

Chapter 14

Connectivity as the Amount of Reachable Habitat: Conservation Priorities and the Roles of Habitat Patches in Landscape Networks

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OBJECTIVES

Landscape connectivity plays an important role in sustaining ecological processes at different spatial and temporal scales (e.g., Crooks and Sanjayan, 2006). Landscape connectivity can help to counteract some of the adverse effects of habitat fragmentation and to facilitate species range shifts in response to climate change. Therefore, maintaining or enhancing landscape connectivity is a key part of current biodiversity conservation efforts. A variety of metrics for analyzing connectivity have been developed, ranging from some derived from or used within metapopulation models (Hanski and Ovaskainen 2000; Moilanen and Nieminen 2002) to others based on network analysis (graph theory) (Ricotta et al. 2000; Urban and Keitt 2001; Estrada and Bodin 2008; Saura and Rubio 2010; Galpern et al. 2011; Rayfield et al. 2011). In particular, graph-based approaches have gained increasing popularity in ecological research and applied conservation planning in recent years (Calabrese and Fagan 2004; Saura and Pascual-Hortal 2007; Urban et al. 2009; Pereira et al. 2011; Awade et al. 2012; Rodriguez-Perez et al. 2014). Graphs are just a data structure, and, similarly to vector or raster data structures in geographical information systems, different outcomes of variable quality can be obtained through their use. A crucial issue

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is how to measure and analyze connectivity in order to capture important aspects and provide meaningful guidance for conservation decisions. Through this lab, students will:

1. Analyze potential weaknesses and limitations of several widespread connectivity metrics for establishing conservation priorities;
2. Understand why connectivity is not only related to connections between habitat patches but should also consider the contribution to connectivity coming from the amount of habitat within individual patches;
3. Measure connectivity as the amount of available (reachable) habitat in the landscape using the Integral Index of Connectivity (*IIC*) and the Probability of Connectivity (*PC*) metrics (and understand their formulas, ingredients, and behavior);
4. Learn to use the Conefor software to quantify landscape connectivity;
5. Evaluate the importance and different roles of individual habitat patches as connectivity providers; and
6. Apply these concepts and tools to a real-world conservation case study;

This lab assumes you have already gained familiarity with the basics of spatial networks in Chapter 12. Here, we go a step further with a more in-depth analysis on how (and which) connectivity metrics can be used to prioritize landscape elements for conservation planning. You will explore situations where many connectivity metrics fail to provide appropriate answers, particularly when used for identification of specific key patches or links essential to connectivity. First, you will perform exercises “by hand” to learn some new metrics (Exercises 1, 2 and 3). In Exercises 4 and 5 you will use Conefor, and in Exercise 6 you will combine Conefor with GIS for the analysis of a real-world example. Several printed handouts (available from the book website) will be helpful as you work through the exercises. While we frame this chapter within the context of a graph-theoretical approach for the analysis of landscape connectivity, the concepts here presented and illustrated are of a wider reach; they apply in general to the way landscape connectivity is conceived and measured and to the quantification of the different roles of habitat patches in landscape networks.

INTRODUCTION

Recall that a landscape graph consists of a set of nodes and links between them (Ricotta et al. 2000; Urban and Keitt 2001; Jordán et al. 2003; Pascual-Hortal and Saura 2006; Galpern et al. 2011; Rayfield et al. 2011). **Nodes** represent differentiated habitat units, which generally correspond to habitat patches (as we will assume hereafter in this lab) but may also correspond to other options such as habitat cells, river segments, management units, or protected areas. Nodes can be weighted to incorporate some characteristic (attribute) of the habitat units such as habitat area, quality, or population size. For simplicity, Parts 1 and 2 of this lab we will assume

that the attribute corresponds to habitat patch area. Later, in Part 3, we will consider a case where habitat quality is incorporated in the attribute of the patches. **Links** represent ecological flow (usually the movement of an organism or species) directly between two habitat patches, without use of any intermediate stepping stone patch. Two patches not directly linked in the graph may still be connected through a **path** (a sequence of links) involving several **stepping stone** patches. A link may correspond to a physical corridor or it may represent potential of an organism to directly disperse between two patches; however, links contain no habitat area. Any landscape element containing habitat is represented as a node even when its main role is to serve as a stepping stone or connector between other habitat areas.

For simplicity in this lab, we assume **undirected graphs** where the possibility of moving from patch i to patch j is the same as moving from j to i . However, the concepts and metrics presented also apply to directed networks with asymmetric connections such as wind-driven dispersal or water flows. In Exercises 1–5 we will consider graphs with **unweighted links** (i.e., binary connection model where two patches are simply considered either directly connected or unconnected, with no intermediate modulation of the quality, strength, feasibility, or frequency of use of that connection). Later, in Exercise 6, we will consider a richer graph representation of the landscape (probabilistic connection model) in which links are **weighted** according to their ability or effectiveness in conducting a movement or ecological flows.

Connectivity: Is it Just Between Habitat Patches?

A classic definition of **landscape connectivity** is “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). This definition implies that landscape connectivity is related to and can be successfully addressed by only considering the number or quality of connections among habitat patches in the landscape. Consider the two landscapes in Figure 14.1. Which landscape is more connected? Consider your answer using some of the metrics you are familiar with from the previous chapter: number of components, number of links or link density.

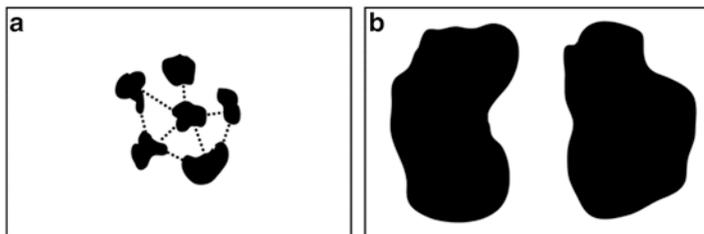


Figure 14.1 Two simple hypothetical landscapes (a, b) illustrating the concept of habitat availability (reachability) at the landscape scale. Habitat patches (nodes) are shown in *black* and the links (direct connections) between the nodes are represented by *dotted lines*. Adapted from Saura (2008)

Using many existing metrics, one would deduce that connectivity is higher in A than in B, since A contains eight links between patches while landscape B has no links. Similarly, landscape A would be regarded as more connected because all habitat occurs within one component, whereas B consists of two completely isolated components (i.e., the two big patches). However, it makes little sense to consider landscape A more connected than B. No matter how well connected patches are in A, together they comprise less amount of available (reachable) habitat than either single patch in B (Pascual-Hortal and Saura 2006). Either one of the big isolated patches in B (on its own) contains more area of connected habitat than the entire area of habitat potentially reached via the links in landscape A. In fact, habitat loss and fragmentation of either patch in landscape B could lead to a pattern similar to landscape A. From the standpoint of conservation, fragmentation of one large patch should not be deemed more beneficial (or more connected) than the original continuous habitat patch.

