Landscape Ecol
DOI 10.1007/s10980-007-9149-8

RESEARCH ARTICLE

Carabids (Coleoptera: Carabidae) in a forest patchwork: a connectivity analysis of the Bereg Plain landscape graph

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Received: 7 August 2006 / Accepted: 9 August 2007

Abstract For many species, one important key to persistence is maintaining connectivity among local populations that allow for dispersal and gene flow. This is probably true for carabid species (Coleoptera:Carabidae) living in the fragmented forests of the Bereg Plain (NE Hungary and W Ukraine). Based on field data, we have drafted a landscape graph of the area representing the habitat network of these species. Graph nodes and links represented two kinds of landscape elements: habitat (forest) patches and corridors, respectively. The quality of habitat patches and corridors were ranked (from low (1) to high (4)), reflecting local population sizes in the case of patches and estimated permeability in the case of corridors. We analysed (1) the positional importance of landscape elements in maintaining the connectivity of the intact network, (2) the effect of inserting hypothetical corridors into the network, (3) the effects of improving the quality of the existing corridors, and (4) how to connect every patch in a cost-effective way. Our results set quantitative priorities for conservation practice by identifying important corridors: what to protect, what to build and what to improve. Several network analytical techniques were used to account for the directed (source-sink) and highly fragmented nature of the landscape graph. We provide conservation priority ranks for the landscape elements and discuss the conditions for the use of particular network indices. Our study could be of extreme relevance, since a new highway is being planned through the area.

Keywords Landscape graph · Reachability · Isolation · Connectivity · Carabidae · Hungary · Directed graph

Introduction

The loss of natural habitats and the fragmentation of those remaining raise important concerns in conservation biology and practice. If individuals cannot disperse between fragmented habitat patches, local populations become isolated and various mechanisms (including random fluctuations, inbreeding and demographical problems, see e.g., Keller and Largiadér

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2003) may cause local extinctions. For many species, the most important key to persistence is maintaining connectivity among habitat patches that can provide the possibility of gene flow among local populations (e.g., Baudry et al. 2003).

A number of principles have recently been proposed to describe how species characteristics and habitat fragmentation interact to determine extinction probability (e.g., Kruess and Tscharntke 1994; Davies et al. 2000). The differential sensitivity of particular species may lead to a disruption of the structure of local communities and their ecological processes. One example is the local extinction of large, mobile, higher predators and the subsequent loss of top-down control on mesopredators and primary consumers (Crooks and Soulé 1999; Kondoh 2003). Interspecific interactions may also be sensitive to fragmentation (Tewksbury et al. 2002) and this potentially leads to significant changes to ecosystem processes.

The effect of fragmentation on population processes is not always immediately clear. Extinction debt (Brooks et al. 1999) or source-sink metapopulation dynamics (Spiller and Schoener 1998) may mask an extinction process in the short run. Moreover, many species live in patchy habitats under natural conditions, so a patchy spatial pattern is not necessarily a result of fragmentation. Despite these difficulties, it is very interesting and important to monitor how landscape ecological processes influence high-level predators, as cascading community ecological processes may project single-species problems to community-wide crises (Crooks and Soulé 1999).

The focus of this study is to examine the habitat network of a set of carabid species (Coleoptera: Carabidae) that inhabit hill and mountain forest patches (hereinafter: “forest specialist carabids”) in the Bereg Plain, NE Hungary and W Ukraine. Carabids are excellent study species for landscape ecology, because their habitat structure is relatively easy to describe (compared to many other organisms, e.g., birds); the ecology of the group is well known and adults can easily be used for experiments. Moreover, many carabids are higher predators and sensitive to fragmentation, potentially participating in trophic cascades. The conservation value of ground beetles is also high (Lövei and Sunderland 1996).

Our study site, the Bereg Plain is located at the foot of the Carpathians and spreads over an area of 6,000 km^2, belonging to Hungary and the Ukraine. The Bereg Plain was covered by continuous woodlands of deciduous trees up to the 18th–19th centuries. Because of the clear-felling of forests and agricultural activity, the former near-continuous forested areas are reduced to small isolated forest fragments separated by agricultural areas and open semi-natural habitats. When the Bereg Plain was covered by continuous forest, species living in closed canopy deciduous forests were able to disperse from the Carpathians to lowland forests. For these species, the Carpathians were a potential colonization source. Even today, a special feature of the carabid fauna in these patches is the occurrence of species characteristic of closed-canopy deciduous forests of hills and mountains. Such species do not usually occur in Hungarian lowlands (Magura et al. 2001b; Ködöböcz and Magura 2005). The local populations in at least some of these fragments are relatively stable, but the entire metapopulation (sensu Pickett and Cadenasso 1995) probably depends on the dispersal of individuals from the source areas in the Carpathians. The fragmentation of the formerly contiguous forests in the Bereg Plain raises the question of whether forest specialist carabids can persist in these patches and whether their persistence can be helped by conservation efforts (e.g., building corridors or protecting the most critical patches and corridors).

