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# Emerging network-based tools in movement ecology

David M. P. Jacoby <sup>a\*</sup> & Robin Freeman<sup>a</sup>

<sup>a</sup> Institute of Zoology, Zoological Society of London, Regent's Park, NW1 4RY, UK

Corresponding author: Jacoby, D.M.P (david.jacoby@ioz.ac.uk)

27 ABSTRACT:

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

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

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## 42 **Reducing complexity in a technological age**

43 Since antiquity the flow of valuable goods such as silk from China, spices from India or ivory  
44 from Africa, have criss-crossed the globe on trade networks that have been heavily  
45 influenced by geography and the prevailing socio-cultural climate [1]; these factors have had  
46 extraordinary impact on the evolution of human society over the last 13000 years [2].  
47 Analogously, animal movement, that is reliant on the underlying geographic landscape and  
48 the social environment in which animals find themselves, can strongly influence the flow of  
49 genetic material, infectious disease and cultural innovations within a population [3–5]. The  
50 analysis of social systems has received considerable attention in the scientific literature and  
51 robust, quantitative analyses of animal social networks are now firmly embedded in  
52 behavioural ecology and evolution [6–9]. Despite considerable theoretical overlap and  
53 broad utility in the study of human mobility and transportation networks (e.g. [10,11]),  
54 movement ecologists have been slow to adopt ‘graph theory’ (see Glossary) as a framework  
55 for quantifying habitat connectivity. In order to help refine our understanding of the  
56 mechanistic links between movement behaviour, the environment and individual  
57 motivation or physiological traits however, dynamic spatially-informed models are key  
58 [12,13], not least because they allow us to visually identify patterns relating to ecological  
59 processes. Recently, with technological developments that have enhanced our ability to  
60 track multiple individuals concurrently over long periods [14–17], the requirement for  
61 analytical methods that allow us to interpret how global patterns are shaped by the  
62 movements of many individuals, have brought network analyses back into the limelight.

63        Networks themselves have an intuitive appeal, utilising metrics that facilitate the  
64 identification of central players, which are key to flow and connectivity within a given

65 system [18](Box 1); this provides a means to explore connectivity at multiple scales,  
66 clarifying the relationship between structure and process in biological systems [19,20].  
67 Analyses of movement data, retrieved from numerous active or passive methods, currently  
68 rely heavily on correlative measures of fixed units (e.g. presence-absence data) to explore  
69 inter- and intraspecific comparisons or environmental predictors of movement. Adopting a  
70 'network perspective' however, helps to quantify dynamics while accounting for the non-  
71 independence of movement steps. Networks achieve this by considering relationships  
72 between network *edges* that represent the transition between paired locations within an  
73 individuals' movement network. The flexibility with which we can define these edges, from a  
74 simple A to B transition for an individual, to the correlation of route similarity between  
75 individuals potentially moving as a collective [21], is crucial for extracting and delineating  
76 behaviour from very large data sets or where we have limited knowledge of the study  
77 system. Consequently, movement networks can be spatially explicit and dynamic,  
78 explanatory or predictive; they provide a powerful means to visualise, interpret and  
79 interrogate animal tracking data, generating new hypotheses with clear applications in  
80 conservation and resource management.

81 In this review, we draw on recent developments in the acquisition and analysis of  
82 spatial data to explore how movement ecology is benefiting from the convergent evolution  
83 of network tools across multiple disciplines. The network approach, for example, will clearly  
84 benefit from advances in the fields of biologging and machine-sensing of behavioural data  
85 which have considerably progressed our understanding of wild animal biology [15,22,23] or  
86 urban planning and modelling of human mobility within geography [10,24–26]. We discuss  
87 how network theory is generating new hypotheses and explore the novel insights into

88 ecological connectivity provided through animal movement networks. Further, we  
89 investigate the interplay between social and spatial networks through recent advances that  
90 allow inference of social networks from the temporary nature of visitation patterns at  
91 logging stations. Still in its infancy, we highlight a number of areas where we see this field is  
92 expanding and discuss the future impact this emergent research theme will have on  
93 individual and collective movement in the context of ecology, evolution and conservation.

