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The use of multilayer network analysis in animal behaviour

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Abstract

Network analysis has driven key developments in research on animal behaviour by providing quantitative methods to study the social structures of animal groups and populations. A recent formalism, known as *multilayer network analysis*, has advanced the study of multifaceted networked systems in many disciplines. It offers novel ways to study and quantify animal behaviour as connected 'layers' of interactions. In this article, we review common questions in animal behaviour that can be studied using a multilayer approach, and we link these questions to specific analyses. We outline the types of behavioural data and questions that may be suitable to study using multilayer network analysis. We detail several multilayer methods, which can provide new insights into questions about animal sociality at individual, group, population, and evolutionary levels of organisation. We give examples for how to implement multilayer methods to demonstrate how taking a multilayer approach can alter inferences about social structure and the positions of individuals within such a structure. Finally, we discuss caveats to undertaking multilayer network analysis in the study of animal social networks, and we call attention to methodological challenges for the application of these approaches. Our aim is to instigate the study of new questions about animal sociality using the new toolbox of multilayer network analysis.

1. Introduction

1.1 'Multi-dimensionality' of animal social behaviour

Sociality is widespread in animals, and it has a pervasive impact on behavioural, evolutionary, and ecological processes, such as social learning and disease spread (Allen, Weinrich, Hoppitt, & Rendell, 2013; Aplin et al., 2014; Silk, Alberts, & Altmann, 2003; White, Forester, & Craft, 2017). The structure and dynamics of animal societies emerge from interactions between and among individuals (Hinde, 1976; Krause, Croft, & James, 2007; Pinter-Wollman et al., 2014). These interactions are typically 'multi-dimensional', as they occur across different social contexts (e.g., affiliation, agonistic, and feeding), connect different types of individuals (e.g., male–male, female–female, or male–female interactions), and/or vary spatially and temporally. Considering such multi-dimensionality is crucial for thoroughly understanding the structure of animal social systems (Barrett, Henzi, & Lusseau, 2012).

Network approaches for studying the social behaviour of animals have been instrumental in quantifying how sociality influences ecological and evolutionary processes (Krause et al., 2007; Krause, James, Franks, & Croft, 2015; Kurvers et al., Krause, Croft, Wilson, & Wolf, 2014; Pinter-Wollman et al., 2014; Sih, Hanser, & McHugh, 2009; Sueur, Jacobs, Amblard, Petit, & King, 2011; Webber & Vander Wal, 2018; Wey, Blumstein, Shen, & Jordán, 2008). In animal social networks, nodes (also called 'vertices') typically represent individual animals; and edges (also called 'links' or 'ties') often represent pairwise interactions (i.e., behaviours, such as grooming, in which two individuals engage) or associations (e.g., spatio-temporal proximity or shared group memberships) between these individuals. Such a network representation is a simplified depiction of a much more intricate, multifaceted system. A social system can include different types of interactions, with different biological meanings (e.g., cooperative or

51   competitive), which standard network approaches often do not take into account, or they do so

52   by analysing networks of different edge types separately (Gazda, Iyer, Killingback, Connor, &

53   Brault, 2015b). Typical approaches ignore interdependencies that may exist between different

54   types of interactions and between different subsystems (Barrett et al., 2012; Beisner, Jin,

55   Fushing, & McCowan, 2015). Furthermore, networks are often studied as snapshots or

56   aggregations of processes that change over time, but dynamics can play a major role in animal

57   behaviour (Blonder, Wey, Dornhaus, James, & Sih, 2012; Farine, 2018; Wey et al., 2008; Wilson

58   et al., 2014). As we highlighted recently (Silk, Finn, Porter, & Pinter-Wollman, 2018), advances

59   in multilayer network analysis provide opportunities to analyse the multifaceted nature of animal

60   behaviour, to ask questions about links between social dynamics across biological scales, and to

61   provide new views on broad ecological and evolutionary processes. In this paper, we introduce

62   the new mathematical formalism of multilayer network analysis to researchers in animal

63   behavior. This formalism provides a common vocabulary to describe, compare, and contrast

64   multilayer network methodologies. Our goal is to review research areas and questions in animal

65   behavior that are amenable to multilayer network analysis, and we link specific analyses to these

66   questions (see Table 1). In the remainder of this section, we describe different types of multilayer

67   networks and detail how they can encode animal data. In Section 2, we review several questions

68   and hypotheses, across social scales, that multilayer network analysis can help investigate. We

69   summarize key questions and provide a guide to available methods and software for multilayer

70   network analysis in Table 1. Throughout Section 2, we present worked examples to illustrate our

71   ideas. In Section 3, we consider some of the requirements and caveats of multilayer network

72   analysis as a tool to study animal social behaviour and discuss several directions for future work.

