Quantifying Landscape Connectivity Using Probability of Connectivity Response Curves

by

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ABSTRACT

Maintenance of habitat connectivity is recommended as a method of promoting biodiversity. A systematic manipulation of a simple theoretical landscape was used to assess how a landscape connectivity index responded to specific changes in habitat distribution. Quantifying the response of the index to changes in the spatial scale of dispersal is proposed as a method of objectively quantifying multiple aspects of landscape structure known to influence habitat connectivity. An ecosystem simulation model was used to assess if the index demonstrated the same patterns of response to changes in complex landscapes, and to quantify impact of logging distribution, roads, natural disturbances and habitat corridors. The high degree of sensitivity to the presence of roads, and the scale of response to different management scenarios highlight the value of the proposed index, and the sensitivity to the assumptions of habitat delineation used in index calculation.

Keywords: connectivity, landscape ecology, forestry, biodiversity

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CHAPTER 1: LANDSCAPE CONNECTIVITY

INTRODUCTION

Managing for diverse social, economic and ecological values is a common theme in sustainable forest management, and the conservation of biodiversity contributes to these values (Ehrlich and Ehrlich 1992, Carey 2003). Modern forest management attempts to maximize the post-harvest habitat value of the forestry land base in order to conserve biodiversity (Lindenmayer 2009). Modern ecosystem management recognizes that ecosystems are not static entities and that periodic disturbances result in a heterogeneous distribution of seral stages and structural conditions across the landscape. By manipulating the location, nature, and timing of harvest, a manager can emulate natural disturbances (Klenk et al. 2009) and in the process create landscapes that are more likely to recover existing flora and fauna (Mitchell et al. 2002, Buddle et al. 2006). Habitat connectivity has been widely recognized as a factor that contributes to maintaining biodiversity in ecosystems affected by anthropogenic disturbances (Taylor et al. 1993, Fahrig 2003, Lindenmayer and Fischer 2007, Brudvig et al. 2009). Promoting connectivity within a landscape contributes to biodiversity conservation by creating conditions where the retained habitat patches conserve species typical of non-disturbed habitat, and serve as routes to facilitate the re-colonization of depopulated areas (Polasky et al. 2005).

Although the concept of habitat connectivity and its value as a conservation strategy make intuitive sense, its application to landscape management has been limited by the lack of a consistently-applied objective metric to quantify connectivity and compare the outcome of management strategies, due primarily to the multitude of proposed metrics. Habitat connectivity has been interpreted from a variety of perspectives, with different metrics proposed to quantify each perspective (Baguette and Van Dyck 2007). The assumptions inherent in each approach will affect the assessment of connectivity for identical distributions of habitat. Furthermore, the spatial scale of examination and the data limitations inherent in landscape scale analyses further complicate the objective quantification of landscape connectivity values. In order to help guide forest management strategies a connectivity metric must realistically represent the impacts of forestry to a range of species.

Values derived from connectivity indices are simply an empirical method of describing the landscape characteristics: they do not carry with them any weighting of what is an ideal landscape structure. The metrics that describe an affected landscape must be compared to a desired or initial landscape composition in order to provide some context to the impacts of anthropogenic disturbances (Nielsen et al. 2007, Matisziw and Murray 2009). Frequently the estimated state of ecosystems prior to anthropogenic disturbances is used as a benchmark when attempting to determine a desirable landscape state. In addition to the difficulties of determining landscape structure outside of the narrow time frame for which we have extensive forest inventories, there is a natural range of variability in age distribution of forests in landscapes subject to natural disturbances (Keane et al. 2009). In order to determine what this range may be, assessments must be performed at a relevant spatial and temporal scale (Mayer and Rietkerk 2004).

CONNECTIVITY DYNAMICS

Habitat connectivity contributes to biodiversity conservation through its impact on metapopulation dynamics. The term metapopulation was first introduced in 1970 by Richard Levins, and can be summarized as a population of populations, where a metapopulation encompasses all individuals of multiple populations of a species that exist within a defined geographic region (Hanski 1999). "Metapopulation biology is concerned with the dynamic consequences of migration among local populations and the conditions of regional persistence of species with unstable local populations" (Hanski 1998). Immigration and emigration rates between habitat patches are understood to impact the persistence of both subpopulations and the metapopulation as a whole (Hanski et al. 2008). Immigration and emigration rates are affected by the ease of dispersal between populations, and the net reproductive output of the source populations. If a landscape is well connected, it allows for the movement of individuals or genetic material between populations, decreasing the probability of extinction for both populations and enhancing metapopulation persistence (Hanski and Ovaskainen 2003, Ovaskainen et al. 2004). Stable metapopulations of species can be maintained in landscapes subject to disturbance regimes if disturbances occur at a frequency and distribution that allows for previously disturbed habitat to regain similar habitat characteristics, making them suitable for colonization, and there is sufficient connectivity between extant populations and areas where a population has been extirpated (With et al. 2006, Vuilleumier et al. 2007, Nabe-Nielsen et al. 2010). A metric that can quantify the limitations to dispersal between habitat patches can therefore be used to assess the how the distribution of habitat affects metapopulation persistence within a landscape. Since species vary in the spatial scale of dispersal, a metric that quantifies the distribution of habitat at a range of spatial scales will provide insight for a larger range of species.

Despite the interactions and similarities between the disciplines of landscape ecology and metapopulation biology, segregation exists between the two disciplines (Moilanen and Hanski 2001, Tischendorf and Fahrig 2001, Prugh 2009, Jacobson and Peres-Neto 2010, Schooley and Branch 2011). Both disciplines are concerned with the emergent properties at larger spatial scales resulting from many small scale relationships. The division between the two disciplines is largely based on the perspective of examination, and exacerbated by different terminology sometimes being used to describe the same concept between disciplines. A widely-cited definition of landscape connectivity is, "the degree to which the landscape facilitates or impedes movement among resource patches", (Taylor et al. 1993). This definition highlights the differences between landscape connectivity, where the degree that landscape structure impedes movement in general is quantified, and patch connectivity, where the movement to/from a specific habitat patch is quantified (Tischendorf and Fahrig 2001). In metapopulation theory, the dynamics of subpopulations are quantified at the patch scale and the impediments to the greater metapopulation persistence is quantified at the landscape scale (Hanski and Ovaskainen 2000). Landscape connectivity metrics are objective methods of combining all patch level connections within a landscape to calculate an assessment of overall connectivity.

For the majority of species within a landscape, metapopulation dynamics play a greater role in species distribution and composition than the survival and dispersal of individuals since local extinctions are an expected occurrence in many metapopualtion models (Hanski 1999). Additionally, in many landscapes site-specific environmental characteristics of a habitat patch play a greater role in determining species composition than connectivity to other habitat patches (St-Laurent et al. 2009). Maintaining landscape connectivity should therefore not be viewed as a “silver bullet” solution that can be expected to satisfy all biodiversity concerns. The connectivity of a landscape will only affect the probability of emigrating individuals reaching other habitat patches, and other metapopulation values must be appropriately managed to ensure that there is a net output of dispersers (Hodgson et al. 2009, 2011). When considering the connections between patches in a landscape, individual dispersal is relevant only in how it defines limitations to emigration, immigration and colonization rates of a metapopulation.

FORESTRY AND CONNECTIVITY

Forestry is widespread in British Columbia, representing one of the dominant land use types, and is understood to affect landscape structure by transforming late seral habitat and re-setting it to early seral habitat that is often inhospitable to many of the species that previously utilized the harvested area (McGarigal et al. 2001, Molina et al. 2006, Nitschke 2008). Forestry reduces the total pool of late seral forest habitat and may fragment remaining late seral habitat with tracts of inhospitable early seral habitat to be crossed (Wulder et al. 2009, Zwolak 2009). Forestry also fragments habitat through the influence of the road network necessary for timber extraction, since roads directly impact populations through mortality, and act as a semi permeable barrier to the dispersal of genetic material (Reed et al. 1996, Holderegger and Di Giulio 2010). The severity of these effects varies between species, based on their motility and habitat requirements, but are generally viewed as fragmenting otherwise contiguous patches of forest habitat and results in negative population impacts (Tinker et al. 1998, Fahrig and Rytwinski 2009). The forests of British Columbia have been subject to a short history of industrial disturbances on the global scale of anthropogenic disturbances. Unlike residential developments, agriculture, or the conversion of forests, logging does not result in a permanent loss of forest habitat and there is the potential for impacted habitat to regain some or all of its former value as succession proceeds (Clark et al. 2003, Welsh et al. 2008). The goal of modern forest management is to determine strategies that will allow for continued resource extraction over time without impacting landscape structure to the point that it results in an unacceptable loss of biodiversity (Boutin et al. 2009). Conceptually, biodiversity is maintained by conserving desirable habitat so that there are patches to support populations of species that use a particular habitat type, and sufficient connectivity between patches to maintain a viable metapopulation in the landscape. In addition to forestry, the distribution of mature forest habitat is affected by natural disturbances, that are widely recognized as playing a key role in the heterogeneous age distribution of forests in North America (Klenner et al. 2000, Amiro et al. 2001). The current policy of forest management in British Columbia recognizes the necessity of concurrently managing for both economic and environmental values (Hoberg and Malkinson 2012). Distributing areas of harvesting so that landscape connectivity is maintained will increase the persistence of late seral species, allowing continued resource extraction while maintaining biodiversity.

The concept of habitat connectivity is a largely theoretical construct with no single widely-adopted metric for assessment, yet it is widely cited as a proposed method of mitigating or preventing anthropogenic ecosystem impacts (Bailey 2007). There are a range of proposed metrics based on either extrapolation of the theoretical basis of habitat connectivity or computer simulations, each with inherent assumptions and limitations in how they quantify landscape connectivity (Schumaker 1996, Tischendorf and Fahrig 2000b, Vos et al. 2008, Watts and Handley 2010, Minor and Lookingbill 2010). An impediment to the management of landscapes for connectivity is the disparity between the scale at which we are interested in managing landscapes, and the scale at which connectivity indices have been empirically validated and can be practically applied.

LANDSCAPE FACTORS

In any examination of connectivity the most basic underlying assumptions are the criteria for delineating acceptable habitat from inhospitable habitat within a landscape (Girvetz and Greco 2007). The delineation of habitat requires a subjective decision of which species assemblies are to be conserved within the landscape. Although there is recognition of the importance of maintaining a heterogeneous distribution of tree species and ages, frequently the habitat type of concern in most forestry conservation strategies is late seral or old-growth forests (Richards et al. 2002, St-Laurent et al. 2008). This focus on late seral habitat does not solely represent a bias towards old forest structure, as there is a lesser need to manage for early seral stage habitat for a variety of reasons. For example, we are able to easily create new early seral habitat by inducing disturbances where we desire that habitat type, compared to late seral habitats which are more difficult to replace since centuries may be required after disturbance to regain previous habitat structure. Also, the species that occupy early seral habitat primarily exploit that niche through high dispersal and establishment capabilities (Franklin 1993, Molina et al. 2006, James et al. 2007). It would therefore be expected that lower levels of connectivity between early seral habitat patches are required to maintain viable metapopulations (Acuna and Estades 2011). Based on these factors, the majority of forestry management is focused on the conservation of late seral forest habitat within landscape units.

Although debate exists as to the best method of quantifying landscape connectivity of delineated habitat patches, there are several basic aspects of landscape structure that exert an influence on connectivity. Currently connectivity is viewed as a function of both the distribution of habitat and how alternative habitat types impede movement between habitat patches (Ricketts 2001, Fahrig 2003, Hodgson et al. 2011). There are several factors of the distribution of habitat that affect the likelihood of dispersal between patches including the fragmentation of habitat, the spatial dispersion of fragmented patches, and the total amount of habitat in the landscape.

Two patches are considered to be fragmented when they are isolated from areas of similar habitat by some expanse of a comparatively inhospitable habitat type (Lindenmayer and Fischer 2006). In the context of quantifying the impacts of forestry on landscape connectivity, early seral harvested sites and their associated road networks are assumed to fragment patches of late seral forest (McGarigal et al. 2001, Houle et al. 2010). At the landscape scale, fragmentation is the degree that total available habitat is fragmented into different patches. When habitat is fragmented into an increased number of patches, it decreases the connectivity of that landscape, and divides large populations into groups of smaller, potentially unconnected subpopulations, therefore decreasing the probability of both population and metapopulation persistence (Andren 1994). Larger distances of inhospitable matrix between fragmented patches increases the dispersion of those patches. The level of dispersion necessary for two patches to be considered unconnected is a function of the assumed dispersal capabilities of a species for that habitat type (Swihart et al. 2003, Bowler and Benton 2005). At the landscape scale, all potential habitat connections are considered to give an assessment of overall habitat dispersion (Anderson et al. 2006). At the patch scale, habitat amount describes the size of each habitat patch. Increased habitat patch sizes are considered beneficial for metapopulation persistence. At the landscape scale, habitat amount refers to the total proportion of the landscape occupied by a specific habitat type.

Habitat amount has been demonstrated to be the primary determinant of species abundance and persistence (Fahrig 2003, St-Laurent et al. 2009). The amount of habitat in a landscape exerts substantial influence on landscape connectivity, to the extent that above a percolation threshold of habitat amount, the distribution of habitat has minimal impacts on connectivity (With and Crist 1995, Flather and Bevers 2002, Holyoak 2008). Management decisions regarding the amount of forest to be harvested or conserved are frequently based on extraneous economic, social and ecological considerations (Snetsinger 2008). Connectivity indices are proposed as a method of determining how the prescribed amounts of harvest should be distributed across a landscape to mitigate the impacts of the inevitable habitat loss on the fragmentation and dispersion of the remaining habitat patches throughout the rotation period (Smith et al. 2009). In this context, an index that is able to distinguish differences in the interdependent factors of habitat amount and distribution is necessary for useful comparisons (Long et al. 2010).

CONNECTIVITY METRICS

The primary conceptual perspectives for quantifying connectivity are structural, functional, and potential connectivity (Doak et al. 1992, Demers et al. 1995, Tischendorf and Fahrig 2000a, 2000b, Calabrese and Fagan 2004, Kindlmann and Burel 2008). Structural connectivity describes only the distribution of habitat patches in a landscape without any consideration of how species move through the landscape. Functional connectivity quantifies actual rates of movement of a species, incorporating as many factors as necessary to accurately describe observed population dynamics (Kadoya 2009). The potential connectivity of a landscape is an intermediate perspective where landscape structure, combined with generalized assumptions of the limitations to dispersal, are used to describe the connectivity of a landscape.

Structural connectivity metrics, such as the number of patches, nearest neighbour distance, patch area, core area, patch perimeter, contagion, fractal dimension and patch cohesion have been widely applied in examinations of habitat distribution, due in part to their low data requirements and ease of calculation (Schumaker 1996, Fagan and Calabrese 2006). Structural connectivity explicitly quantifies a specific landscape characteristic. These indices are not direct measures of landscape connectivity, but rather of habitat characteristics understood to be indicators of a well-connected landscape. These types of simple metrics may accurately capture the influence of landscape changes on a single factor of landscape structure, such as fragmentation, but can be completely insensitive to the dispersion and amount of habitat in the fragmented patches.

Functional connectivity considers the realized movement of populations, individuals or genetic material between different patches of habitat (Kindlmann and Burel 2008). Since different species move through and use habitat at different spatial scales, functional connectivity is species-specific and dependent on both the behaviour of the species of concern and the landscape structure (Kadoya 2009). Two habitat patches can therefore have high functional connectivity for an organism that is able to disperse long distances, but have low functional connectivity for an organism with lower dispersal abilities (Swihart et al. 2003). When the goal of landscape management is to conserve biodiversity, the impacts of anthropogenic disturbances must be considered for species with both large and small dispersal capabilities.

A common method of quantifying functional connectivity is to apply spatially-explicit population models of a focal species to quantify connections between habitat patches and extrapolate those values to a landscape scale metric (Ovaskainen and Hanski 2003, Betts et al. 2006, Horne et al. 2008). Though this approach is useful for the management of a species of concern, it may not necessarily reflect the general patterns of habitat distribution in a landscape (Edenius and Mikusinski 2006). There are many factors that will affect the value of a habitat patch and its contribution to species abundance outside of its connectedness to other habitat patches (Ovaskainen and Hanski 2003, Bowler and Benton 2005, Radford et al.

2005). Spatially-explicit population models will therefore be influenced by a multitude of species-specific factors that may have limited influence on other species that use a habitat type. Some impediments to individual dispersal may indicate a well-connected landscape. For example, intra-specific territoriality could limit an individual's ability to move through a habitat patch, but would indicate a viable metapopulation since habitat patches would need to be occupied by conspecifics in order for territoriality to act as a barrier to dispersal. Establishing a spatially-explicit population model for a focal species is also inherently prone to uncertainty in terms of how well each additional model factor accurately represents the behavior of that species (Beier et al. 2009). The accuracy of these values is important as minor changes to model inputs lead to significant variation in the results of connectivity indices based on population models (Rayfield et al. 2010). In addition to the logistical difficulties of establishing an accurate spatially-explicit population model, there is debate as to the validity of extrapolating results from a focal species to a range of species since it contradicts the theory of niche specialization leading to heterogeneous species distribution (Lindenmayer et al. 2002). When assessing landscape connectivity for the conservation of biodiversity, the goal is to quantify the degree to which anthropogenic disturbances reduce the ability of a variety of species to occupy acceptable habitat that is available in the landscape. These impacts are not likely to be detected by functional connectivity metrics of a single focal species.

For landscape managers seeking to maintain connectivity for biodiversity conservation, connectivity metrics may need to only incorporate general principles of connectivity, such as distance thresholds, to accurately reflect broad scale connectivity (Doerr et al. 2010). If the explicit quantification of functional connectivity is inherently prone to uncertainty in its accuracy and applicability to other environments and species, a more informative perspective would be to quantify how forestry impacts the potential connectivity of a focal habitat type from the perspective of hypothetical species which use the focal habitat type (Watts et al. 2010). In the case of hypothetical species (Huggard et al. 2007), dispersal abilities are not based on any one existing species, but are assigned to fall within the range of dispersal abilities of organisms that exist within that habitat type. Using a measure of potential connectivity, the assumptions incorporated into a metrics calculation can be tailored to reflect the impacts of forestry, independent of species specific factors that would limit dispersal regardless of whether harvesting had occurred.

GRAPH-BASED METRICS

Graph theory has emerged as an effective method of quantifying the sum of patch interactions to give an overall assessment of landscape connectivity (Urban and Keitt 2001, Minor and Urban 2008, Zetterberg et al. 2010). The results of graph-based analyses produce comparable results to those obtained from detailed spatially-explicit habitat models (Minor and Urban 2007), with less detailed inputs required to reflect biological realism (Calabrese and Fagan 2004). A graph network is composed of nodes and links, each of which has defined characteristics. Nodes that are connected by links are defined as belonging to the same component. When applying graph theory to habitat connectivity, different habitat patches constitute the nodes and the movement of individuals or genetic material between patches are the links between nodes. The assumptions inherent in criteria used to describe nodes and links will affect the outcome of any connectivity metrics applied to the graph network and therefore must be recognized. But, this allows for the flexibility to tailor these assumptions to reflect the impacts of forestry. Calculating graph-based metrics with varying assumptions of dispersal capabilities will allow for the quantification of the connectivity impacts of forestry across a range of scales. If identical methods of defining habitat and hypothetical dispersal capabilities are applied to multiple potential distributions of habitat in the same landscape, the distribution of the habitat can be deduced to be the cause of the changes in index results.