94

## 95 **Constructing movement networks**

### 96 *Static or dynamic edges?*

97 Discrete, localised movements from autonomous fixed arrays (AFAs) such as camera traps  
98 or acoustic receivers, or the high resolution GPS tracking of individuals during migration or  
99 collective movement [14,16,21], all present some form of connectivity of landscapes. Such  
100 data is thus amenable to the construction and appraisal of network features (Fig. 1).  
101 Depending on the research question of interest, networks can be either static or dynamic.  
102 Static spatial networks capture the flow of resources or information between locations,  
103 where movement data is pooled across multiple sampling periods creating weighted  
104 network edges, the properties of which inform the directionality and strength of flow within  
105 the system [11,27]. Such networks are important as they can provide a rich understanding  
106 of how fixed environmental constraints drive animal movement decisions [28], and thus  
107 how the environment shapes patterns in social networks. For example, if the environment  
108 restricts movement of animals between areas, this can result in assortative behaviours [29],  
109 and potentially the emergence of local traditions [30]. By contrast, dynamic networks of

110 movement, that is the repeated aggregation of movement steps through time (Fig. 1)  
111 and/or the correlation of edges among individuals through time, can enable us to extract  
112 fundamental behavioural insight from long-term tracking data despite the significant  
113 analytical challenges of incorporating time in networks (Box 2). Dynamic networks for  
114 example, have been used to reveal shared decision-making about movement in non-human  
115 primates [31] and hierarchical group behaviours by examining the lagged correlation of  
116 heading routes in collective flocks of birds [21].

### 117 *Representation of nodes*

118 Networks can take two possible forms; bipartite or ‘two-mode’ networks and unipartite,  
119 ‘one-mode’ networks (Fig. 1). Bipartite networks contain two very distinct types of nodes  
120 (e.g. individuals and locations) and links are established between them. For example,  
121 Fortuna et al. [32] consider the modular structure of bipartite graphs of giant noctule bats,  
122 *Nyctalus lasiopterus* roosting in a network of trees and consider the implications of this  
123 structure on the spread and management of disease. Bipartite networks, often the  
124 analytical precursor of the two forms, can prove useful for explaining modularity (the  
125 clustering of discrete units) and nestedness (hierarchies of visitation) within a network [32–  
126 34]. These metrics can be useful in guiding which network components are likely to be  
127 important when the data are converted to a unipartite network. Importantly, bipartite  
128 networks offer a heuristic framework for systems where there are limited data, but that  
129 enable growth in complexity as more data become available [34]. Alternatively, unipartite  
130 networks, for example, individuals in social networks or locations in movement networks,  
131 reveal structure within nodes of the same type. Where nodes represent fixed spatial  
132 locations (e.g. in AFAs) unipartite networks better represent the movement of the individual

133 or group, albeit in a discretised manner. Comparisons of such networks can reveal  
134 interesting shifts in space use as individuals develop over time [35] or differences between  
135 species [36] that might reflect cryptic, temporal segregation of resource use in spatially  
136 overlapping species. Visualisation of the network structure and the ease with which  
137 networks can be restricted to different time periods, age classes, sexes – as with social  
138 networks – helps quickly identify pertinent questions to explore within the data using  
139 quantitative measures of centrality, connectivity or community formation associated with  
140 graph theory (see Box 1). Network metrics (reviewed comprehensively in [18] and  
141 specifically for animal societies in [37]) report the structural properties of a network at local  
142 (individual nodes) and ‘global’ scales (mean across nodes). These metrics provide dynamic  
143 tools for comparing movement graphs between species [33,38–40] or against theoretical  
144 models [41]. As a word of caution however, the size, density or duration of data can strongly  
145 influence network structure, raising important questions about how best to truly compare  
146 movement networks (see Outstanding Questions); relating these metrics to other  
147 information captured in the data, however, can reveal considerable new ecological insights  
148 into animal ecology (Table 1).

