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RESEARCH ARTICLE

Characterising landscape connectivity for conservation planning using a dispersal guild approach

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Abstract

Context Land use changes have modified the extent and structure of native vegetation, resulting in fragmentation of native species habitat. Connectivity is increasingly seen as a requirement for effective conservation in these landscapes, but the question remains: 'connectivity for which species?'.

Objective The aim of this study was to develop and then apply a rapid, expert-based, dispersal guild approach where species are grouped on similar fine-scale dispersal behaviour (such as between scattered trees) and habitat characteristics.

Methods Dispersal guilds were identified using clustering techniques to compare dispersal and habitat parameters elicited from experts. We modelled least-cost paths and corridors between patches and individual movement probabilities within these corridors for each of the dispersal guilds using Circuitscape. We demonstrate our approach with a case study in the Tasmanian Northern Midlands, Australia.

Results The dispersal guild approach grouped the 12 species into five dispersal guilds. The connectivity modelling of those five guilds found that broadly dispersing species in this landscape, such as medium-sized carnivorous mammals, were unaffected by fragmentation while from the perspective of the three dispersal guilds made up of smaller mammals, the landscape appeared highly fragmented.

Conclusions Our approach yields biologically defensible outputs that are broadly applicable, particularly for conservation planning where data and resources are limited. It is a useful first step in multi-species conservation planning which aims to identify those species most in need of conservation efforts.

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Introduction

Human driven land use changes have modified the extent and structure of native vegetation, resulting in fragmentation of native species habitat. Species movement through landscapes declines as habitat fragmentation increases, with decreased connectivity resulting in reduced population viability and increased extinction risk beyond that caused by habitat loss alone (Caughley 1994; Fischer and Lindenmayer 2006; Brook et al. 2008). Land use between habitat patches can strongly influence connectivity. The most common conservation method to address the impacts of habitat fragmentation is to increase habitat area or increase connectivity between remnant habitat patches through wildlife corridors (Brost and Beier 2012).

A common approach to connectivity modelling is based on least-cost path analysis and graph theory (Urban and Keitt 2001; Adriaensen et al. 2003; Saura and Torné 2009; Foltête et al. 2012). Least-cost paths represent the least costly path across a cost surface, where the values assigned to cells in the cost surface represent the relative energetic costs, difficulty, or mortality risk of moving through that particular land cover type (Adriaensen et al. 2003; Sawyer et al. 2011). Least-cost analysis can also be used to identify least-cost corridors which represent the accumulated costs of movement between two patches (McRae and Kavanagh 2011). The significance of patches and links within a connectivity network can be quantified using the graph theoretic approach and calculation of network measures (Minor and Urban 2008; Rayfield et al. 2011). Another common approach that has been applied to connectivity modelling is based on circuit theory, whereby the landscape is conceptualized 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).

Connectivity modelling has been applied to landscape features or land-facets (Alagador et al. 2012; Brost and Beier 2012), single species (LaRue and Nielsen 2008; Tournant et al. 2013) and multiple single species modelled separately (Beier et al. 2009; Brás et al. 2013). In this paper we develop a modelling approach that is an intermediate between single species models and the landscape features or land-facets approach, characterising connectivity for groups of species based on shared dispersal and habitat characteristics. We extend the guild concept, defined as a "group of species whose members exploit similar resources in a similar manner" (Park and Allaby 2013), to include species with similar dispersal characteristics as well as those that exploit similar resources in a similar manner. Using the guild approach, information about single species can be meaningfully aggregated into common groups, providing greater generalisability of the results (Blaum et al. 2011). Conversely, adopting empirical, single species approaches to understand many species' needs can be practically impossible to implement within time frames and costs reasonable for conservation planning (Noon et al. 2009; Blaum et al. 2011; Rudnick et al. 2012). Our research complements existing approaches to multi-species connectivity modelling for conservation planning which include assessing the overlap between connectivity outputs from multiple single species models (Beier et al. 2009), identifying links between habitats occupied by multiple species with distinct distributions and/or dispersal requirements (Brás et al. 2013) and identifying corridors for a range of dispersal abilities as opposed to specific species (Drielsma et al. 2007; Cushman and Landguth 2012; Synes et al. 2015). Additionally, our methods can potentially be used in experimental studies examining the ecology of connectivity for multiple species (e.g. Haddad et al. 2003; Frey-Ehrenbold et al. 2013).

The objective of this study was to develop the dispersal guild concept and then apply it to conservation planning using an expert-based parameterisation of connectivity modelling using a combination of least-cost path, circuit theory and graph theory methods. The approach can be used as a filtering process for multi-species conservation planning to identify those species in greatest need of conservation efforts. We demonstrate this approach using the Tasmanian Northern Midlands, Australia as a case study using a connectivity modelling framework which describes fine-scale dispersal patterns (Lechner et al. 2015b, c). Through a process of engaging experts in workshops we identified the species of critical concern and the habitat and dispersal characteristics of each. These individual target species were then grouped into dispersal guilds using cluster analysis. Connectivity was then modelled for each of these groups based on their shared dispersal and habitat characteristics. We used Graphab (Foltête et al. 2012) to calculate graph-

metrics and least-cost paths between patches and Linkage Mapper (with Circuitscape) (McRae et al. 2008; McRae and Kavanagh 2011) to characterise least-cost corridors and individual movement probabilities for each of the dispersal guilds. By modelling dispersal guilds it was possible to capture a range of responses to fragmentation and thus identify those groups of species that may benefit from habitat restoration based on the spatial and functional requirements for increased connectivity. We conclude by discussing the application of this method to conservation planning.

