Measuring landscape structural connectivity

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1 Introduction

Landscapes are composed of features such as habitats, ecosystems, or land uses. One way to view a landscape is in a binary form where a landscape feature of interest is present in a series of patches within a matrix of differing landscape conditions (Forman & Godron 1981). When viewed in this context, landscape condition can initially be measured by ‘landscape feature abundance’ that quantifies the proportion of a landscape that is covered by the feature of interest. This enables a simple measure for assessing gains or losses in that feature within a landscape over time. However, alongside reduced feature abundance the fragmentation of landscape features into more, smaller, and isolated patches can also be an important consideration (Fahrig 2003). For example, ‘structural connectivity’ is an additional landscape measure that describes the contiguity of the areas covered by a landscape feature (Tischendorf & Fahrig 2000). Such contiguity can be important for many ecological processes, and hence an increase in fragmentation and the associated decrease in structural connectivity could have important implications for landscape scale processes.

1.1 Objectives

Assuming that landscape feature abundance is already being measured, the objective of this review was:

- to determine what secondary measure can also be calculated to provide additional information on structural connectivity.

1.2 Background and approach

Studies comparing methods that could be relevant in this context agree that it is difficult to select amongst available methods and that any choice is likely to be dependent on individual requirements of a study (Calabrese & Fagan 2004; Neel et al. 2004; Wang et al. 2014; Keeley et al. 2021). Therefore, we adopted the following five principles to guide our review.

1 Determining the specific landscape features of interest would be out of scope.

2 We assumed a binary patch-matrix model of landscapes, with uniformity of conditions assumed within all patches and within the matrix.

3 Landscape feature abundance in the form of the proportion cover of the landscape was taken as the primary measure.

4 We focused on advising on a secondary measure that would provide additional information on structural connectivity in the form of a singular numeric value for the whole landscape.

5 Simpler and more intuitive approaches would be preferred over complex ones, as these would aid in explaining the methods and interpretating the results.

2 Structural versus functional connectivity

In contrast to structural connectivity that is only concerned with contiguity of the landscape feature of interest, ‘functional connectivity’ explicitly considers ecological process-specific criteria associated with connections (such as spread, dispersal, flow, or movement) through the matrix (Tischendorf & Fahrig 2000). This distinction is important, because any connectivity method that requires a parameter such as a distance to establish connections between patches across the matrix would be a functional connectivity measure – and hence out of scope for this review. Our focus on structural rather than functional connectivity excluded connectivity methods such as ProtConn (Saura et al. 2017) or the integral index of connectivity (Pascual-Hortal & Saura 2006), as those use a network model of patches that are connected based on distances (Keeley et al. 2021).

While functional connectivity can provide a more precise measure of connectivity for a specific ecological process, selecting an appropriate connection distance is extremely difficult as it depends on the ecological process to which it is being applied. Also, what is an ‘appropriate’ distance will vary by ecological process and by landscape, meaning that functional connectivity measures may not transfer well between processes and landscapes. In contrast, measures of structural connectivity are easier to parameterise as they do not require any distance to be specified, and while they will likely be a poor measure for any one specific ecological process, they are less likely to suffer from issues of transference between landscapes and processes as they are less specific.

Methods for measuring structural connectivity have been developed in the context of ‘landscape metrics’ that seek to measure landscape feature pattern (Turner & Gardner 2015). Of particular relevance are those landscape metrics that aim to measure landscape (or habitat) fragmentation. In general, as landscape fragmentation increases landscape structural connectivity decreases. Fragmentation metrics are not reliant on a distance parameter and are therefore much easier to parameterise as they simply require the landscape of interest to be presented in a patch-matrix form for the landscape feature of interest.

3 Landscape feature abundance as a structural connectivity metric

The primary landscape metric being measured is the landscape feature abundance (F_a) in the form of the proportion of the landscape covered by patches. This can be defined as Equation (1):

$$F_a = \frac{\sum a_i}{A} \qquad (1)$$

where the sum of the area of each patch (a_i) is divided by the area of the landscape (A).

