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DOES STRUCTURAL CONNECTIVITY FACILITATE DISPERSAL OF NATIVE SPECIES IN AUSTRALIA'S FRAGMENTED TERRESTRIAL LANDSCAPES?

Systematic Review

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Draft protocol published on website: 08 April 2008- Final protocol published on website: 14 November 2008 - Draft review published on website: 11 March 2009 – Final review posted on website: 13 January 2010

Cite as: Doerr, V.A.J., Doerr, E.D., and Davies, M.J. 2010. Does structural connectivity facilitate dispersal of native species in Australia's fragmented terrestrial landscapes? CEE review 08-007 (SR44). Collaboration for Environmental Evidence: www.environmentalevidence.org/SR44.html.

Systematic Review Summary

Background

Habitat loss and fragmentation present increasingly serious problems in the context of global climate change, as smaller populations will be less resilient and isolated populations will have difficulty shifting their ranges to track changing environments. A potential solution is to provide *structural connectivity*—elements of the landscape (typically some form of native vegetation) that physically link isolated patches of habitat. According to metapopulation theory, these linkages will allow individuals and/or their genes to disperse between multiple small patches, allowing these subpopulations to collectively function as larger, more resilient metapopulations. Structural connectivity includes the concept of wildlife "corridors" (linear, continuous connections between patches), but also encompasses a wide variety of landscape elements in the form of corridors, disconnected linear elements that do not directly connect patches, and "stepping stones"— series of isolated features such as individual trees, shrubs, rocky outcrops or small clusters of these features. However, it is unclear whether structural connectivity really does facilitate the movement of native animals and plants between patches (and thus provide *functional connectivity*), or if particular characteristics of structural connectivity influence its effectiveness. Protection and restoration of structural connectivity is already being recommended across Australia, but given the lack of consensus on the relationships between structural and functional connectivity, specific guidelines for managers are lacking. The purpose of this review was to synthesise all available evidence on the relationship between structural connectivity and landscape-scale dispersal movements in Australian terrestrial landscapes in order to identify knowledge gaps and, if possible, to devise general principles for connectivity restoration.

Objectives

Our primary question was:

- Do the various landscape elements that provide structural connectivity in Australian fragmented terrestrial landscapes facilitate dispersal of native species between habitat patches or populations? i.e., do they provide true functional connectivity?

Because we were particularly interested in knowing what form structural connectivity should take in order to be most effective, we also asked the secondary questions:

- Do the various landscape elements that provide structural connectivity differ in how well they facilitate dispersal of individuals between habitat patches or populations?
- What particular characteristics make structural connectivity most effective?

Finally, the effectiveness of structural connectivity may depend not just on its form but also on the species and ecosystem in question. Thus, we aimed to consider whether the effectiveness of different types of connectivity varies among taxonomic groups or other species categories (such as habitat specialists vs. generalists), and between temperate and tropical ecosystems.

Search strategy

Electronic searching using a pre-defined series of search terms was completed in May and June of 2008 using the following databases, catalogues and web-engines: ISI Web of Knowledge (including ISI Web of Science, ISI Proceedings, Current Contents, CAB Abstracts, Zoological Record, and Web Citation Index), Directory of Open Access Journals, Scopus, Australian Agriculture and Natural Resources Online (AANRO), CSPubList (via EnCompass; official

CSIRO publications), CSIRO Library Catalogue (Voyager), Australasian Digital Theses Program, ProQuest Dissertations and Theses, Google Scholar, and AllTheWeb. A special protocol was developed to search for grey literature via university libraries, departments, and state and federal governmental organisations involved in environmental research. Bibliographies of articles viewed at full text, particularly narrative literature reviews, were searched for additional relevant sources. Experts were widely consulted in the development of the review protocol, resulting in the inclusion of two sources of unpublished data in the review.

Selection criteria

Studies were included in the review if they:

- contained data on any terrestrial native Australian species;
- and had at least one study site that contained some type of structural connectivity (spatial heterogeneity) between otherwise isolated patches of native habitat;
- and contained data on movement of species through the connectivity or data that allowed inference of movement (e.g., presence in the connectivity, population genetic data, presence/absence in patches with different types or degrees of connectivity).

Data collection and analysis

The selection criteria were met by 98 sources, representing 80 different studies. As the vast majority of studies did not directly test the primary question of the review, but contained data that could allow it to be evaluated, raw data rather than statistical results were extracted for each species included in each study. These included whether or not there was evidence for movement (or presence) of the species in the structural connectivity, whether or not there was evidence for movement (or presence) of the species in the matrix if that was also studied as a control, as well as the quality of the evidence (e.g., the degree to which movement was directly assessed versus inferred based various assumptions). A suite of other variables was extracted describing the species, the characteristics of the structural connectivity, and the general environment. Additional data on gap distances crossed, either between small elements of structural connectivity or between both structurally connected and isolated patches were also extracted where possible. Almost none of the studies provided data suitable for meta-analysis, so exploratory analyses using summary statistics and hierarchical modelling were undertaken instead.

Main results

The 80 studies included in the review varied enormously in their goals, methodologies, and theoretical frameworks and they measured responses to structural connectivity using more than two dozen different response variables. Too few studies were available on plants or invertebrates to include them in most of our analyses. Almost all studies were conducted in wooded habitat patches and/or in structural connectivity consisting of trees, so relatively little can be concluded about grassland or other non-treed ecosystems. Furthermore, the vast majority of studies only assessed the presence of species within structural connectivity without directly examining movement of species through the connectivity and thus probably tell us more about the value of connectivity as habitat rather than its effectiveness at facilitating movement. Despite these limitations, our exploratory analyses were able to reveal a few clear messages as well as some interesting patterns that suggest foci for future research.

Does structural connectivity help? Native species were more likely to be present in elements of structural connectivity than in the matrix, providing reasonable evidence that these landscape features provide habitat for these species, though only weak evidence that they facilitate dispersal movements. However, studies with specific evidence of movement between patches also generally found that the presence of structural connectivity increased the rates and/or likelihood of such movement. Both simple contingency analyses and HGLM (mixed) models confirmed that increased amounts of structural connectivity were correlated with increased movement between patches. Thus, we found considerable support for a positive answer to the review's primary question (i.e., structural connectivity generally did facilitate greater functional connectivity).

Which types of structural connectivity (corridors, stepping stones, etc.) are better? All forms of structural connectivity for which there were sufficient data for analyses were effective to some degree in both providing habitat and in facilitating movement. In terms of providing habitat, our exploratory analyses suggest that while all forms were better habitat than matrix for most species, continuous corridors were better than discontinuous linear elements which were better than stepping stones. However, in terms of facilitating movement, our analyses suggest that stepping stones (generally, these were scattered paddock trees) were at least as effective if not more effective than continuous corridors.

Does the effectiveness of these different structures vary among ecosystems and species? Effectiveness of structural connectivity at providing habitat varied somewhat according to the environment and the species. Species that disperse terrestrially were less likely to be found living between habitat patches, but where they were found between patches, they were significantly more restricted to elements of structural connectivity (as opposed to the matrix) than aerial dispersers. Similarly, habitat specialists were less likely to be present between patches, but when present were significantly more restricted to disconnected linear element and corridors than habitat generalists. Corridors were less likely to be used as habitat in tropical ecosystems than in temperate ones, and disconnected linear elements were more likely to be used as habitat when they were wider. Both types were less likely to contain reptile species (relative to other taxonomic groups), possibly because most studies focused specifically on wooded landscape elements, which may not constitute habitat for many of the reptiles studied. Interestingly, width had a significant effect on the likelihood of occupancy of disconnected linear elements but no effect on occupancy of continuous corridors.

In general, there were insufficient data and/or variability in the data to assess variation in the effectiveness of the different forms of structural connectivity at facilitating movement. However, similar to our analyses of connectivity as habitat, we did find evidence that wooded corridors were less likely to facilitate movement by reptiles relative to other taxonomic groups. Birds and mammals appeared to have similar responses to structural connectivity, and both groups appeared to be slightly more likely to move through stepping stones (scattered trees) than corridors.

Are gap distances and distances between patches important? Data on critical gap-crossing and interpatch-crossing distance thresholds could be estimated for only a subset of studies and most of these estimates were based on relatively small sample sizes. Based on these limited data we calculated a mean gap-crossing threshold of 106m, indicating that many species are unable to cross open areas (i.e., matrix) that exceed this distance. We also calculated an interpatch-crossing threshold of 1100m, indicating that many species are unable to disperse between patches of habitat separated by >1100m, even where structural connectivity exists between the patches. While it must be reiterated that these threshold values are based on limited data that come primarily from bird and mammal species inhabiting wooded habitats, they should provide a useful starting point for future connectivity research, modelling and planning.

Conclusions

Research implications: Structural connectivity can serve multiple functions in a landscape, providing additional habitat but also facilitating dispersal movements and gene flow between larger patches of habitat. The distinction between these two functions of connectivity is critical because the vast majority of data on the use of structural connectivity by Australian native species have focused on presence in connectivity and thus tested whether the connectivity was providing habitat (94% of the data in this review fall into this category). Yet conclusions are often drawn and management actions undertaken as though the movement function was tested, despite the fact that such tests have rarely been performed. To redress this imbalance more research is urgently needed that examines movements of a wide range of native species (including invertebrates and plant seeds and pollen) through a wide range of heterogeneous, "real" landscapes (including grassland and shrubland systems). Studies should be designed to consider multiple forms of structural connectivity in a comparative framework, to gather data on a large sample of individuals (even where this means limiting the number of species examined in any single study) and to aim for meaningful replication with entire landscapes acting as replicates. Data collection should be particularly focused on recording the details of precise movement paths, accurately characterising all elements of structural connectivity (and the matrix itself) through which movements do and do not occur, and assessing effective dispersal (i.e., post-dispersal contribution to the gene pool). Such data will be critical for developing a meaningful understanding of how different types of structural connectivity contribute to true functional connectivity, and ultimately allow managers to accurately weigh the costs and benefits of different options for preserving or restoring such connectivity.

Management implications: Until the research gaps described above are filled, many aspects of functional connectivity will remain poorly understood. However, management efforts must continue armed with the best available knowledge. Thus, we have attempted to provide guidelines for managing and restoring structural connectivity with the caveat that more research is still needed, so all of our recommendations are intended to be applied in an adaptive management framework. It is particularly important to reiterate that most of the data on which our recommendations are based come from studies of Australian mammals and birds living in woodland and forest ecosystems. Our guidelines (see attached "Summary of Guidelines for Connectivity Management and Restoration" and the full review for more detail) should thus be most applicable in similar systems and applied more broadly only with caution.

This systematic review of available empirical evidence suggests that structural connectivity is currently providing some benefit for native species in Australian landscapes, but that with better information resulting from new research, these benefits and their cost-effectiveness could be significantly improved. Although limited, currently available data indicate that the effectiveness of connectivity initiatives could be enhanced for many species by considering diverse types of structural connectivity (particularly scattered trees separated by no more than ~100m) and by targeting patches less than 1.1km apart for connectivity protection and restoration.

1. Background

1.1 The Problem of Habitat Fragmentation

The modification, loss and fragmentation of natural ecosystems are among the most serious threats to global biodiversity because the resulting altered landscapes invariably support smaller, more isolated populations of native species and increasingly degraded habitats, all of which are likely to reduce population viability and increase risk of extinction. The theory of island biogeography (MacArthur and Wilson 1967) and continued conceptual developments in landscape ecology (e.g., Brown 1971; Wilcox and Murphy 1985) suggest that habitat fragmentation should impact populations through three main effects: edge, area, and isolation effects. Edge effects can include increased rates of predation and altered microclimates which may reduce survivorship and reproductive success. Due to the smaller habitat patches and thus smaller populations created by fragmentation, area effects may include increased levels of inbreeding, reduced genetic variability, and increased sensitivity to stochastic events. These area effects will be further intensified when combined with isolation effects, whereby the possibility of demographic or genetic rescue is reduced or eliminated because individuals cannot disperse between fragments through the matrix of unsuitable habitat. Extensive research has verified these predicted impacts of fragmentation, and numerous syntheses have been produced, so the basic problem is relatively well understood (e.g., Wilcove 1985; Rolstad 1991; Harrison and Bruna 1999; Debinski and Holt 2000; McGarigal and Cushman 2002; Villard 2002; Lindenmayer and Fischer 2006; Fischer and Lindenmayer 2007).

Fragmentation is an even more serious concern now that we know the planet's climate is changing, as global climate change is predicted to force species to locally adapt or move elsewhere in order to survive (Davis and Shaw 2001; Gitay et al. 2002; Parmesan 2006). Yet smaller populations will be less resilient and less able to adapt to altered local conditions, and isolated populations will have difficulty shifting their ranges to track changing environments. This may be of particular concern in Australia, where extensive land clearing was conducted following European settlement, leaving fragments of remnant native vegetation within a matrix dominated by agricultural production (Saunders 1989; Bennett and Ford 1997). The long-term consequences of this fragmentation are expected to be serious with at least some researchers predicting that Australia will lose half of its bird species within the next century (Recher 1990).

1.2 Metapopulations, Patchy Populations and Connectivity Restoration

Action is therefore urgently needed to reverse some of the effects of fragmentation. The most obvious solution would be to restore vast areas of native ecosystems, but such an approach will often be impractical given the range of other human needs (food production, etc.) in fragmented landscapes. However, the theory of metapopulation biology suggests that when a number of small physically isolated populations are linked by some level of dispersal, they can collectively function as one larger, more resilient population (Levins 1969, 1970; Brown and Kodric-Brown 1977; Harrison 1991). In landscapes that have been artificially fragmented by human activities, this may be particularly true when there are relatively high levels of dispersal that produce "rescue effect" metapopulations (those that decline and are then demographically rescued) or even higher levels that produce "patchy populations". This is because classical extinction-recolonisation or source-sink metapopulations that involve lower levels of dispersal may only be viable in the long term if at least some subpopulations can act as sources, sometimes producing many excess individuals who then disperse to other subpopulations. This is unlikely in artificially fragmented landscapes, as such boom-and-bust dynamics may be unlikely to occur in species that evolved in more continuous habitats, and additional threats in fragmented landscapes may make boom cycles rare even if they can occur. Thus, conservation efforts could focus on areas between existing habitat patches, protecting or restoring enough habitat to allow sufficient levels of dispersal to create rescue-effect metapopulations or patchy populations.

Such actions need to occur at local, regional, and even continental scales to ensure benefits accrue at the population level but also that species can move to new areas as necessary under climate change. Fortunately, this need has captured the attention of governments and the public. Connectivity restoration is frequently a goal of private revegetation efforts, local landcare groups, and incentive schemes administered by regional natural resource management bodies. Almost two decades ago, authors first proposed large networks of connected habitats in North America (Harris and Gallagher 1989) and Australia (Hobbs and Hopkins 1991), and governmental and non-governmental organisations have recently initiated a number of major projects involving continental scale connectivity restoration such as Gondwana Link and the Great Eastern Ranges Initiative (formerly known as Alps to Atherton), including its component projects such as Kosciusko-to-Coast and Slopes-to-Summit.

The difficulty is that it is unclear exactly what actions should be taken to restore connectivity to our landscapes. Based on metapopulation theory from which the concept was derived, a connected landscape is one in which individuals of all species (or their propagules or genes) can not only make their normal daily foraging movements, but can disperse from one resource patch to another (see Appendix A for definitions of terms used in this protocol). So how much habitat, what kind of habitat, and in what spatial configuration might be required to facilitate such dispersal? Unfortunately, the many syntheses of the problems of habitat fragmentation tell us relatively little about dispersal, and thus about the appropriate *solutions* to the problem, and new research and syntheses specifically focused on connectivity, as opposed to fragmentation, are required.

1.3 Initial Focus on Corridors

The most commonly proposed solution is to retain or restore habitat corridors. While the interpretation of this term varies (see Simberloff et al. 1992 for six different definitions), we define a corridor as a relatively unbroken (contiguous) linear strip of habitat that connects two or more patches of habitat that are otherwise surrounded by unsuitable areas for the species or community in question (Hobbs 1992; Beier and Noss 1998). We believe this matches the operational definition used by most Australian land managers and by members of the public. The theory behind corridors is that individuals will be exchanged and/or genes will flow between connected patches or populations either because the corridor is occupied by the species or community and thus the corridor creates a continuous population between the two patches, or because dispersing individuals (or seed dispersers or pollinators) will use the corridor to move from one patch to the other. However, the ability of corridors to achieve this goal, and provide for dispersal just as much as continuous habitat would, may depend very much on the dispersal behaviour of the species involved as well as many other characteristics of the corridors themselves, the habitat patches, and the surrounding matrix (Tischendorf and Wissel 1997; Lindenmayer 1998; St Clair et al. 1998; Heinz et al. 2007). As a result, the effectiveness of corridors has been the subject of considerable debate (Noss 1987; Simberloff and Cox 1987; Simberloff et al. 1992; Beier and Noss 1998; Haddad et al. 2000), and there is an imperative to determine which characteristics might make them most effective across different species and even different ecosystems, and whether there are alternatives.

