Emerging network-based tools in movement ecology

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ABSTRACT:

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 establish network theory as a prominent, hypothesis-generating tool in movement ecology.

Keywords: *animal tracking; connectivity; graph theory; spatial networks; social behaviour; telemetry*

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, have criss-crossed the globe on trade networks that have been heavily influenced by geography and the prevailing socio-cultural climate [1]; these factors have had extraordinary impact on the evolution of human society over the last 13000 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 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' (see Glossary) as a framework for quantifying habitat connectivity. In order to help 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 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 an individuals' movement network. 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 behaviour from very large data sets 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 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 a number of 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 the high resolution GPS tracking of individuals during migration or collective movement [14,16,21], all present some form of connectivity of landscapes. Such data is thus amenable to the construction and appraisal of network features (Fig. 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 as 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, that is the repeated aggregation of movement steps through time (Fig. 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 in networks (Box 2). Dynamic networks for example, have been used to reveal shared decision-making about movement in non-human primates [31] and 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 (Fig. 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 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 unipartite network. Importantly, bipartite networks offer a heuristic framework for systems where there are limited data, but that 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 quickly identify pertinent questions to explore within the data using quantitative measures of centrality, connectivity or community formation associated with graph theory (see 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 ecological insights into animal ecology (Table 1).

Generating new insights and ecological applications

In many terrestrial ecosystems, human land use and resource acquisition has 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 proven 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 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 how many individuals are needed 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](see 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 systems, such as public transportation ticketing systems (e.g. London's Oyster card system). Additionally, 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 knowledge of connectivity and multi-individual ranging behaviour is 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 a number of 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 proven key, 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 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 as 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 due 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 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 just a few habitat nodes that are of critical 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 those further away. While this poses a potential challenge to how we develop null models for significance testing of spatial networks (see Box 4), it can also inform 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 rather cryptic species [63].

Capturing visitation chronology and duration

There are ongoing challenges associated with incorporating time in 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 inform temporal analyses as directionality of edges pertain to time also.

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 within 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 address critical ecological questions surrounding the behavioural motivation of animals living in challenging or remote environments. Interestingly, artificial neural networks, used to estimate movement probability kernels, 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 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 proven 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, 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 a number of 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]. Using 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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Glossary

Adjacency matrix: an *n* x *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, through 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, in this instance, the movements between locations within AFA. These models assume that any movement is based purely on the current state, not preceding states and that transition probabilities between states remain the same over time.

Graph theory: a branch of mathematics that allow 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 two dimensional 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 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.

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
Terrestrial				
Common buckeye, *Junonia coenia*; Variegated fritillary, *Euptoieta claudia*	Mark-release-recapture	Inter-patch movements; geographically-weighted proxy for degree	Corridors increase long-distance movements of habitat restricted species	[27]
Cactus bug, *Chelinidea vittiger*	Mark-release-recapture	Betweenness; clustering coefficient; density	Determining which method of network construction best predicts real-world habitat linkages	[86]
Dairy cattle,	Shipment records from Diary 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, *Sciurus niger cinereus*	Simulated dispersion data across suitable habitat	Betweenness; degree distribution; edge redundancy; null modelling	Revealing bottlenecks to dispersal as targets for conservation	[87]
Everglades snail kite, *Rostrhamus sociabilis plumbeus*	Mark-release-recapture	Betweenness; clustering coefficient; density	Determining which method of network construction best predicts real-world habitat linkages	[86]
Giant noctule bat, *Nyctalus lasiopterus*	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, *homo sapiens*	Ship monitoring systems (global database)	Shipping port betweenness centrality; strength; degree distribution	Connectivity of cargo ship ports possess a heavy-tailed distribution	[11]
Human, *homo sapiens*	Mobile phone locational data	Network density; distance clustering; entropy of individual trajectory	Human movement is highly predictable	[10,26]
Human, *homo sapiens*	Mobile phone locational data	Weighted networks; network stability of parasite transmission	Revealing travel routes key to malaria epidemiology	[45]
Mexican spotted owl, *Strix occidentalis lucida*	Modelling of suitable habitat patches	Edge removal; node removal; null modelling	Population predicted to persist despite substantial loss of habitat	[34]

