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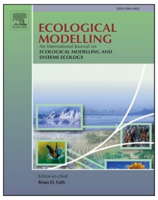

General Landscape Connectivity Model (GLCM): a new way to map whole of landscape biodiversity functional connectivity for operational planning and reporting

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ABSTRACT

Graph-theoretic approaches are commonly used to map landscape connectivity networks to inform environmental management priorities. We developed the new General Landscape Connectivity Model (GLCM), as a operationally practical way of evaluating and mapping habitat networks to inform conservation priorities and plans. GLCM is built on two complementary metapopulation ecology-based measures: Neighbourhood habitat area (*Ni*) and habitat link value (*Li*). *Ni* is a measure of the amount of connected habitat to each location considering its cross-scale connectivity to neighbouring habitat. The remaining *Ni* across a region can be reported as an indicator of Ecological Carrying Capacity for wildlife (plants and animals). *Li* at any location is its contribution to the landscape connectivity of the study region (i.e. which is reported as summed *Ni* across a region) by virtue of providing the 'least-cost' linkages between concentrations of habitat. Mapped *Li* provides valuable insights into the pattern of a region's habitat network, highlighting functioning habitat corridors and stepping-stones, and candidate areas for conservation and restoration. Due to its foundations in ecological theory and its parsimonious design, GLCM addresses a number of criteria we list as important, while addressing criticisms often levelled at graph-theoretical approaches. We present results for three south-east Australian case-studies using continuous-value ecological condition surfaces as input. However, a simple habitat/non-habitat binary surface approximating a threshold ecological condition can also be used. GLCM has been designed to specifically address the need for generic landscape connectivity assessment at regional scales, and broader. It incorporates connectivity analyses across a range of spatial scales and granularities relevant to broad ranges of taxa and movement processes (foraging, dispersal and migration). Successively finer spatial scales are more intensively sampled based on a simple scaling-law. This approach allows analysis resolutions to be determined by data-driven ecological relevance rather than by processing limitations. The operational advantages of GLCM means that landscape connectivity assessments can be readily updated with refined or changed inputs including time-series remote sensing of land cover, or applied to alternative scenarios of land use, ecological restoration, climate projections or combinations of these.

1. INTRODUCTION

1.1. *Landscape connectivity*

The ecological condition of a geographically defined space, or location, is a function of that location's ecological composition, structure and function (Noss, 1990) compared with a benchmark state (Gibbons and Freudenberger, 2006). The ecological connectivity between locations is a key determinant – along with the representation of innate ecosystems (Margules and Pressey, 2000) – to translating ecological condition at one spatial scale to ecological integrity at broader spatial scales; i.e., connectivity makes a collection of habitat elements different

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to the sum of its parts (Batty and Torrens, 2005; Drielsma et al., 2018; With, 2015).

Landscape connectivity – "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al., 1993) – is relevant to home-range and dispersal movements, seasonal migrations and climate-induced shifts in species distributions (Baguette et al., 2013; Laliberté and St-Laurent, 2020; Wu, 1999). These movement processes vary across species (Estes et al., 2018; Walker and Salt, 2012), spanning a broad range of spatial and temporal scales, and functional granularities (Baguette and Van Dyck, 2007). While many ecological processes remain poorly known, complex, or undiscovered (Baguette et al., 2013), it is well understood that the survival of native populations in the wild relies to a large degree on connectivity between their habitats (Baguette et al., 2013; Doerr et al., 2014; Metzger and Décamps, 1997; Noss, 1987; Zia et al., 2011). While this is true in stable climatic conditions, landscape connectivity performs a critical role, facilitating migrations to meet the changing geography of habitat suitability due to climate change (Heller and Zavaleta, 2009; Noss, 1991; Prober et al., 2019). With habitat fragmentation and land-use intensification continuing in many parts of the world, and with the alarming pace of climate change, maintaining landscape movement-function has become a major goal of conservation plans (Fischer and Lindenmayer, 2007; Prober et al., 2019; Watson et al., 2017; Worboys et al., 2010).

It follows that credible, yet operationally-practical landscape connectivity assessment is needed to inform conservation priorities and plans, monitor trends in the levels of 'available' or 'functional' habitat, and to report on the effectiveness of conservation actions in promoting habitat availability (Duflot et al., 2018; Fahrig, 2013; Laliberté and St-Laurent, 2020; Watson et al., 2017). Connectivity assessment can also act as a catalyst for community engagement in innovative conservation and land-use planning (Meppem and Gill, 1998) by providing a link between local conservation action and big picture ecological processes, such as broad-scale and multi-generational migration routes and habitat redistribution networks (Keeley et al., 2019).

Regularly updated remote sensing is becoming increasingly available. This opens the opportunity to operationalise workflows to produce streams of data, that include connectivity assessment. This allows closer monitoring of seasonal effects, longer term trends, and the progress of recovery from major disturbances such as Australia's black summer bushfires in 2019-2020 (Godfree et al., 2021).

The distinction between structural and functional connectivity of habitats (e.g. Baguette and Van Dyck, 2007) is often made. Doerr et al. (2014) describes structural connectivity as "anything that physically links separate populations". In addition to contiguous 'corridors', this definition includes stepping stones (Saura et al., 2014) and "more subtle habitat elements such as scattered trees or shrubs, or even scattered clumps of tussock grass or coarse woody debris" (Doerr et al., 2014). Critical connectivity thresholds have been demonstrated in relation to structural connectivity (Metzger and Décamps, 1997). However, it is often pointed out that in practice the benefits of structural connectivity are rarely validated with empirical evidence (Doerr et al., 2014; Hodgson et al., 2011; Laliberté and St-Laurent, 2020). While over-emphasis on structural connectivity has been heavily critiqued (Hodgson et al., 2011; Hodgson et al., 2009; Moilanen, 2011), it is nonetheless an enduring feature of conservation planning practice (Zeller et al., 2020).

According to Baguette and Van Dyck (2007) "functional connectivity refers to how the behaviour of a dispersing organism is affected by landscape structure and elements". Although functional connectivity is often aligned to the movements of individual species; the relevance of the concept to higher levels of biological organisation (sensu Noss, 1990) is less acknowledged. Aggregated across whole regions, functional connectivity informs on the functional integrity of landscapes (Ludwig et al., 2004; Walston and Hartmann, 2018; Woodwell, 2002).

Close examination of the functional aspects of landscape connectivity inevitably leads to the question of 'connectivity for what?'. Biological entities can be genetic traits, species, species functional groups, ecosystems, or all of biodiversity. Thus, we make the distinction here between species-specific, or even species-process specific connectivity (i.e. home-range movements, dispersals and migrations) (Drielsma and Ferrier, 2009), and more broadly defined structural connectivity. In the case of species-specific connectivity, the source, destination, path and movement abilities are explicitly linked to the biology of a defined species or functionally related group (Drielsma and Ferrier, 2009; Drielsma et al., 2016; Drielsma et al., 2020; Scotts and Drielsma, 2003). Broadly defined structural connectivity has been found to facilitate function more generally (Doerr et al., 2010).

1.2. *Analytic tools*

Increasingly, analytical tools are being deployed for mapping and reporting on landscape connectivity across regions (Correa Ayram et al., 2015; Correa Ayram et al., 2017). Least-cost path analysis provides a powerful means for quantifying or mapping landscape connectivity. However, there are sustained concerns that this approach lacks ecological realism (Moilanen, 2011), or should be better applied to account for functional movement processes (Sawyer et al., 2011; Zeller et al., 2018). Ferrarini (2014) describes "two biologically improbable assumptions" of using least-cost paths: (1) dispersers have complete knowledge of their surroundings, and (2) they select the least-cost route based on this information. Least-cost path algorithms only consider the least-cost route between pairs of locations, ignoring both the added strength and redundancy to habitat networks provided by alternative routes (Moilanen 2011), and the influence of learned behaviour. The application of circuit-theory to landscape connectivity assessment in the program Circuitscape (Dickson et al., 2019; McRae et al., 2008; Shah and McRae, 2008) overcomes the former deficiency by considering all paths between chosen endpoints. However, this is achieved at high computational cost per node pair (path endpoints), and so the number of node pairs that can feasibly be examined is limited. The all-paths approach works well in cases where connectivity assessment is sought between a limited number of known concentrations of habitat. However, the approach quickly becomes intractable in cases where extensive habitats form a fine-grained heterogeneous continuum, that lacks clear *a priori* endpoints for analysis (Ferrarini, 2014; McIntyre and Barrett, 1992; Wiens, 1995; With et al., 1997). In highly variegated environments, represented by high resolution data, large numbers of node pairs are required to adequately sample habitat across a region, and the most pertinent nodes are not easily established.