Dispersal guilds to connectivity analysis methods

Case study

We use a case study in the Tasmanian Northern Midlands to demonstrate the application of the dispersal guild approach to conservation, as this landscape represents a typical connectivity planning problem example, where the focus of conservation is on connecting small fragmented, predominantly woodland remnant habitat. The Tasmanian Northern Midlands is one of fifteen designated Australian Biodiversity Hotspots containing numerous endemic plants and nationally and state listed threatened plants and animals (Department of Environment 2014). Widespread land clearing has left native vegetation highly fragmented, with mostly small and scattered remnants (Mooney et al. 2010). A planned expansion of irrigation schemes in the region will likely lead to agricultural intensification across the landscape (Gadsby et al. 2013), and further fragmentation of habitat in the region.

Expert elicitation

The selection of species, their parameterisation and validation of the model outputs were driven by an expert elicitation approach, over three (approximately 1 day) workshops and through engaging individual experts separately. The aim of each of the three workshops were as follows:

1. To identify target species of conservation concern and available spatial and ecological data.

2. To identify dispersal and habitat characteristics for the target species to be used as inputs into dispersal guild analysis and connectivity modelling.
3. To present and refine draft modelling outputs.

The workshop attendees represented a core group of experts responsible for parameterising and selecting all the target species. This group was made up of 14 individuals over three workshops, with eight to eleven individuals attending per workshop (including the authors). This group included ecologists from academia (7), non-government conservation organisations (4), and government conservation agencies (3). The experts had a broad knowledge of the study area and the species, either through conducting research in the area or engaging in on ground conservation activities. These experts included individuals from three conservation organisations (the Tasmanian Land Conservancy, Greening Australia and Bush Heritage Australia) and the state government who have all been working in the study area for many decades. In addition to the workshop, six other experts were consulted separately to validate parameter estimates derived by the workshop attendees. These other experts had completed or were completing their PhD on specific target species, in many cases within the study area and had strong field experience which included observing and/or trapping the target species. Finally, two recognised field ecologists from academia with broad experience in the ecology of connectivity in Australia were also consulted.

Target species

Species considered to be of importance for conservation in the Tasmanian Northern Midlands were chosen at the first expert workshop. This workshop identified ground-based mammals as a key target group for conservation. Candidate species were reduced to those that depend only on native woodlands, the original vegetation cover that was fragmented by clearing as distinct from native grasslands, non-native vegetation or pasture. For example, the Eastern Quoll (*Dasyurus viverrinus*) was excluded because it readily utilises cleared areas such as non-native pastures and improving landscape connectivity is unlikely to be as important for the conservation of this species as other factors such as managing introduced predators. Twelve ground based mammals were identified and

then grouped into dispersal guilds using a cluster analysis in subsequent workshops.

Approach to characterising connectivity

Our approach to characterising connectivity used in this paper is based on the GAP CLoSR framework for modelling fine-scale dispersal behaviour described in Lechner and Lefroy (2014) and Lechner et al. (2015a, b, c). The framework consists of three key parameters (Fig. 1):

1. *Minimum patch size* The minimum area of habitat that can support a population. Below this minimum patch size, vegetation no longer contributes to habitat but may aid in dispersal such as in the case of a wildlife corridor.
2. *Gap-crossing distance threshold* The maximum distance a species will cross between connectivity elements (such as scattered trees), which limits the distances of open ground (gaps) individuals will move across.
3. *Interpatch-crossing distance* The maximum total distance that a species can move between habitat patches using connectivity elements that are within the gap-crossing distance.

We also included additional parameters characterising land cover for habitat and connectivity elements. Habitat and connectivity elements were classified as either above 1 m (e.g. trees) or below 1 m (e.g. undergrowth) from ground level (Table 1).

The parameters (Table 1) for each of the 12 species were the result of a literature review and discussions with individual experts at the second workshop. These parameters were refined in the final workshop when the outputs from the model were presented to the expert group.

A critical component of the framework is the inclusion of fine-scale dispersal behaviour which is often absent from many common connectivity modelling approaches. In order for species to move long distances between patches there is a need for connectivity elements such as corridors, or stepping stones to facilitate movement (Fischer and Lindenmayer 2002; Van Der Ree et al. 2004).

Dispersal guilds and cluster analysis

Common dispersal and habitat characteristics of the target species were identified using cluster analysis to define the dispersal guilds. Two cluster analysis methods were used; a hierarchical clustering analysis in R using the pvclust package version 1.2-2 (Suzuki and Shimodaira 2006) and the Partitioning Around Medoids (PAM) algorithm (Kaufman and Rousseeuw 1990) in the Cluster package for R 2.15.2. A hierarchical cluster analysis is based on an agglomerative algorithm and produces a dendrogram or tree diagram used to illustrate the arrangement of the clusters. The PAM algorithm groups objects into clusters based on the number of clusters specified beforehand. In our study a range of cluster numbers were tested. To determine the stability of the clustering, which reflects the validity of a cluster solution (i.e. number and grouping), we calculated the average silhouette width, which provides a standard measure of cluster isolation (Kaufman and Rousseeuw 1990). High values of average silhouette width is one way to identify the
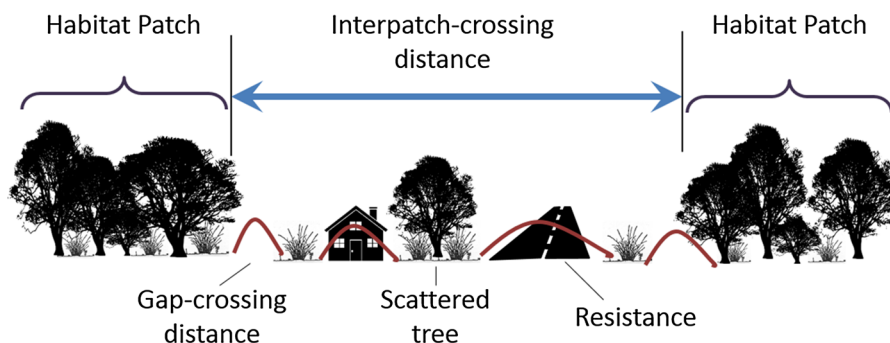