PROBABILITY OF CONNECTIVITY

Of the array of current graph metrics, the probability of connectivity index (*PC*) possesses many qualities that make it well suited to the quantification of the connectivity impacts of forest management. *PC* index values are defined as the probability that two randomly selected habitat patches are considered connected based on the structure of the landscape of examination and defined dispersal behaviour. The probability of connectivity index was reported by Saura and Pascual-Hortal (2007) where it was compared to a variety of existing landscape indices using 13 properties that they argued a viable landscape index should detect (Table 1.1). Since then, the *PC* index has been frequently used and has not been critically refuted. The index has been applied in studies ranging from computer simulations, population distribution studies, and explorations of connectivity theory and metrics (Bodin 2009, Bodin and Saura 2010b, García-Feced et al. 2011, Morzillo et al. 2011, Gurrutxaga et al. 2011, Awade et al. 2012, Zozaya et al. 2012, Mazaris et al. 2013, Bergsten et al. 2013). Some desirable characteristics of the index from the perspective of forestry management include: (1) the index can be applied to both raster and vector data, (2) it has a predefined range of variation between 0 and 1, (3) it detects the effects of stepping-stone habitats, and (4) it performs calculations on a large number of polygons (Saura and Pascual-Hortal 2007). The *PC* index may be calculated using CONEFOR 2.6, a software package that uses node and connection files derived from habitat maps to calculate a suite of connectivity indices (Saura and Torne 2009). CONEFOR is based on the Sensinode 1.0 software developed at Duke University by D.L Urban and uses a graph theoretic approach to calculate a range of connectivity indices. CONEFOR calculates the *PC* metric by applying user-supplied node and connection files for a landscape to the function:

$$PC = {\sum_{i=1}^{n} \sum_{j=1}^{n} P_{ij} a_i a_j} \Big/ {A_L^2} \qquad (1)$$

where:

- a_i= the node attributes of a source polygon,
- a_j= node attributes of a destination polygon,
- P^*_{ij}= the maximum product probability of movement between the two polygons, and
- A_L=total landscape area of both habitat and non-habitat areas.

Node and connection files are derived from GIS landscape maps using the freely available CONEFOR input tools at Jenness Enterprises (Jenness 2008). The node file provides a unique identification number for each habitat patch (node) in the landscape and the value of that node as a habitat patch (a_i). These habitat values are typically an area-weighted habitat suitability value and are defined by the selected habitat assessment criteria included as a variable in the GIS data. The connection file provides information on

Table 1.1 Response of different indices to the 13 properties relevant for their use for quantifying connectivity in landscape conservation planning and change analysis applications (from Saura and Pascual-Hortal, 2007). An ideal index should systematically provide an affirmative answer to each of these questions. An affirmative answer here means that the index consistently achieves that property in every case (i.e., with no variable reaction depending on the particular way a certain type of spatial change occurs).

	PC	Flux	Area Weighted Flux	Patch Cohesion	Correlation Length	Integral Index of Connectivity	Dispersal Success	Search Time	Cell Immigration
-1 Does it have a predefined and bounded range of variation?	Yes	No	No	Yes	No	Yes	No	No	No
-2 Can it be computed both on vector and raster data?	Yes	Yes	Yes	No (*)	No	Yes	Yes	Yes	No
-3 Is it insensitive to subpixel resampling of landscape pattern?	Yes	Yes	Yes	No (*)	Yes	Yes	Yes	Yes	No
-4 Does it indicate lower connectivity when the distance between patches increases?	Yes	Yes	Yes	No	No (**)	No (**)	Yes	Yes	Yes
-5 Does it attain its maximum value when a single habitat patch covers the whole landscape?	Yes	No	No	Yes	Yes	Yes	No	No	Yes
-6 Does it indicate lower connectivity as the habitat is progressively more fragmented?	Yes	No	No	Yes	No	Yes	No	No	Yes
-7 Does it consider negative the loss of a connected patch?	Yes	Yes	Yes	No	No	Yes	Yes	No	Yes
-8 Does it consider negative the loss of an isolated patch?	Yes	No	No	No	No	Yes	No	No	No
-9 Does it consider negative the loss of a part of a patch?	Yes	No	No	No	No	Yes	No	No	Yes
-10 Does it detect as more important the loss of bigger patches?	Yes	No	Yes	Yes	No	Yes	No	No	Yes
-11 Is it able to detect the importance of key stepping-stone patches?	Yes	No	No	No	Yes	Yes	Yes	No	Yes
-12 Is it able to detect as those key stepping-stones patches that when lost leave most of the remaining habitat	Yes	No	No	No	No	Yes	No	No	No
-13 Is it unaffected by the presence of adjacent habitat patches?	Yes	No	No	No	Yes	No	No	No	Yes

the links between different habitat patches (nodes) in the landscape. The values for these links can be supplied either as an externally calculated probability of direct dispersal between two habitat patches based on a custom dispersal kernel (P_{ij}), or as distances between habitat patches (d_{ij}). In instances where connections are supplied as distances, CONEFOR converts the supplied list of distance values (d_{ij}) to probability of direct dispersal (P_{ij}) based on the exponential distance decay kernel,

$$P_{ij}=e^{-kd_{ij}} \tag{2}$$

where k is a constant that calibrates the function to the user-supplied combination of distance and probability (e.g., all other dispersal probabilities are calibrated to user-supplied specification that nodes separated by 100 units have 0.05 probability of dispersal). When the *PC* index is calculated, these probabilities of direct dispersal are converted to the maximum product probability of dispersal, that considers if there is a greater probability of reaching a destination patch by dispersing through intermediate habitat patches than dispersing by a direct route between two patches (Fig. 1).

A criticism of the *PC* index is that it produces results with values much lower than other connectivity metrics (Neel 2008). In response, the authors proposed an adaptation of the *PC* index with a more intuitively interpretable scale of response, the equivalent connected area (ECA) (Saura et al. 2011a). The ECA is calculated as the square root of the numerator used in the calculation of the *PC* index,

$$ECA=\sqrt{\left(\sum_{i=1}^{n}\sum_{j=1}^{n}P_{ij}a_{i}a_{j}\right)} \tag{3}$$

and is equal to the area of land that when contained in a single polygon has the same level of connectivity as the sum of the fragmented habitat patches. This measure does not have a pre-defined range of variation and the scale of potential results will be dependent on the size of the landscape being examined. This index can be adapted to have a predefined range of variation by dividing the ECA by the total area of the landscape of examination. Mathematically this is equivalent to the $\sqrt{PC}$ as the term PC_{Num} is common to the formula

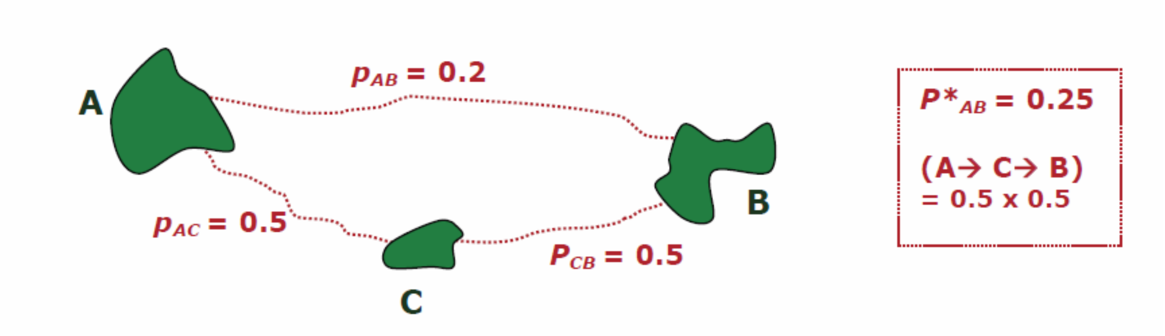

Figure 1.1. A schematic illustration of the difference between the probability of direct dispersal (P_{AB}) and maximum product probability of (P^*_{AB}) between habitat patches *A* and B, from (Saura and Pascual-Hortal 2007)**.**

for both *PC* and *ECA* since the *PC* formula (1) can be simplified to:

$$PC = {PC_{Num}} / {A_L^2} \tag{4}$$

which is equivalent to the equation:

$$\sqrt{PC} = {\sqrt{PC_{Num}}} / {A_L} \tag{5}$$

Substituting *ECA* for $\sqrt{PC_{Num}}$ gives the formula

$$\sqrt{PC} = {ECA} / {A_L} \tag{6}$$

The $\sqrt{PC}$ is therefore equivalent to the proportion of the landscape, that when amalgamated into a single habitat patch, would be equivalent to connectivity of the examined scenario. At sufficiently high dispersal values, all habitat will be considered connected, and the *ECA* will be equal to the total amount of habitat in the landscape, which divided by the total landscape area (A_L) gives the total proportion of the landscape occupied by habitat. Due to this relationship to the total amount of habitat in the landscape I propose the $\sqrt{PC}$ as an intuitively interpretable value and is used in all subsequent analyses.

PCRC

The response curve of the $\sqrt{PC}$ index (*PCRC*) calculated over a range of spatial scales will quantify the overall landscape connectivity of a focal habitat type to a range of species and better quantify the impacts of land use impacts on biodiversity than a single connectivity value based on a single dispersal capability. Plotting connectivity index results against the dispersal distances used for their calculation will result in a response curve of connectivity index values that increases with increased dispersal values as more and more patches are considered to be connected. If a sufficiently large range of values are used, this curve would include all possible perceptions of the landscape's connectivity, from an organism unable to cross any distance of inhospitable matrix, to an organism able to access all available habitat in a landscape. A similar procedure of calculating *PC* index over a range of dispersal thresholds has been previously applied to assess the impact of the distribution of wildlife reserve patches (Laita et al. 2010).

The results of this form of examination represent the maximum potential connectivity of that landscape assuming that the only limitation to dispersal is the distribution of habitat in the landscape. Presenting connectivity metrics in this manner allows for the rapid assessment of a range of relevant landscape characteristics. The *PCRC* intercept represents how the landscape would impede movement of an organism unable to disperse across any gap in the contiguous habitat reflecting the fragmentation of the landscape. The upper asymptote of a *PCRC* reflects connectivity of the landscape when dispersal values are high enough that the entire landscape is considered connected, and is therefore a function of the total amount of the focal habitat type in the landscape. The rate at which $\sqrt{PC}$ values increase with increased dispersal distances is a function of the distances that need to be crossed for habitat patches to be considered connected and will reflect the dispersion of habitat in a landscape. This type of examination better quantifies the impacts of forestry because it simultaneously reflects impacts at a range of spatial scales that would be missed by an assessment that considered only the scale of dispersal of a focal species. Impacts at multiple spatial scales are important to consider since species can be affected by landscape structure at spatial scales outside of their maximum dispersal capabilities (Dyer et al. 2002).

INDEX ASSESSMENTS

In order to be appropriately applied as a landscape management tool, the efficacy of *PCRC* must first be tested. Without a thorough examination of the ways that an index responds to controlled changes in landscape structure, any interpretation of results may be misguided. I assessed the value of *PCRC* to quantify the effects of forestry on landscape connectivity, using a series of examinations where landscape factors were manipulated independently to isolate the response of the index to specific factors known to affect connectivity. To simplify the assessment process, these factors were analyzed in increasingly complex scenarios where additional factors could be examined once the dynamics of the more basic factors had been examined. In Chapter 2, I manipulated the amount, fragmentation, dispersion, and inter-patch connections of habitat in a simple theoretical landscape to calibrate index response to specific types of landscape change. In Chapter 3, I used ecosystem simulation model projections for an existing forest landscape near Clearwater, BC to assess the response of *PCRC* to controlled manipulations of landscape structure, and to compare the outcomes of alternative distributions of conservation areas in landscapes subject to anthropogenic and natural disturbances. In Chapter 4 I will argue the benefits of *PCRC* in assessing changes in landscape structure and its application potential to landscape management.

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CHAPTER 2: QUANTIFYING LANDSCAPE CONNECTIVITY THROUGH THE USE OF CONNECTIVITY RESPONSE CURVES.

INTRODUCTION

Habitat connectivity has become a focus of modern ecosystem management and is widely recognized as a key factor in the conservation of biodiversity (Taylor et al. 1993, Fischer and Lindenmayer 2007, Lindenmayer et al. 2008, Brudvig et al. 2009). For example, in a review of 22 years of recommendations for biodiversity management in the face of climate change, increasing connectivity was the most frequently recommended method of conserving biodiversity (Heller and Zavaleta 2009). Despite this recognition, there are no accepted standards for the measurement of habitat connectivity, or benchmarks against which measurements can be compared (Lindenmayer and Fischer 2007, Kindlmann and Burel 2008). Connectivity promotes biodiversity through its effect on rates of immigration and emigration between habitat patches, processes necessary for the continued persistence of meta-populations within a landscape (Visconti and Elkin 2009). Although connectivity plays an important role in metapopulation dynamics, it can only facilitate movement among otherwise productive populations, and cannot be expected to maintain biodiversity if other habitat values are not managed concurrently.

Biodiversity conservation is focused on maintaining the metapopulation persistence of a range of species (Drielsma and Ferrier 2009). Any metrics intended to guide biodiversity conservation should therefore represent landscape connectivity values from the perspective of a range of species in order to promote a range of viable populations that can serve as sources for re-colonization following disturbance and local extirpation. With these goals in mind, landscape management strategies should focus on the conservation of landscape connectivity as opposed to the functional connectivity of a focal species. Landscape connectivity is widely defined as, "the degree to which a landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993), in contrast to the functional connectivity of a focal species that quantifies rates of dispersal between habitat patches based on spatially-explicit population models (Beier et al. 2008). In addition to the logistical difficulties of establishing accurate spatially-explicit population models, there is debate as to the validity of extrapolating results from a focal species to a range of species, as this contradicts the theory of niche specialization leading to heterogeneous species distribution, where the interaction of environmental tolerances and interspecific competition determine species distribution (Lindenmayer et al. 2002, Ficetola et al. 2007). An alternative approach is to identify a focal habitat type and calculate connectivity based on a range of dispersal capabilities (Laita et al. 2010). Quantifying connectivity from this perspective better approximates the previously stated definition of landscape connectivity, in that it quantifies how the structure of the landscape impedes movement between patches across a range of spatial scales, rather than quantifying dispersal success of a single species.

In order for a connectivity metric to be of practical use in landscape management, it should be robust to application across large spatial extents while retaining sensitivity to fine-scale habitat features. It should also reflect the impacts of biologically relevant landscape structure. Our understanding of landscape structure that promotes connectivity is largely theoretical in nature, due primarily to the difficulties in conducting well designed trials at the spatial and temporal scales inherent in landscape management (Saura et al. 2011b). The agreement between theoretical projections of connectivity values and observed population impacts from the existing empirical evidence has been mixed, and responses are highly species-specific (Debinski and Holt 2000). When assessing the connectivity of a landscape, the two factors considered to be of primary biological significance are the amount of suitable habitat and how that habitat is distributed (Fahrig 2003, Lindenmayer and Fischer 2007, Long et al. 2010). The amount of suitable habitat has a confounding effect on landscape connectivity that differs from the impacts of fragmentation *per se*. (Fahrig 2003, Betts et al. 2006, Koper et al. 2007, Smith et al. 2009, Cushman et al. 2012, Tscharntke et al. 2012). Hence, there is value in an index that responds independently to changes in the amount and distribution of suitable habitat. For a given amount of habitat, fragmentation into a greater number of patches (Saunders et al. 1991, With et al. 2006, Zuckerberg and Porter 2010), and increased spatial dispersion (Tischendorf et al. 2005, Matter et al. 2005, Hinam and St. Clair 2008) have detrimental population effects. Inter-patch connections in the form of corridors and “stepping-stone” habitats are frequently recommended to promote connectivity and have mixed but predominantly beneficial population effects (Perault and Lomolino 2000, Tewksbury et al. 2002, Loehle 2007, Chan-McLeod and Moy 2007, Gilbert-Norton et al. 2010). Biodiversity conservation is frequently focused on the distribution of residual habitat patches and reserves in the face of anthropogenic habitat loss, with increased reserve areas having beneficial effects (Chapin et al. 1998, Lindenmayer et al. 2006, 2008). The allocation of limited habitat reserves necessitates balancing the impacts of patch size and patch dispersion (Acuna and Estades 2011).

CONEFOR is a software package that calculates a range of graph-theoretic connectivity indices (Saura and Torne 2009). The probability of connectivity (*PC*) index was created by the developers of CONEFOR as a response to the conceptual deficiencies they observed in other available connectivity metrics (Saura and Pascual-Hortal 2007). Since its publication, the *PC* index and its derivatives have been widely employed in a range of theoretical and practical applications (Neel 2008, Bodin 2009, Perotto-Baldivieso et al. 2009, Bodin and Saura 2010a, García-Feced et al. 2011, Morzillo et al. 2011, Gurrutxaga et al. 2011, Awade et al. 2012, Zozaya et al. 2012, Rubio et al. 2012, Mazaris et al. 2013, Bergsten et al. 2013).

I examined whether connectivity response curves (*PCRC*) created by plotting $\sqrt{PC}$ index values as a function of the dispersal values used for their calculation are sensitive to changes in landscape structure. The square root of the *PC* index was used due to its intuitive relationship to the amount of habitat in a landscape described below. The amount, fragmentation, and spatial dispersion of suitable habitat within simple landscapes were manipulated in a systematic fashion to isolate how *PCRC* respond to changes in each factor. To have practical use as landscape connectivity metric, *PCRC* should respond to manipulations of each factor in a unique and interpretable fashion. To reflect the currently accepted principles of landscape connectivity, *PCRC* should indicate higher connectivity for scenarios with greater amounts of suitable habitat, scenarios where the extent of suitable habitat is fragmented into a smaller number of patches, and scenarios where fragmented patches are separated by smaller distances. To assess if *PCRC* responds to management strategies intended to promote connectivity, corridor and stepping-stone connections were established between symmetrical distributions of habitat patches, a varying number of habitat reserves were aligned or isolated in a matrix of random habitat, and stepping-stone connections were established between habitat reserves. To reflect the impacts of these strategies, expected under the current accepted principles of habitat connectivity, connections between patches, an increased number of habitat reserves, less dispersion of habitat reserves and habitat reserves with stepping-stone connections should be assessed as having higher levels of connectivity.

METHODS

Connectivity Index Calculation

The CONEFOR software calculates the probability of connectivity (*PC*) index using the function:

$$PC = \sum_{i=1}^{n} \sum_{j=1}^{n} P_{ij} a_i a_j \Big/ A_L^2 \qquad (7)$$

where:

- a_i and a_j= the habitat attributes of patches *i* and *j*
- A_L= total landscape area , and
- P_{ij}*= the maximum product probability of dispersal between patches *i* and *j*.

The maximum product probability of dispersal (P_{ij}*) is the product of the probabilities of moving through adjacent habitat patches to reach a destination habitat patch, and is used in index calculation if that value is larger than the probability of direct dispersal (P_{ij}). Landscape scenarios were translated into the necessary index inputs, the node and connection files, using the CONEFOR Inputs extension for ESRI software created by Jenness Enterprises (Jenness 2008). Node files consist of two columns identifying a unique identification number and habitat value for each polygon within the landscape. Area weighted habitat values (a_i) were calculated as the product of the habitat value and the area in hectares of each polygon. Connection files consist of the unique identification number of the source and destination polygons and the edge to edge Euclidean distance between them.

These Euclidean distances were translated into probabilities of direct dispersal (P_{ij}) by the internal distance decay function of CONEFOR,

$$P_{ij}=e^{-kd_{ij}} \tag{8}$$

where d_{ij} is Euclidean edge to edge distance, and k is a constant used to fit the function to the user-specified relationship between distance and dispersal probability. For these examinations the variable identified as dispersal distance (DispDist) was the threshold value in metres for 5% probability of dispersal between polygons used to calibrate the distance decay function.

