

Algonquin to the Adirondacks (A2A): Using circuit theory to measure landscape connectivity

Laura Roch

A thesis

In the Department

of

Geography, Planning and Environment

Presented in Partial Fulfillment of the Requirements

For the Degree of

Masters of Science (Geography, Urban and Environmental Studies) at

Concordia University

Montreal, Quebec, Canada

February 2015

© Laura Roch, 2015

CONCORDIA UNIVERSITY
School of Graduate Studies

This is to certify that the thesis prepared

By: Laura Roch

Entitled: Algonquin to the Adirondacks (A2A): Using circuit theory to measure landscape connectivity

and submitted in partial fulfillment of the requirements for the degree of

Masters of Science (Geography, Urban & Environmental Studies)

complies with the regulations of the University and meets the accepted standards with respect to originality and quality.

Signed by the final examining committee:

Dr. Alan Nash Chair

Dr. Pascale Biron Examiner

Dr. Jean-Philippe Lessard Examiner

Dr. Jochen A.G. Jaeger Supervisor

Approved by _____
Chair of Department or Graduate Program Director

Dean of Faculty

Date

ABSTRACT

Algonquin to the Adirondacks (A2A):

Using circuit theory to measure landscape connectivity

Laura Roch

The A2A region (93,369 km²) is a diverse landscape with rich biodiversity; and the preservation and restoration of this least degraded north-south corridor east of Lake Superior is a growing concern because of increasing use of this land for agriculture, urbanization, and construction of major highways. Modelling landscape connectivity, which is defined as the degree to which the landscape promotes movement, is central for conservation planning because of its importance for population viability. Electrical circuit theory has recently been incorporated within connectivity models to predict movement patterns and identify important areas or corridors of connectivity. This study used circuit theory to analyse the degree of landscape connectivity within the region between Ontario's Algonquin Provincial Park and New York State's Adirondack Park and identified three important ecological corridors for the movement of wildlife species. Fishers (*Pekania pennanti*) were used as an umbrella species to map the movement of multiple species and was calibrated with live-trapping data and validated with telemetry data. Even with the variations in resolution and focal node placement (the areas between which connectivity is measured), these three main pathways were always present. However, with the additional resistance of roads, the connectivity maps drastically changed, disrupting and almost eliminating all three of these movement corridors. A road mitigation scenario analysis, comparing various mitigation measures for a portion of highway 401 in Ontario, showed that placing wildlife structures at points of highest current is the best method to increase connectivity in this landscape.

Acknowledgements

I would like to thank all those who responded to my emails, be it for data, suggestions or general guidance. Specifically, I would like to send loads of positive energy towards my supervisor Dr. Jochen Jaeger. Jochen has been a part of my academic career going on four years (having also supervised my honours in my undergrad). He has opened up my eyes to the world of landscape and road ecology and has fueled my passion and research into these fields. For that I will be forever grateful. A fury of appreciation must be passed onto Dr. Jeff Bowman, whom without I would be lost in the world of theories. Jeff having a wealth of experience has helped guide the direction of this current research. In addition, he has provided me with data from a range of sources, one source was from a previous master's student of his, Erin Koen, whom must be singled out and given many thanks for all her work and which I have gratefully incorporated within my own research. There are more indirect, though no less significant, help provided by my fellow lab mates (shout out to Juliette, Katrina and Samia), who have had to endure my random outbursts, protests and just plain weirdness. Trevor Smith, a fellow geography master's student, crazy person, and more importantly one of my best friends, has been by my side throughout this roller coaster ride of a masters, words cannot express how grateful I am to have you in my life. Huge thanks to FQRNT and NSERC for funding this research, without which I would have not been able to devote as much attention to my research as I did. To the A2A Collaborative, I hope this research helps in the advancement of your own goals and larger picture for the A2A region. I appreciate all the support you have provided me throughout my project. Last but not least, I would like to give all the rainbows, sunshine and cute puppies to my parents. They have always believed in me and without their support I would be quite lost. A simple thank you does not seem enough, but either way, thank you, I love you guys!

Contribution of Authors

Chapter 3: Co-Authors: Jochen A.G. Jaeger and Jeff Bowman

Table of Contents

List of Figures	vii
List of Tables	viii
List of Acronyms	xi
Chapter 1. Introduction	1
1.1 Landscape connectivity in the A2A region	1
1.2 Research objectives	3
Chapter 2. Literature review	5
2.1 Importance of landscape connectivity	5
2.2 Ecological corridors	7
2.3 Methods for measuring landscape connectivity	9
2.3.1 Landscape pattern indices	9
2.3.2 Individual-based movement models	9
2.3.3 Analytic measures of network connectivity	10
2.3.3.1 Graph theory	10
2.3.3.2 Least-cost theory	11
2.3.3.3 Circuit theory and Circuitscape	12
2.4 Examples of regional connectivity projects in North America	15
2.5 Framework for A2A: Looking at the larger picture	16
2.5.1 Great Lakes Conservation Blueprint for Terrestrial Biodiversity	16
2.5.2 Natural Heritage Systems	20
Chapter 3. Algonquin to Adirondacks (A2A): Using circuit theory to measure landscape connectivity	21
3.1 Introduction	23
3.1.1 What is landscape connectivity and why should decision-makers care?	23
3.1.2 Research objectives	24
3.2 Methods	25
3.2.1 The A2A study area	25

3.2.2 Fishers (<i>Pekania pennanti</i>) as focal species	26
3.2.3 Fisher trapping data	28
3.2.4 Land cover maps	28
3.2.5 Explanatory variables of habitat suitability	29
3.2.6 Habitat suitability modeling	30
3.2.7 Fisher habitat suitability map and validation of the resistance model	31
3.2.8 Connectivity modeling	32
3.3 Results	40
3.3.1 Explanatory variables	40
3.3.2 Habitat suitability modeling.....	40
3.3.3 Resistance scenario validation	42
3.3.4 Connectivity modeling	44
3.3.4.1 Cost surface, circuit outputs, and the influence of different resistance scenarios.....	44
3.3.4.2 Influence of focal node placement.....	48
3.3.4.3 Influence of resolution (square grid cells)	52
3.3.4.4 Influence of roads	54
3.4 Discussion	57
3.4.1 Connectivity maps	57
3.4.2 Influence of resolution and focal node placement	57
3.4.3 Effects of roads and their incorporation in the connectivity analysis	58
3.4.4 Wildlife corridors	60
3.5 Conclusion	62
Chapter 4. Mitigation Scenarios, Habitat Amount, and the Role of Public Participation ...	64
4.1 Road mitigation scenario analysis.....	64
4.1.1 Improving current practice of identifying locations for mitigation measures	64
4.1.2 Research questions and approach	64
4.1.3 Comparing mitigation measures using Circuitscape	65
4.2 Importance of connectivity vs. habitat amount	71

4.3 Issues with the implementation of ecological networks and the role of public participation.....	73
Chapter 5. General conclusions.....	74
5.1 Summary of findings.....	74
5.2 Management implications	75
References.....	77
Appendix.....	89

List of Figures

Figure 2.1: Location of Frontenac Axis (from Frontenac Arch Biosphere Reserve 2009)	20
Figure 3.1: Map of the Algonquin to Adirondacks region (from Ken Buchan 2014)	25
Figure 3.2: Cost surface of scenario R5 (without roads) with a 300 m resolution. Yellow areas represent lowest resistance (i.e. forested areas) and blue areas indicate the highest resistances (i.e. water and urban areas)	44
Figure 3.3: A comparison of the current in runs 6, 2, and 7 with the land cover data. These runs compare the differences between resistance surfaces (R4, R5 and R6). All maps show a 10,000 km ² tile within the A2A region. The urban area in the top left hand corner represents Ottawa. Twenty nodes were randomly placed at a distance of over 40 km around the boundary of A2A for all circuit map outputs. Letters B & C signify main high movement areas; A is not visible as it does not fall within this sub-region	45
Figure 3.4: Current in run 6 for scenario R4 using a resolution of 300 m and 20 random focal nodes. Letters signify main high movement areas	47
Figure 3.5: Current in run 7 for scenario R6 using a resolution of 300 m and 20 random focal nodes. Letters signify main high movement areas	48
Figure 3.6: Current in run 1 for scenario R5 using a resolution of 300 m and four linear focal regions. Current based on quantile classification. Letters signify main high movement areas	49
Figure 3.7: Current in run 2 for scenario R5 using a resolution of 300 m and 20 random focal nodes. Current based on quantile classification. Letters signify main high movement areas	49
Figure 3.8: Current in run 3 for scenario R5 using a resolution of 300 m and six focal nodes placed in each park. Current based on quantile classification from run 1. Letters signify main high movement areas	51
Figure 3.9: Current in run 4 for scenario R5 using a resolution of 300 m and the parks themselves as two focal regions. Current based on quantile classification from run 2. Letters signify main high movement areas	51
Figure 3.10: Comparison of the 150 m and 300 m resolutions for a small section (approx. 10,000 km ²) of the connectivity map	53
Figure 3.11: Comparison of the connectivity network with the additional impact of roads on scenario R5, with a resolution of 300 m and 20 randomly placed focal nodes around the A2A boundary. All maps show a 10,000 km ² tile within the A2A region. The urban area in the top	

left hand corner represents Ottawa. Letters B & C signify main high movement areas; A is not visible as it does not fall within this sub-region55

Figure 3.12: Current in run 10 for scenario R5 with the addition of road classes 1, 2 and 3 using a resolution of 300 m and 20 random focal nodes56

Figure 3.13: Comparing the southern-most corridor (A) with imagery provided by ESRI, in order to get a clearer picture of where and for what reasons high current areas still remain in this location even after the inclusion of all road types in the connectivity analysis.....61

Figure 4.1: Comparison of mitigation scenarios for a portion of the road scenario study area. The circles represent the locations of the wildlife structures. For the scenarios which have randomly placed wildlife structures, one run was selected here as an example output for comparison purposes.....68

Figure 4.2: Comparison of the effective resistances of the three configurations for the eight wildlife structures: evenly (E), at locations of highest current (HC), and randomly (R), to answer four research questions: (1) Does the spatial arrangement of the wildlife structures matter when there are no fences?, and (2) Does the spatial arrangement of the wildlife structures matter when the whole road is fenced. (3) Does the spatial arrangement of the wildlife structures matter when there is 1.5 km of fencing on either side of each wildlife structure?, and (4) Does the spatial arrangement of the wildlife structures matter when there is 600 m of fencing on either side of each wildlife structure? The dark bar in the middle of the box represents the median, the box represents the 25% and 75% quantiles, the dashed lines (whiskers) represent the 5% and 95% quantiles. The blue notched areas indicate 95% confidence intervals around the median71

List of Tables

Table 2.1: Common terms used in circuit theory, their definitions, and units. Adapted from McRae et al. (2008).....12

Table 2.2: Comparison of four regional connectivity projects from North America (examples).17

Table 3.1a: Estimates of various fisher movement parameters: home range size, dispersal distance and daily movement26

Table 3.1b: Justifications for selection or avoidance of various land cover types for fishers26

Table 3.2: Land cover classes in Ontario, Québec and United States land cover databases and their association to each of the aggregated land cover types used in this study (all have resolution of 30 m by 30 m). NoData includes the following classifications in the various datasets: NoData, unclassified, cloud, and shadow.....28

Table 3.3: Summary of various grid cell resolutions, their associated advantages and disadvantages, and the reasons for selecting two square grid cells (150 m by 150 m and 300 m by 300 m) for this connectivity analysis31

Table 3.4a: The resistances assigned to forest, water, wetland, urban areas and proximity to roads for six different scenarios. Description and justification for all scenarios is given in Tab. 3.4b. Scenarios R4, R5 and R6 are based on the model averaged coefficient values from the five top suitability models for fishers. R4 is the global model representing the most complex model, and R5 is representing the simplest and top ranked model, with R6, the second highest ranked model, falling between these two models. Resistances were calculated by the following equation, based on 100 being the maximum allowable resistance and 1 being the lowest:

$$R = \frac{100}{\frac{99}{TS_{max}} \times TS + 1}$$

(^a) The resistance for roads was added to the resistances of the land cover variables. This implies that resistance values could range from 1 to 225 (e.g. 100 for the resistance of PROP_URB + 80 for the resistance of high (1) + 40 for medium (2) + 5 for low (3) intensity roads (there are cases where all three roads intersect the same pixel), see Tab. 3.4b for road classification breakdown). See section 3.4.3 for more information on roads and how they were accounted for.....34

Table 3.4b: Overview of the various resistance scenarios, their associated advantages, disadvantages, and reasons for selection36

Table 3.5: The species, resistance values, methods, and resolutions used in other connectivity studies. (^a) We have grouped resistances into our five land cover classes in order to make

comparisons. This is not an extensive list of all their resistance values; additionally, there is some variation in resistances within these five classes due to how these studies have broken down their categories, i.e. this column provides a general breakdown.....37

Table 3.6: The scenario used, the resolution and the placement of focal nodes in each of the Circuitscape runs39

Table 3.7: Thirty-one candidate habitat suitability models of fishers (*Pekania pennanti*) for the A2A region, ranked with *AICc*, the difference from the top *AICc* model (Δ_i), and model weights (w_i), where K is the number of parameters in the model, N is the sample size and $-2LL$ is the -2 log-likelihood estimate to derive *AICc*. Highlighted in green are the five top models which were model-averaged to estimate the coefficients.....39

Table 3.8: Weighted parameter estimates (i.e. model averaging; Burham & Anderson 2002) for a composite model of fisher (*Pekania pennanti*) habitat suitability in the A2A region using the top five best ranked models, including standard error (SE), 95% confidence intervals, and importance value of the model average variable. The importance values were estimated by adding up the Akaike weights (w_i) of a particular parameter using all the models41

Table 3.9: Validation summary results comparing the amount of current (i.e. movement probabilities) from one sample t-tests for option 1 and for two sample t-tests for options 2A and 2B for both MCP and 95% kernel home ranges43

Table 3.10: Focal node placement, number of focal node pairs, cumulative effective resistance, and their associated effective resistance divided by the number of focal node pairs from the resulting connectivity map using scenario R549

Table 3.11: Size estimates and descriptions of the ecological road effect zone from various sources59

Table 4.1: Description of the mitigation scenarios and their associated effective resistances. The connectivity ranking ranges from 1 (best) to 25 (worst). Wildlife structures have a minimum distance of 300m from one another. The random placement was replicated 20 times, median and range are given.....66

List of Acronyms

A2A	Algonquin to the Adirondacks
AIC	Akaike Information Criterion
GI	Green Infrastructure
GLM	Generalized linear model
HR	Home range
LARCH	Landscape ecological Analysis and Rules for the Configuration of Habitat
MCP	Minimum convex polygons
PATH	Pathway Analysis Through Habitat
QUBS	Queens University Biological Station
SCML	South Coast Missing Linkages
TN	Trap night
TS	Trapping success
TVR	Trap-vaccinate-release
Y2Y	Yellowstone to Yukon

Chapter 1. Introduction

1.1 Landscape connectivity in the A2A region

Modelling landscape connectivity, which is defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993, p. 571), is central for conservation planning. It is generally agreed upon that the fragmentation of natural habitats is one of the most significant risks to the persistence of many species and that landscape connectivity increases population viability (Adriaensen et al. 2003; Beier & Noss 1998; Brown & Harris 2005; Dobson et al. 1999; Gilbert-Norton et al. 2010; Gustafsson & Hansson 1997; Hargrove et al. 2004; Laita et al. 2011; Saunders et al. 1991). For example, connectivity is important for gene flow, source-sink dynamics, metapopulation dynamics, and range expansion (McRae et al. 2008). Landscape connectivity is important for a wide range of ecological processes contributing towards the maintenance of biodiversity and long-term population persistence. With continued habitat loss and fragmentation, measuring and analysing landscape connectivity is becoming increasingly important.

The identification of functional ecological networks is the first step towards developing specific goals for enhancing connectivity between habitats and populations (Koen et al. 2010; McRae 2006). To identify functional networks, a specific species or group of species must be chosen; as connectivity is not just dependent on the features within the landscape (i.e. structural connectivity) but also on the movement ability and behaviour of a particular organism in response to various landscape features (i.e. functional connectivity), and is therefore, species and landscape specific (Adriaensen et al. 2003; Gustafsson & Hansson 1997; Taylor et al. 1993; Tischendorf & Fahrig 2000; Koen et al. 2012). In this study, fishers (*Pekania pennanti*) were chosen as the umbrella species to model movement probabilities. After the selection of a particular species, the mapping of their movement probabilities within the landscape can be performed by using a connectivity model.

Electrical circuit theory has recently been incorporated within connectivity models; it provides “the best-justified method to bridge landscape and genetic data, and holds much promise in ecology, evolution, and conservation planning” (McRae 2006, p. 19885). It has many distinct properties which are advantageous over other commonly used connectivity models (e.g. least-cost path and Euclidian distance) and is used to predict movement patterns and probabilities, generate connectivity measures, and identify important areas or elements of

connectivity (e.g. corridors or pinch points of connectivity) (Koen et al. 2012; Koen et al. 2010; McRae et al. 2008; McRae & Shah 2011).

Resistance is one of the main components of circuit theory and is defined as the opposition that a resistor imposes on the flow of current, where current is the flow of charge. For its application in ecology, a cost or resistance surface is a representation of a landscape's hindrance (or permeability) to animal movement or gene flow and is used to measure functional connectivity between focal nodes. Focal nodes are defined as points or regions between which connectivity is to be modelled. Current is used as a predictor of net movement probabilities; the greater the current, the higher the probability of movement in that area (i.e. high connectivity) (Koen et al. 2012; McRae et al. 2008).

The area around and between Algonquin Park and the Adirondack Park (approximately 93,369 km²) is the region of study for this landscape connectivity analysis. At the region's centre is the intersection of the southwest-northeast axis of the St. Lawrence River and the northwest-southeast axis of the Frontenac Axis. The Frontenac Axis is the least-degraded north-south corridor east of Lake Superior which cuts across the St. Lawrence River, and is situated at the northeastern limit of the deciduous forest, thereby providing an important biogeographical connection between Canada's Boreal forest and the Northern Temperate forest of the United States, and it provides an unique opportunity to protect and re-establish wildlife connectivity (Algonquin to Conservation Association 2012; Keddy 1995; Quinby et al. 1999). Although the Frontenac Axis is much less altered compared to the surrounding area (i.e. its wooded landscape is relatively intact), its function as an ecological linkage is increasingly being threatened by the growing amount of highways and urban development between Toronto, Ottawa and Montreal, and pollution of the St. Lawrence River and therefore, there is an urgent need for its protection (Algonquin to Conservation Association 2012; Quinby et al. 1999).

The Algonquin Provincial Park was created in 1893 and is Ontario's oldest and largest provincial park, with an area of 7,725 km². It is situated in south-central Ontario, within a section of the Canadian Shield between Ontario's Georgian Bay and the Ottawa River. Algonquin Park provides habitat for a wide range of species (34 native species of trees, 53 species of mammals, 272 species of birds, 31 species of reptiles and amphibians, 53 species of fish, 7000 species of insects and 1000 species of plants and fungi) (The Friends of Algonquin Park 2005).

The Adirondack Park situated in New York State was created in 1892 and is the largest publicly protected park in the United States, with an approximate area of 24,281 km², i.e. it is larger than Yellowstone, Everglades, Glacier, and Grand Canyon National Park combined. Almost half belongs to the people of New York and is protected to remain a “forever wild” forest preserve. The rest is private land consisting of farms, homes, timber lands and businesses. The Adirondack region has a wide range of habitats, such as some unique wetland types and old growth forests; and is home to 53 species of mammals and 35 species of amphibians and reptiles (Adirondack Ecological Center 2012; NYS Adirondack Park Agency 2003). In addition, the Adirondack Park has been suggested as a potential core habitat for wolf populations, and with a proposed A2A corridor, this region may have the potential to facilitate wolf recovery and to promote the movement of other species such as the lynx, marten and moose (Quinby et al. 1999).

It is therefore important that the ecological connectivity network between the A2A parks is mapped out, in order to identify areas which have potential high levels of movement and to identify priority conservation areas in order for effective management efforts towards maintaining a connected landscape to take place.

1.2 Research objectives

With the use of circuit theory, landscape connectivity can be mapped in a reliable and efficient way in order to identify areas which have high levels of movement, help identify priority areas for conservation, and to potentially establish the best placement of wildlife structures; e.g. pinch points (high movement areas). Therefore, transportation planners and road construction can integrate these structures into their plans, which is not currently being done systematically nor effectively. Therefore, the main research objective of this study was to analyse the degree of landscape connectivity between Ontario’s Algonquin Provincial Park and New York State’s Adirondack Park and to identify important ecological corridors for the movement of wildlife species within the area between these two parks. In addition to this main objective, there were methodological research questions revolving around (A) which cost surface is most appropriate to use, how (or if), (B) changing focal node placement and (C) resolution would impact the resulting connectivity maps and (D) how do roads influence connectivity in the A2A region (addressed in chapter 3). Once the connectivity network had been mapped, a scenario analysis was conducted on a section of highway 401, where various mitigation measures

were implemented and their impacts on connectivity compared, in an effort to see which mitigation measure is the most beneficial for augmenting connectivity (addressed in chapter 4).

Chapter 2. Literature Review

2.1 Importance of landscape connectivity

Fragmentation of natural areas has many detrimental effects on wildlife populations, such as declines in species abundance and diversity (Fahrig & Rytwinski 2009; Forman et al. 2003; Gilbert-Norton et al. 2010). It is widely agreed upon that landscape connectivity generally augments population viability and that the fragmentation of natural habitats is one of the most significant threats to the long-term persistence of many species (Adriaensen et al. 2003; Beier & Noss 1998; Brown & Harris 2005; Dobson et al. 1999; Gilbert-Norton et al. 2010; Gustafsson & Hansson 1997; Hargrove et al. 2004; Laita et al. 2011; Saunders et al. 1991). Habitat fragmentation impairs the movement of animals, genes, seeds, and pollen, as well as nutrient and energy flows between habitat patches and increases the probability of extinction due to the isolation of populations (Dobson et al. 1999; Rosenberg et al. 1997). Growing concern about habitat fragmentation has led to an increase in research on countering its effects and on developing appropriate measures and tools which will help predict, as well as, monitor various processes of landscape change and fragmentation (Adriaensen et al. 2003; Dobson et al. 1999; Saunders et al. 1991).

An analysis on the effects of roads and traffic on animal abundance and distribution (Fahrig & Rytwinski 2009) outlined four categories of species which respond negatively to roads: (1) species which are attracted to roads but are unable to avoid traffic, (2) species with large ranges of movement and low reproductive rates, (3) small animals who avoid roads and the surrounding habitat and (4) small animals that do not avoid roads and are unable to avoid traffic. Two categories of species exhibited positive responses to fragmentation caused by roads: (1) species that are attracted to roads for resources and are able to avoid traffic and (2) species who avoid roads but whose predators are negatively impacted by roads (Fahrig & Rytwinski 2009). To combat the negative effects of landscape fragmentation caused by transportation infrastructure on wildlife, measures to restore landscape connectivity can be developed, i.e. wildlife crossing structures in combination with fencing (fences aid in funnelling species towards safe passages and prevent them from crossing the road and therefore, reduces wildlife road mortalities) (Jaeger 2007).

Connectivity between habitats and (sub-) populations is essential for a variety of ecological processes such as: “gene flow, meta-population dynamics, demographic rescue, seed dispersal,

infectious disease spread, range expansion, exotic invasion, population persistence and maintenance of biodiversity” (McRae et al. 2008, p. 2712). Habitat connectivity helps in maintaining gene flow and promoting movement, dispersal and recolonization which all contribute towards increasing population size, and prolonging long-term population persistence (Hargrove et al. 2004; Kool et al. 2013). In addition, habitat connectivity helps increase the ability of species to adapt to climate change and natural disturbances; facilitating species to shift and extend their home ranges in search of new resources as their environment changes (Spencer et al. 2010).

Landscape connectivity is defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993, p. 571). Accordingly, connectivity does not just depend on the features within the landscape (i.e. structural connectivity) but also depends on the probability of movement and the behaviour of a particular organism in response to various landscape features (i.e. functional connectivity), and is therefore, species and landscape specific (Adriaensen et al. 2003; Gustafsson & Hansson 1997; Taylor et al. 1993; Tischendorf & Fahrig 2000). As movement is a central process needed for population persistence, landscape connectivity is considered an important measure of landscape structure in addition to landscape composition (i.e. types of habitat) and landscape configuration (i.e. distances between and spatial arrangement of patches) (Gilbert-Norton et al. 2010; Taylor et al. 1993).

There are many methods for measuring landscape connectivity, some of which will be discussed in section 2.4. The method I will be using in this study is the analytical connectivity model of circuit theory (section 2.3.3). Landscape connectivity can be studied as either a dependent or an independent variable (Goodwin 2003). When looking at landscape connectivity in terms of its relationship with landscape structure and movement behaviour, it should be treated as a dependent variable. However, when connectivity is studied in terms of its potential to impact various ecological processes then it should be treated as an independent variable. There are only a few studies which have treated landscape connectivity as a dependent variable and those that have often use modelling (Goodwin 2003). There is a growing demand for studying landscape connectivity as there are mounting concerns about the fragmentation of natural systems and an increasing need for developing adequate tools which evaluate landscape structure in terms of its effects on the ecological processes that depend on connectivity (Adriaensen et al. 2003; McRae et al. 2008; Saunders et al. 1991). This study on the A2A region used this approach

of modelling (using circuit theory) and therefore, landscape connectivity was viewed as a dependent variable.

2.2 Ecological corridors

Ecological corridors are pathways or links of habitat within the landscape matrix which connect two or more habitat patches (Beier & Noss 1998; Gilbert-Norton et al. 2010; Hargrove et al. 2004). Though there is a general consensus on the definition of corridors, there remains a disagreement about if and to what degree corridors act as a tool for conservation. Growing recognition of the importance of interpatch movement of species in the last decade has shifted the focus of conservation strategies onto the development of corridor networks (Goodwin 2003). There are three main types of movement: seasonal movements (migration), dispersal, and daily regular movements. Dispersal is defined as the movement of an organism leaving their birthplace in an effort to find their own adult home range, where they will breed and usually remain for the remainder of their lives. Daily movement consists of movements involved with foraging, feeding and nesting. Ecological corridors can help facilitate and promote all of these types of movement (Dobson et al. 1999).

The importance of ecological corridors for animal movement, population persistence and biodiversity, as well as its relevance for conservation and management efforts has been widely discussed in the literature, with the consensus that corridors aid in increasing connectivity and therefore, are an important tool for conservation and management practices (Beier & Noss 1998; Dobson et al. 1999; Gilbert-Norton et al. 2010; Hargrove et al. 2004; Hilty et al. 2006; Rosenberg et al. 1997). Other generally accepted benefits of corridors are “enhanced biotic movement, extra foraging areas, refuges during disturbances, and enhancement of the aesthetic appeal of the landscape” (Saunders et al. 1991, p. 23). In addition, the corridors themselves may act as additional habitat area for many species (Dobson et al. 1999; Gilbert-Norton et al. 2010; Saunders et al. 1991).

A meta-analysis conducted by Gilbert-Norton et al. (2010) revealed that “there was approximately 50% more movement between habitat patches connected by a corridor than between isolated habitat patches” (p. 665) and that out of 78 experiments analysed, 77% showed that corridors increase movement. However, the remaining studies showed that corridors were not as useful for increasing movement between habitat patches than if a species were to just

travel within the non-habitat matrix (i.e. no corridor present). Some possible explanations into why these corridors did not aid in facilitating movement are that the experiment could have misclassified what is actually habitat and non-habitat, the scale of the experiment could be wrong, in that the individual cannot even perceive the difference between corridors and non-habitat (i.e. scale too small, for example, many of these studies looked at insects, therefore, the possibility that the insect could even detect if a corridor was present could be a source of error), and the quality of the corridor itself may not have been great enough to distinguish it from non-habitat (Gilbert-Norton et al. 2010; Soga & Koike 2012).