Fig. 1 Conceptual model of fine-scale connectivity behaviour of mammal fauna, where the likelihood of individuals moving between two patches is a function of two thresholds, the interpatch-crossing distance and gap-crossing distance, and the dispersal cost of landcover features (such as roads)

Table 1 Habitat values and connectivity elements used to inform dispersal guilds for connectivity modelling

Habitat (patches)	
Habitat cover > 1 m	Woody vegetation taller than 1 m that contributes to habitat to sustain a breeding population
Habitat cover < 1 m	Vegetation (or even man-made structures) shorter than 1 m that contribute to habitat to sustain a breeding population
Ruleset	AND function. If Habitat cover over 1 m = "yes" and Habitat cover under 1 m = "yes", species require both and won't be found where one exists in isolation
Minimum patch size	Habitat comprises areas for species to breed and raise young. Minimum contiguous area considered to meet habitat requirements, for species. This determination of minimum patch size does not accommodate the influence of habitat quality or emigration
Connectivity elements (e.g. Stepping stones or corridors that provide cover)	
Connectivity elements with cover > 1 m	Woody vegetation taller than 1 m that contributes suitable perching/resting places
Connectivity elements with cover < 1 m	Vegetation (or even man-made structures) shorter than 1 m that constitute suitable hiding/resting places
Ruleset	OR function. If connectivity elements with cover over 1 m = "yes" and Stepping stones and corridors with cover under 1 m = "yes", species will use either, whatever is available, it is not necessary that both occur together
Minimum connectivity element size	Most species only require very small features for shelter whilst moving between habitat patches. The size of features included in a model is often limited by available data
Dispersal distances	
Interpatch-crossing distance threshold	Distances between patches
Gap-crossing distance threshold	Distance between connectivity elements

Connectivity elements are identified as cover below the minimum patch size

appropriate number of clusters within which the data naturally falls. PAM uses a medoid as its measure of cluster centre as opposed to a centroid based on mean values. This method is more robust in the presence of noise and outliers than mean-based approaches (e.g. k-mean). The two cluster analysis methods have very different approaches and different graphical outputs, providing a method of testing whether clustering outputs are independent of the assumptions in the clustering methods.

To complete the cluster analysis, categorical variables including habitat above and below 1 m were converted to a matrix of zeros and ones as both cluster analysis methods require all variables to be continuous. The converted categorical data were then combined with the continuous data describing dispersal distances, and singular value decomposition was applied to create new continuous variables, each of which represents a composite of the original datasets.

The outputs of both cluster analysis methods were presented at the third expert workshop for validation. The cluster analysis provided an accessible graphical way of summarising the complex similarity and dissimilarity of ecological parameters between species that may have been difficult for an expert panel to identify from the raw data alone.

A single value for each of the habitat characteristics and dispersal thresholds is required to represent each dispersal guild for connectivity modelling. In this study we used average values for the continuous variables (e.g. interpatch-dispersal distance) and the most common value for the categorical variables (e.g. habitat).

Characterising habitat and dispersal-cost surfaces using spatial data

Habitat and dispersal-cost surfaces were produced for connectivity modelling to spatially represent the attributes of each dispersal guild. All spatial layers, regardless of their original spatial resolution, were aggregated to 50 m, the smallest pixel size at which the connectivity model would run for our study area.

Structural vegetation mapping from Tasmanian Land Conservancy vegetation data (5 m pixel size) was used to spatially represent habitat and connectivity elements (Sprod 2013). The spatial representation of the connectivity elements was used to create the dispersal cost-surface layer. Spatial data were based on TASVEG 2.0 mapping (DPIPWE 2013) and refined through interpretation of aerial imagery. Mapped polygons were refined and then attributed according to estimated density of vegetation structures above and below 1 m height (Table 1).

The above- and below 1 m vegetation classes were converted into two binary layers to spatially represent all combinations of habitat and connectivity described in Table 1. Habitat and connectivity were characterised as: (i) vegetation > 1 m; (ii) vegetation < 1 m; (iii) vegetation > 1 m AND vegetation < 1 m; and (iv) vegetation over 1 m OR vegetation under 1 m (i.e. either i, or ii) (Table 1; Fig. A.1). An AND function represents cases where vegetation above and below 1 m need to be present, while the OR function represents cases where any form of vegetation is present.

The dispersal-cost surface characterises how land cover type between habitat patches reduces or prevents movement. It is a result of combining the gap-crossing layer and the land cover resistance surface.

The gap-crossing distance threshold layer was simulated by creating the gap-crossing layer (see Lechner et al. (2015a, b, c) for more details). The gap-crossing layer identified distances between connectivity elements and patches beyond the movement threshold that act as barriers to dispersal. The input vegetation layers were buffered by half of the gap-crossing distance threshold (Fig. A.2). Where connectivity elements or patches fall within the gap-crossing distance threshold, buffers touch or overlap indicating connectivity between patches. Areas mapped outside the buffer area describe areas in which dispersal cannot take place (i.e. barriers).

Resistance to dispersal between patches is characterised by increased movement costs associated with land cover which is assumed to be linear. For example, 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 study area we used generic land cover classes with dispersal costs assigned to each pixel based on expert opinion for small and medium mammals

(Table A.1). We used the Land Use Tasmania spatial dataset (Brown 2011) for the spatial characterisation of resistance (Fig. A.3 caption for more details).

In the final step, the dispersal-cost surface was created by combining the binary gap-crossing layer with the resistance surface based on land cover. The dispersal-cost values are a function of: (a) pixel size (e.g. if the pixel size is 50 m and there is no resistance the cost should be 50 m); (b) land cover resistance (200 % resistance means a pixel size with of 50 m will have a value of 100 m); and (c) the presence of connectivity elements below the gap-crossing distance identified from the gap-crossing layer.