Clearly, some connectivity metrics indicate higher connectivity in more fragmented landscapes (Tischendorf and Fahrig 2000). In fact, some metrics indicate zero connectivity in landscapes with one contiguous patch, even when the habitat patch occupies the entire landscape (Tischendorf and Fahrig 2000). Approaches and metrics that focus only on the connections between habitat patches (**interpatch connectivity**), while ignoring **intrapatch connectivity** (e.g., area of the patches), are problematic for informing conservation planning priorities or evaluating the impacts of landscape changes (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007). When habitat patterns change through time, or when networks with differing numbers and sizes of patches are compared, metrics that only consider interpatch connectivity can provide misleading results.

The concept of **habitat availability (or reachability)** at the landscape scale helps to address these deficiencies (Pascual-Hortal and Saura 2006; Saura 2008; Saura and Rubio 2010) in two ways. First, it recognizes that a habitat patch provides (by itself) some amount of connected habitat—more connectivity within bigger patches—even when the patch is completely isolated from all other patches. Second, the connected area *within* habitat patches (i.e., **intrapatch connectivity**) should be measured along with the area made available by (or reachable through) connections with other patches (i.e., **interpatch connectivity**) (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010). The habitat availability concept acknowledges that species may be able to reach a larger amount of habitat resources in the landscape *either* through bigger patches (intrapatch connectivity) *or* through more or stronger connections among different patches (interpatch connectivity). More frequently, a combination of both will determine the total amount of available/reachable habitat in the landscape for a given species.

Through this chapter you will learn to understand and appropriately apply habitat reachability metrics which account for intra- and interpatch connectivity.

EXERCISES

Part 1. Understanding the Behavior and Limitations of Commonly Used Connectivity Metrics

Assume one wants to evaluate how important an individual habitat patch (or link) is to the maintenance of overall landscape connectivity, using a given landscape-level connectivity metric X . One approach would be to calculate the relative change in the metric value (dX) after the removal of that patch (or link) from the habitat network:

$$dX (\%) = 100 \cdot \frac{X_{\text{initial}} - X_{\text{removal}}}{X_{\text{initial}}}$$

where X_{initial} is the value of the connectivity metric in the initial or intact landscape and X_{removal} is the metric value after the removal of a particular patch or link from the landscape.

This calculation can be repeated for any (or every) individual element in the landscape, and the resulting dX values would quantify the importance of each patch (or link) in maintaining landscape connectivity. Therefore, ranking patches by dX values can prioritize their value to sustaining connectivity and thus provide guidance on where to concentrate conservation efforts. Similarly, dX values could also be calculated for landscape changes involving the loss of multiple patches and/or links.

There are a myriad of metrics to quantify the connectivity of landscape networks (e.g., Jordán et al. 2003; Galpern et al. 2011; Rayfield et al. 2011). Each would most likely yield different results for dX , and suggest different conservation priorities; therefore it is of utmost importance to scrutinize and understand the actual behavior, performance, and adequacy of various metrics. A key question is: *What properties should a connectivity metric fulfill to be reliable for such conservation planning purposes?*

To address this, you will examine the behavior of several commonly used connectivity metrics in response to changes in habitat networks. Your goal is to evaluate whether these metrics can be reliably used for prioritizing habitat patches and links for connectivity conservation. In particular, you will examine three metrics that are easy to understand, widely used in connectivity analyses, and similar to metrics you learned about in Chapter 12 in this book:

- **Number of Links (NL)**—A link is a direct connection between different habitat patches.
- **Number of Components (NC)**—A component is a set of connected patches in which every patch can be reached from the others through at least one path (sequence of links). There are no links or paths between patches in different components.

- **Mean Component Size (*MCS*)**—The size of a component is the sum of habitat areas for all patches within the component. *MCS* is the average size of all the components in the landscape.

Higher values of *NL* and *MCS* indicate more connectivity while the inverse interpretation applies for *NC*. Upon patch removal, *NL* will never increase (and hence $dNL \geq 0$). In contrast, *dNC* and *dMCS* can potentially yield positive or negative values. Therefore, the most important landscape elements (patches or links) for connectivity according to *NL* and *MCS* would be indicated by the highest *dNL* and *dMCS* values when these elements are removed (which for *dMCS* may correspond either to the highest positive or the least negative values). For *NC*, the most important landscape elements would be those that, when removed, produce the lowest *dNC* values (which may include negative *dNC* values).

EXERCISE 1: Response of Connectivity Metrics to Changes in Habitat Networks with Some Hypothetical Examples

Figure 14.2 shows six different hypothetical landscapes with their corresponding habitat networks (graphs with unweighted links). In each landscape, two different losses can occur—loss of either A or B—which generally correspond to different habitat patches. The exceptions are in landscape L5 where B corresponds to the link between two patches, and in landscape L6 where A corresponds to a component made up of three patches and two links (identified by a dashed line).

Next, we'll assume, due to budget constraints, that only A or B can be protected. Thus, a decision has to be made as to which element will be protected and which will be lost. When a patch is lost, all connected links are considered lost.

Q1 Visually examine the six landscapes in Figure 14.2. Based on your own qualitative visual assessment (no detailed calculations), would the loss of A or B be more detrimental to habitat connectivity and availability (reachability) in each landscape? Which element (A or B) should be prioritized for conservation? Why? Consider that the reasons might be different for each of the six cases.

Q2 Next, you will systematically and quantitatively examine the behavior of *NL*, *NC*, and *MCS* to determine which of the two losses (A or B) is more detrimental to connectivity according to these three metrics. Evaluate using *dNL*, *dNC*, and *dMCS* values or simply from the absolute difference in the metric value before and after a change ($X_{\text{initial}} - X_{\text{removal}}$). Recall that higher *NC* values are assumed indicative of lower connectivity with the reverse is true for *NL* and *MCS*. Use the tables provided in **Handout #1** (available on the website for the book) to organize your calculations. Example calculations are provided for landscapes L1 and L6 in Handout #1.