#### 149 **Generating new insights and ecological applications**

150 In many terrestrial ecosystems, human land use and resource acquisition has led to  
151 widespread landscape fragmentation, isolating organisms to discrete patches of suitable  
152 habitat [42]. Consequently, the influence of fragmentation on animal and plant populations  
153 has proven a rich vein of research with some applying graph theory to assess the relative  
154 importance of individual patches to overall landscape connectivity based on metrics of  
155 edges that link important habitat or resources [34]. Studies on invertebrate pollinators, for

156 example, have revealed the importance of corridors to increase movements between  
157 fragmented habitats within plant-pollinator networks [27,38]. Migration routes in long  
158 distance avian migrants also rely on a mosaic of connected stopover sites to rest, feed or  
159 shelter from bad weather. The arrival and departure of Oriental White Storks, *Ciconia*  
160 *boycciana* at migratory stopover sites were modelled as a network of connected components  
161 to identify the shortest path lengths and associated staging sites fundamental to the  
162 connectivity of the full migration route [43]. There is considerable scope for such tools to  
163 help inform the ways in which we conserve and manage species by measuring or forecasting  
164 the impact of human disturbance on movement or by monitoring endangered species  
165 tagged with tracking devices. As an example, variation in the spatial autocorrelation of  
166 animal movement steps, post reintroduction, is likely to have considerable bearing on how  
167 breeding pairs acclimate to their new environment. Determining how they disperse and  
168 where and when the sexes come together, will inform how many individuals are needed to  
169 support a successful reintroduction programme that is fundamentally rooted in the ecology  
170 of the species in question [44].

#### 171 *Understanding the patterns, dynamics and drivers of mobility*

172 More broadly, network analyses enable us to deconstruct animal movement patterns into  
173 individual behavioural processes (e.g. dispersal patterns) and population-level biological  
174 motivation such as social drivers or environmental factors [28]. Network community  
175 detection algorithms, for example, offer ways to explore the core space use of species at  
176 multiple scales by redefining what comprise the network nodes (e.g. individual receivers,  
177 fixed quadrats, different habitat types) revealing the underlying social and spatial drivers of  
178 movement [33]. Recently, networks have also had significant impact on our understanding



179 of broad-scale patterns of mobility in human societies, not least for modelling global  
180 transport and cargo networks [11,25], with considerable success in recreating and  
181 predicting human movement from networks of mobile phone usage [10,26,45](see Table 1  
182 for summary). How and when we socialise and how this is influenced by routine movements  
183 between familiar locations, can all be captured from networks of mobile phone transmitters  
184 or radio frequency identification systems, such as public transportation ticketing systems  
185 (e.g. London's Oyster card system). Additionally, while social data on conspecifics can be  
186 used to improve predictions about the location of unknown individuals [46], locational data  
187 from animal tracking, can be used strategically to recreate a broader understanding of social  
188 dynamics in a population (Box 3).

189         The emergence of spatial networks in animal movement ecology has been particularly  
190 useful in systems where knowledge of connectivity and multi-individual ranging behaviour is  
191 difficult to study, such as marine systems (e.g. [33,35,39,41,47,48]) where movement must  
192 sometimes be inferred between discrete locational fixes. More widely however, the  
193 development and application of biologging technologies are progressing faster than our  
194 ability to analyse the vast data they generate [15,33,47]. Network analyses, alongside a  
195 number of other burgeoning methodologies (e.g. Bayesian bridges [13]; step-selection  
196 methods [49]; behavioural state modelling [50]), now offer more integrative, comparative  
197 and hypothesis-driven approaches to movement ecology [16,33,35,47]. As such, network  
198 tools are finding a place in conservation and management by enabling us to measure and  
199 quantify singular and correlative linkages between areas maintained by unseen animals,  
200 that traditional static analyses likely miss. This has proven key, for example, for  
201 understanding the fission-fusion dynamics of commercially important fishes between

202 networks of fish aggregating devices [51], for measuring nutrient transfer by marine  
203 predators within mesophotic coral reef communities [39] or for quantifying the transport  
204 and spread of disease within coastal aquaculture farms [52].

