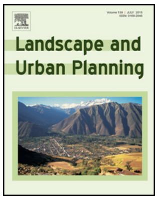
Landscape and Urban Planning 141 (2015) 11–23

Contents lists available at ScienceDirect

Landscape and Urban Planning

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



Research Paper

A framework for incorporating fine-scale dispersal behaviour into biodiversity conservation planning

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HIGHLIGHTS

- We describe a multi-scale connectivity framework for conservation planning.
- The model characterises connectivity at fine resolutions over large spatial extents.
- Graph networks are used at the regional scale and Circuitscape at the local scale.
- The framework was designed specifically to be applied by landuse planners.
- We demonstrate the framework in the Lower Hunter, New South Wales, Australia.

ARTICLE INFO

Article history:
Received 20 March 2014
Received in revised form 15 April 2015
Accepted 22 April 2015

Keywords:
Connectivity
Dispersal
Circuitscape
Graph theory
Least-cost paths
Conservation planning

ABSTRACT

Fine-scale landscape features such as scattered trees are increasingly thought to be critical for dispersal, and need to be considered in connectivity modelling and planning. Yet existing modelling approaches struggle to adequately take fine-scale features and threshold dynamics of dispersal behaviour into account, in part because of computational limitations. We present a framework for modelling connectivity at fine spatial resolutions over large spatial extents. Our framework involves a novel approach to characterising fine-scale dispersal behaviour within the context of existing modelling methods, and uses key parameters of dispersal behaviour to link models and their interpretation at multiple scales. We address computational limitations by creating a gap-crossing threshold layer, which identifies areas where dispersal is possible because of the presence and spacing of fine-scale connectivity elements. This layer is combined with a dispersal-cost layer within a graph-network analysis to identify the optimal least-cost path between patches. Graph metrics are used to assess the importance of specific patches at the regional-scale and to describe connectivity for the whole landscape. A local-scale connectivity model using the Circuitscape software complements the regional analysis outputs by considering all possible pathways across a landscape simultaneously rather than a single least-cost path. The framework was designed specifically to be applied by land use planners who need to quantify the impacts of property development on fine-scale connectivity, yet need to assess implications at the regional scale. We demonstrate the framework by applying it in the Lower Hunter region, Australia.

1. Introduction

Human modification of landscapes results in fragmentation and isolation of populations of native species, increasing the risk of extinction due to demographic and environmental stochasticity (Brook, Sodhi, & Bradshaw, 2008; Caughley, 1994; Lindenmayer & Fischer, 2007). Identifying, conserving or restoring vegetation in locations thought to be critical for supporting dispersal and

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http://dx.doi.org/10.1016/j.landurbplan.2015.04.008

population connectivity is therefore a key focus of conservation efforts (Lindenmayer & Fischer, 2007). Landscape connectivity can be considered as the degree to which a landscape aides or restricts movement between patches of habitat. It includes structural aspects such as the arrangement of landscape elements like “stepping stones” or “corridors”, and functional aspects which characterise how species movement between patches is affected by landscape structure (Hilty & Merenlender, 2006; Taylor, Fahrig, & With, 2006).

Increasingly, empirical studies are revealing that the dispersal movements of animals in fragmented landscapes depend on very fine-resolution elements of structural connectivity such as roadside corridors, and small, isolated features such as individual paddock trees, shrubs, rocky outcrops or small clusters of these features that can act as stepping stones (Bennett, 1990; Carruthers, Bickerton, Carpenter, Brook, & Hodder, 2004; Doerr, Doerr, & Davies, 2010; Gibbons & Boak, 2000; Robertson & Radford, 2009). For conservation planning and management to be effective, connectivity modelling must incorporate this knowledge of fine-scale species dispersal behaviour. Yet conservation planning and prioritisation often occur over relatively large areas, so models to assist planning need to simultaneously incorporate fine-resolution spatial data while modelling their implications over large areas. Unfortunately, our ability to characterise connectivity at fine spatial resolutions over large spatial extents is currently restricted by the computational limitations of common modelling software and desktop PC platforms, so compromise solutions are required (Moilanen, 2011; Pelletier et al., 2014).

Current approaches to connectivity modelling include least-cost path analysis, circuit theory and graph theory, each of which attempts to incorporate more ecological realism in different ways while avoiding computational limits (Adriaensen et al., 2003; Foltête, Clauzel, & Vuidel, 2012; McRae, Dickson, Keitt, & Shah, 2008; Urban & Keitt, 2001). Least-cost path and circuit theory analysis characterise non-habitat using dispersal costs which are intended to represent the energetic costs, difficulty, or mortality risk of moving across these areas (Adriaensen et al., 2003; Sawyer, Epps, & Brashares, 2011). Dispersal cost is typically determined by land cover characteristics, such as levels of urbanisation, combined with species-specific dispersal probability over various distances. Using cost-weighted distance analysis, least-cost pathways between patches of suitable habitat can be calculated. The significance of patches within a connectivity network can be quantified using the graph theoretic approach and calculation of network measures/graph metrics (Minor & Urban, 2008; Rayfield, Fortin, & Fall, 2011; Urban, Minor, Treml, & Schick, 2009). In contrast, circuit theory conceptualises the landscape as a conductive surface within an electrical circuit, characterising “resistance” to movement for every raster grid cell, considering current flow as analogous to individual movement probabilities (McRae et al., 2008).

Although all these approaches have made significant contributions towards modelling landscape connectivity in a useful and appropriate way, they still have a number of critical limitations. First, there is no single method that adequately evaluates the connectivity contributions of both patches and the intervening areas (‘interpatch’ areas). Second, none of these approaches adequately incorporates truly fine-scale features such as scattered trees. Finally, there is increasing evidence that threshold dynamics (Doerr, Doerr, & Davies, 2011; Smith, Forbes, & Betts, 2013) are often not appropriately modelled using cumulative cost approaches. For example, Doerr et al. (2011) found that dispersing and nomadic woodland birds will readily cross gaps between scattered trees of up to 100 m in agricultural land with no apparent cumulative cost. These birds also use a foray search strategy and thus will only continue to move between scattered trees for about 1.1 km before returning, suggesting that dispersal costs begin to sharply accumulate only after a particular distance.

To address these limitations of current connectivity modelling approaches, we developed a framework that uses detailed information on fine-scale dispersal behaviour and empirically derived thresholds. Both fine-scale connectivity and thresholds are generally not well-represented by existing modelling approaches. Our approach rescales the necessary fine-scale data to coarser grain sizes in a way that still preserves the threshold dynamics while addressing the computational limitation associated with processing high spatial resolution data over large extents. The framework is based on regional and local-scale connectivity models using the same underlying data and ecological principles. It was developed in response to requests from end-users in government and non-government agencies who are required to assess the importance of connectivity at local-scale for single or multiple properties such as in response to a development approval and/or environmental impact assessment. Ensuring that local-scale connectivity between or within fine-scale features such as scattered trees and road side corridors are adequately modelled is of key importance for these end-users.

In this paper we describe a framework for characterising connectivity based on fine-scale dispersal behaviour specifically designed for planners who commonly assess developments at the property-scale, yet need to assess implications at the regional scale. The framework includes: (a) a workflow that starts with the identification of key ecological connectivity parameters; (b) pre-processing spatial data based on these parameters; (c) a software tool for automating this processing; and (d) a method for running these spatial data within existing connectivity modelling software. At the regional scale we use the Graphab graph theoretic connectivity model (Foltête et al., 2012) to characterise patch isolation and optimal least-cost paths between patches. Circuit theory connectivity modelling using the Circuitscape software (McRae et al., 2008) is then used to assess connectivity at local-scales for a subset of the region, considering all possible pathways across a landscape simultaneously rather than a single optimal path. We demonstrate this approach using the Lower Hunter Region, Australia as a case study, assessing connectivity between native woody vegetation, parameterised using two thresholds; the interpatch-crossing and the gap-crossing distance, based on a review by Doerr et al. (2010) of Australian connectivity studies.