For all examinations, the $\sqrt{PC}$ was used as the metric of examination due to its intuitive relationship to the total amount of habitat in a landscape. The relationship between *PC* index values and habitat amount can be explained by an alternative exploration of the index proposed by its authors, namely the equivalent connected area (*ECA*) (Saura et al. 2011a). The *ECA* is defined as the area of land that when combined into a single polygon has the same connectivity value as the sum of the fragmented habitat patches and is calculated as the square root of the numerator of the *PC* index equation:

$$ECA=\sqrt{PC_{Num}}=\sqrt{\left(\sum_{i=1}^{n}\sum_{j=1}^{n}P_{ij}a_i a_j\right)} \tag{9}$$

The term PC_{Num} is common to the formula for both *PC* and *ECA* since the *PC* formula (1) can be simplified to:

$$PC={PC_{Num}}\big/{A_L^2} \tag{10}$$

which is equivalent to the equation:

$$\sqrt{PC}={\sqrt{PC_{Num}}}\big/{A_L} \tag{11}$$

Substituting *ECA* in for $\sqrt{PC_{Num}}$ gives the formula:

$$\sqrt{PC} = ECA / A_L \qquad (12)$$

In single habitat patch scenarios, or at sufficiently high dispersal values, all habitat is considered to be connected, and the *ECA* is equal to the total amount of habitat in the landscape. When the *ECA* is divided by the total landscape area (A_L) the result is the proportion of the landscape occupied by that particular habitat. For this reason the $\sqrt{PC}$ is proposed as a more intuitively interpretable value and is used in all subsequent analyses. This transformation of index results does not affect the observed relationships between index values and dispersal distance because the transformation has an equivalent impact at all dispersal values and is not applied to the index inputs prior to their inclusion in index calculation.

For each landscape scenario, the *PC* index was calculated using a range of dispersal distance thresholds ranging from 5 m to 40 000 m at intervals that increased with dispersal values. Under 100 m, the 5% probability of dispersal was defined as occurring at 5, 10, 25, and 50 m; between 100 and 1000 m, dispersal values were increased at 100m intervals; between 1000 and 5000 m dispersal distances were increased at 500m intervals; between 5 000m to 40 000m interval size doubled with each step. This range of dispersal values was intended to demonstrate fine scale connectivity dynamics with low dispersal values, but attain a large enough value to approach the upper asymptote of the maximum possible connectivity for the landscape. To facilitate the calculation of index values for a large number of dispersal thresholds, the *PC* index was calculated using batch files through the command line interface of CONEFOR. The index was calculated in heuristic mode where dispersal probabilities under the 5% threshold were not included in the overall index calculation.

Symmetrical Habitat Distributions

Landscape structure was altered in a simple theoretical landscape consisting of 30 × 30 one hectare pixels. The impact of representing a landscape in a raster (data represented as equally sized 1 ha cells) versus vector (irregular sized polygons of similar contiguous habitat) format was examined by comparing the results calculated from landscapes where each habitat patch is a group of 1 ha pixels (raster), to landscapes where the same habitat patches were simplified to a single habitat patch polygon with a habitat value equal to the total area in hectares. Raster and vector landscapes gave identical results, regardless of the habitat distribution and the dispersal distance for which index values were calculated. The parameters of the response function are therefore also identical and will give the same assessment of connectivity for landscapes represented in raster and vector formats.

The amount and distribution of habitat within the landscape was manipulated systematically by assigning habitat suitability values of zero or one to each pixel within the landscape to create landscapes that differed in the amount, fragmentation, spatial dispersion of suitable habitat, and inter-patch connections in the landscape. Landscapes were created with amounts of suitable habitat ranging from 5% to 75%, at 5% increments (Fig. 2.1 *i*). For each increment in the amount of suitable habitat, scenarios were created where the total amount of habitat was fragmented into one, two, four, five, or nine discrete habitat patches that were separated by identical inter-patch distances for a given amount of suitable habitat (Fig. 2.1 *ii*). To examine the impact of inter-patch distances, the 10% and 25% suitable habitat scenarios were manipulated so that suitable habitat patches were separated by distances of 100 to 500 m at increments of 100 m for all levels of habitat fragmentation (Fig. 2.1 *iii*). The 10% and 25% suitable habitat levels were selected as the subsets for examination to allow for all levels of inter-patch distance to be symmetrically applied within the limitations of the finite boundaries of the simple theoretical landscape.

To assess the effect of inter-patch connections on *PCRC,* the four patch 25% suitable habitat scenario was manipulated to create habitat corridor and “stepping-stone” connections (Fig. 2.1 *iv*). Corridors were created by defining a series of contiguous pixels as suitable habitat between patches; stepping-stones were created by defining a series of non-contiguous pixels as suitable habitat between patches (Fig. 2.1 *iv*). To maintain a constant amount of habitat between scenarios, the habitat area required to create corridors and stepping-stones were removed from the outer edges of the connected patches. Scenarios were created with one inter-patch connection, two connections in series, two parallel connections, three

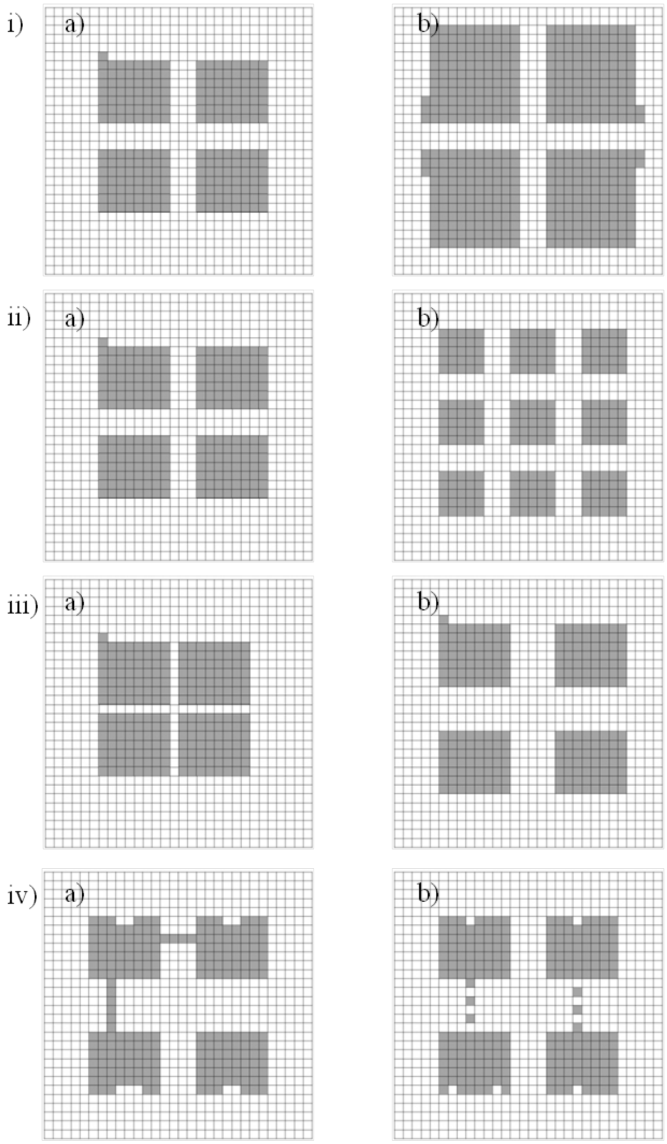

Figure 2.1. Examples of the manipulations of suitable habitat (shaded cells) in the simple landscape to alter i) the amount of suitable habitat (a= 25% and b= 50%) with constant fragmentation and dispersion, ii) suitable habitat fragmentation (a= 4 patches and b= 9 patches) with constant suitable habitat amount and dispersion, iii) suitable habitat dispersion (a= 100 m inter-patch distance and b= 500 m inter-patch distance), and iv) inter-patch connections (a= 2 corridors in series, b=2 stepping-stones in parallel) with constant suitable habitat amount, fragmentation and dispersion.

connections, and four connections between patches, for both stepping-stone and corridor connections (Fig. 2.1 iv).

Reserve Distribution

The distribution of a subset of suitable habitat amounts was manipulated to demonstrate the response of *PCRC* to the distribution of habitat reserves in a landscape. Scenarios with 10%, 25%, and 50% suitable habitat were created with different placements of reserve patches with the remaining amount of habitat distributed randomly across the landscape. Each scenario was replicated 10 times with identical reserve distributions and a different inter-patch matrix of random habitat distribution. Habitat reserves consisted of a contiguous patch that contains 20% of the total amount of habitat in the scenario. Scenarios were created with one, two, or three reserve patches.

Scenarios with three habitat reserve patches were manipulated so that reserve patches were either aligned,thereby reducing inter-patch distance (1 200 m and 800 m), or placed in separate corners of the landscape, maximizing inter-patch distance (2 000 m and 1 600 m). To assess the sensitivity of *PCRC* to inter-reserve connections, each scenario containing more than one reserve patch was established with and without the presence of stepping-stone connections between habitat reserves. Stepping-stone connections were established by defining a series of habitat pixels between habitat reserves as desirable habitat so that there are no habitat gaps larger than 100 m to be crossed.

Statistical Analysis

For each landscape scenario the $\sqrt{PC}$ index results were plotted against the dispersal values used for their calculation to create a connectivity response curve (*PCRC*). Displaying connectivity values in this manner represents the degree to which the landscape structure impedes movement among resource patches for all possible dispersal abilities. A similar conceptual approach has been used to compare differences between connectivity indices and to examine the impact of changes in landscape structure (Laita et al. 2010). The parameters that describe the relationship between dispersal values and $\sqrt{PC}$ for each landscape scenario were calculated by fitting *PCRC* to the logistic response function:

$$\sqrt{PC} = a / \left(1 + e^{b - c\,(DispersalDistance)}\right) \tag{13}$$

using the non-linear least squares (R command nls) package in the R statistical analysis software (R Development Core Team 2011). The parameters *a, b,* and *c* of fitted *PCRC* were used for statistical comparisons between landscape scenarios. The significance of the response of these parameters to changes in different landscape factors was assessed using Tukey's honest significant differences test (de Mendiburu 2013) based on a type II analysis of variance.

RESULTS

PCRC demonstrated several patterns of response that are relevant to interpreting index results when applied to complex landscapes. For all habitat amounts the single patch scenario gives identical index results regardless of the dispersal threshold used for index calculation and is larger than the connectivity values calculated for any other habitat distribution. The $\sqrt{PC}$ index value for these single patch scenarios was equal to the proportion of suitable habitat in the landscape (Fig. 2.2). Regardless of the characteristics of the examined landscapes, increasing dispersal values resulted in an increase in the $\sqrt{PC}$ values.

Amount of Suitable Habitat

The impact of the amount of suitable habitat on index values is evident in the scale of variation between scenarios with different amounts of suitable habitat. As habitat amount increased, there was convergence between scenarios with habitat divided into a different number of habitat patches (Fig. 2.2 *iv*). This convergence is consistent with the concept of a percolation threshold of habitat amount, above which the distribution of habitat exerts minimal influence on connectivity (Metzger and Décamps 1997, King and With 2002). Due to this dynamic, comparisons of specific *PCRC* parameters were limited to habitat amounts of 50% or less suitable habitat. The differences between scenarios is best compared through an examination of the parameters that define the logistic relationship between $\sqrt{PC}$ and dispersal values, the asymptote (*a*), intercept determinant (*b*) , and interaction term (*c*).

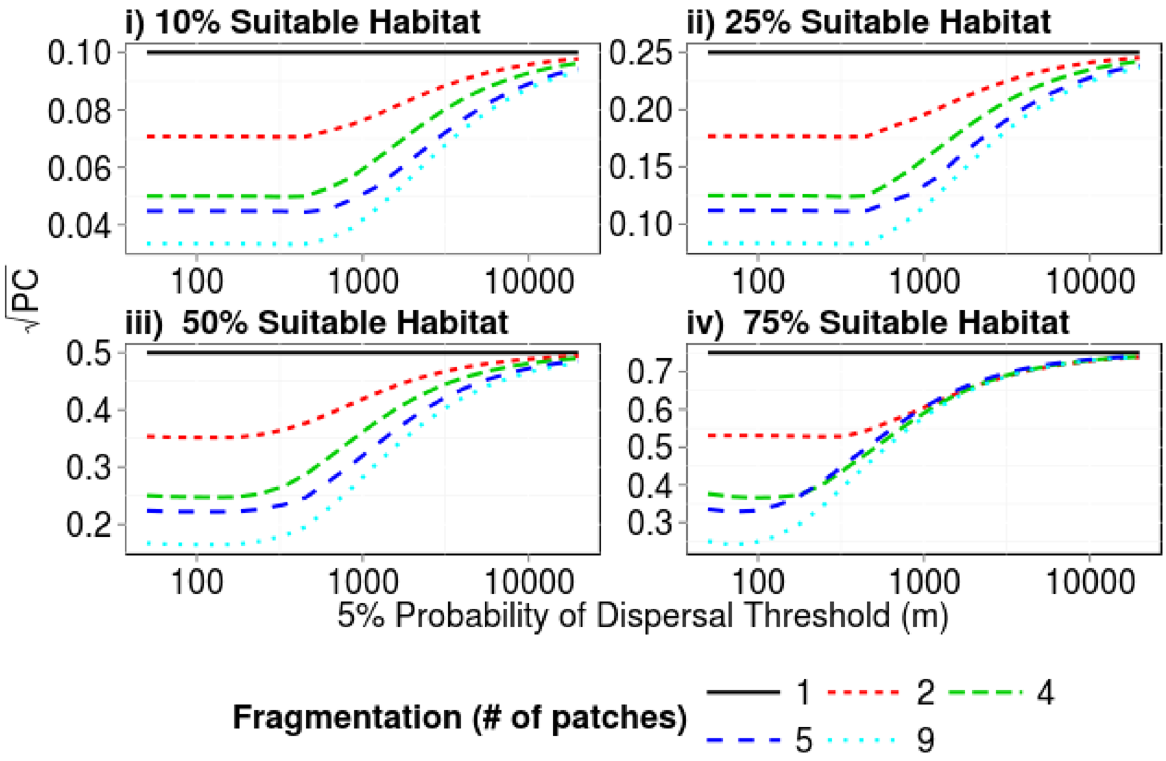

Figure 2.2. Connectivity response curves (*PCRC*) for the relationship between √*PC* and the dispersal distances threshold used for index calculation for a subset of habitat amounts (*i*-*iv*) fragmented into a range of habitat patches (line style)

For all scenarios, the asymptote of *PCRC* demonstrated significant increases to all incremental increases in the amount of suitable habitat in the landscape (Fig. 2.3). The asymptote of a *PCRC* is approached when the dispersal threshold used for index calculation is large enough that all habitat patches within the landscape approach the 100% probability of dispersal. Because the dispersal distance value corresponds to the threshold for a 5% probability of dispersal, dispersal thresholds greater than the maximum dimensions of the landscape are necessary to approach the 100% probability of dispersal. In these situations, the value of P_{ij} has been maximized between all habitat patch connections and the *PC* index value is a function of the amount of habitat in the landscape, and is equal to the index results for the single patch scenario. The asymptote had a significant response to changes in the amount of habitat, but demonstrated no significant response to changes in the distribution of habitat (Fig. 2.3 *i* & *iv*). Asymptote values can therefore be used to isolate the relatively strong response induced by alterations in habitat amount to examine the impacts of habitat distribution. Manipulations of suitable habitat amount resulted in clustered responses for the *PCRC* interaction term (Fig. 2.3 *iii* & *vi*). The pattern of significant differences in interaction term values indicates that this dynamic may be due to inter-patch distances, which are correlated with habitat amount. Due to the dynamic of increasing the amount of habitat within finite boundaries, as habitat amount increased the inter-patch distances that could be held constant between habitat distributions decreased. The intervals of habitat amount where changes in the dispersal interaction term are evident correspond to the habitat intervals where inter-patch distances were decreased.

Fragmentation of Suitable Habitat

Manipulating the number of habitat patches that a given amount of suitable habitat was fragmented into had no significant effect on the asymptote or interaction term values for *PCRC* (Fig. 2.3 *iv* and *vi*). Increasing fragmentation resulted in significant increases in the intercept determinant (Fig. 2.3 *v*), which due to its placement in the logistic response function corresponds to a decrease in the *PCRC* intercept (Fig. 2.2 and 2.4 *v*). The specificity of intercept determinant response to manipulations of suitable habitat fragmentation indicates that any observed changes in intercept determinants are due to the fragmentation of suitable habitat independent of the amount of suitable habitat.

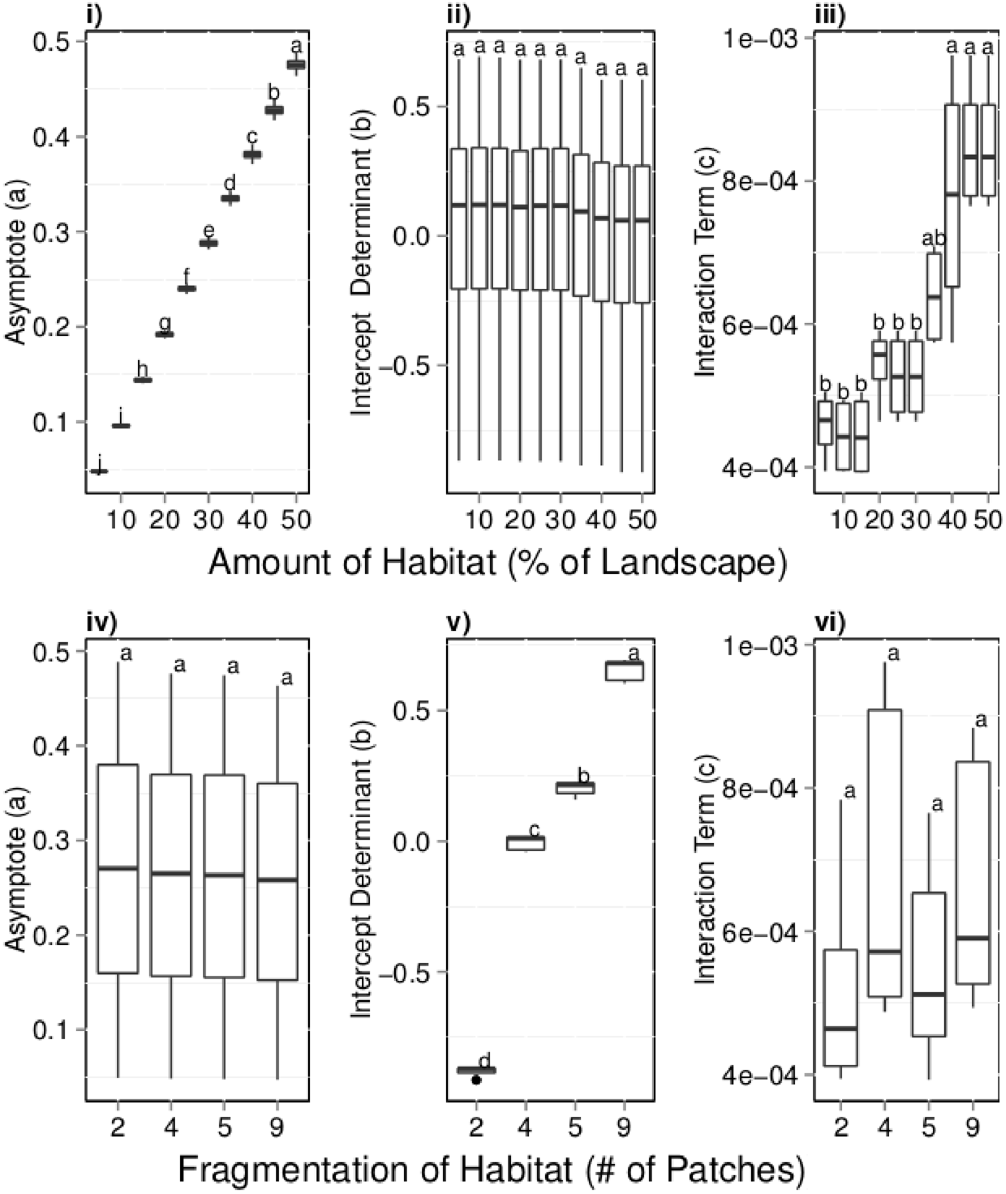

Figure 2.3. Response of *PCRC* asymptote (*i and iv*), intercept determinant (*ii and v*), and interaction term (*iii, and vi*) to manipulations of the amount (*i, ii, iii*) and fragmentation (*iv, v, vi*) of suitable habitat. Letters indicate significant differences based on Tukey's HSD test with α≤0.05. Note that due to the placement in the logistic function higher intercept determinant values (*b*) result in lower *PCRC* intercepts.

