**Population connectivity: recent advances and new perspectives**

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

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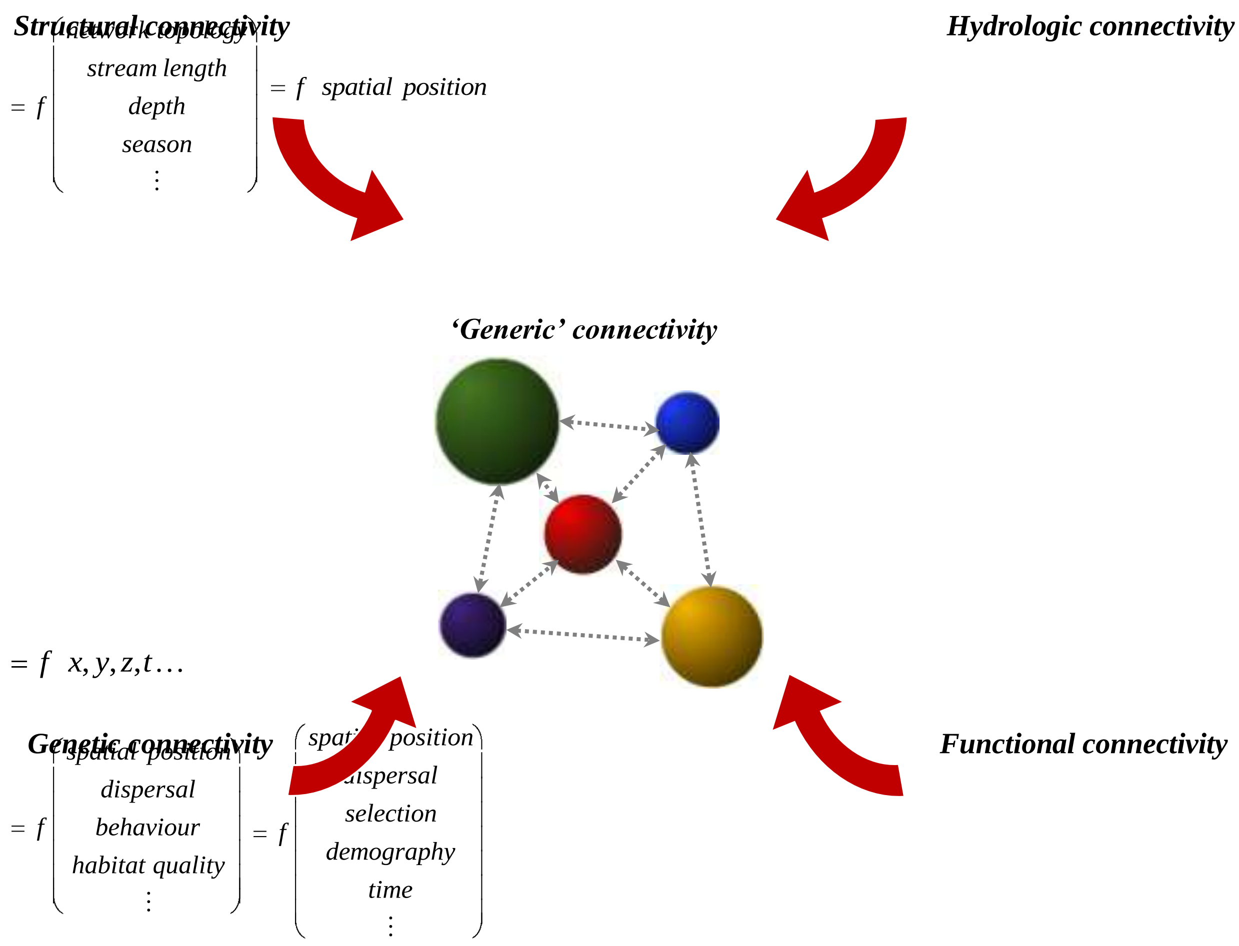
**Panel 1: Deconstructing connectivity**

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?*

*(2) How are distances between landscape elements determined? For example, are they Euclidian distances, least-cost paths, or more complex pathways (e.g. accounting for mortality, competition and selection, reproductive success etc.)?*

*(3) Are distances or potential movement pathways interpreted in a species- or individual-specific manner?*

*(4) Is connectivity being considered from the perspective of a patch (landscape element), between a pair of landscape elements, or as an aggregate property of the entire landscape?*

*(5) Is connectivity used as a stand-alone quantity, as an explanatory variable of a statistical model, or as a part of a 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.

