PROCESS- VERSUS PATTERN-BASED MEASURES OF FRAGMENTATION: A SIMULATED SENSITIVITY ANALYSIS

BARBARA KERR

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
FOR PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF MASTER OF SCIENCE

GRADUATE PROGRAM IN GEOGRAPHY
YORK UNIVERSITY
TORONTO, ONTARIO

May 2024

Abstract

Landscape fragmentation, which has demonstrated links to habitat loss, increased isolation, a loss of connectivity, decreased biodiversity, and reduced connectivity is difficult to quantify. Traditional pattern-based approaches to measuring fragmentation use landscape metrics to quantify aspects of the composition or configuration of landscapes. The objective of this study was to examine the relative improvements of an alternative process-based approach using the cost of traversing a landscape as a proxy for fragmentation and compare it with the traditional approach. One thousand binary landscapes varying in composition and configuration were simulated, and least-cost path analysis provided the data to calculate the process-based metrics, which were compared with the computed pattern-based metrics. The process-based quantification of landscape fragmentation was more sensitive to landscape fragmentation and strongly related to landscape proportion. My study provides a methodological foundation for further studies as it is not associated with a specific species or ecological process, and thus can be easily adapted to numerous settings.

Acknowledgements

First and foremost, I would like to express my deepest appreciation to my supervisor, Dr. Tarmo K. Remmel, for his unwavering support. Without his assistance and dedicated involvement throughout this process, this thesis would not have been completed. I would also like to express my gratitude to my supervisory committee member, Dr. Jennifer B. Korosi, for reviewing my research and her invaluable feedback. My thanks to Dr. Suzanne MacDonald for taking interest in my work and taking time to be part of my examining committee. In addition, I would like to thank the National Science and Engineering Research Council (NSERC) for awarding me a 2022 Canada Graduate Scholarship – Master's (CGS M). This financial support provided equipment and funding for the completion of this thesis.

My thanks go to The Pattern Lab, Faculty of Environmental and Urban Change, for providing space to carry out my research. The Pattern lab and a Discovery Grant to my Supervisor from NSERC (RGPIN-2021-03645) also gave me an opportunity to present my research at the Canadian Association of Geographers annual conferences in 2022 and 2023. I would be remiss if I did not mention the encouragement that I received from my Pattern Lab colleagues, with whom I had the pleasure of working with over the past few years.

Lastly, I would like to acknowledge the support of the Faculties of Environmental and Urban Change and Graduate Studies for affording me the opportunity to grow intellectually and successfully complete this degree.

Table of Contents

List of Tables

List of Figures

1. Introduction

Landscapes include both natural landforms and anthropogenic features and are continually evolving. Because of natural variations in factors such as parent soil materials, climate, topography, and human activities, landscapes can comprise many land cover types, arranged in varying configurations, and imprinted on complex topographic landforms (Forman and Godron 1981; Turner 1989). The amount and type of these various land cover types are typically referred to as the landscape composition while the spatial arrangement of these various components denotes the landscape configuration (Remmel and Csillag 2003; Uuemaa et al. 2009; Riitters 2019).

This spatial arrangement is the result of complex physical, biological, and human interactions (Forman and Godron 1981). The spatial arrangement can be relatively stable over the years or subject to change due to natural events or anthropogenic disturbances (Turner et al. 1989). Landscapes can change over long periods of time as a result of geological forces such as plate tectonics, and glaciation, while disturbances such as forest fires, volcanic eruptions, floods, landslides, and earthquakes cause changes over a shorter time period. Landscapes are also increasingly being altered by clearing natural land cover for agricultural or urbanization purposes (Haddad et al. 2015). This re-shaping of the landscape can result in fragmentation, where regions of natural land cover are portioned into smaller, more isolated areas (Forman and Godron 1986). Studies have indicated that the landscape pattern is more fragmented around urban centres and coasts where human economic activities are more concentrated (Yang and Liu 2005). This study proposes new ways to quantify fragmentation and to test for incremental improvements over existing methods.

Landscape fragmentation, which has demonstrated links to habitat loss, increased isolation, and reduced connectivity all of which can lead to decreased biodiversity (Jaeger 2000; Neel et al. 2004; Kupfer and Franklin 2009; Llausàs and Nogué 2012; Haddad et al. 2015; Ribeiro et al. 2017; Antongiovanni et al. 2018) is difficult to quantify. Globally, the loss of biodiversity is recognized as a major concern because biodiversity plays a significant role in human welfare by providing agricultural, economic, and health benefits (Zhang and Zhou 2019). For example, a diversity of pollinators ensures and stabilizes food supply (Syrbe and Walz 2012). Biodiversity provides economic benefits by providing goods such as forest products (Zhang and Zhou 2019) and fuel (Costanza et al. 1997). Biodiversity has also been a source of unique biological materials for medicine (Costanza et al. 1997; Zhang and Zhou 2019). Biodiversity contributes to healthy ecosystems which in turn provide numerous goods and services to human populations that are critical to the effective functioning of Earth's life support systems (Costanza et al. 1997). For instance, healthy ecosystems perform waste treatment by the removal or breakdown of excess or xenic nutrients and compounds, and provide storage and retention of water in reservoirs and aquifers (Costanza et al. 1997). Finally, diversity within ecosystems may facilitate reorganization after disturbances due to a high number of insurance species (Naeem and Li 1997; Tscharntke et al. 2005) as biodiversity insures ecosystem functions are maintained as different species respond differently to environmental changes (Yachi and Loreau 1999).

The Convention on Biological Diversity under The United Nations Environmental program recognizes three basic elements of biodiversity: genetics, species, and ecosystem diversity (Hoban et al. 2020) that are interrelated (Walz and Syrbe 2013). Genetic diversity quantifies the magnitude of genetic variability within a population and helps populations adapt to changing conditions such as global warming. In addition, research into genetic biodiversity and its connection to human diseases might be important for finding ways to combat human diseases (Zhang and Zhou 2019). Fragmentation can adversely affect species diversity, the number of species in a certain spatial unit (Walz and Syrbe 2013), by increasing vulnerability to invasive species (With 2002). Fragmentation increases the perimeter, or edge, of a land cover type. These increased edges limit the habitat needed by some native species leading in some cases to local extinction and reducing overall biodiversity (Pfeifer et al. 2017).

Fragmentation affects ecosystems by changing the conditions within these smaller areas and the flow of resources (Rutledge 2003). Anthropogenic activities that fragment the landscape can result in changes in ecological processes that lead to further habitat decline and species loss (Hobbs 1993). For example, a synthesis of fragmentation studies found that reduced patch area, increased isolation, and increased edge were all associated with degraded ecosystem functions including reduced carbon and nitrogen retention, productivity, and pollination (Haddad et al. 2015). Fragmentation can alter biodiversity and ecosystem functioning through the non-random loss of species that contribute to the ecosystem processes (Liu et al. 2018). For instance, the decrease of key seed dispersers or pollinators can reduce reproduction, dispersal, and establishment of dependent plant species (Laurance 2008). Reproduction rates, size, and mortality of the various species will change according to resource availability (Rutledge 2003). The effects arising from fragmentation vary widely according to the process or organism of interest. There are differences in the response to fragmentation between generalist and specialist species (Bogaert 2003). For example, species with lower mobility and greater ecological specialization generally respond more negatively to insularization (Laurance 2008). It is important to quantify the pattern of fragmentation to predict its effects and apply conservation or management guidelines, but there has been a lack of agreement on how to measure patterns of landscape fragmentation (Bogaert 2003; Kupfer 2012; Lausch et al. 2015; Frazier and Kedron 2017).

There has been some debate over the role of fragmentation relative to habitat loss in explaining decreases in biodiversity and the degradation of ecosystems (Fahrig 2003; Fahrig et al. 2022). However, in the past, many studies have not differentiated between habitat loss and habitat fragmentation (Fahrig 2003, 2019; Hadley and Betts 2016). For example, if a habitat patch is removed there is a reduction in habitat amount: loss occurs but there is not an increase in fragmentation. Similarly, if a large patch is reduced in size, there is habitat loss but not an increase in fragmentation (Fahrig 2019). Although habitat loss is widely considered to have been a major contributor to a loss of species richness and diversity (Jaeger 2000; Fahrig 2003; Kupfer and Franklin 2009; Fletcher et al. 2018), observational and experimental studies have demonstrated that fragmentation also has multiple simultaneous effects that are interconnected in complex ways and can operate over long time scales (Haddad et al. 2015). Responding to global threats to biodiversity has been challenging because these threats can interact to generate outcomes that may not be predicted by examining their effects in isolation (Driscoll et al. 2021). Threats can co-occur in space and time, but the associations can be coincidental or causal. For instance, fragmentation stemming from land cover change from forest to agriculture, and heat waves caused by climate change, can co-occur coincidently, but interact to have synergistic effects on woodland birds during heat waves (Geary et al. 2019).

Fire can influence fragmentation by destroying and fragmenting habitat or creating and connecting habitat. Where fire and fragmentation influence each other, feedback loops that lead to ecosystem conversions such as from forest to grassland can occur (Driscoll et al. 2021).

Experiments have shown that habitat fragmentation reduces biodiversity and impairs key ecosystem functions, and the effects can operate over long time scales (Haddad et al. 2015). Increasing global urbanization and the resulting landscape fragmentation has stressed the need for more accurate measures for quantifying fragmentation (De Montis et al. 2020). Understanding and managing the impacts of fragmentation has become critical for managing conservation efforts (Pfeifer et al. 2017). The distinction between habitat loss and fragmentation can be important for landscape policy makers and designers as resources are generally limited, and optimizing landscape configuration might be one option for reducing the negative effects of habitat loss on diversity (Hadley and Betts 2016).

Given the potential impact of landscape fragmentation on a wide range of ecological processes (Haddad et al. 2015), it is important to quantify fragmentation. The quantification and monitoring of landscape fragmentation is challenging (Tischendorf and Fahrig 2000; Wickham and Riitters 2019), often context specific, but central to landscape ecology (Llausàs and Nogué 2012; Fahrig 2017). Quantification is a prerequisite to the study of landscape function (Kupfer 2012) and is used to quantify how landscapes change over time (Turner and Gardner 2015), especially in response to different types of disturbances or land-use pressures (Hesselbarth et al. 2019). The quantification of fragmentation is also needed to identify trends and compare different regions, for planning and legislation (Jaeger et al. 2007). The traditional pattern-based approach to measuring fragmentation of landscape metrics relies on measuring the relationships resulting from the composition and configuration of landscape elements. An alternative approach is to develop process-based metrics that are calculated from the process of traversing a landscape to assess the degree of fragmentation.

1.1 Research objectives

The goal of this research was to develop and test process-based fragmentation quantification methods and to then compare those to existing pattern-based fragmentation quantification methods. The three research questions that allowed the research goal to be achieved are as follows:

1. Is a process-based quantification of landscape fragmentation more sensitive to landscape fragmentation than a pattern-based quantification?
2. How sensitive are the pattern- and process-based metrics to landscape simulation parameters?
3. Is there information from process-based metrics that is not provided by pattern-based metrics?

I used simulated landscapes and multiple instances of least cost path (LCP) analysis (as a landscape process) to examine the linkages between states of fragmentation (patterns and metrics) and the LCP processes acting within those fragmented landscapes. The assumption being that changes to the relative proportion of the landscape class of interest (composition) or how the classes are arranged (configuration) will affect movement across landscapes making the trip more, or less costly depending on the underlying spatial structure of the landscape classes. When the landscape structure is altered by fragmentation that should lead to varied measurement results. The sensitivity of the LCP processes due to known landscape fragmentation was simulated and tested. Multiple landscape simulations were valuable in this instance as it would be impossible to manipulate actual landscapes and allow for many cases to be analyzed within a short period of time. In addition, the large number of simulations provided statistical power for hypothesis testing and characterizes the variability in metric results.

1.2 Fragmentation definitions

Fragmentation is a landscape-level process (Fahrig 2003; McGarigal et al. 2005). While fragmentation characterizes the structural state of a landscape at any instantaneous moment, it is also understood to be a process (Forman 1995a; Jaeger 2000; Fahrig 2003; McGarigal et al. 2005). The quantification of fragmentation is a measure of the current structural state of fragmentation along a continuum of change. Fragmentation is part of a broader sequence of spatial processes transforming land from one type to another (Forman 1995a). These spatial processes can overlap throughout the period of land transformation and include perforation, dissection, fragmentation, shrinkage, and attrition (Forman 1995a). These processes, or phases, are not precisely delineated as several can take place at concurrently, but usually one phase can be identified as the dominant process (Jaeger 2000; McGarigal et al. 2005). This earlier concept of five phases of fragmentation (Forman 1995a) was broadened to include the additional phase of incision which falls between perforation and dissection and the renaming of the fragmentation phase to dissipation leaving the term fragmentation as a more comprehensive notion for all six phases (Jaeger 2000). The six phases of fragmentation: perforation, incision, dissection, dissipation, shrinkage, and attrition, are illustrated in Figure 1.

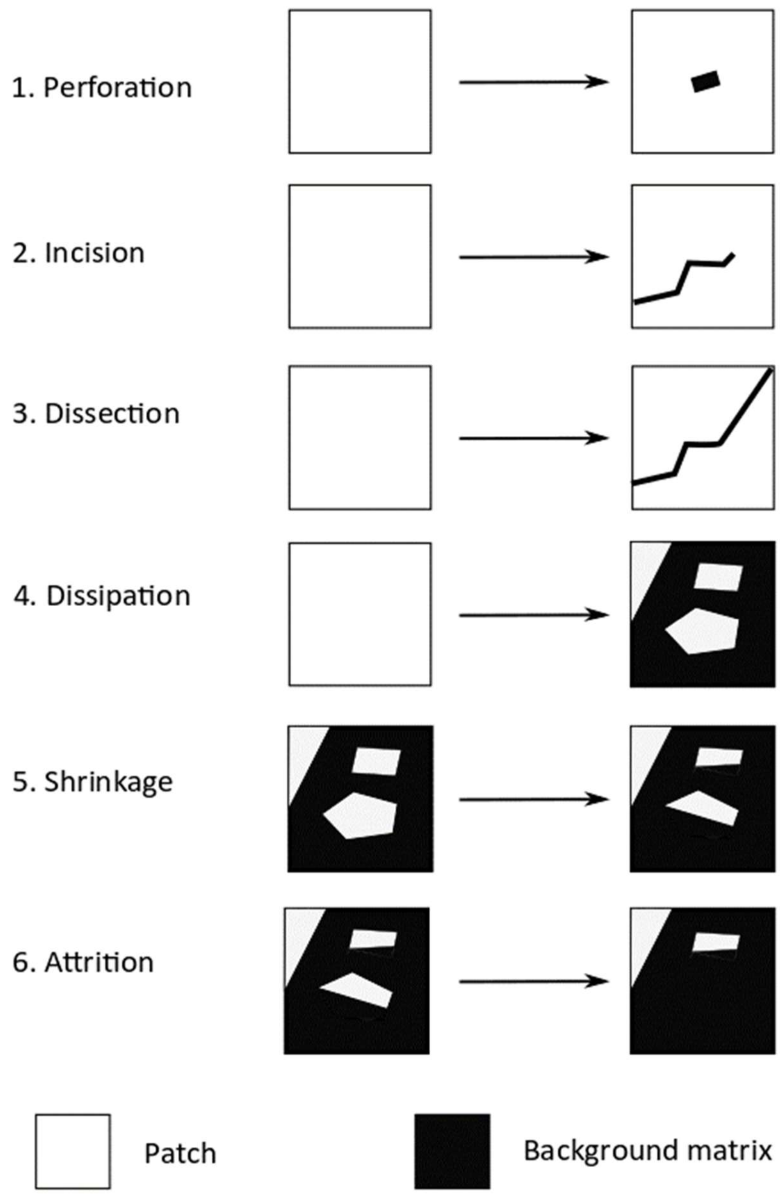


Figure 1. The six fragmentation processes according to Jaeger (2000).

Perforation is the process of making holes in land cover class of interest. This can occur, for example when forested areas are cleared for agricultural fields (Kupfer and Franklin 2009). Perforation creates holes in an otherwise contiguous land cover type leading to a direct loss of habitat and a change in spatial distribution (McGarigal et al. 2005). Incision occurs when a linear element enters a habitat type but does not separate it into two areas (i.e., dissection) (Jaeger

2000). Dissection is the division of an area using equal-width lines such as roads or powerlines (Forman 1995a). In most cases, there is little loss of area, but the linear landscape elements can be a source of disruption for example by providing an avenue for invasive species and affecting connectivity by altering movement patterns (McGarigal et al. 2005). Dissipation is the splitting of an object into smaller pieces and can occur when perforations and dissections grow wider or connect to separate a landscape into multiple smaller components (Kupfer and Franklin 2009). Shrinkage is the decrease in size of objects. Finally, attrition is the disappearance of objects. (Forman 1995a). In Figure 1, only two types of land cover classes are depicted, the white patch class is the class of interest as it is the one being fragmented. In this example, a large expanse of habitat has been transformed into several smaller patches comprising a smaller total area from the original, and the patches are isolated from each other. Thus, there is a change in composition and configuration and the measurement of both aspects is important for monitoring change.

An area of dispute in the conservation research community is known as the single large or several small debate (SLOSS – Single Large Or Several Small) regarding the relative value of large reserves versus collections of small reserves that protect the same total area (Tjørve 2010; Fahrig et al. 2022). Given limited conservation resources, there has been heated discussion regarding the advantages of protecting one large conservation area (SL) versus several small conservation patches (SS) (Hilty 2019). In the mid-1970s, environmental conservationists proposed that when designing nature reserves, for a fixed total area, one large reserve will preserve more species that several smaller ones (Tjørve 2010; Fahrig 2020). Prioritizing the conservation of large patches over small patches has been a practice throughout the world (Lindenmayer 2019; Fahrig 2020; Riva and Fahrig 2022) and may have had the unintended consequence of underrating the importance of small remnant patches in fragmented landscapes (Wintle et al. 2019). It was argued that the negative relationship between patch size and extinction risk would likely lead to lower species richness in a set of small patches relative to a large patch. The extinction risk has been seen as being higher in small patches because smaller populations are more susceptible to environmental stochasticity (Laurance 2002; Riva and Fahrig 2022).

In response to conflicting results, it has been suggested that conservation priorities be modified to recognize the value of small patches where appropriate (Wintle et al. 2019; Riva and Fahrig 2022). For example, small patches can act as stepping stones that promote connectivity in otherwise highly modified and fragmented environments (Herrera et al. 2017), an important consideration in times of increasing climate change (Saura et al. 2014). In other cases, large patches are needed because some species are sensitive to habitat amount (Wang et al. 2014). Recently, it has been recognized that both single large and many small fragments are needed to promote landscape-wide biodiversity (Rösch et al. 2015; Riva and Fahrig 2023). Thus, the quantification and monitoring of landscape fragmentation is of interest to ecologists or wildlife and resource managers with often competing needs.

In addition to measuring the composition of fragmented landscapes, it can also be important to measure the configuration (i.e., the spatial arrangement of the landscape elements). Changes in the landscape configuration measure the degree of isolation or, conversely, connectiveness (Rutledge 2003). Isolation deals with the degree to which patches are spatially isolated from each other (Ene and McGarigal 2023). The actual distance between patches is important for potential patch interactions (Forman and Godron 1981). The functioning of ecosystems and provision of their services is made possible by the flow of organisms, materials, energy and information across landscapes (Crooks and Sanjayan 2006). Landscape connectivity may also be important for species persistence because the survival of a species depends on the rate of local extinctions and the rate of species movement among patches (Turner 1989; Kindlmann and Burel 2008).

Landscape ecology studies the reciprocal interactions that occur between spatial pattern and ecological processes (Turner 1989, 2005; Rutledge 2003). For example, changes in landscape structures can affect the distribution, movement, and persistence of some species (Turner 1989), population dynamics, biogeochemical cycling, biodiversity (Mas et al. 2010), and surface water runoff (Krummel et al. 1987). Maintaining connectivity is seen as an important goal for biodiversity conservation worldwide (Ribeiro et al. 2017). It has been found that extinction cascades are more likely to occur in landscapes with low landscape connectivity and low or degraded native vegetation cover (Fischer and Lindenmayer 2007). Structural connectivity corresponds to the spatial relationships of continuity and adjacency between structural elements of a landscape and is independent of the ecological characteristics of a species. Functional connectivity corresponds to landscape features that facilitate or impede the movement of species among habitats and is integrated with the structural features of a landscape (Correa Ayram et al. 2016; Dutta et al. 2022). What represents functional connectiveness depends on the organism of interest. For example, patches that are connected for bird dispersal might not be connected for salamanders (McGarigal et al. 2005).

Landscape composition can influence landscape configuration and functional connectivity. For example, in landscapes with low forest cover, nearest-neighbour forest patches were often found to be distant from one another, have a large number of patches and increased edge with some interpatch distances being quite large for the three forest birds under study (Bélisle et al. 2001). When the three species of forest birds, the Black-throated Blue Warbler (*Dendroica caerulescens*), the Ovenbird (*Seiurus aurocapillus*), and the Black-capped Chickadee (*Poecile atricapillus*), were translocated to an area with lower forest cover, the birds took longer and were less likely to return to their territories as forest cover decreased. Movement was constrained for these species of birds when they travelled in deforested and fragmented landscapes. This decrease in functional connectivity in this instance is likely to alter the species population structure and dynamic (Bélisle et al. 2001).

Thus, maintaining and restoring connectivity among habitat patches is seen as an effective conservation practice for facilitating species movement, gene flow, and increased population persistence in fragmented landscapes (Dutta et al. 2022). Corridors within a landscape can increase the movement and genetic exchange between populations in different habitat patches and possibly save populations from extinction (Huck et al. 2010; Alexander et al. 2016). Connectivity has also been used to evaluate and model the spread of invasive species (Helfenstein et al. 2014). There are other advantages to understanding the effects of fragmentation and connectivity. For example, one strategy for increasing the productivity of agricultural land is to improve conditions for pollinators. However, it is important to understand how pollinators are affected by habitat quality, structure, and connectivity. For instance, the abundance and diversity of pollinators has been found to decrease in fragmented patterns of forest patches (Mitchell et al. 2014).

1.3 Approaches to understanding and quantifying landscape structure

Landscapes are considered to be a mixture of natural and anthropogenically altered patches of different sizes and shapes (Krummel et al. 1987), making them spatially heterogeneous areas (Turner 1989). In the field of landscape ecology, the question regarding the usefulness of landscapes as units in ecology with a distinctive structure and function that could be analyzed to solve critical ecological questions had been posed (Forman and Godron 1981). A key premise of the discipline has been that there are strong links between ecological pattern and ecological function and process (Turner 1989; Gustafson 1998). In the organism-centred perspective in landscape ecology, the focus is on a particular target habitat according to the species under study and thus, the area of interest depends on the spatial pattern that is meaningful for that species (Antrop 2021). The description and analysis of landscape patterns became a focus in landscape ecology (Costanza et al. 2019) and hundreds of measures of landscape patterns have been developed (Baker and Cai 1992; McGarigal and Marks 1995; Haines-Young and Chopping 1996; Gustafson 1998, 2019; Saura 2004; Cushman and McGarigal 2008; Uuemaa et al. 2009; Frazier and Kedron 2017); a recent contextualizng review organizes these contributions into a logical framework (Remmel and Mitchell 2022).

Evolving methodologies, data acquisition tools and modeling approaches aided by advanced technologies have increased the options available to landscape ecologists for examining landscape ecology questions (Wiens 2008). In particular, landscape fragmentation is an issue that has been garnering increased attention (Fischer and Lindenmayer 2007; Driscoll et al. 2021).

1.4 The patch matrix model

An early approach to understanding landscape structure was the patch matrix model developed in the 1980s (Forman and Godron 1981, 1986; Turner 1989; McGarigal and Marks 1995; Forman 1995a; Lausch et al. 2015). The patch matrix model depicts a landscape as a mosaic of discretely delineated homogenous areas: patches, connecting corridors, and the background matrix. Every point in a landscape is either within a patch, a corridor, or part of the background matrix (Forman 1995a). The common elements found in the patch matrix model are illustrated in Figure 2. In this instance, there are three patches, Patch A, B, and C and two connecting corridors. Patch A is physically connected with Patch B through a corridor and Patch C is physically connected to Patch B through a corridor. The patches and corridors exist within the matrix.

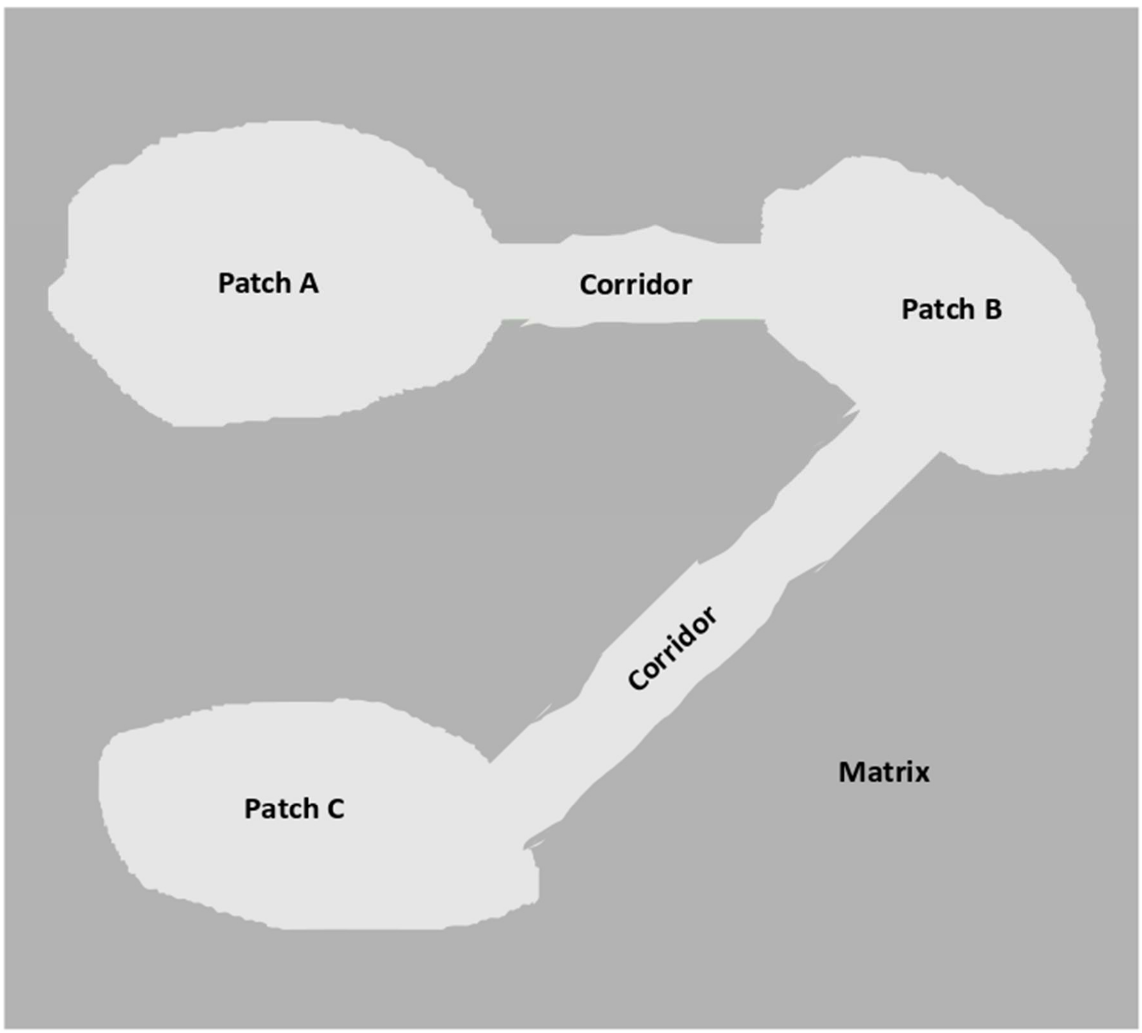


Figure 2. General representation of the Patch Matrix Model including the three main elements: patch, corridor, and background matrix.

A patch is a distinct homogenous landscape feature that differs from its surroundings by some attribute, such as age, size, shape, or content (Wu and Levin 1994). Examples of patches would include features such as marshes or stands of trees. Patches can be characterized by size (total area), interior (core) area, and shape. Patch size affects many values such as potential habitat (forage), and nutrient and water flux has been shown to correlate with species diversity (Forman and Godron 1981). Core area is the amount of usable area within a patch as a function of patch shape (Baskent and Jordon 1995) as defined by the species or process of interest (McGarigal and Marks 1995). For example, many bird species have been found to be more dependent on core area than total area (Baskent and Jordon 1995). Patches are typically described by metrics that consider their area, the length of their edge (i.e., perimeter), and their shape.