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### 206 **Spatial patterns within movement networks**

207 The utility of spatial graphs in ecology has been largely driven by the need to better  
208 understand disease dynamics and rates of transmission within populations and across  
209 geographic landscapes [32,45,53–59]. This body of research has broadly informed how we  
210 model spatial networks of flow and connectivity and use networks as predictive tools  
211 [32,57] incorporating the distance between nodes within the underlying mobility network.

212 It is important to model the modularity and the dynamic structural properties of a  
213 movement network as this can reflect the underlying robustness (or vulnerability) of the  
214 biological landscape through which animals move. Network structure can be characterised  
215 by the distribution of node-based metrics within the population. For example, a power-law  
216 *degree* distribution is indicative of a disproportionately low number of nodes harbouring a  
217 high percentage of the connections; these nodes are the hubs within the network [60] and  
218 might indicate priority areas for conservation due to a high in- and out-flow of individuals. In  
219 fact multiple species of roving herbivorous fish were found to be heavily reliant on a few  
220 well-connected areas of the Great Barrier Reef – monitored using an acoustic AFA –  
221 revealing inherent vulnerabilities in the ‘ultra small-world’ nature of these movement  
222 networks, should these areas with a high degree centrality become perturbed [41]. We  
223 caution however, that without a high number of nodes within a network (e.g. hundreds to

224 thousands), such properties are very difficult to truly determine [61]. Finn et al. [33] argue  
225 that spatial networks are much more likely to take the form of a regular graph where each  
226 node is connected to its nearest neighbour, but this can be dependent on in-built structure  
227 in the data (e.g. array layout or sampling frequency). Another way to assess the robustness  
228 of a measured animal movement network is to evaluate network degradation through the  
229 systematic removal of nodes to mimic habitat loss [35], a tool likely to prove informative for  
230 predictive management. This has been used to good effect to show that the activity space of  
231 pike and spottail sharks [36] and migration routes of oriental white storks [43] become  
232 significantly fragmented, then disconnected, after the removal of just a few habitat nodes  
233 that are of critical ecological importance to these animals. For some ecosystems or species  
234 in particular, these hubs for animal mobility – whether on a migration route (e.g. watering  
235 holes) or part of a core activity area (e.g. latrines) – might not be immediately apparent;  
236 density estimates of individual occurrences for instance, might tell us nothing about the  
237 repeated ranging behaviour or the time associated with such behaviour, that can be  
238 captured by the relative flow of movements to and from the surrounding habitats.

239       Spatial autocorrelation within networks is the likelihood that nodes that are  
240 geographically nearer to each other are more likely than random to share similar metrics  
241 than those further away. While this poses a potential challenge to how we develop null  
242 models for significance testing of spatial networks (see Box 4), it can also inform interesting  
243 questions about how animals use space. The spatial assortment of nodes within a weighted  
244 movement network for example, could be indicative of behavioural mechanisms such as  
245 central place foraging, whereas assortment by habitat type suggests that movement is  
246 perhaps driven predominantly by resource distribution, allowing us to make generalisations

247 about patterns of space use [62]. Further, the correlation of activity at different spatial  
248 nodes can be tracked repeatedly through time to generate hypotheses about peak flow  
249 patterns. We predict that these types of techniques will prove useful for monitoring the  
250 impacts of climate change through time on route determination and repeatability in  
251 migratory animals. For these tools to be robust however, null hypothesis significance testing  
252 is vital [8](Box 4).