Environmental niche modelling of individual species provides a way to define potential distributions which can then be assessed for connectivity, and individual assessments can be aggregated to represent multiple species (Correa Ayram et al., 2017; Scotts and Drielsma, 2003). For many species and more generally within many environments, it is problematic to represent large, irregularly shaped patches with a single node. Doing this can lead to loss of information in terms of landscape heterogeneity (With et al., 1997). It introduces error if perfect connectivity is assumed within patches, and when all parts of a patch are considered equally connected to all parts of other patches. Thus patch-based approaches introduce a problem concerning the placement of nodes in large or irregularly shaped patches. An alternative approach that overcomes these limitations has been developed uses continuous-value rasters (grids) of species distributions (Drielsma and Love, 2021; Drielsma and Ferrier, 2009). That approach builds on the cost-benefit approach (CBA) to measuring habitat configuration (Drielsma et al., 2007a).

The CBA and the spatial links tool (SLT, Drielsma et al., 2007b) are raster-based, least-cost paths (Dijkstra, 1959) graph-theoretic approaches that overcome reliance on patch definition and provide a tractable solution to assessing large and complex landscape configurations. The CBA and spatial links tools have been used as stand-alone applications for evaluating and mapping 'Ecological Carrying Capacity' and 'Ecological Connectivity' (Love et al., 2020). The CBA approach has been integrated into species- and community-level persistence assessments for calculating: ‘Potential Occupancy’ and ‘Metapopulation Capacity’ (Drielsma and Love, 2021; Drielsma and Ferrier, 2009); an index of biodiversity persistence, conservation benefits and unique diversity mapping (Drielsma et al., 2014; Drielsma et al., 2020); and a measure of spatial resilience to climate change (Ferrier et al., 2020; Office of Environment and Heritage (NSW), 2016).

1.3. Taxonomic granularity

Landscape connectivity assessments that incorporate specific habitat and movement abilities of single species, or a limited subset of all species, are perceived to provide particular realism. Umbrella species are sometimes adopted as a strategy to represent many taxa, using one or few high trophic-level species (e.g. Baguette et al., 2013; Williams et al., 2012). A single habitat connection can serve the needs of multiple species, but characterising the entire biota using representative species will necessarily skew results towards well-studied and iconic species (Cushman and Landguth, 2012; Drielsma et al., 2014). This concern has led to some assessments adopting hypothetical, yet representative species (Hand et al., 2014; Noss, 2007), or generic focal species (Doerr et al., 2013; Foster et al., 2017).

More generic level assessment can be helpful in two related ways. Firstly, it can be used in lieu of the difficult task of measuring functional connectivity individually across the entirety of taxa, which includes a number of species that are poorly understood, or are unknown to science. Secondly, and perhaps more aptly, connectivity at the ecosystem level promotes general resilience, defined as “the capacity of social-ecological systems to adapt or transform in response to unfamiliar, unexpected and extreme shocks” (Carpenter et al., 2012; Harwood et al., in review). However, in no way do the strengths of ecosystem-level or structural connectivity (sensu Doerr et al., 2014) preclude or displace the need to explicitly address functional connectivity individually for highly valued individual species, especially those at high risk of extinction.

In assessing landscape connectivity it is a significant challenge to adequately represent movement abilities across the full spectrum of life. Scaling laws help to bring order to otherwise seemingly overwhelming chaos (Loehle, 2004; West and Brown, 2005). They apply to island biogeography, whereby a species-area curve can explain diminishing marginal gains in diversity as the area of habitat increases (Brown et al., 2002; Crawley and Harral, 2001). This reflects the diminishing potential for entry to a habitat patch by larger, more mobile species, and higher-order predators with increasing patch area; the concentration of diversity among invertebrate fauna, and smaller plant life; and the statistical chance of colonisation. Power-law relationships have also been found to describe the distribution of body size among animals (Marquet et al., 2005), body mass and home-range size (Gompper and Gittleman, 1991; Jetz et al., 2004; Rosten et al., 2016), body size and mean average travel distance (Rosten et al., 2016), and the frequency of movement and distance travelled by individual species (Ramos-Fernández et al., 2004).

1.4. Towards a new way to assess landscape connectivity

We set out to develop a landscape connectivity assessment approach that was generic across biodiversity. We developed the new General Landscape Connectivity Model (GLCM) to automate connectivity assessment based on a single spatial input of pre-defined land cover or ecological condition. The approach adopts a fractal design founded on the self-similarity of movement processes that can be assumed across spatial scales, and which can be described by a power law. The GLCM builds a model of landscape connectivity networks, comprising complex patterns, through repeated application of a simple (least-cost path) algorithm across geographic space and across spatial scales, drawing on spatial data of land cover or ecological condition, and a minimal set of movement-related parameters.

In developing GLCM we sought to addresses a range of criteria we find to be important or beneficial in assessing broad-scale landscape connectivity, at least within the context of eastern continental Australia. These criteria are listed in Table 1. GLCM combines (in a scripted environment) the CBA and SLT, thereby incorporating analysis of both spatial context and link value. We substantially enhanced the CBA and the SLT software for computation efficiency, and expanded node sampling to effectively consider all feasible least-cost paths across a study region.

GLCM generates cross-scale, or scale-agnostic, measures of neighbourhood habitat area (Hanski, 1999), and habitat link value (Drielsma et al., 2007b). It maps functional connectivity generically across multiple scales, theoretically accounting for the movement abilities of multiple species and modes of movement (home-range, dispersal and migration). As such GLCM provides a basis for aspects of conservation planning, such as ‘no regrets’ conservation actions to address loss of ecological function arising from clearing of habitat and climate change (Prober et al., 2019).

In this paper, we describe the methods underlying GLCM and present three case studies applied to south-eastern Australia to illustrate differing ways, arising from how the input data is formulated, in which GLCM can be usefully applied. These case-studies have largely been described in published project reports; but here, we consolidate the general approach and place GLCM within the broader context of landscape connectivity assessment methodologies, to both inform conservation planning and to report on status and trends. We argue that GLCM provides a unique perspective on habitat networks that captures sufficient realism in landscape connectivity across spatial scales, while providing operability that facilitates periodic updates for monitoring and reporting.

Through the case studies, we demonstrate GLCM’s flexibility: to map connectivity networks semi-generically across three structurally distinct habitat types (case study 1); to generate generic landscape connectivity mapping, and connectivity indicators for jurisdictional reporting for New South Wales, Australia (case study 2a), and for the Sydney Basin bioregion of Australia, at higher spatial resolution (case study 2b); and to consider temporal and spatial connectivity in the context of climate-induced shifts to environmental niches (case study 3).

Table 1
Criteria for operationalising general landscape connectivity assessment.

Criteria	Utility
Visual representation	Provide insightful maps of landscape connectivity networks which can be used to promote understanding and be used for conservation planning
Reportable metrics	Facilitate periodic monitoring of landscape connectivity and functional integrity across large regions
Landscape variegation	Be able to consider how species rarely respond to landscapes as a binary patch-matrix pattern but often recognise more subtle gradations
Comprehensive paths	Transcend reliance on pre-defined path nodes or a single node per ‘patch’
Realistic paths	Add realism by considering the permeability of paths and the easiest routes, and continuous dispersal kernels to avoid abrupt distance thresholds (Moilanen, 2011)
Multiple scales	Incorporate the movement abilities of multiple taxa and multiple modes of movement
Dual perspectives	View connectivity value of a location from the perspective of it being a source/destination; or as its conduit or link value
Ecological theory	Draw on ecological theory to transform Euclidean distance to cost-distance, and to weight paths by the habitat resources they connect
Computational efficiency	Feasible to assess large regions at high resolution
Operability	Repeatable – can be periodically calculated using a stream of input data

2. METHODS

2.1. A dual perspective on landscape connectivity

GLCM combines dual perspectives on region-wide habitat networks (Duflot et al., 2018) (Fig. 1) using a simple raster geometry to span ecological scales (Fig. 2).