Dispersion of Suitable Habitat

When inter-patch distances were progressively increased for landscapes with 10% or 25% suitable habitat fragmented into two, four, five or nine patches, assessed landscape connectivity decreased across all spatial scales (Fig. 2.4). The intercept and asymptotes demonstrated the same patterns of response to differences in the amount and fragmentation of suitable habitat, but no sensitivity to the manipulations of inter-patch distances (Fig. 2.5 *i, ii, iv,* and *v*). The interaction term significantly decreased with increased inter-patch distances (Fig. 2.5 *iii* & *vi*). There were significant differences in interaction term values between different levels of habitat fragmentation with common inter-patch distances; however, these differences were not sufficiently large to cause any significant grouping of interaction term values between different inter-patch distances.

Inter-patch Connections

Establishing any type of connections between patches in the four patch scenario resulted in higher connectivity values than the scenario lacking inter-patch connections (Fig. 2.6). An increased number of connections between patches resulted in progressively higher assessments of connectivity. Each additional corridor connection resulted in greater increases in connectivity values than each additional stepping-stone connection. Increasing the number of corridor connections resulted in an increase in the intercept of the connectivity response curve and exhibited no subsequent increase in connectivity until dispersal values large enough to cross the gaps between patches without established connections (500 m) are considered. The three and four corridor connection scenarios, where all habitat patches are connected by a corridor, result in constant *PC* index values regardless of the dispersal value considered, indicating that they are being assessed as a single patch. At the lowest dispersal values, an increase in the number of stepping-stone connections resulted in decreased *PC* index values compared to the connection free scenario (Fig. 2.6). When dispersal values are less than the inter-patch distances each stepping-stone is considered an unconnected fragment, which results in the observed decrease in assessed connectivity. As dispersal values were increased above the 100 m gap between stepping-stones, scenarios with more stepping-stone connections were assigned higher *PC* index values than the scenario lacking any inter-patch connections.

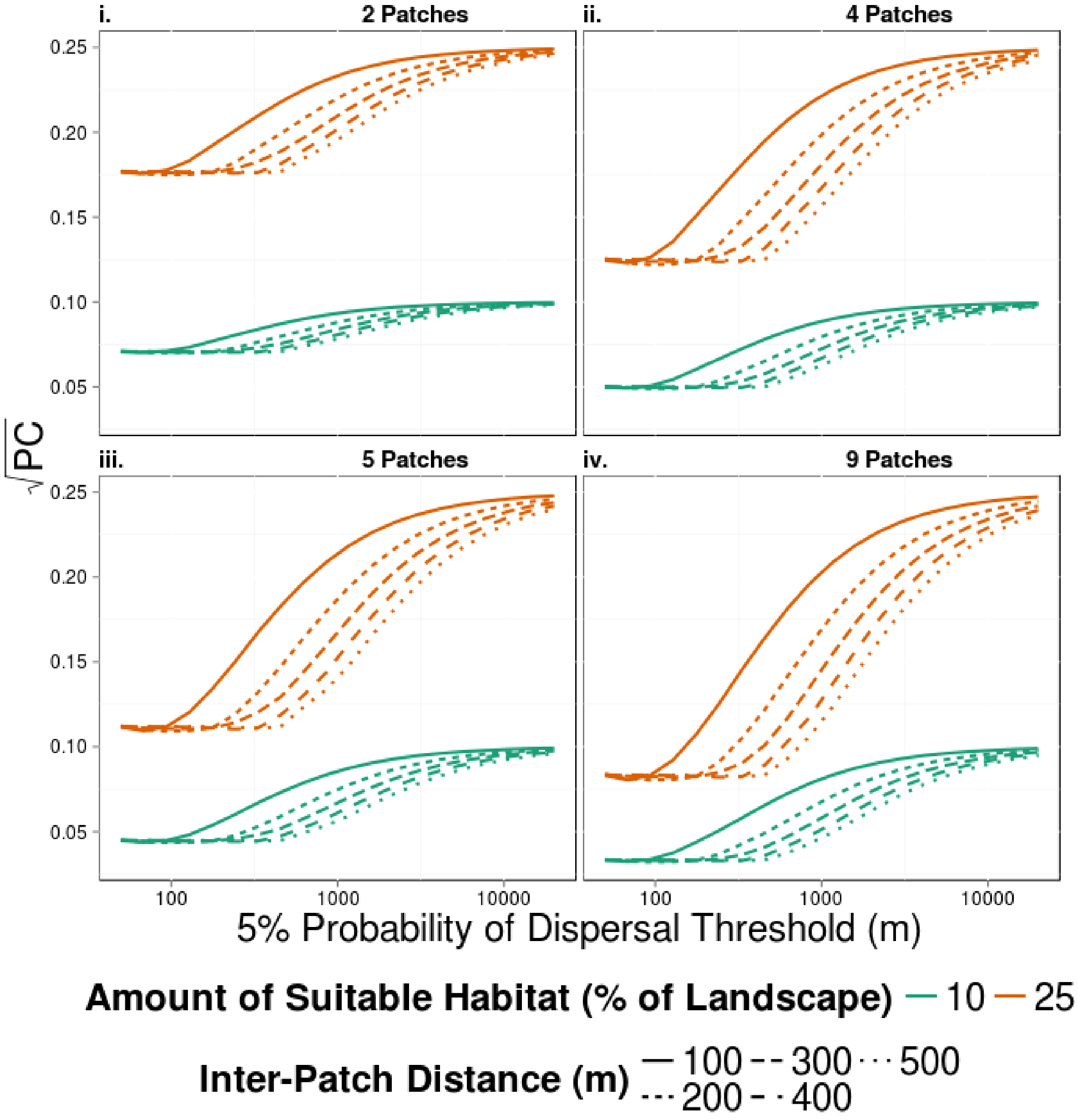

Figure 2.4. Response of *PCRC* to manipulations of the inter-patch distances (100-500m) for two different amounts of suitable habitat (line style) fragmented into two (*i*), four (*ii*), five (*iii*) or nine (*iv*) separate habitat patches.

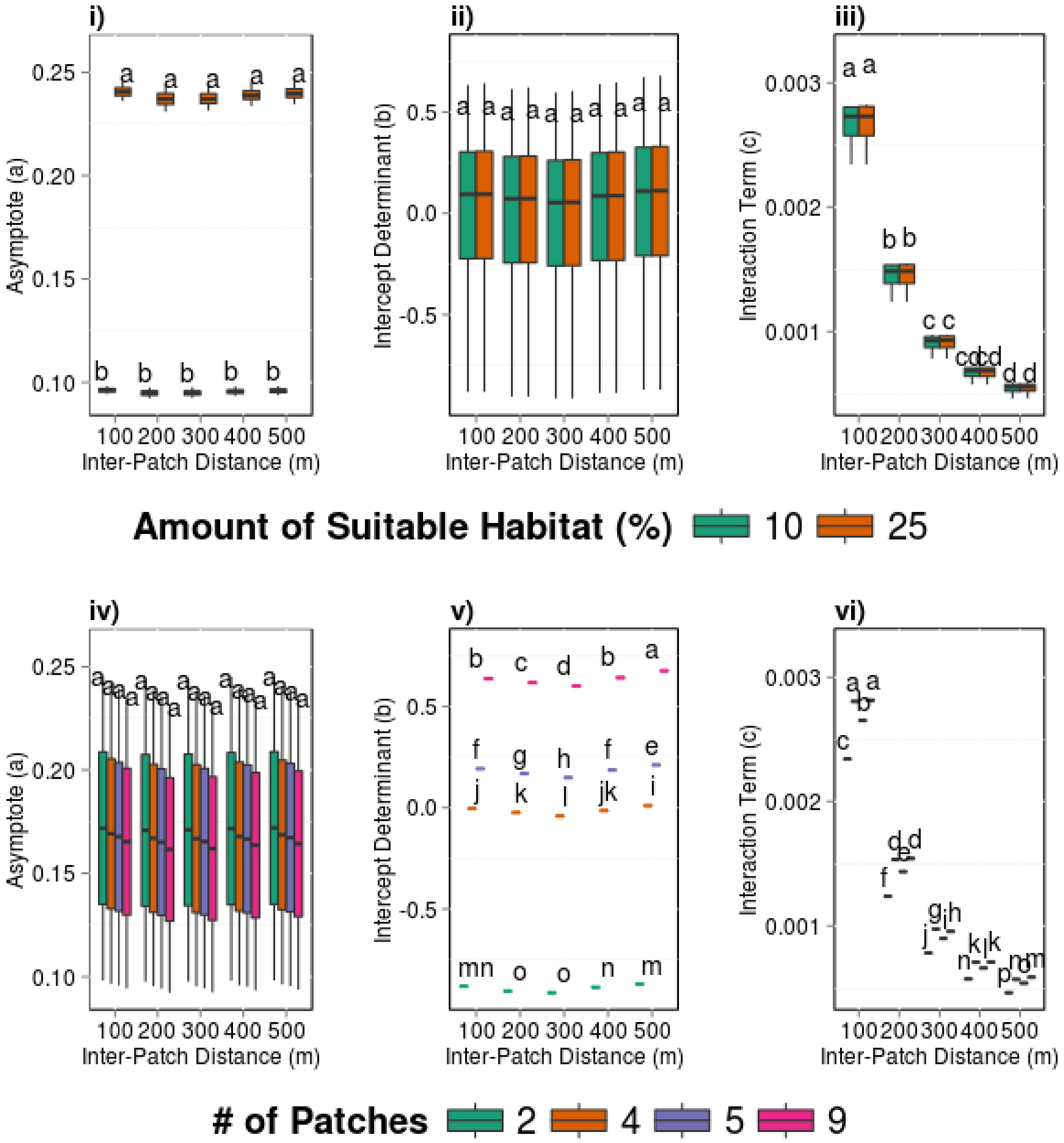

Figure 2.5. Response of parameters that describe the *PCRC* in Figure 2.4 to manipulations of inter-patch distances for different amounts (*i, ii, iii*) and fragmentation (*iv, v, vi*) of suitable habitat. Letters indicate significant differences based on Tukey's HSD test with α≤ 0.05.

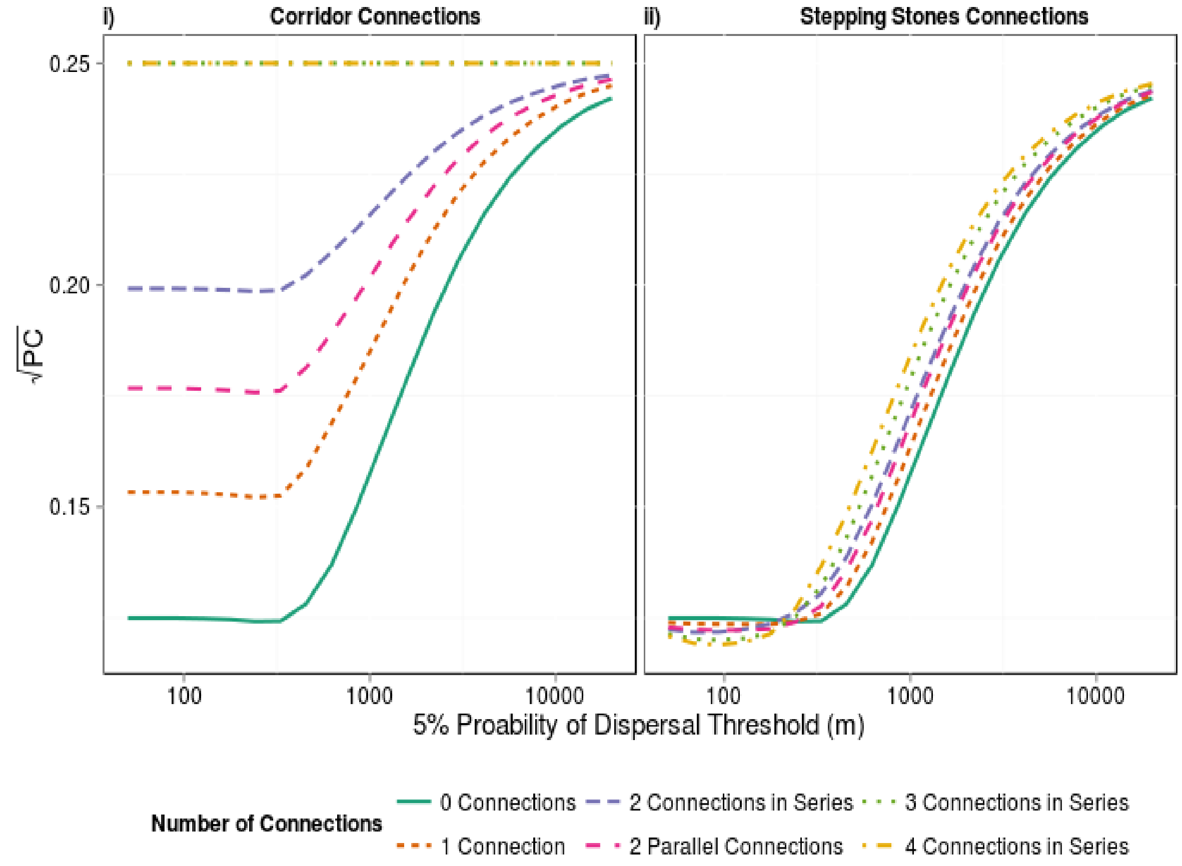

Figure 2.6. *PCRC* response to the addition of corridor (i) and stepping-stone (ii) inter-patch connections between four habitat patches in a landscape scenario with 25% desirable habitat.

Reserve Distribution Scenarios

Increasing the amount of habitat in a landscape that is allocated as habitat reserves versus a random distribution of habitat induced different *PCRC* responses based on the amount of habitat within a landscape. For the 10% and 25% suitable habitat scenarios, increasing the number of habitat reserves created lower levels of fragmentation, indicated by lowered intercept determinant values, but higher levels of habitat dispersion, as indicated by lowered interaction term values (Fig. 2.7 *iv, v,* and *vi*). This response is inferred to be due to lower amounts of suitable habitat in the inter-patch matrix resulting in larger extents of contiguous non-habitat between suitable habitat patches. When suitable habitat amount was increased to 50% the relative assessment of connectivity was reversed with the purely random habitat distribution having the highest levels of connectivity at all spatial scales, and an inverse response of intercept determinants and dispersal interaction terms (Fig. 2.7 *v* and *vi*). This inversed response is inferred to occur due to a percolation threshold of suitable habitat amount being reached. Regardless of habitat distribution it is impossible for habitat to be separated by large distances. Due to this influence, further statistical comparisons included only scenarios with 10% or 25% suitable habitat where the distribution of habitat exerts an influence on overall landscape connectivity. Changes to the amount of suitable habitat allocated as habitat reserves had a significant impact on intercept determinants that was consistent across 10% and 25% suitable habitat (Fig. 2.7 *iv*). The asymptote and intercept determinant demonstrated similar patterns of response across the two lower habitat amounts, with significant differences in parameter values within and across different amounts of habitat. This pattern of response indicates that the primary impact of altering the amount of habitat allocated as reserves is on the dispersion of habitat in the resulting landscape.

Scenarios with stepping-stones and aligned reserve patches gave higher assessed levels of connectivity across all spatial scales than scenarios without stepping-stone connections or isolated reserve patches, indicating that *PCRC* are sensitive to the distribution of reserve patches and the establishment of connections (Fig. 2.8 *i* and *ii*). The asymptote demonstrated no significant response to the manipulations of habitat distribution and connections across different habitat amounts (Fig. 2.8 *iii* and *iv*). The intercept determinant demonstrated no consistent significant response to the distribution of habitat reserves or the

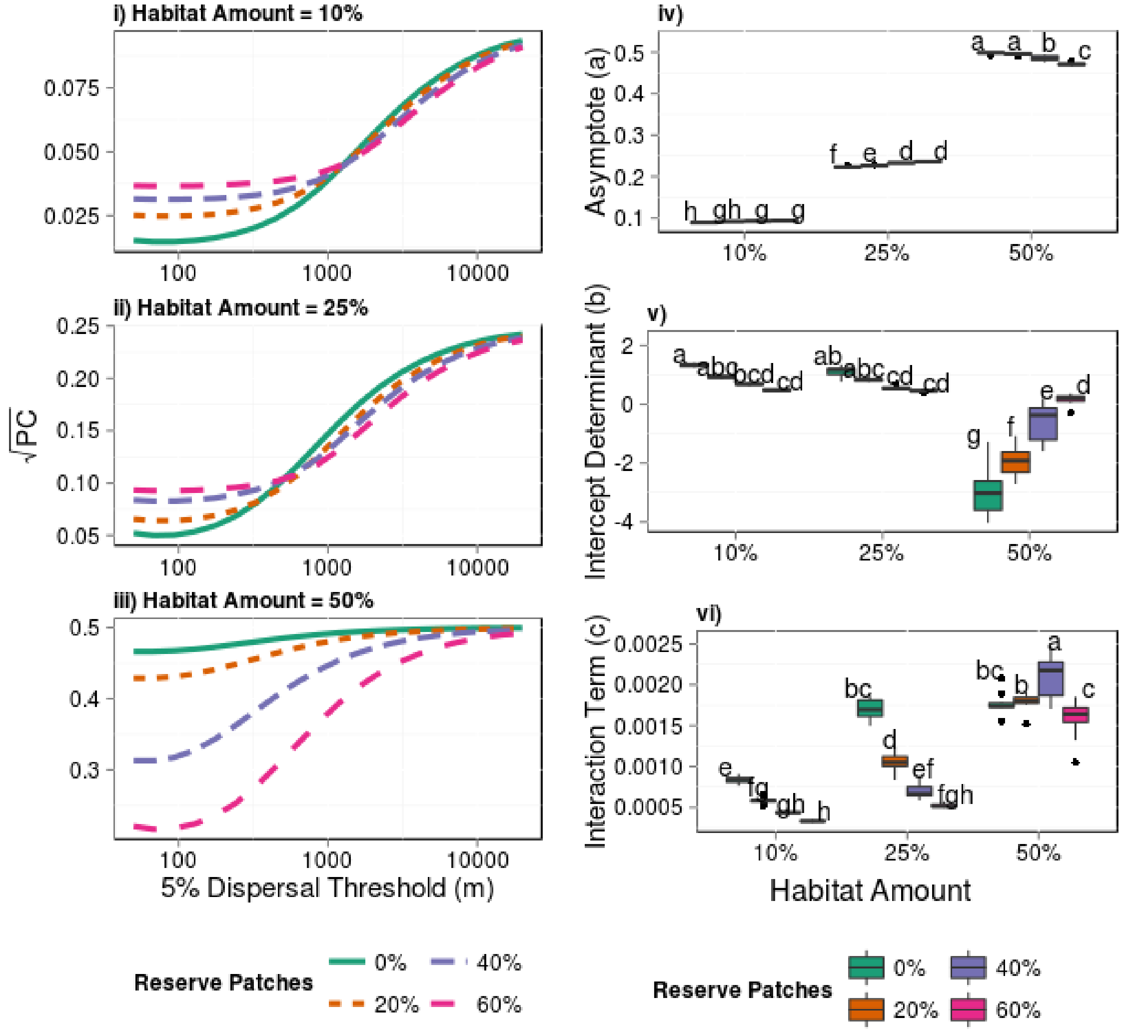

Figure 2.7. *PCRC* and boxplots of *PCRC* parameters for scenarios where a given amount of habitat is distributed either randomly (0% reserves) or in an increasing number of habitat reserve patches (contiguous patches of 20% of the total habitat in the landscape). Letters indicate significant differences based on Tukey's HSD test with $\alpha \leq 0.05$.

