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RESEARCH ARTICLE

Graph-theoretic connectivity measures: what do they tell us about connectivity?

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Abstract Graph-theoretic connectivity analyses have received much attention in connectivity evaluation during the last few years. Here, we explore the underlying conceptual differences of various graph-theoretic connectivity measures. Based on connectivity analyses from three reserve networks in forested landscapes in Central Finland, we illustrate how these conceptual differences cause inconsistent connectivity evaluations at both the landscape and patch level. Our results also illustrate how the characteristics of the networks (patch density) may affect the performance of the different measures. Many of the connectivity measures react to changes in habitat connectivity in an ecologically undesirable manner. Patch prioritisations based on a node removal analysis were sensitive to the connectivity measure they were based on. The patch prioritisations derived from different measures showed a disparity in terms of how much weight they put on patch size versus patch location and how they value patch location. Although graphs operate at the interface of structure and function, there is still much to do for incorporating the inferred ecological process into graph structures and analyses. If graph analyses are going to be used for real-world management and conservation purposes, a more thorough understanding of the caveats and justifications of the graph-theoretic connectivity measures will be needed.

Keywords Functional connectivity · Graph theory · Reserve network · Component · Patch prioritisation

Introduction

Habitat loss and fragmentation pose two primary threats to biodiversity across spatial scales that range from the global to very local ones. Fragmentation confounds and intensifies the effect of pure habitat loss when the amount of habitat falls below a critical threshold (Andren 1994; Mönkkönen and Reunanen 1999). Although habitat loss and fragmentation are separate components affecting the patterning of habitat (i.e. habitat amount and its configuration in a landscape), their independent roles are difficult to evaluate (Fahrig 1997,2003; Bender et al. 1998; Wiegand et al. 2005).

The intertwined ecological consequences of habitat loss and fragmentation can be understood and measured on the basis of the concept of connectivity. Connectivity supports ecological flows in a landscape and, with various mechanisms, influences the viability of spatially structured populations. Habitat connectivity is needed to sustain spatially dependent ecological processes, and it is a necessity for the long-term persistence of biodiversity (Fahrig and

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Merriam 1994; Hanski 1999). Connectivity conservation can also be considered to be a prerequisite for ecologically and economically efficient conservation practices.

The most commonly used definition for landscape connectivity is rooted in a functional connectivity concept, and it is described as 'the degree to which landscape facilitates or impedes movement of organisms among resource patches' (Taylor et al. 1993). Underlying the functional connectivity concept is the idea that the connectivity experienced by an organism is result of the behavioural responses of the organisms to physical landscape structure (e.g. Tischendorf and Fahrig 2000a, b; Bélisle 2005; Kindlmann and Burel 2008). However, all of the definitions of functional connectivity are conceptually so broad that they leave room for a range of interpretations and applications. The very nature of the concept of connectivity has been approached from several (also conflicting) perspectives during the past decade (Tischendorf and Fahrig 2000a, 2001; Moilanen and Hanski 2001; Goodwin 2003), which indicates that the definition of the concept is far from simple, and that the focuses of the researcher are reflected in it.

Graphs are versatile models for analysing a wide range of practical problems concerned with the properties and functions of networks (Gross and Yellen 2006). In landscape ecology, graphs are abstractions of landscapes where habitat patches are represented as spatially explicit nodes and functional connections between the nodes as links (Fall et al. 2007; for in-depth graph definitions in the field of landscape ecology we recommend Bunn et al. 2000, Urban and Keitt 2001; Urban et al. 2009). Graph theory, with its algorithms, has given rise to many connectivity measures with varying degrees of complexity and differing underlying assumptions. Some connectivity measures have been adopted to landscape ecology from the general graph definitions and methodology of other disciplines, while other measures were specifically designed for the evaluation of landscape connectivity. Graph metrics that were developed for the uses of other disciplines may not, however, be suitable for the evaluation of landscape connectivity due to its very special characteristics and needs (Saura and Rubio 2010).

Graphs operate at the interface of structure and process (e.g. Urban and Keitt 2001; Urban et al. 2009). In landscape ecology, graph structures are defined in reference to the dispersal ability of a species and can be analysed as structures as such or with a specific relevance to the underlying process, such as gene flow, flux of dispersing individuals (Urban and Keitt 2001; Minor and Urban 2007a, b), species occurrence (Andersson and Bodin 2009) or species invasions (Ferrari and Lookingbill 2009). Graph-theoretic connectivity measures vary in terms of how they infuse and deal with the underlying ecological process, although they are ultimately founded on the concept of metapopulation with spatially interrelated subpopulations (Urban et al. 2009).

Graph-theoretic connectivity analyses lend themselves to functional connectivity evaluations both at the level of the entire networks and at the level of individual patches. At the network level, they have been used to evaluate network connectedness for a focal species (Keitt et al. 1997; Bunn et al. 2000), in the design of reserve network (Fuller et al. 2006) and in connectivity conservation for the habitat of threatened species (Fall et al. 2007). Connectivity evaluation at the level of individual patches is often called patch prioritisation, because in many cases it is used to select the most valuable patches in a habitat network (Jordán et al. 2003; Rothley and Rae 2005; Pascual-Hortal and Saura 2008). Patch prioritisation has also been used to extract configurational properties of patches into a variable that can be used in statistical analyses to explain ecological process (e.g. species occurrence, colonisation probability) (van Langevelde 2000) or to reveal the roles of patches in a landscape (Keitt et al. 1997; Bunn et al. 2000; Urban and Keitt 2001).

The graph-theoretic connectivity measures do not form a single story about connectivity, but represent a full spectrum of specific measures that capture different aspects of connectivity. This is important to remember when the measures are selected for different kinds of applications and their outcomes interpreted. Pascual-Hortal and Saura (2006) and Saura and Pascual-Hortal (2007) have made a valuable effort in the systematic comparison of different measures and their properties. They have investigated the performance of measures in landscapes varying in their level of habitat loss and fragmentation with an emphasis on the outcome (whether it is desirable or not) rather than on the mechanisms that produced the outcome. Although empirical data sets on the movements of individuals (i.e. realised connectivity) represent the "truth" against which the performance of connectivity measures should be evaluated and calibrated, connectivity measures can also, to some extent, be evaluated and understood on theoretical grounds. Theoretical evaluation is especially suitable for revealing possible unwanted behaviour of the measures (that is not in agreement with the concept of connectivity), and comparisons between measures may provide insights into their characteristics and performance.

Here, we shall first review and compare the available graph-theoretic connectivity measures in terms of their conceptual differences. One of the major factors leading to differences among the measures is whether connectivity can only "prevail" between habitat patches or if intrapatch connectivity is also acknowledged. For instance, what is the connectivity for a landscape that is fully covered by habitat? Zero or the maximum? The non-acceptance that area within a habitat patch may contribute to connectivity may lead to the counterintuitive outcome that connectivity has a positive relationship with fragmentation (Tischendorf and Fahrig 2000b; Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Matisziw and Murray 2008). The relationship of the measure to intrapatch connectivity also largely determines whether the measure explicitly tracks the amount of suitable habitat in a landscape. Although the way how the pairwise distances between patches are determined (e.g. as Euclidean, cost-modified distances or based on simulation) is independent of the connectivity measure, how the connections between patches are defined (e.g. among all pairs of patches or not, as direct connections only or acknowledging paths) can differ widely among measures with anticipated influence on their behaviour.