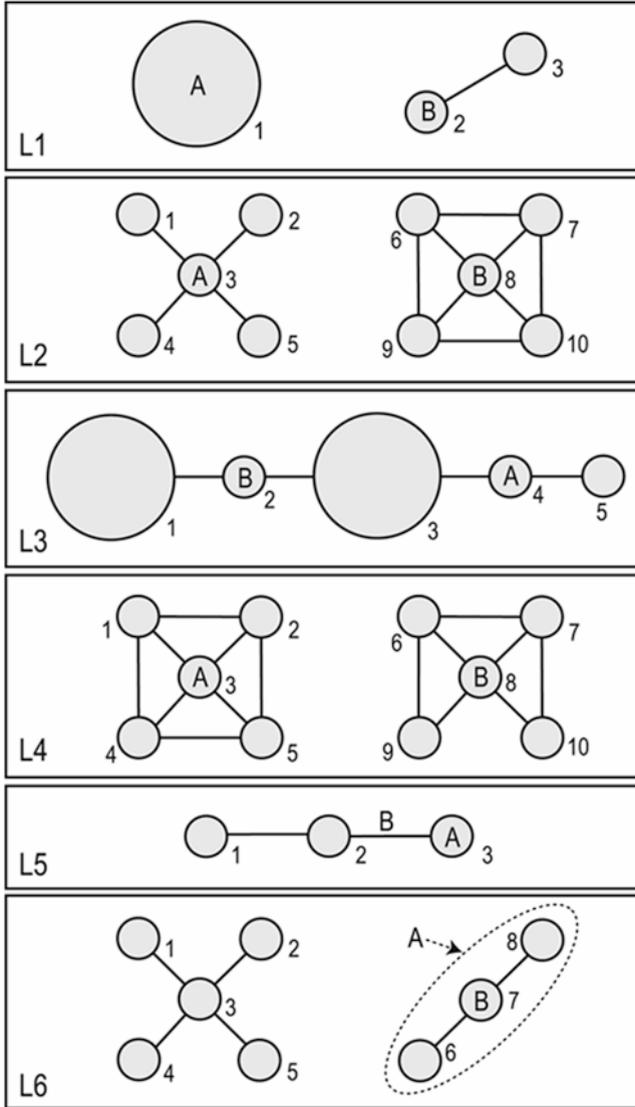


Figure 14.2 Six simple landscapes comprising different sets of habitat patches or nodes (*grey numbered circles*) and links between them (*solid lines*). In each landscape two hypothetical losses can occur indicated by *A* and *B*. The big patches in *L1* (*patch 1*) and *L3* (*patches 1 and 3*) have a habitat area of 9 ha whereas the rest of the patches have a habitat area of 1 ha. See Exercise 1 for additional explanations. Later in Exercise 2, you will need to know that the total area of each landscape is 25 ha.

Q3 What do you conclude about the behavior and reaction to spatial changes of these connectivity metrics? Would you advocate the use of *NL*, *NC*, or *MCS* as a basis for prioritizing landscape elements for the conservation of habitat connectivity and availability or for evaluating the potential impacts of landscape changes in the ecological flows related to connectivity? Why?

Part 2. Integrating Intrapatch and Interpatch Connectivity in a Single Measure: The Integral Index of Connectivity

Next you will explore new connectivity metrics which measure the amount of available (reachable) habitat in the landscape (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010). These metrics integrate both intrapatch (within patch) and interpatch (between-patch) connectivity in a single measure. In doing so, these new metrics address the main primary limitations of previous metrics you have examined.

Now, in Part 2, you will only consider the habitat availability metrics that are based on a binary connection model (graphs with unweighted links). These metrics are the **Integral Index of Connectivity** (*IIC*) and the related **Equivalent Connectivity** metric (*EC(IIC)*). In the particular case where the node attribute corresponds to habitat area, as in exercises in Part 2, the latter metric is referred to as the **Equivalent Connected Area** (*ECA(IIC)*). These metrics are described in Table 14.1. They derive from the same concept and way of measuring connectivity but are expressed in different units and over a different range of variation. Later, in Part 3, we will introduce a probabilistic version of these metrics corresponding to graphs with weighted links.

EXERCISE 2: Understanding *IIC* and *ECA(IIC)* Calculations

1. Examine the definition of the *IIC* and *EC(IIC)* metrics given in Table 14.1. The latter metric will be referred to as *ECA(IIC)* hereafter, since we are using habitat area as the attribute of the nodes. Pay attention to the variable in these metrics that relates to the number of links in the shortest path between patches (nl_{ij}), which can take different values depending on the pair of patches considered, as described next.
 - **Interpatch connectivity** is addressed in several ways. For a **direct link** between two patches, $nl_{ij}=1$ (e.g., patches 2 and 3 in L1 in Figure 14.2). **Indirect connections** occur between patches if i and j belong to the same component (i.e., there is a path from i to j), but have no direct link. In such cases, $1 < nl_{ij} < \infty$. This occurs for example for patches 9 and 10 in L4 in Figure 14.2, where $nl_{ij}=2$. For **unconnected patches** (not connected through any path), $nl_{ij}=\infty$ (no matter how many links are traversed, movement from i

Table 14.1 Habitat availability (reachability) metrics: formulas and description

Metric name	Acronym	Formula	Description	Reference
Integral index of connectivity	<i>IIC</i>	$IIC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i \cdot a_j}{A_L^2}$ $= \frac{IICnum}{A_L^2}$	<p><i>IIC</i> ranges from 0 to 1 and increases with improved connectivity where <i>n</i> is the total number of nodes (usually patches) in the landscape, <i>a_i</i> and <i>a_j</i> are attributes (e.g., habitat area, quality) characterizing habitat resources in patches <i>i</i> and <i>j</i>, and <i>nl_{ij}</i> is the number of links in the shortest path between patches <i>i</i> and <i>j</i> (further details on <i>nl_{ij}</i> are given in Exercise 2). <i>A_L</i> is the maximum landscape attribute, a constant with the same units as <i>a_i</i> and <i>a_j</i> and sets the reference for the maximum <i>IIC</i> attainable (<i>IIC</i> = 1). If patch attributes are habitat areas (as assumed in Exercise 2), then <i>A_L</i> is equal to the total landscape area. Therefore <i>IIC</i> = 1 when the landscape is fully covered by habitat.</p>	Pascual-Hortal and Saura (2006)
Equivalent connectivity for <i>IIC</i>	<i>EC(IIC)</i>	$EC(IIC) = \sqrt{IICnum}$ $= \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i \cdot a_j}$	<p><i>EC(IIC)</i> is the amount of habitat resources (in the same units as the attribute <i>a_i</i>) that a single habitat patch (maximally connected) should have to provide the same <i>IIC</i> value as the actual network currently in the landscape. <i>EC(IIC)</i> may be thought of as a measure of the amount of reachable habitat resources in a landscape. <i>EC(IIC)</i> will not be smaller than the largest <i>a_i</i> and will not exceed the sum of <i>a_i</i> values for all patches in the landscape (total amount of habitat resources). The maximum possible <i>EC(IIC)</i> for a given amount of habitat resources occurs when all the habitat occurs as a single habitat patch (no fragmentation). In the particular case in which the attribute <i>a_i</i> corresponds to patch area, <i>EC(IIC)</i> can be named as Equivalent Connected Area for <i>IIC</i> (<i>ECA(IIC)</i>) and be defined as the size of a single habitat patch that would provide the same <i>IIC</i> value as the actual habitat network in the landscape.</p>	Saura et al. (2011)

(continued)

Table 14.1 (continued)