2. Framework for multi-scale connectivity models based on fine-scale dispersal

Our framework is a six step process for modelling connectivity at local and regional scales based on identifying key ecological rules, particularly threshold dynamics in dispersal, and using them to paramaterise existing graph-theoretic, least-cost path and circuit theory connectivity modelling approaches (Fig. 1). The framework was developed by engaging a range of stakeholders who represented potential end-users from government and non-government agencies. Conservation planning for these organisations is often in response to a development proposal on a single property or multiple properties and needs to occur within short time periods in response to these development requests. Thus approaches commonly developed for academic research such as the construction of a single species connectivity model using empirical data (Rudnick et al., 2012) are not feasible in the timeframes required by these organisations. The framework also needs to utilise the best available science so that the methods are defensible when challenged by development proponents, yet be simple enough to be used without highly specialised GIS expertise and ecological knowledge that these organisations often lack.

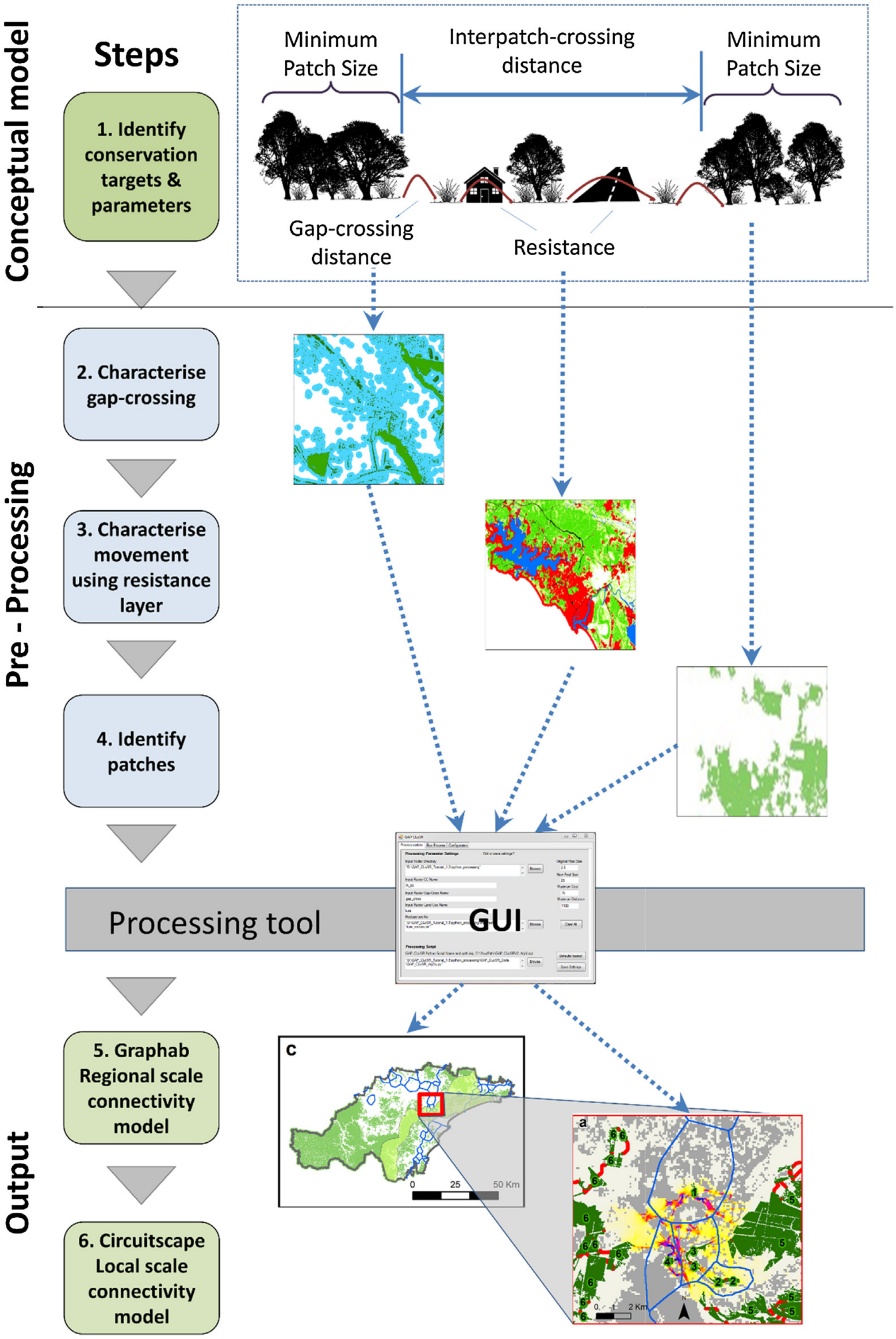

Fig. 1. Flow diagram describing the steps used in parameterising the general connectivity model.

The six step process is explained in the following sections with an example based on a case study in the Lower Hunter Region, an area of approximately 430,000 ha in New South Wales, Australia, approximately 100 km north of Sydney. The region includes a mix of natural and modified environments, from highly urbanised areas and farmlands, to natural habitat across mountain ranges to coastal and estuarine environments. A more detailed version of the Lower Hunter case study including the methods can be found in Lechner and Lefroy (2014).

2.1. Step 1: Identify focal conservation target and key dispersal parameters

The first step of the framework is to identify the focal conservation targets and their key dispersal parameters. The targets may be species, ecological communities or ecological systems (The Nature Conservancy, 2007). Targets should be chosen based on their how they represent biological diversity and/or their status such as a species in decline or protected by legislation (see The

Nature Conservancy, 2007). In the Lower Hunter, we modelled functional connectivity between patches of remnant woody vegetation which provide habitat for the majority of woodland or forest-dependent fauna species and the plant species that depend on these fauna for dispersal. We therefore modelled connectivity between environmentally similar habitats instead of species, similar to the land-facet concept that has been used in Australia (e.g. Drielsma, Howling, & Love, 2012) and internationally (Alagador et al., 2012; Brost & Beier, 2012). A connectivity model such as this reflects a compromise between the uncertainty associated with the complexity of parameterising a multi-species connectivity model, and the simplicity of a structural connectivity model that ignores the complexity of species movement between patches (hereafter we refer to this as a "general connectivity model").

The focal conservation target is modelled with three parameters (Doerr et al., 2010):

(a) minimum patch size;
(b) gap-crossing distance threshold;
(c) interpatch-crossing distance threshold.

The gap-crossing distance threshold describes the maximum distance of open areas (i.e., matrix/non-habitat) that individuals can cross between structural connectivity elements and/or patches (sensu Doerr et al., 2010). For example, the distance between isolated scattered trees, or the size of a break in an otherwise continuously vegetated riparian corridor. Structural connectivity elements are features that do not provide habitat in themselves (unlike patches), but can be used for dispersal. Connectivity elements include wildlife corridors (linear links between patches), disconnected linear elements, and stepping-stones (paddock trees, shrubs, rocky outcrops, or small clusters of these features). The modelling of structural connectivity elements such as scattered trees is not currently considered in connectivity models for conservation planning.

The interpatch-crossing distance threshold is the maximum distance individuals will move between patches when structural connectivity elements are present within the gap-crossing distance. Note that this is distinctly different from a dispersal distance, as individuals could cross many of these interpatch-crossing distances through structural connectivity, but may still need the patches to be close to provide resting and feeding sites. Our use of the term gap-crossing is in accordance with Doerr et al. (2010), rather than other studies that do not differentiate movement between patches from movement between structural connectivity elements (e.g. Duggan, Heske, & Schooley, 2012; Smith et al., 2013). The use of thresholds in our framework also differs from other methods based on a single average dispersal distance and a distance decay function (Hanski, 1994) to model the probability of dispersal at various distances (e.g. Drielsma, Manion, & Ferrier, 2007; Tournant, Afonso, Roué, Giraudoux, & Foltête, 2013).

The choice of dispersal parameters used in the framework and their actual values used in the Lower Hunter case study were recommended from a systematic review of connectivity by Doerr et al. (2010), which synthesised all available evidence on the relationship between structural connectivity and movements of Australian native species. The review involved a meta-analysis of 81 studies (representing 41 species of mammal, 32 birds, 8 reptiles and 5 species each of plants and invertebrates) that contained information on both movement and fine-scale landscape structure, primarily in fragmented woodland and forest environments. The review concluded that scattered trees were just as important for facilitating dispersal and other species movements as were other landscape elements such as linear corridors.

