Population connectivity: recent advances and new perspectives

Johnathan T. Kool^{1,2 *†}, Atte Moilanen³, Eric A. Treml⁴

¹ARC Centre of Excellence for Coral Reef Studies
James Cook University, 10 Angus Smith Drive
Townsville, QLD Australia 4811
Tel: +61 7 4781 6134 Fax: +61 7 4781 3115
e-mail: johnathan.kool@jcu.edu.au

²Australian Institute of Marine Science
PMB 3, Townsville MC
Townsville, QLD Australia 4810

³Finnish Centre of Excellence in Metapopulation Biology
Department of Biosciences
P.O. Box 65 (Viikinkaari 1)
FI-00014 University of Helsinki, Finland

⁴Department of Zoology
University of Melbourne
Melbourne, VIC Australia 3010

*Corresponding Author

†Current address:

Geoscience Australia
Cnr Jerrabomberra Ave and Hindmarsh Drive
Symonston, ACT Australia 2609
Tel: +61 2 6249 5842 Fax: +61 2 6249 9920
e-mail: johnathan.kool@ga.gov.au

Abstract

Connectivity is a vital component of metapopulation and landscape ecology, influencing fundamental processes such as population dynamics, evolution, and community responses to climate change. Here, we review ongoing developments in connectivity science, providing perspectives on recent advances in identifying, quantifying, modelling and analysing connectivity, and highlight new applications for conservation. We also address ongoing challenges for connectivity research, explore opportunities for addressing them and highlight potential linkages with other fields of research. Continued development of connectivity science will provide insights into key aspects of ecology and the evolution of species, and will also contribute significantly towards achieving more effective conservation outcomes.

Introduction

Connectivity has rapidly grown into a field of great interest for scientists and conservation managers (Crooks and Sanjayan 2006; Claudet 2011; Liu et al. 2011; Rayfield et al. 2011; Luque et al. 2012). Connectivity research links a wide variety of subjects in ecology and evolution, including dispersal and migration (Baguette and Van Dyck 2007), the development of population genetic structure (Kool et al. 2011), source-sink dynamics (Figueira and Crowder 2006) and potential responses to climate change (Munday et al. 2009; Wasserman et al. 2012). Connectivity also affects conservation decisions involving aspects of reserve network design (Cerdeira et al. 2010), restoration (Raeymaekers et al. 2008), controlling invasive species (Hulme 2009), and administration of transboundary resources (Chester 2006; Treml and Halpin in press). Over time, perspectives on connectivity have evolved considerably, departing from the view that populations are uniformly distributed and

panmictic, towards a more nuanced notion of networks of patches and demes often engaged in self-replenishment, as well as dynamic and asymmetric exchanges. Yet, despite the attention connectivity has received, much work is still required in order to understand its underlying causes and consequences, and to incorporate our understanding of connectivity into operational management strategies. Although general reviews of population connectivity have appeared elsewhere (Crooks and Sanjayan 2006; Hilty et al. 2006; Cowen and Sponaugle 2009), we here focus on trends in connectivity research, highlight ongoing developments, technologies and applications, and discuss emerging challenges and opportunities.

Conceptualizing connectivity

Initially, connectivity was described in the terrestrial context as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). Over time however, different research perspectives and operational needs have led to alternative ways of defining connectivity [Panel 1]. For example, Piñeda *et al.* (2007) distinguish between transport, dispersal and connectivity in marine systems (connectivity being a function of transport, larval survival, settlement and post-larval survival), Pringle (2003) addresses the importance of hydrologic connectivity, and Lowe and Allendorf (2010) discuss aspects of demographic and genetic connectivity. A challenge in population connectivity research lies in defining what constitutes a population, subpopulation or patch, and in semi-continuous habitats, distinguishing patches may be difficult and/or counterproductive. Consequently connectivity, however defined, may vary greatly, depending not only on the abundance and density of individuals, but also on habitat characteristics and the spatial and temporal scales of interest. For example, low levels of exchange might not be

significant in a short-term demographic context, but might be vital for maintaining genetic diversity (Lowe and Allendorf 2010). Furthermore, population connectivity is not limited to the movement of individuals, but can also be defined according to gene flow (Hedgcock et al. 2007), or even more abstract concepts, such as the transfer of information or behaviour (Ahmad and Teredesai 2006).

Although population connectivity can be interpreted in different ways under different circumstances, the approaches share a fundamental property in common. In all cases, connectivity corresponds to a structured set of relationships between spatially and/or temporally distinct entities, or put another way - connectivity is the outcome of dependencies between populations or individuals. Exploring the nature of these dependencies and relationships, as well as the consequences of their form, is what underpins connectivity research.

Empirically quantifying population connectivity

Direct methods

A variety of different techniques have been used to directly measure connectivity between populations (Table I). Tracking organisms through field observation is the most basic means of evaluating population connectivity, but this can be challenging when monitoring large populations or broad spatial extents, particularly when the organisms being observed are small or cryptic. To address this difficulty, mark-recapture techniques have been used extensively in the past (Webster et al. 2002) and continue to be the primary means of assessing connectivity today (Jacobson and Peres-Neto 2010), providing estimates of population size and movement patterns, often in a habitat-specific context. For organisms

that are too small or fragile to carry physical tags, chemical-based analyses are often used (Rubenstein and Hobson 2004; Hobson 2008; Pauli et al. 2009; Durbec et al. 2010), particularly for aquatic populations. Researchers have been able to identify probable source populations based on chemical signatures present in otoliths and statoliths (sensory bones/stones found in fish and invertebrates respectively) (Thorrold et al. 2007; Woods et al. 2010), and more recently, artificial tagging techniques have been used to label and identify parents and progeny of marine species (Almany et al. 2007). Similar approaches have been used to study terrestrial mammal and bird populations (West et al. 2006; Newsome et al. 2007; Faaborg et al. 2010).

Recently, there has been a dramatic expansion in the ability to remotely monitor animal movements, physiological measurements and associated environmental data (biologging - Rutz and Hays 2009). Large quantities of data are becoming available from these efforts, and are proving invaluable for understanding animal migration, behaviour and ecology for many species at a greater level of detail and at a broader range of scales than previously possible. For example, pop-up satellite archival tags (PSATs) have been used to track large numbers of pelagic predators and sea turtles over extremely large distances (Rutz and Hays 2009). Radar technology is also now providing ways of comprehensively tracking large collections of small and delicate organisms such as butterflies (Ovaskainen et al. 2008c).

Major advances are also being made towards the development of large-scale, fine-grained sensor networks for monitoring animal movement (Porter et al. 2005; Borgman et al. 2007). Cameras and environmental sensors linked to wireless communication systems provide a means of automatically detecting fine-scale movement patterns in real time (Hamilton et al. 2007; Kays et al. 2009). These data can then be filtered and queried to identify and

summarize mass occurrences of movement events. These types of networks have been applied in terrestrial environments for monitoring tiger populations (Karanth et al. 2006), and are becoming increasingly prevalent in coastal and ocean systems as well (Martin Taylor 2009). Imaging systems are also being developed that are capable of capturing images of microscopic plankton (Cowen and Guigand 2008), which can then be processed using algorithms to identify species and characterize their spatial distribution within the water column (Tsechpenakis et al. 2007). Coupling these technologies with ocean sensing grids would provide an unprecedented opportunity to monitor the real-time spatial characteristics of connectivity in aquatic environments.

Connectivity studies have been greatly assisted by the extensive development of GIS and remote-sensing data, however obtaining comprehensive and simultaneous data with a high degree of resolution remains challenging, especially for features that are not highly visible. Further development of remote-sensing platforms will be necessary, as well as comprehensive field research for ground-truthing remotely sensed and modelled data. It will also be important to collect time-series data to assess the effects of temporal changes in connectivity (e.g. successional dynamics, anthropogenic change). Understanding temporal aspects of connectivity will be key for understanding species responses (such as range expansion) to progressive habitat fragmentation and climate change (Heller and Zavaleta 2009).

Indirect methods

Direct tracking of organisms provides the most accurate information on animal movement over demographic time-scales, but over longer time scales (e.g. evolutionary) a different

approach is needed. Population genetics provides a means of assessing connectivity integrated over many generations, compressing time scales that otherwise would not be observable. Rapid expansion in the availability of genetic markers (Parker et al. 1998; Broquet and Petit 2009; Francesco Ficetola and Bonin 2011) and dramatic increases in computing power have opened up new opportunities for identifying patterns of genetic connectivity (Balkenhol et al. 2009; Lowe and Allendorf 2010). Restriction fragment-length polymorphism (RFLP) and mtDNA analyses have largely given way to variable-number tandem repeat (VNTR – e.g. microsatellites) analysis, and with drastic decreases in both the cost and amount of time required to carry out genetic research, large repositories of population genetic data are becoming available for a variety of species and locations (Storfer et al. 2010). These data can be used to examine isolation by distance patterns, to back-trace migration paths and to identify potential stepping-stone populations using specialized software programs (such as MIGRATE-N - Beerli and Palczewski 2010). Assignment tests are also being used to identify barriers, spatial structuring and recent migration patterns (Excoffier and Heckel 2006; Faubet and Gaggiotti 2008). These developments have led to the expansive growth and development of the fields of landscape and seascape genetics (Manel et al. 2003; Holderegger and Wagner 2006; Selkoe et al. 2008).