A summary of the processing rule set:

- Connectivity elements take precedence over all other land cover classes, because dispersal cannot occur in the absence of structural connectivity;
- The dispersal cost for each pixel was calculated as an average of all land covers.

The result was a resistance layer that recognises threshold dynamics by ensuring there was no dispersal where gaps are too large between connectivity elements, but still models cumulative costs where dispersal was considered possible but may be impeded by land use.

Connectivity modelling approach

Connectivity was modelled using Graphab (Foltête et al. 2012) a graph-network connectivity modelling software that uses least-cost paths and Linkage Mapper (McRae and Kavanagh 2011) for identifying least-cost corridors. The least-cost analysis was based on cumulative cost in relation to land cover resistance (Minor and Urban 2007; Dale and Fortin 2010; Etherington and Holland 2013).

Using the graph theoretic approach and the Graphab software we characterised patch isolation by identifying groups of patches that are linked to each other but isolated from other groups of patches. These groups of interlinked patches are known as components. The patterns in the size and shape of the components can be used to characterize fragmentation and isolation, and to locate barriers to connectivity. We also calculated a number of landscape-scale graph-metrics describing component characteristics: mean size of components (km^2), size of the largest component (km^2), number of components and the

integral index of connectivity (IIC) dispersal metric (Minor and Urban 2008; Rayfield et al. 2011). The IIC measures the probability that two points randomly placed in a landscape are in habitat areas that can be reached (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007). High values indicate more connected landscapes.

We then combined the least-cost corridors, representing areas with cost-weighted distances below the interpatch dispersal distance threshold with Circuitscape's Pinch Point Mapper in the Linkage Mapper tool (see McRae and Kavanagh 2011). The Pinch Point Mapper characterises wildlife corridor pinch points based on random walk patterns between patches identified using circuit theory (McRae et al. 2008). Pinch-points (or choke-points) are areas where animal movement is funnelled within corridors and represent areas where linkages are most vulnerable to being severed (McRae et al. 2008). Using this combination of methods means we can characterise connectivity based on the two dispersal thresholds (interpatch and gap crossing) while characterising dispersal behaviour more realistically based on a random walk. This is not possible when modelling with Circuitscape in isolation as it does not allow for maximum dispersal distances.

Sensitivity analysis

The connectivity outputs can be assessed for sensitivity to the input data and parameterisation. A comparison of the modelled connectivity with and without dispersal costs from the gap-crossing layer and land use allows assessment of the importance of interpatch-crossing distance thresholds for landscape-scale connectivity.

The results can be interpreted in two ways:

1. Does uncertainty in the mapping of fine-scale vegetation and land use effect connectivity outputs?
2. Do corridors, vegetation and connectivity elements (e.g. scattered trees) make a key contribution to connectivity?

Further sensitivity analysis that characterises the number of components versus interpatch-crossing distance for all combinations of habitat input layers identifies the critical scales that need to be considered.

Tasmanian Northern Midlands case study

Expert elicitation of dispersal and habitat values for each species

A literature review revealed very few empirical studies that could be used to confidently characterise dispersal distances for our species. As a result, the values for the dispersal and habitat parameters for each species were derived through the consensus of an expert panel in a workshop environment (Table A.2). For some species experts outside of the workshop group were suggested by the panel and contacted or literature was identified. Values derived from outside experts and literature were reviewed by the panel. The experts agreed that the values represent only approximations, so the relative differences between species are likely to be more accurate than the absolute values. The experts also agreed that due to the lack of knowledge of our target species a general sensitivity analysis was useful for assessing the uncertainty on the elicited estimations.

Identify dispersal guilds and connectivity model input parameters

The dendrogram produced by the hierarchical cluster analysis qualitatively identified six groups made up of one to four species (Fig. 2). The output from the PAM clustering method set at six clusters found exactly the same membership as the hierarchical cluster analysis. The average silhouette widths (a method for assessing the strength of clustering) for six clusters calculated with the PAM clustering method was 0.591, which according to Kaufman and Rousseeuw (1990) indicates "reasonable structure has been found". Average silhouette widths below 0.5 indicate weak structure that could be artificial or no structure at all. With five to seven clusters, all had greater than 0.5 average silhouette width (Fig. A.4b), so assigning between five and seven dispersal guilds was supported by this statistical analysis.

