

Connectivity change in habitat networks

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Abstract Habitat management is essential for safeguarding important flora and fauna. Further, habitat connectivity is a crucial component for maintaining biodiversity given that it is known to have implications for species persistence. However, damage to habitat due to natural and human induced hazards can alter spatial relationships between habitats, potentially impacting biodiversity. Therefore, the susceptibility of spatial relationships to patch loss and associated connectivity degradation is obviously an important factor in maintaining existing or planned habitat networks. Identifying patches vital to connectivity is critical both for effectively prioritizing protection (e.g., enhancing habitat connectivity) and establishing disaster mitigation measures (e.g., stemming the spread of habitat loss). This paper presents a methodology for characterizing connectivity associated with habitat networks. Methods for evaluating habitat

network connectivity change are formalized. Examples are presented to facilitate analysis of connectivity in the management of biodiversity.

Keywords Spatial structure · Habitat change · Network analysis · Fragmentation · Nature reserves · Landscape ecology · Conservation ecology

Introduction

Habitat protection and management is vital for mitigating threats to biodiversity. A well-known facet of biodiversity preservation is that, among other things, species are dependent on spatial aspects of their habitat (Cabeza and Moilanen 2001; Moilanen and Nieminen 2002; Lindenmayer et al. 2006). An especially important issue in this regard is connectivity between habitat patches. Connectivity refers to the presence of a path between two locations along which movement can occur, and is an essential relationship among habitat patches, permitting ecological flows, re-colonization, and ecological memory preservation (Merriam 1991; Hess 1996; Hoctor et al. 2000; Fagan 2002; Moilanen and Hanski 2001; Bengtsson et al. 2003; FitzGibbon et al. 2007). Contrasting these beneficial aspects, connectivity can also be associated with undesirable features, such as facilitating the spread of invasive species and disease as well as

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eliminating barriers to other environmental threats like fire (Turner et al. 1989). Given its importance, accounting for spatial connectivity has become a major design concern in habitat management (Williams 1998; Onal and Briers 2005; Matisziw and Murray 2006; Noss and Daly 2006; Fuller and Sarkar 2006).

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. As an example, a habitat assemblage considered amenable to a particular species at one point in time, may not continue to be in the future (Cabeza and Moilanen 2001; Chave et al. 2002; Drechsler 2005; O'Hanley et al. 2007). Moving forward in time, habitat changes are unavoidable and some of these will certainly be detrimental to species persistence. For instance, natural and man-made threats, such as fire, floods, climate change, pollution, urban encroachment, logging, farming and invasive species, can alter habitat, connectivity, and associated biodiversity (Brooks et al. 1999; Midgley et al. 2002; Pino et al. 2005; Scott 2006). Although these sources of environmental decline are ubiquitous, protected areas are particularly at risk given that these are designed to account for existing patterns of biodiversity (Liu et al. 2001; Chave et al. 2002; Drechsler 2005; Hannah et al. 2005; Williams et al. 2005; O'Hanley et al. 2007). Loss or change to a managed component (e.g., patch or corridor) of a habitat network can alter connectivity, thereby rendering the network less effective, or ineffective, for species conservation.

Given uncertainties in the nature of habitat dynamics, developing strategic plans for offsetting or curtailing undesirable changes to connectivity is essential for managing biodiversity (Kurz et al. 2000; Urban and Keitt 2001; Cumming 2002; Jordan et al. 2003; Fuller and Sarkar 2006). In order to facilitate the management of habitat connectivity, many methodologies for evaluating the relative importance of habitat patches to connectivity have been proposed. However, with the exception of a few studies (see Urban and Keitt 2001; Bodin et al. 2006, for example), the overall significance of habitat and associated connectivity under different habitat loss regimes has largely been ignored. From a planning standpoint, effective characterization of the range of possible impacts to connectivity is essential for

understanding the significance of changes to connectivity. Below we review indirect and direct metrics for measuring connectivity and impacts associated with connectivity loss and propose an alternate approach. As part of our proposed approach, notions of patch connectivity (or interaction) and connectivity loss are discussed and formalized. The broader scope of connectivity change within a habitat configuration is then considered, highlighting the measurement of habitat connectivity change under various states of habitat loss. Given the developed approach, the positioning of scenarios of habitat change in relation to their impact on connectivity is then assessed for different habitat configurations, illustrating the influence spatial structure can have on connectivity in habitat networks if there is patch loss. Finally, discussion and conclusions are provided.