In order to explicitly study the source-sink nature of the studied patches, we analysed them as a directed network with a single source and many sinks. A directed network contains links where a link from A to B is not equivalent to a link from B to A (contrary to an undirected network, where no difference exists between a link from A to B and from B to A).

In this study we provide a network analysis of the landscape graph (from a “ground beetle perspective”) to determine: (1) the positional importance of existing landscape elements (patches and corridors) in maintaining connectivity; (2) the advantages of various hypothetical landscape management solutions (creating corridors in different positions); (3) the effects of improving the quality of existing corridors; and (4) the most efficient solution for connecting all patches. Our approach is mostly based on a structural analysis of the landscape graph, and we provide solutions for setting preferences in landscape management. Our study is of immediate and applied interest, because a new highway is planned to be built across the studied area and carabids (as mobile predators) may be among those organisms that are the most sensitive to this kind of disturbance.

Methods

Species

The focal species of our study were forest specialist carabids inhabiting closed deciduous forests of hills and mountains. We have disregarded habitat generalists, because fragmentation is probably less problematic for them (Magura et al. 2001b; Lövei et al. 2006), and a landscape graph analysis may not be sensitive to the distribution of generalist carabids. The reason is that these species inhabit less definitive landscape elements. Typically, there are a variety of factors influencing the distribution of carabids, but vegetation structure seems to be of high importance (Brose 2003a, 2003b; de la Pena et al. 2003). Grazing of herbivores (Suominen et al. 2003) and human activity (Niemelä et al. 2002; Ishitani et al. 2003; Kotze et al. 2003; Magura et al. 2004) may also exert a large, indirect influence on their distribution. The forest specialist carabids analysed here were *Carabus intricatus* (Linnaeus 1761), *Cychrus caraboides* (Linnaeus 1758), *Leistus piceus* (Frölich 1799), *Abax parallelus* (Duftschmid 1812), *Cymindis cingulata* (Dejean 1825), *Carabus arcensis carpathus* (Born 1902), *Pterostichus melas* (Creutzer 1799) and *Molops piceus* (Panzer 1793). These specialist species only occur in old-growth deciduous forest patches, because they require special environmental conditions (cool and wet microclimate, dead and decaying trees, cover of leaf litter and herbs etc.). We have analysed the composite habitat network for all of these species, since they inhabit areas of very similar habitat structure. Lumping species-specific data served for the building of a more robust database at the expense of losing information on interspecific differences. Habitat choice and landscape use by these species are very similar across species (Ködöböcz and Magura 2005).

Collection methods

Carabids were collected between 1995 and 1999. Beetles were sampled using unbaited pitfall traps, consisting of plastic cups (diameter 100 mm, volume 500 ml) filled with 70% ethylene glycol as a killing and preserving solution. Within individual forest patches, there were 9 to 18 traps located at least 10 m from each other and scattered randomly. Each pitfall trap was located at least 50 m from the nearest forest edge, in order to avoid edge effects (Magura et al. 2000). Traps were checked monthly between April and October in each year from 1995 to 1999 (Magura et al. 2001b). Unequal trapping effort did not influence the number and abundance of forest specialist species (Lövei et al. 2006). Further, as we sampled over the whole activity season, trap density is unlikely to affect our results.

The study area and the construction of the habitat network model

The Bereg Plain in NE Hungary and W Ukraine is confined by the Tisza River and the Carpathians (Fig. 1). The analysed old-growth deciduous forest patches, dominated by oak (*Quercus robur*) and populated by varying densities of *Fraxinus angustifolia* spp. *pannonica* and hornbeam (*Carpinus betulus*), are located in an area dominated by agricultural fields, roads and creeks. These deciduous forests are declining and the local populations of specialist carabids living in the forests fragments either become isolated or may disperse between small forest patches, depending on the distance between patches, the properties of the matrix (Baudry and Burel 2004;

Fig. 1 Topographical map of the studied area. Black areas are forests and thin lines mark country borders. The studied forest patches are numbered with the codes displayed in the Tables. For spatial scaling, note that the distance of patch 1 from the largest patch 16 is 40 km and its area totals 1250 ha

Baum et al. 2004) and the presence of corridor-like landscape elements.