Metrics for the probabilistic connection model (graphs with weighted links) used in Part 3			
Metric name	Acronym	Formula	Description
Probability of connectivity	<i>PC</i>	$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i \cdot a_j \cdot p_{ij}^*}{A_L^2}$ $= \frac{PCnum}{A_L^2}$	<p><i>PC</i> ranges from 0 to 1 and increases with improved connectivity. <i>PC</i> is defined as the probability that two individuals of a given species, randomly placed within the landscape, are able to reach each other (i.e., fall into habitat connected to each other). This will happen either if both individuals are placed within the same patch (intrapatch connectivity) or if they are placed in different patches connected through a path (interpatch connectivity). p_{ij}^* is defined as the maximum product probability of all the paths between patches <i>i</i> and <i>j</i> (see Part 3 for further details and examples). All the rest is the same as for <i>IIC</i>.</p>
Equivalent connectivity for <i>PC</i>	<i>EC(PC)</i>	$EC(PC) = \sqrt{PCnum}$ $= \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i \cdot a_j \cdot p_{ij}^*}$	<p><i>EC(PC)</i> is completely analogous in interpretation to <i>EC(IIC)</i> but calculated from <i>PCnum</i> rather than from <i>IICnum</i>. For example, when patch attributes correspond to areas, <i>EC(PC)</i> can be called <i>ECA(PC)</i> and is defined as the size of a single patch providing the same <i>PC</i> value as the actual habitat network. The maximum possible <i>EC(PC)</i> value for a given amount of habitat would be obtained when all habitat occurs as a single habitat patch (no fragmentation) or when the habitat is dissected into different patches but with a maximum interpatch connectivity ($p_{ij}^* = 1$ between all patches).</p>
			<p>Reference Saura and Pascual-Hortal (2007)</p> <p>Saura et al. (2011)</p>

Table 14.2 Calculation of the Integral Index of Connectivity (*IIC*) and the Equivalent Connected Area (*ECA(IIC)*) for **landscape L3** in Figure 14.2. Some missing values need to be filled to complete the calculations

	Patch <i>i</i>	Patch <i>j</i>	<i>a_i</i>	<i>a_j</i>	<i>nl_{ij}</i>	$\frac{a_i \cdot a_j}{1 + nl_{ij}}$	$\sum \frac{a_i \cdot a_j}{1 + nl_{ij}}$
Intrapatch connectivity (<i>i=j</i>)	1	1	9	9	0	81	165
	2	2	1	1	0	1	
	3	3		9	0		
	4	4	1		0	1	
	5	5	1	1	0	1	
Interpatch connectivity for <i>i<j</i>	1	2	9	1	1	4.5	48.63
	1	3	9	9	2	27	
	1	4				2.25	
	1	5	9	1		1.8	
	2	3	1	9	1	4.5	
	2	4	1	1	2	0.33	
	2	5	1	1	3	0.25	
	3	4	9	1		4.5	
	3	5		1	2		
	4	5	1	1	1	0.5	
Interpatch connectivity for <i>i>j</i>	Same as above for <i>i<j</i> (undirected graphs)						48.63
Total connectivity (<i>IICnum</i>)=intrapatch + interpatch connectivity							262.26
<i>IIC</i> = <i>IICnum</i> / <i>A_L</i> ² = 262,26/25 ² = 0.4196							
Equivalent Connected Area (<i>ECA(IIC)</i>) = <i>IICnum</i> ^{0.5} = 16.19 ha							

to *j* will never be achieved) and the numerator equals zero. This is the case for example for patches 1 and 2 in L1.

- **Intrapatch connectivity** is also accounted for. When *i=j* then *nl_{ij}*=0 because no links are needed to reach a patch from itself. This relates to the habitat availability concept, in which a patch itself is considered to provide some connected habitat.
2. Examine the example (partial calculation) of *IIC* and *ECA(IIC)* given in Table 14.2. Determine generally how these numbers correspond to **landscape L3** in Figure 14.2 from which these calculations are derived. Remember that the total landscape area (*A_L* as in Table 14.1) is 25 ha (as in all landscapes in Figure 14.2).
 3. Fill in the missing values in the table (use **Handout #2**) to ensure you understand the formulation of these calculations. Check your answers with your partner (or instructor) at each step, before proceeding.
 - Note patches 1 and 3, which are very large compared to the rest of the network. The large connected areas within these patches will make a large contribution to the value of *ECA(IIC)* due to their high **intrapatch connectivity**.

- Recall that connections are symmetric (as for undirected graphs). Thus, we can simplify the calculations for the **interpatch connectivity** by just considering the cases where $i < j$ and use identical values for $i > j$.
- Due to the contribution of both intrapatch and interpatch connectivity $ECA(IIC) = 16.19$ ha, about 6 ha lower than the total habitat area (22 ha) in the network.

EXERCISE 3: Evaluating Changes in Connectivity (by-hand) Using Habitat Availability Metrics IIC and $ECA(IIC)$

Next you will explore some “by-hand” calculations in two of the simplest landscapes from Figure 14.2 to analyze the behavior of IIC and $ECA(IIC)$. Later you will learn to use Conefor software to perform such computations more rapidly and automatically which will be necessary when we move to analysis of real-world networks with a much larger number of patches.

Examine the example calculations for L1 (shown in a series of three tables in **Handout #3** and described below). Remember that the total landscape area (A_L) is 25 ha for these landscapes. After you follow and understand these calculations for L1, you will follow the same procedure for L5. Recall your work from Table 14.2, which can be a useful guide together with the example calculations given next. Your goal is to determine: Does loss of a or b represent a bigger problem for connectivity?

1. Calculations for intact landscape L1 are shown in **Handout #3** Table (a).
2. If we lose A (patch 1) from the landscape, the table simplifies to that shown in Table (b).

By losing A the IIC value decreases from $IIC_{\text{initial}} = 0.1344$ to $IIC_{\text{remove}} = 0.0048$ (the $IICnum$ value decreases from $IICnum_{\text{initial}} = 84$ to $IICnum_{\text{remove}} = 3$), which yields $dIIC = 96.43\%$. Note that since the IIC and $IICnum$ values are proportional (the former equals the latter divided by A_L^2), $dIIC$ and $dIICnum$ values will be identical, and therefore you can use $IICnum$ to calculate $dIIC$.

3. If we lose B (patch 2) from the landscape, then the table simplifies to that shown in Table (c).

By losing B the IIC value decreases from $IIC_{\text{initial}} = 0.1344$ to $IIC_{\text{remove}} = 0.1312$ ($IICnum$ value decreases from $IICnum_{\text{initial}} = 84$ to $IICnum_{\text{remove}} = 82$), which yields $dIIC = 2.38\%$. This $dIIC$ value is lower than the one obtained by losing A, which was 96.43%. Therefore, the loss of A would cause a much larger decrease in habitat connectivity and availability in this landscape, and thus A is more important than B according to IIC .

4. Following the above example (detailed in **Handout #3**), perform the necessary calculations to analyze the behavior of IIC and $ECA(IIC)$ for **landscape L5**. You may find it helpful to create a similar series of data tables for L5.

Q4 Which of the two possible losses (A or B) would be more detrimental for connectivity (according to $dIIC$ values) in landscape L5?

