

Modelling landscape connectivity for highly-mobile terrestrial animals:

a continuous and scalable approach

by

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ABSTRACT

Assessments of landscape connectivity are increasingly required in natural resource management. Understanding how landscape structure affects the movement and dispersal of animals may be essential for ensuring the long-term persistence of species of conservation concern. Functional connectivity models describing how features on the landscape influence animal movement behaviour have been produced in two different ways. The resistance surface models landscape connectivity as its inverse, the resistance to movement and dispersal, while the landscape graph represents landscape connectivity by describing the relationships among resource patches. Both methods have limitations that make them less effective for modelling highly-mobile and wide-ranging species such as ungulates and carnivores. This thesis develops a method called grains of connectivity that combines the continuous representation of landscape connectivity provided by resistance surfaces and the scalability provided by landscape graphs to create a flexible modelling framework for these species.

The first half of the thesis reviews the conceptual origins of the grains of connectivity method and examines its properties using simulated landscapes. In the second half, empirical evidence of movement and dispersal in a boreal woodland caribou (*Rangifer tarandus caribou*) population is used to validate functional connectivity hypotheses generated using the method. Connectivity for caribou at the temporal scale of generations is examined using a landscape genetics approach, while connectivity at the seasonal scale is assessed using the distribution of caribou telemetry locations.

Grains of connectivity may be most useful for study systems where animals are not found exclusively in well-defined resource patches and there is uncertainty in the behavioural parameters influencing movement and dispersal. Additionally, the scalability of the analysis can be used to selectively remove spatial heterogeneity that may be uncorrelated with movement and dispersal giving an improved description of the pattern affecting the landscape connectivity process.

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To
Florence Woolner and Jenny Morrow

for
their conspiracy and trickery

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INTRODUCTION

1.1. Context

Understanding how and why animals are distributed in space remains a fundamental question in ecology (Begon et al. 2005). Landscape connectivity extends this spatial question into the temporal realm: how *can* animals be distributed in space? What, if anything, may limit or encourage their movement? Natural resource managers are increasingly asking such questions in the course of their work (Freemark et al. 2002, Crooks and Sanjayan 2006). Can landscape change and habitat fragmentation disrupt the ability of animals to move (Epps et al. 2007, Jordan et al. 2007, Saura and Pascual-Hortal 2007, Schwartz et al. 2009)? Can corridors, or a network of protected areas, facilitate movement (Chetkiewicz et al. 2006, Sawyer et al. 2011)? How can biosecurity risks associated with the spread of pests, pathogens and invasive species be reduced (Margosian et al. 2009, Etherington 2012)? Are animals able to migrate in response to climate change (Heller and Zavaleta 2009)?

According to the widely-cited definition, landscape connectivity is "the degree to which landscape facilitates or impedes the movement among resource patches" (Taylor et al. 1993). It is the landscape, its features and their configuration with respect to resources, that will determine how or if animals will be able to change their distribution in space. It follows that in order to make predictions about this landscape for management purposes, or explain how its configuration has influenced ecological processes, a map is needed to identify the landscape features that may be important.

There is now consensus that such a map should not only describe landscape structure, but should also represent an animal's anticipated response to that structure (Goodwin 2003, Bélisle 2005, Kindlmann and Burel 2008). Functional connectivity, as this has been called, imposes a model of animal behaviour and interprets the landscape structure from the perspective of this model. In other words, it creates a map describing how an animal is likely to respond to a specific landscape configuration. Others have referred to this phenomenon as the perception of spatial heterogeneity by an animal, or how an animal "sees" and experiences the landscape structure (Baguette and Van Dyck 2007).

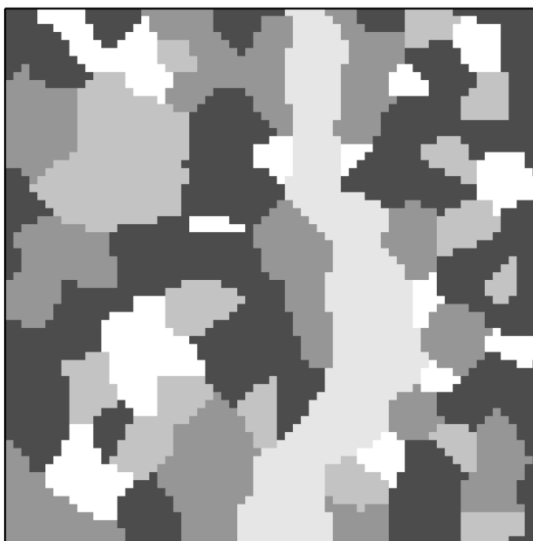
1.2. Resistance surfaces and landscape graphs

There are two distinct ways of producing functional connectivity maps (Fig. 1-1). Resistance surfaces describe landscape connectivity as its inverse, the resistance to movement and dispersal (Sawyer et al. 2011, Zeller et al. 2012). Typically these maps represent the degree to which landscape features contribute to this resistance by influencing animal behaviour and fitness (Fig. 1-1, a; Spear et al. 2010). The surface can be used to represent the landscape connectivity between any two points on the landscape as an effective distance using one of several metrics, of which least-cost path distance is the best-known example (Adriaensen et al. 2003, McRae et al. 2008, Pinto and Keitt 2009).

Figure 1-1. Two methods for mapping and modelling functional connectivity.

(a) Resistance surfaces describe the inverse of landscape connectivity, the resistance to movement and dispersal; (b) Landscape graphs describe the relationships between resource patches.

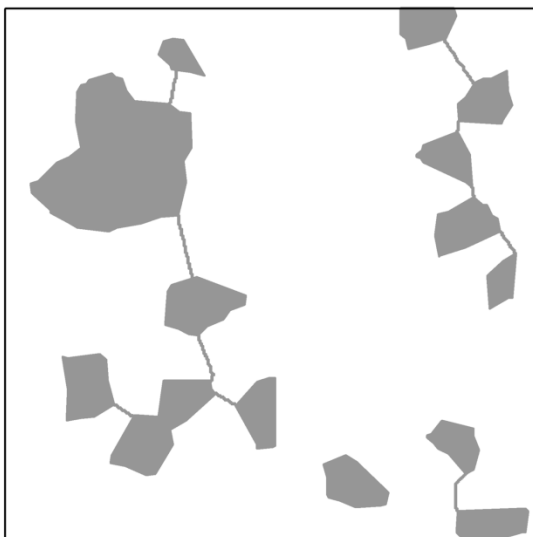
(a) Resistance surface



resistance units
per cell

- 100
- 5
- 8
- 1

(b) Landscape graph



■ graph node
(patch)

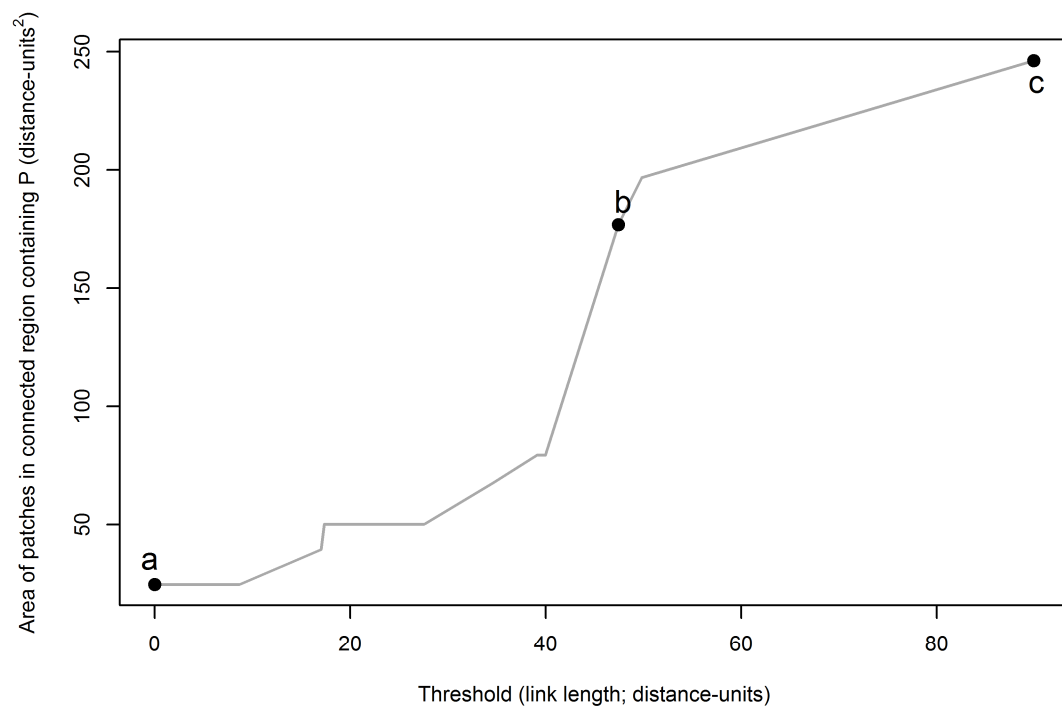
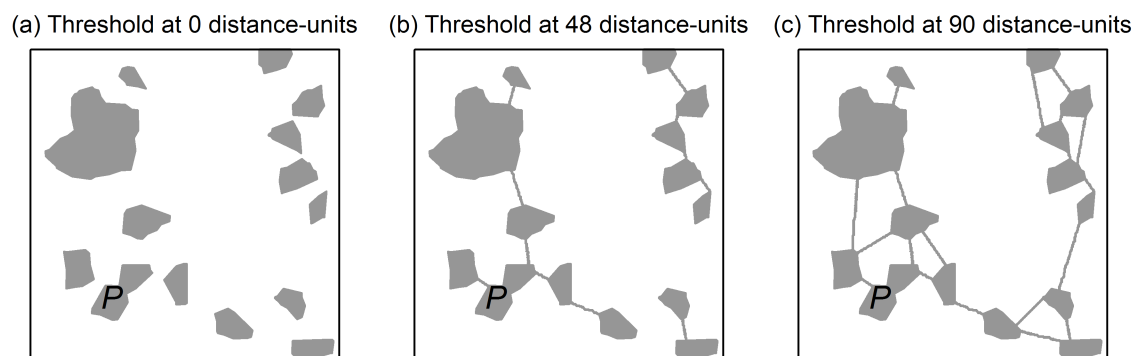
— graph link

A second class of functional connectivity model, the landscape graph, was developed to understand the connectivity relationships among resource patches (Cantwell and Forman 1993, Urban and Keitt 2001, Urban et al. 2009). These models have been preferred for organisms that are restricted to the resource patches such as amphibians in wetlands, or arboreal mammals inhabiting forested islands in agricultural fields (e.g. Bodin et al. 2006, Fortuna et al. 2006). The resulting maps are spatial representations of a mathematical graph or network, where patches are graph nodes, and potential paths for dispersal among patches are the graph links (Fig. 1-1, b; Fall et al. 2007, Dale and Fortin 2010). In their simplest form only a single behavioural parameter is required for these models: the maximum distance an animal is likely to disperse (Urban and Keitt 2001). However, models have been built with many more parameters, notably, in combination with the first type of connectivity model, the resistance surface, where least-cost paths are used to describe the dispersal paths among patches (e.g. Bunn et al. 2000, O'Brien et al. 2006, Jantz and Goetz 2008, Ziólkowska et al. 2012).

Resistance surfaces and landscape graphs, either alone or in combination, provide a flexible modelling framework for mapping the potential for future connectivity, or understanding how landscape has shaped past movement and dispersal. However, both methods have intrinsic limitations. Conceptually, landscape graphs make the most sense for organisms where the patch is easily defined, or has a high probability of use, and the landscape outside the patch, called the matrix, contains the structural features that reduce landscape connectivity (Urban and Keitt 2001, Urban et al. 2009). Many systems of

Figure 1-2. Thresholding a landscape graph to define connected regions at different scales.

Links represent the potential connections between patches. (a, b, c) As the link threshold value increases, longer links are added, resulting in larger connected regions. Thresholding is described in greater detail in Chapter 2. The dimensions of this square landscape are 400 distance units.



interest, however, are not this simple. Natural resource managers may wish to understand landscape connectivity for large terrestrial mammals, such as ungulates or carnivores, where the patch dependency concept can make little sense (Cushman et al. 2006, Epps et al. 2007, Schwartz et al. 2009).

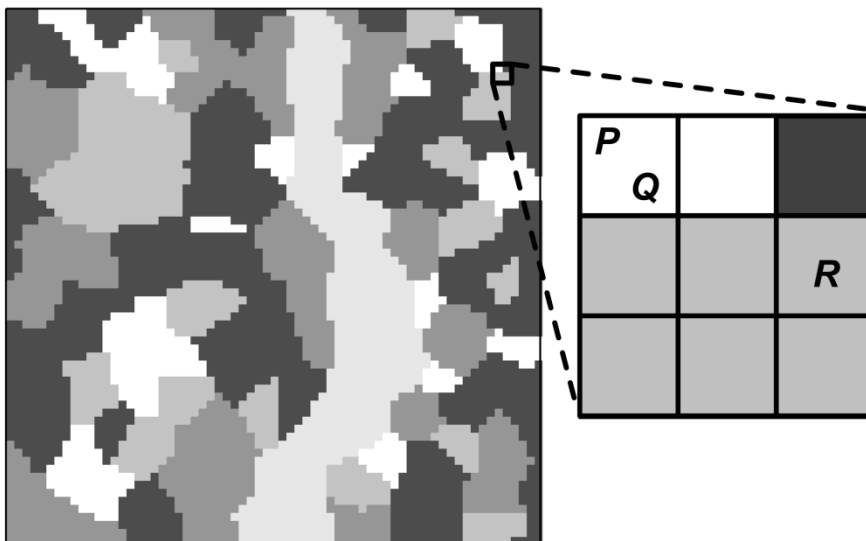
For these species, researchers have turned instead to resistance surfaces (Sawyer et al. 2011, Zeller et al. 2012). Here, the resource patch is not given any special importance and, if it makes sense to model it at all, is represented with a low resistance (e.g. Schwartz et al. 2009). As the word surface implies, landscape connectivity is understood as a continuous property, that, unlike in a landscape graph, can be modelled from or to any point on the landscape; animals need not be found exclusively in any one discrete feature (like a pond or forest fragment) for the model to make sense. This property takes care of the patch dependency limitation, but at the same time dispenses with an additional property of landscape graphs that may be critical for accurate modelling.

A useful property of landscape graphs is that they can be scaled to represent an increasing potential for landscape connectivity (Bunn et al. 2000, Brooks 2006, O'Brien et al. 2006, Treml et al. 2008). This process has been called thresholding, where resource patches are connected and understood to represent a single meta-patch (or in graph-theoretic terms a component) when the length of the links connecting patches is below a threshold value (Fig. 1-2). Building a landscape graph at successive threshold values has been called a scalar analysis of landscape connectivity (Brooks 2003), and can be used to control for the uncertainty in the maximum amount of dispersal an animal may exhibit. Each time

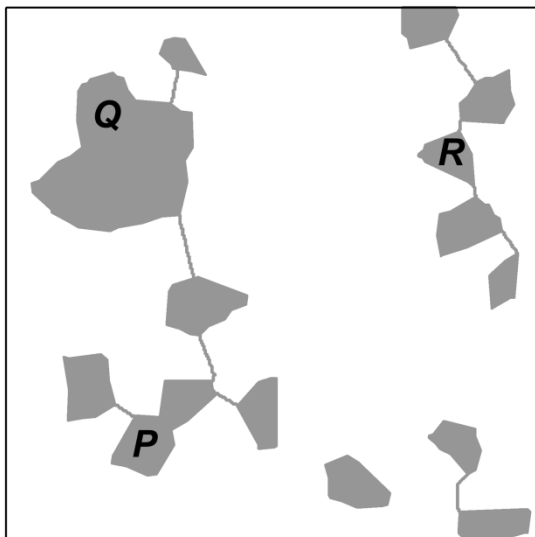
Figure 1-3. Raster cells are conceptually the same as patches in a landscape graph.

Both the cell and the patch define a region of high connectivity. (a, b) According to each model, locations P and Q are connected and are therefore effectively at the same location. Locations P and R are not connected in either model, implying that movement and dispersal between these locations will come at some cost to the animal.

(a) Resistance surface



(b) Landscape graph



the graph is built at a larger threshold value, it describes a state in which there is more landscape connectivity, and as more patches are connected into components, the size of the connected regions on the landscape also increases (Fig. 1- 2, bottom).

Resistance surfaces, on the other hand, have largely been used to model landscape connectivity at only one scale (Anderson et al. 2010). Rasters are the data structure universally used, and the scale of landscape connectivity described is given by the resolution or the grain of the data (Sawyer et al. 2011, Zeller et al. 2012). Fig. 1-3 demonstrates how a single raster cell is conceptually the same as a patch, or a component of connected patches on a landscape graph: both define a region of the map that is highly connected. It is therefore possible to scale landscape connectivity on a resistance surface by reducing the resolution of a raster (Anderson et al. 2010, Cushman and Landguth 2010). The larger cell sizes that result imply that more of the landscape is connected. In practice, however, this type of scaling has seldom been done, perhaps because coarsening the grain of the raster also results in a loss of other information about landscape structure that may be pertinent to connectivity.

Both landscape graphs and resistance surfaces, then, are similar in that they define areas of high landscape connectivity, and describe a functional response to landscape structure between these areas of high connectivity. But they differ fundamentally in how they can be scaled, in the shapes and sizes of the regions of high connectivity they describe, and in their continuous representation of the landscape.

1.3. Towards a continuous and scalable approach

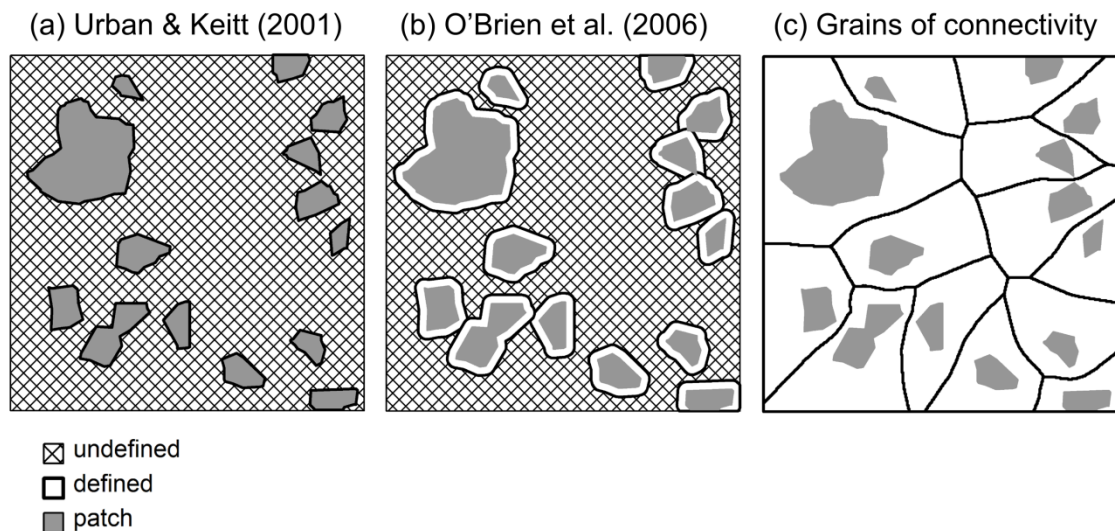
O'Brien et al. (2006) were perhaps the first to recognize the potential for using landscape graphs to model a continuous landscape connectivity process. In their woodland caribou study they built a landscape graph where patches were a vegetation feature selected by caribou. Because animals were not found exclusively in these patch types, they extended the definition of the patch by buffering it. Therefore the patch was understood to stand in for a larger region of the landscape, and in the model became an anchor for the connectivity process. The result was a model of landscape connectivity where more points on the landscape surface could be studied (Fig. 1-4, a, b). Because the model was a landscape graph it could also be scaled to describe higher amounts of connectivity, and as in other landscape graphs, scaling implied that multiple regions containing patches could be connected.

In this thesis, I develop a way of modelling landscape connectivity that extends the buffered patch concept of O'Brien et al. (2006) such that all areas of the landscape surface are defined for the landscape connectivity process (Fig.1- 4, c). Here, the landscape is understood as a continuous¹ but irregular tessellation, much like a resistance surface, where cells are polygons with large areas and variable shapes. On this tessellation, each polygon represents a high connectivity region centred on a focal patch or focal location, and the relationships among these regions are modelled using a landscape graph. I call this method *grains of connectivity* because each tessellation is a scale-dependent representation (i.e. a grain) of functional connectivity. In effect, this

¹Here, and throughout the term *continuous* suggests that the entire landscape surface is defined for the landscape connectivity process (i.e. movement can be modelled to or from any point on the surface). This wording is not intended to imply that these models are continuous functions in the mathematical sense.

Figure 1-4. Using a patch-based landscape graph model to achieve a continuous representation of landscape connectivity.

(a) As originally described (e.g. Urban & Keitt, 2001), connectivity on landscape graphs is only defined for animals that are restricted to patches; (b) O'Brien et al. (2006) used buffered patches to model connectivity for animals that may be found on or near patches. This increases continuity, but areas of the landscape can still be undefined for modelling connectivity relationships; (c) Grains of connectivity achieves continuous coverage of the landscape using a Voronoi tessellation which describes a region of proximity surrounding the patch. Grains of connectivity are explained in detail in Chapters 3, 4 and 5.



combines the continuous modelling of resistance surfaces, with the scalability of landscape graphs. This key contribution provides a means of representing landscape connectivity for study systems where evidence for patch dependency is weak or non-existent, and there is high uncertainty surrounding the behavioural parameters influencing movement and dispersal. Additionally, as I show in this thesis, the scalability of the analysis allows spatial heterogeneity that may be uncorrelated with movement and dispersal to be selectively removed, potentially giving an improved description of the structure affecting landscape connectivity. The overall goal of this work is to explore and test the grains of connectivity method for modelling functional connectivity in highly-mobile and wide-ranging terrestrial species, characterized by home ranges that are larger than the grain of available landscape data.

1.4. Thesis organization

The first half of the thesis is devoted to describing the mechanics of the grains of connectivity method and identifying its properties while the remainder applies the method to map and test functional connectivity hypotheses. The applied work focuses on a boreal woodland caribou (*Rangifer tarandus caribou*) population in central Saskatchewan, Canada. This ecotype of caribou is classified as threatened in Canada (Species At Risk Act; Government of Canada, 2003), and the Smoothstone-Wapeweka range, studied here, has been declared a population that is unlikely to be self-sustaining and at risk of extirpation (Environment Canada 2011a, b). Demographic indicators confirm that the population is under stress (Arsenault and Manseau 2011), and evidence for habitat fragmentation caused by natural and anthropogenic disturbance is plentiful

(Arlt and Manseau 2011). Although empirical support for caribou conservation measures is of great interest (Environment Canada 2011b), woodland caribou are not a convenient model organism to study functional connectivity: they occupy extensive landscapes at low density, they are highly mobile, and observations of movement and dispersal are costly to obtain. However, the challenges are similar in many other large terrestrial mammals of conservation concern, making this study system an excellent opportunity to demonstrate approaches to modelling that are directly relevant to natural resource managers.

The four research chapters in the thesis are written to stand alone as publications and each has its own specific audience and purpose. They are united in demonstrating the potential of grains of connectivity, and related methods, to address applied questions of landscape connectivity. Additionally, two chapters (Chapters 3 and 5) begin to develop a secondary theme. In these I motivate the concept of *functional grain*, originally expressed by Baguette & Van Dyck (2007), to serve as a generic term for the scale-dependent pattern influencing the landscape connectivity process. In this schema, the theoretical construct is the functional grain, and grains of connectivity is one method that can be used to identify this pattern.

An introduction to each of the four chapters follows, indicating the ways in which they contribute to the thematic whole.

1.4.1. Chapter two

This chapter, entitled *Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation* (now published in *Biological Conservation*, vol. 144, pp. 44-55), is a literature review for landscape graphs modelling. The paper surveys numerous variants of this modelling approach, including the minimum planar graph (Fall et al. 2007), that is used in grains of connectivity. This chapter primarily serves as context for the methods that are used in subsequent chapters, and explains how they may be advantageous for conservation and natural resource management.

1.4.2. Chapter three

The contribution of this chapter, entitled *Scaling landscape connectivity: comparing new and existing methods for measuring effective distance at multiple spatial grains* (in peer review), is an introduction to the properties of the grains of connectivity method. It demonstrates how the method works, and tests its effectiveness using simulated functional connectivity hypotheses intended to be representative of a highly-mobile terrestrial species. The paper introduces the concept of functional grain as the grain of the landscape connectivity process, and explores the comparative accuracy of grains of connectivity versus the spatial scaling of a raster resistance surface for representing this functional grain.

1.4.3. Chapter four

A major focus of research in the field of landscape genetics is the influence of reduced landscape connectivity on genetic variation (Manel et al. 2003, Balkenhol et al. 2009, Storfer et al. 2010). This paper, entitled *Grains of connectivity: analysis at multiple spatial scales in landscape genetics* (now published in *Molecular Ecology*, vol. 21, pp. 3996–4009), is intended for this audience. This is the first of two chapters that use empirical data to assess functional connectivity hypotheses for boreal woodland caribou in central Saskatchewan. Genetic similarity among pairs of individual caribou is used as a proxy for dispersal and gene flow over multiple generations, making this a test of the cumulative effects of functional connectivity over long temporal scales. The potential of scaling to remove spatial heterogeneity that may be uncorrelated with movement and dispersal is also explored.

1.4.4. Chapter five

The effects of functional connectivity on animal movement and dispersal may also be evident at shorter temporal scales, such as those captured using seasonal observations of animal distribution. The chapter, entitled *Exploring the dimensions of functional grain: testing patch and resistance models of landscape connectivity across spatial and seasonal scales*, is a direct extension of the work of O'Brien et al. (2006) to the grains of connectivity framework. Telemetry locations from caribou in central Saskatchewan are used to test the correspondence between animal distribution and functional connectivity hypotheses. The concept of functional grain is further developed as describing regions of high connectivity defined by the configuration of resource patches, the resistance of

landscape features or both. This paper also introduces a variant method called lattice grains of connectivity that is intended as a generalized way of producing scalable, continuous surfaces for landscape connectivity modelling.

1.5. Appendices

Two appendices are provided describing software developed to support the analyses in this thesis. The first is an abstract describing the *grainscape* package for R, the software used to implement grains of connectivity analyses in Chapters 3, 4 and 5. The second is an abstract describing the *allelematch* package for R (the publication describing the software is available in *Molecular Ecology Resources*, vol. 12, pp. 771-778). The *allelematch* package is used in Chapter 4 to identify unique multilocus genotypes in a collection obtained by non-invasive sampling of caribou fecal pellets.

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CHAPTER TWO

Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation¹

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2.1. Abstract

Graph theory has become a popular tool for modelling the functional connectivity of landscapes. We conduct a review of studies that use graph theory to model connectivity among patches of habitat (patch-based graphs), with the intention of identifying typical research questions and their associated graph construction and analysis methods. We identify and examine nine questions of conservation importance that can be answered with these types of graph models, discussing appropriate applications of these questions and presenting a guide for using graph methods to answer them. We also investigate how the connectivity predictions of patch-based graphs have been assessed and emphasize the importance of empirical evaluation. Our findings identify commonality among diverse approaches and methodological gaps with an aim to improve application and to help the integration of graph theory and ecological analysis.

2.2. Introduction

Maintaining connectivity and mitigating the fragmentation of habitat may be critical for landscape processes such as gene flow, dispersal, and natural ranging behaviour (Crooks and Sanjayan 2006). Conversely, species invasion, and the spread of pests and pathogens are processes that can be managed by reducing connectivity (Minor and Urban 2008).

Connectivity has consequently emerged as a conservation priority, with management targets including specific connectivity recommendations (Freemark et al. 2002). To support these goals, recent studies have emphasized analyses based on graph theory (also known as network analysis) for modeling the functional response of a target species to landscape pattern (patch size, shape, location). Graph-based landscape models are appealing because they provide a spatial representation that can be examined in relation to land use activities, and offer a well-developed mathematical framework for quantifying the impacts of management decisions for landscape connectivity (Urban et al. 2009).

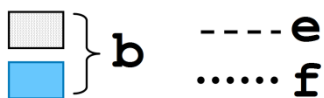
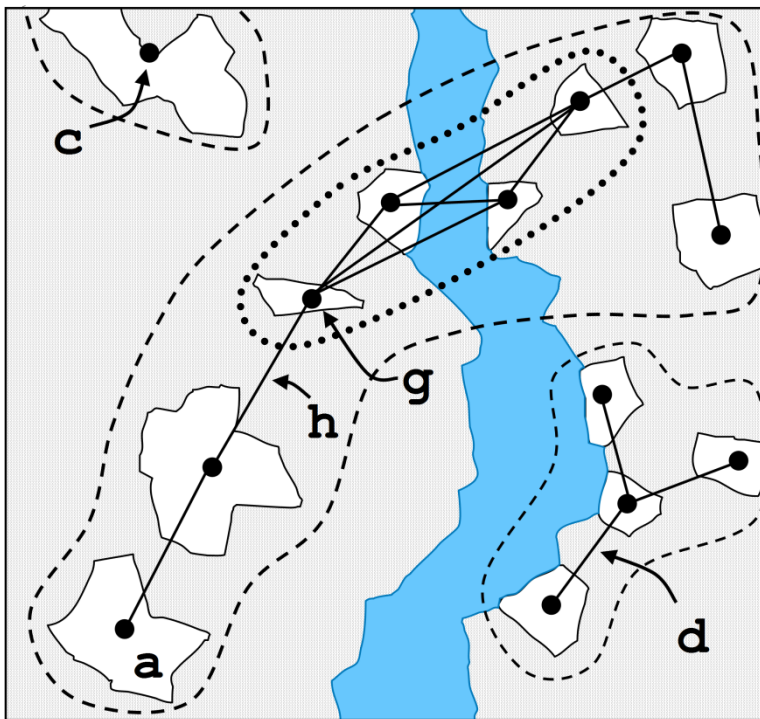
Although graph theory is a relative newcomer to landscape ecology, it has been widely used for diverse applications in natural and social sciences, where the resulting models are variously called graphs or networks. There are several distinct uses of graph theory for landscape modelling (for review see Urban et al. 2009). Graphs have been used to represent spatial relationships among patches of habitat (Urban and Keitt 2001) and among individuals on landscapes (Fortuna et al. 2008) for focal species. Graphs have also been used to model the connectivity among habitat reserves, permitting an

assessment of conservation strategies for multiple species (Fuller et al. 2006). A fourth and most distinct use of graph theory is to produce raster models of landscapes where connectivity is examined at the scale of a single raster cell (Adriaensen et al. 2003, Drielsma et al. 2007, McRae et al. 2008, Pinto and Keitt 2009). These four approaches are unified in their use of graph theory to represent connectivity on landscapes, but they differ in their analysis goals, and in particular, what landscape features and ecological processes the structural elements of the graph represent.

Here, we focus on only one form of landscape graph; graphs that model the relationships among patches of habitat. We refer to these as “patch-based graphs” for clarity. In these models, patches of habitat defined for a focal species (Fig. 2-1, a) are distinguished from the matrix (Fig. 2-1, b) and serve as the nodes (also called vertices; Fig. 2-1, c). The connections among nodes, called links (also called edges; Fig. 2-1, d) suggest the potential for movement or dispersal of a focal species. In the most common application of patch-based graphs, links represent the geographic distance between nodes, and nodes are connected by links only when this distance is below some ecologically-relevant movement threshold for the organism. Groups of connected nodes are called components (Fig. 2-1, e), and these imply that an organism inhabiting any node (i.e. patch) within the component can potentially move or disperse to any other node in the same component. Nodes that have no links to other nodes are also considered to be components (Fig. 2-1, c). A compartment is another term for a group of connected nodes but typically more stringent criteria for group membership apply (e.g. a high density of links among nodes as shown in Fig. 2-1, f). For more formal definitions and discussions of graph properties

Figure 2-1. Illustration of key terms in patch-based graphs.

(a) Patch – the focal habitat on the landscape; (b) Matrix – the landscape excluding the patches, shown here as a stippled surface and a solid-coloured river; (c) Node – the graph element used to represent the patch; (d) Link – the graph element used to represent the connectivity relationship between patches; (e) Components – groups of nodes connected by links; (f) Compartment – a group of nodes identified according to some criterion; this compartment has been identified based on the density of links among nodes, and is part of a larger component. (g) Cut-node – a node which, if removed, would disconnect a component; (h) Cut-link – a link which, if removed, would disconnect a component.



we direct the reader to introductions that have appeared in the landscape ecology literature (Urban and Keitt 2001, Bodin and Norberg 2007, Fall et al. 2007, Estrada and Bodin 2008, Minor and Urban 2008).

In most cases patch-based graphs are models of functional connectivity because their links represent a functional response of the organism to the landscape; that is, the links are not interpreted as structural features of the landscape or as corridors, but rather as representing the connections among patches as the organism might experience them. They can be further classed as models of potential connectivity because the predictions of the graph have not been tested with observations of organism movement. Although empirical measurements of species dispersal or movement may be used as parameters to build the graph, actual connectivity (*sensu* Calabrese and Fagan 2004), or evidence of movement of the focal species in reference to the landscape, is typically not incorporated *a priori*. A growing number of studies, however, have evaluated the potential connectivity predictions of patch-based models using empirical data from the landscape under study (Brooks 2006, O'Brien et al. 2006, Awade and Metzger 2008, Neel 2008, Andersson and Bodin 2009, Minor et al. 2009).

To guide researchers and managers who may wish to use patch-based graphs, we feel a comprehensive and detailed review of methodology is essential. In a recent review Urban et al. (2009) have taken on this challenge in broad terms, motivating the use of graph theory for landscape connectivity and reviewing existing and promising applications for all forms of landscape graphs. However, there remains a need to connect

specific conservation questions with appropriate methods. Here, we aim to complement Urban et al. (2009) by narrowing the scope of our review to patch-based graphs, the most widely published and best developed form of landscape graphs, and by concentrating on the key decisions in both graph construction and connectivity analysis required to answer questions of conservation interest. From this review, we develop a guide to the use of these graphs for achieving conservation research objectives. We also examine how the predictions of these models have been assessed.

2.3. Methods

We reviewed publications that presented patch-based graphs in order to identify a range of conservation questions and the methods used to address them. To find candidate papers, we searched titles, keywords and abstracts in the ISI Web of Knowledge database, using the following keywords in various combinations: *connectivity*, *graph*, *network*, *landscape*, *patch*, *functional connectivity*, and *habitat connectivity*. We focused on the period following the publication of Urban and Keitt (2001), and its empirical counterpart (Bunn et al., 2000), as we see these as key early contributions in the development of patch-based graphs.

From the candidate papers, we selected only research papers, theoretical papers, and reviews that presented models of landscapes where nodes were patches of habitat defined for actual or hypothetical focal species. We added the requirement that the paper present at least one graph of a real landscape in order to exclude publications that were strictly theoretical. Any additional references cited by authors of these papers that met our

Table 2-1. Chronological and alphabetical listing of studies included in the review with actual or hypothetical focal species and approximate study area.