There is some skepticism to this view that corridors are valuable and there are concerns to whether or not they actually provide connectivity (Beier & Noss 1998; Gustafsson & Hansson 1997; Simberloff et al. 1992). However, no study has empirically demonstrated negative consequences of corridors. Some proposed disadvantages of corridors are their potential of increasing the distribution of diseases, invasive species, and fires, increased predation, and the possibility of facilitating inbreeding (Saunders et al. 1991; Simberloff et al. 1992; Wydeven et al. 1998). Another criticism of corridors concerns their high monetary costs of establishing them (Simberloff et al. 1992). However, considering that all types of conservation projects are expensive, the justification of not supporting corridors based on their costs is not a unique argument against corridor development but just a general disadvantage of most conservation projects (Beier & Noss 1998).

Corridor development, their design and dimensions are another source of contention. Questions arise about the optimal or minimum width a corridor should have in order to enhance connectivity. Determining this optimal width of corridors may be the most important criterion of corridor quality and is therefore essential for conservation planners (Gilbert-Norton et al. 2010). Width would vary depending on the species the corridor is designed for, the scale, and the overall purpose of the corridor. Since there are different types of movement, the goal of enhancing a certain type or multiple types of movements would influence the dimension requirements of the corridor (Dobson et al. 1999).

Though evidence on the actual benefits of corridors is not fully established and continues to be questioned, much of the literature assessing the value of corridors still state that a connected landscape is more beneficial for biodiversity than a fragmented one, and that the approach of corridors should be adopted and an attempt should be made to develop and protect a corridor

network wherever possible (Beier & Noss 1998; Gilbert-Norton et al. 2010; Gustafsson & Hansson 1992; Saunders et al. 1991).

There are several ecological corridor network projects which have been created throughout the world. Some examples are the green belts in and around the four largest cities in the Netherlands (Harms & Knapen 1988), the protection of riverine forests in the Pantanal region of Brazil (Quigley & Crawshaw 1992), the California Essential Habitat Connectivity Project (Spencer et al. 2010, section 2.5), and the Yellowstone to Yukon Conservation Initiative (Y2Y) in North America (Yellowstone to Yukon Initiative 2004; section 2.5).

2.3 Methods for measuring landscape connectivity

There are many different types of landscape connectivity measures which range from measures that are based on distances or amount of habitat to those that are based on dispersal success or graph theory (Goodwin 2003). This section presents some of these approaches grouped into three categories: landscape pattern indices, individual-based movement models, and analytic measures of network connectivity (into which circuit theory falls) (McRae et al. 2008).

2.3.1 Landscape pattern indices

Some commonly used landscape pattern indices found in landscape ecology which have frequently been used to measure habitat connectivity are: “number of patches, patch area, core area, patch perimeter, nearest neighbor distance, contagion, perimeter-area ratio, shape index, and fractal dimension” (Schumaker 1996, p. 1213). Through the examination of these indices, it was found that all of these indices were weak predictors of habitat connectivity based on the product-moment correlation coefficients relating each landscape pattern index to dispersal success (Schumaker 1996). Through the investigation on the use and measurement of landscape connectivity, it has been established that a more reliable measure is needed to accurately analyse landscape connectivity (Tischendorf & Fahrig 2000).

2.3.2 Individual-based movement models

Another method for predicting landscape connectivity is individual-based movement models. An example is the Pathway Analysis Through Habitat (PATH) tool, which is used to predict the location of potential corridors between habitat patches. Some useful aspects of this tool are its

integration with random walk theory and its ability to show all potential connectivity paths (Hargrove et al. 2005) (these features are also present in circuit theory, see section 2.3.3).

The tool works as follows: walkers are set to start their journey in each patch of habitat in the landscape and are programmed with user-specific characteristics, enabling them to take on any species' movement behaviour. Once all walkers have been dispatched, the paths of walkers which have successfully dispersed, are inversely weighted by the energy used (this is supplied in the inputs of the land use layer, which specifies: preferences for each type of habitat, energy costs for movement, likelihood of finding food in each habitat and the likelihood of mortality in each habitat) and then added together so that their combined paths depict the pathways where most movement occurs (Hargrove et al. 2005). While the PATH tool has many advantageous characteristics for measuring connectivity, circuit theory also encompasses many of these same advantages (excluding for example, the likelihood of finding food in each habitat) but offers a more simplified approach with fewer inputs and computations, while being able to show the connectivity for the whole landscape (with PATH, not all pixels within the landscape will be given a value of connectivity).

2.3.3 Analytic measures of network connectivity

Network-based measures are being applied more frequently for analysing landscape connectivity as these methods have strong analytical and empirical support (Saura 2010).

2.3.3.1 Graph theory

Graphs are models which are used in various applications when analysing properties and functions of networks. Graphs are representations of landscapes as networks made up of groups (sets) of nodes. Nodes are points of connections which could represent habitat patches, natural areas (e.g. provincial parks) or cells within a raster grid (landscape) connected by edges or links, which are related to functional connections (such as dispersal) between nodes. The weight of each edge corresponds to the strength of that connection between those nodes (Laita et al. 2011; McRae et al. 2008; Saura 2010; Urban et al. 2009; Urban & Keitt 2000).

Graph theory has led to the development of various connectivity measures. Two examples which integrate the concepts of graph theory are least-cost and circuit theory models.

2.3.3.2 *Least-cost theory*

Least-cost models are widely used for designing ecological corridors (Beier et al. 2009). Least-cost models assign costs (or resistance or friction values) to each cell within a grid based on the degree of difficulty it takes to move through this cell. For example, generally, an urban cell would have a greater cost compared to a forest cell, as an urban cell is harder for an animal to cross through (i.e. low probability of movement) than a forest cell (these costs would vary depending on the species being studied). Once costs have been assigned for the entire grid, the best route between pairs of connecting cells are derived, and then a cost-weighted distance is calculated in order to measure the effective distance between these cells (Adriaensen et al. 2003; McRae 2006).

A major advantage of least-cost models compared to, for example, the popularly used Euclidean (shortest) distance to calculate patch connectivity, is that they incorporate not only the structure of the landscape but behavioural aspects as well. This represents a shift from structural to functional connectivity (circuit theory also looks at functional connectivity by using resistance distance (or effective resistance) between any two cells (or nodes) (McRae 2006)). With shortest distance, only structural measures (i.e. physical distance) are used and the characteristics of the landscape between the patches are not included, whereas with least-cost modelling, there are friction values being assigned to each cell within the landscape. This is important because how and to what degree landscape features influence movement is species and process specific (Adriaensen et al. 2003) and as indicated previously, movement is a central process to population persistence (Gilbert-Norton et al. 2010; Taylor et al. 1993).

The disadvantage of least-cost models is that they identify only one pathway between two points; therefore, alternative routes which could exist between them are not accounted for. Circuit theory addresses this issue as it calculates multiple movement pathways (McRae 2006).

A source of uncertainty with least-cost models comes from the selection of the factor weights for each of the landscape features within the model (e.g. road density, elevation, and land cover – what is the order of least to most detrimental to connectivity?) and the resistance values which are assigned to each of the classes within these features (i.e. what should the resistance values be for the land cover classes of forest or urban?) (Beier et al. 2009). This is also a concern with circuit theory, as resistance values are also needed (McRae et al. 2008). However, with an uncertainty analysis or sensitivity analysis, these issues can be better accounted for and

quantified, allowing for decision-makers to be aware of the impact of these uncertainties when making their decisions on conservation and management efforts (Beier et al. 2009).

Adriaensen et al. (2003) concluded that least-cost modelling is a useful, flexible tool for helping understand the relationships between landscape structure and movement. With this understanding, it may be possible to identify priority areas for mitigating conservation actions and predict the effect of various landscape changes on connectivity. Even though there are limitations to least-cost models, they offer much potential for connectivity studies.

2.3.3.3 *Circuit theory and Circuitscape*

Circuitscape (the tool which I applied in my research) is an open-source program that uses circuit theory to predict processes such as gene flow and movement in heterogeneous landscapes. Recently, concepts and algorithms from circuit theory have been adapted to address the problems of measuring ecological connectivity across landscapes (McRae 2006; McRae et al. 2008; Shah & McRae 2008). Circuitscape converts the landscape into a graph, with every cell in the landscape being expressed as a node on the graph (Tab. 2.1). The connections between these cells are called edges, which are related to functional connections (i.e. the three main movement types). The strengths of these connections, referred to as edge weights, are functions of the per-cell conductance values, which are usually expressed as either the average resistance or average conductance of the two cells being connected. In summary, the landscape is represented as a conductive surface, where low resistances are given to more permeable habitats or land covers and high resistances are given to more impermeable habitats (McRae & Shah 2011; McRae et al. 2008; Shah & Beier 2008).

Table 2.1: Common terms used in circuit theory, their definitions, and units. Adapted from McRae et al. (2008).

Term	Units	Definition
Resistance	Ohm	The opposition of a habitat type (or land cover) to movement of a particular organism. The higher the resistance, the greater the difficulty of movement.
Conductance	Siemens	The inverse of resistance, therefore relates to permeability. The higher the conductance, the more that cell (or habitat) facilitates movement.
Resistance distance (or effective resistance)	Ohm	Measures the isolation between two nodes. Incorporates multiple pathways, with the addition of more connections decreasing effective resistance. Therefore, taking into account the minimum movement cost and the number of alternative pathways between two nodes.

Effective conductance	Siemens	Measures connectivity between two nodes. Effective conductance increases as alternative connections between two points are created.
Current	Ampere	Measures the net probability of movement of random walkers, thereby enabling one to predict the areas which have high levels of movement.
Voltage	Volt	Measures the probability that a random walker leaving any location (pixel) will reach a given destination (i.e. the probability of successful dispersal).

As electricity within an electric network has properties of a random walk, resistance distance can be characterized as the probability of a random walker travelling through a network (Doyle & Snell 1984). Another beneficial component of resistance distance is that it provides a measure of isolation assuming a random walk; as random walkers have no prior knowledge of the landscape in which they are travelling (McRae 2006). This differs from least-cost distances where path choice is made under the assumption that an individual has complete knowledge of the landscape, thus resulting in only one pathway of potential movement (McRae et al. 2008).

Similarly, conductance can also be derived. Conductance is the inverse of resistance, in that it is related to the ease of movement or likelihood that a random walker will move through a particular cell (McRae et al. 2008). Voltage is the difference in electrical charge between two nodes in a circuit. In an ecological sense, this can be described as the potential a random walker leaving from any point will successfully arrive at a certain destination (i.e. dispersal success); the higher the voltage the greater the probability of success (McRae et al. 2008).

Once resistance (or conductance) is established for all land cover types, the flow of current through a node can be derived. Current is used to calculate the net flow or probability of movement of random walkers moving from node to node. Current density is used to predict the location of landscape corridors or “pinch points” (areas of high probability of movement or high current density) (McRae et al. 2008).

Circuit theory offers many advantages over other connectivity measures. Two advantages are its close relation to random walk theory and its ability to integrate multiple dispersal pathways (Kool et al. 2013; McRae & Shah 2011; McRae et al. 2008; McRae & Beier 2007). Random-walk theory can be used to predict movement patterns and probabilities of successful dispersal or mortality of random walkers moving across complex landscapes, to generate measures of connectivity of habitat patches, populations, or protected areas, and to identify important connective elements (e.g. corridors) for conservation planning (McRae et al. 2008). Using random walkers to estimate landscape resistance results in resistances to decrease with increasing

connectivity, increasing path width and path redundancy. These relationships make circuit theory very promising and beneficial for modeling individual movement and gene flow (Koen et al. 2010; McRae et al. 2008; McRae 2006).

Some research examples where circuit theory has been applied and verified based on empirical evidence from landscape, genetic, or movement data are available for: American martens (Koen et al. 2012), wolverines (McRae & Beier 2007), fishers (Garroway et al. 2011), lynx (Walpole et al. 2012), golden-headed lion tamarins (Zeigler et al. 2011), Eastern Yellowbelly Racer (Klug et al. 2011), jaguars (Rabinowitz & Zeller 2010), and big-leaf mahoganys (McRae & Beier 2007).

Some disadvantages with circuit theory revolve around how movement is simulated. As with all models, they are simplifications of reality. One such simplification is that movement is based on random walkers. This approach ignores many of the complex details of movement behaviour (Goodwin 2003). Random walkers are non-intelligent organisms, meaning they have no control of their destination, which is not realistic. Species may have previous knowledge of their surroundings or can pick up on environmental indicators which can help them reach suitable habitat. Therefore, their movement is not completely random and may actually be quite informed and more direct (Travis & French 2000).

A main concern, which also applies to least-cost models, surrounds the parameterization of resistance surfaces. Parameterization is a major challenge of developing cost surfaces as the true costs of movement are rarely known. It is difficult to assign resistance values to different landscape elements when the impact of biological functions such as survival, density, and reproduction on movement probabilities, are usually unknown. Ways to get around this lack of knowledge are to use field data (e.g. radio telemetry, point counts, mark-recapture studies), model optimization, or expert opinion (or a combination of the three) (Beier et al. 2009; Koen et al. 2012; Spear et al. 2010). Model optimization uses multiple cost surfaces to represent the same landscape element(s), and compares each cost surface statistically in order to gauge which of these cost surfaces generates the best fit with genetic data (Spear et al. 2010). The methods and assumptions used to create and validate the cost surface are essential to reliably map connectivity; therefore, it is important to be rigorous in one's selection of the most representative cost surface. There is no universal answer to how cost surfaces should be defined as it depends

on a study's objectives, biological and analytical assumptions, and methods used to parameterize the resistances (Beier et al. 2009; Koen et al. 2012; Spear et al. 2010).

Another concern with circuit theory revolves around the effect of the map boundaries (or study area). It is impossible to run circuit theory for all of Canada and the United States (due to computation limitations) in order to model the connectivity between two regions, therefore the researcher needs to set an area limit. However, this area selection creates artificial boundaries, in that, in reality these boundaries do not exist within the landscape, therefore, the boundaries themselves will artificially act as a barrier. Such boundaries limit the space available to random walkers, reducing the number of paths to each node (i.e. it could happen that important connections are missed entirely), thereby increasing perceived resistance. To remove these effects, especially if the extent of the habitat data is limited, a buffer can be applied around the whole study area (or in cases where more data is available, the reach of the study area should be extended). The buffer could be created by randomized habitat data, or favoured with higher quality habitat, or favoured with lower quality habitat. In all cases, the buffer introduced less bias than if no buffer was applied (buffers should only be used if the study would be influenced by map boundaries) (Koen et al. 2010).

Currently, studies using circuit theory have focused on the connectivity of smaller regions, but as landscape level management projects become more prominent, circuit theory should also be applied on larger scales in order to capture a more exhaustive ecological network of connections.

2.4 Examples of regional connectivity projects in North America

Landscape level ecosystem-based management projects are increasingly used for conservation efforts as protected areas are just not enough for fully conserving biodiversity and ecosystem functions. This type of management is identified in Canada's national biodiversity strategy (Vásárhelyi & Thomas, 2006). In addition, multiple regional-scale connectivity projects have been or are currently being implemented in North America. Four examples of such projects are the South Coast Missing Linkages (SCML) (Beier et al. 2005), the California Essential Habitat Connectivity Project (Spencer et al. 2010; this project compared their connectivity maps to the linkage designs derived from the SCML project, building upon the network of these identified linkages), Y2Y (Yellowstone to Yukon Initiative 2004), and A2A (Algonquin to Conservation

Association 2012). A comparison of these four projects, their goals, their importance, and their challenges can be found in Tab. 2.2.

To conserve ecological connectivity, regional connectivity maps need to be developed in order to help guide decision-makers and conservation planners. Seven basic steps towards developing regional connectivity maps were outlined by Beier et al. (2011): 1) state the goal of the map, 2) establish collaborations, 3) define the region, 4) delineate natural landscape blocks, 5) determine which pairs of blocks would benefit from connectivity, 6) depict connectivity areas, and 7) provide guidance to end users. Notwithstanding the variations between each regional project, it is important to establish a general framework or guidelines which can be followed for all projects, in order to facilitate the whole process from the conceptualization of the project to the development of the connectivity maps to implementation and management of these projects (Beier et al. 2011). It is also useful to learn from previous studies, to understand how they did or did not overcome obstacles.

2.5 Framework for A2A: Looking at the larger picture

2.5.1 Great Lakes Conservation Blueprint for Terrestrial Biodiversity

The Great Lakes ecoregion has the greatest biodiversity in Canada (Henson et al. 2005). The region has been important in forming the history and development of Canada, and it currently supports the core industrial economy of Canada, with many people's livelihoods relying on the social, economic and ecological health of the region (nearly one quarter of the Canadian population inhabits this region; Henson et al. 2005).

The Great Lakes span almost one third of the width of North America, cutting across many north-south running natural ecological corridors. Various anthropogenic factors such as growing populations and urban sprawl are further contributing to this barrier effect (Stephenson 2001). In the southern Great lakes area, there are multiple natural corridors present. One is the Frontenac Axis (Fig. 2.1), which links Ontario's Algonquin Provincial Park to New York State's Adirondack Park, extending across the St. Lawrence River in the Thousand Islands.

Table 2.2: Comparison of four regional connectivity projects from North America (examples).

Name of Project	Location	Year	Size	Goal	Importance	Challenges	Mapping Connectivity		Sources
							Method	Species	
Algonquin to the Adirondacks (A2A)	Across the St. Lawrence River in the Thousand Islands area using the Frontenac Axis to link the Algonquin Provincial Park in Ontario to the Adirondack State Park in New York State, a distance of approximately 270 km.	1995	93,369 km ²	A2A mission: "We provide leadership and facilitate collaboration among partners to restore, enhance and maintain ecological connectivity, ecosystem function and native biodiversity while respecting sustainable human land uses in the A2A region" (Algonquin to Adirondacks Conservation Association 2012).	<p>The Frontenac Axis is the most extensive, least degraded north-south corridor across the St. Lawrence River.</p> <p>Algonquin and the Adirondack parks are two of the largest protected parks in eastern North America.</p> <p>This region is part of the ancient eastern deciduous forest which is identified as one of the highly endangered ecosystems in North America.</p> <p>This region ranks second in Canada for biodiversity.</p>	<p>Dealing with the St. Lawrence River and highway barriers (e.g. HWY 401), two of the largest barriers to connectivity.</p> <p>Getting the support and involvement of private landowners (as much of the land in the proposed corridor is private property) and establishing a good transnational relationship between Ontario (Canada) and New York State (US).</p> <p>The lack of federal and New York State laws which have the capacity to potentially support the protected area network once established.</p>	<p>Habitat suitability and least-cost corridor analyses.</p> <p>This current study will use: Habitat suitability and circuit theory analyses.</p>	<p>Single umbrella species: eastern timber wolf.</p> <p>This current study will use a single umbrella species: fishers.</p>	<p>Algonquin to Conservation Association 2012; Brown & Harris 2005; Keddy 1995; Quinby et al. 1999; Stephenson 2001</p>

Name of Project	Location	Year	Size	Goal	Importance	Challenges	Mapping Connectivity		Sources
							Method	Species	
Yellowstone to Yukon (Y2Y)	Extending 3200 km along the Rocky Mountains from the Peel River in the Yukon Territories to the Wind River Range in Wyoming; Yellowstone National Park to the Peel River of Yukon Territory	1993	1.2 million km ²	"Combining science and stewardship, we seek to ensure that the world-renowned wilderness, wildlife, native plants and natural processes of the Yellowstone to Yukon region continue to function as an interconnected web of life, capable of supporting all of its natural and human communities, for now and for future generations" (Yellowstone to Yukon Conservation Initiative 2004).	One of the most intact assemblages of wildlife in the world. One of the largest scale conservation efforts ever undertaken in North America.	- Dealing with the Trans-Canada Highway, Canadian Pacific Railway and mining prospects near Braid Creek in northern British Columbia in and around Muskwa-Kechika wildlands. - Preserving cultural traditions. - Political boundaries and jurisdictions not operating at the same scale as ecological processes necessary to support wildlife populations.	Habitat models and conservation requirements of grizzly bears to identify eight priority areas that function as either core wildlife habitat or as key corridors connecting those areas. (Secondary focus is on birds and fish).	Unique umbrella approach using three large-scale landscape strategies: grizzly bears, twenty focal bird species, and native cutthroat and bull trout (as indicator species to measure the status of rivers in the Y2Y region).	Chadwick 2000; Yellowstone to Yukon Conservation Initiative 2004
South Coast Missing Linkages (SCML)	West of the Sonoran and Mohave Deserts and south of the Santa Ynez and Transverse Ranges, extends 320 km south into Baja California, Mexico.	2000	340,000 km ²	To conserve essential linkages and ecological integrity throughout the South Coast Ecoregion and "to provide one promising recipe for designing plans that conserve and restore connectivity in real landscapes" (Beier et al. 2005, p. 557).	California's most populated ecoregion. The most threatened hotspot of biodiversity in the USA, with over 400 species at risk.	Due to limitations of data and cultural and political differences, details on linkage designs for three linkages which cross into Baja California, Mexico were impossible to acquire.	Habitat suitability and least-cost corridor analyses.	A variety of focal species for each linkage were chosen (selected by experts in five workshops). A total of 109 species were identified in all 15 linkages.	Beier et al. 2005

Name of Project	Location	Year	Size	Goal	Importance	Challenges	Mapping Connectivity		Sources
							Method	Species	
California Essential Connectivity Project	The state of California	2010	424,000 km ²	To identify large remaining intact habitat patches and to model the linkages between them which need to be maintained, especially for serving as corridors for wildlife.	California is one of the 25 most important hotspots of biodiversity on Earth. A connectivity area network is important for maintaining native species and communities, and ecological processes throughout California.	Limited number and quality of datasets. Data sharing and access is critical for future studies. For example, some areas were omitted as they were on military bases.	Habitat suitability (based on an Ecological Condition Index) and least-cost corridor analyses.	Use of state-wide index of ecological integrity or “naturalness” as primary basis for developing land-cover costs. Reason: due to the high biogeographic variability within the state of California, no species or set of species would provide an adequate and unbiased representation of these costs.	Spencer et al. 2010

The distance between the parks is approximately 270 km, with the main section of the Frontenac Axis measuring 100 km long by 60 km wide (Stephenson 2001). The A2A project is a part of this larger effort to design a Great Lakes Conservation Blueprint for Terrestrial Biodiversity (Henson et al. 2005).

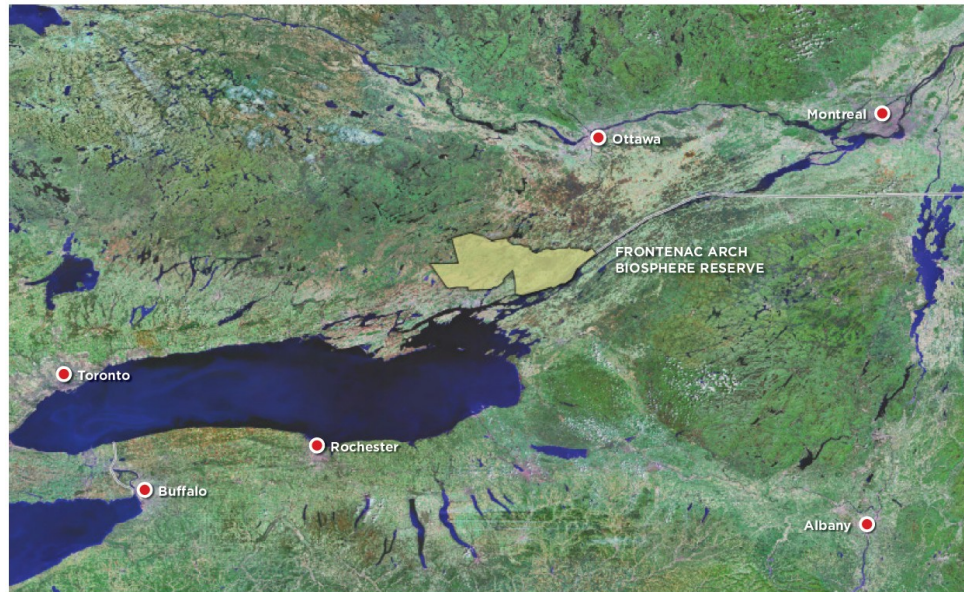


Figure 2.1: Location of Frontenac Axis (from Frontenac Arch Biosphere Reserve 2009)

2.5.2 *Natural Heritage Systems*

The Ontario Ministry of Natural Resources has recently advocated the concept of natural heritage system design and planning at the regional landscape level (Prince Edward County Working Group 2011). This system’s approach brings together science, technology and qualitative information while also engaging multiple stakeholders as decision-makers throughout the whole process (Prince Edward County Working Group 2011).

Natural heritage systems are networks composed of natural elements and areas. These natural areas provide a suite of ecosystem services such as habitat for wildlife, pollination, food and other production (e.g. medicines, biofuels), recreational opportunities, resiliency to environmental changes (Prince Edward County Working Group 2011). The overall A2A project aims at identifying and creating a natural heritage system for this region and to “restore, enhance, and maintain ecological connectivity, ecosystem function and native biodiversity, while respecting sustainable human land uses in the distinctive region of Ontario and New York State that lies between and embraces Algonquin and Adirondacks Parks” (Stephenson 2001, p.307).

Chapter 3. Algonquin to Adirondacks (A2A): Using circuit theory to measure landscape connectivity

I wrote this chapter with my supervisor Dr. Jochen A.G. Jaeger and one of my committee members Dr. Jeff Bowman. This manuscript has not yet been submitted for publication, but we plan on submitting to a peer-reviewed journal. As first author, I was responsible for the development of the research objectives, the spatial and statistical analyses and the writing of the manuscript. Dr. Jochen A.G. Jaeger helped in the development of the research objectives and overall direction of the research, and did manuscript revisions. Dr. Jeff Bowman was involved throughout the process, provided data (telemetry data from one of his previous masters student Erin Koen, and trapping data from the TVR program), helped with the statistical analyses and did manuscript revisions.

Abstract

The A2A region (93,369 km²) is a diverse landscape with rich biodiversity; and the conservation and restoration of this least degraded north-south corridor east of Lake Superior is a growing concern because of increasing use of this land for agriculture, urbanization, and construction of major highways and pollution of the St. Lawrence River. Modelling landscape connectivity is central for conservation planning. It is widely agreed upon that the fragmentation of natural habitats is one of the most significant threats to the persistence of many species. Electrical circuit theory has recently been incorporated within connectivity models to model movement patterns and identify important areas or corridors of connectivity. This study used circuit theory to analyse the degree of landscape connectivity within the area between Ontario's Algonquin Provincial Park and New York State's Adirondack Park and identified three important ecological corridors for the movement of wildlife species. Even with the variations in resolution and focal node placement (the areas between which connectivity is measured); these three main pathways were always present. However, with the additional resistance of roads, the connectivity maps drastically changed, disrupting and almost eliminating all three of these movement corridors. There is a need to restore and maintain connectivity in this region, focusing efforts on these three main pathways for movement. Wildlife structures are one solution which can alleviate the pressures the current road network has on connectivity. Future planning can use these maps as a tool to avoid areas of high movement and maintain their connectivity by selecting areas which will pose the least damage to this corridor network.

Keywords: landscape resistance, habitat suitability, trapping success, fishers, *Pekania pennanti*, functional ecological networks, movement, current

3.1 Introduction

3.1.1 *What is landscape connectivity and why should decision-makers care?*

Modelling landscape connectivity, which is defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993, p. 571), is central for conservation planning. The fragmentation of natural habitats is one of the most significant threats to the persistence of many wildlife populations and landscape connectivity generally augments population viability (Adriaensen et al. 2003; Beier & Noss 1998; Brown & Harris 2005; Dobson et al. 1999; Gilbert-Norton et al. 2010; Gustafsson & Hansson 1997; Hargrove et al. 2004; Laita et al. 2011; Saunders et al. 1991). For example, connectivity is important for gene flow, source-sink dynamics, metapopulation dynamics, range expansion, and adaptation to climate change (McRae et al. 2008).

The identification of functional ecological networks is the first step towards developing specific goals for enhancing connectivity between habitats and populations (Koen et al. 2010; McRae 2006). To be able to identify functional networks, a species or group of species must be chosen; as connectivity is not only dependent on the features within the landscape (i.e. structural connectivity) but also on the movement behaviour of a particular organism in response to various landscape features (i.e. functional connectivity), and is therefore, species and landscape specific (Adriaensen et al. 2003; Gustafsson & Hansson 1997; Taylor et al. 1993; Tischendorf & Fahrig 2000; Koen et al. 2012a, 2012b). A species’ movement probabilities within the landscape can be mapped by using a connectivity model.

