

# Chapter 12

## Assessing Multi-Scale Landscape Connectivity Using Network Analysis

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### OBJECTIVES

Landscape connectivity has implications for many ecological processes, including spread of invasive species and conservation of native ones. Because species have different minimum area requirements and different movement abilities, landscape designs suitable for one species (or group of species) may be inappropriate for other species. Methods from network analysis can be used to combine information on landscape pattern and species life history characteristics for species-specific assessments of potential connectivity. The lab is intended to provide students with the following:

1. An introduction to the concepts of landscape connectivity and network analysis;
2. Practice defining the basic elements of the landscape network including nodes, links, and components;
3. Exploration of simple measures of connectivity related to dispersal, home range, and species persistence;
4. Ways to construct and compare landscape networks for different species with differing perceptions of the landscape;
5. Consider how protected areas form networks of potential connectivity; and
6. Discuss simplifying assumptions of the approach and how methods for quantifying connectivity may differ in contrasting landscapes.

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Exercises in Part 1 assess potential connectivity on a highly fragmented simulated landscape for two species with different life history characteristics, using pencils/markers and the provided map. You will then calculate and compare two simple metrics of landscape connectivity for these two networks. In Part 2, you will examine the consequences of landscape connectivity for protected lands in the Willamette Valley ecoregion of the United States in a more realistic example. You will examine three species with differing minimum area requirements and movement abilities (ranging from large carnivores to rodents). While a variety of software programs can automate most of these analysis procedures, it is worthwhile to construct your first networks “by hand” as you learn the concepts and calculations; thus, the exercises in this chapter have been simplified and do not require a computer. Two subsequent chapters in this text (see Chapters 14 and 20) provide more detailed applications of network analysis that build on and assume familiarity with the concepts in this lab.

## INTRODUCTION

One of the biggest problems in conservation biology and biogeography today is the alteration of landscapes and loss of native habitat (Richardson and Whittaker 2010). Landscape fragmentation has potential implications for many ecological processes. As habitats become more fragmented and separated, and the intervening matrix becomes more dangerous and inhospitable, native populations experience a loss of genetic variation and/or permanent extinction. Barriers to immigration and recolonization may be especially detrimental as species attempt to adapt to other stressors such as those associated with climate change. As a result, it has become essential to accurately measure landscape connectivity and understand its effects on major ecological and evolutionary processes. Landscape ecology offers specific tools for the quantitative study of landscape connectivity among fragmented habitat patches.

### Landscape Connectivity

Landscape connectivity is a measure of how well the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993). In fragmented environments, connectivity of habitat patches is important for movement of genes, individuals, populations, and species over multiple time scales (Fahrig and Merriam 1985). Over the short term, it affects the success of juvenile dispersal and thus recolonization of empty habitat patches (Clergeau and Burel 1997). At intermediate temporal scales, connectivity affects migration, persistence of metapopulations (Hanski and Gilpin 1991; Ferreras 2001), and genetic diversity (Dixo et al. 2009; Angelone and Holderegger 2009). Over longer time frames, connectivity influences the ability of species to adapt, expand, or alter their ranges in response to climate

change (Lyford et al. 2003; Opdam and Wascher 2004). Habitat connectivity is especially important when habitat is degraded, rare, fragmented, or otherwise sparsely distributed (Flather and Bevers 2002; King and With 2002; Fischer and Lindenmayer 2007).