Oriental white storks, *Ciconia boyciana*	Satellite tracking derived stopover sites	Path length	Determining key stopover sites critical to migration route connectivity	[43]
Red Postman, *Helioconius erato*; Common Postman, *Helioconius melpomene*	Mark-release-recapture	Mean strength; degree distribution; clustering coefficient; network diameter	Comparable network structures between species; identifying resource hotspots of high connectivity	[38]
Marine				
Atlantic Salmon, *Salmo salar*; Rainbow trout, *Oncorhynchus mykiss* (farmed)	Fish Health Inspectorate live fish transport database	Degree centrality	Identified sites of increased infection vulnerability and spread in fish farms	[52]
Bonefish, *Albula vulpes*; Great Baracuda, *Sphyraena barracuda*; Permit, *Trachinotus falcatus*	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, *Chlorurus microrhinos*; Rivulated parrotfish, *Scarus rivulatus*; Scribbled rabbitfish, *Siganus doliatus*	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, *Notorynchus cepedianus*	Acoustic telemetry (AFA)	Eigenvector centrality; EDMM analysis	Spatial segregation of the sexes as reveal through combining network statistics with Markov models	[48]
Caribbean reef shark, *Carcharhinus perezi*; Small spotted catshark, *Scyliorhinus canicula*	Acoustic telemetry (AFA)	Degree; edge filtering; betweenness; network density; average path length	Network visualisation help to explore hypotheses and abiotic variables predict movement	[35]
Galapagos shark, *Carcharhinus galapagensis*; Giant trevally, *Caranx ignobilis*	Acoustic telemetry (AFA)	Degree centrality; betweenness	Marine predators are important in the nutrient transfer between reef habitats	[39]
Pigeye shark, *Carcharhinus amboinensis*; spottail shark, *Carcharhinus sorrah*	Acoustic telemetry (AFA)	Eigenvector centrality; closeness; strength; community detection	Marine predators utilise movement corridors between vulnerable core areas	[36]

Schoolmaster snapper, *Lutjanus apodus*; Stoplight parrotfish, *Sparisoma viride*	Acoustic telemetry (AFA)	Eigenvector centrality; EDMM analysis	Inter- and intraspecific differences in spatio-temporal patterns of reef fishes	[67]
Yellowfin tuna, *Thunnus albacares*	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]

[a] See Box 1 for discussion of the different available network metrics

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. Knock-out experiments).

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. Here we outline the utility of such metrics for defining areas of critical importance in movement networks. Unweighted, binary networks (Fig 1i) simply indicate whether an animal has moved between two locations and this relationship can be accompanied by directionality (Fig. 1ii). In movement networks there are also two key temporal measures that accompany an edge: 1) time the edge occurred (T-D), providing some chronology of edge formation and 2) 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 Fig 1iii). 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 transportation networks where busy 'hubs' are better able to deal with higher percentage and heavier weighting of flow [11].

Single node-based centrality measures can inform the relative importance of habitat patches [87] and the distribution of these measures across the network might be used to characterise the robustness of a system to fragmentation and animal dispersal [41,88]. We have encountered *degree* but there are a number of other measures including *edge betweenness* and *eigenvector* centrality that can indicate important 'corridors' that link multiple subgroups of the spatial network (e.g. red node, Fig. 1). Additionally, the *clustering coefficient* and global measures of community detection can apportion the network into subgroups should activity be restricted to statistically higher within- than between-group movements (i.e. spatial assortment represented by the dotted lines in Fig. 1). 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 [88]. For wider ranging or migratory species *shortest path length* (blue lines, Fig. 1) 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].

Box 1 Figure 1. Metrics within unweighted (i), directed (ii) and weighted (iii) elements of a movement network across a small AFA. Here, we represent summed degree weight (node size, iii), community structuring (dotted 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.

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 a number of 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 to undirected networks. Such classifications though, still aggregate movements into a single matrix for each period (although, see [89] for an exception) and this can be rather subjective, potentially leading to the loss of important characteristics of the animal's space use [48,67,76]. Alternatively, with high-resolution tracking, comes the potential to explore the spatio-temporal 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 at 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 (that is 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].

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 allowing greater power to test hypotheses from presence-absence data (Fig. 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 – 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 data set 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 spatio-temporal data stream. 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 further reconcile the link, *in situ*, between population dynamics and animal movement [12].

Box 3 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 ($\sum(\Delta t_m)$) 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 (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 (see [8,37,96] for an overview). Movement networks are also spatially embedded and so 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 due to 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 randomisation procedures and the 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 error (see [8,29] for discussion). Instead, shuffling of the data stream, that is randomisation of the raw visitation pattern and chronology prior to 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 data-stream approaches in order 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 and the spatial component of animal social networks is available and would be recommended for future applications [8,29,96,98].