There are a number of ecological reasons which suggest that alternatives to corridors need to be seriously considered. First, if corridors are to provide for gene flow by providing occupied habitat, then there may be costs to the populations involved, so a thorough weighing of the balance between benefits and costs is required. In particular, edge effects in narrow habitat strips may mean that population sinks may be created when corridors are occupied (Lynch et al. 1996; Cale 1999; Hess and Fischer 2001). Such sinks could potentially decrease both the likelihood of dispersal between patches and the overall viability of the population, even though the corridor might appear to be a success because it is occupied. Second, the corridor concept is based on a binary patch/matrix model of the landscape—that there are distinct, suitable parts of a landscape (patches) and unsuitable parts (matrix), but no "grey area" in between. However, ecologists now recognise that there are other valid landscape models, including the variegated model (McIntyre and Barrett 1992; McIntyre and Hobbs 1999) and continuum models (Manning et al. 2004; Fischer and Lindenmayer 2006), in which different parts of the landscape may vary in their suitability for any given species, resulting in different densities or patterns of use. These models are particularly important in Australia, as many of Australia's ecosystems naturally form a patchy mosaic (e.g., Bentley and Catterall 1997), so native species may have evolved to take advantage of that heterogeneity during dispersal. This means that individuals may not require continuous strips of habitat for dispersal, partly because suitable habitat for dispersal might actually have a very different composition and structure than habitat suitable for long-term survival and reproduction.

1.4 Beyond Corridors: Structural vs. Functional Connectivity

The increased appreciation of these ecological concepts has led scientists to broaden their thinking about connectivity restoration beyond corridors and into the paradigm of structural vs. functional connectivity (With et al. 1999; Uezu et al. 2005; Crooks and Sanjayan 2006; Hilty et al. 2006). Under this new paradigm, structural connectivity is anything that physically links separate populations, and it may consist of just about any kind of landscape heterogeneity in between occupied patches of habitat. Examples of structural connectivity include linear elements such as corridors and partially vegetated drainage lines or fence lines. But structural connectivity may also consist of more subtle habitat elements such as scattered trees or shrubs, or even scattered clumps of tussock grass, rocky outcrops, or coarse woody debris, all of which are sometimes referred to as "stepping stones" because of their scattered, non-linear structure. In contrast, functional connectivity refers to the outcome we desire from these structural features—the degree to which movement and dispersal actually occur, which depends not just on the structure of the connectivity but also on its interaction with species' dispersal and habitat selection behaviour (Lima and Zollner 1996; Johnson et al. 2004; Chetkiewicz et al. 2006). Emphasis is now placed on trying to understand the relationships between structural and functional connectivity, which includes work on corridors but is more broadly focused on movement and gene flow in heterogeneous landscapes. Protection and restoration of diverse types of structural connectivity is already being recommended as an appropriate management strategy (e.g., Fischer et al. 2006), but more specific guidelines for managers are lacking. We need to know exactly which types of structural connectivity really do provide functional connectivity (dispersal in the landscape) for the majority of species in an ecosystem. If multiple types of structural connectivity can successfully provide for dispersal, we also need to understand their relative costs and benefits, in both ecological and economic terms, to best inform conservation planning and management.

1.5 Applying Connectivity Concepts to Management Requires Evidence

These general principles for connectivity restoration—recommendations for what is likely to work best for most species in most systems—can only come from syntheses of many empirical studies, rather than from conceptual or mathematical models. A synthesis that incorporates a variety of types of structural connectivity, not just corridors, has yet to be performed. While the utility of corridors has been tested using theoretical modelling (e.g., Hanson et al. 1990; Tilman et al. 1997), and empirical evidence for use of corridors has been accumulating for a number of years (Saunders and Hobbs 1991; Beier and Noss 1998; Bennett 1998; Haddad et al. 2003; Davies and Pullin 2007), research on other types of structural connectivity is relatively recent. Furthermore, recent evidence comes from a variety of different types of studies (survey, mark-recapture, genetic, radiotracking, etc.), which can make the resulting conclusions difficult to interpret *across* studies. Thus, the time is ripe to attempt a synthesis of the relationships between structural and functional connectivity, particularly in Australia where there may be considerable variation in structural connectivity and how it is used by native species. The systematic review approach may be especially useful, as it provides a rigorous framework in which to attempt a formal comparison of the different types of evidence produced by different types of studies.

In this review, we evaluated whether structural connectivity (i.e., landscape elements of any sort in an otherwise unoccupied/unsuitable matrix) between areas of occupied habitat facilitates functional connectivity (i.e., dispersal of native species) in fragmented terrestrial landscapes in Australia. Furthermore, we identified some of the characteristics of structural connectivity that increase the probability of dispersal. While different characteristics may be important for different species or in different landscapes or ecosystems, we aimed to identify principles for natural resource managers that are as generally applicable as possible, while also distilling recommendations for specific taxa or communities where more general insights do not emerge. Ultimately, our aim was to provide clear, science-based information to natural resource planners and managers about how best to invest in connectivity and to identify critical knowledge gaps that will guide future research to ensure that Australia's significant on-ground expenditures achieve their goals of restoring functional connectivity in Australian landscapes.

2. Objectives

2.1 Primary objective

Our primary aim was to systematically search for and synthesise all available empirical evidence to determine whether structural connectivity really does facilitate dispersal of native species in Australian fragmented landscapes. We considered all types of connectivity and all types of species and environments collectively, as we wanted to determine whether providing structural connectivity was a reasonable *general* aim for Australian land managers. Specifically, we asked the following primary question:

- Do the various landscape elements that provide structural connectivity in Australian fragmented terrestrial landscapes facilitate dispersal of native species between habitat patches or populations? i.e., do they provide true functional connectivity?

2.2 Secondary objective

At the moment, most land managers believe that the answer to the primary question is "yes", and are particularly interested in knowing what form the structural connectivity should take in order to be most effective. Thus, we asked the secondary questions:

- Do the various landscape elements that provide structural connectivity differ in how well they facilitate dispersal of individuals between habitat patches or populations?
- What characteristics make structural connectivity elements most effective?

Specifically, we aimed to evaluate differences in the effectiveness of connectivity based on:

1. the type of connection (e.g., scattered trees, drainage lines, corridors, messy native pastures—whatever types of heterogeneity exist between habitat patches)
2. length of the connection
3. width of the connection, especially for corridor connections

4. vegetation density relative to habitat patches (a measure of quality)
5. composition and structure of the connection
6. maximum gaps to be crossed

2.3 Tertiary objective

It is often argued that the effectiveness of structural connectivity will depend not just on its form (our secondary objective variables) but also on the species and ecosystem in question. Yet in practice, land managers are unlikely to be managing for single species in single locations. Instead, they need some general principles to be distilled from all this variation (e.g., habitat specialists respond similarly, or scattered trees are more effective when they connect woodlands as opposed to forests). Thus, we aimed to consider variation in the following sources of heterogeneity among studies:

1. Taxonomic group of study organism (e.g., birds, mammals, invertebrates, etc.)
2. Ecology, behaviour, and dispersal mechanism of study organism
3. Life history of study species and specifically the life-history stage of individuals included in the study
4. Size of study organism and spatial scale of movements
5. Type of community or ecosystem (e.g., temperate vs. tropical, woodland vs. forest vs. grassland, etc.)
6. Size, number and habitat quality of patches being connected
7. Characteristics of the intervening matrix (crop, pasture, pine plantation, etc.)
8. Whether the connectivity and/or patches are remnant or restored habitat
9. Landscape level characteristics (e.g., total percent cover of native vegetation)
10. Disturbance history of study areas
11. Climatic conditions during study (e.g., drought)
12. Type/purpose of movements studied (daily foraging vs. dispersal vs. migratory or nomadic movements)
13. Study design (replicated comparisons, etc.)
14. Source of information on movement and dispersal (tracking, mark/recapture, population genetic, etc)

3. Methods

3.1 Question formulation

Land & Water Australia (LWA) wished to trial the use of systematic reviews for informing management specifically in Australia, and identified the general issue of connectivity as a desirable subject. Simultaneously, the reviewers were conducting their own research on empirical evidence for the effectiveness of different types of connectivity and attended a short-course on the systematic review approach. Thus, the review questions were developed through discussions between LWA and the reviewers. They were further refined after soliciting comments from 54 stakeholders, representing researchers actively working on connectivity in Australia, state and national governments focused on both policy and management in relation to connectivity, regional natural resource management bodies, and not-for-profit conservation groups engaged in on-ground conservation work.

3.2 Search strategy

3.2.1 General sources

The following electronic databases were searched during May and June of 2008 by one reviewer (MJD) for studies to be included in the review, and citations retrieved were transferred to an EndNote X1.0.1 (Thomson Reuters) database, or to html files for further filtering before inclusion in a final EndNote database:

1. ISI Web of Knowledge
    i. ISI Web of Science
    ii. ISI Proceedings
    iii. Current Contents
    iv. CAB Abstracts
    v. Zoological Record
    vi. Web Citation Index
2. Directory of Open Access Journals
3. Scopus
4. Australian Agriculture and Natural Resources Online (AANRO)
5. CSPubList (via EnCompass; official CSIRO publications)
6. CSIRO Library Catalogue (Voyager)
7. Australasian Digital Theses Program
8. ProQuest Dissertations and Theses

A series of searches was performed, with each search combining two terms: one movement-related term and one term relating to landscape context. Each database was searched using all possible two-term searches based on the following movement and landscape terms:

Movement-related terms:

- colonisation OR colonization
- dispersal
- migration
- movement*

Landscape-context terms:

- connectivity
- corridor*
- fragment*
- isolat *
- landscape*
- matrix
- paddock tree*
- patch*
- stepping stone*

In addition, each database was also searched for the following single terms:

- interpatch*
- gap-crossing

We experimented with incorporating NOT operators into searches to limit the number of hits on unrelated topics. Where databases allowed the inclusion of a large number of search terms, we used the following NOT terms: alloy*, aquatic, bacter*, brain, Campylobacter, capital, cell*, clinical, corrosion, cortex *, cultur*, deep-sea, disease*, evangel*, eye-movement*, fluvial, fung*, gas*, Holocene, ion, medicine, molec*, neur*, marine, motion, patient, phylogenetic, Pleistocene, politic*, polymer*, protein, river*, Salmonella, scripture, sediment, social movement, soil*, speciation, stent, stream*, thermal sensor, train, transport, virus*.

No foreign language searches were conducted, as we anticipated that all research on connectivity in Australia would be published in English, with an aim to inform management within Australia. Note that while the intention was to only include research conducted in Australia, no geographic search terms could be used at this stage (but see **3.3.3 Filtering procedures**). This was because many studies did not include geographic terms in either the title or the abstract, and trials involving the use of geographical terms failed to capture a number of relevant sources.

Searches were also conducted using the internet-based search engines Google Scholar (http://scholar.google.com) and Alltheweb (http://www.alltheweb.com), using the two single-term searches and the five most prolific two-term searches from the Web of Science searches listed above. The first 100 hits from each search on each website were examined for possible inclusion in the review by one reviewer (MJD). Finally, we also searched bibliographies of accepted sources and traditional literature reviews that were identified in searches to identify any additional sources that needed to be considered.

3.2.2 Specifically targeting the grey literature

One of the difficulties with searching for relevant studies in Australia is that much of the research done in Australia is performed by or for government departments and results are often only available in government reports, not peer-reviewed publications. Unfortunately, there are no searchable databases of these reports in Australia. In addition, the Australasian Digital Theses Program database catalogues Masters and PhD theses from every university in Australia, but the extent of chronological coverage seems to vary among institutions. Furthermore, this database does not include Honours theses, which are generally only catalogued by the relevant university department. Thus, we developed a novel systematic search strategy specifically for these types of data sources. The following organisations were contacted:

1. the main library of every research university in Australia
2. every research university department that includes the words, biology, zoology, botany, ecology, evolution, ecosystem, conservation, environment*, forestry or natural resources, in its department name
3. any other university school or department recommended by a university library but not identified using the terms listed above
4. every state government department that conducts or funds environmental research
5. every federal government department that conducts or funds environmental research

Requests were made of each organisation to either search themselves or allow us to search their databases for all theses or reports that have any of the following terms in their titles or as keywords: dispersal, corridor*, connectivity, fragment*, remnant*. Where possible, we targeted our requests to specific individuals in these organisations to improve the likelihood that they would respond to our requests.

3.3 Study inclusion criteria

3.3.1 Standard criteria

All sources identified during the search process were evaluated for inclusion in the review based on pre-determined inclusion and exclusion criteria that matched specific components of the review question. To be included in the review, sources needed to meet all of the following inclusion criteria. They needed to:

- **Subject(s):** contain data on any terrestrial native Australian species including mammals, birds, reptiles, invertebrates or plants (including seeds or pollen)
- **Intervention:** have at least one study site that contained some type of structural connectivity between otherwise isolated patches of native habitat or, even more broadly,

have a study site with significant spatial heterogeneity in structure and occupancy by the subject
- **Outcome:** contain data on movement of subjects between patches, or contain data that may allow inference of movement (e.g., presence in connectivity, population genetic data, presence/absence in patches with different types or degrees of connectivity—see **3.4 Study quality assessment**)

Note that studies needed to contain empirical data to be included in the review—purely theoretical or modelling studies could conceptually inform the review but were excluded from official synthesis. However, a wide variety of types of empirical studies were considered, including presence/absence studies, abundance surveys, mark-recapture or resighting surveys, genetic studies (including both population-level analyses and individual-based analyses like assignment tests), and more direct observations of movement such as radiotelemetry studies. Movements for unknown purposes, induced by translocation or baiting, and for daily foraging purposes were all considered in addition to movements specifically for dispersal, as landscapes that facilitate these other types of movements are likely to help facilitate dispersal as well, and we anticipated that data specifically on dispersing individuals would be highly limited. Only studies conducted in Australia were included, as some of the explicit goals of this review were to trial the systematic review process in Australia and determine whether sufficient empirical information exists to derive evidence-based management decisions specifically for Australia's unique ecosystems.

3.3.2 Criteria for meta-analysis

For inclusion in any potential meta-analyses, studies needed to have a suitable control (i.e., an intervention comparator)—at least one study site with less or no structural connectivity to compare to the study site containing structural connectivity. This could be as simple as a study in a single landscape that assessed movement through both structural connectivity and through the adjacent matrix, but would preferably involve a comparison of landscapes with and without structural connectivity (or at least some replication at the landscape level). Meta-analysis also required studies to express outcomes quantitatively, as the amount of movement in landscapes with more structural connectivity versus those with less or no structural connectivity. Nonetheless, studies with only a structurally connected site or landscape (i.e., that lacked a less-connected comparator) and studies that simply expressed movement as a binary yes/no outcome (i.e., did not provide quantitative movement data) were still included for less formal synthesis.

3.3.3 Filtering procedures

A geographic filter was first applied, to attempt to select sources describing research in Australia. All sources containing "Australia" or the names of any Australian state or territory were automatically included. From the remainder of sources, those that contained any of a range of specific non-Australian geographic terms (e.g., "Europe", "America", "France", etc.) were excluded. All sources were then filtered by title to remove any irrelevant to this review (i.e., that obviously did not meet the inclusion criteria). All three reviewers participated, filtering different but overlapping portions of the dataset in order to perform a kappa analysis to test agreement across reviewers. Reviewers agreed on 97.5% of title filtering decisions, resulting in an agreement rating of 'substantial' (Cohen's Kappa test: K=0.645; Cohen 1960). Sources were then filtered based on their abstracts, primarily by one reviewer (MJD), though approximately 20% of sources were also evaluated by VAJD. The two reviewers agreed on 87% of abstract filtering decisions, also resulting in an agreement rating of 'substantial' (Cohen's Kappa test: K=0.66). Studies were included at each filtering stage if they appeared to match the inclusion criteria or if it was ambiguous whether they met the criteria or not. Final full-text filtering was performed in conjunction with data extraction, with one reviewer (MJD) performing an initial filter and one of the two remaining reviewers (either EDD or VAJD) confirming the filtering decision and extracting relevant data. Any disagreements at this stage of filtering were resolved by discussion and consensus between at least two of the three reviewers.

3.4 Study quality assessment

Each source accepted into the final review was assigned two scores to rank its quality according to two distinct sets of criteria. These scores were thus available for potential weighting of studies in a meta-analysis, but they could also be more simply investigated as different sources of variation among studies that might influence results (see **2.3 Tertiary objective**).

3.4.1 Experimental design

One set of scores relates to the experimental design employed in each study. Scores were assigned based on the categories in Table 1, which is modified from the hierarchy of evidence table presented by Pullin and Knight (2003). We modified this existing table because we wanted to include comparative but descriptive data, as well as anecdotal data, which may provide very weak evidence but can be common in the literature on connectivity and movement.

Table 1. Hierarchy of evidence based on the experimental design of research undertaken. Modified from Pullin and Knight (2003).

Rank	Experimental Design
1	replicated randomised comparisons of more and less connected landscapes
2	replicated (but not randomised) comparisons of more and less connected landscapes (in time or space)
3	nonreplicated comparisons of more and less connected landscapes or sites
4	qualitative or descriptive comparisons of more and less connected landscapes
5	qualitative or descriptive data on more connected landscape(s) or site(s) only
6	anecdotal or single observation

3.4.2 Direct and indirect measures of dispersal

The quality of studies on functional connectivity can also be scored based on the degree to which the actual movement path was known and resulting effective dispersal was actually measured versus how much they were assumed based on surrogate or indirect measures. The "gold standard" for relating structural connectivity to effective dispersal would be a study that documents dispersal paths between patches (so it is known which landscape elements were actually used during interpatch dispersal) and which also documents successful reproduction and thus contribution to the gene pool following dispersal ("effective dispersal"). This first point is particularly important because data merely showing that individuals have transferred between patches (e.g., capture-mark-recapture data) do not demonstrate what features of the landscape were used during that transfer. The second point is important because dispersal without reproduction will not ultimately affect levels of gene flow or "rescue" populations from extinction—the ultimate aim of connectivity. In general, very few studies will meet this gold standard by providing data on both of these aspects of dispersal.