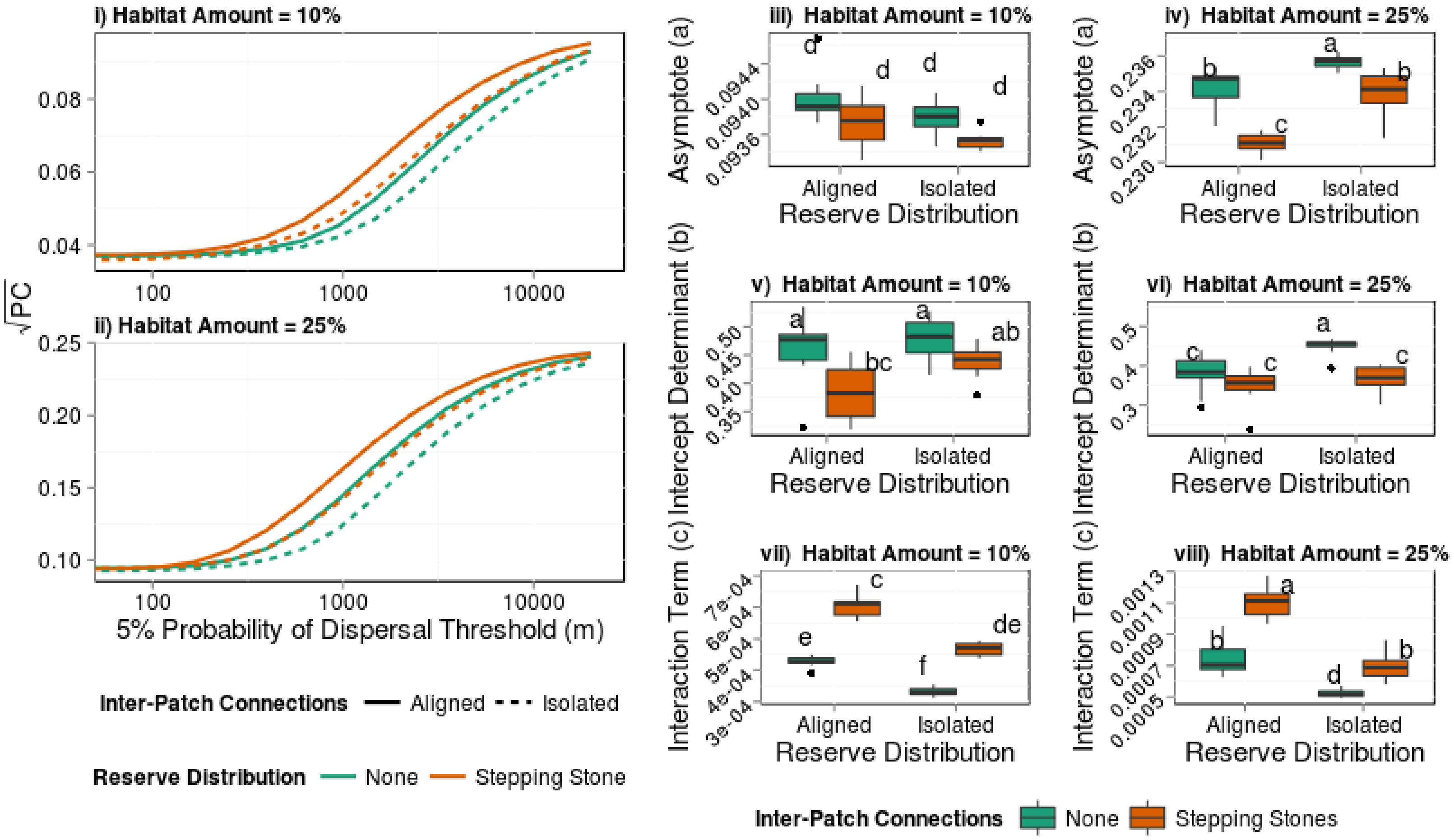

Figure 2.8. *PCRC* and boxplots of *PCRC* parameters for different distributions of habitat reserves with and without stepping-stone connections between habitat reserves. Letters indicate significant differences between groups based on a Tukey's HSD test with an $\alpha \leq 0.05$. The scale of response variable axis differs between habitat amounts, but differences between groups were calculated across all habitat amounts.

addition of stepping-stone connections across habitat amounts because the fragmentation of habitat patches was not manipulated, fragmented patches were simply oriented to minimize the extent of non-contiguous habitat to be crossed. The strongest impact of stepping-stone connections was observed for the interaction term (Fig. 2.8 *vii* and *viii*). Stepping stone connections were observed to result in greater increases in the interaction term for aligned distributions of habitat reserves; however, the interaction between stepping-stones and reserve distribution lacked significance. These results indicate that the *PCRC* assessed stepping-stones as achieving their management goal by reducing the distances of non-habitat to be crossed in order to reach other habitat reserves.

DISCUSSION

A clear understanding of how a landscape metric responds to controlled changes in simple landscapes can help guide the interpretation of index results from complex landscapes. Creating a *PCRC* of the $\sqrt{PC}$ index results over a range of dispersal values demonstrated interpretable responses to manipulations of the amount, fragmentation, and dispersion of suitable habitat in simple landscape scenarios. The specificity of response of the asymptote, intercept and interaction term that describe a *PCRC* to these manipulations indicates that they can be used to assess how alternative landscape management strategies affect each of these relevant landscape factors. The influences of habitat amount can be independently assessed by examining the asymptote values of *PCRC*. A given habitat amount can vary in how fragmented and spatially dispersed it is, and each factor influences habitat connectivity. The intercept and interaction term of *PCRC* can be compared between alternative management strategies to assess the impacts on the fragmentation and dispersion of suitable habitat. When scenarios were created with increased amounts of suitable habitat, decreased fragmentation, decreased spatial dispersion, and increased inter-patch connections, the resulting *PCRC* and parameters had significant positive responses. These parameters can be used by landscape managers to guide decisions on how best to distribute suitable habitat patches to maximize connectivity based on the constraints of habitat amount specific to the landscape of examination. This approach explicitly quantifies the influence of each landscape factor rather than condensing their combined influence into a single value, facilitating identification of which aspects of landscape structure should be managed to maximize connectivity.

The response of *PCRC* to specific types of landscape conditions indicates that there are certain assumptions that must be recognized when interpreting index results. The amount of habitat in a landscape is a primary driver of landscape connectivity and can have a large enough effect to override the effects of habitat distribution (Hodgson et al. 2011). Increased amounts of habitat increase connectivity not only because there is more available habitat, but also because when habitat amount is increased within a finite spatial area it will intrinsically impact the distribution of habitat as well, resulting in percolation threshold amounts of habitat where connectivity is maximized. This habitat amount threshold is reflected in *PCRC* results as any increase in habitat amount results in elevated assessments of connectivity, and at high amounts of habitat distribution exerted less influence on index results. The compartmentalization of index inputs allows for a flexibility of application to a wide range of landscapes and habitat types, but is also a source of potential error in the biological realism of landscape assessment. The criteria used to delineate and quantify the values of habitat patches dictates index values. The applicability of index results is therefore dependent on the degree that the criteria of habitat delineation reflect biologically relevant habitat characteristics.

Conceptually, a connectivity response curve can be constructed using any connectivity metric that incorporates a manipulable spatial component into index calculation, but the *PC* index possesses characteristics that make it well suited to examination of large areas with habitat delineated at a fine scale. The *PC* index's applicability to landscapes represented in a vector format allows for examination of large spatial extents with the types of forest inventory and ecosystem classification maps that are typically available to landscape managers. A metric that can be applied to vector data allows for the examination of large areas without sacrificing the ability to delineate small habitat features, as occurs with raster based metrics. This behaviour is due to the use of a maximum product probability of dispersal with Euclidean edge-to-edge distances in *PC* index calculation. When combined with the use of the maximum product probability of dispersal through alternative dispersal routes, as the *PC* index does, crossing an area of non-habitat will be considered to have a

100% probability of dispersal if there is an alternative route of contiguous habitat around the habitat gap. This method of defining dispersal can result in high values of dispersal probability between patches separated by distances greater than the dispersal threshold. The influence of the method of defining dispersal is evidenced in the pattern of results for single habitat patches and scenarios where all suitable habitat patches are connected by habitat corridors (Fig. 2.2 and 7). In both cases the *PCRC* indicates that connectivity of these contiguous extents of habitat is maximized regardless of the spatial scale of dispersal values considered. Due to this behaviour, corridor connections should not be delineated unless there is strong evidence that the corridor does result in unimpeded movement between habitat patches. The variable identified as dispersal probability in index calculation would therefore be more accurately described as gap crossing probability.

The results of a *PCRC* for a given amount of habitat are only impacted by the gaps in contiguous habitat patches and therefore will not be confounded by species-specific behaviours within habitat patches that are independent of overall landscape composition. An index that attempts to include dispersal dynamics that are not explicitly defined increases the uncertainty of index results when these variables are estimated (Beier et al. 2009). An index that considers movement through desirable habitat patches to be unimpeded therefore avoids adding additional levels of uncertainty to index results, but does not realistically portray the movement of individuals through a landscape as spatially-explicit population models do. From the perspective of landscape management, *PCRC* would reflect the degree to which the landscape facilitates or impedes movement among resource patches at the population level.

The results of *PCRC* are consistent with how the landscape would impede movement of a population that had unlimited generations to move through the landscape, and was limited only by its ability to cross patches of undesirable habitat to the extent defined by the dispersal value supplied for index calculation. Indices calculated using maximum product probability of dispersal with edge to edge Euclidean distances should therefore be viewed as the maximum potential connectivity of that landscape to an organism able to cross gaps equal to or less than the supplied dispersal distance, compared to a spatially-explicit population model, which would be a measure of the realized functional connectivity of the focal species. By examining connectivity from the perspective of a habitat type over a range of dispersal abilities rather than from the perspective of a focal species, the examination can focus explicitly on the habitat characteristics that are assumed to be biologically relevant as defined in the criteria for calculation of habitat suitability values.

PCRC index values do not convey what is a “good” or “bad” landscape composition. A *PCRC* applied in the manner herein quantifies the effects of changes in landscape structure on the amount, fragmentation and dispersion of a defined habitat type, which can be compared between scenarios. The *PC* index varies between 0 and 1.0 and is maximized when the entire landscape is the focal habitat type. This type of situation is neither realistic nor desirable. Based on the currently accepted principles of ecosystem dynamics, any given landscape would be expected to be comprised of a mosaic of habitat types (Carey 2003), and a connectivity index of 1.0 for a certain habitat type would result in an index result of 0.0 for all other habitat types. If index maximization does not represent a desirable landscape condition, an alternative method of defining a desired state is required. In modern ecosystem management the goal is frequently to emulate the landscape patterns created by natural disturbances (Hunter 1993, Mitchell et al. 2002). Since natural disturbances are stochastic, a range of potential landscape conditions can be expected, this range is referred to as the natural range of variability (Landres et al. 1999, Klenner et al. 2008). A reasonable goal for landscape management would be to maintain levels of connectivity that fall somewhere within the natural range of variation. Based on the sensitivities of *PC* based *PCRC* to controlled changes in landscape structure, it could be used as a tool to compare the complex landscapes created by the interaction of land use strategies and natural disturbances to the landscapes predicted from the historical range of variation of natural disturbances. Incorporating the calculation of *PCRC* into the CONEFOR software package would facilitate critical assessments of the validity of this technique. A menu-driven interface in the CONEFOR software would allow for this technique to be applied by a wider range of users, and facilitate its application to studies where the deduced relationships between landscape structure, *PCRC* results, and population dynamics can be empirically validated.

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CHAPTER 3: QUANTIFYING CONNECTIVITY USING GRAPH-BASED CONNECTIVITY RESPONSE CURVES IN COMPLEX LANDSCAPES UNDER SIMULATED FOREST MANAGEMENT SCENARIOS.

INTRODUCTION

Modern forest management is focused on the conservation of biodiversity and habitat values while maintaining timber resources (Fischer et al. 2006, Eriksson and Hammer 2006, Hoberg and Malkinson 2012). Anthropogenic impacts to habitat distribution affect the potential for species to disperse between habitat patches, hence the maintenance of habitat connectivity is widely recommended as a method of promoting ecosystem resilience and biodiversity in landscapes subject to disturbances (Taylor et al. 1993, Fischer and Lindenmayer 2007, Lindenmayer et al. 2008, Brudvig et al. 2009). Careful attention should be paid to maintaining an appropriate spatial pattern of retained mature forest habitat during harvest planning to avoid unnecessary losses of biodiversity in forested landscapes, as many species are known to rely on this habitat type (Raphael et al. 2001). In British Columbia (BC) the distribution of mature forest habitat in a landscape is managed by controlling the amount of forest that can be harvested, the spatial distribution of harvesting, and by excluding harvest from old growth management areas (*OGMA*) (Forest Practices Board 2012). Despite being a frequently recommended management strategy, there are no accepted standards for the measurement of connectivity or its application to forest management strategies (Lindenmayer and Fischer 2007, Kindlmann and Burel 2008, Laita et al. 2011).

To have value as a tool to guide forestry management, a connectivity metric should reflect the accepted principles of landscape connectivity, be sensitive to the impacts of forestry, and be logistically feasible to apply to large spatial areas. Landscape connectivity is widely cited and defined as, “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). This definition highlights the differences between landscape connectivity, where the degree to which landscape structure impedes movement is quantified, and patch connectivity, where movement between specific habitat patches is quantified (Tischendorf et al. 2003). From the perspective of forest management, the resource patches of greatest interest are ecologically mature forest habitats (Spies et al. 2006) and the goal is to distribute forest harvesting to maintain the connectivity of mature forests to mitigate the impacts of harvesting on metapopulation dynamics. Metapopulation persistence is enhanced through increased connectivity by minimizing the impediments to movement between patches and allows the re-colonization of areas that have experienced extinction of local populations (Hanski and Ovaskainen 2003). Although connectivity plays an important role in metapopulation dynamics, it can only facilitate movement among otherwise productive populations, and cannot be expected to maintain biodiversity if other aspects of habitat are not managed concurrently.

The primary factors that facilitate or impede movement between patches of habitat within a landscape are the amount of a specific habitat type, how fragmented it is and the spatial dispersion of habitat patches (Tischendorf et al. 2003, Fischer and Lindenmayer 2007, Long et al. 2010). The fragmentation of habitat reflects the number of separate patches a given amount of habitat is divided into, and the spatial dispersion of habitat describes the distance between fragmented patches. Commercial forestry impacts North American landscapes by reducing the amount of mature forest habitat (Spies et al. 2007) and fragmenting the remaining forest patches with road networks to allow for the extraction of the harvested timber (McGarigal et al. 2001, Houle et al. 2010). Larger amounts of suitable habitat increase landscape connectivity by increasing the pool of potentially connected habitat. For a given amount of habitat, fragmentation into a greater number of patches is considered to decrease the connectivity of available habitat (Saunders et al. 1991, Blaschke 2006, Zuckerberg and Porter 2010). Increasing the distance between fragmented patches further decreases landscape connectivity (Tischendorf et al. 2005, Hinam and St. Clair 2008, Anand et al. 2010).

Plotting the response curve of Pascual and Hortal's (2007) probability of connectivity index (*PCRC*) to changes in the spatial scale of a theoretical disperser is proposed as a method of quantifying landscape connectivity for biodiversity conservation. A similar technique (Laita et al. 2010) has been previously applied to examine the impacts of habitat reserves on landscape connectivity. The probability of connectivity index is a graph-based metric calculated using the CONEFOR software package, developed to address the conceptual deficiencies in other connectivity metrics (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007, Saura and Torne 2009, Saura and Rubio 2010). Graph theory is a method of describing the distribution of habitat as a network of nodes which may be connected by links (Minor and Urban 2008, Zetterberg et al. 2010). Each node and link are assigned numeric values based on the value of each node and the strength of each link so that the emergent properties of the entire network can be quantified (Minor and Urban 2007). Distinguishing how the different aspects of habitat distribution impact landscape connectivity is challenging as the factors of habitat amount and habitat distribution are correlated (Smith et al. 2009). In controlled systematic manipulations of simple landscape scenarios, the asymptote, intercept, and interaction parameters of a generalized logistic function that describe a *PCRC* responded independently to changes in the amount, fragmentation and spatial dispersion of a focal habitat (Chapter 2). The specificity of response of each parameter to a specific type of landscape change allows for the conflicting and correlated influence of habitat amount, fragmentation, and spatial dispersion, to be compared among alternative landscape management scenarios. A similar pattern of response in complex landscapes would indicate that these parameters can be used to assess how forestry impacts landscape connectivity. A *PCRC* quantifies the degree that changes to a landscape impact connectivity based on a range of dispersal capabilities, rather than focusing on the multitude of stochastic and deterministic factors that affect the dispersal of focal species but may not accurately reflect impacts to other species (Lindenmayer et al. 2002). Rather than attempting to manage a landscape on a species by species basis, this approach quantifies the changes in the distribution of a focal habitat type in the landscape relative to a starting condition or desired management state. By examining the patterns of habitat connectivity from all spatial scales, impacts that might otherwise be undetected from a species-specific examination will be observable, and results will better reflect the Taylor et al. (1993) definition of landscape connectivity: “the degree to which the landscape facilitates or impedes movement among resource patches”.

Comparisons of complex ecosystem simulation models were used to a) determine if *PCRC* demonstrated the same patterns of response to manipulations of habitat amount, fragmentation and dispersion in complex landscapes as were observed in simple landscapes,

b) assess if *PCRC* can be used to reflect impacts of forestry predicted by the reviewed literature, and c) apply those responses to compare the efficacy of alternative forest management strategies to promote connectivity in a landscape subjected to both natural and anthropogenic disturbance regimes. Independent parameter responses to controlled manipulations of the amount, fragmentation and dispersion of habitat, as induced by rates and distribution of harvest, will indicate that *PCRC* demonstrate the same sensitivities in a complex landscape that were observed in simple landscapes. A negative response to the presence of road networks, increased rates of harvest, and dispersed patterns of harvest are expected based on the predicted connectivity impacts of forestry on forest dependent species assemblies. Decreased fragmentation and dispersion indices would indicate that distributing *OGMA* as corridors achieved the goal of minimizing losses of landscape connectivity associated with forestry.

