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Review

Emerging Network-Based Tools in Movement Ecology

David M.P. Jacoby^{1,*} and Robin Freeman¹

New technologies have vastly increased the available data on animal movement and behaviour. Consequently, new methods deciphering the spatial and temporal interactions between individuals and their environments are vital. Network analyses offer a powerful suite of tools to disentangle the complexity within these dynamic systems, and we review these tools, their application, and how they have generated new ecological and behavioural insights. We suggest that network theory can be used to model and predict the influence of ecological and environmental parameters on animal movement, focusing on spatial and social connectivity, with fundamental implications for conservation. Refining how we construct and randomise spatial networks at different temporal scales will help to establish network theory as a prominent, hypothesis-generating tool in movement ecology.

Trends

Network theory is developing in its application across multiple disciplines.

Animal movement networks can reveal important insight about ecological connectivity.

Further development is necessary to fully encapsulate temporal dynamics.

We discuss using network metrics to understand spatial and social ecology.

Reducing Complexity in a Technological Age

Since antiquity the flow of valuable goods such as silk from China, spices from India, or ivory from Africa has criss-crossed the globe on trade networks that have been heavily influenced by geography and the prevailing sociocultural climate [1]; these factors have had extraordinary impact on the evolution of human society over the past 13 000 years [2]. Analogously, animal movement, that is reliant on the underlying geographic landscape and the social environment in which animals find themselves, can strongly influence the flow of genetic material, infectious disease, and cultural innovations within a population [3–5]. The analysis of social systems has received considerable attention in the scientific literature, and robust quantitative analyses of animal **social networks** (see [Glossary](#)) are now firmly embedded in behavioural ecology and evolution [6–9]. Despite considerable theoretical overlap and broad utility in the study of human mobility and transportation networks (e.g., [10,11]), movement ecologists have been slow to adopt **graph theory** as a framework for quantifying habitat connectivity. To help to refine our understanding of the mechanistic links between movement behaviour, the environment, and individual motivation or physiological traits, however, dynamic spatially informed models are key [12,13], not least because they allow us to visually identify patterns relating to ecological processes. Recently, with technological developments that have enhanced our ability to track multiple individuals concurrently over long periods [14–17], the requirement for analytical methods that allow us to interpret how global patterns are shaped by the movements of many individuals have brought network analyses back into the limelight.

Networks themselves have an intuitive appeal, utilising metrics that facilitate the identification of central players, which are key to flow and connectivity within a given system [18] ([Box 1](#)); this provides a means to explore connectivity at multiple scales, clarifying the relationship between structure and process in biological systems [19,20]. Analyses of movement data, retrieved from numerous active or passive methods, currently rely heavily on correlative measures of fixed units (e.g., presence/absence data) to explore inter- and intraspecific comparisons or environmental predictors of movement. Adopting a ‘network perspective’, however, helps to quantify dynamics

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Box 1. The Properties of Movement Networks

Most movement networks of locational nodes and movement edges can be analysed with standard metrics that report the structural and connective properties within a network. We outline here the utility of such metrics for defining areas of crucial importance in movement networks. Unweighted, binary networks (Figure I) simply indicate whether an animal has moved between two locations and this relationship can be accompanied by directionality (Figure Iii). In movement networks there are also two key temporal measures that accompany an edge: (i) time the edge occurred (T-D), providing some chronology of edge formation, and (ii) duration (Δt_m), which is the time taken from leaving one node to arriving at another. Weighting the edges informs the frequency with which that movement has occurred and, by averaging the sums of the linked weights arriving and departing from a location, we obtain the relative node *strength* (indicated by node size in Figure Iii). Across the global cargo shipping network, average node strength was found to scale superlinearly with degree – the number of unweighted edges attached to a node – reflecting interesting properties of transport networks where busy ‘hubs’ are better able to deal with a higher percentage and heavier weighting of flow [11].

Single node-based centrality measures can inform the relative importance of habitat patches [86], and the distribution of these measures across the network might be used to characterise the robustness of a system to fragmentation and animal dispersal [41,87]. We have encountered degree, but several other measures including edge betweenness and eigenvector centrality can indicate important ‘corridors’ that link multiple subgroups of the spatial network (e.g., red node, Figure I). In addition, the clustering coefficient and global measures of community detection can apportion the network into subgroups if activity is restricted to statistically-higher within- rather than between-group movements (i.e., spatial assortment represented by the broken lines in Figure I). While the formation of clusters is often likely to favour spatially close locations, in ecosystems that are subject to stochastic fragmentation, such as temporarily flooded ponds, clustering can indicate potential and time-associated habitat to freshwater residents such as amphibians [87]. For wider ranging or migratory species shortest path length (blue lines, Figure I) can illustrate the most efficient routes through a mosaic of habitats, helping to understand the implications of animals that cannot, or fail to, take these routes [43].

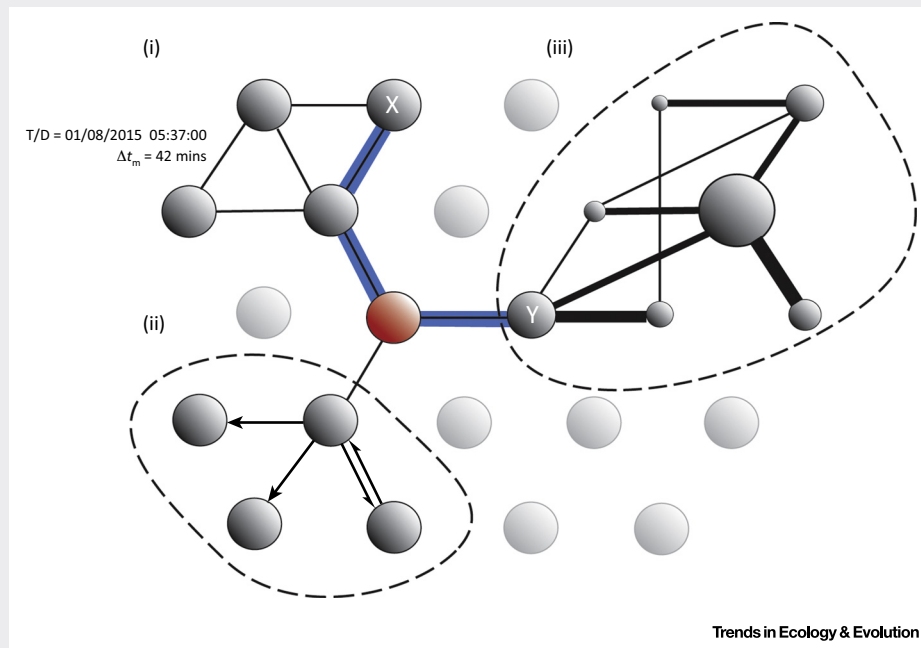


Figure I. Metrics within unweighted (i), directed (ii), and weighted (iii) elements of a movement network across a small AFA. We represent summed degree weight (node size, iii), community structuring (broken line), high betweenness centrality (red node), and shortest path length between location X and Y (blue lines). Each movement edge is associated with a specific time, date, and duration.

while accounting for the non-independence of movement steps. Networks achieve this by considering relationships between network edges that represent the transition between paired locations within the **movement network** of an individual. The flexibility with which we can define these edges, from a simple A to B transition for an individual, to the correlation of route similarity between individuals potentially moving as a collective [21], is crucial for extracting and delineating

Glossary

Adjacency matrix: an $n \times n$ matrix linking all nodes in a network via some form of interaction, in this case movements of animals between one receiver and another. The matrix can be either symmetric or asymmetric to represent non-directed or directed interactions.

