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Research paper

Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach

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ABSTRACT

Due to increasing habitat fragmentation and concern about its ecological effects, there has been an upsurge in the use of landscape connectivity estimates in conservation planning. Measuring connectivity is challenging, resulting in a limited understanding of the efficacy of connectivity estimation techniques and the conditions under which they perform best. We evaluated the performance of four commonly used connectivity metrics – Euclidean distance; least-cost paths (LCP) length and cost; and circuit theory's resistance distance – over a variety of simulated landscapes. We developed an agent-based model simulating the dispersal of individuals with different behavioural traits across landscapes varying in their spatial structure. The outcomes of multiple dispersal attempts were used to obtain 'true' connectivity. These 'true' connectivity measures were then compared to estimates generated using the connectivity metrics, employing the simulated landscapes as cost-surfaces. The four metrics differed in the strength of their correlation with true connectivity; resistance distance showed the strongest correlation, closely followed by LCP cost, with Euclidean distance having the weakest. Landscape structure and species behavioural attributes only weakly predicted the performance of resistance distance, LCP cost and length estimates, with none predicting Euclidean distance's efficacy. Our results indicate that resistance distance and LCP cost produce the most accurate connectivity estimates, although their absolute performance under different conditions is difficult to predict. We emphasise the importance of testing connectivity estimates against patterns derived from independent data, such as those acquired from tracking studies. Our findings should help to inform a more refined implementation of connectivity metrics in conservation management.

1. Introduction

As habitat fragmentation and land-use intensification continue, maintaining the ability for individuals to move among habitat patches and populations has become a major goal of many conservation plans (Fischer and Lindenmayer, 2007). Accordingly, measurements of 'landscape connectivity' often play a large role in land-use management schemes (Moilanen and Hanski, 2001; Moilanen and Nieminen, 2002). Landscape connectivity is a measure of the extent to which landscape structures and elements facilitate or impede movements among resources or habitat patches (Taylor et al., 1993; Tischendorf and Fahrig, 2000). However, direct measures of landscape connectivity are difficult and costly to obtain (Kindlmann and Burel, 2008), and so most quantifications of connectivity are indirect.

Early efforts to estimate landscape connectivity used Euclidean distances between habitat patches (e.g. Green, 1994; Metzger and Décamps, 1997). However, because the dispersal capabilities of organisms are affected by landscape composition and configuration, and so vary across space, Euclidean distances often provide poor estimates of connectivity (Emel and Storfer, 2015; Vuilleumier and Fontanillas, 2007). Subsequently, connectivity has been estimated using various models which are underpinned by cost-surfaces. Cost-surfaces are raster depictions of landscapes in which the difficulty for individuals of some species of interest to traverse different features in the landscape is represented by a cost value (Douglas, 1994; Etherington, 2016). Connectivity tech-

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niques using cost-surfaces fall along a continuum of an individuals assumed familiarity with a landscape (Rayfield et al., 2011). At one extreme is least-cost path (LCP) modelling, which calculates a single route of maximum efficiency (i.e., 'lowest cost') between two points, assuming that an individual has complete and perfect knowledge of the composition and configuration of the landscape (Adriaensen et al., 2003; Douglas, 1994; Etherington, 2016). At the other extreme is circuit-theory, which assumes individuals move randomly through landscapes of which they have no prior knowledge, producing multiple pathways depicting the concentration of individuals' flow between two points (McRae, 2006; McRae and Beier, 2007).

Given the proliferation of cost-surface derived connectivity models a number of studies have explored the factors that influence each model's performance. Most of these studies examine the sensitivity of a single model (Rayfield et al., 2010), or compare the sensitivity of multiple models (Koen et al., 2012), to changes in cost-surface configuration (i.e. spatial structure) and/or composition (i.e. cost values). While such studies explain how connectivity models may react to changes in cost-surfaces they do not indicate how well each model captures the true connectivity of the underlying landscape. Recent studies have used tracking and genetic data to quantify the ability of connectivity models to capture this true landscape connectivity (McClure et al., 2016; Poor et al., 2012; Ruiz-González et al., 2014; Sawyer et al., 2011). The results of these studies have been mixed with regards to which model best represents landscape connectivity. However, these results highlight that the performance of connectivity models is context-dependent; for example, McClure et al. (2016) found that LCP was the best model for predicting the movements of migrating individuals but that circuit-theory was best for naïvely dispersing individuals. This context-dependence means that elucidating universal trends in model performance requires a large number of different contexts to be studied. However, due to the costs involved studies such as those mentioned above are rare and are often conducted only on a small number of species in a small number of landscapes, limiting the generalisability of their results (Spear et al., 2010).