While the landscape feature abundance metric is primarily used to quantify the amount of a landscape feature, it is important to understand this metric will also provide information on structural connectivity. Taken to the extremes, when there are no landscape features there will be no structural connectivity and when landscape features cover the entire landscape then there will be complete structural connectivity. Percolation theory experiments on grids of virtual simulated landscapes called neutral landscape models (NLMs) demonstrate that when landscape features are randomly located within cells on landscapes then a ‘percolation threshold’ where landscape features form a single patch that spans the entire landscape occurs when around 0.6 of a landscape is covered in landscape features for orthogonal cell connections (Gardner et al. 1987) and around 0.4 for orthogonal and diagonal cell connections (Turner & Gardner 2015). This percolation threshold concept is important for structural connectivity, as landscapes can be expected to be largely connected above the threshold and largely disconnected below the threshold.

Of course real landscapes do not have randomly occurring landscape features, and using NLMs with more aggregated patterns of landscape features has indicated that the percolation threshold is less predictable (O'Neill et al. 1992). However, it seemed reasonable to assume that any metric that is being chosen to provide information on structural connectivity in addition to that provided by landscape feature abundance metric needs to primarily focus on landscapes with 0.0 to around 0.5 landscape feature abundance where it is unlikely that a percolation threshold will have been reached and hence structural connectivity will not have been achieved through landscape feature abundance alone.

4 Assessing secondary structural connectivity metrics

4.1 Selection criteria and initial assessment

It is critically important for landscape metrics to be evaluated under a range of conditions so that metric behaviour is well understood (Turner & Gardner 2015). Therefore, we considered only metrics that had undergone independent evaluations via NLM modelling. Wang et al. (2014) provide a useful assessment of 64 landscape metrics that demonstrates how each metric varies as a function of landscape feature abundance and aggregation.

We developed five elimination criteria to reduce this potential list to a smaller set of candidates, as listed in the paragraphs below.

1. *Landscape metrics need to be comparable between different sized landscapes*. Landscape metrics such as the number of patches or total edge length failed in this context, because under the same landscape feature patterns smaller landscapes will naturally have fewer patches and less edge than larger landscapes. Consequently, these metrics cannot be compared between landscapes of different sizes.
2. *Landscape metric must relate specifically to structural connectivity***.** We rejected landscape metrics focused on measuring patch shape and edge.

   In the context of structural connectivity, it does not matter how narrow or complex a connection is, what matters is simply whether a structural connection exists. So, while metrics such as edge density will increase as patches fragment and become less structurally connected, there is also the potential for edge density to increase when structural connections are achieved by linear corridors that have a lot of edge relative to area. Therefore, we excluded such metrics since their behaviour could be misleading in the context of structural connectivity.

   We also rejected landscape metrics calculated from inter-patch distances. For structural connectivity the distance between patches is irrelevant as patches separated by any distance across the matrix are considered unconnected. Therefore, we rejected metrics such as mean Euclidian nearest neighbour index since they would be more relevant for measuring functional connectivity that does allow patch connections via the matrix.
3. *There must be numerical independence from the primary landscape metric of landscape feature abundance.* Given landscape feature abundance is the primary metric, our secondary metric needed to be uncorrelated with landscape feature abundance to provide additional information. This requirement excluded metrics such as aggregation index, area weighted

mean contiguity index, area weighted mean perimeter area ratio, and percentage of like adjacencies.

4 *The discrimination value between aggregation patterns when landscape feature abundance must be less than 0.5.* An important requirement of this work was that the metric could distinguish between landscapes with different levels of feature aggregation when the feature covers 0.5 or less of the landscape, as such landscapes were likely to be below a percolation threshold. This requirement excluded metrics such as connectance index, mean proximity index, largest patch index, splitting index, effective mesh size, and landscape division index.

5 *There must be metric consistency for landscapes of different amounts and aggregation of landscape features***.** Many metrics also demonstrated erratic and inconsistent behaviour as the amount and aggregation of landscape features changed. This eliminated many metrics such as mean contiguity index, perimeter area fractal dimension, and mean proximity index.

After applying these five elimination criteria only three landscape metrics were identified as being worthy of further investigation: clumpiness index, patch cohesion, and patch density. These were examined individually in more detail to assess metric simplicity and intuitiveness, the level of understanding about metric behaviour under different analytical conditions, and to note any major limitations.