Edges are variously described as the outer band of a patch (Forman and Godron 1981), the locations, or border, where different types of qualitatively different land cover types such as forest and agricultural land join (Haines-Young and Chopping 1996), or ecotones where one land cover class transitions to another (Forman and Godron 1981). Edge effect refers to the change in ecological patterns and processes that happen around and within the edge of two adjacent ecosystems (Fonseca and Joner 2007) or a difference in species composition and abundance in the patch edge (Forman and Godron 1981). In general, the level of effect typically decreases away from the boundary or edge of a patch towards the interior or core of the patch (Rutledge 2003; Laurance et al. 2007), although the magnitude and distance of the edge influence can vary along a gradient from steep and short to shallow and long (Harper et al. 2005). Edges are also influenced by neighbouring patches (Rutledge 2003). For example, in the Amazon, where the pastures that encircle forest fragments are regularly burned to control weeds and promote fresh grass, the fires raze and re-open fragment edges thus maximizing edge-related microclimatic stresses (Laurance et al. 2007). The total class edge is often the most important piece of information in the study of fragmentation (McGarigal and Marks 1995).

Some species are more edge tolerant than others. Edge tolerant species are often generalists and invasive that can outcompete native species (Pfeifer et al. 2017; Antongiovanni et al. 2018). Relatively sudden changes in the microenvironment at the edge of a forest fragment, for instance, can lead to effects such as increased light levels, higher wind speeds, lower humidity, and higher temperatures (Schmidt et al. 2017). As the effect of an edge on inputs and outputs of physical resources often decreases from the border of a patch towards the interior it is important, for some species and processes, to divide the patch area into core and edge areas (Rutledge 2003; Vogt and Riitters 2017). The core areas are inset a specified distance from the edge and this distance depends on the process of interest (McGarigal and Marks 1995). The relationship between the core area of a habitat patch and the length of edge is affected by the size and shape of the patch. The shape of a patch often relates the perimeter to the area in some way (Rego et al. 2018). Measures of patch shape metrics endeavor to quantify patch complexity as this can be important for several ecological processes. For example, a compact or rounded patch shape is effective in conserving internal resources (Forman 1995a). Shapes with extensive straight and simple boundaries are often associated with anthropogenic activities (Remmel and Mitchell 2022) such as urbanization, agriculture, and forest harvesting (Krummel et al. 1987). Patch shape is also scale dependent; images presented at finer spatial resolution generally result in more complex patch shapes, while coarser spatial resolution leads to increased generalization (Haines-Young and Chopping 1996). In Figure 3a) the land cover classification displays complex patch shapes with an edge length of 1500 units. In Figure 3b) which was initially obtained at a coarser resolution and re-scaled, the same patches have simpler shapes and relatively decreased edges.

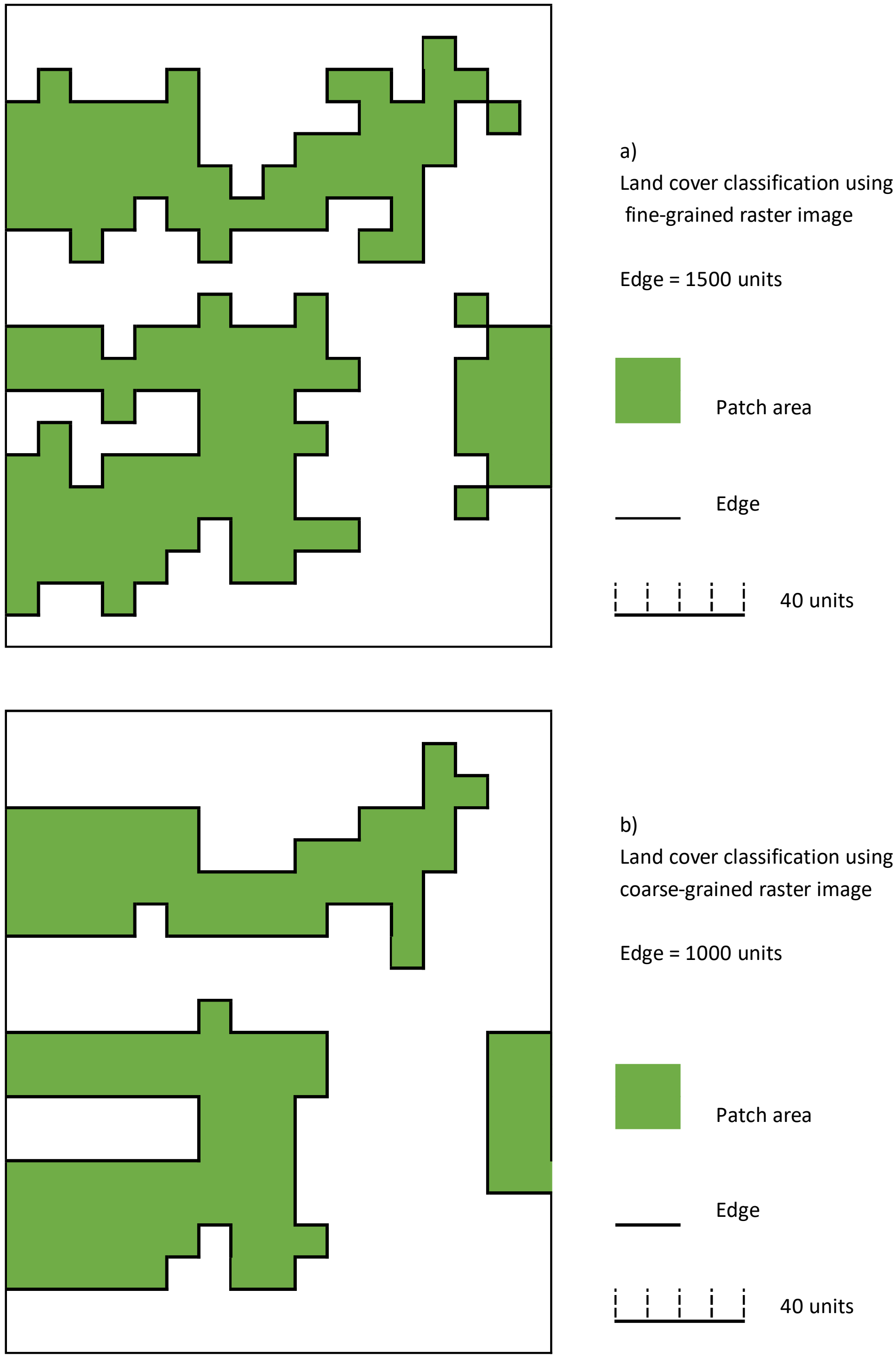


Figure 3. Example of scale effects on patch shape: a) the finer resolution leads to a more complex patch shape and more edge than in b) which was initially obtained at a coarser resolution and re-scaled.

Corridors connect patches and are narrow relative to their length. They may be isolated strips, but usually connect one or more patches (Forman and Godron 1986). Their importance includes the facilitation of movement along the corridor (Forman and Godron 1981). They may function as conduits for organisms, for example for the dispersal of plant seeds, pollen, spores, and insects by redirecting airflow and increasing the likelihood of seed uplift (Damschen et al. 2014). Corridors may also facilitate the movement of species among patches thus increasing gene flow and decreasing the risk of extirpation or extinction (Edelsparre et al. 2018). This movement also includes reestablishment of certain species in the patch after a disturbance leading to species loss (Forman and Godron 1981). However, corridors have also been found to have some unintended effects such as facilitating the movement of predators (Weldon 2006).

Matrix refers to the dominant background land cover type in a landscape (Lausch et al. 2015). It typically has extensive cover and high connectivity (Turner and Gardner 2015). However, the designation of the matrix type depends on the phenomenon of concern and the scale of investigation (McGarigal and Marks 1995). For example, in a study involving geomorphological processes, the geological substrate could define the matrix, whereas in a study involving vertebrate populations, the matrix might be defined by the vegetation structure. Similarly, at a certain scale, mature forest could be the matrix while, at a coarser scale agricultural land may be the matrix with mature forest patches embedded within the agricultural land (Ene and McGarigal 2023).

The patch matrix model, which described any landscape as a combination of patches, corridors, and a background matrix, provided a simple and practical way to describe and quantify landscape structure (Lausch et al. 2015; Hesselbarth et al. 2019). It provided a conceptual framework for the development of many landscape metrics. These metrics have been defined at three levels: patch-level, class level to describe the characteristics of each single class type, and landscape-level to examine the spatial structure in multi-class patch mosaics (Cushman et al. 2008). These mathematical constructs are based on measures related to the spatial pattern of landscape features in terms of their composition and configuration (Gustafson 1998; Remmel and Csillag 2003). However, some researchers argue that landscape metrics are not useful indicators of fragmentation and should only be used to describe landscape pattern with research directly investigating ecosystem processes and fragmentation (Rutledge 2003). Others note that while metrics have been developed for various purposes, such as dominance (O'Neill et al. 1988a), few metrics have been designed specifically to measure fragmentation (Jaeger 2000).

In a review examining research into the description and analysis of landscape patterns, it was reported that the use of pattern metrics has continued to increase over time, and the development and usage has informed research in a wide variety of disciplines including the environmental sciences, urban studies, and forestry (Costanza et al. 2019). The field has also benefitted from research in other disciplines such as the physical sciences, operations research (Gustafson 2019), and mathematical morphology (Riitters et al. 2007). Large data sets are now currently obtainable for the measurement of patterns and there is a call to think critically about the methods and techniques that are used and those that can be developed (Costanza et al. 2019).

Advances in computing, remote sensing, GIS (Geographical Information Systems), and the availability of digital geodata enabled the analysis of vast amounts of land cover information that can inform ecological studies (Walz et al. 2016). These advances also enabled the development of new tools and methods for describing and depicting landscapes such as landscape metrics (Costanza et al. 2019). However, as with traditional cartography, representing an area of Earth's surface in a digital format requires generalizations and simplifications. Factors such as the scale, spatial resolution of the land cover information, and digital data format affect the ultimate depiction of the landscape in digital form.

Scaling issues have been recognized as an ongoing problem in the quantification of landscape pattern (Saura 2004; Gustafson 2019). Scaling differences in ecological studies had been brought to the attention of landscape ecologists (Wiens 1989). However, while ecologists acknowledged that spatial heterogeneity is scale-dependent, a general understanding of the scaling relationships of spatial pattern had not been well developed (Wu et al. 2003). The issue of scale was highlighted in several subsequent landscape pattern studies. For example, researchers found that landscape metrics are sensitive to the unit area or extent over which the metric was computed (O'Neill et al. 1996). Results of a study of 19 commonly used metrics calculated over changing scale indicated that metrics fell into one of three classes: predicable responses, staircase-like responses that were less predictable, and erratic responses (Wu et al. 2003). Additional research showed that in order to adequately capture and monitor landscape heterogeneity, multiscale analysis is needed (Wu 2004; Fu et al. 2021). Thus, there has been a call to take into account the scale at which the metrics were calculated when interpreting them (Gustafson 2019).

While it is preferable to define the extent and spatial resolution appropriate to the phenomenon or organism under study, for practical reasons, they are often controlled by the spatial resolution of the satellite image used. Thus it has been recommended that the satellite sensor that is appropriate for the research question be chosen (Benson and MacKenzie 1995; Cushman and McGarigal 2008). For example, changing the spatial resolution from coarse- to fine- spatial resolution data can result in the identification of features that were not discernable at the coarser spatial resolution (Ostapowicz et al. 2008; Wickham and Riitters 2019).

Landscape metrics have been computed using vector or raster data formats, although the raster format has become more popular because of the ease of performing complex spatial computations on grids (McGarigal et al. 2005) and the availability of satellite data (Mõisja et al. 2016). Vector data characterizes each object as points, lines, and polygons, while the raster format divides data into a grid consisting of individual cells or pixels (Zaragozí et al. 2012). For digital data in vector format, a patch would be represented as a polygon. However, in representing the landscape in raster format each cell is typically assigned to the land cover class that comprises the majority of the cell as projected onto the ground (Cushman and McGarigal 2008). These characteristics of format also influence the applicability of landscape metrics. For example, because vector and raster formats represent lines differently, edge and perimeter metrics will be affected by the choice of digital formats (Cushman and McGarigal 2008).

1.5 Pattern-based quantification of landscape fragmentation

Landscape metrics were developed in the 1980s as a means of characterizing landscapes with respect to a wide array of pattern dimensions (Turner 1989; Gustafson 1998). For example, the number, size, and perimeters of patches were compared across real and simulated landscapes (Gardner et al. 1987) and the contagion index measured the extent to which patches were aggregated or clumped (O'Neill et al. 1988a). As more features of landscape patterns were noted as being potentially important to research, additional metrics to quantify these characteristics were developed (Costanza et al. 2019) and hundreds of metrics have been developed (Frazier and Kedron 2017; Costanza et al. 2019; Remmel and Mitchell 2022). Concurrently, the introduction of software such as *r.le* (Baker and Cai 1992) and *FRAGSTATS* (McGarigal and Marks 1995) made it easier to calculate a wide variety of landscape metrics (Haines-Young and Chopping 1996; Uuemaa et al. 2009). There has been continued work on developing software to calculate these metrics that is designed to overcome some of the constraints of earlier software programs. For example, *landscapemetrics* (Hesselbarth et al. 2019), an extensive collection of widely used metrics, is available in the open-source R environment (R Core Team 2021).

1.6 Fragmentation metrics

The term fragmentation has been used to describe ecological change with respect to habitat loss, composition (number of patches and patch area), shape, and configuration (Rutledge 2003). Thus, research progress has been impacted by the imprecise or inconsistent use of terminology (Fischer and Lindenmayer 2007), as there are a multitude of interpretations of fragmentation (Fahrig 2003). For instance, some studies describe fragmentation at the landscape level while others describe it at a patch level (Fahrig 2003; McGarigal et al. 2005). Generally, as noted earlier, landscape fragmentation refers to the division of an ecosystem into smaller and more isolated patches (De Montis et al. 2020) characterized by increased edge length (Davidson 1998).

Given the large number of interpretations of fragmentation, it is not surprising that there are many metrics that attempt to measure landscape fragmentation. As noted earlier, patches are typically described by their size (area), their edge (perimeter), and their shape – all aspects that are inter-related. The spatial arrangement of these patches across a landscape can be expressed by contagion or the degree of "clumpiness". Contagion measures the extent to which patch types are aggregated, with lower values generally associated with many small, dispersed patches (McGarigal et al. 2005). These characteristics of composition and configuration can also be used to organize the large number of landscape metrics and varying levels of detail that are often found in the literature. For convenience, landscape metrics can be subdivided into categories such as those focused on characterizing aspects related to area, patches, edges, shapes, core areas, nearest neighbours, diversity, contagion, or interspersion (McGarigal and Marks 1995). In another classification, landscape metrics have been categorized by area and edge, shape, core area, aggregation, diversity, and complexity metrics (Hesselbarth et al. 2019). Commonly used fragmentation metrics have also been subdivided into the three categories, including composition, shape, and configuration (Rutledge 2003). However, not all landscape metrics can be easily classified into any single category. For example, mean patch size and the patch density of a particular patch type reflect both the amount of a patch type present and its spatial distribution (McGarigal and Marks 1995).

Commonly used fragmentation metrics that were investigated in this study are listed in the following three tables as categorized in the *landscapemetrics* program (Hesselbarth et al. 2019). Table 1 describes various metrics based on the size of patches and the amount of edge associated with the patch. Table 2 lists metrics based on the shape of patches. As can be seen in **Error! Reference source not found.**, patches with more complex shapes tend to have longer edge lengths and a greater perimeter-to-area ratio. Finally, Table 3 lists the metrics that measure contagion that were used in this study. Contagion measures interspersion as well as patch dispersion (i.e., the spatial distribution of a patch type) (McGarigal and Marks 1995).

Table 1. Selected fragmentation metrics measuring area and edge.

Symbol	Metric	Definition	Reference
area_cv	Coefficient of variation of patch area	Summarizes each class as the Coefficient of variation of all patch areas belonging to a class.	Baker and Cai (1992)
area_mn	Mean patch size	The mean of all patch areas belonging to the class.	Baker and Cai (1992)
area_sd	Standard deviation of patch area	Summarizes each class as the standard deviation of all patch areas belonging to a class.	Baker and Cai (1992)
cai_cv	Coefficient of variation of core area index	The percentage of core area in relation to patch area. Summarizes each class as the Coefficient of variation of the core area index of all patches belonging to a class. Describes the differences among all patches of the same class in the landscape.	McGarigal and Marks (1995)
cai_mn	Mean of core area index	Summarizes each class as the mean of core area index of all patches in a class.	McGarigal and Marks (1995)
cai_sd	Standard deviation of core area index	Summarizes each class as the standard deviation of the core area index of all patches in a class.	McGarigal and Marks (1995)
dcad	Disjunct core area	The number of disjunct core areas per 100 ha relative to the total area.	McGarigal and Marks (1995)
ed	Edge density	Sum of lengths of all edge segments involving the corresponding patch type, divided by total landscape area.	Baker and Cai (1992)
lpi	Largest patch index	Percent of total landscape area occupied by the largest size patch of the class of interest.	Forman (1995); McGarigal and Marks (1995)
te	Total edge	Sum of lengths of all edge segments involving corresponding patch type.	Baker and Cai (1992)

Table 2. Selected fragmentation metrics measuring shape.

Symbol	Metric	Definition	Reference
shape_cv	Covariance of variation shape index	Ratio between the actual perimeter of the patch and the square root of patch area.	Patton (1975); McGarigal and Marks (1995)
shape_mn	Mean shape index	Mean of all patches in the landscape.	McGarigal and Marks (1995)
shape_sd	Standard deviation shape index	Standard deviation of all patches in the landscape.	McGarigal and Marks (1995)
para_cv	Coefficient of variation perimeter area ratio	Summarizes each class as the Coefficient of variation of each. patch. Because it is not standardized to a certain shape, it is not scale independent.	Gardner et al. (1987) Baker and Cai (1992)
para_mn	Mean perimeter area ratio	Summarizes the landscape as the mean of each patch perimeter area ratio.	Baker and Cai (1992);
para_sd	Standard deviation perimeter area ratio	Summarizes the landscape as the standard deviation of each patch perimeter area ratio.	Baker and Cai (1992)

Table 3. Selected fragmentation metrics measuring contagion (aggregation metrics).

Symbol	Metric	Definition	Reference
cohesion	Patch cohesion index	Characterizes the connectedness of patches belonging to a class (aggregated or isolated).	McGarigal and Marks (1995); Schumaker (1996)
division	Division	The probability that two randomly selected cells are not located in the same patch; negatively correlation with effective mesh size.	Jaeger (2000)
enn_cv	Coefficient of variation of euclidean nearest-neighbour distance	Measures the distance to the nearest neighbouring patch of the same class. It is a simple way to describe patch isolation.	Hargis et al. (1998); McGarigal and Marks (1995)
enn_mn	Mean of euclidean nearest-neighbor distance	Summarizes each class as the mean of each patch belonging to a class.	McGarigal and Marks (1995)
enn_sd	Standard deviation of euclidean nearest-neighbor distance	Summarizes each class as the standard deviation of each patch belonging to a class.	McGarigal and Marks (1995)
mesh	Effective mesh size	Number of equal size patches of a particular class required to produce a desired degree of landscape division.	Jaeger (2000)
np	Number of patches	Number of patches of a particular class.	Gardner et al. (1987)
pd	Patch density	Number of patches of a particular class per unit area.	McGarigal and Marks (1995)
split	Splitting index	Describes the number of patches if all patches of a class would be divided into equally sized patches.	Jaeger (2000)

Since there is no single measure of fragmentation, it is difficult to quantitatively evaluate changes in fragmentation or alternative landscape designs (Davidson 1998), or to compare among different studies. One approach to choosing among the plethora of fragmentation metrics is to choose the aspect of fragmentation that is most applicable to the question or species of interest. For instance, for a highly mobile animal, total habitat area might be of more importance than core area or edge length. However, interpreting one measure of fragmentation can be challenging as measures can interact (i.e., they are not independent metrics) and may change in contradictory directions as fragmentation advances (Davidson 1998).

An alternative approach is to combine several metrics to make a single measure (Bogaert et al. 2000; De Montis et al. 2020). One single-valued factor measure of fragmentation, the single measure, $|\phi|$ (Bogaert et al. 2000) proposes a metric that combines total habitat area (α), total habitat perimeter (β), number of patches (ν), and patch isolation(δ). Every component is a normalized value computed from either raster or vector data. The four indices can be combined to a single measure $|\phi|$ using a 4-D space composed of 4 orthogonal coordinates axes with origin *O*. A fragmented patch can be represented by a point or vector in this space measuring the Euclidean distance to the origin $|\phi|_f$ and calculated by

$$|\phi|_f = \sqrt{\alpha_f^2 + \beta_f^2 + \nu_f^2 + \delta_f^2} \quad (1)$$

Points remote to *O* represent patches with a low degree of fragmentation. As the values are normalized, the difference in fragmentation between two patches can be quantified. This single measure $|\phi|$ was used to evaluate four areas with pine forest fragments in Belgium. The use of this single measure prevented misinterpretation of features such as fragmentation number or boundary length. However, a limitation of this measure is that while all major features of fragmentation are incorporated, it does not include interior-to-edge measures or connectivity measures (Bogaert et al. 2000).

Another single factor metric that has been proposed is the Composite Indicator of Landscape Fragmentation (De Montis et al. 2020). It is composed of three indicators: the Infrastructure Fragmentation Index, the Urban Fragmentation Index, and the mesh size density. An application of the composite index was used in a study that examined the effect of landscape fragmentation on transport and mobility infrastructures, human settlements, and patch density per se from 2003 to 2008 of 51 landscape units in Sicily, Italy. The composite index was found to have the advantage of simplification for decision makers, but there was also a loss of information. Continuing work with this composite index may yield useful results in the future (De Montis et al. 2020). It has been suggested that combining several measures to make a single fragmentation measure is most appropriate with the integrity of the entire ecosystem is of more concern rather than the impact on a single species (Davidson 1998).

1.7 Issues with applying landscape metrics

It is difficult to compare fragmentation studies because authors have not only used different definitions of fragmentation but they have measured fragmentation in different ways and at different spatial scales (Fahrig 2003). The large number of metrics available also make it difficult to choose an appropriate metric (Neel et al. 2004). To be meaningful for a particular organism or process, the metric also needs a relevant landscape classification at an appropriate scale (Gustafson 1998). All analyses produce numerical results but the ecological functionality for most of the metrics has not been verified (Baldwin et al. 2004; Turner 2005).

The large number of available metrics spurred research into identifying redundancies (Uuemaa et al. 2009), and many metrics have been shown to be correlated (O'Neill et al. 1988a; Riitters et al. 1995). Through multivariate and factor analysis, one study found that 55 landscape metrics could be initially reduced to a set of 26 metrics. Of these 26 metrics, factor analysis showed that the first six factors explained about 87% of the variation. The suggested six univariate metrics are (1) average perimeter-area ratio, (2) contagion, (3) standardized patch shape, (4) patch perimeter-area scaling, (5) number of attribute classes, and (6) large patch density-area scaling (Riitters et al. 1995). Another study found that 49 class-level metrics could be reduced to 24 independent class-level components and 54 landscape-level metrics could be reduced to 17 independent landscape-level components (Cushman et al. 2008). Recent reviews of the literature have concluded that the abundance of a class and their spatial aggregation are likely to be the two most important factors to know about a landscape (Gustafson 2019).

While landscape metrics have been widely used in the past few decades, they have also been subject to criticism. Some of the criticism refers to the use of metrics for purposes other than what they were designed for rather than deficiencies with the metrics (Kupfer 2012). Nevertheless, several issues surrounding the use of landscape metrics have been identified. For example, the ecological relevance of a particular landscape metric may be presumed without any empirical evidence (Tischendorf 2001; Kupfer 2012). The analysis of datasets is influenced by the scale of observation and by data transformation techniques, such as aggregation, magnification, and resampling (Saura 2004). Thus, landscape metrics based on patterns revealed by rescaled data may not match those in the real landscape (Li and Wu 2004). Finally, several studies have shown landscape metrics to vary with scale, both in spatial resolution (Qi and Wu 1996; Saura 2004) and study area extent (Saura and Martinez-Mlian 2001; Wu 2004; Šímová and Gdulová 2012). Although possible, the statistical comparison of landscape metrics is computationally taxing and limited to binary landscapes only; even then, situations are abundant where a landscape metric does not provide sufficient information about landscapes to even separate vastly different compositional states (Remmel and Csillag 2003; Remmel and Fortin 2013).

Landscape metrics make quantifications based solely on composition and configuration and this includes the metrics that are used to measure fragmentation. Many of the class-level metrics are highly correlated with habitat abundance, which makes it difficult to determine whether it is habitat amount or habitat pattern that accounts for variation in a landscape (Gustafson 1998; Wang et al. 2014). Pattern-based approaches typically focused on human-perceived landscape patterns and their correlation with measures of species occurrence, and originated from island biogeography (Fischer and Lindenmayer 2007), with its analogy between patches of natural vegetation and oceanic islands (Turner and Gardner 2015). Fragmentation studies in the 1980s were characterized by the extension of island biogeography theory to landscape patches (Wiens 2008). It is well recognized that pattern is scale-dependent (Riitters 2019), with patterns only discernable at certain scales. Landscape metrics are based on patterns and do not consider how processes are progressing across a landscape. While hundreds of metrics have been developed based on the patch matrix model, it is recognized that this paradigm can be of limited usefulness and other means of representing landscape patterns may disclose deeper insights (Gustafson 2019). Landscape pattern analysis has been producing tools and insights that are important for landscape ecology and associated disciplines (Costanza et al. 2019).

1.8 Landscape morphology

Landscape morphology is one approach that has moved away from solely indicator-based measures, and incorporates visualization techniques to make landscape analyses more interpretable (Kupfer 2012). Mathematical morphology was considered as a potential approach for characterizing spatial patterns in ecological research and biodiversity assessments (Riitters et al. 2007). Concepts of mathematical morphology had been extensively used in digital image analysis for image filtering, segmentation, and measurements; all tasks that are relevant to earth observation imagery (Soille and Pesaresi 2002). For instance, morphological image processing has been used for classifying spatial patterns at the pixel level on binary land-cover maps (Vogt et al. 2007a), for mapping landscape corridors (Vogt et al. 2007b), and identifying hubs, links, and related structural classes of land cover (Wickham et al. 2010).

For the analysis of fragmentation in forest environments, it can be important to differentiate between internal and external fragmentation (Zipperer 1993). Many forest fragmentation indicators had been related to the concepts of adjacency and connectivity at the pixel level, or by Forman's (Forman 1995b) landscape level concept of the patch corridor matrix and patch mosaic (Vogt et al. 2007a). In a global analysis of forest fragmentation using image convolution, six categories of fragmentation were identified (interior, perforated, edge, transitional, patch and undetermined) from the amount of forest and its occurrence as adjacent forest pixels. The fragmentation model performed well in mapping exercises, but the researchers noted that the model could be improved. For example, some of the fragmentation that was detected was the result of excluding savanna and woody savanna from the forest definition. Including savanna in the definition of forest resulted in an overestimation of perforated and edge area and underestimated interior area in forest types that contain a large amount of savanna (Riitters et al. 2000).

Mathematical landscape morphology was used to segment binary pattern images into one of seven mutually exclusive spatial categories of the foreground pixels: core area, islet, loop, bridge, perforation, edge, and branch (Soille and Vogt 2009). The class of interest belongs to the foreground pixels and the background pixels are the complementary area. Core pixels are within a set edge distance from the nearest background pixel. Islet pixels are foreground connected elements that do not contain any core pixels and are not wide enough to contain core cells and thus do not have edges. Both loop and bridge pixels are connectors. Loop pixels, as the name suggest, return to the same core area while bridge pixels come from two or more core connected components. Perforation pixels form the inside boundary to the background surrounded by core pixels, while edge pixels form an outside boundary between the background and core pixels Finally, pixels that do not belong in any of the preceding categories and emanate from edge, perforation, bridge, or loop pixels. An example of morphological segmentation of binary patterns resulting into seven mutually exclusive classes for foreground pixels is shown in Figure 4.