The review calculated values for a mean gap-crossing distance threshold and an interpatch-crossing distance threshold based on a subset of studies for which such detailed fine-scale information was available. The gap-crossing distance threshold of 106 m represented the maximum distance, averaged across studies, that individuals were likely to travel from one element of structural connectivity to the next. The interpatch-crossing distance threshold of 1.1 km represented the maximum distance, averaged across studies, that individuals were likely to travel through some kind of structural connectivity before turning around. The values for dispersal distances used in the framework will differ with species and environments, however within Australia they represent a useful starting point for parameterising connectivity models.

2.2. Step 2: Characterise fine-scale threshold dynamics

If gap-crossing distance thresholds exist, beyond which dispersers may not cross non-habitat, then there will be some areas of a landscape that can support dispersal movements and others that cannot. This binary distinction modelled in the framework contrasts with other approaches to modelling dispersal potential which are based on continuously varying probabilities. While probabilities may be a more mathematically sophisticated approach, they may not match current empirical understanding if threshold dynamics are present. Our approach incorporates fine-scale dispersal (threshold) dynamics by creating a binary gap-crossing distance threshold layer which identifies areas in which the average distance between structural connectivity elements and patches is below a threshold (in this case 106 m). This step removes the need to model dispersal between all structural connectivity elements, reducing computational demands while still reflecting realistic dispersal behaviour.

The binary gap-crossing distance threshold layer can be created by identifying distances between structural connectivity elements and patches using high resolution spatial data (Fig. 2). The first step in the creation of the gap-crossing layer is mapping vegetation that contributes to structural connectivity elements and patches. In the Lower Hunter this was mapped using SPOT satellite vegetation data at 2.5 m resolution (see Siggins et al., 2006 for relevant metadata and classification accuracy information). In the next step vegetation is buffered by half of the gap-crossing distance threshold, which was 53 m in our case study (Fig. 2a). Therefore if structural connectivity elements or patches are within the gap-crossing distance threshold, the 53 m buffers will touch or overlap and connectivity between will be possible (Fig. 2c). Areas mapped outside the buffer area describe areas in which dispersal cannot take place. The approach described in this study represents one possible method for simulating a binary gap-crossing layer. Another approach that is less computationally intensive, but less precise than this buffer analysis is described in Lechner and Lefroy (2014). Regardless of the method used, a key novel feature of this step is the simulation of fine-scale dispersal based on the presence of structural connectivity through a simple binary gap-crossing layer.

2.3. Step 3: Create dispersal-cost surface

2.3.1. Create resistance layer from land use/land cover (LULC) map

Resistance to dispersal between patches is characterised by increasing the movement costs based on coarse land cover properties. For example, urban areas that contain appropriately spaced structural connectivity elements may still be more costly to move through than agricultural areas containing the same structural connectivity elements. If land cover with high dispersal resistance doubled the movement cost, the interpatch-crossing distance threshold would be reduced from 1.1 km to 550 m.

In the Lower Hunter we used generic land cover classes that are not specific to a particular land cover mapping method. Four land

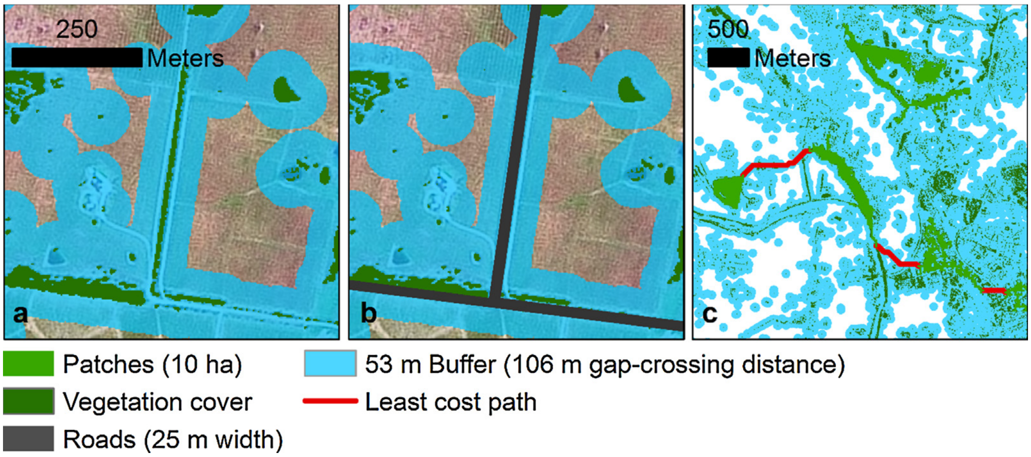

Fig. 2. Processing to create gap-crossing layer. (a) High spatial resolution vegetation data representing structural connectivity elements buffered by half of the gap-crossing threshold distance, which was 53 m in our case study. (b) Vegetation in narrow corridors would disappear when aggregated if the neighbouring pixels included barriers such as roads classified as having infinite cost. (c) Areas mapped outside of the buffer area are dispersal barriers for least-cost path mapping.

Table 1
Land cover dispersal costs under different scenarios of gap-crossing thresholds and dispersal barriers where dispersal cost is characterised as an increase in cost based on a multiplier.

Scenario name and description	Dispersal cost			
	Other	Hydro.	Trans.	Infra.
Default scenario	× 1	× 3	× 2	× 2
Scenario 1: No land cover dispersal costs and gap-crossing threshold layer excluded	× 1	× 1	× 1	× 1
Scenario 2: No land cover resistance, but gap-crossing threshold used	× 1	× 1	× 1	× 1
Scenario 3: Gap-crossing threshold 53 m	Default scenario			
Scenario 4: Gap-crossing threshold 212 m	Default scenario			
Scenario 5: Road Barriers + default parameterisation	× 1	× 3	× 2	Infinite

cover/land use (LULC) classes were identified as being important in the region: Infrastructure (urban and industrial areas), Transportation (roads and train lines), Hydrological (water-bodies such as rivers and lakes) and Other (predominantly agricultural and grazing areas). The movement costs associated with each class are outlined in Table 1 for a default scenario based on best available ecological knowledge.

A key feature of the framework is identifying land cover classes that are considered to have no additional movement costs, where movement is only restricted by the presence or absence of structural connectivity. In the Lower Hunter this was represented by the "Other" land cover class, which is predominantly agricultural and grazing areas. If structural connectivity is present in these areas individuals may move at their maximum dispersal distance.

2.3.2. *Combine gap-crossing layer and land cover resistance surface*

The final step in the creation of the dispersal-cost surface was combining the binary gap-crossing layer with the resistance surface based on land cover. The dispersal-cost value assigned to each pixel is a function of: (a) pixel size (e.g. if the pixel size is 30 m and there is no resistance the cost should be 30 m); (b) land cover resistance (200% resistance means a pixel size with of 30 m will have a value of 60 m); and (c) the presence of structural connectivity elements identified with the gap-crossing layer.

Once again, for computational purposes, a trade-off was required between the spatial extent and the spatial resolution (i.e., pixel size). However, important land cover elements, such as roads, train tracks, fence lines, rivers or streams that are dispersal barriers can occur at fine scales. To address this limitation the pixel size of the dispersal-cost surface was aggregated using a method that preserves dispersal costs in a realistic way, as shown in Fig. 3. A summary of the processing rule set is: (a) structural connectivity elements take precedence over all other land cover classes, because dispersal cannot occur in the absence of structural connectivity; (b) barriers will have infinite cost regardless of their physical size in relation to the aggregated pixel size. This processing step is important to ensure linear features that represent barriers are actually modelled as barriers (Adriaensen et al., 2003; Rothley, 2005) and there are no discontinuities as a result of the aggregation process; and (c) the dispersal cost for a single aggregated pixel is calculated as an average of all land covers except if a barrier or structural connectivity is present as described in (b) and (c). The result is a layer that recognises threshold dynamics by ensuring there is no probability of dispersal where gaps are too large between structural connectivity elements, but still reflects cumulative costs where dispersal is considered possible but may be impeded by land use. Furthermore, as the gap-crossing layer has a greater area than the original vegetation from which it was derived, neighbouring pixels with high or infinite cost such as roads do not remove these elements from the dispersal-cost surface when aggregated and averaged (Fig. 2b). This phenomenon typically occurs when dispersal pathways such as wildlife corridors occur alongside high-cost features such as roadside vegetation.