4.2 Clumpiness index

The clumpiness index (McGarigal et al. 2026) appeared an attractive option in that it consistently differentiates landscapes with differing landscape feature abundance and aggregation and also is completely uncorrelated with landscape feature abundance (Wang et al. 2014). However, it is a more complex and less intuitive metric than many other metrics under consideration, as for each cell it in a raster it compares the frequency of like-adjacent cells to the frequency expected under a random spatial arrangement. The clumpiness index ($CLUMPY$) was calculated using a raster data structure as shown in Equations 2 to 5 below.

$$G_i = \left(\frac{g_{ii}}{\sum g_{ik}}\right) \tag{2}$$

$$CLUMPY\ (where\ G_i \geq\ P_i) = \frac{G_i - P_i}{1 - P_i} \tag{3}$$

$$CLUMPY\ (where\ G_i <\ P_i\ and\ P_i \geq 0.5) = \frac{G_i - P_i}{1 - P_i} \tag{4}$$

$$CLUMPY\ (where\ G_i <\ P_i\ and\ P_i < 0.5) = \frac{G_i - P_i}{-P_i} \tag{5}$$

Where G_i is the proportion of like adjacencies g_{ii} is the number of like adjacencies between cells of the same feature type, g_{ik} is the number of adjacencies between cells of different feature types, and P_i is the proportion of the landscape occupied by the feature type. The clumpiness index has also not been formally published and described, and while several studies have looked at aspects of the metric's behaviour (Neel et al. 2004; Wang et al. 2014) a full exploration of this metric would be advisable before adoption.

4.3 Patch cohesion

Patch cohesion uses information on patch area and perimeter and total landscape area to measure physical connectedness of landscape features (Schumaker 1996). Patch cohesion (PC) is calculated using a raster data structure as shown in Equation 6:

$$PC = \left(1 - \frac{\sum p_i}{\sum(p_i\sqrt{c_i})}\right)\left(1 - \frac{1}{\sqrt{N}}\right)^{-1} \tag{6}$$

using the patch area as the number of cells (c_i) and perimeter as the number of cell edges (p_i) of each patch of contiguous cells and the total number of landscape cells (N).

While we found the *PC* metric straightforward to calculate, how these factors combine numerically in relation to structural connectivity was less clear – which makes interpretation of results harder. Simulation modelling has demonstrated that patch cohesion may relate well to ecological processes such as dispersal (Schumaker 1996; Tischendorf 2001), at least at lower landscape feature abundances (Neel et al. 2004). However, while producing consistent results for varying landscape feature abundance and patch density, patch cohesion has a reasonably linear association with landscape feature abundance below the percolation threshold, and provides no information above the percolation threshold (Gustafson 1998; Wang et al. 2014). Patch cohesion has also been shown to be extremely sensitive to changes in data resolution (Saura 2004). While a modification has been suggested that measures area in areal units rather than cell counts by Saura (2004) it has not be tested, so the behaviour of this modified version is not understood. We viewed this complication as a significant negative as it created the potential for generation of inconsistent metrics between different landscapes.

4.4 Patch density

Landscape feature patch density is a very simple and intuitive metric (McGarigal et al. 2026). It defines patch density (P_d) as in Equation 7:

$$P_d = \frac{n}{A} \tag{7}$$

where the number of patches (n) is divided by the area of the landscape (A). Despite its simplicity patch density appeared to differentiate landscapes very well when landscape feature abundance is below the percolation threshold (Wang et al. 2014). This is an important requirement for a secondary metric. Patch density provided less information at higher landscape feature abundances, but this is because the landscape is above the percolation threshold and so there are likely to be fewer patches. The trend between landscape feature abundance and patch density is not monotonic, so changes in patch density need to be contextualised by landscape feature abundance to understand if any increase or decrease in patch density is desirable or not. The major limitation we found with patch density was that it cannot account for differences in patch size: four patches of equal size would be measured as equivalent to one large patch and three small patches. It was unclear to us whether this would be a significant issue for measuring structural connectivity in combination with landscape feature abundance.

4.5 Assessment summary

Of the three landscape metrics we assessed (Table 1) patch density seemed to meet the criteria most effectively. We therefore recommend it as the most suitable candidate to explore further.