Neighbourhood habitat area (*Ni*) is the amount of structurally connected extant habitat at each location (denoted *i*) weighted by its functional connectivity to *i* (Box 1 provides a glossary of key terms used in this paper). A high value for *Ni* indicates that for *i* there is high availability of connected habitat (quantity and/or quality) presumably providing the resources that support individuals and populations of species typically found at the location. *Ni* summed across a region provides a useful indicator of the functional integrity for that region.

Habitat link value (*Li*) is the contribution of a location (denoted *i*) to the functional integrity of a study region. *Li* mapped across a region provides a visualisation of a study region's connectivity network. This mapping can be used to inform the connectivity strategy (priorities for improving the persistence of biodiversity) by highlighting opportunities for conserving, enhancing and building habitat networks between concentrations of high quality habitat (Baguette et al., 2013; Noss, 1991).

As *Ni* and *Li* are calculated across multiple scales, we can assume that they encompass all forms of organism movement processes: foraging, dispersal and migrations. *Ni* and *Li* originate from metapopulation ecology (Hanski, 1999). Initially they were applied to habitat represented by variably sized, circular habitat patches. GLCM provides higher-level configuration that repeatedly and systematically increments calculations of *Ni* and *Li* across ecological scales using standardised parameterisation. *Ni* is operationalised for raster data using the CBA tool (Drielsma et al., 2007a); and *Li* is derived using the Spatial Links Tool (Drielsma et al., 2007b).

2.2. Neighbourhood habitat area (Ni)

Neighbourhood habitat area (*Ni*) is calculated as:

$$Ni = \sum_j H_j w_{ij}, \tag{1}$$

where H_j is the amount of habitat (quantity and quality) of each neighbourhood cell (indexed by *j*) connected by a least cost path to *i*. This formulation of neighbourhood habitat area is close to Hanski's (Hanski, 1999) 'connectivity of a patch *i*', but here we consider habitat at the source by allowing *i* to equal *j* (Drielsma and Love, 2021). Permeability to movement across a grid cell *i* can be calculated as $w_i = e^{-\alpha d_i}$ where $1/\alpha$ is the average movement ability being analysed and d_i is the cost-distance of traversing cell *i*, with both given in the same units (in our case meters). The concept of cost-distance can be considered inverse to permeability (i.e. $d_{ij} = -1/\alpha \ln w_{ij}$) and is calculated in our case by scaling up the Euclidean distance across *i* (orthogonal grid cell size) by any loss in its habitat value. Thus, w_{ij} is a function of the amount of habitat traversed (the structural component) scaled relative to the movement ability being assessed (the functional component). Once summed across *j*, *Ni* represents the amount of structurally connected habitat weighted by its functional connectivity to ***i***.

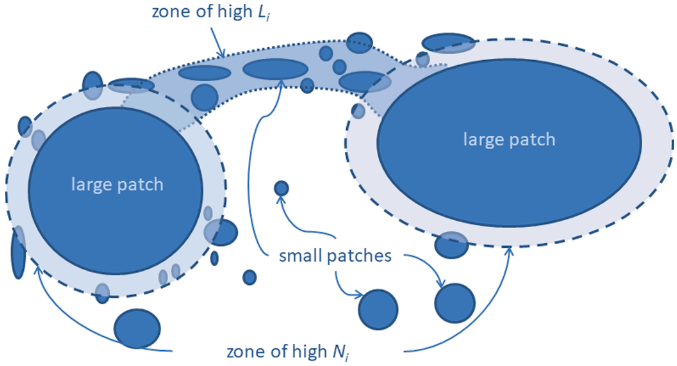


Figure 1. A dual perspective on habitat networks. Locations of high neighbourhood habitat area (N_i) are typically larger or well-connected regions of high habitat condition. High habitat link value (L_i) occurs along important movement pathways within or between habitat following corridors or stepping stones, where present.

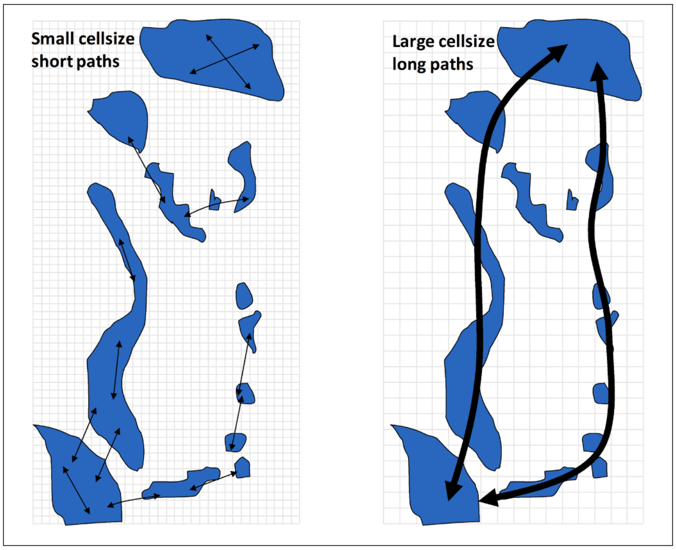


Figure 2. Indicative links, shown as arrows, at a fine spatial scale (left) and coarse spatial scale (right) for a hypothetical landscape represented as irregular habitat patches.

A single petal configuration, which is chosen to achieve balance between computational demand and ecological rigor (Drielsma et al., 2007a), is used throughout any given calculation of *Ni*.

2.3. Habitat link value (Li)

Habitat link value (*Li*) is calculated based on the colonisation potential of a patch (Hanski, 1999):

$$Li = \sum_j \sum_k H_j H_k w_{jk} \tag{2}$$

where w_{jk} is the permeability of the habitat link connecting end nodes *j* and k, and where grid cell *i* is either an end node (i.e. *i*=*j or i*=*k)* or is an element of a set of nodes that form the least cost path between the end nodes (i.e. *i*≠*j and i*≠*k*). Habitat links are calculated as least cost paths connecting units of habitat (sensu Drielsma and Love, 2021). The value of a habitat link is derived from the overall connectivity the link provides to the habitat network based on path length and the quality of the habitat it traverses and connects. As least cost paths are solved for each pair of *j* and *k* (and across scales), habitat link values are accumulated at each grid cell (*i*) that forms part of each link. Thus, a grid cell's final value of *Li* accounts for the number of traversing habitat links and the connectivity value of those links to the habitat network.

A habitat link may comprise a mix of environments along its path. Thus, high *Li* indicates a location that provides connectivity between habitats supporting ecological processes, but each location along a path may not be of high habitat value itself.

2.4. Operationalising connectivity metrics

Operationally, deriving *Ni* and *Li* both involve solving single-source shortest path trees rooted at each grid cell location with least cost paths visiting every neighbourhood location within specified search constraints. For *Ni,* neighbourhood locations (j) may either be individual grid cells within a predetermined analysis window (centred on i) or aggregations of those grid cells into petals (Drielsma et al., 2007a), to improve computational performance. For *Li,* locations j and k are grid cells within a maximum search radius of each other beyond which paths would be irrelevant (w_{jk} approaches 0 as distance exceeds $1/a$), and are therefore not solved. A minimum habitat threshold (H_{min}) can be used when selecting j and k to avoid solving low-valued paths that are unlikely to add appreciable value to any *Li.* A moving analysis window, used for *Ni* (centred on i) and latter implementations of *Li* (centred on j), is used to measure the connections between each grid cell as a focal grid cell out to all neighbourhood locations. For each *Ni,* habitat link values are accumulated at the focal grid cell (i); for *Li,* values are accumulated at each grid cell forming part of the least cost path, according to the colonisation potential calculated for the path.