Instead, most studies use a variety of different surrogates including: following dispersal movements from departure until settlement (but without subsequent monitoring), observing only portions of dispersal (or other movement) paths, inferring dispersal using genetic data, or inferring dispersal based on presence/absence of a species either in the structural connectivity or in patches that differ in the degree to which they are structurally connected to other patches. Thus, each source included in the review was also scored based on the degree to which dispersal paths were fully documented and on the methods used to assess whether effective dispersal had occurred (Table 2). Note that because these methods make different assumptions and may be more or less valid in different circumstances, these scores do not represent a strict hierarchy of evidence. While score 1 provides the strongest evidence for effective dispersal and score 7 provides the weakest, the precise rank order of the other scores may differ. For example, score 5 (when dispersal between patches is known but the movement path is not) can provide strong evidence for the role of connectivity in facilitating movement if the data come from a well-replicated study in which some patches are connected and others are not but only weak evidence in a study with limited replication. Understanding the type of evidence provided by any study is important as it influences the precise interpretation of the results.

Table 2. Types of evidence for effective dispersal based on the degree to which dispersal was actually observed versus inferred from different types of data.

Score	Type of Dispersal Data
1	Dispersers followed directly so movement paths known and subsequent contribution to the gene pool also assessed
2	Movement paths for dispersers fully known (to settlement in new patch) but subsequent genetic contribution unknown
3	Partial movement paths of dispersers known
4	Movement paths known but unknown whether for dispersal or other purposes
5	Dispersal between patches known (e.g., from mark-recapture data, genetic assignment tests, or radiotelemetry data) but movement path not known
6	Dispersal between patches inferred from population genetic data or presence/absence data in patches
7	Dispersal inferred from presence in the connecting landscape element (e.g., in corridor or stepping stone between patches)

3.5 Data extraction

Information was extracted from each source into a specially designed data extraction form by one of two reviewers (EDD or VAJD), and any uncertainty was resolved by consensus between both these reviewers. Subject and outcome data were extracted separately for each species (or species group, e.g., “Araneae”, when that was the lowest level of taxonomic organisation considered in the study), yielding multiple species-based data points nested within studies. Data on interventions and other landscape variables (e.g., habitat type of patches) were extracted for each study. Outcomes were assessed for both intervention landscapes (more structural connectivity) and control landscapes (less or no structural connectivity) where controls were present. Where data on multiple forms of structural connectivity were to be extracted from a study and there was no landscape without connectivity to serve as a control for comparisons, we assumed that continuous corridors provided more structural connectivity than disconnected linear elements which provided more structural connectivity than stepping stones. In many studies, structural connectivity varied within rather than between landscapes. So for these studies, data from the more connected “landscape” were actually data from areas containing structural connectivity and data from the less connected “landscape” were from areas without connectivity (i.e., the matrix) from within the same landscape. The main outcome extracted was simply whether the study provided evidence for movement of each species in each landscape or not (a binary yes/no variable). This provided a single measure that could be used to compare results across studies that quantified movement or a surrogate of movement in very different ways. Rates of movement and their standard errors were also extracted as outcomes wherever possible, regardless of the way in which the study quantified movement and thus of the precise units in which rates were expressed. Appendix B provides a list and brief explanation of all variables extracted and Appendix C provides a sample of the data extraction form.

Variables of interest associated with subjects, such as whether the subject was a specialist on the patch habitat type or not, were not always available from each source. Where possible, general information on the species in that region, or on the species in Australia, was used to populate the database. For example, Saunders and de Rebeira (1991) classified bird species in the Kellerberrin district of Western Australia depending on whether or not they are dependent on native (woody) vegetation in that region. We considered such species "specialists", and we applied this to all studies of these species in the Kellerberrin. Variables of interest associated with intervention and control landscapes, such as distances between patches or density of scattered trees, were not always available from each source. Where possible (and it usually was), we used Google Earth 4.3 (Google Inc.) to look at recent images of the study sites and measure or categorise these landscape variables. Taxonomic names were changed where necessary from those reported in individual sources to match current nomenclature.

3.6 Data synthesis and analysis

Data suitable for meta-analysis—means with standard errors of outcome variables in both control (less or no structural connectivity) and treatment (more structural connectivity) landscapes—were only provided by four studies (van Schagen et al. 1992; Hill 1995; Laurance 1996 and Laurance & Laurance 1999; Lumsden & Bennett 2005), and all four of these studies only assessed presence in connectivity (i.e., they did not assess movement directly). While it is possible to perform meta-analysis without standard errors, weighting all studies equally, this requires mean values of all studies to be presented in the same units. This was not the case in this review, as mean movement "rates" were actually a range of different measures, including abundance and relative density values, proportion of individuals moving, F_{ST} values, etc. Thus, we were unable to perform any formal meta-analyses.

As an alternative, the data were explored using multivariate statistics, as well as simple summary statistics. Note that the vast majority of studies included in the review were not directly testing the primary question of the review themselves, but they contained data that would allow review questions to be evaluated. Thus, summary data on whether or not evidence for movement (or for presence in connectivity) existed for each species considered in each study were extracted and analysed as a function of characteristics of the species, the structural connectivity, and the broader environment. These analyses did not explicitly test the questions or hypotheses proposed (i.e., were not intended to be inferential), but could illuminate interesting patterns in the data across studies that warrant further investigation.

All analyses were performed on two different subsets of the data, rather than the full data set. Data in which movement was inferred because of presence of the species in structural connectivity were analysed separately from data based on all other types of evidence for movement (see Table 2). This was because presence in these elements merely provides evidence that structural connectivity is serving as habitat, which was not a function that this review was designed to assess. Such studies could therefore have been excluded from the review, but they may provide weak evidence for movement through structural connectivity, at least for some types of connectivity (for more discussion of this issue, see **Box 1: Multiple functions of structural connectivity**). Thus, they were included in the review but analysed separately to determine whether, and under what conditions, structural connectivity provides habitat, which may or may not facilitate movement and gene flow.

To address the primary question, contingency analyses were performed to evaluate the prediction that more structurally connected landscapes would provide evidence for movement more often than expected by chance (and less structurally connected landscapes would fail to provide evidence for movement more often than expected by chance). These analyses were performed using the subset of studies that actually provided a comparison between less connected and more connected landscapes (or between less connected and more connected elements of the same landscape). These analyses were also repeated for the subset of those data in which the less structurally connected landscapes provided no structural connectivity at all. For studies that reported relative rates of movement in less and more connected landscapes, we used a nonparametric sign test to compare the frequency with which the rate in the more connected landscape was greater than the rate in the less connected landscape and vice versa, evaluating the prediction that movement rates should be higher in more structurally connected landscapes. Finally, to make use of all the data, not just studies that included a comparator, we used a generalised linear modelling approach with a binary response to model whether landscapes that had some form of connectivity were more likely to exhibit evidence of movement.

To address our secondary and tertiary questions, we also used a generalised linear modelling approach, again as an exploratory technique to investigate potential sources of variation in the effectiveness of structural connectivity at providing habitat and at facilitating movement. We first considered all the landscape data (except for data on plants and in alpine ecosystems where sample sizes were extremely small) and modelled the influence of connectivity type (corridor, stepping stone, etc.) on presence in the connection and evidence of movement. We attempted to fit additional interaction terms where possible (e.g., to test whether corridors were more effective than stepping stones for habitat specialists). We then modelled data for each type of connectivity separately to incorporate variables that could not be included in the larger models, either because interaction terms showed too little variability or because the variables themselves were only applicable to a subset of connectivity types (e.g., width, which was not reported for studies examining stepping stones). Due to time constraints and based on *a priori* rankings of the relative likely importance of different factors, we considered only the following subset of secondary and tertiary level variables in our analyses:

- taxonomic group of the species studied (bird, mammal, etc.)
- whether the species was a specialist or a generalist
- whether the species dispersed terrestrially or aerially
- whether the individuals studied were in the life history stage in which dispersal usually occurs for the species
- whether the study was conducted in a temperate or a tropical ecosystem
- width of corridors or disconnected linear elements
- whether corridors or disconnected linear elements were riparian vs. other types of habitat
- density of habitat elements in stepping stone connections relative to density of patches

Where the data were sufficiently variable to model, we report results of all models rather than a final or best model, as appropriate for exploratory analysis.

For all of these analyses, data on multiple species or in multiple landscapes were often derived from the same study, violating the assumption of independence of data points. Thus, we used hierarchical linear modelling (HLM) to control for predictable differences among studies when evaluating the secondary and tertiary questions, and when evaluating the primary question using a generalised regression approach. HLM is particularly designed for the analysis of nested data without resorting to averaging or data reduction (Raudenbush and Bryk 2002). Data are organised as level-1 units (in this case, species) nested within level-2 units (studies) and restricted maximum likelihood is used to simultaneously solve a level-1 regression equation and a series of level-2 equations. The level-1 equation is essentially a standard regression equation predicting a response based on estimated coefficients (slopes) for each predictor and an estimated intercept. However, the level-2 equations allow these intercepts to vary among level-2 units. The result is that predictable variation across the different studies included in this review can be controlled for while modelling the overall effects of predictor variables (e.g., taxonomic group or connectivity type) across level-1 units. As the outcome variable was always binary (evidence for movement or not), we used hierarchical generalised linear models (HGLM) to model the influence of explanatory variables using a Bernoulli sampling model and a logit link function. Coefficients from these models thus represent the change in the log-odds of movement expected in response to a unit increase in the corresponding predictor variable. All hierarchical modelling was performed using HLM 6.06 (S. Raudenbush, A. Bryk & R. Congdon, Scientific Software International Inc., Lincolnwood, Illinois, USA), while all other analyses were performed using SYSTAT 10 (SPSS Inc., Chicago, Illinois, USA).

Box 1: Multiple functions of structural connectivity

Some researchers have clearly articulated the fact that structural connectivity can serve multiple functions and have been explicit about which functions they were testing (Lindenmayer et al. 1993; Bentley and Catterall 1997; Bennett 1998). Yet overall, there is still a general lack of clarity in the literature about the different functions that structural connectivity may be performing in a landscape, whether those functions always work in concert or whether each can work separately, and how the detailed characteristics of structural connectivity may be related to the functions it can perform. This lack of clarity has sometimes meant that studies testing for one function are often interpreted in the context of a separate function. This mismatch between evidence and conclusions may exist within a single study, but may also result from the sometimes difficult process of translating science into management recommendations. Thus, it is critical that researchers, policy-makers and land managers alike have a basic understanding of the different potential functions of structural connectivity and the types of data that can be used to test for these functions in real landscapes.

<u>Three functions</u>

1. Habitat: Structural connectivity may simply provide habitat for everyday living, supporting territories, feeding sites, roosting sites, etc. This isn't necessarily a "connectivity" function per se, and is thus a secondary goal of structural connectivity. However in many landscapes, elements of structural connectivity actually constitute a significant proportion of remaining native vegetation (i.e., the connections ARE the patches), so provision of habitat may be a critical function of structural connectivity in some landscapes.

2. Interpatch dispersal of individuals within a single generation: Theories of connectivity suggest its primary function should be to facilitate exchange of individuals and genes between patches of habitat, connecting these patches to create a metapopulation or patchy population. The most intuitively simple way for this to occur is if dispersing individuals can move from one patch to another by travelling through the structural connectivity.

3. Interpatch dispersal of genes over multiple generations: Exchange of genes between populations may also occur over multiple generations. If a dispersing individual can leave a patch and settle *within* the structural connectivity, reproduce, and create another disperser who could disperse to a different patch, then interpatch exchange could happen over the course of multiple reproductive periods via the dispersal movements of multiple individuals.

All of these functions can occur simultaneously, but some can also occur in the absence of others. These particular interactions result in four different categories of structural connectivity, as illustrated in Figure 1.

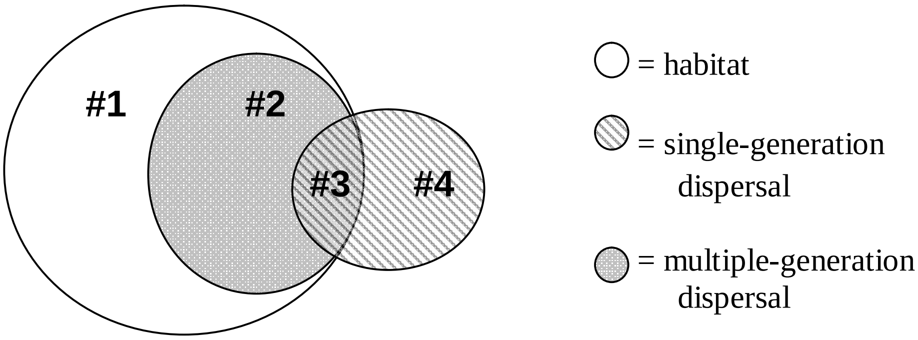

Figure 1. Conceptual representation of the three potential functions of structural connectivity and how they can interact to produce four different categories of structural connectivity. See text for descriptions of these four types.

Note that structural connectivity that facilitates dispersal of genes over multiple generations is, by definition, also providing habitat—the multiple-generation movement can only occur if individuals can settle and reproduce in the connection (#2). In some cases, individuals may also be able to move through these occupied connections in a single generation, so all three functions can occur simultaneously (#3). However, single-generation dispersal may also occur independently of the other functions, for example where habitat is too sparse to allow settlement, but sufficient for facilitating movement of dispersers (#4).

Finally, a connection may be serving as habitat (i.e., individuals of the species in question live their daily lives in the structural connectivity), yet still not facilitate either single-generation or multiple-generation gene flow between patches (#1). This is somewhat counterintuitive, but it could occur for a variety of reasons, including social interactions in which territorial individuals in the connection prevent passage of dispersers, or sink dynamics in which connections are occupied but are too poor in quality (often due to edge effects) to support the production of dispersers. Horskins et al. (2006) argued for the existence of this type of structural connectivity (the kind that only serves the habitat function and does not facilitate gene flow) for fawn-footed melomys (*Melomys cervinipes*) in the Atherton Tablelands. In this study, a wooded corridor was fully occupied by this small mammal species, but genetic differentiation between patches at either end of the corridor was the same as that between patches isolated by agricultural land, yet in both cases, differentiation was greater than between populations in continuous habitat.

<u>Testing for the three functions</u>

1. Habitat: The first step in testing whether structural connectivity serves as habitat may be to assess presence in the connection, which was the most common method employed by studies in this review. However, this criterion is necessary but not sufficient. To be fully functioning as habitat, connections need to support populations that survive and reproduce at levels appropriate to maintain the population. For example, Cale (1999; 2003) found that many corridors that were occupied by white-browed babblers (*Pomatostomus superciliosus*) were actually serving as population sinks and thus probably decreasing rather than increasing overall population viability. This underscores the importance of testing whether structural connectivity is serving as beneficial habitat by assessing population dynamics rather than just species presence. Yet very few studies have assessed such population dynamics in any form of structural connectivity.

2. Interpatch dispersal of individuals within a single generation: As single-generation dispersal may occur in connections that serve as habitat as well as those that don't, presence in a connection is not necessarily related to this potential function of structural connectivity. In this case, actual observations of movements into and ultimately through connectivity (preferably via telemetry to minimise observer bias) would establish that single-generation movement occurs in the connection. But again, this type of evidence is necessary but not sufficient. Genetic assignment tests, comparative population genetic data, or subsequent detailed monitoring of marked dispersers to detect successful reproduction would establish that effective dispersal actually occurred. (See also Table 2, as that loose hierarchy of types of evidence applies best to this potential function of structural connectivity.)

3. Interpatch dispersal of genes over multiple generations: As multiple-generation movement necessarily occurs in connections that also function as habitat, presence in the connection is necessary but not sufficient evidence for this function. Comparative population genetic data or detailed mark-recapture data and population monitoring over multiple generations in both patches and connections would be required to establish the movement of genetic material between patches through structural connectivity.

Implications for management

Why should land managers need to distinguish between these different functions of structural connectivity? At first glance, it would seem logical that managers should simply aim to have connections that serve all three functions. The problem is that the physical characteristics required for structural connectivity to provide each of these functions might be very different. For example, in order to provide habitat without acting as a sink, a corridor might need to be hundreds of metres wide and be carefully managed to maintain a structurally diverse habitat. Yet a very narrow, simple corridor might actually facilitate single generation dispersal. Thus, the decision of exactly what to plant where in restoration projects, or exactly where to put the fence in regeneration or management projects, needs to be made not just based on resources available but on an understanding of the landscape functions that will be achieved (both costs and benefits). Otherwise, there is a risk that the connectivity will fail to provide any of the three possible functions, or will fail to provide the function most needed in that particular landscape.

4. Results

4.1 Review statistics

The numbers of sources included at each stage of the review are presented in Table 3. The inability to use geographical search terms and the diversity of techniques that can be used to study movement meant that initial searches were less targeted than is generally desirable. However, the majority of rejected sources were rejected at the early filtering stages, limiting the number that had to be examined at the full text stage. While 98 sources were accepted into the review (listed in Appendix D), a number of studies were represented by multiple sources which, when combined, provided sufficient information to complete the data extraction form. Thus, the 98 accepted sources represented 80 different studies. As data were extracted separately for each species in each type of structural connectivity studied, this resulted in 2220 lines of extracted data representing 458 different species or species groups (e.g., “ants”).