METHODS

Landscape scenarios were created for a 110 000 ha study area dominated by coniferous forest located approximately 125 km north of Kamloops, BC (51°52'30.92"N, 119°36'16.78"W). The landscape is composed of forests of the Engelmann Spruce-Subalpine Fir and Interior Cedar Hemlock zones outlined in the Biogeoclimatic Ecosystem Classification system used in BC for ecosystem classification (Lloyd 1990). Current forest conditions were assigned a vegetation class based on species and age information derived from the BC Forests and Range Vegetation Resource Inventory (BC Minsitry of Forests, Lands, and Natural Resource Operations 2012). This inventory delineates the landscape based on a range of habitat characteristics including tree species composition, stand age, and crown closure. These factors are used to define forest stands as part of the timber harvest land base or as non-contributing areas where forestry is not economically or operationally feasible. These initial conditions were used to develop landscape scenarios where alternative harvesting strategies were applied over a simulated 50 year period using the Tool for Exploratory Landscape Scenario Analyses (TELSA). TELSA is a spatially-explicit landscape simulation model designed to project ecosystem conditions, incorporating the influence of forest harvesting, natural disturbances, and succession (Kurz et al. 2000). This model has been previously employed as a method of estimating the impacts of management strategies and natural disturbances on forest ecosystems in BC (Klenner et al. 2000, Klenner and Walton 2009). The TELSA model was used to create scenarios where the connectivity impacts caused by roads, changes to the amount and distribution of harvest, natural disturbances, and OGMA could be assessed and compared to the current landscape connectivity (Table 3.1).

Roads

Different combinations of habitat amount and distribution, as outlined below, were assessed with and without the presence of roads (Fig. 3.1 c and d). The existing road network was based on inventories from the BC Ministry of Forests, Lands and Natural Resource Operations. Using the existing road network, additional roads were extended to new harvest areas using the road projection tool of the TELSA model. Loose-surface two lane roads were defined as primary roads and were assigned a width of 30 m intended to represent only the area directly impacted by the maintained surface and rights of ways of existing roads. All remaining roads were defined as secondary roads with a width of 20 m. The projected roads that would be necessary for timber extraction in the planned harvest areas were assigned the smaller width class of 20 m to represent a management strategy of limiting the continued establishment of new primary roads. The footprint of the road network was eliminated from the habitat map created for each landscape scenario.

Harvesting Amount and Distribution

Scenarios were created where harvesting was the only disturbance affecting the landscape, to assess how *PCRC*s respond to controlled changes in landscape structure prior to introducing additional stochastic factors. Two factors were altered in the harvesting regimes; the annual volume of timber harvested and the distribution of these harvested areas across the landscape. The amount of mature forest habitat was manipulated by applying different rates of harvest; “low” (125,000 m^3/year) rates of harvest remove less forest habitat than is replaced through succession and re-growth, whereas “high” rates of harvest (185,000 m^3/year) remove more forest than can be replaced, and result in a decrease in the amount of mature forest habitat in the landscape. For each level of harvesting, scenarios were created where harvesting occurred in either aggregated or dispersed areas of harvest without

Table 3.1. Summary of landscape simulation scenarios including mean and standard deviation of habitat amounts across ten Monte Carlo replicates for the examined landscape scenarios.

Road Presence	Harvest Rate	Harvest Distribution	Fire (% of Historic Rate)	OGMA Distribution	Mean Habitat Area (ha)	Standard Deviation of Habitat Area
Initial State	Initial State	Initial State	Initial State	Initial State	60170.51	NA
Without Roads	Natural Disturbance	Natural Disturbance	100	None	86473.24	2599.50
Without Roads	Low (125K)	Aggregated	0	None	62962.96	271.43
Without Roads	Low (125K)	Dispersed	0	None	62232.62	126.38
Without Roads	High (185K)	Aggregated	0	None	53856.36	459.47
Without Roads	High (185K)	Dispersed	0	None	52705.22	210.21
With Roads	Low (125K)	Aggregated	0	None	61308.99	256.70
With Roads	Low (125K)	Aggregated	0	Corridor	60308.62	153.59
With Roads	Low (125K)	Dispersed	0	Current	59340.32	338.67
With Roads	Low (125K)	Dispersed	0	None	60223.91	121.03
With Roads	Low (125K)	Dispersed	33	Corridor	57656.05	330.09
With Roads	Low (125K)	Dispersed	33	Current	57148.97	305.00
With Roads	Low (125K)	Dispersed	100	Corridor	52257.51	578.94
With Roads	Low (125K)	Dispersed	100	Current	52253.10	503.79
With Roads	High (185K)	Aggregated	0	None	52304.16	438.41
With Roads	High (185K)	Dispersed	0	Corridor	50741.47	139.31
With Roads	High (185K)	Dispersed	0	Current	47877.56	542.25
With Roads	High (185K)	Dispersed	0	None	51012.59	184.39
With Roads	High (185K)	Dispersed	33	Corridor	48137.97	256.07
With Roads	High (185K)	Dispersed	33	Current	44391.48	846.43
With Roads	High (185K)	Dispersed	100	Corridor	45131.24	918.71
With Roads	High (185K)	Dispersed	100	Current	44399.15	853.17

retention (Fig. 3.1 a and b). Dispersed harvesting was defined by a maximum cutblock size of 40 ha, and minimum distance of 150 m from any previous cut block that had not reached a "green-up" stage of regeneration (approximately 17 years since harvest). These characteristics are similar to the conventional harvest design for the area. Aggregated areas of harvest were modeled by removing green-up constraints and conducting subsequent harvests adjacent to recently harvested areas, resulting in larger patches of disturbed areas. For each permutation of harvest amount and distribution, ten Monte Carlo replicates were run. Each replicate followed the same rules regarding harvest distribution and amount, with a different random number seed for designating the initial areas of harvest from the pool of eligible polygons in the study area.

Natural Disturbances

To reflect the influence of natural disturbances on the forests of British Columbia, scenarios were created that included stand replacing fires. Natural disturbances were applied using the TELSA model at rates of 33% or 100% of historical disturbance levels, based on historic fire records from 1926 to present. Similar to the distribution of harvesting, the TELSA model applies equal amounts of disturbance between scenario replicates, but uses a random number seed to determine the timing and size of fires. For each level of natural disturbance, scenarios were created with harvesting occurring at "low" and "high" levels of harvest with a dispersed harvesting distribution. A baseline (no harvesting) landscape condition without anthropogenic disturbances was generated by applying only natural disturbances to the landscape for a period of 150 years. The time period allowed all previously disturbed areas sufficient time to regain value as mature forest habitat based on the 120 year threshold used to delineate mature forest habitat (see below).

Old Growth Management Areas (OGMA)

OGMA are a management designation used to exclude areas from harvest to maintain mature forest habitat. Scenarios with the current OGMA distribution (Fig. 3.2 a), were compared to scenarios with OGMA distributed as corridors in a hypothetical radial pattern across the landscape (Fig. 3.2 b) intended to promote connectivity without considering other habitat requirements such as minimum patch sizes. These comparisons were conducted with and without natural disturbances present in the landscape. The ratio of OGMA allocated in

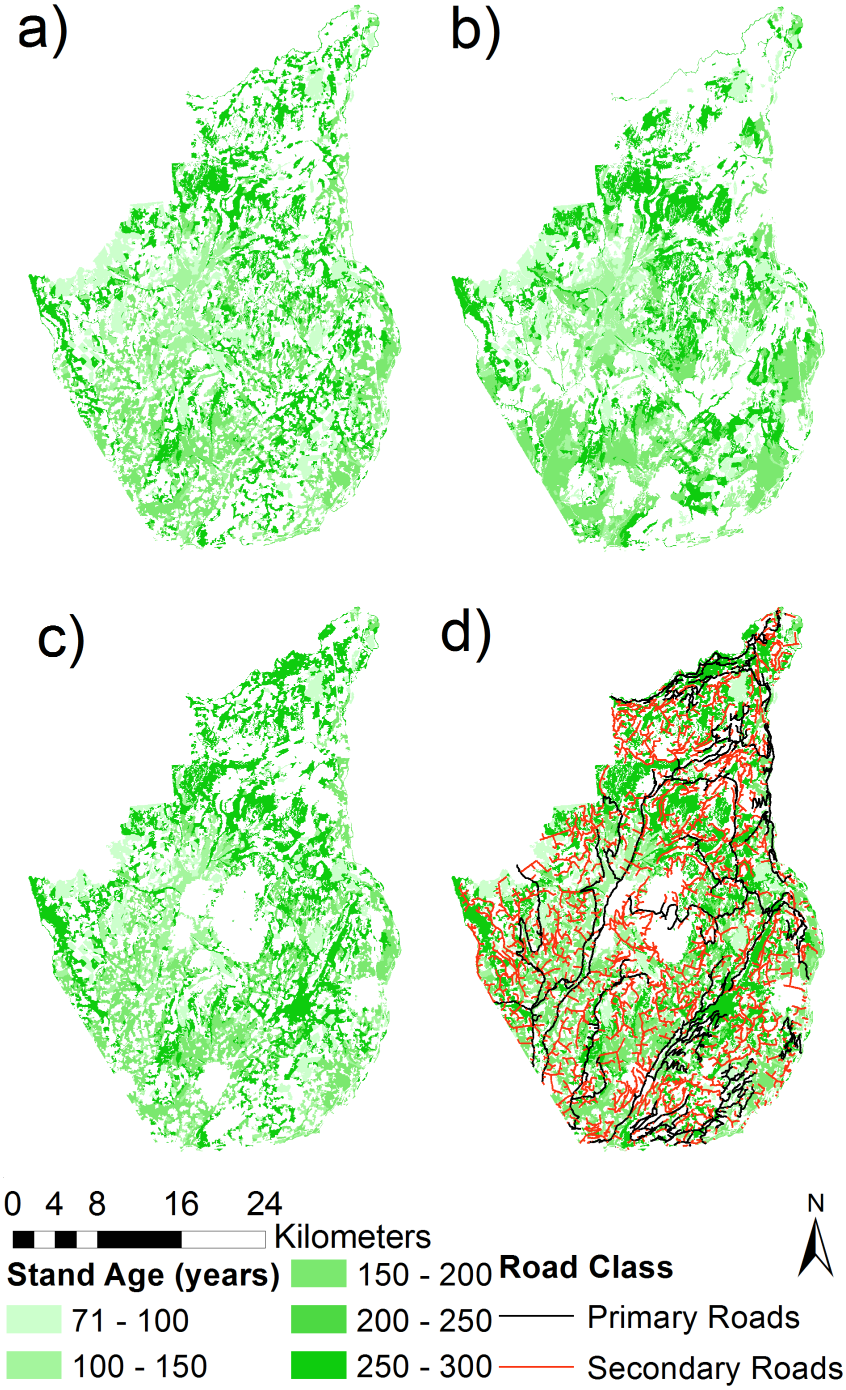


Figure 3.1. Examples of the distribution of mature forest habitat in the North Thompson landscape after 50 years of harvesting at 185 000 m^3/year distributed in either dispersed (a) or aggregated (b) harvesting, dispersed harvesting with natural disturbances at 100% of natural rate (c), and dispersed harvesting with natural disturbances and the accompanying road network (d).

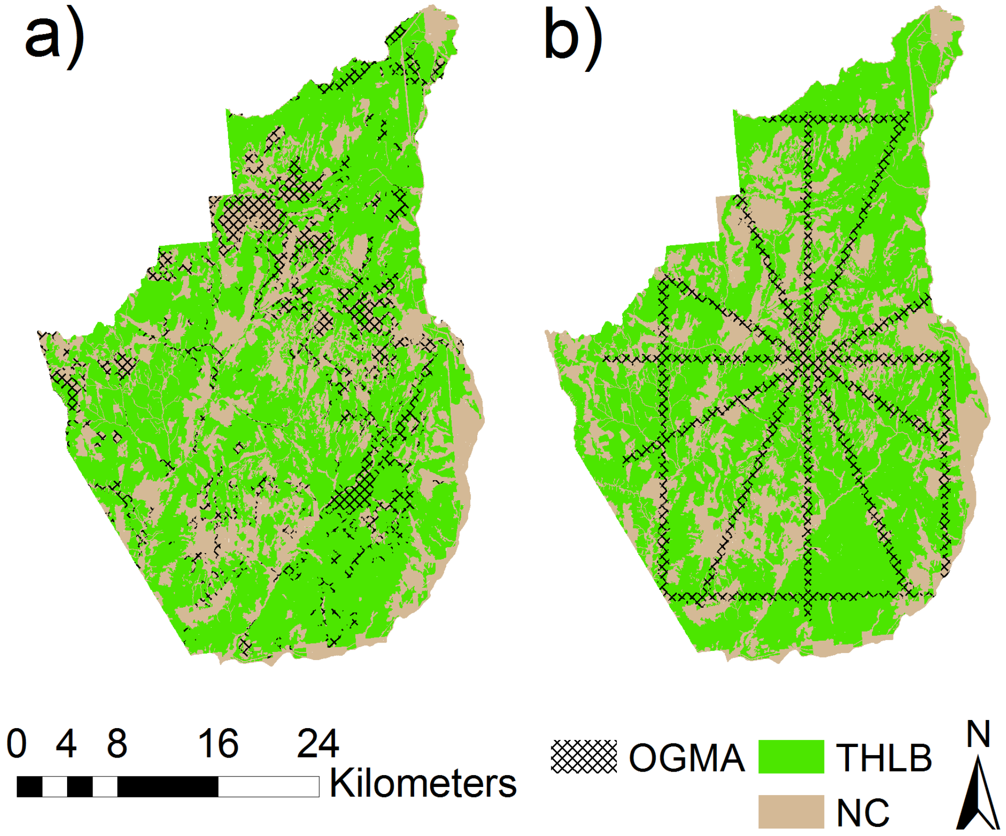


Figure 3.2. Current old growth management areas (OGMA) distribution (a) and conceptual OGMA network distributed as corridors (b) overlaid on the boundaries of the timber harvest landbase (THLB) and non-contributing areas (NC).

non-contributing forests versus areas of the timber harvest land base was maintained constant between the corridor and current OGMA scenarios.

Habitat Delineation

Since the intent was to identify the effect of changes in the distribution of mature forest habitat, the results of fine scale TELSA projections were simplified based on patches of contiguous habitat, defined by the time since the last stand-replacing disturbance. Mature forest habitat was delineated and assigned habitat suitability values using the relationship between stand age and habitat suitability proposed for the American marten (*Martes americana*) in BC (Steventon and Daust 2009). Marten are consistently associated with mature coniferous forest habitat, but have broad habitat plasticity in terms of the tree species composition of that forest (Payer and Harrison 2003). The time required for a disturbed patch to recover value as marten habitat is intended to represent a general criterion for a mature forest focal habitat type, defined by the function,

$$HSI = 1 - e^{\left(-10\left(AGE/OPT_{AGE}\right)^{5}\right)} \tag{1}$$

where HSI= habitat suitability index, AGE=stand age, OPT_{AGE}= age at which habitat value is optimized (120). The median optimization age of 120 years proposed by Steventon and Daust (2009) corresponds to thresholds for mature forest status for all tree species present in the landscape under both provincial and federal classification systems (Gillis et al. 2003). Polygons with habitat suitability index values of less than 0.5 (70.4 years) were defined as unsuitable habitat. The calculated HSI value of each polygon was multiplied by the area in hectares to give an area-weighted habitat value for each polygon that was used as the node attribute variable for index calculation (a_i and a_j).

The edge to edge Euclidean distance (the shortest straight line distance between the boundaries of two polygons) was calculated in metres for all polygon combinations within 2500 m (a value larger than any inter-patch distances present in the landscape) of each source polygon, using the CONEFOR inputs GIS extension created by Jenness Enterprises (Jenness 2008). These Euclidean distances were translated into probabilities of direct dispersal using the internal distance decay function of the CONEFOR software:

$$P_{ij} = e^{-kd_{ij}} \tag{2}$$

where d_{ij} is Euclidean edge to edge distance, and k is a constant used to fit the function to the user defined combination of inter-patch distance and dispersal probability. Manipulations of simple landscape scenarios demonstrated that when Euclidean distances are combined with the maximum product probability of dispersal used to calculate the *PC* index, the values identified as dispersal distance are more accurately defined as gap crossing capability (Chap. 2). For this study the threshold values for 0.05 probability of gap crossing were used to calibrate the distance decay function (Eq. 2), and are the values that connectivity values are plotted against to create *PCRC*.

Index Calculation

The probability of connectivity index is calculated using the software package CONEFOR (Saura and Torne 2009), which applies the function:

$$PC = \left. \sum_{i=1}^{n} \sum_{j=1}^{n} P_{ij} a_i a_j \middle/ A_L^2 \right. \tag{3}$$

to the values supplied in the node and connection files derived from landscape maps where a_i and a_j= the habitat attributes of source and destination patches, A_L= total landscape area, and P_{ij}*= the maximum product probability of dispersal between patches *i* and *j*. The maximum product probability of dispersal (P_{ij}*) is either the product of the probabilities of moving through intermediate habitat patches to reach a destination habitat patch, or the probability of direct dispersal (P_{ij}) calculated by Eq. 2, whichever is larger.

Probability of connectivity index values were calculated for a range of gap-crossing values from 5 to 40 000m, intended to represent all potential dispersal abilities for species that require mature forest habitat. *PCRC* were created by plotting the square root of the probability of connectivity index ($\sqrt{PC}$) values against the gap crossing threshold used in its calculation. The $\sqrt{PC}$ was used to calculate *PCRC* due to its proportional relationship to the amount of habitat in a landscape. The authors of the probability of connectivity index have demonstrated that the numerator of the function used to calculate index values (Eq. 3), is equal to the "equivalent connect area", defined as the size of a single habitat patch that is equivalent to the connectivity of the fragmented patches within the landscape (Saura et al. 2011b). The $\sqrt{PC}$ is equal to the equivalent connected area divided by the total area of the landscape and is therefore a measure of the proportion of the total landscape that when contained in a single polygon has the same level of connectivity as the sum of the fragmented habitat patches. To compare differences in the non-linear responses *PCRC* were fitted to the generalized logistic function:

$$\sqrt{PC} = {a} \Big/ \left(1 + e^{b - c\,(GapCrossing)}\right) \qquad (4)$$

to quantify the asymptote (a), intercept determinant (b) and dispersal interaction term (c) parameters of the *PCRC* for each replicate of the different landscape scenarios using the non-linear least squares fitting method (R command nls) in the R statistical analysis software (R Development Core Team, 2011). The asymptote (a) of the *PCRC* function is the $\sqrt{PC}$ value when all polygons are considered connected and is dependent only on the total amount of habitat, and can be used as an index of the amount of mature forest habitat in each landscape scenario. The intercept is a function of the proportion of the landscape that is connected when any gap size is considered to fragment habitat. The parameter that defines the intercept (b) was used as an index of the fragmentation of mature forest habitat, with higher values indicating more fragmentation. The interaction term (c) defines the degree to which increases in gap crossing thresholds increase $\sqrt{PC}$ values, and was used as an index of the spatial dispersion of mature forest habitat fragments. Higher interaction term values indicate that the same increase in gap crossing values results in greater increases in the number of connected patches, and therefore represent less spatial dispersion of habitat. For each group of scenario replicates these parameters were used to compare impacts of alternative management strategies on the amount, fragmentation and spatial dispersion of habitat. Comparisons were made using boxplots that were grouped according to significant differences from initial landscape conditions at a threshold of $\alpha \leq 0.05$ using Tukey's HSD test (de Mendiburu 2013).