No.	Study	Focal Species	Study Area
1	Kininmonth et al. (2010)	Unspecified coral reef species	Great Barrier Reef, Australia
2	Lookingbill et al. (2010)	<i>Sciurus niger cinereus</i> Delmarva fox squirrel	Delmarva Peninsula, Eastern USA.
3	Minor et al. (2009)	208 species of vascular plant	Washington County, Maryland, USA
4	Vasas et al. (2009)	Eight species of Carabid beetle	Bereg Plain, Hungary and Ukraine
5	Andersson & Bodin (2009)	Eleven species of songbird	Greater metropolitan Stockholm, Sweden
6	Margosian et al. (2009)	Unspecified pests and pathogens of four crops	Continental USA
7	Awade & Metzger (2008)	Two species of songbird	São Paulo State, Brazil
8	Estrada & Bodin (2008)	<i>Lemur catta</i> Ring-tailed lemur	Androy region, Madagascar
9	Jantz & Goetz (2008)	Unspecified terrestrial animals	Maine to North Carolina, USA
10	Minor & Urban (2008)	Unspecified songbirds	North Carolina Piedmont, USA
11	Neel (2008)	<i>Astragalus albens</i> Cushenbury milkvetch	San Bernardino Mtns., California, USA
12	Pascual-Hortal & Saura (2008)	<i>Tetrao urogallus</i> Capercaillie	Catalonia, Spain
13	Rayfield et al. (2008)	<i>Martes americana</i> American marten	South-central Quebec, Canada
14	Treml et al. (2008)	Unspecified corals	Reefs, Tropical Pacific Ocean
15	Bodin & Norberg (2007)	<i>Lemur catta</i> Ring-tailed lemur	Androy region, Madagascar
16	Fall et al. (2007)	<i>Rangifer tarandus caribou</i> Woodland caribou	Central Manitoba, Canada
17	Jordan et al. (2007)	Eight species of Carabid beetle	Bereg Plain, Hungary and Ukraine
18	Minor & Urban (2007)	<i>Hylocichla mustelina</i> Wood thrush	Wake County, North Carolina, USA
19	Pascual-Hortal & Saura (2007)	Unspecified wildlife animal species	Three randomly chosen landscapes, Spain
20	Saura & Pascual-Hortal (2007)	<i>Accipiter gentilis</i> Goshawk	Catalonia, Spain
21	Schick and Lindley (2007)	<i>Oncorhynchus tshawytscha</i> Chinook salmon	Central valley, California, USA
22	Sutherland et al. (2007)	<i>Strix occidentalis caurina</i> Northern spotted owl	Southern British Columbia, Canada
23	Bodin et al. (2006)	<i>Lemur catta</i> Ring-tailed lemur	Androy region, Madagascar
24	Brooks (2006)	Two species: fungal pathogen; salamander	Two areas: 20 x 11 m plot; Eastern USA
25	Fortuna et al. (2006)	Unspecified amphibians	Doñana National Park, Spain
26	O'Brien et al. (2006)	<i>Rangifer tarandus caribou</i> Woodland caribou	Manitoba, Canada
27	Estrada-Pena (2005)	<i>Ixodes ricinus</i> Tick	Rioja, Spain
28	Jordan et al. (2003)	<i>Pholidoptera transsylvanica</i> Bush cricket	Aggtelek Karst, Hungary
29	Urban & Keitt (2001)	<i>Strix occidentalis lucida</i> Mexican spotted owl	South-western USA
30	Bunn et al. (2000)	Two species: small mammal; small songbird	Coastal Plain, North Carolina, USA

criteria were also added. Our discussion references thirty studies that present patch-based graphs of real landscapes (Table 2-1). In all cases but one (Sutherland et al. 2007) the sources of the selected papers were peer-reviewed journals.

Methods for graph construction used by authors are presented first (Section 2.4), followed by a summary of approaches used for measuring connectivity from the graph (Section 2.5). We classify studies that use each method in tables, and opt to highlight a small number of illustrative examples in the text. Conservation applications of these methods, organized by research question, are then discussed (Section 2.6). We conclude by reviewing studies that use actual connectivity data to evaluate graph predictions (Section 2.7).

2.4. Graph construction

Building the graph requires decisions about which landscape features the nodes represent, and which ecological processes the links characterize (Table 2-2). Further, the rule used to assemble the graph (i.e. determining which nodes are connected to one another) must also be considered. In all cases, the graph construction variants chosen will depend on analysis goals, knowledge of the focal species, and available data for model parameterization. We review construction issues related to nodes, links, and graph assembly, and conclude by summarizing the key decisions in landscape graph construction.

Table 2-2. Variations in the construction of patch-based graphs.

Numbers refer to studies in Table 2-1.

Node geometry	
Point	1, 2, 3, 4, 8, 10, 14, 15, 17, 21, 23, 24, 25, 27, 28, 29, 30
Two-dimensional	5, 6, 7, 9, 11, 12, 13, 16, 18, 19, 20, 22, 26
Link representation and geometry	
Euclidean geometry	
Distance	2, 3, 5, 10, 11, 12, 13, 14, 17, 18, 24, 25, 29
Dispersal model	1, 2, 7, 8, 14, 15, 19, 20, 23, 30
Flux/Function of node weights	6, 13, 18, 27, 30
Corridor quality	4, 17
Least cost path geometry	
Distance	9, 16, 22, 26, 30
Structural geometry	
Distance	28
Dispersal model	21
Corridor quality	28
Link types	
Unweighted-undirected	2, 3, 5, 7, 8, 10, 11, 12, 14, 15, 16, 19, 22, 23, 24, 25, 26, 28
Weighted-undirected	4, 6, 7, 9, 13, 17, 19, 20, 27, 28, 29, 30
Unweighted-directed	8, 25
Weighted-directed	1, 8, 14, 18, 21
Graph assembly	
No graph approximation used	1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 14, 15, 17, 18, 19, 20, 23, 25, 30
Graph approximations	
Minimum planar graph	13, 16, 22, 26
Minimum spanning tree	29, 30
Relative neighbourhood network	27
Graph models structural features	4, 21, 28

2.4.1. Node definition

In some study systems it is straightforward to identify habitat patches for use as nodes in the graph (Fig. 2-1, A). Forested patches in a Madagascar agricultural landscape that are habitat for ring-tailed lemurs are simple to identify because the transition between patch and matrix is distinct and the matrix is uniformly uninhabitable (Bodin et al. 2006).

Woodland caribou in Manitoba, Canada, on the other hand, use a variety of forest types with differing frequencies, presenting a variable surface of habitat preference (O'Brien et al. 2006, Koper and Manseau 2009).

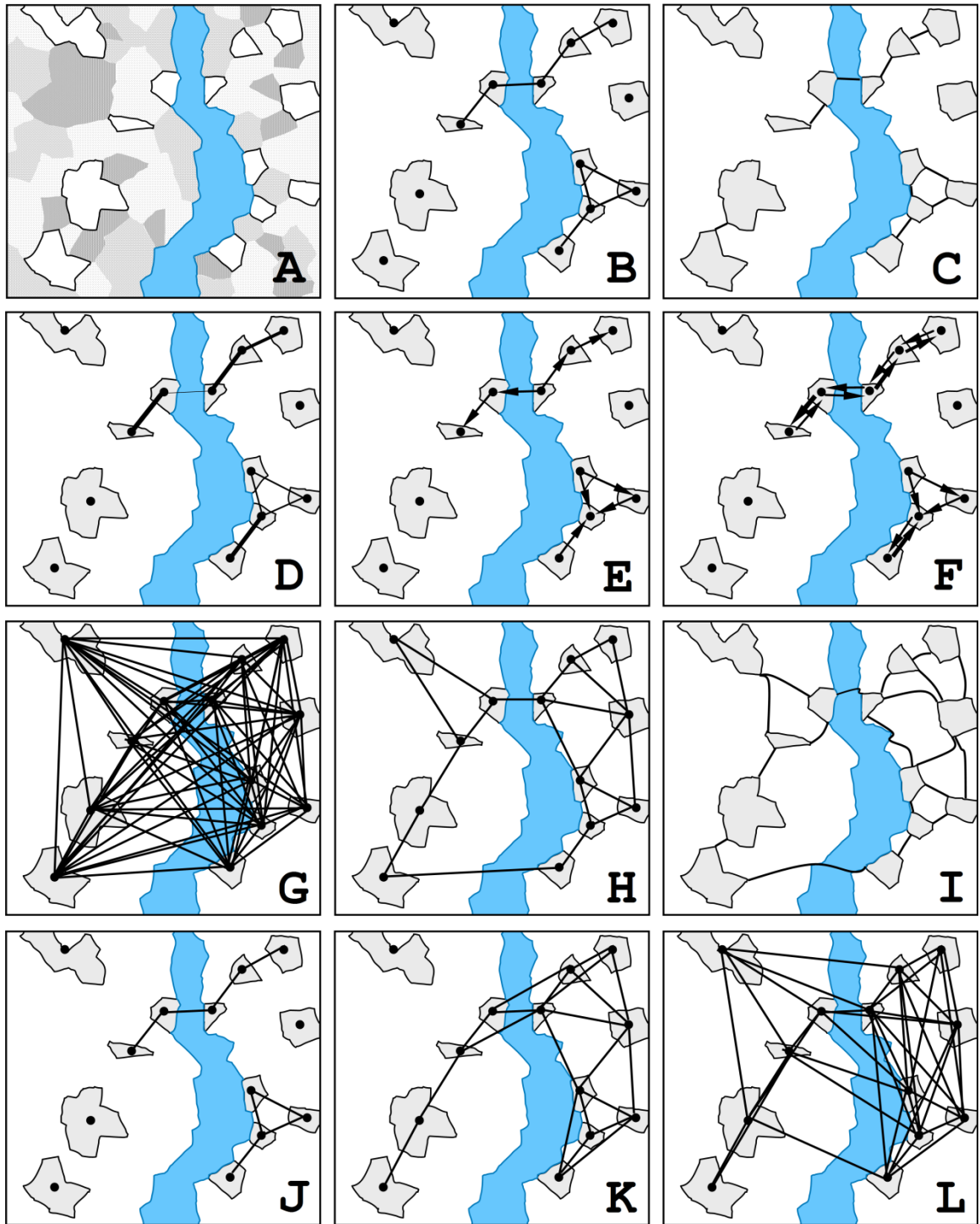
Under both scenarios, nodes can be defined based on the probability that the patch represented by the node is used as habitat. Where observations of the organism on the landscape suggest there is a high probability that certain patches are habitat, node definition has been justified qualitatively (e.g. ring-tailed lemurs; Bodin et al. 2006).

When evidence suggests that the landscape is not strictly dichotomous between habitat and matrix, which is the case for many large and highly mobile mammals (Boyce and McDonald 1999) , or there is uncertainty about which patch types constitute habitat, a quantitative approach is appropriate. In such cases nodes have been defined using combinations of environmental variables (e.g. Pascual-Hortal and Saura 2007, Saura and Pascual-Hortal 2007), or using resource selection functions to identify patches with the highest probability of use (e.g. O'Brien et al. 2006).

Figure 2-2. Examples of graph construction.

(A) Node definition on a landscape; patches are unshaded; stippled areas and solid-coloured river show habitat variation in the matrix; (B) Graph with unweighted undirected links, point node geometry, links representing relationships between patch centroids, assembled at a link threshold; (C) Same as B with two-dimensional node geometry, links representing relationships between patch boundaries; (D) Same as B with weighted undirected links; (E) Same as B with unweighted directed links, all arcs unidirectional; (F) Same as B with weighted directed links, some arcs bidirectional; (G) Same as B, showing the complete graph without link thresholding; (H) Same as B showing minimum planar graph approximation of the complete graph without thresholding; (I) “Spatial graph” – same as C with links representing least-cost paths between patch boundaries, assembled using minimum planar graph approximation of the complete graph without link thresholding (see A for the resistance surface used to model least cost paths, where darker shading indicates greater cost to movement); (J-L) A link thresholding experiment demonstrated for the complete graph presented in G, showing a different link threshold value in each figure.

Figure 2-2. Cont'd.



2.4.2. Node geometry

Nodes can be points, typically at the centroid of the patch (Fig. 2-1, B; Table 2-2), or have two-dimensional geometry (Fig. 2-1, C; Table 2-2). Using patch centroids may bias the spatial location of nodes, for example, when patches tend to be elongate in shape, or inter-patch distances are small relative to patch dimensions. Two-dimensional node geometry (Fig. 2-1, C), although computationally expensive, permits greater accuracy because distances between nodes can be calculated between patch boundaries rather than patch centroids (Minor and Urban 2007). Using centroid-to-centroid measures of connectivity means that movement within a patch is equally weighted with movement outside a patch. At certain scales the node geometry selected will become irrelevant. For example, reef patches in the Tropical Pacific are much smaller in size than vast stretches of ocean that separate them, making point nodes satisfactory (Treml et al. 2008). Spotted owl nesting and home range patches in a forest matrix, however, are sufficiently close and irregularly shaped that two-dimensional node geometry was needed (Sutherland et al. 2007). It should be noted that graphs may be plotted using point nodes even though links have been determined assuming two-dimensional node geometry (i.e. as the distance between patch boundaries).

2.4.3. Node weights

Node weights (also known as node attributes) are typically superimposed on the graph after it has been built to be used as variables in graph connectivity metrics. Weights describe properties of patches such as area, population size, occupancy, and habitat quality. Node weights seldom influence the links, except where links represent flux as a

function of the weights at adjacent nodes (e.g. Schick and Lindley 2007). In most cases, node weights are supplementary variables. For example, the sum of patch areas in a graph component provided a measure of the total area of habitat functionally available to two rainforest bird species (Awade and Metzger 2008). In most published examples the node weights are used to include additional ecological information when describing connectivity. This is in contrast to node geometry which impacts directly on connectivity and is selected to improve the specification of the links. For this reason, a graph with point node geometry and nodes weighted by patch area is distinct from a graph with two-dimensional node geometry where node weights are not used.

2.4.4. Link representation and geometry

The presence of a link between two nodes implies that the nodes are connected. To decide whether or not two nodes should be connected (the process of graph assembly; see Section 2.4.6) some empirical measure describing the strength of the connection between nodes is needed. A suitable measure may describe a resistance to animal movement or dispersal such as geographic distance or alternatively the amount of movement or dispersal expected under some model (e.g. probability of dispersal or flux). We call these measures the link representation (i.e. the biological or landscape property that underlies the link). In most cases the link representation is calculated as some function of the distance between nodes. This requires that consideration is also given to what we call the link geometry (i.e. whether the distance used to calculate the link representation is obtained from a Euclidean or a non-linear path).

Three types of link geometry have been used in published studies (Table 2-2). Euclidean link geometry makes the fewest assumptions (i.e. that on average the movement of the focal species can be described by the most direct route). Euclidean geometry has been applied to birds, insects, and plants, or where the model assumes the matrix is uninhabitable or homogeneous and should be traversed in the most direct manner (e.g. Jordan et al. 2007, Neel 2008, Andersson and Bodin 2009). We describe studies as using structural link geometry (Table 2-2) where nodes are connected by existing, typically non-linear, corridors on the landscape. This approach has been used infrequently, but may be useful where the focal species moves exclusively using easily distinguished structural features, such as rivers or hedgerows (e.g. Jordan et al. 2003, Schick and Lindley 2007).

Least-cost path geometry is an appropriate choice where the routes followed by the focal species are likely to be non-linear (e.g. influenced by different cover types and features), such as is the case for many terrestrial mammals (Adriaensen et al. 2003, Coulon et al. 2004). A disadvantage is that intensive parameterization is required to produce a resistance surface (Spear et al. 2010), presenting practical challenges, in addition to the introduction of error. For certain species, however, the use of least-cost paths may better capture the connectivity relationships among nodes. For example, in a landscape where a barrier separates two nodes, least-cost path geometry may describe a link going around the obstruction, while Euclidean geometry may describe a link directly crossing the obstruction. In the latter case, the distance represented by the link may overestimate the degree to which the two nodes are connected for the organism (Adriaensen et al. 2003).

Typically, least-cost paths are summarized using an effective distance which describes the cost of following the path, and structural geometry is summarized using the total length of the path (e.g. Schick and Lindley 2007, Sutherland et al. 2007, Jantz and Goetz 2008).

In most published studies the Euclidean distance, effective distance, or the length of the path is used as the link representation (i.e. as the magnitude of the connection between nodes). Where more information is available about connectivity, the link representation can potentially be improved by using a dispersal model. Dispersal models produce a probability of dispersal between adjacent nodes by incorporating theoretical assumptions about organism movement (e.g. Treml et al. 2008). The probability of dispersal, rather than the distance, is then used as the link representation. Dispersal models typically also include some measure of distance, but we classify them separately in Table 2-2 because distance is combined with other variables representing properties of the landscape or the focal species (e.g. Schick and Lindley 2007, Treml et al. 2008). Fluxes are another type of link representation where dispersal models are combined with node weights, such as patch area, to improve the estimate. In several cases, links have represented some other function of geographic distance and node weights. For example, links in a graph describing connectivity for maize pests and pathogens were a function of Euclidean distance and the densities of maize at adjacent nodes (Margosian et al. 2009).

Where two-dimensional nodes are used, links can also be given spatial endpoints where they intersect with the node boundary (O'Brien et al. 2006, Fall et al. 2007). The choice

of these endpoints can be made such that the Euclidean or least-cost path between nodes is determined from a specific point on node boundaries, which can potentially be used to improve the accuracy of the link representation.

2.4.5. Link types

Links may or may not have a weight attribute assigned to them (Figs. 2-2, B, D; Table 2-2). When weight attributes are used, they are typically the magnitude of the link representation (e.g., Euclidean distance, effective distance, length of the path, or probability of dispersal). In unweighted graphs, the link representation is used in graph construction rather than appearing explicitly as an attribute in the graph. For example, many unweighted graphs are constructed using a link threshold rule where nodes are connected if the distance between them is smaller than a threshold value (see Section 2.4.6). Weighted graphs can also be constructed using such a rule, but differ from unweighted graphs by adding information about the strength of the connection rather than simply representing the presence or absence of a connection. The decision to use weight attributes is made on the basis of how connectivity will be measured from the graph (i.e. if the metric used will incorporate weight attributes explicitly; see Section 2.5). It may also be useful to construct an unweighted graph based on one link representation and then overlay a second variable as a weight attribute. A graph for Carabid beetles, for example, was built using links representing Euclidean distance between patches and analyzed using weights describing the quality of the landscape corridor suggested by each link (Jordan et al. 2007).

Links may also describe directional connectivity, in which case they are referred to as arcs (Figs. 2-2, E, F). Arcs representing amphibian migration from temporary to perennially flooded ponds in Spain were not weighted (Fortuna et al. 2006), while the arcs representing the pelagic drift of coral larvae in the Tropical Pacific were signed and weighted using a dispersal model that incorporated surface ocean current velocity (Tremblay et al. 2008).

2.4.6. Assembling the graph

Assembling the graph is the final step in graph construction, and there are several variations possible. The most common approach is to create a *complete graph* (Fig. 2-1, G; Table 2-2), which has links between every pair of nodes. Alternatively, approximations of this complete graph can be used, such as the *minimum planar graph* (see below; Fig. 2-1, H; Table 2-2). In most cases, this initial graph should be subjected to a link threshold rule, where links are removed that represent a value beyond some ecologically determined threshold (e.g. greater than the largest observed dispersal distance for the focal species, or below some probability of dispersal). The link-thresholded graph can also be assembled directly to avoid creating the complete graph. For example, forest patches inhabited by coal tits were linked if the Euclidean distance between their boundaries was less than an empirically determined daily movement threshold distance (e.g. Andersson and Bodin 2009).

Complete graphs (Fig. 2-2, G; Table 2-2) contain the maximum information and path alternatives for a given set of nodes, but at a cost of having to represent and process

potentially large numbers of links. The minimum planar graph (Fig. 2-2, H; Table 2-2) has been used to approximate the complete graph, summarizing much of the information in the complete graph using many fewer links (Keil and Gutwin 1992, Fall et al. 2007). Assembly proceeds by tessellating the landscape into a set of convex Voronoi polygons with the nodes at the centre of each polygon (Okabe et al. 2000). Links connect nodes in adjacent polygons, producing a graph where links do not cross one another (i.e. the graph is planar). This results in a simpler graph that is computationally efficient for landscapes of many nodes and can be more easily visualized on a map (Fall et al. 2007), but the absence of links between non-adjacent patches may limit some analysis methods (e.g. some patch removal experiments) and must be taken into account during interpretation of results.

Although not a requirement, minimum planar graphs typically have been built using two dimensional nodes and non-linear least cost path link geometry; a collection of properties that have been called "Spatial Graphs" (Fig 2I; Fall et al. 2007). In Spatial Graphs, the geometry of the patch boundary and the relative positions of neighbouring patch boundaries together determine the endpoints of the links. Spatial Graphs also add the feature that the endpoints of the links have spatial coordinates rather than terminating arbitrarily in adjacent patches.

The minimum spanning tree (Table 2-2) has been used as an approximation of the underlying backbone of connectivity, and does so by identifying links that connect all nodes with minimum total link length (Fall et al. 2007). This form of graph appeared in

initial work (e.g. Bunn et al. 2000, Urban and Keitt 2001), but its absence in more recent work may reflect a consensus that it may capture insufficient information for use in ecological connectivity analysis. Minimum spanning tree graphs, by definition, do not retain the alternate movement pathways.

Where structural link geometry is used (Table 2-2), graph assembly simply models the network of structural features that actually connects patches on the landscape (Urban et al. 2009). Rivers provide an intuitive example of this. For example, a graph describing chinook salmon connectivity among river basins in Central Valley, California, was built to represent the drainage network (Schick and Lindley 2007).

2.4.7. Key decisions in graph construction

In Table 2-3, we summarize seven key decisions in landscape graph construction, focusing on the most widely used construction variants. Typical indications for the use of each construction variant are given with reference to compatibility with the study system and proposed analyses. Node and link geometry, the choice of link representation and the rule used to assemble the graph will all influence the topology of the graph. The degree to which these choices may affect landscape connectivity conclusions, however, has not been comprehensively studied (see however Estrada and Bodin 2008). Node and link weights (i.e. attributes), as typically applied, will not affect graph topology. A decision to include these is indicated by the metric used to measure connectivity from the graph, which is, in turn, suggested by the research question of interest. Finally, the

Table 2-3. Seven decisions in patch-based graph construction.

Construction variant	Typical indications for use of construction variant
<i>1. Choose node geometry:</i>	
(a) Point node geometry	<ul style="list-style-type: none"> ▪ Centroids adequately represent spatial arrangement of patches
(b) Two-dimensional node geometry	<ul style="list-style-type: none"> ▪ Centroids poorly represent the spatial arrangement of patches ▪ Scale of study is such that defining links from patch boundary-to-boundary is necessary to correct bias in the centroid-to-centroid distance
<i>2. Choose node weights:</i>	
(a) Node weights not applied	<ul style="list-style-type: none"> ▪ Analysis focuses on the topological arrangement of connected patches ▪ Connectivity metrics do not incorporate patch variables
(b) Node weights applied	<ul style="list-style-type: none"> ▪ Analysis considers biological or landscape properties of groups of connected patches, in addition to their topological arrangement ▪ Connectivity metrics are used or developed that incorporate population or landscape variables from patches
<i>3. Choose link geometry:</i>	
(a) Euclidean link geometry	<ul style="list-style-type: none"> ▪ Matrix is essentially uniform for focal species ▪ Movement of focal species is, on average, summarized by the most direct route
(b) Least-cost path link geometry	<ul style="list-style-type: none"> ▪ Matrix is not uniform for focal species ▪ Movement of focal species is, on average, summarized by the least-costly route. ▪ Data is available to parameterize the resistance surface used to calculate least-cost paths
(c) Structural link geometry	<ul style="list-style-type: none"> ▪ Focal species moves using landscape features apparent to human observers

Table 2-3. Cont'd.

Construction variant	Typical indications for use of construction variant
<i>4. Choose link representation:</i>	
(a) Distance link representation	<ul style="list-style-type: none"> ▪ Probability of movement is adequately modelled using geographic distance, or costs which represent geographic distance (e.g. effective distance)
(b) Dispersal model link representation	<ul style="list-style-type: none"> ▪ Probability of movement modelling is improved using organism, population or landscape variables that predict dispersal as a function of distance ▪ Data is available to parameterize a dispersal model
(c) Flux link representation	<ul style="list-style-type: none"> ▪ Probability of movement modelling is improved using population or landscape variables from adjacent patches as a function of distance ▪ Node weights are applied
<i>5. Choose link types:</i>	
(a) Unweighted, undirected links	<ul style="list-style-type: none"> ▪ Connectivity metrics used measure the presence or absence of connections among patches
(b) Weighted, undirected links	<ul style="list-style-type: none"> ▪ Connectivity metrics used incorporate link attributes describing the strength of the connection among patches ▪ Graph is built using one link representation, and a second variable is superimposed for analysis purposes
(c) Unweighted, uni- or bidirectional links (arcs)	<ul style="list-style-type: none"> ▪ Connectivity metrics used incorporate the direction of the arc(s) between patches
(d) Weighted, uni- or bidirectional links (arcs)	<ul style="list-style-type: none"> ▪ Connectivity metrics used incorporate the direction and strength of the flows described by arc(s) between patches ▪ Graph is built using one link representation, and a second link representation is superimposed for analysis purposes

Table 2-3. Cont'd.

Construction variant	Typical indications for use of construction variant
<i>6. Choose graph approximation:</i>	
(a) No graph approximation;	<ul style="list-style-type: none"> ▪ Generally applicable
(b) Graph approximation is used	<ul style="list-style-type: none"> ▪ Approximation of complete graph is desired for map-making and visualization or because a large number of nodes makes the complete graph intractable for analysis ▪ Graph approximations will not compromise the analysis (as noted in Section 2.6)
<i>7. Choose link thresholding:</i>	
(a) Graph assembled at one, several or many link thresholds	<ul style="list-style-type: none"> ▪ Generally applicable
(b) No link thresholding	<ul style="list-style-type: none"> ▪ Weighted and/or directed link attributes are used ▪ Connectivity metrics incorporate link weights and/or directions

decision to assemble the graph at one or many link thresholds is determined by analysis goals (see Section 2.6).

2.5. Measuring connectivity from the graph

Building a graph with attention to node definition, node geometry, link representation and graph assembly decisions can produce an informative tool that requires no further work; a map visualization of the graph and the spatial configuration of habitat it describes can be sufficient for many planning exercises (see Section 2.6.1). Typically, however, further analyses are needed to quantify the connectivity of the graph in order to select from multiple alternative models, or describe and test properties of the graph that are not apparent on visualization.

Graph metrics (Table 2-4) are required to quantify the connectivity of the graph and can be broadly classified into: (a) those that assess connectivity for the entire graph; (b) those that assess connectivity by measuring the properties of groups of nodes, such as graph components; and, (c) those that assess connectivity for single nodes. Metrics for the entire graph or groups of nodes can also be developed by summing or averaging single node connectivity metrics across the relevant nodes. Depending on the metric used, it is possible to reference node (i.e. patch) attributes for measuring the connectivity of groups of nodes. For example, summing the area of all patches in a component uses a node weight for this purpose (e.g. Awade and Metzger 2008), or reporting the average link weight across the entire graph can be used to summarize connectivity at a landscape scale (e.g. Rayfield et al. 2008). Equally, patches may be valued for their contribution to

Table 2-4. Three categories of metrics available to measure connectivity from a patch-based graph.

A sampling of the simplest metrics used among the papers reviewed is presented to illustrate key differences among categories. Numbers refer to studies in Table 2-1 that use this metric.

(a) Measure connectivity for the entire graph		
Number of components	A count of the number of components in a graph	6, 10, 11, 14, 19, 30
Mean link weight	The sum of all link weight attributes in the graph divided by the number of links in the graph	1, 13, 14
(b) Measure connectivity for groups of connected nodes		
Number of nodes in largest component	A count of the number of nodes in the largest component	10, 14
Total patch area in a component	The sum of the patch area node attributes for all nodes in a component	5, 6, 7
(c) Measure connectivity for single nodes		
Degree (Indegree / Outdegree)	The number of links incident on a node; or in a graph with directed links the number of incoming or outgoing arcs incident on a node	8, 9, 17, 18, 21, 28
Betweenness centrality	The proportion of all shortest paths between all nodes on the graph that pass through a node	1, 2, 8, 9, 15, 18

landscape scale connectivity, which can be assessed using node removal experiments that examine the change in connectivity across the entire graph (see Section 2.6.6).

Selecting a graph metric presents a challenge to researchers; we counted more than forty metrics among the studies reviewed. As a general rule, we suggest choosing the category of metric appropriate for the analysis and then comparing the results from multiple metrics within that category. We offer appropriate categories of metric for each conservation question discussed in Section 2.6. For some questions, researchers may find it useful to assign node or link weights and develop their own metrics incorporating this information. In one example from Carabids, the number of nodes (or order) in the largest graph component, is combined with demographic data associated with each node to produce an estimate of metapopulation size (Jordan et al. 2007).

2.6. Conservation applications

We identified nine conservation-related research questions that have been asked using patch-based graphs (Table 2-5). These research questions are all ultimately concerned with describing landscape connectivity and do this by exploring different properties of the graph. It is also critical to assess the role that connectivity plays in the spatial structuring of the species of interest, which we address in Section 2.7. For each of the nine questions, we suggest potential applications, approaches for answering the question, and limitations of these approaches. We also note analyses where certain graph construction options are more or less suitable.

Table 2-5. Conservation questions asked by studies reviewed.

Numbers refer to studies in Table 2-1.

Which areas of the landscape are connected? <i>Identification of functionally connected components</i>	2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 21, 22, 23, 26, 27, 28, 29, 30
Which areas of the landscape are highly connected? <i>Identification of community structure compartments</i>	15
What are the critical thresholds at which the landscape is aggregated? <i>Link thresholding experiments</i>	6, 14, 16, 24, 26, 29, 30
What are the implications of the network topology for connectivity? <i>Assessment of the node-degree distribution</i>	1, 2, 10, 24, 25
How does connectivity differ between graphs? <i>Comparison of graphs using various approaches</i>	6, 14, 19, 22, 25, 26, 30
Which patches are important for connectivity? <i>Patch prioritization using node metrics or node removal experiments</i>	2, 8, 9, 11, 12, 14, 15, 17, 18, 19, 20, 21, 25, 28
Which patches are important as sources and which as sinks? <i>Patch prioritization using node metrics or node removal experiments</i>	14, 18, 21, 25
What types of patches are important for connectivity? <i>Node removal experiments</i>	8, 21, 27, 29, 30
Which connections among patches are important for connectivity? <i>Corridor prioritization using link removal or insertion experiments</i>	1, 2, 4, 17, 28

2.6.1. Which areas of the landscape are connected?

Landscape planning for species of concern requires detailed knowledge of the amount and quality of habitat as well as the connectivity or spatial configuration of that habitat (Fahrig 2001, 2002). While not sufficient in itself for landscape planning purposes, a map depicting the spatial configuration of habitat can be an important contribution to the decision process. For example, roads, which may present a strong barrier to connectivity for many mammals (Balkenhol and Waits 2009), can be routed such that they avoid disrupting regions that are essential for maintaining connectivity. Consultations for new reserves or protected areas might draw boundaries around highly connected regions of habitat, or alternately around poorly connected regions of the landscape that are critical corridors (Briers 2002, Fall et al. 2007). In forest management planning, maps can direct harvesting to avoid impact on species at risk and GIS layers describing connectivity can be incorporated into dynamic harvest models (e.g. Sutherland et al. 2007, Rayfield et al. 2008).

Producing an informative map for management begins with assembling the graph using one link threshold representing the best available information on movement or dispersal for the focal species. For distance link representations, this amounts to plotting only those links that are less than the threshold. The resulting map will show connected groups of patches, or components (e.g. Figs. 2-2, J, K, L), and this can be used to visually highlight candidate areas for restoration where connectivity is poor or non-existent.

Maps showing graphs built at additional link thresholds can serve other conservation objectives. Because the exact maximum movement or dispersal distance for an organism may never be known (Bunn et al. 2000, Bowman et al. 2002), an upper and lower estimate of this threshold value can be used to produce two maps to guide decisions. A range of threshold values for movement or dispersal can also be used to depict connectivity hypotheses at different temporal scales, such as for daily foraging, dispersal, or seasonal migration, although caution is appropriate because the parameters used for node definition and link representation may also vary, requiring construction of a new graph.

In association with these maps, it may also be valuable to present measures of functional connectivity. Metrics associated with groups of nodes and with the entire graph will be most useful. For example, the total patch area in each component (e.g. Awade and Metzger 2008), or the mean patch area of all components in the graph (e.g. expected cluster size; O'Brien et al. 2006), are simple but informative metrics for landscape planning.

Where map visualization to identify the spatial extent and configuration of components is of primary interest, we recommend complete graph approximations such as the minimum planar graph (Fig. 2-2, H) or, if there is sufficient data for parameterization, Spatial Graphs, which maintain connection of graph elements and the geographic landscape (Fig. 2-2, I; see Section 2.4.6). When approximations are not used, maps may have many intersecting links that can obscure landscape features and make the map

difficult to interpret for planning purposes (Fall et al. 2007). When map visualization to identify areas with a high density of links is of interest, however, approximations should not be used, and researchers should consider a more formal identification of these highly connected regions of the landscape (see Section 2.6.2).

2.6.2. Which areas of the landscape are highly connected?

This is an extension of the previous question that may also be valuable for landscape planning. The delineation of “highly connected” rather than “connected” areas of the landscape can be achieved by finding community structure in the graph and using this to define compartments (e.g. Fig. 2-1, f). Community structure algorithms (e.g. Girvan and Newman 2002) can identify groups of nodes that are more densely connected and, depending on the criteria used, can exclude the weakly connected areas of the landscape represented by cut-nodes and cut-links (Fig. 2-1, g, h).

Finding compartments based on community structure may be valuable in landscapes that are generally well connected for the focal species, because such compartments are sensitive to the degree of connectivity (Bodin and Norberg 2007). Maps of compartments can then be depicted in a graph assembled at a certain link threshold (e.g. Bodin and Norberg 2007). However, work is still required to explore the ecological interpretations of the available community structure methods, and researchers must also give consideration to the appropriate level of community structure to report (Girvan and Newman 2002, Bodin and Norberg 2007). The use of graph approximations will not be informative, because these will remove links in highly connected areas of the graph.

2.6.3. What are the critical thresholds at which the landscape is aggregated?

Where landscapes are becoming heavily fragmented, it may be important to evaluate the potential resilience of a species to the loss of connectivity (e.g. Bunn et al. 2000). Where species invasion or the spread of pest and pathogens is a concern, connectivity risk assessment may also be pertinent (e.g. Margosian et al. 2009). One approach is to identify a critical link threshold at which the landscape generally becomes disconnected for the focal species. For example, in a graph using distance link representation, a species that has a maximum movement or dispersal distance above a critical threshold experiences much of the landscape as connected, while a species that falls below this threshold will have its movement inhibited by disconnected habitat. This information can be used to determine if habitat restoration is required to improve connectivity, or for invasive species, pests and pathogens, if steps must be taken to mitigate spread. A map can also be made at this link threshold (see Section 2.6.1) and used to suggest specific steps to achieve these conservation goals.

Critical link thresholds at which there are large changes in connectivity can be determined using a link thresholding experiment (one form of link thinning or removal) (e.g. Figs. 2-2, J-L). The graph is assembled at an ordered series of link threshold values, and a connectivity metric is assessed for the entire graph, or for groups of nodes at each step (Urban and Keitt 2001). In many examples, slow increases in the connectivity metric as the link threshold increases are punctuated by rapid increases near key thresholds, reaching a plateau as most nodes in the graph become connected (e.g. Bunn et

al. 2000, Urban and Keitt 2001, Brooks 2006, O'Brien et al. 2006). The critical link thresholds can then be determined mathematically as the points associated with rapid connectivity increases (Brooks 2006).

2.6.4. What are the implications of the network topology for connectivity?

This conservation question offers a second approach to determine resilience and risks associated with connectivity by describing the topology of the entire graph (or network).

Among the papers reviewed, network topology has been chiefly described by determining the frequency distribution of node degree (Table 2-4), a metric describing the number of links incident on a node. Starting with a graph assembled at a link threshold value of ecological interest, the node degree distribution of the graph is compared to simulated distributions representing random, scale-free and other network types (e.g. Brooks 2006, Fortuna et al. 2006, Minor and Urban 2008). Evidence that a network exhibits scale-free characteristics, for example, suggests that connectivity is dependent on a small number of highly-connected hub patches and it, therefore, has a low resilience to the loss of these hub patches and is more susceptible to species invasion and disease spread (Minor and Urban 2008). Graph approximations must be used carefully here as they may eliminate the topological complexity that is being assessed.

This approach may be valuable for preliminary assessments of resilience and risk where spatially-explicit conclusions are not required. For example, a graph describing a pond network demonstrated that connectivity for amphibians with limited dispersal distance was robust to the loss of ephemeral ponds (Fortuna et al. 2006).