Parentage analysis is increasingly being used as a means of assessing demographic connectivity over the time-scale of a single generation (Jones and Ardren 2003; Jones et al. 2005; Planes et al. 2009; Jones et al. 2010). This is typically achieved by comprehensively sampling the population, obtaining molecular marker frequencies (e.g. microsatellites), numerically simulating progeny, and using log-likelihood scores to match the actual progeny with the most likely parent or parent pair (Saenz-Agudelo et al. 2009). Parentage analysis offers tremendous benefits in that it provides quantitative and unambiguous measures of

connectivity (Harrison et al. 2012), as well as a strong means of validating other means of assessing connectivity (Berumen et al. 2010). However, the requirement that the population be comprehensively sampled (Marshall et al. 1998) makes large-scale studies difficult, or in many cases, impossible. Methods have been developed to help account for incomplete sampling (Duchesne et al. 2005; Mobley 2011), but for the time being, this approach will be generally limited to smaller, mostly-closed populations or small groups of populations.

With major developments in next generation sequencing technology (Hudson 2008), extensive analyses of single nucleotide polymorphisms (SNPs) will become increasingly feasible and affordable. This is opening up the potential for genome-wide association studies (GWAS - Donnelly 2008), making it possible to compare differences between individuals and cohorts at the nucleotide level, the lowest possible level of genetic resolution. Reviews by Allendorf et al. (2010), Avise (2010) and Ouborg et al. (2010) all stress the ongoing shift towards the use of genomic data in conservation applications. Making effective use of the rapidly expanding sources of data will necessitate the development of not only new methods for searching and filtering genomic data for intra- and inter-population signals, but also the development of appropriate statistical tests to determine their significance. This will require moving beyond the use of simple genetic models into the extensive application of multivariate analytical techniques (Jombart et al. 2009).

Although population genetic data have the ability to reveal connectivity patterns over long time periods, they also present challenges, since a large amount of variability is introduced into the data as a result of stochastic population processes (e.g. birth, mortality, and mutation) and natural plasticity in biological parameters (e.g. life-history characteristics). The influence of contemporary landscape or seascape patterns can also be confounded by historical

influences, such as demographic bottlenecks, geographic barriers or patterns of anthropogenic habitat loss (Kool et al. 2011). Furthermore, there is also a mismatch between the time scale of genetic processes and the time scales of management interest, and reconciling them will require identifying the characteristic scales of the system, as well as innovative ways of adapting our understanding/knowledge across different scales. However, with the development of multiple genetic marker types, new opportunities will emerge for empirically examining genetic connectivity patterns over various time scales, particularly as our ability to process, analyse and compare very large data sets improves with increased computing power.

Modelling and analysing connectivity

Sampling large spatial and temporal extents with a high degree of resolution is often impossible, and consequently researchers are forced to turn to models in order to investigate these types of environments. There are many challenges associated with modelling and analysing connectivity however (Panel 2), and many different approaches have been used in both metapopulation and landscape ecology (Table II).

Statistics and measures

The earliest and simplest means of assessing connectivity involved using buffer distances or through the use of statistics summarizing the size and arrangement of landscape patches classified in a binary manner (habitat vs. non-habitat - Dale et al. 2002). Dispersal kernels can be used as a means of scaling the effect of distance on connectivity (Moilanen and Nieminen 2002), however this approach typically assumes that the dispersal process is radially symmetric and not influenced by intervening habitat structure, which may not be true (Mitarai et al. 2008). Population geneticists have also made extensive use of isolation by

distance plots, comparing physical distance (typically geographic, but see White et al. 2010) versus some measure of genetic distance (e.g. Pinsky et al. 2010). Saura and Pascual-Hortal (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007) have developed indices that characterize the reachability of habitat patches. Reachability considers habitat patches themselves as spaces where connectivity occurs, taking into account resources existing within patches (intra-patch connectivity), together with those available through connections with other habitat patches (inter-patch connectivity), and consequently connectivity can be generated by large individual high-quality patches, from connections between patches, or a combination of both. Saura and Rubio (2010) also demonstrated how the probability of connection metric (PC) could be expressed in terms of the relative contribution of an individual component towards overall habitat availability in the landscape, and how that score could be partitioned into three components – intra-patch connectivity, dispersal flux through the patch, and the contribution of a component to the connectivity between other habitat patches (i.e. as a stepping-stone). Additional landscape metrics have been reviewed by Kindlmann and Burel (2008).

Pathfinding

Least-cost path (LCP) analysis also provides a means of scaling distance values between patches, and continues to be influential in landscape ecology (Urban et al. 2009). With LCP analysis, connectivity values are based on the path of least resistance between any two landscape elements. Exact and approximate algorithms exist for the computation of LCPs, but computation time remains a challenge for high-dimensional landscapes (Urban et al. 2009). In addition, LCP computation requires species-specific resistance values for different habitat types, which can be difficult to parameterize. Electric circuit theory has also been used in an ecological context to investigate path-type connectivity (McRae et al. 2008), and can be

considered as an extension to LCP analysis. Like LCP analysis, circuit theory operates on the basis of deriving resistance values between patches, but rather than identifying a single path, this framework allows for multiple paths between patches. This is a conceptually important development, since it becomes possible to investigate swaths as connections, as well as multiple corridor routing options (Ferrerias 2001).

Spatially structured diffusion

Spatially structured diffusion provides another way of analysing animal movements in heterogeneous landscapes using mark-recapture and tracking data (Ovaskainen 2004; Ovaskainen et al. 2008a). It operates by incorporating directional biases towards particular habitats at patch boundaries using a diffusion framework. Rather than considering discrete corridors, spatially structured diffusion integrates in a continuous manner across all possible movement pathways, and allows for rigorous estimates of species observability, as well as movement rates and mortalities in different habitat types, and transition rates between different pairs of habitats (Ovaskainen et al. 2008b). Occupancy times in landscape elements, hitting probabilities of landscape elements, quasi-stationary occupancy distributions, time evolution of occupancy distribution as function of initial condition, and occupancy probability densities between two observation points can also be derived directly from the diffusion process (Ovaskainen 2008).

Individual-based simulation

For complex environments with extremely high levels of spatial and temporal variability, individual-based models (IBMs) (Grimm and Railsback 2005) are being used to generate increasingly realistic simulations based on real-world data (Paris et al. 2007; Kool et al. 2010). IBMs operate on the basis of programmatically assigning properties and behaviour to

individuals and then allowing them to interact within a stochastic simulation environment (Levey et al. 2008; Kool et al. 2011). Although individual-based models are flexible in terms of their structure and dynamics, they require programming expertise, are difficult to parameterize rigorously, and cannot be manipulated, analysed and reconfigured in the manner of algebraic equations.

Graph theory

Graph theory has been extensively used to study the structure and properties of connectivity networks, as well as providing a means of displaying and visualizing them (Urban et al. 2009; Galpern et al. 2011; Luque et al. 2012). Graph theory provides a means of efficiently analysing large and complex networks, as well as their emergent properties and key structural characteristics. For example, measures of centrality (e.g., betweenness, degree, closeness) identify the position or role of a node with respect to its neighbours or the entire network (Estrada and Bodin 2008; Opsahl et al. 2010), and detecting nodes that exert a high degree of influence over the dynamics of the entire system. Network community structure can be evaluated through various clustering methods (Clauset et al. 2004; Palla et al. 2005), characterizing associations between individuals or groups. The degree distribution of a network is the probability distribution of the number of edges a node will have across the entire network, providing an indication of resilience and communicability within the network (Minor and Urban 2008). A network with a skewed degree distribution and several large hubs would suggest resilience to random node failure, and fast spread across the network (Proulx et al. 2005). Metanetworks (networks that model the relationships between other networks) have also been proposed as a means of linking species networks with spatial networks (Luque et al. 2012; Rubio and Saura 2012). For in-depth reviews of graph and network metrics, refer to Rayfield et al. (2011). Although it is important to be mindful of

some of the potential limitations of relying on a graph-theoretic approach (Moilanen 2011), with recent applications in both terrestrial and marine systems (Treml et al. 2008; Minor et al. 2009; Erös et al. 2012), as well as rapidly expanding interest in the analysis of social networks (Bodin and Crona 2009; Borgatti et al. 2009) suggests that graph theory will remain an active part of connectivity research for some time.

Matrix analysis

Matrix models provide another means of analysing connectivity flows (Caswell 2001), and have recently been used to project connectivity structure over time (Kool 2009), providing a link between individual-based biophysical dispersal models and population genetic structure (Foster et al. 2012). The sensitivity and elasticity of connectivity matrices (Caswell 2001, 2007) can be used to identify connections that exert the greatest influence on the overall system, and ordering matrices through sorting (Tsafirir et al. 2005), reduction (Bode et al. 2006) or recursive partitioning (Jacobi et al. 2012) makes it possible to evaluate natural clusters of exchange. More advanced techniques, such as singular value decomposition, and matrix perturbation theory for analysing connectivity and designing optimal networks have also been explored (Aiken and Navarrete 2011; Jacobi and Jonsson 2011).

Linkages between approaches

Many similarities exist between the various connectivity measures and analyses used in landscape ecology, metapopulation ecology, and connectivity research (Table IIb). Cluster analysis based on nearest-neighbour distances is closely connected to the construction of minimum spanning tree type graphs. Critical distances used in graph theory are structurally the same as buffer or neighbourhood measures in metapopulation studies and statistical habitat modelling (Visconti and Elkin 2009). Pair-wise distance matrices used inside

connectivity measures can be constructed based on declining-by-distance dispersal kernels or via least cost path computations (Urban et al. 2009). Graph theoretic approaches and matrices can be explicitly linked via the construction of an adjacency matrix representing the strength of connections between nodes. Caswell (2001) noted that matrix models can be linked to IBMs, and arise naturally from stochastic models where each individual moves through its life cycle independently. The various methods are in many cases closely related ways of approaching the same problem - characterizing relationships among patches, populations or demes. Rather than focusing on a particular modelling framework, it is more profitable to classify spatial studies and connectivity measures according to their structural characteristics (Panel 1).