Table 3. Number of sources included after each systematic review filtering stage.

Systematic review stage	**No. of sources**
Sources identified from electronic database searches after removal of duplicates*	24,851
Sources remaining after geographical filter*	15,358
Sources remaining after title and abstract filter	690
Sources included in review after full-text filtering	98

* does not include results from search engine searches, targeting the grey literature, or database searches that could not be directly imported into EndNote.

Of the 690 sources to be examined at the full text filtering stage, only seven were rejected because the sources could not be obtained. Three sources from the grey literature were rejected because the same information was published in a peer-reviewed publication as well, so we extracted the data from the peer-reviewed source. A number of sources were rejected because there was insufficient information in the document to extract data on either the more connected landscape(s) or on a measure of movement, despite the fact that the study design could have yielded this information. This was either because the landscape was not described in sufficient detail (and we were unable to locate it definitively on Google Earth; 36 sources), or because movement information was presented too generally, and often combined across landscape types (66 sources). A list of these sources is presented in Appendices E and F respectively. It might be possible to include these sources after contacting authors to obtain additional information, but that was beyond the scope of the current review.

Twenty-eight sources were rejected because they only described isolated landscapes, and thus did not provide the intervention (structural connectivity) that the review was designed to evaluate. However, these sources did provide information on distances between patches that species were willing or not willing to cross in the absence of structural connectivity. These distances were extracted and used along with interpatch movement distances from studies fully included in the review to evaluate possible threshold interpatch distances in the presence and absence of structural connectivity. Finally, a number of theoretical sources, traditional reviews, and examples of high quality empirical research performed overseas were saved in a separate EndNote library to provide theory and other background information for this review.

4.2 Description of studies

The majority of studies were survey-based and presented data on presence of species within elements of structural connectivity, and thus provided evidence for structural connectivity as habitat. Only 35 studies provided evidence of movement *per se*, either measured directly or inferred. Of those 35, none provided the “gold standard” evidence—known movement paths with known contribution to the local gene pool in the new patch. The numbers of studies that provided different types of movement evidence are detailed in Table 4. Despite the fact that movement of dispersers is what is required to ensure functioning rescue-effect metapopulations or patchy populations (the primary goal of connectivity), only 11 studies were able to provide data on movements of individuals in the dispersal life-history stage.

As expected, more information was available for particular parts of Australia where connectivity research has been concentrated, such as the sheep-wheat belts of Western Australia and New South Wales/Victoria (Table 4). While this suggests that significant portions of Australia are underrepresented, these regions are the ones that have been most fragmented by human activities, and thus where outcomes of research are likely to be used to guide restoration. Mammals were the best-represented taxonomic group, following closely by birds, and followed much more distantly by reptiles, invertebrates, and plants (Table 4). The majority of studies were conducted on corridors (Table 4). Almost all of the data on stepping stones came from landscapes where scattered paddock trees were the stepping stones, while only five studies collected data on movement through other types of stepping stones such as shrubs, rocky outcrops, or small clumps of woodland or forest. Though there were notable exceptions (e.g., Fischer and Lindenmayer 2002), most of the data on paddock trees as stepping stones came from studies that did not identify these trees as elements of structural connectivity (or generally even note their existence), instead treating paddocks containing them as hostile matrix. In these cases, it was only by locating study landscapes on Google Earth that we were able to classify these areas correctly as containing potential stepping stones.

Table 4. Numbers of studies included in the systematic review (out of a total of 80 studies) that possessed different non-mutually-exclusive characteristics.

No. of studies	Characteristics of the studies
54	evidence that connectivity used as habitat based on presence/absence of species in the connectivity itself
9	movement evidence based on known movement paths between patches
8	movement evidence based on knowledge of a partial movement paths
14	movement evidence based on known transfers between patches but without knowledge of the habitat elements used (i.e., movement paths unknown)
3	movement evidence based on population genetic data to assess relative levels of gene flow in different landscapes
4	movement evidence inferred from patterns of species presence and absence in more and less connected patches
11	evidence of movement by individuals in the dispersal life-history stage
15	conducted in sheep-wheat belt of southwestern Western Australia
13	conducted in and around the Atherton Tablelands in Queensland
6	conducted in the southeastern corner of Queensland
19	conducted in the sheep-wheat belt of New South Wales and Victoria
10	conducted in the southern and southeastern coastal forests
41	data on mammals
32	data on birds
8	data on reptiles
5	data on invertebrates
5	data on plants
63	landscapes contained corridors
9	landscapes contained disconnected linear elements
30	landscapes contained stepping stones
65	peer-reviewed publication
15	in grey literature only

4.3 Summary statistics: primary question

For the subset of studies that compared sites without structural connectivity to sites with some form of structural connectivity, we scored each observation (species within studies) according to whether the answer to the primary question was yes—whether there was movement through structural connectivity but no movement through matrix lacking structural connectivity—and calculated the percentage of yes answers. We repeated these summaries for the subset of studies that calculated movement rates, scoring these studies as supporting the primary question if the rate of movement was higher in the more connected landscape. As detailed above, we summarised data on presence in connectivity (evidence that connectivity serves as habitat) separately from other types of data which provide better evidence for movement *per se*.

Presence in connectivity**:** 45.2% of observations in studies that compared presence of species in areas without structural connectivity to areas with structural connectivity (total n=586) provided support for the primary question. When we looked at studies that calculated rates in less and more connected sites, 59.6% of observations (total n=641) supported the primary question. The difference in these two values suggests that a number of additional species may have been present in both the matrix and in connectivity, but that they were present in greater numbers or at greater densities in the connectivity.

Evidence for movement**:** Similarly, 42.1% of observations in studies that compared evidence for movement *per se* in landscapes without structural connectivity versus those with structural connectivity (total n=75) provided support for the primary question. When we looked at observations from studies that calculated movement rates in less and more connected landscapes, 51% (total n=51) supported the primary question. The difference in these two values suggests that for some species, the matrix or low levels of structural connectivity were crossable but that movement rates increased with increasing amounts of structural connectivity.

4.4 Quantitative analyses

4.4.1 Primary question

Presence in connectivity**:** Contingency analyses revealed that structural connectivity provided habitat more often than expected by chance compared to the matrix (Fisher's exact test, n=1172, p<0.001). More structural connectivity also provided habitat more often than expected by chance compared to less structural connectivity (Fisher's exact test, n=1910, p<0.001). When we controlled for consistent differences among studies using HGLM, we obtained the same result—species were more likely to be present in structural connectivity compared to the matrix (HGLM: t-ratio=9.514, df=51/2574, p<0.001; coefficient ±SE=1.795±0.189). Finally, when comparing rates, more structural connectivity provided habitat for more individuals or greater densities of species than less connectivity did (Sign test, n=641, p<0.001).

Evidence for movement**:** Contingency analyses revealed that movement occurred more often than expected by chance in landscapes with structural connectivity compared to those with no connectivity at all (Fisher's exact test, n=150, p<0.001). Analysing studies that compared sites with more and less structural connectivity, more structural connectivity also facilitated movement more often than expected by chance (Fisher's exact test, n=184, p<0.001). When we controlled for consistent differences among studies using HGLM, we obtained the same result—species were more likely to move into or through structural connectivity compared to the matrix (HGLM: t-ratio=2.446, df=32/197, p=0.016; coefficient ±SE=2.011±0.822). Finally, when analysing studies with comparative quantitative data, we found that more structural connectivity generally facilitated greater rates of movement than less connectivity did (Sign test, n=51, p=0.025).

4.4.2 Secondary & tertiary questions

***Presence in connectivity*:** Compared to the matrix, species were much more likely to be present in all types of structural connectivity, though stepping stones did not appear to function as habitat as well as the other connectivity types (Table 5). Species that disperse terrestrially were less likely to be found living between habitat patches, but where they were found were significantly more restricted to elements of structural connectivity than aerial dispersers (as indicated by the significant interaction terms; Table 5). Similarly, habitat specialists were less likely to be present between patches, but when present were significantly more restricted to disconnected linear element and corridors (but not stepping stones) than habitat generalists (Table 5).

Table 5. Results of hierarchical generalised linear models examining the influence of connectivity type and other sources of variation on presence of species in connections

Variable(s) in model	Coefficient ± SE	t-ratio	p-value
Corridors	1.958 ± 0.207	9.462	<0.001
Disconnected linear elements	1.654 ± 0.166	9.974	<0.001
Stepping stones	1.020 ± 0.433	2.355	0.019
(model df = 51/2572)			
Aerial/Terrestrial dispersal*	1.138 ± 0.326	3.490	0.001
Corridors	2.883 ± 0.163	17.738	<0.001
Disconnected linear elements	2.485 ± 0.234	10.636	<0.001
Stepping stones	2.227 ± 0.288	7.741	<0.001
Aerial x Stepping stones	-1.388 ± 0.564	-2.462	0.014
Aerial x Linear elements	-0.887 ± 0.327	-2.708	0.007
Aerial x Corridors	-1.024 ± 0.331	-3.094	0.002
(model df = 51/2542)			
Specialist/Generalist*	-1.294 ± 0.437	-2.961	0.004
Corridors	1.385 ± 0.233	5.939	<0.001
Disconnected linear elements	1.154 ± 0.243	4.747	<0.001
Stepping stones	0.910 ± 0.294	3.094	0.002
Specialist x Stepping stones	0.291 ± 0.483	0.602	0.547
Specialist x Linear elements	1.016 ± 0.539	1.885	0.059
Specialist x Corridors	1.129 ± 0.409	2.758	0.006
(model df = 49/2253)			

* these variables and other binary variables in subsequent models were coded such that the coefficients describe the effect of the first category relative to the second category as a baseline (e.g., the effect of aerial movement relative to terrestrial movement)

When we modelled evidence for presence specifically in corridors, to investigate any other conditions under which corridors might be most likely to provide habitat (Table 6), we excluded constructed corridors such as highway underpasses due to small sample size. We found that species were no more likely to be present in wider corridors than narrower ones (range of widths in the data: 1-110m). Surprisingly, riparian corridors were less likely to have species present in them than other types (woodland or forest) and species were less likely to be present in tropical corridors compared to temperate corridors. However, multicollinearity between these two variables (all tropical corridors were riparian corridors) means that we cannot distinguish between their effects. There were also differences among taxonomic groups, with reptiles less likely than other taxa to be present in corridors.

Table 6. Results of hierarchical generalised linear models examining the influence of sources of variation on presence of species specifically in corridors

Variable(s) in model	Coefficient ± SE	t-ratio	p-value
Width (model df = 34/1238)	-0.003 ± 0.006	-0.469	0.639
Riparian/Other types (model df = 38/1306)	-0.625 ± 0.308	-2.027	0.043
Reptiles/Other taxa (model df = 38/1306)	-0.339 ± 0.147	-2.313	0.021
Tropical/Temperate (model df = 38/1306)	-0.655 ± 0.320	-2.046	0.041

When we modelled evidence for presence specifically in disconnected linear elements, to investigate any other conditions under which these elements might be most likely to provide habitat (Table 7), there were insufficient data to include invertebrates in the model, but reptiles were less likely to be present in these elements. In addition, wider elements and riparian elements were both more likely to have species present. Disconnected linear elements in temperate and tropical environments appeared to be equally effective.

Table 7. Results of hierarchical generalised linear models examining the influence of sources of variation on presence of species specifically in disconnected linear elements

Variable(s) in model	Coefficient ± SE	t-ratio	p-value
Width (model df = 6/633)	0.016 ± 0.005	3.455	0.001
Riparian/Other types (model df = 7/635)	0.975 ± 0.279	3.499	0.001
Reptiles/Other taxa (model df = 7/635)	-1.044 ± 0.439	-2.377	0.018
Tropical/Temperate (model df = 7/635)	-0.670 ± 0.990	-0.677	0.498

When we modelled evidence for presence specifically in stepping stones, to investigate any other conditions under which stepping stones might be most likely to provide habitat (Table 8), there were no differences among taxonomic groups in tendency to be present in stepping stones, though there were insufficient data to include reptiles in the model. The density of stepping stones also had no effect on their likelihood of having native species present.

Table 8. Results of hierarchical generalised linear models examining the influence of sources of variation on presence of species specifically in stepping stones

Variable(s) in model	Coefficient ± SE	t-ratio	p-value
Mammal/Other taxa	0.224 ± 0.401	0.559	0.576
Invert/Other taxa	2.123 ± 1.723	1.233	0.219
(model df = 14/337)			
Density	4.823 ± 3.48	1.383	0.168
(model df = 13/333)			

***Evidence for movement*:** There were too few observations of disconnected linear elements or of invertebrates in any type of structural connectivity to include them in hierarchical models. Modelling the other connectivity types and taxonomic groups, there was much more evidence of movement in corridors and stepping stones compared to the matrix. However, unlike the results based on presence in connectivity, stepping stones may actually have been more effective at facilitating movement than corridors, based on the magnitude of the coefficient (the effect size; Table 9). We attempted to incorporate interaction terms into this model to investigate whether the effectiveness of these two types of structural connectivity differed depending on characteristics of the species or ecosystem, but there was insufficient variation in the data to run these models.

Table 9. Results of hierarchical generalised linear models examining the influence of connectivity type on evidence of movement in connections

Variable(s) in model	Coefficient ± SE	t-ratio	p-value
Corridors	1.919 ± 0.389	4.938	<0.001
Stepping stones	2.538 ± 0.661	3.838	<0.001
(model df = 32/196)			

When we modelled evidence for movement specifically in corridors, to investigate the conditions under which or the types of species for which corridors might be most effective (Table 10), we excluded constructed corridors such as highway underpasses due to small sample size. There was also insufficient variation to investigate effects of dispersal method (aerial vs. terrestrial), specialist vs. generalist, or life-history stage. When we attempted to model variation in corridor effectiveness across all taxonomic groups, there was insufficient variation to simultaneously model all groups. However, when we considered each group separately (e.g., birds vs. all other types), we found that reptiles were less likely to be moving in corridors than the other species groups. Corridors in temperate and tropical ecosystems appeared to be equally effective at facilitating movement, and corridor width had no influence on whether or not there was evidence for movement (range of widths in the data: 1-350m).

Table 10. Results of hierarchical generalised linear models examining the influence of sources of variation on evidence of movement specifically in corridors

Variable(s) in model	Coefficient ± SE	t-ratio	p-value
Width (model df = 18/74)	0.007 ± 0.012	0.552	0.582
Reptiles/Other taxa (model df = 22/80)	-1.795 ± 0.791	-2.267	0.026
Tropical/Temperate (model df = 22/80)	-0.926 ± 0.938	-0.987	0.327

When we modelled evidence for movement specifically in stepping stones, to investigate the conditions under which or the types of species for which stepping stones might be most effective (Table 11), there was insufficient variation to investigate effects of density of stepping stones, temperate vs. tropical ecosystems, different taxonomic groups, or specialists vs. generalists. Aerial and terrestrial dispersers were equally likely to be moving in stepping stones, as were individuals within dispersal vs. other life-history stages.

Table 11. Results of hierarchical generalised linear models examining the influence of sources of variation on evidence of movement specifically in stepping stones

Variable(s) in model	Coefficient ± SE	t-ratio	p-value
Aerial/Terrestrial dispersal (model df = 16/37)	-0.499 ± 1.367	-0.365	0.717
Dispersal/Other life-history stage (model df = 16/37)	-1.252 ± 1.470	-0.852	0.400

4.5 Summary statistics: secondary & tertiary questions

For variables where there were insufficient data or insufficient variation to include them in the quantitative analyses described above, we were still able to calculate the percentages of observations in different categories that provided a yes or no answer to the primary question (see **4.3 Summary statistics: primary question**).

***Life-history stage*:** Summary statistics suggest that while structural connectivity may often simply facilitate daily movements of resident individuals, it may be almost as successful at facilitating movements of dispersers. Among comparisons where the individuals studied were in the dispersal life-history stage, 38.5% (total n=13) provided positive support for the primary question. Where individuals were not in the dispersal life-history stage or life-history stage was unknown, 43.5% (total n=62) provided support for a positive response to the primary question.

Scale: Based on the summary information, species that tend to have smaller home ranges could be more likely to use structural connectivity as habitat, but it is unclear whether home range size influences the likelihood of moving through structural connectivity. Home range sizes were categorised at three levels: <1 hectare, multiple hectares, or 1 km^2 or more. Of landscape comparisons where outcomes were based on presence in connectivity, 80% of observations of species with the smallest home range size (total n=5) positively supported the primary question, 61.6% of those with the intermediate home range size (total n=159) supported the primary question, and only 33.3% of those with the largest home range size (total n=18) supported the primary question. All but one of the comparisons in which outcomes were based on assessing movement (n=36) were of species with home ranges at the scale of hectares, so comparative percentages could not be calculated.

***Dispersiveness*:** Our summary statistics suggest that sedentary and migratory or nomadic species may be equally likely to use structural connectivity as habitat, but it is unclear whether dispersiveness influences the likelihood of moving through structural connectivity. Where outcomes were based on presence in connectivity, 47% of the landscape comparisons involving sedentary species (total n=251) and 49% of landscape comparisons for migratory or nomadic species (total n=51) provided positive support for the primary question. Again, all but one of the comparisons in which outcomes were based on evidence for movement (n=39) were of sedentary species, so comparative percentages could not be calculated.