In the Lower Hunter the original pixel size of 12.5 m (1:25,000) for the LULC and 2.5 m for the canopy cover layer were aggregated to 25 m. We found that 25 m was the finest pixel size that could be processed by the Graphab connectivity software in a study of this spatial extent (4300 km^2), patch size and configuration.

2.4. *Step 4: Identify minimum patch size*

The landscape was characterised as either a patch of suitable habitat or non-habitat. This conforms to the discrete patch-matrix

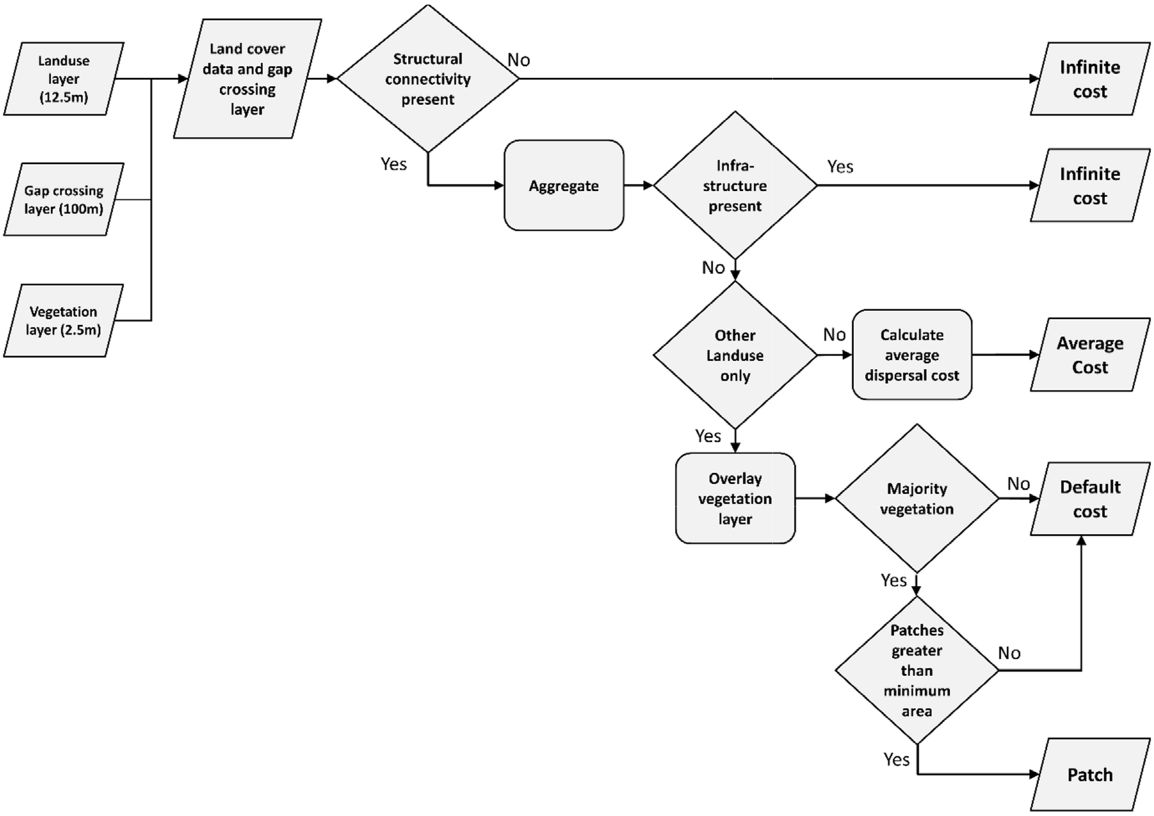

Fig. 3. Processing flow chart describing the derivation of a raster layer that represents patches of habitat and dispersal costs at a coarser pixel size than the original input data.

paradigm commonly used in landscape ecology (Forman & Godron, 1986) and most connectivity studies in Australia (Doerr et al., 2010). Habitat is characterised by identifying a minimum vegetation patch size. In the Lower Hunter we used a minimum patch size of 10 ha, as a variety of Australian studies have suggested that woodland birds in particular are often absent from patches smaller than 10–20 ha (see Doerr et al., 2010).

Patches are calculated from the outputs of the previous processing steps using the aggregated pixel values where vegetation is in the majority and pixels did not contain other land cover classes such as infrastructure, hydrology or transport. Using aggregated data was especially important in the Lower Hunter case study as there are likely to be gaps in the canopy at the pixel size of the SPOT 2.5 m (Siggins et al., 2006) typical of woodlands and forests that do not reflect gaps within the habitat.

2.5. Step 5: Regional-scale connectivity model based on graph theoretic approach and least-cost paths

The graph theoretic approach is used within the Graphab software (Foltête et al., 2012) to represent the landscape as a set of nodes and edges, where the nodes are patches within a network and the edges represent connectivity pathways between nodes (Minor & Urban, 2007). Linkages between patches are characterised using least-cost analysis which identifies the single most optimal link between patches based on cumulative cost in relation to land cover resistance (Etherington & Penelope Holland, 2013; Minor & Urban, 2008).

Patches that are linked to each other but isolated from other patches form components – groups of interconnected patches. Whether a patch is linked to another patch will depend on distances between patches, the interpatch-dispersal distance threshold, the resistance of the landcover and presence of structural connectivity at the gap-crossing distance thresholds. The first step in an analysis based on this framework is interpreting connectivity visually from the spatial configuration and extent of components to identify where connectivity is potentially present and which areas are isolated.

In the next step graph metrics can be used to characterise the complex patterns of connectivity resulting from the location of multiple nodes and the links between them across a network. A wide variety of graph metrics have been developed to describe these patterns at the patch-scale and at the landscape-scale (Rayfield, Fortin, & Fall, 2010). Patch-scale graph metrics can be calculated for each patch to describe the role of a patch in providing connectivity for a whole network. Of key importance for conservation planning is identifying patches that are critical for maintaining connectivity across a network (Minor & Urban, 2008). In contrast, landscape-scale graph metrics are calculated as a single value intended to describe connectivity for the whole landscape and are useful for comparisons between landscapes or scenarios.

Of key importance in the selection of graph metrics is using metrics that account for the many ways in which dispersal patterns can be described (see Baranyi, Saura, Podani, & Jordán, 2011; Rayfield et al., 2011 for more information on the choice of graph metric). In the Lower Hunter we selected five patch-scale and seven landscape-scale metrics (Table 2) to examine a broad range of components of heterogeneity and ensure that each of the broad categories of spatial heterogeneity described in Rayfield et al. (2010) was measured: route-specific flux, route redundancy, route vulnerability and connected habitat area. The definition of the broad categories of spatial heterogeneity can be found in Supplementary material S1. The result of a regional analysis is an understanding of which patches and links in the landscape appear critical for supporting existing regional networks and thus could be prioritised for long-term protection. It also reveals where components are

Table 2
Patch and landscape-scale graph metrics used in the case study. For Rayfield et al.'s (2011) broad categories of spatial heterogeneity see Supplementary material S1.

Graph metric	Ecological description	Rayfield et al. (2011) Connectivity characteristic	Reference
Patch-scale graph metrics			
Node degree	The number of links associated with a focal patch	Route-specific flux	(Ricotta, Stanisci, Avena, & Blasi, 2000)
Clustering coefficient	The level of redundancy for the patch within a network	Route redundancy	(Minor & Urban, 2008; Ricotta et al., 2000)
Connectivity correlation	The degree of compartmentalisation or presence of sub-networks. Important for reducing the spread of cascading disturbances	Route vulnerability	(Minor & Urban, 2008)
Delta Integral index of connectivity (dIIC)	The loss of habitat availability caused by the removal of the focal patch relative to the connectivity network	Connected habitat area	(Pascual-Hortal & Saura, 2006; Saura & Pascual-Hortal, 2007)
Delta Harary index	Importance of the patch for connecting patches across the landscape	Route-specific flux	(Ricotta et al., 2000)
Landscape-scale graph metrics			
Mean size of components (km^2)	Describes the level of isolation between groups of landscape patches	Route-specific flux	(Urban & Keitt, 2001)
Size of largest component (km^2)	Describes the level of isolation between groups of landscape patches	Route-specific flux	(Urban & Keitt, 2001)
Number of components	Simple measure that describes the number of isolated areas in the landscape	Route-specific flux	(Urban & Keitt, 2001)
Harary index	The number of patches that contribute to linking patches across the landscape. High value indicates low number of patches and connected landscape	Route-specific flux	(Ricotta et al., 2000)
Class coincidence probability	Measure of dispersal relative to component isolation based on the probability that two randomly located points are found in the same component	Connected habitat area	(Pascual-Hortal & Saura, 2006)
Expected cluster size (km^2)	The mean area that a disperser has access to	Connected habitat area	(O'Brien, Manseau, Fall, & Fortin, 2006)
Integral index of connectivity (IIC)	Probability that two dispersers randomly located in the landscape can access each other	Connected habitat area	(Pascual-Hortal & Saura, 2006)

unconnected, which could indicate priority locations for restoring connectivity.