Challenges and opportunities

Modelling and analysing connectivity presents a number of challenges. Landscape dynamics (e.g. successional changes, fragmentation) have the potential to confuse connectivity observations, leading to underestimates or even an apparent lack of connectivity effects (Hodgson et al. 2009a), and imperfect detection of species in sites has long been recognized as a problem for metapopulation studies, leading to biases in parameter estimation, including overestimation of population turnover, extinction and colonization rates, dispersal distances and connectivity as a whole (Mackenzie et al. 2003). Overestimation of connectivity can then lead to underestimation of conservation needs. One way of addressing this is through the use of stochastic state-space models (Patterson et al. 2008b). Under this framework, a process model is coupled with a separate observation model, providing a means of partitioning the sources of variability that are truly associated with the process from those associated with observation. Spatial autocorrelation is also an important consideration for connectivity studies (González-Megías et al. 2005). Autocorrelation in observations can

occur due to correlation in local habitat quality, spatially correlated dynamics or synchronizing factors such as weather (Van Teeffelen and Ovaskainen 2007). If spatial autocorrelation is ignored, then events are taken as independent when in truth they are not, leading to incorrect parameter estimates and false estimates of statistical significance. Autocorrelation is particularly a problem when habitat data are represented using high-resolution grids of semi-continuously varying habitat quality (Drielsma and Ferrier 2009), and consequently individual spatial units (i.e. individual raster cells) cannot be taken as dynamically independent from their neighbourhood. This has operational significance because most spatial habitat data currently exists in raster format, and high-resolution analyses are necessary to link the data with on-the-ground conservation applications (Elith and Leathwick 2009).

A number of opportunities exist for moving connectivity research forward by taking advantage of advances made in other fields. Some of the challenges facing connectivity researchers correspond to problems in other disciplines, and existing solutions can be brought to bear in a biological context. For example, solvers for the knapsack problem from computer science have been applied to optimizing environmental designs (Higgins et al. 2008), and the entire framework of graph-theoretic connectivity is an import from mathematical/computational sciences (Urban and Keitt 2001). Allesina and Pascual (2009) demonstrated how an adaptation of the Google PageRank algorithm could be used to identify key species whose loss could result in cascading extinctions, and the same could be used to identify groups of co-dependent patches or demes. Stochastic control theory (Wang et al. 2008) could be used to develop management strategies that dynamically respond to changes in connectivity, and bandwidth-allocation models (Ogryczak et al. 2008) could be modified to determine how resources could be most effectively distributed to maintain existing

connectivity structure. Many of these questions relating to connectivity research appear to fall under the domain of complex adaptive systems, and complexity in general (Miller and Page 2007). However, it is also important to recognize that populations are not binary switches, and ecological systems frequently exhibit non-linear and strategic behaviour. By design, many algorithms and analytical methods focus on maximal or minimal aspects of the system, but in many cases, the variability and distribution of responses are just as important, sometimes even more. Developing ways of assessing and testing how models, metrics and analyses results are affected by different forms of variability, as well as behaviour that evolves over time will be essential for moving forward with population connectivity research.

Management applications

Connectivity is a critical consideration in biodiversity conservation and management. Interactions between humans and landscapes occur through spatially defined interactions, which influence connectivity (Crooks and Sanjayan 2006). Spatial considerations were originally incorporated into conservation through the use of critical maximum dispersal distances and minimum patch size requirements, and spatial aggregation was achieved using boundary length penalties (Sarkar et al. 2006). Boundary length penalties penalize high edge-to-area ratios when carrying out optimization of reserve networks, leading to more globular delineations for individual sites and to more aggregated network solutions. This technique is still widely used in reserve network design, since structural aggregation is beneficial from both an ecological and economic perspective with respect to reserve establishment and management (Ball et al. 2009).

Presently, many different connectivity indices, both structural and functional, can be calculated using publicly available software packages such as FRAGSTATS (McGarigal et al. 2002), PATHMATRIX (Ray 2005), Conefor (Saura and Torné 2009), Marine Geospatial Ecology Tools (MGET - Roberts et al. 2010), or generic GIS software. These connectivity measures can be used as explanatory variables in further statistical analysis and modelling of conservation decisions. Conservation-oriented single-species spatial analysis can be carried out using empirically fitted metapopulation models (Drielsma and Ferrier 2009) or spatial population viability analyses (Naujokaitis-Lewis et al. 2009), although data demands of detailed dynamic models are generally high. Detailed mechanistic analyses of dispersal are also possible, for example, via spatially structured diffusion. Additionally, specialized software exists for advanced path-based analysis (McRae et al. 2008), and corridor building (Cushman et al. 2009).

Several software packages are publicly available for addressing connectivity in multi-species systematic conservation planning. The ResNet software package incorporates connectivity considerations into reserve network design via path-like graph-theoretic considerations (Ciarleglio et al. 2009). MARXAN and MARXAN with Zones implement patch size requirements and the boundary length penalty technique (Ball et al. 2009; Watts et al. 2009). The grid-based Zonation software implements species-specific parametric neighbourhood responses in a non-directional (terrestrial) environment (Moilanen and Wintle 2007) and for freshwater networks with strongly directed connectivity (Leathwick et al. 2010). It also implements pair-wise and many-to-one connectivity responses between species, between environments, between existing and proposed conservation areas (Lehtomäki et al. 2009), or between the present and the future in the climate change context (Carroll et al. 2010).

Despite significant progress during the past decade, many challenges remain in understanding how to best include connectivity in conservation management, when the needs of multiple species and environments, habitat quality and connectivity, direct costs and opportunity costs, short-term and long-term objectives, and multiple alternative conservation actions must be balanced (Pressey et al. 2007). Johst et al. (2011) were able to develop an analytical method for examining trade-offs between different landscape attributes, but integrating multiple forms of connectivity into the same analysis, using sparse data to effectively parameterize conservation analyses, and understanding the most robust and appropriate use of connectivity criteria in spatial conservation planning are all areas requiring further study. There are also questions regarding appropriate role of connectivity in conservation relative to strategies that primarily target habitat area or habitat quality - the two most fundamental determinants of regional carrying capacity for any species (Hodgson et al. 2009b). Using simulations, Visconti and Elkin (2009) were able to quantitatively show that connectivity metrics that take into account patch quality performed significantly better with regards to correctly ranking patches according to their contribution to overall metapopulation viability. Reinforcing connectivity for one species may add breeding habitat for another, implying potentially great benefits from strategies such as agri-environment schemes (Donald and Evans 2006). However, working with connectivity alone does not provide information regarding what is necessary or adequate for conservation. While connectivity can inform decision-makers about patterns of dispersal and colonization, alone it does not provide comprehensive information on local population dynamics, age/stage structure, or population growth and extinction.

As another general concern, connectivity is an uncertain management criterion despite it being the one most commonly proposed as a solution for conservation under climate change (Heller and Zavaleta 2009). There are numerous conceptual and operational definitions for

connectivity, making discussion about connectivity prone to linguistic uncertainty in communication. Choices of connectivity metrics are also prone to human decision uncertainty about what form of connectivity measure is applied and for what species (or other biodiversity features). Further complicating use of connectivity as a management criterion is epistemic uncertainty (lack of knowledge) about the correct structure and parameterization of connectivity. Consequently, application of connectivity in multi-species conservation management needs to be implemented with care and in a manner robust to uncertainty. While our ability compute connectivity metrics improves, our understanding about the appropriate use of connectivity in conservation management does not improve at the same rate, and our linguistic and decision uncertainty have not been reduced.

Synthesis

A significant part of the value of connectivity research lies in assembling the individual pieces of a landscape or seascape together into an integrated spatially and temporally explicit whole. Studying populations in an integrated manner makes it possible to test the consistency of our understanding of the system, and reveals if critical components are not being accounted for. Moreover, by examining the various components in concert, other aspects emerge. The first is the critical importance of scale. Depending on the spatial and temporal scales at which one observes a landscape or seascape, patches may change, blend into one another, or cease to effectively exist altogether. Understanding the scales at which different landscape processes operate, as well as ways of identifying those scales is essential for devising efficient monitoring strategies, as well as determining functional connections. This is no trivial task, since scales will vary not only among the different processes, but also according to how individual species perceive and use their environment. Consequently, in

494 addition to seeking out unifying principles, it is equally important to critically evaluate the
495 causes and consequences of variability between individuals, species and assemblages, and to
496 address the interactions between them. Fusing the homogeneity of an integrated design with
497 variability down to the genetic level requires reconciling top-down, holistic approaches with
498 bottom-up, reductionist approaches. The complexity of dispersal and connectivity,
499 augmented by the need to account for additional factors such as the role of demographic
500 processes or to integrate with social and economic systems might seem cause for despair, but
501 this is a challenge for which connectivity researchers are well-suited. Teasing signal from
502 noise, partitioning intra- and inter-group variation, and developing conceptual models that
503 explain system behaviour using the minimum amount of detail required are common practice
504 in connectivity research. Fortunately, is it not necessary to develop methods entirely *de novo*.
505 Although models designed for mechanical systems may be too simple for biological systems,
506 they can at least serve as a basis for further development. Communication across disciplines
507 will also be crucial when developing conservation and management strategies. Connectivity
508 scientists need to be transparent about what their measurements and models mean, and the
509 assumptions behind them. It is also essential to distil and simplify this knowledge into an
510 accessible form - through the development of tools, and outreach beyond scientific
511 publications. From managers, a clear articulation of their needs is required, as well as a
512 transparent assessment of constraints: logistical, social and economic. Naturally, this will be
513 an iterative and interactive process, but facilitating these connections, as well as identifying
514 where productive new linkages could be formed will be important moving forward. Lastly,
515 understanding the implications of long-term connectivity will involve strengthening links
516 with population genetic theory, including aspects of speciation and biogeography. Over time,
517 inter-population processes will be dependent on intra-population ones, such as reproductive
518 success, carrying capacity and habitat quality. Fundamentally, an improved understanding of

connectivity is needed to fully appreciate the likely development of biodiversity patterns under climate change and other human pressures.