Electrical circuit theory currently provides “the best-justified method to bridge landscape and genetic data, and holds much promise in ecology, evolution, and conservation planning” (McRae 2006, p. 19885). It has many advantages over other commonly used connectivity models (e.g. least-cost path and Euclidian distance) and is used to predict movement patterns and probabilities, generate connectivity measures, and identify important elements of connectivity (e.g. corridors and pinch points of connectivity) (Koen et al. 2012a; Koen et al. 2010; McRae et al. 2008; McRae & Shah 2011).

One of its main components is resistance. Resistance is the opposition that a resistor poses on the flow of electric current (flow of charge). As the flow of current within an electric network has properties of a random walk, resistance distance can be characterized as the probability of a random walker travelling through a network (Doyle & Snell 1984). For its application in

ecology, resistance is framed as the hindrance of a land cover type to the movement or gene flow of a particular species. A cost or resistance surface is a representation of a landscape's opposition to animal movement and is used to measure functional connectivity between focal nodes. Focal nodes are defined as points or regions between which connectivity is to be modelled. The greater the current, the higher the probability of movement in that area; this would relate to a more connected location in the landscape (Koen et al. 2012a; McRae et al. 2008; McRae & Beier 2007). Landscape resistance can be based on habitat suitability indices, where high habitat suitability relates to a low resistance (Lapoint et al. 2013; Poor et al. 2012; Sawyer et al. 2011; Walpole et al. 2012; Zeller et al. 2012).

The Algonquin to Adirondacks (A2A) region has high biodiversity, and the Frontenac Axis is a central component in the maintenance of this least degraded north-south corridor east of Lake Superior, and is a critical link between Canada's Boreal Forest and the Northern Temperate Forest of the United States (Algonquin to Adirondacks Conservation Association 2012; Keddy 1995; Quinby et al. 1999). Landscape-level ecosystem-based management projects are increasingly used for conservation efforts as protected areas are just not enough for fully conserving biodiversity and ecosystem functions. Therefore, this type of management is identified in Canada's national biodiversity strategy (Vásárhelyi & Thomas, 2006). It is important that the ecological connectivity network in the A2A region is mapped in order to: identify areas which have high levels of movement, help identify a priority network of wildlife corridors for conservation, and to determine the best placement of wildlife structures; e.g. pinch points (high movement areas). Accordingly, transportation planners and road construction can integrate wildlife structures into their plans, which is currently not being done systematically nor effectively in North America.

3.1.2 Research objectives

The main objective of this study was to analyse the degree of landscape connectivity between Ontario's Algonquin Provincial Park and New York State's Adirondack Park and to identify important ecological corridors for the movement of wildlife species between these two parks. In addition, there were also methodological research questions:

- (A) What is the most appropriate resistance scenario to accurately map connectivity?
- (B) Where should focal nodes be placed for an analysis of the A2A region?

- (C) How does changing map resolution affect the resulting maps of connectivity?
- (D) How do roads influence connectivity in the A2A region?

3.2 Methods

3.2.1 The A2A study area

The area around and between Algonquin Park and the Adirondack Park (approximately 93,369 km², Fig 3.1) is the region of study for this landscape connectivity analysis. It is part of a larger long-term initiative which aims “to protect, restore, enhance and maintain ecological connectivity and ecosystem function for the conservation of native biological diversity and for the delivery of ecosystem services to sustain healthy people and a healthy economy for generations to come” (Algonquin to Adirondacks Conservation Association 2012, “Our Mission”, para.1). The idea of better linking the two parks ecologically across the Frontenac Axis emerged in the 1990s when conservationists conceptualized a connected and sustainable network of ecosystems framed by these two parks. The A2A region is a diverse landscape with rich biodiversity (Algonquin to Adirondacks Conservation Association 2012; Keddy 1995; Quinby et al. 1999); and its preservation and restoration is a growing concern because of increasing use of this land for agriculture and urbanization, and increasing threats from the construction of major highways and pollution of the St. Lawrence River (Keddy 1995).

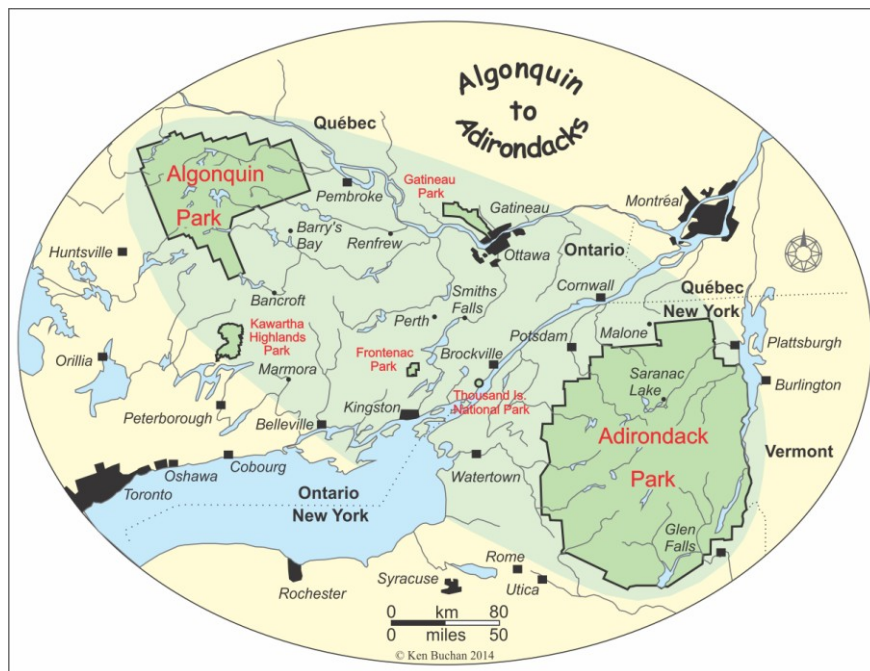


Figure 3.1: Map of the Algonquin to Adirondacks region (from Ken Buchan 2014)

3.2.2 Fishers (*Pekania pennanti*) as focal species

In this study, fishers (*Pekania pennanti*), medium-sized mustelids endemic to North America (Powell 1993; Powell et al. 2003; Tully 2006), were selected as our focal species because fishers are considered habitat generalists, habitat use by fishers has been well studied, and data are available for the A2A region (telemetry, gene flow, harvest data, anecdotal observations). While it is unfeasible to map out the connectivity for all species, fishers act as an umbrella species as they are generalist predators and have a wide range of habitat requirements (Bowman et al. 2006; Garroway et al. 2011; Tully 2006; Rohweder et al. 2012; Tab. 3.1a, b).

Table 3.1a: Estimates of various fisher movement parameters: home range size, dispersal distance and daily movement.

Home Range Size	Source
40 km ² (males), 15 km ² (females)	Powell & Zielinski (1994); Carroll et al. (2001)
34 km ² (males), 19 km ² (females)	Arthur et al. (1989)
Dispersal Distance	Source
10-100 km	Powell & Zielinski (1994)
4 km (males), 1.3 km (females)	Matthews et al. (2013)
29 km (males), 6 km (females)	Aubry & Raley (2006)
41.3 km (males), 16.7 km (females)	Weir & Corbould (2008)
25 km (males), 37 km (females)	York (1996)
17.3 km (males), 14.9 km (females)	Arthur et al. (1993)
Average 19.2±12.1 km ²	Kelley (1977), from Allen (1983) (in New Hampshire)
Daily Movement	Source
5-6 km	Kelly (1997); Arthur & Krohn (1991); Jones (1991)
Up to 5 km	Powell (1979), from Allen (1983)
Average of 2.5 km	Kelley (1977), from Allen (1983) (in New Hampshire)
General comments	
“Movements are mainly concentrated along drainages, ridgelines, and lake shores, while straight line movements are usually the result of cross-country excursions.”	deVos (1951), from Allen (1983)

Table 3.1b: Justifications for selection or avoidance of various land cover types for fishers.

Justification	Sources
<i>Forest</i>	
“Dense coniferous and mixed coniferous/deciduous forests are the preferred habitat of the fisher”	Allen (1983)
Coniferous forests	Powell (1982), from Arthur et al. (1989)

Mature conifer and mixed conifer-deciduous forests	deVos (1952); Coulter 1966; Kelly (1977); Powell (1977), from Arthur et al. (1989)
Optimal fisher habitat includes a mixture of forest types	Arthur et al. (1989)
Fishers in Maine tolerated a fairly high degree of human activity (includes: low density housing, farms, roads, small clear cuts, gravel pits and intense trapping pressure). However, there was a lot of forested areas in the surroundings.	Arthur et al. (1989)
<i>Wetlands</i>	
In New Hampshire, fishers chose to inhabit wetland associated forests.	Allen (1983)
Forests interspersed with an evergreen wetland can provide high quality habitat for fishers.	Allen (1983)
Forested wetlands and swamps are mentioned as potential high use habitat based on questionnaire results filled out by Ontario trappers, indicating where fishers were most often seen.	Allen (1983); deVos (1952); Kelly (1977)
Scrub stands and wetlands were used infrequently during all seasons.	Arthur et al. (1989)
<i>Agricultural lands (open areas)</i>	
Absent from recently logged and burnt forest stands	Allen (1983); deVos (1951)
Avoidance of open areas	Allen (1983); Kelly (1977); deVos (1952); Raine (1983); Arthur et al. (1989)
<i>Water</i>	
It is not uncommon for fishers to swim significant distances. There is also anecdotal evidence of fishers swimming among the St. Lawrence Islands (OMNR unpublished data). It has been found that fishers have immigrated to Ontario across the St. Lawrence River from Adirondack, New York.	Carr (2007a)
There are accounts of fishers swimming a mile across a lake. In addition, fishers are often found swimming in rivers and lakes in the Adirondacks.	Seton (1929)
Rivers can act as barriers to fisher movement. However, Carr et al. (2007a) had found the opposite to be true (see above for details). This may be explained because the St. Lawrence River usually freezes during the winter which would aid in the fisher's ability to cross. Therefore, fast flowing rivers may be more likely limit movement of dispersers.	Garroway et al. (2011)

During the 1920s and 1930s, fishers had been extirpated from most of southern Ontario due to overharvesting, degradation and loss of habitat, climate change, and societal perspectives towards predator control. Starting in the 1990s through to today, fishers have recolonized much of their former range due to reintroduction initiatives, harvest regulations and regeneration of forests, with populations in Ontario continuing to expand. Potential sources for this fisher recolonization include remnant populations found in Algonquin Park and Adirondack Park, with genetic support supporting that Adirondack fisher population has recently expanded into Ontario

from New York (Carr et al. 2007a, 2007b; Garroway et al. 2011; Koen et al. 2010; Koen et al. 2007a, 2007b; Lancaster et al. 2008; Tully 2006).

3.2.3 Fisher trapping data

The dataset used to develop the model of fisher habitat suitability (based on live-trapping success (TS)) and the cost surface for the connectivity model, is from an extensive live-trapping program (trap-vaccinate-release (TVR)) that took place from 1995 to 2006 (inclusive), data we report on is up to 2004), between June and October. Trapping was conducted for 448,654 trap nights (Bowman et al. 2006), with the main goal of vaccinating potential carriers of raccoon rabies in order to prevent the spread of rabies in Ontario (Rosatte et al. 1992, 2001). This dataset is available over a 950 km² study area bordered by the St. Lawrence River to the south, the latitude 45°00'N to the north and the longitude 75°15'W to the east and the longitude 76°00'W to the west (Tully 2006). The trapping areas were created by dividing the 950 km² study area into cells which averaged 12 km² in size. The trapping protocol involved setting up 100 Tomahawk model 106 and 108 live traps per night per cell, which were baited with sardines, and checked daily for captures. Captured fishers were released unmarked during the start-up of the program, however, they were marked during the later years (starting from 1999) of the study. The Ontario Ministry of Natural Resources Animal Care Committee approved all animal handling procedures (Bowman et al. 2006). As not all trapping cells were used for trapping each year, we used an annual average of captures per 100 trap nights (TN) as a measure of fisher habitat suitability.

3.2.4 Land cover maps

We used three land cover datasets: the Provincial land cover database for Ontario (OMNR 2000), the National land cover database for New York State (U.S. Geological Survey 2001) and Geobase for Québec (Government of Canada et al. 2000) in ArcGIS 10.1 (ESRI 2012) for habitat suitability modeling. Land cover types were aggregated into forest, wetlands, agricultural fields (including barren, shrubland, grassland and pasture land covers), urban, and water (Tab. 3.2).

Table 3.2: Land cover classes in Ontario, Québec and United States, land cover databases, and their association to each of the aggregated land cover types used in this study (all have resolution

of 30 m by 30 m). NoData includes the following classifications in the various datasets: NoData, unclassified, cloud, and shadow.

Land cover classes used in this study	Provincial land cover database (Ontario)	National land cover database (US)	Geobase land cover (Québec)
Forest	Dense deciduous forest, Dense coniferous forest, Coniferous plantation, Mixed forest mainly deciduous, Mixed forest mainly coniferous, Sparse coniferous forest, Sparse deciduous forest	Deciduous forest, Evergreen forest, Mixed forest	Forest/tree classes, Coniferous forest, Coniferous dense, Coniferous open, Coniferous sparse, Deciduous forest, Broadleaf dense, Broadleaf open, Broadleaf sparse, Mixed forest, Mixedwood dense, Mixedwood open, Mixedwood sparse
Wetlands	Coastal mudflats, Intertidal marsh, Supertidal marsh, Freshwater/Inland marsh, Deciduous swamp, Coniferous swamp, Open fen, Treed fen, Open bog, Treed bog	Woody wetlands, Emergent herbaceous wetlands	Wetland, Wetland-treed, Wetland-shrub, Wetland-herb
Agricultural land (includes other open areas such as: shrubland, grassland, pasture and barren lands)	Tundra heath, Recent cutovers, Recent burns, Old cuts and burns, Mine tailings/Quarries/Bedrock outcrops, Pasture and abandoned fields, Cropland, Alvar	Perennial Ice/Snow, Barren Land (Rock, Sand, Clay), Dwarf shrub, Shrub/Scrub, Grassland/Herbaceous, Sedge/Herbaceous, Lichens, Moss, Pasture/Hay, Cultivated crops	Barren/non-vegetated, Snow/ice, Rock/rubble, Exposed land, Sparsely vegetated bedrock, Sparsely vegetated till-colluvium, Bare soil with cryptogam crust-frost boils, Bryoids, Shrubland, Shrub tall, Shrub low, Prostrate dwarf shrub, Herb, Tussock graminoid tundra, Wet sedge, Moist to dry non tussock graminoid/dwarf shrub tundra, Dry graminoid, prostrate dwarf shrub tundra, Grassland, Cultivated agricultural land, Annual cropland, Perennial cropland and pasture
Water	Water	Open water	Water
Urban	Settlement and developed land	Developed (Open space), Developed (Low intensity), Developed (Medium intensity), Developed (High intensity)	Developed

3.2.5 Explanatory variables of habitat suitability

We measured six explanatory variables to develop additive models of habitat suitability for fishers and to infer movement within a landscape (Walpole et al. 2012). Five variables, (1) proportion of forest, (2) proportion of wetlands, (3) proportion of agricultural lands, (4) proportion of water, and (5) proportion of urban area were calculated within each of the trapping

cells. The sixth variable, proximity to roads (road classes 1, 2 and 3, see below Tab. 3.4b), calculated the Euclidean distance from the centroid of each trapping cell to the nearest road and was measured with Near in ArcGIS 10.1 Proximity toolset (ESRI 2012)¹. Roads are significant barriers to animal movement as they eliminate habitat and interrupt major travel corridors between habitat patches (Forman & Deblinger 2000; Forman et al. 2003). A correlation matrix was created to explore if any pairs of variables were highly correlated (one variable from any correlation greater than 0.70 would be removed from further analysis; Sheskin 2004).

3.2.6 Habitat suitability modeling

We developed 31 habitat suitability models for fishers using five of our six initial explanatory variables (proportion of agricultural land was removed, as it was highly negatively correlated with proportion of forest, $r = -0.818$, and forest is the main habitat for fishers).

To represent fisher habitat suitability, our response variable was mean *TS* of fishers per 100 TN, which was calculated by using the TVR trapping data:

$$TS_i = \frac{\text{Fishers trapped in year } i}{\# \text{ TN of year } i} \times 100 \quad (1a)$$

$$MEAN_{TS} = \sum_{i=\text{year } 1995}^{\text{year } 2004} TS_i \div \# \text{ of years fishers were trapped for a given trapping cell}$$

For model selection, we ranked each of the 31 models with Akaike's Information Criterion (*AIC*), corrected for small sample sizes (AIC_c , i.e. $n/K < \text{approximately } 40$, where n is the sample size and K is the number of parameters):

$$AIC_c = -2(\log - \text{likelihood}) + 2K + \frac{2K(K + 1)}{(n - K - 1)} \quad (2)$$

(Burnham & Anderson 2002; Mazerolle 2004).

The value of *AIC* favours models that have a high goodness of fit and a low number of parameters and was used to compare a series of models, where the model with the lowest *AIC* is considered the best model to approximate reality (Burnham & Anderson 2002; Mazerolle 2006; Mazerolle 2004).

¹ For a note on using road data from 2011, see Appendix 1.

Using the global model, we estimated the dispersion parameter (\hat{c}), which measures the deviance over the residual degrees of freedom, and found that $\hat{c} < 1$ for the global model, indicating no overdispersion. The top models were selected based on natural breaks in the relative importance values and delta AIC_c (i.e. when Δ_i was < 3 , where Δ_i is the measure of each model relative to the best model and is calculated by $\Delta_i = AIC_i - \min AIC$). Accordingly, we model-averaged the top five models to calculate weighted parameter estimates and weighted unconditional standard errors.

3.2.7 Fisher habitat suitability map and validation of the resistance model

We mapped habitat suitability of fishers based on the model-averaged coefficients from the best ranked models. We overlaid square grid cells of 300 m by 300 m and 150 m by 150 m over the study area and applied the weighted composite model to each cell to calculate habitat suitability for that cell (Tab. 3.3).

Table 3.3: Summary of various grid cell resolutions, their associated advantages and disadvantages, and the reasons for selecting two square grid cells (150 m by 150 m and 300 m by 300 m) for this connectivity analysis.

Resolution	Advantages	Disadvantages	Reason for Selection
30 m × 30 m	- Highest resolution (i.e. resolution of land cover data).	- Computational time is long. - Scale not large enough to contain multiple land cover types necessary for precise estimates of habitat suitability for fishers. - Have to break up the landscape into sections, in order to run Circuitscape.	Did not choose.
60 m × 60 m	- High resolution which therefore can capture fine connectivity details.	- Scale may not be large enough to contain multiple land cover types necessary for precise estimates of habitat suitability for fishers. - Have to break up the landscape into sections, in order to run Circuitscape. - Computational time is long.	Did not choose.
90 m × 90 m	- Can capture fine connectivity details. - Can capture roads without having to distort too much the actual width of the roads. - Contains multiple land cover types necessary for precise estimates of habitat suitability for fishers.	- Have to break up the landscape into sections, in order to run Circuitscape. - Computational time is long. - Fishnet tool which creates the grids cannot run for the entire landscape, exceeds memory capacity of 2GB.	Did not choose.
150 m × 150 m	- Contains multiple land cover types necessary for precise estimates of habitat suitability for fishers. - Has been used as a grid size by	- Hard to capture roads. Roads could be accounted for by taking the vector file and converting it to the raster; however, width could be exaggerated	- Has been used in a previous study. - A 50% increase in resolution from the

	Walpole et al. (2012).	as roads would be given a width of 150 m.	300 m pixel resolution for which can be run for the entire landscape. - Can run Circuitscape once for entire study area (no need to break up the landscape).
300 m × 300 m	- Can run for entire A2A region (i.e. no stitching required). - Contains multiple land cover types necessary for precise estimates of habitat suitability for fishers. -Computational time is the shortest compared to other resolutions. -Is approximately a tenth of the distance a fisher travels on a daily basis (approx. 1.5-3 km) and is much smaller than a fisher’s home range (sizes range depending upon location and gender).	- Hard to capture roads. Roads could be accounted for by taking the vector file and converting it to the raster; however, width could be exaggerated as roads would be given a width of 300 m. - Harder to capture fine connectivity details compared to higher resolutions.	- Have already calculated the proportions of land cover types in each pixel. - Can run Circuitscape once for entire study area (no need to break up the landscape).

We also used an additional dataset of fisher telemetry data from 61 fishers radio collared and tracked using ground and aerial telemetry in Leeds and Grenville County in eastern Ontario from February 2003 to January 2005 (Koen 2005), to test which resistance scenario (Tab. 3.4a, 3.4b) most accurately reflected fisher movements. This was done by comparing each scenario’s circuit outputs (using eight nodes at a map resolution of 150 m) with the calculated home ranges using both 95% minimum convex polygons (MCP) and 95% kernel estimates, of 30 of the 61 fishers (some individuals were removed due to mortality, or loss of radio transmissions, Koen et al. 2007a), using one sample and two sample t-tests in R. We expected that the current density from these resulting connectivity maps would be greater within the real home ranges than outside these areas. We applied three validation options and compared mean current density between real home ranges and (1) overall telemetry area (one sample t-test), (2) randomly generated home ranges, where random home ranges were constricted to areas where real home ranges were not located (two sample t-test), and (3) randomly generated home ranges, where randomly generated home ranges were able to occupy any area available in the overall telemetry area (two sample t-test).

3.2.8 Connectivity modeling

We assigned resistances to various land cover types based on the weighted composite fisher habitat suitability models, where resistances were calculated by:

$$R = \frac{X}{\frac{X_{max}-X_{min}}{TS_{max}} \times TS + 1} \quad (3)$$

where R is the resistance for each of the square grid cells, TS is trapping success, TS_{max} is maximum trapping success, X_{max} is the maximum resistance value corresponding to the lowest trapping success, and X_{min} is the minimum resistance value according to the highest trapping success. Any negative predicted TS values (e.g. for urban areas) were changed to zero, so that no negative resistances could result. The +1 in the denominator was added in order to prevent infinite resistance values when TS is zero. We used 100 as our X_{max} and 1 as our X_{min} . We wanted to capture a range of resistance scenarios to explore how changes in resistances influence the connectivity maps and which scenario was most supported by the fisher telemetry validation dataset (Tab. 3.4a and 3.4b). Tab. 3.4a shows the resistances of the six scenarios investigated. The first three scenarios (R1 - R3) are based on fisher's habitat requirements and preferences described in the literature. They are also based on the results from the habitat suitability models, using the hierarchy of the weighted composite coefficients from the top five ranked models and then I experimented with said order, due to variations in the literature on fisher habitat preferences. The last three scenarios (R4 - R6) are also based on the results from the habitat suitability models, where R4 represents the global model, R5 represents the top ranked model, and R6 the second highest ranked model. All six scenarios were compared for the situation (1) without roads, (2) with the addition of high impacting roads (r_1), (3) with high and medium impacting roads (r_12), and (4) with high, medium and low impacting roads (r_123). Further description and justification for all scenarios can be found in Tab. 3.4b. Resistances used in other studies are given in Tab. 3.5. Reasons for using a resistance surface can be found in Appendix 2. We modeled functional connectivity using circuit theory (McRae et al. 2008) in Circuitscape 3.5.8 (McRae & Shah 2008-09). Tab. 3.6 provides a description of the various runs (scenario, resolution, and focal node placement), using the eight neighbouring cell connection scheme and pairwise mode (iterates across all pairs of focal nodes).

Table 3.4a: The resistances assigned to forest, water, wetland, urban areas and proximity to roads for six different scenarios. Description and justification for all scenarios is given in Tab. 3.4b. Scenarios R4, R5 and R6 are based on the model averaged coefficient values from the five top suitability models for fishers. R4 is the global model representing the most complex model, and R5 is representing the simplest and top ranked model, with R6, the second highest ranked model, falling between these two models. Resistances were calculated by the following equation, based on 100 being the maximum allowable resistance and 1 being the lowest:

$$R = \frac{100}{\frac{99}{TS_{max}} \times TS + 1}$$

(^a) The resistance for roads was added to the resistances of the land cover variables. This implies that resistance values could range from 1 to 225 (e.g. 100 for the resistance of PROP_URB + 80 for the resistance of high (1) + 40 for medium (2) + 5 for low (3) intensity roads (there are cases where all three roads intersect the same pixel), see Tab. 3.4b for road classification breakdown). See section 3.4.3 for more information on roads and how they were accounted for.

Explanatory Variables	<i>Resistance scenarios without the integration of roads</i>					
	R1	R2	R3	R4	R5	R6
FOREST	1	1	1	Y = a + b ₁ *FOREST + b ₂ *URBAN + b ₃ *WATER + b ₄ *WETLANDS + b ₅ *PROXIMITY TO ROADS	Y = a + b ₁ *FOREST	Y = a + b ₁ *FOREST + b ₂ *URBAN
WATER	20	1.5	2			
WETLANDS	30	2	1.5			
URBAN	100	100	100			
	<i>Resistance scenarios with the integration of roads^a</i>					
High intensity roads	R1_r1	R2_r1	R3_r1	R4_r1	R5_r1	R6_r1
High + medium intensity roads	R1_r12	R2_r12	R3_r12	R4_r12	R5_r12	R6_r12
High + medium + low intensity roads	R1_r123	R2_r123	R3_r123	R4_r123	R5_r123	R6_r123

ROADS	<i>Additional resistances for roads</i>		
	High (1)	Medium (2)	Low (3)
	80	40	5

Table 3.4b: Overview of the various resistance scenarios, their advantages, disadvantages, and reasons for selection.

Scenarios	Description		Justification
R1	Will assign resistances for variables using the focal statistics tool using the neighbourhood operation of majority. This means that the greatest proportion of land cover within a grid cell will be given that corresponding resistance value.		The hierarchy of resistances is based on the model averaged coefficient values from the top five habitat suitability models for fishers. Resistances are framed between 1 for the most suitable habitat for fishers, i.e. forest, to the least suitable habitat, i.e. urban areas.
R2	Will assign resistances for variables using the focal statistics tool using the neighbourhood operation of majority. This means that the greatest proportion of land cover within a grid cell will be given that corresponding resistance value.		The hierarchy of resistances is based on the model averaged coefficient values from the top five habitat suitability models for fishers. Difference between this scenario and R1 is that resistances of water and wetlands are closer to that of forests. This is to emphasize that anthropogenic barriers are more detrimental to fisher movement than natural barriers.
R3	Will assign resistances for variables using the focal statistics tool using the neighbourhood operation of majority. This means that the greatest proportion of land cover within a grid cell will be given that corresponding resistance value.		The hierarchy of resistances is based on the model averaged coefficient values from the top five habitat suitability models for fishers, except for proportions of water and wetlands (the difference between this scenario and R2), where ordering is reversed based on literature that wetlands are suitable habitat for fishers (refer to Tab. 3.1b).
R4	Will assign resistances based on the model averaged coefficient values from the top five habitat suitability models for fishers for all explanatory variables.		To see the effect of the resulting connectivity map using the full habitat suitability equation ($Y = a + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$).
R5	Will assign resistances based on the model averaged coefficient values from the top five habitat suitability models for fishers for only the proportion of forest explanatory variable.		Proportion of forest is the only variable whose confidence intervals do not overlap zero, indicating that the variable was biologically meaningful (Walpole et al. 2012).
R6	Will assign resistances based on the model averaged coefficient values from the top five habitat suitability models for fishers for the proportion of forest and urban areas explanatory variables.		Proportion of forest and proportion of urban area have the highest importance values (see Tab. 3.6). In addition, this is based on the literature describing habitat suitability for fishers, where forests are their primary habitat and that fishers tend to avoid urban areas (refer to Tab. 3.1b).
Roads			
Intensity	Road type in New York (Tigerlines 2011)	Road type in Ontario & Quebec (Canvec 2011)	Justification
High (1)	Primary road (S1100), Secondary roads (S1200), Ramp (S1630), Road Median (S2000)	Freeway(1), Expressway/Highway (2), Arterial (3), Ramp (9)	Primary roads, usually multiple lanes, paved and with high traffic volume.
Medium (2)	Local neighbourhood road, rural road, city road (S1400), Service drive usually along a limited access highway (S1640)	Collector (4), Local Street (5), Local Strata (6), Local unknown (7), Service lane (12)	Secondary roads, usually paved and with lower traffic volume than high roads.