Along with the assessment of the default parameterisation, the sensitivity of the connectivity model to choices in the model parameterisation needs to be tested. In this paper we illustrate the contribution of the gap-crossing layer and the aggregation method to the connectivity model by testing five sensitivity analysis scenarios which compare the presence and absence of the gap-crossing layer, gap-crossing distance thresholds and the characterisation of dispersal barriers (Table 1). For each scenario, landscape or network-scale graph metrics can be calculated to assess overall differences in connectivity patterns. The differences in the graph metrics and the least-cost pathways and components can also be assessed visually to evaluate the parameters most sensitive to uncertainty.

2.6. Step 6: Local-scale connectivity model based on Circuitscape

After Graphab is used to identify the single most optimal links between patches, Circuit theory connectivity modelling using the Circuitscape software (McRae et al., 2008) is used to assess a subset of the region in response to specific planning questions, characterising connectivity for all pixels in the landscape simultaneously. Circuitscape models the landscape as analogous to an electrical circuit, characterising movement across a resistance surface as current flowing through a circuit, in order to derive all possible pathways to traverse the landscape from one point or region to another. Maps of current density flow measured in Amps can be created by modelling electrical current from multiple individual pairs of sources (patches or groups of patches) to highlight alternative pathways and "pinch points" of high current density, where loss of a small area could disproportionately compromise connectivity (McRae et al., 2008).

Circuitscape can be used with exactly the same input datasets as used in the regional analysis with Graphab. Although Circuitscape allows for the gap-crossing distance threshold to be incorporated, it does not enable the interpatch-crossing distance threshold to be incorporated (as Graphab does). Due to computational limitations associated with the current desktop version of Circuitscape (Mcrae & Shah, 2009; Pelletier et al., 2014), it can only be run on a subset of the study area at the same spatial resolutions as the regional modelling. It is important that the subset includes the core area being tested and a buffer area to avoid biased landscape resistance estimated with circuit theory (Koen, Garroway, Wilson, & Bowman, 2010).

Circuitscape is used within our framework for the following types of analysis: (a) an assessment of potential interpatch path redundancy where least-cost pathways between patches have been identified and (b) an assessment of potential areas for rehabilitation or protection at pinch points in areas beyond the interpatch-crossing dispersal distance. In the first type of analysis dispersal between patches based on the optimal paths identified by Graphab can be compared to the Circuitscape analysis. In this case each patch is considered as a focal node. Using this method, potential redundancy or bottlenecks to connectivity between patches can be identified. This type of analysis is especially important where there are two large neighbouring patches with only a single least cost-path representing connectivity between those patches. Planners need to assess whether the least-cost path is a unique link between patches or connectivity can occur at other locations between the patches. In the second analysis, connectivity can be assessed between components where all patches within a component are treated as a single node. As dispersal beyond the interpatch-crossing distance threshold is allowed it is therefore also useful to identify areas suitable for connectivity restoration. An example of these two types of analyses is provided using the Lower Hunter case study. In both analyses we used pairwise analysis with four neighbourhood connections and current density was log-transformed following Mcrae and Shah (2009).

3. Pre-processing tool

Steps 1–4 have been automated in a freely available software tool which can be accessed from a graphical user interface or directly using the Python programming language. The tool utilises the ArcGIS 10.1 Python libraries and is part of the General Approach to Planning Connectivity from Local Scales to Regional (GAP CLoSR) framework (see www.github.com/GAP-CLoSR).

4. Case study to illustrate the application of the framework

In the following section we provide a brief overview of all the outputs, paying special attention to the unique outputs of this framework using examples from the Lower Hunter case study.

4.1. Regional-scale connectivity model using Graphab

The first step in the framework is assessing regional-scale connectivity using Graphab. These outputs, especially the location and shape of the least-cost paths have straightforward interpretations and explicit relationships to the ecological parameters and can be easily verified with aerial photo or field observations. For example, it is simple to relate component boundaries to interpatch-crossing distance threshold and landcover between patches or the pattern of a least-cost path to the presence of structural connectivity (e.g. Fig. 2).

The spatial configuration and extent of components (isolated groups of interlinked patches) identified by Graphab provides a simple way of assessing fragmentation based on functional connectivity. In the Lower Hunter, the component boundaries identified two large components in the west and the east (Fig. 4, Component 1 and 2). The western component (Fig. 4, Component 1) included 80% of total patch area in the Lower Hunter region, demonstrating that these patches are connected for dispersal purposes. A highly fragmented area, consisting of small components made up of one or a few small patches can be found in the centre of the Lower Hunter from Branxton to Newcastle and Morriset, isolating the two largest components in the east and west.

In the next step more complex outputs from patch-level graph metrics were applied to assess the importance of a specific patch or linkage. The dIIC is a graph metric that characterises patches based on their importance for connectivity relative to their area (Fig. 4). In the Lower Hunter the larger patches also connected multiple smaller patches, producing the highest dIIC values. The Clustering coefficient graph metric, in contrast, describes patch redundancy, useful for identifying stepping stones for connectivity. Patches with high Clustering coefficient were often smaller and thus had low dIIC value (Compare Fig. 4 inset versus Fig. 5 inset).

A final stage in the regional-scale analysis is to visually test the sensitivity of the regional model to the ecological parameterisation by assessing differences in least-cost paths, components and patch metrics, or quantitatively test sensitivity through landscape graph-metrics with the five scenarios (Fig. 6, Fig. S1 and Table 3). This analysis is important as the parameterisation of these types of models is likely to be driven by expert opinion with high uncertainty compared to empirical data. Fig. 6 provides an illustration of the impact of two of the unique features of the processing methods described in this framework, the gap-crossing layer and the preservation of barriers regardless of pixel size. In the Lower Hunter the sensitivity analysis showed that parameterisations that reduced resistance, such as Scenario 1: No cost and Scenario 4: Gap-crossing 212 m, increased connectivity as shown by a reduction in the number of components and increase in some landscape metrics such as the Haray Index. The impact of a reduction in the gap-crossing distance threshold could be identified through the loss of least-cost pathways connecting patches (Fig. 6a versus Fig. 6d). Finally, dispersal barriers such as roads which are smaller than the pixel size are preserved through the frameworks processing methods, resulting in reduced connectivity between patches that were connected in all other scenarios (Fig. 6e).

4.2. Local-scale connectivity model using Circuitscape

The first local-scale analysis provides an example of how Circuitscape can be used to assess potential interpatch path redundancy (Fig. 7). Graphab connectivity analysis identifies the single most optimal least-cost path between two patches, but does not identify if there are multiple possible routes between patches. Assessing current density patterns such as pinch points, which are areas of high current density, enables path redundancy and areas where there are few options for linking patches to be assessed qualitatively. In the area of the Lower Hunter shown in Fig. 7, current density values were visually homogenous where the land-use is predominantly grazing with scattered trees that provide structural connectivity and allow for dispersal. The local-scale analysis showed that the least cost paths identified by the regional analysis may not be the only possible functional connections between patches, particularly where scattered trees may be widespread. Thus, while the least-cost path locations could be targeted for management to maintain current connectivity values (including prevention of land use change), the precise location of such management activities could deviate from the least-cost path where necessary to accommodate the preferences of local land owners.

