Ecological Modelling 386 (2018) 47–58

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Increasing the function in distance-based functional connectivity assessments: a modified spatial interaction model (SIM) approach

Shantel J. Koenig*, Darren J. Bender

Department of Geography, University of Calgary, 2500 University Drive NW, Calgary, Alberta, T2N 1N4, Canada

ARTICLE INFO

Keywords:
Functional connectivity
Spatial interaction model
Effective distance
Movement
Least-cost path
Connectivity model

ABSTRACT

Assessments of connectivity are subject to the limitations imposed by the technique used to model species movement. Least-cost path analysis is one such commonly applied technique that has a number of associated limitations that are often discounted, such as the assumption of individual omniscience or symmetrical movement between patches. We contend that not accounting for methodological limitations may lead to inaccurate assessments of connectivity, and thus there is a need for more robust and adaptable approaches. Using simulated data and in a case study on Ord's kangaroo rat (*Dipodomys ordii*), we present an approach that uses effective distance, in this case calculated from least-cost paths, in combination with a spatial interaction model (SIM), which allows one to incorporate additional landscape characteristics and interactions influencing movement, thereby overcoming key assumptions and limitations associated with the least-cost framework. We show how various factors influencing connectivity can be incorporated, how outputs from the SIM can be used to quantify connectivity, how outputs from different models may be compared, and, importantly, that in both a simulated and empirical case study application, the assessment of functional connectivity is sensitive to small changes to the model.

1. Introduction

A species' capacity to persist in a heterogeneous environment depends on its ability to move successfully between patches of suitable habitat that promote reproduction and survival. Described in terms of connectivity, the ability to interpret, measure, and quantify how well or poorly individuals move between patches has provided a metric that can be somewhat elusive to assess accurately, robustly, and consistently (Crooks and Sanjayan, 2006).

A complete understanding of connectivity requires that both habitat patches and the space between patches, the matrix, are properly represented and accounted for (Tischendorf and Fahrig, 2000; Ricketts, 2001; Kuefler et al., 2010, Murphy et al., 2010, Kennedy et al., 2011; Ziolkowska et al., 2014), thereby ensuring that both the structural (i.e., landscape composition and configuration) and functional (i.e., species behaviour and landscape interactions) components are accounted for and represented (Prugh, 2009; Watts and Handley, 2010; Courbin et al., 2014). In practice, however, accounting for the multitude of factors that specifically determine functional connectivity for a species can be challenging.

Data on the actual route(s) travelled between patches provides the most accurate information on connectivity for a species, because a travelled route reflects both movement choices and the actual distance traversed between locations (Graves et al., 2007; Sawyer et al., 2011; Milanesi et al., 2016). However, determining actual routes requires intensive monitoring that may be logistically infeasible, so often route data simply do not exist (Fagan and Calabrese, 2006; Kindlmann and Burel, 2008; Zeller et al., 2012). Instead, much effort has been applied to developing models that account for the ways in which the matrix influences movement between patches and provide predictions for paths or corridors that provide a measure of effective distance between patches; patches that are effectively "closer" are assumed to have greater functional connectivity.

Currently, least-cost methods are the most well-known and frequently applied method for calculating effective distances among patches to assess functional connectivity (Sawyer et al., 2011; Ayram et al., 2016; Etherington, 2016). Least-cost approaches rely on a raster surface model of the resistance or permeability of the landscape (Adriaensen et al., 2003), and commonly a habitat selection model, such as a resource selection function (RSF), is used to assign resistance values. Then, paths and effective or cost distances are calculated based on the resistance values, and connectivity is assessed based on these distances.

Generated in this way, least-cost paths (LCPs) measure functional connectivity to a certain degree by accounting for matrix heterogeneity

* Corresponding author.
E-mail addresses: skoenig@fieraconsulting.ca, sjkoenig@ucalgary.ca (S.J. Koenig), dbender@ucalgary.ca (D.J. Bender).

https://doi.org/10.1016/j.ecolmodel.2018.08.007
Received 2 February 2018; Received in revised form 12 August 2018; Accepted 13 August 2018

and differential landscape use by a species; however, when solely based on habitat selection or suitability, these paths assume that species direct their movements based on habitat preferences or resource requirements and that poor or unsuitable habitat will be avoided during movements (Coulon et al., 2015). For many species, other factors affect and determine a species' movements in the matrix, so movement between patches, and thus connectivity, is determined across a wider spectrum of landscape features than just suitable or selected for habitat (Belisle, 2005; Cline and Hunter, 2014; Vasudev and Fletcher, 2015; Vasudev et al., 2015; Keeley et al., 2017). Therefore, basing a resistance layer only on variables related to habitat selection does not comprehensively depict all the relevant landscape properties (composition and configuration) that determine connectivity and species' movement abilities (motivation, cognition, and physical capacities) (Sawyer et al., 2011; Zeller et al., 2012; Mateo-Sanchez et al., 2015; Abrahms et al., 2017). In such cases, the assessment or prediction of functional connectivity will be lacking or inaccurate (Chetkiewicz et al., 2006; Abrahms et al., 2016).