Introduction to Conefor Software

Although it is advisable to use hand calculations initially to fully understand these metrics, this is cumbersome and infeasible in realistic networks. Fortunately, these metrics have been implemented in the Conefor software available for download at <http://www.conefor.org>. Conefor calculates both the overall metrics for the whole landscape (e.g., IIC and $EC(IIC)$) and the patch-level importance ($dIIC$) for every patch in the network, among other outputs.

INPUT

Conefor requires two input files for each network you wish to analyze: the **node file** and the **connection file**. Both are simple text files (with columns separated by tabs or spaces) that can be produced with any basic text editor (later in Part 3 you learn how to automatically generate these files using a custom-made GIS extension).

The **node file** simply has one row for each node and two columns. The first column identifies each node by a distinct node ID (integer value), and the second column contains its corresponding attribute value for that node (a_i and a_j in equations in Table 14.1, usually corresponding to habitat area).

In the case of landscape L3 in Figure 14.2, the node file is simply:

1	9
2	1
3	9
4	1
5	1

The **connection file** identifies connections between each pair of nodes, presented in three columns. The first two columns contain a pair of node IDs, whereas the third column characterizes the direct connection between the node pair. In our example, where connections correspond to binary links, they are represented as 1 (linked) or 0 (not linked). Alternatively, distances or probabilities for each pair of nodes could be used. Because our connections are symmetric (undirected graphs), each pair of nodes needs to be listed only once, although both directions will be considered in the calculations. The ordering of pairs in the file has no effect on Conefor calculations.

In the case of landscape L3, the connection file would be as follows:

1	2	1
1	3	0
1	4	0
1	5	0
2	3	1

2	4	0
2	5	0
3	4	1
3	5	0
4	5	1

The above format is used in a **full connection file** where **all pairs** of nodes are listed once.

It is also possible to list only node pairs with direct connections (links, 1 values only), to create a **partial connection file**. In such a file, any missing node pairs are considered not directly connected. The partial connection file is much shorter, with one line for each link, as follows:

1	2	1
2	3	1
3	4	1
4	5	1

EXERCISE 4: Using Conefor to Calculate the Importance of Nodes and Links

1. Copy the entire folder **Exercise 4** to C:\temp\ or C:\workspace\
2. Open and examine the digital node, full, and partial connection files for L3 with any text editor. Do they match the above description?
3. See the **Conefor Instructions Handout** for steps 3–7.
Using Conefor, be sure you can successfully run the example for L3 (using the provided files) before proceeding to subsequent steps. Calculate the *IICnum*, *IIC*, and *ECA(IIC)* values for this landscape and check that you obtain the same values as in Table 14.2 above. **Save your output files.**
4. Build node and partial connection files for the other five landscapes in Figure 14.2. *NOTE:* Each of these files should end with a blank line.
5. Using Conefor, calculate the *dIIC* values for each of the possible changes (A or B) in each of the six landscapes. **Save your output files.** In almost all the cases, loss of A or B corresponds to specific patches and the *dIIC* values will be calculated by Conefor in the node importance file. Exceptions include **B in L5 and A in L6**, explained next.
6. B in L5 corresponds to the loss of a **link**. Thus, the *dIIC* value for this link is in the link importance file resulting from the link removal analysis in Conefor.
7. Loss of A in L6 involves **multiple patches and links**. Conefor will not automatically calculate the corresponding *dIIC* value. In this case you need to:
 - Get the *IIC* or *IICnum* value corresponding to L6 (in the initial landscape, using the node and connection files created in step 4).

- Build node and partial connection files corresponding to landscape L6 after the entire component A has been lost.
- Use these files in Conefor to calculate the *IIC* or *IICnum* values for this modified network.
- Calculate *dIIC* for the metric values before and after the loss of component A.

NOTE: Remember that the values of *dIIC* and *dIICnum* are, by definition, identical since A_L is a constant that remains unvaried before and after any change in the landscape. You can therefore use either *IIC* or *IICnum* values to obtain the requested *dIIC* values.

8. Complete the table in **Handout #4**. The results for L1 (from Exercise 3) are already included. Compare your Conefor results for L5 with your manually calculated results from Exercise 3.

Q5 When considering the *dIIC* values, which of the two losses (A or B) is more detrimental to connectivity in each landscape? Does *IIC* identify conservation priorities in a way that is more relevant to your responses to Q1? Explain why.

Understanding Three Distinct Fractions of Landscape Connectivity

Now that you are familiar with the habitat availability (reachability) metrics, we will examine the ingredients of the *IIC* metric in more detail and explore how these can be used to gain a more thorough understanding of the role of specific habitat patches in a network.

The *dIIC* values for a given patch can be partitioned into three distinct fractions which quantify the different ways a patch can contribute to habitat connectivity and availability in the landscape (i.e., contribute to the amount of reachable habitat) (Saura and Rubio 2010):

$$dIIC = dIIC_{intra} + dIIC_{flux} + dIIC_{connector}$$

The **intra fraction** (*dIIC_{intra}*) is the contribution of the patch in terms of **intra-patch connectivity**, corresponding to $a_i \cdot a_j / (1 + nl_{ij})$ when $i = j$ and, therefore, $nl_{ij} = 0$. It corresponds to the amount of habitat resources (habitat area, quality, or other attribute) provided by the patch (i.e., the amount available or reachable from within that patch). *dIIC_{intra}* is **completely independent of the patch's connections** to other patches. This metric returns the same value even if the patch is completely isolated.

The **flux fraction** (*dIIC_{flux}*) corresponds to the **dispersal flux** (weighted by the focal patch attribute) through the connections of the focal patch with all other patches in the network. It assumes the focal patch is the starting (or ending) point of

the dispersal flux. This fraction depends on both the attribute of the focal patch and its position within the network. It corresponds to the sum $a_i \cdot a_j / (1 + nl_{ij})$ for each node pair where $i \neq j$. This fraction measures how well connected the focal patch is to the rest of the habitat in the landscape. It does not quantify the patch's importance for maintaining connectivity among the other patches, however, which is quantified by the next fraction.

The **connector fraction** (*dIICconnector*) quantifies the contribution of the analyzed (focal) patch as a connecting element or **stepping stone** between other patches. This fraction depends only on the **topological position** of the patch in the network. The connector fraction for a focal patch is independent of the attributes of the focal patch, but accounts for attributes of other patches connected via it. Thus, the connector fraction for a patch will be higher when it connects patches with more habitat resources (higher a_i).

dIICconnector for focal patch k corresponds to a part of the sum of $a_i \cdot a_j / (1 + nl_{ij})$ for each pair of patches i and j in which $i \neq k$, $j \neq k$, and k is part of the shortest path between i and j . A given patch k will contribute to *dIIC* through the connector fraction only when it is part of the shortest path between at least two other patches. The value of *dIICconnector* for patch k also depends on any alternative paths which, upon loss of patch k , still allow movement among other patches. If remaining alternative paths are nearly as good, the connector fraction for k will be low; if patch k is irreplaceable (its role cannot be compensated for by other patches or paths after its loss), then it will present a higher *dIICconnector* value. See Saura and Rubio (2010) and Bodin and Saura (2010) for further details and equations.