Indirect and direct connectivity metrics

An intuitive way of viewing the spatial relationship among habitat patches is through their representation as a network of connected patches. In network representations of habitats, nodes reference individual patches while arcs reference cases where direct interaction (no intervening patches) between patch pairs is feasible. As such, various landscape connectivity metrics have been proposed based upon constructs drawn from graph theory and network analysis (see Keitt et al. 1997; Urban and Keitt 2001; Calabrese and Fagan 2004). An important distinction among network connectivity metrics is whether connectivity is measured directly or indirectly. On one hand, *indirect* metrics can provide some general insight on habitat network characteristics related to size and form (e.g., compact versus dispersed), and level of node (patch) adjacency. Commonly used indirect metrics include the cyclomatic number, correlation length, nodal degree, network diameter, as well as alpha, beta and gamma indices (see Haggett and Chorley 1969; Cantwell and Forman 1993; Keitt et al. 1997; Ricotta et al. 2000; Urban and Keitt 2001; Jordan et al. 2003; Rothley and Rae 2005). However, connectivity, or rather the availability of a path of movement between all pairs of network nodes (patches), is not explicitly measured by indirect metrics. For instance, one indirect measure, network diameter, refers to the maximum

shortest path (as measured in number of arcs) in a network. That is, diameter only provides knowledge of connectivity between a single pair of nodes in the network and does not account for presence/absence of connectivity between all other pairs of nodes. Thus, while it can be used to indirectly approximate connectivity in some cases, its use in characterizing network connectivity in general is questionable (see Grubestic et al. 2008). Given that indirect metrics do not account for connectivity between all pairs of nodes in a network, their use in the analysis of network connectivity change is rather limited, as concluded in Jordan et al. (2003) and Pascual-Hortal and Saura (2006) among others.

Direct measures of connectivity, on the other hand, explicitly account for the availability of potential paths among nodes (patches) in a network. A simple way to evaluate inter-nodal connectivity is by assessing the presence of a shortest, or least cost, path between two nodes (see Daskin 1995, for example). If a shortest path of non-infinite cost exists, then the nodes are connected and the length of the path provides an indication of inter-nodal accessibility (ease of movement). The sum of all shortest paths in a network is often interpreted as a measure of dispersion, and the sum of all shortest paths incident to an individual node as a measure of nodal accessibility (see Shimbelt 1953). A common adaptation of such an approach is summing the inverse shortest path distance between all network nodes (Ricotta et al. 2000; Jordan et al. 2003; Pascual-Hortal and Saura 2006).¹ Other shortest path-based metrics have been proposed to quantify the importance of an individual network node or arc to system-wide movements (Freeman 1977; Bodin and Norberg 2007). Unlike indirect measures of connectivity, direct measures have been shown to be more effective in evaluating change in habitat connectivity given patch loss (Jordan et al. 2003; Pascual-Hortal and Saura 2006).

Despite their ability to account for movement potential in a network, shortest path-based measures do have limitations as is true with other landscape indices (see Li and Wu 2004). First, since inter-patch distance is involved, changes to these metrics do not

always represent changes in connectivity, but rather changes to the accessibility or efficiency of movement between connected components. That is, lower total distance between connected patches is not necessarily indicative of higher inter-patch connectivity given that lower total inter-patch distance can also be a result of fewer connected patches. This is particularly evident in non-linear measures, such as the inverse shortest path, where a spatial bias toward shorter path lengths is introduced. Further, while it may be reasonable in many contexts that increased inter-patch distance decreases network accessibility, there is no certainty that a species will perceive accessibility as a function of shortest paths. Third, measures based on shortest paths are not standardized across networks with respect to connectivity loss/gain, preventing cross-network comparison. Finally, the non-linear expression of the inverse shortest path measure can render habitat management/design optimization models substantially more challenging, if not impossible to solve. Although distance is certainly an important consideration in network assessment, what is needed is a means for directly evaluating connectivity, permitting a more concise interpretation of connectivity in habitat networks.

An alternative direct connectivity metric

In order to examine habitat connectivity and its dynamics, a generalized measure of connectivity accounting for the presence/absence of an unobstructed path of movement between each pair of habitat patches is desirable. To illustrate this strict definition of connectivity, consider the eight potential habitat configurations in Fig. 1. The spatial relationships between the habitat patches in each configuration can be conceptualized by representing each habitat assemblage as a network, where each patch is a network node and spatial relationships (e.g., adjacency) among nodes are represented as arcs. Figure 2 depicts the habitat configurations from Fig. 1a and f as networks. For both configurations in Fig. 2, note that a path of movement (connectivity) exist between all pairs of habitat patches or nodes. For example patches 9 and 10 are connected as reflected in Fig. 2a by the existence of a single arc (a single step path) linking the nodes; and patches 6 and 10 are connected given the availability of a multi-step

¹ This non-linear treatment of distance is often attributed to Harary (1969), but has long been used in studies examining spatial interaction (see Zipf 1946).