2.6.5. How does connectivity differ between graphs?

Patch-based graph comparison has not been the subject of any focused attention, but it may be a promising avenue for future research. Comparison of graphs for multiple species can be used to assess relative risks associated with species invasion and disease spread (e.g. Margosian et al. 2009). A series of graph construction treatments where link representation, link weights, or node weights are varied can also be used to explore how differences in ecological parameters affect connectivity (e.g. Fortuna et al. 2006, Treml et al. 2008). Graphs describing connectivity in the past and in the present can be compared to assess the impact of landscape change (e.g. O'Brien et al. 2006) and evaluate the success of landscape restoration efforts. Equally, planned or potential changes to land use or land cover such as road construction or natural and human disturbances can be represented on a graph and compared to the present configuration (e.g. Sutherland et al. 2007). Comparing graphs for multiple landscapes may also be helpful for assessing potential landscapes for species reintroduction, for triage cases, and for site comparisons in environmental impact assessments.

The comparison of different link thresholds for a single landscape is not typically the focus, because in this case we expect, *a priori*, connectivity to change with link threshold value. Rather, graph comparison will be of interest where the parameters used to construct each graph are different (e.g. graphs are of several landscapes, or graphs explore different hypotheses for a single landscape). Comparing graphs can be done using one, or preferably several, graph metrics that describe connectivity for the entire

graph (e.g. Margosian et al. 2009). Comparisons of node-degree distributions (Section 2.6.4; Fortuna et al. 2006) for different graphs have been used, as has the comparison of critical link thresholds (Section 2.6.3; e.g. Bunn et al. 2000, O'Brien et al. 2006). New approaches may also be found in other disciplines where graph comparison is well-developed (e.g. cospectrality of graphs used for pattern recognition; Wilson and Zhu 2008).

2.6.6. Which patches are important for connectivity?

When nodes are well-defined and distinct from the matrix and there is a high probability that the patches represented by nodes are used as habitat (see Section 2.4.1), finding nodes that are important for landscape-scale connectivity may have several applications. For a species of concern, patches which play an important connectivity role can be identified and given conservation priority (e.g. Pascual-Hortal and Saura 2008) or selected for a protected area network (e.g. Minor and Urban 2008). For invasive species, pests and pathogens, these patches could be removed to interrupt spread (e.g. Estrada-Pena 2005).

Identifying patches with high connectivity importance has been termed patch prioritization (Pascual-Hortal and Saura 2007), and has been done in two ways. In the first approach, node metrics (e.g. Table 2-4) are determined for each node on the graph, and high scoring nodes are given high priority. For example, the betweenness centralities of nodes representing forested roadless areas in Maine and New Hampshire, U.S.A., were used to identify a corridor suitable for terrestrial wildlife (Jantz and Goetz 2008).

In the second approach, node removal experiments are performed where the node and its associated links are removed from the graph, and the change in value of a metric for the entire graph is determined. The node is then returned to the graph and the process is repeated. Nodes that cause large reductions in the total connectivity of the graph are prioritized. A node removal experiment for ticks in Rioja, Spain identified habitat patches that lowered the total traversability of the landscape, a result which could be applied to limit their spread (Estrada-Pena 2005).

Using node weights is often informative in patch prioritization. Metrics that incorporate the value of node weights can be used to combine other ecological parameters with connectivity. For example, using patch area as a node weight in a node removal analysis has been used to create a habitat availability metric that incorporates connectivity (Pascual-Hortal and Saura 2006). Because alternate pathways may not be present, graph approximations should be used with caution in removal experiments. Finally, ranking the importance of a patch for connectivity using several methods is recommended in order to seek a consensus (e.g. Minor and Urban 2008).

2.6.7. Which patches are important as sources and which as sinks?

The goal in this question is also the identification of priority patches for a conservation response (see Section 2.6.6), but the emphasis is on source and sink attributes of those patches. Where species recovery is a concern, important source patches can be identified as candidates for restoration or conservation (Schick and Lindley 2007, Treml et al.

2008). To capture directional connectivity, graphs must be constructed with directed links (arcs) and link representation may require heavy parameterization to produce informative directional estimates (e.g. Schick and Lindley 2007, Treml et al. 2008; but see Fortuna et al 2006). Node based metrics and node removal are also appropriate, using metrics that summarize the net effect of arcs at each node (e.g. node strength; Schick and Lindley 2007), or across the graph (e.g. population independence; Schick and Lindley 2007).

2.6.8. What types of patches are important for connectivity?

Sometimes it may be useful to identify the general characteristics of priority patches (see Section 2.6.6); to generate rules of thumb that can be applied in other systems where studies are not feasible (e.g. Estrada-Pena 2005, Schick and Lindley 2007). To do this, a subset of nodes is selected according to a criterion of conservation importance. Patches that have high node-based connectivity values, are spatially remote, have extreme node weights, or are randomly chosen, may be removed sequentially and the impact on the connectivity of the entire graph determined. This approach is similar to node removal, except that nodes are not returned to the graph at each repetition. For example, the removal of patches that had a high connectivity (assessed using a single node connectivity metric) caused a faster change in overall connectivity for chinook salmon than the removal of random patches or patches with high population sizes, suggesting that these types of patches should be prioritized for restoration (Schick and Lindley 2007).

2.6.9. Which connections among patches are important for connectivity?

Where links can be readily translated into structural features of the landscape, a corridor prioritization can help identify links of management interest. Links representing potential corridors that have a high priority can be selected for restoration or conservation (e.g. Jordan et al. 2003, Jordan et al. 2007, Vasas et al. 2009). The effect of inserting links into the graph can also be determined to assess alternative corridor construction or restoration scenarios (e.g. Jordan et al. 2007). The analysis is similar to a node removal exercise (see Section 2.6.6); links are removed or inserted and the change in an entire graph connectivity metric recorded.

2.7. Evaluating graph predictions with empirical data

Patch-based graphs can be compelling conservation tools. This is, in part, because they describe connectivity with a picture that is intuitive and easy to interpret (Urban et al. 2009). Without empirical evaluation of their predictions, however, these models remain elaborate suppositions that managers may feel reluctant to use given the costly and often controversial decisions they face. Improving confidence in a model requires testing its predictions with actual connectivity data obtained from the landscape (Urban et al. 2009).

Tests using patch-based graph models have begun to appear, but much work remains to articulate a general approach to this problem. The most common method is to assemble the graph at one or many link thresholds of ecological significance and measure the association of the study organism with the graph components. This has been done using presence/absence, abundance, and telemetry data. For example, the predictions of a

graph describing forested patches in a park in Maryland, USA were assessed using partial Mantel tests, which showed that network distance between patches (a metric which incorporates the component structure of the graph) better explained species compositions than the Euclidean distance between patches (Minor et al. 2009). Coal tits in an urban landscape in Stockholm, Sweden were significantly present in components of a graph model built at a link threshold of 50 m (Andersson and Bodin 2009). The R^2 value from simple linear regressions of abundance against total component area were used to select the better of two link threshold graphs for songbirds in Brazilian Atlantic rainforest (Awade and Metzger 2008). And, for graphs built at certain link thresholds, woodland caribou telemetry points were significantly closer to larger components when compared to random locations, suggesting caribou select larger areas of functionally connected habitat at these thresholds (O'Brien et al. 2006).

Spatial autocorrelation in genetic data has also been used to test the predictions of a patch-based graph, and this has been termed scale matching. In the only example we found of this approach, the genetic neighbourhood, a measure describing the scale at which gene flow is operating, determined for a plant pathogen and a salamander, matched the critical link thresholds of landscape aggregation for these species (Section 2.6.3; Brooks 2006). This result suggests that dispersal and subsequent gene flow are happening over an area of approximately the same size as an average component on a patch-based graph.

The association of the study organism with the patch rather than with the component has been used in one test of a patch-based graph. For the endangered plant *Astragalus albens*, patches with a higher importance for connectivity, determined in a node removal experiment, also had significantly higher indices of genetic diversity. Graph models built at link thresholds above that expected for gene flow in this plant did not demonstrate this significant relationship (Neel 2008).

Genetic approaches, in general, may be a promising way forward. Obtaining genetic data at a landscape scale has become feasible in many study systems; recent advances in non-invasive genetic sampling (i.e. of hair and fecal material), for example, now enable the collection of large sample sizes for wildlife (e.g. Solberg et al. 2006, Ball et al. 2010). The use of genetic data to test landscape connectivity models is a major focus of landscape genetics (Manel et al. 2003), where other landscape graph approaches, particularly raster-based graphs (Adriaensen et al. 2003, McRae et al. 2008), have been used to examine how landscape features facilitate or resist gene flow (e.g. Coulon et al. 2004, Cushman et al. 2006). For patch-based graphs, the association of genetic observations with graph components or compartments is a potential approach (see Chapter 4). For example, if poor connectivity is presenting resistance to dispersal and ultimately to gene flow we might expect individuals sampled in the same component to have more similar genotypes than individuals sampled in separate components.

2.8. Concluding remarks

We have reviewed how patch-based graphs have been used to investigate landscape connectivity for conservation applications. When connectivity among reserves rather than patches is of interest (e.g. Fuller et al. 2006), many of the graph construction and analysis techniques reviewed here will apply. However, landscape models of connectivity where nodes represent a single raster cell (e.g. Adriaensen et al. 2003, McRae et al. 2008) are not interchangeable. Although it is possible to incorporate these landscape models into patch-based graphs (e.g. least-cost path link geometry; Section 2.3.4), their primary goal is to represent connectivity between two points on a landscape. Patch and matrix are not distinguished explicitly, but rather through the parameterization of the raster cells; i.e. habitat is assigned a low resistance, while inhospitable areas of the landscape are assigned a high resistance. Raster-based models on their own have chiefly been used to investigate barriers or facilitators, such as roads and topography, to actual connectivity on a landscape (e.g. Cushman et al. 2006).

The software to construct and analyse patch-based graphs requires development to make these tools accessible to researchers and practitioners. We counted only three publicly accessible patch-based graph specific software packages among the papers we reviewed and these can together only perform a subset of the construction variants and analyses we have described. The packages are Conefor Sensinode (Saura and Torne 2009; available at <http://www.conefor.org/>), SELES (Fall and Fall 2001; available at <http://seles.info/>) and JMatrixNet (available at <http://www.ecology.su.se/jmatrixnet/>). In many cases, authors have developed their own tools or repurposed others for patch-based graphs (e.g.

Margosian et al. 2009). We feel a comprehensive software package is now essential; it should provide the capacity to extract one-dimensional and two-dimensional node and link information from landscape rasters, incorporate a wide selection of graph construction variants and metrics, as well as perform analyses such as link thresholding and node removal experiments. For extension analyses, graphs should be exportable in formats compatible with standard graph analysis software such as the igraph library for R and Python (Csardi and Nepusz 2006), Ucinet (Borgatti et al. 2002), and Pajek (Batagelj and Mrvar 2004).

Perhaps the most exciting contribution of patch-based graphs is the broad range of possibilities that the toolkit presents for ecological connectivity analysis. Indeed, there are many graph and network analysis techniques available, as yet unused in the context of patch-based graphs, which can only broaden the utility of the approach. We note that no two studies have constructed patch-based graphs in the same way, and despite this apparent complexity, the meaning of the models remains intuitive and their predictions visually accessible. We see these qualities as critical for engaging stakeholders and other non-specialists if graphs are used to support the decision-making process. In particular, using patch-based graphs to combine connectivity with information on the amount and quality of habitat (e.g. as node weights) summarizes several important ecological properties of the landscape, that are essential for conservation decisions (Pascual-Hortal and Saura 2007), in a way that can be effectively communicated. As a final caveat, we urge those using patch-based graphs in a decision-making process to assess the relative importance of conserving connectivity compared to, for example, conservation decisions

based only on the amount and quality of habitat. This remains an important area for further theoretical and empirical consideration (Hodgson et al. 2009, Saura and Rubio 2010).

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2.10. Author contributions

All authors were involved in the conceptual development of this paper. P. G. conducted the literature review and wrote the manuscript. M. M. and A.F. contributed to and commented on several drafts.

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CHAPTER THREE

Scaling landscape connectivity: comparing new and existing methods for measuring effective distance at multiple spatial grains

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3.1. Abstract

Landscape connectivity can be measured between two point locations using an effective distance. Typically, raster models of landscape resistance are used to calculate these metrics. Because organisms may perceive landscape heterogeneity at different scales (i.e. functional grains), using a raster with too fine or too coarse a spatial grain (i.e. analysis grain) may lead to biased estimates of effective distance. We adopted a simulation approach where the true functional grain and effective distance were defined and these were used to test the accuracy of three types of effective distance metric: least-cost paths, circuit theory resistance, and grains of connectivity, a new method that we introduce which uses an irregular tessellation of the resistance surface to coarsen the landscape data while also respecting landscape structure. We found that matching functional and analysis grain sizes led to the highest accuracy when measuring effective distance, affirming the importance of multiscale analysis. The use of areal approaches, such as cell aggregation or moving windows to achieve this match, did not generally improve accuracy over analysis at the base grain of the landscape data. Our grains of connectivity method correctly described coarse functional grains and found the true effective distance with high accuracy. A key advantage of our new method is the potential to scale landscape data to achieve a spatially-explicit description of the pattern influencing landscape connectivity. Appendices are provided that demonstrate the construction of grains of connectivity models and how they can be used to calculate effective distance.

3.2. Introduction

Estimates of landscape connectivity are frequently required in landscape ecology and helpful for the conservation and management of fragmented landscapes (e.g. Baguette and Van Dyck 2007, Beier et al. 2009, Urban et al. 2009, Sawyer et al. 2011, Luque et al. 2012). Much work in landscape genetics also relies on models of landscape connectivity, where the reduction in, or absence of, landscape connectivity can be used to explain patterns in gene flow and genetic similarity (e.g. Cushman et al. 2006, Schwartz et al. 2009, Shirk et al. 2010, Storfer et al. 2010).

Landscape connectivity is often understood as a functional response of an organism to landscape structure (Calabrese and Fagan 2004). Because organisms perceive spatial heterogeneity on landscapes at different functional grains (Baguette and Van Dyck 2007) estimates of connectivity must also consider the scale at which the heterogeneity, or pattern, affecting connectivity is measured. In order to respect the fundamental dependencies between scale, pattern and process (Wiens 1989, Levin 1992, Wu 2004), the pattern (how the landscape is connected) must be described at the same scale as the process (how organisms move and disperse). Failure to match these scales can produce incorrect conclusions about how or if the landscape is functionally connected for the species of interest (Cushman and Landguth 2010).

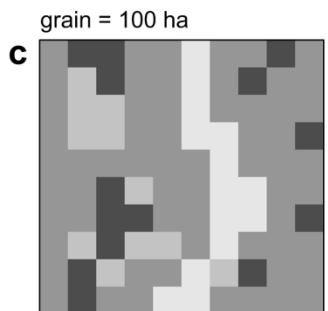
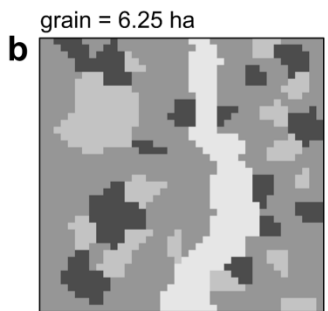
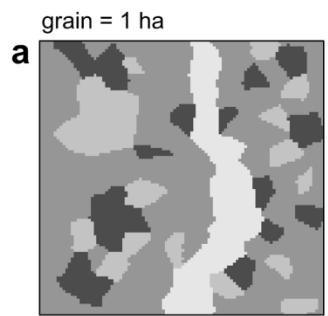
However, identifying the correct functional grain remains a challenge, and requires difficult to acquire empirical estimates of perceptual range and dispersal capability (Baguette and Van Dyck 2007). For example, highly-mobile terrestrial organisms, such

as large mammals, are likely to perceive landscapes and to disperse at relatively coarse functional grains. Woodland caribou, a large ungulate, has been shown to select for connected areas of habitat between 20 km² and 100 km² in area (O'Brien et al. 2006). Potentially, for mobile species, the functional grain could be orders of magnitude larger than the grain of the landscape data. The fine-grained variation found on remotely-sensed landcover maps, in these cases, may not be important for the movement and dispersal process, and can be rather a kind of noise that can obscure the coarser patterns in landscape features influential for connectivity (Anderson et al. 2010).

One approach for removing the noise and revealing the pattern is to coarsen the spatial grain of the landcover raster (Anderson et al. 2010). Scaling of rasters has been done using areal methods where cells are aggregated to reduce resolution, or variation is smoothed using a moving window (e.g. Cushman and Landguth 2010). These steps can typically retain key landscape features when the optimal grain is not too much coarser than the grain of the original raster (e.g. Fig. 3-1, a, b). However, when the grain required is orders of magnitude coarser than the original grain (e.g. Fig. 3-1, c, d), as it may need to be for mobile species, areal methods may obscure or eliminate small footprint features influential for connectivity, such as roads and rivers. In addition, there is a practical upper limit to the grain area using these approaches, with very coarse grains resulting in the loss of nearly all information about the landscape (Fig. 3-1, d).

Figure 3-1. Changing the analysis grain by areal methods.

This can retain information about landscape structure when the change in grain area is relatively small (a and b). When grain size changes by orders of magnitude nearly all information about the landscape is lost (c and d). The effects of changing the grain using a modal cell aggregation rule are shown.

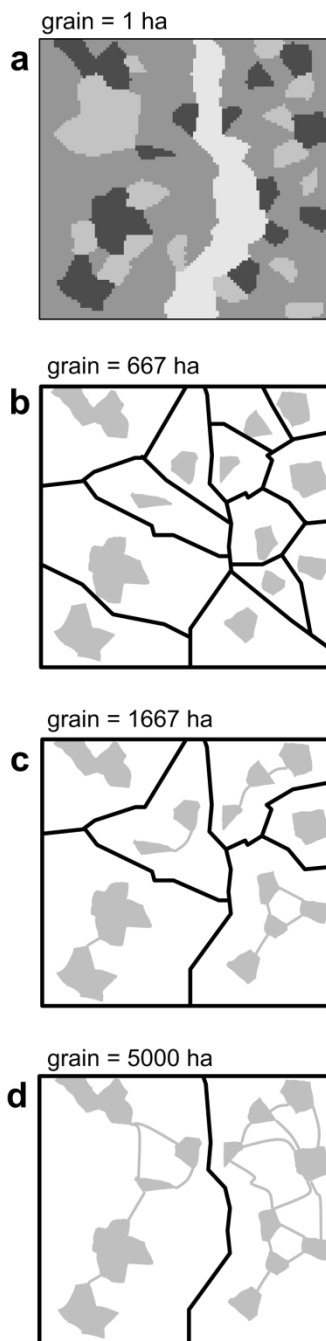


Patch-based landscape graphs (Urban and Keitt 2001, Fall et al. 2007, Galpern et al. 2011) provide an alternative approach to scaling. These methods can be used to aggregate habitat patches at different thresholds of dispersal ability (scalar analysis; Brooks 2003), essentially describing the landscape at a series of functional grains rather than areal grains (Bunn et al. 2000, O'Brien et al. 2006, Margosian et al. 2009). Here, we introduce a method that extends patch-based graphs by modelling the relationships among regions of the landscape. This method, called grains of connectivity, uses a Voronoi tessellation of a landscape raster to find polygons describing regions of proximity around habitat patches (Okabe et al. 2000, O'Brien et al. 2006, Fall et al. 2007). These Voronoi polygons are analogous to the cells in a typical raster, but unlike grid cells they can vary in shape and area in order to represent functionally connected regions of the landscape (Fig. 3-2). Like areal scaling, the grains of connectivity method coarsens the grain of a raster, and filters out landscape features that do not impact the relationships between adjacent polygons. Importantly, it can also scale to much larger grains than areal methods, which may be essential for describing pattern influencing connectivity for highly mobile organisms. Please see Appendices 3-1 to 3-4 for an overview of minimum planar graph and grains of connectivity modelling (see also Galpern et al. 2012).

When landscape connectivity is measured between two point locations, it has been called an effective distance (Adriaensen et al. 2003). Distances calculated using least-cost paths first appeared (Adriaensen et al. 2003), followed by methods that consider multiple paths simultaneously (e.g. circuit theory resistance distance, conditional minimum transit cost; McRae et al. 2008, Pinto and Keitt 2009). In all cases, distances are determined by

Figure 3-2. Changing the analysis grain using grains of connectivity, a method that describes functional grain.

This can retain information about landscape structure at much larger grain areas, correctly representing small footprint features such as the river. Grain is changed using a Voronoi tessellation (b) of a resistance surface (a) and by producing a landscape graph of patches (c and d). This method is explained further in the text.



producing a cost or resistance surface which parameterizes the effects of landscape features on movement and dispersal (Fig. 3-3, a). These surfaces are typically raster grids, and effective distance is calculated by adopting a graph-based representation of the relationships among raster cells and finding a path between cells containing the point locations using a random-walk or Dijkstra's algorithm (Fig. 3-3, b; Dijkstra 1959, Adriaensen et al. 2003, McRae et al. 2008). An effective distance can be measured from a grain of connectivity in an analogous manner. For example, we find a network distance as the shortest distance between Voronoi polygons containing the point locations (Fig. 3-3, c). In this way grains of connectivity provides a scalar landscape graphs extension of least-cost paths; this network distance is essentially a least-cost path through a much coarser and irregular grain, and the distance separating polygons is itself an effective distance measured on the original raster grid (see Appendices 3-1 to 3-4).

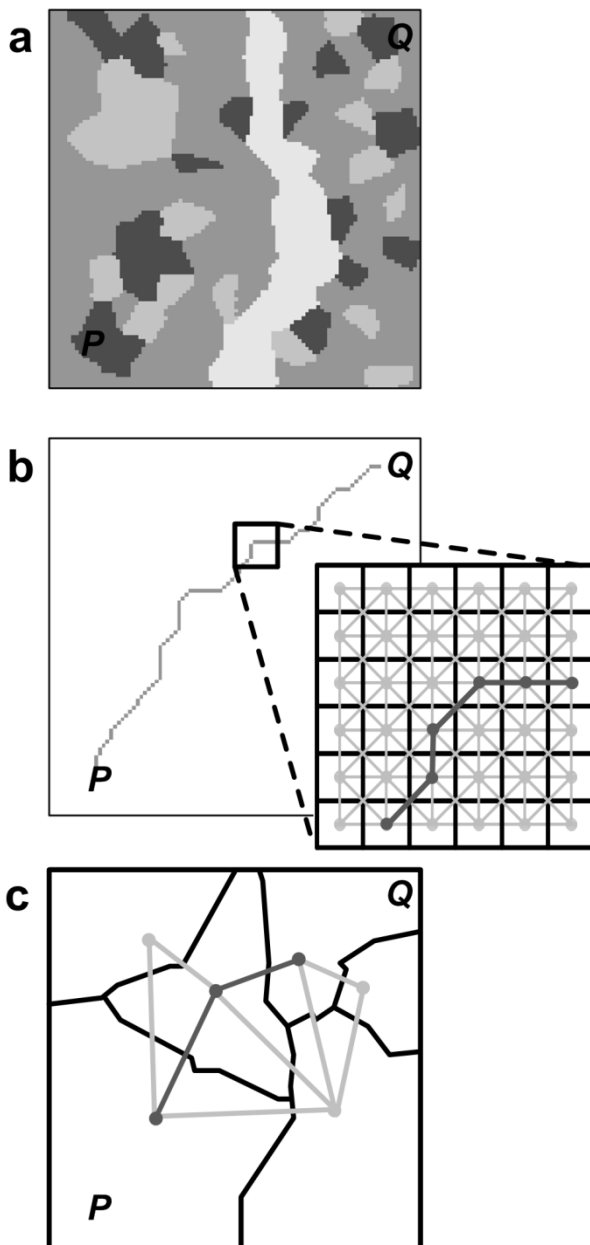
3.2.1. Objectives

In any of these measures of effective distance, if the measurement grain is mismatched with the functional grain, we should expect metrics to incorporate some amount of error (Cushman and Landguth 2010). Our objective in this paper is to compare the accuracy of three types of effective distance metrics: the grains of connectivity method, least-cost paths and circuit theory-derived resistances. Using artificial land cover rasters, we ask if these methods are capable of correctly measuring pattern in landscape resistance that we simulated to operate at grains that were much coarser than, or similar to, the original raster. We also examine the effect of changing the grain size, using both areal and grains

Figure 3-3. Two approaches to find effective distances from a resistance surface.

A surface describing the resistance of landscape features (a). Raster-based methods such as least-cost paths (b) are affected by fine-grained variation.

Shortest network distances calculated using a grain of connectivity have many fewer steps (c), and potentially can filter out fine-grained variation that may contribute to error when measuring effective distance



of connectivity approaches, and explore the sensitivity of our conclusions to resistance parameterization.

3.3. Methods

We tested a new method, called grains of connectivity, that can be used to find effective distances between point locations. We determined these distances by first building a minimum planar graph (MPG), a patch-based landscape graph that models landscape connectivity using least-cost paths between focal high-quality habitat patches (Fall et al. 2007, Urban et al. 2009, Galpern et al. 2011). We then used the complement of the MPG, a Voronoi tessellation of the patches in the graph (Okabe et al. 2000, Fall et al. 2007), to describe regions of proximity in resistance units around those patches (e.g. polygons in Fig. 3-2, c). Tessellations at different scales (i.e. spatial grains) were achieved by thresholding the MPG at varying maximum amounts of least-cost path distance (e.g. Fig. 3-2, b, c, d; Brooks 2003). We describe these tessellations as grains of connectivity. A grains of connectivity graph was then built by finding the mean least-cost path distance between patches in each Voronoi polygon and using this to weight links (Fig. 3-3, c). Finally, the effective distance between two locations was the shortest network distance on the grains of connectivity graph between polygons containing those locations. Appendices 3-1 to 3-4 provide a detailed presentation of grains of connectivity and the grains of connectivity network distance.

To explore the performance of the grains of connectivity network distance and two other effective distance metrics, we constructed artificial landscapes with three different

patterns, and analyzed them at multiple spatial scales. For each pattern we defined how a hypothetical organism might perceive the landscape, and declared this the functional grain. We then tested whether least-cost paths, circuit theory resistance distance, and grains of connectivity network distance (Adriaensen et al. 2003, McRae et al. 2008) were able to accurately describe this functional grain when measured at a series of grain sizes.

We began by simulating a patchy landscape 400 x 400 cells in dimension with four cover classes (algorithm as in Rayfield et al. 2010). Circular high-quality habitat patches were then superimposed on the landscape in either a regular or irregular pattern depending on the treatment. A resistance value (equal to 1, 2, 3, 4 or 5) was assigned to each of these five cover classes, with high-quality habitat assigned the lowest resistance (i.e. 1).

For the first artificial landscape (treatment 1) we positioned high-quality patches in a regular pattern and superimposed an additional landscape feature, a radial structure, that divided the landscape into three regions (Fig. 3-4, right). The resistance value of this feature was initially set to 20. We proposed a hypothetical organism that could move freely within these regions but experienced resistance to movement and dispersal only when crossing the arms of the radial structure. Each arm of the structure had a different thickness, meaning that these regions of the landscape differed from one another in their relative proximity. A correct representation of the connectivity on this landscape for this hypothetical organism would produce ranked pairwise distances shown in Fig. 3-4 (centre bottom) for the six sampling locations shown in Fig. 3-4 (A to F). Such a matrix implies that the resistance associated with the land cover on the map is essentially noise and that

the radial feature, a pattern that is evident at a broad extent, defines the shape and size of the functional grain influencing connectivity.

In a second landscape (treatment 2), rather than adding a structure, we created pattern through the irregular placement of high-quality habitat patches (Fig. 3-5, right). Here we proposed an organism that could move freely within each of the four regions of the map, but experienced resistance to movement only when moving among these regions. We proposed that resistance due to all landscape features within these regions was essentially noise, and that the connectivity relationships among these regions would be approximately proportional to their proximity in Euclidean space (i.e. that resistance to movement is lowest when moving horizontally between regions, intermediate when moving vertically, and highest when moving diagonally.) Thus the four regions of the map, each containing a cluster of high-quality habitat, defined the shape and extent of the functional grain. The expected effective distance matrix given these hypothetical conditions and eight sampling locations (Fig. 3-5, A to H) is given by the ranked pairwise distances (Fig. 3-5, centre bottom). The goal in this treatment was to examine landscape pattern in patch spatial configuration and whether it could be captured by the effective distance metrics.

In a third landscape (treatment 3) we used only the regular placement of high-quality habitat patches and proposed an organism that experienced landscape resistance at the grain of the original raster (Fig. 3-6, right). In this case we used the least-cost path distances among six locations (Fig. 3-6, A to F) to create the expected effective distance

Figure 3-4. Treatment 1.

Effective distances measured using grains of connectivity (GOC) are most accurate at capturing a functional grain (i.e. a pattern affecting connectivity) that is coarser than the raster grain when the pattern has been created by an influential small footprint feature. (Left) Accuracy of effective distance methods of describing the expected effective distances at a range of analysis grains. (Centre top) The shape and configuration of Voronoi polygons at the most accurate GOC analysis grain. (Centre bottom) The expected effective distances given the landscape pattern and the proposed functional grain. (Right) The resistance surface used in this treatment. Darker shading indicates a higher resistance to movement and dispersal.

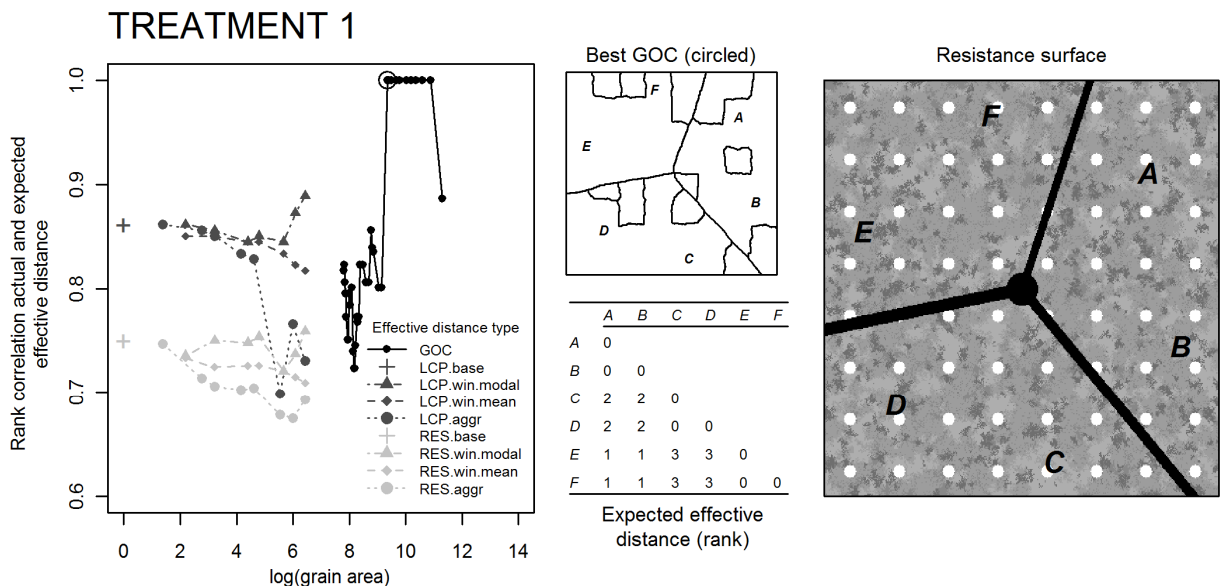


Figure 3-5. Treatment 2.

Effective distances measured using grains of connectivity (GOC) are most accurate at capturing a functional grain (i.e. a pattern affecting connectivity) that is coarser than the raster grain when the pattern created by the spatial configuration of high-quality habitat patches. See Fig. 3-4 caption for explanation of sub-figures.

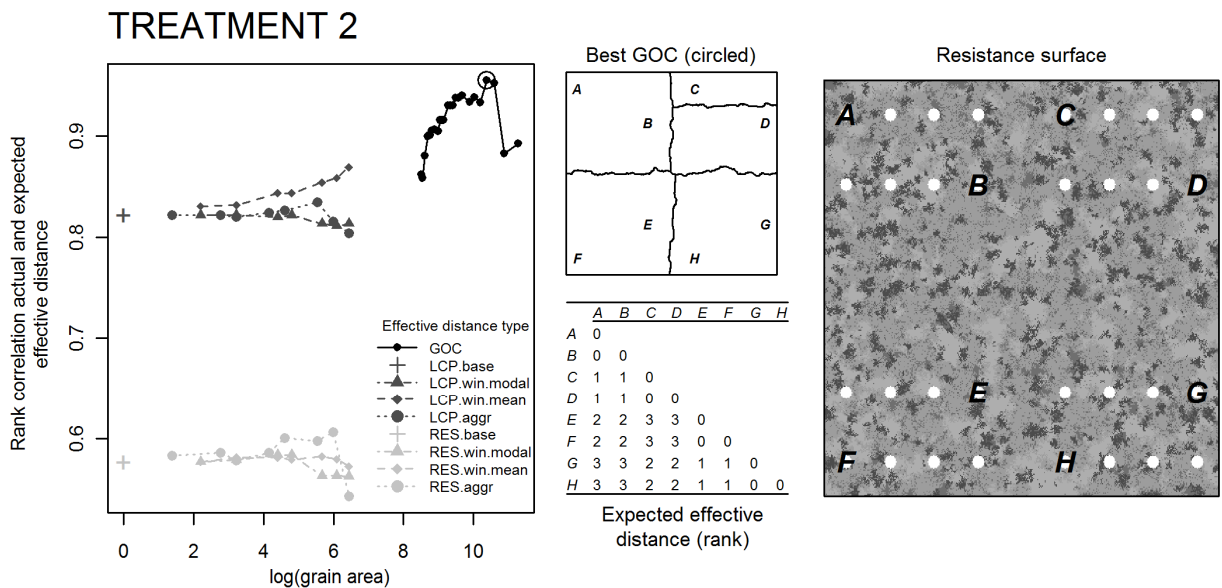
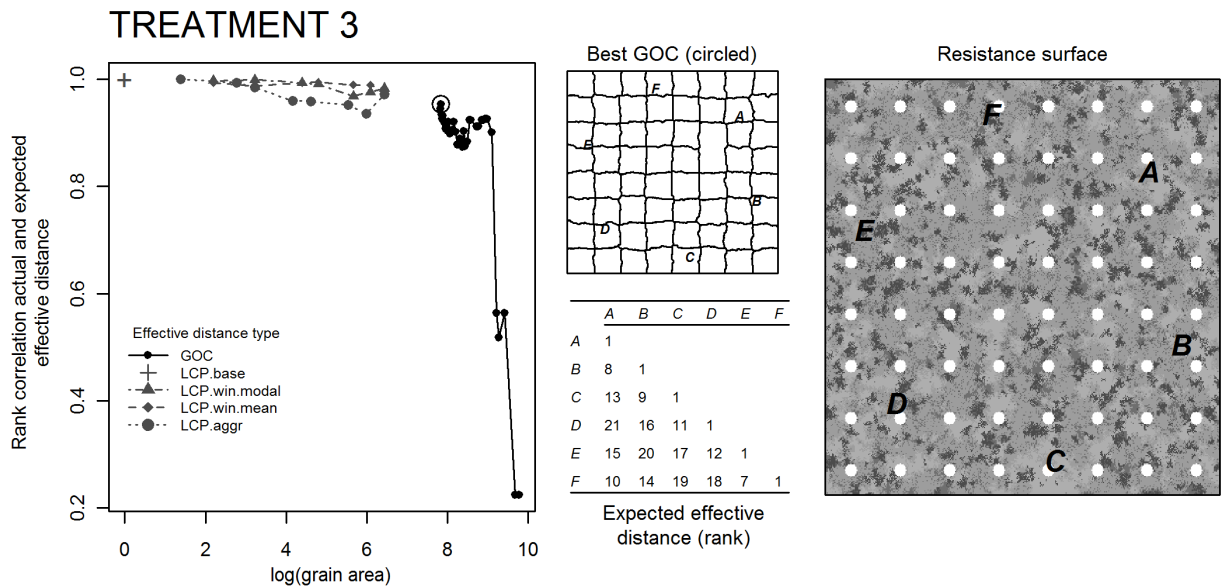


Figure 3-6. Treatment 3.