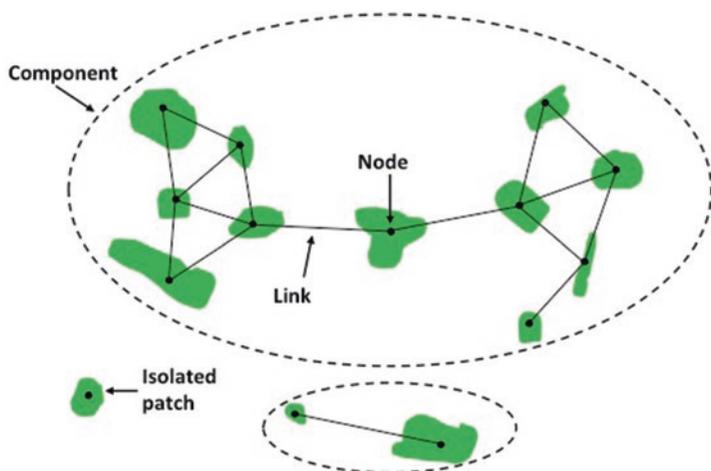
Landscape connectivity can be defined in many ways (Calabrese and Fagan 2004). **Structural connectivity** refers simply to landscape pattern and is not necessarily associated with the movement behavior of any particular organism. **Functional connectivity**, on the other hand, includes information on the movement of organisms in response to landscape pattern; this is a species-specific measure of connectivity. Functional connectivity may take two forms: **actual connectivity**, which requires detailed observations of the movement of individuals, and **potential connectivity**, where life history data on mobility are used to estimate movement pathways. Potential measures of connectivity, such as those derived from network analysis, are thought to be the most cost effective for addressing questions of basic ecology and applied natural resource management in both terrestrial and marine ecosystems (Calabrese and Fagan 2004; Grober-Dunsmore et al. 2009).

It is also necessary to distinguish between **landscape connectivity**, where connectivity is seen as a property of the entire landscape, and **patch connectivity**, where connectivity is seen as a patch-level attribute (Kindlmann and Burel 2008). Within a landscape, each patch may have a different level of connectivity—some may be highly connected to other patches while others may be completely isolated. Methods of network analysis, based on the mathematics of graph theory, are useful here as well. The patch-based data structure lends itself naturally to assessment at both of these levels.

## Network Analysis

Network analysis has been proposed as a simple solution to unify and evaluate multiple aspects of habitat connectivity (Kadoya 2009; Urban et al. 2009). Although relatively recently introduced to landscape ecology (Urban and Keitt 2001; Jordan et al. 2003), network analysis is a well-developed body of research often used in the computer and social sciences that quantifies connectivity and flow in networks (Harary 1969). A **network** is a set of **nodes** (points) connected by **links** (lines); a link between points indicates a connection between them. In the case of landscape networks, nodes represent habitat patches or local populations, and links indicate interaction or dispersal among populations (Figure 12.1). The approach can quantify either structural or functional connectivity, but, because it typically uses information on dispersal processes to define patch connections, it is especially useful for quantifying potential connectivity.

Nodes and links are the two fundamental elements that define the landscape network. Discrete patches of habitat are represented as nodes, invoking an island view of discrete habitat islands in a “sea” of nonhabitat (i.e., the matrix). The network approach connects patches with links if they are within some user-specified (and



**Figure 12.1** An example of a landscape network with network features identified. Links are drawn from node to node (i.e., *patch centroids*), as is conventional, even though the distances are measured from patch edge to edge. All patches (*shaded polygons*) in this example are considered large enough to be suitable habitat for the species of study. Largest component = 0.77; link density = 0.18; degree centrality of labeled node = 2 links; domain of labeled node = 10 nodes

preferably ecologically relevant) distance of each other or connected by corridors. Networks can be represented graphically, as in Figure 12.1, or in a connectivity matrix. A connectivity matrix is a table with information about the connectivity (or lack thereof) of every pair of nodes. The links might be binary (connected or not) or they might be weighted, specifying the strength of a connection between two nodes. For example, the weights might represent geographic distance or likelihood or rate of dispersal. Links also might indicate movement in multiple directions among patches or they might be directional, designating preferred pathways of flow.

Scores of metrics are available for characterizing connectivity based on properties of the network (Pascual-Hortal and Saura 2006; Bodin and Norberg 2007; Kindlmann and Burel 2008). Some of these are relevant to properties of the entire landscape—i.e., landscape connectivity. Others assess connectivity of an individual habitat patch—i.e., patch connectivity (Table 12.1). At the landscape scale, groups of connected patches are called **components** (Figure 12.1). By definition, dispersal can occur among patches within a component but not among patches of different components. One rather intuitive measure of landscape connectivity is an index of the size of the **largest component**, simply calculated as the proportion of suitable habitat on the landscape that is connected within the largest component (Ferrari et al. 2007). This metric is informative about the potential for large-scale population processes on the landscape: many small components suggest isolated subpopulations, while large components suggest a well-mixed population.