73

74   **1.2 What are multilayer networks?**

75   Multilayer networks are assemblages of distinct network 'layers' that are connected (and

76   hence coupled) to each other via interlayer edges (Boccaletti et al., 2014; Kivelä et al., 2014). A

77   multilayer network can include more than one 'stack' of layers, and each such facet of layering is

78   called an 'aspect'. For instance, one aspect of a multilayer network can encode temporal

79   dynamics and another aspect can represent the types of social interactions (Fig. 1 and Appendix

80   I).

81   The recent formalism of *multilayer networks* has opened up new ways to study

82   multifaceted networked systems (Boccaletti et al., 2014; Kivelä et al., 2014). The application of

83   multilayer networks to questions in animal behaviour is still in its infancy, but multilayer

84   network analysis has facilitated substantial advances over monolayer (i.e., single-layer) network

85   analysis in many other fields (Aleta & Moreno (2018) and Kivelä et al. (2014)). For example,

86   multilayer network approaches have made it possible to identify important nodes that are not

87   considered central in a monolayer network (De Domenico, Solé-Ribalta, Omodei, Gómez, &

88   Arenas, 2015). Multilayer approaches applied to studying information spread on Twitter (where,

89   e.g., one can use different layers to represent 'tweets', 'retweets', and 'mentions') have

90   uncovered information spreaders who have a disproportionate impact on social groups but were

91   overlooked in prior monolayer investigations (Al-Garadi, Varathan, Ravana, Ahmed, & Chang,

92   2016). Multilayer modelling of transportation systems has improved investigations of congestion

93   and efficiency of transportation. For example, each layer may be a different airline (De

94   Domenico, Solé-Ribalta, et al., 2015) or a different form of transportation in a city (Chodrow et

95   al., 2016; Gallotti & Barthélemy, 2015; Strano, Shai, Dobson, & Barthélemy, 2015). Modelling

96   dynamical processes on multilayer networks can result in qualitatively different outcomes

97   compared to modelling dynamics on aggregate representations of networks (see Appendix II for

98   a discussion of aggregating networks) or on snapshots of networks (De Domenico, Granell,

99   Porter, & Arenas, 2016). For instance, the dynamics of disease and information spread can be

100 coupled in a multilayer framework to reveal how different social processes can impact the onset

101 of epidemics (Wang, Andrews, Wu, Wang, & Bauch, 2015). Historically, the usage of

102 'multiplexity' dates back many decades (Mitchell, 1969), and the new mathematical formalism

103 (De Domenico et al., 2014; Kivelä et al., 2014; Newman, 2018c; Porter, 2018) has produced a

104 unified framework that makes it possible to consolidate analysis and terminology. For reviews of

105 previous multilayer network studies and applications in other fields, see (Aleta & Moreno, 2018;