***Matrix type*:** Our summary statistics suggest that structural connectivity may be more likely to serve as habitat when it is embedded in a grassy matrix, rather than a matrix of woody vegetation not traditionally thought to serve as habitat, though it is unclear how differences in the matrix influence the use of structural connectivity for movement. Where outcomes were based on presence in connectivity, 46.3% of comparisons between no and more structural connectivity in the context of a grassy matrix (total n=540) positively supported the primary question, while only 32.6% of such comparisons in the context of a woody matrix (total n=46) positively supported the primary question. Note that this may be because both the woody matrix and the structural connectivity were serving as habitat, the woody matrix was preferentially used as habitat, or because neither the matrix nor the connectivity were occupied. All but three of the 72 observations where outcomes were based on assessing movement itself were within a grassy matrix, so comparative percentages could not be calculated.

***Patch size*:** It is unclear whether structural connectivity functions better, either as habitat or at facilitating movement, as a function of patch size. Where outcomes were based on presence in connectivity, only two mean patch sizes were represented (45 ha and 91 ha), and landscape comparisons involving these patch sizes reported similar levels of support for the primary question (41.7% total n=60, and 50% total n=76, respectively). A greater number of different mean patch sizes were represented in the landscape comparisons in which outcomes involved some measure of movement (range: 5-300 ha), so we explored any potential relationship between patch size and the answer to the primary question using hierarchical generalised linear modelling. Patch size appeared to have no influence on the answer to the primary question (HGLM: t=-0.573, df=6/34, p=0.570), though this was based on only seven different studies, so sample size of independent data was extremely limited.

***Landscape cover*:** It is unclear whether structural connectivity is more or less likely to be serving as habitat in landscapes that have a greater percent cover of intact native vegetation, though there may be a trend for it to be more likely to serve as habitat in more intact landscapes. Where outcomes were based on presence in connectivity, a reasonable range of landscape cover values were present in the data (range: 5-30%), so we explored any potential relationship between landscape cover and the answer to the primary question using hierarchical generalised linear modelling. Landscape cover did not influence the answer to the primary question (HGLM: t=1.412, df=6/317, p=0.159), though if a trend exists, it was a positive one. Note that this too was only based on seven different studies, so sample size of independent data was extremely limited. It is unclear whether the amount of remaining vegetation in the landscape influences the ability of structural connectivity to facilitate movement. Where outcomes were based on measures of movement, there were only three landscape cover values represented (2% total n=1, 7% total n=20, and 15% total n=2). Ninety percent (total n=22) of the comparisons made in landscapes with 7% cover and with 15% cover positively supported the primary question (and the one comparison made in the landscape with 2% cover did not), but there were insufficient data to compare percentages to landscapes with more or less cover.

***Remnant vs. revegetated connectivity*:** Remnant structural connectivity and revegetated structural connectivity may be just as likely to serve as habitat (though almost certainly for a different suite of species), but there is a possibility that revegetated connectivity is less likely to facilitate movement. Where outcomes were based on presence in connectivity, 46.2% of comparisons between no and more remnant structural connectivity (total n=403) positively supported the primary question, and 44.3% of such comparisons involving revegetated connectivity (total n=122) positively supported the primary question. However, where outcomes were based on assessing movement itself, only 30% of comparisons involving revegetated connectivity (total n=10) supported the primary question, compared to 43.9% of landscape comparisons involving remnant structural connectivity (total n=57).

4.6 Gap-crossing and interpatch distance thresholds

Species may have a threshold distance beyond which they are unwilling to cross any gaps in the structural connectivity, such as distances between scattered trees or gaps in a disconnected linear element. Data on gap-crossing distances (though they were not always reported as such) could be extracted from 20 studies. Two of these studies provided observations that were identified as extreme outliers in box plots using the methods of Tukey (1977). These outliers were excluded from the following summary statistics as species insensitive to gap distances, and new box plots were generated to depict results graphically (Figure 2). Only a few studies had collected enough data over a diversity of gap distances to suggest a threshold—a maximum distance beyond which species would not cross. The mean of this maximum gap distance (±SD) across studies and species was 164 ± 90m (n=5). More commonly, studies provided what we termed the "minimum threshold"—the largest gap distance that the study could confirm was crossed by at least some individuals. The mean of this gap distance across studies and species was 106 ± 82m (n=23). Any actual threshold gap-crossing distance would presumably be somewhat larger than this value as estimates from many studies were based on very small sample sizes, but based on the available data, inferences could not be drawn about larger gaps. A few studies also reported mean gap distances crossed, suggesting a distance commonly crossed rather than a maximum threshold. The grand mean across these studies was 70 ± 5m (n=3).

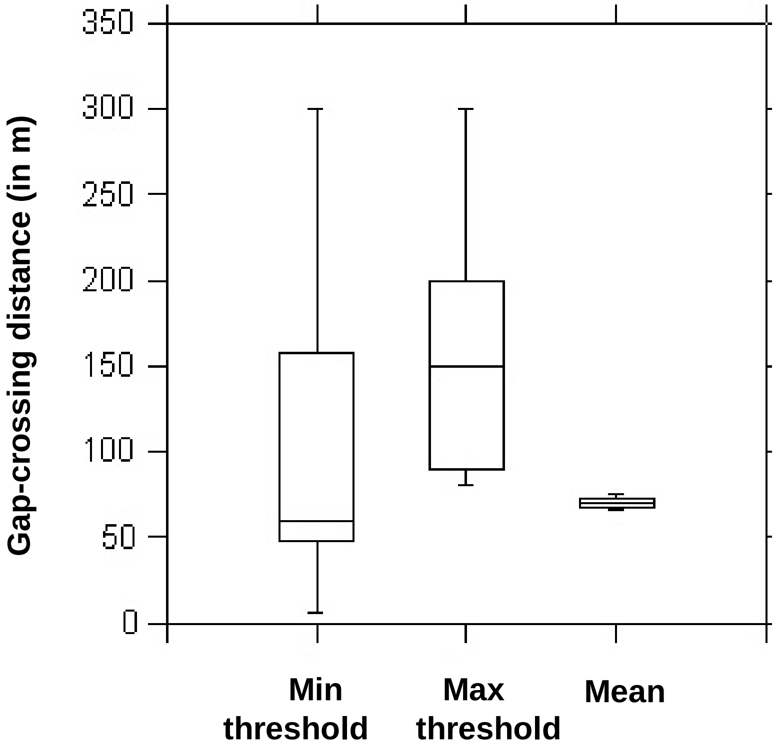

Figure 2. Box plots of gap-crossing distances across species and studies. The minimum of the threshold is the largest gap species were observed crossing, the maximum of the threshold is the smallest distance species were known not to cross, and the mean is the grand mean across studies that quantified sufficient gap crossing to present summary statistics.

Species may still be willing to and/or capable of crossing larger expanses of matrix when another habitat patch is the destination, as opposed to an element of structural connectivity such as a stepping stone. Furthermore, such an interpatch crossing distance may be greater (but not necessarily infinite) when there is some form of structural connectivity that can be used for movement between the patches. Based on all types of data in which a maximum distance moved between patches was extracted, the mean of the maximum interpatch movement distances observed across studies where there was no structural connectivity (excluding extreme outliers as above) was 71 $\pm$ 26m (n=29) while the mean of the maximum interpatch movement distances observed where there was some form of structural connectivity was 1100 $\pm$ 1516m (n=72; Figure 3). Thus, structural connectivity appeared to significantly increase interpatch crossing distances (t-test for samples with unequal variance: t=-5.757, df=71, p<0.001).

If we also included the data extracted from sources that studied isolated landscapes only (sources technically excluded from the full review), then the mean of the maximum interpatch movement distances observed in the absence of structural connectivity increased to 390 $\pm$ 463m (n=111; Figure 3), which was still significantly smaller than the interpatch movement distances observed where there was some form of structural connectivity (t-test for samples with unequal variance: t=-3.861, df=80, p=0.001). However, this large increase could be at least partially attributable to authors classifying study landscapes as "isolated" when they in fact contained some structural connectivity. As we have seen, this would most likely be stepping stones in the form of scattered trees, which until recently were often overlooked as a form of structural connectivity.

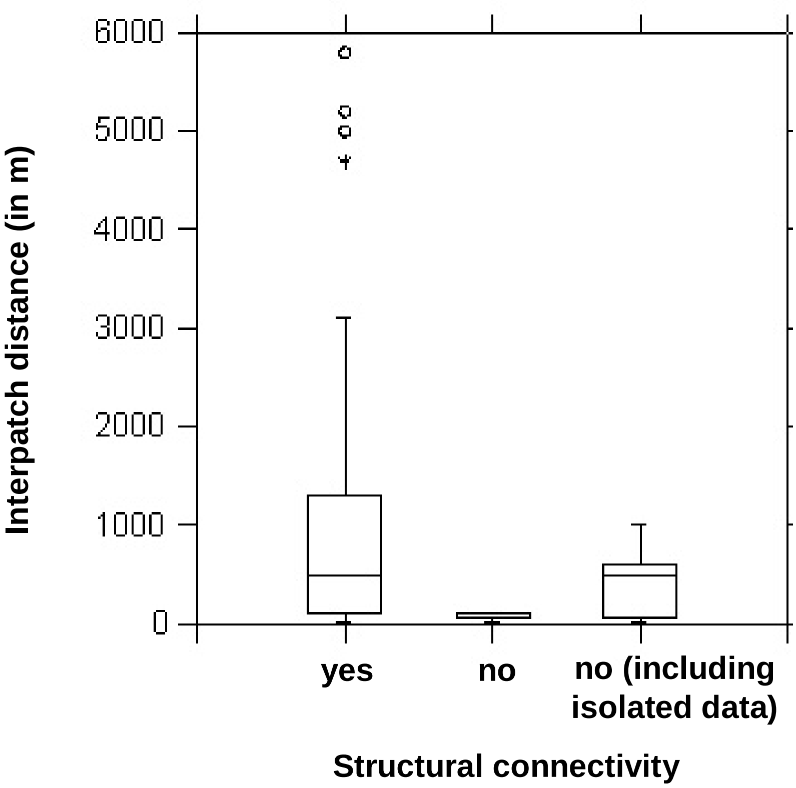

Figure 3. Box plots of interpatch crossing distances across species and studies. From left to right: crossing distances observed with structural connectivity between patches, crossing distances observed without any structural connectivity in studies included in the review, crossing distances observed without any structural connectivity in both studies included in the review and those excluded because they only contained data on isolated landscapes.

4.7 Outcome of the review

The 80 studies included in the review varied enormously in their goals, methodologies, and theoretical frameworks and they measured responses to structural connectivity using more than two dozen different response variables. These inconsistencies, and the fact that only a handful of studies provided comparative data and information from which variances could be estimated, eliminated any possibility of performing a proper meta-analysis, though we were able to perform some exploratory multivariate analyses. Too few studies were available on plants or invertebrates to include them in most of these analyses. Most of the studies focused on mammals or birds, with a much smaller number on reptiles (see Table 4). Almost all studies were conducted in wooded habitat patches and/or in structural connectivity consisting of trees, so relatively little can be concluded about grassland or other non-treed ecosystems. Despite these limitations, our exploratory analyses were able to reveal a few clear messages as well as some interesting patterns that suggest foci for future research.

Native species were more likely to be present in elements of structural connectivity than in the matrix, providing reasonable evidence that these landscape features provide habitat for these species, though only weak evidence that they facilitate dispersal movements. However, studies with specific evidence of movement between patches also generally found that the presence of structural connectivity increased the rates and/or likelihood of such movement. Both simple contingency analyses and HGLM (mixed) models confirmed that increased amounts of structural connectivity were correlated with increased functional connectivity. Thus, we found considerable support for a positive answer to the review's primary question.

All forms of structural connectivity for which there were sufficient data for analyses were effective to some degree in both providing habitat and in facilitating movement (two distinctly different functions). In terms of providing habitat, our exploratory analyses suggest that while all forms were better habitat than matrix for most species, continuous corridors were better than discontinuous linear elements which were better than stepping stones (e.g., scattered paddock trees). However, in terms of facilitating movement, our analyses suggest that stepping stones were at least as good if not better than continuous corridors. Data supporting the use of stepping stones for movement came from a number of bird and mammal species as well as a single reptile species (Figure 4).

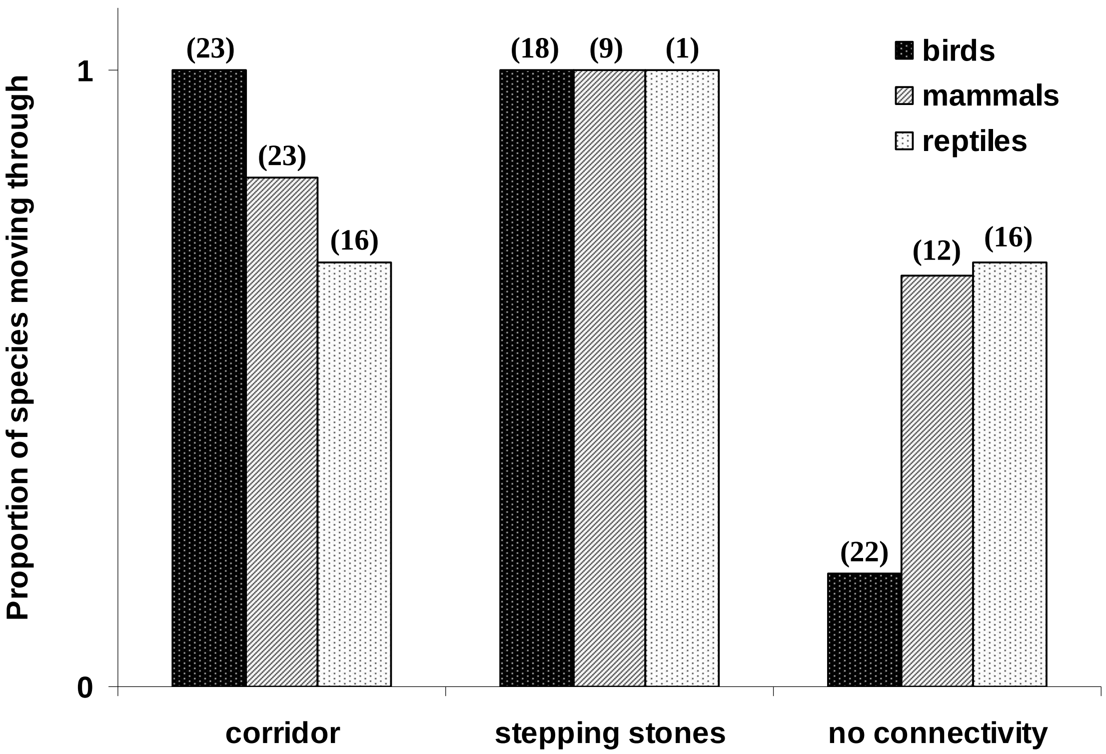

Figure 4. Proportion of bird, mammal, and reptile species that used different types of connectivity to move between patches of habitat. The sample size of species examined in each connectivity type is shown above the bars. The data come from 10 studies of birds, 23 of mammals, and 3 of reptiles.

Effectiveness of structural connectivity at providing habitat varied somewhat according to the environment and the species. Species that disperse terrestrially were less likely to be found living between habitat patches, but where they were found were significantly more restricted to elements of structural connectivity than aerial dispersers. Similarly, habitat specialists were less likely to be present between patches, but when present were significantly more restricted to disconnected linear element and corridors (but not stepping stones) than habitat generalists. Corridors were less likely to be used as habitat in tropical ecosystems than in temperate ones, and disconnected linear elements were more likely to be used as habitat when they were wider. Both types were less likely to contain reptile species (relative to other taxonomic groups), possibly because most studies focused specifically on wooded landscape elements. Interestingly, width had a significant effect on the likelihood of occupancy of disconnected linear elements but no effect on occupancy of continuous corridors.

In general, there were insufficient data and/or variability in the data to assess variation in the effectiveness of the different forms of structural connectivity at facilitating movement. However, similar to our analyses of connectivity as habitat, we did find evidence that wooded corridors were less likely to facilitate movement by reptiles relative to other taxonomic groups.

Data on critical gap-crossing and interpatch-crossing distance thresholds could be estimated for only a subset of studies and most of these estimates were based on relatively small sample sizes. Thus, it was impossible to determine how much of the variation observed in these thresholds was due to variation among species as opposed to variation among studies (i.e., differences in methodology and sampling effort). However, based on these data we were able to calculate a mean gap-crossing threshold of 106m and an interpatch-crossing threshold of 1100m. Thus, many species may not be able to cross gaps through matrix of >106m and may not be able to disperse between patches of habitat separated by >1100m, even where structural connectivity exists between patches. These values should provide a useful starting point for future connectivity research, modelling and planning.

5. Discussion

5.1 Evidence of effectiveness

Structural connectivity can serve multiple functions in a landscape, providing additional habitat but also facilitating dispersal movements and gene flow between larger patches of habitat. Sometimes these functions occur in concert, but it is possible to have structural connectivity that provides habitat (i.e., is occupied) but which does not facilitate gene flow, just as it is possible to have structural connectivity that helps animals (and possibly plants) disperse between patches but which they do not attempt to settle or live in for any extended period. As the movement functions of structural connectivity are the ones the concept of connectivity was originally designed to provide (Taylor et al. 1993; Hilty et al. 2006), this review was specifically intended to evaluate the effectiveness of structural connectivity at facilitating movement. However, because providing habitat is a secondary function of structural connectivity, because this is the function the majority of empirical studies attempt to test, and because some structural connections that provide habitat will also facilitate movement, we also evaluated the effectiveness of structural connectivity at providing this secondary function.