In our review, we shall briefly describe a number of graph-theoretical measures that are used in the evaluation of landscape connectivity. We shall use simple examples to illustrate what kind of counterintuitive connectivity evaluations the measure may possibly produce and with which mechanisms. We draw on a connectivity concept that recognises both habitat amount and connections among and inside patches as contributing to connectivity (the so-called habitat availability concept described by Saura and Pascual-Hortal 2007; and Pascual-Hortal and Saura; 2008). In contrast to the original definition of functional connectivity by Taylor et al. (1993), this concept acknowledges within resource patch connectivity and recognises habitat amount as a critical factor contributing to dispersal among resource patches. The sizes of a source and a target patch are linked with the dispersal probability between the patch pair within a given time period (more dispersing individuals with increasing donating area; growing chance of ending in a target patch with increasing number of dispersing individuals, and with the increasing size of a target patch). The connectivity based on this concept may be briefly described as the amount of habitat that is available to a species dispersal (given its assumed dispersal ability) at the landscape level. The concept can easily be extended to dispersal flux if the habitat area is assumed to scale linearly with the number of migrants. The connectivity rises if (i) for a given amount of habitat, the connection status is improved or (ii) for a given connection status, the amount of habitat increases. The connection status is improved when the degree of linkage among patches increases and more so when either the strength of connections among the patches increases (so that proximal patches contribute more to connectivity than distant ones) or the habitat area that is linked increases.

In the second part of the article, we analyse empirical data from three reserve networks located in forested landscapes in Central Finland to illustrate how the underlying conceptual differences in the connectivity measures influence the connectivity ratings at the network and patch level. At the network level, we compare the performance of the connectivity measures in terms of how they react when the existing forest reserve network is augmented with small-sized woodland key habitats (WKHs). The numerical value of a connectivity measure should, if lined with the connectivity concept, react positively to the addition of WKHs into the reserve network, as both habitat area and the number (and strength) of interpatch connections increase. At the patch level, we compare the prioritisations obtained from different measures.

Review of the graph-theoretic connectivity measures

We classify the graph-theoretic connectivity measures broadly into two groups: network coherence measures and flux measures (which corresponds to the division of the measures into indirect and direct ones by Matisziw and Murray 2008). The coherence measures provide information about some element of network structure (in respect to coherence or fragmentation in reverse) taking into account species dispersal abilities. Coherence measures usually react strongly to the component structure of the network, acknowledging a ‘single component’ structure as the one maximising connectivity with a given amount of habitat. In contrast, the flux measures summarise interpatch connections between all pairs of patches. The flux measures can either take into account direct interpatch connections only (direct links) or also allow paths, i.e. indirect links via stepping stone patches. The flux measures mainly aim to evaluate the rate of flow of dispersing individuals at the level of the entire habitat network.

We have summarised in Table 1 the various connectivity measures that have been used in landscape ecological connectivity analyses, and below we shall discuss in detail the ones that are most commonly used.

Network coherence measures

Graph diameter is the longest path between any two habitat patches in the graph, where the path length between the patches is itself the shortest possible path (Bunn et al. 2000). As Ferrari et al. (2007) stated, ‘a large graph diameter can either be positive or negative [*for an individual traversing a landscape*] and needs to be interpreted with caution’. Graph diameter is purely a topological measure, which does not take patch areas into account, and generally increases with the increasing number of patches brought about by fragmentation. Graph diameter is usually calculated for the largest component, and within that component, it only provides information on the connectivity between a single pair of patches. *Characteristic path length*, CPL (or average path length) is the average of the shortest path lengths calculated between all pairs of reachable patches in a network. According to Minor and Urban (2007a, b), ‘if CPL is short, all patches tend to be easily reachable’. As the measure concentrates only on reachable pairs of patches, CPL is also short when a network is composed of isolated, internally well-connected components

Table 1 Summary of the connectivity measures used in graph-theoretic connectivity analyses

Measure			References
Network coherence measures			
Characteristic path length, CPL		B	Minor and Urban (2007)
Coincidence probability (class/landscape, CCP/LCP)	C	B	Pascual-Hortal and Saura (2006)
Correlation length	C	B	Keitt et al. (1997), Rothley and Rae (2005)
Expected cluster size, ECS	C	B	O’Brien et al. (2006), Fall et al. (2007)
Graph diameter	C	B	Bunn et al. (2000), Bodin and Norberg (2007), Ferrari et al. (2007), Minor and Urban (2007)
Graph-derived proportional measures, e.g.,			
Ratio of graph diameter to the size of the largest component	C	B	Minor and Urban (2007)
Ratio of the proportion of habitat in the largest patch to the proportion of habitat in the largest cluster (F-measure)	C	B	Ferrari et al. (2007), Lookingbill et al. (2010)
Flux measures			
(Area-weighted) flux (AW)F		P	Bunn et al. (2000), Urban and Keitt (2001)
Harary index, H		B	Jordán et al. (2003)
Habitat availability indices			
Integral index of connectivity, IIC		B	Pascual-Hortal and Saura (2006), Pascual-Hortal and Saura (2008)
Probability of connectivity, PC		P	Saura and Pascual-Hortal (2007)
Total network connectivity		P	Matisziw and Murray (2008)

Measures based on component approach are marked with C. Binary and probabilistic connectivity models are marked with B and P, respectively (comprised possibly of few patches). Thus, fragmentation, in the form of isolated components, may lead to a false indication of connectivity. In the case of a single component network, CPL reaches a minimum value of one when all patches are within one step from each other—irrespective of the number of patches and habitat amount involved.

Correlation length measures the average distance an individual with a given dispersal ability can move before reaching a barrier (Keitt et al. 1997). Correlation length is calculated as an area-weighted mean radius of gyration of all the components in a landscape as follows (for raster data):

$$C_d = \frac{\sum_{i=1}^{NC} n_i.R_i}{\sum_{i=1}^{NC} n_i},$$

where NC is the number of components in the landscape, n_i is the number of habitat cells (i.e. pixels) in component i, and:

$$R_i = \frac{1}{n_i}\sum_{j=1}^{n_i}\sqrt{\left(x_j-\overline{x_i}\right)^2+\left(y_j-\overline{y_i}\right)^2},$$

where R_i is the radius of gyration of component i, $\overline{x_i}$ and $\overline{y_i}$ are the mean x and y coordinates of the habitat cells in component i, and x_j and y_j are the coordinates of the jth habitat cell in component i.

Similar to the graph diameter, there is the undesired property in the correlation length that it is positively related to increasing fragmentation. For example, two connected patches score higher in correlation length than one patch with the same total area. Increasing interpatch distances (within the dispersal ability of a species) also increase the value of this measure, although any species would likely benefit from the proximity of the patches. Correlation length does not explicitly account for the total habitat area, because the habitat area is masked by the extent and shape of a component. Habitat area in a component can be small, but if distributed evenly within a component, it can still provide an opportunity for high average dispersal distances.