106 Boccaletti et al., 2014; D 'Agostino & Scala, 2014; Kivelä et al., 2014; Pilosof, Porter, Pascual,

107 & Kéfi, 2017).
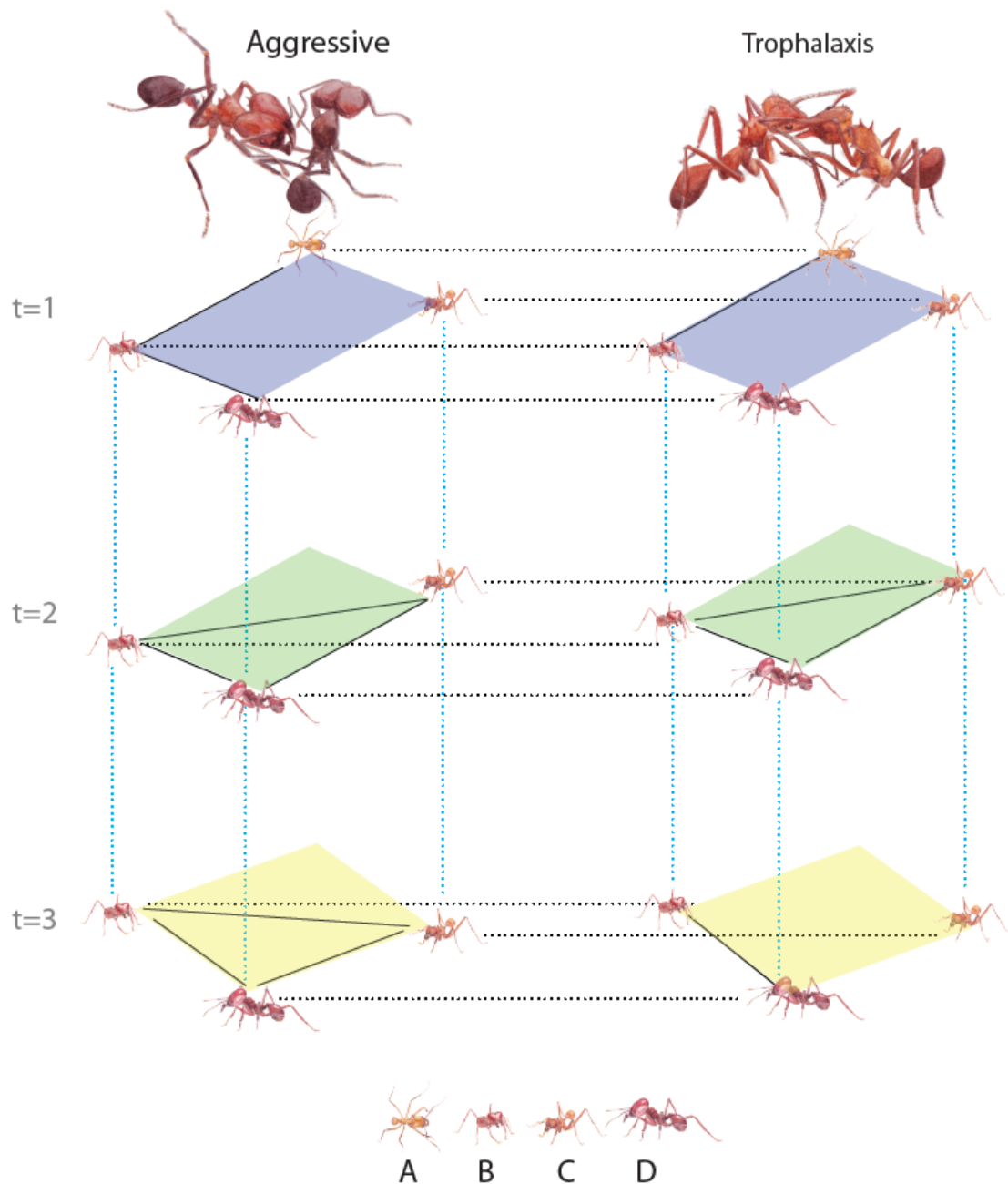
Figure 1: A hypothetical multilayer network. Four ants interact at different time points and in two different ways. Each diamond represents a layer. The stack of three layers on the left represents aggressive interactions, and the stack of three layers on the right represents trophalactic interactions. Each colour represents a different time point (blue is $t=1$, green is $t=2$, and yellow is $t=3$). Solid lines represent intralayer (i.e., within-layer) interactions, dotted blue

114 lines represent interlayer (i.e., across-layer) relationships in the temporal aspect, and dotted black

115 lines represent interlayer edges in the behavioural aspect. These interlayer interactions connect

116 replicates of the same individuals across different layers. See Appendix I for further discussion

117 and for a presentation of the mathematical formalism.

118

119 **1.3 Types of multilayer networks**

120 The mathematical framework of multilayer networks was developed recently to create a unified

121 formalism (De Domenico et al., 2014; Kivelä et al., 2014; Mucha, Richardson, Macon, Porter, &

122 Onnela, 2010; Porter, 2018). One can use this multilayer network framework, which we follow

123 in this paper and detail in Appendix I, to represent a variety of network types and situations. In

124 contrast to monolayer networks, which are traditional in network analysis and which consist of

125 only a single network 'layer', multilayer networks can include many different types of data that

126 are commonly collected in studies of animal behaviour. For example, types of social interactions,

127 spatial locations (with connections between them), and different measures of genetic relatedness

128 can all constitute layers in a multilayer network. Node attributes can include behavioural or

129 physical phenotypes, sex, age, personality, and more. Edge attributes, such as their weight or

130 direction, can encode interaction frequencies, distances between locations, dominance, and so on.

131 Commonly studied variants of multilayer networks that can accommodate such data include the

132 following.

133   (1) *Multiplex networks* (i.e., *edge-coloured networks*) are networks in which interlayer

134   edges connect nodes to themselves on different layers (Fig. 1 and Appendix I). It is

135   often assumed, for convenience, that all layers consist of the same set of nodes, but

136   this is not necessary.