253

#### 254 **Future research directions**

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

#### 264 *Capturing visitation chronology and duration*

265 There are ongoing challenges associated with incorporating time in movement networks.  
266 We foresee great potential in methods that search for repeated topologies (e.g. temporally  
267 recurring motifs) or that adopt time-ordered and time-aggregated networks within the  
268 movement structure [64–66], combined with behavioural state modelling that allows us to

269 explore transitional shifts [48,50,67]. Furthermore, we anticipate entropy maximisation  
270 techniques being incorporated into movement networks to predict probable flow strength  
271 and directionality based on the relative loading of units – this could be individuals or  
272 resources – at each node within the spatial network. Such techniques have proven  
273 extremely successful in a geographic context for predicting the emergent patternation of  
274 the 2011 London riots for example [24], or the chronology and dimensionality of human  
275 settlements in the Middle Bronze and Iron Ages in Syria [68]. Such innovations are likely to  
276 help inform temporal analyses as directionality of edges pertain to time also.

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

### 287 *Route repeatability and refinement*

288 With recent evidence that repeatable social network positions can be indicative of  
289 personality traits within animals [70–72], we foresee an interesting avenue of research  
290 determining whether individual movement trajectories through a landscape might show  
291 consistent variation or perhaps plasticity during ontogeny. Here, visitation chronology can

292 be captured as a bipartite network, the properties of which might be compared across  
293 individuals in the population. This could have interesting implications for animals moving in  
294 groups: Using light-weight, GPS trackers for example, route fidelity in *solo* homing pigeons  
295 become refined in accuracy over repeated journeys [73]; these routes might then  
296 recapitulate under 'social' *flocking* scenarios in ways that are predictive of social  
297 relationships [74]. Similarly, the migratory journeys of Atlantic Puffins are strongly  
298 recapitulated within individuals following their own routes during what otherwise appear to  
299 be dispersive migrations [75]. In fact recent advances in the analyses of vast trajectory data  
300 within geography and urban planning suggest that network analyses can improve the  
301 positional accuracy of GPS data to reduce data redundancy and better interpolate or  
302 explore individual and collective trajectories [76]. With such huge data from these fields,  
303 researchers can now fully harness the predictive power of network tools for understanding  
304 emergent spatial patterns across many different contexts [24,68]. In species for which such  
305 tracking data is not feasible, simple, binary presence-absence data, analysed as a connected  
306 network, can help us address critical ecological questions surrounding the behavioural  
307 motivation of animals living in challenging or remote environments. Interestingly, artificial  
308 neural networks, used to estimate movement probability kernels, offer movement models  
309 that now integrate the spatial structure, the spatial variability of the resource landscape and  
310 individual memory of previously visited locations, strengthening the link between pattern,  
311 personality and process [13,77]. Further questions of interest are listed in the Outstanding  
312 Questions.

313 **Concluding remarks**

314 Spatial connectivity in biological systems can be quantified at myriad scales and using  
315 broadly different data collection methods. Only recently has technology enabled us to  
316 monitor, round-the-clock, the behaviour of tens, hundreds, or even thousands of individuals  
317 concurrently for periods of weeks, months or even years [14–16,78–80]. Graph theory has  
318 already proven an intuitive and informative paradigm for the measurement and appraisal of  
319 complex connected systems from social networks to transport systems and beyond  
320 [25,60,81]. Network-based analyses offer a robust, quantitative set of metrics that  
321 complement traditional means of understanding movement ecology within AFAs of camera  
322 traps, acoustic receivers, mobile phone masts, RFID stations, or from continuous satellite  
323 tracking data. With the current unprecedented availability of high-resolution and/or long-  
324 term tracking data, it is more important than ever that we begin to connect the tools  
325 available to the appropriate research questions [82]. In addition to movement, the temporal  
326 component associated with arrival and departure of animals at network nodes can offer  
327 information on the social interactions of free ranging tagged animals through analysis of  
328 individual co-occurrences [83,84]. These methods are one of a number of burgeoning  
329 disciplines – including *data mining* [23], *machine learning* [85] and *automated image-based*  
330 *tracking* [17] – that utilise recent advances in computational power to analyse large,  
331 complex time-series data and that are guiding more integrative, comparative and  
332 hypothesis-driven approaches in the field of animal movement ecology [23,47]. Using  
333 network-based tools to understand the movement, flow and connectivity of habitats and  
334 individuals in the wild, offers new opportunities to unravel underlying mechanisms and to  
335 provide crucial new understanding of the ecology and behaviour of free-ranging animals.

