Advances in Landscape Connectivity Assessment for Species Conservation

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Summary

Metrics of functional connectivity are necessary to understand the influence of habitat loss and fragmentation on biodiversity outcomes. Effective metrics must capture three landscape characteristics: i) habitat availability, ii) probability of movement between habitat patches and iii) habitat quality. Patch area has generally been used as a surrogate for quality such that a bias towards fewer, larger patches exists in connectivity research (mirrored across conservation science). We argue that this approach neglects species of conservation concern in highly fragmented landscapes that may persist where dispersal and habitat availability override minimum patch size requirements. We provide solutions to address this bias.

KEYWORDS: Connectivity; Ecology; SLOSS; Functional; Landscape

1 Introduction

Recent approaches to measuring landscape connectivity are predicated on the assumption that fewer large patches are preferable to a greater number of small patches. Most are general forms or extensions of the incidence function proposed by Hanski (1994), culminating with the probability of connectivity metric (PC; Pascual-Hortal and Saura, 2008), which has been adapted by others to consider, for example, matrix resistance and edge removal (e.g., Watts and Handley, 2010). The inherent bias towards large patches appears to stem from two underlying assumptions: that patch size can be considered as a surrogate for quality for all species groups (and that they are homogenous throughout); and that fragmentation necessarily equates to a loss of functional connectivity. In contrast to this, work arising from the SLOSS (Single Large or Several Small) debate (see Fahrig, 2021) suggests that assumptions related to the general case that fewer bigger patches (Single Large/SL) are better than more numerous smaller patches (Several Small/SS) for biodiversity (SL>SS) may not always hold. For this reason, current connectivity modelling approaches may not effectively capture landscape-scale connectivity for all species groups.

An illustration of the problem is provided in **Figure 1**. Here the scenario with a greater number of patches will always present a lower measure of landscape connectivity. This is because most functional connectivity metrics are derived from the sum of the product of patch sizes and the probability of movement between patches. Due to the greater number of trips through the matrix required to access all available habitat in **Figure 1B** (SS), this will always result in lower connectivity estimates. However, the assumption that SS implies lower connectivity is only ecologically meaningful for interior specialists with minimum patch size requirements and poor dispersal abilities.

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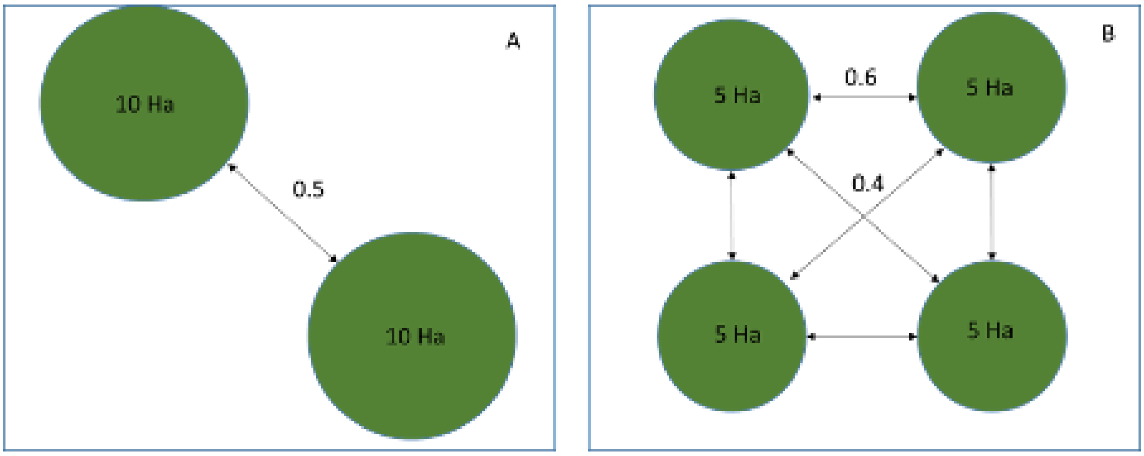

Figure 1. A) SL configuration: two 10 Ha patches with 0.5 probability of movement. **B)** SS configuration: four smaller patches (5 Ha) with 0.6 and 0.4 movement probabilities.

Recent reviews on the impact of fragmentation on landscape-scale species richness have highlighted that SS>SL often holds for a given amount of habitat in the landscape (Fahrig, 2017, 2020). These findings and their likely mechanisms have important implications for landscape and spatial-ecological theory.