Effective distances measured at fine grains are most accurate at capturing a functional grain (i.e a pattern affecting connectivity) that is at the same grain as the raster. The pattern is created by the land cover at the raster grain. See Fig. 3-4 caption for explanation of sub-figures.



matrix (Fig. 3-6, centre bottom). Because we were comparing against least-cost paths, we did not examine circuit theory resistance distances for this case. The purpose of this treatment was to examine if effective distances calculated at grains coarser than the pattern of interest could correctly capture pattern evident at fine grains.

For each of these landscape treatments we manipulated the grain of measurement using four different methods. For rasters we used moving windows at seven different grain sizes to smooth variation. Moving windows were applied with both a mean (win.mean) and a modal function (win.modal). We also produced lower resolution rasters at eight different grains using a modal cell aggregation rule (aggr). For these areal methods the upper grain size used was that where only two classes of feature remained on the raster. Grains of connectivity were determined for each landscape at threshold intervals of 1 resistance unit, and those that produced different grains were retained. The upper grain size was where the landscape was divided into two polygons.

We found pairwise least-cost path distances (LCP) and circuit theory resistance distances (RES) for the specified sampling locations at each raster grain as well as at the grain of the original raster (base). We also found the grains of connectivity network distance (GOC) for each grain of connectivity.

Finally, to understand how the parameterization of landscape features affects conclusions, we used the first landscape (treatment 1) and assigned one of ten levels of resistance (5, 10, 15, 20, 25, 50, 100, 200, 400, or 800) to the radial structure. We examined accuracy

at identifying the correct effective distances using least-cost paths and circuit theory resistance methods for the base grain, and for the grains of connectivity method at all grains.

In all cases we measured the accuracy of the effective distance metric using a rank correlation (Spearman's r) between the actual and expected effective distances for each pair of sampling locations. We depicted the grain of connectivity with the highest accuracy (Best GOC) by plotting the outline of each Voronoi polygon at that grain.

All analyses were conducted in R 2.14.1 (R Development Core Team 2012). Landscape simulation and the areal manipulations of grain size on raster grids were done using the *raster* package (Hijmans and van Etten 2011). Grains of connectivity and the grains of connectivity network distances were determined using the *grainscape* package (Galpern et al., in prep.). Least-cost path and circuit theory resistance distances were calculated using the *gdistance* package (van Etten 2010).

3.4. Results

3.4.1. Accuracy at identifying functional grain

The highest accuracies were found where the grain used to measure the effective distance, the analysis grain, matched the functional grain. In treatments 1 and 2 (Figs. 3-4 and 3-5, left) the functional grain, or pattern influencing connectivity, was the division of the landscape into three or four regions. The GOC method found these functional

grains (Best GOC) as well as the resistance associated with moving between these regions, and accurately reproduced the expected effective distances among the reference locations. In treatment 1, the most accurate GOC grain (Best GOC; Fig. 3-4, centre top) showed more than the expected three regions because there are insufficient sampling points to differentiate between this grain and one with fewer polygons. Perfect accuracy is achieved, however, because the sampling points are grouped together correctly and the proximities of these three regions are as expected. In treatment 2 the most accurate GOC grain (Best GOC; Fig 3-5, centre top) does not completely capture the four expected regions, and finds five instead, indicating that the GOC effective distances are subject to some amount of error. In treatment 3 (Fig. 3-6, left), the proposed functional grain was many times smaller, and defined as the area of a single raster cell. In this case the pattern was created by the land cover features on the artificial landscape, and the expected effective distances were the accumulated resistance of least-cost paths at this grain. Using grains of connectivity, in treatment 3, where the smallest possible analysis grain was about 2500 times greater in area than the proposed functional grain (Best GOC; Fig. 3-6, centre top), produced less accurate results than using least-cost paths at most grain size and scaling methods.

3.4.2. Effects of changing analysis grain

Changing the analysis grain using an areal approach yielded relatively small differences in the accuracy of effective distance. In treatment 1 (Fig. 3-4, left) the use of a modal moving window (win.mean) where the most frequent cell value in the neighbourhood is assigned to the window, improved accuracy at coarse analysis grains. In treatment 2

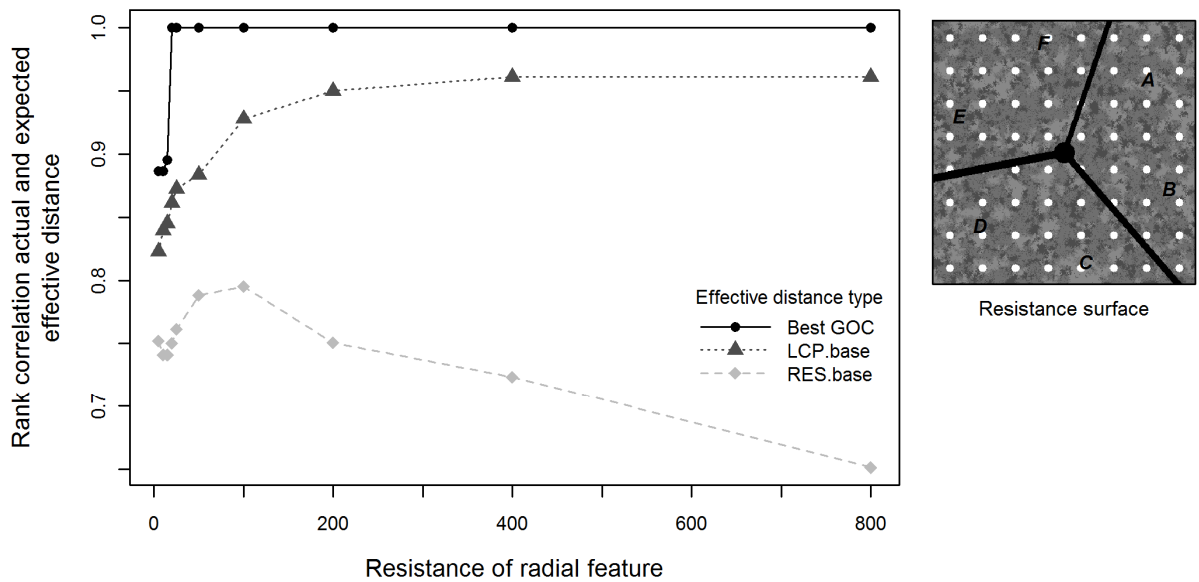
(Fig. 3-5, left) a mean moving window (win.mean) also improved accuracy at coarse analysis grains. In treatment 3 (Fig. 3-6, left) all areal methods to increase analysis grain size resulted in poorer accuracy than the base grain, although the effect on accuracy was small (Fig. 3-6, left). Finally, the accuracy of GOC reached its maximum as the analysis grain approached the expected functional grain size (Figs. 3-4 to 3-6, left), but the approach was not monotonic on either side of this maximum, exhibiting a threshold response instead. In treatment 3, the accuracy of GOC fell as the mismatch between the functional grain and the analysis grain became extreme (Fig.3-6, left).

3.4.3. Effects of changing resistance value

When the resistance value assigned to the radial feature in treatment 1 was manipulated, the three types of effective distance metric performed differently (Fig. 3-7). GOC showed a threshold response, finding the best analysis grain to describe the pattern when the resistance of the radial feature exceeded a minimum (resistance=20; Fig. 3-7). LCP measured at the base analysis grain (LCP.base) showed an asymptotic response, where the effective distance metric performed with increasing accuracy as the resistance value increased, and nearly matched the accuracy of GOC when this value was set above 200 units (Fig. 3-7). RES measured at the base analysis grain (RES.base) achieved an intermediate maximum in accuracy, but declined as the resistance value increased (Fig. 3-7).

Figure 3-7. Effects of manipulating the resistance value of the radial feature.

The accuracy of effective distances measured using grains of connectivity (Best GOC) is least sensitive to the resistance value assigned to the radial structure (treatment 1). Effective distances calculated using least-cost paths (LCP.base) can also accurately describe the pattern, but require the resistance value of the radial structure to be set much higher. Resistance distances calculated using circuit theory (RES.base) performed less accurately than either of the other two methods.



3.4.4. Relative accuracy of effective distance metrics

LCP and GOC metrics generally performed more accurately than RES in treatments 1 and 2 where the functional grain was much coarser than the analysis grain. We did not test RES in treatment 3 where the functional grain was the same as the grain of the landscape data, because LCP was used to define the expected distances.

3.5. Discussion

Our simulations assumed that there is an optimal spatial grain at which an organism perceives landscape pattern during movement and dispersal (i.e. a functional grain for landscape connectivity). We conjectured that if the analysis grain does not correspond to this functional grain, measures of landscape connectivity (e.g. effective distances that describe landscape resistance to movement) will be biased because they will incorporate too much or too little spatial heterogeneity. By defining a correct functional grain for a hypothetical organism we asked if effective distance measured using least-cost paths (Adriaensen et al. 2003), circuit theory resistance (McRae et al. 2008), or a method we introduced called grains of connectivity, could find the true landscape resistance to movement this organism would experience.

3.5.1. Matching analysis and functional grains

Using three simulated landscapes we found that effective distance metrics were most accurate when the analysis grain matched the hypothesized functional grain. This was true both when the functional grain was the same grain as the landscape data, and when it was much coarser than the landscape data. These results support the expectation that the

scales of pattern measurement and ecological process should be comparable to ensure accurate conclusions (Wiens 1989, Wu 2004, Anderson et al. 2010). In a similar exercise Cushman & Landguth (2010) found that using an analysis grain finer than the functional grain (in this case simulated using a stochastic gene flow simulation) had a relatively small effect on accuracy. Our results also found a small reduction in accuracy when using too fine an analysis grain. However, in qualitative terms, the effect of underestimating the grain size is more significant. Had we conducted an analysis at the finest grain we might have concluded that landscape features were influencing connectivity between all locations, and overlooked the potentially important observation that certain pairs of locations are effectively at the same location in terms of their connectivity (e.g, locations with a zero rank expected effective distance in Figs. 3-4, 3-5). We would have missed the high connectivity, and therefore negligible landscape resistance, associated with moving between these points even though the two locations are not superimposed; in other words, we would have failed to recognize the role of spatial configuration in landscape connectivity.

Increasing the analysis grain should better approximate these conditions, because using a larger grain area creates larger homogeneous regions; i.e. by increasing the size of the raster cell, simplifying landscape heterogeneity, or both (e.g. Figs. 3-1, 3-2). However, we found that increasing the analysis grain using areal approaches such as cell aggregation rules or moving windows yielded no consistent improvement when the functional grain was coarse. Using too coarse an analysis grain has been cited as a potential pitfall in least-cost path analysis because it may miss important landscape

variation affecting connectivity (Chetkiewicz et al. 2006, Beier et al. 2009, Sawyer et al. 2011). In contrast to these predictions, we found that using the coarsest analysis grain achievable by an areal approach produced a relatively small reduction in accuracy when the functional grain was much finer.

Areal approaches simplify variation in a uniform manner and are therefore arbitrary with respect to landscape pattern (e.g. Fig. 3-1). Where the landscape heterogeneity affecting connectivity is a continuous variable, such as elevation or moisture, it is possible that this simplification could approximate the correct functional grain. However, if the relevant landscape heterogeneity is discrete, such as topographic features, patches of cover vegetation, or human disturbance, an orthogonal approach is very likely to obscure pattern. Ungulates, for example, may perceive their landscape in terms of the avoidance of roads and buildings (Coulon et al. 2008, Polfus et al. 2011). These are discrete small footprint features that are likely to be eliminated when the map is rendered at a sufficiently coarse grain to reduce other variation (e.g. in vegetation features) that is potentially unimportant.

The grains of connectivity approach to increasing the analysis grain can overcome the orthogonal limitations of areal approaches. Using this method we produced analysis grains that described the locations of small footprint features on the base grain (e.g. Fig. 3-4, centre top; polygon boundaries) as well as areas containing landscape variation unimportant for connectivity (e.g. Figs. 3-4, 3-5, centre top; polygon regions). Grains of connectivity were also highly accurate at finding coarse functional grains. This

underlines the potential of the method to differentially smooth heterogeneity, a process which is governed by the resistance value that is assigned to landscape features (see Appendix 3-1).

3.5.2. Resistance parameterization

In least-cost path or circuit theory based analyses, the assignment of resistance values has been shown to influence conclusions, and sensitivity analyses have been strongly recommended (Beier et al. 2009, Rayfield et al. 2010, Spear et al. 2010, Sawyer et al. 2011). We have shown that the grains of connectivity method is less sensitive to the assignment of resistance values than other methods. The threshold response to increasing the resistance of the radial feature suggested that there was a narrower range in parameter values over which accuracy is variable compared to other methods (Fig. 3-7; Best GOC). It is important to note that the "best" grain of connectivity on which this observation is based requires testing multiple grains and using some criterion to select an optimal one.

Although there may be less sensitivity if such a multiscale approach is used, the shape of Voronoi polygons is still reliant on the relative resistances assigned to features.

Therefore calls to ensure that resistance parameters are correctly estimated using justifiable means, and that parameters reflect the costs of movement and dispersal, do still apply (e.g. Spear et al. 2010). In addition, it appears that the differences between resistance values need not be large to capture the relevant functional grain. This has the potential to further improve accuracy because high contrasts in resistance values, at least

in analyses that use least-cost paths, have been shown to increase sensitivity (Rayfield et al. 2010).

Our results also support the conclusion that least-cost path and circuit theory-based analyses are sensitive to the magnitude of resistance assigned to certain features (Rayfield et al. 2010, Sawyer et al. 2011). Interestingly, in the single treatment we examined, increasing the resistance value improved results for least-cost paths, implying that by selectively assigning a high resistance to a feature it is possible to render variation in other features relatively unimportant for the effective distance. The absence of alternative paths around the radial feature are likely causing this result (i.e. paths between different regions of the landscape must cross the feature, and therefore all paths between regions have a much higher effective distance than paths within a region).

In disturbed landscapes it may be common for there to be no alternative to crossing a high resistance feature. In a landscape genetic study of mountain goats, for example, a resistance surface was used where roads and high elevations were assigned high resistances (> 10 000 units) effectively creating a network of barriers. The authors of this study found that effective distances measured using circuit theory explained genetic relatedness (Shirk et al. 2010). It is possible that these results were influenced by these high resistance features, where effective distances across them were orders of magnitude larger than other distances, making the cost of crossing other features relatively unimportant.

Assigning high resistances to certain features and using fine-grained landscape data may be one way to model areas of high connectivity because it can potentially smooth out unimportant variation, but this requires *a priori* identification of these features. In cases where there are no obvious high resistance features, or the amount of resistance may be a cumulative effect of multiple features, this approach will likely be unsuccessful. A key contribution of grains of connectivity is defining these high resistance, low connectivity, regions. The Voronoi polygon in a grain of connectivity represents a region where resistance is below a certain threshold and, for the purposes of measuring effective distance, any features within this region are ignored (Appendices 3-1 to 3-4; Fig. 3-3, b). A transition across a Voronoi polygon boundary therefore represents a resistance higher than the threshold amount, and its value combines information from multiple landscape features that may be affecting movement between the polygons. Thus, the boundaries of the polygons can be understood as meta-features that represent low connectivity and resistance to movement. In some cases these meta-features may correspond spatially to actual features (e.g. the radial features in Fig. 3-4, right), and in others to the reduced connectivity created by combinations of landscape features (e.g. Fig. 3-5, right).

3.5.3. Circuit theory at coarse functional grains

In our simulations, the circuit theory resistance metric was less accurate than the least-cost path metric in the two treatments where comparison was possible. The potential of circuit theory to model multiple movement pathways in ways that least-cost paths cannot is compelling; in certain landscape configurations, circuit theory identifies greater connectivity between locations than least-cost paths because it considers multiple

alternative routes in parallel (McRae et al. 2008). It could be argued that the landscape dominated by a radial feature (Fig. 3-4) is, therefore, not a fair test of circuit theory because alternative paths around the barrier do not exist. However there is no such limitation in Fig. 3-5, and yet in both cases the method performed less accurately. We caution that this poorer performance may only extend to identifying patterns at coarse grains relative to the landscape data, and because of our study design we were unable to meaningfully measure the accuracy of circuit theory at finer grains (see *Methods*). These results, however, suggest that further investigation is warranted to understand the landscape conditions where circuit theory is more or less suitable than least-cost paths.

3.5.4. Study limitations

Conducting stochastic simulations, by using multiple random landscapes with controlled properties for example, would help confirm the generality of the conclusions we have drawn. Instead, we have adopted a case study approach in order to better focus on the properties of these metrics and illustrate their relative performance. Therefore the possibility that some of our conclusions are specific to the scenarios we have illustrated should be considered, and accuracy differences among least-cost paths and circuit theory metrics may potentially be within sampling error. Additionally, in two treatments we modelled functional grains that were coarser than the grain that could be achieved using areal scaling methods. We therefore did not test the performance of areal scaling methods for functional grains of comparable area. However, the orthogonality limitations of areal scaling and the likelihood that that landscape pattern in discrete

feature classes will be obscured (see above) suggest that there will be limits to the accuracy of these approaches.

3.5.5. Applications

Although we have demonstrated that mismatching the grain of analysis and the functional grain is important for accuracy, our results also demonstrated that using least-cost path analysis at the finest grain could still be very accurate. In all landscapes we studied, the rank order of effective distances remained highly correlated with the expected pattern across a broad range of analysis grains. This implies that using a standard least-cost path approach may yield fair approximations of the correct effective distance no matter the functional grain at which the organism perceives spatial heterogeneity. In landscape genetics studies, then, where the objective is to correlate effective distance measures of landscape resistance to genetic distance (e.g. Cushman et al. 2006, Schwartz et al. 2009, Shirk et al. 2010), using least-cost paths at the finest grain may capture a large proportion of the variation in landscape resistance, and therefore could be used to provide evidence of landscape influence on gene flow. We note, however, that in a woodland caribou landscape genetic study we found that coarse grains of connectivity, and not fine-grained rasters, produced conclusive evidence of landscape influence of gene flow (Galpern et al. 2012), suggesting that other factors, such as the strength of the spatial genetic structure, may also play a role.

Even in cases where the finest analysis grain may be adequate for correlative purposes, measuring landscape connectivity at multiple scales could still help highlight the causal

mechanisms of resistance. Consider the high degree of accuracy possible when using grains of connectivity (e.g. Figs. 3-4, 3-5). In these cases there existed a grain of connectivity that very closely depicted the simulated functional grain and described the effective distance among locations. The Voronoi polygons produced by this method provide a spatially-explicit description of landscape pattern creating resistance, a tool that is potentially more useful than the relative influence of landscape features that can be obtained by testing a fine-grained resistance surface (e.g. Schwartz et al. 2009). For example, at the finest grain we would have overlooked the importance of the spatial configuration to landscape connectivity, and we may have incorrectly concluded that certain landscape features were presenting resistance (see above).

We foresee great potential for multiscale analyses, such as grains of connectivity, that attempt to model the functional grain influencing movement and dispersal. As with other methods of measuring landscape connectivity, finding ways to test these models using empirical evidence of movement and dispersal, and applying more powerful approaches to identify supported grains, will remain important (Jaquiéry et al. 2011, Sawyer et al. 2011, Galpern et al. 2012).

3.5.6. Conclusions

We demonstrated that matching the analysis grain with the functional grain (i.e. the perception of landscape heterogeneity for a hypothetical organism) can improve accuracy in effective distance measurements. Using areal approaches to change the grain and find this match was not accurate when the functional grain was coarse relative to the

landscape data. Although these methods smooth variation, they do so uniformly, which at coarse grain sizes obscures pattern. Grains of connectivity, a multiscaled approach that describes regions of proximity and the relationships among these regions, can coarsen landscape data without obscuring pattern. We found that this method could accurately depict the functional grain pattern and represent this in effective distance measurements. A key advantage of a multiscaled analysis may be the potential to achieve a spatially-explicit description of the pattern influencing landscape connectivity.

3.6. Acknowledgements

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3.7. Author contributions

Both authors were involved in the conceptual development of this paper. P.G. designed and conducted the simulations and wrote the manuscript. M. M. contributed to and commented on several versions of the manuscript.

3.8. Appendices

Appendix 3-1

Producing grains of connectivity models and finding the grains of connectivity network distance.

Appendix 3-2

Illustration of minimum planar graph and grains of connectivity modelling at four selected resistance thresholds (for Treatment 1).

Appendix 3-3

Illustration of minimum planar graph and grains of connectivity modelling at four selected resistance thresholds (for Treatment 2).

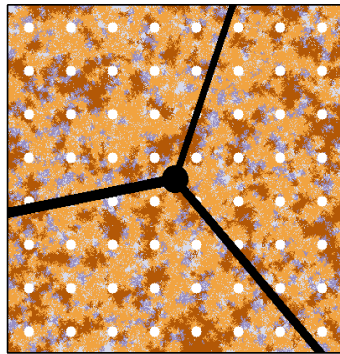
Appendix 3-4

Illustration of minimum planar graph and grains of connectivity modelling at four selected resistance thresholds (for Treatment 3).

Appendix 3-1. Producing grains of connectivity models and finding the grains of connectivity network distance.

The following figures describe eight steps in the production of a grains of connectivity model, and then demonstrate how it is used to find the effective distance between two locations. The land cover raster used in Treatment 1 is shown here. The process begins by finding the minimum planar graph (MPG). Then, a grain of connectivity and a grain of connectivity graph (GOC graph) is found. Finally, a shortest path algorithm is used to find a network distance through the GOC graph.

Appendix 3-1. Cont'd.



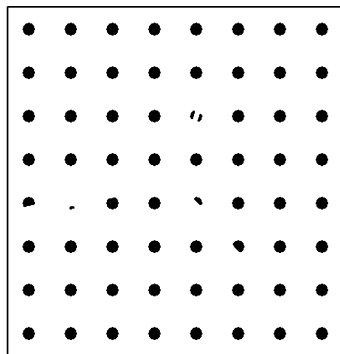
land cover
(resistance units
per cell)

- 1
- 2
- 3
- 4
- 5
- 20

100 cells

STEP 1

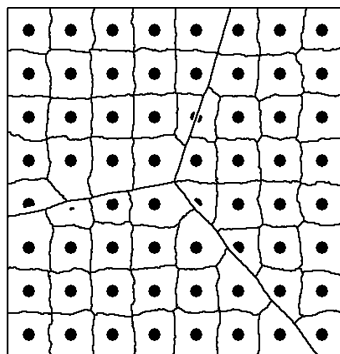
A land cover raster is rendered as a resistance (or cost) surface, where features are assigned a resistance value. Higher values indicate greater resistance to movement (i.e. reduced landscape connectivity). The raster from Treatment 1 is used in the following series.



● focal patch

STEP 2

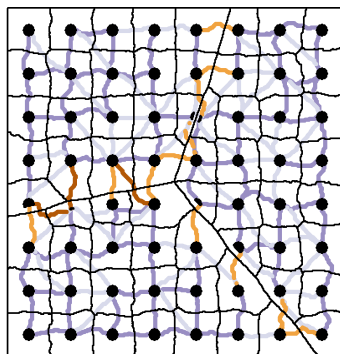
Focal patches are identified on the land cover raster (STEP 1). These patches are typically contiguous areas with a low or negligible amount of landscape resistance. Focal patches could be selected using any biological or landscape criterion, however (e.g. using a minimum area, or minimum core area). In this example, patches represent all areas of the lowest resistance land cover feature (resistance = 1).



● focal patch
— Voronoi polygon

STEP 3

Regions of proximity are found surrounding the focal patches. Polygons describing these regions are identified using a two-dimensional generalization of the Voronoi tessellation (e.g. Okabe et al., 2000) where the focal patches are the generators, and distance is represented in resistance units (STEP 1) measured from the perimeter of the patches (Fall et al., 2007)



● MPG node
(focal patch)
— Voronoi polygon

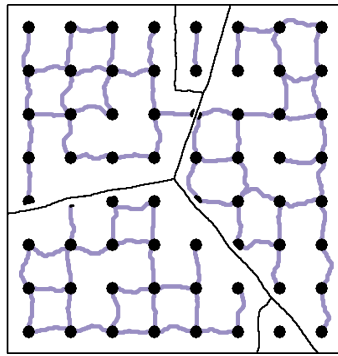
MPG link (least-cost path)
(resistance units)

- 70 - 106
- 107 - 199
- 200 - 299
- 300 - 430

STEP 4

The minimum planar graph (MPG) is extracted, where focal patches serve as nodes, and least-cost paths between nodes serve as links. Links in an MPG are made only between nodes that share adjacent Voronoi polygons (STEP 3). The MPG is an approximation of the complete graph (i.e. a graph where all pairs of nodes are connected) with many fewer links (Fall et al., 2007).

Appendix 3-1. Cont'd.

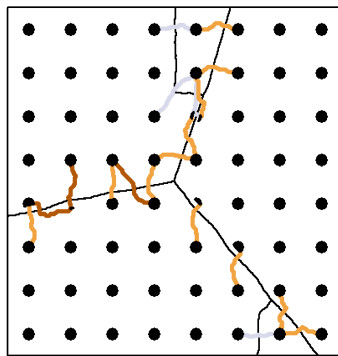


Threshold = 106 resistance units

- MPG node (focal patch)
- Voronoi polygon
- MPG link (least-cost path) (resistance units)
 - 70 - 106
 - 107 - 199
 - 200 - 299
 - 300 - 430

STEP 5

The MPG (STEP 4) is reconstructed at a resistance threshold (also known as scalar analysis; Brooks, 2003), where links joining nodes are removed from the MPG if their weight (i.e. the length of the least-cost path they represent) is greater than a threshold value. Following thresholding, if nodes are still joined by links, their Voronoi polygons (STEP 3) are combined. The resulting set of polygons is a grain of connectivity, where the region of each polygon describes an area of proximity for an organism given a maximum threshold of least-cost path distance.

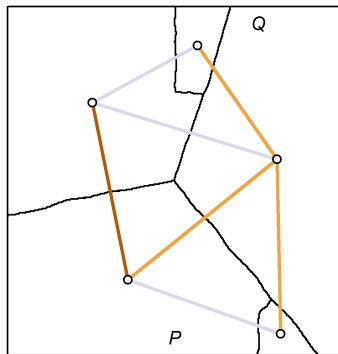


Threshold = 106 resistance units

- MPG node (focal patch)
- Voronoi polygon
- MPG link (least-cost path) (resistance units)
 - 70 - 106
 - 107 - 199
 - 200 - 299
 - 300 - 430

STEP 6

Links in the MPG (STEP 4) that connect adjacent polygons in the grain of connectivity (STEP 5) are identified. By definition, these links have weights that are greater than the resistance threshold value.

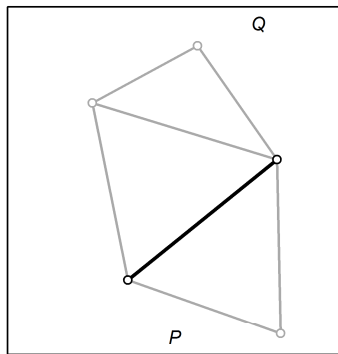


Threshold = 106 resistance units

- GOC node (arbitrary location)
- Voronoi polygon
- GOC link (resistance units)
 - 70 - 106
 - 107 - 199
 - 200 - 299
 - 300 - 430

STEP 7

A new graph, called a grains of connectivity graph (GOC graph), is constructed, where nodes represent Voronoi polygons, and links between nodes in adjacent polygons represent the mean link weight of all MPG links between those polygons (STEP 6). Other functions can also be used to weight links in the GOC graph (e.g. minimum, median, or a count of links connecting adjacent polygons).



Threshold = 106 resistance units

- GOC node (arbitrary location)
- GOC graph
- shortest path through GOC graph between polygons containing P and Q

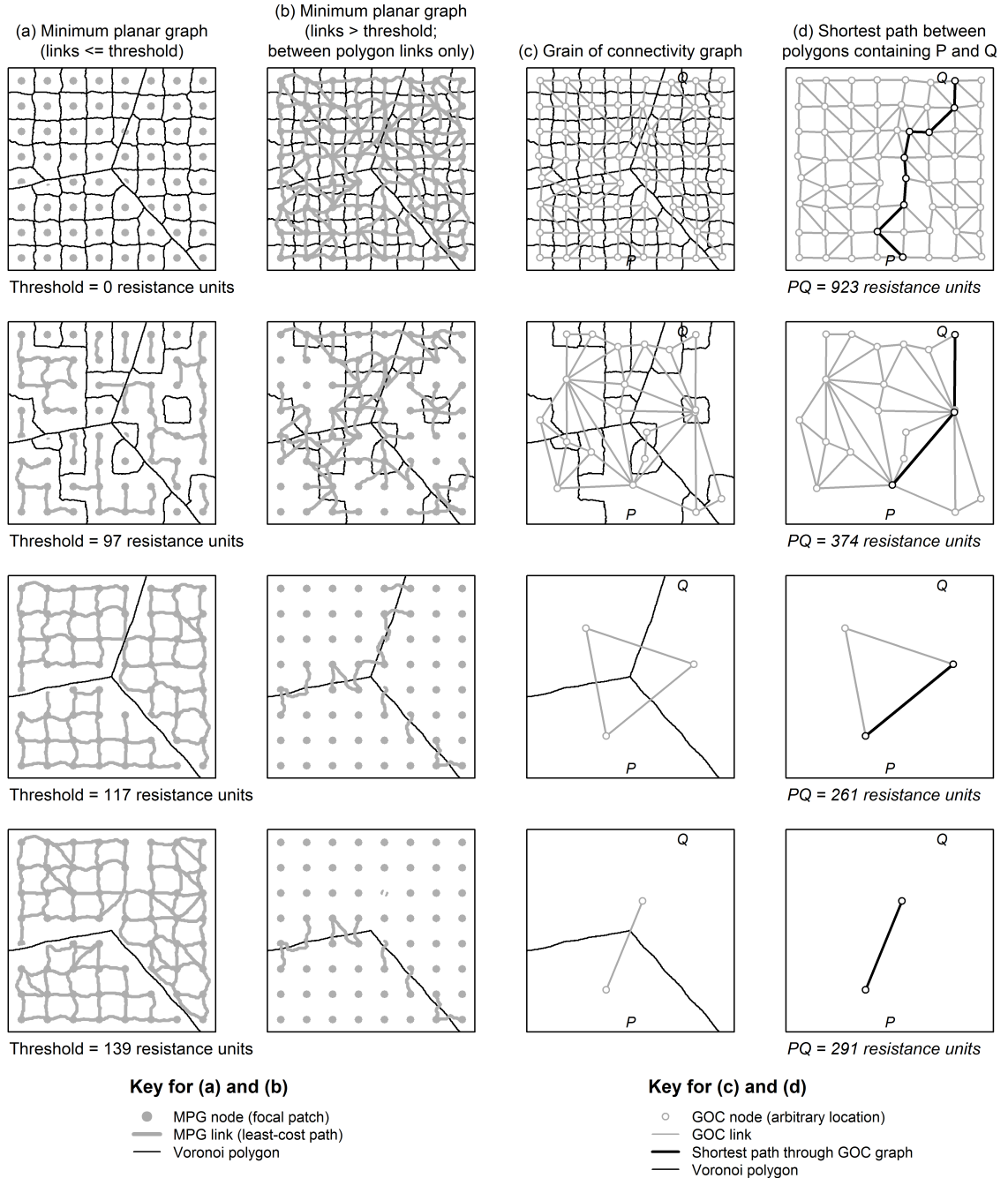
STEP 8

Given a GOC graph (STEP 7) the grains of connectivity network distance is found between two locations on the landscape. This effective distance metric is the shortest length path through the GOC graph connecting the Voronoi polygons containing the locations found using Dijkstra's algorithm (Dijkstra, 1959). In this example, the effective distance between P and Q is 270 resistance units.

Appendix 3-2. Illustration of minimum planar graph and grains of connectivity modelling at four selected resistance thresholds (for Treatment 1).

Four resistance thresholds (0, 97, 118 and 139 resistance units) were selected to illustrate the production of a minimum planar graph (MPG), grain of connectivity, and a grains of connectivity graph (GOC graph) at different grain sizes. Note how that as resistance threshold increases, grain size also increases. In addition, the shortest path between two locations is also a function of the grain size/resistance threshold used.

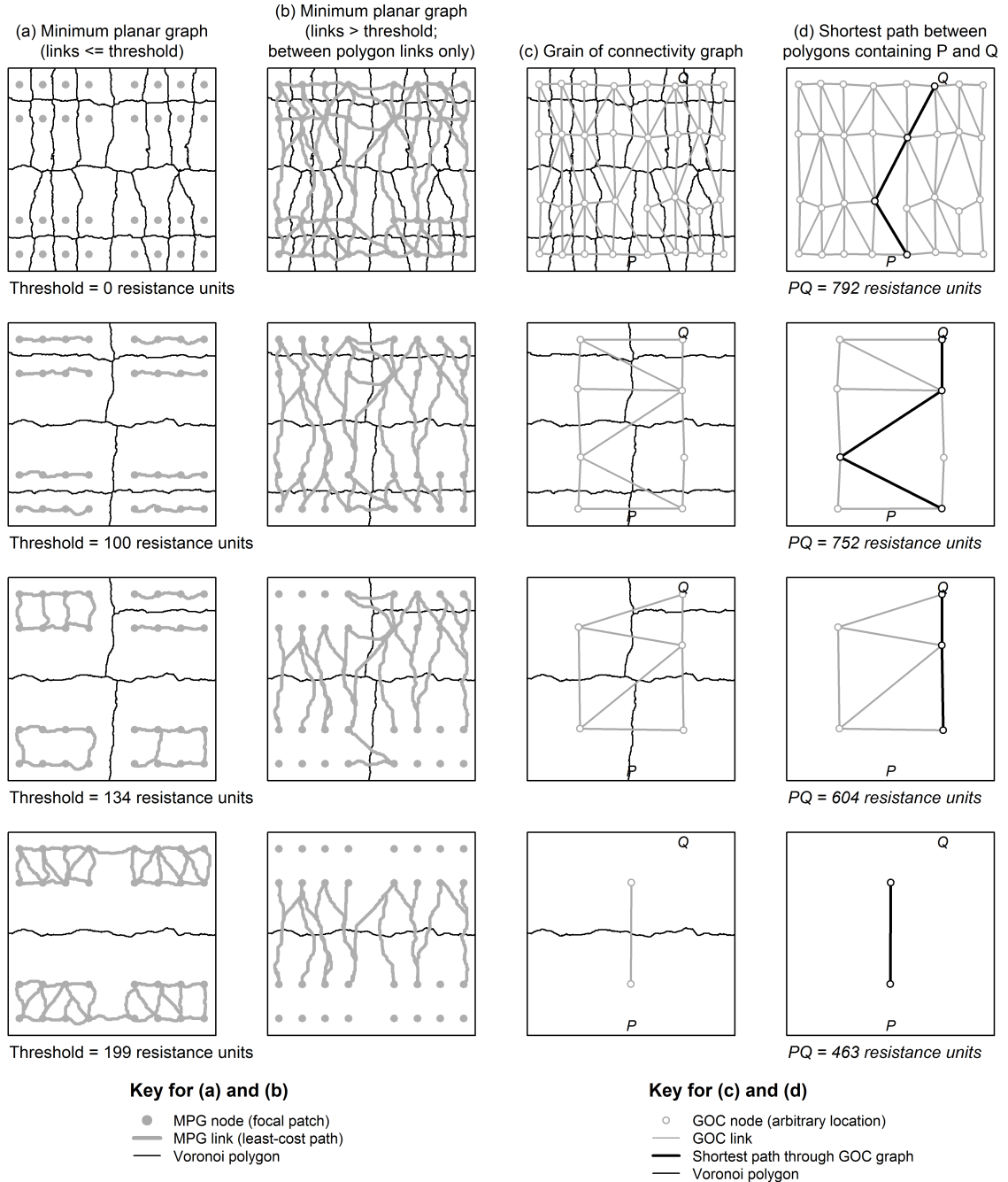
Appendix 3-2. Cont'd.



Appendix 3-3. Illustration of minimum planar graph and grains of connectivity modelling at four selected resistance thresholds (for Treatment 2).