Another basic measure of landscape-level connectivity is the link density of the network. **Link density** is defined as  $L/[n(n-1)/2]$  where  $L$  and  $n$  are the number of

**Table 12.1** Definitions of network connectivity metrics used in these exercises

	Term	Units	Definition
Landscape-level metrics	<i>Largest component</i>	Unitless	Area of habitat contained in the largest component ( $H_{LC}$ ) divided by the total amount of suitable habitat area ( $H_T$ ) where only patches $\geq$ minimum size are considered suitable. $H_{LC}/H_T$
	<i>Link density</i>	Unitless	Number of links ( $L$ ) in the network divided by the maximum number of links possible. $L/[n(n-1)/2]$ ; where $n$ = number of suitable nodes
Patch-level metrics	<i>Degree centrality</i>	Links	Total number of links for a node. This is a very local measure of patch connectivity (i.e., only accounts for nearest neighbors)
	<i>Domain</i>	Nodes	Total number of nodes reachable from the node. This is a larger-scale measure of patch connectivity (i.e., extending to entire component)

links and nodes in the network, respectively (Royer et al. 2008). The denominator represents the maximum POSSIBLE number of links of links in the network. Landscapes with a large number of links relative to the number of patches should be well connected. The more links, the greater the redundancy in the network and the less vulnerable the landscape to the loss of any individual connection (e.g., through loss of habitat or addition of a dispersal barrier such as a road). Systematically removing either the nodes (Urban and Keitt 2001) or links (Lookingbill et al. 2010) from a network and evaluating the effects on connectivity can be an informative exercise for evaluating the vulnerability of landscapes to habitat loss and fragmentation.

Connectivity metrics also can be used to examine more localized issues of patch occupancy, population stability, and genetic diversity. Patch-level metrics are useful for this purpose because they can quantify the structural importance of habitat patches within the landscape network (Galpern et al. 2011). Two commonly used measures are degree centrality and domain (Table 12.1). **Degree centrality** is the number of direct connections for a given habitat patch (nearest neighbors). This is ecologically similar to the number of patches within a given distance or patch density (e.g., van Dorp and Opdam 1987). A **hub** is a node with very high degree (i.e., a patch with many neighbors), while an **isolated node** has no neighbors (Figure 12.1). From an applied perspective, hubs might be identified and targeted for protection to facilitate rapid species migration. **Domain** is a measure of the number of other nodes that are reachable from a node, which is equivalent to the size of the component containing the node (De Nooy et al. 2005). While these patch-level metrics describe connectivity of individual patches, they measure connectivity at different scales. Degree measures connectivity at the most local scale (the number of immediate neighbors), while domain measures how connected a patch is to the broader landscape.

## Conservation Networks

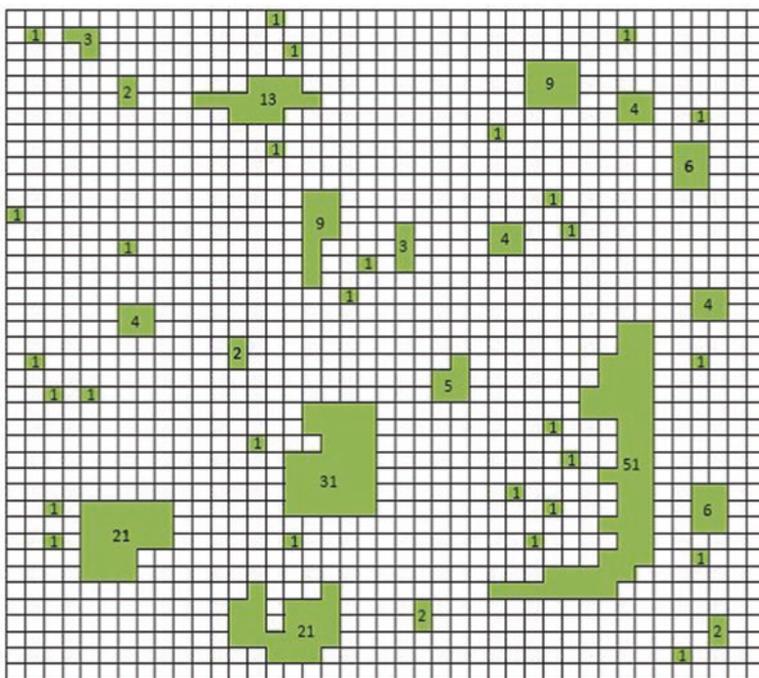
Landscape ecology has become highly invested in habitat connectivity and its implications for populations (Tischendorf and Fahrig 2000; Fahrig 2003; Calabrese and Fagan 2004; Crooks and Sanjayan 2006; Fischer and Lindenmayer 2007), and the application of network analysis has erupted over the last few years. Network analysis offers a valuable set of tools for conservation that are visually intuitive, computationally efficient, and easily interpretable for conservation management. In particular, a network representation is often used to invoke a metapopulation model with subpopulations interacting across a fragmented landscape (Estrada-Pena 2005). Network analysis has been applied to the design and assessment of reserve networks (Saura and Pascual-Hortal 2007; Minor and Lookingbill 2010), the identification of important movement corridors or habitat linkages (Jordan et al. 2003; Morzillo et al. 2011), and the detection of population sources and sinks (Minor and Urban 2007; Treml et al. 2008). Because the construction of the landscape network is dependent upon species life history characteristics, most of these applications are species specific.