We assumed a typical dispersal range of 1 km for the studied flightless specialist species (Thiele 1977). We identified 16 forest patches (15 small ones and the Carpathians as a practically continuous forest patch, coded N1–N16), as well as 9 forest corridors (coded L1–L9; Fig. 2a). We analysed this landscape graph and created modified versions by inserting 18 hypothetical green corridors (coded L10–L27; Fig. 2b). Building these corridors would entail establishing a series of forest patches with a size of 50 × 50 m and distances from one another of not more than 1 km; so that these could serve as stepping-stones between habitat patches. We used the recommended patch size in order to have core zones: edge effects have been found to negatively influence forest specialist carabids staying within 10–30 m of the matrix (Magura et al. 2000, 2001a). We did not analyse an additional 93 hypothetical corridors, because those were either topographically impossible (e.g., a corridor between N8 and N12; Fig. 2a), or apparently meaningless (for example, building a green corridor between N1 and N3 would not substantially increase connectivity; Fig. 2a).

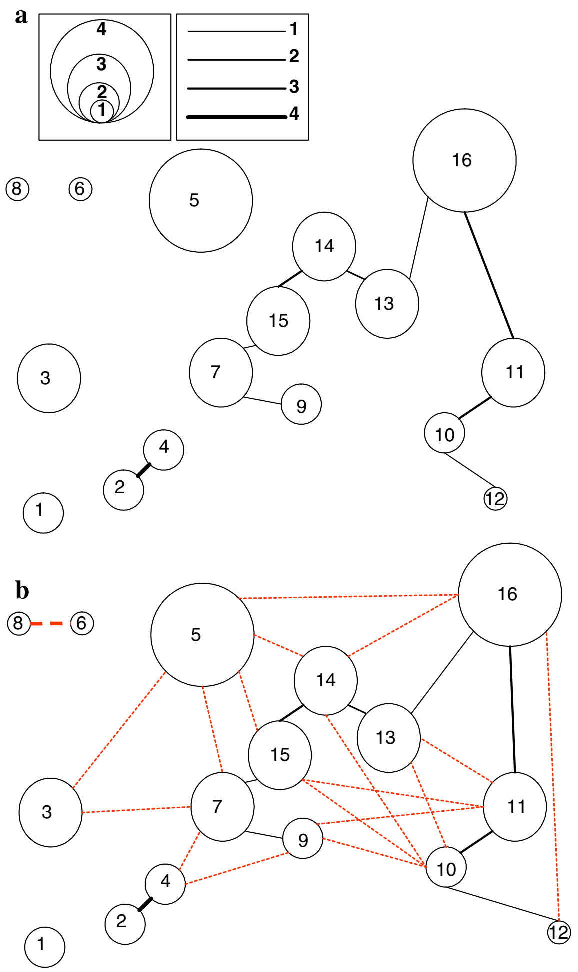

Fig. 2 Topology of landscape elements. Nodes and links represent habitat patches and corridors, respectively. Numbers correspond to patch codes given in Table 1 (i.e., “5” corresponds to node “N5”, for simplicity, while corridor L1 connects “2” to “4”, see Table 1). Quality values are illustrated by node size and link width, according to the top left insets in (**a**). The hypothetical corridors, whose insertion effects have been studied, are also presented by dashed lines in (**b**)

However, certain possibilities of the latter were also tested, although only in combinations with others (L28–L37, see Table 2). The quality of both patches and corridors (including the hypothetical ones) were weighted (respectively, from 1 (low) to 4 (high)) reflecting local population sizes for patches and permeability for corridors.

Local population size was the annual average combined number of individuals trapped for the eight studied species: patch values of 1, 2, 3 and 4 correspond to 0–10, 11–100, 101–1000 and >1001 individuals, respectively (these are qualitative weights on graph nodes). Local population size as an indicator of habitat quality is problematic because of source-sink network effects. In this case, however, it seems to be less problematic, because every patch (except N16) is also likely to be a sink (this is why we also studied a directed network, beyond the more general analysis of the undirected landscape graph). Thus, differences in local population size reflected differences in quality of the given patches.

The width of links corresponded to the estimated permeability of corridors (here, we provided a “semi-quantitative” weight on graph links, based on field data). We assumed the existence of a corridor between two patches if their distance did not exceed 1,000 m and there was no unpenetrable barrier between them. This critical distance was chosen because even poor colonist forest specialists can cover this distance through inhospitable habitats. The highest permeability score (4) was given to corridors of length up to 100 m with no barrier (e.g., corridor L1 between N2 and N4), a value of 3 was given to 300–500 m long corridors with no barriers (e.g., L4 between N14 and N15), a value of 2 was given for corridors that were longer but <1000 m or relatively easily penetrable barriers, like a road (e.g., L5 between N13 and N14), and, finally, the lowest score (1) was given to corridors with hardly penetrable barriers, like a small creek (e.g., L2 between N7 and N9). In summary, distance between patches and matrix properties determined corridor quality.

We also analysed the modified network where the quality of individual corridors was improved one by one to attain maximum permeability (L1*–L9*; "*" marks improved quality). For reasons of simplicity, we did not take into account the area of patches (but see Pascual-Hortal and Saura 2006).