Low (3)	Vehicular trail (S1500), Alley (S1730), Private road for service vehicles (logging, oil fields, ranches) (S1740), Parking lot road (S1780),	Alleyway/lane (8), Resource/Recreation (10), Rapid transit (11)	Incorporates some non-paved roads as well as paved roads, but with low traffic volume.
Non-barrier	Bike path or trail (S1820), Walkway/Pedestrian trail (S1710), Stairway (S1720), Bridle path (1830)	Winter road (13)	Non paved and/or seasonal and/or non-vehicular traffic.

Table 3.5: The species, resistance values, methods, and resolutions used in other connectivity studies. ^(a) We have grouped resistances into our five land cover classes in order to make comparisons. This is not an extensive list of all their resistance values; additionally, there is some variation in resistances within these five classes due to how these studies have broken down their categories, i.e. this column provides a general breakdown.

Species	Resistances ^a	Method	Resolution	Focal Node Placement	Source
Fisher (also bobcat, mink and moose)	Ranged from 1 to 10 (highest). Forest: 1 Wetlands: 3 (Palustrine shrub wetland), 5 (Wetland forests), 10 (Palustrine and estuarine emergent wetland) Agricultural/ open areas:8-10 Water: 10 Urban: 10	Least cost path and circuit theory. Used habitat suitability models. For fishers, habitat suitability model was based on land cover alone.	5 m	Nodes as high quality suitability areas	Rohweder et al. (2012)
Mink	Ranged from 1 to 10 (highest). Forest: 4 Wetlands: 1 Agricultural/ open areas:6-8 Water: 1 Urban: 10	Least cost path and circuit theory. Used habitat suitability models. For fisher habitat suitability model was based on land cover alone.	5 m	Nodes as high quality suitability areas	Rohweder et al. (2012)
None, but instead used a measure of landscape structure: the hardness of barriers, the connectedness of natural cover, and the arrangement of land uses.	Ranged from 0 to 100 (highest). Forest: 10 Wetlands: 10 Agricultural/ open areas:10 (grassland), 50 (bare ground), 80 (cultivated crops) Water: 50 Urban: 100	Local connectedness and circuit theory	Local connectedness: 90 m Circuit theory: 270 m	Study area divided up in 53 tiles, used the edges of the buffered tiles as the ground and source (can imagine these as linear nodes).	Anderson et al. (2012)
Large forest-bound mammals	Ranged from 0 to 100 (highest). Forest: 1 Wetlands: 10 Agricultural/ open areas: 67 (cultivated crops), 88 (grassland), 88(bare ground) Water: 88 (peat bogs, salt marshes, inland marshes) Urban: 100	Least cost path and Linkage Mapper tool.	Landscape-level analysis: 1 km	Nodes based on the identification of the core habitats	EEA (2014)

Range of species	Ranged from 0 to 20 (highest). Forest: 0 Wetlands: 0 Agricultural/ open areas: 0 (grassland), 5 (bare ground), 15 (cultivated crops) Water: 20 Urban: 20	Least cost path	30 m Buffered roads 25m	A range in focal nodes depending on the specie being investigated (nodes were selected by using the core habitat areas. A total of 850 natural landscape blocks were found)	Spencer et al. (2010)
None, but is meant to be representative of a range of species.	Unnatural areas, impermeable: 1000 Unnatural, but permeable: 100 Natural: 10	Circuit theory	100 m	50 randomly placed nodes buffered (approx. $\geq 20\%$ of study area width) outside of study area	Koen et al. (2014)
Canada lynx	Used model coefficients as the resistances.	Circuit theory	150 m	Two linear nodes buffered (approx. 40 km) outside of study area	Walpole et al. (2012)
Marten	Did multiple iterations of cost surface parameterization. E.g. good habitat: 1, while poor habitat ranged from 2 up to 1024.	Circuit theory and least cost. Using habitat suitability to imply movement.	500 m	29 nodes (sites where genetic relatedness among populations of martens were sampled)	Koen et al. (2012)
Wolverine	Not disclosed in paper.	2-dimensional isolation by distance, least cost path, and circuit theory.	5 km	Replaced habitat cells by nodes	McRae & Beier (2007)

Table 3.6: The scenario used, the resolution and the placement of focal nodes in each of the Circuitscape runs.

Runs	Scenario	Resolution	Focal Node Placement
1	R5	300 m	Four linear bands of pixels (a band for each cardinal direction) positioned over 40 km from this boundary in order to avoid bias due to edge effects (Koen et al. 2010).
2	R5	300 m	Twenty randomly placed focal nodes at a buffer distance of 40 km along the

			boundary of the study area.
3	R5	300 m	Six focal nodes within each of the two parks.
4	R5	300 m	The parks themselves act as two focal regions.
5	R5	150 m	Twenty randomly placed focal nodes at a buffer distance of 40 km along the boundary of the study area.
6	R4	300 m	Twenty randomly placed focal nodes at a buffer distance of 40 km along the boundary of the study area.
7	R6	300 m	Twenty randomly placed focal nodes at a buffer distance of 40 km along the boundary of the study area.
8	R5 + roads (1)	300 m	Twenty randomly placed focal nodes at a buffer distance of 40 km along the boundary of the study area.
9	R5 + roads (1,2)	300 m	Twenty randomly placed focal nodes at a buffer distance of 40 km along the boundary of the study area.
10	R5 + roads (1,2,3)	300 m	Twenty randomly placed focal nodes at a buffer distance of 40 km along the boundary of the study area.

3.3 Results

3.3.1 Explanatory variables

For 93 trapping cells from the TVR dataset, the proportions of forest, wetlands, agricultural lands, urban areas, and water were calculated (in percentages); we also calculated the distances to the nearest road (km) for each cell (Appendix 3). Proportions were calculated by taking the amount of a particular land cover type in each trapping cell divided by the area of that cell.

3.3.2 Habitat suitability modeling

The habitat suitability models containing the variable proportion of forests best predicted fisher *TS* within the TVR study area (Tab. 3.7).

Table 3.7: Thirty-one candidate habitat suitability models of fishers (*Pekania pennanti*) for the A2A region, ranked with *AICc*, the difference from the top *AICc* model (Δ_i), and model weights (w_i), where K is the number of parameters in the model, N is the sample size and $-2LL$ is the -2 log-likelihood estimate to derive *AICc*. Highlighted in green are the five top models which were model-averaged to estimate the coefficients.

Model	Models for fisher habitat suitability	K	N	$-2LL$	$AICc$	Δ_i	w_i
2	PROP_FOR	3	93	-51.53	-130.73	0.00	0.23
28	PROP_URB + PROP_FOR	4	93	-51.95	-128.73	2.00	0.08
31	PROP_FOR + PROP_WET	4	93	-51.71	-128.62	2.11	0.08
18	PROP_WAT + PROP_FOR	4	93	-51.59	-128.57	2.16	0.08
25	PROX_ROAD_KM + PROP_FOR	4	93	-51.54	-128.55	2.18	0.08

1	PROP_URB	5	93	-43.95	-127.44	3.29	0.04
4	PROX_ROAD_KM	5	93	-43.53	-127.25	3.48	0.04
3	PROP_WET	5	93	-42.73	-126.91	3.82	0.03
5	PROP_WAT	5	93	-42.70	-126.89	3.84	0.03
29	PROP_URB + PROP_FOR + PROP_WET	5	93	-52.08	-126.55	4.18	0.03
15	PROP_WAT + PROP_URB + PROP_FOR	5	93	-52.06	-126.54	4.19	0.03
22	PROX_ROAD_KM + PROP_URB + PROP_FOR	6	93	-51.95	-126.49	4.24	0.03
19	PROP_WAT + PROP_FOR + PROP_WET	6	93	-51.72	-126.39	4.34	0.03
26	PROX_ROAD_KM + PROP_FOR + PROP_WET	6	93	-51.71	-126.39	4.34	0.03
11	PROP_WAT + PROX_ROAD_KM + PROP_FOR	6	93	-51.60	-126.34	4.39	0.03
21	PROX_ROAD_KM + PROP_URB	3	93	-44.56	-125.52	5.21	0.02
14	PROP_WAT + PROP_URB	3	93	-44.29	-125.40	5.33	0.02
30	PROP_URB + PROP_WET	7	93	-44.07	-125.31	5.42	0.02
6	PROP_WAT + PROX_ROAD_KM	4	93	-43.77	-125.17	5.56	0.01
27	PROX_ROAD_KM + PROP_WET	3	93	-43.59	-125.10	5.63	0.01
20	PROP_WAT + PROP_WET	4	93	-42.81	-124.76	5.97	0.01
16	PROP_WAT + PROP_URB + PROP_FOR + PROP_WET	3	93	-52.12	-124.28	6.45	0.01
24	PROX_ROAD_KM + PROP_URB + PROP_FOR + PROP_WET	4	93	-52.09	-124.27	6.46	0.01
8	PROP_WAT + PROX_ROAD_KM + PROP_URB + PROP_FOR	4	93	-52.06	-124.25	6.48	0.01
12	PROP_WAT + PROX_ROAD_KM + PROP_FOR + PROP_WET	4	93	-51.72	-124.11	6.63	0.01
7	PROP_WAT + PROX_ROAD_KM + PROP_URB	5	93	-44.94	-123.45	7.28	0.01
23	PROX_ROAD_KM + PROP_URB + PROP_WET	5	93	-44.60	-123.30	7.43	0.01
17	PROP_WAT + PROP_URB + PROP_WET	4	93	-44.31	-123.18	7.55	0.01
13	PROP_WAT + PROX_ROAD_KM + PROP_WET	5	93	-43.77	-122.94	7.79	0.00
9	PROP_WAT + PROX_ROAD_KM + PROP_URB + PROP_FOR + PROP_WET	5	93	-52.13	-121.94	8.79	0.00
10	PROP_WAT + PROX_ROAD_KM + PROP_URB + PROP_WET	6	93	-44.94	-121.16	9.57	0.00

The weighted composite model based on the top five models indicated that proportion of forests, proportion of water, proximity to roads, and proportion of wetlands had a positive relationship with habitat suitability for fishers. However, only the confidence interval of the estimate of proportion of forests did not overlap zero (Tab. 3.8); therefore the biological meaningfulness might be called into question for all other variables for which the confidence intervals overlapped zero (Mazerolle 2004).

Table 3.8: Weighted parameter estimates (i.e. model averaging; Burham & Anderson 2002) for a composite model of fisher (*Pekania pennanti*) habitat suitability in the A2A region using the top five best ranked models, including standard error (SE), 95% confidence intervals, and

importance value of the model average variable. The importance values were estimated by adding up the Akaike weights (w_i) of a particular parameter using all the models.

Parameter	Weighted Parameter Estimates	SE	95% Confidence Interval		Importance Value
			Upper	Lower	
<i>PROP_FOR</i>	0.3011	0.1013	0.4996	0.1025	0.7399
<i>PROP_WAT</i>	0.1679	0.7321	1.6029	-1.2671	0.2770
<i>PROX_ROAD</i>	0.0043	0.0521	0.1066	-0.0979	0.2855
<i>PROP_URB</i>	-0.1394	0.2182	0.2882	-0.5670	0.3058
<i>PROP_WET</i>	0.1012	0.2413	0.5742	-0.3717	0.2786
<i>Intercept</i>	0.0044	0.0466	0.0958	-0.0869	NA

3.3.3 Resistance scenario validation

Based on the results of the validation and the weighted composite models (Tab. 3.9), scenario R5 was selected as the main cost surface for the connectivity analysis of the A2A region (however, in terms of analysing the impact of cost surfaces on the connectivity in this region scenarios R4 and R6 were also compared). R5 was the simplest and top model from our habitat suitability modelling results (proportion of forest is the sole variable, and it is the only variable whose confidence intervals do not overlap zero). The validation results were quite similar when comparing the various scenarios when no roads were added (Tab. 3.9). Though R1 had the lowest p -value, all other scenarios were more or less in the same range, and all were supported by the telemetry data as valid resistance surfaces to measure connectivity (except when comparing the MCP home ranges, R2, R3 and R4 all failed at capturing fisher movement). An interesting observation is how dramatically the p -values responded to the addition of roads, with the support of these scenarios as valid resistance surfaces increasing significantly for r_1 and r_{123} . This demonstrates that roads play a major role in the movement of fishers in the landscape and are important to include in the connectivity analysis. The smaller p -values for the 95% kernel home ranges compared to the MCP home ranges indicate that they can be more precise in estimating home ranges (Seaman et al. 1999).

Table 3.9: Validation summary results comparing the amount of current (i.e. movement probabilities) from one sample t-tests for option 1 and for two sample t-tests for options 2 and 3 for both MCP and 95% kernel home ranges.

Scenario	Minimum Convex Polygon Home Range									95 % Kernel Home Range								
	Option1			Option2			Option3			Option1			Option2			Option3		
	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value	<i>t</i>	df
R1	2.770E-03	2.99	29	1.859E-02	2.49	29.14	1.907E-02	2.48	29.07	1.481E-04	4.11	29	1.933E-03	3.40	29.28	1.916E-03	3.41	29.12
R2	2.933E-02	1.96	29	1.020E-01	1.68	29.00	1.016E-01	1.69	29.00	2.695E-04	3.88	29	4.299E-03	3.09	29.05	4.235E-03	3.1	29.02
R3	3.581E-02	1.86	29	1.144E-01	1.62	29.00	1.136E-01	1.63	29.00	3.352E-04	3.80	29	4.686E-03	3.06	29.05	4.612E-03	3.07	29.02
R4	3.479E-02	1.88	29	1.023E-01	1.68	29.01	1.029E-01	1.68	29.00	6.495E-04	3.56	29	5.863E-03	2.97	29.09	5.882E-03	2.97	29.07
R5	1.136E-02	2.40	29	4.894E-02	2.05	29.06	4.934E-02	2.05	29.03	1.385E-03	3.27	29	1.013E-02	2.75	29.07	1.013E-02	2.75	29.07
R6	1.224E-02	2.37	29	5.125E-02	2.03	29.06	5.151E-02	2.03	29.03	1.410E-03	3.26	29	9.834E-03	2.76	29.13	1.028E-02	2.74	29.07
R4_r1	3.069E-07	6.34	29	8.400E-04	3.70	30.77	9.644E-04	3.65	30.11	1.224E-09	8.47	29	1.929E-04	4.19	33.24	2.016E-04	4.19	31.81
R5_r1	7.723E-07	6.01	29	2.401E-03	3.30	30.76	2.401E-03	3.31	30.32	1.199E-09	8.48	29	1.271E-04	4.34	32.70	1.108E-04	4.4	31.95
R6_r1	7.891E-07	6.00	29	2.310E-03	3.32	30.95	2.244E-03	3.33	30.42	1.203E-09	8.48	29	1.193E-04	4.36	32.93	1.127E-04	4.41	31.20
R4_r12	4.18E-02	1.79	29	1.21E-01	1.59	29.01	1.21E-01	1.59	29.00	3.629E-09	8.03	29	5.451E-04	3.83	32.56	3.586E-04	31.48	31.48
R5_r12	2.47E-02	2.05	29	8.65E-02	1.77	29.02	8.61E-02	1.77	29.00	1.202E-09	8.48	29	1.274E-04	4.34	32.70	1.186E-04	4.39	31.09
R6_r12	2.54E-02	2.03	29	8.80E-02	1.76	29.02	8.75E-02	1.76	29.00	1.204E-09	8.48	29	1.196E-04	4.36	32.94	1.297E-03	3.54	30.46
R4_r123	5.728E-08	6.97	29	3.600E-04	3.99	31.42	3.732E-04	3.99	30.69	1.225E-09	8.47	29	7.345E-04	3.70	34.43	3.011E-04	4.05	32.00
R5_r123	4.803E-08	7.04	29	5.012E-04	3.88	31.40	4.264E-04	3.95	30.46	1.200E-09	8.48	29	1.274E-04	4.34	32.70	1.184E-04	4.39	31.09
R6_r123	4.775E-08	7.04	29	4.710E-04	3.89	31.63	3.950E-04	3.97	30.62	1.203E-09	8.48	29	1.196E-04	4.36	32.94	1.128E-04	4.41	31.20

3.3.4 Connectivity modeling

3.3.4.1 Cost surface, circuit outputs, and the influence of different resistance scenarios

To get an overall understanding of the landscape, the cost surface using scenario R5 is shown below (Fig. 3.2). Even before running Circuitscape, one can already identify areas where movement will be more likely (i.e. low resistance) and can envision pinch points of connectivity (certain sections along the Saint Lawrence River), which become more apparent in the following circuit outputs.

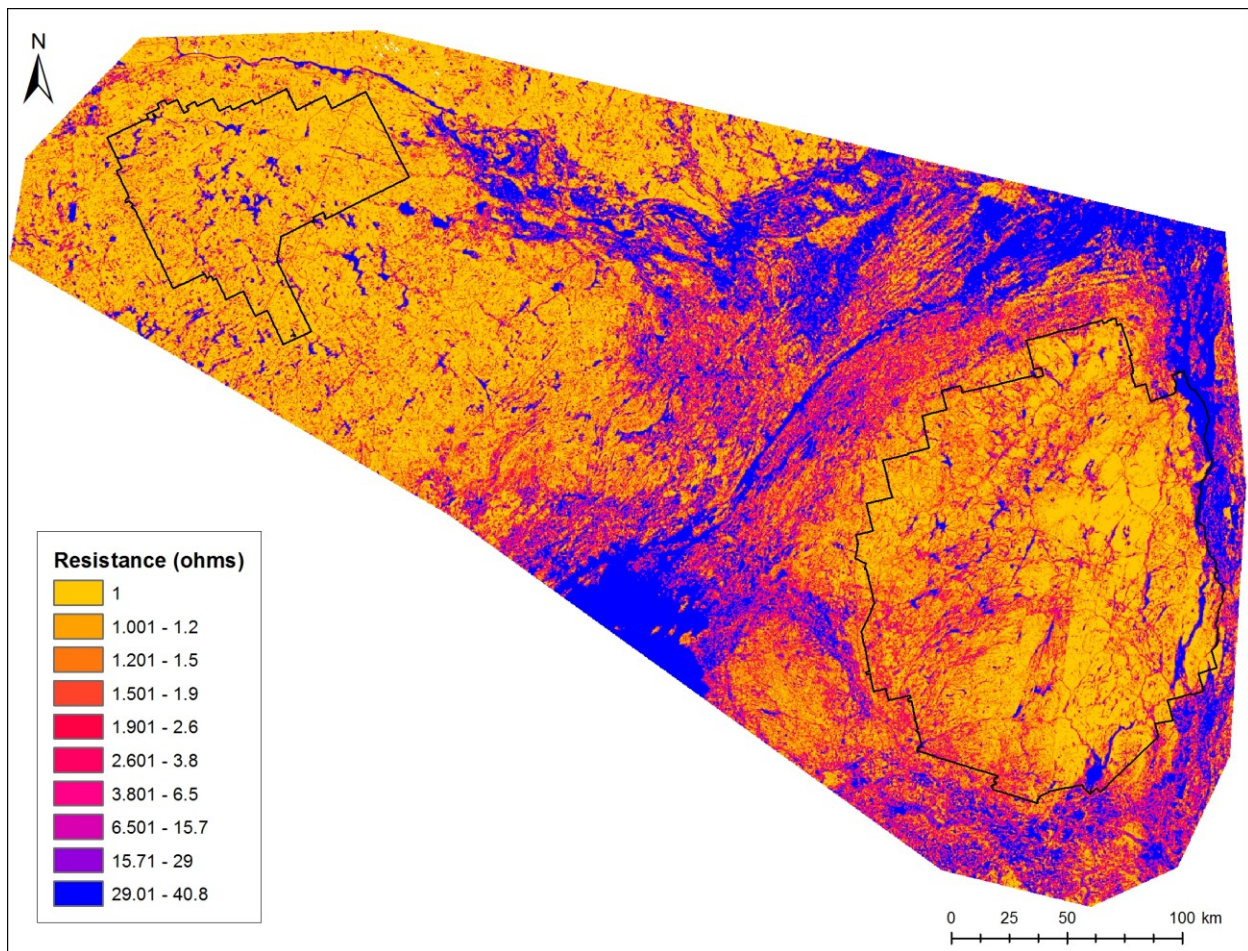


Figure 3.2: Cost surface of scenario R5 (without roads) with a 300 m resolution based on a quantile distribution. Yellow areas represent lowest resistance (i.e. forested areas) and blue areas indicate the highest resistances (i.e. water and urban areas).

We visually inspected the various circuit output maps and compared them to the land cover map to identify trends in fisher movement in this A2A landscape (Fig. 3.3).

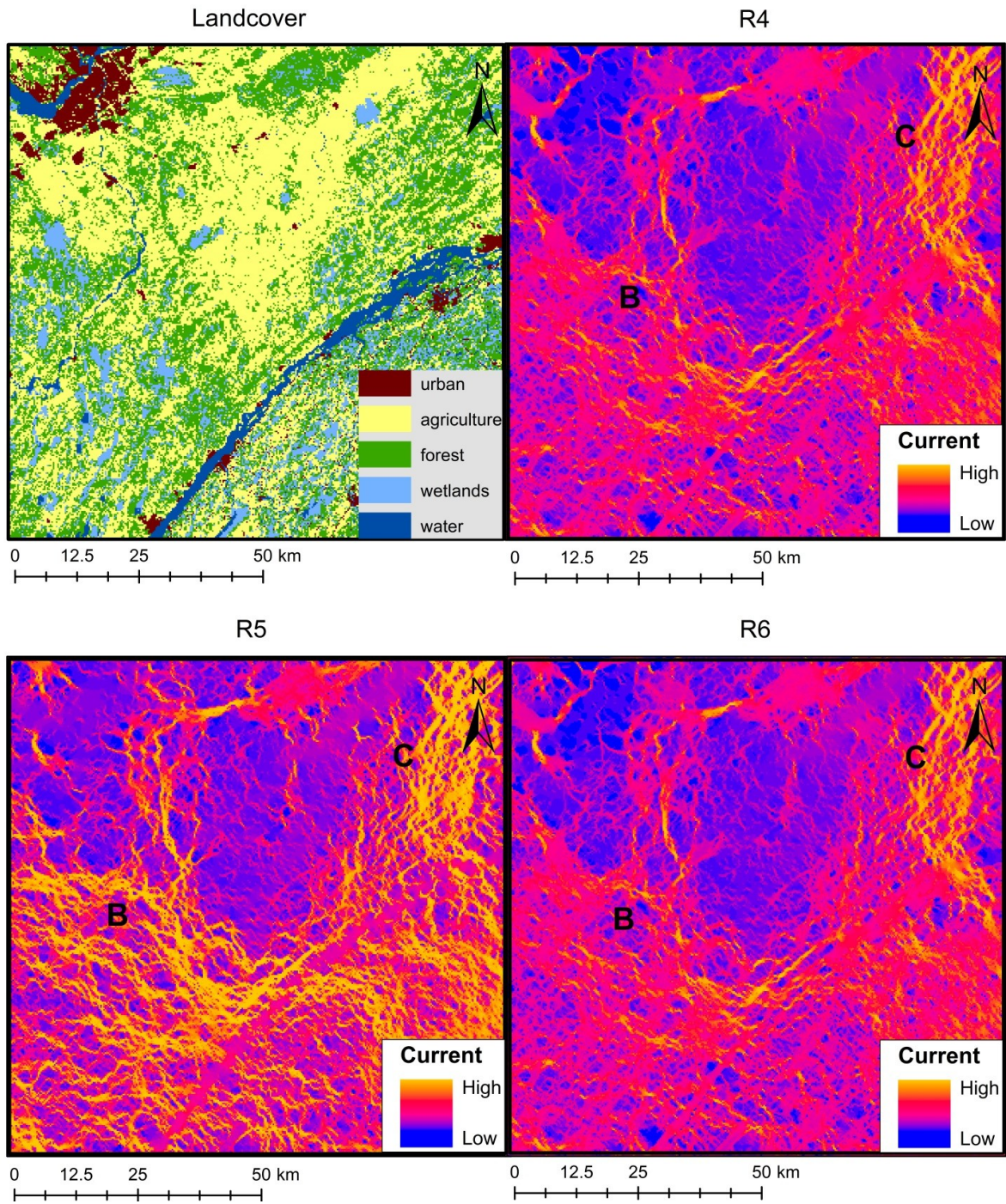


Figure 3.3: A comparison of the current in runs 6, 2, and 7 with the land cover data. These runs compare the differences between resistance surfaces (R4, R5 and R6). All maps show a 10,000 km² tile within the A2A region. The urban area in the top left hand corner represents Ottawa. Twenty nodes were randomly placed at a distance of over 40 km around the boundary of A2A for all circuit map outputs. Letters B & C signify main high movement areas; A is not visible as it does not fall within this sub-region.

In the R4 scenario circuit output (run 6, Fig. 3.4), agricultural lands negatively impact the amount of fisher movement quite strongly. The current is moderately high outside of Algonquin Park, spilling out over the adjacent forested lands. The agricultural lands act as a funnel, directing movement towards the Saint Lawrence Islands, thereby pooling current in this area and delineating a main corridor (A) of movement to the Adirondack Park. This is the location of the Frontenac Axis, which has been established as the least degraded north-south corridor across the Saint Lawrence River. In addition to this high current pathway, two other main corridors can be distinguished which connect to the Adirondack Park. One is located further upstream of the Saint Lawrence (B). This pathway flows through the wetland and forested areas which are surrounded by agricultural lands, passing northeast of the urban areas of Prescott and Ogdensburg. The other main corridor is situated west of Cornwall, descending down from Québec (C). A fourth area of high movement is found in the Gatineau region (D); this area is composed of mostly forested lands with some lakes dispersed intermittingly within the forested region.

In contrast to scenarios R5 (run 2), R4 has higher current in water (the same is the case with scenario R6 (run 7)). The Saint Lawrence River has many sections of high current, which biologically does not necessarily indicate a high amount of fisher movement. Fishers can travel in water, however, they are not aquatic creatures, and would not usually swim in the river in this manner.

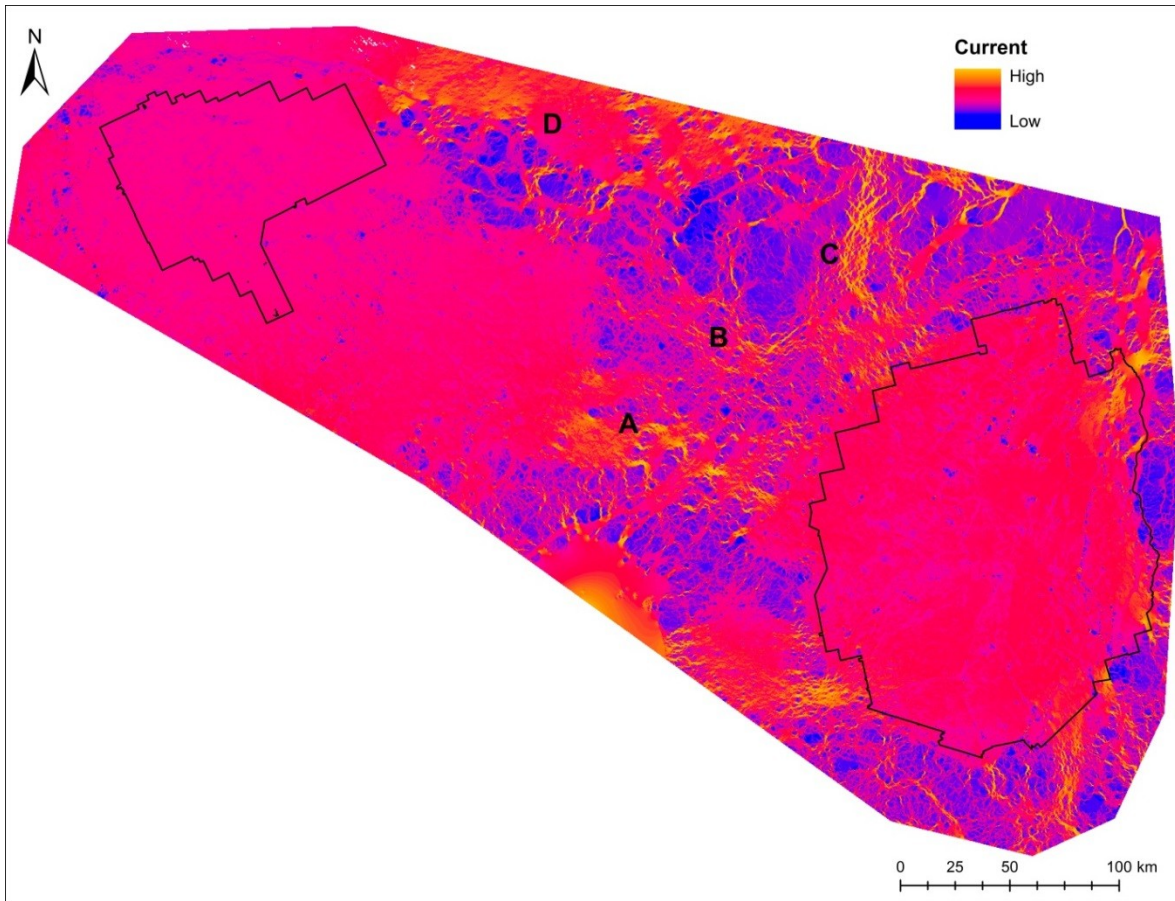


Figure 3.4: Current in run 6 for scenario R4 using a resolution of 300 m and 20 random focal nodes. Letters signify main high movement areas.