***Effectiveness at providing habitat*:** Across all analyses, structural connectivity was always more likely to provide habitat (to contain species that also live in adjacent patches) compared to the matrix. Furthermore, the more structural connectivity present, the better. Comparing sites with more vs. less structural connectivity, those with more connectivity were likely to have more species present in the connectivity and in greater numbers or densities. Comparing presence in structural connectivity and in the matrix, just under half of the observations were of species that were apparently unwilling to live in the matrix but were willing to live in the structural connectivity, suggesting that they were benefiting from the structural connectivity. This also suggests that over half of all species were not strongly benefiting from structural connectivity as habitat, either because they were willing to live in the matrix or because they were unable to live in the types of structural connectivity studied.

Effectiveness at facilitating dispersal: Just as above, across all analyses, structural connectivity was always more likely to provide evidence of movement compared to the matrix. Furthermore, the more structural connectivity present, the better. When comparing sites with more vs. less structural connectivity, those with more connectivity were likely to have more evidence of species' movement and to facilitate greater rates of movement. Again, when comparing evidence of movement in structural connectivity and in the matrix, just under half of the observations were of species that were benefiting from the structural connectivity—that were not observed or inferred to move across matrix, but were observed or inferred to move through structural connectivity. This suggests that over half of all species were not strongly benefiting from structural connectivity as conduits for movement, either because they were willing to move across the matrix or because they were unable to move through the types of structural connectivity studied.

5.2 Variation in effectiveness

While an overall positive effect of structural connectivity was found, there were still sources of variation in the degree to which elements of structural connectivity provided habitat and/or facilitated dispersal.

***Variation in effectiveness at providing habitat*:** All types of structural connectivity (corridors, disconnected linear elements and stepping stones) were more likely to provide habitat than the matrix (mostly mixed agricultural land and some forestry plantations), and this was particularly true for terrestrial dispersers. Stepping stones were slightly less effective than the other connectivity types, particularly for habitat specialists, who were more likely to be present in corridors and disconnected linear elements. This may be because stepping stones were almost exclusively scattered trees, with no shrubs or other types of understorey or ground-layer complexity. Summary statistics suggested that structural connectivity may be more likely to provide habitat when surrounded by agricultural land rather than plantation forest, species with larger home ranges may be less likely to live in structural connectivity, structural connectivity is equally effective for sedentary vs. migratory or nomadic species, and revegetated connectivity is just as effective as remnant connectivity.

***Corridors as habitat*:** Contrary to popular opinion, the likelihood of species being present in a corridor was unrelated to the width of the corridor. However, this does not mean that corridor width is irrelevant to management. Species may be present in corridors with a wide range of widths, but may only survive and reproduce well (thus avoiding the problem of population sinks) in corridors with certain widths (see **Box 1** and **5.3.2 Questions that could not be addressed due to insufficient data**). Corridors were less likely to serve as habitat for reptiles. This may simply be because all the corridors studied were corridors of woody vegetation of some sort. Many reptiles require rocky outcrops, coarse woody debris, or other types of non-vegetated habitat elements (Smith 1999; Stow and Sunnucks 2004; Fischer et al. 2005), which, if present in the form of a corridor, might still support the presence of reptiles. All tropical corridors were riparian corridors, so we could not distinguish between the effects of these variables. As these corridors were less likely to support species, we suspect that tropical is the important variable. Tropical corridors may be less effective at providing habitat than temperate corridors because, as many others have suggested, edge effects tend to be stronger at the harder boundaries between tropical ecosystems and agricultural land (Laurance et al. 2002; Ries et al. 2004).

***Disconnected linear elements as habitat*:** In disconnected linear elements, reptiles were also less likely to be present, possibly for the same reasons as above. However, in contrast to corridors, wider disconnected linear elements were more likely to have species present within them, and temperate and tropical linear elements were equally effective. Differences in the corridor and linear element results were surprising, and require further investigation.

***Stepping stones as habitat*:** Finally, stepping stones (which were almost always scattered trees, see **5.3.2 Questions that could not be addressed due to insufficient data)** did not vary in their effectiveness at supporting species presence across taxonomic groups or as a function of the density of scattered trees. However, data on stepping stones were limited, and this would be a fruitful topic for further investigation.

Variation in effectiveness at facilitating dispersal: Data on dispersal or even inferred dispersal were much more limited than data on presence in structural connectivity. As a result, only corridors and stepping stones could be evaluated for their abilities to facilitate possible dispersal movements. Evidence for movement was much more prevalent in both types of structural connectivity compared to the matrix (which was mostly mixed agricultural land). Stepping stones appeared to be more effective at facilitating movement than corridors, which was opposite to their effectiveness at providing habitat, despite their lack of habitat complexity. Summary statistics suggested that revegetated (i.e., planted) structural connectivity could be less likely to facilitate movement than remnant structural connectivity. This requires further investigation as, if the pattern is real, it could be the result of differences in age (such that revegetated connections will eventually become just as effective), quality, or both.

***Corridors for movement*:** Just as for effectiveness at providing habitat, the likelihood of finding evidence for movement through a corridor was unrelated to its width, and reptiles were less likely to be found moving in corridors, possibly for the same reasons as detailed above. In contrast to the results for effectiveness at providing habitat, corridors in temperate and tropical ecosystems appeared to be equally effective at facilitating movement. Thus, tropical corridors may be less likely to serve as habitat, but may still allow dispersal (making tropical corridors more likely to be type #4 functional connections, see Box 1).

***Stepping stones for movement*:** Unfortunately, data on movement specifically through stepping stones were particularly limited and very few sources of variation could be investigated. Aerial and terrestrial dispersers were equally likely to be moving in stepping stones, as were individuals within dispersal vs. other life-history stages. These results suggest that stepping stones may be broadly effective at encouraging dispersal movements in fragmented landscapes, but there are insufficient data to evaluate the exceptions to this generality.

***Gap and interpatch crossing distances*:** Gap-crossing and interpatch-crossing data can provide an alternative way of identifying the specific characteristics that structural connectivity might need to have in order to be effective at facilitating movement. It was rarely possible to identify actual thresholds from the studies included in this review, but maximum observed distances can set a minimum possible threshold value. Standard deviations of the potential maximum and the potential minimum of the threshold across species were large, suggesting significant differences in gap tolerances between species, but much of this variation would also be due to variation in sample sizes between studies (as sample size increases, the maximum observed gap-crossing distance should asymptote at the gap-crossing threshold value for the species). However, by ensuring distances between stepping stones or gaps in disconnected linear elements do not exceed the mean of the minimum threshold values (106m), or even the mean gap distances crossed regardless of threshold values (70m), it may be possible to ensure effectiveness of structural connectivity for a majority of species.

Interpatch crossing distances were significantly increased through the provision of structural connectivity. Again, there was considerable variation in maximum distances crossed between patches, especially when structural connectivity was present. However, the mean values for interpatch crossing distances with and without structural connectivity may suggest the range of interpatch distances in which structural connectivity is most likely to be effective. Based on the data from this review, structural connectivity is likely to be helpful between patches that are separated by at least 71m but no more than 1100m. The existence of this upper limit is thought to be related to the specific behaviours that many species use during dispersal such as foray search (Conradt et al. 2003), in which there may be a maximum foray distance individuals are willing to travel regardless of the habitat or landscape.

5.3 Review limitations

5.3.1 Limiting inference from the analyses performed

It must be stressed that data were insufficient to perform meta-analysis, so the analyses presented here are exploratory only. They are not direct tests of the review questions, though they will hopefully stimulate more targeted research on connectivity. They are useful for revealing broad patterns, particularly across studies examining different types of structural connectivity, which have never been synthesised before. These broad patterns can be used to develop more robust and specific management recommendations than are currently available, but particularly given the exploratory nature of the analyses, such recommendations should be incorporated into an adaptive management framework, in which adjustments will continually be made as new information becomes available.

5.3.2 Questions that could not be addressed due to insufficient data

Researchers and managers alike have generally assumed that the effectiveness of structural connectivity may depend on many different factors, including characteristics of the environment as well as the species using the connectivity (Wilson and Lindenmayer 1995; Bennett 1998). This review was only partly able to address the most commonly-suspected sources of variation.

***Taxonomic group*:** Different taxonomic groups might show very different responses to structural connectivity. Plants in particular and invertebrates (and to a lesser extent, reptiles) were underrepresented in existing studies, so we were able to draw few if any conclusions about them.

Scale and dispersiveness: The effectiveness of connectivity for any given species may vary depending on the scale at which the species normally experiences its environment (i.e., the size of its normal home range) and whether it is nomadic or migratory and thus sometimes experiences its environment at much broader scales. Taken together, the studies included in this review suggested that these differences are unrelated to use of structural connectivity, but data were quite limited. Home ranges and sedentary tendencies for any given species can differ in different environments, so data on these factors need to be specific to the location in which connectivity research is conducted, which requires more detailed population-level approaches than have normally been employed.

Width & quality of the connection**:** Corridor width has probably been the source of variation most discussed by managers but, while some individual studies tested for and found positive effects of corridor width (usually on species richness), others found no effect, and no effect was evident when analysed across all studies in this review. That could be because a sufficient range of corridor widths was not represented, but the presence data included corridors up to 110m wide and the movement data included corridors up to 350m wide. However, the interest in corridor width is really a specific case of asking about the habitat quality of structural connectivity. Do connections need to provide high quality habitat, with limited influence of edge effects, or is low quality habitat sufficient? And the appropriate answers to these questions are likely to differ depending on the intended function of the connection (see Box 1).

If movement within a single generation is the aim, structural connectivity does not have to be occupied, so width and quality may not be important variables. Empirical data are sorely lacking to test this, particularly as tests need to assess potential costs as well as benefits of dispersing via lower quality structural connectivity, such as increased contact with aggressive species that may prefer narrow, structurally simple connections (like noisy miners; *Manorina melanocephala*). In contrast, if movement across multiple generations is the aim, connections not only have to be occupied, they have to support viable populations, rather than population sinks. Thus, to support sufficiently high levels of survival and reproduction, they may need to provide quite high quality habitat. Hypotheses and management guidelines can be derived from the extensive literature on patch quality and edge effects. For example, some Australian research on edge effects suggests that effects extend 150-200m from the edge, so corridors may need to be >350m wide to have even a small amount of habitat uninfluenced by edge (Goldingay and Whelan 1997; Clarke and Oldland 2007). However, testing whether a connection is truly providing good quality habitat requires data on population dynamics, not just presence or even density/relative abundance, and such data are exceedingly limited in Australian environments (but see Cale 1999; 2003).

Non-woody connections, especially stepping stones**:** Almost all studies included in this review exclusively focused on structural connectivity that consisted of woody vegetation (i.e., structural connectivity that is easily visible to a human, including from a satellite image or GIS map). While many native species do require native woody vegetation, others have different habitat needs and we therefore know next to nothing about potential structural connectivity types and their effectiveness for these species, which include all grassland specialists and many reptiles. The importance of these other types of connectivity can be discussed in a theoretical and conceptual sense, but it cannot be evaluated without empirical data from alternative types of connections. This is particularly problematic in the case of stepping stones, as virtually all examples were specifically scattered trees and did not even include other types of woody vegetation. While these stepping stones appeared to provide habitat and facilitate movement in quite a number of cases, it is unclear whether they could be more effective if they incorporated additional habitat elements.

Variegated landscapes & a softer matrix**:** The designs of almost all studies in this review, and thus the structure of our own data extraction and analysis approaches, are based on the patch-matrix landscape model in which some areas serve as habitat while others do not. However, habitat is not necessarily so binary, but may be more likely to be variegated or represent more of a continuum, in which different areas may be used at different densities and for different purposes (McIntyre and Barrett 1992; McIntyre and Hobbs 1999; Fischer et al. 2004; Manning et al. 2004). Under these alternative models, it has been suggested that softening the matrix—ensuring native perennials are used as pasture grasses, coarse woody debris is left on the ground, tussocks are allowed to develop to provide structural complexity, etc.—could make the matrix more likely to be occupied and used for dispersal. Testing for the effectiveness of stepping stones, particularly at providing habitat, is partly addressing these alternative landscape models. But very few empirical studies have been designed or described with these alternative models in mind. It is possible that studies included in the review were actually conducted in landscapes that match a variegated or continuum model much better than a patch-matrix model, but authors failed to sufficiently describe the landscape in those terms. Alternatively, it is possible that most empirical studies are conducted in landscapes that match the patch-matrix model because it is easier to design studies in these types of landscapes, even though they may not be representative. Either way, there is a need for empirical studies to evaluate the role of structural connectivity in less binary landscapes (Radford and Bennett 2007).

***Metapopulation dynamic context*:** From early conceptual development, it was never envisioned that structural connectivity would be helpful regardless of what was being connected. It is not a solution to habitat fragmentation in and of itself, but metapopulation theory suggests it should work given the right population dynamic context. Structural connectivity is thought to be a way to connect *a sufficient number* of patches, which are each *of sufficient size and quality* to support populations that are each viable in the short term (but not the long term), with the end result being a functioning rescue-effect metapopulation or a patchy population that should be viable in the long term (Wilson and Lindenmayer 1995; Bennett 1998; Verboom and Pouwels 2004; Hilty et al. 2006). But empirically testing this whole concept—testing whether each of these different components of a functioning metapopulation is present or not and whether that influences the effectiveness of structural connectivity—is a daunting task. As a simpler surrogate, researchers have suggested that the effectiveness of structural connectivity should be tested in landscapes with different patch sizes or different proportions of remaining native vegetation. At some threshold value of increasing patch size, populations that are large enough to be viable in the long term will be contained *within* patches so metapopulations become unnecessary. Similarly at sufficiently high levels of habitat extent, structural connectivity will naturally exist due to lower levels of habitat loss and so metapopulations should already be functioning (Andren 1994; Radford and Bennett 2007). In this review, too few studies reported patch sizes or landscape cover of native vegetation and among those that did, there was too little variation to assess the influence of these variables, let alone whether these surrogates are actually related to metapopulation structure and function.

5.3.3 Limits to conclusions based on indirect measures of effective dispersal

Even when studies provided evidence of movement *per se*, rarely were these movements of dispersal-age individuals actively dispersing. Yet the primary function of structural connectivity is to facilitate dispersal, and it is possible that species require different types of structural connectivity specifically for dispersal movements. We were occasionally able to model life-history stage in our analyses, to see whether effectiveness of connectivity differed depending on whether the subject was likely to be a disperser or not. But in general, there was insufficient variation in the data to analyse dispersal movements in particular compared to foraging or other types of movements. Not only was evidence for movement rarely targeted to dispersers, it was also usually indirect or partial, so the conclusion that movement occurred through structural connectivity was reliant on untested assumptions (see **3.4.2 Direct and indirect measures of dispersal**). And finally, movement data were rarely accompanied by assessments of subsequent reproduction (either observational or via genetic data), so any contribution to the gene pool in the settlement patch, the ultimate aim, remained unknown.

6. Reviewers' Conclusions

6.1 Implications for research

6.1.1 Imbalance in connectivity research to date

The findings of this review have major implications for research into the relationship between structural and functional connectivity (i.e., between landscape structure and the movement of organisms and their genetic material across landscapes). Many of these implications arise from knowledge or research gaps identified, but also from the way the review process has forced us to refine and focus the critical questions and hypotheses about connectivity. Much of the research that is perceived as being relevant to understanding connectivity is really about understanding the effects of fragmentation, and while fragmentation and connectivity are closely related phenomena, they are not the same thing. The majority of this previous research has involved using various survey techniques to identify ecological patterns related to fragmentation (e.g., patterns of patch occupancy or relative densities of different species in various landscape elements). These sorts of studies have played a critical role in identifying and characterising the negative effects of habitat fragmentation and patch isolation on populations of native species. However, it is notoriously difficult to infer ecological processes from ecological pattern, and if we wish to address the problem of fragmentation then we must focus more effort on understanding the processes of animal movement that ultimately determine the degree of functional connectivity in a given landscape.

Of the studies included in the review, 68% yielded data on presence in connectivity while only 44% provided data on movement processes (either directly observed or indirectly inferred). However, presence in connectivity data from any given study typically encompassed a moderate to large number of different species while studies with movement data generally focused on only one or at most a few species. Thus, at the species level 94% of data that could be extracted for the review were on presence in connectivity and thus could only address the question of whether the connectivity was providing habitat. Less than 6% of the data characterised known or inferred movements and were thus relevant to assessing the primary function of structural connectivity.

We suspect that this imbalance is due, at least in part, to the increasingly widely held attitude (among many researchers, land managers, and funding bodies) that, to properly inform natural resource management decisions, research must occur at large scales and on large numbers of species – ideally on entire communities or ecosystems. However, we believe that an understanding of the processes of animal movement, dispersal behaviour and the dispersal of pollen and seeds, particularly at large scales, must be built from studies of individual species, which is the level organisation at which these processes occur. Just as the success of modern medicine has been built on a thorough understanding of how individual cells, organs and elements of the immune system function with the ultimate aim of ensuring the health of the entire body, the management of functional connectivity at whatever scale must be fundamentally based on a sound understanding of how different species move through and respond to varying forms of structural connectivity with the ultimate aim of ensuring the health of the entire ecosystem. Broader scale research on communities and ecosystems at landscape scales will then allow exploration of emergent properties at these larger scales.