Summary

From advances in physical tracking, to the application of new genetic techniques, as well as ongoing developments in modelling and analysis, it is clear that much work has been done, and is still going on to improve our understanding of connectivity. Methods for measuring connectivity have greatly improved in both extent and resolution, spatially and temporally. A wide range of options exist for monitoring organisms at a variety of scales in terrestrial and aquatic environments. Similarly, many techniques are available to characterizing connectivity and to represent its underlying processes. From relatively simple measures, such as summary statistics through to dynamic individual-based models and spatially structured diffusion models, researchers have many choices depending on data availability and structure, as well as how the results will ultimately be used. It is also important to give strong consideration to how connectivity data and models can be integrated into conservation and management strategies. To this end, a number of software tools have been developed, but ensuring that this information is effectively used will require careful consideration of what operational definitions of connectivity are most relevant to the problem at hand, as well as its relative importance in the decision-making process. Also, while our understanding of connectivity is improving, there will still be a strong need to gather field data on individual and species-level behaviour, habitat quality, and demography. Nevertheless, the progress to date in detecting and recognizing connectivity patterns, and understanding the processes responsible for generating them is highly encouraging, and we look forward to seeing the benefits that an improved understanding of connectivity will provide in the future.

Acknowledgments

J.K. would like to thank Bob Pressey and Program 6 (Conservation Planning) of the ARC Centre of Excellence for Coral Reef Studies and the Australian Institute of Marine Science for providing financial support for this work. He also thanks Stephanie Januchowski-Hartley, Tom Brewer, Claire Paris and Bill Laurance for their input on draft versions of the manuscript. Ideas developed during conversations with Hugo Harrison also contributed significantly to the population genetics section, and several key ideas were generated during discussions with Bob Warner, particularly regarding the importance of demographic effects. A.M. thanks the ERC grant StG 260393 - GEDA and the Academy of Finland Centre of Excellence Programme 2012-2017 for support. Funding for E.T. was provided by Australian Research Council grant DP0878306, and a World Wildlife Fund Kathryn Fuller Science for Nature Postdoctoral Fellowship.

References

- Ahmad MA, Teredesai A (2006) Modeling spread of ideas in online social networks. Proceedings of the fifth Australasian conference on Data mining and analytics - Volume 61. Australian Computer Society, Inc., Sydney, Australia, pp. 185-190
- Aiken CM, Navarrete SA (2011) Environmental fluctuations and asymmetrical dispersal: generalized stability theory for studying metapopulation persistence and marine protected areas. *Mar. Ecol. Prog. Ser.* 428:77-88
- Allendorf FW, Hohenlohe PA, Luikart G (2010) Genomics and the future of conservation genetics. *Nat. Rev. Genet.* 11(10):697-709
- Allesina S, Pascual M (2009) Googling Food Webs: Can an Eigenvector Measure Species' Importance for Coextinctions? *PLoS Comput. Biol.* 5(9):e1000494
- Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local Replenishment of Coral Reef Fish Populations in a Marine Reserve. *Science* 316(5825):742-744

574 Avise JC (2010) Perspective: Conservation genetics enters the genomics era. *Conserv. Genet.*
575 11(2):665-669

576 Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional
577 grain as a key determinant for dispersal. *Landsc. Ecol.* 22(8):1117-1129

578 Balkenhol N, Gugerli F, Cushman S et al (2009) Identifying future research needs in
579 landscape genetics: where to from here? *Landsc. Ecol.* 24(4):455-463

580 Ball IR, Possingham HP, Watts M (2009) Marxan and relatives: Software for spatial
581 conservation prioritisation. In: Moilanen A., Wilson K. A., Possingham H. P. (eds), *Spatial*
582 *conservation prioritisation: Quantitative methods and computational tools.* Oxford University
583 Press, Oxford, UK, pp. 185-195

584 Beerli P, Palczewski M (2010) Unified Framework to Evaluate Panmixia and Migration
585 Direction Among Multiple Sampling Locations. *Genetics* 185(1):313-326

586 Berry O, Tocher MD, Sarre SD (2004) Can assignment tests measure dispersal? *Mol. Ecol.*
587 13(3):551-561

588 Berumen M, Walsh H, Raventos N et al (2010) Otolith geochemistry does not reflect
589 dispersal history of clownfish larvae. *Coral Reefs* 29(4):883-891

590 Bode M, Bode L, Armsworth PR (2006) Larval dispersal reveals regional sources and sinks
591 in the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 308:17-25

592 Bodin Ö, Crona BI (2009) The role of social networks in natural resource governance: What
593 relational patterns make a difference? *Glob. Env. Change* 19(3):366-374

594 Borgatti SP, Mehra A, Brass DJ, Labianca G (2009) Network Analysis in the Social Sciences.
595 *Science* 323(5916):892-895

596 Borgman C, Wallis J, Enyedy N (2007) Little science confronts the data deluge: habitat
597 ecology, embedded sensor networks, and digital libraries. *International Journal on Digital*
598 *Libraries* 7(1):17-30

599 Broquet T, Petit EJ (2009) Molecular Estimation of Dispersal for Ecology and Population
600 Genetics. *Ann. Rev. Ecology, Evolution, and Systematics* 40(1):193-216

601 Cantrell RS, Cosner C (2003) *Spatial Ecology via Reaction-Diffusion Equations.* John Wiley
602 and Sons, Chichester, UK

603 Carroll C, Dunk JR, Moilanen A (2010) Optimizing resiliency of reserve networks to climate
604 change: multispecies conservation planning in the Pacific Northwest, USA. *Glob. Change*
605 *Biol.* 16(3):891-904

606 Caswell H (2001) *Matrix population models : construction, analysis, and interpretation.*
607 Sinauer Associates, Sunderland, Mass.

608 Caswell H (2007) Sensitivity analysis of transient population dynamics. *Ecol. Lett.* 10(1):1-
609 15

610 Cerdeira JO, Pinto LS, Cabeza M, Gaston KJ (2010) Species specific connectivity in reserve-
611 network design using graphs. *Biol. Conserv.* 143(2):408-415

612 Chester CC (2006) Conservation across borders: biodiversity in an interdependent world.
613 Island Press, Washington, DC

614 Ciarleglio M, Wesley Barnes J, Sarkar S (2009) ConsNet: new software for the selection of
615 conservation area networks with spatial and multi-criteria analyses. *Ecography* 32(2):205-209

616 Claudet J (2011) Marine Protected Areas: A Multidisciplinary Approach. Cambridge
617 University Press, Cambridge, MA

618 Clauset A, Newman MEJ, Moore C (2004) Finding community structure in very large
619 networks. *Phys. Rev. E* 70(6):066111

620 Cowen RK, Guigand CM (2008) In situ ichthyoplankton imaging system (ISIIS): system
621 design and preliminary results. *Limnology and Oceanography: Methods* 6:126-132

622 Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Ann.*
623 *Rev. Mar. Sci.* 1:443-466

624 Crooks KR, Sanjayan M (eds) (2006) Connectivity Conservation. Cambridge University
625 Press, Cambridge, UK

626 Cushman SA, McKelvey KS, Schwartz MK (2009) Use of Empirically Derived Source-
627 Destination Models to Map Regional Conservation Corridors

628 Utilización de Modelos Fuente-Destino Empíricamente Derivados para Cartografiar
629 Corredores de Conservación Regionales. *Conserv. Biol.* 23(2):368-376

630 Dale MRT, Dixon P, Fortin M-J, Legendre P, Myers DE, Rosenberg MS (2002) Conceptual
631 and mathematical relationships among methods for spatial analysis. *Ecography* 25(5):558-
632 577

633 Donald PF, Evans AD (2006) Habitat connectivity and matrix restoration: the wider
634 implications of agri-environment schemes. *J. Appl. Ecol.* 43(2):209-218

635 Donnelly P (2008) Progress and challenges in genome-wide association studies in humans.
636 *Nature* 456(7223):728-731

637 Douglas DH (1994) Least-cost Path in GIS Using an Accumulated Cost Surface and
638 Slopelines. *Cartographica The International Journal for Geographic Information and*
639 *Geovisualization* 31(3):37-51

640 Drielsma M, Ferrier S (2009) Rapid evaluation of metapopulation persistence in highly
641 variegated landscapes. *Biol. Conserv.* 142(3):529-540

642 Duchesne P, Castric T, Bernatchez L (2005) pasos (parental allocation of singles in open
643 systems): a computer program for individual parental allocation with missing parents. *Mol.*
644 *Ecol. Notes* 5(3):701-704

645 Durbec M, Cavalli L, Grey J, Chappaz R, Nguyen The B (2010) The use of stable isotopes to
646 trace small-scale movements by small fish species. *Hydrobiologia* 641(1):23-31

647 Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and
648 Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*
649 40(1):677-697

650 Erös T, Olden J, Schick R, Schmera D, Fortin M-J (2012) Characterizing connectivity
651 relationships in freshwaters using patch-based graphs. *Landsc. Ecol.* 27(2):303-317

652 Estrada E, Bodin Ö (2008) Using network centrality measures to manage landscape
653 connectivity. *Ecol. Appl.* 18(7):1810-1825

654 Excoffier L, Heckel G (2006) Computer programs for population genetics data analysis: a
655 survival guide. *Nat. Rev. Genet.* 7(10):745-758

656 Faaborg J, Holmes RT, Anders AD et al (2010) Recent advances in understanding migration
657 systems of New World land birds. *Ecol. Monogr.* 80(1):3-48