Four resistance thresholds (0, 100, 139 and 199 resistance units) were selected to illustrate the production of a minimum planar graph (MPG), grain of connectivity, and a grains of connectivity graph (GOC graph) at different grain sizes. Note how that as resistance threshold increases, grain size also increases. In addition, the shortest path between two locations is also a function of the grain size/resistance threshold used.

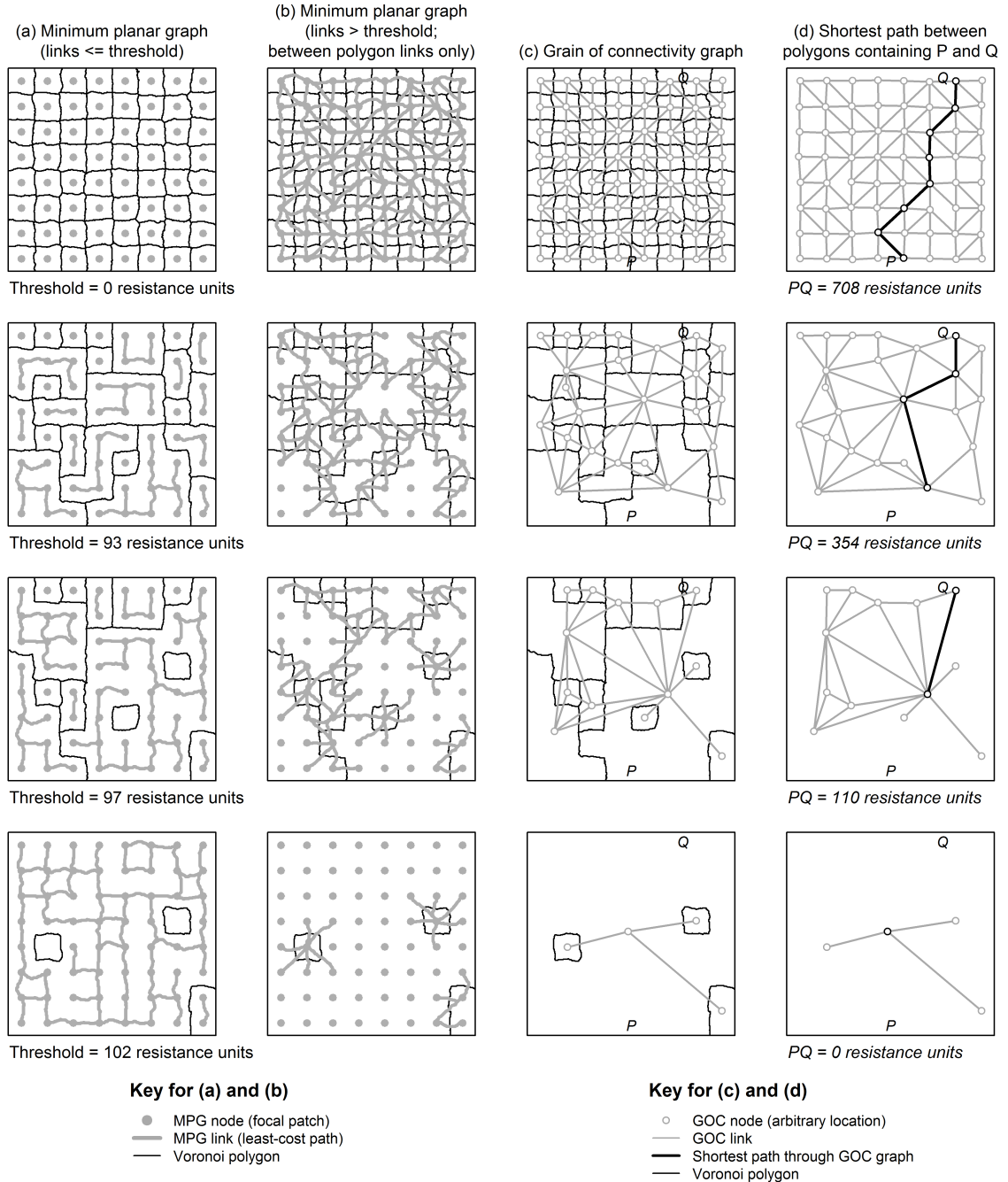
Appendix 3-3. Cont'd.



Appendix 3-4. Illustration of minimum planar graph and grains of connectivity modelling at four selected resistance thresholds (for Treatment 3).

Four resistance thresholds (0, 93, 97 and 102 resistance units) were selected to illustrate the production of a minimum planar graph (MPG), grain of connectivity, and a grains of connectivity graph (GOC graph) at different grain sizes. Note how that as resistance threshold increases, grain size also increases. In addition, the shortest path between two locations is also a function of the grain size/resistance threshold used.

Appendix 3-4. Cont'd.



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CHAPTER FOUR

Grains of connectivity: analysis at multiple spatial scales in landscape genetics¹

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4.1. Abstract

Landscape genetic analyses are typically conducted at one spatial scale. Considering multiple scales may be essential for identifying landscape features influencing gene flow. We examined landscape connectivity for woodland caribou (*Rangifer tarandus caribou*) at multiple spatial scales using a new approach based on landscape graphs that creates a Voronoi tessellation of the landscape. To illustrate the potential of the method, we generated 5 resistance surfaces to explain how landscape pattern may influence gene flow across the range of this population. We tested each resistance surface at the spatial grain typical of landscape genetic studies (200 m grid squares). We then used our method to produce up to 127 additional grains for each resistance surface. We applied a causal modelling framework with partial Mantel tests, where evidence of landscape resistance is tested against an alternative hypothesis of isolation-by-distance, and found statistically significant support for landscape resistance to gene flow in 89 of the 507 spatial grains examined. We found evidence that major roads as well as the cumulative effects of natural and anthropogenic disturbance may be contributing to the genetic structure. Using only the original grid raster yielded no evidence for landscape resistance to gene flow. Our results show that using multiple spatial grains can reveal landscape influences on genetic structure that may be overlooked with a single grain, and suggest that coarsening the grain of landcover data may be appropriate for highly-mobile species. Grains of connectivity and related analyses have potential landscape genetic applications in a broad range of systems.

4.2. Introduction

Landscape genetics is an emerging field with the goal of understanding how landscape influences genetic variation (Balkenhol et al. 2009, Storfer et al. 2010). Where habitat loss and fragmentation have occurred, landscape connectivity may also be reduced, presenting risks for the maintenance of genetic variation and for population persistence (Lynch et al. 1995, Crnokrak and Roff 1999, Crooks and Sanjayan 2006). The restriction of dispersal and gene flow makes small and isolated populations susceptible to the loss of genetic variation through genetic drift (Keyghobadi 2007).

The central importance of scale has long been recognized in ecology, where identifying a relationship between pattern and process may depend on the scale at which the pattern is described (Wiens 1989, Levin 1992, Wu 2004). In landscape genetics, pattern that may influence connectivity, and therefore gene flow, may only be identifiable at certain scales of analysis (Anderson et al. 2010, Cushman and Landguth 2010a). Work on western toads, for example, has shown that variation in landcover variables measured at fine spatial scales, in combination with variation in topographic variables measured at coarse scales may collectively influence landscape genetic relationships (Murphy et al. 2010). Because of the importance of matching the scales of pattern and process, and the potential for incorrectly attributing the factors influencing gene flow, analyzing connectivity at multiple scales may be essential (Anderson et al. 2010, Cushman and Landguth 2010a).

A common method for describing connectivity in landscape genetics begins by representing the landscape as a raster, a regular grid of pixels where each is assigned a resistance for the landscape feature it represents. The resistance value for each pixel is the hypothesized reduction in gene flow associated with the landscape feature, and can be thought of as a surrogate measure for a reduction in landscape connectivity. From this resistance (or cost) surface, the effective distance for gene flow between two locations on the landscape can be calculated using least-cost paths or circuit theory, where the locations may represent groups or single individuals (Adriaensen et al. 2003, McRae et al. 2008, Pinto and Keitt 2009).

A modification of this method has been proposed to describe landscape pattern at multiple spatial scales (e.g. Anderson et al. 2010). By varying the spatial grain of analysis (sensu Dungan et al. 2002) of the grid raster, for example, by averaging resistance values using moving windows or by resampling rasters to larger pixel sizes (McRae et al. 2008, Cushman and Landguth 2010a), it may be possible to exclude local variation in landscape pattern that is unimportant for gene flow. A recent formal evaluation of scale issues in landscape genetics suggests that conducting analyses at a finer spatial grain than that at which gene flow operates may increase power to detect landscape influences on genetic structure (Cushman and Landguth 2010a). These authors found that changing the thematic resolution of the raster (i.e. the intervals at which environmental variability is described) had a greater effect than changing the spatial grain. While these results compellingly suggest the reduced importance of spatial grain, these simulations did not examine gene flow processes operating at spatial grains widely

divergent from those at which the pattern was measured. There is, as yet, no evidence that using the finest-grained data available is adequate if gene flow responds to pattern at grains that are coarser by orders of magnitude (i.e. if the grain of the phenomenon is many times coarser than the grain of the analysis). For this reason, multiscale analysis may still be appropriate for achieving a match between the scale of landscape pattern description and the gene flow process it is being used to understand.

In the case of highly mobile terrestrial mammals, where dispersal is likely to occur over large distances, gene flow processes might be expected to respond to pattern at much coarser grains than for species with more limited dispersal capability. In other words, gene flow may be more influenced by patterns evident at broader extents than by fine-grained variation in landscape features. It is possible to test this assertion by using a raster resistance surface where each pixel describes an area several kilometres in radius. A grain this coarse would reduce unimportant variation in landcover or topographic variables by averaging out local detail, for example, but it may also obscure or incorrectly render the pattern in small footprint features that might have a high impact, such as roads and rivers. Therefore, a method that can coarsen the grain while retaining some pattern from the original grain may be helpful.

Here we propose changing the grain of analysis not by areal means (e.g. McRae et al. 2008, Cushman and Landguth 2010a), but by identifying patterns in functional landscape connectivity for the focal species. The product is a series of related models, where each is analogous to a raster resistance surface, but has a unique grain reflecting a functional

connectivity hypothesis. Because the grain describes patterns in connectivity, sets of features that reduce connectivity can be identified. The method used to produce these grains comes from the patch-based landscape graphs tradition where landscape connectivity is modelled by building graphs (also called networks) describing the resistance to movement or dispersal between patches of habitat (Urban and Keitt 2001, Fall et al. 2007, Galpern et al. 2011). Our method then divides the landscape into regions representing connected groups of patches in this graph to produce a tessellation, where each polygon in the tessellation represents many pixels of the original raster. The polygons describe areas of connectivity for the organism within which we hypothesize gene flow will occur. By systematically changing how we produce the underlying graph, a process called thresholding (e.g. O'Brien et al. 2006), many *grains of connectivity* can be examined.

We illustrate our method using genetic data for a population of boreal woodland caribou (*Rangifer tarandus caribou*) in central Canada. We begin by hypothesizing a series of alternative explanations for landscape resistance in the form of 200 m pixel radius grid rasters, and then test each of these rasters at multiple grains of connectivity. We test each hypothesis against an alternative hypothesis of isolation-by-distance using a causal modelling framework with partial Mantel tests (Cushman et al. 2006, Shirk et al. 2010). In addition, we contrast our results with those that would have been obtained at the spatial grain of the original raster. Our primary goal is to demonstrate a method for testing landscape genetic hypotheses at multiple spatial grains, and to explore the properties of this method using current analytical and inferential approaches in the field.

4.3. Materials and methods

Boreal woodland caribou are designated as threatened under Canada's Species at Risk Act (Government of Canada, 2003). The Smoothstone-Wapeweka caribou population occupies a 25,000 km² range (approx.; centred at 54° 17' N, 105° 31' W) within the Boreal Plains ecozone in central Saskatchewan, Canada. A recent investigation of population genetic structure including genotypes from this caribou range, as well as the neighbouring province of Manitoba, found no evidence of distinct genetic populations within the study area (Ball et al. 2010). However, accumulating evidence suggests the population is under stress. A mark-recapture study using genetic markers estimated that there are 154 animals in the western half of the study area, and the population is in demographic decline (Rettie and Messier 1998, Arsenault and Manseau 2011, Hettinga et al. 2012). Animals in this population are typically characterized as sedentary, and telemetry observations (1992 to 1995 and 2004 to 2008) of adult females reveal home ranges have become increasingly restricted (Minimum convex polygon: mean = 221 km², sd = 145, n = 23; Arsenault & Manseau, 2011).

4.3.1. Noninvasive genetic sampling and genotyping

We conducted noninvasive sampling of fecal pellets in the winters of 2007 and 2008 by flying linear transects spaced 3 km apart to achieve systematic coverage of the study area. The helicopter stopped to collect samples where recent caribou activity was evident in the snow. DNA was extracted from the tissue present in the outer mucosal layer of each sample, quantified and normalized through dilution and then genotyped at 10

microsatellite loci (BM848, BM888, BMS1788, MAP2C, RT5, RT6, RT7, RT9, RT24 and RT30; Bishop et al. 1994, Wilson et al. 1997, Cronin et al. 2005) following an existing protocol (Ball et al. 2007, Ball et al. 2010). Because tissue is sampled directly from the mucosal coat during winter sampling, there is high quality and quantity DNA available (Ball et al. 2007, Ball et al. 2010) reducing the challenges typically associated with fecal DNA profiling (e.g. Waits and Paetkau 2005). Profiles were scored by at least two observers to ensure an interpretation consistent with previously determined scoring guidelines. Because individuals are typically sampled multiple times in this protocol, we used the ALLELEMATCH package for R, a genotype matching and clustering tool, to validate profiles and remove duplicate profiles (Galpern et al. 2012). Identical profiles were those that matched at 18 out of 20 alleles and had match probabilities below a threshold of 0.0001 (Psib; Woods et al. 1999). Samples with identical profiles were identified as validated for their genotype and culled to remove duplication. Any unique individuals were profiled a second time to confirm the genotype. We sampled a random subset of 10% of the samples and re-profiled them to estimate an error rate (see Hettinga et al. 2012). For additional genotyping information please see Ball *et al.* (2010) which included a subset of the population under study. For subsequent landscape genetic analyses we found the genetic distances between all pairs of the remaining profiles using the proportion of shared alleles metric (Dps; Bowcock et al. 1994, Shirk et al. 2010).

4.3.2. Resistance surfaces

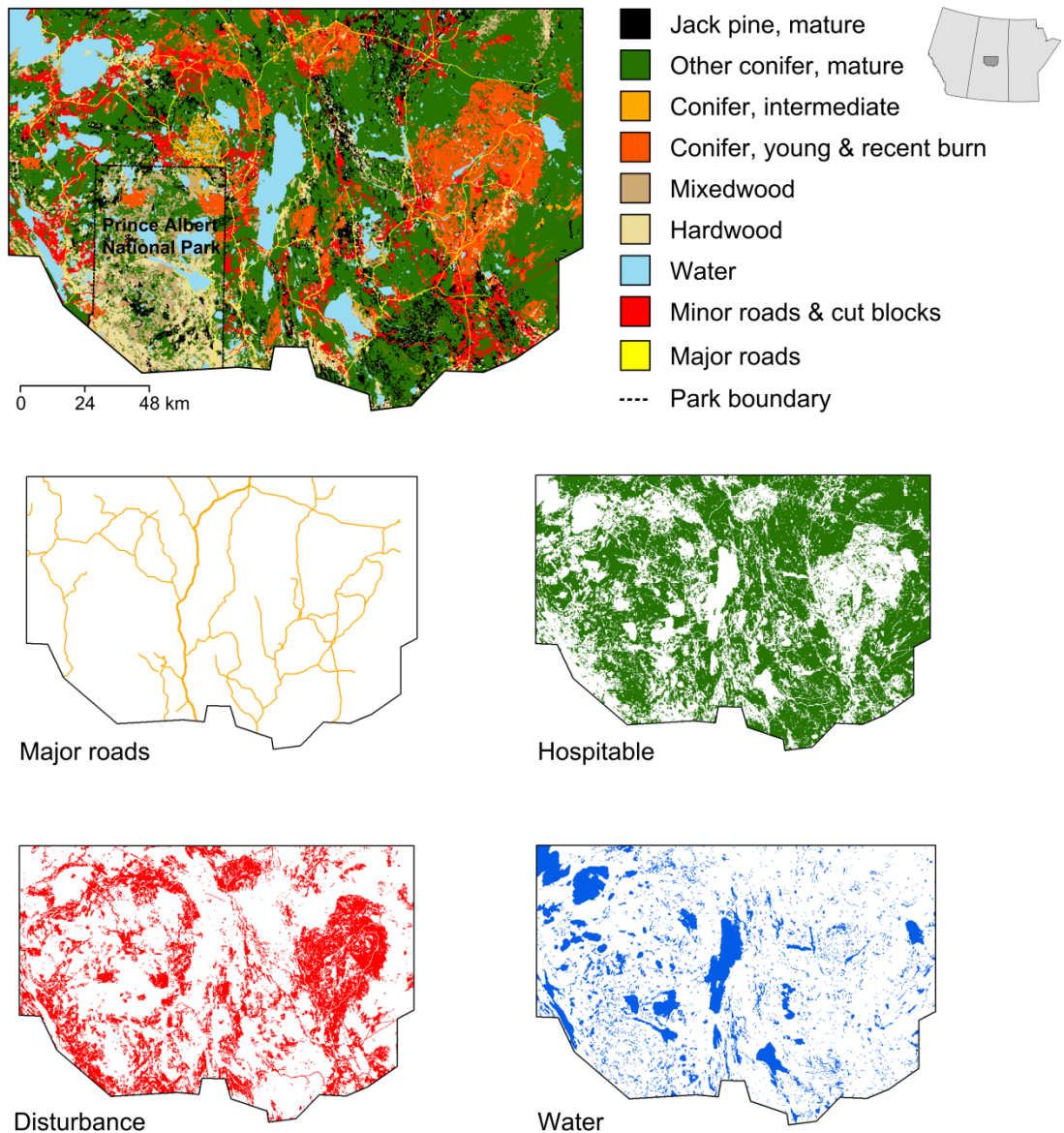
We developed a map describing landcover, roads, as well as sites of other natural and anthropogenic disturbances in the manner described by Arlt & Manseau (2011) for an

overlapping study area. This map, rasterized at 200 m pixel radius, served as the basis of subsequent steps (Fig. 4-1). We next built a series of surfaces describing hypothesized resistance to gene flow for landscape features on this map (e.g. Cushman et al. 2006). Because finding appropriate and empirically-supported resistance values for each feature can be challenging (Shirk et al. 2010, Spear et al. 2010), we combined several strategies. We estimated resistance to gene flow for vegetation features using GPS telemetry observations from eighteen adult female caribou collared in the study area during 2004-2008 (Arlt 2009). Resistance values were the inverse of the odds ratio from a generalized estimating equation model describing the probability of caribou occurrence in a vegetation feature relative to a reference high quality habitat feature (O'Brien et al. 2006, Koper and Manseau 2009). We selected mature jack pine dominated stands as the reference feature because this resource was the most limited of the candidate high quality mature coniferous habitats. Resistance values for a provincial highway, minor forestry roads, gravel roads, cut blocks, lakes and rivers could not be determined empirically because caribou were seldom observed in association with these features. Cut blocks and minor forestry tracks were assigned the same resistance value as that determined for young coniferous stands as these features are similar in physiognomy, and lakes and rivers were assigned a relatively high value (100) because resource selection function analyses suggest that caribou avoid these features (O'Brien et al. 2006, Arlt 2009, Koper and Manseau 2009). In order to thoroughly explore the effect of major roads (gravel roads and provincial highway) we adopted an experimental approach where resistance values were assigned to one of five levels: no resistance to gene flow (resistance=1); equivalent to the largest vegetation feature (resistance=10); equivalent to the largest

Figure 4-1. Habitat map for woodland caribou in the Smoothstone-Wapaweka range, Saskatchewan, Canada.

Habitat map (top) and four maps highlighting distinctive sets of landscape features from the habitat map (bottom).

Smoothstone-Wapaweka woodland caribou range, Saskatchewan, Canada



natural feature (resistance=100); or, greater than the largest natural feature (resistance=200, 400). We produced five grid raster resistance surfaces that differed only in terms of this major roads resistance value (Appendix 4-1).

4.3.3. Analysis at multiple scales

We examined each resistance surface at its original grid grain (sensu Dungan et al. 2002) and at additional grains by further processing of the surface. These additional grains were determined by patterns of landscape connectivity rather than pixel radius, and were composed of polygons that were heterogeneous in area and shape.

To produce these additional grains we developed a method based on patch-based landscape graphs (Urban and Keitt 2001, Fall et al. 2007, Galpern et al. 2011). In landscape graphs, patches of habitat are identified and a network is constructed describing the potential connections among patches. Our method adds two steps: (1) we tessellate the landscape into regions that contain connected groups of patches; and (2) we build a new graph of the resistance relationships among these regions. We call a given tessellation of the landscape a grain of connectivity because the polygons in the tessellation describe a hypothesized region of proximity for the organism within which there is high connectivity and, therefore, negligible resistance to gene flow. In contrast to typical landscape graphs, we model connectivity relationships among regions of the landscape rather than patches, a difference that allows us to model organisms that are not restricted to a certain patch class, but may select for that class.

To help describe the method, we applied it to an artificial 400 x 400 pixel landscape with five feature classes (Figs. 4-2 to 4-4). First, we produced a resistance surface from the raster landcover data in which each feature class was assigned a resistance value (Fig. 4-2, a). Second, we identified patches of one feature class as the focal patches (Fig. 4-2, b). Third, we created a Voronoi tessellation of the resistance surface where Voronoi polygons describe a region of proximity in resistance units from the perimeter of each focal patch (Fig. 4-2, c). This process is a generalization of the Voronoi tessellation (e.g. Okabe et al. 2000) for two-dimensional objects, where distance is measured in terms of resistance units and the generators are two-dimensional patches rather than points. Fourth, we extracted the minimum planar graph (Fig. 4-2, d), a simplified landscape graph model that approximates all potential connections with many fewer links (Fall et al. 2007). The minimum planar graph we used is a form of "Spatial Graph" where potential connections among focal patches are described by least-cost paths between the boundaries of those patches through the original raster resistance surface. Fifth, we superimposed the minimum planar graph on the Voronoi tessellation to create a new graph (Fig. 4-2, e), where each graph node represented a Voronoi polygon, and the link weights of the minimum planar graph (least-cost path lengths) served as link weights in the new graph.

To produce multiple grains of connectivity, we adopted a thresholding (or scalar) approach (Brooks 2003). If polygons were separated by graph links with weights less than or equal to a maximum amount of resistance (the resistance threshold) they were combined to produce larger polygons (Fig. 4-3). If two or more links were collapsed into

Figure 4-2. Producing the finest grain of connectivity.

Beginning with a grid raster resistance surface (a) where pixels representing landscape features are each assigned a resistance value, identify focal habitat patches (b) to serve as the nodes of the graph. Using these two-dimensional node patches and the resistance surface perform a Voronoi tessellation (c) to produce a minimum planar graph (d) where links between nodes are least-cost paths between the perimeters of node patches. Finally create a new graph (e) where each node represents an entire Voronoi polygon from c and links have the accumulated resistance of the corresponding least-cost path link in d. This final graph shows the finest grain of connectivity possible for this resistance surface using these focal patches.

Figure 4-2. Cont'd.

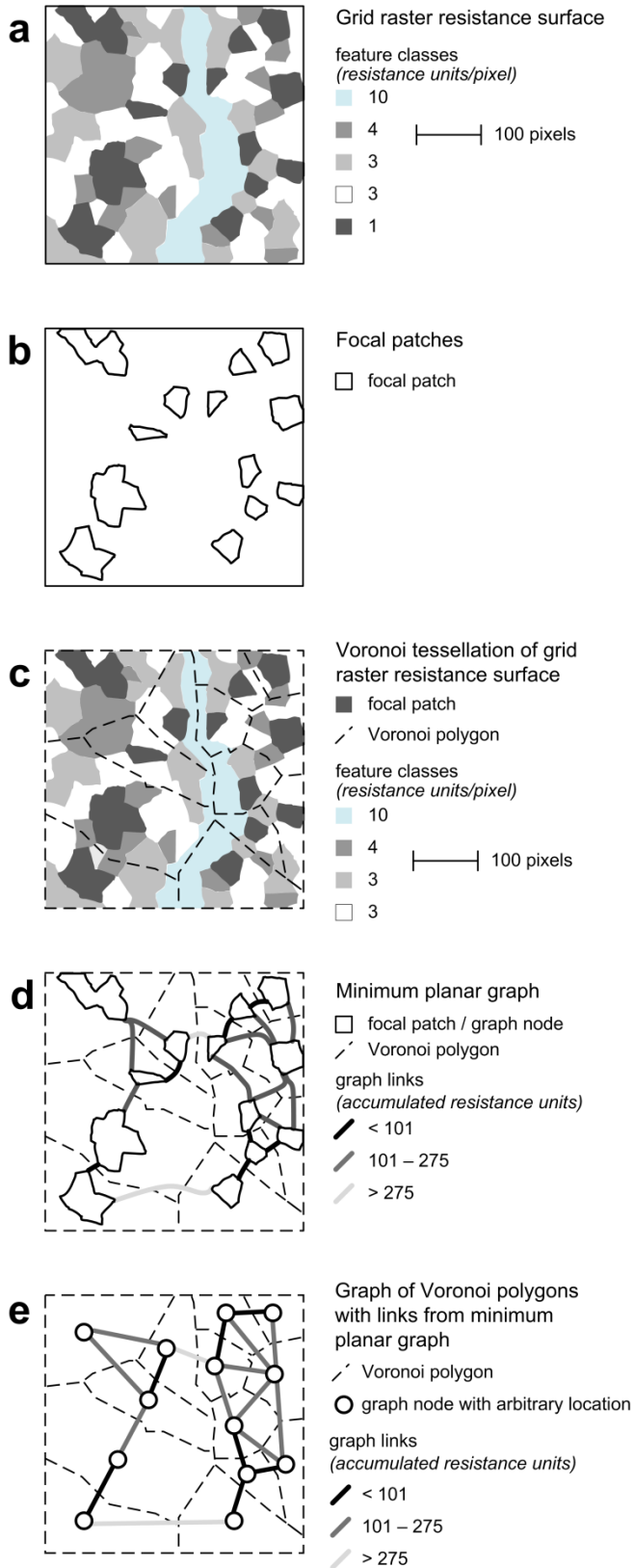


Figure 4-3. Producing multiple grains of connectivity using a thresholding approach.

The graph of Voronoi polygons (a) reproduced from Fig. 4-1, e is simplified by combining Voronoi polygons that are separated by a maximum or threshold resistance (b and c). A larger value for the link threshold produces a coarser spatial grain. Where two or more links are collapsed into one, the new resistance assigned to that link is the mean resistance of the original links (see sample link weight calculations below figure).

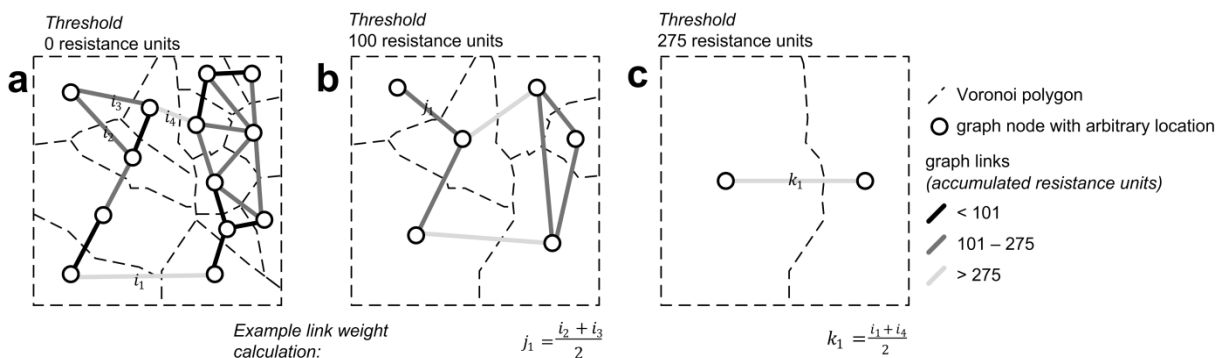
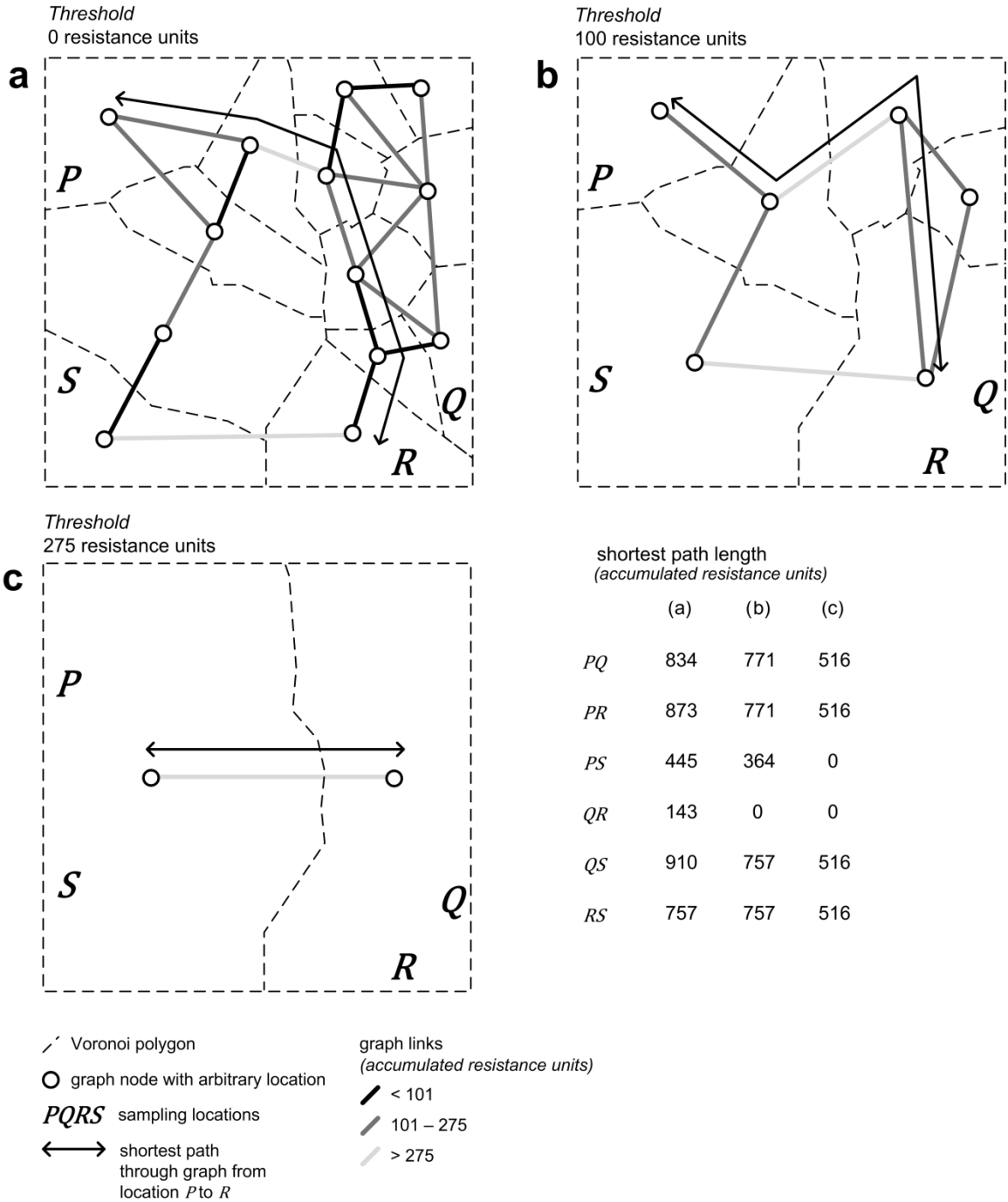


Figure 4-4. Producing IBR hypotheses from grains of connectivity.

The landscape resistance between pairs of sampling locations changes with grain (a, b and c). The accumulated resistance between locations is the length of the shortest path between the polygons containing these locations (e.g. arrows). Note that in some cases (b and c) sampling locations may be grouped in the same polygon resulting in zero-length paths.

Figure 4-4. Cont'd.



one by the combination of polygons, the new link was assigned the mean weight of the collapsed links. At the coarsest grain of connectivity shown (Fig. 4-3, c), the model assumes a negligible resistance to gene flow inside the two polygons, while gene flow between the polygons will face resistance proportional to the mean of two links on the original graph (Fig. 4-3, a, i_1 and i_2). In this example (Fig. 4-3, c), these links represent the cost of crossing the highest resistance feature (a river) on the original raster resistance surface (Fig. 4-2, a).

Finally, we found the accumulated landscape resistance between sampling locations of individuals (Fig. 4-4) in a manner analogous to finding the least-cost paths between sampling locations on a grid raster. Typical implementations of least-cost path analysis represent the grid raster as a graph where each pixel is a node that is connected to its eight neighbours. These methods use Dijkstra's algorithm to return the length of the shortest path through this graph (Dijkstra 1959). Our method adopted the same approach, although unlike typical least-cost path implementations, our graphs have many fewer links and nodes that are not connected symmetrically to all neighbours. As a result of the thresholding, the accumulated resistance between pairs of sampling locations also varied (Fig. 4-4). Samples collected in the same polygon were considered to be at the same spatial location for the purposes of testing resistance to gene flow. For this reason, grains where all sampling locations fall in the same polygon were not testable because there is no hypothesized resistance to gene flow (i.e. all shortest path distances between individuals were zero).

To model grains of connectivity for woodland caribou on the Saskatchewan landcover map, we chose mature jack pine dominated stands as the focal patches in our landscape graphs. Our rationale for using this feature class was the same as for selecting the reference feature in our generalized estimating equation models (see above). We chose resistance thresholds to ensure a broad range of patterns were available for testing; small intervals were used to capture pattern at lower thresholds of connectivity where vegetation patterns are likely to be more influential (resistance thresholds < 950 units; 10 unit interval), while higher thresholds were spaced at larger intervals because trials of the method indicate that patterns tend to become more stable at successive thresholds (resistance thresholds > 1000 units; 100 unit interval). All analysis steps were completed in R 2.13.1 (R Development Core Team 2012), using the *grainscape* package for R (Galpern et al., in prep.). Graph and spatial analysis routines in *grainscape* depend on the packages *gdistance*, *igraph*, *sp* and *raster* (Pebesma and Bivand 2005, Csardi and Nepusz 2006, van Etten 2010, Hijmans and van Etten 2011), as well as the software package SELES (Fall and Fall 2001). For the accumulated resistance between sampling locations on the original grid rasters we used the R package *gdistance* (van Etten 2010).

4.3.4. Assessment of IBR hypotheses

To make inferences about landscape influences on spatial genetic structure, we used both grid and grains of connectivity models to find the accumulated landscape resistance between the sampling locations of all pairs of individuals. These pairwise resistances form an isolation-by-landscape-resistance hypothesis (IBR), and typically, isolation-by-distance (IBD; Wright 1943) is used as an alternative hypothesis (e.g. Cushman et al.

2006, Shirk et al. 2010). We measured IBD in a manner that reflected the grain of the IBR hypothesis. For grains of connectivity, IBD hypotheses were the Euclidean distances between the centroids of polygons containing the sampling locations of pairs of caribou. This enabled a measurement of geographic distance at the same spatial grain as landscape resistance. For the grid models, the IBD hypothesis was the Euclidean distance between point sampling locations.

We elected to examine IBR and IBD between individuals rather than groups of individuals because simulations indicate that this approach has more power to detect subtle gradients in genetic structure (Cushman and Landguth 2010b). Genetic distances, IBR and IBD hypotheses among pairs of individuals were produced as symmetrical distance (or dissimilarity) matrices for all grid and grains of connectivity models. Matrices for all grains and hypotheses were the same dimension (i.e. contained pairwise genetic, landscape resistance, or geographic distances for all individuals in the study). We followed a causal modelling framework with partial Mantel tests (Cushman et al. 2006). We used pairs of partial Mantel tests with 10^4 permutations of the residuals from a null regression model (zt 1.1; Bonnet and Van de Peer 2002) to test the influence of the two hypotheses on genetic distance. The strongest support for an IBR hypothesis was indicated when IBR significantly explained genetic distance with IBD partialled out (Genetic \sim IBR | IBD, $r_p > 0$, $P < 0.05$) and IBD was non-significant with IBR partialled out (Genetic \sim IBD | IBR, $P \geq 0.05$). We interpreted cases where IBR and IBD were both significant as confounding the role of the two biological explanations and, therefore, as being inconclusive about the resistance hypothesis. Cases where only IBD was

supported, or where neither IBR nor IBD were supported, suggested that landscape pattern at that grain was not important for gene flow.