6.1.2 Redressing the imbalance

If real progress in understanding the relationship between structural and functional connectivity is to be achieved then the imbalance described in the previous section must be redressed. We must recognise that corridors and other landscape elements can provide either habitat or conduits for movement (or both or neither), and that these two potential functions of structural connectivity may be independent of each other with very different factors influencing each of them (see Box 1). This review shows clearly that most research to date has really addressed the "corridors as habitat" function without always recognising that such data on their own tell us relatively little about functional connectivity in a metapopulation context. Furthermore, our analyses of data on presence in connectivity (i.e., addressing the connectivity-as-habitat function) often produced very different results than analyses of data on movement, underscoring the independence of these two potential functions of structural connectivity.

Functional connectivity is fundamentally determined by the interactions between structural connectivity (the various features of the landscape that can potentially facilitate movement of native species through the matrix) and the dispersal behaviours (and other movement behaviours) exhibited by different species (Belisle 2005; Chetkiewicz et al. 2006). Therefore, if our currently crude understanding of functional connectivity is to improve, then research must focus on both variation in landscape features and on how this variation influences the movements and gene flow of native species. Furthermore, this research must feature appropriate replication, reasonably large sample sizes, and above all an appropriate comparative framework, as has been previously emphasised (Nicholls and Margules 1991; Inglis and Underwood 1992). In fact, a variety of elements of functional connectivity (not just continuous corridors) should be replicated and, as much as possible, entire landscapes should be replicated to facilitate valid inference regarding the effects of variation in aspects of structural connectivity on the resulting functional connectivity of landscapes.

6.1.3 Focus on movement paths and movement rates of dispersers

While previous authors have provided similar recommendations about experimental design, there has been relatively little discussion in the literature about the appropriate response variables or outcomes to quantify. Given that a primary goal of managing connectivity is generally to create rescue-effect metapopulations or patchy populations (rather than source-sink or extinction-recolonisation systems) and that these functions are dependent on sufficient movement of individuals and/or their genes, much more research should be specifically focused on direct observation and quantification of animal movement as a response to variation in structural connectivity. As discussed above (see **3.4.2 Direct and indirect measures of dispersal**), the best movement data in terms of understanding functional connectivity must describe the precise movement paths followed by individuals moving between patches. Therefore, whenever practicable, studies should utilise radiotelemetry or other techniques that can be used to reveal these paths, allowing accurate and precise determination of the relative use of different elements of structural connectivity. Doerr & Doerr (2005) provide a number of relevant recommendations for studying and characterising dispersal movement paths.

Methods such as capture-mark-recapture and genetic assignment tests have the potential to identify movements at various scales, but reveal no information about movement paths and thus use of elements of structural connectivity can only be inferred. Where such methods are to be employed, we recommend greater sample sizes and more replication of landscapes with and without structural connectivity to increase the power of inferences regarding the use of these elements.

Studies of interpatch and other larger-scale movements will make efficient use of their limited resources to the extent that they can target individuals most likely to make such movements. For the majority of animal species, these will be pre-breeding natal dispersers and a further advantage of radiotelemetry is that it allows data collection effort to be concentrated efficiently on such target individuals. Quantitative comparisons of movement in different landscapes will probably be best accomplished using some form of movement rate such as the proportion of individual dispersers living in a pair of patches that successfully cross to the other patch, or by calculating preferences for different elements of structural connectivity based on usage of those elements corrected for their relative availability.

6.1.4 Focus on thresholds

If new research on movement through structural connectivity is to provide meaningful guidance for managers, then far more attention must be given to determining the critical threshold distances that represent key transitions in the decision rules governing dispersal behaviour of native species. As described above, we believe that the two key thresholds will be the gap-crossing threshold, which represents the maximum distance an individual will move through the hostile matrix to travel from one patch or element of structural connectivity to reach another patch or bit of connectivity, and the interpatch distance threshold, which describes the maximum distance an individual will travel between patches (through matrix as well as through various elements of structural connectivity). Gap-crossing thresholds have been widely incorporated into a variety of types of spatially explicit models that are already being used to estimate current functional connectivity of landscapes and to predict future connectivity under different scenarios, but the estimates currently in use are based on very little empirical data. We are introducing the concept of interpatch distance threshold largely to accommodate the increasing evidence that many species use some form of foray-based search strategy during dispersal (Conradt et al. 2001; Conradt et al. 2003; Doerr and Doerr 2005), and thus may be unwilling to move long distances between patches even if they are connected by continuous corridors. Much more research that assesses these threshold distances for Australian native species is urgently required if efforts to model, protect and restore functional connectivity across Australian landscapes are to have real impact.

6.1.5 Better characterisation of landscapes and structural connectivity

Even if researchers record the movement paths of long-distance dispersers with perfect precision, their data will be meaningless if not combined with detailed characterisation of the nature, location and extent of structural connectivity in the landscape. In this regard, it is crucial that we look beyond our recent obsession with continuous corridors and consider all forms of structural connectivity as potentially providing functional connectivity. The exploratory analyses contained in this review suggest that stepping stones in particular deserve greater attention and it is worth noting that nearly half of the data on the use of stepping stones analysed in this review were from areas identified by the authors of the studies as empty paddock (i.e., matrix) and it was only by examining these study areas on Google Earth that we identified them as paddocks containing substantial numbers of paddock trees (i.e., stepping stones). Researchers interested in functional connectivity must be prepared to find it in unlikely places and should pay attention to the presence not only of scattered paddock trees but also to scattered shrubs, tussock grasses, coarse woody debris, boulders and any other features that may provide havens for rest and refuge within the matrix. Efforts should be made to characterise not only location and extent of these various forms of structural connectivity but also variation within them including factors that may reflect their relative quality (e.g., structural complexity, width of corridors, density of paddock trees or other stepping stones, etc). We also need to be willing to appreciate the matrix as something other than a unitary, unvaryingly “hostile” feature of a landscape. This may involve moving beyond simple binary patch-matrix models to consider the shades-of-grey landscapes envisioned by alternative frameworks such as variegated landscape models and continuum models (see Radford and Bennett 2007).

6.1.6 Other gaps in previous research

We noted a number of research gaps as revealed through the course of our exploratory analyses. For example, one such gap was research on the effectiveness of structural connectivity consisting of revegetated areas relative to that consisting of remnant vegetation. Previous research on the relationship between structural and functional connectivity has also tended to neglect certain taxonomic groups, with reptiles, invertebrates and particularly plants being under-represented. Although we are advocating a new wave of research focused more explicitly on movement paths and distance thresholds in the context of well-characterised replicated landscapes containing a variety of structural connectivity, it is important to be aware of these gaps in previous work. Where gaps have emerged in past research, they are probably likely to emerge again, so we recommend that research effort be spread across all taxonomic groups. Similarly, revegetated landscape features must not be ignored by future research, so that we can begin to understand the time frames required if we wish to improve functional connectivity by planting native vegetation in whatever configurations.

6.1.7 Effective dispersal and the importance of genetic studies

Genetic analyses have an important role to play in connectivity research. No study provided "gold-standard" evidence of effective dispersal (see Section 3.4.2 above) because the few studies that provided data on detailed movement paths did not continue monitoring dispersers beyond settlement and carry out genetic parentage analyses or population genetic analyses to document gene flow. Continuing improvements to genetic assignment tests (which identify likely dispersers by assigning them, with varying degrees of confidence, to their patch of origin) provide a powerful tool for identifying dispersal events over potentially very long distances, whereas following dispersers over very long distances clearly presents challenges for methods like radiotelemetry. We suggest that whenever possible studies should adopt a combined approach and attempt to link direct observations of movement with genetic data analyses.

In addition, interpatch dispersal of genes over multiple generations may be important for many species, particularly for plants, and population genetic data may be the only way to establish such multi-generational gene flow. Despite the voluminous data documenting the presence of species in elements of structural connectivity, evidence for multi-generational dispersal through these features was sparse. It is clear that presence in connectivity does not always guarantee gene flow, due to sink population dynamics and/or social and competitive limits on dispersal behaviour (Wilson and Lindenmayer 1995; Horskins et al. 2006). Additional research documenting presence in corridors (or other connectivity elements) will be of little value in furthering our understanding of functional connectivity unless it also examines the population dynamics within and gene flow through the corridor. Such analyses will provide crucial information about the factors influencing multi-generational dispersal via various elements of structural connectivity and about the relative importance of multi-generational versus single-generation dispersal.

Despite the importance of population genetic data in establishing effective dispersal, particularly over multiple generations, and the apparent wealth of genetic studies in ecology, it seems surprising that only three genetic studies were included in the review (Banks et al. 2005; Driscoll and Hardy 2005; Horskins et al. 2006). Many genetic studies were rejected because they lacked proper comparators to address the review questions, often consisting of only a single fragmented landscape or comparing such a landscape to a single large continuous area of habitat. Such comparisons allow inference about the effects of isolation, but not of connectivity. Most other genetic studies were rejected because they lacked sufficient information about the study landscapes. We suspect that this was a particular problem for genetic studies because they tended to be carried out across a larger spatial scale than most other studies, making it less likely that the authors would characterise the structural connectivity between distant patches in any detail, and also making it harder for the reviewers to identify patches and structural connectivity using Google Earth. For population genetic data to properly inform management and restoration of structural connectivity, studies must adopt an appropriate scale (e.g., be conducted using adjacent patches) and carefully characterise replicate landscapes in terms of the variety of landscape elements present.

6.1.8 Final thoughts

The results of this review do at least clearly demonstrate that the answer to our primary question is "yes" – structural connectivity does generally provide for functional connectivity. Or to state this as an even simpler conclusion: the presence of vegetation generally facilitates the presence and the movements of native species. This is hardly earth-shattering, but we suggest that it should mean an end to studies investigating the presence or movements of species in unusually simplified landscapes. If one compares movement between two completely isolated patches and two patches connected by a corridor then one can be fairly confident that there will be more movement between the connected patches for most species, but corridors are not the only possible solution to the problem of habitat fragmentation. Structural connectivity comes in many forms and future research must begin to compare the effectiveness of these different forms in different contexts under varying conditions and for diverse taxonomic groups.

6.2 Implications for management and policy

Given the fact that clear information is still lacking about many aspects of connectivity, and that analyses presented in this review were exploratory and frequently limited by a lack of data, it is not possible to set firm rules for the management and restoration of structural connectivity throughout Australia. However, as millions of dollars worth of management and restoration of connectivity are already occurring, there is a strong need for any small amount of information that might make structural connectivity more cost-effective. Based on the results of this review, it is possible to devise evidence-based guidelines rather than rules or prescriptions. These guidelines must be incorporated into an adaptive management framework, with explicit recognition that further research must be funded and exact prescriptions may change as new information becomes available, particularly on corridor widths and potential sink population dynamics when connections are functioning as habitat.

GUIDELINES FOR MANAGING & RESTORING STRUCTURAL CONNECTIVITY

These guidelines can be used by anyone wishing to plan and undertake on-ground works to improve the health of natural ecosystems, regional funding bodies wishing to evaluate the likely environmental benefits of applications they receive for incentive funding, and policy-makers working to design incentive schemes, offset programs, and management regulations. It must be stressed that most of the data on which these recommendations are based come from studies of mammals and birds living in woodland and forest ecosystems. These guidelines should thus be most applicable in similar systems and applied more broadly only with caution.

STEP 1: Evaluate the landscape context to see if connectivity management and restoration is appropriate

Structural connectivity is best protected and restored where there are multiple patches of a particular ecosystem type that are still of some minimum size and that aren't too far apart. Ask the following questions about a landscape that is a candidate for connectivity restoration:

- Are there multiple patches of the ecosystem in question that are at least 10-20ha in size?
- Are those patches reasonable quality examples of the ecosystem, rather than severely degraded?
- Are those patches no more than 1.1km apart?

If the answers to all the above questions are yes, move on to Step 2. If an answer to any one of the above questions is no, focus on creating the above conditions by restoring ***patches*** of native vegetation/habitat and improving their quality (rather than restoring connectivity) and/or find another landscape in which to manage and restore connectivity.

(Side note: This does not mean that any existing structural connectivity that does not meet these conditions should be abandoned or not managed. For example, many travelling stock reserves are frequently talked about as "corridors" but they do not meet the above conditions. In these situations, there is probably much more benefit to be gained by managing these areas ***as patches***, rather than as connectivity, and thus focusing on increasing their size, reducing the proportion of edge habitat, and improving habitat/vegetation quality.)

STEP 2: Consider the types of structural connectivity that are likely to function appropriately, given your goals and local environment

Some thought is required at this stage about what functions are desired from the connectivity—is it sufficient for it to facilitate movement (the primary goal of structural connectivity) or must it also provide habitat (a secondary goal)? Habitat may be a desired function based on tourism or public perception issues, or for ensuring the provision of some ecosystem services (like pollination) throughout a landscape, but the costs of providing enough structural connectivity to serve this function may be much larger than if movement is the only desired function.

In both temperate and tropical environments when the desired function is movement (but not necessarily the provision of habitat):

Stepping stones (such as scattered paddock trees) may be the best choice. Ensure that:

- gaps between them are no more than ~100m
- consider trying to provide stepping stones that are more than just scattered trees—include scattered shrubs, logs on the ground, and even small rocky areas

Corridors can also work (and possibly also disconnected linear elements—basically corridors with gaps that don't connect directly to patches). Remember that:

- width is not as important a factor as the distance between patches being connected (see Step 1 above)

In tropical environments when the desired function is provision of habitat as well as movement:

Disconnected linear elements may be the best choice. However, it is unclear why they appeared to be better than corridors. It may be that tropical disconnected linear elements tend to be much wider than tropical corridors (an interaction we were unable to test), so this requires further investigation. Regardless of whether disconnected linear elements or corridors are used, ensure that:

- they are as wide as possible, at least 80m (but keep in mind that recent research on edge effects suggests that 350m may be the true minimum width)
- gaps within them or between them and patches are no more than ~100m
- principles for ensuring high quality vegetation/habitat for the ecosystem in question are applied to the corridors and linear elements just as much as to the patches

In temperate environments when the desired function is provision of habitat as well as movement:
Corridors may be the best choice. Remember that:

- width may not be as important as the distance between patches being connected (see Step 1 above), but the risk of establishing population sinks is currently unknown so use a precautionary principle—as wide as possible, keeping in mind that recent research on edge effects suggests that 350m may be the true minimum width
- principles for ensuring high quality vegetation/habitat for the ecosystem in question should be applied to the corridors just as much as to the patches

Disconnected linear elements can also work. Remember that:

- the same principles as above for corridors should apply
- gaps within them or between them and patches should be no more than ~100m

Stepping stones are not necessarily the best choice for providing habitat for species that normally reside in denser patches. However:

- stepping stones such as scattered paddock trees may actually be providing critical habitat specifically for open woodland species; thus, they should be managed ***as patches*** for that particular ecosystem type
- such open woodland patches could then secondarily facilitate movement (but not provide habitat) for species that are specialists on the denser patches in the landscape, so see above for characteristics they need to possess

STEP 3: Given the options above depending on environment and desired functions for structural connectivity, select which option to pursue by considering costs and other benefits desired in the landscape
For most of the function-environment combinations discussed above, there are still a few options for the type of structural connectivity that could be effective. Deciding between those options will largely depend on their relative costs, any constraints that exist in the landscape that may make some options difficult to implement, and any other benefits the different options might provide.

For example, a wide corridor may be significantly more costly to restore, while stepping stones may be less costly and easier to integrate with pasture production (and thus more acceptable to private land owners). Yet stepping stones are likely to be more difficult to implement and maintain in cropping areas compared to grazing or mixed systems. Where drainage lines exist in the system in between patches, corridors or disconnected linear elements might be preferred where possible, because they could also serve to control erosion and restore proper hydrodynamic processes. Any type of revegetation or regeneration may be more difficult to achieve in areas with a history of fertiliser applications. In these areas, corridors or disconnected linear elements may be preferred because they would cover a smaller total area than stepping stones, and thus fertiliser use could still occur over a larger production area. Alternatively, given the cost of fertiliser, landowners may prefer stepping stones to maximise ecosystem services and achieve success with lower-input farming practices.

A complete review of these additional considerations would be helpful, but is beyond the scope of this review. However, many of the costs and additional benefits of structural connectivity will be quite site-specific due to different physical features of the landscape, management histories, and landowner values and goals. Thus, some decision-making within the boundaries framed by the options above will always be required.

STEP 4: Monitor the results of connectivity management actions and be prepared to adjust management activities as new information becomes available
The guidelines presented here are based on a very small number of studies that truly assessed movement in fragmented landscapes – many more are needed. Thus, it is particularly helpful if connectivity management and restoration programs can be designed from the beginning to incorporate replicated monitoring efforts with appropriate controls. While most managers may lack the resources to directly study movement of native species themselves, they can link with researchers to ensure management actions are applied in an experimental framework, with replication and controls, and to publish findings and thus make them widely available to other managers and researchers. Recommended management actions can then be revised based on data from this ongoing monitoring as well as new research performed elsewhere, ensuring that functional connectivity is truly managed using an adaptive management approach.