We note that the usefulness of corridors for several species is questionable (Collinge 2000; Haddad et al. 2003). Depending on the properties and the quality of corridors, they may facilitate the movement of some species (Beier and Noss 1998; Berggren et al. 2002), while hinder others (Selonen and Hanski 2003; Henein and Merriam 1990; Tischendorf and Wissel 1997; Tischendorf et al. 1998). Corridors are generally beneficial to carabid dispersal (Burel 1989, 1992). The evaluation of corridors and the role of the matrix are important. Corridors that are not used by animals should not be defined as such (Selonen and Hanski 2003). Similarly, matrix areas that are frequently and easily used are not matrix areas and should be defined as part of a preferred patch (cf. Baum et al. 2004). In spite of theses difficulties, we believe that the habitat network we constructed is a good model for the studied organisms.

Methods of network analysis

Landscape graphs are characterised by a wide array of techniques (Cantwell and Forman 1993; Schumaker 1996; O'Neill et al. 1998; Tischendorf and Fahrig 2000a, b; Urban and Keitt 2001; Turner et al. 2001), many of which are supported by graph theory (e.g., Shimazaki et al. 2004). Landscape graphs are mathematical representations of habitat structure, where nodes (representing patches) are linked ("links" stand for corridors) to one another providing information on habitat topology (e.g., whether habitat arrangement is spider-, chain- or loop-like, Pickett and Cadenasso 1995). For studying a special problem, techniques most adequate for the properties of the landscape graph (e.g., data quality) need to be selected.

We analysed our landscape graph with structural indices that enabled us to weight nodes (characterising habitat patch quality) and links (characterising the permeability of corridors). Carabids in this system are regarded as a source-sink metapopulation, where continuous immigration is needed for sink patches (the forest fragments) from the source area (the Carpathians). It is unknown whether the local

Table 1 The code and identity of habitat patches and corridors in the intact landscape graph

Intact graph		
Habitat patches		
Code	Name	Quality
N1	Bockerek	2
N2	Déda H	2
N3	Lónya	3
N4	Déda U	2
N5	Dobrony	4
N6	Peres	1
N7	Rafajna	3
N8	Téglás	1
N9	Gút	2
N10	Alsóremete	2
N11	Beregújfalu	3
N12	Puskino	1
N13	Munkács	3
N14	Alsókerepec	3
N15	Gát	3
N16	Carpathians	4
Corridors		
Code	Position	Quality
L1	N2/N4	4
L2	N7/N9	1
L3	N7/N15	1
L4	N14/N15	3
L5	N13/N14	2
L6	N13/N16	1
L7	N11/N16	3
L8	N10/N11	3
L9	N10/N12	1

Quality is estimated based on field data and expert (from 1 to 4) reflecting local population size for patches and permeability for corridors. See the details in Methods section

Table 2 The code and identity of designed corridors

designed corridors		
code	position	length
L10	N3/N5	13
L11	N3/N7	11
L12	N4/N7	4
L13	N4/N9	5
L14	N5/N7	8
L15	N5/N14	10
L16	N5/N15	13
L17	N5/N16	7
L18	N6/N8	1
L19	N9/N10	9
L20	N9/N11	9
L21	N10/N13	13
L22	N10/N14	14
L23	N10/N15	12
L24	N11/N13	9
L25	N11/N15	10
L26	N12/N16	4
L27	N14/N16	2
L28	N1/N2	3
L29	N1/N3	6
L30	N1/N7	7
L31	N2/N3	8
L32	N2/N7	4
L33	N3/N6	16
L34	N3/N8	17
L35	N5/ N6	2
L36	N6/N16	8
L37	N8/N16	14

Length gives the number of established stepping-stones when opening a new corridor. Designed corridors are always of quality 1 except for L18 which is of quality 2

populations are self-sustainable, because the habitat network of the analysed carabids is poorly connected. The graph is unconnected (individuals cannot disperse between every pair of patches) and several network indices are sensitive to infinite distance values. We used several network indices in order to characterize different aspects of this fragmented source-sink habitat network.

These indices were used to answer the four major questions stated at the end of Introduction. First, we quantified (1) the effects of removing nodes (marked by N1–N16) and links (marked by L1–L9) from the intact network (Fig. 2a). Subsequently, we calculated (2) the effects of adding single links according to Fig. 2b (L10–L27), and (3) the effects of improving the quality of existing links (L1*–L9*). Finally, we determined (4) the best solution for connecting every patch by adding combinations of links (L10–L37).