1.1 Should Larger patches be prioritised in landscape decisions aimed at species conservation?

The tendency to assume that fewer larger patches should support greater species richness is derived from foundational statements contained within key theoretical developments in ecology, such as the equilibrium theory of Island Biogeography and Diamond (1975). However, the idea that greater patch size is the primary driver of species richness or population sizes has only been partially supported in the subsequent empirical literature (Fahrig, 2020), and alternative theories explaining this have been posited (e.g., Fischer et al., 2006; Powell et al., 2015). The assumption that SL>SS in terms of species richness is closely linked to the idea that edge is associated with low quality habitat, fragmentation and species loss. However, the preponderance of SS>SL in the empirical evidence suggests that a) edge-exploiting species contribute significantly to species richness and b) sufficient interior habitat can be provided by SS or mixed configurations. From a connectivity modeling perspective, the inability of current approaches to delineate adequately interior from edge habitat (and quality) is therefore a limitation.

1.2 Does fragmentation lead to lowered functional connectivity?

If an increased number of journeys through the matrix are required to make use of the available habitat (**Figure 1**), then mortality risk increases and overall immigration success between patches decreases. However, it has been proposed that the higher ratio of edge-to-area and potentially lower between-patch distances in fragmented landscapes can increase encounter rates, thereby mitigating (or enhancing) the impacts of fragmentation (Saura et al., 2014). Given that fragmentation has come to denote the very opposite of connectivity, untangling this misuse is of paramount importance if the conservation biology and landscape connectivity fields are to be re-aligned.

2 Methods

In order to address these limitations, we present a new method for the calculation of functional landscape connectivity that builds upon the Probability of Connectivity function (Saura and Pascual-Hortal, 2008):

$$\frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j P_{ij}^*}{A_L^2}$$

(1)

where a_i and a_j are the areas of habitat patches *i* and *j*, and A_L is the total landscape area (including habitat and non-habitat patches). Movement probability between patches p_i and p_j is defined as the maximum probability of movement based on shortest paths in a probabilistic patch-based graph. We update this approach to include proper consideration of the edge implications of non-habitat patches in the landscape and changes in functional connectivity as a function of fragmentation. To consider properly the area of edge within each patch, we model edge effects using a distance decay function (a negative exponential). The model then selects for either interior specialists, edge specialists, or generalists (which are an input parameter). To address the bias whereby fragmentation always leads to lower estimates of functional connectivity we include edge-area ratio as a positive factor and set intra-patch movement to zero. The model is implemented as a function in R.

2.1 Model evaluation

We created several hypothetical landscape scenarios (**Figure 2**) to assess whether the method behaved in line with mechanisms discussed above. To evaluate modelling outcomes for different species along the interior-to-edge spectrum we tested the following hypotheses:

1. In a neutral landscape, interior, edge and generalist species should respond differently to increases in edge impacts. As edge impacts increase, connectivity estimates for edge specialists should increase, whilst connectivity estimates for interior specialists should decrease. This should hold true in SL, SS and mixed landscapes (**Figure 2**).

2. In addition to edge intensity, species of different specialisms should likewise respond differently according to their sensitivity to edge effects. Here we supposed that both interior and edge specialists should suffer as a result of increased sensitivity to edge. However, in SS landscapes, edge specialists should suffer less (as there will be higher edge-interior habitat ratio) and in SL landscapes, interior specialists should outperform edge species due to lower edge-interior habitat ratios. In mixed landscapes we assumed that the difference between edge and interior specialists should be smallest.

3. If within-patch movement is cost-free, then the difference in functional distances versus scenarios where cost is incurred should be greater for SS than for SL scenarios.

4. SL>Mixed>SS should only occur for interior specialists when extinction-related processes (sensitivity to edge) are more pronounced than colonization rates.