Species have different perceptions of the landscape in which they live. These perceptions inform what constitutes a patch of suitable habitat, as well as the willingness to traverse through the matrix to a neighboring patch (Pe'er and Kramer-Schadt 2008). In network terms, the nodes and the links in any network will likely differ for different species on the same landscape. Large-scale conservation plans should consider landscape connectivity from the perspective of all relevant species groups. Generalizations for different species groups are valuable for multi-species applications such as designing green infrastructure or marine protected-area networks. For mammals, there is a strong linear relationship between what a species perceives as a patch (a function of home range size) and its maximum possible dispersal distance (Bowman 2003). Both of these factors scale with body size such that small mammals have small home ranges and short dispersal distances; intermediate-sized mammals have intermediate home ranges and intermediate dispersal distances; and large mammals have large home ranges and longer dispersal distances. This allometric scaling relationship can be used to construct landscape networks to evaluate connectivity of protected-area networks for general classes of mammals based on their body size (see West et al. 1997 for further background on allometric scaling laws).

Spatial data about the protected areas in the United States are available from the Conservation Biology Institute (CBI 2012). Such data could represent potential patches for use in a network analysis. For example, reserves could be identified that meet the minimum home range requirements of a particular group of species (e.g., 1000 ha for large mammals). Two reserves could be considered linked if they were as close as (or closer) than the maximum dispersal distance for the species group (e.g., 100 km for large mammals). Network representations could be constructed for different species groups, and the resulting networks would differ in both the spatial configuration of patches (e.g., the reserves included in a large-mammal protected-area network would be a subset of the reserves in a small-mammal protected-area network) and the rules used to create links (e.g., large mammals have the potential to travel farther than small mammals).

To learn the basic concepts of network analysis, Part 1 begins with a simulated landscape and hypothetical species to illustrate two metrics of landscape connectivity. In Part 2, we present protected-area networks based on CBI data for three mammals in the Willamette Valley ecoregion of the western United States. The three networks facilitate comparisons among species inhabiting the same landscape in order to illustrate metrics of patch connectivity.

## Part 1. Introduction to Landscape-Level Connectivity



**Figure 12.2** Hypothetical landscape for Exercise 1. Habitat patches are labeled according to their size. The total number of habitat cells (*shaded*) on the landscape is 230 divided among 48 patches. Note that not all of this area is suitable for both species and depends on the size of the patch

### EXERCISE 1: Constructing Networks by Hand

In this exercise, you will assess potential connectivity for two species on a simulated landscape with a high level of fragmentation (13% of the habitat remains on the landscape). Your first step is to construct the landscape networks using a pencil, the map found in Figure 12.2, and the life history characteristics described below. You will then calculate two simple metrics of landscape connectivity and compare

the values for the two networks. Although computer programs can be used to automate most of these processes, it is a worthwhile exercise to practice constructing a network by hand.