Table 1. Summary of three candidate landscape metrics' suitability as a secondary measure of structural connectivity against selection criteria

Assessment	Clumpiness index	Patch cohesion	Patch density
Initial assessment criteria			
Metric comparable between different sized landscapes	Yes	Yes	Yes
Metric relates specifically to structural connectivity	Yes	Yes	Yes
Numerical independence from the primary landscape metric of landscape feature abundance	High	Medium	High
Discrimination between aggregation patterns when landscape feature abundance is less than 0.5	Medium	Medium	High
Metric consistency for landscapes of different amounts and aggregation of landscape features	High	High	High
Metric-specific assessments			
Metric simplicity and intuitiveness	Low	Medium	High
Level of understanding about metric behaviour under different analytical conditions	Low	Medium	High
Major limitation	Not formally published	Sensitive to changes in data resolution	Does not account for patch area
Summary			
Overall suitability as a secondary structural connectivity metric to compliment landscape feature abundance	Low	Medium	High

5 Landscape data requirements

Data requirements for calculating landscape metrics are more easily met for structural connectivity than for functional connectivity (Calabrese & Fagan 2004), making consistent calculation across space and time more achievable. In terms of calculating the patch density metric, it seems advisable to us to use a vector rather than a raster data format for two reasons. First, a vector data format is more likely to capture narrow linear elements of patches that may be important for structural connectivity that could be lost when using raster cells that may be large relative to the feature (O'Neill et al. 1996). Second, using a raster data format introduces the risk of inconsistent application of the metric. For example, when using a raster data format, a decision must be made as to whether connections occur just between orthogonal neighbour cells or also between diagonal neighbours. There is no consensus amongst researchers on which approach is more appropriate, which would create the potential for different choices, either made deliberately or by accepting default values in software, to affect results. Therefore, we consider the use of a vector data model preferable, and note that such a model can be easily applied to calculate both landscape feature abundance and patch density.

Even when using vector data, we found evidence that connectivity metrics remain sensitive to spatial scale (O'Neill et al. 1996; Turner & Gardner 2015). Therefore, we note that when comparing metric values across space or time it will be important to ensure that ideally the same data sets are used, or at least data sets produced with the consistent spatial and thematic scales.

6 Visualisation of multiple simple metrics

The proliferation of landscape metrics has possibly been driven by a desire to overcome limitations with simpler metrics. For example, the landscape feature abundance metric gives no indication about the spatial arrangement of landscape features and hence could be comprised of a single large patch or a multitude of very small patches. Patch density also gives no indication of whether a landscape is covered in small or large patches. Yet despite these limitations at least one modelling study has found both landscape feature abundance and patch density to be consistently correlated with dispersal so the information from both metrics likely has value for measuring connectivity (Tischendorf 2001).

To resolve these issues with individual metrics researchers have tried combining the information from multiple simpler metrics into a single metric (Turner and Gardner 2015). This is advantageous in that it produces a single number that can then be easily compared to assess changes within and between landscapes. However, more complex metrics are harder to compute and perhaps more critically are much harder to intuitively understand.

An alternative to combining multiple simple metrics into more complex metrics that are harder to understand is to simultaneously visualise multiple simple metrics that compliment each other. For measuring structural connectivity, the landscape feature abundance and patch density metrics appear to be highly complementary (Wang et al. 2014). By visualising landscapes in a two-dimensional structural connectivity state space formed by these metrics (Figure 1) we can compare how landscapes differ and with time-series landscape data plot trajectories of structural connectivity (O'Neill et al. 1996).