In scenario R5 (run 2, Fig. 3.7, see section 3.3.4.2) the same three main movement pathways, as indicated in scenario R4, are present. A main difference in the overall current map between scenarios R4 and R5 is the reduction in movement associated to water. R5 has many more pockets of very low current (blue areas in the circuit output maps) embedded in the matrix of the higher current areas (e.g. Algonquin Park itself and just outside the park), as this is where the water bodies are located.

In scenario R6 (run 7, Fig. 3.5), the same broad patterns of connectivity are present as in the previous two scenarios. The main differences to R5 are that there are more areas with low current (or areas which had low current in R5 have further decreased in connectivity in R6). This is intuitive, as in R6, urban areas were integrated into the habitat model and so these areas now have a higher resistance compared to R5 when only the variable of forest habitat was included.

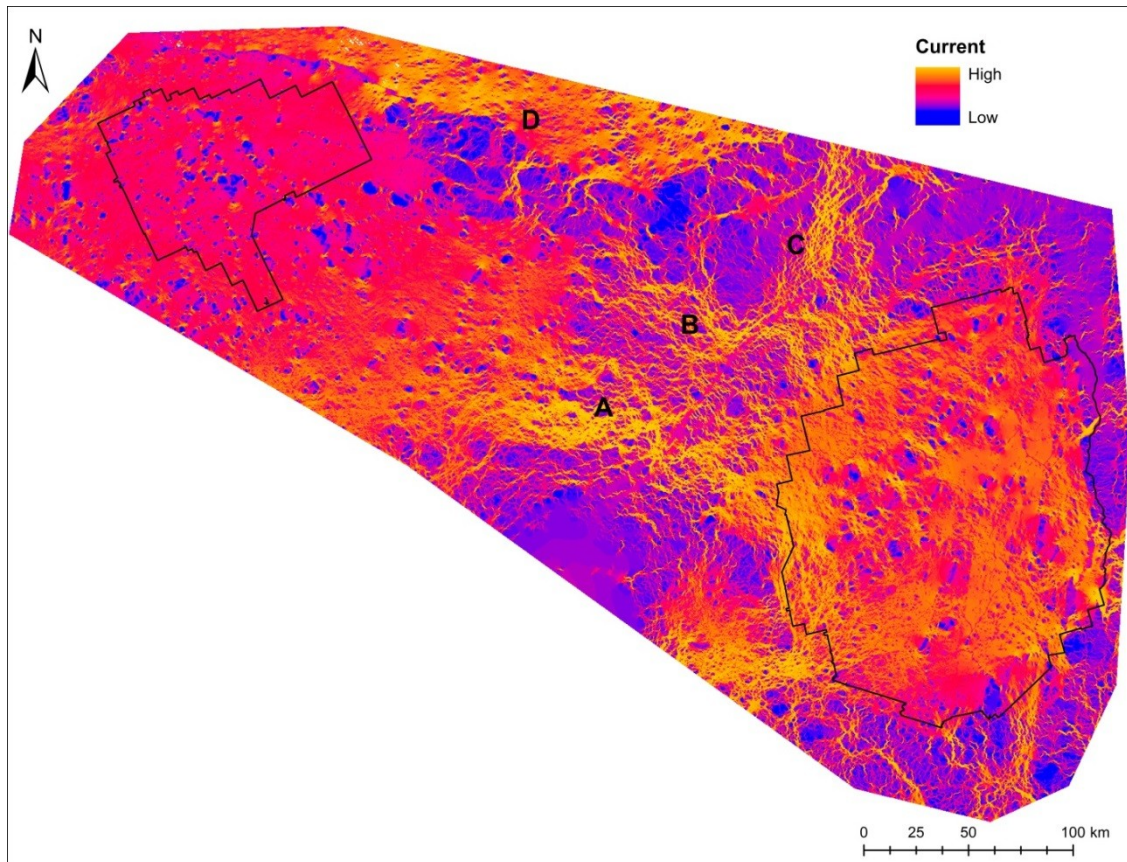


Figure 3.5: Current in run 7 for scenario R6 using a resolution of 300 m and 20 random focal nodes. Letters signify main high movement areas.

3.3.4.2 *Influence of focal node placement*

We also explored how the resulting connectivity maps would be influenced by various focal node placements (runs 1-4, Tab. 3.6, Figures 3.6, 3.7, 3.8 and 3.9). The comparisons between placing four linear bands at each cardinal direction over 40 km away from the A2A region (Fig. 3.6; Appendix 4), and placing 20 random nodes over 40 km away (Fig. 3.7; Appendix 4), around the A2A boundary, showed one major change in current: a strong decrease in current in the Gatineau region when using four linear focal nodes. There is not a universal amount of nodes to reliably depict connectivity, however it has been demonstrated that 15-20 node pairs are usually adequate, as at this point an asymptote is reached when comparing full pairwise current density estimates (Koen et al. 2014). Though there were slight differences in current throughout the A2A region between these two runs, the main pattern of connectivity remained the same. The connectivity maps resemble each other visually when comparing them using a quantile distribution, but their effective resistance differs (Tab. 3.10), with effective resistance measuring

the isolation between two nodes (the lower the effective resistance the more connected these nodes are). Reasons why effective resistance differs between focal node placements, even after they have been divided by the number of node pairs, is due to varying focal node sizes and distances between node pairs. Due to these differences in effective resistance, caution must be used in visual comparisons between connectivity maps. If for example, the same quantile classification from the 20 random nodes was applied to the four linear band nodes, the current map would look all blue (i.e. low connectivity), but this is only because highest current in the 20 random nodes overpowers the high current in the four linear band nodes. To make comparisons, the classifications need to be adjusted accordingly. The highest current areas in all focal configurations are in the same location; i.e., the main pattern of connectivity remains the same.

Table 3.10: Focal node placement, number of focal node pairs, cumulative effective resistance, and their associated effective resistances divided by the number of focal node pairs from the resulting connectivity map using scenario R5.

Focal Nodes	Number of Focal Node Pairs	Cumulative Effective Resistance (ohms)	Effective Resistance (ohms)
Four linear bands	6	8.290	1.382
Twenty random nodes	190	1897.044	9.984
Six nodes in each park	66	157.810	2.391
Parks themselves as two nodes	1	1.438	1.438

When placing the focal nodes inside the two parks (Fig 3.8), the resulting connectivity map is dramatically different than for the previous two focal node configurations. As the nodes were now within the study region, this greatly skewed the distribution of the current. As the current was being forced into these nodes, they were concentrated points of high movement, thereby decreasing the current significantly elsewhere. However, this circuit output still shows the identical three main movement corridors found for all other focal node placements.

When turning the two parks entirely into focal nodes themselves (i.e. as focal regions), this has a similar effect to the placement of six nodes within the parks, albeit less extreme (Fig. 3.9). The parks themselves become two beacons of high current, and though the main pattern of connectivity is present, it is difficult to focus in on areas of high and low current as the region has been saturated in current.

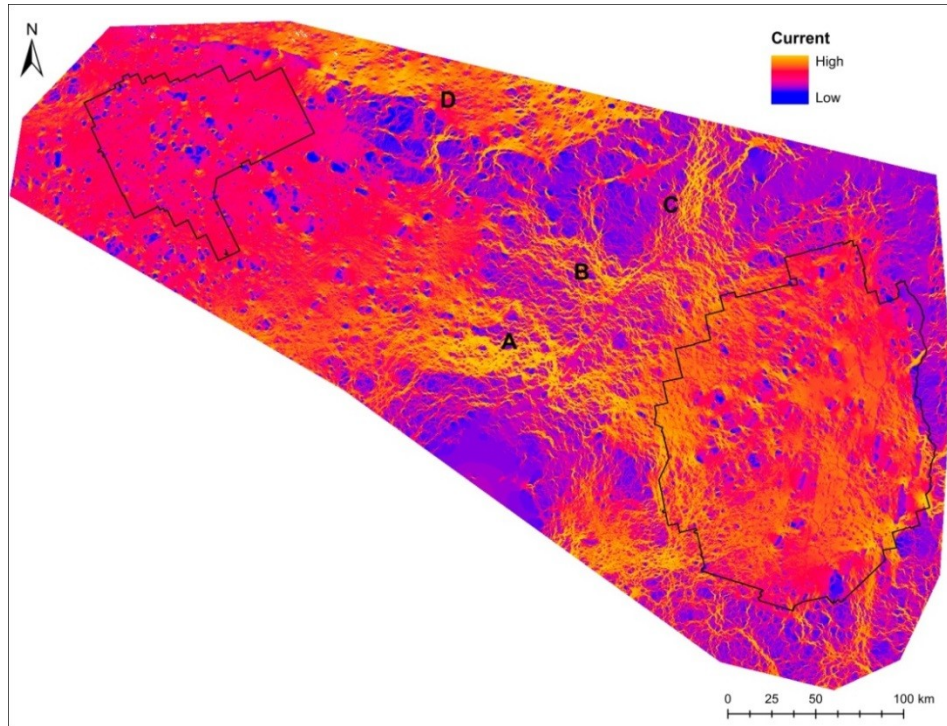


Figure 3.6: Current in run 1 for scenario R5 using a resolution of 300 m and four linear focal regions. Current based on quantile classification. Letters signify main high movement areas.

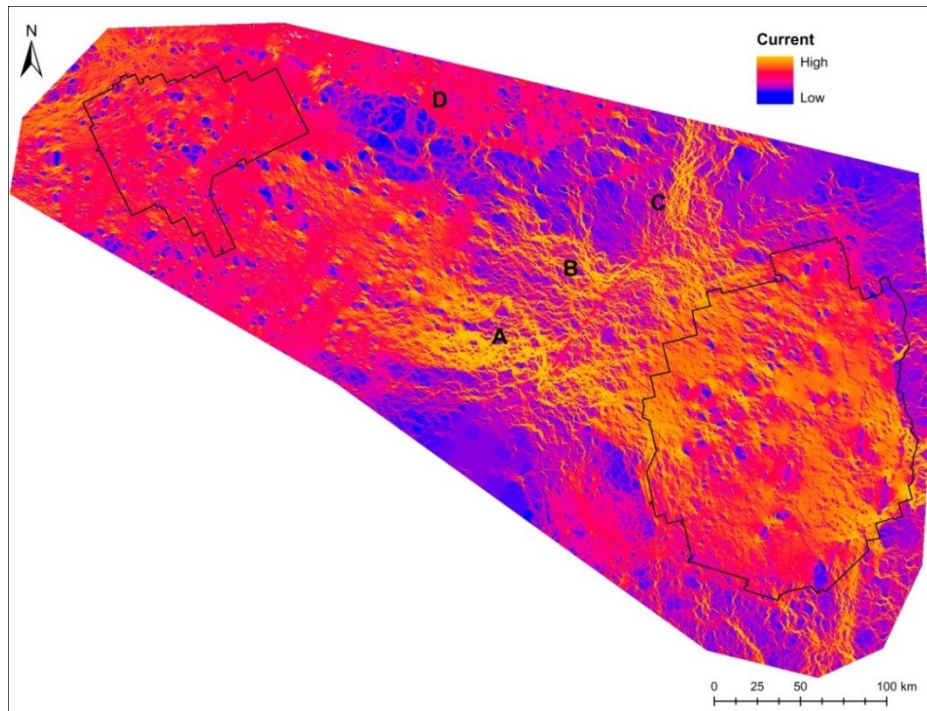


Figure 3.7: Current in run 2 for scenario R5 using a resolution of 300 m and 20 random focal nodes. Current based on quantile classification. Letters signify main high movement areas.

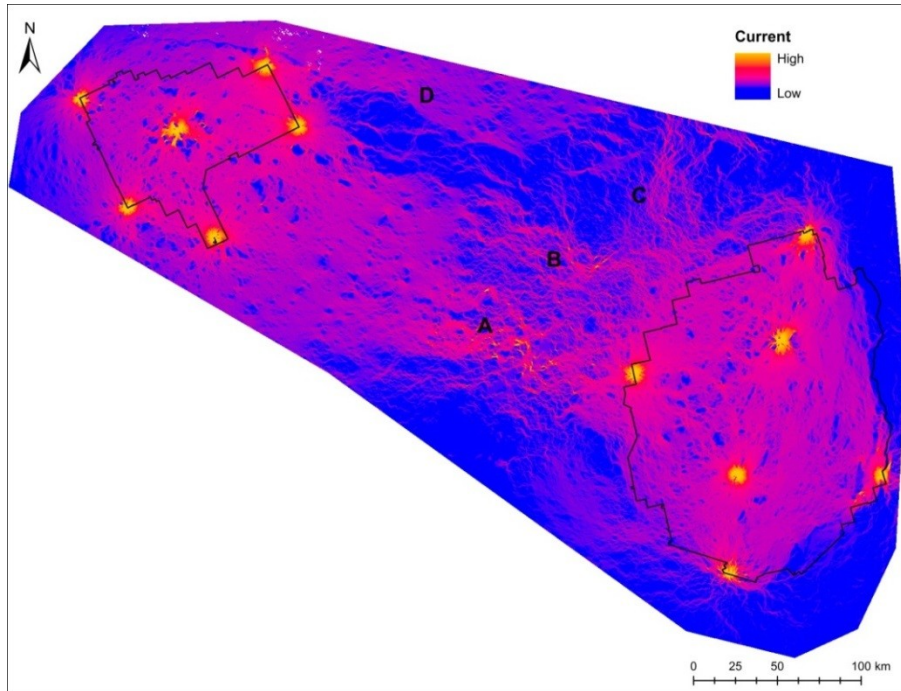


Figure 3.8: Current in run 3 for scenario R5 using a resolution of 300 m and six focal nodes placed in each park. Current based on quantile classification from run 1. Letters signify main high movement areas.

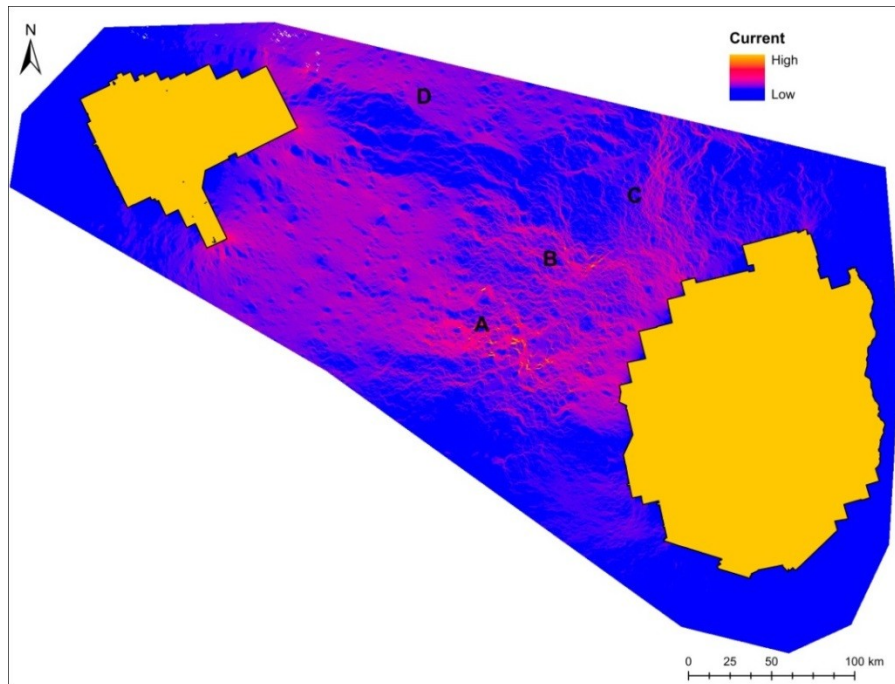


Figure 3.9: Current in run 4 for scenario R5 using a resolution of 300 m and the parks themselves as two focal regions. Current based on quantile classification from run 2. Letters signify main high movement areas.

3.3.4.3 *Influence of resolution (square grid cells)*

Another secondary objective of this study was to analyse how resolution would affect the resulting connectivity maps. By comparing 150 m and 300 m resolutions, there was no overall change in the connectivity pathways, however when zooming more into the maps, there were some slight differences (Fig. 3.10). As expected, with a higher resolution, more details are visible in the connectivity maps. If resolution would continue to become finer, one could further isolate specifically the areas of high movement. However, to visualize the broader patterns of movement, a coarser resolution is sufficient. A price does come with higher resolution; the computational time is longer and data capacity of the Circuitscape program itself can be exceeded. To overcome this problem, the landscape could be divided into smaller sections and run on these individual tiles (Pelletier et al. 2014), or alternatively, selected areas derived from the coarser resolution Circuitscape run, could be targeted for further investigation (e.g. areas which showed high probability of movement). This could be valuable for areas where current is shown to cross over sections of major barriers such as roads or waterways. Being able to identify where animals are more likely to cross can help planners focus their efforts and perhaps bring more support to building wildlife structures in these areas.

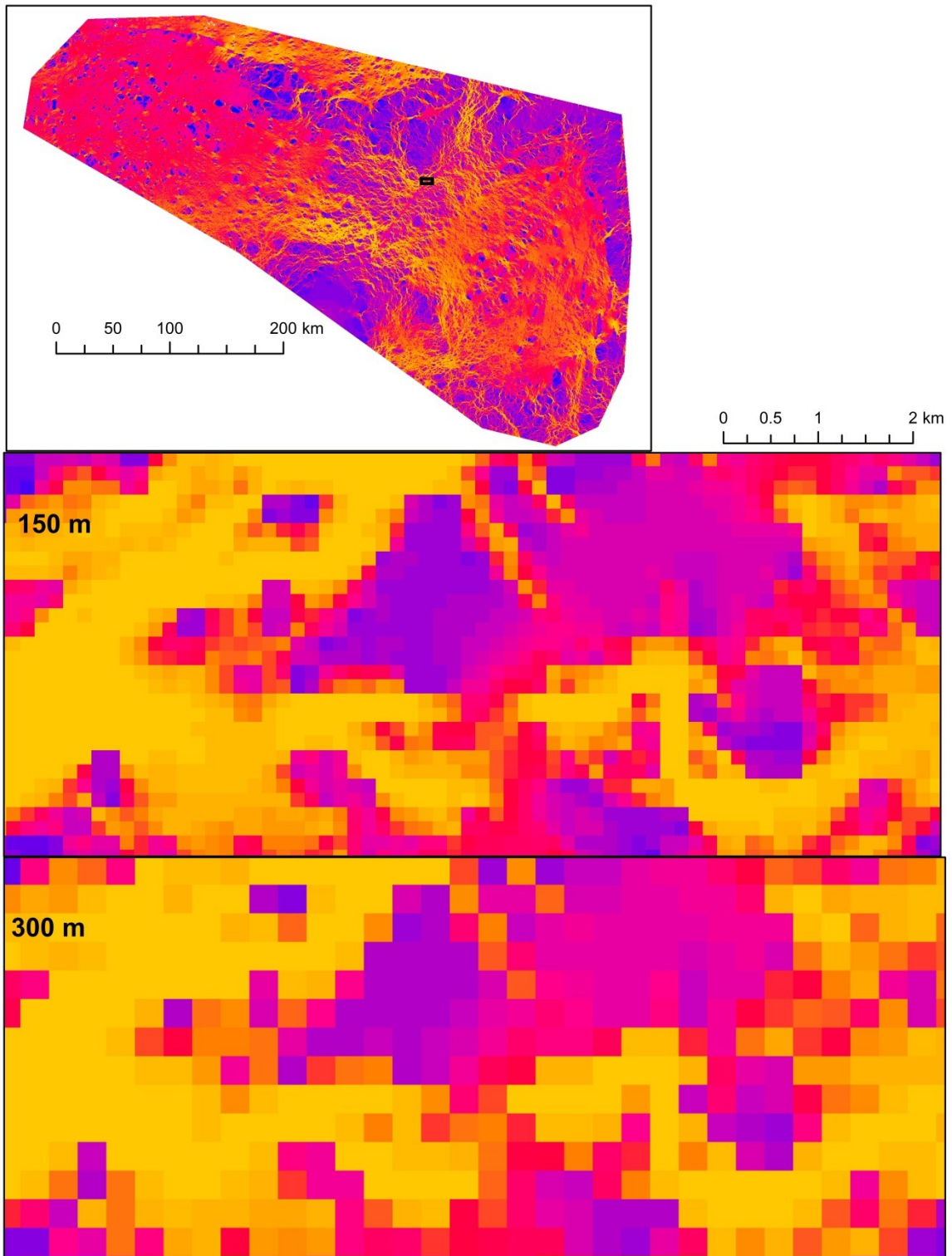


Figure 3.10: Comparison of the 150 m and 300 m resolutions for a small section (approx. 10,000 km²) of the connectivity map.

3.3.4.4 *Influence of roads*

The three previous scenarios (R4, R5 and R6) did not integrate the impacts of roads on the movement of fishers (R4 did indirectly incorporate roads, by including the variable proximity to roads, but did not include the resistance of the road itself). The following maps show the impacts of the addition of various classes of roads (Tab. 3.4b, Fig. 3.11).

With the additional resistance of class 1 roads, movement throughout the A2A region decreased dramatically. Two of the main movement pathways which were evident in R5 without roads, were almost eliminated (B and C). The southernmost pathway (A) was still present, but its overall current was reduced. Another interesting difference between R5 without roads and R5 with class 1 roads was how the previous universal spilling of current out from the Algonquin became more directed towards the southern section of the A2A region. This difference in effect creates a more visually distinctive ecological corridor between the two parks. This can be explained by the large amount of roads concentrated in the center of the A2A region (section 3.4.3).

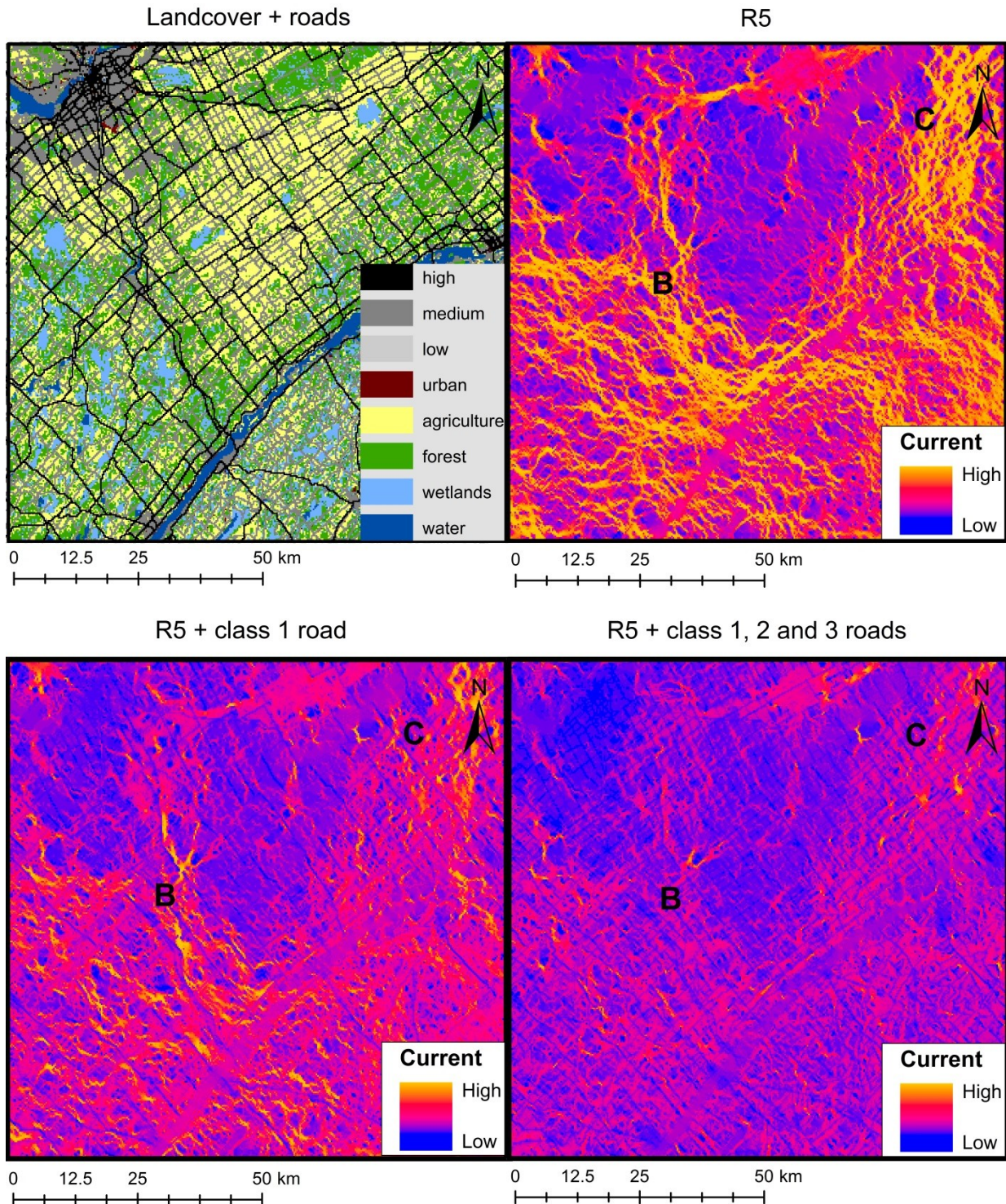


Figure 3.11: Comparison of the connectivity network with the additional impact of roads on scenario R5, with a resolution of 300 m and 20 randomly placed focal nodes around the A2A boundary. All maps show a 10,000 km² tile within the A2A region. The urban area in the top left hand corner represents Ottawa. Letters B & C signify main high movement areas; A is not visible as it does not fall within this sub-region.

In R5 with the additional resistance of road classes 1 and 2, current was further reduced. Continuing with adding more and more roads into the connectivity analysis further highlights the remaining high current areas. The two parks themselves became more distinguished as areas of high movement (and few roads). The urban areas in particular were avoided more (as shown by darker and darker blues). The Gatineau region was still mostly high in current; however the effects of development on the eastern side of the region were visible, which showed a steady decrease in current.

In the last road scenario (Fig. 3.12), which incorporated all levels of roads, the overall connectivity of the A2A continued to decrease. The high current pathways in R5 were almost completely eliminated when all roads were included within the landscape.