Fig. 1 Alternative habitat network configurations

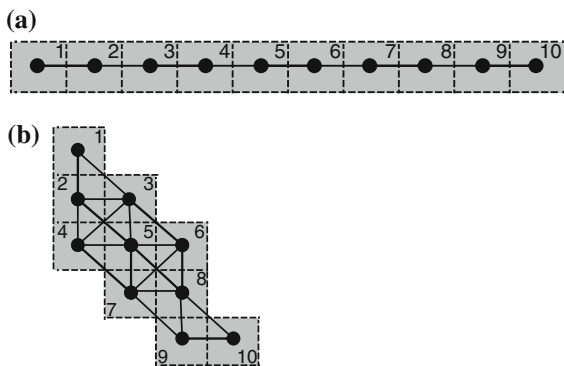
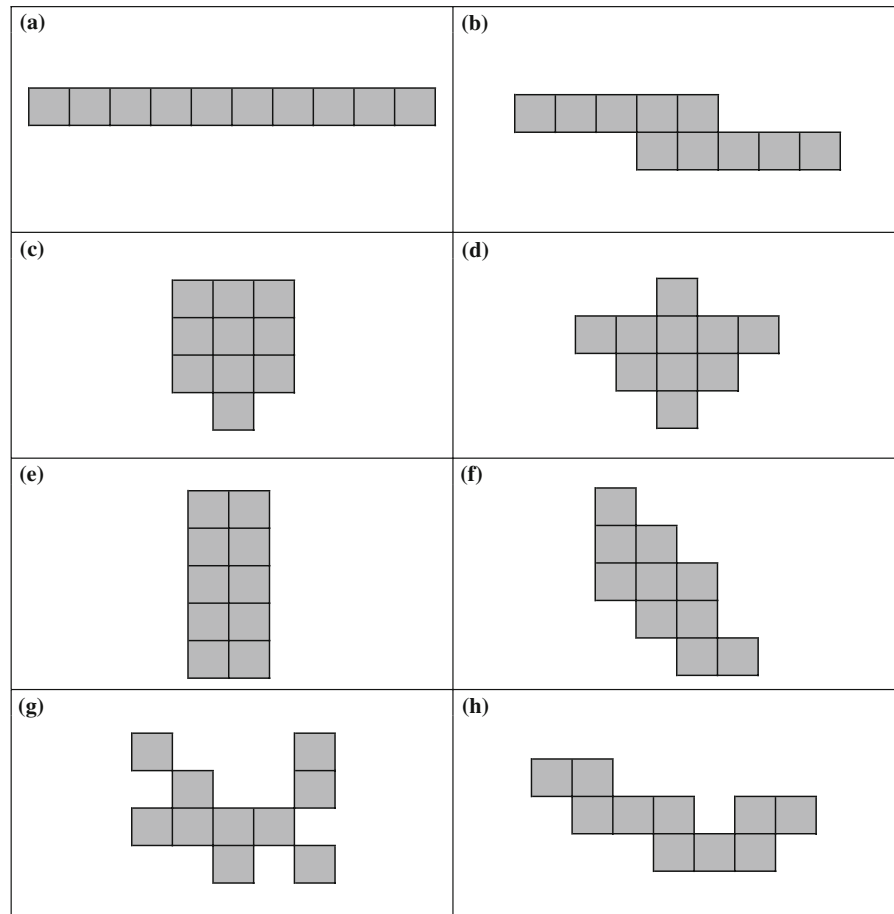


Fig. 2 Network representation of habitat configurations (a) and (f) in Fig. 1

path (i.e., sequence 6-7-8-9-10). In configurations like Fig. 2b, two patches might be both connected via multiple paths (e.g., patches 8 and 10).

In what follows, we propose a new approach for measuring habitat connectivity. Given a network

representation of a habitat assemblage, G with N nodes and E arcs, a direct measure of network connectivity is the sum of the total connectivity between nodes. To formalize this notion of connectivity, consider the following notation: i = index of patches (j defined similarly); $f(G,i,j)$ = indicator function for connectivity between patches i and j , given G

$$Z_{ij} = f(G,i,j) = \begin{cases} 1 & \text{if connectivity exists between patches } i \text{ and } j \\ 0 & \text{otherwise} \end{cases}$$

Like other direct metrics, the proposed measure of connectivity presumes the ability to assess the existence of a viable path of movement between each pair of patches in a network. Defining what constitutes a viable path between two patches i and j can depend on any function of a number of parameters, $f(G,i,j)$, given the characteristics of the species of

interest and their perception of connectivity. For instance, considerations might include practical limitations to species dispersal (e.g., distance), the ease of movement through intervening habitat (e.g., cost), capacities of corridors to effectively handle movements, or the qualities of patches.² Once plausible conditions for movement are established and connectivity between each pair of patches is assessed, total network connectivity, C , can then be measured as:

$$C = \sum_i^N \sum_j^N Z_{ij} \tag{1}$$

In cases where connectivity exists between every pair of patches, as is true for each configuration in Fig. 1, $C = (N^2)$. Therefore, for each arrangement of ten patches in Fig. 1 there is connectivity between all 100 patch pairs, so $C = 100$. This measure assumes intra-patch connectivity is counted as well. That is, if a patch exists, it is obviously connected to itself. If intra-patch connectivity is ignored, total connectivity would be $N(N - 1)$.

The eight habitat assemblages in Fig. 1 are equivalent in that initially, there is connectivity between all patches in each assemblage. However, patch loss can impact connectivity in different ways, depending on the network structure associated with the configuration. To examine the potential impact of patch loss on connectivity in the initial undisrupted network G , define G' as the network after patch loss, where $G' \subseteq G$. Thus, Z'_{ij} indicates connectivity in the modified network. Total connectivity for the degraded network is now $C' = \sum_i \sum_j Z'_{ij}$. We know that $C' \leq C$, so network connectivity with respect to patch loss can be defined as the ratio:

$$\Omega = C' / C \tag{2}$$

Given this, values of Ω will range from zero to one ($\Omega \in [0,1]$). Therefore, Ω is a measure of relative connectivity attributable to patch loss. It is important to note that Ω remains valid and measurable in the presence of subgraphs (e.g., network fragmentation).