Autonomous fixed arrays (AFA): a cluster of sedentary biologging devices capable of wirelessly receiving or capturing long-term information (months to years) on animal space-use by logging presence/absence, where animals are often individually identifiable (e.g., radio-frequency or acoustic receivers, camera traps).

Bipartite graph: the modelled relationship between two different classes of node, in this instance a matrix of individuals-by-location.

Empirically derived Markov model

(EDMM): deterministic model that accounts for the temporal dynamics of transitions between states or, for example, the movements between locations within AFA. These models assume that any movement is based purely on the current state, and not on preceding states, and that transition probabilities between states remain the same over time.

Graph theory: a branch of mathematics that allows us to model the structure of pairwise relations between objects in the form of a network. Objects are typically represented by nodes or vertices and relations by edges between nodes.

Infinite Gaussian mixture models

(IGMM): a probabilistic Bayesian model, with an undefined prior number of mixture components, used to statistically infer aggregated or clustered distributions within data from course observations and/or time-series sampling of the population.

Kernel utilisation distribution

(KUD): a 2D probability density function that estimates the probability of finding an animal within an area based on a given set of recorded locations.

Movement network: movements of an individual or group of organisms between locations, modelled using graph theory.

Social network: the structure describing a series of nodes or individuals and the accumulated dyadic linkages formed through some

behaviour from very large datasets or where we have limited knowledge of the study system. Consequently, movement networks can be spatially explicit and dynamic, explanatory, or predictive; they provide a powerful means to visualise, interpret, and interrogate animal tracking data, generating new hypotheses with clear applications in conservation and resource management.

In this review we draw on recent developments in the acquisition and analysis of spatial data to explore how movement ecology is benefiting from the convergent evolution of network tools across multiple disciplines. The network approach, for example, will clearly benefit from advances in the fields of biologging and machine-sensing of behavioural data which have considerably progressed our understanding of wild animal biology [15,22,23] or, further a field, from urban planning and modelling of human mobility within geography [10,24–26]. We discuss how network theory is generating new hypotheses and explore the novel insights into ecological connectivity provided through animal movement networks. Further, we investigate the interplay between social and **spatial networks** through recent advances that allow inference of social networks from the temporary nature of visitation patterns at logging stations. Still in its infancy, we highlight several areas where we see this field is expanding and discuss the future impact this emergent research theme will have on individual and collective movement in the context of ecology, evolution, and conservation.

Constructing Movement Networks

Static or Dynamic Edges?

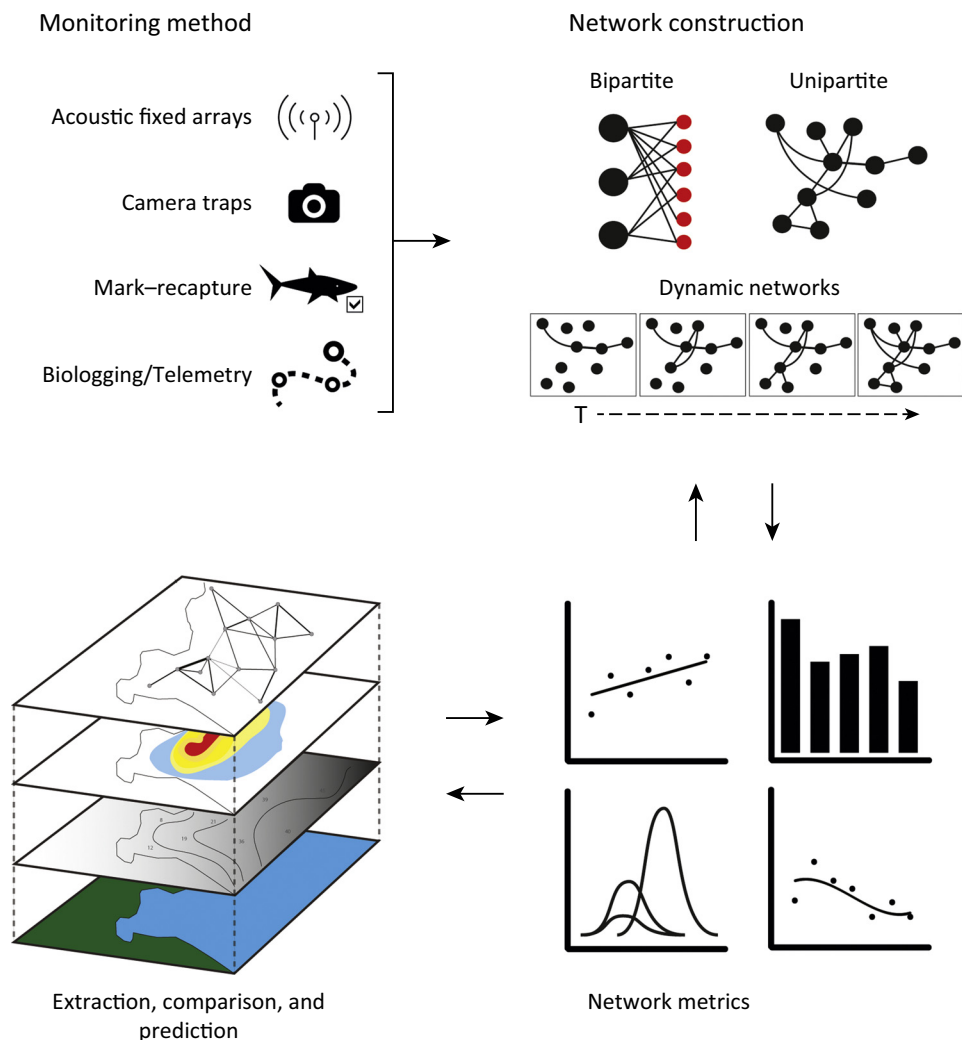
Discrete, localised movements from **autonomous fixed arrays** (AFAs), such as camera traps or acoustic receivers, or high-resolution GPS tracking of individuals during migration or collective movement [14,16,21], all present some form of connectivity of landscapes. Such data are thus amenable to the construction and appraisal of network features (Figure 1). Depending on the research question of interest, networks can be either static or dynamic. Static spatial networks capture the flow of resources or information between locations, where movement data is pooled across multiple sampling periods creating weighted network edges, the properties of which inform the directionality and strength of flow within the system [11,27]. Such networks are important because they can provide a rich understanding of how fixed environmental constraints drive animal movement decisions [28], and thus how the environment shapes patterns in social networks. For example, if the environment restricts movement of animals between areas, this can result in assortative behaviours [29], and potentially the emergence of local traditions [30]. By contrast, dynamic networks of movement – the repeated aggregation of movement steps through time (Figure 1) and/or the correlation of edges among individuals through time – can enable us to extract fundamental behavioural insight from long-term tracking data despite the significant analytical challenges of incorporating time into networks (Box 2). Dynamic networks, for example, have been used to reveal shared decision-making about movement in non-human primates [31] and to study hierarchical group behaviours by examining the lagged correlation of heading routes in collective flocks of birds [21].