Expected cluster size (first introduced by O'Brien et al. 2006) represents an area-weighted mean cluster (i.e. component) size calculated as:

$$\text{ECS} = \frac{\sum_{i=1}^{NC} a_i^2}{a},$$

where NC is the number of components in the landscape, a_i is the habitat area in component i and a is the total habitat area over all components of the graph.

ECS is the size of the component in which a point randomly located within a habitat area is expected to reside at a given threshold distance w. ECS carries information on the amount of habitat within a component, but it still does not react ecologically meaningfully to the amount of habitat in a landscape. For example, the value of ECS increases with the loss of isolated patches/components with a small habitat area, although the total habitat area in the landscape diminishes.

Landscape coincidence probability, LCP, is the probability that two points located randomly within a landscape reside in the same habitat component (Pascual-Hortal and Saura 2006). It is computed as:

$$\text{LCP} = \sum_{i=1}^{NC}\left(\frac{c_i}{A_L}\right)^2,$$

where NC is the number of components in the landscape, c_i is the sum of the sizes of all the patches belonging to component i and A_L is the total landscape area.

LCP is reactive to the amount of habitat in the landscape and shows a decrease with increasing fragmentation. It evaluates (like ECS) reachability between patches as defined by the component structure only, but does not provide information about the internal connectivity of components (discussed in more detail in 'Discussion' section).

Flux measures

Flux measures can be based on a binary or a probabilistic connection model. The probabilistic connection model weights the links with the dispersal probability between two habitat patches. The probability of direct dispersal between patches is determined on the basis of a chosen dispersal kernel, most often a decreasing exponential function of the interpatch distance:

$$p_{ij} = e^{-k\cdot d_{ij}},$$

where k is a constant and d_{ij} is the distance (Euclidean or effective distance) between patches i and j.

Area-weighted flux, AWF, evaluates the area-weighted flux between all pairs of patches:

$$\mathrm{AWF} = \sum_{i=1}^{n} \sum_{j=1, i \neq j}^{n} p_{ij} \cdot a_i \cdot a_j,$$

where n is the total number of patches, p_{ij} is the probability of direct dispersal between patches i and j, and a_i and a_j are the sizes of patches i and j.

AWF does not account for the dispersal potential within a patch itself as it concentrates only on the flux between patches. For this reason, it does not react ecologically meaningfully to the amount of habitat in a landscape; for example, it neglects the loss of an isolated patch ($p_{ij} = 0$) regardless of its size. It also reacts in an undesirable way to fragmentation as, for example, the connectivity value increases with an increasing number of habitat patches when the habitat area and interpatch distances are controlled for. The connection model of the measure does not allow for indirect interpatch connections mediated by stepping stone patches.

Connectivity measures rooted in habitat availability (Integral index of connectivity and Probability of connectivity, presented below) integrate the habitat area existing within patches with the area made available by the interpatch connections into a single measure (Pascual-Hortal and Saura 2006, 2008; Saura and Pascual-Hortal 2007). If habitat patch area (or other patch attribute) is used as a surrogate for the number of dispersing individuals, habitat availability measures are easily interpreted as flux measures. Habitat availability measures avoid undesired responses to increased fragmentation and habitat loss.

Integral index of connectivity, IIC, is a habitat availability measure with a binary connection model (Pascual-Hortal and Saura 2008):

$$\mathrm{IIC} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \frac{a_i \cdot a_j}{1 + l_{ij}}}{A_{\mathrm{L}}^2},$$

where n is the total number of patches, a_i and a_j are the sizes of patches i and j, l_{ij} is the number of links in the shortest path between patches i and j (and equals zero for $i = j$), and A_{L} is the total landscape area. IIC reaches unity when the landscape is occupied by the given habitat.

As shown by Pascual-Hortal and Saura (2006), IIC can reliably provide information on habitat amount and the degree of connectivity between patches, but with the restrictions brought about by its binary view of connectivity (Saura and Pascual-Hortal 2007). IIC evaluates the strength of connections between patches in a topological sense (i.e., the inverse of 1 + the number of links in the shortest path separating the patches), and thus recognises the increasing topological distances between patches as lower connectivity. IIC favours habitat located in a single large patch (in which the habitat area is separated by 0 links), whereas patches with direct or indirect connections (a path length of one link or more) are downscaled by the increasing denominator. For example, two directly connected patches would have lower connectivity than one large patch of the same total area.

Probability of connectivity, PC, measure (Saura and Pascual-Hortal 2007) is calculated as:

$$\mathrm{PC} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \cdot a_j \cdot p_{ij}^{*}}{A_{\mathrm{L}}^2},$$

where n is the total number of patches, a_i and a_j are the sizes of patches i and j, and A_{L} is the total landscape area. p_{ij}^{*} is defined as the maximum product probability of all possible paths between patches i and j. Product probability of a path is the product of all the link weights (p_{ij}) included in the path. For patches close enough, p_{ij}^{*} is reduced to the direct dispersal probability p_{ij}, but for more distant patches the 'best path' passes through stepping stone patches. When $i = j$, the p_{ij}^{*} equals 1.

It has been recommended that PC be used as a connectivity measure, because it is, according to Saura and Pascual-Hortal (2007), the only measure having all the properties of an ideal connectivity measure. It reacts meaningfully to habitat loss and network fragmentation. PC also possesses the richest connection model of the measures in widespread use in connectivity evaluation. PC does not, however, account for other connections between any two patches besides the most probable path (i.e. it does not react to the number of connections between the patches).

Empirical comparison of the performance of the graph-theoretic connectivity measures: habitat network analyses in forested landscape in Finland

With our empirical analyses, we wanted to address the following questions: (i) How do different graph-theoretic connectivity measures perform when the existing reserve network is augmented with small-sized WKHs? (Network level), (ii) How consistently do patch prioritisations based on different measures value patches, and how sensitive are these prioritisations to the density of habitat patches in a landscape? (Patch level). Patch density may have important consequences for the ability of measures to consistently value patches because network properties and the roles of patches in sparse networks differ in an anticipated way from those of denser networks. We used data from three habitat networks, which were composed of reserve patches of a given habitat type added with WKH patches of the same habitat type. The habitat types were herb-rich forests, spruce mires and heath forests. The total landscape area (matrix and habitat area included) in all the networks was ca. 500 km^2. Networks varied more than 10-fold in terms of the patch number (i.e. graph order) and density (number of patches per landscape area); the herb-rich forest network had 42 (17 reserves; 25 WKHs), the spruce mire network 158 (134 reserves; 24 WKHs) and the heath-forest network 528 (242 reserves; 286 WKHs) patches. The total habitat area in the herb-rich forest network was 79 ha (36% of the area in WKHs), in the spruce mire network 283 ha (10% of the area in WKHs) and in the heath-forest network 2634 ha (6% of the area in WKHs) representing more than 30-fold difference in habitat area. The networks were located in Central Finland (61°26′–63°37′N, 24°6′–26°46′E); the herb-rich forest and spruce mire networks were in the northern parts of the area, and the heath-forest network was in the south. The networks are described in more detail in Laita et al. (2010).