658 Faubet P, Gaggiotti OE (2008) A New Bayesian Method to Identify the Environmental
659 Factors That Influence Recent Migration. *Genetics* 178(3):1491-1504

660 Ferreras P (2001) Landscape structure and asymmetrical inter-patch connectivity in a
661 metapopulation of the endangered Iberian lynx. *Biol. Conserv.* 100(1):125-136

662 Figueira W, Crowder L (2006) Defining patch contribution in source-sink metapopulations:
663 the importance of including dispersal and its relevance to marine systems. *Popul. Ecol.*
664 48(3):215-224

665 Fleming PJS, Tracey JP (eds) (2008) *Aerial Surveys of Wildlife: Theory and Applications.*
666 CSIRO Publishing, Collingwood, VIC

667 Foster NL, Paris CB, Kool JT et al (2012) Connectivity of Caribbean coral populations:
668 complementary insights from empirical and modelled gene flow. *Mol. Ecol.* 21(5):1143-1157

669 Francesco Ficetola G, Bonin A (2011) Conserving adaptive genetic diversity in dynamic
670 landscapes. *Mol. Ecol.* 20(8):1569-1571

671 Fujiwara M, Anderson K, Neubert M, Caswell H (2006) On the Estimation of Dispersal
672 Kernels from Individual Mark-Recapture Data. *Environ. Ecol. Stat.* 13(2):183-197

673 Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: A guide
674 to construction, analysis and application for conservation. *Biol. Conserv.* 144(1):44-55

675 González-Megías A, Gómez JM, Sánchez-Piñero F (2005) Consequences of spatial
676 autocorrelation for the analysis of metapopulation dynamics. *Ecology* 86(12):3264-3271

677 Grimm V, Railsback SF (2005) *Individual-based modeling and ecology* Princeton University
678 Press, Princeton

679 Hamilton MP, Graham EA, Rundel PW et al (2007) New Approaches in Embedded
680 Networked Sensing for Terrestrial Ecological Observatories. *Environmental Engineering*
681 *Science* 24(2):192-204

682 Harrison Hugo B, Williamson David H, Evans Richard D et al (2012) Larval Export from
683 Marine Reserves and the Recruitment Benefit for Fish and Fisheries. *Current Biology*
684 22(11):1023-1028

685 Hedgecock D, Barber PH, Edmands S (2007) Genetic Approaches to Measuring
686 Connectivity. *Oceanography* 20(3):70-79

687 Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: A
688 review of 22 years of recommendations. *Biol. Conserv.* 142(1):14-32

689 Higgins AJ, Hajkowicz S, Bui E (2008) A multi-objective model for environmental
690 investment decision making. *Computers & Operations Research* 35(1):253-266

691 Hilty J, Lidicker Jr. WZ, Merenlender A (2006) Corridor ecology: the science and practice of
692 linking landscapes for biodiversity conservation. Island Press, Washington, D.C.

693 Hobson KA (2008) Applying Isotopic Methods to Tracking Animal Movements. In: Keith A.
694 H. and Leonard I. W. (eds), *Terrestrial Ecology*. Elsevier, pp. 45-78

695 Hodgson JA, Moilanen A, Thomas CD (2009a) Metapopulation responses to patch
696 connectivity and quality are masked by successional habitat dynamics. *Ecology* 90(6):1608-
697 1619

698 Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009b) Climate change, connectivity and
699 conservation decision making: back to basics. *J. Appl. Ecol.* 46(5):964-969

700 Holderegger R, Wagner H (2006) A brief guide to Landscape Genetics. *Landsc. Ecol.*
701 21(6):793-796

702 Holmes EE, Lewis MA, Banks JE, Veit RR (1994) Partial Differential Equations in Ecology:
703 Spatial Interactions and Population Dynamics. *Ecology* 75(1):17-29

704 Hudson ME (2008) Sequencing breakthroughs for genomic ecology and evolutionary
705 biology. *Mol. Ecol. Res.* 8(1):3-17

706 Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era
707 of globalization. *J. Appl. Ecol.* 46(1):10-18

708 Jacobi MN, André C, Döös K, Jonsson PR (2012) Identification of subpopulations from
709 connectivity matrices. *Ecography*: DOI: 10.1111/j.1600-0587.2012.07281.x

710 Jacobi MN, Jonsson PR (2011) Optimal networks of nature reserves can be found through
711 eigenvalue perturbation theory of the connectivity matrix. *Ecol. Appl.* 21(5):1861-1870

712 Jacobson B, Peres-Neto P (2010) Quantifying and disentangling dispersal in
713 metacommunities: how close have we come? How far is there to go? *Landsc. Ecol.*
714 25(4):495-507

715 Jaquiéry J, Broquet T, Hirzel AH, Yearsley J, Perrin N (2011) Inferring landscape effects on
716 dispersal from genetic distances: how far can we go? *Mol. Ecol.* 20(4):692-705

717 Johst K, Drechsler M, van Teeffelen AJA et al (2011) Biodiversity conservation in dynamic
718 landscapes: trade-offs between number, connectivity and turnover of habitat patches. *J. Appl.*
719 *Ecol.* 48(5):1227-1235

720 Jombart T, Pontier D, Dufour AB (2009) Genetic markers in the playground of multivariate
721 analysis. *Heredity* 102(4):330-341

722 Jones AG, Ardren WR (2003) Methods of parentage analysis in natural populations. *Mol.*
723 *Ecol.* 12:2511-2523

724 Jones AG, Small CM, Paczolt KA, Ratterman NL (2010) A practical guide to methods of
725 parentage analysis. *Mol. Ecol. Res.* 10(1):6-30

726 Jones GP, Planes S, Thorrold SR (2005) Coral Reef Fish Larvae Settle Close to Home.
727 *Current Biology* 15(14):1314-1318

728 Karanth KU, Nichols JD, Kumar NS, Hines JE (2006) Assessing tiger population dynamics
729 using photographic capture-recapture sampling. *Ecology* 87(11):2925-2937

730 Kays R, Kranstauber B, Jansen P et al Camera traps as sensor networks for monitoring
731 animal communities. In: *Local Computer Networks, 2009. LCN 2009. IEEE 34th*
732 *Conference on*, 2009. p. 811-818

733 Kindlmann P, Burel F (2008) Connectivity measures: a review. *Landsc. Ecol.* 23(8):879-890

734 Kool JT (2009) An object-oriented, individual-based approach for simulating the dynamics of
735 genes in subdivided populations. *Ecol. Inform.* 4:136-146

736 Kool JT, Paris CB, Andréfouët S, Cowen RK (2010) Complex migration and the
737 development of genetic structure in subdivided populations: an example from Caribbean
738 coral reef ecosystems. *Ecography* 33:597-606

739 Kool JT, Paris CB, Barber PH, Cowen RK (2011) Connectivity and the development of
740 population genetic structure in Indo-West Pacific coral reef communities. *Global Ecology*
741 *and Biogeography* 20(5):695-706

742 Leathwick JR, Moilanen A, Ferrier S, Julian K (2010) Complementarity-based conservation
743 prioritization using a community classification, and its application to riverine ecosystems.
744 *Biol. Conserv.* 143(4)

745 Lehtomäki J, Tomppo E, Kuokkanen P, Hanski I, Moilanen A (2009) Applying spatial
746 conservation prioritization software and high-resolution GIS data to a national-scale study in
747 forest conservation. *For. Ecol. Manage.* 258(11):2439-2449

748 Levey DJ, Tewksbury JJ, Bolker BM (2008) Modelling long-distance seed dispersal in
749 heterogeneous landscapes. *J. Ecol.* 96(4):599-608

750 Liu J, Hull V, Morzillo AT, Wiens JA (2011) *Sources, Sinks and Sustainability*. Cambridge
751 University Press, Cambridge, MA

752 Lowe WH, Allendorf FW (2010) What can genetics tell us about population connectivity?
753 *Mol. Ecol.* 19(15):3038-3051

754 Luque S, Saura S, Fortin M-J (2012) Landscape connectivity analysis for conservation:
755 insights from combining new methods with ecological and genetic data. *Landsc. Ecol.*
756 27:153-157

757 Mackenzie DI, Nichols JD, Hines JE, Knutson MG, Franklin AB (2003) Estimating site
758 occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*
759 84(8):2200-2207

760 Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining
761 landscape ecology and population genetics. *Trends Ecol. Evol.* 18(4):189-197

762 Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-
763 based paternity inference in natural populations. *Mol. Ecol.* 7(5):639-655

764 Martin Taylor S (2009) Transformative ocean science through the VENUS and NEPTUNE
765 Canada ocean observing systems. *Nuclear Instruments and Methods in Physics Research*
766 *Section A: Accelerators, Spectrometers, Detectors and Associated Equipment* 602(1):63-67

767 McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial Pattern Analysis
768 Program for Categorical Maps. University of Massachusetts, Amherst,

769 McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model
770 connectivity in ecology, evolution, and conservation. *Ecology* 89(10):2712-2724

771 Miller JH, Page SE (2007) *Complex Adaptive Systems: An Introduction to Computational*
772 *Models of Social Life*. Princeton University Press, Princeton, NJ

773 Millsbaugh J, Marzluff JM (eds) (2001) *Radio Tracking and Animal Populations*. Academic
774 Press, Salt Lake City, UT

775 Minor ES, Tessel SM, Engelhardt KAM, Lookingbill TR (2009) The role of landscape
776 connectivity in assembling exotic plant communities: a network analysis. *Ecology*
777 90(7):1802-1809

778 Minor ES, Urban DL (2008) A graph-theory framework for evaluating landscape
779 connectivity and conservation planning. *Conserv. Biol.* 22(2):297-307