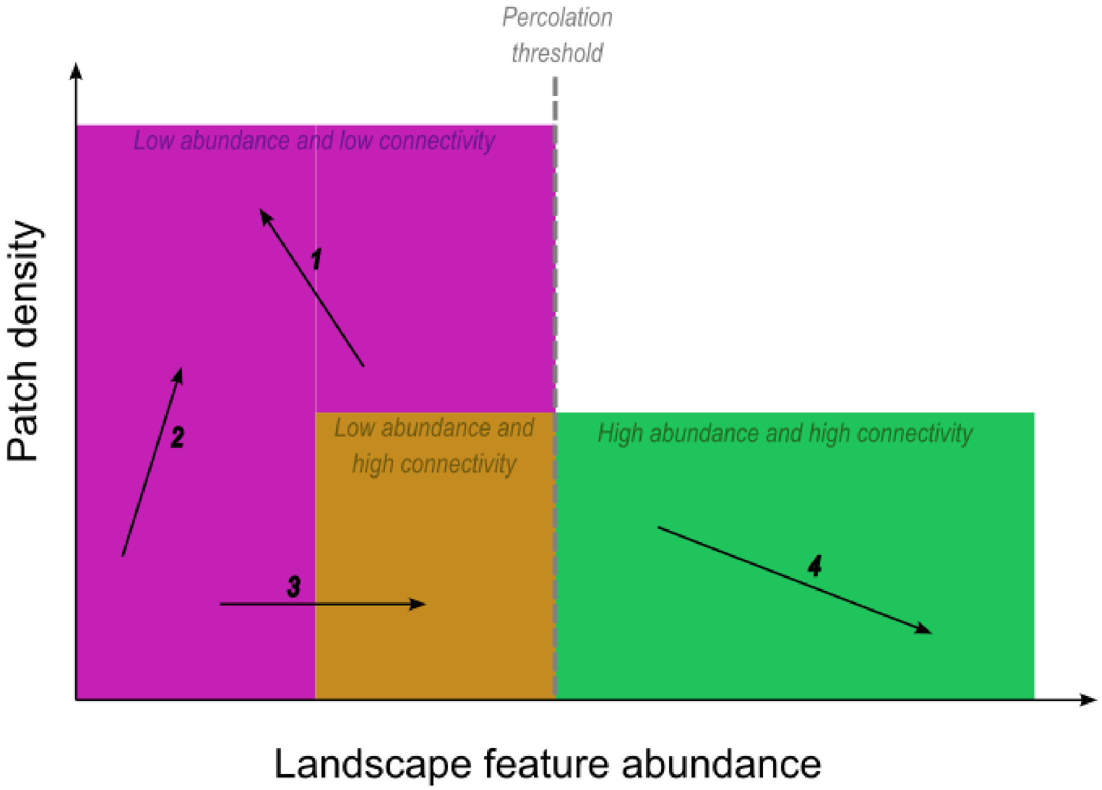

Figure 1. Examples of structural connectivity state space trajectories, with arrows indicating hypothetical changes in landscape arrangement between two time points for four different trajectories (see main text Section 6 for full description of trajectories). The colours differentiate key zones of differing combinations of landscape feature abundance and patch density around the percolation threshold.

In Figure 1, Trajectory 1 indicates a landscape whose features are become both less abundant and also more fragmented as patch density increases. Trajectory 2 indicates a landscape with increasing feature abundance in the form of new patches as the patch density is increasing. Trajectory 3 indicates a landscape with increasing abundance in the form of extensions to existing patches as patch density is constant. Trajectory 4 indicates an increase in abundance and the coalescence of existing patches as the patch density is decreasing. Where structural connectivity is viewed as desirable then trajectories 2, 3, and 4 are all positive trends, with only trajectory 1 being a non-desirable trend.

7 Recommendations and conclusions

From the 64 landscape metrics systematically assessed by Wang et al. (2014) that we reviewed, we found only the clumpiness index, patch chosen, and patch density to be possible options in this study.

- *Recommendation 1:* We recommend patch density as the most viable option given the assessment criteria, but only if patch density is simultaneously considered alongside landscape feature abundance.

General advice for use of landscape metrics is that any new approaches should be tested with NLMs (Turner & Gardner 2015). While neither landscape feature abundance nor patch density are new metrics, our recommendation to use them in combination to measure structural connectivity would be a new approach.

- *Recommendation 2*: Before adopting these metrics to measure structural connectivity we recommend conducting some simple NLM modelling to understand the behaviour and sensitivity of the combination of metrics to changes in landscape feature amount and patterns so that important landscape changes can be reliable detected (O'Neill et al. 1996; Remmel & Csillag 2003).
- *Recommendation 3:* We also recommend examining some real New Zealand landscapes, particularly those that are known to exhibit differences in structural connectivity over space and time, to better understand if landscape feature abundance and patch density in combination can capture landscape changes considered relevant.

7.1 Conclusions

In reviewing previous work comparing structural connectivity metrics it was apparent to us that there is no pre-existing definitive guidance on how to choose a connectivity metric, but the urgency of issues related to connectivity requires some decision to be made (Calabrese & Fagan 2004).

We consider that his uncertainty around what metric to choose should not preclude those responsible for making land management decisions from beginning to make measurements. The underlying landscape data forming the basis of the patch-matrix landscape model will always be available, so we think it would be a relatively trivial task to change landscape metrics in the future (as methods and knowledge develop) to produce improved views of how landscapes have changed.

We conclude that the recommended approach based on using the simple metrics of landscape feature abundance and patch density in combination could form a reliable baseline approach that can be superseded by future approaches that can be proven to be better.

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