2.5. *Spatial Inputs*

GLCM requires up to two geospatial raster inputs: land cover or ecological condition (or equivalent representation of habitat, ecosystem or vegetation quality data); and habitat permeability. Respectively, these represent the habitat resource, or 'benefit' at path nodes, and the relative inverse perspective of 'cost-distance' to biota of traversing each location (Drielsma and Ferrier, 2006). The ecological condition grid represents each location's capacity to provide the resources necessary to support plant and animal species native to an area, calculated relative to an ideal reference state for the location. These measures are not produced within GLCM as they're fit-for-purpose, user-defined inputs (e.g. Harwood et al., 2016; Love et al., 2020; Williams et al., 2021). We employ a raster-based grid data-structure whereby ecological condition and habitat permeability values for each grid cell are the estimated average value within the grid cell's extent (GLCM then considers the grid cell's broader landscape context). Habitat condition and permeability can be represented simply as binary, high versus low grid cell values; or, as for the three case studies presented below, continuous valued surfaces (McIntyre and Barrett, 1992; Wiens, 1995; With, 2015). The spatial resolution of input rasters determines that of the combined outputs. Finer grain source data is preferred as it increases the potential bandwidth of ecological scales represented in the analysis, allowing it to account for more local movements associated with less space-demanding and less mobile species.

Ideally, habitat permeability is generated as a separate input along with ecological condition. Optionally, permeability can be calculated within GLCM by applying a linear transformation of ecological condition into cost-distance as a proxy for movement ability (e.g. see Love et al., 2020). In our case studies (see section below) a minimum cost-distance assigned to highest-quality habitat was set to the Euclidean orthogonal grid cell size; the maximum cost-distance, for grid cells devoid of habitat, was calculated by multiplying the grid cell size by a 'cost ratio' (denoted ε) of 2.5. Permeability (W_i) values for average movement abilities being analysed at each scale were then calculated from H_i, linearly scaled between these minimum and maximum cost-distances.

The selected value of ε is a defining trait of any GLCM analysis. Following parameterisations in a number of studies (e.g. Drielsma et al., 2016; Drielsma et al., 2017), we chose a cost ratio value of $\varepsilon = 2.5$, which we consider provides an acceptable balance in trading between alternative movement profiles. A higher cost ratio limits exploration of higher cost regions in the grid as W_{ij} decays more rapidly resulting in lower values for *Ni* and *Li.* A lower cost ratio allows paths to traverse higher cost regions further, before their contribution to *Ni* or *Li* becomes insignificant; potentially increasing connectedness of habitat and ultimately resulting in higher connectivity values overall. To investigate if our models were overly influenced by our choice of ε we conducted a sensitivity analysis on case study 2 (see Supplementary S9).

2.6. *The scaling approach*

A simple raster geometry is employed within GLCM to sample *Ni* and *Li* uniformly across ecological scales, whereby each scale is subjected to an identical analysis in terms of analysis window dimensions (number of grid cells), range of grid cell permeability values and, for the *Ni* analysis, the petal configuration used (e.g. see Fig. 3a). Sampling across spatial scales is informed by a power law such that, at each successive sampling (starting with the original data's finest granularity), potential movement ability (1/a) and grid cell size are doubled, hence the spatial resolution of the analysis is systematically halved (i.e. to coarser granularity) (Brown et al., 2002; Drielsma et al., 2018) (see Box 2). Complexity is managed in this process by working with 'number of cells' (rather than geographic distance) as distance units, which remain constant across the spatial scales.

A 'jittering' process (see Figure 3b and Supplementary S5) was applied to all but the finest scale analysis, whereby multiple shifted grid cell offsets (Love et al., 2020) are used to resample the finest scale source data (ecological condition and permeability) to each coarser resolution. With jittering, grid cell offsets are shifted a fraction of the coarser grid cell size in both the x and y directions so that in each instance of spatial scale and offset, the aggregation of source grid cells into coarser analysis grid cells is unique. Thus, the jittering process reduces information loss that usually results when a single grid origin for resampling is chosen, and it improves visual representation (see Table 1) by reducing the imprint of grid cell circumscription artefacts which would otherwise prevail in output maps.

Ni and *Li* analysis are performed independently using matching scaling parameters for each offset within each resolution (Love et al., 2020).

2.7. *Aggregation stage*

The final aggregation, across scales, offsets and methods (*Ni* and *Li*), is set to the source data's original (finest) resolution using a simple schema (e.g. see Supplementary S4). As all the required influence across scales is handled in the scaling (power law) approach, aggregation of components requires limited standardisation to achieve the aim of equal weighting across scales (we only need to account for differences in the number of offsets analysed at each resolution). In the final aggregation, the ecological condition surface itself is also included as a component of *Ni* at its original resolution, as it implicitly represents *Ni* within the bounds of each grid cell. Assuming perfect connectivity within the grid cell ($W_{ij} = 1.0$), this equates to H_i.

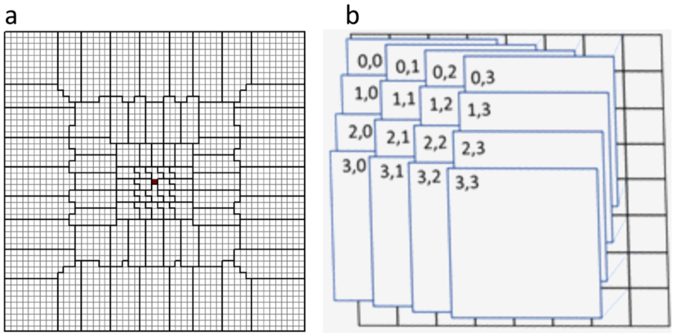


Figure 3. a) The raster geometry for *Ni* analysis for case study 2. The cells within the neighbourhood window at each resolution (light grid) are assigned to a common petal arrangement (heavy lines); b) Multi-scale analysis sampling showing a single cell location (blue) for each of the 16 overlapping pixel offsets used for the 360-meter analysis resolution relative to the original 90-meter resolution raster cells, shown in black.

3. RESULTS

We present three case studies, for comparison. Each has been described in separate project reports: case study 1 (Drielsma et al., 2012); case study 2 (Love et al., 2020); and case study 3 (Drielsma et al., 2015). The case studies cover overlapping sub-continental study regions in south-eastern Australia (see top of Fig. 4). They illustrate a diversity of applications as well as an evolution of the GLCM approach in terms of methods, data and software (see Table 2). Zoomed in examples of spatial inputs and outputs for the three case studies are provided in Fig. 4, and for their complete extent in Supplementary S1, S2, S3, and S8. Supplementary S5 also presents an additional fine-scaled analysis using case study 2 methods, but is a local application for the greater Sydney region to help instil landscape connectivity into the NSW 'Greening our City' program to "increase the tree canopy and green cover across Greater Sydney by planting 1 million trees by 2022" (New South Wales Government, 2017). Thus, we refer to case study 2a (all of NSW) and case study 2b (the Greater Sydney region). Details of the methods for each case study are provided in Supplementary S4, S5 and S6.

The three case studies are nested within a common study region comprising: major urban population and growth centres surrounded by fragmented grassland and woodland habitats within an intensively farmed sheep-wheat agricultural region; a high diversity of ecosystems ranging from desert rangelands, to sub-tropical rainforests, and alpine woodlands and heath; over 870 national parks and public reserves (in the state of New South Wales); an extensive network of travelling stock route reserves (Lentini et al., 2013); extensive areas likely to be critical to carbon sequestration forestry (Polglase et al., 2011); a key part of the Great Eastern Ranges conservation connectivity corridor (Mackey et al., 2010); and, the Gondwana Rainforests and Greater Blue Mountains UNESCO listed World Heritage Areas.

For each case study a suitable buffer area (c. 200 km) was added to avoid edge artefacts arising from the analysis. Where necessary, ecological condition data to fill the buffer extent were derived using a less rigorous methodology (Love et al., 2020). Water and sea were considered high-quality ecological condition to ensure connections with coastal areas were not inappropriately devalued.

The ecological condition surfaces used as inputs to the three case studies were derived semi-inferentially through an aggregation of information from multiple sources, including remotely sensed measures of vegetation cover (Love et al., 2020). Remotely sensed foliage projective cover (FPC) was used to estimate a woody cover component of ecological condition. Raw FPC values were transformed using logistic functions with inflection points set to lower bound thresholds based on benchmarks with high perceived condition for different vegetation types (Ayers et al., 2005; Drielsma et al., 2012). Transformed FPC values were combined across vegetation types and further modified based on tenure, land-use and land cover, to provide the best available indication of understory and ground cover ecological condition (Dillon et al., 2009). Case study 2a included an additional measure of stable green vegetation based on Landsat-derived fractional cover metrics. Stable green vegetation combines measures of annual mean green vegetation cover with its mean intra-annual range over a 10-year period. This was included in modified landscapes where it was qualitatively found to provide a useful gradient between frequently cropped or heavily grazed lands and those less intensively utilised lands which have consistently higher ground cover (Love et al., 2020).