² See Hanski and Ovaskainen (2003), Ovaskainen (2004), McRae (2006), and North and Ovaskainen (2007) for other factors potentially impacting the form of $f(G,i,j)$.

Measuring connectivity loss

The significance of directly measuring connectivity using Ω is the capability to examine impacts due to patch loss. Figure 3 illustrates various habitat patch loss scenarios for the configuration shown in Fig. 1f. In Fig. 3a node 8 is removed from the network. The loss of a node implies that any arcs connecting that

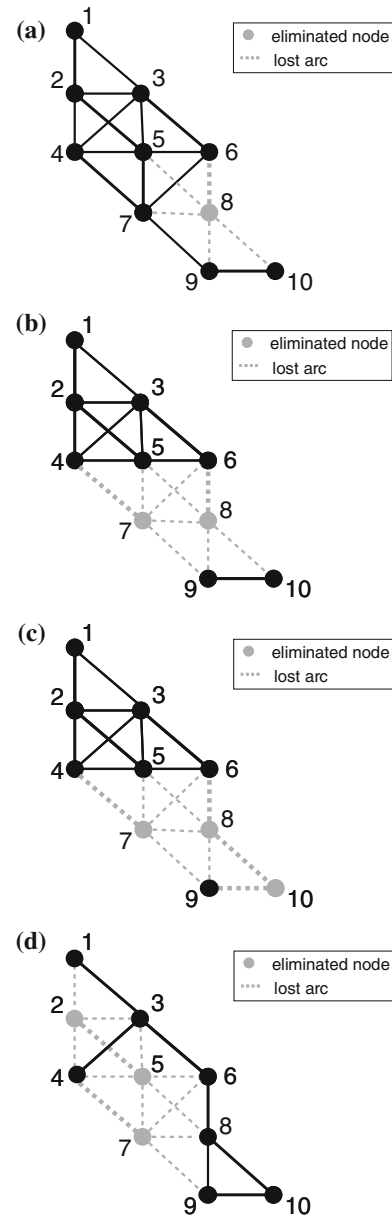


Fig. 3 Network change associated with patch loss for configuration (f) in Fig. 1

node to the remaining network are no longer available. In this case, the five arcs directly connected to node 8 are effectively eliminated. Given this situation, only connectivity between patch 8 and the other habitat patches is impacted since there are still available paths connecting each remaining pair of patches. Thus, $C' = 81$ for Fig. 3a, and $\Omega = 0.82$, indicating that 81 pairs of habitat patches are connected, so 19% of network connectivity has been lost. Figure 3b depicts the simultaneous loss of nodes 7 and 8 (patches 7 and 8), eliminating the nine incident arcs and splitting the network into two subgraphs. In this instance, the impact to habitat connectivity is more dramatic, with $C' = 40$ and $\Omega = 0.40$.

Although the network connectivity, C , of Fig. 2a, b are equivalent, their network topologies are quite different. For Fig. 2b, any *single* node can be lost without impacting connectivity (or the availability of a path) between remaining patch pairs. However, in Fig. 2a only one path exists between each patch pair and in many cases the impacts to connectivity can be more severe. Figure 4a illustrates the loss of node 5 associated with the configuration given in Fig. 2a. In this case, the network is split into two subgraphs and connectivity between 59 patch pairs is lost, so $\Omega = 0.41$. The loss of two patches, as detailed in Fig. 4b, further fragments the network into three subgraphs (e.g., isolated units or fragments), disrupting 74% of network connectivity ($\Omega = 0.26$). Through simple comparison of the configurations shown in Fig. 2a, b, it is easy to see that habitat connectivity is susceptible to patch loss, and is strongly influenced by spatial structure.

Since C directly measures connectivity and is not obscured by other parameters (e.g., distance), a lower