Overall network connectivity measures were calculated with a threshold distance ranging from 200 m to 25 km. Patch importance measures were calculated at the thresholds distances of 500 m, 1 km, 2.5 km, 5 km, 7.5 km and 10 km. Link weights were determined based on Euclidean edge-to-edge distances between patches. For overall network connectivity analyses, we formed two separate networks for each habitat type: one composed of reserve patches only and another network with WKHs added. We plotted the connectivity of both networks to the same graph to see how the measure reacts to the addition of WKHs over the range of threshold distances. The network measures used for overall network analyses were: correlation length; expected cluster size (ECS); landscape coincidence probability (LCP); area-weighted flux (AWF); integral index of connectivity (IIC) and probability of connectivity (PC). For probabilistic measures, AWF and PC, we defined a dispersal probability of 0.05 to correspond to the threshold distance (i.e. the cut-off dispersal distance, if exceeded a patch pair is not connected by a link) used in analyses based on the binary connection model.

For patch prioritisations, we determined how consistently the different connectivity measures value individual patches. Patch prioritisations were calculated with a node removal analysis; each patch was systematically removed from the network, and the reconstructed network was compared with the original network which included the patch (Keitt et al. 1997). The connectivity loss caused by the removal of a patch measures the contribution of the patch to the network connectivity. We compared patch prioritisations for four measures that account for patch area, two of them binary (IIC and LCP) and two probabilistic (AWF and PC). We analysed the proportion of patch importance that was explained by patch area. The proportion was given by the coefficient of determination (R^2) of the regression of the log-transformed patch prioritisation values against the log-transformed patch area. To see how consistently prioritisations derived from different measures value patches, we calculated Pearson's correlations and partial correlations (controlling for patch area) for each measure pair as a function of threshold distance. Correlations were calculated for log-transformed variables. Partial correlations show how consistently different measures value the locations of patches (with the assumption that the part of the prioritisation not explained by patch area represents its locational value in a network). We also calculated full and partial correlations for prioritisations including only the 20 top-ranking patches based on the IIC values averaged over all threshold distances. IIC does not naturally represent any standard, but being rather widely applied it offers an interesting reference for the performance of other measures. By concentrating on the "top-20" patches, we determined whether measures value more consistently the top patches rather than all patches in their prioritisations as the prioritisations are usually used for recognising the most valuable patches.

Graphs were analysed with Conefor Sensinode v.2.2 (Saura and Torné 2009) (for AWF, IIC, LCP and PC) and Spatially Explicit Landscape Event Simulator v.3.3 SELES (Fall and Fall 2001) (for correlation length and ECS).

Results

As expected on the basis of the review above, connectivity evaluations of the connectivity measures differed from each other (Fig. 1). Correlation length, expected cluster size and LCP levelled-off when patches occured as one component. This happened, for example, in the spruce mire network with WKHs when species' dispersal ability exceeded 3 km. After the levelling-off, these network coherence measures did not show further changes with improving dispersal ability. IIC, AWF and PC, however, showed a rise in connectivity with increasing threshold distance even after the network is composed of one component. It remains that IIC levelled-off after all patches are in direct connection with each other. This happened when the threshold distance corresponded to the maximum distance between the pairs of patches. Probabilistic measures (AWF and PC) react in a similarly, despite the underlying differences in their connection models. Both measures showed a rise in connectivity with increasing threshold distance until the probability of dispersal between all pairs of patches reached 1.

Expected cluster size and correlation length did not react in line with the connectivity concept when adding WKHs to the network (Fig. 1). At small threshold distances, they indicated lower connectivity for networks with WKHs than for reserves-only networks. At small threshold distances, the WKH patches increased the number of components in the landscape and, being small-sized, decreased the average component size indicated by expected cluster size (habitat area of component) and correlation length (component extent). LCP, IIC, AFW and PC all recognised that WKHs contributed to increased connectivity, yet differently. For example, probabilistic measures showed a considerably smaller contribution of WKHs to connectivity than binary measures. How WKHs affected connectivity with increasing threshold distance also differed among measures. Binary measures showed a rather rapid rise in connectivity at the threshold distances of ca. 200 m to 5 km. For IIC, this rise with threshold distance was smoother than for other binary measures, which showed a stepwise pattern. Probabilistic measures did not show any range of threshold distances as being critical for connectivity, but expressed a steady rise in connectivity with threshold distance.

Connectivity measures showed different patch prioritisation performances in terms of how much emphasis they put on the effect of patch configuration versus patch size at different threshold distances (Fig. 2). For AWF, the importance of patch size to patch prioritisations rose steadily with increasing threshold distance. The PC measure emphasised, more than AWF, the value of patch size at small threshold distances in patch prioritisations. With IIC and LCP, the relative effect of patch size increased pronouncedly with the threshold distance until the patch importance values were totally determined by patch size. In the herb-rich forest and the spruce mire networks, however, the effect of patch size on patch prioritisations for the two binary measures dropped at intermediate distances (at ca. 1–2.5 km), suggesting the importance of patch configuration at this scale.

Network density had an influence on the relative importance of patch size over patch configuration. In the lowest density network (herb-rich forest), patch importance was determined to a greater extent by patch size at small threshold distances, compared to the other two networks of larger density. In the herb-rich forest network, patch size explained over 60% of patch importance values across all threshold distances for prioritisations based on IIC, LCP and PC. In the other two networks, patch size accounted less for patch priority, ca. 30–60% at small threshold distances. In the herb-rich forest network, the three measures weighted consistently the relative role of patch size on prioritisations across threshold distances. In the spruce mire and the heath-forest networks, the binary, IIC and LCP, and probabilistic PC measures diverged from each other in performance; binary measures put clearly more emphasis on the role of patch size at threshold distances greater than 2.5 km.