137   a. In ***multirelational networks,*** each layer represents a different type of

138   interaction. For example, a network of aggressive interactions can be

139   connected with a network of affiliative interactions through interlayer edges

140   that link individuals to themselves if they appear in both layers (Fig. 1;

141   horizontal dotted black lines).

142   b. In ***temporal networks,*** each layer encodes the same type of interactions during

143   different time points or over different time windows. In the most common

144   multiplex representation of a temporal network, consecutive layers are

145   connected to each other through interlayer edges that link individuals to

146   themselves at different times (Fig. 1; vertical dotted blue lines).

147 (2) In ***interconnected networks*** (i.e., ***node-coloured networks***)*,* the nodes in different

148   layers do not necessarily represent the same entities, and interlayer edges can exist

149   between different types of nodes. (See our discussion of the mathematical formalism

150   and an example figure in Appendix I.)

151   a. ***Networks of networks*** consist of subsystems, which themselves are networks

152   that are linked to each other through interlayer edges between the subsystems'

153   nodes. For example, one can model intra-group interactions in a population-

154   level network of interactions between social groups, which are themselves

155   networks.

156   b. In ***inter-contextual networks,*** one can construe each layer as representing a

157   different type of node. For example, interactions between males can be in one

158   layer, interactions between females can be in a second layer, and inter-sex

159   interactions are interlayer edges. See Fig. 1 of Silk, Weber, et al. (2018) and

160   Fig 1. of Silk, Finn, Porter, & Pinter-Wollman (2018).

161   c. *Spatial networks*, which we define here as networks of locations, can be

162   linked with social networks of animals that move between these locations

163   (Pilosof et al., 2017; Silk, Finn, Porter, & Pinter-Wollman, 2018). Our use of

164   the term "spatial networks" refers to networks that are embedded in space,

165   rather than networks that are influenced by a latent space (Barthélemy, 2018).

166 Throughout this paper, we use the term "multilayer networks" to refer to any of the variants

167 above, unless we specify that a method applies to only one or a subset of specific network types.

168 For a review of other types of multilayer networks, see (Kivelä et al., 2014).

169

170 2. Novel insights into animal sociality: From individuals to populations

171   We propose that a multilayer network approach can advance the study of animal

172 behaviour and expand the types of questions that one can investigate. Specifically, we discuss

173 how a multilayer framework can enhance understanding of (1) an individual's role in a social

174 network, (2) group-level structure and dynamics, (3) population structure, and (4) evolutionary

175 models of the emergence of sociality.

176

177 2.1 An individual's role in society

178   Traditionally, the use of network analysis to examine the impact of individuals on their

179 society has focused on the social positions of particular individuals using various centrality

180 measures (such as degree, eigenvector centrality, betweenness centrality, and others (Pinter-

181 Wollman et al., 2014; Wasserman & Faust, 1994; Wey et al., 2008; Williams & Lusseau, 2006)).

182   It is common to construe individuals with disproportionally large centrality values as influential

183   or important to a network in some way (but see (Rosenthal, Twomey, Hartnett, Wu, & Couzin,

184   2015) for a different trend). The biological meaning of 'importance' and corresponding centrality

185   measures differ among types of networks and is both system-dependent and question-specific.

186   Consequently, one has to be careful to avoid misinterpreting the results of centrality calculations.

187   Centrality measures have been used to examine which individuals have the most influence on a

188   group in relation to age, sex, or personality (Sih et al., 2009; Wilson, Krause, Dingemanse, &

189   Krause, 2013) and to study the fitness consequences of holding an influential position (Pinter-

190   Wollman et al., 2014). A multilayer approach can advance understanding of roles that

191   individuals play in a population or a social group, and it can potentially identify central

192   individuals who may be overlooked when using monolayer approaches on "multidimensional"

193   data.