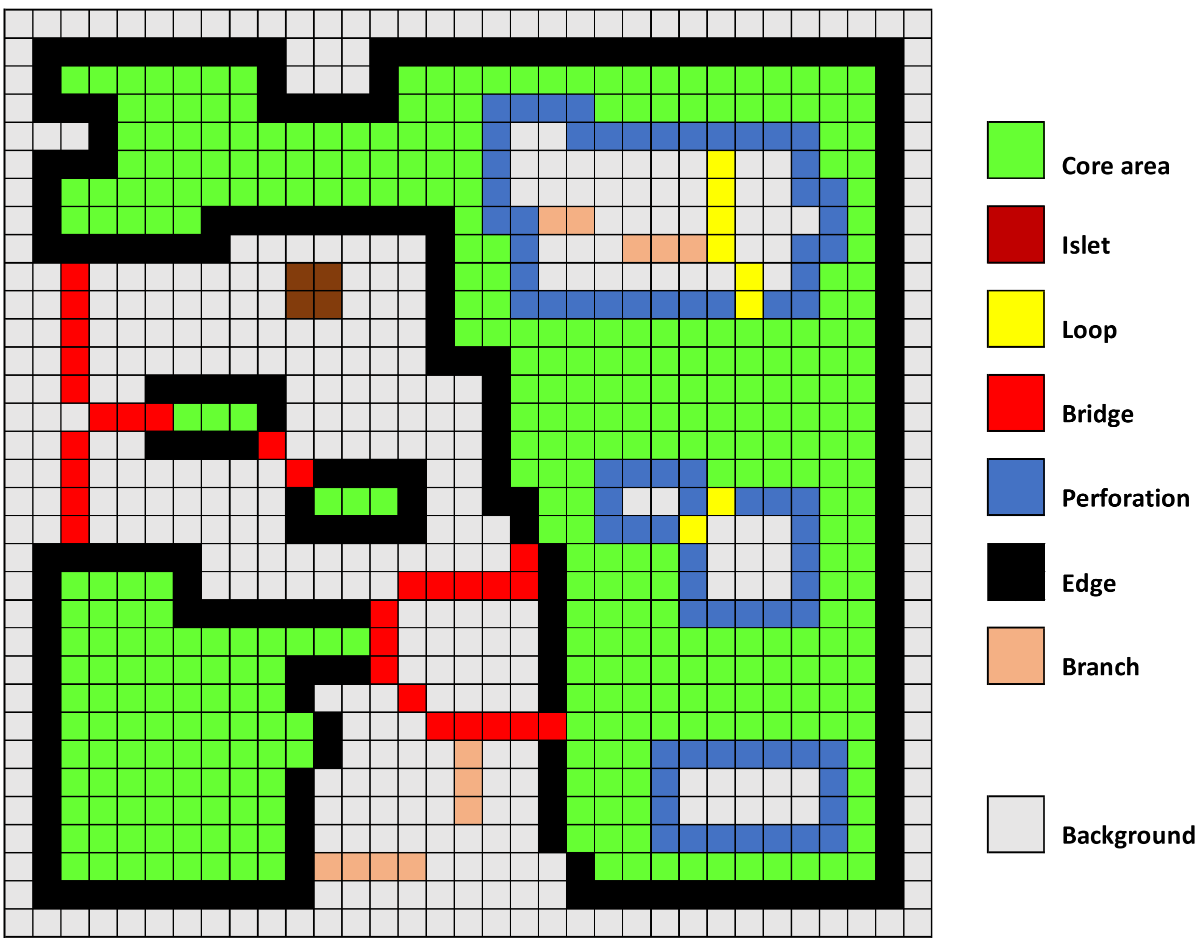


Figure 4. Example of morphological segmentation of binary patterns resulting into seven mutually exclusive classes for foreground pixels.

The principles of morphological segmentation of binary patterns are conceptually simple but the formal definition of the morphological class depends on a series of advanced mathematical morphology operations which were not easy to implement. A free software package which included a set of customized, thematically grouped raster image analysis methodologies was developed to objectively design and quantify various spatial properties of image objects in digital raster data. The package is called the Graphical User Interface for the Description of Objects and their Shapes Toolbox (GuidosToolbox) (Vogt and Riitters 2017). The core of the program is a generic and universal pattern analysis framework called morphological spatial pattern analysis (MSPA) (Riitters et al. 2009).

The morphological segmentation of binary patterns has proven to be an effective method for describing spatial patterns with emphasis on connections and has been used to analyze patterns related to landscape fragmentation (Soille and Vogt 2022). For example, it was used for analysis of a multispecies ecological network in Italy and its changes over three decades (Modica et al. 2021). For urban landscape management and urban planning purposes, MSPA was used to quantify the structural composition, connectivity, and fragmentation of the tree canopy network across the Greater Boston metropolitan area (Ossola et al. 2019). MSPA has also been used to quantify the cover density of an invasive alien species Winter Heliotrope (*Petasites pyrenaicus*). This approach offered an accurate and objective alternative to traditional visual estimation throughout seasonal variations and growth stages (Carlier et al. 2020).

1.9 Process-based quantification of landscape fragmentation

Models are often useful in landscape studies because it is frequently difficult to perform experiments at the ideal spatial or temporal scale (Turner et al. 1989). For instance, 1000 replications of simulated landscapes established the empirical distributions of six widely used landscape metrics as functions of landscape composition and configuration (Remmel and Csillag 2003). Individual movement, mortality, and boundary reactions across 1632 simulated landscapes were used to analyze the response of three landscape connectivity measures, dispersal success, search time and cell immigration, to habitat fragmentation revealing that the three measures were not interchangeable (Tischendorf and Fahrig 2000).

Neutral models have been used to establish a base against which data and hypotheses can be tested (Gardner et al. 1987). Percolation theory had inspired the use of neutral model landscapes (Gustafson 2019). Simulated landscapes provided multiple replications of a landscape to analyze broad-scale landscape pattern in conjunction with percolation theory to define the appropriate scales at which disturbance and landscape processes interact (Gardner et al. 1987). They can be used to predict when landscapes will become fragmented (With 1997).

Imported from the physics literature, percolation theory, which looks at the flow of particles or energy through a porous lattice of grid cells, was applied to the movement of water through soil. The idea of soil percolation was used to try to understand the movement of animals or a disturbance in relation to the spatial aggregation of suitable and unsuitable habitat patches. In bond percolation, movement can only occur in four directions from the cell of interest (i.e., along the edges of the cell). It can also be described as movement only in the four cardinal directions: north, south, east, west, known as rook's case connectivity (Luo et al. 2018). This is in contrast to site percolation, where movement can also occur at the vertices of the cell, the queen's case connectivity (Luo et al. 2018). Percolation theory was used as the basis for generating and analyzing patterns of two-dimensional arrays, which are similar to maps of landscape patterns (Turner 1989). These arrays provide a neutral model of a two-dimensional landscape map because being generated by a simple random process, they are neutral to the physical and biological processes that shape landscape patterns (Gardner et al. 1987).

Percolation theory also relates the connectiveness of the matrix to the proportion of the landscape occupied by patches by defining when a matrix inversion occurs. The background class ceases to be the most dominant and most connected landscape type (Antrop 2021). Using the rook's case connectivity, a critical proportion of the focal class probability occurs where the largest cluster will connect the map continuously from one side to the other occurs at 0.5928 (Gardner et al. 1987), for very large arrays. Thus, a hypothetical species restricted to a single habitat, could be expected to successfully disperse across a landscape if the proportion of occurrence of this habitat exceeded 0.5928 (Turner et al. 1989; Turner and Gardner 2015).

Results from a sequence of neutral modelling studies indicate that the amount of habitat (i.e., the composition) is the single best predictor of landscape pattern (Gardner and Urban 2007). Studies have also shown that humans are more sensitive to changes in composition than configuration (Boots and Csillag 2006).

Agent-based modelling has been shown to be useful for studying the interactions between coupled human and natural systems that change landscapes over time (Bone et al. 2014). In ecological studies, agent-based models were first used to study tree communities in 1972 (DeAngelis and Diaz 2019). With an increase in computational power in the 1980s, interest grew in using models based on individual organisms rather than on populations or highly aggregated state values. One advantage of the agent-based models was that they integrated many different levels in the traditional hierarchy of ecological processes. Another advantage was that many of the properties of individual organisms and the mechanisms by which they interacted with their environment could be measured for use in the models (Huston et al. 1988). In the last few decades, agent-based models have become established in many areas of ecology (DeAngelis and Diaz 2019).

Agent-based models, are increasingly being used in natural resource management and planning (McLane et al. 2011; Høye et al. 2012; Gustafson 2019). For example, landscape connectivity, the capacity of a landscape to facilitate species movement between areas of good habitat is an important component of ecologically functional ecosystems (Zeller et al. 2012; Kanagaraj et al. 2013). To integrate the individual behaviour of bighorn sheep, their perceptual range, and movement decisions into corridor models that could enhance the ecological realism of subsequent connectivity design, an agent-based model was developed for bighorn sheep in the Okanagan Valley of British Columbia, Canada. A virtual grid was developed from government open-data sites. Each spatial data layer included slope in degrees, percent crown cover, lakes, rivers, and roads. The bighorn sheep agents' movement would be implemented as what the authors refer to as a pseudo-biased random walk. A randomized list of the eight adjacent cells to the agent's current location is generated. The agent would evaluate the attributes of the surrounding grid cells in the order they appear in the list. They would move towards the first favourable habitat found on the list. The simulation ends when all agents are removed from the simulation because they have become stuck, leave the spatial extent, or 2,000 steps have elapsed. At the conclusion of the simulation, the number of times an agent used each pixel on the landscape was aggregated into a single map. Results indicated that a combination of road interventions to make roads more permeable to sheep with increasing collision risk, and restoring natural fire regimes in key areas of the study regime were likely to increase bighorn sheep connectivity (Allen et al. 2016).

There has been increasing interest in using least-cost path (LCP) analysis to examine landscape connectivity across fragmented landscapes (Adriaensen et al. 2003; Correa Ayram et al. 2016; Etherington 2016; Savary et al. 2022) and to inform habitat linkage design (Sawyer et al. 2011). In a review related to connectivity and conservation from 2008 to 2013, not only was there a substantial increase in the number of publications, but LCP analysis was also the most used method (Correa Ayram et al. 2016). This may be in part because tool boxes for LCP analysis are available in GIS packages (Rayfield et al. 2010).

LCP modelling was initially developed in context of geographic transportation (Diniz et al. 2020). The LCP finds the most cost-effective path from a start point to finish. The most cost-effective path is the route of maximum efficiency between two positions as a function of both the distance travelled and the costs incurred (Etherington 2016). The amount and spatial configuration of habitats is used to develop a cost surface, also known as a resistance surface, where every grid cell is classified as to how much it hinders or facilitates species movement. The cost surface is a spatial representation of the cost of movement across a each cell comprising a landscape (Dutta et al. 2022). Resistance to movement can represent the willingness of an organism to cross a specific environment, a physiological cost of moving through this environment, a reduction in survival for this organism, or a combination of all these factors (Zeller et al. 2012). An algorithm calculates the cumulative cost of specific paths (Adriaensen et al. 2003).

One objective of LCP modelling is to provide a measure of connectivity between two locations that is more ecologically realistic than using Euclidean distance because the LCP takes into account the perceived ecological costs of traversing a landscape (Etherington and Holland 2013). The calculation of the LCP provides two important types of ecological information: the spatial location of the path, and the accumulated cost summed along the path, also known as the cost distance (Savary et al. 2022) or effective distance (Adriaensen et al. 2003). The length of the LCP has sometimes been used in studies and models instead of the accumulated cost, although there is concern that this might be a misleading measure as it does not include the costs incurred and might be little better than Euclidean distance (Etherington and Holland 2013). Instead of simply estimating isolation as Euclidean distance (Spear et al. 2010), the use of cost surfaces permitted a transition from connectivity models based on homogenous landscapes to one that included the different landscape characteristics (Diniz et al. 2020).

LCP modelling has been used to assist in identifying potential corridors to connect populations that have become isolated through habitat loss and fragmentation such as in the case of reintroducing a swift fox (*Vulpes velox)* population into a suitable habitat in the North American Great Plains. The LCP analysis pinpointed a potential dispersal corridor that could facilitate movement between two existing swift fox populations and four potential reintroduction sites (Alexander et al. 2016). Actual species movement data is not always available for ecological management solutions. Theoretical corridors derived from LCP analysis were compared with actual dispersal routes for grey wolves (*Canis lupus*) and the Eurasian lynx (*Lynx lynx)* in Poland, and found to be mainly within the range of real routes (Huck et al. 2010). In developing ecological corridors (i.e., interconnected networks of urban green and blue spaces) urban planners have found that the theoretical LCPs were indeed heavily used by grassland-dwelling moths and forest-dwelling passerine birds (Balbi et al. 2021).

Population persistence has been characterized as a function of colonization and extinction rates. Patch colonization by dispersing individuals has contributed to the stabilization of metapopulations and thus connectivity has been an important aspect of landscape studies. In earlier conceptual approaches based on island biogeography (MacArthur and Wilson 1967), the non-habitat matrix was considered to be homogeneous (Gustafson 2019). Studies that expanded the island biogeography view beyond the binary patch model included the incorporation of the effect of characteristics of the matrix in determining patch isolation (Knaapen et al. 1992), recognizing that because of landscape structure, dispersal routes would likely not be the shortest distance between two habitat patches (Gustafson and Gardner 1996), and ecological connectivity models based in electrical circuit theory (McRae et al. 2008).

A review of the state-of-the-art article noted that the use of alternatives to the binary patch model, such as the application of resistance or least-cost surfaces to predict animal movement across landscapes had the potential to advance landscape ecological knowledge (Gustafson 2019). A process-based approach to quantifying fragmentation is an alternative to the pattern-based approach. In addition, using simulated landscapes avoids the problems of extent and grain that affect the measurement of fragmentation derived from pattern-based landscape metrics. The process-based approach is also not linked or limited to any specific ecological processes.

2. Methods

To answer the research questions, the research methods involved three components: generating simulated landscapes, calculating pattern-based metrics, and setting up the LCP model to calculate the process-based metrics. Computation and analysis of the three components was accomplished using R Statistical Software (R Core Team2021; v4.1.2).

2.1 Generating simulated landscapes

Manipulating and controlling natural landscapes is not realistic. Therefore, I simulated a series of 1000 binary landscapes with 256^2 pixels each. The landscapes varied by both relative class proportion and spatial autocorrelation, but scale was held constant. Landscapes were simulated using a Conditional Autoregressive (CAR) model (Remmel and Csillag 2003) which was parameterized with a proxy measure for spatial autocorrelation and then density sliced to produce the desired binary proportion of land cover classes. The two land cover classes were white cells (low-cost to traverse) and black cells (high-cost to traverse). Class proportion varied from 1% white cells to 99% white cells. The parametrization of spatial autocorrelation varied from 0.00000 to 0.2499999, with these values, when multiplied by 4, returning a value similar to the typical value of rho that is used for characterizing spatial autocorrelation (comparable to Moran's *I*). This parameterization of spatial autocorrelation will be referred to as rho.

The procedure for generating simulated landscapes (Remmel and Csillag 2003) was selected because it is highly recommended in the literature (Turner 2005; Wang et al. 2014) and readily incorporated into our workflow in the R environment. The landscapes are comprised of discrete spatial units (cells). Each cell can be described by its location along the *x*-axis and *y*-axis as a Cartesian coordinate. The origin (0,0) is the bottom left corner of the simulated landscape. The *x*-axis includes columns 1 to 256 and increases from left to right, while the *y*-axis includes rows 1 to 256 and increases from bottom to top as shown in Figure 5. The four examples of simulated landscapes include the extremes of high and low input parameters (Figure 5). The landscape in 5a has low proportion of white cells (the class of interest) and low spatial autocorrelation. The landscape in Figure 5b has a high proportion of white cells and low spatial autocorrelation. The landscape Figure 5c has both a low proportion of white cells and low spatial autocorrelation. Finally, the landscape in Figure 5d has a low proportion of white cells and high spatial autocorrelation. The 1000 simulated landscapes represent the study area for this research.

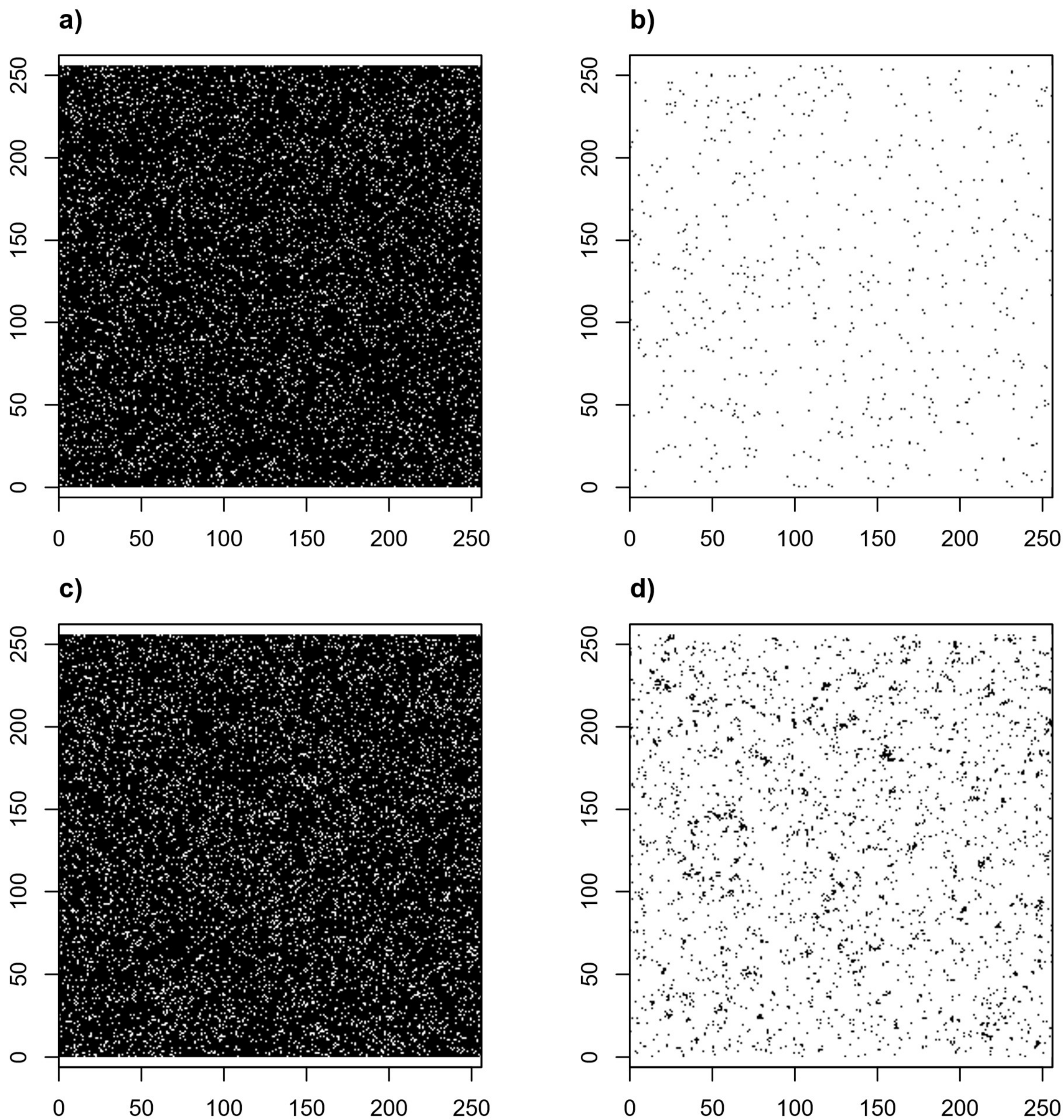


Figure 5. Four examples of simulated landscapes: a) has a low proportion white cells and low spatial autocorrelation, b) has a high proportion white cells and low spatial autocorrelation, c) has low proportion of white cells and high spatial autocorrelation, and d) has a high proportion of white cells and high spatial autocorrelation.

2.2 Calculating pattern-based metrics

The composition (*proportion*) and configuration (r*ho*) parameters used to simulate each replicate landscape were recorded along with the resulting landscape. To provide a basis for comparison, traditional pattern-based metrics that have often been used to measure fragmentation, were calculated and recorded for each simulated landscape. These landscape metrics were computed by the *landscapemetrics* package for R which includes the most frequently used metrics (Hesselbarth et al. 2019). In the program *landscapemetrics*, the distance units of the projection are assumed to be meters, and the package converts units internally and returns results in either meters, square meters, or hectares. However, in this study the values are relative since the extent and spatial resolution were maintained constant throughout the study. A list of the 72 variables that were recorded for the pattern-based results for each of the 1000 landscape simulations is detailed in Table 4.

Table 4. Variables recorded for each pattern-based result.

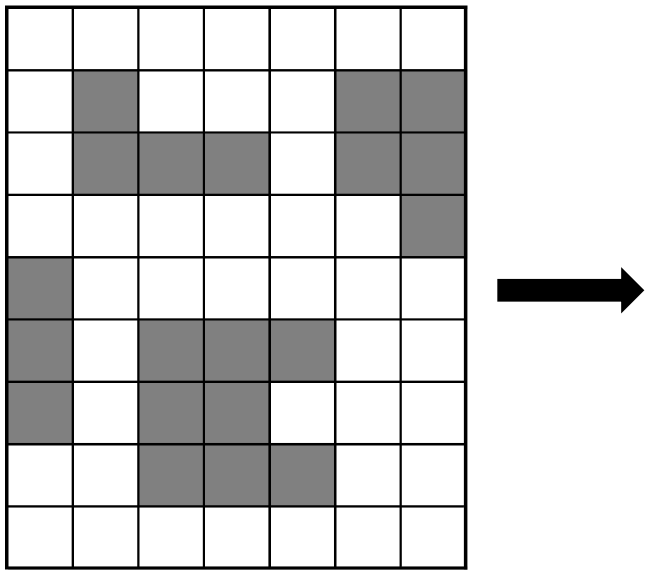
Variable	Description	Unit or range
1.	Date and time stamp	Day, month, date, time (h:m:s)
2.	Landscape size	$2^8 \times 2^8$
3.	Proportion white cells	1% – 99%
4.	Rho	0.000000 – 0.249999
5.	Cutpoint (to obtain categorical maps)	$6.271e^{-10}$ – $1.549e^{-07}$
6.	Landscape ID number	1 – 1000
7. – 72.	Metrics included in *landscape metrics package*	Depending on metric

The landscape number was unique and allowed for the two data frames, (i.e., the pattern-based metrics results and the process-based metrics results) to be joined in one data table. Although the *landscapemetrics* package (Hesselbarth et al. 2019) contains the most common metrics, not all of these metrics measure fragmentation. For example, the landscape metric entropy measures a diversity of landscape classes. Thus, only 23 of these metrics as listed in Table 1-3 were included in the analysis.

2.3 Setting up the LCP model

The goal of the LCP model was to analyze the cost, or difficulty, of traversing the cells of a simulated landscape from the west side to the east side. The cells were either costly or inexpensive to cross. In this case, costly cells were given a relative value of 100, and inexpensive cells were given a value of 1. The minimum cost to traverse a landscape would be 256, and the maximum cost would be 25,600. The LCP analysis would determine the optimal route for minimizing the cumulative cost. Thus, the total cost of crossing a landscape was a proxy for fragmentation, with more fragmented landscapes incurring higher costs. Each transit across the landscape was computed by LCP analysis for a random starting and ending point combination that connected the western and eastern margins of the landscape.

LCP requires a cost surface raster to calculate the optimal path between the two randomized points. The cost surface defines the cost (or impedance) to move through each cell. As shown in Figure 6, the cost surfaces, also known as the friction raster, were derived from each simulated landscape by recoding low-cost cells with a relative cost value of 1 and recoding high-cost cells with a cost of 100. The cost of traversing a high-cost cell was 100 times more expensive than crossing a low-cost cell. There were no absolute barriers to crossing the landscape, but additional substantial cumulative costs would be incurred by traversing a high-cost cell rather than travelling around it; this forced the LCP to follow the least accumulative cost path. The values of 1 for traversing a low-cost cell and 100 for traversing a high-cost cell were chosen to achieve tangible differences in path choices. Each simulated landscape had an associated cost raster.



1	1	1	1	1	1	1
1	100	1	1	1	100	100
1	100	100	100	1	100	100
1	1	1	1	1	1	100
100	1	1	1	1	1	1
100	1	100	100	100	1	1
100	1	100	100	1	1	1
1	1	100	100	100	1	1
1	1	1	1	1	1	1

Figure 6. Cost rasters are derived from simulated landscapes with white cells equal to a cost of 1, and black cells equal to a cost of 100 each time the cell is traversed.

The R package *leastcostpath* (2.0.12, Lewis 2022) was used to calculate the LCP that approximated the difficulty of moving across each of the simulated landscapes. The program *leastcostpath* was built on classes and functions delivered in the R package *gdistance* (van Etten 2017). Each simulated landscape was portrayed on a 256 × 256 pixel grid. For this study, movement to adjoining cells used rook's case connectivity. In rook connectivity only the common sides of the cells define the neighbour relation as shown in Figure 7.

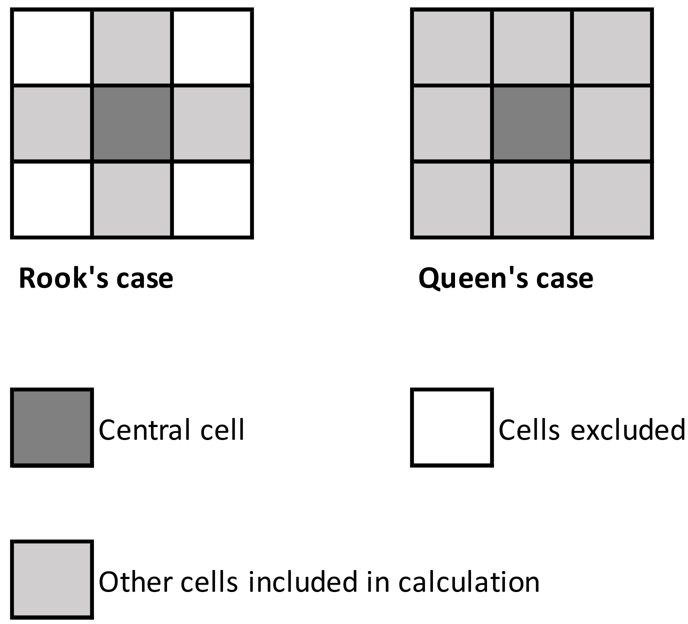


Figure 7. Comparison of rook and queen case contiguity.

The start point of the LCP was randomly assigned in the first column, and the end point was randomly assigned in the last column. For example, in Figure 8 the start point was (1,1) and the objective was to find the LCP to point (256, 121) using the cost raster assigned to the associated simulated landscape. The LCP under these conditions is indicated by the yellow route. As is characteristic of LCP analysis, the spatial location of the path, as well as the accumulated cost summed along the path, is calculated.

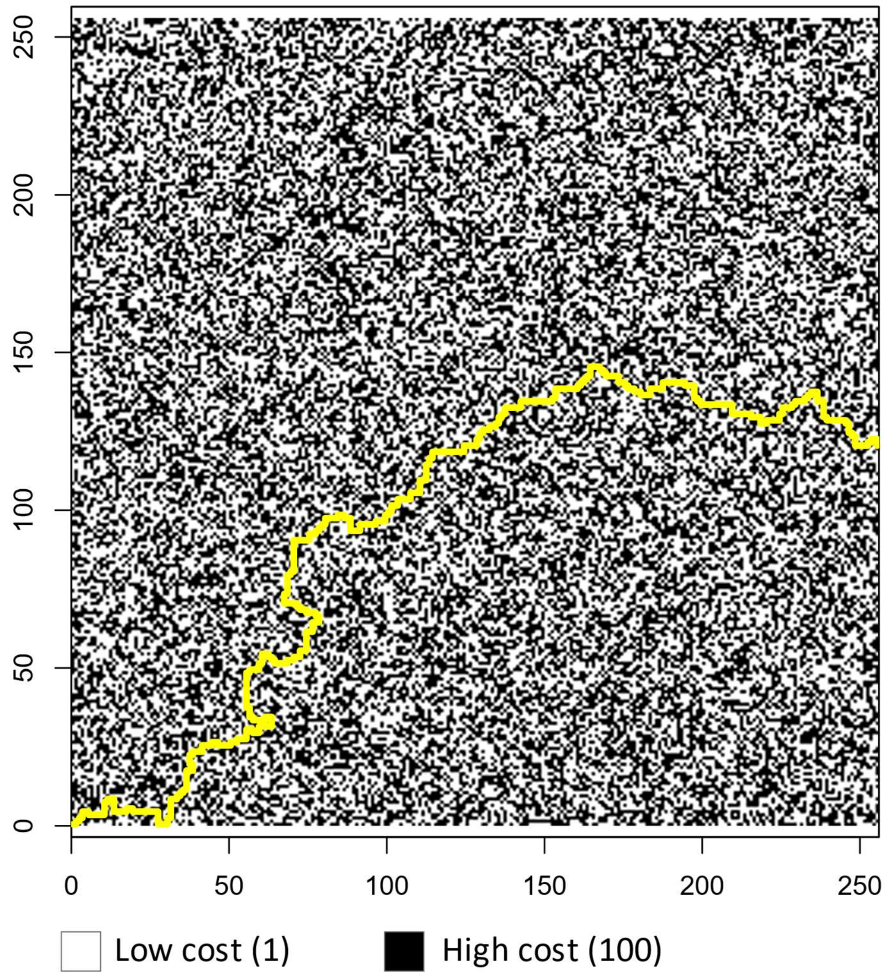


Figure 8. Example of one LCP on a landscape with 53% low-cost cells and rho of 0.203618 starting in position (1,0) and ending position (256, 121).