1. Print (or copy) Figure 12.2.
2. From this map of potential habitat, identify the suitable habitat patches (or nodes) that meet the minimum area requirement for a hypothetical small mammal (see Table 12.2). Shade or color these areas.
3. Next, on either separate pieces of paper or in different colors on the same map, identify and shade the patches that meet the minimum area requirements for a large mammal as defined in Table 12.2 (i.e., identify its suitable habitat).
4. Using the maximum dispersal distances (defined in Table 12.2), draw the links among nodes of suitable habitat for each of the two species. Links should be drawn and measured as the shortest distance between patches. To do this, start counting from the edge of a habitat patch; diagonal distances count as only one cell length so it is possible to move in eight directions from a given cell (i.e., an 8-neighbor rule). If the edge of a new habitat patch is reached within the allowable number of steps, then the two patches are connected. Dispersal can occur across any kind of cell (habitat or nonhabitat).
5. Using the definitions provided in Table 12.1, calculate the **largest component index** and **link density** for each of the two species and add these values to Table 12.2.

- Q1** Which species had the greatest connectivity for this landscape (by measure 1 (the largest component index), by measure 2 (link density)? Show your work.
- (a) How do you think the differences in landscape-level connectivity would affect the long-term persistence of the two species on the sample landscape?
  - (b) Landscape connectivity measures by themselves may not provide sufficient information for a species conservation plan. How might the total amount of habitat and number of patches in each of the networks also be important for the long-term persistence of a species? What other information about the landscape would be useful?

**Table 12.2** Landscape-level connectivity metrics for Exercise 1

	Minimum habitat requirement (cells)	Maximum dispersal distance (cells)	Largest component index	Link density
Small mammal	1	2		
Large mammal	16	32		

The largest component index and link density should be calculated for the two species and inserted in the table

- Q2** Define the concept of an umbrella species as it is applied to conservation (you may need to look this term up in an ecology text if you not familiar with it).
- What can you say about the ability to generalize about connectivity from one species to another based on the results from this exercise?
  - Given what you have observed about the habitat connectivity and total amount of habitat area for these two species on the sample landscape, what specific conservation actions would you recommend for the small mammal? for the large mammal?
- Q3** A developer would like to remove some of the habitat to create a subdivision on a parcel of property, four cells in area, somewhere on the landscape.
- Where would be the most detrimental place(s) to locate this subdivision (circle on Figure 12.2)? Would this location be the same for the two species? Provide a rationale for your choice(s).
  - To offset development elsewhere, the developer is required by law to create four cells of new habitat somewhere on the landscape. What would be the best strategy for adding this habitat to the existing map (ignore the loss of habitat described in the previous question)? Options may include adding property to existing patches, creating new patches, random placement of new habitat, etc. You should consider multiple strategies and the potential impacts to each of the two species, but ultimately a total of only four new habitat cells will be created. Draw the four cells on Figure 12.2 and provide a rationale for your choice.