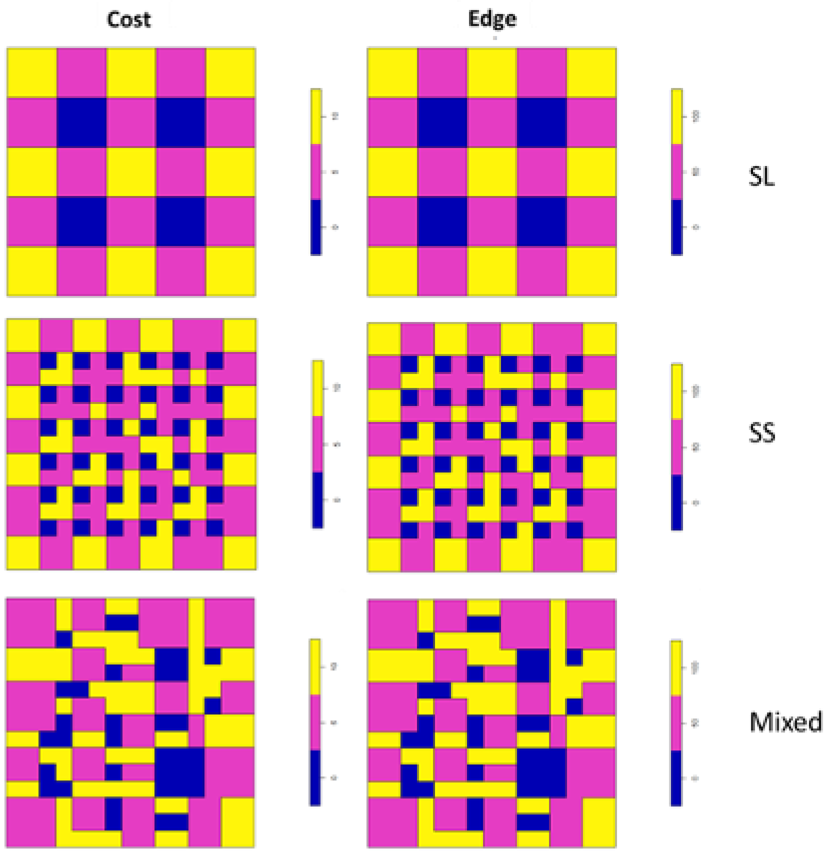

Figure 2. Three simulated landscapes: SL, SS and mixed. Zero values (dark blue polygons) represent habitat patches.

3 Results

Our results reflected expectations around responses for interior and edge specialists, with connectivity for interior specialists falling at a greater rate in SS versus SL landscapes with increasing edge sensitivity. The mixed landscape appears to have a buffering impact whereby observed differences in response to the sensitivity parameter for edge and interior specialists were minimised (**Figure 3**).

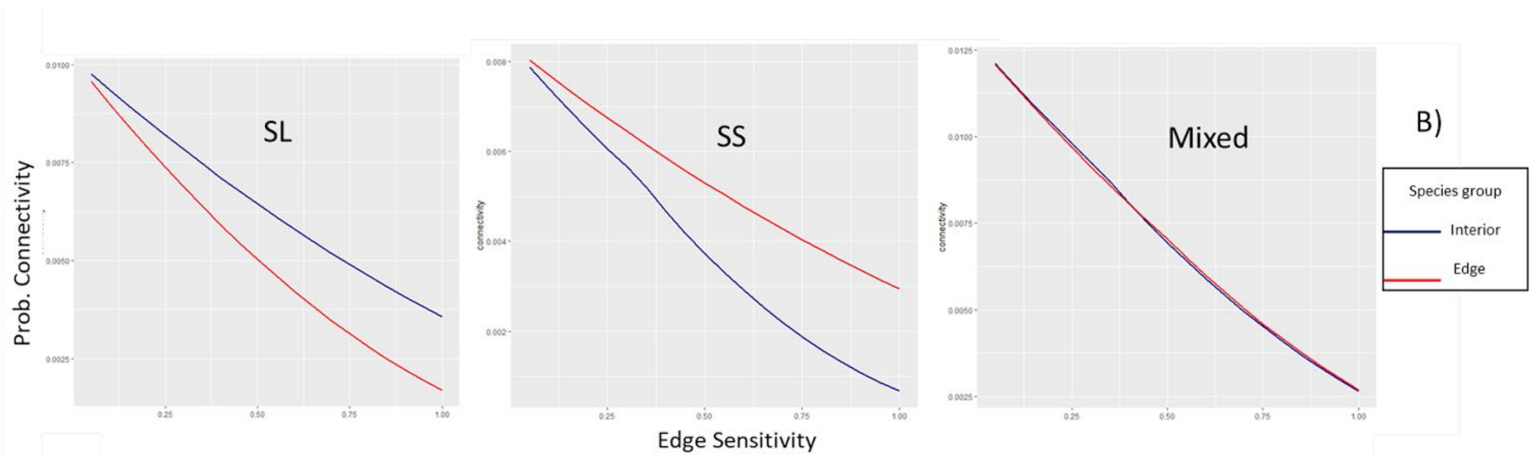

Figure 3. Connectivity metric response to edge sensitivity of interior and edge specialists for SL, SS and Mixed landscapes.