780 Mitarai S, Siegel DA, Winters KB (2008) A numerical study of stochastic larval settlement in
781 the California Current system. *J. Mar. Sys.* 69(3-4):295-309

782 Mobley KB (2011) Grandfathering in a new era of parentage analysis. *Mol. Ecol.* 20(6):1080-
783 1082

784 Moilanen A (2011) On the limitations of graph-theoretic connectivity in spatial ecology and
785 conservation. *J. Appl. Ecol.* 48:1543-1547

786 Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. *Ecology*
787 83(4):1131-1145

788 Moilanen A, Wintle BA (2007) The Boundary-Quality Penalty: a Quantitative Method for
789 Approximating Species Responses to Fragmentation in Reserve Selection. *Conserv. Biol.*
790 21(2):355-364

791 Munday P, Leis J, Lough J et al (2009) Climate change and coral reef connectivity. *Coral*
792 *Reefs* 28(2):379-395

793 Munro AR, Gillanders BM, Thurstan S, Crook DA, Sanger AC (2009) Transgenerational
794 marking of freshwater fishes with enriched stable isotopes: a tool for fisheries management
795 and research. *J. Fish Biol.* 75(3):668-684

796 Musyl MK, Domeier ML, Nasby-Lucas N et al (2011) Performance of pop-up satellite
797 archival tags. *Mar. Ecol. Prog. Ser.* 433:1-28

798 Naujokaitis-Lewis IR, Curtis JMR, Arcese P, Rosenfeld J (2009) Sensitivity Analyses of
799 Spatial Population Viability Analysis Models for Species at Risk and Habitat Conservation
800 Planning. *Conserv. Biol.* 23(1):225-229

801 Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic
802 ecology. *Front. Ecol. Environ.* 5(8):429-436

803 Ogryczak W, Wierzbicki A, Milewski M (2008) A multi-criteria approach to fair and
804 efficient bandwidth allocation. *Omega* 36(3):451-463

805 Opsahl T, Agneessens F, Skvoretz J (2010) Node centrality in weighted networks:
806 Generalizing degree and shortest paths. *Social Networks* 32(3):245-251

807 Ouborg NJ, Pertoldi C, Loeschcke V, Bijlsma RK, Hedrick PW (2010) Conservation genetics
808 in transition to conservation genomics. *Trends in Genetics* 26(4):177-187

809 Ovaskainen O (2004) Habitat-specific movement parameters estimated using mark-recapture
810 data and a diffusion model. *Ecology* 85(1):242-257

811 Ovaskainen O (2008) Analytical and numerical tools for diffusion-based movement models.
812 *Theor. Popul. Biol.* 73(2):198-211

813 Ovaskainen O, Luoto M, Ikonen I, Rekola H, Meyke E, Kuussaari M (2008a) An Empirical
814 Test of a Diffusion Model: Predicting Clouded Apollo Movements in a Novel Environment.
815 *Am. Nat.* 171(5):610-619

816 Ovaskainen O, Rekola H, Meyke E, Arjas E (2008b) Bayesian methods for analyzing
817 movements in heterogeneous landscapes from mark-recapture data. *Ecology* 89(2):542-554

818 Ovaskainen O, Smith AD, Osborne JL et al (2008c) Tracking butterfly movements with
819 harmonic radar reveals an effect of population age on movement distance. *PNAS*
820 105(49):19090-19095

821 Palla G, Derenyi I, Farkas I, Vicsek T (2005) Uncovering the overlapping community
822 structure of complex networks in nature and society. *Nature* 435(7043):814-818

823 Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef:
824 effects on population connectivity. *Mar. Ecol. Prog. Ser.* 347:285-300

825 Parker PG, Snow AA, Schug MD, Booton GC, Fuerst PA (1998) What molecules can tell us
826 about populations: Choosing and using a molecular marker. *Ecology* 79(2):361-382

827 Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based
828 landscape connectivity indices: towards the prioritization of habitat patches and corridors for
829 conservation. *Landsc. Ecol.* 21(7):959-967

830 Patterson TA, Evans K, Carter TI, Gunn JS (2008a) Movement and behaviour of large
831 southern bluefin tuna (*Thunnus maccoyii*) in the Australian region determined using pop-up
832 satellite archival tags. *Fish Oceanogr.* 17(5):352-367

833 Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008b) State-space
834 models of individual animal movement. *Trends Ecol. Evol.* 23(2):87-94

835 Pauli JN, Ben-David M, Buskirk SW, Depue JE, Smith WP (2009) An isotopic technique to
836 mark mid-sized vertebrates non-invasively. *J. Zool.* 278(2):141-148

837 Pineda J, Hare JA, Sponaugle S (2007) Larval Transport and Dispersal in the Coastal Ocean
838 and Consequences for Population Connectivity. *Oceanography* 20(3):22-39

839 Pinsky ML, Montes HR, Palumbi SR (2010) Using isolation by distance and effective density
840 to estimate dispersal scales in anemonefish. *Evolution* 64:2688-2700

841 Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a
842 network of marine protected areas. *PNAS* 106:5693-5697

843 Porter J, Arzberger P, Braun H-W et al (2005) Wireless Sensor Networks for Ecology.
844 Bioscience 55(7):561-572

845 Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA (2007) Conservation planning
846 in a changing world. Trends Ecol. Evol. 22(11):583-592

847 Pringle C (2003) The need for a more predictive understanding of hydrologic connectivity.
848 Aquatic Conservation: Marine and Freshwater Ecosystems 13(6):467-471

849 Proulx SR, Promislow DEL, Phillips PC (2005) Network thinking in ecology and evolution.
850 Trends Ecol. Evol. 20(6):345-353

851 Raeymaekers JAM, Maes GE, Geldof S, Hontis I, Nackaerts K, Volckaert FAM (2008)
852 Modeling genetic connectivity in sticklebacks as a guideline for river restoration.
853 Evolutionary Applications 1(3):475-488

854 Randall LA, Diehl RH, Wilson BC, Barrow Jr. WC, Jeske CW (2011) Potential use of
855 weather radar to study movements of wintering waterfowl. J. Wildl. Manage. 75(6):1324-
856 1329

857 Ray N (2005) PATHMATRIX: a geographical information system tool to compute effective
858 distances among samples. Mol. Ecol. Notes 5(1):177-180

859 Rayfield B, Fortin M-J, Fall A (2011) Connectivity for conservation: a framework to classify
860 network measures. Ecology 92(4):847-858

861 Recio MR, Mathieu R, Denys P, Sirguey P, Seddon PJ (2011) Lightweight GPS-Tags, One
862 Giant Leap for Wildlife Tracking? An Assessment Approach. PLoS One 6(12):e28225

863 Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (2010) Marine Geospatial Ecology
864 Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R,
865 MATLAB, and C++. Environmental Modelling & Software 25(10):1197-1207

866 Rubenstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and
867 stable isotopes. Trends Ecol. Evol. 19(5):256-263

868 Rubio L, Saura S (2012) Assessing the importance of individual habitat patches as
869 irreplaceable connecting elements: An analysis of simulated and real landscape data.
870 Ecological Complexity 11:28-37

871 Rutz C, Hays GC (2009) New frontiers in biologging science. Biology Letters 5(3):289-292

872 Saenz-Agudelo P, Jones GP, Thorrold SR, Planes S (2009) Estimating connectivity in marine
873 populations: an empirical evaluation of assignment tests and parentage analysis under
874 different gene flow scenarios. Mol. Ecol. 18(8):1765-1776

875 Sarkar S, Pressey RL, Faith DP et al (2006) Biodiversity conservation planning tools: present
876 status and challenges for the future. Annu. Rev. Environ. Resour. 31:123-59

877 Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in
878 landscape conservation planning: Comparison with existing indices and application to a case
879 study. Landscape and Urban Planning 83:91-103

880 Saura S, Rubio L (2010) A common currency for the different ways in which patches and
881 links can contribute to habitat availability and connectivity in the landscape. Ecography
882 33(3):523-537

883 Saura S, Torné J (2009) Conefor Sensinode 2.2: A software package for quantifying the
884 importance of habitat patches for landscape connectivity. *Environmental Modelling &*
885 *Software* 24(1):135-139

886 Selkoe KA, Henzler CM, Gaines SD (2008) Seascape genetics and the spatial ecology of
887 marine populations. *Fish. Fish.* 9(4):363-377

888 Slone DH (2011) Increasing accuracy of dispersal kernels in grid-based population models.
889 *Ecol. Model.* 222(3):573-579

890 Storfer A, Murphy MA, Spear SF, Holderegger R, Waits LP (2010) Landscape genetics:
891 where are we now? *Mol. Ecol.* 19(17):3496-3514

892 Sutherland WJ (ed) (2006) *Ecological Census Techniques: A Handbook*. Cambridge
893 University Press, Cambridge, UK

894 Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity Is a Vital Element of
895 Landscape Structure. *Oikos* 68(3):571-573

896 Thorrold SR, Zacherl DC, Levin LA (2007) Population Connectivity and Larval Dispersal
897 Using Geochemical Signatures in Calcified Structures. *Oceanography* 20(3):80-89

898 Treml EA, Halpin PN (in press) Marine population connectivity identifies ecological
899 neighbors for conservation planning in the Coral Triangle. *Cons. Lett.*

900 Treml EA, Halpin PN, Urban DL, Pratson LF (2008) Modeling population connectivity by
901 ocean currents, a graph-theoretic approach for marine conservation. *Landsc. Ecol.* 23(S1):19-
902 36

903 Tsafrir D, Tsafrir I, Ein-Dor L, Zuk O, Notterman DA, Domany E (2005) Sorting points into
904 neighborhoods (SPIN): data analysis and visualization by ordering distance matrices.
905 *Bioinformatics* 21(10):2301-2308