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541

542 Glossary

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

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

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

553 **Empirically derived Markov model (EDMM):** deterministic model that accounts for the  
554 temporal dynamics of transitions between states or, in this instance, the movements  
555 between locations within AFA. These models assume that any movement is based purely on  
556 the current state, not preceding states and that transition probabilities between states  
557 remain the same over time.

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

561 **Infinite Gaussian Mixture Models (IGMM):** a probabilistic Bayesian model, with an  
562 undefined prior number of mixture components, used to statistically infer aggregated or

563 clustered distributions within data from course observations and/or time series sampling of  
564 the population.

565 **Kernel utilisation distribution (KUD):** a two dimensional probability density function that  
566 estimates the probability of finding an animal within an area based on a given set of  
567 recorded locations.

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

570 **Social network:** the structure describing a series of nodes or individuals and the  
571 accumulated dyadic linkages formed through some form of direct interaction. For animal  
572 social networks this might take the form of agonistic or grooming behaviours, shared group  
573 membership or communicative interactions.

574 **Spatial network:** a network graph where nodes have a fixed geographic location and edges  
575 are derived from counts or ratios of directed animal movements between the nodes; spatial  
576 networks will have a fixed distribution of inter-node distances. Movement networks are an  
577 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 <sup>a</sup>	New ecological insights	Refs
<b>Terrestrial</b>				
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	[86]
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	[87]
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	[86]
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 critical to migration route connectivity	[43]
Red Postman, <i>Helioconius erato</i> ; Common Postman, <i>Helioconius 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]

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### Marine

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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>Sphyrna 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 reveal 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 help 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 the nutrient transfer between reef habitats	[39]
Pigeeye 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 spatio-temporal 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]

579

<sup>a</sup> See Box 1 for discussion of the different available network metrics

580

581 **Figure 1. Using graph theory to analyse ecological data**

582 Animal movement data can be gathered through numerous active and passive monitoring  
583 techniques and with careful consideration can be used to construct static or dynamic,  
584 bipartite or unipartite networks. Network metrics help to describe the important structural  
585 properties at multiple scales informing the generation of hypotheses about when, where  
586 and how animals interact with their environments. Quantitative network tools can then be  
587 employed to make comparisons between species, individuals or different temporal scales or  
588 to make predictions about the impact of habitat change on movement ecology (e.g. Knock-  
589 out experiments).

590 **Box 1. The properties of movement networks**

591 Most movement networks of locational *nodes* and movement *edges* can be analysed with  
592 standard metrics that report the structural and connective properties within a network.  
593 Here we outline the utility of such metrics for defining areas of critical importance in  
594 movement networks. Unweighted, binary networks (Fig 1i) simply indicate whether an  
595 animal has moved between two locations and this relationship can be accompanied by  
596 directionality (Fig. 1ii). In movement networks there are also two key temporal measures  
597 that accompany an edge: 1) time the edge occurred (T-D), providing some chronology of  
598 edge formation and 2) duration ( $\Delta t_m$ ), which is the time taken from leaving one node to  
599 arriving at another. Weighting the edges informs the frequency with which that movement  
600 has occurred and by averaging the sums of the linked weights arriving and departing from a  
601 location, we obtain the relative node *strength* (indicated by node size in Fig 1iii). Across the  
602 global cargo shipping network, average node strength was found to scale superlinearly with  
603 *degree* – the number of unweighted edges attached to a node – reflecting interesting  
604 properties of transportation networks where busy ‘hubs’ are better able to deal with higher  
605 percentage and heavier weighting of flow [11].