The results from the cluster analysis were then presented to the expert group in workshop 3. The expert group agreed with the clustering except for the Ring-tailed Possum (*Pseudocheirus peregrinus*). They recommended that the Ring-tailed Possum should be grouped with the other arboreal species. It was grouped in a class of its own due to the fact that it is
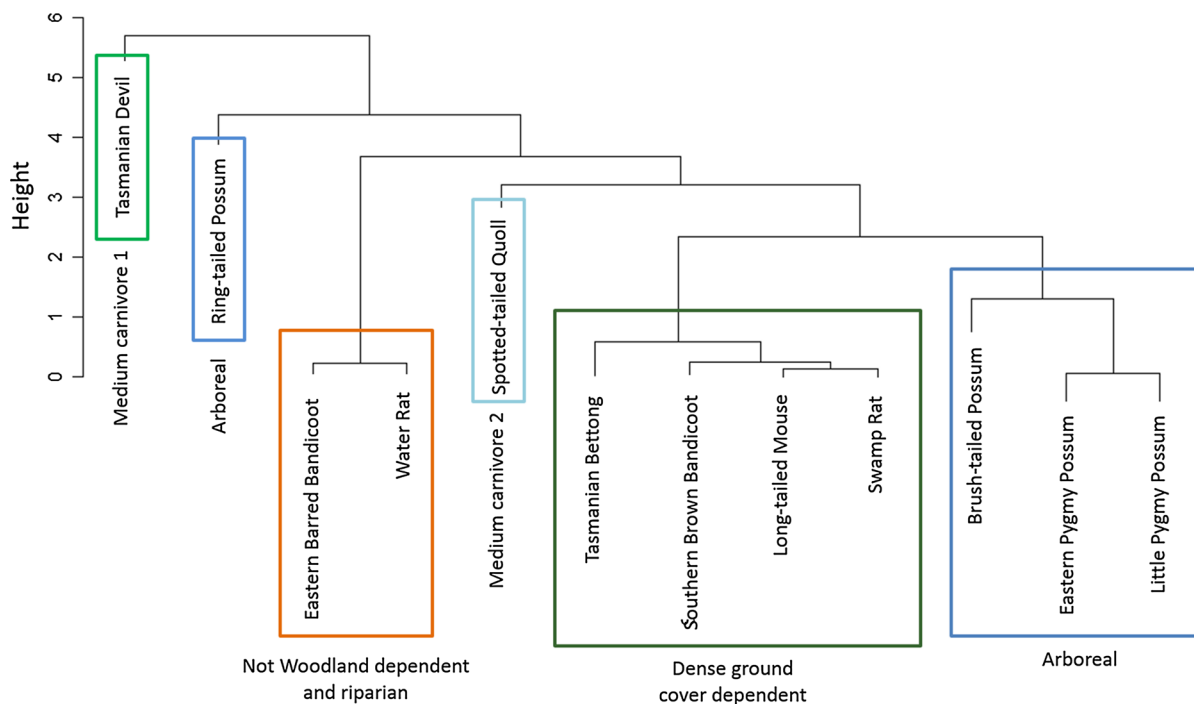
Fig. 2 Hierarchical cluster analysis where height describes the similarity between individual species. Labelled dispersal guilds identified post hoc through discussion with experts. *Each colour* represents a dispersal guild. Note that the Ring-tailed Possum was included in the Arboreal dispersal guild based on expert opinion even though it is found in a separate cluster

the only species which used connectivity elements over 1 m and elements under 1 m (Table A.2). The expert panel also agreed with the identification of the Tasmanian Devil (*Sarcophilus harrisii*) and Spotted-tailed Quoll (*Dasyurus maculatus*) as separate single-species dispersal guilds as their characteristics were unique.

Five dispersal guilds from the original six cluster groupings were agreed to by the expert panel. The expert panel labelled the guilds according to the ecological characteristics that united group members (Fig. 2; Table 2). The cluster analysis identified three guilds made up of smaller mammals with shorter interpatch-crossing and gap-crossing dispersal distances and smaller habitat requirements. Two separate single-species dispersal guilds were made up of medium carnivores with long, but distinct dispersal distances.

For each dispersal guild, a single value for each of the habitat characteristics and dispersal thresholds is required for connectivity modelling. For the two medium carnivore guilds their original values were used, while for the three other dispersal guilds the average values were used. In cases with categorical variables the combination of vegetation above- and/or below 1 m that was found in the majority of cases was used (Table 2).

Dispersal guild connectivity outputs

The connectivity analysis of the five dispersal guilds (Figs. 3, 4; Figs. A.5–A.9) showed large differences in the effects of fragmentation. For the two medium carnivores the landscape essentially appears connected. For the Tasmanian Devil, all patches were connected directly or indirectly to other patches (Fig. 3) and all but 4 patches were connected for the Spotted-tailed Quoll (Fig. A.6). Additionally, the least-cost corridor analysis showed that the medium-sized carnivore guilds with long interpatch and gap crossing dispersal distances utilises more of the matrix than the guilds with shorter dispersal distances (Figs. 3, 4).

From the perspective of the three dispersal guilds of smaller mammals, the landscape appears highly fragmented with the majority of the connected areas

Table 2 Average and majority values for habitat, patch size, connectivity elements and dispersal distance thresholds

Group name	Habitat cover > 1 m	Habitat cover < 1 m	Min patch size (ha)	Interpatch distance (m)	Connectivity elements with cover > 1 m	Connectivity elements with cover < 1 m	Gap crossing (m)
Medium carnivore-Tasmanian Devil	Yes	No	800	10,000	Yes	Yes	2000
Medium carnivore-Spotted-tailed Quoll	Yes	No	150	10,000	Yes	No	750
Not Woodland dependent or riparian	No	Yes	16	1000	No	Yes	150
Dense ground cover dependent	Yes	Yes	30.5	900	No	Yes	107.5
Arboreal	Yes	No	3.5	1650	Yes	Yes	200

in the east and west of the study area and most patches in the central region isolated or connected to relatively few patches (Figs. A.5–A.9). The average component size was between 20 and 28 km² (Table 3). The graph metric value reflects the visual patterns with the IIC having higher values for the medium carnivores versus the small mammals indicating greater connectivity at the landscape scale (Table 3).

Sensitivity analysis

The sensitivity analysis found that all but one of the dispersal guilds,'Arboreal', showed very similar connectivity outputs in terms of the component patterns regardless of the dispersal costs. In the case of medium mammals the landscape is always connected, but the availability of pathways vary and in the case of the two guilds of small mammals, 'Not Woodland dependent and/or riparian' and 'Dense ground cover dependent', most patches and the majority of the large components are isolated due to their relatively short interpatch-crossing distances. However, the 'Arboreal' dispersal guild showed large differences with or without the inclusion of fine-scale connectivity elements and land use. An assessment of the number of components versus interpatch-crossing distance for all combinations of habitat input layers found that at interpatch-crossing distances of approximately 1000 m there is a rapid drop off in connectivity within the landscape

(Fig. 5). This analysis, however, did not include the impact of the gap-crossing threshold.