Representation of Nodes

Networks can take two possible forms; bipartite or ‘two-mode’ networks, and unipartite ‘one-mode’ networks (Figure 1). Bipartite networks contain two very distinct types of nodes (e.g., individuals and locations) and links are established between them. For example, Fortuna *et al.* [32] consider the modular structure of **bipartite graphs** of giant noctule bats, *Nyctalus lasiopterus*, roosting in a network of trees, and they consider the implications of this structure on the spread and management of disease. Bipartite networks, often the analytical precursor of the two forms, can prove useful for explaining modularity (the clustering of discrete units) and nestedness (hierarchies of visitation) within a network [32–34]. These metrics can be useful in guiding which network components are likely to be important when the data are converted to a

form of direct interaction. For animal social networks this might take the form of agonistic or grooming behaviours, shared group membership, or communicative interactions.

Spatial network: a network graph where nodes have a fixed geographic location and edges are derived from counts or ratios of directed animal movements between the nodes; spatial networks will have a fixed distribution of inter-node distances. Movement networks are an example of a spatially restricted network.



Trends in Ecology & Evolution

Figure 1. Using Graph Theory To Analyse Ecological Data. Animal movement data can be gathered through numerous active and passive monitoring techniques and, with careful consideration, can be used to construct static or dynamic, bipartite or unipartite networks. Network metrics help to describe the important structural properties at multiple scales, informing the generation of hypotheses about when, where, and how animals interact with their environments. Quantitative network tools can then be employed to make comparisons between species, individuals, or different temporal scales, or to make predictions about the impact of habitat change on movement ecology (e.g., knockout experiments).

unipartite network. Importantly, bipartite networks offer a heuristic framework for systems where there are limited data, but which enable growth in complexity as more data become available [34]. Alternatively, unipartite networks, for example, individuals in social networks or locations in movement networks, reveal structure within nodes of the same type. Where nodes represent fixed spatial locations (e.g., in AFAs), unipartite networks better represent the movement of the individual or group, albeit in a discretised manner. Comparisons of such networks can reveal interesting shifts in space-use as individuals develop over time [35] or differences between species [36] that might reflect cryptic, temporal segregation of resource-use in spatially overlapping species. Visualisation of the network structure and the ease with which networks can be restricted to different time-periods, age classes, sexes – as with social networks – helps to quickly identify pertinent questions to explore within the data using quantitative measures of

Box 2. The Importance of Time in Movement Networks

The interaction of animals and their environment is a spatial and temporal process. Static spatial networks condense time, reflecting the overriding structure and its associated processes. Sometimes, incorporating a temporal element is important, however, and this can be done at several scales. Movement networks might be considered at daily, seasonal, annual, or other meaningful periods to reveal how changes in conditions correlating with these arbitrary periods influence how animals move [35]. We might partially capture this by having directional edges. This perspective generates very different structures and patterns from undirected networks. Such classifications, however, still aggregate movements into a single matrix for each period (but see [88] for an exception), and this can be rather subjective, potentially leading to the loss of important characteristics of individual space-use [48,67,76]. Alternatively, with high-resolution tracking comes the potential to explore the spatiotemporal autocorrelation of multiple individuals to understand behaviours such as collective movement and leadership [21].

The directional transition between one node and another is accompanied by a measure of time relating to previous and subsequent detections. Decisions taken by the animal within this time are generally unknown due to the resolution of the data; however, individual consistency in these transition times, or changes under different scenarios, still inform the dynamics of movement. For example, the route-directedness of animals between areas of abundant resources (which could reasonably be expected to negatively correlate with transition time) might increase during times when patchy areas of resource become unavailable. While analyses of dynamic networks are still far from resolved, there have been interesting developments that treat these transitions as states of a Markov chain [48,50,67], where the edges in the network represent the probability of transitioning between areas or patches. Using data from acoustically tagged sevengill sharks, *Notorynchus cepedianus*, Stehfest *et al.* [48] compare **empirically derived Markov models** (EDMM) and network analyses of shark movements. They found that both methods were comparable for revealing sex-specific differences in movement, but that the EDMM preserved the chronological detection sequence, thus performing better in defining priority areas [48]. In addition to EDMMs, calculating multiple measures of movement counts across successive time-steps, and then fitting linear models to dyadic strength (i.e., the connectivity of two locations through repeated flow of animals between them), offers one way of monitoring the shifting dynamics of movement patterns through time [69].

centrality, connectivity, or community formation associated with graph theory (Box 1). Network metrics (reviewed comprehensively in [18] and specifically for animal societies in [37]) report the structural properties of a network at local (individual nodes) and 'global' scales (mean across nodes). These metrics provide dynamic tools for comparing movement graphs between species [33,38–40] or against theoretical models [41]. As a word of caution, however, the size, density or duration of data can strongly influence network structure, raising important questions about how best to truly compare movement networks (see Outstanding Questions); relating these metrics to other information captured in the data, however, can reveal considerable new insights into animal ecology (Table 1).

Generating New Insights and Ecological Applications

In many terrestrial ecosystems, human land-use and resource acquisition have led to widespread landscape fragmentation, isolating organisms to discrete patches of suitable habitat [42]. Consequently, the influence of fragmentation on animal and plant populations has proved to be a rich vein of research, with some applying graph theory to assess the relative importance of individual patches to overall landscape connectivity based on metrics of edges that link important habitat or resources [34]. Studies on invertebrate pollinators, for example, have revealed the importance of corridors to increase movements between fragmented habitats within plant–pollinator networks [27,38]. Migration routes in long-distance avian migrants also rely on a mosaic of connected stopover sites to rest, feed, or shelter from bad weather. The arrival and departure of oriental white storks, *Ciconia boyciana*, at migratory stopover sites were modelled as a network of connected components to identify the shortest path lengths and associated staging sites fundamental to the connectivity of the full migration route [43]. There is considerable scope for such tools to help to inform the ways in which we conserve and manage species by measuring or forecasting the impact of human disturbance on movement or by monitoring endangered species tagged with tracking devices. As an example, variation in the spatial autocorrelation of animal movement steps, post reintroduction, is likely to have considerable bearing on how breeding pairs acclimate to their new environment. Determining how they disperse, and where and when the sexes come together, will inform on the number of individuals

Table 1. Application of Network Metrics To Explore Animal Movement and Landscape Ecology