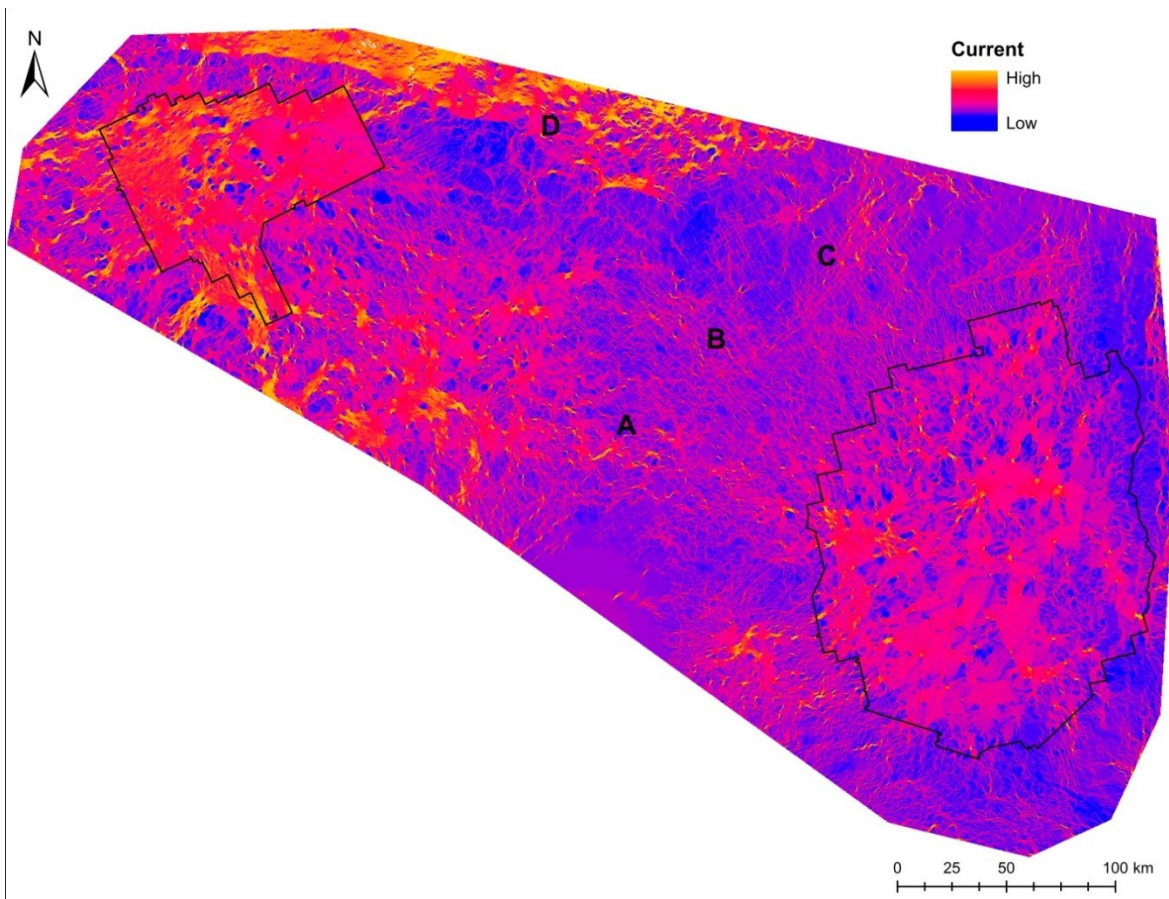


Figure 3.12: Current in run 10 for scenario R5 with the addition of road classes 1, 2 and 3 using a resolution of 300 m and 20 random focal nodes.

3.4. Discussion

3.4.1 *Connectivity maps*

Based on the comparisons of connectivity amongst the different scenarios used to populate the resistance surface, and as confirmed previously by the validation results (Tab. 3.9), all scenarios had similar outputs for the ecological corridor network for fishers. The main movement pathways were the same in all three scenarios (R4, R5, and R6). If a choice needed to be made, however, R5 would be recommended to model fisher movement, due to its simplicity and minimal data requirements. In addition, based on our habitat suitability model selection results (section 3.3.2); R5 was the only model whose variable was considered biologically meaningful (as forest was the only variable whose confidence intervals did not span zero, Tab. 3.8; Walpole et al. 2012).

3.4.2 *Influence of focal node placement*

Using 20 randomly placed nodes buffered outside the study region has been demonstrated as a reliable method in predicting functional connectivity across a region (Koen et al. 2014; Pelletier et al. 2014) and therefore, was used for our other connectivity comparisons. Though the resulting connectivity maps looked similar when focal nodes were either four linear bands, or 20 random nodes, effective resistance greatly differed. One must be cautious to not overestimate the overall connectivity of the region when using only a handful of focal nodes because connections can be overlooked, high resistance areas could be missed and therefore, using 15-20 focal nodes has been shown as adequate for depicting connectivity. Placing the focal nodes within the study region is not ideal when trying to model the connectivity over an entire region, and can lead to false interpretations of movement and result in a saturation of current in some locations, making it difficult to narrow down areas of high or low current. As current is being forced into these nodes (because these are the areas between which connectivity is being measured), this creates high current around these areas, which is not representative of actual movement. To account for this false current, a buffer of 40 km can be applied (and later removed from the output current maps), which was done in the other focal node placement runs, and has been supported as an appropriate distance to eliminate this effect (based on the width of the region, Koen et al. 2010). Therefore, based on these findings and support from the literature,

buffering the area and placing the focal nodes outside this buffer and clipping the circuit output to the study area afterwards, is preferable over placing focal nodes within the study region.

3.4.3 Effects of roads and their incorporation in the connectivity analysis

Habitat fragmentation from transportation networks is one of the most serious risks to biodiversity (Benítez-López et al. 2010). Roads are significant barriers to animal movement and significant ecological effects extend outward from a road and impact areas used by mammals such as deer, fishers, and black bears, which were located up to several kilometres from the highways, i.e. effects of the resulting “road-effect zone” (Forman & Deblinger 2000, Table 3.11). To account for the effects of roads in this connectivity analysis, we used two different measures. Firstly, we included proximity to roads as one of the explanatory variables in our habitat suitability models (R4). This variable explains the resistance a road has on the surrounding environment by lowering the probability of movement along or near roads due to lower habitat suitability. However, this variable does not capture the effort it takes an animal to physically cross the road. Therefore, we also included the resistance of roads. Class 1 roads were assigned a resistance similar to that of urban areas (100) however, slightly lower (80) in order to capture the more permeable nature of roads, depending on their size (number of lanes) and traffic volume. As the road layer was in vector format it was converted to the resolution size of the land cover layer (i.e. 300 m). Although this resolution may seem large, there are sizes similar to and even larger than 300 m for the size of the road effect zone (Tab. 3.11) and therefore, we find this value to be reasonable to account for roads.

Highway 401, which runs parallel to the Saint Lawrence in Ontario has been considered a major challenge to the A2A Collaborative's vision of a connected landscape between these two parks. Though our circuit outputs confirmed that the 401 is a major barrier to animal movement (as shown by the disruption of two of the three main corridors), it is not a complete barrier to movement and must not be used as a reason to question this vision of a connected and healthy landscape. It can be made more permeable by wildlife passages (Chapter 4).

Our connectivity comparisons with the additional resistance of roads and how they greatly reduced the amount of movement throughout the A2A region enforce the importance of properly managing and conserving these remaining important areas for movement before future roads are constructed and more movement pathways are lost or disrupted. The expansion of roads in

Southern Ontario is continuing at an alarming rate; demonstrating the high rate of development and pressing need to develop a plan of action for the remaining roadless areas (Fenech et al. 2005). Remaining roadless areas and low traffic areas have been indicated as important conservation targets and should be inventoried and be given a legal status for protection (Selva et al. 2011). These areas are integral for maintaining ecological integrity, biodiversity and connectivity. By using Circuitscape, these roadless areas are associated with higher movement probabilities and should be viewed as a high priority for conservation efforts.

Table 3.11: Size estimates and descriptions of the ecological road effect zone from various sources.

Size of Road Effect Zone	Description	Source
300 m/side	Average distance from the highway that ecological impacts extend.	Forman & Deblinger (2000)
>100 m	Minimum distance from the highway that ecological impacts were observed.	Forman & Deblinger (2000)
>1 km	Movement corridors and suitable habitat disrupted for mammals such as deer, moose, fisher and black bear.	Forman & Deblinger (2000)
100-200 m	Distance within lower population densities were observed for large mammals. However other animals which tend to avoid roads include anthropods, small mammals, forest birds and grassland birds.	Forman & Alexander (1998)
<1 km	Effect of infrastructure on bird population densities.	Benítez-López et al. (2010)
<5 km	Effect of infrastructure on mammal population densities.	Benítez-López et al. (2010)
A couple of meters up to 17 km	Abundances were affected at a range of distances from infrastructure, with the larger sized mammals being affected at greater distances.	Benítez-López et al. (2010)
1 km/side	Indirect habitat loss due to displacement or avoidance is unclear, but this is the likely average for a highway in heavily forested or vegetated areas.	Ruediger (1996)
3 km/side	Likely average for a highway in open habitats.	Ruediger (1996)
5 m - 100 m	The effect zone where a detectable impact on ecological communities has been shown assuming the road is minor road of 5 m width (study done in UK).	Underhill & Angold (2000)
Other general comments about the effect of roads for fishers and martens		
NA	Marten tracks (and track density) were significantly fewer near roads than away from roads at distances of 800 m and 1000 m.	Robitaille & Aubry (2000)
NA	Roads may show negative correlations with fisher distribution either by providing access to trappers or by their association with habitat degradation.	Carroll et al. (2001)
NA	Reported a negative association between detections of fishers and roads. Where fishers were detected significantly more often in areas with greater than average density of low use roads and less often in areas with moderate and high road use.	Dark (1997)
NA	Negative association between fisher detections and traffic.	Harris et al. (1997)
NA	“The probability of small mammals crossing lightly traveled roads 6-15 m wide may be < 10% of that for movements within adjacent habitats”.	Forman & Alexander (1998), p. 215

3.4.4 *Wildlife corridors*

These resulting current maps can be used as a tool to identify an ecological corridor network for this region and help prioritise areas in need of conservation (i.e. high current locations or bottleneck areas (pinch points of current) would relate to a higher priority). After all road types were included in the connectivity analysis, the southern-most corridor (A) remained the most intact. As shown in figure 3.13, the main reason for this is due to less development in this area, as this is the location of the Frontenac Provincial Park, which is situated in the greater Frontenac Axis (Fig. 2.1). In addition, the Thousand Islands provide stepping stones for movement in order to cross the Saint Lawrence River. This demonstrates the importance of this region (the Frontenac Axis) as a bridge of movement between these two parks and perhaps should be viewed as a national priority as a critical ecological corridor. This is also supported by Quinby et al. (1999) as their finding for the location of a corridor using least-cost theory.

Though we based our cost surface on one species (fishers) as it served as an umbrella species to capture the movement of other species, there are other alternatives which could be used to incorporate a more multi-species approach. Koen et al (2014) based their resistances on the permeability of the landscape as a method to simulate movement for multiple species, where resistances were either: 10 (natural cover), 100 (unnatural but permeable) and 1000 (unnatural and impermeable). Whichever method one chooses, selecting areas of highest current (or bottlenecks) would be a good way to identify conservation targets. Other countries have used various methods to implement such corridor networks, with various degrees of success and legal support. In Switzerland, with the use of GIS and indices of permeability, a corridor network was outlined and areas of highest fragmentation were identified. These results were adopted in ministerial guidelines, are federally supported as the national ecological network and have been incorporated in the master plans of two-thirds of the Swiss cantons. In 2002, a federal restoration plan was initiated for the 51 wildlife corridors of national importance that have been disrupted and require wildlife structures to restore connectivity (Holzgang et al. 2001). In the Netherlands, with the use of a population viability analysis (using an expert-based model LARCH- Landscape ecological Analysis and Rules for the Configuration of Habitat) as well as local knowledge, a corridor network was developed, which later identified 43 priority sites (bottlenecks) for increasing population viability which was incorporated into the government approved national Long-Term Defragmentation Programme (Van der Grift 2005).

Identifying an ecological corridor network and prioritising areas for conservation is only the first step, for these corridors to have any opportunity to be properly preserved or restored, these plans must be adopted in policies, laws and be incorporated in planning agendas.

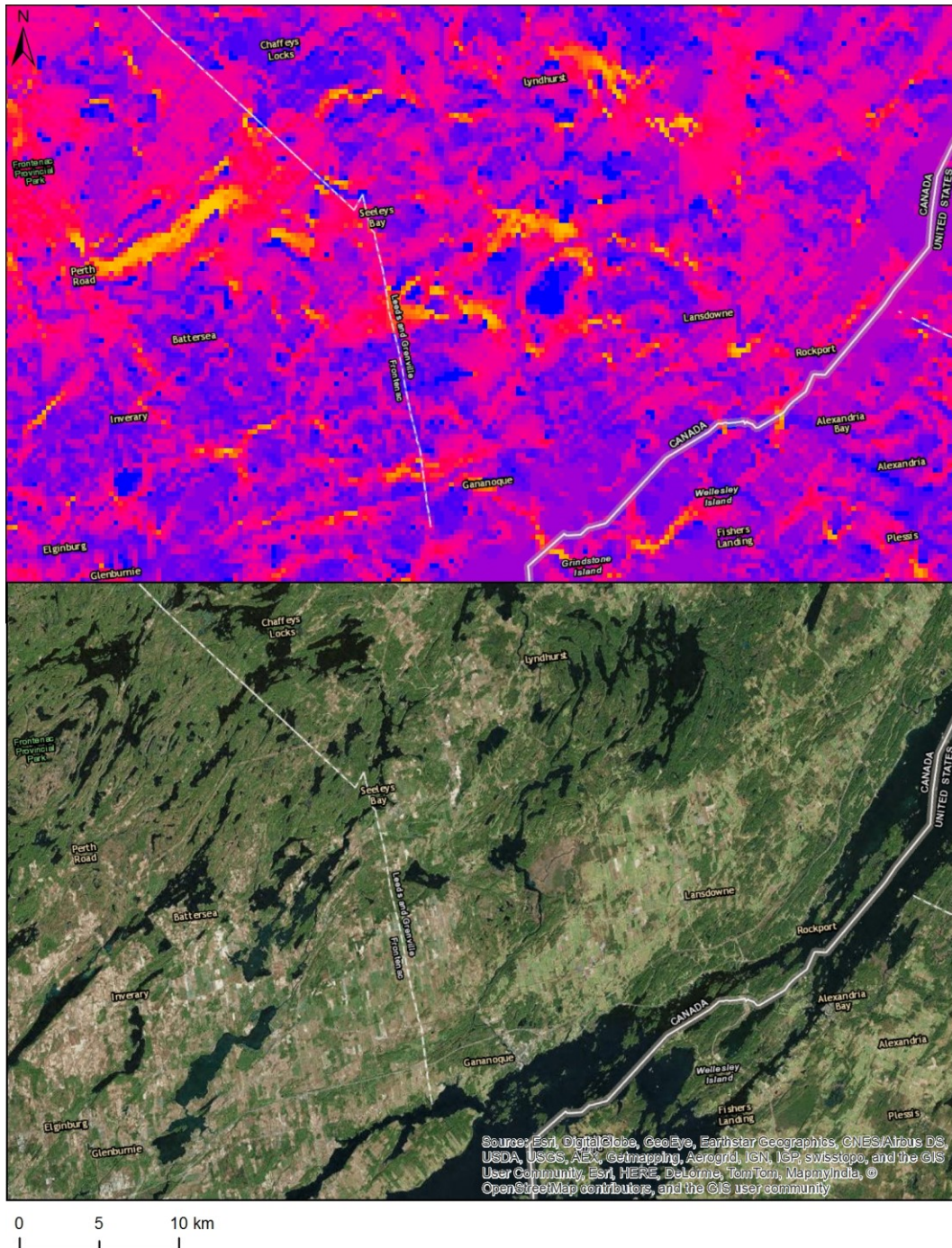


Figure 3.13: Comparing the southern-most corridor (A) with imagery provide by ESRI, in order to get a clearer picture of where and for what reasons high current areas still remain in this location even after the inclusion of all road types in the connectivity analysis.

3.5. Conclusion

The connectivity maps of the A2A region will serve as useful tools to bring attention and support of the goals and vision of the A2A Collaborative to the general public, to landowners in the region, NGOs, planners, and ministries, in an effort to get them actively involved in the planning processes which will shape their land and future, as well as the future for generations to come. It must be noted that the idea behind A2A is not necessarily that there should be individuals moving from Algonquin Park to the Adirondack Park (or vice versa), but that wildlife can move freely and persist within this whole region. We also hope that this study demonstrates the need for more landscape-scale analyses of functional ecological networks and helps support the use of circuit theory as a valid tool to measure landscape connectivity. Our results demonstrate that scenario R5 is the best model for fisher movement, due to its simplicity, minimal data requirements, and validation by fisher telemetry data. Without the consideration of roads, three main ecological corridors were present between A2A. However, when roads were added into the connectivity analysis, this disrupted and almost eliminated all three of these wildlife corridors confirming the negative impacts of roads as well as visually reinforcing the importance of roadless areas and highlighting areas in need of conservation efforts. Based on these results, it is critical that actions towards the restoration and maintenance of the connectivity in this region are undertaken; continued studies using different species or using the approach by Koen et al. (2014) at finer resolutions can be done in order to narrow down these important corridors for movement, however, even this analysis has shown that connectivity is already heavily disrupted and therefore needs to be addressed before more pathways are lost.

We need to envision what we want for our future landscapes in order to develop plans for ecological corridor networks and for prioritizing areas for conservation as land use activities such as urban development and farming continue to shape the landscape and transport networks continue to expand. We can learn from other countries about different possibilities and techniques for shaping our future landscapes. In Europe, a green infrastructure (GI) is their vision for the future. GI is a “strategically planned network of high quality natural and semi-natural areas with other environmental features, which is designed and managed to deliver a wide range of ecosystem services and protect biodiversity in both rural and urban settings” (European Commission 2013, p.7). A strategic approach, which would identify problem areas in a systematic way, find solutions and prioritize concrete actions, enables clear targets for

individual organizations and local projects to strive for and can be scaled up to support the larger picture, where collectively they can contribute to making a real difference. We believe that this sort of planning needs to be implemented in Canada.

Chapter 4. Mitigation Scenarios, Habitat Amount, and the Role of Public Participation

4.1 Road mitigation scenario analysis

4.1.1 Improving current practice of identifying locations for mitigation measures

Currently, the most common approach to identify areas for wildlife structures (e.g. wildlife passages and/or fencing) is to conduct a road mortality hotspot analysis. It is expected that these road mortality hotspots are related to the location of habitat, thereby increasing the probability of an animal confronting the road and attempting to cross. These hotspot locations would therefore indicate areas where mitigation measures should be implemented. However, such hotspots may not be present in areas where wildlife populations have already been reduced due to the pressures of roads in the previous years (Fahrig et al. 1995). Areas which have few roadkills but high habitat suitability may be sites where installing mitigation could help restore wildlife populations and therefore might be equally or more effective as mitigation sites than areas which exhibit high amounts of roadkill as indicated by the hotspot analysis (Eberhardt et al. 2013). Therefore, this road scenario analysis may prove to be beneficial in identifying sites for mitigation as circuit theory maps out all movement pathways, thereby eliminating the issues surrounded by solely using a hotspot analysis. If some low road-kill areas were indeed areas of high movement probabilities, this would be picked up with the circuit analysis, while road mortality hotspots will also be indicated by circuit theory.

4.1.2 Research questions and approach

I performed a scenario analysis on the validation area (3123.46 km²), which was used to test the suitability of the various resistance scenarios (section 3.2.7), using scenario R5 and the 150 m resolution. A series of scenarios representing different mitigation measures along highway 401 in Ontario was conducted in order to answer four research questions:

- 1) Does the spatial arrangement of the wildlife structures matter when there are no fences?
- 2) Does the spatial arrangement of the wildlife structures matter when the whole road is fenced?
- 3) Does the spatial arrangement of the wildlife structures matter when there is 1.5 km of fencing on either side of each wildlife structure?
- 4) Does the spatial arrangement of the wildlife structures matter when there is 600 m of fencing on either side of each wildlife structure?

For each question, I placed eight wildlife structures (1) randomly (replicated 20 times), (2) at the highest points of current, and (3) spaced evenly along highway 401. Identification of points of highest current was done using two different methods: all at once, this means that all wildlife structures were added right away, and one at a time, this means that the highest point of current was selected and a wildlife structure placed there, then Circuitscape was run again, and using this circuit output the next highest point of current was selected and a wildlife structure added; the process continuing until eight structures were added. Also depending on the research question being investigated, points of highest current could have been selected in a number of ways: (1) before the road was added (i.e. based on S0), (2) after the road was added (i.e. based on S1) or after the road and fencing was added (i.e. based on S2). The number of wildlife structures was selected based on the recommendations by Bissonette & Adair (2008), who used an isometrically-scaled home range (HR) metric ($HR^{0.5}$) to calculate the recommended distance between wildlife structures. In the case of fishers, I averaged their home range based on the sources from Tab 3.1a for both males and females, resulting in an averaged home range of 27 km² and, using the $HR^{0.5}$ metric, got a wildlife structure placement distance of 5.20 km. Highway 401 spans a length of 44.54 km in the study area, corresponding to eight wildlife structures to be placed along it ($44.54 \text{ km} / 5.20 \text{ km} = 8.56$). Bissonette & Adair (2008) recommend the wildlife structures to be evenly distributed (i.e. each placed 5.57 km from each other = $44.54 \text{ km} / 8$). This is one of the wildlife structure configurations.

Fencing was treated as essentially a complete barrier to movement and therefore was assigned a resistance of 1000. This resistance was added directly to the resistance of highway 401. The different fence lengths between Q3 and Q4 reflect the wish of transportation agencies to avoid fencing the entire road to save cost. As a result of the different methods of placing wildlife structures for points of highest current, fence lengths were not the same within each research question (Tab. 4.1). The ramifications of this are discussed further in section 4.1.3.

4.1.3 Comparing mitigation measures using Circuitscape

To measure the changes in connectivity between scenarios, effective resistance was calculated and compared and the resulting maps were investigated visually. A decrease in the effective resistance would indicate an increase in connectivity within the landscape. Tab. 4.1 describes the

mitigation scenarios and shows the results of this scenario comparison, figure 4.1 shows a visual connectivity comparison of the Circuitscape maps of a portion of the validation area.

Table 4.1: Description of the mitigation scenarios and their associated effective resistances. The connectivity ranking ranges from 1 (best) to 25 (worst). Wildlife structures have a minimum distance of 300 m from one another. Since the random placement was replicated 20 times, median and range are given.

Scenario	Description			Total Fence Lengths (km)	Effective Resistance (Ω)	Connectivity Ranking
	Hwy 401 (Y/N)	Fences	Placement of Passages			
0	N	None	None	NA	625.805	1
1	Y	None	None	NA	631.551	12
2	Y	Entirely	None	44.54	633.069	25
3	Y	None	Randomly	NA	631.513 (631.494 - 631.527)	11
4	Y	None	At highest current: using S0 – all at once	NA	631.458	4
4a	Y	None	At highest current: using S1 – all at once	NA	631.457	3
4b	Y	None	At highest current: using S1 – one at a time	NA	631.450	2
5	Y	None	Evenly	NA	631.513	10
6	Y	Entirely	Randomly	44.54	632.203 (631.954 - 632.448)	23
7	Y	Entirely	At highest current: using S0 – all at once	44.54	632.164	21
7a	Y	Entirely	At highest current: using S1- all at once	44.54	632.092	20
7b	Y	Entirely	At highest current: using S2 – all at once	44.54	632.263	24
7c	Y	Entirely	At highest current: using S1 – one at a time	44.54	631.787	18
7d	Y	Entirely	At highest current: using S2 – one at a time	44.54	631.787	19
8	Y	Entirely	Evenly	44.54	632.200	22
9	Y	1.5 km	Randomly	24	631.686 (631.596 - 631.759)	16
10	Y	1.5 km	At highest current: using S0 – all at once	9.75	631.486	8
10a	Y	1.5 km	At highest current: using S1 – all at once	11.7	631.506	9
10b	Y	1.5 km	At highest current: using S1 – one at a	24	631.577	15

			time			
11	Y	1.5 km	Evenly	24	631.758	17
12	Y	600 m	Randomly	9.6	631.563 (631.536 - 631.590)	13
13	Y	600 m	At highest current: using S0 – all at once	6	631.468	5
13a	Y	600 m	At highest current: using S1 – all at once	6.45	631.473	6
13b	Y	600 m	At highest current: using S1 – one at a time	9.6	631.483	7
14	Y	600 m	Evenly	9.6	631.573	14

The best mitigation scenario in terms of lowest effective resistance, is the one with no fences and eight manually placed wildlife structures at highest current (S4), while the mitigation scenario with highest resistance is the one with the road entirely fenced with no wildlife structures (S2).

In order to answer the research questions, I replicated the random placement of the wildlife structures twenty times, calculated their effective resistances and plotted them alongside with the effective resistances of the other scenarios. If the effective resistances from the twenty replicates of the randomly generated wildlife structures do not overlap with the other configurations, this would provide strong evidence of a significant difference between their effective resistances (i.e. they would differ in most cases) and would indicate which scenario can best increase connectivity in this landscape.

Even with all these various mitigation measures, no scenario shows an effective resistance as low as S0 and none as high as S2. Accordingly, these two are ranked 1 and 25. However, there are 11 scenarios which are better than S1, demonstrating that mitigation measures do help increase connectivity once a road has been constructed.

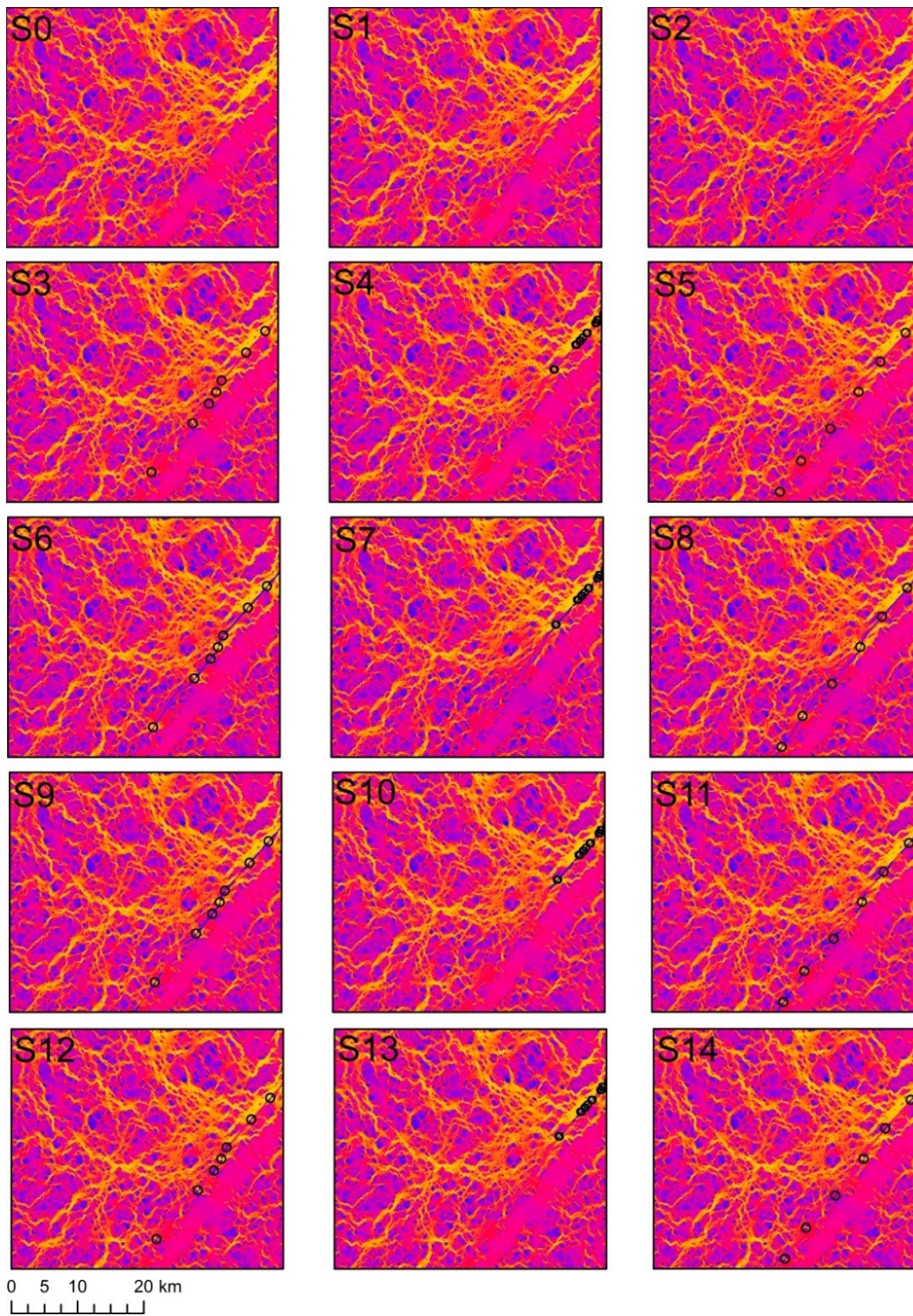


Figure 4.1: Comparison of mitigation scenarios for a portion of the road scenario study area. The circles represent the locations of the wildlife structures. For the scenarios which have randomly placed wildlife structures, one run was selected here as an example output for comparison purposes.