The second local-scale analysis shows how Circuitscape can be used to assess potential areas for restoration or protection in areas beyond the interpatch-crossing dispersal distance and where no structural connectivity occurs (Fig. 8). This location is highly fragmented and composed of 8 separate components that included one or more patches. Circuitscape showed high current density values near the patch locations (focal nodes), where dispersal costs were low, along pathways that have short distances between remnants, and at pinch points where there were few options for dispersal (Fig. 8). This area included multiple narrow high current density pathways between patches suggesting that options for connecting this landscape are limited. These pathways may be good candidates for restoration by adding patches or structural connectivity elements. These restoration scenarios could be then tested with Graphab as the least-cost path method better represents our conceptual model of connectivity that includes interpatch-crossing dispersal thresholds.

5. Discussion

We have presented a general connectivity modelling framework to accommodate fine-scale dispersal behaviour within a regional-scale analysis. This is achieved by integrating Graphab and Circuitscape analyses, using a gap-crossing distance threshold layer and aggregating data in a way that ensures that barriers are recognised, while addressing computational limitations associated with modelling connectivity using high spatial resolution data (Moilanen, 2011). Key to our method is the incorporation of landscape connectivity elements such as scattered trees that have been identified as critical for dispersal (Carruthers et al., 2004; Doerr et al., 2010; Gibbons & Boak, 2000), but are only identifiable in fine-scaled spatial data (Lechner, Stein, Jones, & Ferwerda, 2009).

5.1. Applying the framework outputs to conservation planning

The framework should initially be followed in a step-by-step fashion as described in Section 2, however, the order in which the outputs are interpreted can be altered in response to conservation

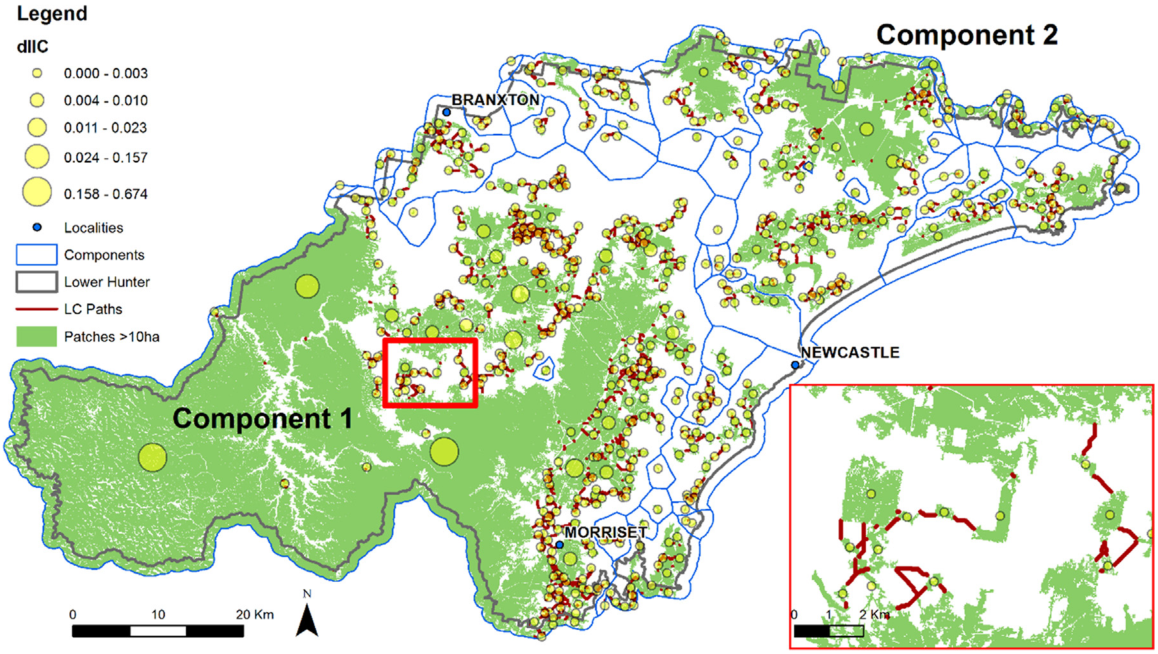

Fig. 4. Regional-scale connectivity analysis using least–cost paths for patches greater than 10 ha using Graphab. The circles located at the centre of patches vary in size in proportion to the dIIC index, a measure of the probability that two randomly located points in a habitat patch are connected. The letters (A–C) denote the three largest patches in the landscape.

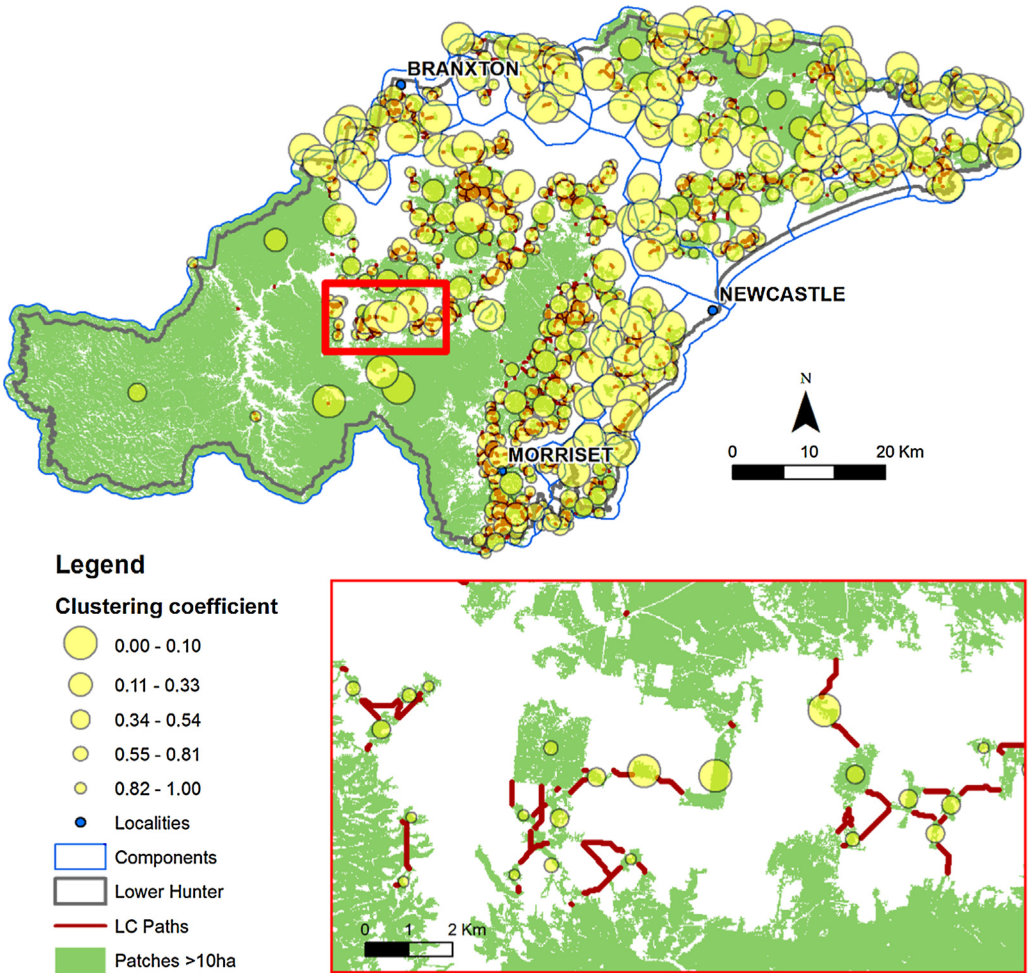

Fig. 5. Regional-scale connectivity analyses based on least–cost paths for patches greater than 10 ha using Graphab. The circles located at the centre of patches vary in size in proportion to the Clustering coefficient value, a measure of patch redundancy in a connectivity network.