Given the limited generalisability of current empirical studies, we adopted a 'virtual ecologist' approach in which we assessed the performance of multiple connectivity models (and their associated metrics) over a range of conditions via simulation (Zurell et al., 2010). We developed a spatially explicit agent-based model (ABM) that represented individuals dispersing through landscapes and from this we quantified simulated 'true' landscape connectivity. We then assessed model performance by comparing each connectivity model's estimates of landscape connectivity to the simulated 'true' connectivity. Using this approach we aimed to: 1) determine the predictive performance of a suite of widely used connectivity estimation techniques; 2) examine to what extent predictive performance was dependent on landscape structure; and 3) explore how sensitive predictive performance was to organism behavioural traits. By using the 'virtual ecologist' approach to address these aims (Zurell et al., 2010), we were able to analyse each connectivity model over a large range of conditions so producing generalisable results.

2. Materials and methods

We used an ABM to simulate 'true' landscape connectivity values against which we evaluated the relative ability of four connectivity metrics (Euclidean distance; least-cost paths length; least-cost paths accumulated cost; and resistance distance) generated using three connectivity models (Euclidean distance; least-cost paths modelling; and circuit-theory) to accurately represent landscape connectivity. We ran our simulation over landscapes with a wide range of compositions and configurations using simulated animal movements with varying behavioural characteristics. In this section, we first report on our ABM design (Section 2.1), then on the calculation of connectivity metrics (Section 2.2), and finally on the experimental design of our study (Section 2.3).

2.1. Agent-based model design

Our ABM used the open-source programming framework NetLogo v.5.1.0 (Wilensky, 1999) in conjunction with R v.3.2.3 (R Core Team, 2015), including the RNetlogo library v 1.4 (Thiele et al., 2012), and Python v.2.7.11 languages for the development of the connectivity models and assessment of their related metrics. The ABM description below follows the overview, design, concepts and details (ODD) protocol (Grimm et al., 2010). In Sections 2.1.1–2.1.3 we describe the surface level procedures of the model. The detailed formulaic descriptions of the sub-models underlying these procedures are given in Section 2.1.4.

2.1.1. Overview

2.1.1.1. Purpose. The purpose of our ABM was to generate 'true' connectivity values for a landscape, by virtue of the dispersal of naïve individuals from the centre of the landscape in search of habitat patches in which to settle; this represents, for example, the movements that occur after a translocation event. Our ABM did not, nor did it attempt to, perfectly emulate the observed movements of a specific taxa, but rather we sought to provide a simple representation of movement dynamics through spatially heterogeneous environments. Dispersal between habitat patches was selected as a movement type as it can be simulated with the fewest explicit assumptions, as opposed to movements such as migration that assume some degree of familiarity with a movement route. Additionally, because single dispersal events typically occur over relatively short time periods we did not represent energetic requirements. Mortality was not represented in the ABM because the data used to inform connectivity estimates are usually acquired from the individuals that survive a dispersal event; the agents in our model may be viewed as those surviving individuals.

2.1.1.2. Entities, state variables, and scales. The spatial domain of the ABM was a 100×100 cell regular lattice (grid). Each cell in the lattice was classified into a landscape type and assigned a corresponding cost value that represented the difficulty of an agent traversing the cell (see "*Landscape generation procedure*"). As the model depicts a generic species with simplified movements that may occur over multiple scales, no explicit spatial scale was defined. While time-steps were not defined explicitly, each represented the period required for an agent to travel a distance equivalent to moving from the centre of one cell to the centre of one of its neighbours.

Each landscape had eight habitat patches arranged concentrically around the landscape's midpoint, with orthogonal patches being slightly closer to the central cell than diagonal patches (Fig. 1). Simulation trials showed that using 16 or 32 patches did not result in qualitatively different outcomes (Supplementary Materials). A uniformly spaced concentric ring of habitat patches was selected as this minimised shadowing (i.e. habitat patches acting as barriers to habitat patches behind them), which frequently occurred when habitat patches were randomly located. Habitat patches were circular with a diameter of 10 cells and a cost value of one. The total number of agents reaching any part of each individual habitat patch was recorded.

The ABM contained one type of mobile agent. Agents were initially located at the centre of the landscape, facing a random direction. Each agent moved through the landscape until they reached one of the eight habitat patches, or left the simulation landscape (see "*move procedure*"). Model agents were characterised by