These three fractions allow for multifaceted, integrated connectivity analyses in which the different roles of habitat patches are measured using identical units and can be directly compared and summed (Saura and Rubio 2010). *dIICintra* measures intrapatch connectivity, while *dIICflux* and *dIICconnector* measure interpatch connectivity. A patch will be more or less important (*dIIC*) due to one or more of these three fractions, depending on its local characteristics (i.e., attributes) and its topological position within the network. Since, by definition, links do not contain any habitat area, they do not provide intrapatch connectivity (thus, *dIICintra*=0); nor can they be the starting or ending flux of any dispersal flux (thus, *dIICflux*=0). As such, links can only contribute to *dIIC* through the *dIICconnector* fraction. Because the connecting role of nodes and links is measured in the same way by the *dIICconnector* fraction, their contributions can be directly compared.

EXERCISE 5: Examining Results from Intra, Flux, and Connector Fractions

Q6 Without making any calculations, which of the patches in each of the six networks in Figure 14.2 contribute via the intra fraction? Which contribute through the flux fraction? And which patches contribute through the connector fraction? Why?

- Q7** Go back to your results from Conefor where you calculated $dIIC$ (for Q5). Examine the values for the three fractions ($dIIC_{intra}$, $dIIC_{flux}$, $dIIC_{connector}$) for all the patches in Figure 14.2. How do these results compare to your answer to the previous Q6? Which patches present the highest values of each fraction in each landscape?
- Q8** Without making any calculations, if the same procedure and fractions were used to evaluate links rather than patches, which links in the six landscapes in Figure 14.2 would have no importance according to $dIIC$? Why?
- Q9** Use Conefor to calculate the $dIIC$ values for each link in landscapes L2, L3, and L4, selecting the link removal mode under the link importance options (See Conefor Instructions Handout). Do these results match to your answer to previous Q8? Among the links with $dIIC > 0$, which are the most important and the least important ones in each landscape? Why?

Part 3. Connectivity Conservation Planning for an Endangered Bird in Spain

The previous exercises demonstrated how IIC reacts to certain changes in habitat networks and how it can prioritize landscape elements for conservation, and also helped you understand what aspects of connectivity are being measured by this metric. Next, you will learn how to use habitat availability metrics and the Conefor software in a real-world case study for an endangered bird species in the region of Catalonia in Spain.

In Exercise 6, you will analyze connectivity using the probabilistic PC metric (Table 14.1). This metric considers more complex information about links using graphs with weighted links, but is otherwise conceptually similar to IIC . The dPC values can be partitioned in three distinct fractions as for $dIIC$ (i.e., dPC_{intra} , dPC_{flux} , $dPC_{connector}$). An Equivalent Connectivity metric ($EC(PC)$) can also be calculated from the numerator of PC and it is denoted $ECA(PC)$ when the node attribute is area (Table 14.1). You will also use Conefor with ArcGIS (or QGIS) to link GIS data to graph-based connectivity analyses. Upon completion, you will be able to adapt and apply the IIC and PC metrics and Conefor to other study areas and species for your own project.

Understanding the Probability of Connectivity (PC) Metric

PC is based on a probabilistic connection model. Links are weighted by p_{ij} which is the **probability of direct dispersal** between patches i and j . The **product probability of a path** is the product of all p_{ij} along the path. If intermediate patches are

traversed, the product probability of a path incorporates all intermediate links (Saura and Pascual-Hortal 2007).

A key ingredient in the formulation of *PC* is the **maximum product probability** (p^*_{ij}) (Table 14.1). This is the only ingredient that differs from *IIC*. p^*_{ij} identifies the maximum product probability among all possible paths between patches i and j to determine the “best” path (and thus, $p^*_{ij} \geq p_{ij}$).

When patches i and j have a **strong direct connection** (e.g., close to each other), the maximum product probability path is the direct link connecting i and j , and then $p^*_{ij} = p_{ij}$. In contrast, if patches i and j are weakly or not connected through the direct link, the “best” (maximum product probability) path may follow several intermediate steps via **stepping stone patches**, yielding $p^*_{ij} > p_{ij}$. When two patches are completely isolated from each other (either due to great distance or barriers such as a road) and there is no possibility for movement between both patches, then $p^*_{ij} = 0$.

When $i = j$ then $p^*_{ij} = 1$ because it is 100% certain that a patch can be reached from itself. This relates to the habitat availability (reachable habitat) concept, which accounts for the amount of habitat resources available within a patch (the intrapatch connectivity).

The **maximum product probability path (quantified by p^*_{ij}) is not necessarily the same as the shortest path for *IIC*** where it is quantified as the number of links (nl_{ij}). An example using Figure 14.2 is instructive to consider. For example, in L2, assume $p_{ij} = 0.5$ for all links except $p_{6,7} = 0.1$. Given this, the direct link yields $p_{6,7} = 0.1$ whereas an indirect link (via patch 8) yields $p^*_{6,7} = 0.25$ (8 is a stepping stone, therefore $0.5 \times 0.5 = 0.25$). Thus, a two-link path is a better option than the direct link between 6 and 7. The direct link between patches 6 and 7 is the shortest path according to *IIC*, but for *PC*, movement is better conducted via patch 8, when p_{ij} values are incorporated.

Status of the Endangered Capercaillie in Spain

The capercaillie is one of the most endangered forest-dwelling bird species in Spain (Canut et al. 2011). We focus on the subspecies of capercaillie (*Tetrao urogallus aquitanicus*) endemic to the Pyrenees and its distribution in Catalonia (NE Spain), a region of 32,000 km² (Figure 14.3). Its habitat in Catalonia is concentrated in upper montane and subalpine forests of the Pyrenees and Pre-Pyrenees (Figure 14.3). Decreasing populations with poor breeding success raise concerns about long-term persistence and habitat fragmentation is a major concern (Canut et al. 2011). Common conservation measures focus on protection of vital areas (leks, hibernating and breeding sites, etc.); however, this approach may not be sufficient to meet the birds' broad spatial requirements. Sustaining functional connectivity among subpopulations to facilitate dispersal and minimizing mortality risk (Canut et al. 2011) requires identification and conservation of areas most critical for habitat connectivity and habitat availability. You will address this using the *PC* metric and actual geodata on habitat quality for this species, with some simplifications and modifications for teaching purposes.