Application of the results

For our specific case study we found that broadly dispersing medium-sized carnivores, are unlikely to have their landscape-scale connectivity increased with revegetation efforts in the Tasmanian Midlands because no or few habitat patches are considered isolated from their perspective. In such instances benefits may result from increasing the condition of habitat through restoration and critical components of wildlife corridors (i.e. pinch-points) or from addressing other threats such as devil facial tumour disease (Hawkins et al. 2006) or the effects of competition from introduced predators such as cats (Hollings et al. 2013). Where habitat patches for species are separated by more than the interpatch-crossing distance, revegetation may be effective, and our results provide a guide as to suitable areas for such activity. This might suit the dispersal guilds 'Not Woodland dependent or riparian' and 'Dense ground cover dependent' with average interpatch-crossing distances of 1000 and 900 m respectively. The corridor analysis (Figs. 3, 4) showed particularly striking differences in the use of the matrix between the medium carnivores and the small mammal dispersal guilds.

Connectivity was also examined for all species by plotting the number of components against the

Fig. 3 Connectivity analysis for the "Medium Carnivore–Tasmanian Devil" dispersal guild with an interpatch-crossing distance threshold of 10,000 m. *Black lines* indicate least cost paths (*LC*) between connected patches. *Least-cost corridors width calculated with 10,000 m cost-weighted distance threshold. Pinch-points identified with Circuitscape within corridors
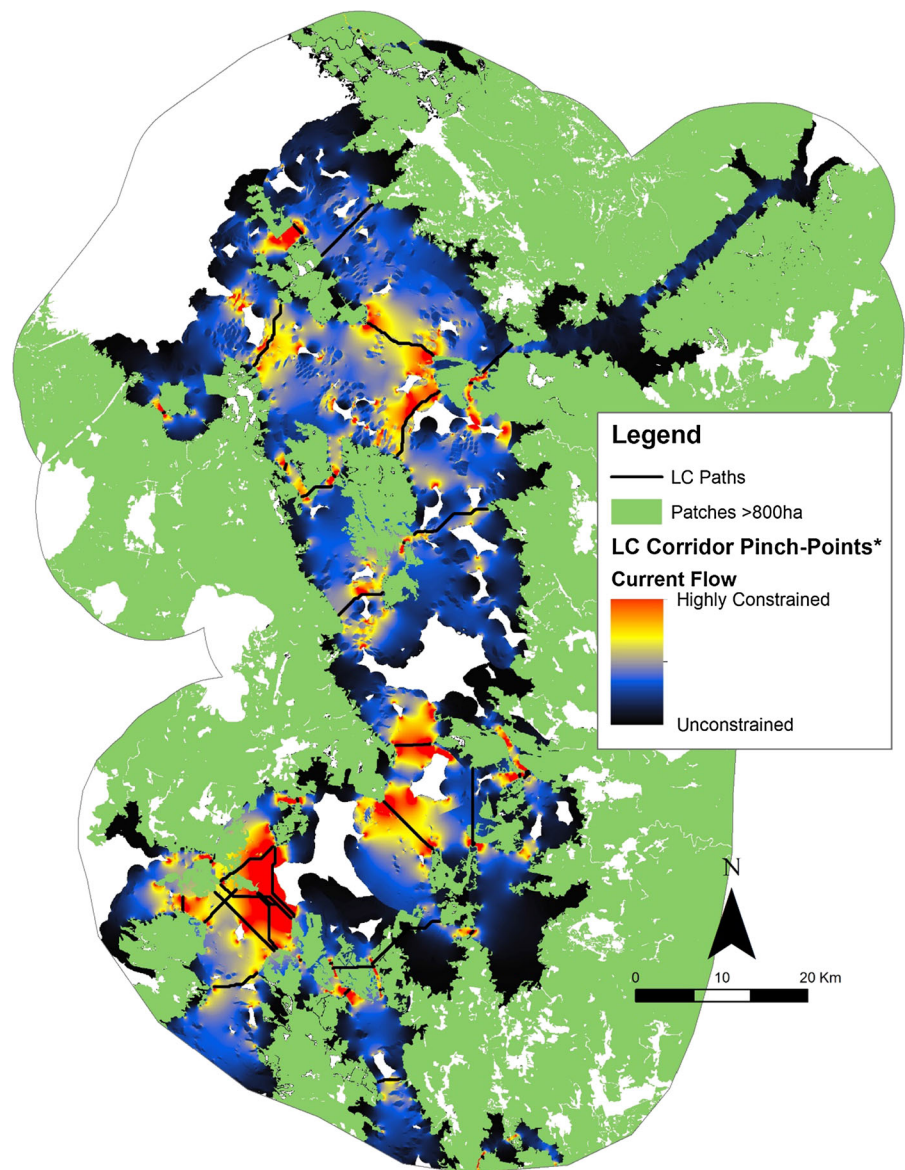

interpatch-crossing distance. This shows that the landscape becomes very fragmented for species with interpatch-crossing distances less than 1000 m. Four of the species tested (Long-tailed Mouse (*Pseudomys higginsi*), Swamp Rat (*Rattus lutreolus*), Eastern Pygmy Possum (*Cercartetus nanus*) and Little Pygmy Possum (*Cercartetus lepidus*)) have interpatch-crossing distances less than or equal to 1000 m. For those four species, the results show that the landscape is highly fragmented from their perspective. Reconnecting the landscape may have positive impacts on landscape movement of these species. A similar pattern can be seen when plotting the IIC versus the interpatch-crossing distance (Fig. A.10).

The outputs of our study could be refined with local knowledge of species distribution. In their current form, the outputs can provide general guidance as to where connectivity may be limiting (or not-limiting) and for which species connectivity may be limited and therefore aid in identifying where future conservation challenges may lie. The dispersal guild method can be expanded to assess future scenarios, barriers, and identify locations for revegetation (e.g. McRae et al. 2012; Foltête et al. 2014; Lechner et al. 2015a).