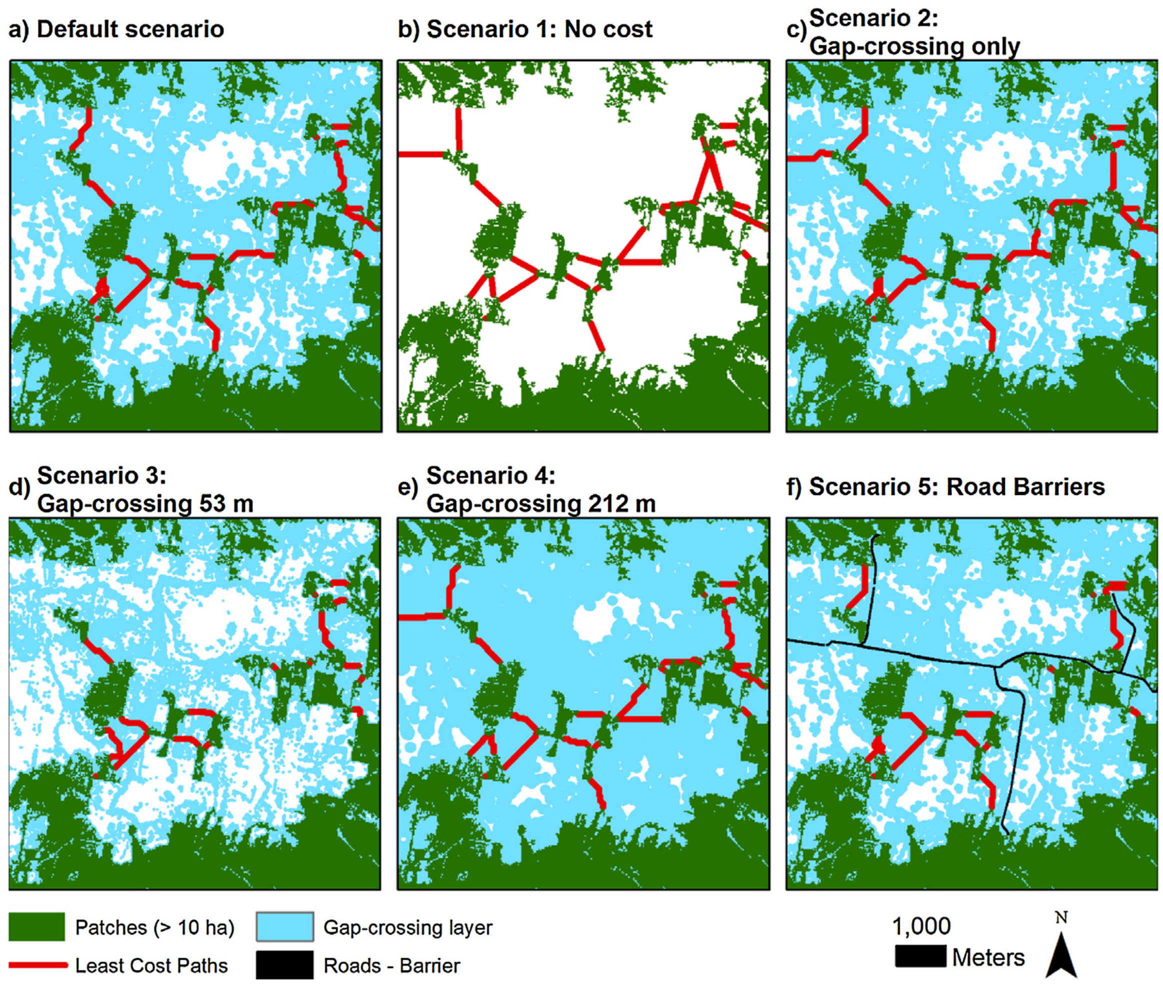

Fig. 6. Comparison of least-cost paths for different scenarios of gap-crossing thresholds and barriers for a subset of the Lower Hunter study area.

objectives and the landscape and planning contexts. The graph-based analysis outputs at the regional scale should first be used to provide a strategic broad-scale overview of connectivity through the identification of patterns of isolation and connection described by the components and the identification of important patches using patch-scale graph metrics, often a principle goal for land use planners (Bergsten & Zetterberg, 2013). For example, in the Lower Hunter the regional-scale analysis revealed a lack of functional connectivity between the east and west of the region. Addressing this may be a strategic long-term goal for the region (Lechner, Brown, & Raymond, 2015).

The regional-scale analysis is likely to be relatively static over time, however, the assessment of development applications at the property level, a more regular task, will require local-scale analysis. At the local-scale a combination of all the frameworks outputs should be used (e.g. Figs. 7 and 8). Circuitscape is used along with the regional-scale modelling outputs (components boundaries and patch-scale graph metrics) for targeted analysis at the local-scale. Only local-scale analysis using Circuitscape can guide the exact placement of protection, restoration or conservation activities within properties, as the least-cost paths alone do not provide the full picture. The regional scale analysis, however, is required to ensure that the areas assessed in the local-scale analysis are considered within their regional context. For example, the Circuitscape analysis described in Fig. 7 is only sensible if the importance of connecting patches outside the local-scale study boundary is considered, based on their regional significance. It is critical to recognise that Circuitscape cannot incorporate the interpatch-crossing distance threshold, so its appropriate interpretation is aided by additional reference to the regional-scale

Table 3
Landscape-scale graph metric values for default and gap-crossing thresholds and dispersal barrier scenarios. Landscape with a total patch area of 2363 km^2 and 574 patches.

Network characteristic	Default scenario	Scenario 1: No cost	Scenario 2: Gap-crossing only	Scenario 3: Gap-crossing 53 m	Scenario 4: Gap-crossing 212 m	Scenario 5: Road barriers
Mean size of components (km^2)	42	139	33	33	55	17
Size of largest component (km^2)	1864	1938	1863	1863	1885	1679
Number of components	56	17	72	72	43	140
Class coincidence probability	0.635	0.701	0.634	0.634	0.651	0.514
Expected cluster size (km^2)	1500	1657	1497	1497	1538	1214
IIC	0.022	0.022	0.021	0.021	0.022	0.019
Harary index	10,868	15,466	9381	9381	11,962	2490

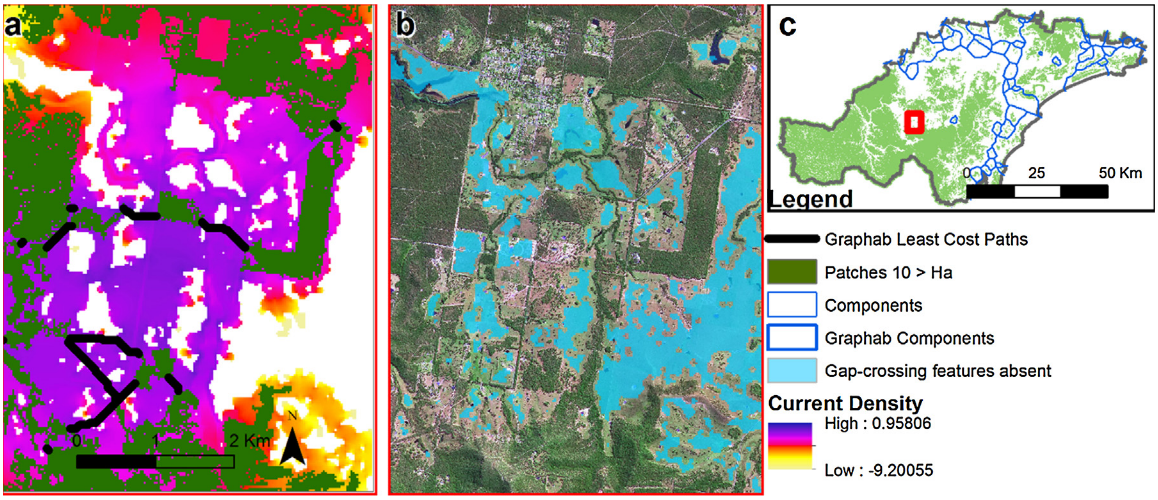

Fig. 7. (a) Local-scale Circuitscape analysis describing connectivity between patches in order to characterise redundancy in the least-cost paths previously identified using Graphab. (b) Satellite imagery for same location. (c) Location of local-scale analysis.

analysis and to the key dispersal parameters defined in the model.

We suggest, like other authors (Baranyi et al., 2011; Rayfield et al., 2011), that a number of graph metrics are tested to assess the full range of responses of graph metrics to a connectivity network at both the regional and local scales. Different graph metrics can produce very different patch-scale patterns (Compare Fig. 4 inset versus Fig. 5 inset). In the Lower Hunter we found all graph metrics apart from Clustering coefficient were positively correlated with patch area and each other, and therefore only Clustering coefficient and one other metric are required to describe the full range of patterns of spatial heterogeneity for the region.