The LCP model became the base from which landscape fragmentation was assessed with five process-based variables: (1) number of steps, (2) cumulative cost to traverse the landscape from west to east, (3) cost per step, (4) Manhattan distance, and (5) ratio of the number of steps relative to the Manhattan distance.

The number of steps (Steps) is the length of the LCP for the specific starting and ending point combination and is one cell wide. For the LCP depicted in Figure 8, it took 540 steps to cross from the starting position at (1, 0) to the end position at (256, 121). Thus, the first process-based variable, number of steps in the LCP (Steps), is 540.

The LCP in Figure 8 crossed 524 white cells (cost of 1 each) and 16 black cells (cost of 100 each) resulting in a cumulative cost (TotalCost) of 2124. The cumulative cost is the second process-based variable. Having ascertained the number of steps taken along the LCP and the cumulative cost, the third process-based variable of cost per step (CostSteps) is 2124/540 = 3.93.

The fourth process-based metric calculates the Manhattan distance from the start point in (1,0) to the end point (256,121). Movement is restricted to north-south and east-west directions only, or as strictly horizontal and vertical paths. The Manhattan distance is the sum of absolute distances between two data points in a grid as shown in Equation 2.

$$Manhattan\ distance = |x_1 - x_2| + |y_1 - y_2| \qquad (2)$$

In the example of Figure 8 with a start point at (1, 1) and ending at (256, 121), applying Equation 1 would calculate the Manhattan distance as 376 as shown in Equation (3).

$$\begin{aligned} &|x_1 - x_2| + |y_1 - y_2| \\ &\quad = |0.5 - 255.5| + |0.5 - 121.5| \\ &\quad = 376 \end{aligned} \qquad (3)$$

The Manhattan distance provides the minimum orthogonal distance between the start and end points. The fifth process-based variable, the distance ratio (DistanceRatio), calculates the ratio of the number of steps relative to the Manhattan distance. In the example of Figure 8, the distance ratio is 540⁄376 = 1.44.

A series of 100 LCPs were calculated for each of the 1000 simulated landscapes using a randomly selected start, to a randomly selected end point, on the first and last columns respectively. Multiple traverses with randomly selected start and end points sought to capture the variability of each landscape. The LCP for each simulated landscape was calculated 100 times with 100 randomly generated start and end points. The random element in this model allows for multiple potential paths to be taken through a landscape and to capture their variability. This variability is a key measure of how well the LCP process characterizes the fragmentation of the landscape.

The Manhattan distance provided a relative minimum distance for each of the randomly start and end points transits: a neutral path that does take impedance into account. Then the fifth variable, the distance ratio, can be calculated to compare the various LCPs within the same landscape. See Figure 9 for an example of 100 traverses (shown in red) across a simulated landscape with a proportion of 53% low-cost cells and a rho of 0.203618.

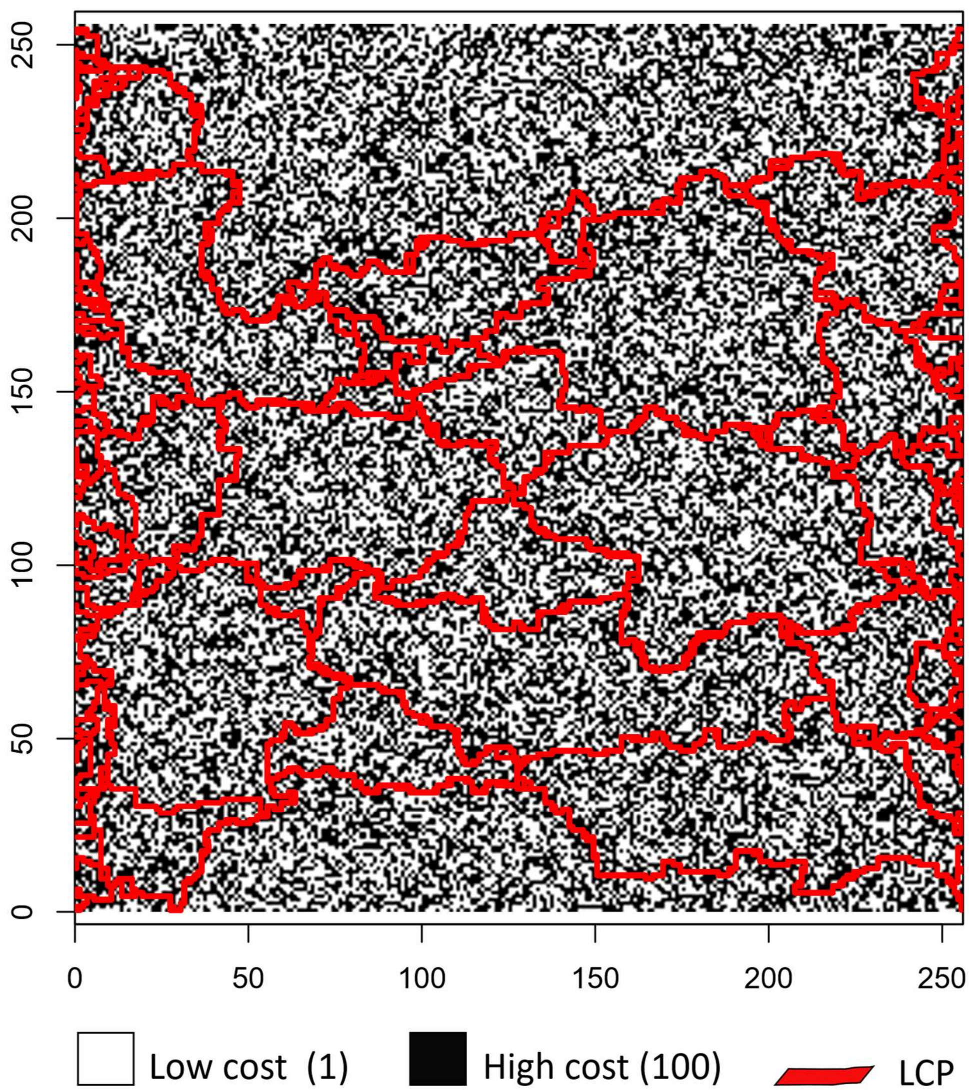


Figure 9. Example of 100 transits across a landscape with a proportion of 53% low-cost cells and a rho of 0.203618.

The landscape number with the associated proportion and rho were recorded. This unique landscape number permitted the comparison between the pattern-based metrics and the pattern-based metrics. The cost surface was derived from the simulated landscape. For each of the 100 traverses of a landscape, the five process-variables were calculated and recorded. Thus, the more fragmented the landscape, the higher the cost to traverse because of having to take a large number of steps, needing to cross high-cost cells, or a combination of both. The unique Landscape Number, composition, configuration, LCP details and values for the 5 process-based variables were recorded (Table 5).

Table 5. Variables recorded for each process-based result.

Variable	**Description**	**Unit or range**
1.	Landscape Number	1 – 1000
2.	LCP repetition	1 – 100
3.	Number of cell neighbours	4 (Rook's Case)
4.	Proportion	1% – 99%
5.	Rho	0.000000 – 0.249999
6.	Start of LCP on west side (col 1)	Row 1 – 256
7.	End of LCP on east side (col 256)	Row 1 – 256
8.	Number of steps	≥ 256
9.	Total cost	≥ 255
10.	Cost per step	≥ 1
11.	Manhattan distance	≥ 256
12.	Ratio of number of steps to Manhattan distance	≥ 1

The overall procedure to answer the research questions is illustrated in Figure 10.

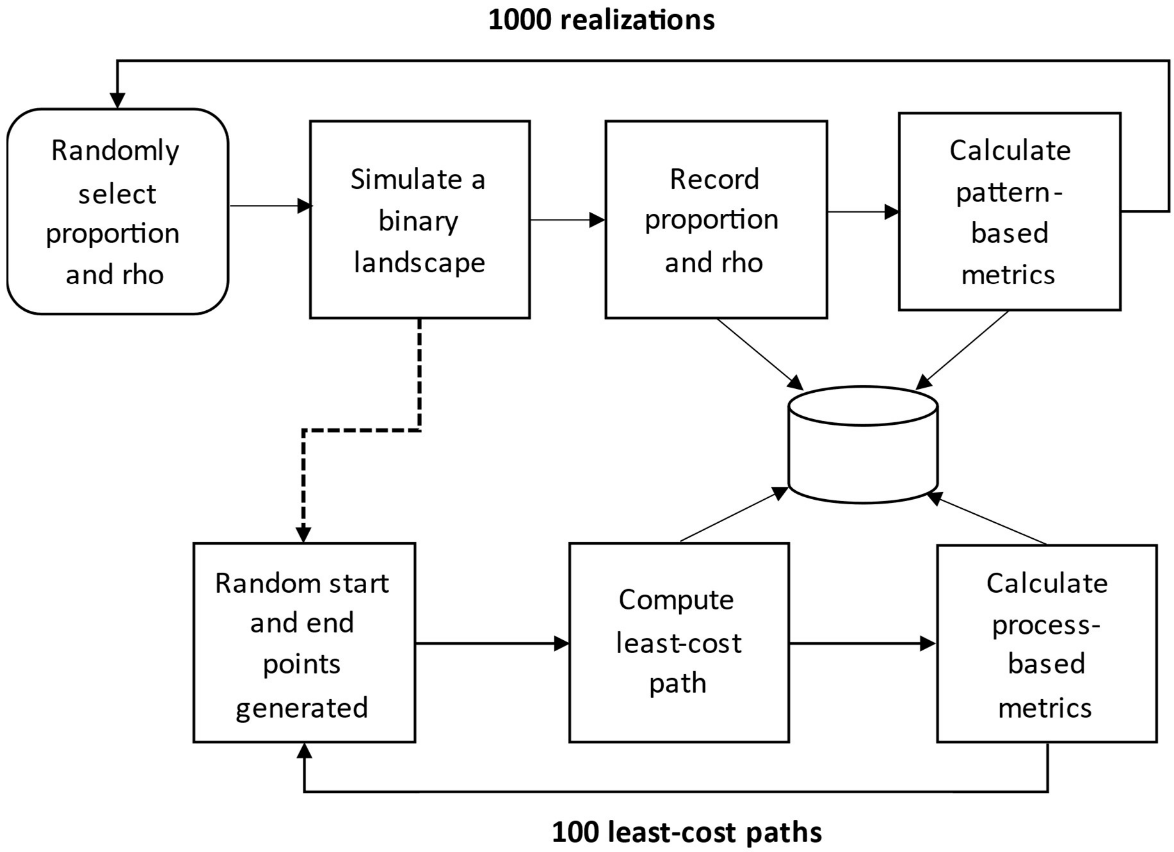


Figure 10. Workflow to create simulated landscapes, pattern-based, and process-based metrics.

2.4 Data analysis

The data analysis was performed within the R environment. Two data frames constructed: one for the pattern-based metrics and one for the process-based metrics. The unique landscape number assigned to each simulated landscape provided the common key for joining the two data frames.

To visualize the data, histograms were produced for the input parameters, pattern-based metrics, and process-based metrics. The 1000 binary landscapes were simulated to pull proportion parameters from a uniform distribution to ensure that each proportion had an equal probability of occurring.

A key objective of statistics is to describe the strength and nature of the relationship between two variables (Gomez et al. 2010). Scatter, and box plots were created to show the relationship between both types of metrics and the input parameters. Finally, the pattern-based metrics were plotted against the process-based metrics to check for correlations.

To examine the sensitivity of the pattern-based and process-based metrics to the input parameters (composition and configuration), correlation tests were run to measure the strength and relationship between the metric and the input parameters of composition (proportion) and configuration (rho). A Pearson correlation coefficient was computed to assess the strength and direction of the relationship between a metric and the two input parameters. A correlation test was performed to test the null hypothesis.

H_0: There is no relationship between pattern-based metric x measure of fragmentation and composition (proportion).

H_1: There is a positive (or negative depending on the particular metric) relationship between pattern-based metric x and composition (proportion).

H_0: There is no relationship between process-based metric x measure of fragmentation and configuration (rho).

H_1: There is a positive (or negative relationship depending on the particular metric) between process-based metric x and composition configuration (rho).

3. Results

The objective of this research was to develop and test process-based fragmentation quantification and to then compare that to existing pattern-based fragmentation quantification methods. To achieve this objective 1000 simulated landscapes were created using a Conditional Autoregressive (CAR) model and pattern-based fragmentation metrics commonly used to measure fragmentation were calculated. For each landscape, 100 LCPs were computed based on randomized start and end locations; this data was used to calculate five process-based metrics, along with their variability, and could be compared with the pattern-based metrics for each simulated landscape, level of composition, or level of spatial autocorrelation present.

3.1 Summary statistics input parameters

Descriptive statistics for the two landscape simulation input parameters of proportion and rho are provided in Table 6.

Table 6. Descriptive statistics for proportion and rho.

Statistic	**Proportion**	**Rho**
Minimum	1.00	0.0001579
Median	51.00	0.1252756
Mean	50.32	0.1260088
Theoretical mean	50.00	0.1249995
Maximum	99.00	0.2499865
Std Dev	27.77	0.0725600
Theoretical Std Dev	28.29	0.0721685
Actual Range	98.00	0.2498286
Theoretical Range	98.00	0.2499998
Skew	-0.04	0.0101047

For proportion, the full range of possible values from 1% to 99% low-cost cells was generated. The distribution of the percentage of low-cost cells (white) across the simulated landscapes, grouped in intervals of 5%, is shown in Figure 11. Each possible proportion of 1% to 99% low-cost cells is represented. The distribution for proportion appears to be fairly uniform. Expected frequency would be 10 occurrences per one percent proportion, or as shown in Figure 11, fifty occurrences per five percent proportion.

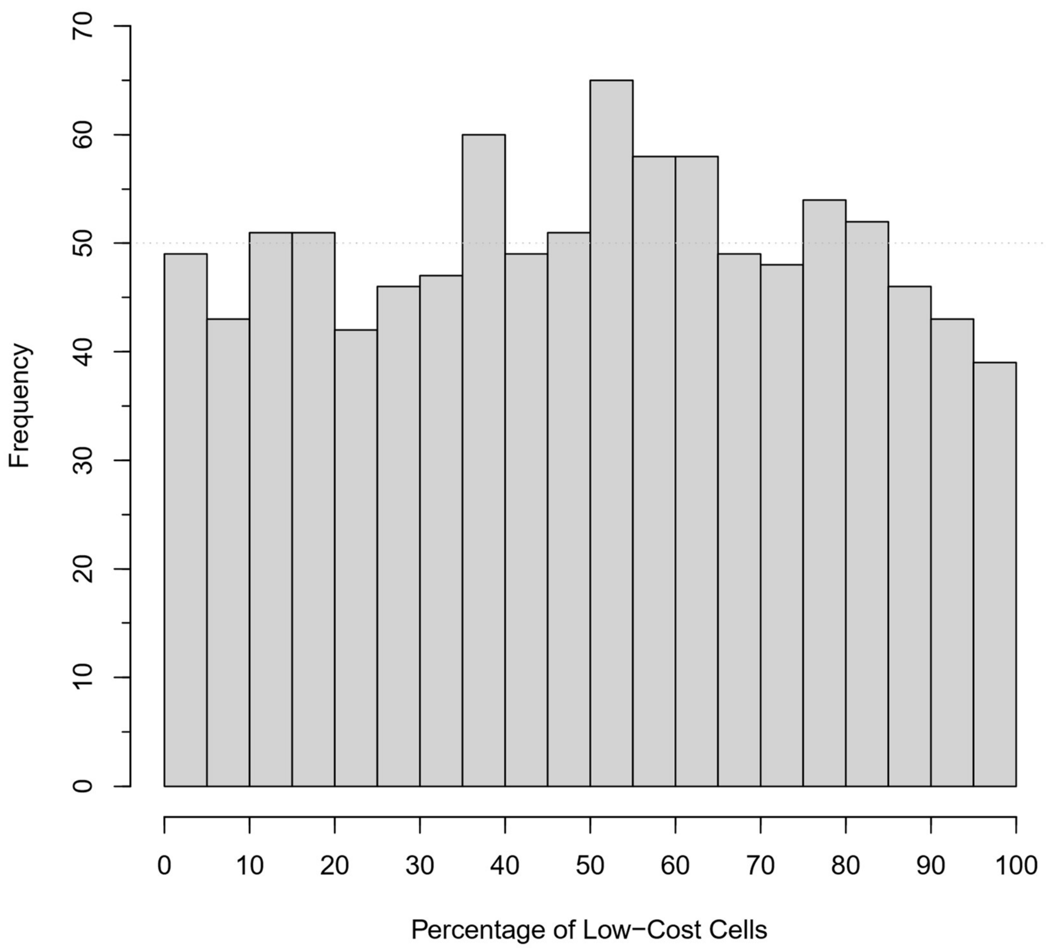


Figure 11. Distribution of percentage of low-cost (white) cells for 1000 simulated landscapes.

For rho (clustering), the full range of possible values from 0.01 to 0.25 was generated. The distribution of rho across the simulated landscapes in intervals of 0.01 is shown in Figure 12. The distribution of rho dataset appears to be relatively uniform. Expected frequencies would be 40 occurrences per 0.01 values of rho.

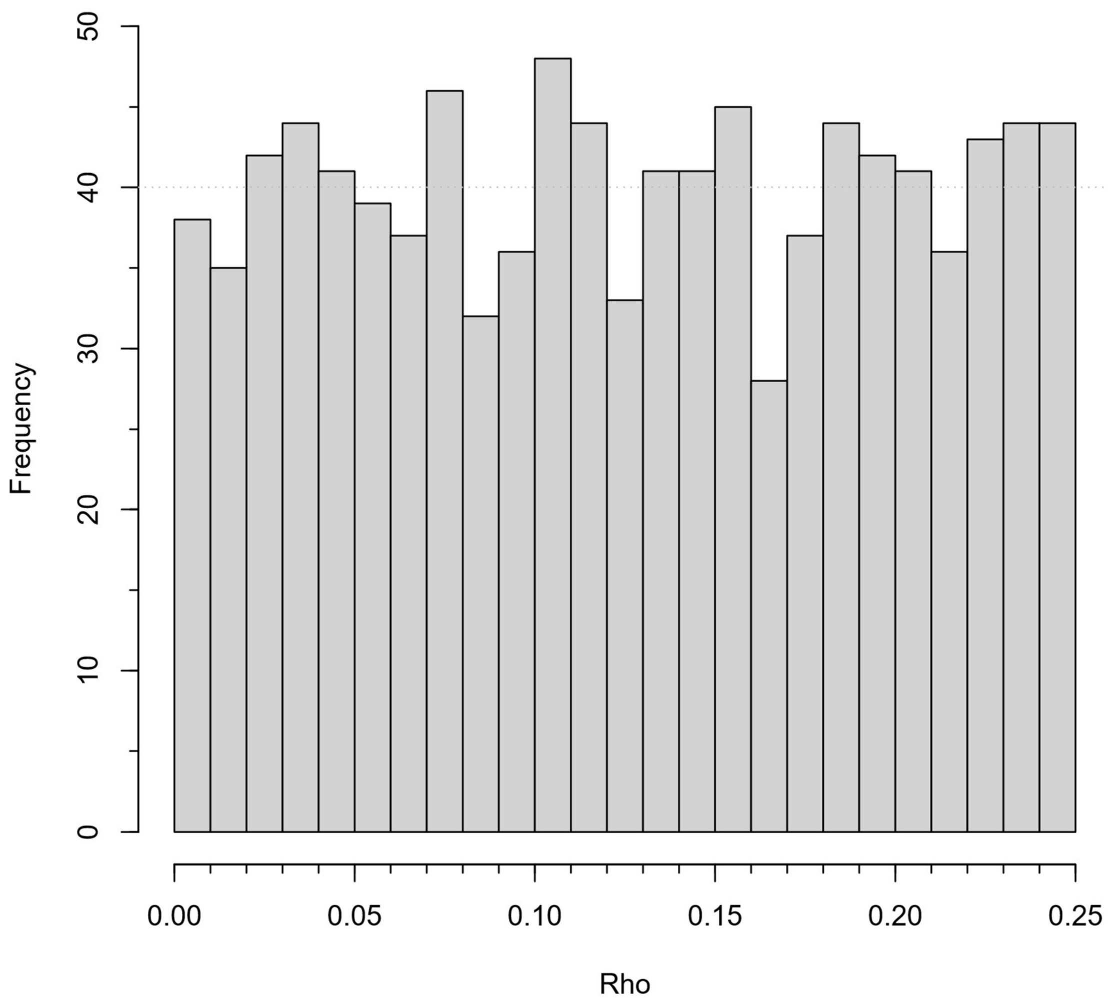


Figure 12. Distribution of rho values for 1000 simulated landscapes.

3.2 Summary statistics for pattern-based metrics

Descriptive statistics for the 25 pattern-based metrics used to measure landscape fragmentation are provided in Table 7.

Table 7. Summary statistics for pattern-based metrics commonly used to measure fragmentation.

Metric	Minimum	Median	Mean	Maximum	Std Dev
area_cv	1482	4056	3870	5980	1539.15
area_mn	1.198	2.061	3.669	12.992	3.09
area_sd	67.85	85.19	101.77	260.61	38.93
cai_cv	306.2	816.2	1871.8	6934.7	1849.99
cai_mn	0.0118	0.15717	0.19708	1.08031	0.17
cai_sd	0.739	1.412	1.483	4.239	0.56
dcad	0.01695	37.63835	27.71100	49.67584	18.48
ed	12.07	255.32	255.59	332.90	94.48
lpi	48.91	73.00	73.63	99.00	14.53
te	71190	1505925	1330602	1963500	557272
shape_cv	10.83	78.60	121.11	386.74	103.68
shape_mn	1.009	1.436	1.398	1.856	0.24
shape_sd	0.1093	1.1496	1.8279	5.8411	1.62
para_cv	4.59	18.38	16.79	24.32	4.55
para_mn	0.1073	0.1159	0.1174	0.1328	0.01
para_sd	0.006096	0.021172	0.019394	0.026136	0.00
cohesion	99.44	99.55	99.58	99.82	0.11
division	0.01992	0.46710	0.40235	0.65473	0.18
enn_cv	2.25	4.62	5.90	38.77	3.81
enn_mn	60.27	60.84	61.52	93.39	2.15
enn_sd	1.36	2.81	3.71	36.21	2.78
mesh	2036	3143	3525	5781	1064
np	454	2862	2719	4925	1524
pd	7.697	48.523	46.099	83.499	25.84
split	1.020	1.877	1.822	2.896	0.51

The commonly used pattern-based metrics for quantifying fragmentation use various attributes of patch characteristics (such as area and shape) and configurations to calculate a metric value. When plotted, the 25 pattern-based metrics displayed a symmetric relationship about the proportion mean of 50%. There is not a one-to-one relationship between a metric value and landscape proportion (of low-cost cells). The pattern-based metrics portrayed either a unimodal, bimodal, or convex relationship with proportion.

Four of the pattern-based metrics displayed a unimodal symmetrical distribution against proportion: Edge density (ed), Total edge (te), Covariance of variation shape index (shape_cv), and Standard deviation shape index (shape_sd) as shown in Figure 13. Edge density and Total edge are equivalent, in this case, as Edge density is standardized to total landscape area and all 1000 simulated landscapes have equal areas. Edge density equals the sum of all edges in relation to landscape area. It describes the configuration of the landscape because, for example, an aggregation of the same class will result in low edge density. The total edge includes all edges. It measures the configuration of the landscape because a highly fragmented landscape will have many edges. Total edge equals 0 when there is no class edge in the landscape and increases, without limit, as the landscape becomes more fragmented. Edge density and Total edge equal zero if only one patch is present and increase without limit as the landscapes become more fragmented. These two graphs (Figure 13a and 13b) indicate that for the class of interest, landscapes become increasingly more fragmented until the landscape reaches 50% proportion (of low-cost cells) and then fragmentation decreases from 50% to 99% proportion. They do not portray a one-to-one function as a metric value is associated with two different landscape proportions. The Covariance of variation shape index equals 0 if all patches have an identical shape index and increases, without limit, as the shape index increases. A higher shape index indicates more complicated patch shapes and thus suggests more fragmentation. In Figure 13c the Coefficient of variation shape index, which describes the ratio between the actual perimeter of the patch and the square root of patch area, increases without limit as the complexity of the patch shape increases up to 50% proportion and then decreases as does Figure 13d the Standard deviation shape index. In these four cases, Edge density, Total edge, Covariance of variation shape and Standard deviation shape index, each metric value is associated with two proportions, and lacks a one-to-one relationship.

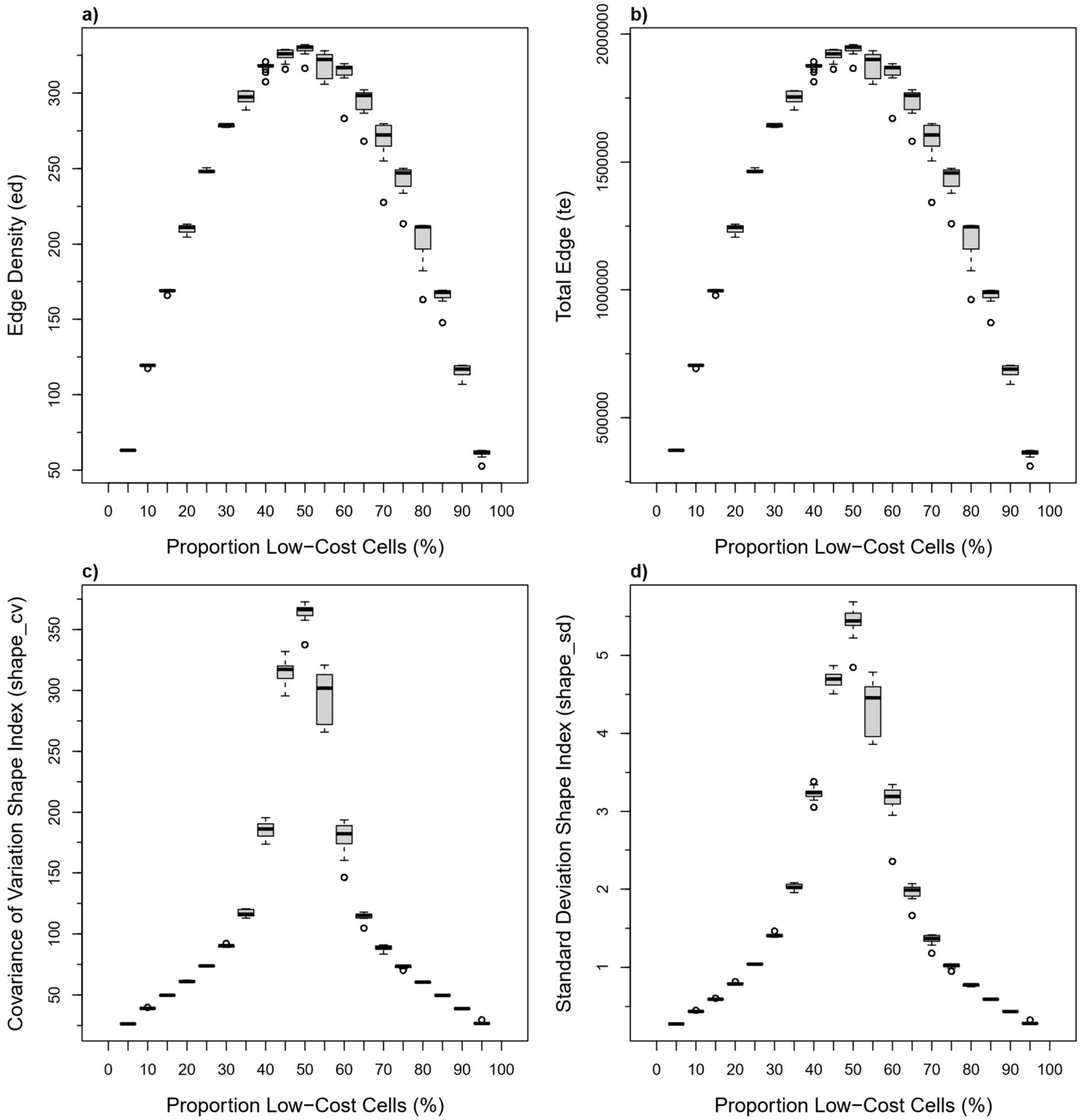


Figure 13. Symmetric unimodal pattern-based metrics versus proportion boxplots: a) Edge density, b) Total edge, c) Coefficient of variance shape index, and d) Standard deviation shape index.