Fig. 4 Connectivity analysis for the 'Dense ground cover dependent' dispersal guild with an interpatch-crossing distance threshold of 900 m. Component boundaries in *blue* are located at the midpoint between patches identifying groups of patches that are linked, *red lines* indicate least cost paths between connected patches. *Least-cost corridors width calculated with 900 m cost-weighted distance threshold. Pinch-points identified with Circuitscape within corridors. *Inset* illustrates that connectivity for this guild exists only at fine scales
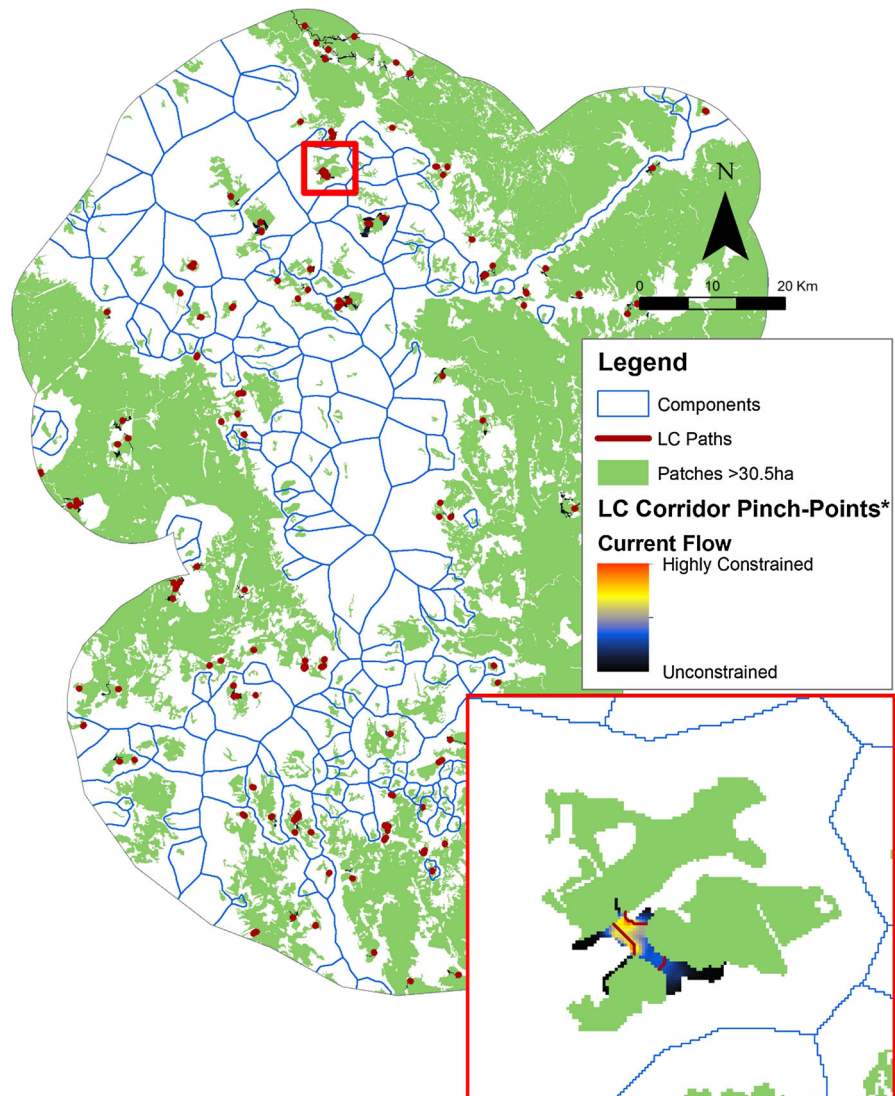
Application of dispersal guilds to conservation planning

The methods outlined in this study show great potential in conservation planning for targets that are intermediate between single species and general landscape features. The dispersal guild approach provides a way of using a relatively rapid assessment based on expert opinion to prioritise conservation effort for groups of species that view the landscape differently. Our approach to grouping species is supported by a recent empirical study by Brodie et al. (2014) which assessed single-species and multiple species habitat corridors in the tropical forests of Borneo and suggested that multispecies habitat connectivity plans should be tailored to groups of ecologically similar species to maximize effectiveness. Our approach presents a form of filtering in multispecies conservation planning by identifying those species that are likely to experience greatest benefit form conservation efforts (e.g. Noon et al., 2009). Such coarse filter approaches have been used previously for characterising connectivity for environmentally-similar habitats (Alagador et al. 2012) or land-facets (Beier and Brost 2010; Brost and Beier 2012), whereas our approach explicitly identifies which groups of species are affected by different aspects of fragmentation such as lack of connectivity

Table 3 Landscape-scale characteristics of the five dispersal guilds

| Graph metric	Medium carnivore Tasmanian Devil	Medium carnivore Spotted-tailed Quoll	Not woodland dependent or riparian	Dense ground cover dependent	Arboreal
Mean size of components (km^2)	5461	1411	22	28	20
Size of largest component (km^2)	5461	5632	2583	2539	4089
Number of components	1	4	221	166	297
Patches	21	76	448	278	1393
Total area (km^2)	5461	5644	4810	4681	5876
Integral index of connectivity	0.090	0.091	0.040	0.038	0.069

(a)

(b)