There are a wide range of metrics available that primarily describe spatial patterns, not necessarily ecological dynamics (Foltête, Girardet, & Clauzel, 2014) and thus it may not be straightforward to interpret their ecological meaning. This is true for the

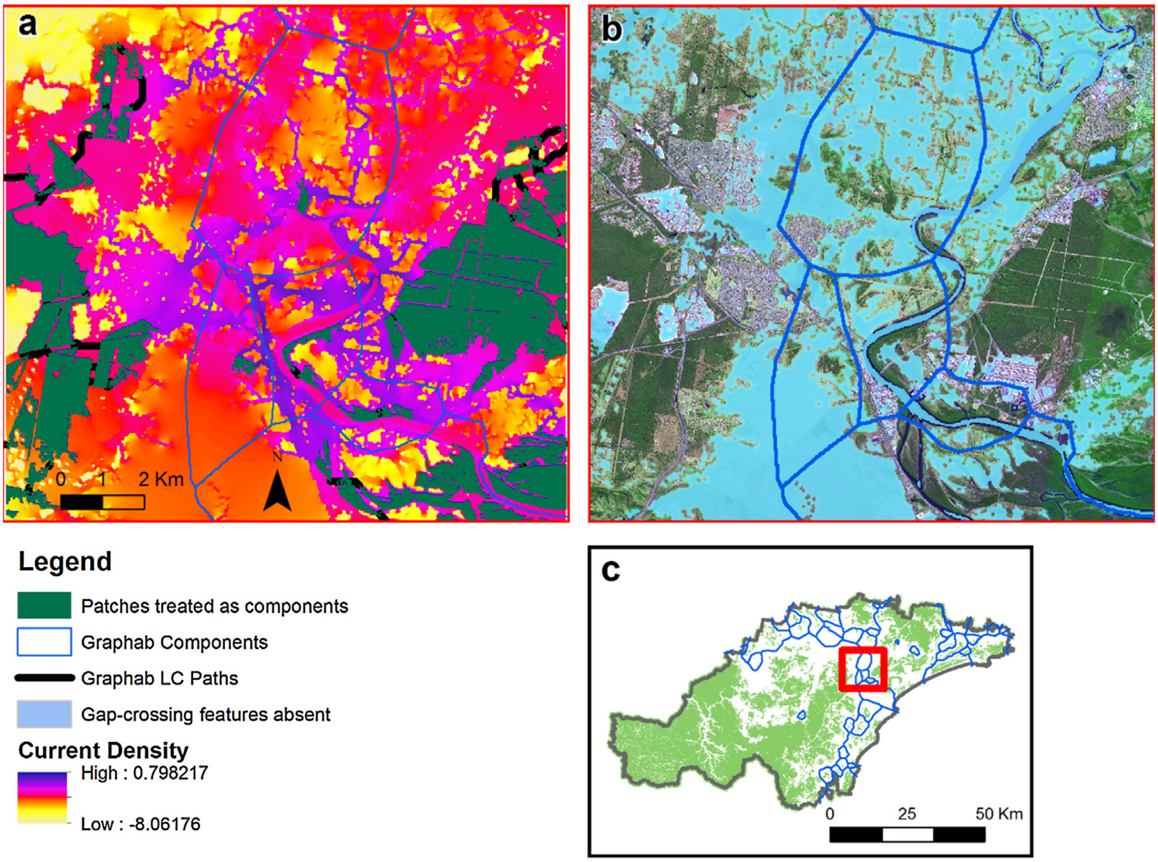

Fig. 8. (a) Local-scale Circuitscape analysis describing connectivity between six components in the centre of the study area. Least-cost paths identified from Graphab regional-scale model. (b) Connectivity was modelled between 8 components in order to characterise redundancy in the least-cost paths previously identified using Graphab. (c) Location of local-scale analysis.

graph metrics and also the Circuitscape outputs. The current density values of Circuitscape pixels reflect the probability that a random walker will pass through a specific cell while moving from one patch to another (McRae et al., 2008). Pixel values may therefore need to be interpreted qualitatively in light of the multiple factors that affect these probabilities, such as patterns of resistance and dispersal barriers and patch locations (sources). For example, it is clear that there are less options for connectivity in the local-scale analysis described in Fig. 7 than Fig. 8, partly due to large areas identified as barriers by the gap-crossing layer. Empirical data could be used to validate current density values such as road mortality data (e.g. Koen, Bowman, Sadowski, & Walpole, 2014), or current density values could be assessed with expert site-based knowledge to characterise the relative importance of a current density values for connectivity.

5.2. *Operationalising connectivity modelling*

This work is part of an emerging body of research focusing on operationalising the graph theoretic approach for conservation planning (Foltête et al., 2014; García-Feced, Saura, & Elena-Rosselló, 2011; Girardet, Foltête, & Clauzel, 2013; Zetterberg, Mörtberg, & Balfors, 2010), beyond its application in research. In contrast to other published literature on connectivity describing specific techniques (Pelletier et al., 2014), methodological limitations (Moilanen, 2011), or the identification of focal targets (Brost & Beier, 2012), our aim is to provide a practical tool. The framework therefore begins with a conceptual model to describe the ecology of connectivity, incorporates a GIS tool to process the data while addressing methodological limitations, and includes methods for interpreting outputs.

The methods developed in this study were based on discussions with government and non-government land management and conservation organisations that operate at the local and regional scales in the Lower Hunter. One of the challenges for these organisations is that the skills and ability to characterise connectivity within a GIS typically reside outside the organisation, preventing the exploration of GIS data in response to changing circumstances (Bergsten & Zetterberg, 2013; Whitten, Freudenberger, Wyborn, Doerr, & Doerr, 2011). The method developed here specifically set out to overcome this lack of capacity, being relatively simple, based on commonly available spatial datasets and well supported software, and using ecological parameters that are simple to derive and test in the field and applicable for many locations across Australia (Doerr et al., 2010). The software used within the framework was chosen for its ease of use based on our experience training land use planners. However, the framework may be used with different connectivity modelling software such as Conefor sensinode (Saura & Torné, 2009) to apply the graph theoretic approach and the corridor mapping tool in ArcGIS to identify least-cost corridors. Furthermore, as expertise develops within organisations, parts of the framework can be further improved to overcome some of their limitations. For example, tiled omnidirectional Circuitscape connectivity mapping (Pelletier et al., 2014) can be used to analyse current density across the whole region as opposed to a subset of the data.

The framework and specific methods developed in this study are distinctive additions to the suite of decision support tools available to conservation planners as they enable available information on dispersal behaviour of animals and animal-dispersed plants to be incorporated into connectivity modelling. It is important to recognise that the method described here only models connectivity. If species persistence is the goal of conservation planning, other methods, such as population viability assessment, need to be used to complement this approach (e.g. Akcakaya, 2002; Southwell, Lechner, Coates, & Wintle, 2008). However, connectivity modelling methods are more robust in the data-poor situations common to landscape planning, in contrast to these more spatially complex approaches (Bergsten & Zetterberg, 2013; Minor & Urban, 2007). A key future area of research is to assess how the various errors associated with producing the high spatial resolution remote sensing data (Lechner, Langford, Bekessy, & Jones, 2012) and the corresponding gap-crossing layer and least-cost path assessments are likely to affect model outputs. Where possible, both these input data and the modelled connectivity pathways should be validated in the field.

6. Conclusion

While no single model may ever be ideal, our approach to connectivity modelling attempts to balance ecological complexity and robustness with usability and computational efficiency. The framework presented here provides a nested approach to assessing connectivity at the regional scale which preserves the ecological integrity of dispersal behaviour at fine spatial scales. This is essential to identify fine-scale connectivity elements and determine which local-scale options can most effectively improve regional-scale conservation planning.

Acknowledgments

This project was funded by the Australian Government Sustainable Regional Development Program in conjunction with the National Environmental Research Program's Landscapes and Policy research Hub. We would like to thank the reviewers for providing detailed and constructive feedback and sincerely think the manuscript is much improved because of their contributions. We would also like to thank the following people and organisations; Michael Lacy, Tom Barrett, Michael Drielsma, Jamie Love, Meredith Laing, Ellen Saxon, HCCREMs, Sue Gould, Dave Osborn and Randal Storey. Special thanks to Robbie Economos and colleagues at Lake Macquarie Council who improved the gap-crossing layer modelling method. Finally, thanks to the many other people who provided feedback.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2015.04.008

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