Society of London, series B 267: 1311–1313.

Crooks K.R. and Soulé M.E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400: 563–566.

Dias P.C. 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11: 326–330.

Dunning J.B., Danielson B.J. and Pulliam H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Fahrig L. and Merriam G. 1985. Habitat patch connectivity and population survival. Ecology 66: 1762–1768.

Gilbert F., Gonzalez A. and Evans-Freke I. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. Proceedings of the Royal Society of London, series B 265: 577–582.

Hanski I. 1998. Metapopulation dynamics. Nature 396: 41–49.

Hanski I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.

Harary F. 1969. Graph Theory. Addison Wesley, Cambridge, Massachusetts, USA.

Higashi M. and Burns T.P. (eds) 1991. Theoretical Studies on Ecosystems – the Network Perspective. Cambridge University Press, Cambridge, UK.

Ivanciuc O., Balaban T.-S. and Balaban A.T. 1993. Design of topological indices. Part 4. Reciprocal distance matrix, related local vertex invariants and topological indices. Journal of Mathematical Chemistry 12: 309–318.

Johnson M.P. 2000. Temporally explicit habitat ecology and the coexistence of species. Proceedings of the Royal Society of London, series B 267: 1967–1972.

Jordán F. 2000. A reliability-theory approach to corridor design. Ecological Modelling 128: 211–220.

Jordán F. 2001. Adding function to structure – comments on Palmarola landscape connectivity. Community Ecology, 2: 133–135.

Keitt T.H., Urban D.L. and Milne B.T. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology [online] 1:(1):4, URL: http://www.consecol.org/vol1/iss1/art4.

Keymer J.E., Marquet P.A., Velasco-Hernández J.X. and Levin S.A. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. The American Naturalist 156: 478–494.

Kruess A. and Tscharntke T. 1994. Habitat fragmentation, species loss, and biological control. Science 264: 1581–1584.

Lande R. 1988. Genetics and demography in biological conservation. Science 241: 1455–1460.

Meglécz E., Pecsenye K., Varga Z. and Solignac M. 1998. Comparison of differentiation pattern at allozyme and microsatellite loci in *Parnassius mnemosyne* (Linnaeus, 1758) (Lepidoptera) populations. Hereditas 128: 95–103.

Metzger J.P. and Décamps H. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. Acta Oecologica 18: 1–12.

Nagy B., Rácz I. and Varga Z. 1999. The orthopteroid insect fauna of the Aggtelek karst region (NE Hungary) referring to zoogeography and nature conservation. In: Mahunka S. (ed.), The fauna of the Aggtelek National Park. Akadémiai Kiadó, Budapest, Hungary, pp. 83–102.

O'Neill R.V., Krummel J.R., Gardner R.H., Sugihara G., Jackson B., DeAngelis D.L. et al. 1988. Indices of landscape pattern. Landscape Ecology 1: 153–162.

Orci K.M. 1997. A comparative study on grasshopper (Orthoptera) communities in the Aggtelek Biosphere Reserve. In: Tóth E. and Horváth R. (eds), Research in Aggtelek National Park and Biosphere Reserve. ANP directorate, Aggtelek, Hungary, pp. 109–116.

Pickett S.T.A. and Cadenasso M.L. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269: 331–334.

Pimm S.L. 1991. The Balance of Nature? University of Chicago Press, Chicago, Illinois, USA.

Plavsic D., Nikolic S., Trinajstic N. and Mihalic Z. 1993. On the Harary index for the characterization of chemical graphs. Journal of Mathematical Chemistry 12: 235–250.

Pulliam H.R. 1988. Sources, sinks, and population regulation. The American Naturalist 132: 652–661.

Rácz I., Varga Z., Mezô H. and Parragh D. 1997. Studies on the Orthoptera fauna of the Aggtelek Karst. In: Tóth E. and Horváth R. (eds), Research in Aggtelek National Park and Biosphere Reserve. ANP directorate, Aggtelek, Hungary, pp. 99–108.

Ricotta C., Stanisci A., Avena G.C. and Blasi C. 2000. Quantifying the network connectivity of landscape mosaics: a graph-theoretical approach. Community Ecology 1: 89–94.

Saccheri I., Kuussaari M., Kankare M., Vikman P., Fortelius W. and Hanski I. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392: 491–494.

Schumaker N.H. 1996. Using landscape indices to predict habitat connectivity. Ecology 77: 1210–1225.

Spiller D.A. and Schoener T.W. 1998. Lizards reduce spider species richness by excluding rare species. Ecology 79: 503–516.

Shaffer M.L. 1981. Minimum population sizes for species conservation. BioScience 31: 131–134.

Sugihara G. 1984. Graph theory, homology and food webs. Proceedings of Symposia in Applied Mathematics 30: 83–101.

Taylor P.D., Fahrig L., Henein K. and Merriam G. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571–573.

Thomas C.D. 2000. Dispersal and extinction in fragmented landscapes. Proceedings of the Royal Society of London, series B 139: 139–145.

Tiebout H.M. III and Anderson R.A. 1997. A comparison of corridors and intrinsic connectivity to promote dispersal in transient successional landscapes. Conservation Biology 11: 620–627.

Tilman D., May R.M., Lehman C.L. and Nowak M.A. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Tischendorf L. and Fahrig L. 2000a. On the usage and measurement of landscape connectivity. Oikos 90: 7–19.

Tischendorf L. and Fahrig L. 2000b. How should we measure landscape connectivity? Landscape Ecology 15: 633–641.

Turner M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Reviews of Ecology and Systematics 20: 171–197.

Turner M.G., Gardner R.H., Dale V.H. and O'Neill R.V. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55: 121–129.

Urban D. and Keitt T. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82: 1205–1218.

Varga Z. 1997. Biogeographical outline of the invertebrate fauna of the Aggtelek Karst and surrounding areas. In: Tóth E. and Horváth R. (eds), In Research in Aggtelek National Park and Biospherre Reserve. ANP Directorate, Aggtelek, Hungary, pp. 87–94.

Varga Z.V., Sipos J., Orci K.M. and Rácz I. 2000. Semi-arid grasslands on the Aggtelek Karst: phytocoenological relationships, Orthopteranand Lepidopteran communities. In: Virágh K. and Kun A. (eds), Vegetation and Dynamism. MTA ÖBKI, Vácrátót, Hungary, pp. 195–238, (in Hungarian).

Varga-Sipos J. and Varga Z. 1997. Phytocenology of semi-dry grasslands in the Aggtelek Karst area (N Hungary). In: Tóth E. and Horváth R. (eds), In Research in Aggtelek National Park and Biosphere Reserve. ANP Directorate, Aggtelek, Hungary, pp. 59–78.

Wiens J.A., Stenseth N.C., Van Horne B. and Anker Ims R. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369–380.

Zabel J. and Tscharntke T. 1998. Does fragmentation of Urtica habitats affects phytophagous and predatory insects differentially? Oecologia 116: 419–425.