Q1: Does the spatial arrangement of the wildlife structures matter when there are no fences?

The order of best to worst mitigation scenarios is S4b, S4a, S4, S5 and S3 (the median) (Tab. 4.2). As the effective resistance of any variation on S4 does not overlap those of S3, placing wildlife structures at points of highest current is therefore significantly better as a mitigation measure to increase connectivity in this landscape (Fig. 4.2). S5 and the average of S3 are very close to each other (S5 falls within the 95% confidence interval of the median of S3) so their performance to increase connectivity is similar, but some random placements result in lower resistance than the even placement.

Q2: Does the spatial arrangement of the wildlife structures matter when the whole road is fenced?

The order of best to worst mitigation scenarios is S7c and S7d, S7a, S7, S8, S6 (the median) and S7b (Tab. 4.2). This is the only case where one of the variations (S7b) of placing wildlife structures at the points of highest current is not a better mitigation measure than the other two configurations (S6 and S8, Fig. 4.2). In addition, S8 falls with the 95% confidence interval of the median of S6 so their ability to increase connectivity is the same.

Q3: Does the spatial arrangement of the wildlife structures matter when there is 1.5 km of fencing on either side of the wildlife structures?

The order of best to worst mitigation scenarios is S10, S10a, S10b, S9 (the median) and S11 (Tab. 4.2). As the effective resistance of any variation of placing wildlife structures at points of highest current (S10) does not overlap those of S9, it is significantly better as a mitigation measure to increase connectivity in this landscape (Fig. 4.2). Though S11 is at the top of the range of S9, it does not fall within the 95% confidence intervals of the median of S9 and therefore, S11 is significantly different from S9 in terms of their average effects on connectivity, with S9 being a better mitigation measure than S11.

Q4: Does the spatial arrangement of the wildlife structures matter when there is 600 m of fencing on either side of the wildlife structures?

The order of best to worst mitigation scenarios is S13, S13a, S13b, S12 (the median) and S14 (Tab. 4.2). As the effective resistance of any variation of placing wildlife structures at points of highest current (S13) does not overlap those of S12, it is therefore significantly better as a mitigation measure to increase connectivity in this landscape (Fig. 4.2). Though S14 and the range of S12 overlap, S14 does not fall within the 95% confidence interval of the median of S12, therefore, they are significantly different from each other in terms of their effects on connectivity, with S12 being a slightly better mitigation measure on average than S14.

One might intuitively think that the scenarios which select wildlife structure placements based on the “one at a time” method would always yield the best connectivity results, because every passage that is added would impact the connectivity of the landscape and so by selecting passages one by one, this accounts for these shifts in connectivity and therefore would pick up on any changes of the areas of highest current, as shown with Q1 and Q2; however, this pattern is not seen for Q3 and Q4. Reasons for this difference may stem from the fact that these scenarios add fencing associated to each of the wildlife structures at each run, so the fencing lengths will create a barrier at locations, where perhaps current would have flowed previously. Compare this to the “all at once” method, where fence lengths are not influencing the high current locations. For this “one at a time” case, fencing may not have the length of exactly 1.5 km (Q3) or 600 m (Q4), as now the only criterion is that the wildlife structures be placed at a minimum distance of 300 m of each other, so high current areas can be closer to each other (for the “all at once” method) and therefore could have less fencing (Tab. 4.2). It can therefore hard to distinguish exactly which method is more appropriate to use due to these potential effects associated with the various amounts of fencing between scenarios. However, any method of high current wildlife structure placement is still better than evenly or randomly placing the structures.

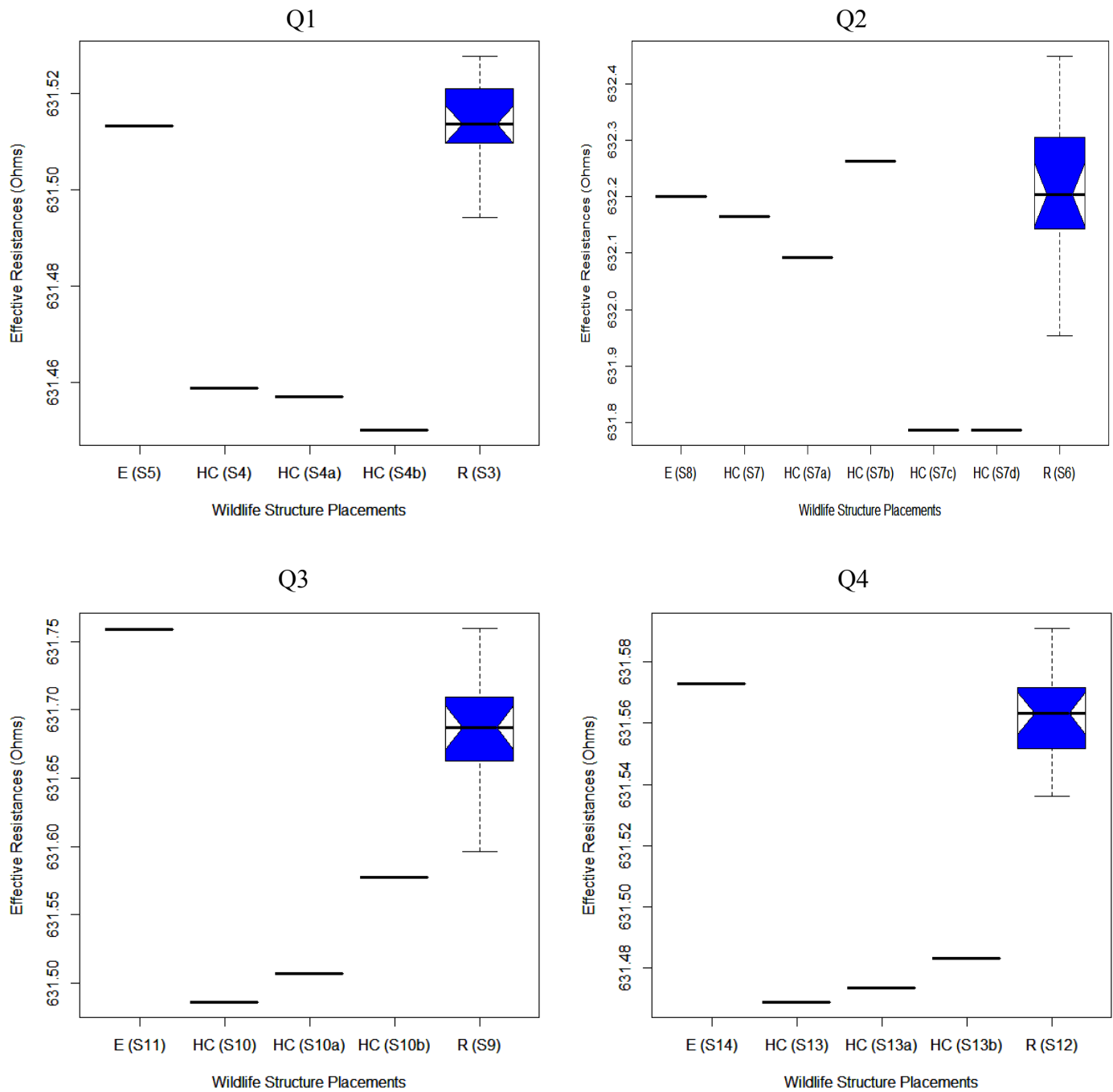


Figure 4.2: Comparison of the effective resistances of the three configurations for the eight wildlife structures: evenly (E), at locations of highest current (HC), and randomly (R), to answer four research questions: (1) Does the spatial arrangement of the wildlife structures matter when there are no fences?, and (2) Does the spatial arrangement of the wildlife structures matter when the whole road is fenced. (3) Does the spatial arrangement of the wildlife structures matter when there is 1.5 km of fencing on either side of each wildlife structure?, and (4) Does the spatial arrangement of the wildlife structures matter when there is 600 m of fencing on either side of each wildlife structure? The dark bar in the middle of the box represents the median, the box represents the 25% and 75% quantiles, the dashed lines (whiskers) represent the 5% and 95% quantiles. The blue notched areas indicate 95% confidence intervals around the median.

In all four cases, placing wildlife structures at points of highest current is better than spacing them evenly. Information on the connectivity of a landscape helps better predict where animals are expected to be moving, thereby indicating areas where movement should be maintained or restored (i.e. locations for wildlife structures) and estimate the degree to which they help augment connectivity. When wildlife structures are simply spaced evenly along a road, or even randomly (results from Q2 being an exception), this valuable knowledge is neglected.

It may be surprising that the scenarios which included fencing decreased connectivity (i.e. increased overall effective resistance). However, fencing was given a very high resistance value (of 1000) and it is intuitive that the resulting effective resistance would increase due to this addition of high resistance. Therefore, comparing effective resistance may not be the best method to demonstrate the beneficial effects fencing may or may not have on connectivity, but can be combined with information about road-kill locations.

4.2 Importance of connectivity vs. habitat amount

In a recent workshop on the use of Circuitscape to measure connectivity (in Peterborough in October 2014), participants were instructed to add in 10,000 pixels of housing into an artificial landscape in such a fashion to maintain as much connectivity between four parks (i.e. focal nodes) as possible. This exercise was done to get participants accustomed to the Circuitscape software, but also brought up an important issue of the differences and conflicts between maintaining habitat amount and increasing connectivity. This issue has not really been addressed in my findings and so I discuss it here.

In this exercise, connectivity was measured using the Circuitscape software and scenarios were compared by calculating the overall effective resistance (housing vs. non-housing). The landscape included pixels of natural habitat (coded by low resistances) and pixels of non-natural habitat (coded by moderate resistance, with the housing pixels having a higher resistance than these non-habitat pixels). Different strategies were implemented among participants. Most groups did not focus on what the previous pixels were (i.e. habitat or non-habitat) before, but thought it would be best if the housing pixels were all in large blocks around the four parks. However, there was one group that had a mission of never transforming a natural habitat pixel to housing (i.e. they wanted habitat amount to remain unchanged), and so their configuration of houses was drastically different, with houses being placed all around the map in various

segments. The groups that blocked housing together in any type of pixel, had similar effective resistances, whereas the group that did not build over natural habitat may be expected to have the best results (i.e. the lowest effective resistances). However this was by far not the case, but their effective resistances were much higher, because their housing areas intersected the pathways between the four parks (due to limited amount of space in this artificial landscape) as a consequence of protecting all pixels of natural habitat.

This result points to an important consideration: Connectivity is not the only factor in the issues of population persistence, but habitat amount is more important than connectivity (Fahrig 2001; Flather & Bevers 2002). Imagine tiny patches of habitat across the landscape; once connectivity is mapped out, current would be shown connecting these patches. However, what are the sizes of these patches, how much food is available, how many species can live there? Large contiguous patches of habitat are what sustain large populations (Fahrig 2002, 2001; Thornton et al. 2011), so even if these little patches are connected, this does not guarantee population persistence. Habitat amount and connectivity should go hand in hand if the goal is a healthy, prosperous landscape where wildlife and people can live together.

4.3 Issues with the implementation of ecological networks and the role of public participation

A survey on New York State landowners found that only 17% of the respondents (out of a total of 47 households) had previous knowledge of a proposed A2A corridor (Brown & Harris 2005). However, after the completion of the survey, 64% of the landowners were in support of the project, with 45% wanting to be actively involved with the planning process (Brown & Harris 2005). As 60% of the land in the A2A region is private property, involving landowners in the plan for developing this ecological network, is highly important because the support and involvement of these private landowners will be crucial for making A2A a reality (Algonquin to the Adirondacks 2012; Brown & Harris 2005).

This leads to the concept of comanagement, commonly known as bottom-up planning, which seeks to merge environmental protection with indigenous or landowner rights (Brown & Harris 2005; Campbell & Vainio-Mattila 2003; Forgie et al. 2001). The integration of active public participation is needed in order for successful sustainable development to occur (Brown & Harris 2005; Campbell & Vainio-Mattila 2003; Forgie et al. 2001). Respecting landowner rights,

establishing clear and unified lines of communication and integrating research and education in the public domain are important aspects that have been recognized and now need to be addressed for the A2A project to proceed (QUBS 2012a, 2012b).

The inclusion of bilateral policy and legislation is essential in regional projects which span across two nations. If these ecological networks are to be implemented for purposes of facilitating movement and conserving biodiversity then the establishment of appropriate legislation would help support this cause. Currently in the US, there is an overall lack of legislation to authorize, distribute funding, and impose regulations necessary to establish an ecological corridor network that would be legally binding (Vásárhelyi & Thomas 2006). In Canada, the Canada National Parks Act and the Species at Risk Act could be used to establish a protected ecological network (Vásárhelyi & Thomas 2006).

Chapter 5. General conclusions

5.1 Summary of findings

The mapping of landscape connectivity between Ontario's Algonquin Provincial Park and New York State's Adirondack Park has identified three main large-scale ecological corridors and many more corridors that are important on a regional scale. These connectivity maps have also visually demonstrated the severely negative effects of roads on wildlife movement. Based on the comparison of resistance scenarios, though many of the cost surfaces have been validated and supported by the fisher telemetry data as good representations to measure fisher movement probabilities, R5 has been chosen as the best scenario to model fisher movement due to its simplicity, its minimal data requirements and its support by the habitat suitability modelling results. From the various focal node placements runs, it has been determined that using 20 randomly placed nodes buffered outside the study region is the most reliable configuration in adequately predicting functional connectivity across a region. By comparing the effect of changing resolution on the resulting connectivity map, the overall picture of connectivity remained the same, however as expected, with finer resolution, one can narrow down the areas of high or low current, thus being able to identify critical areas of movement which is important for management purposes. The highway 401 mitigation scenario results showed that placing wildlife structures at points of highest current is the most efficient way to increase connectivity across the landscape.

5.2 Management implications

As fishers and many other species have large home ranges, management efforts must reflect this scale and therefore, should consider large landscape-scale approaches (Harris et al. 1997; Powell & Zielinski 1994). Due to human activities, ecosystems and landscapes are changing rapidly in southern Ontario and in New York State. Understanding how these changes impact connectivity alongside other ecosystem services is important for effective conservation efforts.

Circuit theory can be used effectively as an approach to analyse connectivity for large landscapes, as is demonstrated in this study. With more and more connectivity studies incorporating this method into their analyses, comparisons between regions and species can be done (if the researcher is transparent and divulges their resistance values, along with the other settings used in their analysis). A visual blueprint is a first concrete step towards making informed decisions about the future of the landscape.

The A2A Collaborative has been a strong advocate in the support of a connected landscape between the Algonquin and Adirondack parks. Finding a common vision and getting the involvement of the public, as well as other conservation authorities and various levels of government, is critical for the advancement of this project. These maps are not necessarily what the protected ecological connectivity network should look like, but it is a starting point for people to come together and begin working on the next steps. Perhaps the next step is to study other species, or change the importance of a certain land cover, or incorporate social or economic factors into these maps. We can draw on the experiences and findings of other countries to help shape our own vision, as well as learn from their mistakes and triumphs. In Europe, ongoing efforts are aiming at a strategic approach, which enables concrete targets and actions individual organizations and local projects can work towards, where their efforts can be scaled up to support the larger picture, where collectively these organizations can contribute to making a real difference. Is this the direction Canada should aim for? If so, we need to create these plans, develop actionable targets and prioritize areas in need of conservation efforts, and have this plan supported by appropriate legislation.

As restoration of connectivity in this landscape is a goal of the A2A Collaborative, future research can use my results to focus on these remaining high current areas in order to recreate the picture of connectivity before the road network was included in the analysis. Using higher

resolution data in these areas, in conjunction with different species or by using the multi-species approach by Koen et al. (2014), can lead to more precise findings about the location of these ecological corridors. In addition, future research can hone in on areas where current is highest when crossing major barriers such as the highway 401 or the Saint Lawrence River, and can be used as a method for establishing a need for mitigation measures or restoration/conservation of habitat in these areas. In comparison with other countries such as Switzerland, which is approximately 50% of the size of this study area and who have identified 51 corridors of national importance, the three corridors my findings identified are only the main building blocks to create a more extensive ecological corridor network. Zooming into these three large pathways, one can distinguish multiple corridors within each of these three broad corridors, and with finer resolution this could help further narrow down more site-specific corridors and lead to a more exhaustive ecological corridor network for this region.

Climate change is an important driver of land cover change, and how it will affect the future landscape and connectivity of the A2A region is currently unknown. There has been research which has used circuit theory to map out such potential changes in Scotland's woodland network (Gimona et al. 2012), and a similar analysis could be of interest for this region. These maps will be a tool to help fuel action, and to get the much needed backing behind this wonderful vision of a connected and healthy landscape.

References

- Adirondack Ecological Center. (2013). Adirondack Flora and Fauna. Retrieved from <http://www.esf.edu/aec/adks/florafauna.htm>
- Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning* 64, 233-247.
- Aengst, P. (2000). The Yellowstone to Yukon initiative: A new conservation paradigm to protect the heart of North America. L. M. Darling, editor. 2000. *Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk*, Kamloops, B.C., 15 - 19 Feb., 1999. Volume Two. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo Kamloops, B.C. 520pp.
- Algonquin to Adirondacks Conservation Association. (2012). Retrieved October 24th, 2012, from <http://www.a2alink.org/vision.html>
- Allen, A.W. (1983). *Habitat suitability index models: Fisher*. Western Energy and Land Use Team, Division of Biological Services, Research and Development, Fish and Wildlife Service, U.S. Department of the Interior. FWS/OBS-82/10.45. 19 pp.
- Anderson, M.G., Clark, M., & Olivero, S.A. (2012). Resilient Sites for Terrestrial Conservation in the Northeast and Mid-Atlantic Region. The Nature Conservancy, Eastern Conservation Science. 168 pp.
- Beier, P., & Noss, R.F. (1998). Do habitat corridors provide connectivity?. *Conservation Biology* 12(6), 1241-1252.
- Beier, P., Penrod, K.L., Luke, C., Spencer, W.D., & Cabañero, C. (2005). South coast missing linkages: restoring connectivity to wildlands in the largest metropolitan area in the United States. In K.R. Crooks & M.A. Sanjayan (Eds.), *Connectivity and Conservation* (pp.555-586). Cambridge, England: Cambridge University Press.
- Beier, P., Majka, D.R., & Newell, S.L. (2009). Uncertainty analysis of least-cost modelling for designing wildlife linkages. *Ecological Applications* 19(8), 2067-2077.
- Beier, P., Spencer, W., Baldwin, R.F., & McRae, B.H. (2011). Toward best practices for developing regional connectivity maps. *Conservation Biology* 25(5), 879-892.
- Bélisle, M. (2005). Measuring landscape connectivity: The challenge of behavioural landscape ecology. *Ecology* 86(8), 1988-1995.

- Benítez-López, A., Alkemade, R., Verweij, P.A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation* 143, 1307-1316.
- Bissonette, J.A., & Adair, W. (2008). Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation* 141, 482-488.
- Bowman, J., Donovan, D., & Rosatte, R.C. (2006). Numerical response of fishers to synchronous prey dynamics. *Journal of Mammalogy* 87, 480-484.
- Brown, R., & Harris, G. (2005). Comanagement of wildlife corridors: the case for citizen participation in the Adirondack to Adirondack proposal. *Journal of Environmental Management* 74, 97-106.
- Burnham, K.P., Anderson, D.R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd edition). New York: Springer-Verlag.
- Campbell, L.M., and Vainio-Mattila, A. (2003). Participatory Development and Community-based Conservation: Opportunities Missed for Lessons Learned? *Human Ecology*, 31(3): 417-437.
- Carr, D., Bowman, J., Kyle, C.J., Tully, S.M., Koen, E.L., Robitaille, & Wilson, P.J. (2007a). Rapid homogenization of multiple sources: genetic structure of a recolonizing population of fishers. *Journal of Wildlife Management* 71, 1853-1861.
- Carr, D., Bowman, J., Kyle, & Wilson, P.J. (2007b). Density-dependent dispersal suggests a genetic measure of habitat suitability. *Oikos* 116, 629-635.
- Chadwick, D.H. (2000). *Yellowstone to Yukon*. Washington, DC: National Geographic Society.
- Driezen K., Adriaansen F., Rondini C., Doncaster C.P., & Matthysen, E. (2007). Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). *Ecological Modelling* 209, 314–322.
- Dobson, A., Ralls, K., Foster, M., Soulé, M.E., Simberloff, D., Doak, D., Estes, J.A., Mills, L.S., Mattson, D., Dirzo, R., Arita, H., Ryan, S., Norse, E.A., Noss, R.F., & Johns, D. (1999). Corridors: Reconnecting fragmented landscapes. In M.E. Soulé & J. Terborgh (Eds.), *Continental conservation: design and management principles for long-term, regional conservation networks* (pp.129-170). Washington, DC: Island Press.

- Doyle P.G., & Snell, J.L. (1984). *Random walks and electric networks*. Washington, DC: The Mathematical Association of America.
- Eberhardt, E., Mitchell, S., & Fahrig, L. (2013). Road kill hotspots do not effectively indicate mitigation locations when past road kill has depressed populations. *The journal of Wildlife Management* 77(7), 1353-1359.
- European Environment Agency (EEA) (2014). Spatial analysis of green infrastructure in Europe. EEA Technical report No 2. Publications of the European Union: Luxembourg. Retrieved from <http://www.upv.es/contenidos/CAMUNISO/info/U0651121.pdf>
- European Commission. (2013). Building a green infrastructure for Europe. Luxembourg: Publications office of the European Union (ISBN 978-92-79-33428-3). 24p.
- Fahrig, L. (2001). How much habitat is enough?. *Biological Conservation* 100 (1), 65-74.
- Fahrig, L. (2002). Effect of habitat fragmentation on the extinction threshold: A synthesis. *Ecological Applications* 12, 346-353.
- Fahrig, L., & Merriam, G. (1985). Habitat patch connectivity and population survival. *Ecology* 66(6), 1762-1768.
- Fahrig, L., & Rytwinski T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14(1), 21. [online] URL: <http://www.ecologyandsociety.org/vol14/iss1/art21/>
- Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D., & Wegner, J.F. (1995). Effect of road traffic on amphibian density. *Biological Conservation* 73: 177-182.
- Fenech, A., & Taylor, B., & Hansell, R., & Whitelaw, G. (2005). Changes in the Major Roads of Southern Ontario, Canada 1935-1995: Implications for Protected Areas. In Fenech, A., & MacIver, D., & Auld, H (eds). *Integrated Mapping Assessment* (p.183-219). Meteorological Service of Canada, Environment Canada. Toronto, Ontario, Canada. 285p.
- Forgie, V., Horsley, P., & Johnston, J. (2001). Facilitating community-based conservation initiatives. *Science for conservation* (p. 6-15). Wellington, New Zealand: Department of Conservation.
- Forman, R.T.T., & Deblinger, R.D. (2001). The ecological road-effect zone of a Massachusetts (U.S.A) suburban highway. *Conservation Biology* 14 (1), 36-46.

- Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., Fahrig, L., France, R., Goldman, C. R., Heanue, K., Jones, J.A., Swanson, F. J., Turrentine, T., & Winter, T. C. (2003). *Road ecology — Science and solutions*, Island Press, Washington DC, USA. 481pp.
- Flather, H.C., & Bevers, M. (2002). Patch reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159 (1), 40-56.
- Garroway, C.J., Bowman, J., Carr, D., & Wilson, P.J. (2008). Applications of graph theory to landscape genetics. *Evolutionary Applications* 1, 93-101.
- Garroway, C.J., Bowman, J., & Wilson, P.J. (2011). Using a genetic network to parameterize a landscape resistance surface for fishers, *Martes pennanti*. *Molecular Ecology* 20, 3978-3988.
- Goodwin, J.B. (2003). Is landscape connectivity a dependent or independent variable?. *Landscape Ecology* 18, 687-699.
- Gilbert-Norton, L., Wilson, R., Stevens, J.R., & Beard, K.H. (2010). A meta-analytic review of corridor effectiveness. *Conservation Biology* 24(3), 660-668.
- Gimona, A., Poggio, L., Brown, I., & Castellazzi, M. (2012). Woodland networks in a changing climate: threats from land use change. *Biological Conservation* 149, 93-102.
- Gustafsson, L., & Hansson, L. (1997). Corridors as a conservation tool. *Ecological Bulletins* 46, 182-190.
- Hanski, I. (1999). Habitat connectivity, habitat continuity, and metapopulation in dynamic landscapes. *Oiko* 87(2), 209-219.
- Hargrove, W.W., Hoffman, M.F., & Efroymson, A.R. (2004). A practical map-analysis tool for detecting potential dispersal corridors. *Landscape Ecology* 20, 361-373.
- Harms, W.B., & Knaapen, J.P. (1988). Landscape planning and ecological infrastructure: The Randstad study. In Schreiber, K.-F. (Ed.), *Connectivity in landscape ecology* (pp.163-167). Schöningh, Muenster.
- Harris, John E., and Chester V. Ogan., Eds. 1997. Mesocarnivores of Northern California: Biology, Management, and Survey Techniques, Workshop Manual. August 12-15, 1997, Humboldt State Univ., Arcata, CA. The Wildlife Society, California North Coast Chapter, Arcata, CA. 127 p.

- Harvey, A. (Ed.). (1998). *A sense of place: Issues, attitudes and resources in the Yellowstone to Yukon ecoregion*. Canmore, Alberta: Yellowstone to Yukon Conservation Initiative.
- Henson, B.L., Brodribb, K.E. & Riley, J.L. (2005). *Great lakes conservation blueprint for terrestrial biodiversity, volume 1*. (Nature Conservancy of Canada ISBN 0-9695980-5-X). Retrieved from http://science.natureconservancy.ca/initiatives/blueprints/greatlakes_w.php
- Hilty, J.A., Lidicker, Z.W., Merenlender, M.A. (2006). *Corridor ecology: The science and practice of linking landscapes for biodiversity conservation*. Washington, DC: Island Press.
- Holzgang, O., Pfister, H.P., Heynen D., Blant, M., Righetti, A., Berthoud, G., Marchesi, P., Maddalena, T., Müri, H., Wendelspiess, M., Dändliker, G., Mollet, P., & Bornhauser-Sieber, U. (2001). Les corridors faunistiques en Suisse. Cahier de l'environnement n° 326, Office fédéral de l'environnement, des forêts et du paysage (OFEFP), Société suisse de Biologie de la Faune (SSBF) & Station ornithologique Suisse de Sempach, Bern, 120 p.
- Jaeger, J.A.G. (2007). Effects of the configuration of road networks on landscape connectivity. In Irwin, C.L., Nelson, D., & McDermott, K.P. (Eds.), *Proceedings of the 2007 International Conference on the Ecology and Transportation*. Raleigh, NC: Center for Transportation and the Environment, North Carolina State University.
- Keddy, C. (1995). *The conservation potential of the Frontenac Axis: Linking Algonquin Park to the Adirondacks*. Ottawa, Ontario: The Canadian Parks and Wilderness Society. Retrieved September 26th, 2012, from <http://www.a2alink.org/uploads/7/6/8/5/7685208/keddy-a2a-report3.pdf>
- Klein, D.J., & Randic, M. (1993). Resistance distance. *Journal of Mathematical Chemistry* 12, 81-95.
- Klug, P.E., Wisely, S.M., & With, K.A. (2011) Population genetic structure and landscape connectivity of the Eastern Yellowbelly Racer (*Columber constrictor flaviventris*) in the contiguous tallgrass prairie of northeastern Kansas, USA. *Landscape Ecology* 26, 281-294.
- Koen, E.L., Bowman, J., & Findlay, C.S. (2007a) Fisher survival in eastern Ontario. *Journal of Wildlife Management* 71, 1214-1219.