606 Single node-based centrality measures can inform the relative importance of habitat  
607 patches [87] and the distribution of these measures across the network might be used to  
608 characterise the robustness of a system to fragmentation and animal dispersal [41,88]. We  
609 have encountered *degree* but there are a number of other measures including *edge*  
610 *betweenness* and *eigenvector* centrality that can indicate important ‘corridors’ that link  
611 multiple subgroups of the spatial network (e.g. red node, Fig. 1). Additionally, the *clustering*  
612 *coefficient* and global measures of community detection can apportion the network into



613 subgroups should activity be restricted to statistically higher within- than between-group  
614 movements (i.e. spatial assortment represented by the dotted lines in Fig. 1). While the  
615 formation of clusters is often likely to favour spatially close locations, in ecosystems that are  
616 subject to stochastic fragmentation such as temporarily flooded ponds, clustering can  
617 indicate potential and time-associated habitat to freshwater residents such as amphibians  
618 [88]. For wider ranging or migratory species *shortest path length* (blue lines, Fig. 1) can  
619 illustrate the most efficient routes through a mosaic of habitats helping to understand the  
620 implications of animals that cannot, or fail to take these routes [43].

621

622 **Box 1 Figure 1.** Metrics within unweighted (i), directed (ii) and weighted (iii) elements of a  
623 movement network across a small AFA. Here, we represent summed degree weight (node  
624 size, iii), community structuring (dotted line), high betweenness centrality (red node) and  
625 shortest path length between location X and Y (blue lines). Each movement edge is  
626 associated with a specific time, date and duration.

627 **Box 2. The importance of time in movement networks**

628 The interaction of animals and their environment is a spatial and *temporal* process. Static  
629 spatial networks condense time reflecting the overriding structure and its associated  
630 processes. Sometimes, incorporating a temporal element is important however, and this can  
631 be done at a number of scales. Movement networks might be considered at daily, seasonal,  
632 annual or other meaningful periods to reveal how changes in conditions correlating with  
633 these arbitrary periods influence how animals move [35]. We might partially capture this by  
634 having directional edges. This perspective generates very different structures and patterns  
635 to undirected networks. Such classifications though, still aggregate movements into a single  
636 matrix for each period (although, see [89] for an exception) and this can be rather  
637 subjective, potentially leading to the loss of important characteristics of the animal's space  
638 use [48,67,76]. Alternatively, with high-resolution tracking, comes the potential to explore  
639 the spatio-temporal autocorrelation of multiple individuals to understand behaviours such  
640 as collective movement and leadership [21].

641 The directional transition between one node and another is accompanied by a  
642 measure of time relating to previous and subsequent detections. Decisions taken by the  
643 animal within this time are generally unknown due to the resolution of the data, however,  
644 individual consistency in these transition times, or changes under different scenarios still  
645 inform the dynamics of movement. For example, the route directedness of animals between  
646 areas of abundant resources (which could reasonably be expected to negatively correlate  
647 with transition time), might increase during times when patchy areas of resource become  
648 unavailable. While analyses of dynamic networks are still far from resolved, there have been  
649 interesting developments that treat these transitions as states of a Markov chain [48,50,67],

650 where the edges in the network represent the probability of transitioning between areas or  
651 patches. Using data from acoustically tagged sevengill sharks, *Notorynchus cepedianus*,  
652 Stehfest et al. [48] compare empirically derived Markov models (EDMM) and network  
653 analyses of shark movements. They found that both methods were comparable for  
654 revealing sex-specific differences in movement but that the EDMM preserved the  
655 chronological detection sequence thus performing better at defining priority areas [48]. In  
656 addition to EDMs, calculating multiple measures of movement counts across successive  
657 time steps and then fitting linear models to dyadic strength (that is the connectivity of two  
658 locations through repeated flow of animals between them) offers one way of monitoring  
659 the shifting dynamics of movement patterns through time [69].