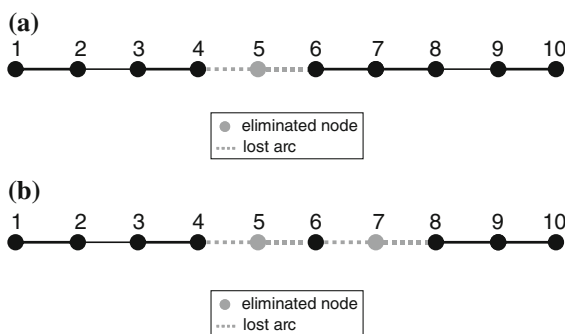


Fig. 4 Impact of patch loss on configuration (a) in Fig. 1

value of C is always indicative of lower connectivity. While this statement may sound rather obvious, the same is not true for other direct measures of connectivity, however, such as those based on shortest paths. As an example, Figs. 3c, d illustrate two different scenarios involving the loss of three nodes (patches). As can be readily observed in Fig. 3c, one patch becomes isolated from the other six, while in Fig. 3d all remaining habitat patches retain connectivity with one another. The scenario in Fig. 3c has $C' = 37$ ($\Omega = 0.37$) and the scenario in Fig. 3d has $C' = 49$ ($\Omega = 0.49$), so connectivity is not at all the same. Attributing each arc within the network with unit distance (distance = 1.0), an inverse shortest path-based measure, or the so called Harary index (see Jordan et al. 2003; Pascual-Hortal and Saura 2006) can be computed for comparison.³ For the scenario in Fig. 3c, the Harary index is 12.5 while for the scenario in Fig. 3d the index is 12.3333, implying that the network in Fig. 3c has greater connectivity between habitat patches. Obviously there is a problem then. To understand what is happening, it is evident that the scenario in Fig. 3c retains inter-patch connectivity between only 30 patch pairs, and the inter-patch distances are rather small. This is in contrast to the scenario in Fig. 3d where inter-patch connectivity is maintained between 42 patch pairs, but at the expense of longer path lengths. Clearly, in this case, the Harary index is problematic because it incorrectly interprets lower total inter-patch distance as higher connectivity despite the obvious fragmentation.

Measuring connectivity change

With the capability of measuring connectivity change comes the recognition that there are likely some scenarios of connectivity change that are more important (decrease/increase connectivity the most) than others, and vice versa. Figures 3 and 4 examine ad hoc scenarios involving the loss of one or a few patches from two habitat configurations. It should be apparent, however, that many other scenarios of

³ The Harary Index: $1/2 \sum_i \sum_{j \neq i} 1/d_{ij}$ where $d_{ij} =$ $\begin{cases} l_{\text{shortest path cost, if an } i, j \text{ path(s) is available}} \\ \infty, \text{ otherwise} \end{cases}$.

single or multiple patch loss are possible, and would no doubt impact network connectivity differentially as a result. Figure 5 summarizes the range of possible disruption outcomes associated with the configuration given in Fig. 2a. For example, if an end patch (node 1 or 10) is lost in Fig. 2a, 19 habitat pairs would be disconnected ($\Omega = 0.81$). Such a situation for this configuration represents the *least impact, best-case* scenario, or *upper-bound* on connectivity disruption for the loss of a single patch because Ω is the largest value for all potential disruption scenarios associated with Fig. 2a (see Fig. 5). The loss of node 5 in Fig. 2a results in $\Omega = 0.41$ (59% reduction in connectivity), which is the *most damaging, worst-case* scenario, or *lower-bound* on connectivity disruption involving the loss of a single patch for this configuration (see Fig. 5). Establishing upper and lower bounds for network connectivity is essential for evaluating and understanding possible connectivity impacts. Aside from the best-case and worst-case scenarios, other scenarios of intermediate connectivity impact exist, and in total, characterize the *range* or *variability* of possible disruptions (see Fig. 5).

The significance of patch loss on habitat connectivity under various states of habitat disruption can now be formalized by expanding our notation: k = index of patch loss scenarios; p = number of patches lost; Φ_p = set of scenarios involving p lost patches; $|\Phi_p|$ = cardinality of set Φ_p ; Ω_{pk} relative

connectivity associated with scenario k for p lost patches; Ω_{pk} is a more general specification of relative connectivity, Ω . The lower bound (Ω_p^{\min}) on network connectivity given the loss of p patches can be defined as:

$$\Omega_p^{\min} = \min_{k \in \Phi_p} \Omega_{pk} \tag{3}$$

An upper bound (Ω_p^{\max}) on network connectivity given the loss of p patches can also be established:

$$\Omega_p^{\max} = \max_{k \in \Phi_p} \Omega_{pk} \tag{4}$$

Given the upper and lower bounds on relative connectivity, the range (Ω_p^{range}) of relative network connectivity is then:

$$\Omega_p^{\text{range}} = \Omega_p^{\max} - \Omega_p^{\min} \tag{5}$$

If all levels of p are examined simultaneously in one graph, extending what is shown in Fig. 5 to include $p = 2, 3, 4, \dots, N$, a connectivity frontier is defined (see Matisziw et al. 2007; Murray et al. 2007). However, this is nothing other than a collection of connectivity ranges, Ω_p^{range} , one for each value of p . One way to summarize the set of Ω_p^{range} values, or the connectivity frontier, is to sum the range as follows:

$$\Gamma = \sum_p \Omega_p^{\text{range}} \tag{6}$$

Additionally, as a measure of central tendency for the distribution of patch loss scenarios, the mean connectivity impact (Ω_p^{μ}) over the range of possible scenarios associated with a loss of p patches can be stated as:

$$\Omega_p^{\mu} = \frac{\sum_{k \in \Phi_p} \Omega_{pk}}{|\Phi_p|} \tag{7}$$

Understanding the significance of patch loss scenarios is illustrated next in the context of these range bounds.