A further four of the pattern-based metrics displayed a slight bimodal symmetrical distribution around 50% proportion of low-cost cells: Disjunct core area (dcad), Division (division), Coefficient of variation perimeter-area ratio (para_cv), and Standard deviation perimeter-area ratio (para_sd) as shown in Figure 14. Disjunct core area density (Figure 14 a) equals the number of disjunct core areas per 100 ha relative to the total area. It equals zero when no patch of the class of interest contains a disjunct core area and increases without limit as disjunct core areas become present (i.e., patches become larger and less complex). Division (Figure 14b) is an aggregation metric. It equals 0 if only one patch is present and approaches 1 if all patches are single cells. The Coefficient of variation perimeter-area ratio (Figure 14c) and the Standard deviation perimeter-area ratio (Figure 14d) are shape metrics and describe the complexity of patches. They equal zero if the perimeter-area ratio is identical for all patches and increases as the variation of the perimeter-area ratio increases. These metric values correspond with at least two and in some cases four proportion values and therefore there is not a one-to-one relationship.

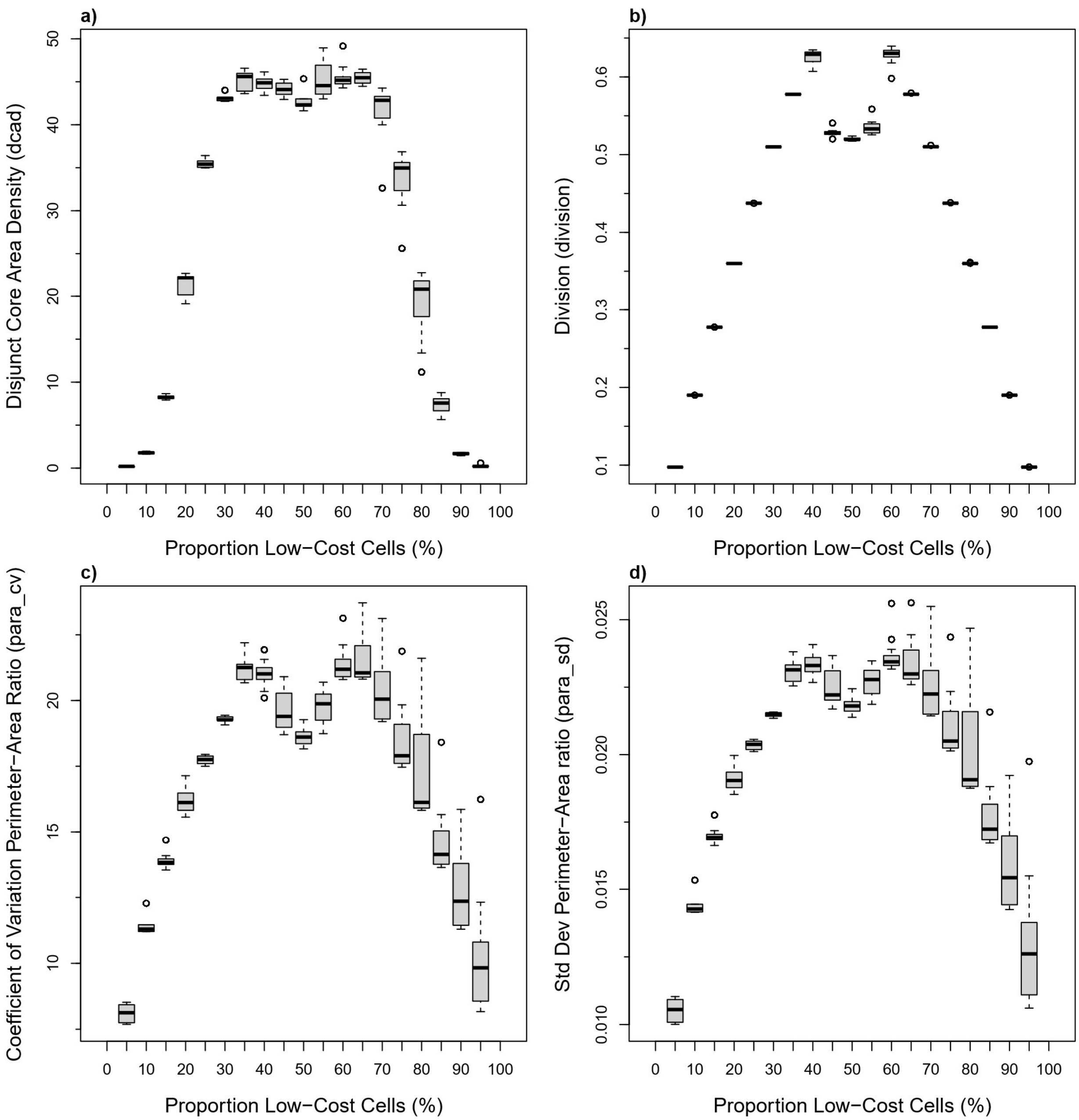


Figure 14. Slightly bimodal pattern-based metrics versus proportion boxplots: a) Disjunct core area density, b) Division, c) Coefficient of variation perimeter-area ratio, and d) Standard deviation perimeter-area ratio.

The majority of the pattern-based metrics displayed a bimodal relationship with the proportion of low-cost cells (Figure 15 and Figure 16). These metric values correspond with at least two and in some cases four proportion values; therefore, there is not a one-to-one relationship.

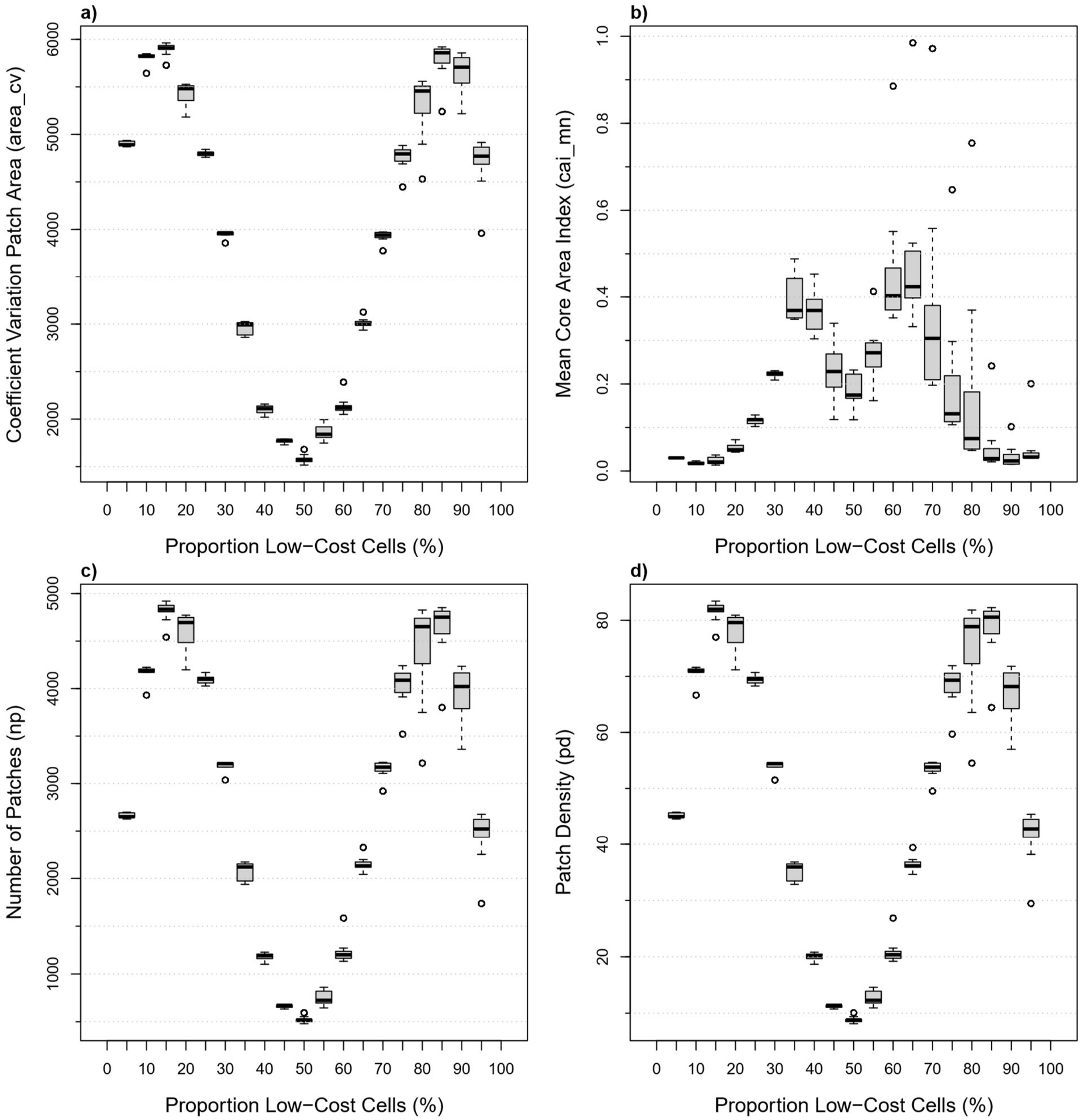


Figure 15. Four of the Bimodal pattern-based metrics versus proportion: a) Coefficient of variation patch area, b) Mean core area, c) Number of patches, and d) Patch Density.

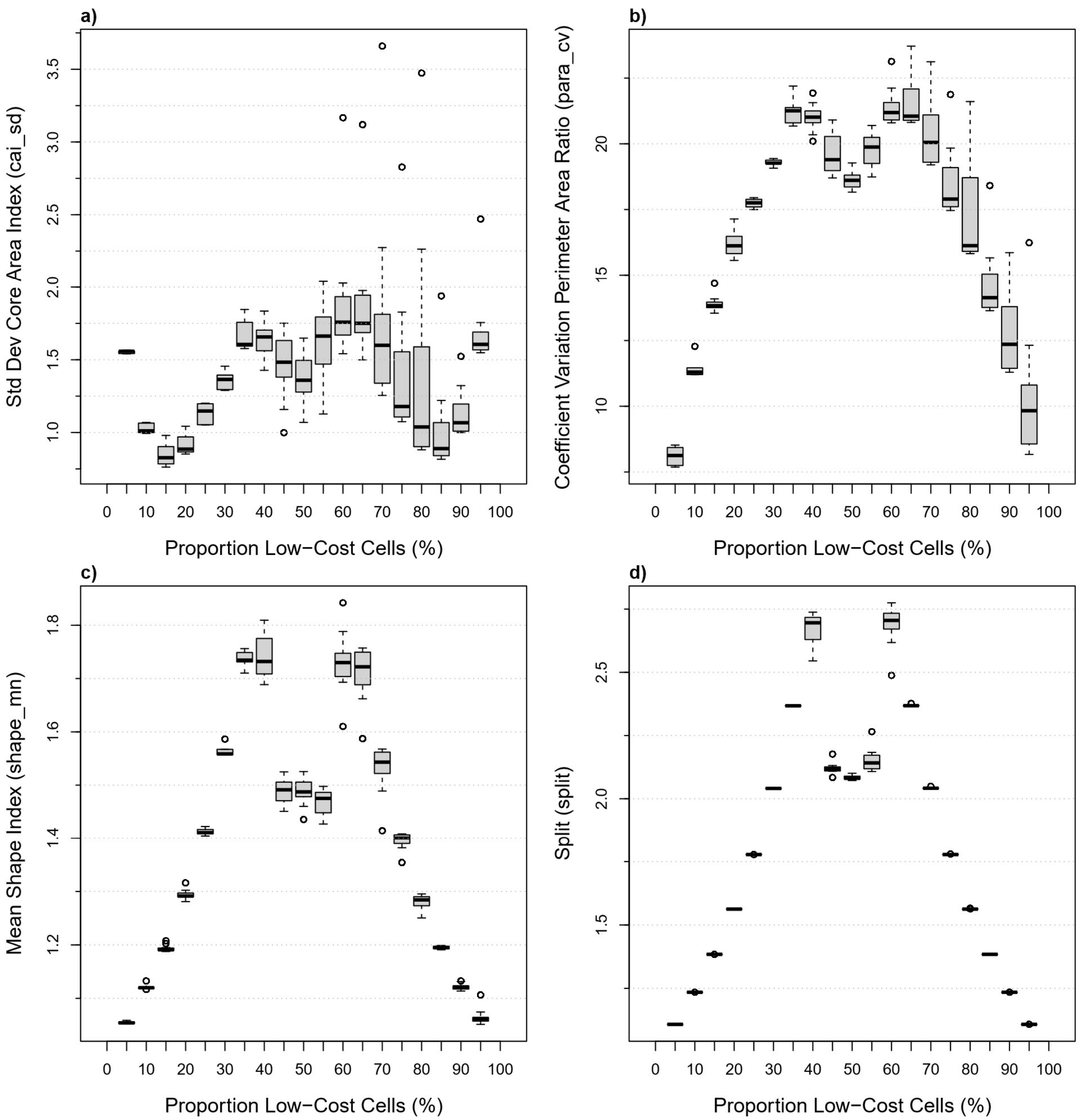


Figure 16. Four bimodal pattern-based metrics versus proportion: Standard deviation core area index, Coefficient of variation perimeter-area ratio, and Mean shape index, and split.

The four remaining metrics, Coefficient of variation Euclidean nearest-neighbour (enn_cv), Mean Euclidean nearest neighbour (enn_mn), Standard deviation Euclidean nearest-neighbour (enn_sd), and Largest patch index (lpi) are unimodal functions with the minimum value occurring at or around 50% proportion of low-cost cells (Figure 17). The Coefficient of variation Euclidean nearest neighbour distance is an aggregation metric and is a simple way to describe patch isolation. It measures the distance to the nearest neighbouring patch of the same class and equals zero if the nearest neighbour distance is identical for all patches. The Mean Euclidean nearest neighbour distance approaches zero as the distance to the nearest neigbour decreases meaning that patches are more aggregated. The Standard deviation of Euclidean nearest neighbour distance equals zero if the Euclidean nearest neighbour distance is identical for all patches and increases without limit as the variation of the Euclidean nearest neighbour distance increases. The Largest patch index is the percentage of the landscape covered by the corresponding largest patch of each class. It approaches zero when the largest patch is becoming small and equals 100 when only one patch is present. These metric values correspond with two proportion values and so there is not a one-to-one relationship.

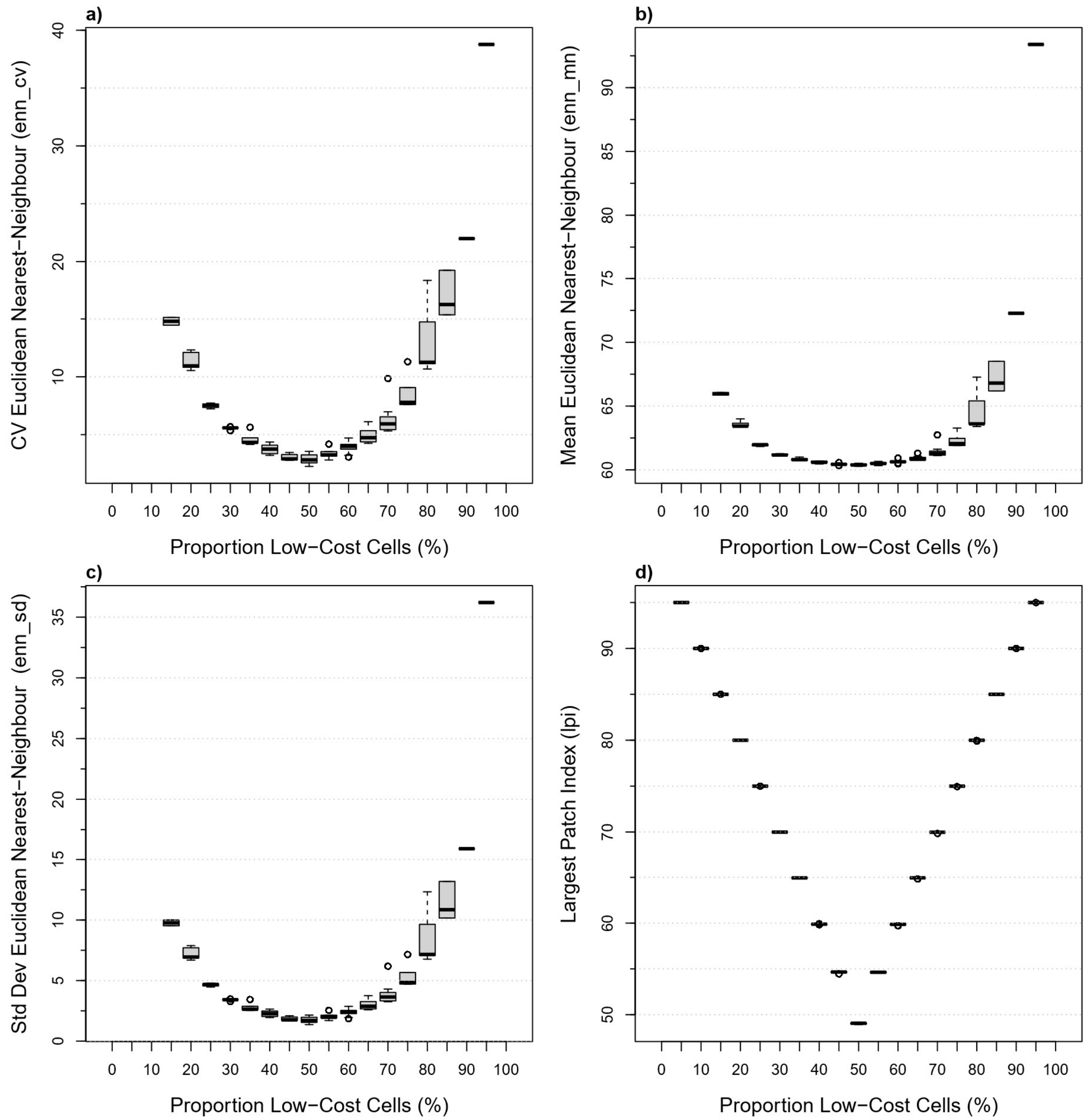


Figure 17. Unimodal function metrics with minimum at 50% proportion: a) Coefficient of Variance Euclidean nearest-neighbour, b) Mean Euclidean nearest-neighbour, c) Standard deviation Euclidean nearest-neighbour, and d) Largest patch index.

In addition to the lack of a one-to-one relationship, some pattern-based metrics gave very little information regarding the level of fragmentation. For example, cohesion is a measure of aggregation. It ranges from 0% to 100% and approaches zero when patches are more isolated. However, in over 1000 simulated landscapes of proportions varying from 1% to 99%

low-cost cells, all cohesion values fell within a very narrow range between 99.44% to 99.82%. There is little differentiation based on proportion.

A narrow range of values is also evident in the right skew of several pattern-based metrics, such as a) Mean of patch area, b) Coefficient of variation core area index, c) Standard deviation core area index, and d) Mean of Euclidean nearest-neighbour index (Figure 18).

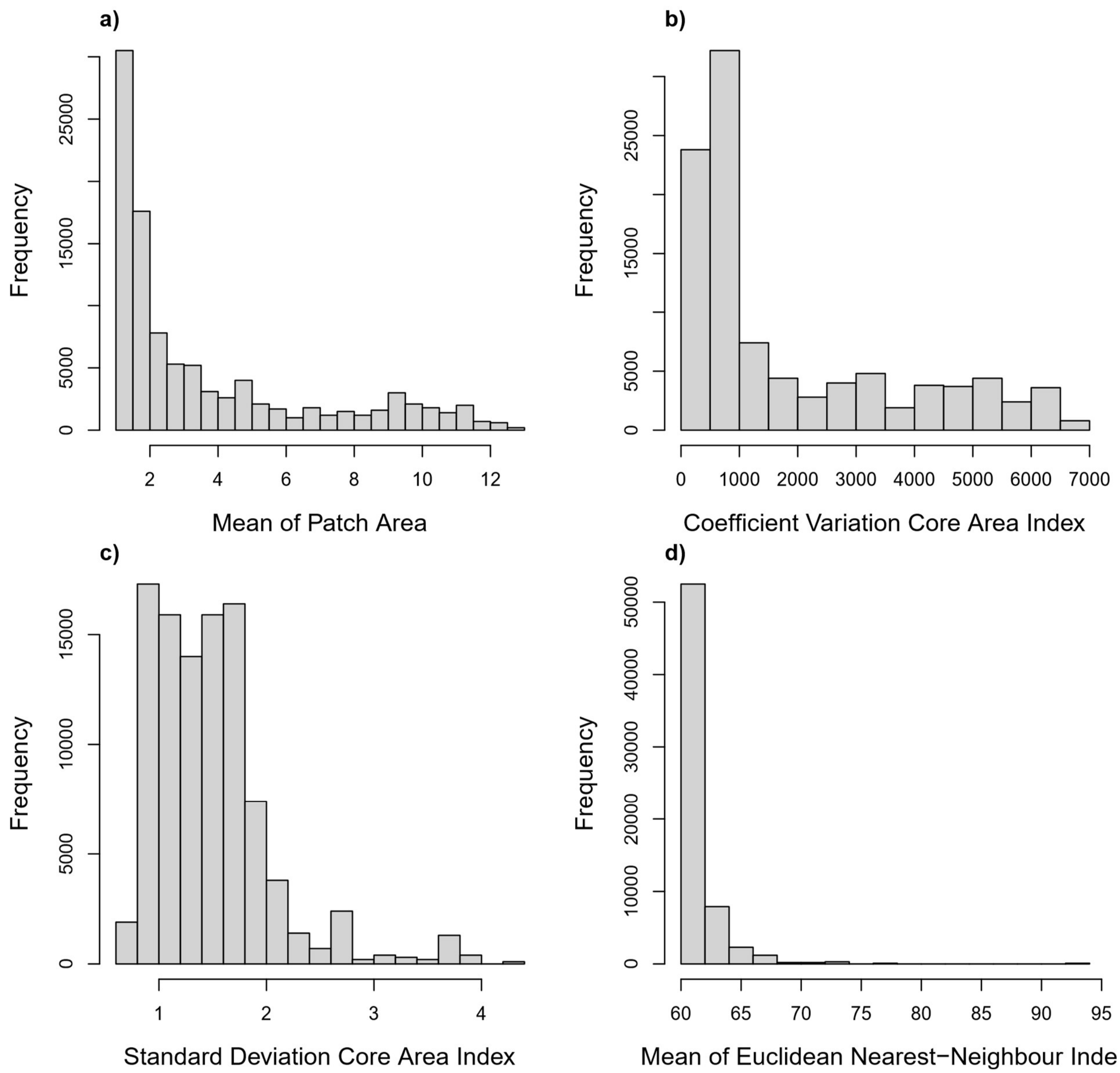


Figure 18. Right skewed histogram for a) Mean of patch area, b) Coefficient variation core area index, c) Standard deviation core area index, and d) Mean of Euclidean nearest-neighbour index.

In these four pattern-based examples the data is highly skewed. The mean of patch area (area_mn) approaches zero if all patches are small and increases without limit as the patch area increases. The coefficient of variation of core area index (cai_cv) and standard deviation core area index (cai_sd) equal zero if the core area index (the percentage of core area in relation to patch area) is identical for all patches. The mean of the Euclidean nearest-neighbour (enn_mn) approaches zero as the distance decreases and increases without limit as patches become more isolated.

One of the criticisms of patten-based metrics has been redundancy among metrics. A correlation matrix indicates the dependence between multiple variables at the same time. The following correlogram (Figure 19) highlights the most correlated variables. The correlation coefficients are coloured according to the value. Positive correlations are displayed in blue and negative correlations are displayed in red. Colour intensity and the size of the circle are proportional to the correlation coefficients in the right side of the correlogram. The lightly coloured correlation coefficients indicate that there is very little correlation.

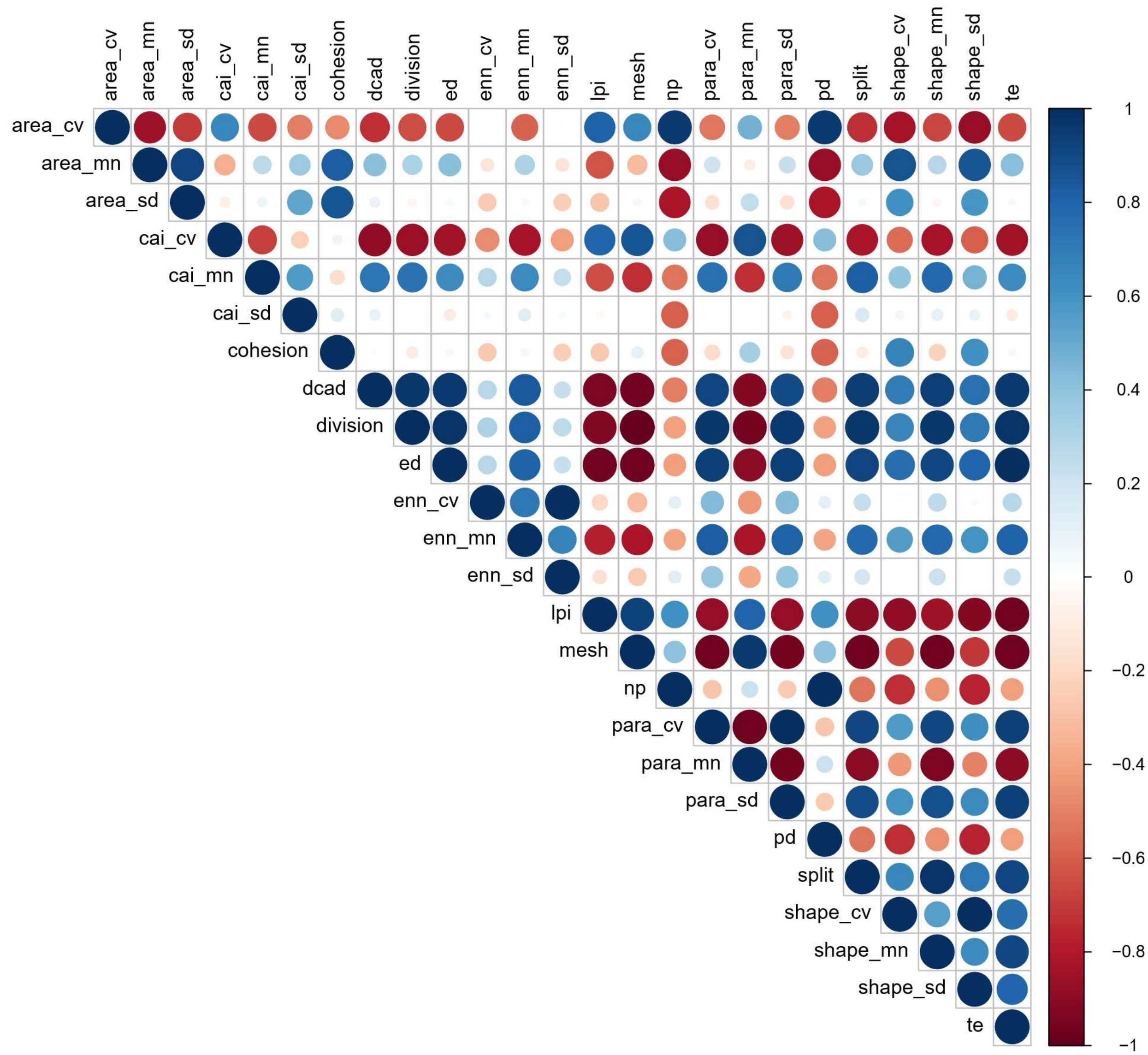


Figure 19. Correlogram showing the correlation coefficient among the pattern-based metrics. The area of the circles shows the absolute value of corresponding correlation value.

3.3 Summary statistics process-based variables

For each simulated landscape, 100 LCPs with random start and end points were generated and the values of the five process-based fragmentation metrics were calculated for each path. Three of the process-based variables, Steps, Total cost, and Manhattan distance, are primary variables. Cost per step (Total Cost / Steps) and Distance ratio (Steps / Manhattan distance) are derived variables. The descriptive statistics for these five process-based metrics are shown in Table 8.

Table 8 Descriptive statistics for the process-based variables.

	Minimum	**Median**	**Mean**	**Maximum**	**Std Dev**
Steps	256.0	386.0	395.3	798.0	77.11
Total Cost	257	2676	2676	45549	9009.20
Cost per step	1.000	5.707	20.410	99.236	25.87
Manhattan Dist.	256	331.0	340.9	511.0	60.20
Distance Ratio	1.000	1.086	1.172	2.661	0.21

The five process-based metrics did not portray symmetrical graphs around 50% proportion. The number of steps (Steps) to traverse the landscape increased as the proportion of low-cost cells increased, until it peaked at around 59%. The number of steps to traverse the landscape then dropped sharply as shown in Figure 20.