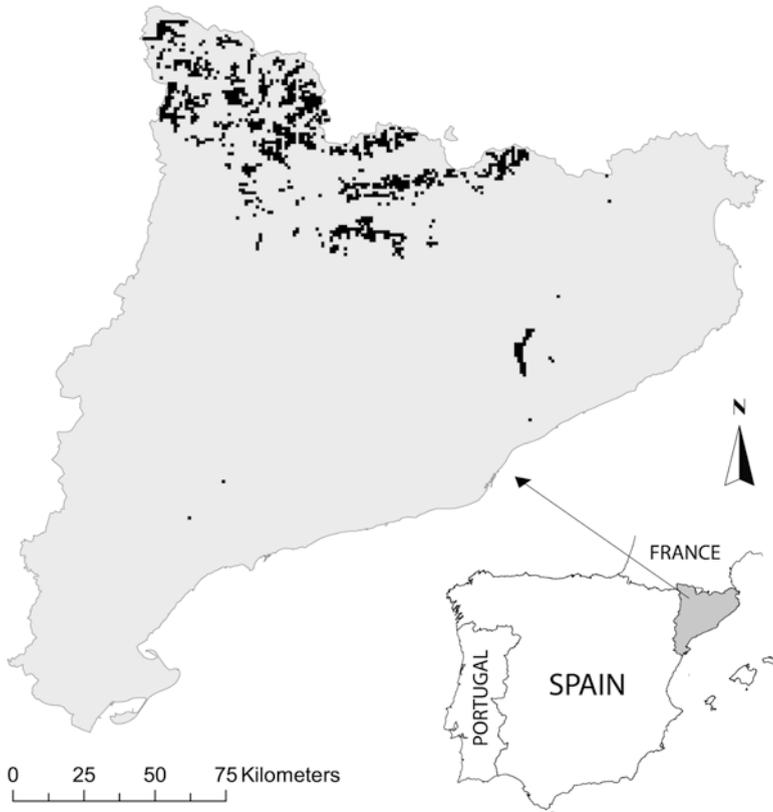


Figure 14.3 Location of the study area (Catalonia, NE Spain) and capercaillie habitat shown in *black* (see text for further details)

Habitat Mapping, Habitat Quality, and Node Creation

Habitat distribution data for the capercaillie in Catalonia (Figure 14.3) were obtained from the Catalan Breeding Bird Atlas 1999–2002 (Estrada et al. 2004). Presence–absence data were gathered in ~3000 UTM 1×1 km cells. Field survey data were used to build a niche-based model estimating probability of occurrence (ranging from 0 to 1) in 1×1 km cells (described further in Estrada et al. 2004). Probability of occurrence can be used as a measure of habitat quality, so cells with a higher probability were considered more suitable and able to support more individuals (Estrada et al. 2004). The **habitat distribution layer (capercaillie.shp)** is a slightly modified and simplified version of these data. Only cells with a probability of capercaillie occurrence ≥ 0.1 are considered habitat for Exercise 6. Cells were grouped into **117 habitat patches (or nodes)** comprising 1173 km² total habitat (Figure 14.3). **Habitat quality** was calculated as the average probability of occurrence for all the 1×1 km cells within a patch.

Both the amount and the quality of habitat are relevant patch characteristics for this habitat analysis. Thus, the **area-weighted habitat quality** is used as the node attribute (a_i) which corresponds to the product of habitat area \times habitat quality. The values of habitat area and quality are provided for each patch in the GIS layer. Remember, since the patch attribute is not simply area, we will use *EC* (Equivalent Connectivity) rather than *ECA* (Equivalent Connected Area).

Defining Links and Direct Dispersal Probabilities

Determining the strength of the links between habitat patches (p_{ij} values) involves two basic components (explained step-by-step, later in Exercise 6):

- **Conefor Inputs extension.** This runs in ArcGIS (or QGIS) and can be used to compute distances between the edges of habitat patches (d_{ij}) which are measured as Euclidean (straight-line) distances. This extension creates the connection file in the input format required by Conefor.
- **Median dispersal distance (d)** relates to the median distance individuals can reach when dispersing. When running Conefor, you will need to specify this distance. You will use a **5000 m** median dispersal distance for capercaillie (derived from Menoni (1991) for the Pyrenees). By definition, $p_{ij}=0.5$ for links between patches separated by distance d . For each pair of patches, p_{ij} values are calculated by Conefor using a (fairly typical) decreasing exponential function based on distance (e.g., Bunn et al. 2000; Hanski and Ovaskainen 2000; Urban and Keitt 2001; Saura and Pascual-Hortal 2007) where $p_{ij}=1$ when the distance between patches is zero. The exponential decay rate is determined by the probability and dispersal distance specified by the user (here 0.5, and 5000 m, respectively). Thus, in our case, patches separated by less than 5000 m will get assigned $p_{ij}>0.5$, while patches separated by distances larger than d will be assigned $p_{ij}<0.5$.

EXERCISE 6: Network Analysis for Capercaillie Habitat

Now you will analyze connectivity of the capercaillie habitat network using the *PC* metric from Conefor. This will enable you to evaluate the contribution of individual patches by examining *dPC* and its three fractions *dPCintra*, *dPCflux*, and *dPCconnector* for each node. In addition to the capercaillie (with median dispersal distance $d=5000$ m), you will also consider two hypothetical species dwelling in the same habitat with different dispersal abilities ($d=500$ m and $d=50,000$ m). You will compare results and conservation guidelines for these three species.

To do so, follow these steps, referring to the **Conefor Instructions Handout** when needed:

1. Make sure that the point (and not the comma) is set as the decimal symbol in the regional configuration settings in your computer. Conefor will expect all the numerical values having the point as the decimal separator and no thousand separator, and will write the results in the same format. In North America, you will likely not need to worry about this step.
2. Copy the entire folder **Exercise 6** to C:\temp\ or wherever your instructor is certain you have full read/write permissions.
3. Using ArcGIS or QGIS, open the capercaillie habitat layer (**capercaillie.shp**) and a layer of the study area boundary (**catalonia.shp**), located within the Exercise 6 folder. Examine the distribution of the habitat patches.
4. In the GIS, open and examine the attribute table in the **capercaillie.shp** file and make the following changes:
 - Create two new fields in the attribute table that correspond to the two columns needed in the Conefor node file. One field will contain a unique identifier (an integer) for each node whereas the other field (floating type) will contain the patch attribute. Name these two new fields **NodeID** and **AreaQual**, respectively.
 - Fill the **NodeID** field with unique integer values for each feature (patch). In ArcGIS this can be done using the internal feature identifier of the layer (FID) as $\text{NodeID} = \text{FID} + 1$, so that NodeID ranges from 1 to the total number of patches. If using QGIS, use the variable \$id to calculate the new field NodeID as $\text{NodeID} = \text{\$id} + 1$.
 - Calculate **AreaQual** so that it contains the value of the attribute for each patch. Recall that here, this attribute equals the product of habitat patch area \times habitat quality.
5. Use the provided **Conefor Inputs extension for ArcGIS** or QGIS to generate the node and connection files in the format required for Conefor. The Conefor Inputs extension will calculate Euclidean (straight-line) edge-to-edge distances (here in meters) between all pairs of patches in the layer, and present this information in the **connection file**. (*NOTE:* In ArcMap, you may need to select **Customize—Toolbars**—and select **Conefor**):
 - In the ArcGIS extension, select to compute distances between all features.
 - Select to calculate distances from feature edges.
 - In the ArcGIS extension, use the **ASCII text** file as the output option.
 - The names of the node and connection files will typically be: **nodes_capercaillie.txt** and **distances_capercaillie.txt**.
Check the online Conefor Inputs extension user manual (available from www.conefor.org) for further details on the usage of the extension if needed.
6. Open the two text files generated by the Conefor Inputs extension with any text editor and check for consistency before proceeding. (*NOTE:* The point “.” should be the decimal separator symbol and no thousand separator should be in the numbers. For example, 1234.5 is correctly formatted whereas 1,234.5 or 1234,5 is not. Refer back to Step 1 if needed.)