Positioning scenarios of connectivity change

As previously discussed, for any habitat configuration many potential patch loss scenarios exist. For example, the loss of a single patch (e.g., Fig. 5) might be considered, or alternatively the simultaneous loss of any number of patches might be of interest. Since there are ten patches in the habitat configurations

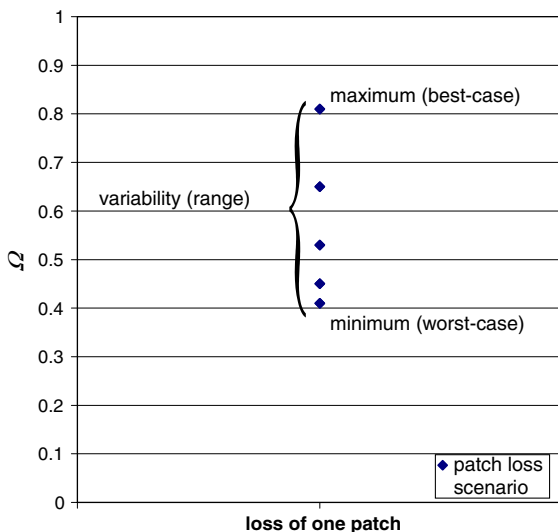


Fig. 5 Range of connectivity impact, Ω , associated with loss of a single patch on the configuration shown in Fig. 2a

shown in Fig. 1, there are $2^{10} - 1$, or 1,023, possible scenarios of patch loss disrupting connectivity in any configuration (i.e., 10 scenarios involving loss of one patch, 45 scenarios involving simultaneous loss of two patches, 120 scenarios involving simultaneous loss of three patches, 210 scenarios involving the loss of four patches, 252 scenarios involving the loss of five patches, 210 scenarios involving the loss of six patches, 120 scenarios involving the loss of seven patches, 45 scenarios involving the loss of eight patches, 10 scenarios involving the loss of nine patches, and 1 scenario involving the loss of all ten patches).

Given the range of patch loss scenarios, an important question is which scenarios are of interest for better habitat management? This question can be approached in several ways. One is to assess a few scenarios for each level of patch loss based on a strategy of sequential disruption of habitat patches. For example, Keitt et al. (1997) simulate possible scenarios by systematically removing individual habitat patches from a network and computing change to a connectivity index. In their analysis, the ecological importance of patch loss is determined by its impact on the network. Urban and Keitt (2001) and Rothley and Rae (2005) expand on this general idea and remove arcs and nodes from a habitat network at random, as well as in sequential order, based on patch characteristics. Following each patch removal, recruitment potential, dispersal flux, and graph diameter were evaluated. Formally, these approaches entail evaluating $k \in \Phi'_p$, where $\Phi'_p \subseteq \Phi_p$. While this type of approach can identify potentially important scenarios, the full range of scenarios (Φ_p) is not generally evaluated. That is, many or most scenarios in Φ_p (or $\cup_p \Phi_p$) are not considered, resulting in a limited characterization of impacts to connectivity, especially with respect to worst-case or best-case impacts to network configurations.