We predicted that SS landscapes should be much more sensitive to reducing cost of movement through patches, especially at lower dispersal distances. **Figure 4** confirms this expectation.

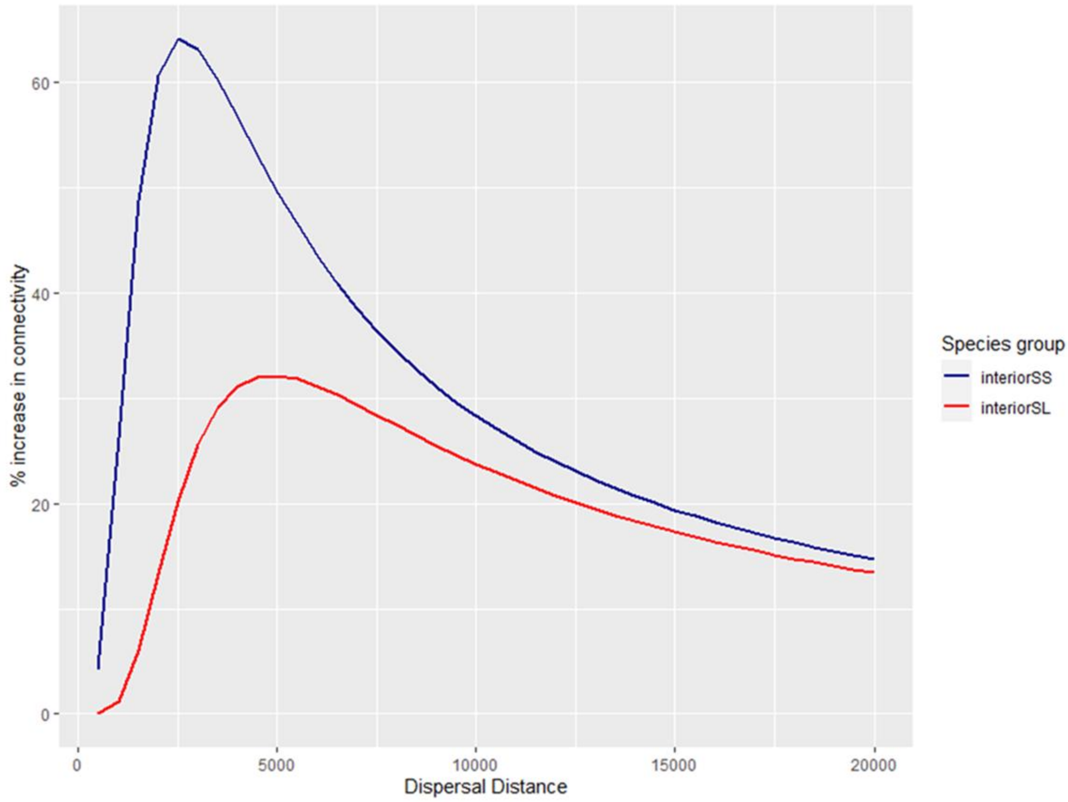

Figure 4. Percentage change in the connectivity metric for interior species in SL (red) and SS (blue) configurations (results for edge species are identical and not shown).

3.1 Aggregated results for simulated heterogeneous landscapes

Our expectation that the method should replicate the ascendency of SL over SS and mixed configuration only when extinction parameters were high relative to colonization rates for interior specialists was observed. Response to increasing colonization rates for low and high edge sensitivity values are shown in **Figure 5**.