The patch prioritisations based on different measures correlated highly in the networks (Fig. 3). This is because all of the prioritisations were to a high degree driven by patch sizes (Fig. 2). The correlations thus mainly reflected the characteristics of

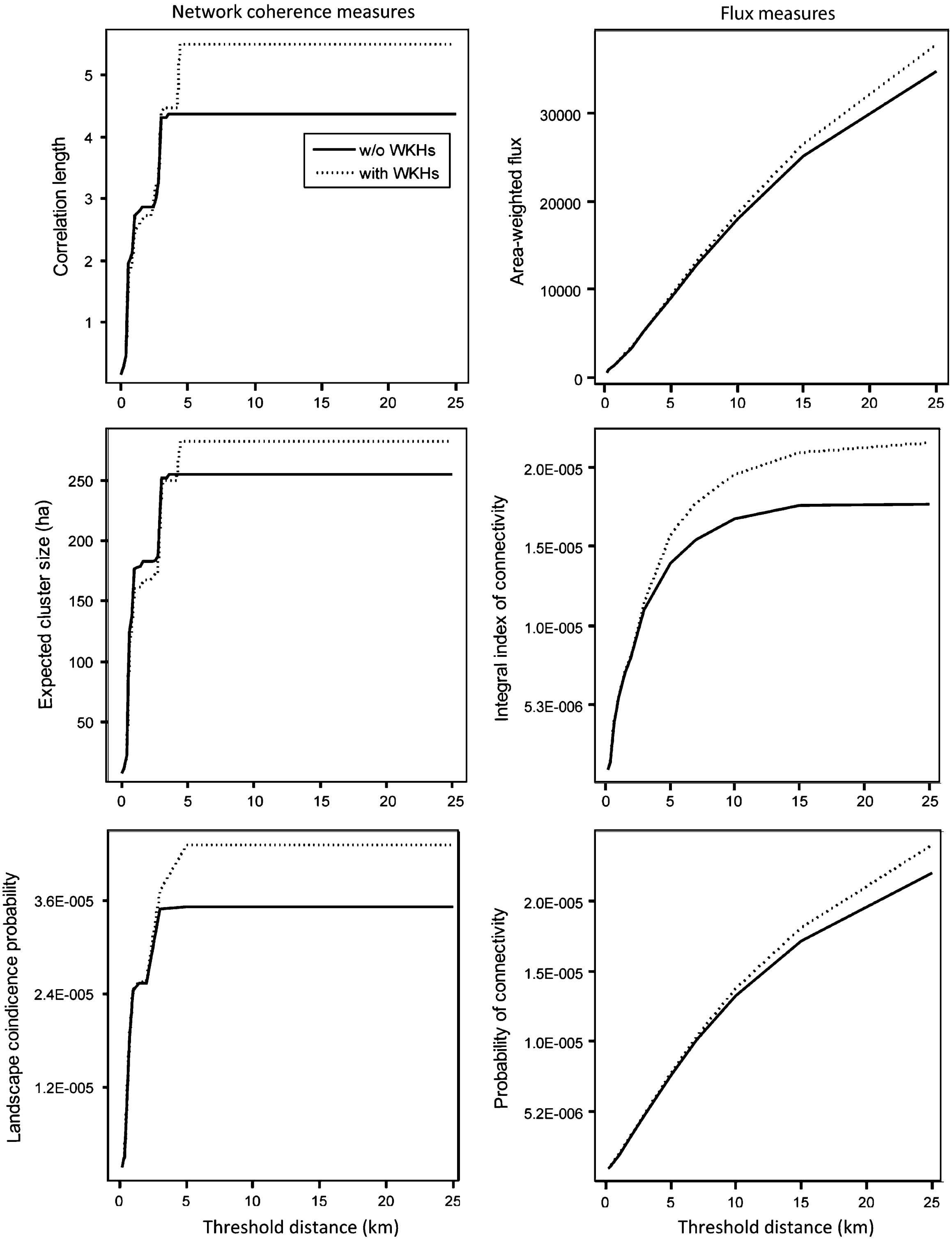


Fig. 1 Comparisons of measure performances as a function of threshold distance for the reserve network of spruce mires with and without woodland key habitats (WKHs)