Additional Considerations:
These guidelines are designed based on very general analyses, to help as many species as possible with one set of actions, but they will not necessarily be successful for all species. Invariably, a number of species will still be unwilling to disperse using these forms of structural connectivity and will remain isolated and more vulnerable to extinction. The analyses and summary statistics presented here suggest that some species (e.g., reptiles) may be particularly likely to remain at risk. Thus, additional actions will be required if the needs of these species are to be met. In some cases, this may be as simple as remembering to apply these guidelines to multiple ecosystem types in a region, rather than just the woodland or forest systems that are often easier for people to see and identify with. In other cases, such as for endangered species with unique ecologies, additional actions may need to be based on detailed species-specific research.

Final Policy Note:

> One of the challenges that the issue of connectivity presents for integrating science and policy is that the details matter when it comes to connectivity. Relatively small and not always intuitive differences in structural connectivity can mean the difference between something that helps many small patches function appropriately and remain healthy vs. something that provides no benefit or may even cause accelerated declines in adjacent patches if it serves as a population sink. Unfortunately, it can be very difficult to design policy that effectively incorporates fine ecological detail. Thus, there is an imperative for policy makers and scientists to come together to develop policy that works, from both political and ecological perspectives.

7. Acknowledgements

We would like to thank all the stakeholders and colleagues who provided constructive comments on the review protocol, helping to shape it into a much better review, particularly the following people who provided the most extensive comments: Jerry Alexander (Department of Sustainability and Environment, Victoria), Andrew Bennett (Deakin University), David Carr & David Freudenberger (Greening Australia), Don Driscoll & Joern Fischer (Australian National University), Donna Hazell (Southern Rivers Catchment Management Authority), Jim Radford (Bush Heritage Trust), Doug Robinson (Trust for Nature), and Mark Sheahan & Robert Taylor (New South Wales Department of Environment and Climate Change (DECC)). We will be forever grateful to the Library and Document Delivery staff at CSIRO (particularly Wendy Hirst, Trudi Prideaux, and Anne Towill) who helped us structure our searches, identify all possible relevant databases, and most importantly helped us acquire hundreds of sources quickly and efficiently. Thanks also to the university libraries and academic departments we contacted, and to Greg Lollback and Gary Howling from DECC, who helped us search for and acquire theses and other sources in the grey literature. We are grateful to Gavin Stewart and Andrew Pullin of the Centre for Evidence-based Conservation for being ready and willing to provide support whenever we needed it.

8. Potential Conflicts of Interest and Sources of Support

There are no conflicts of interest to declare. This systematic review was funded by Land & Water Australia (LWA) and the Commonwealth Scientific and Industrial Research Organisation (CSIRO).

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10. Appendices

Appendix A – Glossary of terminology **

Structural Connectivity – habitat features in a fragmented or heterogeneous landscape that physically link other features, especially when they link discrete areas of habitat occupied by a particular species or community (e.g., patches)

Functional Connectivity – the degree to which organisms actually move through the landscape, especially between discrete areas of occupied habitat (e.g., patches) and especially for dispersal & gene flow

Connectivity – we adopt the definition of landscape connectivity first proposed by Taylor et al. (1993), who defined it as "the degree to which the landscape facilitates or impedes movement among resource patches"; thus, a landscape with high connectivity is one that provides functional connectivity regardless of what it looks like in terms of structural connectivity

Dispersal – movement of organisms or propagules that may potentially result in gene flow, including the movement of individuals from their place of birth to the site of their first breeding (natal dispersal), movement from one breeding site to another breeding site (breeding dispersal), movement of seeds (seed dispersal), and movement of pollen (pollen dispersal)

Effective dispersal – occurs when dispersal movements result in actual gene flow (e.g., natal dispersal followed by successful reproduction, seed dispersal followed by successful establishment and reproduction, etc.)

Patch – a discrete area of habitat occupied by a species, surrounded by areas not occupied by that species that are known or thought to be unsuitable as habitat (e.g., matrix); note therefore that a patch may not be clearly observable in a structural sense to researchers, and thus this definition of patch is compatible with landscape models such as the variegated model and continuum model as well as the patch-matrix model

Matrix – unoccupied region, thought or known to be unsuitable as habitat, surrounding patches of suitable habitat

Habitat – a place suitable for survival and/or reproduction of a particular plant or animal species; note that structural connectivity could thus be used by a species for dispersal, but not considered habitat

Corridor – a landscape element that connects two or more patches in a relatively unbroken (contiguous) line; thus, a form of structural connectivity

Disconnected Linear Element – a landscape element that is located between patches that is relatively linear in shape but which does not physically connect patches because it contains gaps and/or does not actually adjoin patches; thus, a form of structural connectivity

Stepping stone – a landscape element that is located between patches but does not adjoin patches and is one of a series of such disconnected elements (e.g., scattered trees in pasture or crop); thus, a form of structural connectivity

Gap-crossing – movement across matrix (e.g., from a patch to a stepping stone). Gap-crossing studies have typically involved experimental translocation of individuals across gaps and observing their behaviour after release, or audio playback of species-specific calls to attempt to lure individuals across gaps.

** Note: ALL of these terms are likely to be species specific (i.e., what is suitable habitat for one species is not for another), but an overarching goal of the review is to uncover general principles in how the *landscape structure* of habitat influences functional connectivity.

Appendix B – Variables extracted and brief explanation

ShortReference: the parenthetical reference for the source

Locality: description of the region of Australia in which the study was conducted (e.g., the Kellerberrin/SW sheep-wheat belt, southern coast forests, etc.)

CommonName: a common name for the species in question (note: may be just a broad taxonomic group if that is as detailed as the study is)

LatinName: the scientific name of the species (or species group) in question

SpeciesType: a code specifying whether it is a bird, mammal, reptile, invertebrate, plant pollen or plant seed

LHistoryStage: a code specifying whether the individuals included in the study were the correct life-history stage to be dispersers (natal) or not (or unknown)

Spec/General: a code specifying whether the species specialises on the habitat type of patches (see below), or whether the species can inhabit the matrix habitat, at least in part

Scale: a code specifying the scale of the total area of an individual's normal home range (m^2, ha, km^2)

Dispersiveness: a code specifying whether the species is sedentary (i.e., a year-round resident), or whether it is nomadic or migratory, or wind-dispersed or animal-dispersed for seeds and pollen

Social: a code specifying whether the species can regularly, at some time of the year, be found living in groups

DispMethod: a code specifying whether the species uses aerial or terrestrial locomotion *during dispersal*, or is volant (i.e., glides in the air)

PatchType: a code specifying the general type of ecosystem that patches or occupied areas of the landscape contain (temperate woodland, temperate forest, temperate grassland, tropical forest, tropical savannah, or rocky habitats/boulder fields)

MatrixType: a code specifying the general type of ecosystem present in the less or non-occupied areas of the landscape (native pasture/grassland, improved/exotic pasture, crop, any mix of those three, woody but non-habitat for the species, rocky habitats, or built environments (roads, urban))

PatchSize: either the mean or midpoint of the range (where mean not provided) of patches/occupied areas of habitat, expressed in hectares

LscapeCover: % of the landscape still covered in original native ecosystem type

LCComp: a code specifying the habitat type of the structural connectivity present in the less connected landscape(s) (woodland, forest, grassland, riparian, trees only, shrubs only, rocky/boulders, logs & other structures, built structures (tunnels, ropes), or not applicable/no structural connectivity)

LCAge: a code specifying whether the structural connectivity in the less connected landscape(s) is remnant, regenerated habitat, or revegetated/built

LCType: a code specifying whether the structural connectivity in the less connected landscape(s) is predominantly corridors, disconnected linear elements, or stepping stones (including scattered trees)

LCMinDist: the minimum distance between patches in the less connected landscape(s) in metres

LCMaxDist: the maximum distance between patches in the less connected landscape(s) in metres

LCMeanDist: the mean distance between patches in the less connected landscape(s) in metres

LCWidth: mean or midpoint of the range (where mean not provided) of the width of any structural connectivity in the less connected landscape(s) in metres

LCDensity: between 0 and 1—representing the relative vegetation density of any structural connectivity in the less connected landscape(s) compared to patches. If the structural connectivity is just as dense as the patches, this will be 1. If it is half as dense, it will be 0.5, etc.

LCOccupied: a code specifying yes or no, depending on whether any structural connectivity in the less connected landscape(s) is occupied by the species in question or not

MCComp: a code specifying the habitat type of the structural connectivity present in the more connected landscape(s) (woodland, forest, grassland, riparian, trees only, shrubs only, rocky/boulders, logs & other structures, built structures (tunnels, ropes), or not applicable/no structural connectivity)

MCAge: a code specifying whether the structural connectivity in the more connected landscape(s) is remnant, regenerated habitat, or revegetated/built

MCType: a code specifying whether the structural connectivity in the more connected landscape(s) is predominantly corridors, disconnected linear elements, or stepping stones (including scattered trees)

MCMinDist: the minimum distance between patches in the more connected landscape(s) in metres

MCMaxDist: the maximum distance between patches in the more connected landscape(s) in metres

MCMeanDist: the mean distance between patches in the more connected landscape(s) in metres

MCWidth: mean or midpoint of the range (where mean not provided) of the width of any structural connectivity in the more connected landscape(s) in metres

MCDensity: between 0 and 1—representing the relative vegetation density of any structural connectivity in the more connected landscape(s) compared to patches. If the structural connectivity is just as dense as the patches, this will be 1. If it is half as dense, it will be 0.5, etc.

MCOccupied: a code specifying yes or no, depending on whether structural connectivity in the more connected landscape(s) is occupied by the species in question or not

MvmtLC: a code specifying yes or no, depending on whether the study shows any evidence of between-patch movements in the less connected landscape(s)

RateLC: any kind of quantitative measure of movement in the less connected landscape(s) (e.g., density of individuals present in the connection, proportion of individuals that moved, F_{ST}, etc.)

SE_LC: if the above measure is a mean, the standard error of that mean

MaxDistLC: the maximum distance between patches in the less connected landscape(s) that individuals moved or are inferred to have moved, in metres

MvmtMC: a code specifying yes or no, depending on whether the study shows any evidence of between-patch movements in the more connected landscape(s)

RateMC: any kind of quantitative measure of movement in the more connected landscape(s) (e.g., density of individuals present in the connection, proportion of individuals that moved, F_{ST}, etc.)

SE_MC: if the above measure is a mean, the standard error of that mean

MaxDistMC: the maximum distance between patches in the more connected landscape(s) that individuals moved or are inferred to have moved, in metres

UnitsForRates: description of what the rate numbers are (e.g., density of individuals present in the connection, proportion of individuals that moved, F_{ST}, etc.)

Purpose: a code specifying what the purpose of the movements was (daily foraging, dispersal, migration or nomadic movements, induced via translocation or baiting, or unknown)

MaxGapCrossed: the maximum distance a species can cross matrix between elements of structural connectivity (as opposed to between patches), in metres (Note: this is only available for studies that quantify a fairly large amount of movement, and have a maximum gap crossing distance clearly smaller than the maximum possible in the landscape—i.e., it is difficult to identify true maxima.)

MinGapCrossed: the minimum maximum—the maximum observed distance a species crossed matrix between elements of structural connectivity (as opposed to between patches), in metres, where an insufficient amount of data were collected to identify a true maximum

MeanGapsCrossed: the mean distance a species was observed to cross matrix between elements of structural connectivity (as opposed to between patches), in metres

SEGapsCrossed: standard error of the above mean

ReferenceType: a code specifying whether the reference is a published, peer-reviewed source or whether it is a thesis or otherwise in the grey literature

QualityScore1: a code specifying the design of the study (see Table 1)

QualityScore2: a code specifying how close the study came to quantifying movement directly versus inferring it indirectly (see Table 2)

Notes: other information about the structure of the study that might make it unusual or help clarify structure of the less and more connected landscapes

APPENDIX C – Portion of data extraction form

(Page 1 of 4 for the same set of sources; grey areas indicate information was not available or no less connected landscape was studied))

ShortReference	Locality	CommonName	LatinName	SpeciesType	LHistoryStage	Spec/General	Scale	Dispersiveness
Arnold & Weeldenburg 1990	Kellerberrin, WA	Crested Pigeon	*Ocyphaps lophotes*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Galah	*Cacatua roseicapilla*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Australian Magpie	*Gymnorhina tibicen*	B	N	G	H	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Magpie-lark	*Grallina cyanoleuca*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Australian Raven	*Corvus coronoides*	B	N	G	K	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Australian Ringneck	*Barnardius zonarius*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Mulga Parrot	*Psephotus varius*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Black-faced Woodswallow	*Artamus cinereus*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	White-browed Babbler	*Pomatostomus superciliosus*	B	N	S	H	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	White-fronted Chat	*Ephthianura albifrons*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Yellow-throated Miner	*Manorina flavigula*	B	N	S	H	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Singing Honeyeater	*Lichenostomus virescens*	B	N	S		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Grey Shrike-thrush	*Colluricincla harmonica*	B	N	S	H	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Rufous Whistler	*Pachycephala rufiventris*	B	N	S	H	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Willie Wagtail	*Rhipidura leucophrys*	B	N	G	H	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Grey Fantail	*Rhipidura fuliginosa*	B	N	S		M
Arnold & Weeldenburg 1990	Kellerberrin, WA	Red-capped Robin	*Petroica goodenovii*	B	N	S	H	S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Inland Thornbill	*Acanthiza apicalis*	B	N	S		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*	B	N	G		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Chestnut-rumped Thornbill	*Acanthiza uropygialis*	B	N	S		S
Arnold & Weeldenburg 1990	Kellerberrin, WA	Weebill	*Smicrornis brevirostris*	B	N	S	H	S
Arnold et al. 1991	Kellerberrin, WA	kangaroo (2 species)	*Macropus spp.*	M	N	G	K	S
Arnold et al. 1991	Kellerberrin, WA	Western grey kangaroo	*Macropus fuliginosus*	M	N	G	K	S
Arnold et al. 1991, 1993	Kellerberrin, WA	Euro	*Macropus robustus*	M	N	G	K	S
Arnold et al. 1993	Kellerberrin, WA	Euro	*Macropus robustus*	M	D	G	K	S
Arnold et al. 1993	Kellerberrin, WA	Euro	*Macropus robustus*	M	N	G	K	S
Banks et al. 2005b	mtn slope forests, NSW	Agile Antechinus	*Antechinus agilis*	M	N	S	H	S
Bennett 1988, 1990	southern forests, VIC	Short-beaked Echidna	*Tachyglossus aculeatus*	M	N	G	H	S
Bennett 1988, 1990	southern forests, VIC	Koala	*Phascolarctos cinereus*	M	N	S	H	S
Bennett 1988, 1990	southern forests, VIC	Sugar Glider	*Petaurus breviceps*	M	N	S		S
Bennett 1988, 1990	southern forests, VIC	Common Ringtail Possum	*Pseudocheirus peregrinus*	M	N	G		S

(Page 2 of 4 for the same set of sources)

Social	DispMethod	PatchType	MatrixType	PatchSize	LscapeCover	LCComp	LCAge	LCType	LCMinDist	LCMaxDist	LCMeanDist	LCWidth	LCDensity	LCOccupied
Y	A	W	M		10									
Y	A	W	M		10									
Y	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
Y	A	W	M		10									
Y	A	W	M		10									
Y	A	W	M		10									
Y	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
N	A	W	M		10									
Y	A	W	M		10									
Y	A	W	M		10									
Y	A	W	M		10									
Y	T	W	M	77	10	T	M	S	700	4700	1800		0.01	N
Y	T	W	M	77	10	W	M	C				30	0.3	N
Y	T	W	M	77	10	W	M	C				30	0.3	N
Y	T	W	M	77	10									
Y	T	W	M	74	10	T	M	S	50	2000	683		0.01	N
Y	T	F	W	30	2	NA	NA	NA	250	3000				N
N	T	F	M	41	10									
N	T	F	M	41	10									
Y	V	F	M	41	10									
N	T	F	M	41	10									

(Page 3 of 4 for the same set of sources)

MCComp	MCAge	MCType	MCMinDist	MCMaxDist	MCMeanDist	MCWidth	MCDensity	MCOccupied	MvmtLC	RateLC	SE_LC	MaxDistLC	MvmtMC	RateMC	SE_MC
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	1000	14000	7000	29	1	Y					Y		
W	M	C	200	5000	1600	30	0.75	Y	Y			4700	Y		
W	M	C	800	5200		30	0.75	Y	N	4.2			Y	8.01	
W	M	C	800	5200		30	0.75	Y	N	4.2			Y	8.01	
W	M	C	1300			30	0.75	Y					Y		
W	M	C	100	350	225	30	0.75	Y	Y			2000	Y		
I	M	C	250	3000		113	1	Y	Y	0.02		3000	Y	0.05	
F	M	C				18.5	1	Y					Y		
F	M	C				18.5	1	Y					Y		
F	M	C				18.5	1	Y					Y		
F	M	C				18.5	1	Y					Y		

(Page 4 of 4 for the same set of sources; final Notes column omitted)

MaxDistMC	UnitsForRates	Purpose	MaxGapCrossed	MinGapCrossed	MeanGapsCrossed	SEGapsCrossed	ReferenceType	QualityScore1	QualityScore2
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
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		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6
5000		U					P	3	3
5200	fecal pellets per 100m2	U					P	2	6
5200	fecal pellets per 100m2	U					P	2	6
14800		D					P	5	4
350		U					P	3	4
3000	r of genotypes	U					P	2	5
		U					P	5	6
		U					P	5	6
		U					P	5	6
		U					P	5	6

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