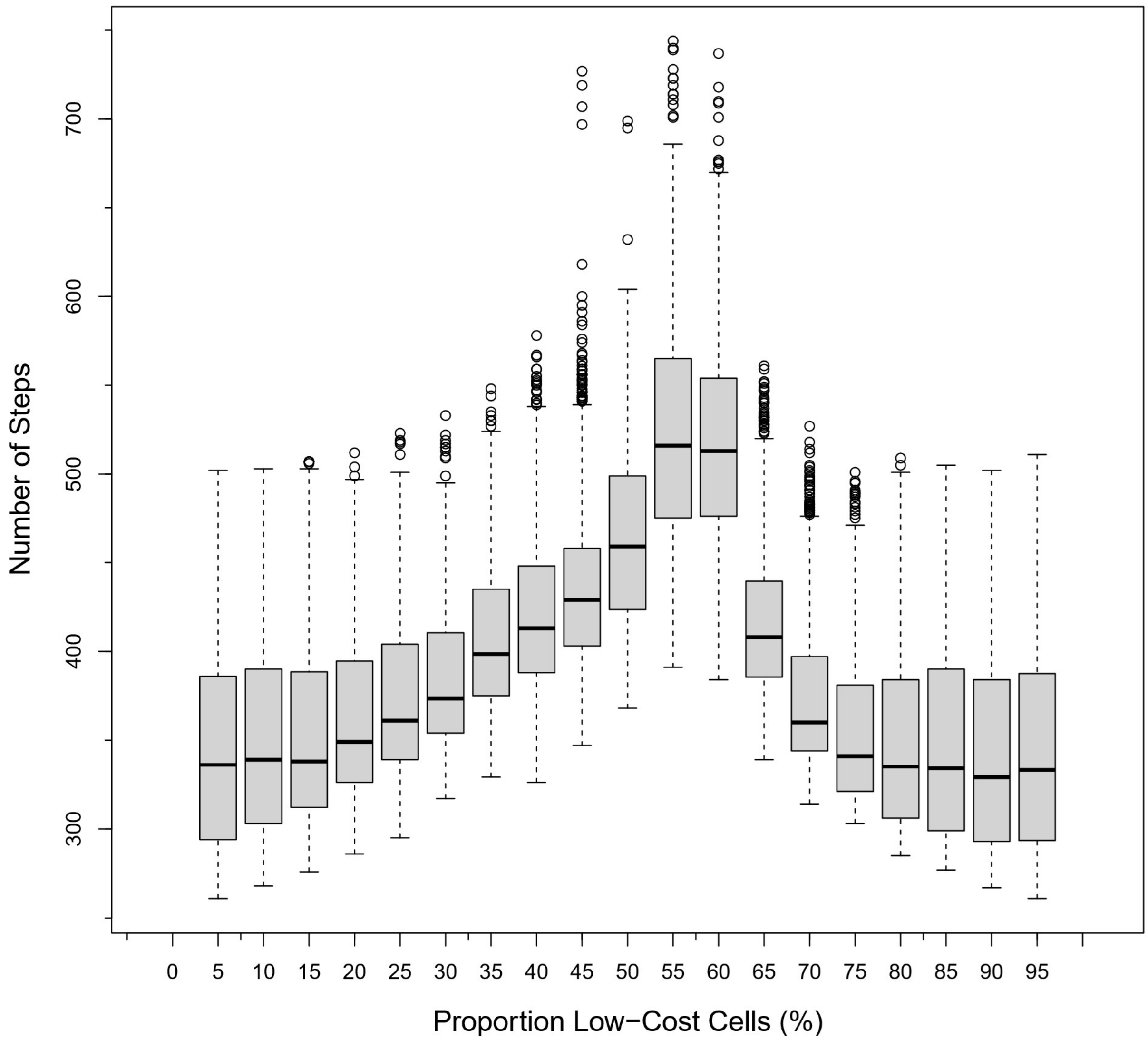


Figure 20. Number of steps versus the proportion of low-cost cells (%).

The cumulative cost (TotalCost) to traverse the landscape yielded one-to-one values based on landscape proportion. The total cost to traverse a landscape decreases sharply from 1% proportion of low-cost cells until approximately 59% proportion of low-cost cells, after which there is negligible difference in cost. There is little difference in the total cost to traverse the landscape between the proportion of 59% to 99% low-cost cells. In summary, as the number of low-cost cells increases, the cost to traverse the landscape decreases (Figure 21).

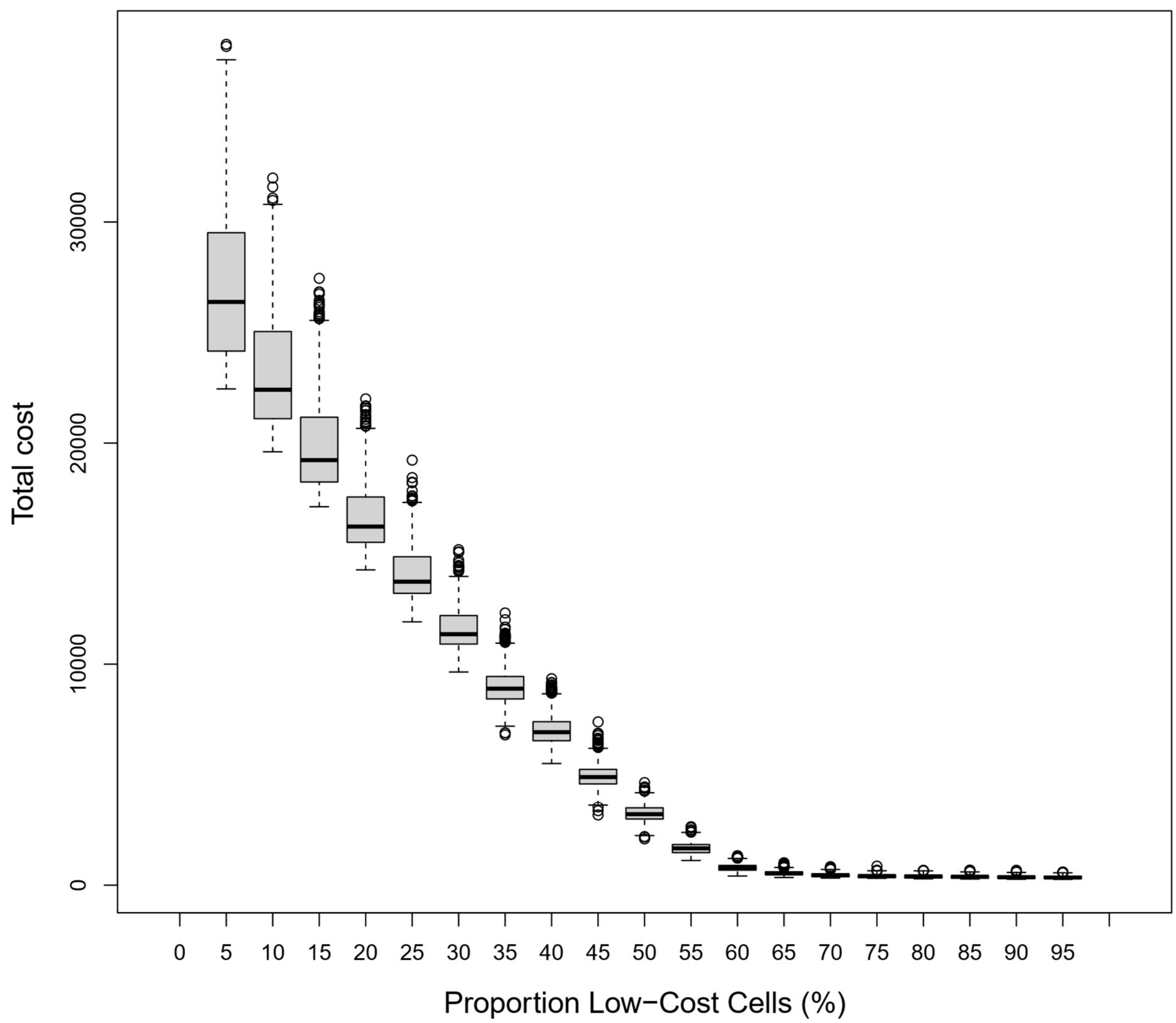


Figure 21. The total cost of traverse versus proportion of low-cost cells (%).

As the values of Total cost cover a large range, the data is also displayed on a logarithmic scale (Figure 22).

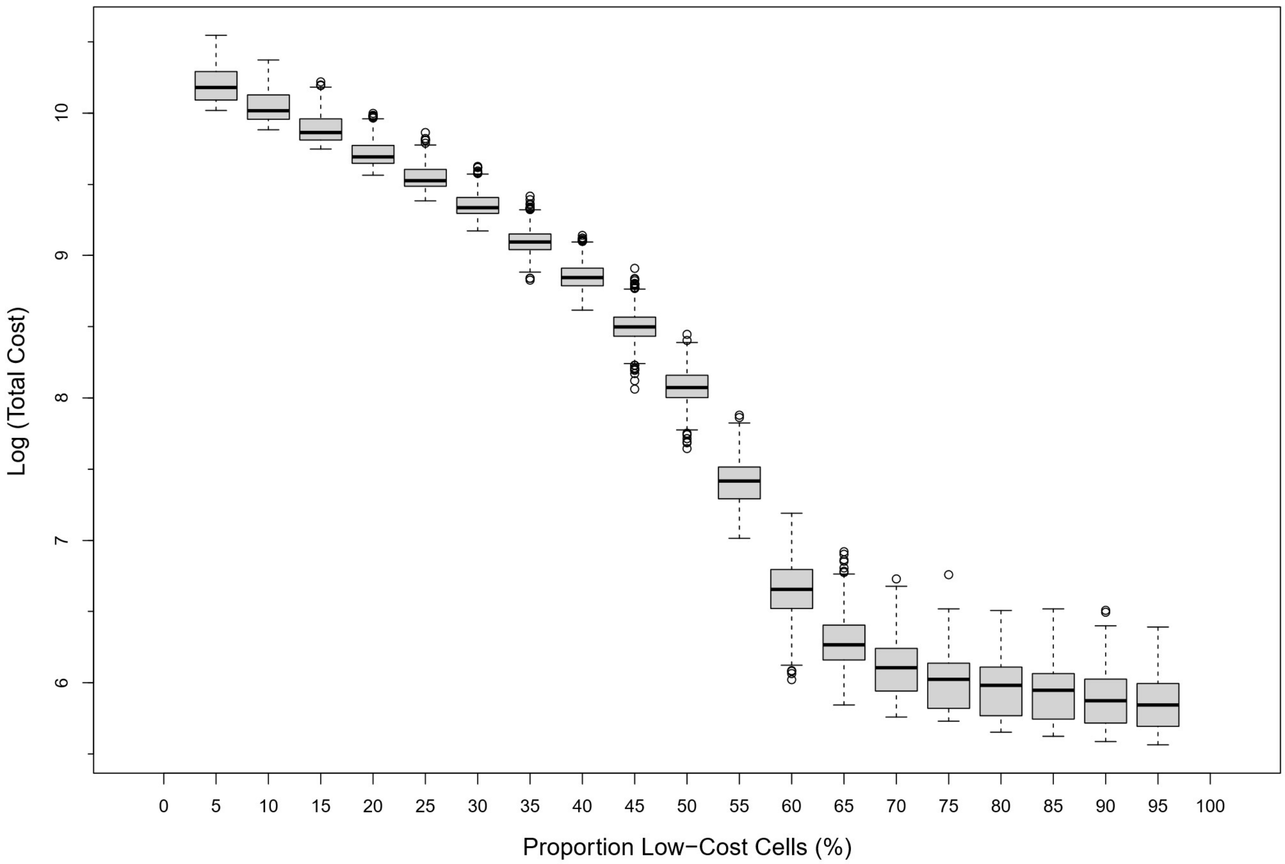


Figure 22. The log scale of Total cost to traverse the landscape versus proportion of low-cost-cells.

The cost per step (CostSteps) is derived from the total cost divided by number of steps on the LCP. The cost per step decreases sharply as the proportion of low-cost cells increases until the proportion of low-cost cells reaches approximately 59%. Between 60% and 100% proportion of low-cost cells, the cost to traverse the landscape is minimal (Figure 23).

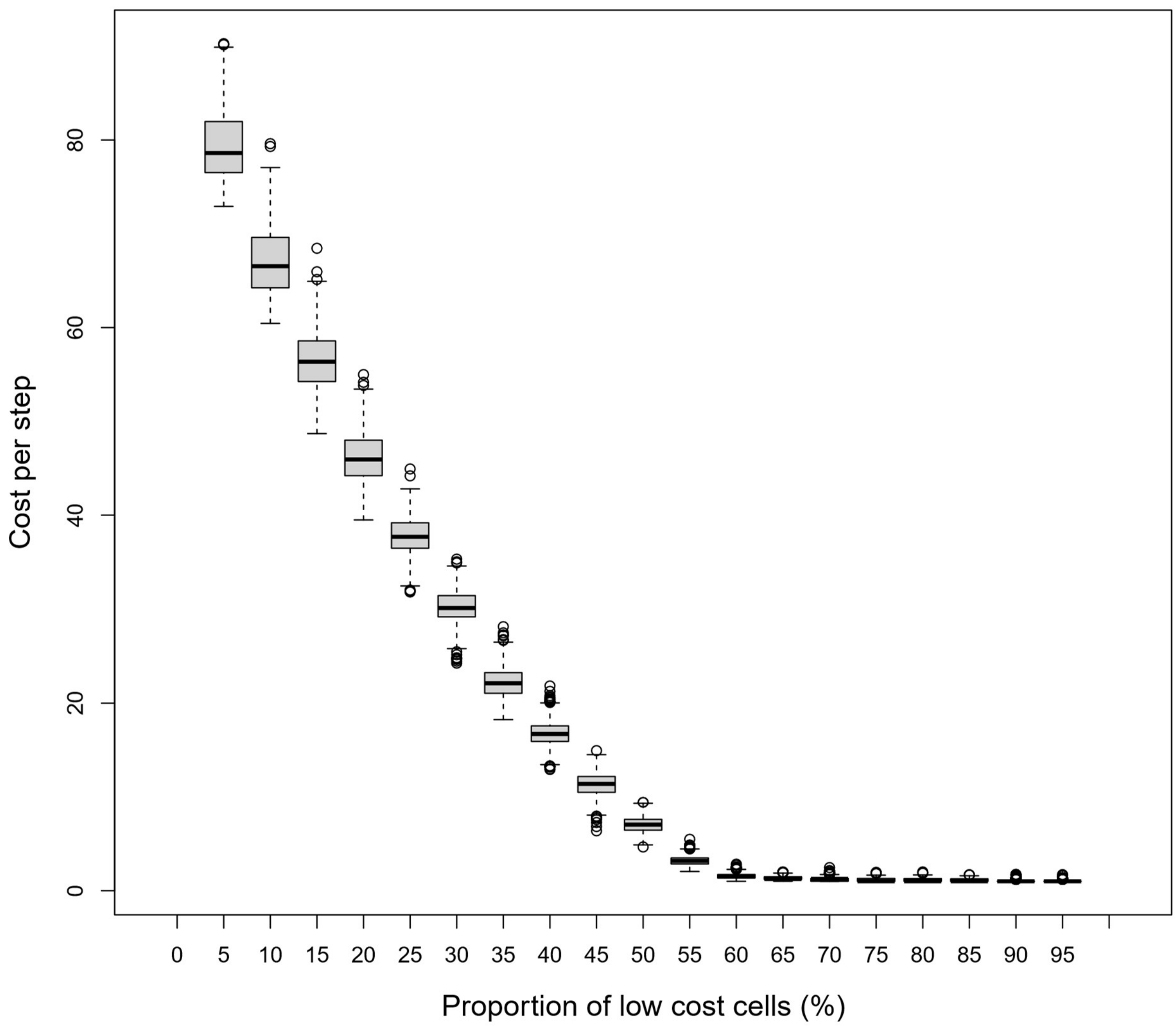


Figure 23. The cost per step versus proportion of low-cost cells (%).

The process-based metric Manhattan Distance (ManhattanDist) remained uniform in relation to proportion of low-cost cells with only minor fluctuations as shown in Figure 24.

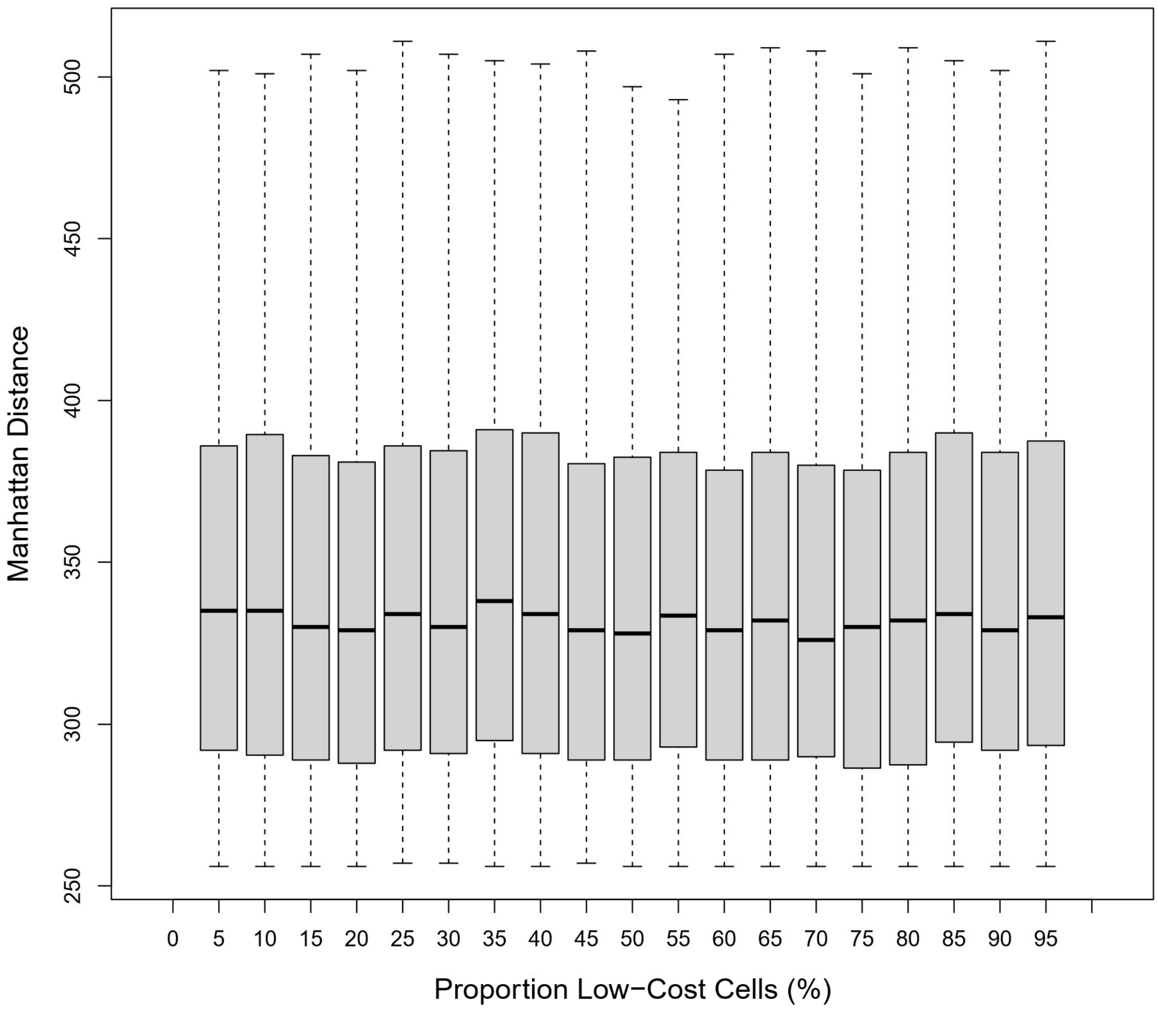


Figure 24. Manhattan distance versus the proportion low-cost cells (%).

Distance ratio is the ratio of the number of steps of the LCP of a traverse to the Manhattan Distance. It is similar to the total number of Steps, in that the graph peaks at around 59% proportion of low-cost cells and then drops sharply (Figure 25).

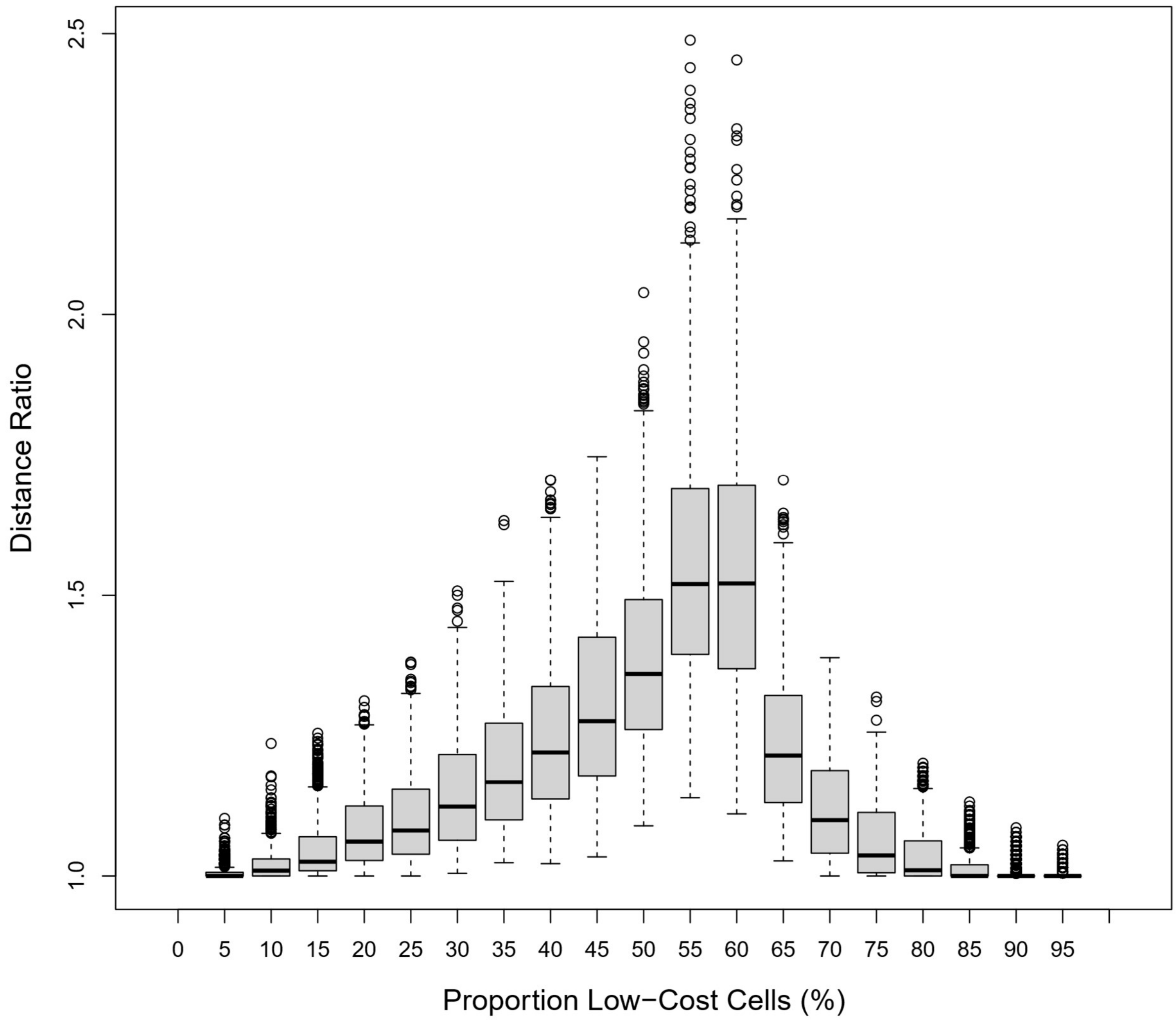


Figure 25. Distance ratio versus proportion of low-cost cells (%).

3.4 Sensitivity of pattern-based and process-based metrics to input parameters

For both the pattern-based and the process-based metrics, a Pearson product-moment correlation was computed to assess the relationship between a metric and the two input parameters of composition (proportion) and configuration (rho). The *a priori* level was set at $p \leq$

0.01. The pattern-based metrics had a negligible or extremely weak association with both proportion and rho (Table 9).

Table 9. Correlations between pattern-based metrics and input parameters. r values with p ≤ 0.01 are bolded.

Pattern metric	***r*: Proportion**	***r*: Rho**
area_cv	-0.034	-0.017
area_mn	0.014	-0.021
area_sd	0.022	-0.016
cai_cv	**-0.129**	**-0.132**
cai_mn	**0.104**	**0.249**
cai_sd	**0.142**	**0.244**
dcad	0.011	0.001
ed	-0.003	-0.027
lpi	0.011	-0.018
te	-0.003	-0.027
para_cv	**0.104**	**-0.157**
para_mn	-0.076	**-0.107**
para_sd	**0.111**	0.163
cohesion	-0.009	-0.015
division	0.016	0.021
enn_cv	**0.169**	**0.256**
enn_mn	0.098	**0.130**
enn_sd	**0.172**	**0.256**
mesh	-0.016	-0.021
np	-0.034	-0.020
pd	-0.034	-0.020
split	0.015	0.014

Although a few metrics displayed a significant result ($p < 0.01$) the relationships are extremely weak. Even the strongest correlation of $r = 0.256$ with rho only explains 6.5% of the variance. A linear regression was run between proportion and the following four pattern-based metrics: Coefficient of variation core area index (cai_cv), Standard deviation core area index (cai_sd), Coefficient of variation Euclidean nearest neighbour distance (enn_cv), and Standard deviation Euclidean nearest neighbour distance (enn_sd) with the linear regression line shown in red (Figure 26).

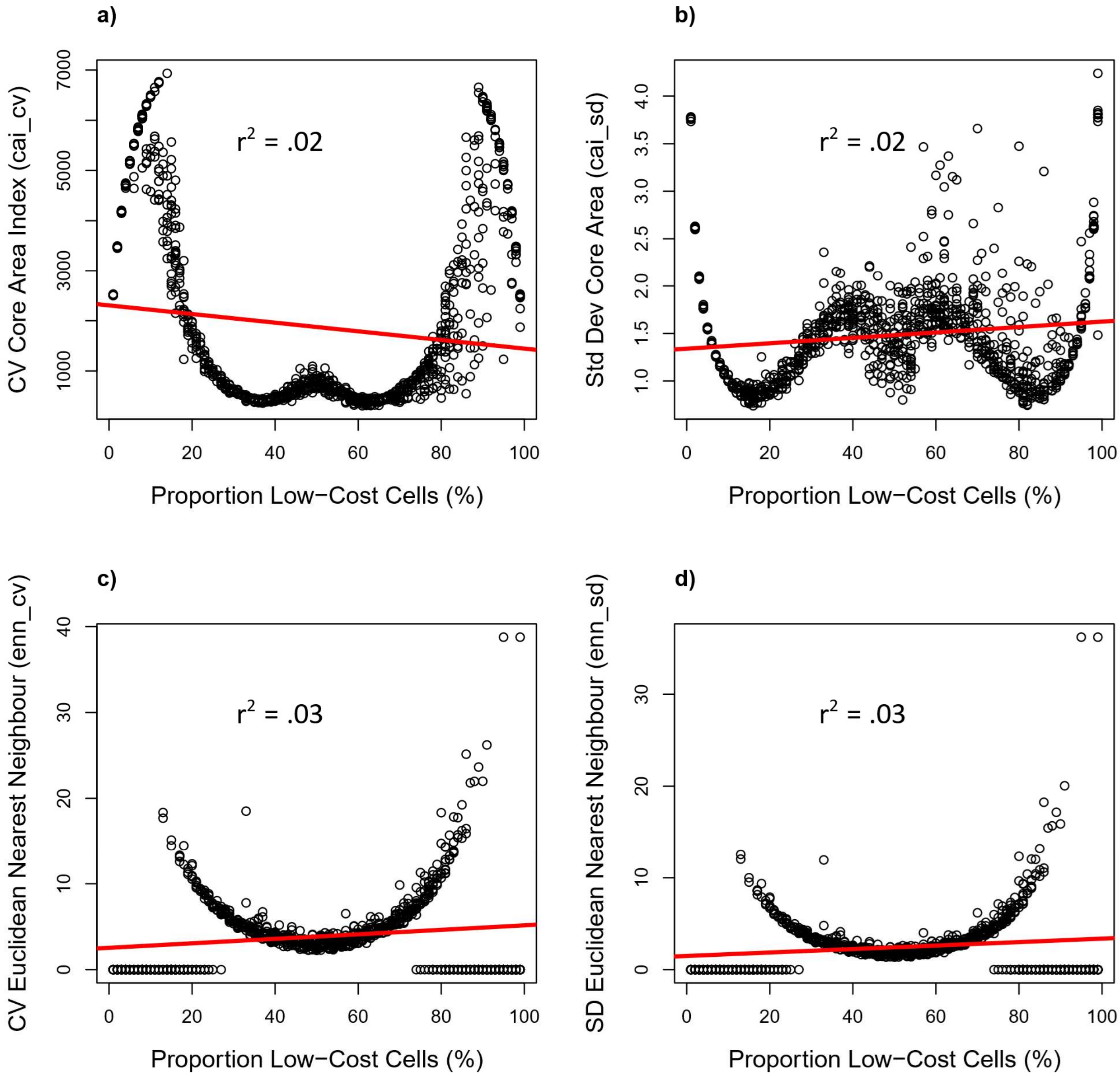


Figure 26. Extremely weak statistically significant correlations ($p < .01$) with Proportion: a) CV core area, b) Std dev core area, c) CV Euclidean nearest neighbour, and d) SD Euclidean nearest neighbour. Linear regression line is indicated in red.