Species	Data Collection Method	Movement Network Analyses ^a	New Ecological Insights	Refs
<i>Terrestrial</i>				
Common buckeye, <i>Junonia coenia</i> ; variegated fritillary, <i>Euptoieta claudia</i>	Mark–release–recapture	Inter-patch movements; geographically weighted proxy for degree	Corridors increase long-distance movements of habitat-restricted species	[27]
Cactus bug, <i>Chelinidea vittiger</i>	Mark–release–recapture	Betweenness; clustering coefficient; density	Determining which method of network construction best predicts real-world habitat linkages	[89]
Dairy cattle	Shipment records from Dairy Herd Improvement Database	In degree; out degree	Key advances in understanding infection chains and disease outbreak across the dairy industry	[40,53,55]
Delmarva fox squirrel, <i>Sciurus niger cinereus</i>	Simulated dispersion data across suitable habitat	Betweenness; degree distribution; edge redundancy; null modelling	Revealing bottlenecks to dispersal as targets for conservation	[86]
Everglades snail kite, <i>Rostrhamus sociabilis plumbeus</i>	Mark–release–recapture	Betweenness; clustering coefficient; density	Determining which method of network construction best predicts real-world habitat linkages	[89]
Giant noctule bat, <i>Nyctalus lasiopterus</i>	Radio tracking to and from roost trees	Degree centrality; betweenness centrality; community detection; null modelling	Spatial and social segregation of the population influences rate and shape of disease dynamics	[32]
Human, <i>homo sapiens</i>	Ship monitoring systems (global database)	Shipping port betweenness centrality; strength; degree distribution	Connectivity of cargo ship ports possess a heavy-tailed distribution	[11]
Human, <i>homo sapiens</i>	Mobile phone locational data	Network density; distance clustering; entropy of individual trajectory	Human movement is highly predictable	[10,26]
Human, <i>homo sapiens</i>	Mobile phone locational data	Weighted networks; network stability of parasite transmission	Revealing travel routes key to malaria epidemiology	[45]
Mexican spotted owl, <i>Strix occidentalis lucida</i>	Modelling of suitable habitat patches	Edge removal; node removal; null modelling	Population predicted to persist despite substantial loss of habitat	[34]
Oriental white storks, <i>Ciconia boyciana</i>	Satellite tracking-derived stopover sites	Path length	Determining key stopover sites crucial to migration route connectivity	[43]

Table 1. (continued)

Species	Data Collection Method	Movement Network Analyses ^a	New Ecological Insights	Refs
Red postman, <i>Heliiconius erato</i> ; common postman, <i>Heliiconius melpomene</i>	Mark–release–recapture	Mean strength; degree distribution; clustering coefficient; network diameter	Comparable network structures between species; identifying resource hotspots of high connectivity	[38]
<i>Marine</i>				
Atlantic salmon, <i>Salmo salar</i> ; rainbow trout, <i>Oncorhynchus mykiss</i> (farmed)	Fish Health Inspectorate Live Fish Transport Database	Degree centrality	Identified sites of increased infection vulnerability and spread in fish farms	[52]
Bonfish, <i>Albula vulpes</i> ; great baracuda, <i>Sphyræna barracuda</i> ; permit, <i>Trachinotus falcatus</i>	Acoustic telemetry (AFA)	Degree distribution; community detection algorithms	Differentiation of species movement strategies as either central place forager or territory holder	[33]
Blunt-head parrotfish, <i>Chlorurus microrhinos</i> ; rivulated parrotfish, <i>Scarus rivulatus</i> ; scribbled rabbitfish, <i>Siganus doliatus</i>	Acoustic telemetry (AFA)	Path length; clustering coefficient; ‘small world’ structural properties	Reef species make predictable movements that are heavily reliant on a few well-connected parts of the reef.	[41]
Broadnose sevengill shark, <i>Notorynchus cepedianus</i>	Acoustic telemetry (AFA)	Eigenvector centrality; EDMM analysis	Spatial segregation of the sexes as revealed through combining network statistics with Markov models	[48]
Caribbean reef shark, <i>Carcharhinus perezi</i> ; small spotted catshark, <i>Scyliorhinus canicula</i>	Acoustic telemetry (AFA)	Degree; edge filtering; betweenness; network density; average path length	Network visualisation helps to explore hypotheses, and abiotic variables predict movement	[35]
Galapagos shark, <i>Carcharhinus galapagensis</i> ; giant trevally, <i>Caranx ignobilis</i>	Acoustic telemetry (AFA)	Degree centrality; betweenness	Marine predators are important in nutrient transfer between reef habitats	[39]
Pigeye shark, <i>Carcharhinus amboinensis</i> ; spottail shark, <i>Carcharhinus sorrah</i>	Acoustic telemetry (AFA)	Eigenvector centrality; closeness; strength; community detection	Marine predators utilise movement corridors between vulnerable core areas	[36]
Schoolmaster snapper, <i>Lutjanus apodus</i> ; stoplight parrotfish, <i>Sparisoma viride</i>	Acoustic telemetry (AFA)	Eigenvector centrality; EDMM analysis	Inter- and intraspecific differences in spatiotemporal patterns of reef fishes	[67]
Yellowfin tuna, <i>Thunnus albacares</i>	Acoustic telemetry (AFA)	Mean degree; network density; fragmentation; mean strength	Layout of artificial fish aggregating devices (FAD) can influence tuna connectivity, cohesion. and management	[51]

^aThe different available network metrics are discussed in [Box 1](#).

necessary to support a successful reintroduction programme that is fundamentally rooted in the ecology of the species in question [44].

Understanding the Patterns, Dynamics, and Drivers of Mobility

More broadly, network analyses enable us to deconstruct animal movement patterns into individual behavioural processes (e.g., dispersal patterns) and population-level biological motivation such as social drivers or environmental factors [28]. Network community detection algorithms, for example, offer ways to explore the core space-use of species at multiple scales by redefining what comprise the network nodes (e.g., individual receivers, fixed quadrats, different habitat types), revealing the underlying social and spatial drivers of movement [33]. Recently, networks have also had significant impact on our understanding of broad-scale patterns of mobility in human societies, not least for modelling global transport and cargo networks [11,25], with considerable success in recreating and predicting human movement from networks of mobile phone usage [10,26,45] (Table 1 for summary). How and when we socialise, and how this is influenced by routine movements between familiar locations, can all be captured from networks of mobile phone transmitters or radio-frequency identification (RFID) systems such as public transport ticketing systems (e.g., London's Oyster card system). In addition, while social data on conspecifics can be used to improve predictions about the location of unknown individuals [46], locational data from animal tracking can be used strategically to recreate a broader understanding of social dynamics in a population (Box 3).

The emergence of spatial networks in animal movement ecology has been particularly useful in systems where connectivity and multi-individual ranging behaviour are difficult to study, such as marine systems (e.g., [33,35,39,41,47,48]) where movement must sometimes be inferred between discrete locational fixes. More widely, however, the development and application of biologging technologies are progressing faster than our ability to analyse the vast data they generate [15,33,47]. Network analyses, alongside several other burgeoning methodologies (e.g., Bayesian bridges [13]; step-selection methods [49]; behavioural state modelling [50]), now offer more integrative, comparative, and hypothesis-driven approaches to movement ecology [16,33,35,47]. As such, network tools are finding a place in conservation and management by enabling us to measure and quantify singular and correlative linkages between areas maintained by unseen animals, that traditional static analyses likely miss. This has proved to be crucial, for example, for understanding the fission–fusion dynamics of commercially important fishes between networks of fish aggregating devices [51], for measuring nutrient transfer by marine predators within mesophotic coral reef communities [39], or for quantifying the transport and spread of disease within coastal aquaculture farms [52].

Spatial Patterns Within Movement Networks

The utility of spatial graphs in ecology has been largely driven by the need to better understand disease dynamics and rates of transmission within populations and across geographic landscapes [32,45,53–59]. This body of research has broadly informed how we model spatial networks of flow and connectivity, and how we can use networks as predictive tools [32,57] incorporating the distance between nodes within the underlying mobility network.