RESULTS

Roads

The inclusion of a road network had the most pronounced effect on the assessed connectivity between scenarios (Fig. 3.3). Simply including roads necessitates the removal of the road network's footprint from the total available habitat, resulting in differences of 1.4%-1.8 % in the amount of habitat between scenarios (Table 3.1). However, this decrease in the amount of mature forest habitat was minor when compared to the differences induced by altering the rate of harvest, which decreased the mature forest habitat between 8% and 9%. The fragmentation and spatial dispersion indices demonstrated a different pattern of response to the inclusion of a road network than were observed for habitat amount index values. Scenarios that lacked roads demonstrated only minor differences between asymptote and intercept values, indicating that there are very few limitations to dispersal between habitat patches. As a result, the values of fragmentation and spatial dispersion indices are completely segregated on the basis of the road factor (Fig. 3.4 ii and iii). To control for the strong influence of road networks on *PCRC*, statistical comparisons of the effects of harvest amount and distribution were blocked for the effect of roads, allowing for a more focused examination of the impacts of harvesting strategies.

Harvesting Rate and Distribution

Compared to the current distribution of mature forest habitat connectivity, impacts were minimized by lower rates of aggregated harvest (Fig. 3.2 and 3.4). The scenario that included only natural disturbances demonstrated the highest level of connectivity, to the extent that intercept values were larger than the asymptote values observed in other scenarios (Fig. 3.3). Manipulations of the rates of harvesting between scenarios had the largest impact on the asymptote of *PCRC*, indicating that the asymptote responds to changes in the amount of habitat in a landscape (Fig. 3.4 i). The rate of harvest resulted in significant differences in fragmentation and spatial dispersion indices (Fig. 3.4 ii and iii), though not to the degree of habitat amount index response, or the degree of impact of roads. The results of *PCRC* indicate that aggregated areas of harvest reduce impacts to the amount and fragmentation of habitat compared to scenarios with the same rates of dispersed harvesting (Fig. 3.4 i and ii). Dispersed harvesting scenarios reduced the spatial dispersion of habitat in the landscape (Fig.

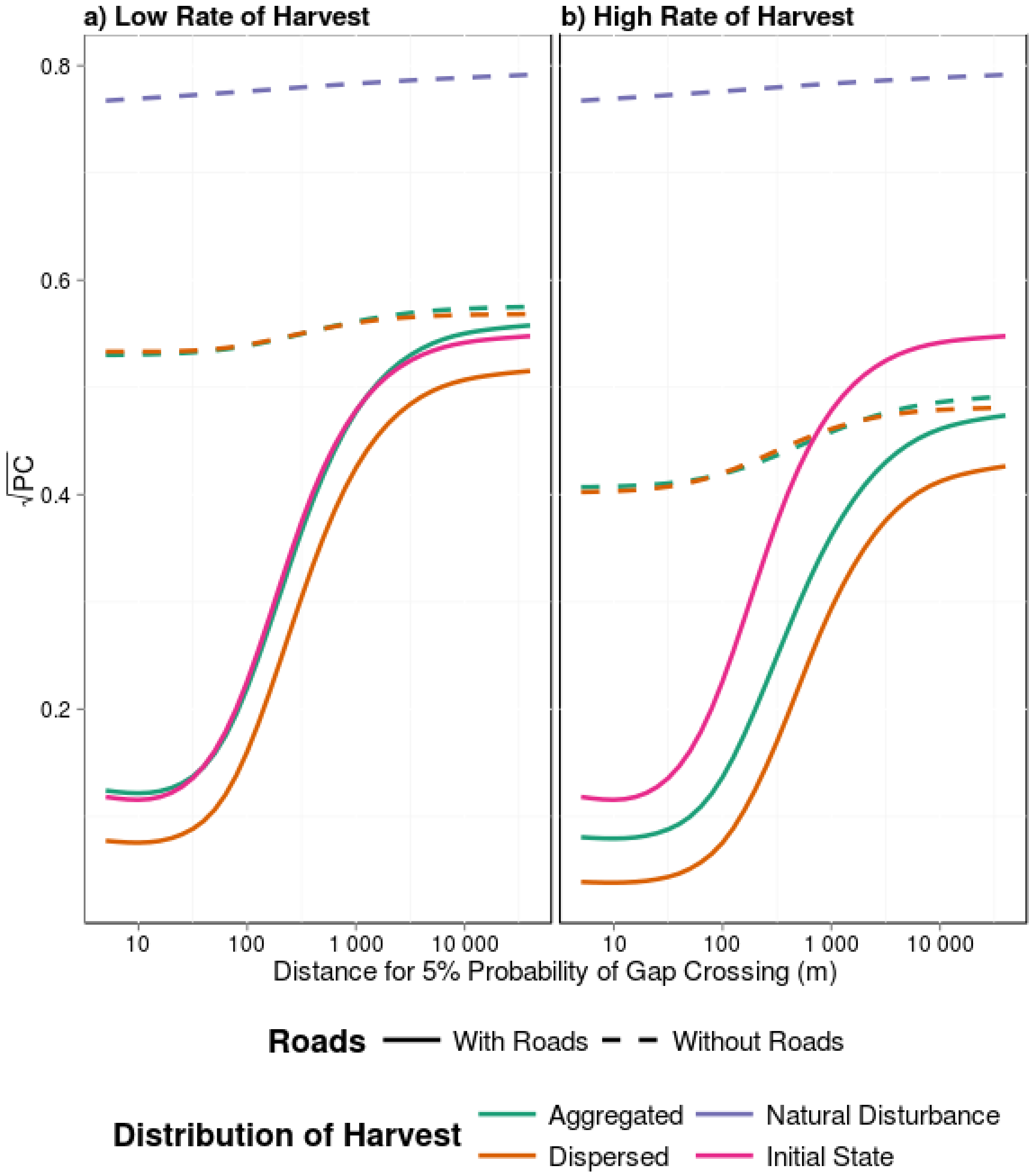


Figure 3.3. LOESS smoothed connectivity response curves (*PCRC*) at low (a) and high (b) rates of harvest comparing ten replicates of scenarios with aggregated and dispersed distributions of harvest (colour) to the distribution of mature forest habitat that currently exists (Initial State) and the distribution expected in a landscape subject to only natural disturbances (Natural Disturbance Only), with and without the presence of roads (line style).

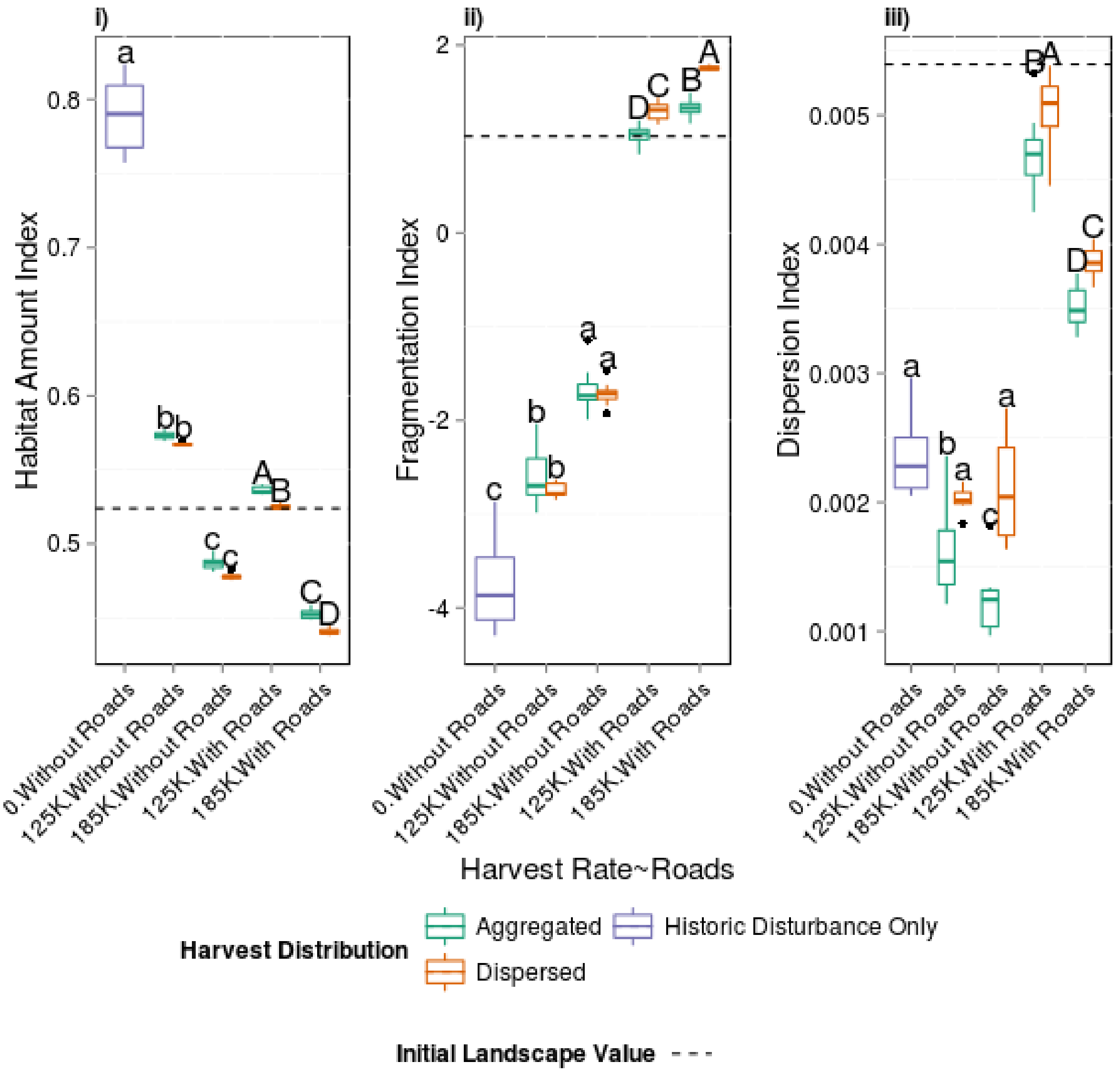


Figure 3.4. Comparison of *PCRC* parameters of habitat amount (i), fragmentation (ii), spatial dispersion (iii) from the *PCRC* in Figure 3.3. Scenarios are displayed according to the presence of roads for each rate of harvest (x axis), and distribution of harvest (box colour). Letters indicate significant differences in the deviation from the initial landscape state (dotted line) based on Tukey's HSD test with α≤ 0.05. Tukey tests were performed blocking for the effect of roads; capital letters indicate differences between scenarios with roads and lower case letters indicate differences between scenarios without roads.

3.4 iii). An increased rate of harvest exacerbated the effect of harvest distribution on fragmentation. These factors combined indicate that the amount of habitat in the landscape is the factor that exerts the greatest influence on *PCRC* results. The habitat amount index responded to changes in the distribution of harvest (Fig. 3.4 i) due to the differences in total habitat amount that arise when employing volume-based harvesting limits. Although the total volume removed from the landscape is equal, the differences in timber volume per hectare results in differences in the total area harvested and therefore creates differences in the remaining mature forest habitat between scenarios with common rates of harvest (Table 3.1). The habitat amount, fragmentation and dispersion indices each responded to the changes induced by different amounts and distribution of harvest, but also responded to landscape changes other than those they were predicted to detect.

Natural Disturbances

Including natural disturbances in scenarios further reduced the amount of mature forest habitat, resulting in lower connectivity values at all spatial scales (Fig. 3.5). The changes in the amount of habitat in the landscape caused by natural disturbances are quantified by decreases in the *PCRC* asymptote, regardless of the level of harvesting or designation of OGMA applied to the landscape (Fig. 3.6 i and iv). Increased rates of natural disturbances resulted in increased habitat fragmentation; these differences were exacerbated at high rates of harvest (Fig. 3.6 v). The same pattern of response was observed for the spatial dispersion of habitat fragments (Fig. 3.6 iii and vi). These results indicate that the primary impact of natural disturbances is a reduction in the total amount of mature forest habitat that is compounded by impacts to the fragmentation and spatial dispersion.

Compared to the initial state of the landscape, distributing OGMA in corridors reduced the impact of harvesting on landscape connectivity (Fig. 3.5). The establishment of corridors had the effect of increasing the total amount of mature forest habitat, and decreasing fragmentation of that habitat, evidenced in the response of the indices of habitat amount and fragmentation (Fig. 3.6). The efficacy of corridor-based OGMA at minimizing the impacts of harvesting on landscape connectivity varied according to the rates of harvest and natural disturbances present in the landscape. Increased rates of harvesting and natural disturbances decreased the differences between alternative OGMA distributions for all

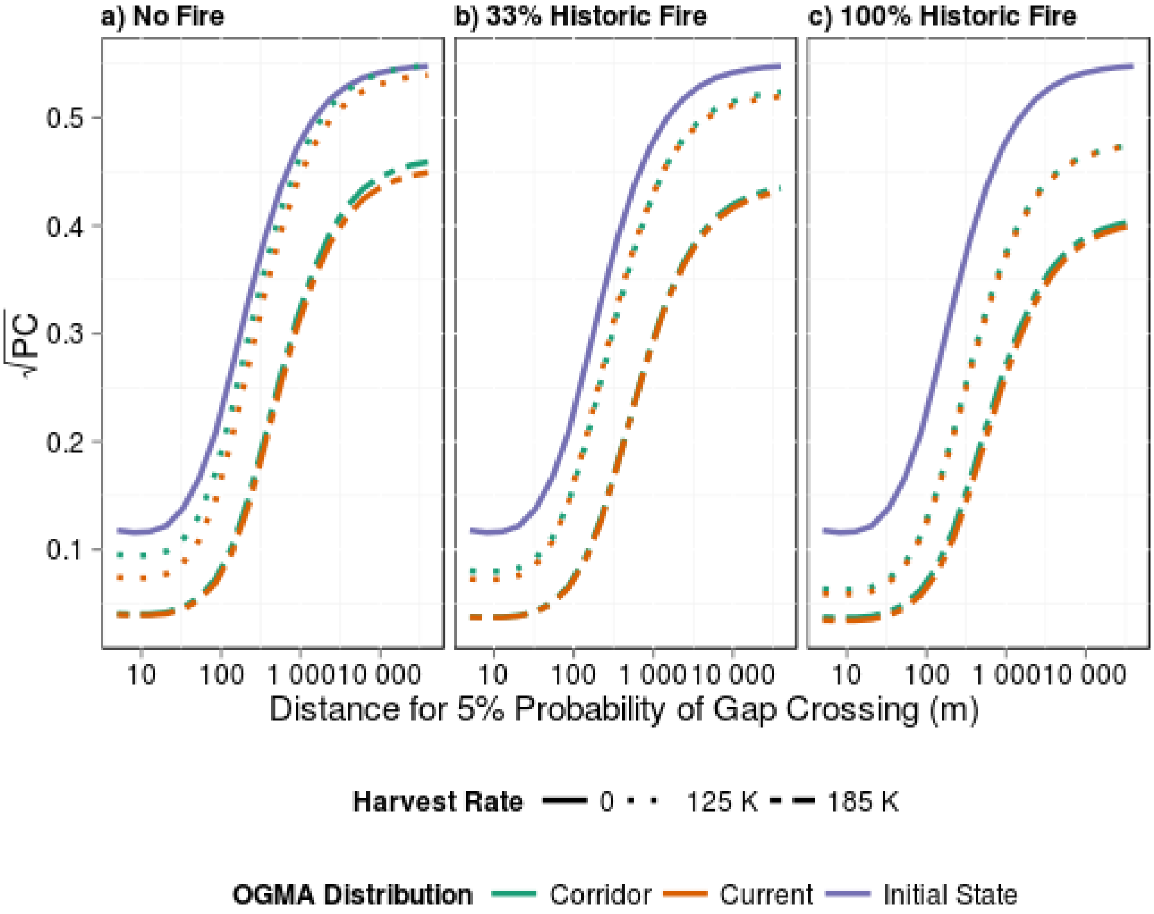
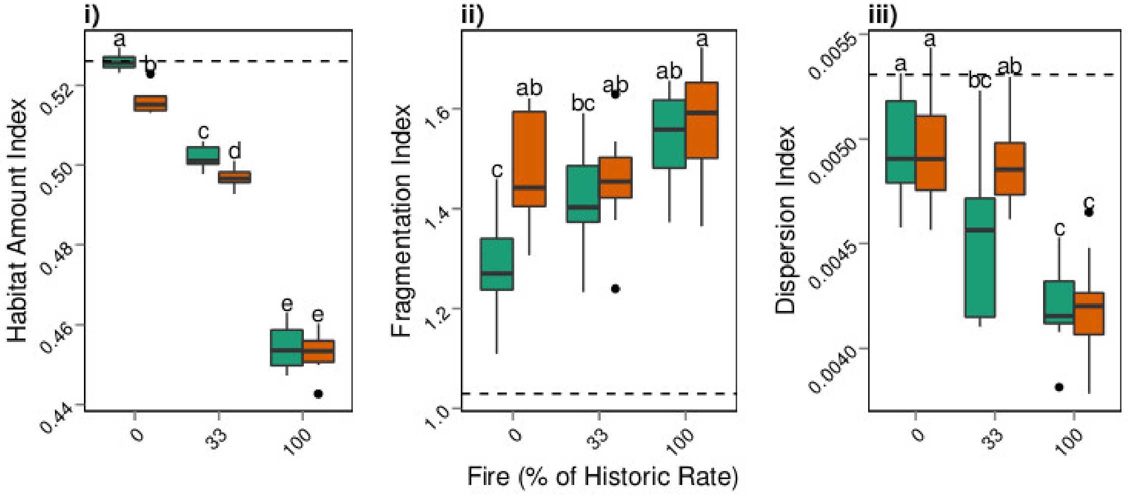


Figure 3.5. LOESS smoothed connectivity response curves (*PCRC*) for ten replicates of scenarios comparing the impact of OGMA distribution (line colour) on landscape connectivity after 50 years of simulated harvesting at rates of 125 000 m3/year or 185 000 m3/year (line type), with natural disturbances occurring at 0 (a), 33 (b), or 100 (c) percent of the historic rate.

a) 125K Harvest



b) 185K Harvest

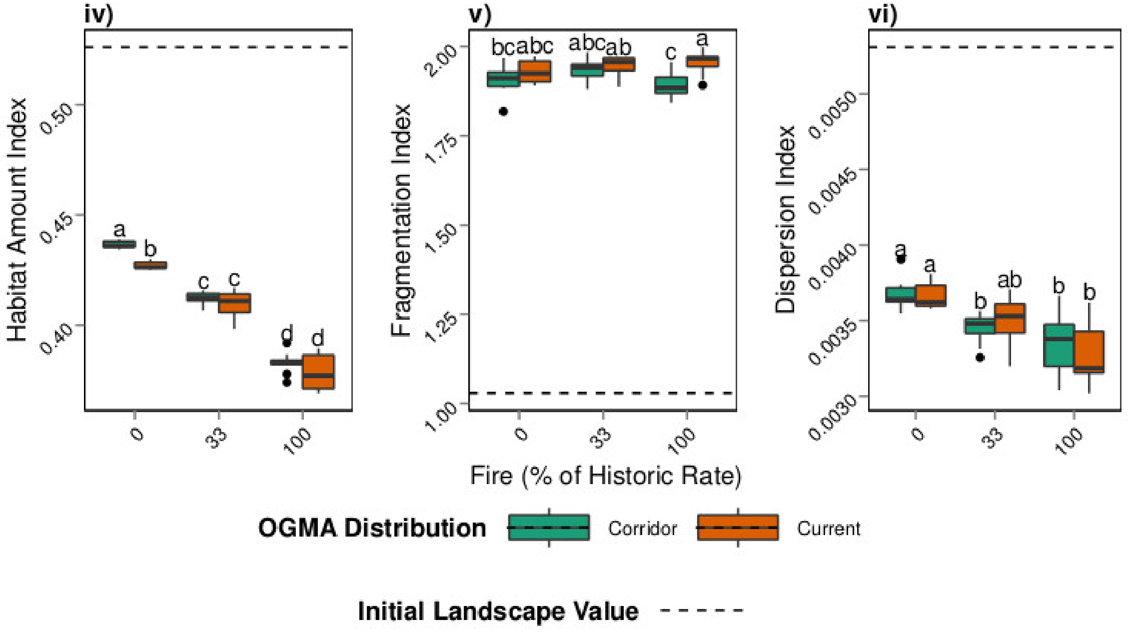


Figure 3.6. Comparison of *PCRC* parameters of habitat amount (i, iv), fragmentation (ii, v), spatial dispersion (iii, vi) from the *PCRC* in Figure 3.5. Scenarios are displayed according to the rate of harvest (a and b), rate of natural disturbances (x axis), and distribution of OGMA (box colour). Letters indicate significance differences in the deviation from the initial landscape condition (dotted line) between groups with a common rate of harvest based on Tukey's HSD test with α≤ 0.05.

connectivity parameters (Fig. 3.6). This interaction is most evident in the index of fragmentation (Fig. 3.6 ii and v).