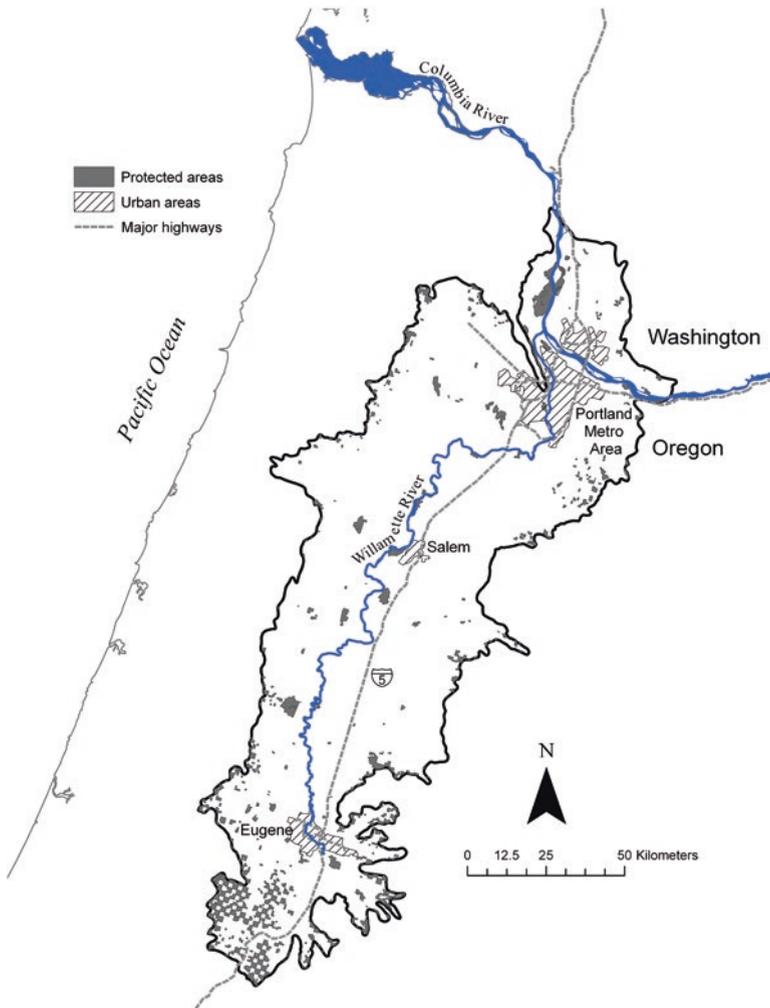
## Part 2. Consequences of Connectivity

### EXERCISE 2: Analyzing Landscape- and Patch-Level Connectivity

In this exercise, you will examine the consequences of landscape connectivity among protected lands in the Willamette Valley ecoregion of the United States from the perspectives of a regional planner, wildlife biologist, and pathologist. A map of the ecoregion derived from the Conservation Biology Institute (CBI) GIS-based Protected Areas Database is provided (Figure 12.3).

Only sites with a land stewardship status 1 or 2 in the USGS GAP analysis program will be considered strictly “protected” in your analysis (Scott et al. 2001), thus ensuring the highest level of biodiversity protection. Any adjacent protected areas with differing ownership, but sharing a boundary, were merged into a single unit (i.e., patch or node) for subsequent network analysis.

The potential connectivity of three different species has been analyzed for this map of protected areas (Figure 12.4). Each species has different minimum area requirements and movement abilities which are related as per Bowman (2003).



**Figure 12.3** Overview map of the Willamette Valley ecoregion showing prominent landscape features and all protected lands

Tables of landscape- (Table 12.3) and patch-level (Table 12.4) connectivity metrics have been provided for each of the species. You will use this information to answer questions about the size and spatial configuration of the protected areas for the three species, and how the life history differences among species should influence their management.

1. Examine the three separate representations of potential connectivity based on the distribution of protected areas (Figure 12.4). One is for wolves with a home range of 1000 ha and a dispersal distance of 100 km; a second is for foxes with a



**Figure 12.4** Landscape networks of potential connectivity for protected areas in the Willamette Valley ecoregion calculated for mice (*Panel a*), foxes (*Panel b*), and wolves (*Panel c*) based on the parameters provided in Table 12.3. Nodes represent protected lands of sufficient size to provide suitable habitat for the species and do not represent actual presence or absence of species

**Table 12.3** Landscape-level connectivity metrics for protected areas in the Willamette Valley ecoregion calculated for three species

	Home range (ha)	Maximum dispersal distance (km)	Largest component index	Link density
Mouse	1	1	0.35	0.02
Fox	100	10	0.45	0.07
Wolf	1000	100	1.0	0.67

**Table 12.4** Patch-level connectivity metrics for protected areas in the Willamette Valley ecoregion calculated for three species

Node	Size (ha)	Mouse		Fox		Wolf	
		Degree (links)	Domain (nodes)	Degree (links)	Domain (nodes)	Degree (links)	Domain (nodes)
1	4499	2	9	4	6	1	2
4	222	2	9	2	6		
5	783	9	9	2	6		
13	101	0	0	0	0		
15	166	0	0	3	6		
17	404	0	0	3	6		
20	249	2	4	3	6		
23	752	0	0	0	0		
26	206	0	0	2	2		
30	127	2	2	2	2		
39	146	1	1	2	2		
41	231	0	0	2	2		
44	238	1	1	1	6		
46	867	1	1	2	2		
48	133	1	1	2	2		
53	358	0	0	0	0		
54	184	1	1	1	1		
55	539	1	1	1	1		
56	959	0	0	0	0		
58	1108	0	0	0	0	2	2
63	2172						
66	133						
75	132						
Mean		1.2	2.0	1.5	2.5	1.3	2.0

For simplicity of presentation, values are provided for only a subset of the 76 nodes contained within the mouse-based network; mean values have been calculated over all nodes. Blanks have been left in the table for the values for the last three nodes and should be filled in as part of Exercise 2. *NOTE:* Mean values are provided as the average number of links per node and average number of nodes reachable per node

home range of 100 ha and a dispersal distance of 10 km; and the third is for mice with a home range of 1 ha and a dispersal distance of 1 km.