It is important to model the modularity and the dynamic structural properties of a movement network because this can reflect the underlying robustness (or vulnerability) of the biological landscape through which animals move. Network structure can be characterised by the distribution of node-based metrics within the population. For example, a power-law degree distribution is indicative of a disproportionately low number of nodes harbouring a high percentage of the connections; these nodes are the hubs within the network [60], and might indicate priority areas for conservation owing to a high in- and out-flow of individuals. In fact, multiple species of roving herbivorous fish were found to be heavily reliant on a few well-connected areas

Box 3. Spatial and Social Interactions Within AFAs

Movement and social behaviour are intrinsically linked, and the concept of encounter rates is a central tenant in ecology, having broad influence on community structuring [12], predator–prey dynamics [90], and information transfer [91], driving the evolution of socially-dependent behaviours such as cooperation [92]. The movement network approach, applied to passive telemetric data [35], delves deeper than traditional analytical methods to consider the connectivity of habitats via the animals that move between the receivers, thus allowing greater power to test hypotheses from presence/absence data (Figure 1A,B). Indeed flow within a system is heavily dependent upon the structural properties of the network, revealing a great deal about the connective importance of individual nodes [18], and can help – in the context of spatial networks – to better inform areas to prioritise for conservation.

An interesting development of this conceptual framework is that, by considering the nodes of an AFA as inherently connected, the arrival and departure of individual animals at receiver locations can be mapped in space and time to explore co-occurrences and social interactions in free-ranging, fully unperturbed animals. Using a rich, long-term dataset of electronically tagged great tits, *Parus major*, in Wytham Woods, Oxfordshire (UK), researchers at the Edward Grey Institute first conceived the idea that wild social interactions might be inferred based on the arrival and departure of individuals in an array of RFID receivers [83] (Figure 1C). Statistically-significant ‘gathering events’, which can be thought of as social sampling periods, can be revealed through the application of data-mining techniques (e.g., GMMs) to the spatiotemporal datastream. This approach has recently facilitated the study of long-term, dynamic social networks in passerine birds, providing substantial insight into the ecological and evolutionary implications of social interactions in the wild [28,84,93–95]. This system relies upon attracting individuals to the receivers (i.e., PIT tag readers at feeding stations) to infer interactions during feeding bouts. It remains to be seen, however, whether the same approach can be used to sample incidental wild social interactions using passive AFAs. If successful, this approach will help to further reconcile the link, *in situ*, between population dynamics and animal movement [12].

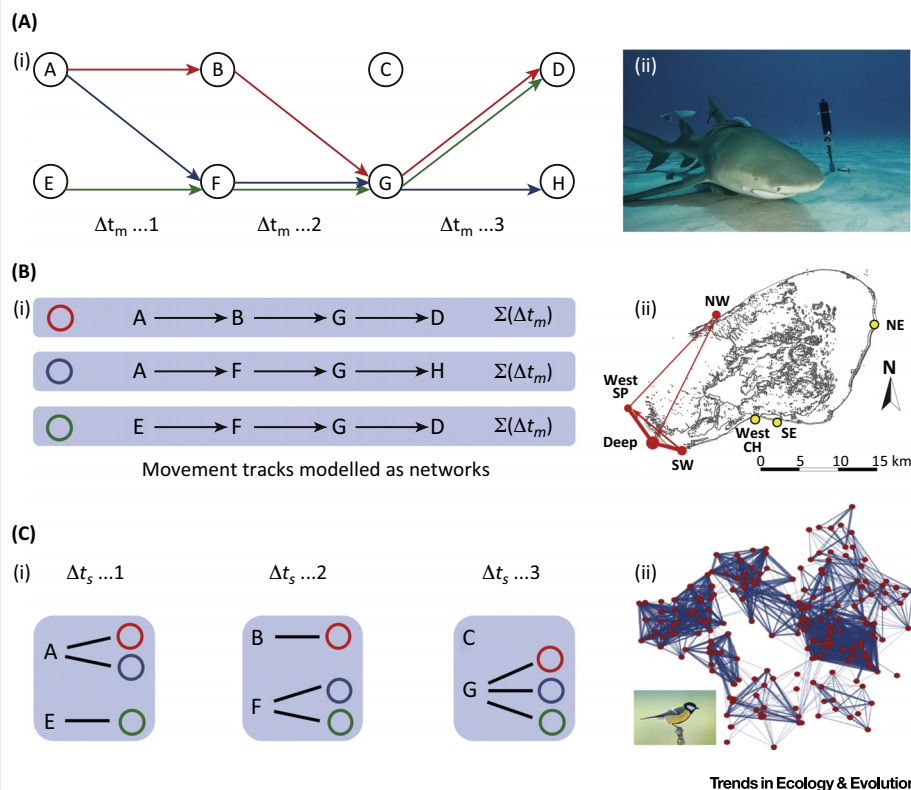


Figure 1. Simplified Schematic Illustrating the Construction and Application of Movement and Social Networks from AFA Data. (A) AFA of eight receivers where a time (Δt_m) is associated with the movement (m) of an individual(s) between locations (i), a lemon shark, *Negaprion brevirostris* approaching an acoustic receiver (ii) (credit Matt Potenski). (B) Movement networks with a corresponding total time $\Sigma(\Delta t_m)$ of three differently coloured individuals through our hypothetical AFA (i) and a real movement network of giant trevally, *Caranx ignobilis*, through an AFA at Pearl and Hermes Atoll in the Pacific Ocean (ii), redrawn from [39]. (C) Social co-occurrences (s) of individuals within a time frame (Δt_s) determined using a Gaussian mixture model (IGMM) (i); great tits, *Parus major* (credit Luc Viatour, CC BY-SA), have been extensively studied using passive integrated transponder (PIT) tags and receivers at feeding stations to infer social foraging networks in the wild (ii), redrawn from [84].

Box 4. Null Modelling of Spatial Data

Null models that incorporate randomisation procedures enable us to control for the non-independence associated with network data (overviewed in [8,37,96]). Movement networks are also spatially embedded, and thus null models must account for the spatial relationships between nodes. Spatially informed null models are already prevalent in animal social network analysis to control the confound that some habitats are more likely to see aggregation of individuals as a result of variation in the optimality of habitat types [8,29,96]. However, there are numerous ways in which network data can be randomised. Given the linear nature of mobility we would expect movement networks in most instances to be highly structured, and the randomisation procedures and test statistics chosen for hypothesis-testing must reflect this.

Node permutation of a movement **adjacency matrix** allows randomisation of the locations visited while retaining the number of possible locations. Alternatively, edge permutation (i.e., movements, directed or undirected) can be used to test whether the observed frequency with which animals move between areas is a non-random process. Both procedures however, have limitations that increase the likelihood of type I and type II errors ([8,29] for discussion). Instead, shuffling the datastream, in other words randomisation of the raw visitation pattern and chronology before constructing a network, provides a more biologically-meaningful method for determining whether movement is truly non-random [96]. A novel randomisation procedure outlined in [97] combines both node-based and datastream approaches to permute data gathered via GPS tracking devices. Further, multiple null models can be used to evaluate competing hypotheses [25]. Choosing a test statistic that is relevant to spatially restricted nodes is also important, and edge-based metrics such as least-cost path, route path diameter, and route redundancy can be highly informative for understanding the connectivity of spatial networks [20]. Further detailed discussion of randomising spatial networks and the spatial component of animal social networks is available and would be recommended for future applications [8,29,96,98].

of the Great Barrier Reef – monitored using an acoustic AFA – revealing inherent vulnerabilities in the ‘ultra small-world’ nature of these movement networks should these areas with a high degree centrality become perturbed [41]. We caution, however, that without a high number of nodes within a network (e.g., hundreds to thousands) such properties are very difficult to truly determine [61]. Finn *et al.* [33] argue that spatial networks are much more likely to take the form of a regular graph where each node is connected to its nearest neighbour, but this can be dependent on in-built structure in the data (e.g., array layout or sampling frequency). Another way to assess the robustness of a measured animal movement network is to evaluate network degradation through the systematic removal of nodes to mimic habitat loss [35], a tool likely to prove informative for predictive management. This has been used to good effect to show that the activity space of pigeye and spottail sharks [36], and migration routes of oriental white storks [43], become significantly fragmented, then disconnected, after the removal of only a few habitat nodes that are of crucial ecological importance to these animals. For some ecosystems or species in particular, these hubs for animal mobility – whether on a migration route (e.g., watering holes) or part of a core activity area (e.g., latrines) – might not be immediately apparent; density estimates of individual occurrences, for instance, might tell us nothing about the repeated ranging behaviour, or the time associated with such behaviour, that can be captured by the relative flow of movements to and from the surrounding habitats.