Network parameters

We quantified our landscape graph with several network indices that are described in the following paragraphs: (1) the degree of network nodes (i.e., the number of neighbour patches directly connected to patch i; D_i); (2) topological distance (d) and topographical distance (d_{tgr}, reflecting corridor quality: the length and width of corridors); and (3) metapopulation size (*MPS*, reflecting patch quality). Using these variables, we constructed a combined importance index (I^*). This technique reflects the quality and basic structural properties of the habitat network, increasing the reality of the graph model. Since this metapopulation system is typically of sink-source nature, we quantified the maximum population size connected to the source habitat (C_{source}) and the distance-based maximum reachability of patches from the source (reachability, $R_{16}^{D;tgr}$).

Degree

The position of node i was characterised by its degree (D_i) value giving the number of neighbouring patches directly connected to i (Wassermann and Faust 1994). Generally, a habitat patch with high D_i will tend to have a high I^*. A D_i value was also calculated for corridors, where the value was calculated as the average degrees of the joint nodes.

Topological distance and topographical distance

The d_{ij} topological distance of two nodes, i and j, is the minimum number of links forming a path through which i is reachable from j in a network (Wassermann and Faust 1994). The topographical distance (d_{tgr}) is a more realistical corridor index that incorporates both the number of links between two nodes and the permeability of the corridors by summing link values along pathways (high permeability meaning low topographical distance). The connectedness of graph node *i* was calculated as the average of the $d_{tgr;ij}$ distance values, $d_{avtgr;i}$. Small distance values represent more central nodes in a network (a habitat patch with low $d_{avtgr;i}$ is more important in maintaining connectivity than one with a higher d_{avtgr}). The distance of nodes *i* and *j* is infinite if they belong to different graph components (there is no path between them); therefore, we calculated the $d_{tgr;ij}$ (and consequently I^*) only for nodes belonging to the largest component of the network.

Metapopulation size

Patch quality was characterized by the estimated local population size (estimated by $LPS_i = \{1, 2, 3, 4\}$ for patch *i*). The sum of LPS_i values of all patches connected to the major component of the landscape graph gives the metapopulation size (*MPS*, assuming that unconnected local populations do not belong to the metapopulation, Urban and Keitt 2001). If a node or a link is removed from the landscape graph, then, in some cases, it becomes more fragmented (Keitt et al. 1997 and Urban and Keitt 2001). The maximally connected-local-population size (*MPS*) is the largest sum of the local population size values of connected patches (metapopulation size). In the intact network, *MPS* equals 24 (i.e., the sum of LPS_i values). If node or link *i* is deleted from the graph, the resulting *MPS* value of the new graph will be MPS_i, thus, a relative value of a landscape element is related to its effect on the *MPS*.

Importance index

The importance index (I^*) was calculated for the elements (nodes and links) of the intact landscape graph (Fig. 2a). This was a modified version of a similar index (Jordán et al. 2003), by ignoring the clustering coefficient, because of the very low connectivity of this network. Thus, I^* was calculated as

$$I_i^* = D_i / (d_{avtgr;i} + MPS_i).$$

This index is a combined index reflecting the pure topological properties of the network (*D*), as well as the quality of both habitat patches (*MPS*) and corridors (*d*).

C_{source}: metapopulation size connected to the source habitat

The metapopulation size connected to the source habitat (C_{source}) is equal to the *MPS* that includes patch N16 (the Carpathians). The analysis of C_{source} differs from preceding indices in that it assumes that dispersal is not limited by distance and is particularly relevant if the metapopulation is sensitive to the loss of genetic variability. If a species is on the brink of extinction, the total number of individuals participating in gene flow is more important than the conditions and speed of dispersal events.

Reachability from the source habitat

Finally, the calculation of the reachability index assumes that dispersal depends on topographic distance and that the contiguity with the source habitat (N16) is critical for persistence. We employed a distance-weighted reachability measure, where the weighting is the combination of topological distance values from N16 and estimated link weights (reflecting corridor permeability). This is modified from Borgatti (2003) and only briefly discussed here. Reachability is calculated as:

$$R_{16}^{D;tgr} = \sum_i \frac{LPS_i}{d_{tgr;16,i}} \bigg/ 4n$$

where the local population size in patch *i* (LPS_i) was weighted by its topographical distance from the Carpathians ($d_{tgr;16,i}$), and was normalized with the size of the network (*n*, the number of nodes) and the possible maximum for LPS_i, (which equals 4 in this case).