3.1. Case study 1 – Connections of three vegetation structural classes

Case study 1 (see Supplementary S4 for methods and S1 for results) was developed to support conservation and restoration activities undertaken as part of the Great Eastern Ranges initiative, a connectivity conservation initiative focused on the Great Dividing Range and the Great Escarpment which runs the length of eastern Australia (Mackey et al., 2010). In contrast to case studies 2 and 3, which considers a single generic entity, case study 1 considers 3 entities of vegetation structural classes (open forest, closed forest and woodland). Case study 1 therefore involved three separate parallel analyses, one for each of three vegetation structural classes.

3.2. Case study 2 – Landscape Connectivity of New South Wales

Case study 2a (see Supplementary S2, S5, S7 and S8) presents an assessment undertaken as part of the New South Wales Biodiversity Indicator Program in which the Ecological Condition indicator was further developed into indicators of Ecological Connectivity and Ecological Carrying Capacity (Love et al., 2020) using a GLCM analysis at 90 m grid cell resolution. Case study 2a was greater in extent and finer-grained compared to case study 1. The application employed a single continuous surface of ecological condition.

Improvements to software performance after the case study 1 analysis allowed an all-pairs analysis using higher resolution input data. The all-pairs approach generates every plausible path from every grid cell to every other grid cell within the bounds of parameterised search constraints. The parameterised constraints used by the approach include a maximum search radius and maximum 'effective' path distance, beyond which least-cost paths are mathematically implausible (maximum attainable w_{ij} beyond the threshold is insignificant) and are not generated; and a minimum ecological condition threshold, below which sites cannot contribute due to very low H_i, and are therefore not processed as path nodes.

Case study 2 included the development of *Ni* as a regional (NSW state-wide) indicator of ecological carrying capacity (Baguette et al., 2013; Department of Planning Industry and Environment NSW, 2020; Love et al., 2020). *Ni* is aggregated across the study region to report on the proportion of all possible (original, pre-disturbance, or benchmark) connected habitat that remains (denoted *Nr*) within a given habitat network or scenario.

$$Nr = \frac{\sum Ni}{\sum Ni*} \tag{2}$$

where *Ni** is the original or benchmark *Ni* at each location (which is constant across a region; but for operational purposes is calculated in order to account for edge effects near the study region boundary).

In case study 2a *Ni* and *Li* are not combined into a single spatial layer. Rather, summed *Ni* evaluates the total connectivity for a region; and mapped *Li* provides a graph (or map) of the connectivity network, or can also be considered a measure of the contribution of each location to the network.

Fig. 5 focuses on a portion of the case study 2a extent, showing outputs for each scale/granularity combination as well as the combined output. Maps of the combined *Li* output for the entire extent of case study 2a is provided in Supplementary S2 and S8.

Case study 2b (see Supplementary S5) follows the general methods of case study 2a, but is calculated at significantly higher spatial resolution (2 - 32 metres cell size).

3.3. Case study 3 – south east Australia climate change connections

Case study 3 (Drielsma et al., 2017; Drielsma et al., 2015) (and see Supplementary S6) applies the *Li* approach used in case study 1 to explicitly define habitat networks within the context of shifting ecological niches due to climate change. Thus, this example was developed as an aid to regional climate adaptation planning by identifying candidate areas for climate-ready conservation management and ecological restoration. The approach is part of an active area of model development that includes employing a climate-informed analogy of *Ni* as an indicator of spatial resilience to climate change (Harwood et al., in review).

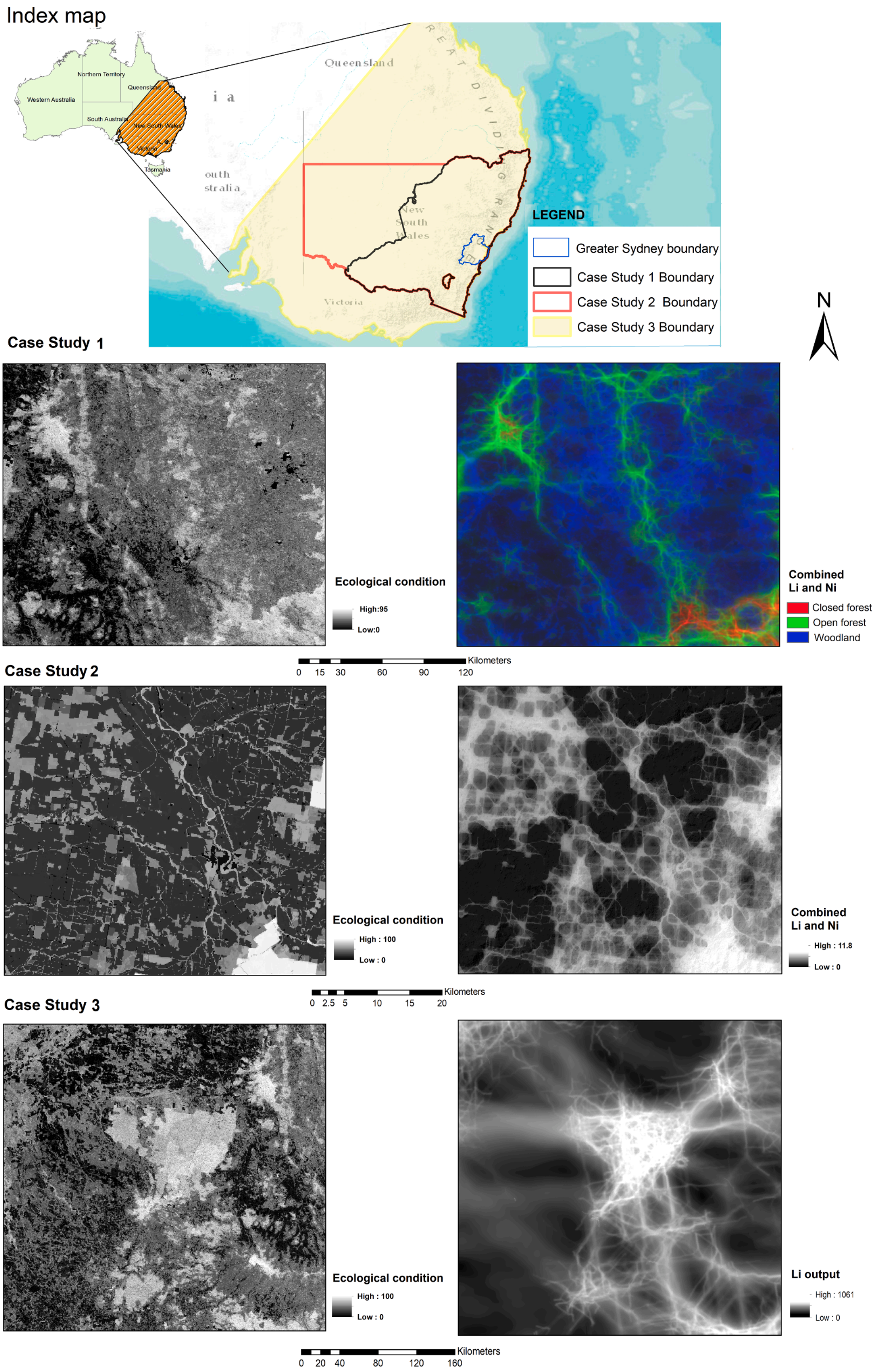


Figure 4. Study areas location map (top) and zoomed in example areas (below) showing inputs (left) and GLCM outputs (right) for the case studies. For case study 1 each of the three vegetation structural class entities were used to colour an image using ESRI Arcmap's composite bands function. Each gridcell is coloured according to its apportioned fit to these three outputs and: Closed Forest – red; Open Forest – green; and Woodland - blue. Combinations of these colours reflect the dual roles of areas spanning more than a single entity. The results from case studies 2 and 3 are shown as monochrome continuous surfaces where lighter shades represent higher *Ni* and *Li*, combined as indicated in Table 2. The Greater Sydney region boundary, shown in blue in the location map depicts the region for which the case study 2 analysis was extended to include fine-scale analysis using 2 metres resolution input data.