Spatial autocorrelation within networks is the likelihood that nodes that are geographically nearer to each other are more likely than random to share similar metrics than are those further away. While this poses a potential challenge to how we develop null models for significance testing of spatial networks (Box 4), it can also guide interesting questions about how animals use space. The spatial assortment of nodes within a weighted movement network, for example, could be indicative of behavioural mechanisms such as central place foraging, whereas assortment by habitat type suggests that movement is perhaps driven predominantly by resource distribution, allowing us to make generalisations about patterns of space-use [62]. Further, the correlation of activity at different spatial nodes can be tracked repeatedly through time to generate hypotheses about peak flow patterns. We predict that these types of techniques will prove useful for monitoring the impacts of climate change through time on route determination and repeatability in migratory animals. For these tools to be robust, however, null hypothesis significance testing is vital [8] (Box 4).

Future Research Directions

As graph theory and its utility continue to develop in parallel across multiple disciplines, from physics to the computer sciences, and from genetics to mathematical biology, the potential to broaden the scope of these exciting tools in movement ecology grows. We predict significant developments in this field by combining network-based approaches with other measures of individual biology such as machine-sensed energetics (e.g., accelerometer tags), genetic profiling, and personal observations of behaviour, providing multiple attributes that can be associated with the network nodes and edges. Such holistic, integrated approaches have already proven highly successful in providing a deep mechanistic understanding of behaviour in somewhat cryptic species [63].

Capturing Visitation Chronology and Duration

There are ongoing challenges associated with incorporating time into movement networks. We foresee great potential in methods that search for repeated topologies (e.g., temporally recurring motifs) or that adopt time-ordered and time-aggregated networks within the movement structure [64–66], combined with behavioural state modelling that allows us to explore transitional shifts [48,50,67]. Furthermore, we anticipate entropy maximisation techniques being incorporated into movement networks to predict probable flow strength and directionality based on the relative loading of units – this could be individuals or resources – at each node within the spatial network. Such techniques have proven extremely successful in a geographic context for predicting the emergent patternation of the 2011 London riots for example [24], or the chronology and dimensionality of human settlements in the Middle Bronze and Iron Ages in Syria [68]. Such innovations are likely to help to inform temporal analyses because the directionality of edges also pertains to time.

Understanding the mechanisms behind movement through time might also be facilitated by adopting a multiplex approach to connectivity [69]. This would provide two interesting developments in how we analyse movement networks: first, by quantifying the trajectory of changes in continuous measures of dyadic metrics, deviations from this trajectory will highlight the timing and magnitude of non-random changes in movement patterns, allowing us to detect subtle but significant shifts in behaviour [69]. Second, looking for correlative relationships between multiple measures of habitat connectivity, for example the transfer of material carried on the prevailing wind or current, will provide a means of measuring the influence of environmental parameters on movement that account for directionality and transition time that cannot be captured without dynamic analyses.

Route Repeatability and Refinement

With recent evidence that repeatable social network positions can be indicative of personality traits within animals [70–72], we foresee an interesting avenue of research determining whether individual movement trajectories through a landscape might show consistent variation or perhaps plasticity during ontogeny. Here, visitation chronology can be captured as a bipartite network, the properties of which might be compared across individuals in the population. This could have interesting implications for animals moving in groups: using light-weight GPS trackers for example, route fidelity in solo homing pigeons become refined in accuracy over repeated journeys [73]; these routes might then recapitulate under ‘social’ flocking scenarios in ways that are predictive of social relationships [74]. Similarly, the migratory journeys of Atlantic puffins are strongly recapitulated by individuals following their own routes during what otherwise appear to be dispersive migrations [75]. In fact, recent advances in the analyses of vast trajectory data within geography and urban planning suggest that network analyses can improve the positional accuracy of GPS data to reduce data redundancy and better interpolate or explore individual and collective trajectories [76]. With such huge data from these fields, researchers can now fully harness the predictive power of network tools for understanding emergent spatial

patterns across many different contexts [24,68]. In species for which such tracking data is not feasible, simple, binary presence/absence data, analysed as a connected network, can help us to address crucial ecological questions surrounding the behavioural motivation of animals living in challenging or remote environments. Interestingly, artificial neural networks, used to estimate movement probability kernels (**kernel utilisation distribution**, KUD), offer movement models that now integrate the spatial structure, the spatial variability of the resource landscape, and individual memory of previously visited locations, strengthening the link between pattern, personality, and process [13,77]. Further questions of interest are listed in the Outstanding Questions.

Concluding Remarks

Spatial connectivity in biological systems can be quantified at myriad scales and by using broadly different data collection methods. Only recently has technology enabled us to monitor, round-the-clock, the behaviour of tens, hundreds, or even thousands of individuals concurrently for periods of weeks, months, or even years [14–16,78–80]. Graph theory has already proved to be an intuitive and informative paradigm for the measurement and appraisal of complex connected systems from social networks to transport systems and beyond [25,60,81]. Network-based analyses offer a robust, quantitative set of metrics that complement traditional means of understanding movement ecology within AFAs of camera traps, acoustic receivers, mobile phone masts, and RFID stations, or from continuous satellite tracking data. With the current unprecedented availability of high-resolution and/or long-term tracking data, it is more important than ever that we begin to connect the tools available to the appropriate research questions [82]. In addition to movement, the temporal component associated with arrival and departure of animals at network nodes can offer information on the social interactions of free-ranging tagged animals through analysis of individual co-occurrences [83,84]. These methods are one of several burgeoning disciplines – including data mining [23], machine learning [85], and automated image-based tracking [17] – that utilise recent advances in computational power to analyse large, complex time-series data and that are guiding more integrative, comparative, and hypothesis-driven approaches in the field of animal movement ecology [23,47]. The use of network-based tools to understand the movement, flow, and connectivity of habitats and individuals in the wild offers new opportunities to unravel underlying mechanisms and to provide crucial new understanding of the ecology and behaviour of free-ranging animals.