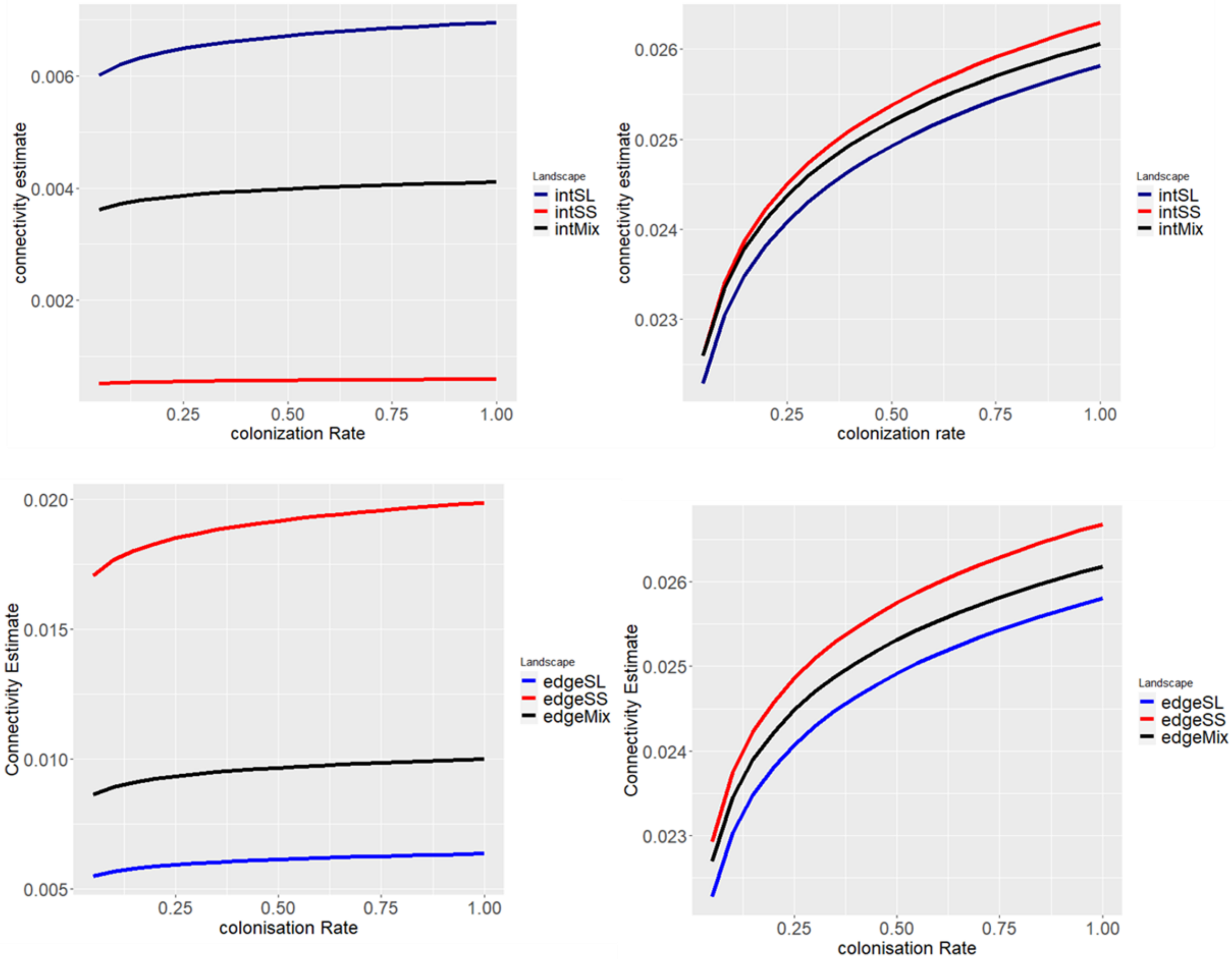

Figure 5. Metric response to colonization rate for SL, SS and mixed landscapes for low and high edge sensitivity.

Conclusions

There is a need to bring the current breadth of connectivity research to bear on important developments in theoretical ecology and conservation biology. Existing metrics are biased towards generalists or interior specialists, yet do not adequately account for the ecology of either with respect to landscape configuration. The method presented here addresses some key oversights in existing connectivity work and aligns landscape ecology with findings and mechanisms coming to light through key debates in ecology. By highlighting and addressing these limitations, we believe that there are opportunities to better integrate landscape connectivity assessments into ecological research.

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Biographies

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Dr Ewan McHenry is a Conservation Advisor (Landscape Ecology) at the Woodland Trust. He is a specialist in population ecology and the use of quantitative methods to understand conservation outcomes and evidence.