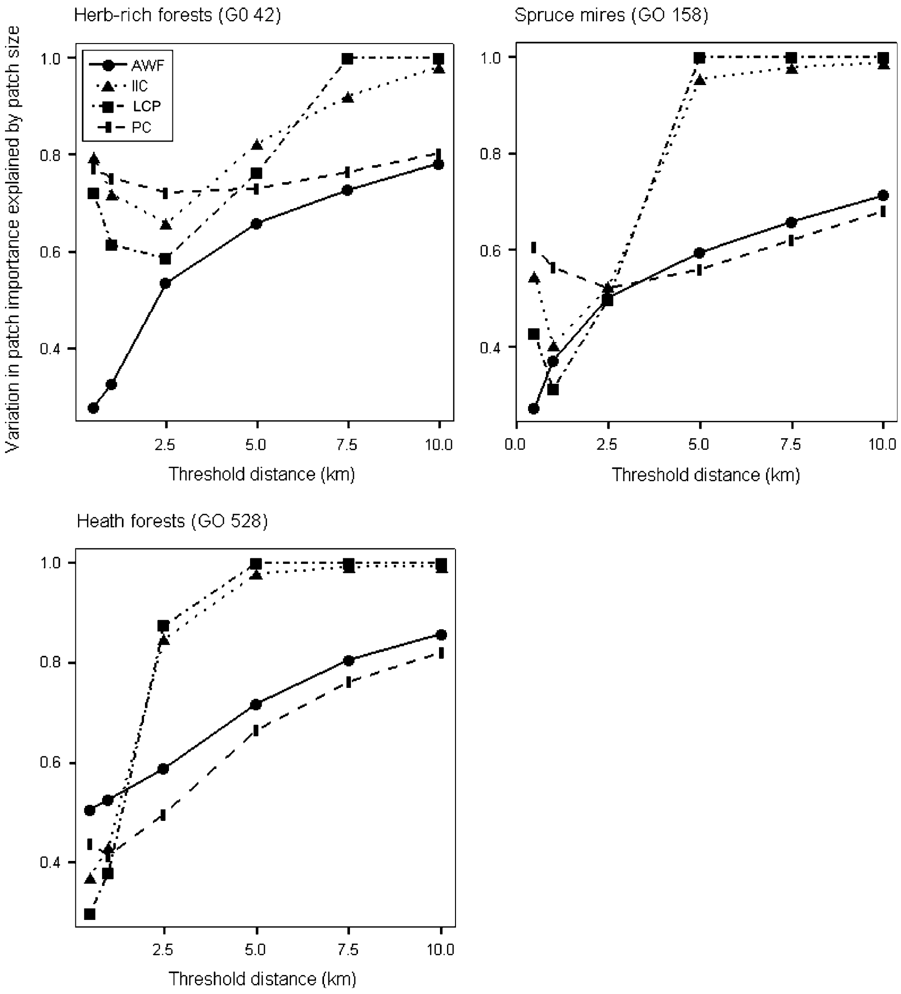


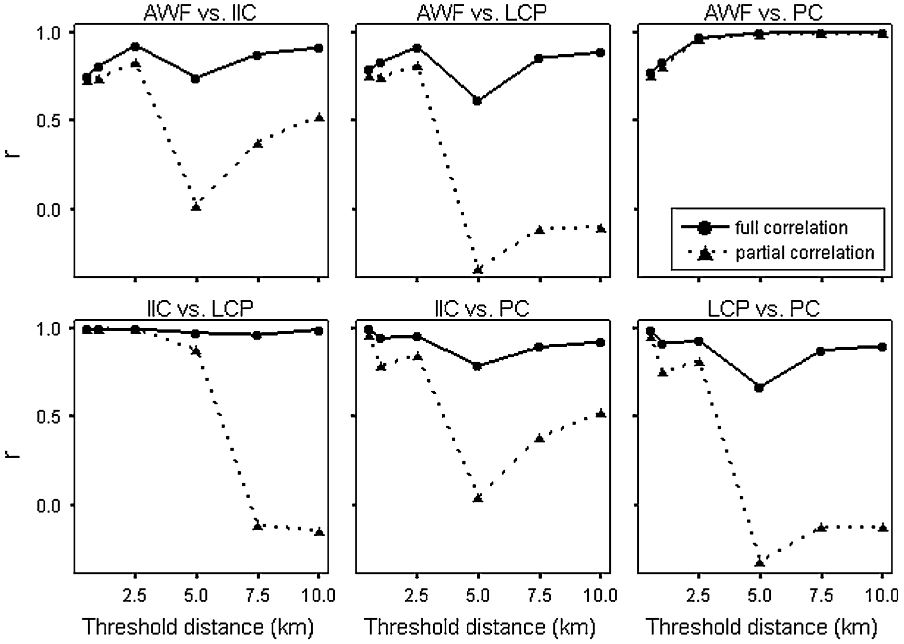
Fig. 2 Comparisons of four connectivity measures (AWF, IIC, LCP, and PC) for the effect of patch size on the patch prioritisation values at different threshold distances for three habitat networks that vary in terms of their graph order (GO). The effect of patch size is calculated by regressing log-transformed patch importance values against log-transformed patch areas and reported as a coefficient of determination (R^2)

measures in terms of how much they value patch size in their prioritisations. When the effect of patch size on the correlation was controlled for, the measures showed differences in their evaluations of the influence of patch location. The two probabilistic measures, AWF and PC, evaluate consistently the configuration component of prioritisations. LCP-valued locations of patches in a different manner compared to other measures at great threshold distances (>5 km). There even existed negative correlations for the prioritisations (AWF vs. LCP, LCP vs. PC and IIC vs. LCP) indicating that measures can value locations of patches quite inconsistently. IIC-valued patch locations more in accordance with probabilistic measures than LCP, but showed deviations from the probabilistic measures at large threshold distances.

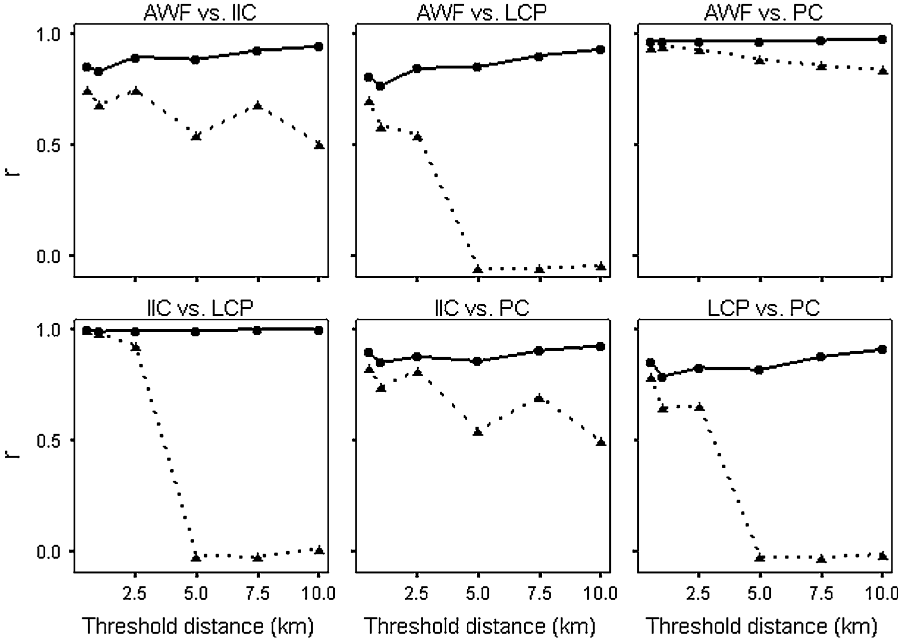
In the sparse network of herb-rich forests, the top-patches were even more inconsistently valued in prioritisations than all patches as a whole (Fig. 4). In this network, binary measures valued top patches more for their location than patches as a whole (results not shown), which seemed to increase differences in patch prioritisations derived from different measures. This is especially reflected in the increasing disparity between probabilistic and binary measures for the top patches. The difference was more pronounced at the intermediate threshold distances. In contrast, in the dense network of heath forests, different measures scored top patches with approximately the same consistency as all patches as a whole (Fig. 4). In that network, the binary measure IIC valued top-patch locations in accordance with probabilistic measures.

Fig. 3 Pairwise comparisons of patch prioritizations based on different measures (AWF, IIC, LCP, and PC) as a function of threshold distance for the networks of herb-rich and heath forests. Comparisons are based on Pearson's correlations coefficients calculated for the log-transformed patch importance values. Partial correlations show the correlations for the importance values after the effect of patch size is controlled for