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References

- Seland, E.H. (2013) Networks and social cohesion in ancient Indian Ocean trade: geography, ethnicity, religion. *J. Glob. Hist.* 8, 373–390
- Diamond, J.M. (1998) *Guns, Germs, and Steel: A Short History of Everybody for the Last 13,000 years*, Vintage
- Allen, J. et al. (2013) Network-based diffusion analysis reveals cultural transmission of lobe feeding in humpback whales. *Science* 340, 485–488
- Bohonak, A.J. (1999) Dispersal, gene flow, and population structure. *Q. Rev. Biol.* 74, 21–45
- Fèvre, E.M. et al. (2006) Animal movements and the spread of infectious diseases. *Trends Microbiol.* 14, 125–131
- Pinter-Wollman, N. et al. (2014) The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* 25, 242–255
- Krause, J. et al. (2014) *Animal Social Networks*, Oxford University
- Groft, D.P. et al. (2011) Hypothesis testing in animal social networks. *Trends Ecol. Evol.* 26, 502–507
- Kurvers, R.H.J.M. et al. (2014) The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol. Evol.* 29, 326–335
- Louail, T. et al. (2015) Uncovering the spatial structure of mobility networks. *Nat. Commun.* 6, 6007
- Kaluza, P. et al. (2010) The complex network of global cargo ship movements. *J. R. Soc. Interface* 7, 1093–1103
- Morales, J.M. et al. (2010) Building the bridge between animal movement and population dynamics. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 365, 2289–2301
- Dalziel, B.D. et al. (2008) Fitting probability distributions to animal movement trajectories: using artificial neural networks to link distance, resources, and memory. *Am. Nat.* 172, 248–258
- Kays, R. et al. (2015) Terrestrial animal tracking as an eye on life and planet. *Science* 348, aaa2478
- Rutz, C. and Hays, G.C. (2009) New frontiers in biollogging science. *Biol. Lett.* 5, 289–292

Outstanding Questions

Temporal

To what degree are patterns of animal/environment interaction repeated? For example, are there repeated structural patterns or 'motifs' within movement networks?

Can we detect temporal resource partitioning? For example, are overlapping spatial networks structured such that resources are shared through temporal segregation?

Are sequences of spatial networks stable over time (in chronology and duration)?

Do environmental dynamics (e.g., water appearance/flow, wind speed/direction) correlate with dynamics of movement?

How can we best utilise temporal shifts in the network and individual edge durations? For example, can this inform changes in navigational abilities between individuals or under different conditions?

Spatial

Can we identify drivers of repeated space use? For example, are there correlates of repeated network flow?

Do areas that are assorted by spatial location or those that are assorted by habitat type have more similar network properties? Is this assortment evidence for spatial autocorrelation or individual habitat preferences?

Can we use these methods to better predict animal space use?

Can network methods help us to understand more about the global connectivity of migratory animals from pre-existing population data?

Scale and Sampling

How representative are our individual-based movement networks of real population-level space-use and dispersal? How many individuals are likely to provide a representative sample? Could this be reasonably resolved through simulation?

At what temporal scale do we capture important ongoing processes?

How do different array/node designs generate different networks and what influence does this have on what we

16. Hussey, N.E. *et al.* (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348, 1255–1262
17. Dell, A.I. *et al.* (2014) Automated image-based tracking and its application in ecology. *Trends Ecol. Evol.* 29, 417–428
18. Newman, M. (2010) *Networks: An Introduction*, Oxford University Press
19. Cowan, R. and Jonard, N. (2004) Network structure and the diffusion of knowledge. *J. Econ. Dyn. Control* 28, 1557–1575
20. Dale, M.R.T. and Fortin, M.-J. (2010) From graphs to spatial graphs. *Annu. Rev. Ecol. Syst.* 41, 21–38
21. Nagy, M. *et al.* (2010) Hierarchical group dynamics in pigeon flocks. *Nature* 464, 890–893
22. Kabra, M. *et al.* (2013) JAABA: interactive machine learning for automatic annotation of animal behavior. *Nat. Methods* 10, 64–67
23. Krause, J. *et al.* (2013) Reality mining of animal social systems. *Trends Ecol. Evol.* 28, 541–551
24. Davies, T.P. *et al.* (2013) A mathematical model of the London riots and their policing. *Sci. Rep.* 3, 1303
25. Choi, J.H. *et al.* (2006) Comparing world city networks: a network analysis of internet backbone and air transport intercity linkages. *Glob. Netw.* 6, 81–99
26. Song, C. *et al.* (2010) Limits of predictability in human mobility. *Science* 327, 1018–1021
27. Haddad, N.M. (1999) Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecol. Appl.* 9, 612–622
28. Farine, D.R. *et al.* (2015) The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. *R. Soc. Open Sci.* 2, 150057
29. Farine, D.R. (2014) Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Anim. Behav.* 89, 141–153
30. Aplin, L.M. *et al.* (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518, 538–541
31. Strandburg-Peshkin, A. *et al.* (2015) Shared decision-making drives collective movement in wild baboons. *Science* 348, 1358–1361
32. Fortuna, M.a. *et al.* (2009) The roosting spatial network of a bird-predator bat. *Ecology* 90, 934–944
33. Finn, J.T. *et al.* (2014) Applying network methods to acoustic telemetry data: modeling the movements of tropical marine fishes. *Ecol. Modell.* 293, 139–149
34. Urban, D. and Keitt, T. (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology* 82, 1205–1218
35. Jacoby, D.M.P. *et al.* (2012) Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods Ecol. Evol.* 3, 574–583
36. Lédée, E.J.I. *et al.* (2015) A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species. *Anim. Behav.* 103, 17–28
37. Croft, D.P. *et al.* (2008) *Exploring Animal Social Networks*, Princeton University Press
38. de Lima, L.L.F. *et al.* (2015) Application of network theory to mark recapture data allows insights into population structure of two *Heliconius* species. *Netw. Biol.* 5, 43–54
39. Papastamatiou, Y. *et al.* (2015) Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. *Mar. Ecol. Prog. Ser.* 521, 155–170
40. Nöremark, M. *et al.* (2011) Network analysis of cattle and pig movements in Sweden: measures relevant for disease control and risk based surveillance. *Prev. Vet. Med.* 99, 78–90
41. Fox, R.J. and Bellwood, D.R. (2014) Herbivores in a small world: network theory highlights vulnerability in the function of herbivory on coral reefs. *Funct. Ecol.* 28, 642–651
42. Foley, J.A. *et al.* (2005) Global consequences of land use. *Science* 309, 570–574
43. Shimazaki, H. *et al.* (2004) Network analysis of potential migration routes for oriental white storks (*Ciconia boyciana*). *Ecol. Res.* 19, 683–698
44. Ewen, J.G. *et al.* (2012) *Reintroduction Biology: Integrating Science and Management*, Wiley-Blackwell
45. Wesolowski, A. *et al.* (2012) Quantifying the impact of human mobility on malaria. *Science* 338, 267–270
46. Li, J. *et al.* (2015) Social information improves location prediction in the wild. *Proc. 2015 Int. Work. Trajectory Based Behav. Anal.*
47. Donaldson, M.R. *et al.* (2014) Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Front. Ecol. Environ.* 12, 565–573
48. Stehfest, K.M. *et al.* (2015) Markov models and network analysis reveal sex-specific differences in the space-use of a coastal apex predator. *Oikos* 124, 307–318
49. Miller, J.A. (2015) Towards a better understanding of dynamic interaction metrics for wildlife: a null model approach. *Trans. GIS* 19, 342–361
50. Patterson, T.A. *et al.* (2009) Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *J. Anim. Ecol.* 78, 1113–1123
51. Stehfest, K.M. *et al.* (2013) Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. *Anim. Behav.* 85, 839–848
52. Munro, L.A. and Gregory, A. (2009) Application of network analysis to farmed salmonid movement data from Scotland. *J. Fish Dis.* 32, 641–644
53. Dubé, C. *et al.* (2008) Comparing network analysis measures to determine potential epidemic size of highly contagious exotic diseases in fragmented monthly networks of dairy cattle movements in Ontario, Canada. *Transbound. Emerg. Dis.* 55, 382–392
54. Godfrey, S.S. (2013) Networks and the ecology of parasite transmission: a framework for wildlife parasitology. *Int. J. Parasitol.* 43, 235–245
55. Keeling, M.J. *et al.* (2010) Individual identity and movement networks for disease metapopulations. *Proc. Natl. Acad. Sci. U.S.A.* 107, 8866–8870
56. Proulx, S.R. *et al.* (2005) Network thinking in ecology and evolution. *Trends Ecol. Evol.* 20, 345–353
57. Salathé, M. *et al.* (2010) A high-resolution human contact network for infectious disease transmission. *Proc. Natl. Acad. Sci. U.S.A.* 107, 22020–22025
58. Adelman, J.S. *et al.* (2015) Feeder use predicts both acquisition and transmission of a contagious pathogen in a North American songbird. *Proc. Biol. Sci.* 282, Published online September 22, 2015. <http://dx.doi.org/10.1098/rspb.2015.1429>
59. Vanderwaal, K.L. *et al.* (2013) Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *J. Anim. Ecol.* 83, 406–414
60. Watts, D.J. *et al.* (1998) Collective dynamics of 'small-world' networks. *Nature* 393, 440–442
61. James, R. *et al.* (2009) Potential banana skins in animal social network analysis. *Behav. Ecol. Sociobiol.* 63, 989–997
62. Börger, L. *et al.* (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* 11, 637–650
63. Wilson, A.D.M. *et al.* (2015) Integrating network analysis, sensor tags, and observation to understand shark ecology and behavior. *Behav. Ecol.* Published online July 25, 2015. <http://dx.doi.org/10.1093/beheco/arv115>
64. Blonder, B. *et al.* (2012) Temporal dynamics and network analysis. *Methods Ecol. Evol.* 3, 958–972
65. Holme, P. and Saramäki, J. (2012) Temporal networks. *Phys. Rep.* 519, 97–125
66. Blonder, B. and Dornhaus, A. (2011) Time-ordered networks reveal limitations to information flow in ant colonies. *PLoS ONE* 6, 1–8
67. Garcia, J. *et al.* (2015) Spatial behavior of two coral reef fishes within a Caribbean marine protected area. *Mar. Environ. Res.* 109, 41–51
68. Davies, T. *et al.* (2014) Application of an entropy maximizing and dynamics model for understanding settlement structure: the Khambur Triangle in the Middle Bronze and Iron Ages. *J. Archaeol. Sci.* 43, 141–154
69. Hobson, E.a. *et al.* (2013) An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. *Anim. Behav.* 85, 83–96