Table 2
Configuration and parameterisations for the three GLCM case studies.

Attribute	Description	Case study 1[1]	Case study 2a[2] and 2b	Case study 3[3]
Ni derived		yes	yes	no
Li derived		yes	yes	yes
Entities	Biological unit for analysis	3 structural vegetation classes	(2a) Ecological Condition; (2b) tree cover	Ecological Condition
Multi-scale analysis	scales sampled	5	7	6
Climate projections		None	None	MPI8.5 from 1990 to 2050
Li sampling		Semi-random	All feasible end nodes	Semi-random
Ni, Petals used y/n		yes	no	yes
Raster geometry – Source and destination window sizes		Src:51 Dest:9	Src:25 Dest:25	na
Final surface		*Ni* and *Li* combined	*Ni* and *Li* separate	*Li* only
Ni – number of iterations	A new 'dynamic' measure of *Ni* that accounts for cascades of connections uses an iterative approach[4]	1 iteration	3 iterations	1 iteration
Movement distances		*Ni*: 2.50 - 40.00 km Li: 31.25 - 500.00 km	(2a) *Ni*: 0.25 - 8.00 km Li: 2.25 - 144.00 km	*Li* 31.25 - 500.00 km -
Spatial resolutions		250 m - 4000 m	(2a) 90 m - 5760 m; (2b) 2 m – 32 m	250 m - 8000 m
Jittering		yes	yes	no
Indicators		no	Summed *Ni*; mapped *Ni* and *Li*	no
Combined layer	as per Supplementary S1, S2, S3 and S8	Combined *Ni* and *Li*	*Ni* and *Li* separate	*Li* only
Minimum view scale		1:750,000	(2a) 1:200K; (2b) 1:5K	1:750,000

[1] Drielsma et al., 2012
[2] Love et al., 2020
[3] Drielsma et al., 2015
[4] Drielsma, M.J. et al., 2021

4. DISCUSSION

Conservation decision-making is typically mired by high levels of epistemological uncertainty (Burgman, 2005) and complexity that calls for pluralist perspectives (Funtowicz et al., 1999). This issue is amplified when decision-making is directed at vast geographic areas, multitudes of biota, environments, interactions, and uncertain futures (Prober et al., 2019; Prober et al., 2017). It follows that a variety of fit-for-purpose assessment approaches are needed, including ones that can readily generate generic assessment across broad regions.

The architecture of GLCM circumvents the complexity of ecological systems, by embracing detail in spatial data, which can be readily captured with new and emerging technologies; while adopting simple assumptions within a fractal framework to account for movement processes which are not well known collectively across all taxa. The approach offers a useful supplement to field-based assessment that can otherwise lack broad perspective.

Rather than focusing on actual or putative species, or species functional groups, GLCM considers a wide band of spatial scales and granularities that are reflective of a comprehensive range of biological movements (Cushman and Landguth, 2012; Noss, 1991; Rayfield et al., 2016). As such it is fit for purpose for operationalising assessment of landscape connectivity across broad regions and for setting priorities for conservation actions aimed at building general ecological resilience across regions (e.g. Jalkanen et al., 2020). However, this generic approach has not been developed to enable detailed planning for the conservation of individual, highly threatened species. The latter requires species-specific parameters based on empirical evidence of individual species movement biology and ecological requirements (e.g. Landi et al., 2018).

4.1. *The three case studies*

The results from the three case studies differ in a number of ways due to how each approached the problem of scale and resolution, the use of ecological entities (species, ecosystems) and, in case study 3, ecological forecasting (Clark et al., 2001). In general terms, case study 1 and 3 were designed to provide regional to sub-continental scale perspectives, with case study 3 being configured to capture expected ecosystem migration pathways due to climate change. Case study 2 is a finer-grained 'current climate' scenario perspective, that provides a clearer view of ecological network processes at the landscape scale than at broader scales.

In general, the results from the three case studies highlighted the uneven distribution of connectivity remaining in the variably utilised landscape of south-eastern Australia, reflecting the uneven impacts of land-use and intensification across the study area. Along the coast, many areas of native vegetation have been removed to accommodate urban development, infrastructure, and a mosaic of productive and intensive land uses. Native vegetation remains relatively intact along the slopes and ranges where land is more rugged, where soils often have lower fertility, and where a higher level of protection is afforded by extensive conservation reserves (Pressey et al., 1996). Much of the native vegetation in the more arable central part of the case study region has been highly modified or degraded or replaced with cropping and grazing systems. The native vegetation that remains, is often along roadsides, travelling stock route reserves (Lentini et al., 2013), riparian zones of waterways, or in smaller nature reserves.

Insights gleaned from the case studies included: confirmation of the north-south Great Eastern Ranges corridor as a continental-scale spine of connectivity paralleling the Australian east coast, and augmented with a number of (often tenuous) east-west linkages (coastal to inland) that are likely to be critical for faunal climate migrations toward cooler, moister coastal habitats; and the critical role of large remnant patches, such as the Pilliga forest in the otherwise heavily fragmented central region of the New South Wales state jurisdiction.

More detailed patterns can be discerned when the data is viewed at finer resolutions. This is well illustrated by the Greater Sydney region assessment (case study 2b) which goes down to 2 metre resolution. There the role of parkland, street trees, roads and infrastructure can be discerned.

Case study 2 provides a rare example of how landscape connectivity is actually being monitored (Watson et al., 2017) across a large datasets.

4.2. *Using GLCM to guide management and report on change*

The case studies provided a source of information for land managers and policy makers to explore how decisions and actions at local scales can support retention, maintenance or strengthening of ecological networks at regional and larger scales.

GLCM provides a data-driven evaluation and visualisation of a region's complete suite of habitat networks, including the relative ecological strength of links, the spatial context of locations, connectivity pinch-points, and barriers to movement (although exact delineation of