Combined effects of corridors

In addition to estimating the importance of existing landscape elements, we proposed a plan for connecting all habitat patches by newly established corridors (and stepping-stones if necessary). Here the combined effect of the corridors needs to be calculated: if we establish three corridors, the best solution is not necessarily the insertion of the best three based on their individual effects (Borgatti 2003). If we assume that the habitat network is a source-sink system, and we do not consider dispersal as a limiting factor, our priorities could be the following: (1) connect all patches to the Carpathians (maximize the size of the core, C_{source}), (2) solve this problem with the fewest corridors and stepping-stones possible, and (3) all patches need to be as close to the Carpathians as possible (maximize reachability, $R_{16}^{D;tgr}$). Obviously, priorities could change and, accordingly, the best solution would be different. Based on these priorities, a computer programme was developed to identify the optimal combination of $k = 1,2,...,11$ inserted corridors (based on the calculated index values). The programme provided the 100 best combinations of corridors, where ranking followed first (a) the maximum values of C_{source},. When C_{source} was equal, ranking considered (b) the minimum number of stepping-stones, and in cases where both were equal, the ranking was by (c) $R_{16}^{D;tgr}$ values. From these 11×100 combinations, for each number of stepping-stones, the one with the highest C_{source} value was chosen.

Results

First we analysed the structural importance of existing landscape elements in the intact network.

Table 3 The importance ranks of different landscape elements in the intact network (based on their loss quantified by I* importance index, C_{source} core index and $R_{16}^{D;tgr}$ reachability index), the ranked effects of inserting new corridors (based on core and reachability index), and the effects of improving previously existing ones (based on reachability)

I*		C_{source}—loss		C_{source}—insertion		$R_{16}^{D;tgr}$—loss		$R_{16}^{D;tgr}$—insertion, improvement	
N13	0.1081	N16	X	L12	28	N16	X	L6*	0.1690
L5	0.0967	N13	10	L13	28	L7	0.0916	L7*	0.1511
N14	0.0958	L6	10	L14	28	L6	0.0957	L17	0.1404
L6	0.0920	N14	13	L15	28	N11	0.0977	L27	0.1339
N16	0.0909	L5	13	L16	28	N13	0.1021	L15	0.1305
L4	0.0825	N15	16	L17	28	L5	0.1074	L5*	0.1298
N15	0.0812	L4	16	L11	27	L4	0.1141	L16	0.1296
L7	0.0758	N11	18	L18	24	N14	0.1146	L20	0.1292
N11	0.0748	L7	18	L19	24	L8	0.1150	L25	0.1289
L3	0.0693	N7	19	L20	24	L3	0.1193	L14	0.1284
N7	0.0664	L3	19	L21	24	N15	0.1217	L12	0.1283
L8	0.0658	N10	21	L22	24	N10	0.1227	L13	0.1277
N10	0.0645	L8	21	L23	24	L9	0.1228	L8*	0.1277
L9	0.0432	N9	22	L24	24	L2	0.1229	L11	0.1275
L2	0.0430	L2	22	L25	24	original	0.1248	L19	0.1271
N12	0.0274	N12	23	L26	24	L1	0.1248	L26	0.1267
N9	0.0273	L9	23	L27	24	N7	0.1273	L3*	0.1262
		N1	24	L10	24	N12	0.1310	L9*	0.1259
		N2	24	original	24	N9	0.1311	L23	0.1258
		N3	24			N1	0.1331	L4*	0.1258
		N4	24			N2	0.1331	L2*	0.1252
		N5	24			N3	0.1331	L1*	0.1248
		N6	24			N4	0.1331	L10	0.1248
		N8	24			N5	0.1331	L18	0.1248
		L1	24			N6	0.1331	L21	0.1248
		original	24			N8	0.1331	L22	0.1248
								L24	0.1248
								original	0.1248

Here we did not take the direction of graph links into account (we did not regard the habitat as a source-sink system). Under this scenario, the loss of the Munkács forest patch (N13) resulted in the greatest loss of connectivity of the landscape graph compared to the loss of any other single patch (based on the I^* index, Table 3). The loss of the Gút (N9) and Puskino forests (N12) caused the least reduction in connectivity, since these patches are at the periphery of the largest component of the graph. Among the corridors, the most important one (based on I^*), coded L5, connects the Munkács forest (N13) to the Alsókerepec forest (N14). Patches and corridors not connected to the Carpathians (N16) were not considered for the calculation of this index, (for both realistic and technical reasons). This index is useful if we are interested in a two-way dispersal of individuals (i.e., if the source-sink nature of the carabid metapopulation seems to be unimportant).

Second, we compared the effects of newly established corridors to the effect of losing existing ones (Table 3). In the intact network, the sum of estimated local population values connected to the Carpathians (including the latter) was 24. The removal of the corridor from the Carpathians to the Munkács forest (L6), or losing the Munkács forest itself (N13), would cause the largest loss of connectivity in the network (based on the C_{source} index). In both cases several patches with large local populations would be separated from the source. Losing unconnected patches and corridors had no effect on this property, and a number of insertions did not influence C_{source}. Six different corridor insertions lead to equally good solutions, because these connected either the Déda