2. Examine the tables of connectivity metrics for each of the three networks (Tables 12.3 and 12.4). In particular, note that Table 12.4 provides information for individual patches. These values have been calculated using Pajek (De Nooy et al. 2005) a freely available Windows-based program for analyzing large networks (<http://pajek.imfm.si/>).
3. Fill out the missing values in the three bottom rows of Table 12.4. Use the information from the maps and tables to answer the questions below.

**Q4** Compare the overall landscape-level connectivity for the three different species (i.e., largest component index and link density).

- (a) Which species would have the highest connectivity assuming it relied solely on protected lands? Which species is potentially least connected?
- (b) How do these results compare to your expectations from Exercise 1? Do you see similar or dissimilar patterns?

**Q5** Compare the mean patch-level connectivity metrics for the three species (i.e., degree centrality and domain).

- (a) Which species seems to be best connected by these measures? Which species is potentially least connected?
- (b) How does this compare with your assessment from Question 4? Which species would you expect to experience the most problems due to isolation in the ecoregion according to these results?

**Q6** Imagine you were asked to prioritize regional spending for habitat improvement on protected lands. Consider the relative importance of a specific patch (patch 1) to connectivity.

- (a) Is the patch equally important to the overall, broad-scale connectivity of the landscape for all three species relative to other protected areas in the ecoregion? Are other patches more important?
- (b) Is the patch equally important to local dispersal movement for all three species relative to other protected areas in the ecoregion?

**Q7** Imagine you were a wildlife biologist tasked with establishing a reintroduction program for an endangered species of fox. Which patch would be the most logical location to transplant new individuals to maximize rapid dispersal of the species to other nearby patches? Include in your justification a statement about which metric is most important for this type of decision.

**Q8** Consider a mouse-borne pathogen that threatens humans and has begun to invade the ecoregion. Which patches would be logical locations to focus eradication efforts to try to control the spread of this disease? Include in your justification a statement about which metric is most important for this type of decision.

## SYNTHESIS

- Q9** For learning purposes, several simplifying assumptions were made in this exercise. For example, what implicit assumptions were made about the matrix when constructing these networks? What types of land covers and landscape features might violate these assumptions?
- Q10** Patch 1 in Exercise 2 represents the Sauvie Island Wildlife Area. What are two specific challenges that might reduce the actual connectivity of this patch to the rest of the protected areas in the Willamette Valley?
- Q11** Consider a landscape with a highly connected network of wetland patches.
- Imagine a four-lane highway planned to cross the landscape and intersect the network. What species groups are likely to be most negatively affected by the road? Why? Do not restrict your answer only to mammals.
  - Now imagine that instead of a road, portions of the upland landscape were proposed to be logged. What effects might this disturbance have on the landscape network? What types of species would likely be most affected? Why?
  - What strategies might be implemented to try to reduce the negative impacts of the road and/or the logging?
- Q12** Methods from network analysis can also be used to evaluate connectivity of riverscapes or seascapes (e.g., Grant et al. 2007; Treml et al. 2008; Almany et al. 2009; Grober-Dunsmore et al. 2009).
- What types of additional considerations might be required in conducting a network analysis of freshwater mussel populations within a stream network?
  - What additional factors should be considered in quantifying connectivity for marine environments?
  - Consider a scenario in which multiple sites are being assessed for potential inclusion into an existing marine protected-area (MPA) network. How might an emphasis on connectivity in deciding among the different sites be at odds with other network objectives?

## CONCLUSIONS

The ability to move among habitat patches is vital to ecosystem processes ranging from biological invasions to fire spread and climate adaption. Network analysis provides useful quantitative measures of potential connectivity. However, these measures are scale (and species) specific; thus, more research is needed to develop coherent strategies for the design of multi-species management plans. The development of new methods for quantifying the effect of the matrix on connectivity is another active and important research direction. In many cases, management actions

taken within the matrix may be the most effective approach to promoting connectivity. With these advances in the science and theory of connectivity, network analysis will continue to provide a robust set of tools to be applied to conservation challenges across terrestrial, aquatic, and marine environments.

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<sup>1</sup>NOTE: An asterisk preceding the entry indicates that it is a suggested reading.

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