Original Articles

Understanding the impacts of temporal variability on estimates of landscape connectivity

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A B S T R A C T

Landscape connectivity estimates are widely used to inform species conservation management. However, although many landscapes and species behaviours change over time, such as between seasons, the vast majority of studies view connectivity as static. Calls have therefore been made to use multiple connectivity estimates to adequately capture periodic (e.g., seasonal) temporal changes. These periodic temporal changes are also influenced by stochastic perturbations, such as extreme weather events, and this variability is likely to increase due to ongoing climate change. We aimed to investigate: 1) how variability interacts with periodic landscape changes to alter connectivity estimates, and 2) how these alterations change over longer time-periods. To achieve this we used a virtual ecology approach in which we simulated 100 landscapes. Each simulation ran for 20 seasons with the landscape experiencing regular seasonal changes. Each simulation was then rerun five times with increasing levels of variability super-imposed on the seasonal dynamics. Connectivity for each landscape and every season was calculated using least-cost paths modelling, and the differences between connectivity estimates calculated. We found that the variation in connectivity estimates between seasons increased with temporal variability. Differences in connectivity accumulated over time, meaning that as the variability increased connectivity estimates changed more quickly and by larger amounts. Our study demonstrates that increasing temporal variability will become a challenge for the successful use of static connectivity estimates.

1. Introduction

Understanding how organism movements are impacted by landscape features is key to identifying areas in need of protection or rehabilitation (Donald and Evans 2006; Rudnick et al., 2012). While not universal (e.g., see Haddad et al., 2014), a number of benefits can result from increasing an organism's ability to move through a landscape, including increased gene flow (McRae and Beier 2007; Cushman and Lewis 2010) and decreased risk of local extinction (Stelter et al., 1997; Keymer et al., 2000). As a result, obtaining a measure of landscape connectivity – that is, the extent to which landscape structure (composition and configuration) facilitates or impedes movement through a landscape (Taylor et al., 1993) – is a key goal for many conservation managers (Rayfield et al., 2011). However, directly measuring connectivity is difficult and costly (Kindlmann and Burel 2008; Zeller et al., 2012). Therefore a range of indirect connectivity estimation techniques have been developed, many of which are based around cost-surfaces, raster representations of landscapes that characterise the difficulty for an individual of some species of interest to traverse a grid cell (Etherington 2012).

A number of studies have investigated the sources (e.g., error in the underlying classification of remotely sensed imagery used in habitat mapping, misestimated cost values for different habitat types) and impacts of uncertainty on connectivity estimates and have developed methods to mitigate them (Quinby et al., 1999; Kautz et al., 2006; Beier et al., 2009; Graves et al., 2012; Simpkins et al., 2017). Most of these studies have focused on the spatial uncertainties in estimating connectivity in temporally static landscapes (Zeigler and Fagan 2014). This focus on the purely spatial aspects of connectivity is an understandable initial step and has resulted in the development of useful techniques with which to identify and reduce uncertainty. However, an emphasis on the spatial aspects of uncertainty has meant that there has been relatively little work investigating the temporal aspects of connectivity and associated uncertainties (Zeigler and Fagan 2014; Mui et al., 2016).

Both landscape structure and organism behaviour exhibit temporal variability (Fahrig 1992; Mui et al., 2016). This dynamism has long been recognised in metapopulation studies (e.g. Johst et al., 2002; Akçakaya et al., 2004; Snäll et al., 2005), although this understanding has been largely applied to habitat patches rather than the surrounding

matrix (Zeigler and Fagan 2014). Connectivity between habitat patches may, however, shift dramatically through time with connections opening and closing due to changes in landscape structures or in how an organism perceives the landscape (Wimberly 2006). Changes in connectivity due to landscape structural change are exemplified by ephemeral waterways linking permanent waterbodies, with connectivity increasing when waterways are filled but declining when they dry out (e.g. Bishop-Taylor et al., 2017; DeAngelis et al., 2010; Kerezsy et al., 2013; Perry and Bond 2009). Connectivity may also change in response to changes in organism behaviour such as shifts in energetic demands between seasons (e.g. Mui et al., 2016). Behavioural changes may occur in the presence of a heterospecific species; for example some avian species in Florida increase movements between habitat patches over risky landscapes in the presence of tufted tit-mice (*Baeolophus bicolor*) (Sieving et al., 2004). Connectivity changes may occur regularly (i.e., periodically) over short timespans, such as seasonal changes, and these changes can be important for conservation management planning. These connectivity changes may be especially important in highly dynamic landscapes, such as agricultural areas (Burel and Baudry 2005), where connectivity will be shifting near constantly.