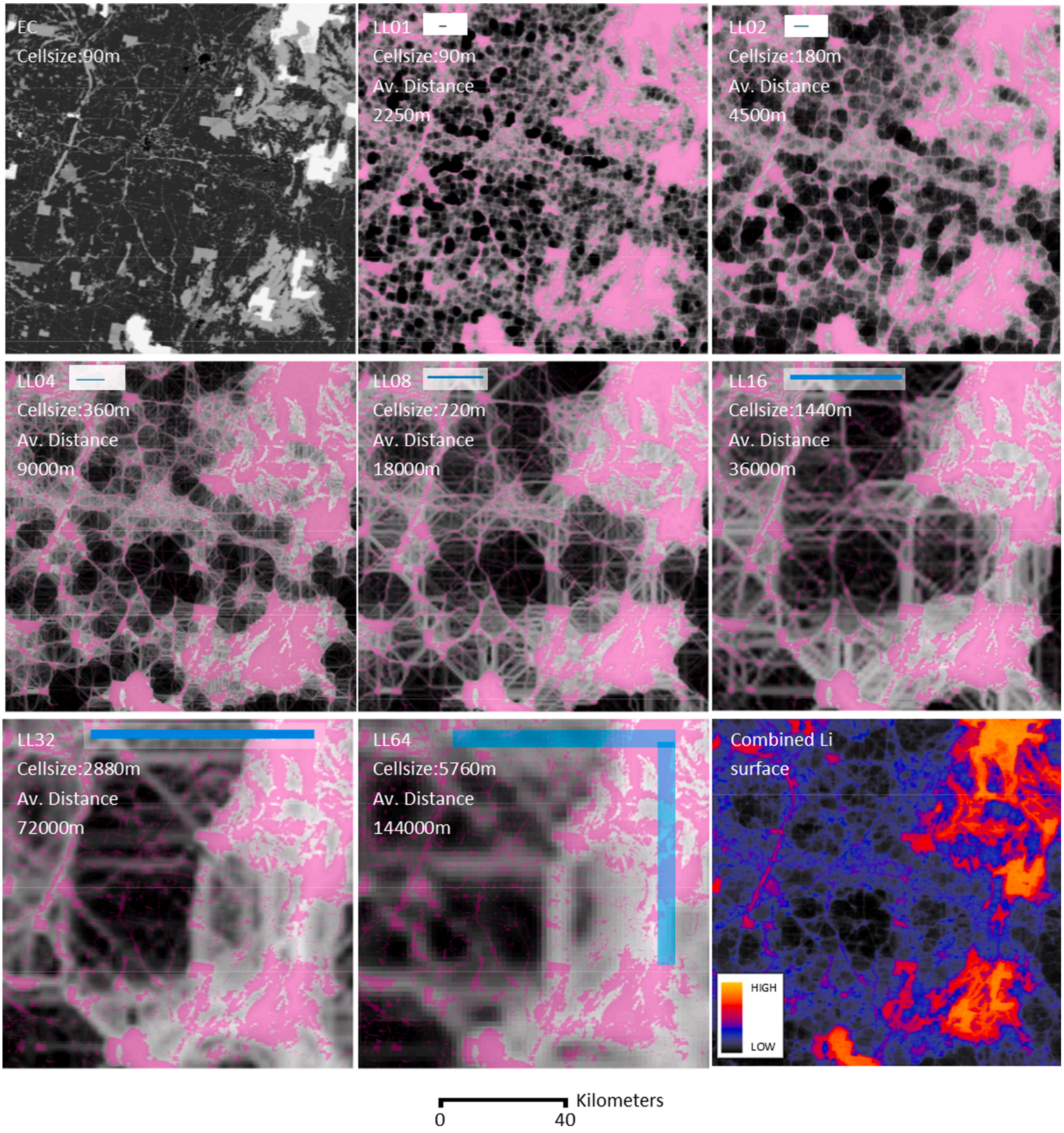


Figure 5. Component *Li* outputs for each scale/granularity component and the combined output, for a portion of the case study 2 extent. For each component the cell size and average movement distance is indicated by the width and length of the blue line, respectively.

these features requires additional context-specific interpretation). These features are illustrated in example spatial products from the case study 2a analysis. Fig. 6 provides a detailed map from an example landscape in southern NSW (comprising less than 2% of the full analysis extent for case study 2a; Supplementary S8, provides the map for all of NSW).

The highlighted areas in Fig. 6 show examples of features which can lead to on-ground targeted management actions to protect or enhance landscape connectivity. These maps provide an index of the contribution of each location to landscape connectivity in their current state. This information, when used in conjunction with complementary information, helps to highlight places where ecological restoration could be most effective in strengthening existing ecological networks.

4.3. *GLCM and its place alongside alternative approaches*

GLCM was designed to address ecological network function (Gaston, 2010) generically across all biodiversity, including common species; and presumably, unknown species which would otherwise be overlooked. We argue that GLCM best meets the criteria we listed in Table 1 as a whole, at least in respect to the demand we encounter for generic broad-scale landscape connectivity assessment in NSW, Australia. Although we do not offer a systematic review of alternative methods for assessing landscape connectivity, we recognise that alternative approaches can also address individual criteria to varying degrees, as well as additional criteria, not listed here. In respect to some criteria, alternative approaches can also outperform GLCM. For example: the

Box 1
Glossary of terms

Cost-benefit tool (CBA)	used to assess the neighbourhood habitat area of a location
ε	Cost ratio – the ration of the cost-distance of more permeable habitat to least permeable
Ecological Condition	a measure of each location's capacity to provide the structures and functions necessary for the persistence of all plant and animal species native to an area
GLCM	General Landscape Connectivity Model
Functional Connectivity	connectivity that is based on organisms' behavioral responses to individual landscape elements (patches and edges) and the spatial arrangement of the entire landscape.
Hj	the amount of habitat (quantity and quality) of each neighbourhood location
Landscape Connectivity	the extent to which a landscape facilitates or impedes the movements of organisms
Habitat Link Value (*Li*)	The contribution of a location to the integrity of a habitat network. The contribution of a location to the integrity of a habitat network (see Drielsma et al. 2007b)
Neighbourhood habitat area (*Ni*)	Measure of structurally connected existing habitat at a location in a landscape (see Drielsma et al. 2007a)
Structural Connectivity	connectivity that is based on the structure of the landscape with relationship to any behavioral characteristics of organisms
Spatial Links Tool (SLT)	used to assess the habitat link value of a location
w_{ij}	Permeability (inverse of cost-distance) of a path between locations *i* and *j*

approach of Lechner et al. (2015) is superior in respect to computational speed and therefore interactivity, while it doesn't recognise the variegation of landscapes that GLCM can; and, due to computational considerations, GLCM draws on least-cost paths only and cannot feasibly include all-paths analysis, as Circuitscape does (but for only a limited set of path nodes).

GLCM provides an assessment of the strength of habitat links based on the quanta of habitat at link nodes and the permeability of links. It does not seek to assess persistence as other complementarity-based approaches do (e.g. see Drielsma et al., 2014; Drielsma et al., 2012; Ferrier and Drielsma, 2010; Moilanen et al., 2009). However, GLCM has been successfully integrated into one such assessment (see Drielsma et al., 2020).

Each species interacts with the landscape in a unique way that cannot be understood from a portrayal of generic landscape connectivity alone (e.g. Delmas et al., 2019). Where the consequences of ill-informed decisions can lead to extinctions, more detailed information including field-based observations, and more biologically detailed and persistence-based assessments may be needed (Foster et al., 2016; Poiani et al., 2000; Possingham et al., 1993; Taylor et al., 2016). For such cases some of the authors have developed an approach (Drielsma and Love, 2021; Drielsma and Ferrier, 2009) that also addresses most of the criteria in Table 1 while it contrasts with GLCM's genericism by working with individual species distribution models, informed by biological data, and by applying species-specific movement abilities within a metapopulation persistence framework.