Old Growth Management Areas

At high rates of harvest, the pool of eligible stands in the timber harvest land base is reduced, decreasing the number of potential locations for subsequent areas of harvest, that causes greater similarity in landscapes between replicates of a management scenario. Natural disturbances diminished the benefit of allocating OGMA in corridors (Fig. 3.5 and 3.6). Natural disturbances do not observe restrictions imposed on landscapes by forest managers and their stochastic distribution can result in stand-replacing disturbances in areas intended to be maintained in a mature forest state, thus decreasing connectivity. When a small number of corridors are responsible for maintaining habitat connectivity, a single natural disturbance can exert a substantial effect on overall landscape connectivity.

DISCUSSION

Controlled manipulations of the amount and distribution of mature forest resulted in interpretable *PCRC* responses. Manipulations of the rate of harvest were reflected in the habitat amount index (*PCRC* asymptote), while manipulations of the distribution of harvest produced significant responses in the fragmentation (*PCRC* intercept determinant) and spatial dispersion (*PCRC* interaction term) indices. These responses lacked the specificity of response to different types of landscape manipulations that were observed in previous examinations of simple landscapes. This is potentially due to the relatively large amounts of habitat in the examined landscape scenarios. Applying additional habitat suitability criteria to stand age will reduce the proportion of the landscape considered suitable habitat.

PCRC demonstrated a response to anthropogenic landscape changes that is consistent with how forestry is expected to impact connectivity. Increased rates of harvest and dispersed distributions of harvest decreased habitat amount and increased fragmentation, while decreasing the spatial dispersion of habitat. The factor that had the largest influence on landscape connectivity values was the presence of road networks. The scale of response to the presence of a road network shows that roads exert a strong influence on the assessed connectivity of landscapes through their influence on habitat fragmentation, and indicates that any examination of the impacts of management strategies should include roads in their delineation of habitat patches. The strong influences of roads on connectivity index values reflects the empirically supported theory that the road networks associated with forest management exert a significant influence on populations separated by roads, and may play a greater role than the harvesting itself (Reed et al. 1996, Tinker et al. 1998). This sensitivity is due to the method of characterizing inter-patch connections. When the maximum product probability of dispersal is used with edge to edge Euclidean distances, any patches that are connected by a series of contiguous intermediate patches will be considered fully connected regardless of the distance through intermediate patches of mature forest habitat. As a result, there is an implicit assumption that dispersers are able to move around disturbed areas to cross the small gaps created by roads rather than crossing the larger gaps created by harvesting. This behaviour indicates that *PCRC* represent the landscape under the assumption that there are no impediments to movement through contiguous patches of the focal habitat.

Model scenarios where OGMA were distributed to form corridors were evaluated as being less fragmented than scenarios with the current OGMA distribution, though this benefit was diminished when harvest rates or the incidence of natural disturbances were high. This indicates that as habitat amount is decreased, the landscape is more prone to the disruption of habitat connections by natural disturbances. Conducting multiple replicates of scenarios with natural disturbances can be used to determine if a small number of connections are responsible for the maintenance of landscape connectivity rendering the landscape vulnerable to disruption. Management strategies that result in a high degree of variability between replicates with natural disturbances would indicate that the habitat patches that are responsible for maintaining landscape connectivity are prone to disruption by natural disturbances. Robust landscape management strategies should therefore focus on identifying management strategies that demonstrate minimal variance between replicates, indicating that there are redundant routes of dispersal between habitat patches**.**

The application of a spatially-explicit population model of a focal species is inherently prone to uncertainty in terms of how well each additional model factor accurately represents the behaviour of that species (Beier et al. 2008). The accuracy of these values is important as minor changes to model inputs lead to significant variation in connectivity indices (Rayfield et al. 2010). In addition to the logistical difficulties of establishing a spatially-explicit population model there is debate as to the validity of extrapolating results from a focal species to a range of species since it contradicts the theory of niche specialization leading to heterogeneous species distribution (Lindenmayer et al. 2002). In cases where the environmental requirements of the focal species are applicable to a range of species, deriving a measure of functional connectivity using a spatially explicit population model would represent only species with similar dispersal capabilities. If connectivity values were calculated based on the dispersal abilities of the marten, whose habitat requirements were used to delineate the focal mature forest habitat type, its dispersal distance of over 100 km (Broquet et al. 2006) is unlikely to represent the metapopulation impacts of other mature forest species such as the forest lichen Methuselah's beard (*Usnea longissima*) which has dispersal distances estimated to be as low as 5 m (Esseen et al. 1981). Since biodiversity conservation is focused on conserving meta-populations of a range of species, rather than explicitly defining how the landscape is perceived by a focal species, there may be greater utility in quantifying the degree that landscape structure impedes movements between patches based on generalized assumptions of the factors that affect habitat suitability and impede dispersal over a range of spatial scales.

The assumptions of the criteria for habitat delineation and dispersal probabilities will influence index results. A *PCRC* is simply a method of quantifying all potential connections in a landscape based on the applied criteria for habitat suitability and dispersal; the degree to which *PCRC* accurately represents landscape connectivity is therefore dependent on the validity of these criteria. In this examination, the results of model simulations were delineated based on a simple criterion, stand age. By basing habitat suitability values solely on a factor that is altered by harvesting, different patterns of habitat could be modelled through manipulations of harvest rate and distribution to test the sensitivity of the index to specific types of landscape changes. This simple criterion led to the majority of the landscape being considered suitable habitat, resulting in model scenarios where percolation thresholds were reached. This effect was exacerbated by the method of quantifying inter-patch connections. The probability of dispersal was quantified based on edge to edge

Euclidean distances and therefore assumes that movement through habitat patches is unimpeded, and better represents the impediments to populations able to cross habitat gaps of different sizes, rather than individuals able to disperse different distances. These assumptions were sufficient to assess the ability of the index to detect specific types of landscape change; however management of ecosystem types of concern will require more specific criteria for habitat delineation and connections. The manipulations of OGMA were intended to maximize habitat connectivity. These manipulations did not exert a strong positive influence on landscape connectivity, indicating that either corridors do not promote landscape connectivity, *PCRC* are insensitive to the presence of corridors, or that the examined landscape scenarios were already well connected, leaving little room for improvement. Given the empirical support for the benefits of habitat corridors (Beier and Noss 1998, Perault and Lomolino 2000, Tewksbury et al. 2002, Hudgens and Haddad 2003), the response of *PCRC* to the presence of corridors in simple landscape scenarios (Chapter 2), and the relatively high proportion of habitat in the examined scenarios, a highly connected initial state is the most likely cause of this lack of response. Conducting similar analyses with more stringent criteria for habitat delineation can be used to determine if the high proportion of the landscape identified as suitable habitat is responsible for this behaviour.

Decisions on the amount and distribution of harvesting are frequently based on extraneous factors. Currently in BC the conservation of biodiversity is identified as a primary management goal, but only when it does not unduly impact timber supply (Hoberg and Malkinson 2012). The locations on a landscape where harvesting occurs will, by default, be dictated to a large extent by the logistics and economics of operating at those points. Due to these factors, the pool of land eligible to be designated as habitat for conservation is limited and management strategies are similarly limited in terms of the actions that can be taken. The allocation of conservation areas will be similarly constrained by management for landscape characteristics other than connectivity. With appropriately tailored assumptions for index inputs *PCRC* can be used by landscape managers to assess the relative contribution of habitat amount, fragmentation and spatial dispersion to landscape connectivity and select the best option of feasibly applicable management strategies for conserving landscape connectivity and, by extension, biodiversity.

CONCLUSION

This study revealed that *PCRC* demonstrated similar sensitivities to manipulations of landscape structure in complex scenarios as were observed in simple landscapes, however the same specificity of response was not observed. The asymptote, intercept, and interaction term of the logistic function that describe *PCRC* can be used as indices to reflect how the amount, fragmentation and spatial dispersion of habitat influence landscape connectivity. Rather than presenting connectivity from the perspective of a focal species, this approach quantifies the degree that changes in landscape structure impede dispersal across at range of spatial scales, based on the assumptions inherent in how the index characterizes habitat patch connections. Maximizing the amount of retained mature forest was identified as the best method of promoting landscape connectivity. Distributing OGMA to form corridors within a landscape had a minimal effect on reducing the loss of connectivity caused by sustained harvesting. This effect was further reduced when natural disturbances are included in landscape scenarios. The decreased specificity of index response to different types of landscape changes and the minimal connectivity benefits gained through establishing corridors may be due to the high proportion of the landscape considered desirable habitat and should be tested by comparing scenarios where more exclusive criteria for habitat delineation are applied. Within the management constraints of a landscape, *PCRC* can be used to compare the connectivity impacts of alternative management strategies, based on the assumptions of habitat delineation and movement resistance.

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CHAPTER 4: MANAGEMENT APPLICATION

In this thesis, I have highlighted the need for the maintenance of connectivity across a range of spatial scales when attempting to conserve biodiversity. Based on this consideration, and a review of existing metrics, I proposed that probability of connectivity response curves (*PCRC*)) (created by plotting the results of probability of connectivity index (Saura and Pascual-Hortal 2007) against the range of dispersal thresholds used for index calculation) is a viable method of objectively quantifying how the distribution of habitat in a landscape would impede movement between habitat patches for all species that use the focal habitat type. The strengths of the *PC* index compared to other landscape connectivity metrics are highlighted in Table 1.1. The advantages of applying the *PC* index as a *PCRC* compared to other conceptual methods of quantifying connectivity are summarized in Table 4.1. Using systematic manipulations of a simple theoretical landscape, I demonstrated that using the *PC* index to create *PCRC* results in a metric that responds independently to manipulations of the amount, fragmentation and dispersion of the habitat in a landscape. The application of *PCRC* to temporal and spatial model projections of a large forested landscape, subjected to a range of anthropogenic and natural disturbances, demonstrated how the index can be used to compare the outcomes of different management strategies and illustrated how the assumptions incorporated into the criteria of habitat delineation and dispersal probabilities will influence index results.

The benefit of applying a *PCRC,* rather than simple structural or focal species based approaches to quantify landscape connectivity, is that it simultaneously represents the impacts of changes in landscape structure across a range of spatial scales for any habitat that can be objectively defined. Typically, the focal species used in landscape analysis are mid to large-sized vertebrates. The multifaceted habitat requirements of higher organisms make them well suited as indicators of complex habitat structure, however they are unlikely to reflect the impediments to movement between patches for smaller animals and plants. These species would be expected to have some of the highest dispersal capabilities of all species in

Table 4.1 Comparison of probability of connectivity response curves (*PCRC*) to other common methods of assessing landscape connectivity.

	PCRC	Spatially Explicit Population Models for a Focal Species	Graph Structural Metrics	Simple Structural Metrics
Example	This thesis	Probability of survival and dispersal (Kanagaraj et al. 2013)	Proportion of habitat in largest component (Minor and Lookingbill 2010)	Edge amount (Holien 1997)
Type of connectivity	Potential	Functional	Structural	Structural
Applicability	Broad	Narrow	Broad	Broad
Data requirements	Intermediate	High	Low	Low
Computational Complexity	Intermediate	High	Intermediate	Low
Key assumptions or requirements	Appropriate delineation of habitat and dispersal limitations.	Appropriate assessment of habitat value and definition of dispersal behaviour.	The examined aspect of graph structure represents connectivity.	The examined habitat structure is representative of connectivity.
Model output	The distribution of focal habitat type.	Population impacts for a defined species based on assumptions of habitat use and dispersal capabilities.	Characteristics of a network graph that function as indicators of habitat connectivity.	Characteristics of habitat distribution that function as indicators of habitat connectivity.
Model limitations	Dependent on accuracy of habitat delineation and dispersal limitations.	High specificity of models limits application to other species.	Sensitive to very specific aspects of landscape structure which may not accurately reflect all connectivity impacts.	Sensitive to very specific aspects of landscape structure which may not accurately reflect all connectivity impacts.
Key benefits	Quantifies distribution of a focal habitat type. Gives insight on connectivity for a range of species. Well suited to comparisons of alternative landscape states	Quantification of expected population impacts. Well suited to guide management of habitat for a defined species.	Ease of calculation. Applicability to large habitat networks	Ease of calculation. Incorporates few assumptions.

the landscape, and would therefore not be expected to accurately represent movement between habitat patches for species with smaller dispersal capabilities. Calculating a *PCRC* for a focal habitat type provides a useful analysis of how habitat is distributed in the landscape by responding to the fragmentation, dispersion and amount of the focal habitat. Simultaneously reflecting impacts on these landscape factors gives an objective index of overall landscape connectivity, applicable to any species that occupies the focal habitat type. The flexibility of index input requirements allows application of a *PCRC* to any landscape analysis where a focal habitat type can be objectively defined and the limitation to dispersal estimated.

A *PCRC* is simply an alternative method of applying the *PC* index and as such incorporates all of its benefits outlined in Table 1.1 and referenced in subsequent chapters. The authors of the *PC* index recommend applying the *PC* index to examine a landscape at a defined spatial scale and calculating the *dPC* index value of each habitat patch in a landscape (Saura and Rubio 2010, Bodin and Saura 2010b). CONEFOR quantifies *dPC* by calculating *PC* index values iteratively for the landscape with each polygon sequentially removed from the landscape to determine it's relative contribution to the overall landscape values. This technique excels at prioritizing habitat areas for conservation as the relative value of each habitat polygon is calculated. In a *PCRC* the *PC* is calculated iteratively for a range of spatial scales allowing specific types of changes in habitat distribution to be detected and quantified. A similar conceptual approach has been used to identify the appropriate spatial scale for management (O’Brien et al. 2006) and as a method of quantifying the impact of habitat reserves (Laita et al. 2010). I propose that *PCRC* are a viable method of quantifying specific types of changes in the distribution of a focal habitat type that are known to impact landscape connectivity, and is a useful tool for comparing alternative landscape scenarios. By applying a standardized method of quantifying landscape connectivity between scenarios, differences in index results likely reflect the changes in habitat distribution.

In order to be appropriately applied as a management tool, the assumptions and limitations of *PCRC* must be recognized. *PCRC* is a method of quantifying how the distribution of habitat, as defined by habitat suitability criteria, impedes movement between fragmented habitat patches, based on the assumptions of the dispersal kernel. Index inputs are compartmentalized in the calculation of the *PC* index. Habitat suitability criteria and the impediments to dispersal between habitats can therefore be tailored to reflect the ecosystem and management goals being examined. This flexibility allows for application to any scenarios where a habitat map has been constructed based on criteria deemed relevant by the user. The efficacy of *PCRC* in quantifying how landscape structure impedes movement between habitat patches is dependent upon the degree to which habitat suitability criteria reflect the true value of the focal habitat type to desired species assemblies. When identical criteria are applied to the initial and projected state of a landscape, the impacts of changes in landscape structure can be quantified and compared.

In my study, alternative landscape management scenarios were analyzed with a simplistic delineation of habitat, based solely on the time since the last stand-replacing disturbance, regardless of forest type. This created a situation where the only determinants of habitat distribution were the harvesting and natural disturbances that were manipulated between scenarios. The use of simple criteria to quantify index inputs facilitated objective assessment of the index to specific types of landscape change. This simplistic criterion for habitat delineation leads to a higher proportion of the landscape being considered "habitat" than may be realistic. Applying increasingly specific criteria for habitat delineation will further diminish the amount of suitable habitat in the landscape, avoiding the potential for landscapes where a percolation threshold is reached causing the distribution of that habitat to have only minor impacts.

Sustainable forest management is focused on managing forests so that they provide environmental, social, and economic values for present and future generations (Hickey and Innes 2008). The future state of forest ecosystems will be affected by the impacts of forest management, natural disturbances, and the changing environmental conditions that are predicted due to anthropogenically-induced climate change (Nitschke and Innes 2008). Computer models can be used to predict the range of landscape conditions that may be produced by the interactions of these influences (Pearson et al. 2002, del Barrio et al. 2006). The conservation of connectivity is the most widely recommended action to mitigate the impacts of climate change on biodiversity (Heller and Zavaleta 2009). *PCRC* can be incorporated as an additional landscape metric in simulation models to identify which strategies minimize impacts to landscape connectivity under different climate change scenarios, thereby promoting the conservation of biodiversity.

A *PCRC* approach should not be used in isolation to assess the impacts of forest management strategies. This method of quantifying landscape structure will not account for all habitat characteristics that are necessary for the management of viable populations. Scenarios that maximize connectivity may have detrimental impacts on other important landscape factors, such as patch size requirements, or combinations of different habitat features to satisfy different life history requirements (e.g. habitat for cover and foraging). In sustainably-managed landscapes, social and economic values need to be concurrently managed in addition to biodiversity. Hence, management decisions will rarely be based solely on the impacts to landscape connectivity. *PCRC* allow for comparison of connectivity impacts of different potential management scenarios that satisfy other primary management goals. *PCRC* are an objective method of quantifying overall landscape connectivity based on defined assumptions of habitat suitability and dispersal limitations, representing an additional metric for use in the analyses of cumulative impacts of landscape changes on biodiversity.

PCRC are most effective for quantifying the changes in connectivity for an affected landscape. This is a valuable characteristic as it is conceptually impossible to define what the connectivity of specific habitat type should be, as this necessitates a subjective decision on which habitat types are desired. Landscapes are composed of a mosaic of habitat types that support the diversity of species that occur within that landscape. Increasing the amount of one habitat will invariably decrease the amount of other habitats, hence managers must make decisions on how to balance the appropriate distribution of different habitats within a landscape. Balancing habitat values could be guided by calculating multiple *PCRC* for different habitat types that occur in a landscape and examining how different management strategies impact each habitat type. When identical criteria are applied to different potential landscape compositions, conclusions can be drawn on how different anthropogenic disturbances and management strategies affect habitat distribution. By examining the response of the asymptote, intercept determinant and interaction term of *PCRC* between scenarios it can be determined if the loss of habitat (indicated by changes in the asymptote) result in fragmentation of habitat patches (indicated by changes in the intercept determinant) or increase the spatial dispersion of habitat patches (indicated by changes in the interaction term). Based on the demonstrated responses to known changes in landscape structure *PCRC* can be used by landscape managers to assess how potential management scenarios will affect the distribution of habitat, to select strategies that promote landscape connectivity thereby enhancing biodiversity conservation.

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