Resistance-based least-cost models have other limitations to consider. The least-cost approach assumes that individuals have sufficient knowledge of the landscape (individual omniscience), which allows one to know their desired destination and to choose an optimal route between two locations (Douglas 1994, Adriaensen et al., 2003; Coulon et al., 2015; Etherington, 2016). This assumption discounts that for some species perceptual range would limit the ability to select a precise, optimal path (Zollner, 2000; Olden et al., 2004; Pe'er and Kramer-Schadt, 2008; Prevedello et al., 2010; Vinatier et al., 2011; Fletcher et al., 2013), and therefore, effective distance may overestimate connectivity. Similarly, a calculated path does not provide any indication of the likelihood of a species travelling the whole length of the path or how that likelihood changes with distance, and thus should be considered alongside information on a species' dispersal characteristics (Creech et al., 2014), such as a distance-decay function or dispersal kernel (Skelsey et al., 2013). Additionally, a LCP is calculated in a way that results in a symmetrical path between patches, which assumes that the same path is travelled, and thus the same effort is invested, independent of which patch is the origin and which patch is the destination (Belisle, 2005). Finally, least-cost routes are unable to account for the influence that patch traits, such as habitat quality or spatial configuration of source and destination patches (e.g., attraction to or preference for clusters of habitat) may have on connectivity (Fahrig, 1997; Rodenhouse et al., 2003; Visconti and Elkin, 2009; Schooley and Branch, 2011; Betts et al., 2015).

Extensions of the least-cost approach to overcome limitations have been proposed. Least-cost corridors (Beier et al., 2009; Pinto and Keitt, 2009; Savage et al., 2010), resistance kernel modelling (Compton et al., 2007; Cushman et al., 2013), and composite least-cost approaches (e.g., Brodie et al., 2015; Ribeiro et al., 2017) address the need to consider alternative or multiple routes when assessing connectivity; however, these approaches remain limited to symmetrical patch relationships and do not consider patch characteristics, such as habitat quality, that may determine connectivity. Thus, to date there has been no consensus as to which approach provides the most consistent or generalizable method for providing estimates of effective distance, because strong correlations to empirical data on connectivity tend to vary depending on the species and situation (Spear et al., 2010; Sawyer et al., 2011; Zeller et al., 2012; Milanesi et al., 2016; Simpkins et al., 2017). Certainly, there is a need for alternative approaches for assessing connectivity that can accommodate more complex dispersal behaviours and/or landscape interactions.

Despite a growing acceptance that least-cost-based assessments of connectivity require more information than just landscape resistance (e.g., Vasudev et al., 2015; Benz et al., 2016; Abrahms et al., 2017; Keeley et al., 2017), the historical and continued prominence of the least-cost approach within connectivity research and management must be considered (e.g., Stevenson-Holt et al., 2014; Alexander et al., 2016; Ayram et al., 2016; Jackson et al., 2016; Milanesi et al., 2016). With this in mind, we propose an approach for assessing connectivity that allows one to address the limitations that may be associated with applying LCPs, such as the assumptions of sufficient landscape knowledge and symmetrical paths between patches, and not accounting for patch traits. Our approach retains a resistance-based landscape representation and the LCP model effective distances, and then applies a second model – a spatial interaction model (SIM) – that allows one to incorporate additional landscape characteristics and interactions influencing movement that LCPs are not able to account for. This second model provides count outputs that reflect numbers of movements among areas of interest (i.e., patches) to provide a more complete and comparable assessment of connectivity (Coulon et al., 2015).

More specifically, in our approach the calculated LCP effective distances are the starting point representation of movement through the matrix, by accounting for one aspect of species behaviour (e.g., habitat selection). Then, a SIM is used to easily incorporate additional relevant components of the connectivity landscape, such as physical features (e.g., barriers) or species' behaviours (e.g., motivation or dispersal traits) and/or add variables that describe attributes of patches that may increase their attractiveness or emissivity. Functional connectivity is then quantified and assessed using predictions of counts in and out of patches calculated from the SIM.

In this paper, we first present and demonstrate our method using simulated data by assessing the difference between a habitat selection-based connectivity model and a set of adjusted models that incorporate movement and/or dispersal factors that may influence functional connectivity. Then we apply our approach in a case study on a regional metapopulation of the endangered Ord's kangaroo rat (*Dipodomys ordii*) in Canada to compare connectivity assessments between a habitat selection-based model and alternative models that account for dispersal-specific factors. Importantly, this allows us to test whether a simple, habitat selection-based approach is a reasonable and stable approximation for assessing connectivity for this endangered species; if the habitat selection based connectivity predictions are substantially different from alternative models that account for dispersal and/or movement behaviour, then there is reasonable evidence that relying only on habitat selection to assess connectivity risks making erroneous management decisions for kangaroo rats in the study region. As part of our demonstration and case study, we suggest ways to interpret and present outcomes of our adapted connectivity modelling method.

2. Methods

2.1. Overview of spatial interaction models

Our approach uses a spatial interaction model (Wilson, 1967, 1970), a model commonly applied by social scientists to assess human connectivity, as a complementary step to a LCP analysis to assess functional connectivity for a species. Like many ecological connectivity models, distance is a primary determinant of connectivity; however, the model also includes variables that describe the attractiveness of destinations and the emissivity of origins. A SIM can take several forms depending on the input data available. We use a variation of the production-constrained SIM, which uses known or accurately estimated counts of patch emigration and the effective distance between patches to calculate predictions of 1) total immigration into each patch, and 2) pairwise exchange for each patch pair.

In our scenarios, the SIM takes the form:

$$T_{ij} = A_i W_j O_i D_j C_{ij} \tag{1}$$

where:

$$A_i = \left\{ \sum_j W_j C_{ij} \right\}^{-1} \tag{2}$$