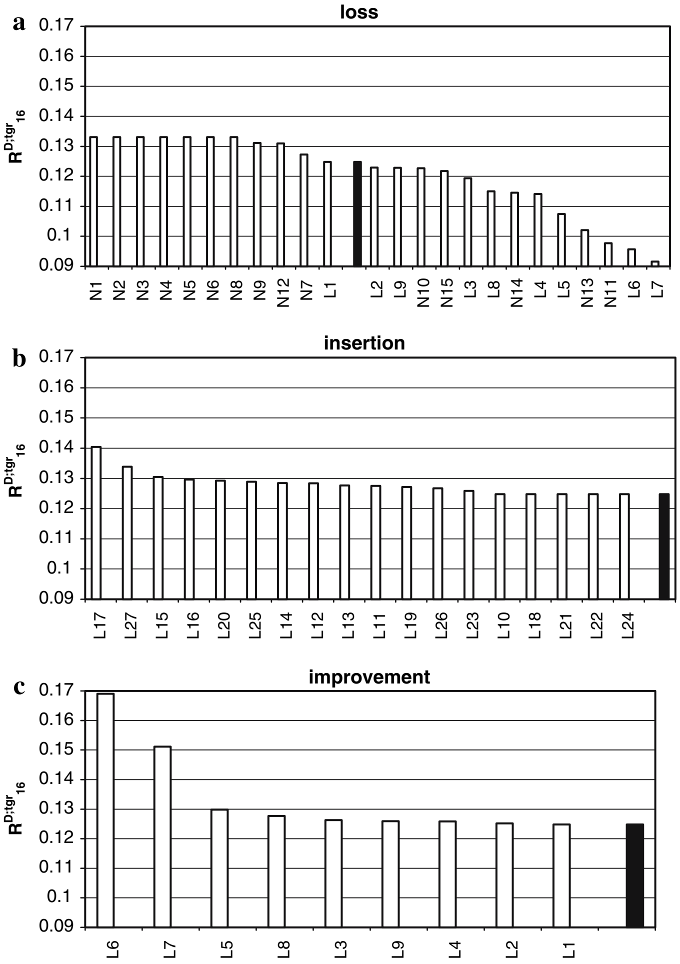

Fig. 3 The reliability of the reachability ($R_{16}^{D;tgr}$) index illustrated by the ranks of different landscape management solutions: (**a**) the loss of patches and corridors; (**b**) the insertion of new corridors; (**c**) improving existing corridors. The value of the intact landscape graph is the dark bar and displayed in each case for comparison. Improvement and insertion are either neutral or positive, while losses may be both negative and positive (i.e., the measure is not consistent for the analysis of the latter)

forest (N2 and N4) or the Dobrony forest (N5) to the main component. The difference between these solutions is related to distance values only expressed by the next index.

Third, we also considered how to improve the quality of the existing corridors. The reachability index ($R_{16}^{D;tgr}$) considers a directed network and compares the effects of corridor deletions, insertions and improvements. This approach focused on the topographical distance-based reachability of nodes measured from the Carpathians (N16). Note that the highest increase of the original value (0.1248) was reached by improving the quality of corridors connecting the Carpathians to the Munkács (L6) or the Beregújfalu (L7) forests, followed by inserting a new corridor, L17 (Table 3). This index was not suitable for estimating the effect of losing patches, since it is normalized with the network size; therefore, the loss of an unconnected patch indirectly increases the reachability of the remaining ones. This index was useful to compare the insertion of new corridors with the improvement of existing ones. However, this was misleading in a few cases: insertions and improvements are neutral or improve the network, but node deletions had both positive and negative effects (Fig. 3).

Table 4 The effects of the insertion of multiple corridors in different combinations on the values of different connectivity indices. "# of insertions" means the number of established corridors, "corridors" identifies the identity of corridors in the network, while "length" gives the number of established stepping-stones required. The maximum of C_{source} core index equals to 39; this is the case when all patches are connected

# of insertions	Corridors	C_{source}	$R_{16}^{D;tgr}$	Length
0	-	24	0.124771	0
1	18	24	0.124771	1
	27	24	0.133873	2
	28	24	0.124771	3
	12	28	0.128345	4
	32	28	0.128345	4
2	12, 18	28	0.128345	5
	18, 32	28	0.128345	5
	12, 27	28	0.138188	6
	27, 32	28	0.138188	6
	28, 32	30	0.129833	7
	13, 28	30	0.128881	8
	17, 35	29	0.142349	9
	28, 30	30	0.129517	10
	12, 17	32	0.14397	11
	17, 32	32	0.14397	11
3	12, 17, 35	33	0.145923	13
	17, 32, 35	33	0.145923	13
	17, 28, 32	34	0.145458	14
	13, 17, 28	34	0.144506	15
	13, 14, 28	34	0.132558	16
	17, 28, 30	34	0.145142	17
	12, 17, 30	34	0.145808	18
	17, 30, 32	34	0.145808	18
	17, 31, 32	35	0.146202	19
4	17, 28, 29, 32	37	0.147333	20
	13, 17, 28, 29	37	0.146069	21
5	17, 28, 29, 32, 35	38	0.149286	22
6	17, 18, 28, 29, 32, 35	39	0.150707	23
7	17, 18, 27, 28, 29, 32, 35	39	0.161054	25
8	17, 18, 26, 27, 28, 29, 32, 35	39	0.163007	29