A statistically significant ($p \leq .01$) but extremely weak positive relationship was found between rho and the following pattern-based metrics: Mean core area (cai_mn), Standard deviation core area (cai_sd), Coefficient of variation Euclidean nearest neighbour distance (enn_cv), and Standard deviation Euclidean nearest neighbour distance (enn_sd). A linear regression model was run for these four correlations and shown as a red line (Figure 27).

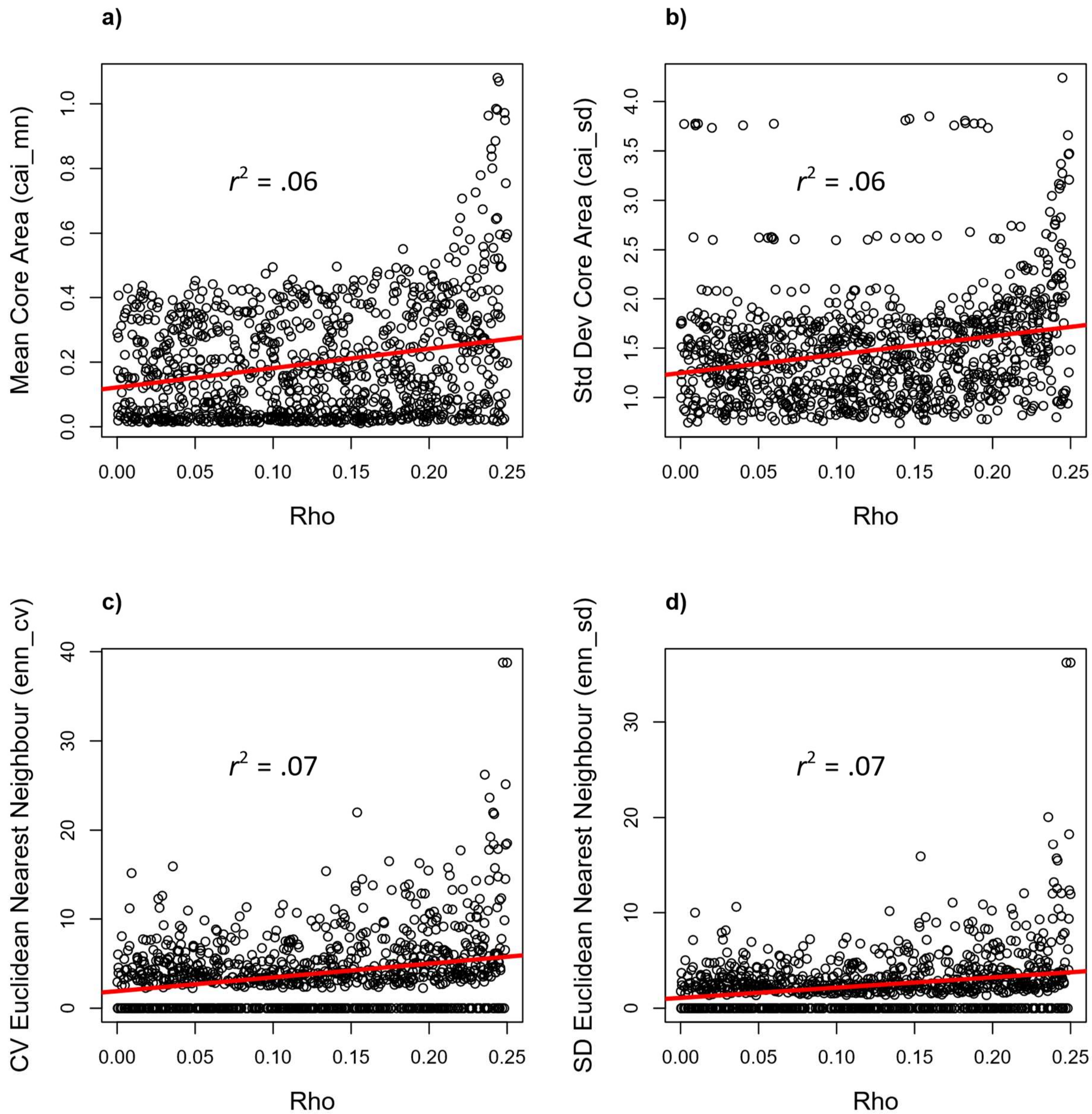


Figure 27. Statistically significant (p≤.01) but extremely weak positive relationship between rho and a) Mean core area, b) Std dev core area, c) CV Euclidean nearest neighbour, and d) Std Dev Euclidean nearest neighbour. Linear regression line is indicated in red.

The majority of the pattern-based metrics appeared to have no discernible relationship between the metric and rho. A sample of four pattern-based metrics: Mean patch area, Edge density, Cohesion, and Standard deviation shape index are shown (Figure 28).

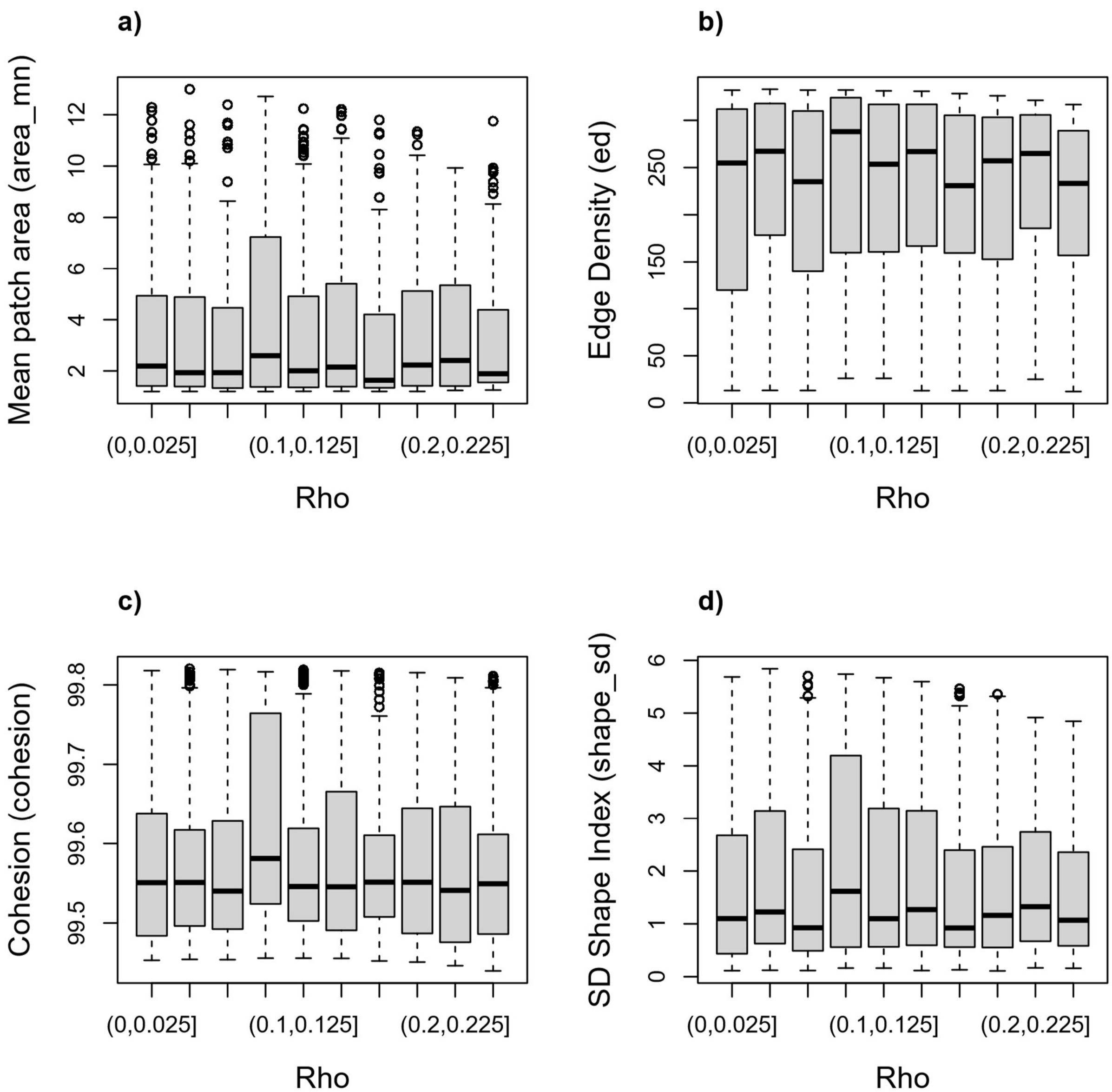


Figure 28. Selected metrics showing no discernible relationship between the pattern-based metric and rho: a) Mean patch area, b) Edge density, c) Cohesion, and d) Standard deviation shape index.

For the process-based metrics, the correlation results were mixed. Correlation tests found a strong negative relationship between two of the process-based metrics: total cost and cost per step with proportion, while the process-based metrics had no significant association with rho (Table 10).

Table 10. Correlations between the process-based metrics and the two input parameters.

Metric	***r*** **Proportion**	***r*** **Rho**
Steps	0.00	0.024
Total Cost	**-0.90**	-0.035
Cost per Step	**-0.88**	0.035
Manhattan Distance	-0.03	0.016
Distance Ratio	0.01	0.022

The number of steps to traverse the landscape (Steps), Manhattan Distance (ManhattanDist), and the Distance Ratio (DistanceRatio) did not appear to be associated with the proportion of low-cost cells. There was, however, a strong negative correlation between the cumulative cost (TotalCost) to traverse the landscape and the proportion of low-cost cells. There was also a strong negative correlation between the cost per Step (CostSteps) and the proportion of low-cost cells (Proportion).

A linear model of Total cost explains over 81% of the variance and has highly significant coefficients for the intercept and the independent variable as well as a highly significant overall model *p*-value. However, a plot of Proportion versus Total cost indicates that the plot has curvature that is not explained well by a linear model. A quadratic model, however, explains over 99% of the variance. The graph also suggests two functions: 1% - 59% and a second function for 59% - 99% proportion. A quadratic model describes proportion from 1% to 59% proportion and is plotted in red while a linear model describes proportion greater than 59% and is plotted in green (Figure 29).

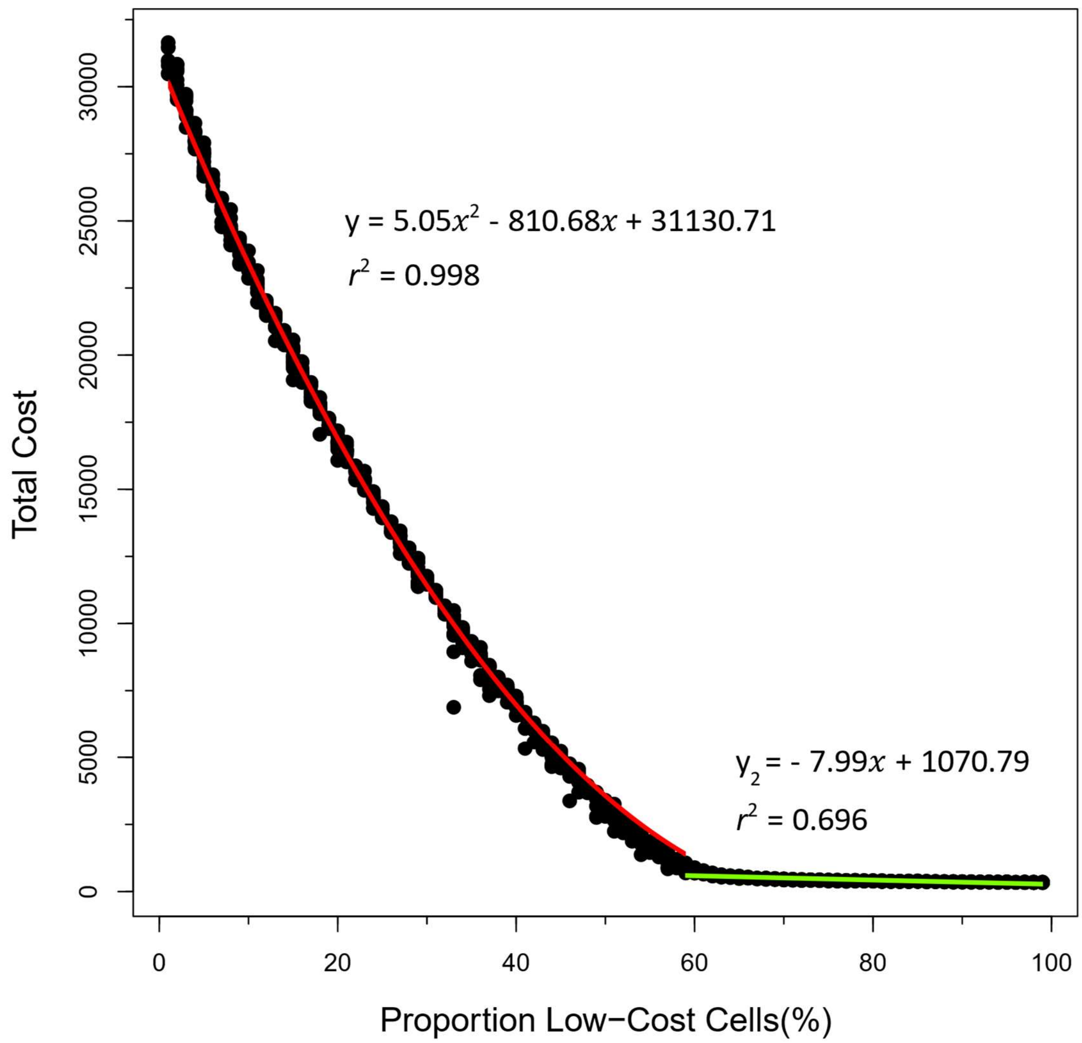


Figure 29. The significant relationship between total cost and proportion: a quadradic function in red between 1% to 59% and a linear function in green between 59% to 99% proportion.

A linear model of cost per step explains over 78% of the variance and has highly significant coefficients for the intercept and the independent variable as well as a highly significant overall model *p*-value. However, a plot of proportion versus cost per step indicates that the plot has curvature that is not explained well by a linear model. The graph also suggests two functions: 1% - 59% and a second function for 59% - 99% proportion. A quadratic model explains over 99% of the variance and is plotted in red, while a linear function is plotted in green (Figure 30).

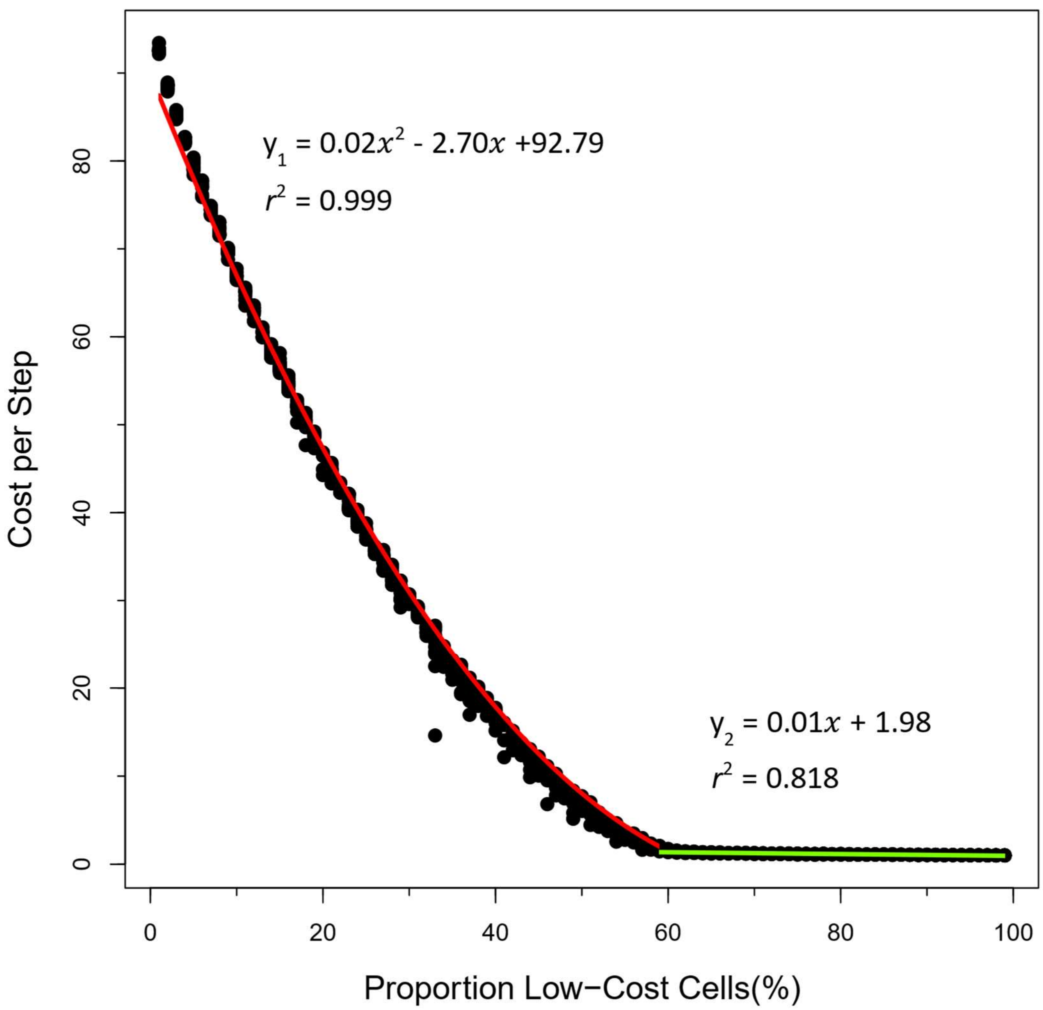


Figure 30. The significant relationship between cost per step and proportion: a quadradic function between 1% to 59% and a linear function between 59% to 99% proportion.

There were no significant correlations between rho and the five process-based metrics: Steps, Total cost, Cost per Step Manhattan Distance, and Distance Ratio (Figure 31).

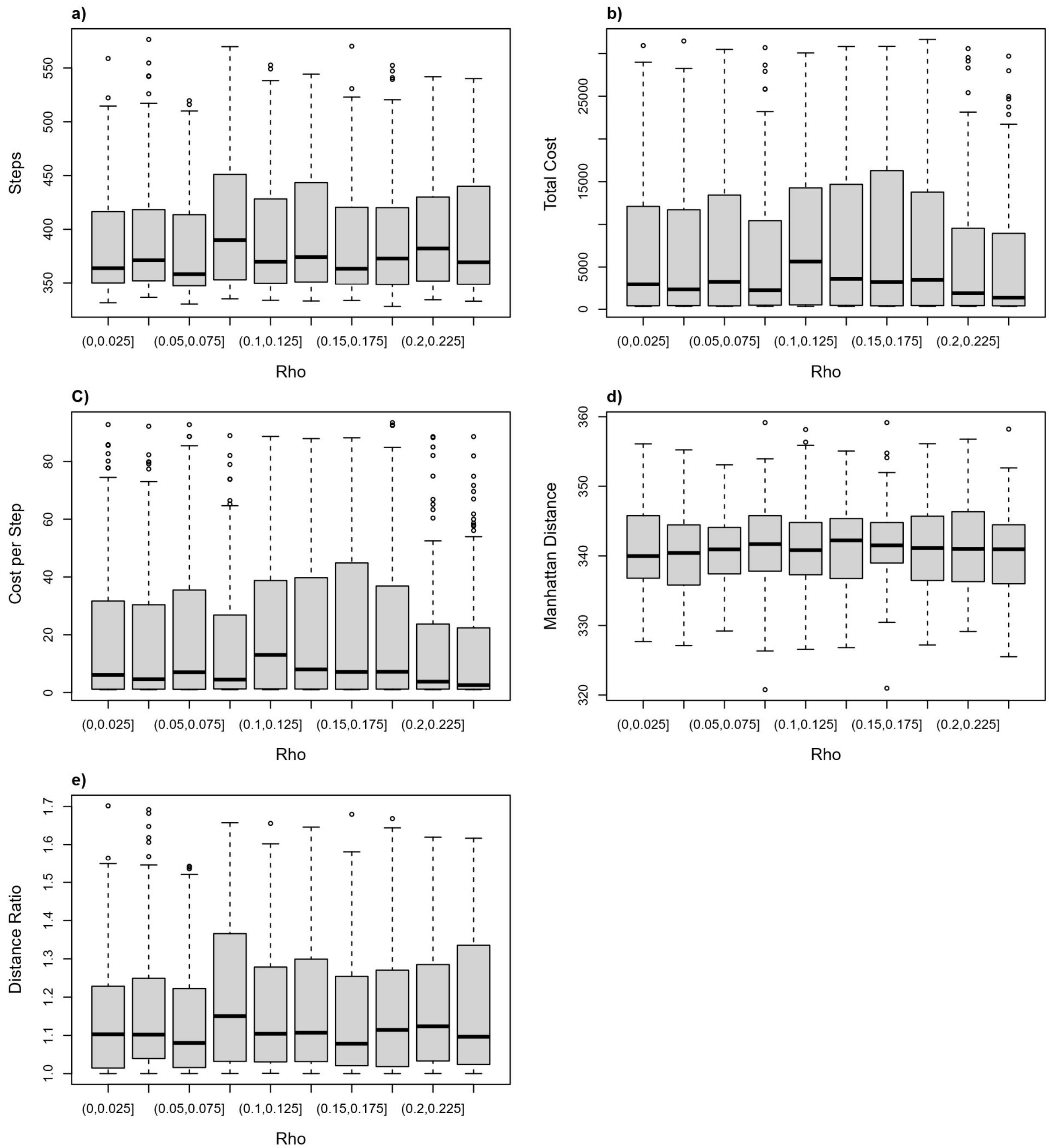


Figure 31. The five process-based variables display no discernible relationship with rho.

4. Discussion

Landscape fragmentation is an area of concern for ecologists because of the potential negative impact on ecological systems. Over the past 40 years, many landscape metrics based on landscape pattern have been developed to quantify fragmentation. However, issues with the use of these pattern-based metrics have been identified including, for example, conceptual flaws in landscape pattern analysis, inherent limitations of landscape metrics, improper use of metrics, and redundancy (Riitters et al. 1995; Li and Wu 2004). The purpose of my study was to investigate if a process-based quantification of landscape fragmentation was more sensitive to landscape fragmentation than a pattern-based quantification? How sensitive are the pattern- and process-based metrics to landscape simulation parameters? Is there information from process-based metrics that is not provided by pattern-based metrics?

The data suggests that two of the process-based metrics, cumulative cost (TotalCost) and cost per step, reliably specify a level of landscape fragmentation as a function of composition (proportion). This relationship is a one-to-one function thus conveying unambiguous information about the level of landscape fragmentation and indicates a significant association. Cumulative cost has been found to capture more information than the LCP length (i.e., Steps) alone and to be an appropriate measure of connectivity (Etherington and Holland 2013).

Conversely, the pattern-based method of computing metrics yielded confounding information, as there were identical metric values at more than one level of landscape composition. All the pattern-based fragmentation metrics plotted as symmetrical graphs centred around 50% composition (proportion). This makes it difficult, for example, to use them to examine changes in a landscape over time. Other research that was used to illustrate typical relationships between habitat amount and some measures of fragmentation, such as number of patches, mean patch size, mean nearest neighbour distance and size of largest patch (Fahrig 2003) did not result in symmetrical image graphs. For instance, mean patch size would be expected to increase linearly with proportion, while the size of the largest patch would be expected to be a S-curve (Fahrig 2003). The one-to-one values yielded by the process-based metrics of cumulative cost (TotalCost) and cost per step (CostSteps), are an improvement over the pattern-based metrics because they are straightforward in their application.

Neither the pattern-based, nor the process-based, metrics exhibited a significant relationship with the configuration (rho) input parameter. It was not surprising that neither the pattern-based nor the process-based metrics showed a significant association between a metric and configuration. Composition has been found to be a more significant factor in determining metric values (Riitters 2019). Nevertheless, configuration can be important for many ecological processes because it helps define structural connectivity (Mitchell et al. 2013) and configuration measures complement composition measures allowing for more sophisticated geographic analysis (Syrbe and Walz 2012). The lack of significant results does not negate the possible benefits of including configuration values in landscape analysis. Habitat in actual landscapes is usually highly aggregated (e.g. Fortin et al. 2003; Remmel & Csillag 2003). Narrowing the range of the input parameter of configuration to more aggregated results in the landscape simulations, might lead to different results.

The two process-based metrics, cumulative costs and cost per step, were significantly negatively associated with the proportion input parameter. The pattern-based metrics were not significantly associated with proportion. Statistical testing also showed that two of the process-based metrics, cumulative cost to cross the landscape (TotalCost) and the cost per step (CostSteps) were negatively associated with composition (Proportion). As the proportion of low-cost cells increases, the cost (i.e., the proxy for fragmentation) decreases. Only one of the pattern-based metrics, the mean of Euclidean nearest-neighbor distance (enn_mn), showed a very weak association between the mean of Euclidean nearest-neighbor distance (enn_mn) and composition (Proportion). However, based on other studies, it would be expected that this metric decreases, not increases, with the increase in habitat abundance (Fahrig 2003; Wang et al. 2014).

The sudden change in the relationship between the cumulative cost (TotalCost) and composition, and cost per step (CostSteps) and composition at 59% composition appears to be linked with percolation theory. An important conclusion of percolation theory relates to the probability of percolating clusters that stretch from one side of the grid to the other (O'Neill et al. 1988b). The percolation threshold value of p_c = 0.59 is restricted to an underlying random spatial distribution, a square grid lattice and a movement rule according to the rook's case (With and King 1997), as is the case with the 1000 simulated landscapes. The probability of a percolating cluster changes over a narrow range as shown in the cumulative cost metric (Figure 21) and the cost per step metric (Figure 23). The transition between a percolating state and a non-percolating state is a phase transition (Riitters et al. 2009). The abruptness of this change is another reason for having robust fragmentation measures for monitoring change. In addition to providing a robust measure of fragmentation, the process-based metrics provided other information not supplied by pattern-based metrics. The number of steps needed to traverse the landscape (Steps) indicated that the steps required are lowest when the landscapes are increasingly uniform. The ratio of number of steps to the Manhattan distance (DistanceRatio) indicated that distances are shortest when landscapes are increasingly uniform.

5. Conclusions

I tested the relative improvements of a process-based method for quantifying landscape fragmentation. I measured the sensitivity of this process-based approach for capturing subtle fragmentation effects and then compared it against existing pattern-based approaches of characterizing fragmentation. The goal was to test for potential benefits of a quantification metric that is based on a simulated stochastic process acting on the landscape to arrive at a quantification, rather than a static metric based purely on composition and configuration. One thousand simulated landscapes, varying in composition (proportion) and configuration (rho), provided the study site. Multiple LCPs with random start and end points along opposing landscape margins were determined for each of the 1000 simulated landscapes. The cost to traverse a landscape was a proxy for a fragmentation measure.

This new approach of developing a process-based fragmentation quantification method yielded a measure that was more sensitive to landscape fragmentation than a pattern-based quantification. Specifically, two of the variables, cumulative cost (TotalCost) and the derived value cost per step (CostSteps), are strongly related to landscape composition with a one-to-one relationship. The pattern-based quantification metrics did not result in one-to-one values between the metric and proportion.

Neither the pattern-based nor the process-based metrics were sensitive to the input parameter of configuration. The process-based quantification method yielded metrics that were strongly negatively correlated with the input parameter of composition between 1% and 59% proportion of the class of interest. Beyond 59% proportion, the cost to traverse the landscape was negligible. Where the landscape was highly fragmented, the cost to traverse the landscape was high.

This process-based method also overcame the significant issue of scale by holding the extent and grain of the landscape constant over 1000 simulated landscapes. It can easily be implemented and modified through readily available free open-source software. My study provides a methodological foundation for further studies as this process-based approach is not associated with a specific species or ecological process, and thus can be easily adapted to numerous settings.