Relative to a static snapshot of a landscape, connectivity may change through time in a number of ways. Connectivity can increase relative to some initial estimate if low-cost connections between points in the landscape develop or high-cost barriers are removed. For example, the removal of late successional forest during clearcutting enhanced inter-patch connectivity for the marsh fritillary butterfly (*Euphydrus aurinia*) because it made the matrix more structurally similar to habitat patches (Wahlberg et al., 2002; Zeigler and Fagan 2014; Blixt et al., 2015). Connectivity may also decrease relative to an initial estimate due to increases in the distance between habitat areas, increased difficulty in traversing the matrix, or the formation of barriers, such as occurs when connecting waterways dry out (e.g. Roe et al., 2009). It is, therefore, important to attempt to develop multiple connectivity measures for a landscape to capture regular (e.g. seasonal) changes over the time-period of interest (Mui et al., 2016). However, generating multiple connectivity estimates is likely to be difficult and costly because it requires high-resolution landscape and movement data. Due to the difficulty and costs involved in their creation it is important that any connectivity estimate calculated with the goal of capturing regular changes is able to predict the size and direction of connectivity changes for as long a timespan as possible.

Being able to predict periodic changes in connectivity (e.g. due to seasonal hydrological dynamics) is becoming increasingly difficult under ongoing climate change. Increases in the energy in the atmosphere along with increasing air and water temperatures, push local precipitation regimes towards their extremes, amplify the frequency of extreme weather events, and alter disturbance regimes (Solomon et al., 2009; Turner 2010; Pachauri et al., 2014). These changes can increase the variability of systems and may cause connectivity to shift in unpredictable ways that may enhance regular seasonal changes or override them altogether. Increasing variability may reduce the timespan over which a set of connectivity estimates are useful, particularly in ecosystems that are highly sensitive to these changes.

We investigated the robustness of connectivity estimates generated for simulated landscapes experiencing regular (seasonal) changes in connectivity in the context of differing amounts of inter-seasonal variability. We focused on two aspects of connectivity change: 1) how do differing levels of variability alter connectivity estimates between seasons and, 2) how do these alterations accumulate through multiple seasons? In order to investigate these questions we adopted a virtual ecology approach (Zurell et al., 2010). We simulated a number of cost-surfaces that served as our baseline landscapes. Each surface then underwent cost changes across multiple seasons with various amounts of inter-seasonal variability superimposed on the underlying seasonal dynamic. The connectivity of each surface for every season was then estimated and the similarity between estimates calculated. The use of a

virtual ecology approach allowed us to investigate a large number of different landscapes over multiple seasons with a large degree of control as to the amount of variability introduced.

2. Materials and methods

2.1. Generation of initial cost-surface

Cost-surfaces were made up of a 100×100 cell regular grid generated using the random clusters nearest-neighbour neutral landscape function in the NLMpy package in Python V2.7. (Saura and Martínez-Millán 2000; Etherington et al., 2014). We used this neutral landscape function because it approximates the patchy or fragmented landscapes in which connectivity studies are often conducted (Zeller et al., 2012). Cost-surfaces were divided into 10 element classes. Each surface element class (i.e., habitat type) was assigned a cost value corresponding to the surface class generated by the random clusters algorithm. Cost values ranged from 10 to 100. Various spatial arrangements were generated by modifying:

1. The maximum cluster size (i.e. maximum number of cells in a single cluster), determined by altering the proportion of cells selected to form unique clusters in the random clusters algorithm. Proportions ranged from 0.2 to 0.5.
2. The proportion of cells in a cost-surface that were of the lowest cost class, the remainder of the surface was divided equally between the other classes. Proportions ranged between 0.1 and 0.5.

We used Latin hypercube sampling to obtain even coverage across the cost-surface generation parameter space (McKay et al., 1979), sampling 100 points in the two-dimensional parameter space. Seasonal changes were then applied to each of the 100 cost-surfaces for 20 seasons with no variability added; this seasonal process was then repeated across five different levels of variability.

2.2. Seasonal change and inter-seasonal variability

At the start of a model iteration (i.e. time 0) each cost-surface element class was assigned a cost change value D, drawn from a uniform probability distribution:

$$D \sim U(-5,5) \tag{1}$$

The range of this distribution was selected to ensure that the rank order of cost-surface elements did not change (although this assumption may not hold in reality), while also ensuring that the mean cost of the surface remained fairly constant. During the first season the cost change value (D) for each element was added to the initial cost value (C_i) to create a new cost value (C_{i+1}). In the following season the cost change value (D) was subtracted from the cost value of the previous season (C_{i+1}) to create a new cost value (C_{i+2}). The value of C_{i+2} equalled the value C_i of when no inter-seasonal variability was added.

$$C_{i+t} = \begin{array}{l} C_i + D, \ t \in \{\mathbb{O}\} \\ C_i - D, \ t \in \{\mathbb{E}\} \end{array} \tag{2}$$

Where: C_{i+t} was the cost value of for the season t, C_i was the cost value of the previous season, D was the cost change value, $\mathbb{O}$ was the set of odd seasons, and $\mathbb{E}$ was the set of even seasons. This cycle of change for alternate seasons continued throughout the model run, with each run lasting 20 seasons (10 season pairs, hereafter termed 'years'). A minimum cost value of 0 was set to prevent negative cost values occurring as these are uncommon in the literature and are difficult to interpret biologically (Zeller et al., 2012).

In simulations where inter-seasonal variability was added a variability value V was drawn from a Gaussian distribution ($\mu = 0$; $\sigma = SD$) at the start of each season. The variability value (V) was redrawn for