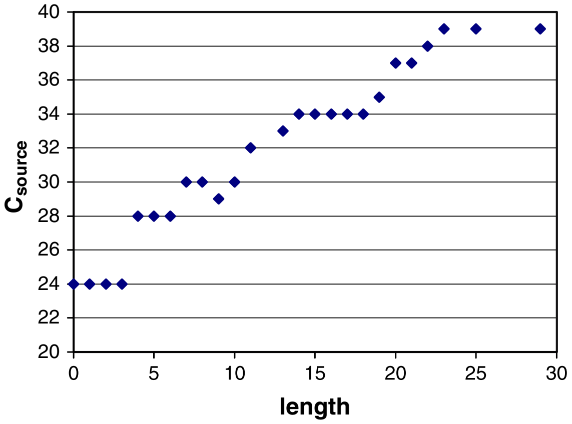

Fig. 4 The effect of the length of inserted corridors on the value of the connectivity index C_{source}. Note that, depending on topology, inserting shorter corridors may result in similar or higher connectivity

Finally, we proposed a plan for connecting all patches to the Carpathians in an efficient way, where "efficient" was defined as the minimum number of stepping-stones needed to establish certain combinations of corridors and "effect" was measured by the C_{source} index, or (if it does not change) by reachability. At least six corridors with 23 stepping-stones must be inserted to connect all patches. Nevertheless, with the addition of another corridor with only two stepping-stones, the distance-based reachability of the network ($R_{16}^{D;tgr}$) was increased (Table 4 and Fig. 4). If resources are limited and only few stepping-stones can be established, our analysis suggested that 4, 7, 11, 14 or 20 stepping-stones (see Fig. 4), established in the positions listed in Table 4, were the ones that gave the most cost-effective solution. These results only provide an illustrative example, since the optimal solution heavily depends on the priorities set (cf. also Urban and Keitt 2001 for the minimum spanning tree analysis of landscape graphs).

Discussion

The conservation of different species living in different habitats requires different landscape management strategies. In the case of forest specialist carabids inhabiting the forest patches of the Bereg Plain, the problematic task is to increase the connectivity of a highly fragmented, source-sink system, where persistence requires continuous recolonisation from the Carpathians. We applied several network analytical indices for characterising the landscape graph of the habitat of the studied species. Based on topological properties and the estimated qualities of both corridors and patches, we evaluated the relative positional importance of landscape elements (patches and corridors) in maintaining the connectivity of the habitat, and consequently in enabling dispersal and gene flow. The habitat network was constructed based on field data and information on the dispersal properties of the species involved.

Given our assumptions on carabid dispersal and land use, the results suggest that relatively simple manipulations could increase the connectivity of the network. Several indices unequivocally indicated the importance of the Munkács forest (N13), the corridors adjacent to it (L5, L6) and the corridor between the Beregújfalu forest and the Carpathians (L7). Attention should focus primarily on these landscape elements. Improving the quality of certain corridors (the ones coming from the Carpathians, L6 and L7) provides the best solution. Other improvements (e.g., L5) are less effective than establishing new corridors in certain arrangements (e.g., L17, between the Dobrony forest and the Carpathians). The network that we analysed in this study was very simple. Still, our study is of high practical relevance considering that (1) the construction of a new highway crossing this area is in the planning phase, and (2) the studied specialist carabids are highly sensitive to fragmentation and are important predators that influence top-down trophic control.

We suggest that the main directions of future research in this area should be (1) improving these methods in order to study more species and their interactions (metacommunities) and (2) considering financial aspects in optimising solutions in a more detailed way. Since habitat network connectivity analysis has recently become a key issue in setting conservation priorities (Briers 2002), landscape engineering and management require new quantitative methods for finding optimal solutions (Jordán 2000; Étienne 2004). This includes studying the relative positional importance of landscape elements in habitat networks (Verboom et al. 2001; Jordán et al. 2003).

Acknowledgements We are grateful for Zoltán Peresztegi-Nagy for developing a computer programme for one part of the analysis, András Báldi and Gábor Lövei for useful discussions and three anonymous reviewers for their comments on the manuscript. We thank K. Csepi and G. Lövei for linguistic revision. FJ and TM were supported by grants from the Hungarian Scientific Research Fund (OTKA T 37726 and F 61651, respectively). FJ was also supported by Society in Science: the Branco Weiss Fellowship from ETH Zürich, Switzerland.

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