(a) Herb-rich forests



(b) Heath forests

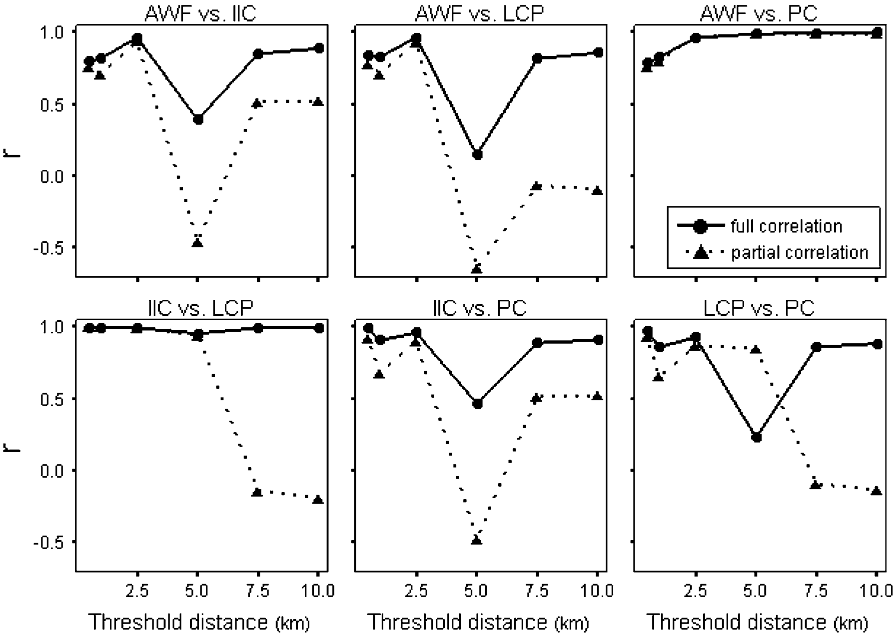


Discussion

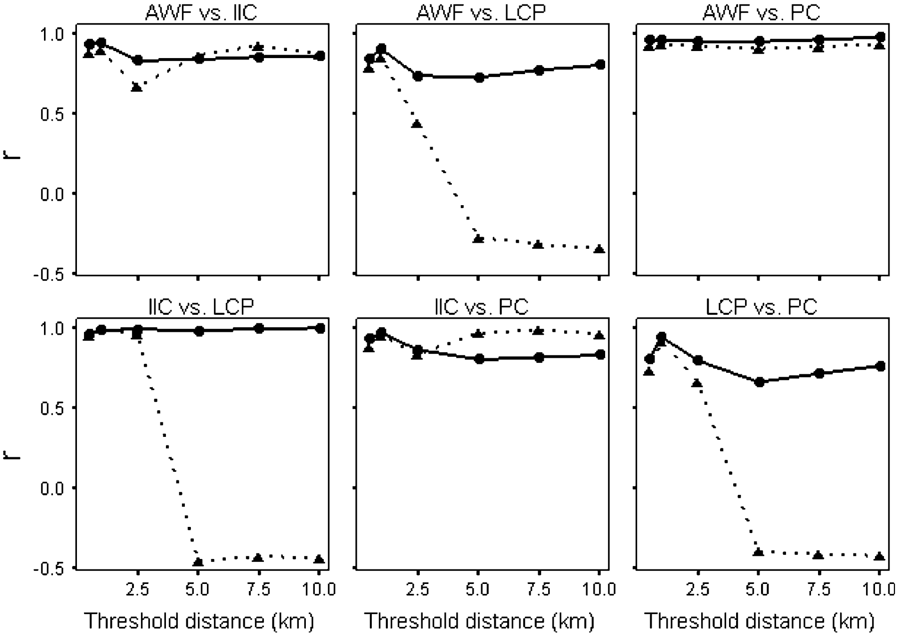
According to our conceptual and empirical comparisons, many connectivity measures do not react to changes in the amount and connection status of habitat in line with the connection concept defined. Measures that show ecologically problematic performance at the network level (graph diameter,

Fig. 4 Pairwise comparisons of patch prioritizations for 20 top patches based on different measures (AWF, IIC, LCP, and PC) as a function of threshold distance in the networks of herb-rich and heath forests

(a) Herb-rich forests



(b) Heath forests



correlation length, ECS) are not appropriate ‘stand-alone’ measures of landscape connectivity, but can nevertheless be used for descriptive purposes. Such descriptive information accompanied with a graphical presentation may give valuable insights into the characteristics of a network. On the other hand, connectivity measures responding in agreement with the connectivity concept at the network level differ greatly in terms of their connectivity model. Our empirical results give important insights of the implications of the connectivity model on the performance of measures at the landscape and patch level—not so evident when evaluated on conceptual grounds.

Because a small increase in dispersal ability (as well as a change in spatial pattern) may produce a sharp rise in connectivity, it has been suggested that connectivity possesses a transition range (e.g. With and Crist 1995; Keitt et al. 1997; and for the more general context of percolation theory, see Gardner et al. 1987; Stauffer 1987; With and King 1997). Transition range divides the species into two groups: those that perceive the landscape as disconnected and those that perceive it as connected. Our connectivity profiles (Fig. 1) indicate that the existence of the transition range is only evident for measures using a binary connection model. In contrast, measures that weigh interpatch distance by dispersal probability did not show a sudden shift in connectivity, but rather a gradual monotonic increase with increasing dispersal distance (as also reported by Saura and Rubio 2010). Empirical data would be needed to evaluate whether this transition range expressed by binary measures is also reflected in the realised ecological processes. If so, the binary measures may be used alongside with probabilistic measures as they are able to provide this additional insight to the interaction between landscape structure and species dispersal.

Our results show that connectivity evaluations of coherence measures are uninformative after the landscape consists of a single component (Fig. 1). Measures that view components as binary structures and do not account for their internal structure may be ecologically unrealistic. This especially holds for networks that show a high level of compartmentalisation. For example, if only one link (its length near the dispersal ability of organisms) is bridging two compartments, the dispersal of organisms may be restricted to within compartment rather than within component. The potential value of this one single link may be related to the process under focus and its associated time frame, because the probability of rare events increases as the time frame is extended. For processes that operate over long time periods (e.g. gene flow), weak connections among components may also be valuable, whereas for a process of a shorter time frame (e.g. population persistence in a fragmented landscape), the value of one weak connection is possibly only negligible. If it is necessary to correct this dependence on one link, an easy remedy would be to set a minimum number of links (greater than one) that should bridge a patch in a component, so that the component-based connectivity would lie on a stronger basis. Connectivity measures that are founded on the component approach (summarised in Table 1) are all confined to this possibly restrictive connectivity concept. Besides being widely used as a conceptual basis for connectivity measures, there has also been a growing interest in using components as landscape ecological units of analyses (e.g. Castellon and Sieving 2007; Minor et al. 2009).

Patch prioritisations based on different measures can produce inconsistent outcomes, which was evident also for the most valuable patches usually identified for conservation purposes (Figs. 3, 4). Our results show that the disparity between patch prioritisations derived from different measures may stem from two mechanisms: the measures place a different emphasis on patch size compared to patch location or they differ in how they value the locations of patches. When the results from graph analyses are interpreted, it is important to remember that the mere choice of a measure affects the relative importance of a patch area versus its topological properties. If the interpretation is biased in topological aspects, small patches may score too high relative to their ecological value. In our analysis, we interpreted the prioritisation value of a patch to be a combined outcome of its size and location in a network. The locational value of a patch can be further divided into two components; a patch can either be a flux donator/receiver in its own pairwise connections and/or a connecting element (i.e. a stepping stone) in the paths among other patches (Saura and Rubio 2010). This elaborated division may give additional insights into the behaviours of different measures in evaluating patches relative to their locations.

Networks that vary in patch density (depicted by the number of patches in a network per landscape area) provide testing grounds for the performance of connectivity measures. When there are more patches spread out in a landscape, their mean interpatch distance decreases, and the nature of their connections may also change (for example, the relative influence of indirect patch connections may increase in sparser networks). Dense networks may also exhibit a greater redundancy in interpatch connections than sparse networks, so that connections between pairs of patches are not necessarily only dependent on a single ‘route’. This redundancy is an important network property that should be understood when the results from node removal analyses are interpreted (as shown by Bodin and Saura 2010). Of course, a network with a small number of patches may have them all very locally gathered, and thus, from the point of view of configuration, show more characteristics of a dense network than a sparse one. This was not, however, the case in our networks, because the average nearest neighbour (NN) distance decreased with network density (herb-rich forests 924.97 m; spruce mires 441.51 m; heath forests 306.04 m). The average NN index (the ratio of the observed NN distance divided by the expected one based on random locations, calculated with ArcMap v. 9.2), which expresses the degree of patch clustering, was also at the same level in all three networks (herb-rich forests 0.64; spruce mire 0.59; heath forests 0.62). In our patch prioritisation results, the sparse network was more susceptible to inconsistent patch prioritisations than the dense one. We see that the conceptual differences between measures may become more evident in the patch prioritisations of sparse networks, but more specific mechanisms and generalisations would require prioritisation results to be analysed from a larger pool of networks. But regardless of network density, we recommend the comparison of prioritisation results from several measures to get a broader picture of the values and roles of patches in a network.