4.3.5. Interpretation of IBR hypotheses

To demonstrate the properties of the grains of connectivity method, we selected a single grain for visualization from each of the five resistance surfaces where only the IBR hypothesis was supported. In each case we chose the grain that produced the highest partial Mantel statistic for the IBR hypothesis. We produced maps showing the polygons at these selected grains of connectivity to illustrate how the method has simplified the resistance surface through changes to the size and shape of the polygons.

We also further examined all grains of connectivity and the original grid rasters on which they were based to determine which features were most influential for least-cost paths at different grains, and to demonstrate, in general, how changing the grain influences resistance. To find the most influential features at a grain of connectivity, we recorded the landscape features traversed by the least-cost paths retained when calculating the resistance between polygons (e.g. to find Fig. 4-3, c, k_l we examined the least-cost paths from Fig. 4-2, d used to estimate Fig. 4-3, a, i_l and i_d). We then calculated the resistance-weighted proportional contribution of sets of landscape features in these links (sets given in Appendix 4-1, italics) to the total accumulated resistance between polygons. For the original grid resistance surfaces on which these grains were based, we performed a comparable calculation, using the resistance-weighted proportional contribution of feature classes on the raster as a measure of influence.

4.4. Results

4.4.1. Genotyping

Screening of profiles (N=166) indicated that many were duplicates. Sibling probability of identity for this data set was 9.7×10^{-5} . We identified and removed six profiles with single allele dropouts by comparing these to other perfectly matching profiles in a clustering procedure. We found 95 unique individuals, 43 of which had been sampled 2 to 5 times each. Six individuals sampled at more than one site were assigned to the site of their first chronological observation. For these individuals the number of alleles per locus ranged from 7 to 14, and heterozygosity at each locus from 0.46 to 0.88. Data were available for individuals at 37 sampling sites.

4.4.2. Assessment of IBR hypotheses

We tested 507 IBR hypotheses, five of these were the original grid raster resistance surfaces (Table 4-1). These surfaces consisted of 815 400 cells 0.04 km^2 in area. The grains of connectivity exhibited complex variation in the spatial characteristics of the tessellations as the resistance threshold changed (Fig. 4-5). The number of polygons in these hypotheses varied from 25 to 2366, mean polygon areas varied from 11.8 km^2 to 1115.1 km^2 and maximum polygon areas varied from 265.5 km^2 to $22\,417.4 \text{ km}^2$.

Table 4-1. Overview of IBR hypotheses.

(a) Summary data on hypotheses tested; (b) Results of causal modelling of these hypotheses, giving the number of hypotheses in each causal modelling category.

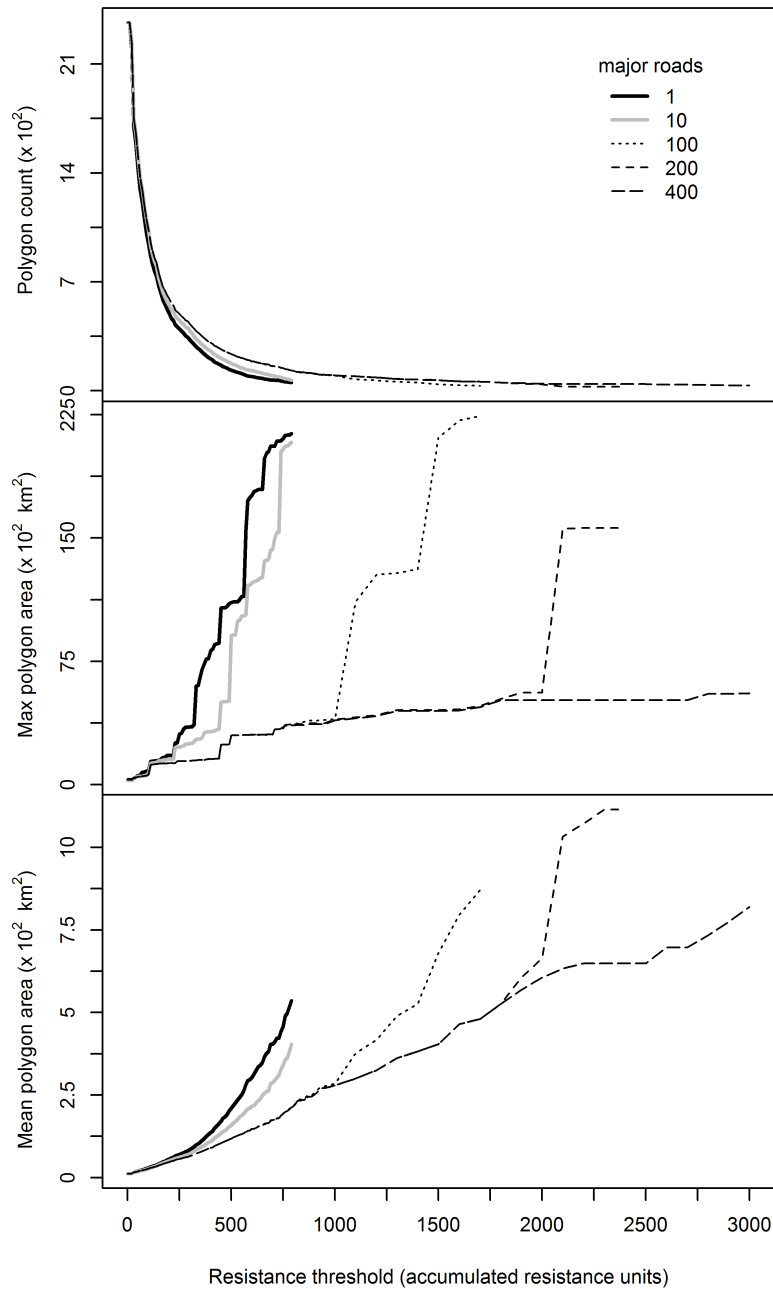
	Grid	Grains of connectivity
(a) IBR hypotheses tested		
Resistance surfaces	5	5
Grains per surface	1	80 to 127 ¹
Total hypotheses	5	502
(b) Causal modelling²		
IBR only supported	0	89
IBD only supported	0	48
IBR and IBD supported	5	0
Neither IBR nor IBD supported	0	365

¹Grains of connectivity were not testable when all sampling locations fell in one polygon

²Support for causal models tested at an alpha level of 0.05 using partial Mantel tests with 10⁴ permutations.

Figure 4-5. The spatial characteristics of Voronoi polygons.

The count and area of polygons in a grain of connectivity is determined both by the resistance threshold and the underlying resistance surface upon which the grain of connectivity is based.



Simple Mantel correlations between genetic distances and IBD hypotheses varied with the grain ($r=0.22$ for 5 grids; $r_{\text{mean}}=0.18$, $r_{\text{sd}}=0.05$, for 502 grains of connectivity; $P < 0.0001$). Log transforming the IBD hypothesis did not improve the correlation ($r=0.17$ for grids; $r_{\text{mean}}=0.14$, $r_{\text{sd}}=0.04$ for grains of connectivity; $P < 0.0001$). IBR and IBD hypotheses, however, were highly correlated ($r_{\text{mean}}=0.79$, $r_{\text{sd}}=0.002$ for grids; $r_{\text{mean}}=0.93$, $r_{\text{sd}}=0.03$ for grains of connectivity; $P < 0.0001$).

We found the strongest support for IBR in 89 of the grains of connectivity hypotheses (Table 4-1; Fig. 4-6; IBR only supported). In these cases, polygons in the tessellations were many times larger in areal terms than the cell sizes typically used in grid rasters (see Appendix 4-2). The remaining grains of connectivity IBR hypotheses were not significant when tested against a corresponding IBD hypothesis (Table 4-1; Fig. 4-6; IBD only supported; Neither IBR nor IBD supported). All five grid hypotheses were confounded with IBD preventing a conclusion about the role of landscape pattern at these grains (Fig. 4-6; IBR and IBD supported; see Appendix 4-3).

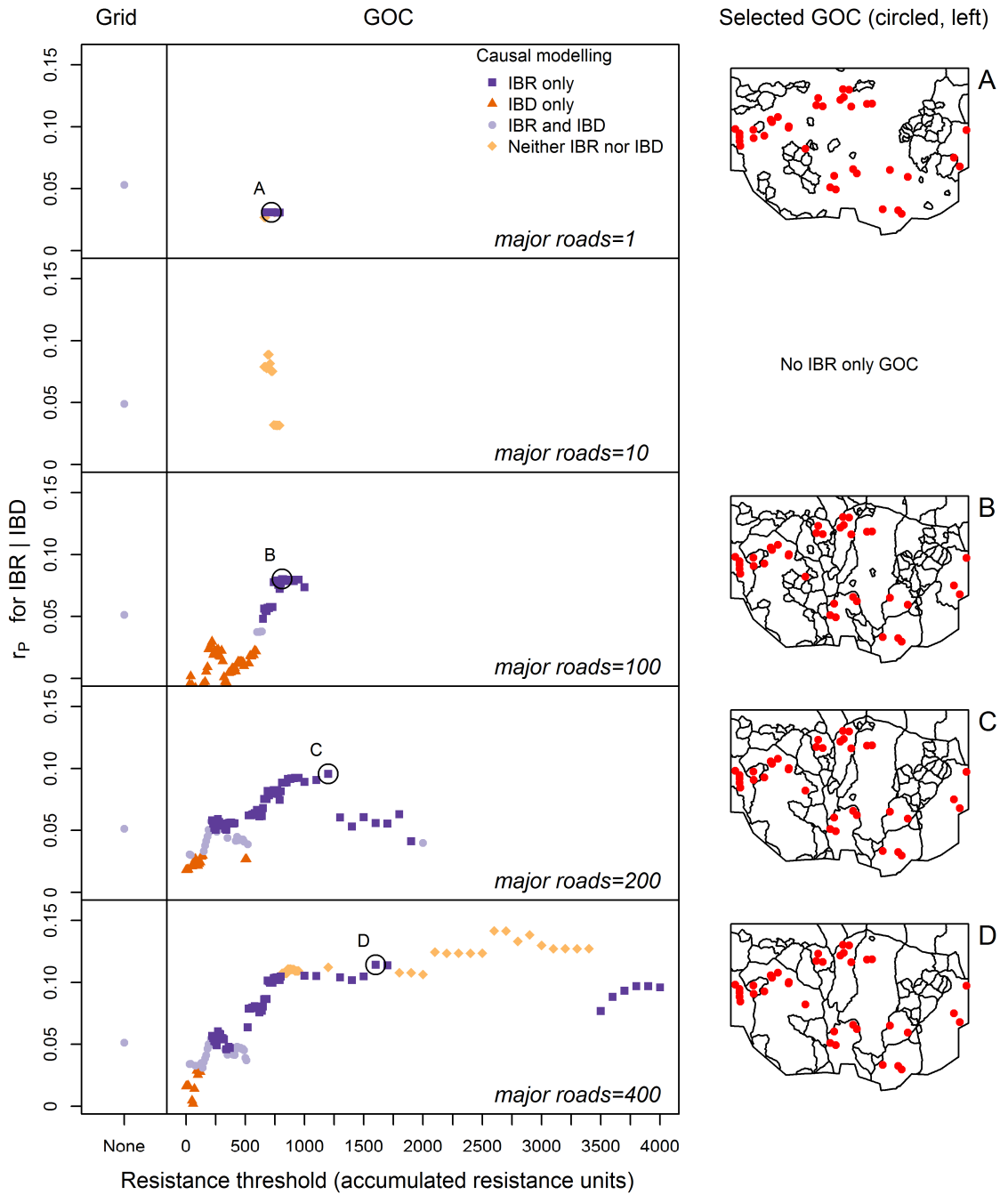
4.4.3. Interpretation of supported IBR hypotheses

Grains of connectivity IBR hypotheses based on four of the five original grid resistance surfaces were supported in the causal modelling framework (Fig. 4-6; IBR only supported; also see Appendix 4-2). However, interpreting results using only the resistance parameters of the original grid can be misleading because landscape resistance distances for grains of connectivity models are determined by the links between polygons and the resistance associated with any given link combines the

Figure 4-6. Partial Mantel test results.

Results demonstrate the high variability in explanatory power of the IBR hypotheses based on grains of connectivity (GOC; right) compared to those based on the original grid rasters (Grid; left). Rows show resistance surfaces that are identical except for the resistance assigned to major roads. Eighty-nine hypotheses based on four of five resistance surfaces show evidence of isolation-by-landscape-resistance in a causal modelling framework (IBR only). Circles and letters (A, B, C, D) indicate significant grains of connectivity hypotheses that meet the criteria for further examination (see text) and these grains have been visualized (maps at right). Red points on maps are sampling locations.

Figure 4-6. Cont'd.



resistance of multiple types of features (Figs. 4-3, 4-4). In addition, sampling locations falling within a polygon have, by definition, zero landscape resistance distances among them. This means that the shape, size and location of polygons (i.e. spatial configuration) may also influence results by defining which sampling locations are connected without resistance. Therefore, in our interpretation we consider both the spatial configuration of polygons and the multiple features creating resistance between polygons.

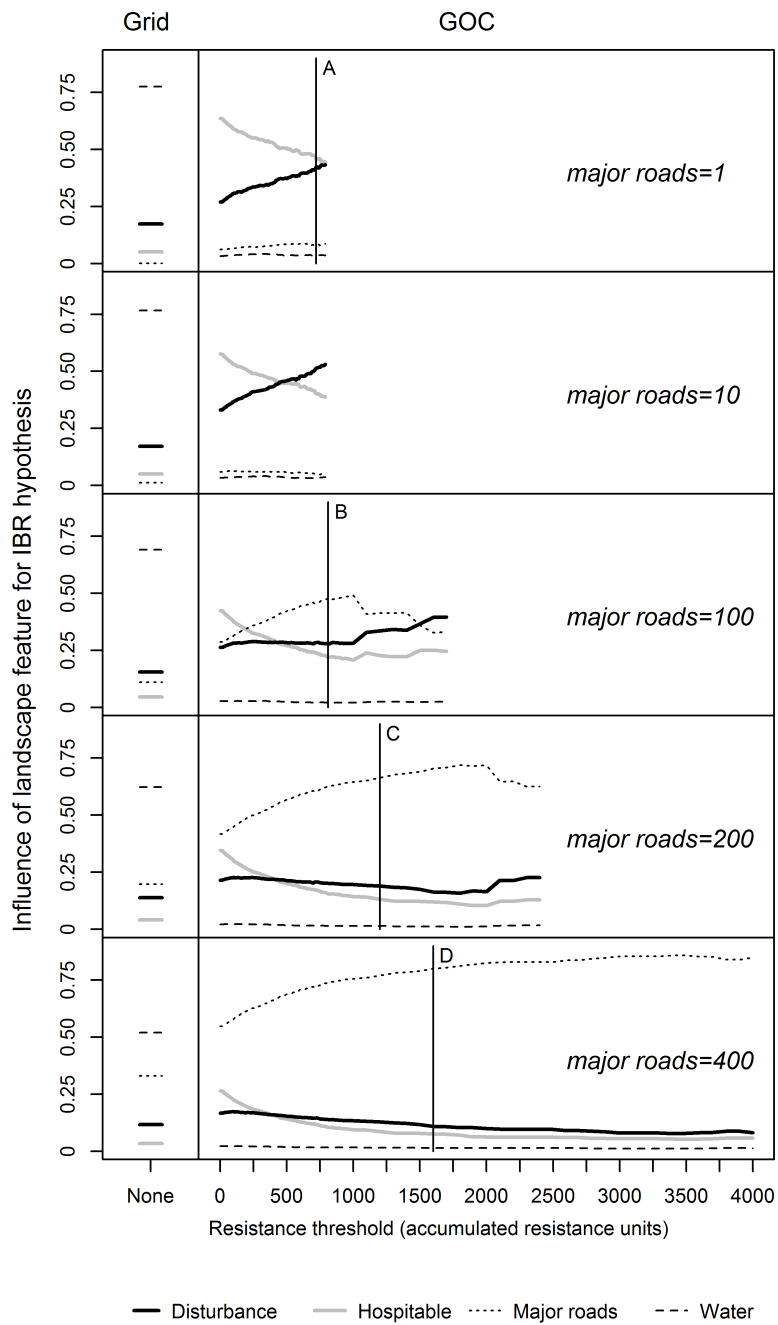
We explored these using four grains of connectivity that met the criteria for selection noted in *Methods* (Fig. 4-6, A, B, C, D; see Appendix 4-2). Among these selected grains we found two distinct spatial configurations. The first described a highly-connected landscape with sampling locations in two polygons (Fig. 4-6; A; major roads=1). This pattern produced a significant but relatively weak partial correlation with genetic distance ($r_p=0.0308$; Appendix 4-2). The introduction of a higher roads resistance to the underlying resistance surface produced a second distinct spatial configuration with many more polygons (Fig. 4-6, B, C, D; major roads ≥ 100). This pattern produced a stronger partial correlation with genetic distance (max $r_p=0.1140$). Although the three selected configurations were similar in these cases, the resistance threshold associated with the configurations was different. Notably, higher resistance thresholds appeared to improve the partial Mantel statistic (Fig. 4-6, B, C, D).

We used influence plots (Fig. 4-7) to explore the landscape features represented in the resistance between polygons. Again, two patterns emerged in the four selected cases. In the first pattern (Fig. 4-7, A) links between polygons had approximately equal

Figure 4-7. The influence of landscape features on the resistance among polygons varies with grain and resistance surface.

Sets of landscape features are those depicted in Fig. 4-1 (bottom). Left panel shows influence for the original grid rasters (Grid), and right panel for connectivity models derived from that grid (GOC). Rows show resistance surfaces that are identical except for the resistance assigned to major roads. Vertical lines with labels (A, B, C, D) indicate the resistance threshold of the four significant grains of connectivity that met the criteria for further examination (see text).

Figure 4-7. Cont'd.



contributions from disturbance features such as minor forestry tracks, cut blocks and early-successional vegetation, as well as from hospitable coniferous features. This is a case where the cumulative effect of multiple low resistance features is structuring the resistance between polygons. In the second pattern (Figs. 4-7, B, C, D), major roads contributed the largest proportion of resistance to the links, implying that resistance to gene flow between polygons is dominated by these features

4.4.4. Comparison of grid and grains of connectivity IBR hypotheses

Changing the grain of analysis using grains of connectivity produced relatively high variability among IBR hypotheses (Fig. 4-6, r_p , GOC). In contrast, analyses at the scale of the original grid raster resulted in nearly identical explanations of genetic structure, despite large differences in the resistance values assigned to major roads (Fig. 4-6, r_p , Grid; see Appendix 4-3). A probable cause of this low variability is that other features that were not manipulated were dominant; i.e. the influence of major roads on the resistance surface was sufficiently low that these features did not have much effect on the length of least-cost paths. Indeed, influence plots (Fig. 4-7, Grid) indicated that water features, and not roads, contributed the majority of the resistance on the grid representations of the landscape. Therefore, least-cost paths on these grids would tend to avoid lakes more, on average, than they would any other feature. Examining these same surfaces using grains of connectivity, however, showed that using much coarser grains introduced variability by reducing the influence of some landscape features, and increasing the influence of others (Fig. 4-7, GOC). The change of grain produced this variation, in part, because the least-cost paths between the areas of high connectivity (i.e.

the polygons) also changed. For example (Fig. 4-7, major roads = 400) resistance between two sampling locations is, on average, more influenced by roads when grains of connectivity are used than when the original grid is used. Also, water features that are dominant on the grid, have very low influence at all grains of connectivity. These results suggest that using grains of connectivity effectively accomplishes a re-parameterization of the grid resistance surface, in some cases increasing, and in others decreasing, the influence of features for connectivity.

4.5. Discussion

We analyzed landscape pattern and its effect on gene flow using both grid rasters and grains of connectivity to determine shortest paths between pairs of animals. We found evidence of landscape resistance to gene flow operating at a range of spatial grains many times coarser than the original landscape raster, suggesting that the landscape patterns influencing gene flow in this woodland caribou population are operating at very broad extents. We found no evidence of landscape resistance to gene flow that could be separated from geographic distance using the original landscape raster. Our results reinforce the value of examining pattern at multiple spatial scales, and particularly for wide-ranging organisms like woodland caribou, the possibility that pattern may be resolved using units hundreds of square kilometres in area.

4.5.1. Grains of connectivity

Examination of pattern at multiple scales remains an important challenge in ecology, and methods for decomposing pattern generated by phenomena operating at multiple spatial

scales such that its scale-specific effect can be quantified continues to be the focus of active research (Levin 1992, Keitt and Urban 2005, Bolliger et al. 2007, Anderson et al. 2010). We have shown that by varying the resistance threshold it is possible to test multiple grains of connectivity representing a variety of scale-specific patterns. This is in contrast to the grid raster approach at a single grain, where the hypotheses we tested produced virtually identical results despite differing widely in the parameterization of a landscape feature. We also found that different resistance surface parameterizations can converge on similar conclusions when examined at different scales (e.g. Fig. 4-6., B, C, D). Importantly, this finding suggests that using a multiscaled approach may be able to reduce the sensitivity of results to the parameterization of resistance features, an effect that has received extensive commentary (e.g. Rayfield et al. 2010, Spear et al. 2010).

Our findings underline that researchers must also give careful consideration to the grain of analysis, and test multiple grains because the optimal grain for capturing pattern will likely never be known *a priori*. For wide ranging organisms in particular, where the process of gene flow may occur over broad extents, some spatial simplification of the landscape data may be required to smooth out unimportant variation, and highlight the pattern driving the process. Analysis at multiple grains may also be necessary to account for uncertainty in a species' perception of its environment (e.g. Sawyer et al. 2011).

An important contribution of the grains of connectivity approach is the potential to improve this match between the scale of landscape pattern and the process of gene flow. Rather than describing the dominant cover in a region of the landscape, the polygons in a

grain of connectivity directly describe the pattern, or spatial configuration of landscape features, that may influence gene flow. These polygons identify regions of the landscape thought to have high connectivity, with resistance among polygons modelled in a way that is analogous to typical least-cost path or circuit theory applications (e.g. Cushman et al. 2006, Schwartz et al. 2009). Our approach achieves a coarser representation of the landscape than has typically been used in landscape genetics and therefore an omission of features that may be unimportant. A coarser representation also has the potential to compensate for the spatial uncertainty in sampling locations caused by organisms with large home ranges (e.g. Graves et al. 2012) which can potentially bias the connectivity estimates.

Coarser grains are achieved by increasing the resistance threshold, which also increases the area of polygons. However, this is more flexible than increasing the grain of analysis by an areal approach (Anderson et al. 2010, Cushman and Landguth 2010a). Resampling or smoothing with moving windows may be useful for evaluating higher order pattern in landcover types, or in continuous landscape features such as topography, but these are less likely to capture landscape pattern associated with small footprint features that occur over a large spatial extent, such as the roads and cut blocks in this study. In contrast, small footprint features contribute to the pattern in our approach when their spatial location and resistance are such that they will influence connectivity. Although the spatial grain may be coarser than the original raster and therefore some variation has been smoothed out, all the feature classes on the original raster are still represented insofar as they contribute to the links between polygons. Further investigation using simulated

genetic data is needed to understand the comparative efficiency of grains of connectivity and areal scaling of raster grids at capturing gene flow operating at a broad range of grain sizes.

The method used for testing grains of connectivity is similar to an existing landscape genetic approach. Isolation-by-barrier (IBB) hypotheses have been used by some authors to test the influence of specific features like roads, rivers, and valleys on gene flow (e.g. Cushman et al. 2006, Shirk et al. 2010). These models produce a similarly structured distance matrix that also contains information about spatial configuration at coarse grains; sampling locations on one side of a barrier are assigned zero distances, while those separated by one or more barriers are assigned a non-zero distance. Our approach differs in that the polygon boundary describes the approximate location of the "barrier" (which can be understood as the absence of high connectivity), and the distance separating locations on either side of a polygon boundary are the resistances of landscape features that must be traversed to enter the polygon. Grains of connectivity essentially provides a systematic way of producing a series of related IBB hypotheses, where the threshold parameter gives the minimum resistance to gene flow associated with this "barrier". In contrast to existing uses of IBB hypotheses, the identification of these "barriers" is based on a functional connectivity hypothesis rather than on the assignment of a resistance value to features thought to be important (e.g. Shirk et al. 2010).

4.5.2. Potential applications

Grains of connectivity may be advantageous for modelling biological phenomena that operate at spatial grains that are much coarser than the grain of landscape features represented on typical landcover and remotely-sensed maps. However, as a general approach for coarsening the grain of landscape data, the method may also be suitable for modelling phenomena that operate at finer grains (e.g. dispersal for less mobile species, or those that are more influenced by patterns in vegetation). Equally, the method will work for organisms that are restricted to certain patch types, or exist in discrete populations. In this study we defined the focal patch in our landscape graph model (e.g. Fig. 4-2, b) in terms of its selection by caribou and not because caribou are found exclusively in these features. The focal patch could easily be defined in other ways that are relevant for the study system (see for review Galpern et al. 2011). For example, in an amphibian landscape genetic study, wetlands may be suitable as focal patches in the landscape graph, and the grains of connectivity might be shown using nodes and links, rather than as Voronoi polygons, in order to represent the regions of high connectivity in a meaningful way for the species (e.g. as Fig. 4-2, d, rather than its equivalent Fig. 4-2, e).

Grains of connectivity is just one application of patch-based landscape graph modelling to landscape genetics. We can foresee partitioning the resistance surface using other scalable properties of patch-based graphs, such as network community structure (e.g. Bodin and Norberg 2007). Much potential still remains for using patch-based graph models to understand landscape influences on gene flow (Galpern et al. 2011).

4.5.3. Limitations of the analysis

Improving statistical methods in landscape genetics is a central task, and additional work is needed to develop a powerful and accurate approach (Jaquiéry et al. 2011). A concern with the causal modelling framework we adopted is that there is no means of ranking the many hypotheses in terms of their relative support (Shirk et al. 2010). Partial Mantel tests used in the framework remain controversial, and suffer from a lack of statistical power as well as a tendency to underestimate the variation explained by landscape resistance (Legendre and Fortin 2010). While using partial Mantel tests is appropriate when hypotheses must be formulated using distances (Legendre and Fortin 2010), and studying landscape resistance at the among-individual level with these tests has been shown to be effective (e.g. Cushman and Landguth 2010b), using multiple statistical methods may be a more robust approach to confirm conclusions (e.g. Jaquiéry et al. 2011).

There is also an increased probability of type I error resulting from the 507 hypothesis tests we conducted. Because each hypothesis described spatial configurations that are difficult to define *a priori*, we feel that this large number of tests was required to systematically examine contrasting explanations for gene flow. Approaches to select a subset of grains to test are certainly warranted, however, and remain an important area for future research.

We used metrics that model the movement pathways of organisms as the minimum-weight path through a graph (e.g. least-cost paths, Fig. 4-2, d, links; shortest paths between polygons, Fig. 4-4). These approaches can be criticized for failing to capture multiple movement pathways that are apparent to organisms, and circuit theory has been proposed to address this concern (McRae et al. 2008). We foresee that grains of connectivity could equally incorporate circuit theory principles; for example, by applying random walk algorithms when finding link lengths on the minimum planar graph, and determining the resistance between polygons.

Some of the features we reported to have influenced gene flow (e.g. roads, disturbance features) have appeared within the last 40 years (Arlt and Manseau 2011), which may be insufficient time for genetic drift to have created the observed genetic structure, even under an extreme scenario of no gene flow among regions of the landscape. Genetic drift is both a function of the number of generations elapsed and the effective population size (Nei and Chakravarti 1977). While we were not able to estimate effective population size, the woodland caribou in this population are few in number (see *Methods*).

Combined with telemetry evidence that these caribou have limited home ranges (see *Methods*), we find it plausible that population size and rates of gene flow could be sufficiently low for drift to have produced a measurable effect. Accumulating evidence suggests woodland caribou avoid roads of any size, as well as forests in early successional stages, which may be the mechanism behind the reduced dispersal and gene flow our results imply (Koper and Manseau 2009, Polfus et al. 2011).

4.6. Conclusion

We examined the effects of landscape connectivity on gene flow in a multiscale analysis. Using this approach we identified landscape influences on spatial genetic structure that would have been missed if analysis had been conducted only at the spatial grain of a grid raster. Our results underline the importance of multiple grains of spatial analysis, and suggest that further investigation of spatial grains hundreds of square kilometres in size may be appropriate for highly-mobile species. Grains of connectivity, and related patch-based landscape graphs methods, hold much promise for multiscale modelling in landscape genetics.

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4.8. Author contributions

All authors were involved in the conceptual development of this paper. P. G. conducted the landscape genetic analyses and wrote the manuscript. M. M. and P. J. W. contributed

samples, landscape data, and genetic data. They both contributed to and commented on several versions of the manuscript.

4.9. Appendices

Appendix 4-1

Parameters used to generate five resistance surfaces.

Appendix 4-2

Results for selected grains of connectivity models.

Appendix 4-3

Results for grid models for five resistance surfaces tested.

Appendix 4.1. Parameters used to generate five resistance surfaces.

Landscape feature	Resistance value
<i>Hospitable landcover</i>	
Jack pine dominated, mature	1.00
Treed muskeg	1.00
Jack pine, black spruce, mature	1.14
Spruce, mature	1.38
Black spruce, larch, mature	1.54
<i>Disturbance landcover</i>	
Mixedwood	2.86
Conifer, intermediate	4.25
Hardwood	4.96
Conifer, young and recent burn	10.39
Cut blocks ¹	10.39
Minor roads (Forestry tracks) ¹	10
<i>Water</i>	
Open water ¹	100
Open muskeg	4.59
<i>Roads</i>	
Major roads (Gravel roads and highway) ^{1,2}	1, 10, 100, 200, 400

¹Resistance values were not estimable (see text).

²Five resistance surfaces were produced differing only in this parameter (see text).

Appendix 4-2. Results for selected grains of connectivity models.

The table shows one IBR only grain of connectivity model for each resistance surface (the model with the highest IBR | IBD partial Mantel statistic; see text).

These models were selected for further examination (see Figs. 4-6 and 4-7).

Major roads (resistance units)	Label on Figures 4-6 and 4-7	Resistance threshold ¹ (resistance units)	Mean polygon area (km ²)	Polygon count	Paired partial mantel tests			
					IBR IBD r_p	IBR IBD P	IBD IBR r_p	IBD IBR P
1	A	720	422.4	66	0.0309	0.0308	-0.0261	0.0528
10	—	—	—	—	No IBR only model			
100	B	810	224.8	124	0.0802	<0.0001	-0.0112	0.2580
200	C	1200	324.2	86	0.0956	<0.0001	-0.0210	0.1060
400	D	1600	464.6	60	0.1140	<0.0001	-0.0294	0.0532

¹Minimum path distance possible for any transition between two polygons; i.e. the minimum resistance of crossing a polygon boundary

Appendix 4-3. Results for grid models for five resistance surfaces tested.

No grid model produced an IBR only hypothesis. In all cases both IBR and IBD were supported in the causal modelling framework.

Major roads (resistance units)	Paired partial mantel tests			
	IBR IBD r_p	IBR IBD P	IBD IBR r_p	IBD IBR P
1	0.0532	0.0026	0.0954	<0.0001
10	0.0491	0.0038	0.0967	<0.0001
100	0.0513	0.0030	0.0962	<0.0001
200	0.0514	0.0027	0.0962	<0.0001
400	0.0513	0.0032	0.0963	<0.0001

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CHAPTER FIVE

Exploring the dimensions of functional grain: testing patch and resistance models of landscape connectivity across spatial and seasonal scales

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5.1. Abstract

Modelling how organisms perceive heterogeneity in landscape structure may be essential for understanding landscape connectivity. Aggregations of patches that animals perceive as high quality, or regions of the landscape that present low fitness costs to movement, create a spatial pattern that we describe as a functional grain. If animals are responding to this pattern, they may be distributed in larger more connected regions of the landscape. The response to landscape features may also be seasonally-dependent, varying with life history stage. We used telemetry observations from a woodland caribou population (*Rangifer tarandus caribou*) in three seasons, and tested hypothetical functional grains defined by the spatial configuration of patches (patch only), by landscape resistance to movement (matrix only), and by a combination of the two (patch + matrix). We developed a measure of fit that describes caribou distribution with respect to larger more connected regions in the grain, and used this to ask: (1) are seasonal caribou locations consistent with a random functional grain, implying that landscape connectivity has not shaped their distribution? and (2) given a functional grain model, are seasonal caribou locations distributed in larger connected regions than random points, implying that caribou are responding in some measure to the shape, size, and location of the connected regions. We found significant support for functional grains defined by a matrix model, in both late winter and summer seasons, where the resistance of landscape features such as roads and highways are the most influential features. Grains defined only by patch spatial configuration fit the data no better than random grains, underlining the importance of landscape resistance for connectivity in highly-mobile organisms such as caribou. We found the least support for functional grains during the calving season, where caribou

may be moving to predator-safe locations without regard to landscape configuration. The grains of connectivity approach that we applied to create hypothetical functional grains provides a flexible means for modelling the functional response of organisms to heterogeneity at multiple spatial scales, and therefore for achieving a closer match between landscape pattern and the process it is being used to understand.

5.2. Introduction

Landscape connectivity continues to be of wide interest to ecologists and land managers (Urban et al. 2009, Sawyer et al. 2011). Knowledge of how landscape features affect the movement and dispersal of organisms may be critical for addressing the impacts of habitat fragmentation (Fischer and Lindenmayer 2007), preventing the spread of pathogens and invasives (Margosian et al. 2009), building protected area networks (Minor and Lookingbill 2010), and facilitating migratory responses to climate change (Heller and Zavaleta 2009).

Exploring how organisms perceive heterogeneity is an essential step in modelling movements on landscapes (Anderson et al. 2010). Animals may perceive landscapes at a certain functional grain (Baguette and Van Dyck 2007). The concept of functional grain implies that movements that are finer than a certain spatial grain are by-products of other routine behaviours such as foraging or predator avoidance, and therefore present no additional fitness or energetic costs. Conversely, movements that are coarser than this spatial grain represent a fitness cost to the organism (e.g. because they may interrupt routine behaviours, or increase predator exposure). It is at this coarser movement scale that dispersal and landscape connectivity comes into play: where the movement of organisms engaging in cost-minimizing behaviour is influenced by the spatial configuration of habitat and the resistance of features in the matrix.

In this paper, we adopt a similar, but scalable, concept of functional grain. We understand the functional grain as the grain at which landscape connectivity operates: as an

interaction between landscape structure and animal perception. Just as functional connectivity is the interaction between structural connectivity and animal response to that structure (Calabrese and Fagan 2004), functional grain represents the interaction between spatial grain and animal response to structure perceived at that grain. Functional grains are therefore scale-dependent representations of functional connectivity. In spatial terms, a functional grain corresponds to a pattern consisting of regions of relatively high connectivity, where the boundaries of these regions are associated with landscape structure perceived as costly by an organism. A functional grain therefore defines a set of regions of high connectivity within which movements are not costly and where landscape heterogeneity, such as the configuration and resistance of features, are not influencing movement.

Elsewhere, in landscape genetics, this idea has been presented as the "grain of the landscape connectivity process," where the emphasis has been on ensuring that landscape connectivity is described at a spatial grain of comparable area to that of the process, in order to achieve accuracy in measurement (Anderson et al. 2010, Cushman and Landguth 2010). In either terminology, representing a functional grain, or the grain of the process, requires some approach that can highlight landscape heterogeneity that an organism may perceive as costly. Defining this perception, however, is challenging as this requires behavioural evidence (e.g. the maximum distance over which dispersal is likely to occur) and a description of the fitness costs an organism experiences during movement, both of which may prove difficult or impossible to obtain (Bunn et al. 2000, Baguette and Van Dyck 2007).