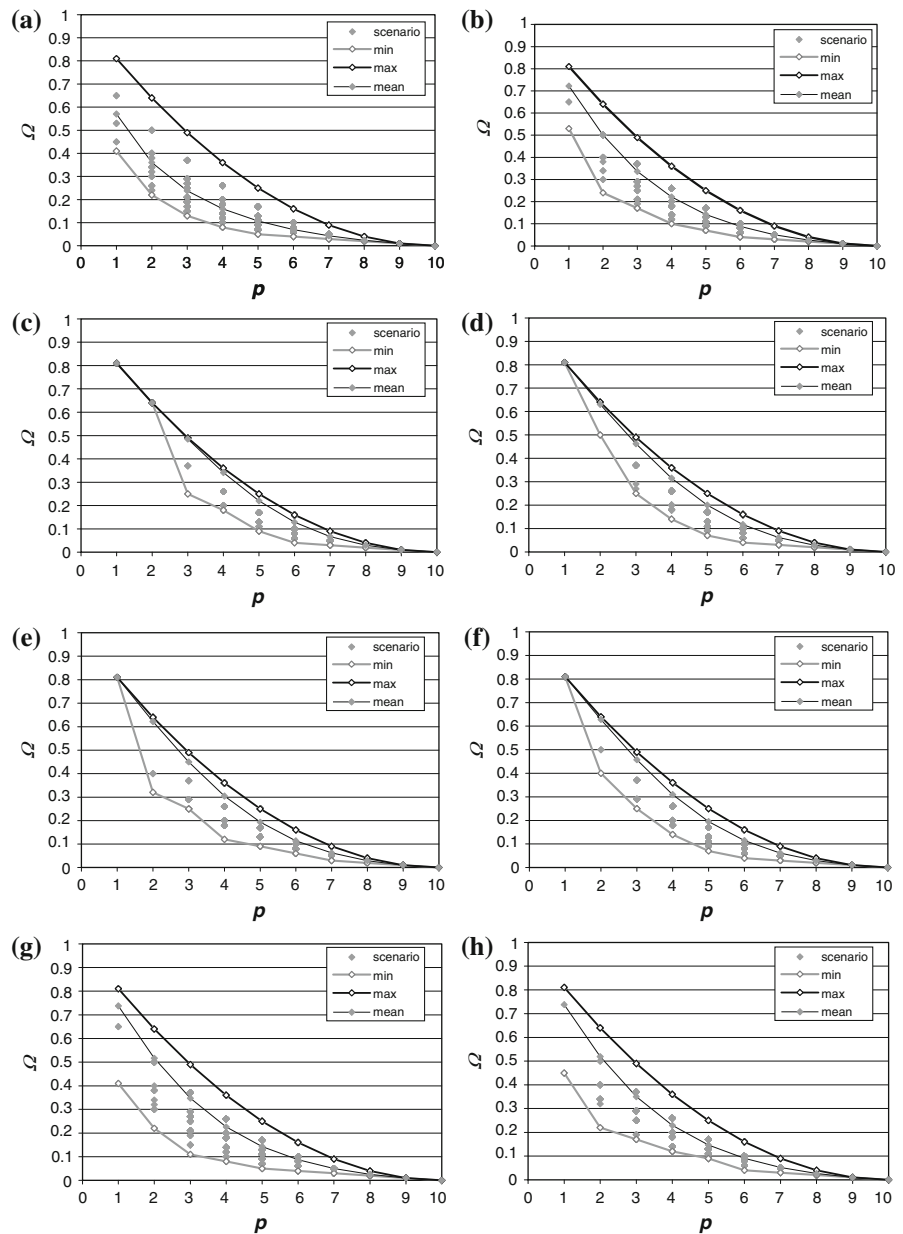
Figure 6 illustrates the full range of patch loss scenarios ($\sum_{p=1}^n |\Phi_p| = 1,023$) for each of the habitat configurations shown in Fig. 1. Highlighted in each figure pane is the maximum, minimum, and average Ω associated with each level of p . For each of the eight configurations, the patch loss maximums, Ω_p^{\max} , are identical. This is due to the fact that for each configuration, at least one scenario involving the loss of p patches exists that does not impact connectivity between the remaining patches. However, each

network configuration can differ significantly in terms of Ω_p^{range} . For instance, for the habitat network in Fig. 2a (see also Figs. 1a and 5) there are five possible scenarios involving the loss of one patch. These scenarios include the best-case, worst-case, and three intermediate cases. When two patches are lost for the network shown in Fig. 2a, Ω_p^{range} increases as illustrated in Fig. 6a.

The range of patch loss scenarios for the network in Fig. 2a contrasts with that from the network associated with the more clustered arrangement shown in Fig. 1c. In the latter configuration, there is no variability in connectivity loss due to the removal of one or two patches (Fig. 6c). It is only in a simultaneous removal of three patches that multiple, unique scenarios of connectivity loss arise (Fig. 6c). Though three unique scenarios could arise in this instance, Ω_p^{μ} is very close to Ω_p^{\max} . This indicates that the majority of scenarios for $p = 3$ ($k \in \Phi_3$) would result in the lowest level of connectivity loss, with only a few scenarios resulting in significant loss of connectivity. Further, the worst-case impact involving three patches ($\Omega_3 = 0.25\%$ or 75% connectivity loss) is considerably less than the corresponding worst-case impact for the configuration in Fig. 1a ($\Omega_3 = 0.13\%$ or 87% connectivity loss). Thus, it is easy to see that in terms of spatial structure for scenarios involving elimination of less than six patches ($p = 6$), the habitat configuration in Fig. 1c appears to be much less vulnerable to connectivity degradation than the one shown in Fig. 1a.

Based on visual inspection of the distribution of relative connectivity for the habitat configurations assessed (Fig. 6), less dense arrangements (less individual patch adjacency) appear to have both a wider range of potential scenarios of connectivity loss for the various levels of patch elimination assessed (Ω_p^{range}) as well as a greater degree of within-range variability (Ω_p^{μ}) (see Fig. 6a, b, g, and h). On the other hand, more clustered arrangements (increased individual patch adjacency) tend to have narrower ranges of connectivity impacts as well as lower within-range variability (see Fig. 6c, d, e, and f). These differences are even clearer when evaluating the total range (Γ) for each configuration. Γ is highest for the configurations in Fig. 1g ($\Gamma = 1.88$), a ($\Gamma = 1.86$), h ($\Gamma = 1.70$), and b ($\Gamma = 1.64$). Γ is lowest for the more clustered arrangements depicted in Fig. 1c ($\Gamma = 0.78$), d ($\Gamma = 0.98$), f ($\Gamma = 1.08$), and e

Fig. 6 Patch loss scenarios and bounds for each habitat configuration



($\Gamma = 1.14$). Thus, higher Γ appears to be indicative of higher overall susceptibility to connectivity degradation, at least with respect to the entire range of patches lost ($p = 1-10$ in this case).