Keitt et al. (1997) suggested that patch configuration plays the most prominent role in landscape connectivity for species with intermediate dispersal ability, whereas for poor or good dispersers the patch value is more determinant. This is because poor dispersers are mostly confined to local patches irrespective of patch configuration, while good dispersers are not dispersal limited, and thus the patch size dominates the patch location in importance. Binary measures (IIC and LCP) and PC showed this pattern in their patch prioritisations, although PC valued configuration in a smoother manner than the binary measures (Fig. 2). However, AWF was not able to recognise the value of patch configuration at intermediate threshold distances (Fig. 2), suggesting that AWF cannot reliably value patch configuration from the perspective of dispersing individuals.

The relative influence of patch size (over configuration) on patch prioritisations was, at small threshold distances, greater in the sparsest network than in the two denser networks (Fig. 2). This indicates that individuals in sparse networks are confined to individual patches/isolated parts of a network. In such cases, the other patches are out of reach to individuals irrespective of their configuration, and habitat area as a currency of (intra- and interpatch) connectivity gets relative high values. Once again AWF deviated from the other measure of connectivity and did not detect this enhanced value of patch size in the sparsest network.

Our analysis showed that all connectivity measures react in their own characteristic ways (dictated by their connectivity model) to the removal of a patch. The mechanisms leading to evident differences in patch prioritisations among measures are intractable based on correlations alone, but would require additional investigation. The node removal analysis presents different kinds of challenges to and requirements on the connectivity measures than the measurement of landscape-level connectivity, because the evaluation of changes induced by patch removal brings about elements that are not exposed when working with intact networks. For the interpretation of the results from node removal analysis, it is important to understand how the given measure reacts to a connectivity change induced by patch removal. For example, the node removal analysis based on component-based measures cannot value a patch location unless the patch bridges otherwise isolated components. In the “non-split” cases, the prioritisation of a patch is only based on its contribution to habitat area. Measures based on the shortest paths (e.g. IIC and PC), on the other hand, may react unpredictably to patch loss because the measures also rate the possible new shortest paths formed in a network (Bodin and Saura 2010). Besides the patch prioritisations based on node removal analysis, there exist also alternative methods to evaluate the connectivity contributions of individual patches (e.g. Estrada and Bodin 2008). These alternatives, rooted in the concept of network centrality, operate on intact networks and have a very different philosophical background from the approach based on node removal analyses. As shown by Bodin and Saura (2010), these approaches may be used to complement each other in order to have a more comprehensive picture of patch value in a network.

Probabilistic connectivity measures track the enhancement in connectivity brought about by increasing dispersal ability of a species much further than do binary measures, which has implications for both landscape- and patch-level connectivity evaluations. Whether the realised connectivity tracks this enhancement captured by probabilistic measures may be related to the process under focus. As speculated by Bodin and Saura (2010), the binary connection model offered by IIC may be suitable for a process like gene exchange, which may be more reactive to a few realised transmission events (and so, to a mere existence of links rather than their strengths) than an actual transmission rate. The probabilistic connectivity models, on the other hand, may give a better basis for tracking quantities (e.g. dispersal flux) moving in a network.

Borgatti (2006) showed that the selection of optimal nodes may strongly depend on the goal. A different set of patches is selected when the purpose is to identify the patches whose removal would cause the greatest network fragmentation compared with a set that most efficiently promotes connections to other patches. This ultimate target of patch prioritisations is not usually explicitly stated or even considered in landscape ecological applications, although it should be inherent to the whole process of patch prioritisation. Graph-theoretic analyses can also be sensitive to the underlying assumptions regarding the dispersal behaviour of individuals. Connectivity at a landscape or patch level cannot be evaluated without a reference as to how individuals disperse in a network (e.g. Borgatti 2005; Urban et al. 2009). The most sophisticated graph-theoretic connectivity measures (IIC and PC) are based on the concept of the shortest paths. Insights provided by empirical connectivity data are needed to better understand which kinds of species and processes (and over which time frames) would possibly experience connectivity in terms of direct connections instead of paths. Moreover, dispersing individuals may not be restricted to the shortest paths, but alternative paths may also be important.

We would like to note that in many cases the actual *level* (quantitative variable) of connectivity is more important than judging whether a landscape is in the connected or disconnected *stage* (binary variable) for any given species. It is important to keep in mind that the total landscape area remains the same irrespective of the dispersal ability, and the level of connectivity is conditional on the total habitat area in a landscape. It is the network topology that determines how the connectivity changes with increasing dispersal ability. Conservation should offer both elements: habitat area as well as its appropriate configuration to allow efficient species dispersal. Even the sparsest of networks show levelling-off in connectivity with increasing dispersal ability, but there is no much use of this topological connectedness if the habitat area in a system is minimal. There have been recent attempts to minimise the total area of protected area network while maintaining the connectivity (e.g. Rothley and Rae 2005). We are afraid that connectivity is not yet understood thoroughly enough for this to be a safe approach. If no certainty exists that the connectivity measures capture the ecological process in focus, ecologically effective conservation should preferably address the question: How can we maximise connectivity for a given amount of habitat?

Scope for the future

The network robustness is an issue often neglected in the evaluation and design of habitat networks (see e.g. Matisziw and Murray 2008; McRae et al. 2008). Robust networks must contain nodes that are apparently redundant at the moment, in order to be resilient to future habitat loss or local extinctions. Robustness stems from the system redundancy, i.e. multiple pathways between pairs of patches. Matisziw and Murray (2008) deal with an important part of connectivity conservation by stating that 'although ensuring a desired level of connectivity in a habitat network might be relatively easy to accomplish at the outset, long- term management of connectivity is much more complex'. Indeed, patch loss can impact connectivity in different ways and patch configurations differ in their robustness to the effects of patch loss. Most network measures do not hold information about network robustness, but only evaluate a network in one point of time. This is definitely an issue that needs further attention.

Graph-theoretic connectivity approaches most often view the connection between two patches as occurring via one link (the shortest/least-cost one), and additionally via one path (the shortest one) if indirect connections are also acknowledged. This is a problem that needs to be addressed, because in reality multiple connections certainly increase connectivity. This is supported by empirical evidence from a connectivity evaluation carried out in a circuit-theoretic framework showing that multiple connections between patches enhance gene flow (McRae and Beier 2007). Multiple connections can occur at two levels: between two patches that are in direct contact and at the larger network level, so that a patch pair is linked via more than one path. The former form of multiple connections has already received attention from several perspectives (e.g. Pinto and Keitt 2009; Urban et al. 2009; Vogt et al. 2009; Lookingbill et al. 2010), and if it can be compressed into one value depicting the isolation between two patches, it can be easily applied to any graph-theoretic connectivity measure. For example, circuit-theoretic resistance distance (a measure of isolation between pairs of patches) decreases with an increasing number of alternative connections between patches (McRae et al. 2008). The latter form of multiple connections, i.e. multiple paths among patches, has not yet been incorporated into graph-theoretic connectivity measures. Graph theory itself does not set limits, but provides potential for acknowledgement of more versatile connections among patches than have been acknowledged so far.

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