906 Tsechpenakis G, Guigand C, Cowen RK Image Analysis Techniques to Accompany a new In
907 Situ Ichthyoplankton Imaging System. In: *OCEANS 2007 - Europe*, 2007. p. 1-6

908 Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M (2003) Remote
909 sensing for biodiversity science and conservation. *Trends in Ecology and Evolution*
910 18(6):306-314

911 Urban D, Keitt T (2001) Landscape connectivity: A graph-theoretic perspective. *Ecology*
912 82(5):1205-1218

913 Urban DL, Minor ES, Treml EA, Schick RS (2009) Graph models of habitat mosaics. *Ecol.*
914 *Lett.* 12(3):260-273

915 Urbano F, Cagnacci F, Calenge C, Dettki H, Cameron A, Neteler M (2010) Wildlife tracking
916 data management: a new vision. *Phil. Trans. R. Soc. Lond. B* 365(1550):2177-2185

917 Van Teeffelen AJA, Ovaskainen O (2007) Can the cause of aggregation be inferred from
918 species distributions? *Oikos* 116(1):4-16

919 Visconti P, Elkin C (2009) Using connectivity metrics in conservation planning – when does
920 habitat quality matter? *Diversity and Distributions* 15(4):602-612

- 921 Wang A, Afshar P, Wang H (2008) Complex stochastic systems modelling and control via
922 iterative machine learning. *Neurocomputing* 71(13-15):2685-2692
- 923 Wang K, Franklin SE, Guo X, Cattet M (2010) Remote Sensing of Ecology, Biodiversity and
924 Conservation: A Review from the Perspective of Remote Sensing Specialists. *Sensors*
925 10:9647-9667
- 926 Waples RS, Gaggiotti OE (2006) What is a population? An empirical evaluation of some
927 genetic methods for identifying the number of gene pools and their degree of connectivity.
928 *Mol. Ecol.* 15:1419-1439
- 929 Wasserman TN, Cushman SA, Shirk AS, Landguth EL, Littell JS (2012) Simulating the
930 effects of climate change on population connectivity of American marten (*Martes americana*)
931 in the northern Rocky Mountains, USA. *Landsc. Ecol.* 27:211-225
- 932 Watts ME, Ball IR, Stewart RS et al (2009) Marxan with Zones: Software for optimal
933 conservation based land- and sea-use zoning. *Environmental Modelling & Software*
934 24(12):1513-1521
- 935 Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds:
936 unraveling migratory connectivity. *Trends Ecol. Evol.* 17(2):76-83
- 937 West JB, Bowen GJ, Cerling TE, Ehleringer JR (2006) Stable isotopes as one of nature's
938 ecological recorders. *Trends Ecol. Evol.* 21(7):408-414
- 939 White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ (2010) Ocean currents
940 help explain population genetic structure. *Proceedings of the Royal Society B: Biological*
941 *Sciences* 277(1688):1685-1694
- 942 Williamson David H, Jones GP, S.R. T, Frisch AJ (2009) Transgenerational marking of
943 marine fish larvae: stable-isotope retention, physiological effects and health issues. *J. Fish*
944 *Biol.* 74(4):891-905
- 945 Woods RJ, Macdonald JI, Crook DA, Schmidt DJ, Hughes JM (2010) Contemporary and
946 historical patterns of connectivity among populations of an inland river fish species inferred
947 from genetics and otolith chemistry. *Can. J. Fish. Aquat. Sci.* 67:1098-1115

948

949

950

Panel 1: Deconstructing connectivity

Existing definitions of connectivity lie along a continuum ranging from the simple – e.g. examining aspects such as patch adjacency or straight-line relationships between objects, to the very complex – e.g. incorporating factors such as mobility, perceptual ability, and species-specific biological considerations. These definitions are not necessarily mutually exclusive and may overlap with one another (e.g. it is possible to consider functional genetic connectivity). In all cases however, the idea of connectivity being a structured set of inter-population relationships remains consistent.

f is a function linking the input variables to the output connectivity values. $x,y,z,t...$ is a set of arbitrary variables.

Rather than pursuing a single 'ideal' operational definition of connectivity, the following questions can instead be used to distinguish between different analytical frameworks, and to clarify various study objectives:

- (1) How is landscape structure characterized? Is a simple, binary habitat/non-habitat classification used, or is continuous or semi-continuous variation in quality allowed?

- 977 (2) *How are distances between landscape elements determined? For example, are they Euclidian distances, least-*
978 *cost paths, or more complex pathways (e.g. accounting for mortality, competition and selection, reproductive*
979 *success etc.)?*
- 980 (3) *Are distances or potential movement pathways interpreted in a species- or individual-specific manner?*
- 981 (4) *Is connectivity being considered from the perspective of a patch (landscape element), between a pair of*
982 *landscape elements, or as an aggregate property of the entire landscape?*
- 983 (5) *Is connectivity used as a stand-alone quantity, as an explanatory variable of a statistical model, or as a part of a*
984 *full population model, allowing Population Viability Analysis (PVA)-like evaluations of population survival?*

Panel 2 - Challenges and considerations for connectivity studies

General challenges and considerations

- Different conceptual and operational definitions for functional connectivity are required.
- Species are likely to have alternative dispersal modes.
- Monitoring and modeling long-distance dispersal can be challenging.
- The effects of spatial autocorrelation on parameterization and interpretation need to be considered.
- Species interdependencies and community effects should be considered, particularly in the context of conservation planning.
- Connectivity calculations for high-dimensional problems can require significant computing resources.
- Determining connectivity for non-stationary distributions (e.g. due to climate change) may need to be considered.

Data requirements and challenges

- Minimally, information regarding location and size of habitat patches are necessary for deriving distance-based measures, such as nearest neighbour distances, buffer measures and many graph-based metrics.
- Identifying the scale(s) at which species use the landscape (dispersal capability) makes it possible to use species-specific buffer or kernel-type connectivity measures.
- Neighbourhood characteristics provide a better understanding of local landscape characteristics, and improve estimates of emigration and immigration rates. Unfavourable habitat surrounding a patch will tend to decrease dispersal to and from the patch, reducing its functional connectivity.
- Detailed information about landscape structure is needed for detailed analysis of movement including development of path-type measures. It is assumed that different habitats have different species-specific effects on movement.
- Data regarding species behaviour, including perceptual ability and behaviour at habitat boundaries improves analyses of movement paths and probabilities. Direct observations, satellite tracking data or mark-recapture data are usually needed to parameterize these models.
- Demographic information such as population size, reproduction rates, and mortality are necessary for parameterising full population models that have connectivity as a component. These data can be difficult to obtain, and are typically species- and environment-specific.
- Estimates of environmental change are needed to assess the effects of processes such as succession, climate change or anthropogenic changes on connectivity, particularly over long spatial distances or time intervals.

Habitat-specific challenges and considerations

Terrestrial environments

- Effectively 2-dimensional landscapes.
- Radially symmetric responses are frequently assumed.
- Landscape barriers, such as roads, rivers or urban areas may be important for ground-dwelling species.
- Landscape traversability (e.g., differential costs of moving through forest vs. agriculture) is an important consideration.

Riverine environments

- Typically represented using 1 or 2 dimensions.
- Strongly asymmetric flow between upstream and downstream locations is common.
- Strong physical barriers (e.g. waterfalls, dams) often exist.
- Large temporal fluctuations are common.

Marine environments

- Truly 3-dimensional.
- Fluid dynamics (e.g. advection and diffusion by winds and ocean currents) are important processes, and are computationally intensive to model.
- Complete dispersal barriers are less common than in terrestrial or riverine systems, and are often cryptic.
- Strong asymmetries in connectivity patterns are common.
- Species-specific transport mechanisms can be challenging to identify, and demographic rates (e.g. mortality) can be difficult to obtain.

989 **Table I:**

990 This table summarizes and compares different methods of measuring population connectivity. Direct methods are
 991 techniques that can detect the physical movement of individuals between populations. Indirect methods make
 992 strong inferences regarding movement between populations.

993
 994 *Extent:* The typical order of magnitude of the extent of the study area covered by the technique. In spatial terms,
 995 this corresponds to the bounding box, or areal range that the technique operates at. In temporal terms, this is the
 996 duration over which such studies typically occur.

997
 998 *Resolution:* The typical order of magnitude at which the technique is able to resolve differences between objects. In
 999 spatial terms, this corresponds to the pixel size of an image, or the accuracy of determining the position of a tracking
 1000 device. In temporal terms, this is the minimum time difference that is possible between successive measurements.

1001
 1002 *Environment:* The environment for which the technique is primarily suited: terrestrial, aquatic (marine or
 1003 freshwater), or any.

1004
 1005 *Data type:* The geometry typically obtained by this technique, point locations, line tracks, patches or displacements.
 1006 Displacements only measure the differences between start and end locations with no regard to processes occurring
 1007 between the two.

1008
 1009 *Sample scale:* The level at which the sample data is typically collected. Individual means that individual organisms
 1010 are marked, tagged, observed. Population means that multiple individuals are monitored simultaneously.

1011
 1012 *Constraints:* Limitations associated with the use of the technique. Note that indirect methods place additional
 1013 demands in terms of processing requirements (e.g. genetic analysis) and technical aspects of data analysis.

1014
 1015 *Selected references:* Reviews or illustrative applications of the technique.

Table I: Methods for empirically quantifying population connectivity.