**Table I:**

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

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

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

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

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

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

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

*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 |
| Direct methods | *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 |
| Direct methods | *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. | Millspaugh and Marzluff 2001 |
| Direct methods | *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 |
| Direct methods | *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 |
| Direct methods | *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 |
| Direct 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 |
| Indirect methods | *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 |
| Indirect methods | *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 |
| Indirect methods | *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. | Jaquiéry et al. 2011; Foster et al. 2012 |

**Table IIa: Characteristics of connectivity models**

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

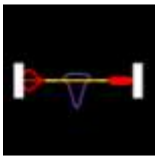
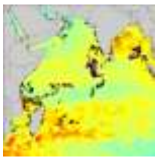
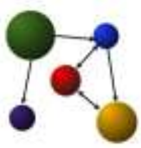
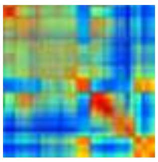
*Domain:* Discrete environments are patches or populations with a defined boundary and homogeneous interior, and are typically represented using polygons. Semi-continuous domains are typically cell or pixel-based discretizations of landscape features (e.g. raster landscapes). Continuous domains are infinitely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

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

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

In order to move from individual (local approaches) to summarized or integrated representations, aggregations or 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 | $G_i = \frac{\sum_{j=1, j \neq i}^{n} w_{ij} y_j}{\sum_{j=1, j \neq i}^{n} y_j}$ | *Neighbourhood statistics* | Any | Typically aggregated | Analytical | Dale et al. 2002; Kindlmann and Burel 2008 |
| | 2 |  | *Dispersal kernels* | Continuous | Integrated | Analytical | Fujiwara et al. 2006; Slone 2011 |
| | 3 |  | *Least cost path analysis* | Semi-continuous | Single | Algorithmic | Douglas 1994 |
| | 4 |  | *Circuit theory* | Semi-continuous | Multiple, Integrated | Algorithmic | McRae et al. 2008 |
| | 5 |  | *Spatially structured diffusion* | Continuous (structured) | Integrated | Analytical | Ovaskainen 2004; Ovaskainen et al. 2008a |
| | 6 |  | *Individual-based models* | Any | Multiple | Algorithmic | Grimm and Railsback 2005 |
| Analysis of Connectivity | 7 |  | *Graph theory* | Discrete, semi-continuous | Multiple | Algorithmic | Minor and Urban 2008; Urban et al. 2009 |
| | 8 |  | *Matrix theory* | Discrete, semi-continuous | Single* | Analytical | Caswell 2001 |
| | 9 |  | *Differential Equations* | Continuous | Integrated | Analytical | Holmes et al. 1994; Cantrell and Cosner 2003 |

*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)* | |
| *Neighbourhood statistics (1)* | *Graph Theory (7)* | Join count statistics can be linked to graph theory through the construction of spanning trees. |
| | *Matrix Theory (8)* | Statistics can be obtained through aggregating and summarizing the matrix data. |
| | *Differential Equations (9)* | Statistics can be obtained through integrating, differentiating, combining, or solving sets of equations. |
| *Dispersal kernels (2)* | *Spatially structured diffusion (5)* | 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. |
| | *Graph Theory (7)* | 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. |
| | *Matrix Theory (8)* | 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. |
| | *Differential Equations (9)* | 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. |
| *Least cost path analysis (3)* | *Circuit Theory (4)* | 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. |
| | *Graph Theory (7),* *Matrix Theory (8)* | 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. |
| | *Differential Equations (9)* | Shortest paths across surfaces defined by differential equations can be solved numerically or using Euler-Lagrange equations. |
| *Circuit Theory (4)* | *Individual-based models (6)* | 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. |
| *Spatially structured diffusion (5)* | *Individual-based models (6)* | 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. |
| | *Differential Equations (9)* | Spatially structured diffusion directly uses partial differential equations. |
| *Individual-based models (6)* | *Graph Theory (7), Matrix Theory (8)* | 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. |
| *Graph Theory (7)* | *Matrix Theory (8)* | Graphs can be built directly using connection information stored in adjacency or distance matrices and vice-versa |
| | *Differential Equations (9)* | 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. |