An alternative approach is to identify a landscape pattern, and then ask if this pattern fits empirical evidence of the process (e.g. O'Brien et al. 2006, Anderson et al. 2010, Cushman and Landguth 2010, Galpern et al. 2012). If animals are responding to a functional grain, given sufficient time, this may influence gene flow, resulting in patterns of genetic similarity consistent with the grain (Galpern et al. 2012). Equally, over shorter time scales, organisms may respond to functional grain patterns in their distribution, and we might expect organisms to select larger, more connected, regions of the landscape described by the grain (O'Brien et al. 2006).

Testing these questions requires a method for generating hypothetical functional grains. One approach is to scale landscape resistance surfaces by increasing the size of the spatial grain (e.g. Anderson et al. 2010, Cushman and Landguth 2010). Resistance surfaces are typically in raster format and they model the inverse of landscape connectivity: the resistance of the landscape to movement and dispersal (McRae et al. 2008, Sawyer et al. 2011). In these models, the raster cell can be understood as the region of high connectivity in the functional grain, and the value assigned to each cell is the amount of resistance that must be overcome to move out of this region (e.g. Galpern and Manseau 2012). As raster data is upscaled, the size of the cell increases, and so does the region of high connectivity. This type of areal scaling has the secondary effect of simplifying the raster, and therefore removing spatial heterogeneity that may be uncorrelated with movement and dispersal (Anderson et al. 2010). However, such simplification may be arbitrary with respect to the landscape, and can obscure small footprint features that are

influential in structuring the functional grain and are therefore important for a connectivity assessment (Galpern and Manseau 2012).

Here, we adopt another method to identify hypothetical functional grains that can accommodate pattern consisting of discrete features (O'Brien et al. 2006, Galpern et al. 2011, Galpern et al. 2012). Grains of connectivity can flexibly identify regions of high connectivity on a resistance surface and model the resistances among them by using landscape graphs methods (Galpern and Manseau 2012, Galpern et al. 2012). A common assumption of landscape graph modelling is the requirement that organisms are restricted to well-defined habitat patches except during dispersal (Urban and Keitt 2001, Galpern et al. 2011). Grains of connectivity extends this approach to make it suitable for highly mobile organisms where habitat may be better described as a probability region than an identifiable patch (Galpern and Manseau 2012, Galpern et al. 2012). Rather than modelling patches exclusively, the method finds a region of proximity in the vicinity of a focal patch or a focal location. This region is found using a Voronoi tessellation and the resulting Voronoi polygons describe proximity in landscape resistance units.

A powerful property of grains of connectivity, and of landscape graphs, is their scalability (Brooks 2003). All landscape graph methods can depict landscape connectivity at different scales by thresholding the graph at a maximum expected dispersal distance for the organism, sometimes called a gap-crossing distance (Bunn et al. 2000, Urban and Keitt 2001, Brooks 2003). This permits a multiscale analysis that can accommodate uncertainty in this movement distance, a challenging parameter to obtain in

many species (Bunn et al. 2000). In grains of connectivity, because the graph represents polygons in a tessellation, multiscale analysis also increases the size of the regions of high connectivity by combining polygons. This has the secondary effect of selectively removing spatial heterogeneity: features are removed if they create less resistance than a threshold amount, where resistance is measured cumulatively and radiating outwards from the focal patch or focal location used to structure the tessellation (Galpern and Manseau 2012).

Organisms may also have changing perceptions of spatial heterogeneity at different stages of their life history. If this is true, testing the importance of landscape connectivity at different temporal scales would require a dynamic definition of functional grain. For example, during juvenile dispersal organisms may have evolved a maximum movement threshold or gap crossing distance (Baguette and Van Dyck 2007), but during other stages it is conceivable that movement may have a lower maximum threshold, or instead be a response to landscape composition such as habitat area or quality. The scalability of grains of connectivity is useful in this regard, as the method can also accommodate uncertainty associated with the maximum movement distance at different life history stages (Bunn et al. 2000).

Here, we use grains of connectivity to model hypothetical functional grains for the threatened boreal woodland caribou (*Rangifer tarandus caribou*) at multiple spatial scales. By altering how grains of connectivity models are produced, we create hypotheses describing landscape connectivity as the spatial configuration of patches, as

the resistance of landscape features, or as a combination of both, and then test the predictions of these models at three different temporal extents. We investigate whether caribou are distributed on the landscape in a manner that reflects these hypothetical functional grains using telemetry data collected in three behaviourally-defined seasons. Specifically, we ask two questions: (1) are seasonal caribou locations consistent with a random functional grain, implying that landscape connectivity has not shaped their distribution? and (2) given a functional grain model, are seasonal caribou locations distributed in larger connected regions than random points, implying that caribou are responding in some measure to the shape, size, and location of the connected regions? Using the three types of models, we also investigate the influence of patch spatial configuration and landscape resistance for these conclusions.

5.3. Methods

Boreal woodland caribou have been assigned a threatened designation under Canada's *Species at Risk Act* (Government of Canada 2003). The Smoothstone-Wapeweka caribou population in central Saskatchewan, Canada (approx. 25,000 km² range; centred at 54° 17' N, 105° 31' W) is in demographic decline, and the landscape has been highly fragmented by forest harvesting activities (Arlt and Manseau 2011, Arsenault and Manseau 2011, Galpern et al. 2012). The sensitivity of woodland caribou to anthropogenic disturbance has been well-documented (e.g. Dyer et al. 2001, Polfus et al. 2011). Telemetry evidence indicates a restriction in the average home ranges of animals over a 16 year period (Arsenault and Manseau 2011) and landscape genetic studies

suggest that natural and anthropogenic disturbance may be influencing genetic structure by reducing rates of gene flow within the population (Galpern et al. 2012).

Seventeen adult female caribou were collared in the study area in 2005 and 2006 using Lotek GPS collars (Lotek Wireless Inc., 115 Pony Drive, Newmarket, Ontario).

Locations were recorded every 4 h and grouped according to seasons defined by movement rates calculated from the data (Dyke 2008). We used points during the late winter season (16 January-27 March 2005 to 2008) to assess landscape connectivity models at a time where deep snows often restrict movement and habitat selection is strongest (Brown et al. 2007, Koper and Manseau 2009). Points during the calving (29 April – 7 June 2005 to 2008) and summer seasons (7 July – 12 August 2005 to 2008) were used to assess our models at two additional temporal extents where female caribou may prioritize predator avoidance when calves are at heel (Rettie and Messier 2001). The number of locations per animal ranged from 368 to 1391 in late winter, 132 to 826 during calving, and 125 to 662 during summer. These data were used to characterize the distribution of animals during three seasons.

5.3.1. Modelling landscape connectivity at multiple spatial scales

We produced landscape connectivity models representing three ways in which caribou may perceive landscape heterogeneity: (1) a model describing patch spatial configuration (patch model); (2) a model describing both patch spatial configuration and the resistance of landscape features (patch + matrix model); and, (3) a model describing the resistance of landscape features (matrix model). We used a grains of connectivity approach

(Galpern and Manseau 2012, Galpern et al. 2012) to create hypothetical functional grains from these models at a range of spatial scales. Grains of connectivity is similar to patch-based landscape graph modelling, and creates a Voronoi tessellation of the landscape (Okabe et al. 2000, Urban and Keitt 2001, Fall et al. 2007, Galpern et al. 2011) that can potentially represent features that are influential for connectivity, while removing those that may be less influential (Galpern and Manseau 2012).

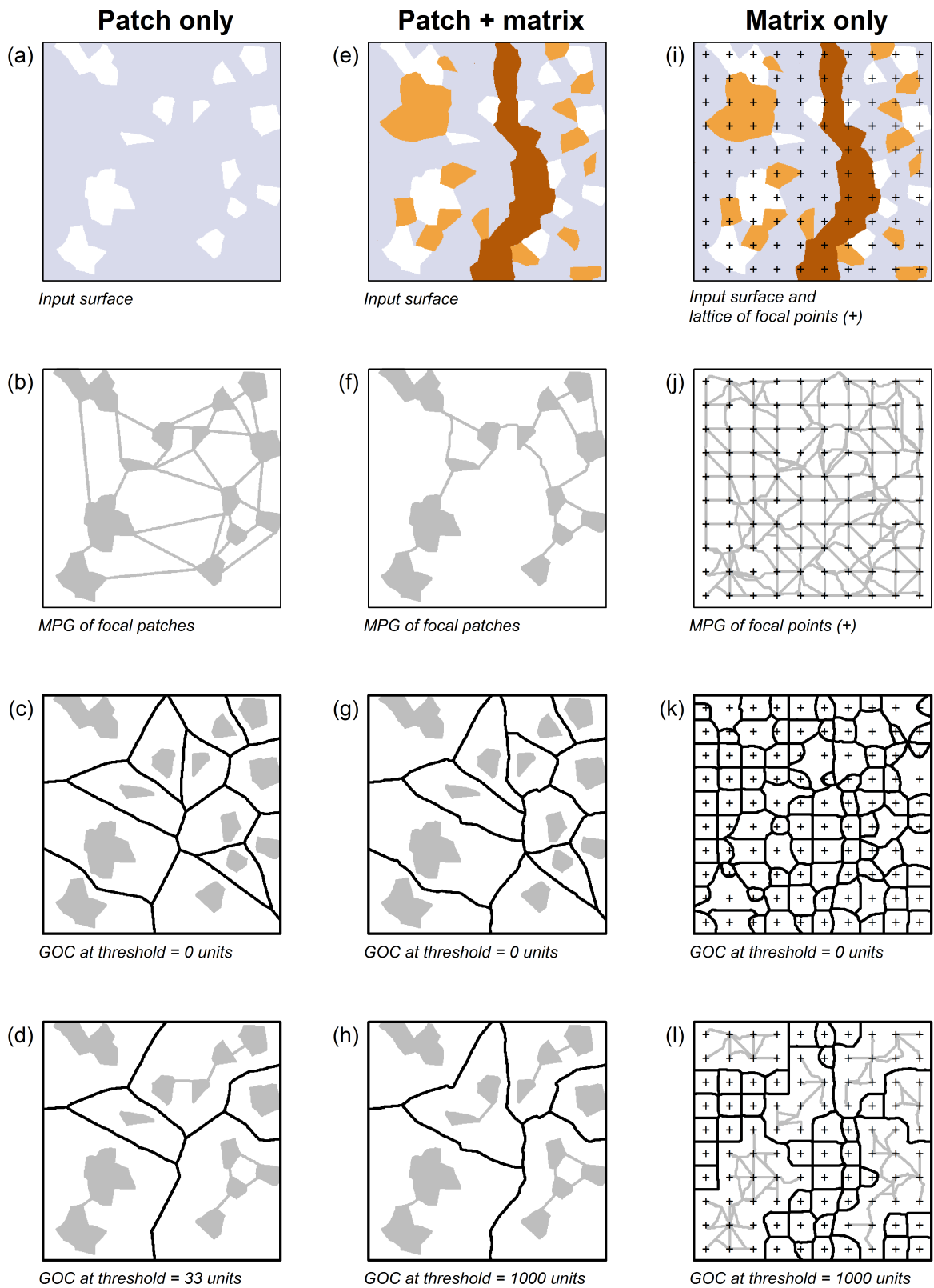
We illustrate this approach using an artificial landscape (Fig. 5-1). For models examining patch spatial configuration, the process begins with a raster resistance surface describing the location of focal patches (Fig. 5-1, a, unshaded regions), which are typically spatially rare habitat of high importance for the organism. The remainder of the landscape (Fig. 5-1, a, shaded) is assigned a resistance value of 1, implying that landscape resistance is equivalent to geographic distance (patch model; Fig. 5-1, a-d). To capture the effects of landscape features in the matrix between patches, a raster resistance surface can be included (patch and matrix model; Fig. 5-1, e-h), describing both the locations of the focal patches, and the relative resistance to connectivity imposed by landscape features (darker regions indicate higher resistance; Fig. 5-1, e).

In either case, a minimum planar graph (MPG) is extracted (Fig. 5-1, b, f). This is a network model that approximates the connectivity relationships between all pairs of patches using links that describe the Euclidean distance or, alternatively, the least-cost distance, associated with movement and dispersal between patches (Fall et al. 2007). The

Figure 5-1. Three ways of producing hypothetical functional grains using the grains of connectivity method.

(a to d) Modelling landscape connectivity as the spatial configuration of patches (patch only): (a) landscape raster showing locations of focal patches (unshaded regions); (b) minimum planar graph (MPG) is extracted modelling the connectivity relationships among these patches, and when the resistance of landscape between patches is set to 1 (shaded), the links represent geographic distances between patch perimeters; (c) grain of connectivity (GOC), a tessellation describing regions of proximity around these patches, is also produced when extracting the MPG. (d) multiple spatial grains are found by thresholding the MPG at different maximum movement distances (links) and combining polygons from the GOC. (e to h) Including information about resistance to movement in the landscape (patch + matrix): (e) same as a, with resistance of other landscape features included (darker shades indicate higher resistance); (f) same as b, with links as effective distance of least-cost paths between patch perimeters; (g) same as c, with regions of proximity around patches in resistance units; (h) same as d, with thresholding at different amounts of effective distance. (i to l) Excluding information about patch spatial configuration (matrix only): (i) same as e, with a lattice of focal points superimposed; (j) same as f, with links as effective distance between focal points; (k) same as g, with regions of proximity around focal points (called a lattice GOC model); (l) same as h.

Figure 5-1. Cont'd.



complement of the MPG is a tessellation that divides the landscape into regions of proximity around the focal patches (Fig. 5-1, c, g). This is done using a generalization of the Voronoi tessellation (Okabe et al. 2000, Fall et al. 2007) for two-dimensional generators that we call a grain of connectivity (GOC). When a non-uniform resistance surface is used, the tessellation describes proximity in resistance units (Fig. 5-1, g) rather than geographic distance units (Fig. 5-1, e) leading to differences in the shape and extent of the polygons that make up the tessellation. Finally, to analyze connectivity at multiple grain sizes, the GOC is simplified (Fig. 5-1, d, h) using a scalar approach (Brooks 2003) that thresholds the MPG according to a maximum link weight in geographic or least-cost distance units that can be understood as a maximum movement threshold required for two patches to be connected (Bunn et al. 2000, Urban et al. 2009). Polygons in the GOC are combined to reflect the structure of the MPG at a given threshold. A polygon therefore describes a region of high connectivity, and a polygon boundary represents the approximate locations of sets of features that may collectively impose resistance to movement. We used these polygons to define the spatial extent of landscape that is effectively homogeneous for connectivity (i.e. as a hypothetical functional grain). We have described grains of connectivity with additional detail elsewhere (Galpern and Manseau 2012, Galpern et al. 2012).

We introduced a third application of the GOC technique to investigate the role of landscape configuration at multiple spatial grains without also explicitly modelling patch spatial configuration (matrix model; Fig. 5-1, i to l). Lattice GOC finds the connectivity relationships for a lattice of focal points superimposed on the raster resistance surface

(Fig. 5-1, i). It extracts and thresholds a GOC model in an identical manner, except these systematically positioned focal points replace focal patches on the raster.

To model the Saskatchewan landscape for caribou we used a landscape map (Fig. 5-2) and a resistance surface (Table 5-1) previously shown to influence gene flow in this population at several spatial grains (Galpern et al. 2012). We restricted our modelling to a focal extent chosen to circumscribe the 100% minimum convex polygon of telemetry locations (Fig. 5-2, a). Mature jack pine, a spatially rare vegetation feature selected by caribou (Koper and Manseau 2009) was used as the focal patch type in the patch models (Fig. 5-2, b). For all three model types, we produced grains of connectivity at 150 resistance thresholds. Focal points in the lattice GOC model were separated with a radius of 3600 m. To enable a standard comparison between models we derived a new connectivity metric identical in form to the expected cluster size (ECS; O'Brien et al. 2006, Fall et al. 2007). We found the expected polygon area (EPA) for a given grain and model as

$$EPA_g = \frac{\sum_{j=1}^m PA_j^2}{A}$$

where there are m polygons in a grain, PA_j is area of the polygon j at grain g , and the total landscape area is given by A . EPA describes the size of the polygon into which a randomly selected point is expected to fall. It can be understood both as a central tendency in grain size and as a metric of connectivity for an entire landscape. To reduce the number of grains tested, we selected grains for further analysis based on their EPA , retaining for each model between 6 and 12 grains that were approximately evenly spaced

Figure 5-2. Sampling distribution and landscape features in the Smoothstone-Wapaweka woodland caribou range in Saskatchewan, Canada.

(a) Home ranges (100% minimum convex polygon) for seventeen female caribou used in this study. (b) Simplified landcover data used to determine locations of focal patches and the matrix model of landscape resistance.

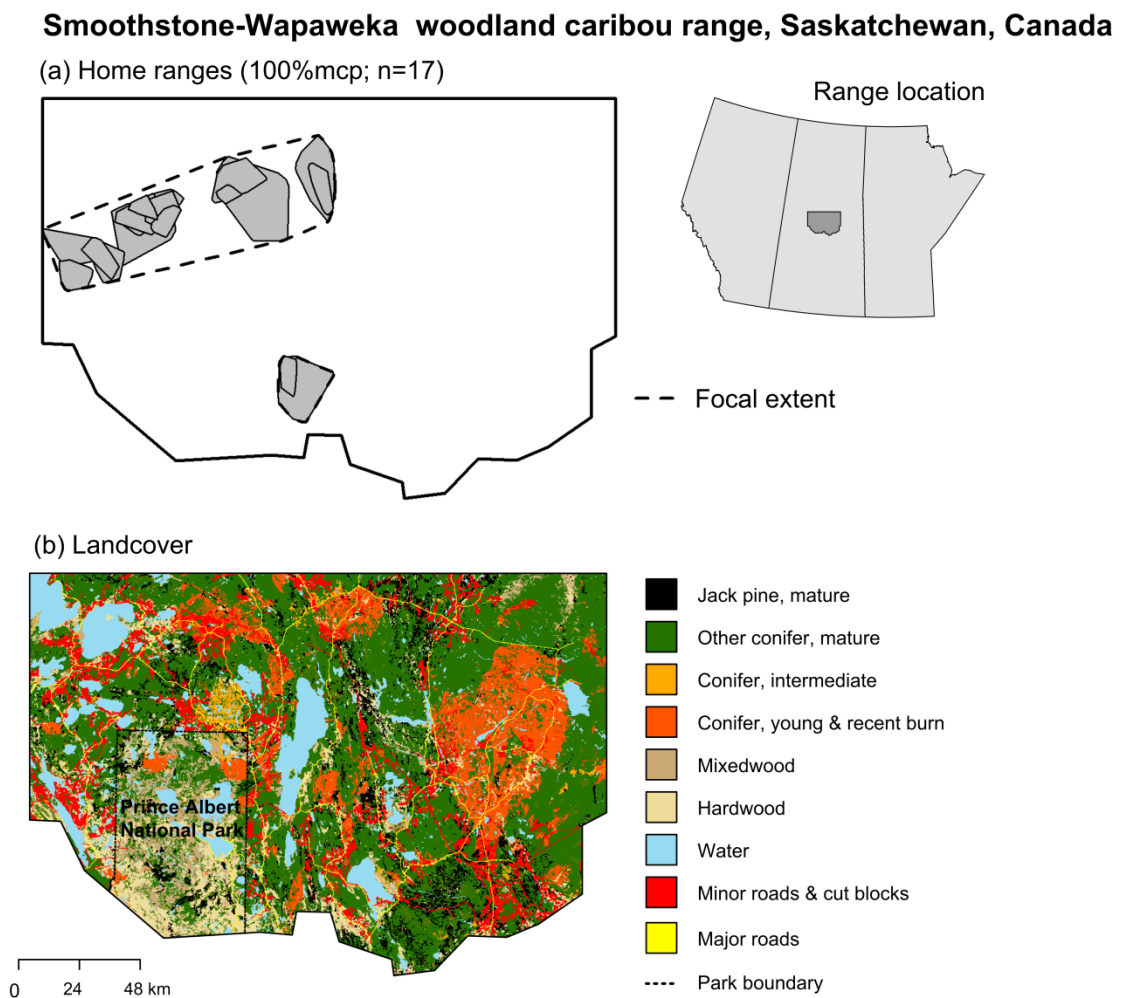


Table 5-1. Parameters used to generate the matrix model landscape resistance surface.

Landscape feature	Resistance value
Jack pine dominated, mature ¹	1.00
Treed muskeg	1.00
Jack pine, black spruce, mature	1.14
Spruce, mature	1.38
Black spruce, larch, mature	1.54
Mixedwood	2.86
Conifer, intermediate	4.25
Open muskeg	4.59
Hardwood	4.96
Minor roads (Forestry tracks)	10
Conifer, young and recent burn	10.39
Cut blocks	10.39
Open water	100
Major roads (Gravel roads and highway)	400

¹Feature class used for focal patches

in their *EPA* up to a maximum *EPA* of 400 km², above which the focal extent was generally dominated by a large polygon.

5.3.2. *Testing model predictions*

First, we asked whether seasonal caribou points were distributed in a manner that was consistent with a random functional grain (i.e. a pattern where ecological correlates of landscape connectivity such as patch spatial configuration and matrix resistance were not included). To make this null model we produced Voronoi tessellations (Okabe et al. 2000), by distributing point generators randomly within the focal extent (Fig. 5-2, a) where the resulting Voronoi polygons were clipped by the extent. Random tessellations at different grain sizes were produced by varying the number of generators, allowing the shape, size, and location of the polygons, and consequently *EPA*, to vary randomly. We used 35 treatments each with a different number of generators (20 to 450), and for each treatment we found a distribution of 100 random tessellations for a total of 3500 random functional grains. To assess whether seasonal caribou points were distributed in a manner consistent with these random functional grain models, or alternatively, consistent with a non-random patch, matrix or patch + matrix model, we found the point mean polygon area (*point* \overline{PA}) for a given grain and model as

$$\textit{point } \overline{PA}_g = \frac{\sum_{i=1}^n PA_i}{n}$$

where there are n points, and PA_i is area of the polygon containing point i at grain g .

Evidence against a null model and support for an alternate at a given grain was found by comparing the *point* \overline{PA} for the alternate model to a bin of random functional grains with an *EPA* of ± 25 km² of the alternate. Statistical significance was recorded where *point* \overline{PA} for the alternate was greater than that for 95% of the random functional grains

in the bin. Because we were unable to control the distribution of *EPA* for the random grains, bins could not contain a constant number of random grains.

Second, as an alternative way of testing the fit of the data to a given model, we asked whether seasonal caribou locations were more consistent with the predictions of the model, than were random points on the landscape. We defined the fit of the model as evidence of caribou locations in larger polygons on average than random points. To do this, we compared the actual locations with 100 sets of random points of equal size (O'Brien et al. 2006) distributed within the focal extent (Fig. 5-2, a) on habitat types (Table 5-1) in proportion to their use of that habitat. We again used the point mean polygon area (*point \overline{PA}*) as a means of comparison, but instead calculated it for different sets of points. Evidence that seasonal location data fit a given model was declared where the *point \overline{PA}* for the seasonal locations was greater than that for 95 of the 100 sets of random points.

All steps were completed using R 2.14.1 (R Development Core Team 2012). We used our own *grainscape* package to find grains of connectivity (v0.1; Galpern et al, in prep), as well as *deldir igraph*, and *raster* packages to perform point Voronoi tessellation, graph and spatial analyses respectively (Csardi and Nepusz 2006, Hijmans and van Etten 2011). The extraction of the MPG was done by *grainscape* using SELES v3.4 software (Fall and Fall 2001) that is bundled with the package.

5.4. Results

5.4.1. *Modelling landscape connectivity at multiple spatial scales*

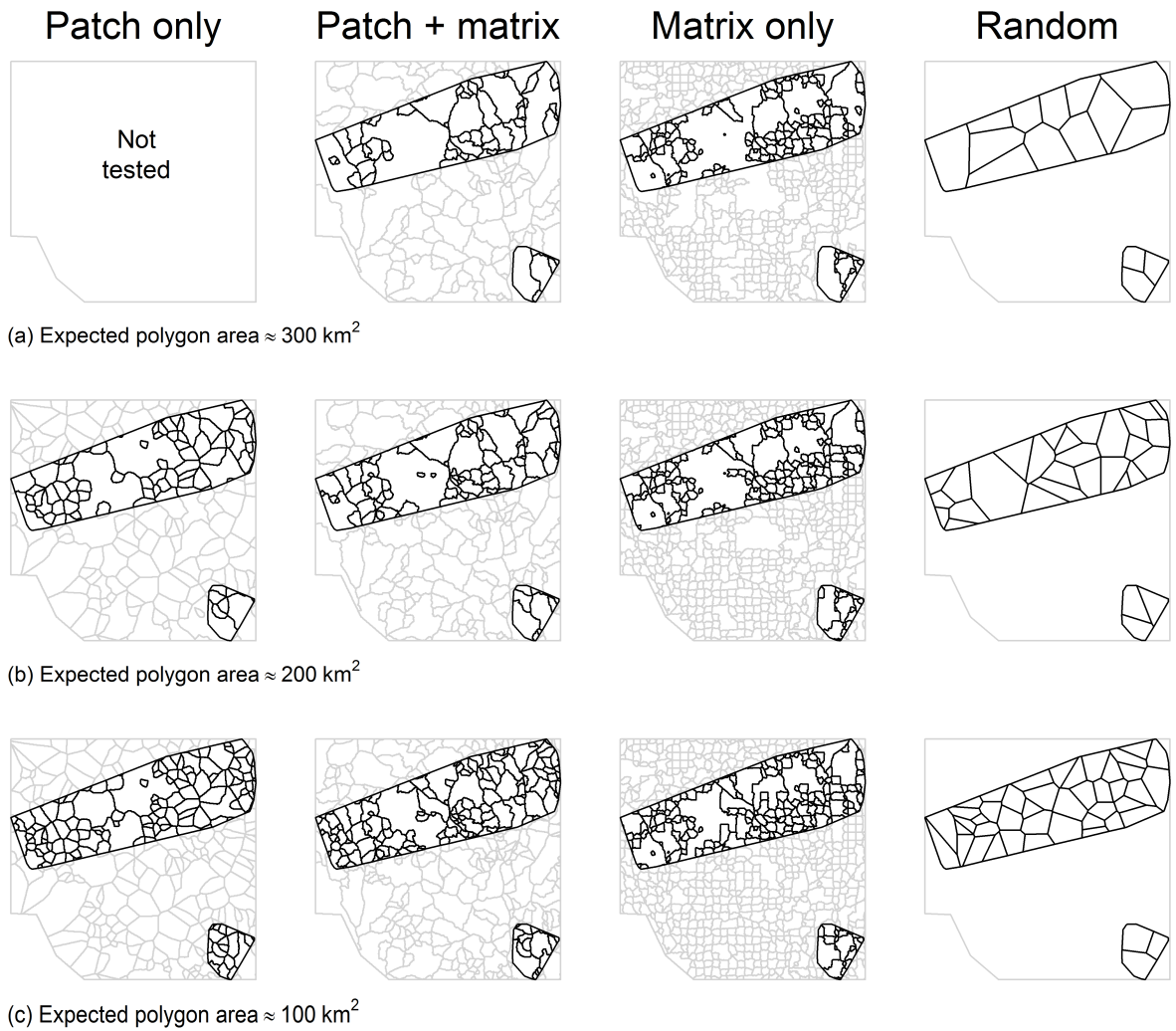
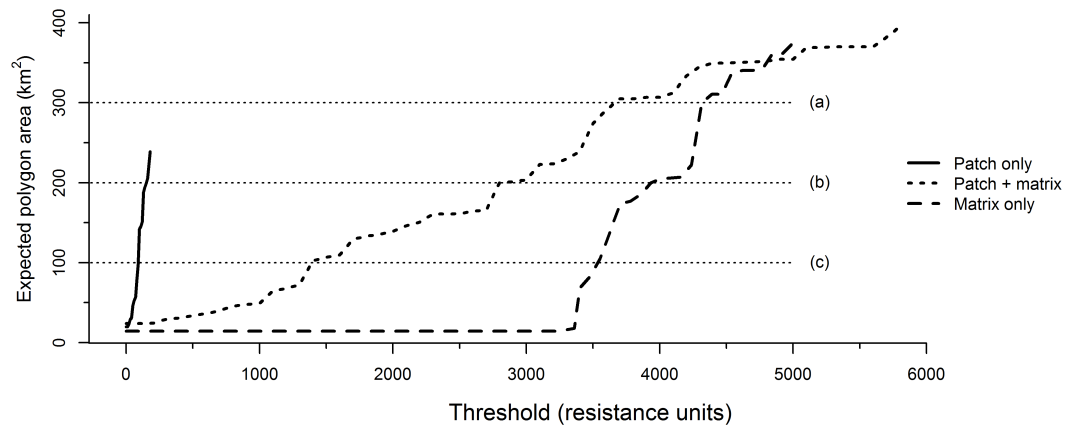
In landscape graph and grains of connectivity modelling the resistance threshold expresses a theoretical maximum movement distance for the organism. In patch only models this resistance threshold is equivalent to a geographic distance separating patches, while in other models the threshold is an effective distance (Adriaensen et al. 2003). This is the model parameter that we manipulated to investigate the role of connectivity at multiple spatial scales (Bunn et al. 2000, O'Brien et al. 2006, Urban et al. 2009). When this value is increased, more focal patches or points on the landscape become connected, which has the effect of producing larger regions of high connectivity (i.e. larger polygons). The relationship between threshold and the expected polygon area (*EPA*; Fig. 5-3) is an increasing function, although the correlation between these variables depends on the landscape structure. Fewer polygons with larger areas also implies the amount of spatial heterogeneity described by the functional grain decreases.

Fig. 5-3 (top) illustrates that the resistance threshold is not a consistent means of describing the connectivity or spatial heterogeneity implied by a functional grain when multiple models are being compared. Similar values of *EPA*, a connectivity and spatial scaling metric, are described at very different thresholds depending on the model (Fig. 5-3, a, b, c). This is partly because threshold is only comparable with reference to a standard set of graph nodes used to build the MPG (i.e. Fig. 5-1, b, f, j), and this set of nodes differs depending on whether patches or a lattice of points is used in the model. When the three models were examined at the same *EPA*, they described generally similar

Figure 5-3. Expected polygon area (EPA) provides a consistent way to compare models at the same spatial grain.

EPA is a measure describing the coarseness of the functional grain or alternatively the expected area of a region of high connectivity. Increasing the resistance threshold, a graph parameter that specifies the maximum dispersal distance for two locations on the landscape to be connected, also causes an increase in EPA, demonstrating how the area of this region and maximum movement are related. (a, b, c) When EPA is held constant, the three types of landscape connectivity model (patch only, patch + matrix, matrix only), and a random functional grain model representing the absence of landscape connectivity, differ in the shape, size and location of the polygons that describe the hypothetical functional grain. EPA is used in this study to compare models with one another, and with random models, as it provides a consistent means of describing both the spatial heterogeneity of a model and the landscape connectivity it implies.

Figure 5-3. Cont'd.



sets of polygons (Fig. 5-3, a, b, c). Differences in the count, shape, and size distribution of those polygons among the models are a consequence of how landscape heterogeneity is incorporated in each case. Three examples of random functional grains, however, indicate very different counts, shapes and size distributions (Fig. 5-3, random) from the models at the same *EPA*, demonstrating that this null hypothesis controls for spatial grain size but not for polygon count, shape or location.

5.4.2. Testing model predictions

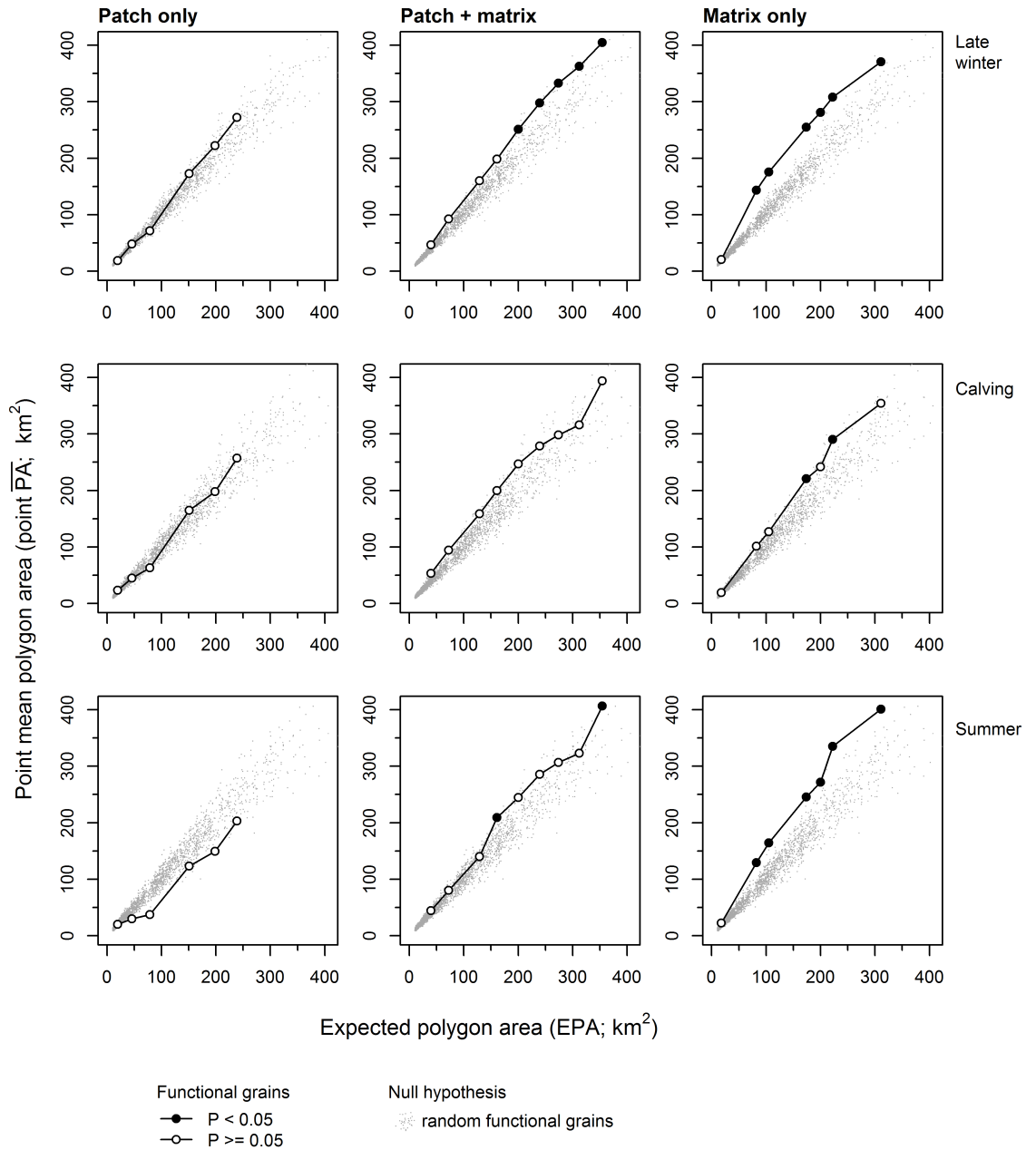
By comparing against random functional grains, we found evidence that caribou are responding to the connectivity of their landscape at a range of functional grains. We found that the point mean polygon area (*point \overline{PA}*), an index of how large the polygon (or region of high connectivity) is on average for all caribou locations, was never significantly higher than the random expectation when only a patch model was used (Fig. 5-4, patch only). In other words, the shapes and locations of polygons produced using only patch spatial configuration are no more informative than using a random tessellation to explain caribou distribution.

The introduction of a matrix model of landscape resistance changed these results, and led to several significant grains when using late winter and summer seasonal locations (Fig. 5-4, patch + matrix). The removal of the influence of patch spatial configuration in the model, produced a still broader range of significant grains overall (Fig. 5-4, matrix only). The largest deviations from the random expectation appeared in the matrix only model for late winter and summer locations, suggesting that the functional grain pattern

Figure 5-4. Tests of three types of functional grain models in three seasons using a random functional grain null hypothesis.