	Method	Extent (typical order of magnitude)		Resolution (typical order of magnitude)		Environment	Data type	Sample scale	Constraints	Selected References
		Spatial	Temporal	Spatial	Temporal					
Direct methods	Visual observation	Hundreds of metres or less	Study duration, typically daily or aggregated over time	Metres or less	Instant	Any	Any	Individuals	Sampling effort, species visibility at observation distance. Data recording and processing effort.	Sutherland 2006
	Mark-recapture	Conditioned on species mobility, typically kilometres	Study duration, conditioned on species mobility and life span.	Conditional on sampling effort and species behaviour	Conditional on sampling effort and species behaviour	Any	Displacement	Individuals	Tagging and sampling effort, organism must be able to carry the marker, and able to withstand handling. Isotopes require hard structures.	Sutherland 2006; Munro et al. 2009; Williamson et al. 2009
	Radio tracking	Hundreds of metres to kilometres	Study duration, typically daily or aggregated over time	Metres	Seconds to Days	Typically terrestrial, some aquatic using sound	Points or routes	Individuals	Tagging and sampling effort, organism must be able to carry the transmitter, and able to withstand handling. Signal transmission is also necessary.	Millsaugh and Marzluff 2001
	Geographic Positioning System (GPS) sensor	Global	Days to months	Metres	Seconds to Days	Terrestrial	Points or routes	Individuals	Tagging effort, organism must be capable of bearing the transmitter, and strong enough to withstand handling. Signal transmission is also necessary.	Urbano et al. 2010; Recio et al. 2011
	Pop-up Satellite Archival Tag (PSAT)	Global	Days to months	Metres	Instant to Days	Aquatic	Points or routes	Individuals	Tagging effort, organism must be capable of bearing the transmitter, and strong enough to withstand handling. Signal transmission is also necessary for collection.	Patterson et al. 2008a; Musyl et al. 2011
	Satellite/aerial surveys	Hundreds of metres per frame to global coverage	Varies by platform and program duration	Centimetres to metres	Varies by platform	Typically terrestrial	Points or patches	Population	Organism must be visible from a vertical aerial perspective.	Turner et al. 2003; Fleming and Tracey 2008; Wang et al. 2010
Indirect methods	Radar	Kilometres	Years (station lifetime)	Sub-metre	Seconds	Terrestrial, aquatic surface	Points or patches	Population	Typically requires a radar installation, though portable radar has been developed.	Ovaskainen et al. 2008c; Randall et al. 2011
	Parentage analysis	Any	Single generation	Parental home/breeding range size	Single generation	Any	Displacement likelihood	Individuals within population	Requires comprehensive sampling of the population. Adequate genetic markers must be developed.	Jones et al. 2005; Jones et al. 2010
	Genetic assignment	Any	Multiple generations	Subpopulation	Multiple generations	Any	Displacement likelihood	Population	Multiple, meaningful markers must be developed. Population assignment depends on genetic models and their associated assumptions.	Berry et al. 2004; Waples and Gaggiotti 2006
	Genetic similarity	Any	Multiple generations	Subpopulation	Multiple generations	Any	Displacement as genetic distance	Population	Multiple, meaningful markers must be developed. Similarity measures depend on genetic models and associated assumptions.	Jaquière et al. 2011; Foster et al. 2012

1017 **Table IIa: Characteristics of connectivity models**

1018 This table summarizes and compares different connectivity modelling approaches. The methods above the blue line
1019 provide ways of estimating connectivity values between objects, whereas those beneath the blue line provide a
1020 means of analysing aspects of local to system-wide network structure and behaviour.

1021
1022 *Domain:* Discrete environments are patches or populations with a defined boundary and homogeneous interior, and
1023 are typically represented using polygons. Semi-continuous domains are typically cell or pixel-based discretizations of
1024 landscape features (e.g. raster landscapes). Continuous domains are infinitely divisible and are typically defined
1025 using equations or a mesh framework (e.g. finite element method or triangulated irregular network).

1026
1027 *Path Type:* Single path methods only allow a single value to describe the connection strength between populations.
1028 Multiple path methods allow multiple channels to influence connectivity between populations. Integrated paths
1029 provide analysis integrated across a distribution of paths.

1030
1031 *Derivation:* Analytical methods have an algebraic foundation and are solved using equations. Algorithmic methods
1032 are required when analytical solutions are complicated or impossible, and are executed out by following a block of
1033 sequential instructions, frequently in a repetitive or recursive manner. Note that many analytical equations can be
1034 characterized and solved by algorithms, and some algorithms (particularly homogeneous recursions) can be
1035 formulated as analytical equations.

1036
1037 In order to move from individual (local approaches) to summarized or integrated representations, aggregations or
1038 convolutions over some form of distance are required, which requires specifying a scale for the analysis.

Table IIa

			Technique	Domain	Path Type	Derivation	Selected References
Estimation of Pair-Wise Connectivity Values	1	$G_i = \frac{\sum_{j=1, j \neq i}^n w_{ij} y_j}{\sum_{j=1, j \neq i}^n y_j}$	<i>Neighbourhood statistics</i>	Any	Typically aggregated	Analytical	Dale et al. 2002; Kindlmann and Burel 2008
	2		<i>Dispersal kernels</i>	Continuous	Integrated	Analytical	Fujiwara et al. 2006; Slone 2011
	3		<i>Least cost path analysis</i>	Semi-continuous	Single	Algorithmic	Douglas 1994
	4		<i>Circuit theory</i>	Semi-continuous	Multiple, Integrated	Algorithmic	McRae et al. 2008
	5		<i>Spatially structured diffusion</i>	Continuous (structured)	Integrated	Analytical	Ovaskainen 2004; Ovaskainen et al. 2008a
	6		<i>Individual-based models</i>	Any	Multiple	Algorithmic	Grimm and Railsback 2005
Analysis of Connectivity	7		<i>Graph theory</i>	Discrete, semi-continuous	Multiple	Algorithmic	Minor and Urban 2008; Urban et al. 2009
	8		<i>Matrix theory</i>	Discrete, semi-continuous	Single*	Analytical	Caswell 2001
	9		<i>Differential Equations</i>	Continuous	Integrated	Analytical	Holmes et al. 1994; Cantrell and Cosner 2003

1041 *Although matrix elements are single, it is possible for them to contain nested functions.

Table IIb: Linkages between approaches for modelling and analysing connectivity

Modelling/analytical approaches		Linkage Explanation
From (Table Ia row)	To (Table Ia row)	
<i>Neighbourhood statistics (1)</i>	<i>Graph Theory (7)</i>	Join count statistics can be linked to graph theory through the construction of spanning trees.
	<i>Matrix Theory (8)</i>	Statistics can be obtained through aggregating and summarizing the matrix data.
	<i>Differential Equations (9)</i>	Statistics can be obtained through integrating, differentiating, combining, or solving sets of equations.
<i>Dispersal kernels (2)</i>	<i>Spatially structured diffusion (5)</i>	Spatially structured diffusion adds spatial structure to the diffusion process / Dispersal kernels can be constructed from spatially explicit diffusion models by averaging across all points in all directions over different lag distances.
	<i>Graph Theory (7)</i>	Dispersal kernels can be used to link weights for graph based analysis / Graph connections can be aggregated at various distance intervals to generate dispersal kernels.
	<i>Matrix Theory (8)</i>	Values for connectivity matrix elements can be obtained from dispersal kernels by using the kernel as a lookup function in conjunction with information about distances between populations.
	<i>Differential Equations (9)</i>	If parametric, dispersal kernels can be used to define differential equations / Sets of differential equations can directly define or be combined to generate a dispersal kernel.
<i>Least cost path analysis (3)</i>	<i>Circuit Theory (4)</i>	Circuit theory can be viewed as an extension to least cost path analysis, allowing for multiple pathways, and addressing strength of corridor use across the landscape.
	<i>Graph Theory (7), Matrix Theory (8)</i>	Connectivity values between pairs of patches or populations derived from LCP analyses can be used as individual cell entries in a connectivity matrix or individual links in a graph.
	<i>Differential Equations (9)</i>	Shortest paths across surfaces defined by differential equations can be solved numerically or using Euler-Lagrange equations.
<i>Circuit Theory (4)</i>	<i>Individual-based models (6)</i>	Using the values from a circuit theory layer, individual pathways can be reconstructed using a cellular automaton-type approach. The resistance values from circuit theory also correspond to the movement rules that an individual follows when traversing a given habitat type / Multiple paths derived from individual based models can be summarized using focal or block statistics to yield surfaces resembling circuit pathways.
<i>Spatially structured diffusion (5)</i>	<i>Individual-based models (6)</i>	Individual paths can be generated from a diffusion process using differential equation solvers in conjunction with a random walk model / Individual-based models could also be used to generate spatial diffusion-type surfaces using focal or block statistics.
	<i>Differential Equations (9)</i>	Spatially structured diffusion directly uses partial differential equations.
<i>Individual-based models (6)</i>	<i>Graph Theory (7), Matrix Theory (8)</i>	Matrix models arise from individual-based stochastic models where each individual moves through its life cycle independently. Probabilities or numbers of successful individuals making the transition between patches can be used as matrix cell entries or graph edge values.
<i>Graph Theory (7)</i>	<i>Matrix Theory (8)</i>	Graphs can be built directly using connection information stored in adjacency or distance matrices and vice-versa
	<i>Differential Equations (9)</i>	Differential equations and graph theory (and consequently matrix theory) can be linked by considering differential equations as the continuous (or limit) form of difference equations for discrete systems. Difference equations can be used to describe relationships between semi-continuous locations in space and time.

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Kool, JT;Moilanen, A;Trembl, EA

Title:

Population connectivity: recent advances and new perspectives

Date:

2013-02-01

Citation:

Kool, J. T., Moilanen, A. & Trembl, E. A. (2013). Population connectivity: recent advances and new perspectives. *LANDSCAPE ECOLOGY*, 28 (2), pp.165-185. <https://doi.org/10.1007/s10980-012-9819-z>.

Persistent Link:

<http://hdl.handle.net/11343/282796>