understand about a species or animals' space use?

Methodological

Can we define a best-practice methodology for comparing networks given that structure can vary substantially depending on sampling and spatio-temporal scale?

Do we need shared repositories for movement network data? Would these facilitate meta-analysis and macro-ecological questions? Are traditional data repositories sufficient?

70. Jacoby, D.M.P. *et al.* (2014) Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behav. Ecol. Sociobiol.* 68, 1995–2003
71. Wilson, A.D.M. *et al.* (2013) Network position: a key component in the characterization of social personality types. *Behav. Ecol. Sociobiol.* 67, 163–173
72. Aplin, L.M. *et al.* (2015) Consistent individual differences in the social phenotypes of great tits. *Anim. Behav.* 108, 117–127
73. Meade, J. *et al.* (2005) Homing pigeons develop local route stereotypy. *Proc. Biol. Sci.* 272, 17–23
74. Freeman, R. *et al.* (2011) Group decisions and individual differences: route fidelity predicts flight leadership in homing pigeons (*Columba livia*). *Biol. Lett.* 7, 63–66
75. Guilford, T. *et al.* (2011) A dispersive migration in the Atlantic puffin and its implications for migratory navigation. *PLoS ONE* 6, e21336
76. Guo, D. *et al.* (2010) A graph-based approach to vehicle trajectory analysis. *J. Locat. Based Serv.* 4, 183–199
77. Chapman, B.B. *et al.* (2011) To boldly go: individual differences in boldness influence migratory tendency. *Ecol. Lett.* 14, 871–876
78. Heupel, M.R. *et al.* (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar. Freshw. Res.* 57, 1–13
79. Ropert-Coudert, Y. and Wilson, R. (2005) Trends and perspectives in animal-attached remote sensing. *Front Ecol Env.* 3, 437–444
80. Cooke, S.J. *et al.* (2004) Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* 19, 334–343
81. Dorogovtsev, S.N. and Mendes, J.F.F. (2013) *Evolution of Networks: From Biological Nets to the Internet and WWW*, Oxford University Press
82. Börger, L. (2016) Stuck in motion? Reconnecting questions and tools in movement ecology. *J. Anim. Ecol.* 85, 5–10
83. Psorakis, I. *et al.* (2012) Inferring social network structure in ecological systems from spatio-temporal data streams. *J. R. Soc. Interface* 9, 3055–3066
84. Psorakis, I. *et al.* (2015) Inferring social structure from temporal data. *Behav. Ecol. Sociobiol.* 69, 857–866
85. Olden, J.D. *et al.* (2008) Machine learning methods without tears: a primer for ecologists. *Q. Rev. Biol.* 83, 171–193
86. Lookingbill, T. *et al.* (2010) Combining a dispersal model with network theory to assess habitat connectivity. *Ecol. Appl.* 20, 427–441
87. Fortuna, M.a. *et al.* (2006) Spatial network structure and amphibian persistence in stochastic environments. *Proc. Biol. Sci.* 273, 1429–1434
88. Boogert, N.J. *et al.* (2014) Developmental stress predicts social network position. *Biol. Lett.* 10, 20140561
89. Fletcher, R.J. *et al.* (2011) Social network models predict movement and connectivity in ecological landscapes. *Proc. Natl. Acad. Sci. U.S.A.* 108, 19282–19287
90. Sims, D.W. *et al.* (2006) Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proc. Biol. Sci.* 273, 1195–1201
91. Goodale, E. *et al.* (2010) Interspecific information transfer influences animal community structure. *Trends Ecol. Evol.* 25, 354–361
92. Axelrod, R. and Hamilton, W.D. (1981) The Evolution of Cooperation. *Science* 211, 1390–1396
93. Aplin, L.M. *et al.* (2013) Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecol. Lett.* 16, 1365–1372
94. Farine, D.R. *et al.* (2015) Interspecific social networks promote information transmission in wild songbirds. *Proc. Biol. Sci.* 282, 20142804
95. Furnston, T. *et al.* (2015) A significance test for inferring affiliation networks from spatio-temporal data. *PLoS ONE* 10, e0132417
96. Farine, D.R. and Whitehead, H. (2015) Constructing, conducting, and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163
97. Godfrey, S.S. *et al.* (2014) A contact-based social network of lizards is defined by low genetic relatedness among strongly connected individuals. *Anim. Behav.* 97, 35–43
98. Farine, D.R. (2013) Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol. Evol.* 4, 1187–1194