660

661 **Box 3. Spatial and social interactions within AFAs**

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

672 An interesting development of this conceptual framework is that by considering the  
673 nodes of an AFA as inherently connected, the arrival and departure of individual animals at  
674 receiver locations can be mapped in space and time to explore co-occurrences and social  
675 interactions in free-ranging, fully unperturbed animals. Using a rich, long-term data set of  
676 electronically tagged great tits, *Parus major* in Wytham Woods, Oxfordshire (UK),  
677 researchers at the Edward Grey Institute first conceived the idea that wild social interactions  
678 might be inferred based on the arrival and departure of individuals in an array of RFID  
679 receivers [[83], Figure 1C]. Statistically significant ‘gathering events’, which can be thought  
680 of as social sampling periods, can be revealed through the application of data mining  
681 techniques (e.g. GMMs) to the spatio-temporal data stream. This approach has recently  
682 facilitated the study of long-term, dynamic social networks in passerine birds providing  
683 substantial insight into the ecological and evolutionary implications of social interactions in  
684 the wild [28,84,93–95]. This system relies upon attracting individuals to the receivers (i.e.

685 PIT tag readers at feeding stations) to infer interactions during feeding bouts. It remains to  
686 be seen however, whether the same approach can be used to sample incidental wild social  
687 interactions using passive AFAs. If successful, this approach will help further reconcile the  
688 link, *in situ*, between population dynamics and animal movement [12].

689

690 **Box 3 Figure 1.** Simplified schematic illustrating the construction and application of  
691 movement and social networks from AFA data. **(A)** AFA of eight receivers where a time ( $\Delta t_m$ )  
692 is associated with the movement ( $m$ ) of an individual(s) between locations (i), a lemon  
693 shark, *Negaprion brevirostris* approaching an acoustic receiver (ii) (credit Matt Potenski). **(B)**  
694 Movement networks with a corresponding total time ( $\sum(\Delta t_m)$ ) of three differently coloured  
695 individuals through our hypothetical AFA (i) and a real movement network of giant trevally,  
696 *Caranx ignobilis* through an AFA at Pearl and Hermes Atoll in the Pacific Ocean (ii), redrawn  
697 from [39]. **(C)** Social co-occurrences ( $s$ ) of individuals within a time frame ( $\Delta t_s$ ) determined  
698 using a Gaussian Mixture Model (i); great tits, *Parus major* (credit Luc Viatour, CC BY\_SA),  
699 have been extensively studied using Passive Integrated Transponder (PIT) tags and receivers  
700 at feeding stations to infer social foraging networks in the wild (ii), redrawn from [84].

701 **Box 4 Null modelling of spatial data**

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

712 Node permutation of a movement adjacency matrix allows randomisation of the  
713 locations visited while retaining the number of possible locations. Alternatively, edge  
714 permutation (i.e. movements, directed or undirected) can be used to test whether the  
715 observed frequency with which animals move between areas is a non-random process. Both  
716 procedures however, have limitations that increase the likelihood of type I and type II error  
717 (see [8,29] for discussion). Instead, shuffling of the data stream, that is randomisation of the  
718 raw visitation pattern and chronology prior to constructing a network, provides a more  
719 biologically meaningful method for determining whether movement is truly non-random  
720 [96]. A novel randomisation procedure outlined in [97], combines both node-based and  
721 data-stream approaches in order to permute data gathered via GPS tracking devices.  
722 Further, multiple null models can be used to evaluate competing hypotheses [25]. Choosing  
723 a test statistic that is relevant to spatially restricted nodes is also important and edge-based

724 metrics such as least-cost path, route path diameter and route redundancy can be highly  
725 informative for understanding the connectivity of spatial networks [20]. Further detailed  
726 discussion of randomising spatial and the spatial component of animal social networks is  
727 available and would be recommended for future applications [8,29,96,98].

728