- Koen, E.L., Bowman, J., Findlay, C.S., & Zheng, L. (2007b). Home range and population density of fishers in eastern Ontario. *Journal of Wildlife Management* 71, 1484-1493.
- Koen, E.L., Garroway, C.J., Wilson, P.J., & Bowman, J. (2010). The effect of map boundary on estimates of landscape resistance to animal movement. *PLoS ONE* 5(7), 1-7.
- Koen, E. L., Bowman, J., & Walpole, A.A. (2012). The effect of cost surface parameterization on landscape resistance estimates. *Molecular Ecology Resources* 12, 686-696.
- Koen, E.L., Bowman, J., & Garroway, C.J. (2012). Landscape resistance and American marten gene flow. *Landscape Ecology* 27, 29-43.
- Koen, E. L., Bowman, J., Sadowski, C., & Walpole, A.A. (2014). Landscape connectivity for wildlife: development and validation of multispecies linkage maps. *Methods in Ecology and Evolution* 5, 626-633.
- Kool, J.T., Moilanen, A., & Treml, E.A. (2013). Population connectivity: recent advances and new perspectives. *Landscape Ecology* 28, 165-185.
- Laita, A., Kotiaho, J.S., & Mönkkönen, M. (2011). Graph-theoretic connectivity measures: what do they tell us about connectivity?. *Landscape Ecology* 26, 951-967.
- Lancaster, P.A., Bowman, J., & Pond, B.A. (2008) Fishers, farms, and forests in eastern North America. *Environmental Management* 42, 93-101.
- Langen, T.A., & Welsh, R. (2006). Effects of a problem-based learning approach on attitude change and science and policy content knowledge. *Conservation Biology* 20(3), 600-608.
- LaPoint, S., Gallery, P., Wikelski, M., & Kays, R. (2013). Animal behaviour, cost-based corridor models, and real corridors. *Landscape Ecology* 28, 1615-1630.
- LaRue A.M., & Nielsen, K.C. (2008). Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. *Ecological Modelling* 212, 372-381.
- Magle, S.B., Theobald, D.M., & Crooks, K.R. (2009). A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. *Landscape Ecology* 24, 267-280.
- Mattson, D.J., Clark, S.G., Byrd, K.L., Brown, S.R., & Robinson, B. (2011). Leaders' perspectives in the Yellowstone to Yukon conservation initiative. *Policy Science* 44, 103-133.

- Mazerolle, M.J. (2004). Appendix 1: Making sense out of Akaike's Information Criterion (AIC): its use and interpretation in model selection and inference from ecological data. Retrieved from <http://avesbiodiv.mncn.csic.es/estadistica/senseaic.pdf>
- Mazerolle, M.J. (2006). Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia- Reptilia* 27, 169-180.
- McGregor, T. (2003). Conservation on a regional scale: Assessing the Yellowstone to Yukon initiative. Unpublished master's thesis, University of Waterloo, Ontario.
- McGregor, T., Murphy, S., & Slocombe, S. (2002). Why Y2Y? Understanding the role of large landscape corridor initiatives in regional conservation planning, using the Yellowstone to Yukon conservation initiative as a case study. *Proceedings of Parks Research Forum of Ontario*, Ridgetown, Ontario, 25-27 April, 2002.
- McRae, B.H. (2006). Isolation by resistance. *Evolution* 60, 1551-1561.
- McRae, B.H., & Beier, P. (2007). Circuit theory predicts Gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the USA* 104, 19885-19890.
- McRae, B.H., & Shah, V.B. (2011) Circuitscape user guide. ONLINE. The University of California, Santa Barbara. Retrieved September 26th, 2012, from <http://www.circuitscape.org>
- McRae, B.H., Dickson, B.G., Keitt, T.H., & Shah, V.B. (2008). Using circuit theory to model connectivity in ecology and conservation. *Ecology* 10, 2712-2724.
- Minor, E.S., & Urban, D.L. (2008). A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology* 22(2), 297-307.
- Moilanen, A., & Hanski, I. (2001). On the use of connectivity measures in spatial ecology. *Oikos* 95(1), 147-151.
- NYS Adirondack Park Agency. (2003). The Adirondack Park. Retrieved from http://apa.ny.gov/About_Park/index.html
- Pelletier, D., Clark, M., Anderson, M.G., Rayfield, B., Wulder, M.A., & Cardille, J.A.. (2014). Applying circuit theory for corridor expansion and management at regional scale: tiling, pinch points, and omnidirectional connectivity. *PLoS ONE* 9(1), 1-11.

- Poor E.E., Loucks C., Jakes A., & Urban D.L. (2012). Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. *PLoS ONE* 7(11), 1-12.
- Powell, R.A. (1993). *The Fisher Life History, Ecology, and Behaviour*. Minneapolis, MN: University of Minnesota Press.
- Powell, R.A. and W.J. Zielinski. (1994). The fisher. In *The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States* (Pages 38-73). L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski, tech. eds. Gen. Tech. Rep. Rm-254. Ft. Collins, CO: USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station. 184 p.
- Powell, R.A., Buskirk, S.W., & Zielinski, W.L. (2003). Fisher and Marten. In Feldhamer, G.A., Thompson, B.C., & Chapmand, J.A. *Wild Mammals of North America*. The Hopkins University Press.
- Prince Edward County Working Group. (2011). *Our Land: Healthy – Vibrant – Valued*. A Natural Heritage System for Prince Edward County and Neighbouring Communities. Retrieved from http://www.pecounty.on.ca/government/eng_dev_works/development_services/pdf/Addendum21ANaturalHeritageSystemReport.pdf
- Queens University Biological Station (QUBS). (2012a). Working toward a Strategic Roadmap for Connectivity, A2A Workshop #1 Proceedings. Canada, Ontario. Retrieved from http://www.a2alink.org/uploads/7/6/8/5/7685208/a2a_workshop_proceedings_april_28_2012.pdf
- Queens University Biological Station (QUBS). (2012b). Working toward a Strategic Roadmap for Connectivity: Forming a Collaborative Network, A2A Workshop #2 Proceedings. Canada, Ontario. Retrieved from http://www.a2alink.org/uploads/7/6/8/5/7685208/a2a_workshop_proceedings_october_20_2012_.pdf
- Quigley, H.B., & Crawshaw, P.G. Jr. (1992). A conservation plan for the jaguar, *Panthera onca* in the Pantanal region of Brazil. *Biological Conservation* 61, 149-157.

- Quinby, P., Trombulak, S., Lee, T., Lane, J., Henry, M., Long, R., & MacKay, P. (1999). Opportunities for wildlife habitat connectivity between Algonquin Park, Ontario, and the Adirondack Park, New York. Vermont: The Great Laurentian Wildlands Project.
- Urban, D.L., Minor, E.S., Treml, E.A., & Schick, R.S. (2009). Graph models of habitat mosaics. *Ecology Letters* 12, 260-273.
- Urban, D., & Keitt, T. (2001). Landscape connectivity: A graph-theoretic perspective. *Ecology* 82(5), 1205-1218.
- Rabinowitz, A., & Zeller, K.A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation* 143, 919-945.
- Rohweder, J.J., De Jager, N.R., & Guntenspergen, G.R. (2012). Anticipated effects of development on habitat fragmentation and movement of mammals into and out of the Schoodic District, Acadia National Park, Maine. U.S. Geological Survey Scientific Investigations Report 2012–5149, 30 p.
- Rosenberg, D.K., Noon, B.R., & Meslow, C.E. (1997). Biological corridors: form, function, and efficacy. *Bioscience* 47 (10), 677-687.
- Rosatte, R. C., ET AL. (2001). Emergency response to raccoon rabies introduction into Ontario. *Journal of Wildlife Diseases* 37, 265–279.
- Rosatte, R. C., Power, M.J., MacInnes, C. D., & Campbell, J.B. (1992). Trap–vaccinate–release and oral vaccination for rabies control in urban skunks, raccoons, and foxes. *Journal of Wildlife Diseases* 28, 562–571.
- Rousset, F. (1997). Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145, 1219-1228.
- Rykiel, E.J., Jr. (1996). Testing ecological models: the meaning of validation. *Ecological Modelling* 90, 229-244.
- Saunders, D.A., Hobbs, R.J., & Margule, C.R. (1991). Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5(1), 18-32.
- Saura, S. (2010). Measuring connectivity in habitat mosaics: the equivalence of two existing network indices and progress beyond them. *Community Ecology* 11(2), 217-222.
- Sawyer, S.C., Epps, C.W., & Brashares, J.S. (2011). Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *Journal of Applied Ecology* 48, 668–678.

- Schumaker, H. N. (1996). Landscape indices to predict habitat connectivity. *Ecology* 77(4), 1210-1225.
- Seaman, D. E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., & Gitzen, R.A. (1999). Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management* 62 (2), 739-747.
- Selva, N., Krefk, S., Kati, V., Schluck, M., Jonsson, B-G., Mihok, B., Okarma, H., & Ibisch, P.L. (2011). Roadless and low-traffic areas as conservation targets in Europe. *Environmental Management* , 48 (5), 865–877.
- Seton, E.T. (1929). Lives of game animals. Doubleday, New York, New York, USA.
- Simberloff, D., Farr, J.A., Cox, J., & Mehlman, D.W. (1992). Movement corridors: Conservation bargains or poor investments?. *Conservation Biology* 6(4), 493-504.
- Shah, V.B. (2007). An Interactive System for Combinatorial Scientific Computing with an Emphasis on Programmer Productivity. PhD thesis, University of California, Santa Barbara.
- Shah, V.B., & McRae, B.H. (2008). Circuitscape: a tool for landscape ecology. In: G. Varoquaux, T. Vaught, J. Millman (Eds.). Proceedings of the 7th Python in Science Conference (SciPy 2008), pp. 62-66.
- Sheskin, D. (2004). *Handbook of parametric and nonparametric statistical procedures: Third edition*. Boca Raton, Florida: CRC Press.
- Soga, M., & Kioke S. (2012). Relative importance of quantity, quality and isolation of patches for butterfly diversity in fragmented urban forests. *Ecological Research* 27, 265-271.
- Spear, S.F., Balkenhol, N., Fortin, M.J. McRae, B.H., & Scribner, K. (2010). Use of resistance surfaces for landscape genetic studies: consideration for parameterization and analysis. *Molecular Biology* 19, 3576-3591.
- Spencer, W.D., Beier, P., Penrod, K., Winters, K., Paulman, C., Rustigian-Romsos, H., Strittholt, J., Parisi, M., & Pettler, A. (2010). California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.
- Stephenson, B. (2001). The Algonquin to Adirondack conservation initiative: a key macro-landscape linkage in eastern North America. In D. Harmon (Ed.), *Crossing Boundaries in*

- Park Management: Proceeding of the 11th Conference on Research and Resource Management in Parks and on Public Lands* (303-310). Michigan: The George Wright Society.
- Taylor, P.D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos* 68(3), 571-573.
- Tischendorf, L., & Fahrig, L. (2000). On the usage and measurement of landscape connectivity. *Oikos* 90(1), 7-19.
- Tischendorf, L., & Fahrig, L. (2001). On the use of connectivity measures in spatial ecology: A reply. *Oikos* 95(1), 152-155.
- The Friends of Algonquin Park. (2005). *Introduction to Algonquin Park*. Retrieved from The Science Behind Algonquin's Animals on December 6th, 2012, from <<http://www.sbaa.ca/about.asp?cn=275>>
- Thornton, D.H., Branch, L.C., & Sunquist M.E. (2011). The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology* 26, 7-18.
- Travis, J.M.J., & French, D.R. (2000). Dispersal functions and spatial models: Expanding our dispersal toolbox. *Ecology Letters* 3, 163-165.
- Tully, S.M. (2006). *Habitat selection of fishers (Martes pennant) in an untrapped refugium: Algonquin Provincial Park*. Unpublished master's thesis, Trent University, Peterborough, Ontario.
- Van Der Grift, E. (2005). Defragmentation in the Netherlands: A success story?. *GAIA* 14(2), 144-147.
- Vásárhelyi, C., & Thomas, V.G. (2006). Evaluating the capacity of Canadian and American legislation to implement terrestrial protected areas networks. *Environmental Science & Policy* 9, 46-54.
- Walpole, A.A., & Bowman, J. (2012). Functional connectivity of lynx at their southern range in periphery in Ontario, Canada. *Landscape Ecology* 27, 761-773.
- Wydeven, P.A., Fuller, K.T, Weber, W., & MacDonald, K. (1998). The potential for wolf recovery in the northeastern United States via dispersal from southeastern Canada. *Wildlife Society Bulletin* 26(4), 776-784.
- Yellowstone to Yukon Conservation Initiative. (2012). Retrieved October 24th, 2012, from

<http://y2y.net/>

Zeigler, S.L., Neel, M.C., Oliveira, L., Raboy B.E., & Fagan F.W. (2011). Conspecific and heterospecific attraction in assessments of functional connectivity. *Biodiversity and Conservation* 20, 2779-2796.

Zeller K.A., McGarigal K., & Whiteley A.R. (2012). Estimating landscape resistance to movement: a review. *Landscape Ecology* 27, 777–797.

Appendix

Appendix 1: Use of 2011 road data

As the road data used to calculate proximity to roads was from 2011, falling outside of the trapping years of 1995-2004, I did a visual inspection of the 2004 Ontario roads layer from DMTI Spatial that I was able to acquire from Alex Guindon, Concordia University's geospatial and data services librarian. Based on this visual inspection, there are only minimal changes in the road network between these two points in time. Intuitively, one might imagine that there would be more roads within the 2011 dataset; however, there are many instances where roads are shown in this 2004 dataset that are not present at the later time (2011). These additional roads in the 2004 dataset were classified as "local roads", defined as either a subdivision road in a city or a gravel road in a rural area. As these roads are found in rural areas, these are gravel roads. These additional roads range from dead-end streets to horseshoe type additions to some cases where they connect two roads together, and even in these cases the road would not be the nearest road to the centroid of the trapping cells, even if they had been included within the analysis. However, there is one case of a road which intersects a trapping cell (123) where it would have been the nearest road if had been included. These additional roads from 2004 fall into the low impacting roads class from the 2011 dataset, and so even if they were not included in the analysis their effects on the movement of fishers are very small (due to their low traffic volume and surface type). The slight additions of roads in the 2011 dataset compared to 2004 are mostly dead-end offshoots from another road or the occasional small horseshoe. It must also be noted that these layers are from two different sources: CanVec (2011) and DMTI Spatial (2004), and therefore their accuracies and procedures for mapping vary and many differences between these two maps can also be attributed to these effects. Unfortunately, I was unable to get older road data from CanVec due to how they update their data, in effect replacing their older data with the newer versions. I also compared the 2011 data with 1995 road data from Fenech (2005). Though only major, secondary, primary and expressways are shown in this 1995 dataset, they match those of the 2011 data, showing that no high or medium impacting roads were added after 1995.

Models are approximations of reality and as researchers we can only do our best with the data that is available and make appropriate generalizations and assumptions. Ideally, one would have

to take the road network from each individual trapping year and then calculated proximity to roads for every year to account for any changes in the road network.

In addition, we validated our suitability models with data from a telemetry study which extended past the trapping dataset (2003 up to 2005), while our land cover is static, only showing year 2000, so there are several aspects which are not ideal. However, these comparisons with older road data indicate that the analysis is valid and the models used are sound.

Appendix 2: Use of resistances or conductances

The way the cost surface is parameterized using resistances or conductances, in Circuitscape, can potentially influence the outcome of the model. In an email discussion with Brad McRae (the main author of Circuitscape), I expressed concerns about the calculation of averaging conductances as is done in Circuitscape when conductances are entered. As resistance is the inverse of conductance (Tab. A1), the results of averaging resistances and averaging conductances, should be the same, however this is not the case (when substituting the values of one for the other, Tab. A1).

Table A2: Equation used for averaging conductance in Circuitscape (McRae & Shah 2011) and comparison with resistance (R is resistance, V is voltage, I is current and G is conductance).

<p>Equation for resistance</p> $R = \frac{V}{I}$	<p>Equation for conductance</p> $G = \frac{I}{V}$
<p>Equation for average resistance</p> $R_{ab} = \frac{R_a + R_b}{2}$	<p>Equation for average conductance in Circuitscape</p> $G_{ab} = \frac{G_a + G_b}{2}$
<p>Example where $R_a = 1\ ohm$ and $R_b = 10\ ohms$</p> $R_{ab} = \frac{R_a + R_b}{2} = \frac{R_a + R_b}{2} = \frac{1 + 10}{2} ohms = 5.5\ ohms$	<p>Example where $R_a = 1\ ohm$ and $R_b = 10\ ohms$</p> $G_{ab} = \frac{G_a + G_b}{2} = \frac{\frac{1}{R_a} + \frac{1}{R_b}}{2} = \frac{\frac{1}{1} + \frac{1}{10}}{2} si = 0.55\ si$ <p>Resulting in $R_{ab} = \frac{1}{G_{ab}}$</p> $\frac{1}{0.55\ si} = 1.818\ ohms$

Based on these concerns, this study parameterized random walk probabilities in resistances in accordance with the rules of circuit theory, unlike the equation for averaging conductances (according to McRae & Shah 2011). Brad McRae supports that most users use average resistances and that it is a good choice for parameterizing a cost surface (B. McRae, personal communication, December 2012). This is also reinforced by Koen et al. (2012) as their recommendation for the most accurate parameterization and functional connectivity estimates is

based on coding cost surfaces as resistances. Resistance surfaces have also been used in other studies (Garroway et al. 2011; Koen et al. 2010; McRae & Beier 2007; Zeigler et al. 2011).

Appendix 3: Summary of explanatory variables within TVR trapping cells.

Table A3: Proportion of urban area, agricultural land, forest, wetland, water (in percentage of total cell area) and distances (km) to the nearest road for each of the 93 TVR trapping cells (range of 1.168 km² to 34.394 km²) included is the annual average of fisher captures per 100 trap nights (i.e. TS) in each trapping cell.

CELL_ID	CELL_SQKM	TS_100TN	URB	AGRO	FOR	WET	WAT	PROX_ROAD
1	19.113	0.000	0.000	84.151	11.753	0.607	3.503	0.395
2	8.185	0.000	0.000	84.165	14.119	0.429	1.265	0.562
3	11.154	0.000	0.000	54.584	3.058	38.205	4.180	0.683
4	14.586	0.000	0.000	89.863	5.251	0.253	4.628	0.088
5	13.780	0.000	0.000	84.377	5.911	5.460	4.226	0.524
6	13.620	0.000	0.000	87.824	12.020	0.145	0.000	0.021
7	12.335	0.000	0.000	77.767	17.840	3.758	0.693	0.190
8	16.316	0.000	0.000	80.374	10.083	6.062	3.497	0.042
9	16.428	0.000	0.000	71.244	19.592	3.271	5.873	0.365
10	14.323	0.000	0.000	73.604	20.283	0.170	5.925	0.060
11	9.183	0.114	0.000	29.403	56.905	8.301	5.430	0.265
12	13.629	0.089	0.000	34.701	61.914	2.153	1.182	0.884
13	12.886	0.206	0.000	45.222	51.571	2.919	0.279	0.909
14	18.186	0.046	0.000	67.922	29.109	2.930	0.000	0.649
15	17.452	0.217	0.000	35.583	60.145	2.970	1.346	0.717
16	12.219	0.000	10.231	40.350	44.511	3.698	1.223	0.563
17	14.533	0.000	13.085	34.381	48.414	3.449	0.700	0.661
18	10.387	0.000	3.371	53.853	39.513	2.634	0.676	0.986
19	4.169	0.000	39.335	40.954	17.552	1.792	0.410	0.010
20	13.435	0.058	0.100	50.162	38.124	11.120	0.509	1.012
21	13.209	0.000	0.000	43.239	49.194	7.338	0.164	0.920
22	9.101	0.051	0.000	39.408	41.020	19.630	0.000	0.543
23	12.671	0.158	0.000	19.340	58.781	21.890	0.000	0.181
26	10.993	0.049	4.339	32.684	59.325	0.917	2.694	0.841
27	16.409	0.032	0.000	29.942	60.345	4.218	5.392	0.828
28	8.793	0.082	0.000	25.026	66.622	7.370	0.993	0.048
29	10.595	0.119	0.000	24.499	64.273	9.608	1.733	0.456
30	11.600	0.117	0.000	46.948	42.774	9.070	1.234	0.869
31	8.772	0.139	0.000	23.597	72.607	2.565	1.139	1.081
32	6.626	0.167	0.000	62.901	35.926	0.896	0.204	0.564

33	14.074	0.058	0.000	75.772	18.922	3.306	2.059	0.243
34	13.914	0.025	0.000	81.799	17.238	0.983	0.000	0.382
35	8.864	0.036	0.000	75.500	22.226	2.264	0.000	0.968
36	11.632	0.111	0.000	39.917	58.750	1.037	0.286	0.484
37	13.006	0.153	0.000	35.949	62.667	0.747	0.609	0.890
38	10.088	0.084	0.000	55.868	42.610	0.883	0.660	0.942
39	10.575	0.075	0.000	78.334	21.558	0.153	0.000	1.087
40	9.299	0.055	0.000	50.356	46.146	1.781	1.694	1.078
41	19.774	0.000	0.000	15.379	37.981	41.454	5.125	1.694
42	12.012	0.092	0.000	78.603	20.919	0.187	0.277	0.680
43	10.072	0.163	0.000	73.319	26.405	0.295	0.000	0.898
44	9.676	0.156	0.000	53.361	44.748	1.749	0.205	0.584
45	9.712	0.214	0.000	67.833	31.924	0.278	0.000	1.028
46	12.724	0.048	0.000	20.124	70.889	3.056	5.934	0.081
47	12.383	0.044	0.000	49.284	49.836	0.589	0.276	0.153
48	11.457	0.181	0.000	17.989	73.159	4.548	4.234	0.163
49	16.017	0.165	0.000	48.334	48.598	2.911	0.129	1.481
50	5.858	0.041	0.000	72.960	25.580	1.444	0.000	0.635
51	10.778	0.072	0.000	51.044	46.285	0.952	1.779	0.582
52	11.114	0.149	0.000	3.328	84.945	2.899	8.827	1.228
53	8.593	0.283	0.000	5.321	61.691	25.001	7.981	1.141
54	8.114	0.084	0.000	42.291	49.612	6.943	1.165	0.529
55	1.168	0.000	0.000	74.182	20.876	3.312	1.849	0.061
56	8.586	0.145	0.000	41.581	46.811	10.272	1.384	0.819
60	9.396	0.000	1.130	57.206	37.004	3.650	0.967	0.630
70	2.954	0.000	76.567	7.587	8.501	0.000	7.191	0.004
71	9.881	0.261	0.000	50.260	42.044	3.197	4.500	0.118
72	13.499	0.102	0.087	61.336	33.728	0.787	4.120	0.128
73	8.391	0.249	1.856	39.107	54.970	3.389	0.772	0.853
74	19.432	0.151	0.065	39.591	52.032	5.664	2.608	0.698
75	12.918	0.076	0.000	68.830	31.081	0.042	0.000	0.819
76	15.430	0.208	0.000	78.109	21.465	0.443	0.000	0.017
77	17.178	0.000	0.000	70.273	29.177	0.534	0.000	0.178
78	14.222	0.075	0.000	66.517	32.914	0.481	0.076	0.796
79	17.853	0.053	0.000	58.528	39.649	0.706	1.074	0.885
80	11.636	0.026	0.000	70.421	29.545	0.085	0.000	0.715
81	15.281	0.131	0.000	65.531	33.313	0.654	0.507	0.672
82	12.030	0.086	0.000	67.653	22.721	2.102	7.511	0.412
83	34.392	0.000	12.045	44.455	38.887	3.525	1.094	0.906
84	17.521	0.047	0.000	48.710	42.700	5.676	2.902	0.941
85	14.268	0.018	0.000	68.584	27.073	2.334	2.018	0.744

86	5.020	0.025	0.000	62.835	33.703	0.179	3.406	0.239
87	16.316	0.113	0.000	21.182	71.776	2.366	4.766	1.327
88	13.512	0.095	0.000	30.993	59.223	8.026	1.752	0.838
91	13.372	0.458	0.000	18.368	59.491	21.282	0.828	1.097
92	12.140	0.042	0.000	40.188	51.775	7.925	0.111	0.237
119	17.296	0.000	0.000	61.631	22.974	15.397	0.000	0.575
122	17.213	0.000	0.000	32.261	60.077	6.672	0.973	0.425
123	13.011	0.000	0.000	30.054	63.193	5.976	0.775	1.018
124	9.398	0.201	2.404	71.586	19.795	6.244	0.000	1.338
125	13.848	0.000	1.677	62.156	13.401	22.038	0.656	0.337
126	13.747	0.000	0.000	26.836	25.946	33.769	13.461	1.265
127	11.467	0.437	0.000	67.833	28.811	1.240	2.103	0.805
129	16.392	0.563	0.000	25.454	40.471	22.649	11.453	0.289
130	17.842	0.420	0.000	19.789	67.981	8.404	3.813	0.106
135	18.629	0.328	0.329	32.765	58.994	6.802	1.029	0.681
136	19.561	1.233	0.138	41.336	53.248	5.374	0.000	0.590
137	13.190	0.114	0.000	15.686	75.423	5.131	3.746	0.825
143	14.840	0.651	0.000	37.717	51.484	8.576	2.226	1.508
145	9.159	0.275	0.000	35.985	59.382	4.619	0.000	0.983
146	15.325	0.452	0.000	11.528	79.598	4.751	4.181	1.017
154	14.089	0.914	0.000	33.109	55.313	5.979	5.621	0.233
155	14.783	0.080	0.000	43.676	49.064	6.472	0.731	0.762

Appendix 4: Location of focal nodes

Figure A4a: Linear focal node placement (grey lines)

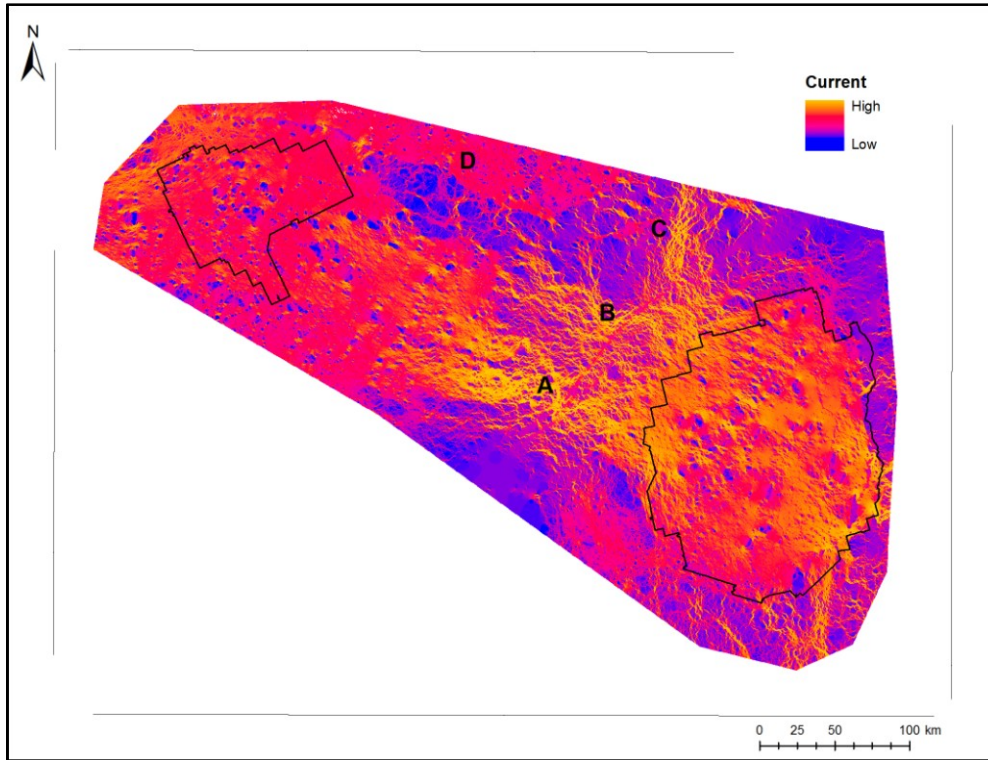


Figure A4b: Random focal node placement (black dots)