Conclusion

The spatial structure of habitat is an important consideration in maintaining biodiversity. Habitat

connectivity is recognized as being an especially critical aspect in this regard. Though adequate connectivity might be present initially in a habitat network, there is no guarantee that it will persist throughout time. Within a habitat network, changes can adversely impact patch connectivity and, hence, biodiversity and species persistence.

The spatial structure of habitat configurations can influence the resilience of habitat to connectivity loss. Network representations of habitat structure have

been shown to be essential for examining potential impacts to connectivity. Given a habitat network, total network connectivity, C , is an important indicator of habitat structure. C is proposed here because it has a number of features desirable for the analysis of habitat connectivity. First, it directly conveys information on the exact number of patch pairs that are connected (or are not connected) in a network. This consistent interpretation of connectivity is essential in allowing meaningful comparison between different habitat configurations. Secondly, C (and associated measures) is not subject to the spatial bias associated with incorporating actual inter-patch distances as required by other direct connectivity measures (see section “Measuring connectivity loss”), since a decrease in C is always indicative of connectivity degradation. Finally, the linear exposition of C increases its potential for use in planning models (e.g., reserve design models). Given C , relative connectivity, Ω , is therefore an effective measure for tracking structural changes due to patch loss.

Additionally, C is relatively flexible given that it can be easily modified to incorporate other features associated with connectivity. For instance, intra-patch connectivity as discussed thus far assumes patches are equal in their individual contributions to connectivity (e.g., size) and, hence, a patch’s connectivity with itself is equivalent to its connectivity with other network patches. This condition need not be the case in general, however, as intra-patch connectivity Z_{ii} can be weighted by some measure of its internal connectivity, a_i (e.g., $a_i Z_{ii}$). However, when using internal characteristics of habitat patches to approximate intra-patch interaction, scale issues can arise. In such cases, it might be necessary to downscale the spatial resolution of habitat patches. Additionally, if information on actual or potential levels of species interaction between (or within) patches, ϕ_{ij} , is available then they can be used to weight patch connectivity (e.g., $\phi_{ij} Z_{ij}$).

For C and associated measures, it is shown that for any habitat configuration, a range of connectivity loss scenarios are possible. Further, we detail how distributional characteristics of the range of scenarios can be formalized for any configuration. This capability to more completely characterize the range of possible disruptive scenarios and establish upper and lower bounds on connectivity is what distinguishes this paper from other efforts in landscape ecology. While

previous methodologies have focused on analysis of a limited number of potential disruptive scenarios, clearly more exist and must be contextualized within the broader scope of connectivity vulnerability. The framework for assessing distributional characteristics of connectivity loss detailed in this paper can be applied to the analysis of any type of networked structure.

To illustrate the proposed measures, a comparison of eight different habitat configurations was presented. Impacts to patch connectivity were explored under various patch loss scenarios. The analysis demonstrated that connectivity vulnerability is strongly dependent on the spatial distribution of patches within a network, with some network configurations proving to be less vulnerable than others.

While complete enumeration was used in this analysis to characterize the range of potential scenarios of patch loss and impacts to connectivity, enumeration may not be feasible in cases where the number of habitat patches is large or where computational resources are limited. In such instances, other methods exist for generating loss scenarios (e.g., ad hoc selection, simulation, mathematical modeling, etc.) that can be used to derive an appropriate representation of the range of loss scenarios possible (see Murray et al. 2008). Regardless of the methodology used to generate scenarios, the approach presented in this paper permits evaluation of those scenarios in relation to their impact on connectivity. Of course, the better the sampling of scenarios, the better the characterization of potential impacts of patch loss on connectivity.

Analysis of connectivity change has important implications for accounting for connectivity in habitat design and management. Assessing statistical characteristics of patch loss and connectivity degradation can yield valuable insights. In some cases, minimizing habitat network susceptibility to connectivity loss might be desirable. Such efforts might focus on increasing the lower bound on connectivity loss. On the other hand, increased susceptibility to connectivity loss might be desirable. For instance, the capability to readily reduce patch connectivity to prevent against spread of invasive species could be beneficial (Cumming 2002). In this instance, planning efforts might be geared toward addressing the upper bound. Other possible uses for this systematic examination of structural vulnerability include

selecting between feasible reserve assemblages and prioritizing patch fortification, management, and mitigation efforts. Furthermore, while the topic of risk of patch loss is not addressed in this paper as all scenarios are weighted equally, information on scenario risk could easily be incorporated in this analysis framework. If risk was also computed for each scenario, then that information could also be associated and charted in the connectivity frontier adding yet another dimension for planners to consider in their decision-making efforts. Finally, while the discussion in this paper has focused on the impact of patch losses on connectivity, the developed framework is equally applicable to evaluating the effects of linkage (arc) loss between patches as well as on patch/or linkage acquisition on connectivity. To evaluate the effects of patch/linkage gain, one would instead simply need to assess the impact of scenarios involving the addition of p patches or linkages to the habitat network relative to the desired state—where connectivity exists between all habitat patches (e.g., $C = (N^2)$). Therefore, assessing patch/linkage acquisition impacts would focus on increasing the upper and lower bounds on connectivity versus lowering the upper bound and lower bound as is done in the case of addressing patch loss.

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