6. References

Adriaensen F, Chardon JP, De Blust G, et al (2003) The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64:233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Alexander JL, Olimb SK, Bly KLS, Restani M (2016) Use of least-cost path analysis to identify potential movement corridors of swift foxes in Montana. JMAMMAL 97:891–898. https://doi.org/10.1093/jmammal/gyw032

Allen CH, Parrott L, Kyle C (2016) An individual-based modelling approach to estimate landscape connectivity for bighorn sheep (Ovis canadensis). PeerJ 4:e2001. https://doi.org/10.7717/peerj.2001

Antongiovanni M, Venticinque EM, Fonseca CR (2018) Fragmentation patterns of the Caatinga drylands. Landscape Ecology 33:1353–1367. https://doi.org/10.1007/s10980-018-0672-6

Antrop M (2021) Landscape mosaics and the patch-corridor-matrix model. In: The Routledge Handbook of Landscape Ecology, 1st edn. Routledge, London, pp 25–48

Baker W, Cai Y (1992) The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. Landscape Ecology 7:291–302. https://doi.org/10.1007/BF00131258

Balbi M, Croci S, Petit EJ, et al (2021) Least-cost path analysis for urban greenways planning: A test with moths and birds across two habitats and two cities. J Appl Ecol 58:632–643. https://doi.org/10.1111/1365-2664.13800

Baldwin D, Weaver K, Schnekenburger F, H. Perera A (2004) Sensitivity of landscape pattern indices to input data characteristics on real landscapes: implications for their use in natural disturbance emulation. Landscape Ecology 19:255–271. https://doi.org/10.1023/B:LAND.0000030442.96122.ef

Baskent E, Jordon G (1995) Characterizing spatial structure of forest landscapes. Canadian Journal of Forest Research 25:1830–1849

Bélisle M, Desrochers A, Fortin M-J (2001) INFLUENCE OF FOREST COVER ON THE MOVEMENTS OF FOREST BIRDS: A HOMING EXPERIMENT. Ecology 82:1893–1904. https://doi.org/10.1890/0012-9658(2001)082[1893: IOFCOT]2.0.CO;2

Benson BJ, MacKenzie MD (1995) Effects of sensor spatial resolution on landscape structure parameters. Landscape Ecol 10:113–120. https://doi.org/10.1007/BF00153828

Bogaert J (2003) Lack of Agreement on Fragmentation Metrics Blurs Correspondence between Fragmentation Experiments and Predicted Effects. Conservation Ecology 7:. https://doi.org/10.5751/ES-00495-0701r06

Bogaert J, Van Hecke P, Eysenrode DS-V, Impens I (2000) Landscape Fragmentation Assessment Using a Single Measure. Wildlife Society Bulletin (1973-2006) 28:875–881

Bone C, Johnson B, Nielsen-Pincus M, et al (2014) A Temporal Variant-Invariant Validation Approach for Agent-based Models of Landscape Dynamics: Agent-based Models of Landscape Dynamics. Transactions in GIS 18:161–182. https://doi.org/10.1111/tgis.12016

Boots B, Csillag F (2006) Categorical maps, comparisons, and confidence. J Geograph Syst 8:109–118. https://doi.org/10.1007/s10109-006-0018-9

Carlier J, Davis E, Ruas S, et al (2020) Using open-source software and digital imagery to efficiently and objectively quantify cover density of an invasive alien plant species. Journal of Environmental Management 266:110519. https://doi.org/10.1016/j.jenvman.2020.110519

Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in biodiversity conservation: A review of recent studies and applications. Progress in Physical Geography: Earth and Environment 40:7–37. https://doi.org/10.1177/0309133315598713

Costanza JK, Riitters K, Vogt P, Wickham J (2019) Describing and analyzing landscape patterns: where are we now, and where are we going? Landscape Ecol 34:2049–2055. https://doi.org/10.1007/s10980-019-00889-6

Costanza R, d'Arge R, de Groot R, et al (1997) The value of the world's ecosystem services and natural capital. Nature 253–260

Crooks K, Sanjayan M (2006) Connectivity conservatio. Cambridge university Press, Cambridge, UK

Cushman SA, McGarigal K (2008) Landscape Metrics, Scales of Resolution. In: von Gadow K, Pukkala T (eds) Designing Green Landscapes. Springer Netherlands, Dordrecht, pp 33–51

Cushman SA, McGarigal K, Neel MC (2008) Parsimony in landscape metrics: Strength, universality, and consistency. Ecological Indicators 8:691–703. https://doi.org/10.1016/j.ecolind.2007.12.002

Damschen EI, Baker DV, Bohrer G, et al (2014) How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. Proc Natl Acad Sci USA 111:3484–3489. https://doi.org/10.1073/pnas.1308968111

Davidson C (1998) Issues in measuring landscape fragmentation. Wildlife Society Bulletin 26:32–37

De Montis A, Serra V, Ganciu A, Ledda A (2020) Assessing Landscape Fragmentation: A Composite Indicator. Sustainability 12:9632. https://doi.org/10.3390/su12229632

DeAngelis DL, Diaz SG (2019) Decision-Making in Agent-Based Modeling: A Current Review and Future Prospectus. Front Ecol Evol 6:237. https://doi.org/10.3389/fevo.2018.00237

Diniz MF, Cushman SA, Machado RB, De Marco Júnior P (2020) Landscape connectivity modeling from the perspective of animal dispersal. Landscape Ecol 35:41–58. https://doi.org/10.1007/s10980-019-00935-3

Driscoll DA, Armenteras D, Bennett AF, et al (2021) How fire interacts with habitat loss and fragmentation. Biological Reviews 96:976–998. https://doi.org/10.1111/brv.12687

Dutta T, Sharma S, Meyer NFV, et al (2022) An overview of computational tools for preparing, constructing and using resistance surfaces in connectivity research. Landsc Ecol 37:2195–2224. https://doi.org/10.1007/s10980-022-01469-x

Edelsparre AH, Shahid A, Fitzpatrick MJ (2018) Habitat connectivity is determined by the scale of habitat loss and dispersal strategy. Ecol Evol 8:5508–5514. https://doi.org/10.1002/ece3.4072

Ene E, McGarigal K (2023) Fragstats Documentation. In: Fragstats. https://www.fragstats.org/index.php/documentation. Accessed 12 Oct 2023

Etherington TR (2016) Least-Cost Modelling and Landscape Ecology: Concepts, Applications, and Opportunities. Curr Landscape Ecol Rep 1:40–53. https://doi.org/10.1007/s40823-016-0006-9

Etherington TR, Holland EP (2013) Least-cost path length versus accumulated-cost as connectivity measures. Landscape Ecol 28:1223–1229. https://doi.org/10.1007/s10980-013-9880-2

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Evol Syst 34:487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig L (2019) Habitat fragmentation: A long and tangled tale: XXXX. Global Ecol Biogeogr 28:33–41. https://doi.org/10.1111/geb.12839

Fahrig L (2017) Ecological Responses to Habitat Fragmentation Per Se. Annual Review of Ecology, Evolution, and Systematics 48:1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig L (2020) Why do several small patches hold more species than few large patches? Global Ecol Biogeogr 29:615–628. https://doi.org/10.1111/geb.13059

Fahrig L, Watling JI, Arnillas CA, et al (2022) Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. Biological Reviews 97:99–114. https://doi.org/10.1111/brv.12792

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecol Biogeography 16:265–280. https://doi.org/10.1111/j.1466-8238.2007.00287.x

Fletcher RJ, Didham RK, Banks-Leite C, et al (2018) Is habitat fragmentation good for biodiversity? Biological Conservation 226:9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Fonseca CR, Joner F (2007) Two-Sided Edge Effect Studies and the Restoration of Endangered Ecosystems. Restoration Ecology 15:613–619. https://doi.org/10.1111/j.1526-100X.2007.00273.x

Forman RTT (1995a) Some general principles of landscape and regional ecology. Landscape Ecol 10:133–142. https://doi.org/10.1007/BF00133027

Forman RTT (1995b) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge

Forman RTT, Godron M (1981) Patches and Structural Components for a Landscape Ecology. BioScience 31:733–740. https://doi.org/10.2307/1308780

Forman RTT, Godron M (1986) Landscape ecology. Wiley, New York

Frazier AE, Kedron P (2017) Landscape Metrics: Past Progress and Future Directions. Curr Landscape Ecol Rep 2:63–72. https://doi.org/10.1007/s40823-017-0026-0

Fu G, Wang W, Li J, et al (2021) Prediction and Selection of Appropriate Landscape Metrics and Optimal Scale Ranges Based on Multi-Scale Interaction Analysis. Land 10:1192. https://doi.org/10.3390/land10111192

Gardner RH, Milne BT, Turner MG, O'Neill RV (1987) Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecol 1:19–28. https://doi.org/10.1007/BF02275262

Gardner RH, Urban DL (2007) Neutral models for testing landscape hypotheses. Landscape Ecology 22:15–29. https://doi.org/10.1007/s10980-006-9011-4

Geary WL, Nimmo DG, Doherty TS, et al (2019) Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. J Appl Ecol 1365-2664.13427. https://doi.org/10.1111/1365-2664.13427

Gomez B, Jones JP III, Jones JP (2010) Research Methods in Geography: A Critical Introduction. John Wiley & Sons, Incorporated, Chicester, UNITED KINGDOM

Gustafson EJ (1998) Quantifying Landscape Spatial Pattern: What Is the State of the Art? Ecosystems 1:143–156. https://doi.org/10.1007/s100219900011

Gustafson EJ (2019) How has the state-of-the-art for quantification of landscape pattern advanced in the twenty-first century? Landscape Ecology 34:2065–2072. https://doi.org/10.1007/s10980-018-0709-x

Gustafson EJ, Gardner RH (1996) The Effect of Landscape Heterogeneity on the Probability of Patch Colonization. Ecology 77:94–107. https://doi.org/10.2307/2265659

Haddad NM, Brudvig LA, Clobert J, et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:. https://doi.org/10.1126/sciadv.1500052

Hadley AS, Betts MG (2016) Refocusing Habitat Fragmentation Research Using Lessons from the Last Decade. Curr Landscape Ecol Rep 1:55–66. https://doi.org/10.1007/s40823-016-0007-8

Haines-Young R, Chopping M (1996) Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. Progress in physical geography 20:418–445

Harper KA, Macdonald SE, Burton PJ, et al (2005) Edge Influence on Forest Structure and Composition in Fragmented Landscapes. Conservation Biology 19:768–782. https://doi.org/10.1111/j.1523-1739.2005.00045.x

Helfenstein J, Bauer L, Clalüna A, et al (2014) Landscape ecology meets landscape science. Landscape Ecol 29:1109–1113. https://doi.org/10.1007/s10980-014-0055-6

Herrera LP, Sabatino MC, Jaimes FR, Saura S (2017) Landscape connectivity and the role of small habitat patches as stepping stones: an assessment of the grassland biome in South America. Biodivers Conserv 26:3465–3479. https://doi.org/10.1007/s10531-017-1416-7

Hesselbarth MHK, Sciaini M, With KA, et al (2019) landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42:1648–1657. https://doi.org/10.1111/ecog.04617

Hilty JA (2019) Corridor ecology: linking landscapes for biodiversity conservation and climate adaptation, 2nd edn. Island Press, Washington, DC

Hoban S, Bruford M, D'Urban Jackson J, et al (2020) Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. Biological Conservation 248:108654. https://doi.org/10.1016/j.biocon.2020.108654

Hobbs RJ (1993) Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt. Biological Conservation 64:193–201. https://doi.org/10.1016/0006-3207(93)90321-Q

Høye TT, Skov F, Topping CJ (2012) Interpreting outputs of agent-based models using abundance–occupancy relationships. Ecological Indicators 20:221–227. https://doi.org/10.1016/j.ecolind.2012.01.017

Huck M, Jędrzejewski W, Borowik T, et al (2010) Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. Acta Theriol 55:177–192. https://doi.org/10.4098/j.at.0001-7051.114.2009

Huston M, DeAngelis D, Post W (1988) New Computer Models Unify Ecological Theory. BioScience 38:682–691. https://doi.org/10.2307/1310870

Jaeger JAG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecology 15:115–130. https://doi.org/10.1023/A:1008129329289

Jaeger JAG, Schwarz-von Raumer H-G, Esswein H, et al (2007) Time Series of Landscape Fragmentation Caused by Transportation Infrastructure and Urban Development: a Case Study from Baden-Wurttemberg, Germany. E&S 12: art22. https://doi.org/10.5751/ES-01983-120122

Kanagaraj R, Wiegand T, Kramer-Schadt S, Goyal SP (2013) Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. Biological Conservation 167:298–309. https://doi.org/10.1016/j.biocon.2013.08.030

Kindlmann P, Burel F (2008) Connectivity measures: a review. Landscape Ecol s10980-008-9245–4. https://doi.org/10.1007/s10980-008-9245-4

Knaapen JP, Scheffer M, Harms B (1992) Estimating habitat isolation in landscape planning. Landscape and Urban Planning 23:1–16. https://doi.org/10.1016/0169-2046(92)90060-D

Krummel JR, Gardner RH, Sugihara G, et al (1987) Landscape Patterns in a Disturbed Environment. Oikos 48:321–324. https://doi.org/10.2307/3565520

Kupfer JA (2012) Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. Progress in Physical Geography 36:400–420. https://doi.org/10.1177/0309133312439594

Kupfer JA, Franklin SB (2009) Linking Spatial Pattern and Ecological Responses in Human-Modified Landscapes: The Effects of Deforestation and Forest Fragmentation on Biodiversity. Geography Compass 3:1331–1355. https://doi.org/10.1111/j.1749-8198.2009.00245.x

Laurance WF (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biological Conservation 141:1731–1744. https://doi.org/10.1016/j.biocon.2008.05.011

Laurance WF (2002) Hyperdynamism in fragmented habitats. Journal of Vegetation Science 13:595–602. https://doi.org/10.1111/j.1654-1103.2002.tb02086.x

Laurance WF, Nascimento HEM, Laurance SG, et al (2007) Habitat Fragmentation, Variable Edge Effects, and the Landscape-Divergence Hypothesis. PLoS ONE 2:e1017. https://doi.org/10.1371/journal.pone.0001017

Lausch A, Blaschke T, Haase D, et al (2015) Understanding and quantifying landscape structure – A review on relevant process characteristics, data models and landscape metrics. Ecological Modelling 295:31–41. https://doi.org/10.1016/j.ecolmodel.2014.08.018

Li HB, Wu JG (2004) Use and misuse of landscape indices. Landscape Ecology 19:389–399

Lindenmayer D (2019) Small patches make critical contributions to biodiversity conservation. Proc Natl Acad Sci USA 116:717–719. https://doi.org/10.1073/pnas.1820169116

Liu J, Wilson M, Hu G, et al (2018) How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship? Landscape Ecol 33:341–352. https://doi.org/10.1007/s10980-018-0620-5

Llausàs A, Nogué J (2012) Indicators of landscape fragmentation: The case for combining ecological indices and the perceptive approach. Ecological Indicators 15:85–91. https://doi.org/10.1016/j.ecolind.2011.08.016

Luo Q, Griffith DA, Wu H (2018) On the Statistical Distribution of the Nonzero Spatial Autocorrelation Parameter in a Simultaneous Autoregressive Model. IJGI 7:476. https://doi.org/10.3390/ijgi7120476

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, New Jersey

Mas J-F, Gao Y, Pacheco JAN (2010) Sensitivity of landscape pattern metrics to classification approaches. Forest Ecology and Management 259:1215–1224. https://doi.org/10.1016/j.foreco.2009.12.016

McGarigal K, Cushman S, Regan C (2005) Quantifying terrestrial habitat loss and fragmentation: A protocol. Department of natural resources conservation, University of Massachusetts, MA

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen Tech Rep PNW-GTR-351 Portland, OR: US Department of

Agriculture, Forest Service, Pacific Northwest Research Station 122 p 351:. https://doi.org/10.2737/PNW-GTR-351

McLane AJ, Semeniuk C, McDermid GJ, Marceau DJ (2011) The role of agent-based models in wildlife ecology and management. Ecological Modelling 222:1544–1556. https://doi.org/10.1016/j.ecolmodel.2011.01.020

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) USING CIRCUIT THEORY TO MODEL CONNECTIVITY IN ECOLOGY, EVOLUTION, AND CONSERVATION. Ecology 89:2712–2724. https://doi.org/10.1890/07-1861.1

Mitchell MGE, Bennett EM, Gonzalez A (2014) Forest fragments modulate the provision of multiple ecosystem services. J Appl Ecol 51:909–918. https://doi.org/10.1111/1365-2664.12241

Mitchell MGE, Bennett EM, Gonzalez A (2013) Linking Landscape Connectivity and Ecosystem Service Provision: Current Knowledge and Research Gaps. Ecosystems 16:894–908. https://doi.org/10.1007/s10021-013-9647-2

Modica G, Praticò S, Laudari L, et al (2021) Implementation of multispecies ecological networks at the regional scale: analysis and multi-temporal assessment. Journal of Environmental Management 289:112494. https://doi.org/10.1016/j.jenvman.2021.112494

Mõisja K, Uuemaa E, Oja T (2016) Integrating small-scale landscape elements into land use/cover: The impact on landscape metrics' values. Ecological Indicators 67:714–722. https://doi.org/10.1016/j.ecolind.2016.03.033

Naeem S, Li S (1997) Biodiversity enhances ecosystem reliability. Nature 390:507–509. https://doi.org/10.1038/37348

Neel MC, McGarigal K, Cushman SA (2004) Behavior of class-level landscape metrics across gradients of class aggregation and area. Landscape Ecology 19:435–455. https://doi.org/10.1023/B:LAND.0000030521.19856.cb

O'Neill R, Krummel J, Gardner R, et al (1988a) Indices of landscape pattern. Landscape Ecology 1:153–162. https://doi.org/10.1007/BF00162741

O'Neill RV, Hunsaker CT, Timmins SP, et al (1996) Scale problems in reporting landscape pattern at the regional scale. Landscape Ecol 11:169–180. https://doi.org/10.1007/BF02447515

O'Neill RV, Milne BT, Turner MG, Gardner RH (1988b) Resource utilization scales and landscape pattern. Landscape Ecol 2:63–69. https://doi.org/10.1007/BF00138908

Ossola A, Locke D, Lin B, Minor E (2019) Yards increase forest connectivity in urban landscapes. Landscape Ecol 34:2935–2948. https://doi.org/10.1007/s10980-019-00923-7

Ostapowicz K, Vogt P, Riitters KH, et al (2008) Impact of scale on morphological spatial pattern of forest. Landscape Ecol 23:1107–1117. https://doi.org/10.1007/s10980-008-9271-2

Pfeifer M, Lefebvre V, Peres CA, et al (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551:187–191. https://doi.org/10.1038/nature24457

Qi Y, Wu J (1996) Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. Landscape Ecol 11:39–49. https://doi.org/10.1007/BF02087112

R Core Team (2021) R: A language and environment for statistical computing

Rayfield B, Fortin M-J, Fall A (2010) The sensitivity of least-cost habitat graphs to relative cost surface values. Landscape Ecol 25:519–532. https://doi.org/10.1007/s10980-009-9436-7

Rego FC, Bunting SC, Strand, Eva K. (2018) Applied landscape ecology. Wiley, Hoboken, NJ

Remmel TK, Csillag F (2003) When are two landscape pattern indices significantly different? Journal of Geographical Systems 5:331–351

Remmel TK, Fortin M-J (2013) Categorical, class-focused map patterns: characterization and comparison. Landscape Ecol 28:1587–1599. https://doi.org/10.1007/s10980-013-9905-x

Remmel TK, Mitchell SW (2022) Landscape pattern analysis. In: Francis RA, Millington JDA, Perry GLW, Minor ES (eds) The Routledge handbook of landscape ecology. Routledge, London, p 472

Ribeiro JW, Silveira dos Santos J, Dodonov P, et al (2017) LandScape Corridors (lscorridors): a new software package for modelling ecological corridors based on landscape patterns and species requirements. Methods in Ecology and Evolution 8:1425–1432. https://doi.org/10.1111/2041-210X.12750

Riitters K (2019) Pattern metrics for a transdisciplinary landscape ecology. Landscape Ecol 34:2057–2063. https://doi.org/10.1007/s10980-018-0755-4

Riitters K, Vogt P, Soille P, Estreguil C (2009) Landscape patterns from mathematical morphology on maps with contagion. Landscape Ecol 24:699–709. https://doi.org/10.1007/s10980-009-9344-x

Riitters K, Wickham JD, O'Neill R, et al (2000) Global-Scale Patterns of Forest Fragmentation. CE 4:art3. https://doi.org/10.5751/ES-00209-040203

Riitters KH, O'Neill RV, Hunsaker CT, et al (1995) A factor analysis of landscape pattern and structure metrics. Landscape Ecology 10:23–39

Riitters KH, Vogt P, Soille P, et al (2007) Neutral model analysis of landscape patterns from mathematical morphology. Landscape Ecol 22:1033–1043. https://doi.org/10.1007/s10980-007-9089-3

Riva F, Fahrig L (2022) The disproportionately high value of small patches for biodiversity conservation. Conservation Letters n/a:e12881. https://doi.org/10.1111/conl.12881

Riva F, Fahrig L (2023) Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay. Ecology Letters 26:268–277. https://doi.org/10.1111/ele.14145

Rösch V, Tscharntke T, Scherber C, Batáry P (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. Oecologia 179:209–222. https://doi.org/10.1007/s00442-015-3315-5

Rutledge D (2003) Landscape indices as measures of the effects of fragmentation: can pattern reflect process? Dept of Conservation, Wellington, New Zealand

Saura S (2004) Effects of remote sensor spatial resolution and data aggregation on selected fragmentation indices. Landscape Ecology 19:197–209. https://doi.org/10.1023/B:LAND.0000021724.60785.65

Saura S, Bodin Ö, Fortin M-J (2014) EDITOR'S CHOICE: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. J Appl Ecol 51:171–182. https://doi.org/10.1111/1365-2664.12179

Saura S, Martinez-Mlian J (2001) Sensitivity of Landscape Pattern Metrics to Map Spatial Extent. PHOTOGRAMMETRIC ENGINEERING 10

Savary P, Foltête JC, Garnier S (2022) Cost distances and least cost paths respond differently to cost scenario variations: a sensitivity analysis of ecological connectivity modeling. International Journal of Geographical Information Science 36:1652–1676. https://doi.org/10.1080/13658816.2021.2014852

Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes?: Least-cost modelling for habitat linkage design. Journal of Applied Ecology 48:668–678. https://doi.org/10.1111/j.1365-2664.2011.01970.x

Schmidt M, Jochheim H, Kersebaum K-C, et al (2017) Gradients of microclimate, carbon and nitrogen in transition zones of fragmented landscapes – a review. Agricultural and Forest Meteorology 232:659–671. https://doi.org/10.1016/j.agrformet.2016.10.022

Schumaker NH (1996) Using Landscape Indices to Predict Habitat Connectivity. Ecology 77:1210–1225. https://doi.org/10.2307/2265590

Šímová P, Gdulová K (2012) Landscape indices behavior: A review of scale effects. Applied Geography 34:385–394. https://doi.org/10.1016/j.apgeog.2012.01.003

Soille P, Pesaresi M (2002) Advances in mathematical morphology applied to geoscience and remote sensing. IEEE Trans Geosci Remote Sensing 40:2042–2055. https://doi.org/10.1109/TGRS.2002.804618

Soille P, Vogt P (2022) MORPHOLOGICAL SPATIAL PATTERN ANALYSIS: OPEN SOURCE RELEASE. Int Arch Photogramm Remote Sens Spatial Inf Sci XLVIII-4/W1-2022:427–433. https://doi.org/10.5194/isprs-archives-XLVIII-4-W1-2022-427-2022

Spear SF, Balkenhol N, Fortin M, et al (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19:3576–3591. https://doi.org/10.1111/j.1365-294X.2010.04657.x

Syrbe R-U, Walz U (2012) Spatial indicators for the assessment of ecosystem services: Providing, benefiting and connecting areas and landscape metrics. Ecological Indicators 21:80–88. https://doi.org/10.1016/j.ecolind.2012.02.013

Tischendorf L (2001) Can landscape indices predict ecological processes consistently? Landscape Ecology 16:235–254

Tischendorf L, Fahrig L (2000) How should we measure landscape connectivity? Landscape Ecology 15:633–641. https://doi.org/10.1023/A:1008177324187

Tjørve E (2010) How to resolve the SLOSS debate: Lessons from species-diversity models. Journal of Theoretical Biology 264:604–612. https://doi.org/10.1016/j.jtbi.2010.02.009

Tscharntke T, Klein AM, Kruess A, et al (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8:857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Turner M (1989) LANDSCAPE ECOLOGY: The Effect of Pattern on Process. Annual Review of Ecology and Systematics 20:27

Turner M, Gardner RH (eds) (2015) Landscape Ecology in Theory and Practice. Springer New York, New York, NY

Turner M, O'Neill R, Gardner R, Milne B (1989) Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecology 3:153–162. https://doi.org/10.1007/BF00131534

Turner MG (2005) Landscape Ecology: What Is the State of the Science? Annu Rev Ecol Evol Syst 36:319–344. https://doi.org/10.1146/annurev.ecolsys.36.102003.152614

Uuemaa E, Antrop M, Roosaare J, et al (2009) Landscape metrics and indices: an overview of their use in landscape research. Living reviews in landscape research 3:1–28

van Etten J (2017) *R* Package **gdistance** : Distances and Routes on Geographical Grids. J Stat Soft 76:. https://doi.org/10.18637/jss.v076.i13

Vogt P, Riitters K (2017) GuidosToolbox: universal digital image object analysis. European Journal of Remote Sensing 50:352–361. https://doi.org/10.1080/22797254.2017.1330650

Vogt P, Riitters KH, Estreguil C, et al (2007a) Mapping Spatial Patterns with Morphological Image Processing. Landscape Ecol 22:171–177. https://doi.org/10.1007/s10980-006-9013-2

Vogt P, Riitters KH, Iwanowski M, et al (2007b) Mapping landscape corridors. Ecological Indicators 7:481–488. https://doi.org/10.1016/j.ecolind.2006.11.001

Walz U, Hoechstetter S, Drăguţ L, Blaschke T (2016) Integrating time and the third spatial dimension in landscape structure analysis. Landscape Research 41:279–293. https://doi.org/10.1080/01426397.2015.1078455

Walz U, Syrbe R-U (2013) Linking landscape structure and biodiversity. Ecological Indicators 31:1–5. https://doi.org/10.1016/j.ecolind.2013.01.032

Wang X, Blanchet FG, Koper N (2014) Measuring habitat fragmentation: An evaluation of landscape pattern metrics. Methods in Ecology and Evolution 5:634–646. https://doi.org/10.1111/2041-210X.12198

Weldon AJ (2006) How Corridors Reduce Indigo Bunting Nest Success: Corridors and Nest Success. Conservation Biology 20:1300–1305. https://doi.org/10.1111/j.1523-1739.2006.00403.x

Wickham J, Riitters KH (2019) Influence of high-resolution data on the assessment of forest fragmentation. Landscape Ecol 34:2169–2182. https://doi.org/10.1007/s10980-019-00820-z

Wickham JD, Riitters KH, Wade TG, Vogt P (2010) A national assessment of green infrastructure and change for the conterminous United States using morphological image processing. Landscape and Urban Planning 94:186–195. https://doi.org/10.1016/j.landurbplan.2009.10.003

Wiens JA (1989) Spatial Scaling in Ecology. Functional Ecology 3:385. https://doi.org/10.2307/2389612

Wiens JA (2008) Allerton Park 1983: the beginnings of a paradigm for landscape ecology? Landscape Ecol 23:125–128. https://doi.org/10.1007/s10980-008-9195-x

Wintle BA, Kujala H, Whitehead A, et al (2019) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. Proc Natl Acad Sci USA 116:909–914. https://doi.org/10.1073/pnas.1813051115

With KA (2002) The Landscape Ecology of Invasive Spread. Conservation Biology 16:1192–1203. https://doi.org/10.1046/j.1523-1739.2002.01064.x

With KA (1997) The Application of Neutral Landscape Models in Conservation Biology. Conservation Biology 11:1069–1080

With KA, King AW (1997) The Use and Misuse of Neutral Landscape Models in Ecology. Oikos 79:219. https://doi.org/10.2307/3546007

Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology 19:125–138. https://doi.org/10.1023/B:LAND.0000021711.40074.ae

Wu J, Levin SA (1994) A Spatial Patch Dynamic Modeling Approach to Pattern and Process in an Annual Grassland. Ecological Monographs 64:447–464. https://doi.org/10.2307/2937145

Wu J, Shen W, Sun W, Tueller PT (2003) Empirical patterns of the effects of changing scale on landscape metrics

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc Natl Acad Sci USA 96:1463–1468. https://doi.org/10.1073/pnas.96.4.1463

Yang X, Liu Z (2005) Quantifying landscape pattern and its change in an estuarine watershed using satellite imagery and landscape metrics. International Journal of Remote Sensing 26:5297–5323. https://doi.org/10.1080/01431160500219273

Zaragozí B, Belda A, Linares J, et al (2012) A free and open source programming library for landscape metrics calculations. Environmental Modelling & Software 31:131–140. https://doi.org/10.1016/j.envsoft.2011.10.009

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landscape Ecol 27:777–797. https://doi.org/10.1007/s10980-012-9737-0

Zhang Z, Zhou J (2019) From ecosystems to human welfare: the role and conservation of biodiversity. Cienc Rural 49: e20170875. https://doi.org/10.1590/0103-8478cr20170875