(c)
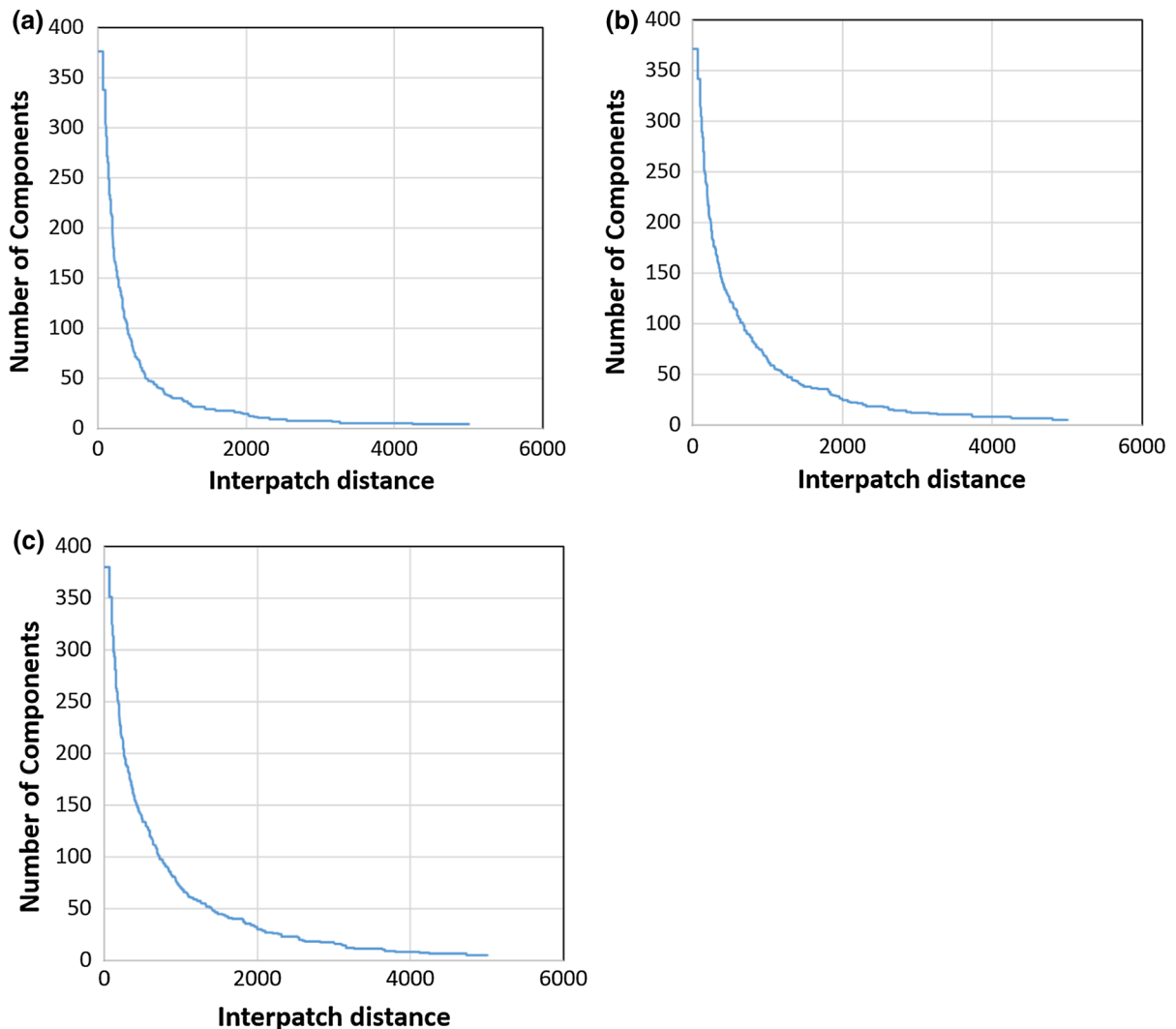
Fig. 5 Interpatch-dispersal distance sensitivity analysis for vegetation **a** over 1 m, **b** over 1 m and under 1 m, and **c** under 1 m characterised by the number of components versus the interpatch-crossing distance. For this analysis the gap-crossing distance was excluded

elements, potential pinch-points and distances between patches. The method described in this paper also differs from existing, commonly applied single species approaches or other approaches aimed at modelling connectivity for multiple species (e.g. Beier and Brost 2010; Brás et al. 2013; Brodie et al. 2014; Koen et al. 2014).

Dispersal guilds could be used as part of a conservation action planning process to assess the viability of focal conservation targets (Poiani et al. 2000; The Nature Conservancy (2007) "Step 3: Assess Viability of Focal Conservation Targets" and CMP (2013) "1D. Analyze the Conservation Situation") and identify the relative benefit different guilds would be likely to derive from alternative interventions (wildlife corridors, improved habitat quality, increased habitat patch size). For example, the case study graphically highlighted that investment in improved connectivity would be less effective than improving habitat area or quality for those species where the dispersal distance and gap-crossing threshold exceed the general level of fragmentation. The thresholds of connectivity and patterns of connectivity associated with each guild could be used in a triage approach, where conservation efforts are best directed at areas where investment is likely to produce the greatest benefit (Bottrill et al. 2008).

Our method can be applied rapidly, within approximately three months, providing experts with sufficient knowledge are available. The expert-based approach is particularly suited to connectivity modelling that uses simple thresholds such as the inter-patch and gap-crossing dispersal distance where species exhibit threshold dynamics such as a foray search strategy (Doerr et al. 2011; Smith et al. 2013) that can be modelled using cumulative cost approaches. It is important though to ensure that: (a) experts have sufficient knowledge for parameterising the model, (b) the required parameters are explained clearly to the experts and (c) it is understood that approximations are suitable for this process. While expert opinion is considered to be suboptimal for parameterising connectivity models (Clevenger et al. 2002; Zeller et al. 2012; Cushman et al. 2013) the alternative of empirical field based research would be a much greater undertaking for multiple species (Compton et al. 2007; Rudnick et al. 2012). Furthermore, the literature review, which was supported by data from a 2014 meta-analysis of all empirical studies of connectivity in Australia (Doerr et al. 2014), found very few empirical studies with the necessary parameters for our model or parameters that could be applied outside of the original study area due to locally unique characteristics. Thus in many cases an expert approach would be the only practical option.

Conclusions

Decision makers need tools that are sufficiently flexible and dynamic to assess connectivity without being too complex, difficult to use or time-consuming. The approach described here of characterising dispersal guilds provides greater generalizability than single species connectivity modelling, and is therefore likely to be better suited to a whole of landscape, multi-species approach to conservation planning. It provides a biologically defensible first pass connectivity assessment using available expert knowledge when the time or resources are not available to collect quantitative dispersal and distribution data for numerous species. The outputs provide a useful basis from which to prioritise conservation investment for connectivity and further research.

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