Significant functional grains ($P < 0.05$) indicate where caribou seasonal locations fit the functional grain better than random functional grains. Uncertainty in caribou perception of spatial heterogeneity is controlled by testing multiple functional grain sizes (levels of EPA). The fit of a functional grain to the seasonal locations at a given grain size is given by *point* \overline{PA} . Significance is declared where observed fits are greater than 95% of the random functional grain fits at an equivalent EPA ($\pm 25\text{km}^2$). At all grain sizes, functional grains based only on patch spatial configuration (patch only) provide no fit improvement over random tessellations. Overall, there is the least support for functional grains during the calving season.

Figure 5-4. Cont'd.



produced by our landscape resistance model (Table 5-1) is most aligned with the distribution of caribou during these seasons. Generally, these results emphasize that the patterns in connectivity produced by landscape resistance may be more important than pattern produced by patch spatial configuration, at least during these seasons. Caribou use of the landscape during calving may not be well explained by any of our functional grain models, with only two significant grains showing relatively small deviations from the random expectation (Fig. 5-4, matrix only, calving).

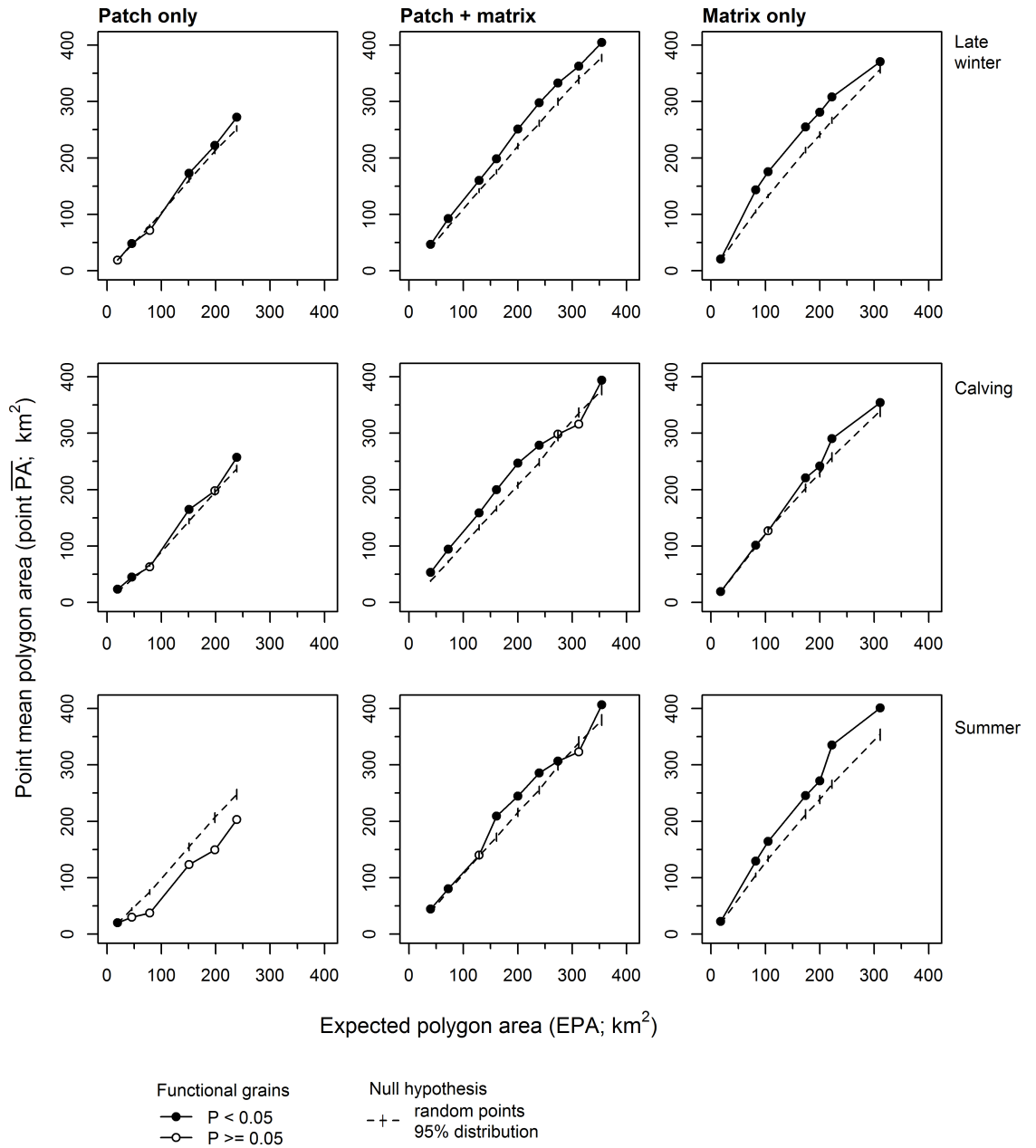
Using sets of random points asks whether caribou are using larger polygons in a given set than would be expected at random. This is in contrast to using random functional grains, which asks if a functional grain is better aligned with the data than a random set of polygons. Because there is no base standard of comparison, a random points null hypothesis is not useful for evaluating the relative performance of the models, and, instead, we use it as a secondary test of whether or not a model is consistent with the data. We found evidence that caribou were using significantly larger polygons than randomly distributed points in nearly all grains tested, regardless of model or season (Fig. 5-5). An exception to this pattern was observed with summer seasonal locations and a patch only model. Here, we found significant evidence that caribou may be selecting smaller polygons than expected under this model, allowing us to conclude that this model is a poor fit to the data (Fig. 5-5, patch only, summer).

The *point* \overline{PA} for the two null hypotheses was closely aligned across spatial scales (results not shown), but the spread was not. Random points produced a much smaller

Figure 5-5. A secondary test of the three types of functional grain models in three seasons using a random points null hypothesis.

Significant functional grains ($P < 0.05$) indicate where caribou seasonal locations fit the functional grain better than sets of random points. Uncertainty in caribou perception of spatial heterogeneity is controlled by testing multiple functional grain sizes (levels of EPA). The fit of a functional grain to either the seasonal locations or random points at a given grain size is given by *point* \overline{PA} . Significance is declared where observed fits are greater than 95 of 100 random sets of points. In most cases, caribou are found in larger, more connected regions of a given functional grain than would be expected at random. This test is less informative as it does not indicate whether these larger polygons are larger than might be expected in a random tessellation of a similar grain size.

Figure 5-5. Cont'd.



null distribution leading to the declaration of more significant grains. However, the grains and models giving the largest deviations from random, and therefore the strongest support for a functional grain, were similar using both null hypotheses.

5.5. Discussion

Our results demonstrate that landscape connectivity can be modelled and tested as the response of an organism to a connected area of the landscape. In the functional grain approach that we have adopted, landscapes are divided into areas of high connectivity shaped by a combination of landscape structure and how the organism perceives that structure. We validated hypothetical functional grains using telemetry locations and found that caribou were responding to functional grain patterns in at least two of three behaviourally-defined seasons, by selecting larger, more connected, areas of the landscape than would be expected at random.

Despite the considerable attention that has been paid to landscape connectivity, there are relatively few examples where landscape connectivity hypotheses have been tested empirically (Galpern et al. 2011, Sawyer et al. 2011). Much of the validation work has been in landscape genetics where landscape connectivity is often modelled as a least-cost or circuit theory resistance distance and tested against genetic evidence of dispersal (Epps et al. 2007, McRae et al. 2008, Schwartz et al. 2009, Wasserman et al. 2010). The least-cost approach has also been applied to presence-absence and telemetry data (Beazley et al. 2005, Chetkiewicz and Boyce 2009, Cushman and Lewis 2010, Richard and Armstrong 2010), however in all cases the emphasis has been on understanding how a

reduction in landscape connectivity between points on the landscape can explain the observed data.

Patch-based landscape graphs have been used to turn the question around, and instead report evidence of connectivity as an association of organisms with highly connected regions. Patterns of presence-absence (Andersson and Bodin 2009, Awade et al. 2012), the abundance of organisms (Awade and Metzger 2008), and the distribution of telemetry locations (O'Brien et al. 2006) in association with components of connected patches have been used to validate these models. We have taken a similar approach, although instead of components of patches we have shown a response to components of Voronoi polygons. This important difference has allowed us represent more information about landscape structure than normally appears in a patch-based landscape graph. In particular, the landscape resistance surface (matrix), if included, not only influences which focal locations are connected at certain thresholds, it also affects the shapes of the polygons in the tessellation. Also, the use of regions rather than patches relaxes the assumption that the model organism will be found exclusively in one type of habitat. Patch habitat, if it is used in the model, becomes instead an anchor for landscape configuration (e.g. a feature for which proximity may be important).

To understand the influence of our modelling decisions, we explored the role of patch spatial configuration and landscape resistance in defining the shape of these polygons. A key finding was that functional grains based on only a patch model were generally poor predictors of the distribution of caribou; in other words, that the configuration of habitat

patches may not be influential for landscape connectivity. However, landscape configuration, as described by landscape resistance surface (matrix), appears to be an important influence for connectivity in our data. These results are supported by individual-based simulations of dispersal, which have shown landscape configuration defined using landscape resistance, rather than habitat area, has a significant effect on genetic differentiation (Cushman et al. 2012). For caribou, and possibly other mobile species with lower patch dependence, these observations underline the importance of using resistance surfaces, either on their own, or as part of a patch-based graph.

Modelling and testing of landscape connectivity at multiple spatial scales may be essential because using too coarse a spatial grain can miss important ecological correlates of the process (Sawyer et al. 2011). Equally, using too fine a spatial grain may reduce accuracy by incorporating landscape noise that is unimportant for connectivity (Anderson et al. 2010, Cushman and Landguth 2010, Galpern and Manseau 2012). Here, we adopted a multiscale approach, allowing uncertainty about the appropriate grain size, or its correlate, the maximum movement threshold, to have limited impact on our conclusions. In practice, this means that the conservation actions based on these results will also incorporate this uncertainty, as the true dimensions of the functional grain may be difficult or impossible to measure directly (Bunn et al. 2000). Although statistical significance generally remained constant across functional grain sizes, implying a degree of scale independence, the deviation from the random expectation did not, suggesting that a more sophisticated approach for model selection may be useful for narrowing the range of supported grain sizes.

The only clear evidence of spatial scale dependence in our results was found at the smallest grain size tested. Functional grains of this scale could not be distinguished from random functional grains (Fig. 5-4). Importantly, this implies that upscaling remotely-sensed landscape data to spatial grains that are many times larger may be appropriate for highly-mobile wildlife like caribou. We have drawn the same conclusion using genetic data for this study system, where we found evidence of landscape structure influencing gene flow at grains thousands of times coarser in area than the map data (Galpern et al. 2012). Overall, these parallels suggest that the grain of the process for landscape connectivity – or in our terms, the functional grain – is likely very coarse relative to map data for highly mobile species like caribou, and the possibility of bias introduced by including too much landscape heterogeneity should be investigated.

We also found evidence of a seasonal dependence in our results, suggesting that the dimensions of functional grain may be defined both in space and in time. The reasons for these differences may be landscape-related. For example, the resistance of features and how they are perceived by caribou may be dynamic, changing perhaps in synchrony with vegetation phenology, seasonal variation in highway traffic volume, or snow, water and ice conditions (e.g. Rettie and Messier 2000, Dyer et al. 2001, Brown et al. 2007, Polfus et al. 2011). As a result our landscape resistance model may be incorrectly optimized for the calving period, where we found the least evidence for a non-random distribution of caribou with respect to functional grain. Alternatively, it may be that functional grain or landscape connectivity in general is not important during this stage of life history.

Calving may be a time of year where females select habitat primarily to minimize predator exposure and improve access to high quality forage when calves are at heel (Rettie and Messier 2001). The females that we collared may be moving to predator-safe locations (e.g. islands) and traditional calving areas without regard to the configuration of the landscape.

Although our results support landscape resistance as an influence on landscape connectivity, we have not tested the implications of the parameters in this model. In our approach, the relative resistance values of landscape features affects the shape of the Voronoi polygons, and the magnitude of these parameters affects which parts of the landscape are connected at a given scale (Fig. 5-1, g, h, k l). In other applications of resistance surfaces, incorrect parameterization of landscape features has been noted to strongly influence conclusions, and sensitivity analyses have been proposed to address this (Sawyer et al. 2011). However, we have shown elsewhere that multiscale analysis can compensate for this sensitivity, in part, because differently parameterized models can produce identical conclusions when they are examined at a range of scales (Galpern et al. 2012).

Highways and major forestry roads received the highest resistance value in our matrix model (Table 5-1), implying that they have an important role in structuring the shapes and the sizes of the polygons in the functional grain. Our results indicated that caribou may be selecting larger regions than would be expected at random, where the pattern of roads on the landscape is at least partly responsible for defining the size of these regions.

Roads also appear to play a role in the genetic differences among caribou on this landscape (Galpern et al. 2012), and we find it plausible that they should also influence animal movement and dispersal at the shorter temporal extents that can be discerned from telemetry data. Avoidance of roads and other anthropogenic activities has been widely demonstrated in caribou and other ungulates (Dyer et al. 2001, Polfus et al. 2011), supporting the high resistance value assigned to these features.

Finally, we introduced a new approach to scaling landscapes and identifying functional grains that borrows from patch-based graphs. Lattice GOC is a variant of grains of connectivity where identifying an appropriate patch type in the model is not necessary, and instead functional grains are identified based only on patterns in the resistance surface. Patches are an influential parameter in a patch-based graph or GOC model and their replacement with a systematically positioned lattice of focal points both simplifies models and reduces uncertainty associated with focal patch identification. Patches can still be represented in the model as lower resistance features; as can be seen in both heuristic (Fig. 5-1, h, l) and real landscapes (Fig. 5-3, a, b, c) patches still influence the shape of the functional grain, but to a lesser extent. A valuable contribution of this form of spatial scaling, over alternatives such as areal scaling using cell aggregation or moving windows (Cushman and Landguth 2010), is that much larger spatial grain sizes can be achieved without obscuring features that may be functionally important to caribou (Galpern and Manseau 2012). Lattice GOC, because it requires only a landscape resistance surface as input, is a straightforward way to perform spatial scaling that may be particularly useful for landscape genetic studies, where resistance surface models have

been favoured for testing connectivity across broad extents of time and space (e.g. Epps et al. 2007, Schwartz et al. 2009).

5.6. Conclusion

We modelled hypothetical functional grains that give spatially-explicit descriptions of how caribou may perceive landscape heterogeneity, and asked if animals were responding to these patterns by selecting larger, more connected areas within the pattern. When a model of landscape resistance, approximating the fitness costs of dispersal, was used to define the functional grain pattern, we found evidence of non-random distribution of caribou. However, describing landscape connectivity as only the spatial configuration of patches produced functional grains with similar fits to the data as random patterns, underlining the influence of the landscape outside patches for connectivity. We also found that support for functional grains in caribou appears to be a seasonal phenomenon, and that regions of high connectivity may have large areas with respect to the grain of remotely-sensed landscape data. Describing hypothetical functional grains using a grains of connectivity approach provides an alternative way to model landscape connectivity that may be particularly useful for highly mobile organisms like caribou. A key advantage is the flexibility to scale landscape heterogeneity and the response of organisms to that heterogeneity in order to better match landscape pattern and evidence of the process.

5.7. Author contributions

Both authors were involved in the conceptual development of this paper. P. G. conducted analyses and wrote the manuscript. M. M. contributed landscape and telemetry data, and commented on several versions of the manuscript.

5.8. References

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CONCLUSION

6.1. A continuous and scalable approach

This thesis has been concerned with identifying the landscape structure that influences movement and dispersal in order to produce functional connectivity assessments of landscapes. I have hypothesized that, for highly-mobile mammals such as boreal woodland caribou, much of the spatial heterogeneity on a remotely-sensed map is essentially noise that may not affect movement and dispersal. Interpreting evidence of connectivity or predicting future connectivity, then, may require simplification of landscape data to highlight the pattern in landscape structure that is influencing the process. The thesis presents a method for upscaling, and therefore for simplifying, the landscape data, intended to retain pattern that may be functionally important for connectivity.

Grains of connectivity begins with the observation that if animals are able to move and disperse over greater distances, more resources required by the animal may become accessible and, consequently, more of the landscape area becomes functionally-connected and available to them. As this functionally-connected region grows in size, the area of the landscape influencing movement and dispersal decreases in proportion. In the graph-theoretic terminology of Chapter 2: adding graph links creates larger components implying a more connected landscape, and having fewer isolated nodes means less of the landscape area is presenting resistance to connectivity.

This simple relationship can be used to let increases in a functional scalar (the maximum movement or dispersal threshold) coarsen the spatial grain of landscape data and, therefore, to simplify it in a way that reflects function. Achieving this duality between function and spatial grain requires understanding the landscape not as a series of discontinuous patches, but rather as a continuous tessellation, where each polygon in the tessellation describes a region of proximity.

Regions of proximity have been defined in this thesis using ecological variables in several different ways (see Chapter 5), but in all cases have relied on a generalization of the Voronoi tessellation proposed by Fall et al. (2007). These authors use this tessellation to make a type of landscape graph called the minimum planar graph (see Chapter 2), advantageous because the number of links in the graph grows linearly rather than exponentially as nodes are added. The Voronoi tessellation plays two separate roles in a grains of connectivity model: it defines the topology of the graph, and it offers the ability to represent connectivity relationships among a continuous set of ecologically-defined regions. It is this second use of the tessellation that makes grains of connectivity distinctive from other landscape graph or minimum planar graph applications. In two chapters I have adopted the term functional grain (*sensu* Baguette and Van Dyck 2007) to describe the ecological concept underlying this set of regions (Chapters 3 and 5).

All landscape graph methods have the flexibility to model at multiple scales, accommodating uncertainty about the maximum amount of movement and dispersal an animal can exhibit. In grains of connectivity, the relationship between the distance scalar

and spatial grain means that scaling has the added benefit of accommodating uncertainty about which elements of landscape structure are influencing connectivity. This property may be particularly important when a resistance surface is used to define the regions of proximity, making results less sensitive to the assignment of resistance parameters (see Chapters 3 and 4).

Typically, resistance surfaces and not landscape graphs have been used to represent continuous connectivity relationships for highly-mobile and wide-ranging species (e.g. Cushman et al. 2006, Schwartz et al. 2009). These models can also be scaled to coarsen spatial grain, and therefore to accommodate uncertainty about landscape structure (Anderson et al. 2010, Cushman and Landguth 2010), but this type of scaling is orthogonal in nature and less likely to reflect the influential pattern (see Chapter 3). Grains of connectivity, however, outperforms resistance surfaces in terms of accuracy (Chapter 3) and in reporting evidence of an effect of landscape connectivity on dispersal (Chapter 4), which may reflect its strength at highlighting the landscape structure that matters.

In summary, grains of connectivity offers a continuous and scalable approach to modelling landscape connectivity. The flexibility of the method may be useful for identifying the landscape pattern influencing connectivity in many species of conservation interest: it relaxes the patch dependency of landscape graphs while using the scalability of these models to accommodate uncertainty in functional parameters such as dispersal distances and the resistances of features.

In the remaining sections, I first frame the key findings of this thesis as a series of recommendations for natural resource management. Second, I discuss how grains of connectivity methods may be applied to a variety of management questions. Third, I review how several findings may be relevant for boreal woodland caribou research. Finally, I present future research directions.

6.2. Recommendations for natural resource management

The implicit goal in much of this thesis has been to improve the quality of connectivity model predictions for natural resource management. In this section, I review how the main conclusions can be applied by researchers and practitioners studying highly-mobile and wide-ranging terrestrial species.

6.2.1. Model landscape connectivity at multiple scales

Multiscale analysis may be essential for addressing uncertainty about the scales at which ecological processes operate (Wiens 1989, Levin 1992). Results from this thesis underline the importance of doing this when modelling landscape connectivity.

Significant evidence of a functional connectivity hypothesis explaining dispersal and subsequent gene flow was found at spatial grains that were orders of magnitude coarser than raster landscape data (Chapter 4). Equally, functional connectivity hypotheses did not significantly differ from random hypotheses for explaining the distribution of animals at the finest spatial grains tested (Chapter 5). Also, in both of these tests, evidence for connectivity shaping ecological processes was not uniformly strong or significant across

scales, suggesting that conducting analyses at a single scale that is mismatched with the connectivity process could lead to incorrect conclusions.

Applying this recommendation requires identifying a series of candidate spatial grain sizes, or alternatively maximum movement thresholds; at a minimum an upper and lower limit should be identified. Modelling a corridor to connect protected areas, a frequent application of landscape connectivity analysis (Chetkiewicz et al. 2006), could use the grains of connectivity graph (see Chapters 3 and 4) constructed at these scales to find a shortest path between the areas. The spread of corridor paths could be entered into the planning process for evaluation.

Identifying the types of landscape features that influence movement and dispersal, important both for parameterizing models to map functional connectivity and for developing management policy (Sawyer et al. 2011), will also benefit from a multiscale approach. In these cases, uncertainty about the importance of features for creating resistance (e.g. the parameter values on a resistance surface) may influence conclusions (e.g. Spear et al. 2010, Zeller et al. 2012). Chapters 3 and 4 offer evidence that differences in resistance parameterization can lead to comparable conclusions when examined at multiple scales. Because the limits of this effect require further exploration, a robust approach when drawing conclusions about features is to report and compare results across several contrasting scales.

6.2.2. Select a scaling method that is appropriate for the landscape data

Following recommendations by Anderson et al. (2010), researchers studying animals with home range sizes larger than the spatial grain of the landscape data should begin with the finest resolution data available and scale up. Grains of connectivity may be helpful for upscaling landscape data consisting of discrete features (e.g. landcover data) because it can retain features that are influential in a functional connectivity hypothesis (Chapters 3 and 4). Methods such as aggregation can also be used to reduce the grain size, but these are likely to obscure small features at coarse grains, such as roads and rivers, that may be influential out of proportion to their footprint (Chapters 3 and 4). In cases where the landscape features hypothesized to be most influential can be represented by one or more continuous variables (e.g. slope, temperature, primary productivity), scaling methods such as aggregation or moving windows may be preferable because of their orthogonality, and therefore, their parsimony.

6.2.3. Validate landscape connectivity models using a relevant temporal scale

Validation of the model input parameters, such as determining the maximum movement and dispersal threshold or confirming that resistance values for features represent their true fitness costs, may be challenging or impossible in natural systems (Bunn et al. 2000, Spear et al. 2010). An alternative, and the one favoured in this thesis, is to ask if the predictions of a functional connectivity hypothesis are supported by empirical evidence of movement and dispersal obtained from the same landscape.

Much work in landscape genetics is organized around this goal (e.g. Chapter 4; Cushman et al. 2006, Epps et al. 2007, Schwartz et al. 2009). The temporal extent of the empirical evidence is generational, with genetic relationships among animals representing the cumulative effects of dispersal over multiple generations. This may be the most informative temporal scale to assess when managing populations to ensure long-term persistence. Alternatively, when managing to ensure animals have seasonal access to a required resource, finer-scaled movement data may be more appropriate (e.g. Richard and Armstrong 2010).

Results in this thesis show that qualitatively, the pattern of influential features and the spatial scales at which they were significant, are comparable using movement data at two distinct temporal extents. For example, late winter telemetry points (Chapter 5) and genetic similarity data (Chapter 4) for a caribou population both indicated support for the same model at a similar range of grain sizes. While this observation suggests that testing models may not require attention to the temporal extent of the corroborating data, there was also evidence of the opposite. Telemetry points from the calving season did not, generally, support the model (Chapter 5).

A robust solution, then, is to ensure that the movement data used to test the model matches the question of management interest. If connectivity is being modelled to build a corridor, then it may best be validated using genetic data that can capture the long time frames over which the corridor is to be effective. Equally, when the goal is managing access to a resource required seasonally, or at one stage in life history, models could be

validated with direct evidence of individual movement, such as telemetry data (e.g. Chapter 5; Richard and Armstrong 2010).

6.2.4. Ask if a resource patch concept is meaningful

Before selecting a modelling strategy, researchers should consider if a resource patch concept is essential, a structuring influence, or largely irrelevant to the study system. Representing landscape connectivity using the spatial configuration of resource patches may be most meaningful for organisms that are restricted to, or dependent on, a certain habitat type (Urban and Keitt 2001, Urban et al. 2009). For others, including many highly-mobile and wide ranging terrestrial species, a resource selection paradigm may be more meaningful, where habitat is better understood as a probability surface (e.g. O'Brien et al. 2006, Koper and Manseau 2009). In these cases, the patch concept may still be relevant as an "anchor" habitat for which proximity is important. In woodland caribou, for example, the mature jack pine patches used as the focal habitat in grains of connectivity models (Chapters 4 and 5) may be used as shelter for predator avoidance (Brown et al. 2007), making these features an important structuring influence.

It is also possible that the spatial configuration of a particular resource is not meaningful at all for connectivity, and it is uniquely the pattern of resistance presented by landscape features that is influential for movement and dispersal. Lattice grains of connectivity may be useful in these cases; it replaces patches with a lattice of focal points, superimposed on a resistance surface at a finer grain than that expected to influence landscape connectivity (Chapter 5). This is a non-orthogonal and functional approach to

scaling resistance surfaces that theoretically can be used to replace any current application of these models.

6.3. Applications of grains of connectivity in a broad range of study systems

This thesis has focused on a landscape modelling method intended for terrestrial organisms that are highly-mobile; or more precisely, for organisms that: (1) have a home range area exceeding the grain area of available map data and (2) are likely to face resistance to movement created by landscape features occurring between regions of higher quality habitat. Many ungulates and carnivores of management interest fall into this category, for example. These specifications, however, are not restrictive, and there are other systems of interest where patch-based or lattice grains of connectivity may prove useful (see also Section 4.5.2).

Mammal or reptile species that might not be considered "highly-mobile" can have home range areas that exceed the grain of relevant land cover data (Turner et al. 1969, Harestad and Bunnell 1979, Christian and Waldschmidt 1984, Lindstedt et al. 1986). In these cases, the scalability of the patch-based grains of connectivity approach may prove advantageous for the same reasons as it does for highly-mobile species: it can be used to progressively remove variation on the land cover map that is potentially unimportant for movement and dispersal. For less mobile species, it is possible that raster-based resistance surface modelling will provide a good enough approximation given that the relevant grains may not be much larger in area than a raster cell. However, patch-based grains of connectivity allows researchers to explicitly model the patch relationships,

which may improve models for species with obligate relationships to particular sites or land cover types (e.g. lemurs; Bodin et al. 2006). In the same way, the potential for movement and dispersal of certain amphibian species could be modelled using wetlands or other water bodies as patches (e.g. Fortuna et al. 2006).

Plant species that rely on terrestrial animals for pollination or seed dispersal (e.g. Howe and Smallwood 1982, Carthew and Goldingay 1997) can also be modelled using grains of connectivity. Multiscale analyses provides a means of accommodating uncertainty both in the functional response of the pollinating or dispersing animal to landscape features and in which species are responsible. The potential for animal pollination from known source locations, for example, could be visualized using one or a series of grains, and the resulting maps used to assess risks for rare and endangered plants. The lattice approach may be helpful for plant species with environmental tolerances that are too narrow to be discernible using landscape-scale data, eliminating the need to identify patches inhabited by both the plant and animal species in question. Equally, assessing risks and mitigating the spread of pests and pathogens with terrestrial animal hosts can be approached in the same manner. Diseases of veterinary interest, such as bovine tuberculosis, chronic wasting disease and anthrax that can be spread by ungulates (Schmitt et al. 1997, Dragon et al. 1999, Habib et al. 2011), could be managed by mapping polygons in a lattice grain of connectivity where the risk of infection is highest, given known disease loci.

However, for species where connectivity is largely determined by an abiotic process (such as wind pollination or water dispersal of larvae) and for volant animals (such as

insects, birds and bats) grains of connectivity models may be misleading. In these cases other variants of landscape graphs that do not explicitly model the landscape surface outside the resource patch may be more suitable (see Chapter 2). Grains of connectivity, then, may be most useful where connectivity is a function of an animal behaviour influenced by the composition and configuration of landscape features outside the resource patch.

6.4. Boreal woodland caribou

The animals have been bystanders in this thesis, serving as a model system rather than as the objects of interest (Chapters 4 and 5). However, there is urgent need for empirical work to support the recent federal initiative, *Recovery Strategy for the Woodland Caribou, Boreal Population* (Environment Canada 2011). This document acknowledges the importance of connectivity among ranges, and proposes that certain populations should be prioritized for recovery because their geographic position serves as an essential link for the entire distribution of caribou. The grains of connectivity method could be applied at these broad extents to determine if landscape between the core areas of neighbouring ranges can provide a corridor. One approach may be to use a parameter set validated using genetic data (e.g. Chapter 4).

Chapters 4 and 5 presented evidence that highways and major forestry roads may be a structuring influence on movement and dispersal at two temporal extents. These observations do not imply that roads serve as barriers to movement, but rather as features that reduce the potential for movement and dispersal. Nor will all roads serve equally in

this way. The essence of grains of connectivity used to demonstrate these effects, is that a feature will influence movement and dispersal only when its position with respect to other features accumulates a total amount of resistance. Observations of caribou at roadsides (K. Whaley, personal communication) therefore should not immediately refute these conclusions. Replication of this study in other caribou landscapes, combined with the use of additional genetic markers to improve resolution of movement, is required to confirm the importance of linear features for caribou connectivity.

Finally, suggestive evidence that telemetry and genetic data can produce the same conclusions about landscape connectivity for caribou (Section 6.2.3) should be viewed cautiously. These results may reveal only that disturbances in this range have had a particularly strong impact: they have restricted movement at a seasonal as well as dispersal scales, and because of a small effective population size, the reduction in gene flow has produced a detectable genetic signal. Individual-based simulations (e.g. CDPOP; Landguth and Cushman 2010) may help to identify when movement data representing different temporal extents can be used interchangeably.

6.5. Future research directions

6.5.1. *Functional grain*

I have adopted the term *functional grain* to describe the scale-dependent pattern influencing functional connectivity (Chapters 3 and 5). The concept of functional grain was originally presented by Baguette and Van Dyck (2007) as follows:

When the landscape grain is smaller than the perceptual range of the individual, there is no real difference between movements within and between habitats; dispersal occurs as a by-product of routine, explorative movement. [...] Contrarily, if the grain of resources is larger than the perceptual range of the animal, dispersal bears larger costs for the individual: as searching time increased, predation or other mortality risks, and deferred costs become higher. According to this hypothesis, the spatial scale determining the functional landscape grain depends on the perceptual range of the individuals, which itself may vary according to landscape structure and configuration (pp. 1122-1123).

Here, functional grain can be understood as an interaction between the grain of the resources (or the landscape structure) and the perceptual range of an animal. A landscape can be understood to be connected for an animal when the perceptual range is coarser than the grain at which habitat is distributed. Equally, if the perceptual range is finer than the grain of habitat distribution, costly dispersal behaviour is required, meaning that landscape connectivity is effectively reduced (Baguette and Van Dyck 2007).

I have presented functional grain as the ecological pattern of interest when modelling landscape connectivity at multiple scales. Others have described this as the grain of the process (e.g. Cushman and Landguth 2010). In spatial terms, functional grain is a pattern of high connectivity areas, where the boundaries of these areas represent regions of lower connectivity (cell boundaries in a raster model, and the boundaries of Voronoi polygons in a grains of connectivity model). The functional grain concept also helps demonstrate how the goals of grains of connectivity and areal scaling methods (such as aggregation or moving windows) are aligned: both attempt to describe this pattern in different ways. In the first case, by modelling it directly, and in the second case by approximating it. Finally, another way to understand this pattern is as a set of ecological neighbourhoods

(Addicott et al. 1987). According to this concept, ecological neighbourhoods for an organism are defined by an ecological process, a time scale, and the organism's activity during this time.

Additional work is needed to articulate a more comprehensive definition of functional grain and demonstrate its properties. The idea may have heuristic value for connecting the concepts of scale, landscape pattern, and the ecological mechanisms that are responsible for landscape connectivity.

6.5.2. *Model selection*

The phenomenological approach, where functional connectivity models are proposed and tested against evidence of movement or dispersal, is unsatisfactory without some method to compare model fit. For testing genetic data, the available inferential methods are controversial and work in this area remains at the leading edge of research (Legendre and Fortin 2010, Guillot and Rousset 2011, Jaquiéry et al. 2011). A model selection procedure has been applied in some cases (e.g. Pavlacky et al. 2009, Garroway et al. 2011), but no single approach has emerged that combines a robust assessment of the role landscape resistance plays over and above geographic distance (e.g. IBD; Wright 1943) while enabling a comparison among models. One way forward may be to represent dispersal and subsequent gene flow, not as a genetic distance relationship, but as a spatial distribution of alleles. This change may allow analyses from spatial ecology that can be used with generalized linear modeling and model selection procedures (e.g. spatial eigenfunctions; Griffith and Peres-Neto 2006).

For telemetry data, model selection has been successfully used to differentiate among resistance surfaces using a case-control design where actual movement steps are compared to random ones (Richard and Armstrong 2010). With either type of data, however, the inclusion of scale as a model parameter will rapidly increase the number of models to be compared. The *a priori* selection of relevant scales to reduce the number tested will be important in this regard (Chapter 4).

6.5.3. Is modelling landscape connectivity important for natural resource management?

As a final caveat to this thesis, and as a matter for future research, the question of whether any of this matters is serious and relevant. For example, Hodgson et al. (2009) have argued that connectivity is strongly influenced by habitat area and quality, and that connectivity objectives can be achieved by managing for these properties instead of connectivity. Habitat area and quality may be easier to measure and conceptualize, and consequently simpler to manage than connectivity from both a policy and practical perspective. Simulations are one way to examine the relationships between habitat area, quality and connectivity. Exploring these at multiple spatial scales may be essential.

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A P P E N D I X A - 1

GRAINSCAPE: an R package for grains of connectivity and minimum planar graph analyses of landscape connectivity

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Abstract

Landscape connectivity modelling to understand the movement and dispersal of organisms has been done using raster resistance surfaces and landscape graph methods. Grains of connectivity (GOC) models combine elements of both approaches to produce a continuous and scalable tool that can be applied in a variety of study systems. The GRAINSCAPE package for R implements grains of connectivity analyses. It accepts raster-based resistance surfaces as input and returns raster, vector and graph-based data structures to represent connectivity at multiple scales. These outputs can be further analyzed in R or exported in other formats. Effective distances describing connectivity between geographic locations can be determined at multiple scales; such analyses can contribute to corridor identification, landscape genetics, as well as other connectivity assessments. Minimum planar graph (MPG; Fall et al. 2007) models of resource patches on landscapes can also be generated using the software. SELES software (Fall and Fall 2001) is distributed with the package, and is used to produce the MPG and perform a generalization of the Voronoi tessellation used in GOC models. Routines also depend on the SP, RASTER, RGEOS and IGRAPH packages which are automatically installed as required (Pebesma and Bivand 2005, Csardi and Nepusz 2006, Hijmans and van Etten 2011, Bivand and Rundel 2012). GRAINSCAPE is currently only available for Windows-based platforms, and can be downloaded from the R-Forge repository at <https://r-forge.r-project.org/projects/grainscape/>.

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APPENDIX A - 2

ALLELEMATCH: an R package for identifying unique multilocus genotypes where genotyping error and missing data may be present¹

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Abstract

We present ALLELEMATCH, an R package to automate the identification of unique multilocus genotypes in data sets where the number of individuals is unknown, and where genotyping error and missing data may be present. Such conditions commonly occur in noninvasive sampling protocols. Output from the software enables a comparison of unique genotypes and their matches, and facilitates the review of differences among profiles. The software has a variety of applications in molecular ecology, and may be valuable where a large number of samples must be processed, unique genotypes identified, and repeated observations made over space and time. We used simulations to assess the performance of ALLELEMATCH and found that it can reliably and accurately determine the correct number of unique genotypes ($\pm 3\%$) across a broad range of data set properties. We found that the software performs with highest accuracy when genotyping error is below 4%. The R package is available from the Comprehensive R Archive Network (<http://cran.r-project.org/>). Supplementary documentation and tutorials are provided.