7. Use Conefor to perform a network connectivity analysis with the *PC* metric using the node and connection files generated in the previous step. Specify the median dispersal distance for the capercaillie ($d=5000$ m, corresponding to a $p_{ij}=0.5$). **See the Conefor Instructions Handout** for more details on using this software.
8. Save the following two files generated by Conefor:
 - **overall metric values** (containing the *PCnum* and *EC(PC)* values for the entire habitat network)
 - **node importances** (containing the values of *dPC* and its three fractions for every patch). The node importance file will also contain the *dA* values for every node, which is the percentage (%) of the total landscape attribute within a particular node (i.e., a_i for a patch i divided by the sum of a_i for all nodes). *dA* is not a connectivity metric but rather a useful “network-independent” reference to compare with the connectivity metrics, as you will do later in this exercise.
9. Open the node importance file as a table in ArcGIS or QGIS and join the numerical results to your original capercaillie habitat layer, based on the common field (node ID).
10. Repeat the analyses in steps 7 and 8 for two other hypothetical species with different median dispersal distances of $d=500$ m and $d=50,000$ m. See the **Conefor Instructions Handout** for more details if needed.

Q10 What is the Equivalent Connectivity *EC(PC)* value for capercaillie habitat in Catalonia? How can this value be interpreted? What are the *EC(PC)* values for the other two hypothetical species with $d=500$ m and $d=50,000$ m?

Q11 Without using Conefor, what are the minimum and maximum possible values of *EC(PC)* for this set of habitat patches? Consider two hypothetical species with zero and infinite dispersal abilities to answer this question.

Q12 Visually examine the capercaillie connectivity results using GIS. You might consider seven classes and natural breaks (jenks) to classify patches by importance values. According to *dPC*, which habitat areas are most important in maintaining overall habitat connectivity and availability?

Q13 How do the three fractions of the *dPC* metric (*dPCintra*, *dPCflux*, *dPCconnector*) distinguish the roles of different patches in the habitat network? Which patches likely exchange a larger number of individuals with other habitat areas? Which patches are best connected to the rest of the habitat in the landscape? Which patches function as important, somewhat irreplaceable stepping stones?

Q14 How important is the contribution of the three *dPC* fractions to total habitat connectivity and availability for the capercaillie? To answer this, determine the relative contribution made by each fraction. Compute this as the ratio between the sum of the delta values for a particular fraction across all the

patches, divided by the sum of the total dPC values across all patches. See the **Conefor Instructions Handout** for details.

- Q15** Given the relative importance of these three fractions, which of the three patch roles is more appropriate for this network and species? How should management approach the spatial priorities for capercaillie conservation?
- Q16** Respond to the same questions as in Q14 and Q15, but now consider the other two species using the same habitat ($d=500$ m and $d=50,000$ m). Do the primary roles of habitat patches change as different species are considered? What implications does this have for the conservation of each species?
- Q17** Determine the sum of the dPC values for all the habitat patches for the capercaillie ($d=5000$ m). Does this value exceed 100%? Why?
- Q18** Plot the dA values (X -axis) against the dPC values (Y -axis) for capercaillie patches ($d=5000$ m). How similarly do dA and dPC prioritize patches? That is, are the most important patches ranked similarly?
- Q19** Produce three new plots as above but instead with each of the dPC fractions (dPC_{intra} , dPC_{flux} , $dPC_{connector}$) in the Y -axis. Which of the fractions are more and less related to the local patch attributes (dA)? Why is this so?
- Q20** Produce similar plots for the two species where $d=500$ m and $d=50,000$ m. What has changed, and why? Do local attributes (of individual patches) have more or less weight on the prioritization of patches given by the metric of habitat connectivity and availability?

CONCLUSIONS

Many connectivity metrics have been developed and the choice of metric depends on the question at hand. However, to inform conservation planning or to evaluate the impacts of landscape change, metrics that only consider interpatch connectivity may provide misleading results. Connectivity should not be solely conceived of, or defined as, connectivity among patches in many cases. Rather, connectivity should be viewed as a landscape-level property describing the amount of habitat resources a species can reach: a combination of the resources within patches as well as those which can be reached via connections to other patches. Ecologically, it seems reasonable that the amount of reachable habitat may be more related to species persistence than (a) the total amount of habitat in the landscape (which ignores the likelihood of movement among the different patches) and (b) the connections among patches (which may not compensate for having less total habitat distributed in many smaller patches).

The *IIC* and *PC* metrics have been developed to address this new way of conceiving connectivity as the amount of reachable habitat. They provide enriched indicators which incorporate the role of habitat amount and local patch characteristics in influencing connectivity. At the same time, they move beyond spatially blind assessments by incorporating connectivity among patches. The *intra*, *flux*, and *connector* fractions allow for comparison of the different ways habitat patches contribute to habitat connectivity and availability. These fractions are measured in a common currency within an integrated conceptual and analytical framework enabling objective decision-making. When using *IIC* or *PC*, there is no risk of either overemphasizing or underestimating the importance of connecting elements between habitat patches when setting conservation priorities, since both alternatives are integrated and jointly considered in the same analysis.

FURTHER APPLICATIONS

Through this chapter, you have learned to understand the *IIC* and *PC* metrics and the Conefor freeware package, and applied them to a real-world case study. There are however many other ways in which these concepts can be applied. The same analytical approach and metrics can be applied to guide restoration to increase landscape connectivity, or to help to identify focal areas to halt the spread of undesired diseases, forest fires, or invasive species. Additional applications throughout the world are provided at <http://www.conefor.org/applications.html>, where more details and references are available. Additional applications include using *IIC* and *PC* in the analysis of pond or river networks, endangered species conservation plans, design of urban ecological networks, seed deposition patterns by frugivorous birds, and applications in combination with least-cost paths and circuit theory models. Other applications include assessments of directional (non-symmetrical) connectivity, evaluations of transnational protected area networks, mitigating barrier effects of transportation infrastructure, quantifying network vulnerability, evaluating long-distance spread over multiple generations, as well as assessments of the role of connectivity in influencing species diversity, distributions, colonization, or genetic diversity. The inspiration found in such applications, together with the understanding and practical skills that you have acquired throughout this chapter, should enable you to adapt and apply these approaches to other landscape management plans and research projects.

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