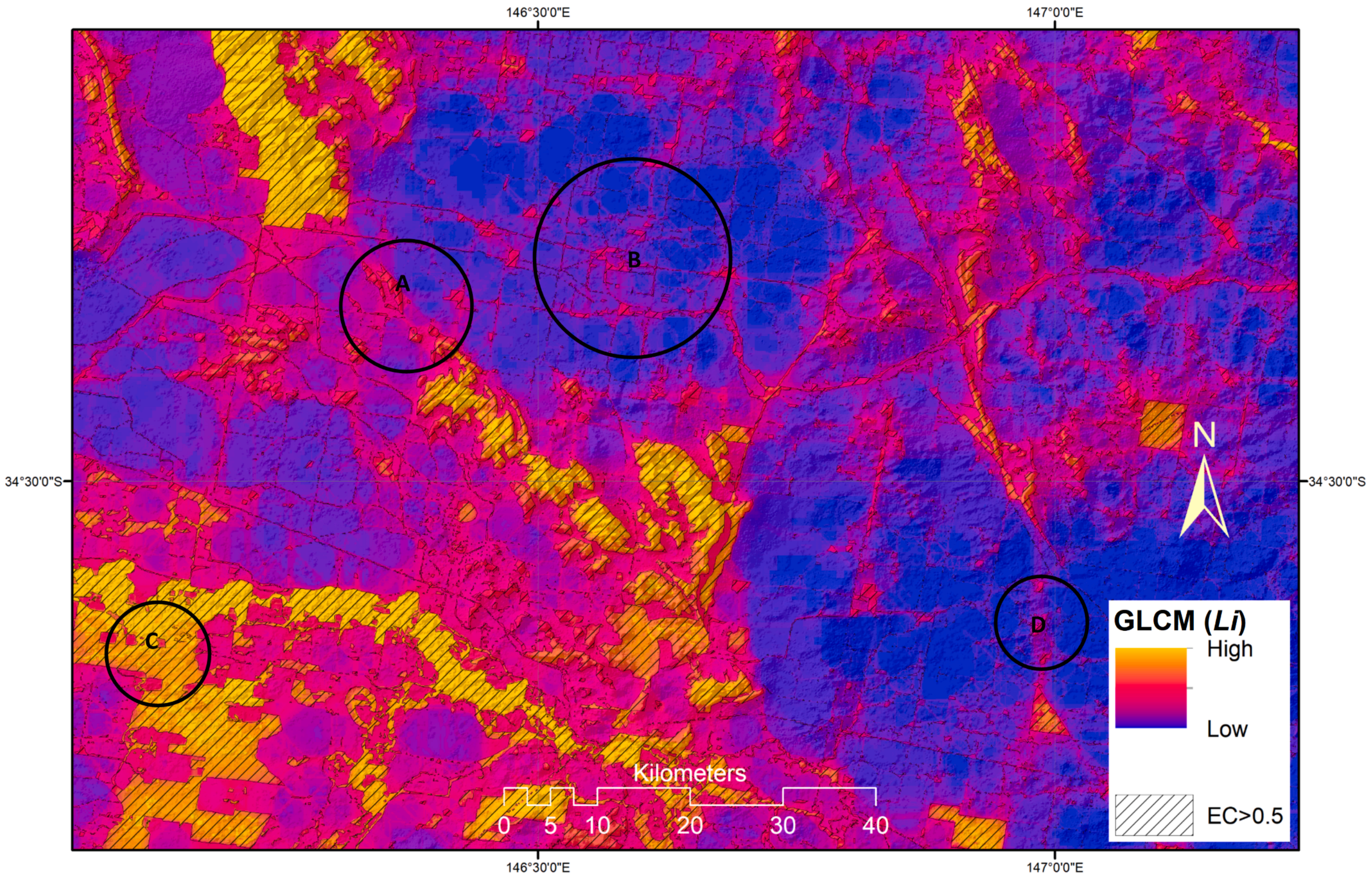
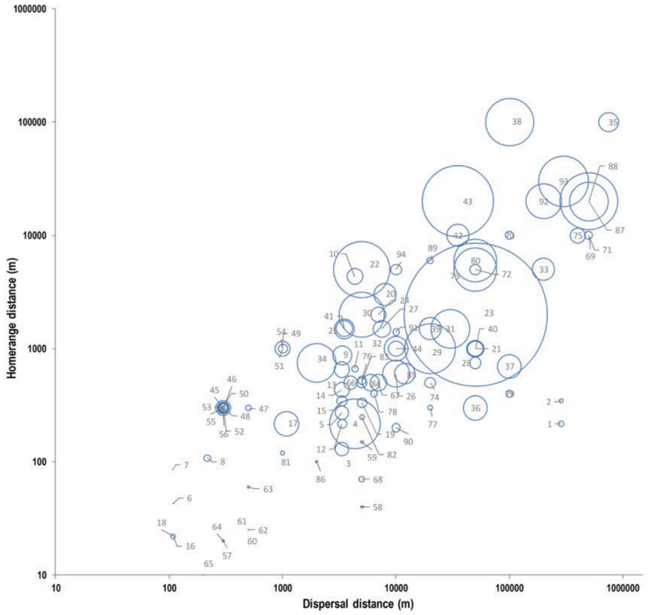


Figure 6. Example of mapped GLCM *Li* output from southern NSW, Australia (from case study 2a). Hatching shows areas with ecological condition at levels greater than 0.5 (on a scale from zero to one), which indicate where relatively intact habitat occurs in relation to the GLCM *Li* output. Areas can be identified as being part of: stepping stones (e.g. circle A); inter-connected networks (e.g. circle B) where multi-lateral connectivity occurs; large contiguous areas of habitat (e.g. circle C), which supports ubiquitous connectivity within patches; or linear habitat links, or 'corridors', which support linear connectivity (e.g. circle D). In each case the map indicates the relative benefit (in terms of landscape connectivity) of protecting remaining habitat, or restoring lost or degraded habitat.



BOX 2. Estimated home range movements against dispersal movement for 94 threatened fauna entities on a log-log chart.

The data was collated from three assessments of threatened species in NSW, Australia (Drielsma et al., 2016; NSW Department of Environment Climate Change and Water, 2009; Taylor et al., 2012). Entities included individual species and functional groups. The chart shows a reasonably even spread of these species along each axis, demonstrating the presence of a power law in relation to movement abilities. The chart also indicates estimated minimum area needed to support a viable population as the size of the bubbles, which generally increases with movement ability.

4.4. *The mathematical model*

The all-pairs approach implemented in GLCM allows for a consistent and controlled sampling of entire study regions. This prevents the problem of over-sampling paths in areas with a greater proportion of intact quality habitat, and under-sampling or ignoring degraded areas and small patches which are prevalent in many regions. Under-sampling the low quality or highly fragmented habitat would undervalue the important marginal contributions of remnant habitat in partially cleared landscapes such as stock reserves or paddock trees in the highly fragmented NSW wheat-sheep agricultural region of central NSW, Australia (Law et al., 2000; Lentini et al., 2011). Sampling bias was completely removed in the most recent version of GLCM (case study 2) by implementing a complete, all-pairs sampling strategy, allowing the algorithm to resolve patterns of habitat connectivity more efficiently than with the heuristic approach (adopted in case study 1 and 3). The all-pairs approach is also fully deterministic, which ensures repeatability and consistency across space and across any set of scenarios.

We expect that GLCM's scaling approach, along with the use of petals and jittering, diminishes over-reliance on single-scale least-cost by capturing wider links at successively coarser spatial scales, and by examining all-pairs of feasible nodes, including multiple proximal nodes. This ensures that many alternative paths, relevant to different species and modes of movement, are captured. So, while GLCM does not consider all alternative paths between individual node pairs (it does not do all-paths); it comprehensively captures potential node pairs across space and across scales.

4.5. *The generic approach*

GLCM can also be applied to actual species or species groups, where scale, resolution, and habitat quality are informed by knowledge of the biological entities chosen (Correa Ayram et al., 2017). We justify our generic approach, demonstrated by the three case studies, in terms of its ability to consider the otherwise intractable complexity of multiple taxa, in variegated environments, through time. GLCM provides pragmatic information in data-poor settings, and augments more detailed species- or community-level assessments which might lack geographic coverage, or which are biased towards a limited set of biological entities.

The generic approach has implications for its use. The promotion of landscape connectivity is intended to reduce pressures affecting the viability of populations generally, and to ensure that ecosystem processes remain intact (Gaston, 2010).

5. CONCLUSION

GLCM utilizes ecological theory to integrate habitat value with connectivity across a network. It considers all-pairs connectivity across a region within a computationally optimised application and is designed to operate across the full range of habitat values present in a region using continuous-valued raster data. This alleviates the need to define or assign weights to discrete habitat patches or make *a priori* judgements as to which habitat nodes to include in an analysis. The approach can be applied consistently and repeatedly to large regions represented by highly granular, complex models of ecological condition. Given sufficiently detailed input data, GLCM allows analysis resolutions to be determined by data-driven ecological relevance rather than by processing limitations.

GLCM outputs can be used for reporting on status and trends in landscape connectivity, and for contributing to broad-scale conservation planning or localised actions that seek to build or strengthen habitat networks to support biodiversity persistence, especially through climate change.

The operational advantages of GLCM mean that landscape connectivity assessment can be practically updated with refined or changed inputs including time-series of remotely sensed data, or it can be applied to alternative scenarios of land use, restoration, climate projections or combinations of these.

5.1. *Software*

The neighbourhood habitat area analysis for calculating *Ni* is performed using the spatial CBA tool (Drielsma et al., 2007a) and *Li* was calculated using the spatial links tool (Drielsma et al., 2007b), both are part of a larger biodiversity tools software package that's been developed in-house and will be made available via the NSW government's SEED portal (https://www.seed.nsw.gov.au/). The spatial CBA tool relies on a NVidia CUDA capable GPU. The spatial rescaling of inputs for both *Ni* and *Li* was performed in Python using ESRI's Arcpy module (Supplementary S8). Combining analysis outputs across scales was performed using ArcMap's grid cell statistics tool with the analysis grid cell size set to the original finest resolution of ecological condition.

The current version of the CBA tool is computationally optimised with GPU processing, which permits rapid calculation (less than 1 hour for over 10^8 grid cells in case study 2).

Author CRediT statement

Michael Drielsma: Conceptualization, Supervision, Writing- original draft preparation, review and editing, Visualisation **Jamie Love:** Conceptualization, Methodology, Software, Formal analysis, Writing – review and editing **Subhashni Taylor:** Writing – review and editing **Rajesh Thapa:** Formal analysis, Map production, Writing – review and editing **Kristin Williams:** Conceptualization, Writing – review and editing

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2021.109858.

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