194   An individual's role in a social group is not restricted to its behaviour in just one social or

195   ecological situation. A multilayer approach creates an opportunity to consolidate analyses of a

196   variety of social situations and simultaneously examine the importances of individuals across and

197   within situations. Many centrality measures have been developed for multilayer networks, and

198   different ones encompass different biological interpretations. For instance, eigenvector

199   'versatility' (see Appendix I for its mathematical definition) is one way to quantify the overall

200   importance of individuals across and within layers, because this measure takes into account

201   multiple layers to identify individuals who increase group cohesion in multiple layers and bridge

202   social situations (De Domenico, Solé-Ribalta, et al., 2015). In a multirelational network, an

203   individual can have small degree (i.e., degree centrality) in each layer, which each represent a

204   different social situation, but it may participate in many social situations, thereby potentially

205   producing a larger impact on social dynamics than individuals with large degrees in just one or a

206   few social situations. One can also account for the interrelatedness of behaviours in different

207   layers in a multilayer network when combining interlayer centralities, if appropriate for the study

208   system (De Domenico, Solé-Ribalta, et al., 2015). For example, it is not possible for two

209   individuals to engage in grooming interactions without also being in proximity. By accounting

210   for interrelatedness between proximity and grooming when calculating multilayer centralities

211   and versatilities, it may be possible to consider grooming interactions as explicitly constrained by

212   proximity interactions and thereby incorporate potentially important nuances.

213   The appropriateness of a versatility measure differs across biological questions, just as

214   various centrality measures on a monolayer network have different interpretations (Wasserman

215   & Faust, 1994; Wey et al., 2008). Versatility measures that have been developed include

216   shortest-path betweenness versatility, hub/authority versatility, Katz versatility, and PageRank

217   versatility (De Domenico, Solé-Ribalta, et al., 2015). Experimental removal of versatile nodes,

218   similar to the removal of central nodes in monolayer networks (Barrett et al., 2012; Firth et al.,

219   2017; Flack et al., 2006; Pruitt & Pinter-Wollman, 2015; Sumana & Sona, 2013), has the

220   potential to uncover the effects of the removed nodes on group actions, group stability, and their

221   impact on the social positions of other individuals. However, which versatility measure gives the

222   most useful information about an individual's importance may depend on the level of

223   participation of an individual in the different types of behaviours that are encoded in a multilayer

224   network. Further, if layers have drastically dissimilar densities, one layer can easily dominate a

225   versatility measure (Braun et al. 2018); see our discussion of caveats in Section 3. In addition to

226   calculating node versatility, one can examine versatility of edges to yield interesting insights into

227   the importances of relationships with respect to group stability and cohesion. Such an approach

228 can help reveal whether interlayer interactions are more important, less important, or comparably

229 important than intralayer interactions for group cohesion. Examining edge versatility can also

230 illuminate which interactions between particular individuals (within or across layers) have the

231 largest impact on group activity and/or stability; and it may be helpful for conservation efforts,

232 such as in identifying social groups that are vulnerable to fragmentation (Snijders, Blumstein,

233 Stanley, & Franks, 2017).

234 A multilayer approach can help elucidate the relative importances of different individuals

235 in various social or ecological situations. For example, a node's 'multidegree' is a vector of the

236 intralayer degrees (each calculated as on a monolayer network) of an individual in each layer.

237 Differences in how the degrees of individuals are distributed across layers help indicate which

238 individuals have influence over others in the different layers. For example, if each layer

239 represents a different situation, individuals whose intralayer degree peaks in one situation may be

240 more influential in that context than individuals whose intralayer degree is small in that situation

241 but peaks in another one. Because multidegree does not account for interlayer connections,

242 quantitatively comparing it with versatility or other multilayer centralities, which account

243 explicitly for interlayer edges (Kivelä et al., 2014), can help elucidate the importance of

244 interlayer edges and thereby highlight interdependencies between biological situations. Such

245 behavioural interdependencies may elucidate and quantify the amount of behavioural carryover

246 across situations (i.e., 'behavioural syndromes') (Sih, Bell, & Johnson, 2004) if, for example,

247 measures that account for interlayer edges explain observed data better than measures that do not

248 take into account such interdependencies.

249 As a final example, one can use a multilayer approach to examine temporal changes in an

250 individual's role (or roles) in a group. A multilayer network in which one aspect represents time

251 and another aspect represents situation (Fig. 1) can reveal when individuals gain or lose central

252 roles and whether roles are lost simultaneously in all situations or if changes in one situation

253 precede changes in another. Comparing monolayer (e.g., time-aggregated) measures and

254 multilayer measures has the potential to uncover the importance of temporal changes in an

255 animal's fitness.

256

2.1.1 Roles of individuals in a group: Baboon versatility in a multiplex affiliation network

258 To demonstrate the potential insights from employing multilayer network analysis to

259 examine the roles of individuals in a social group using multiple interaction types, we analysed

260 published affiliative interactions from a baboon *Papio cynocephalus* group of 26 individuals

261 (Franz, Altmann, & Alberts, 2015b, 2015a) (Fig. 2). One can quantify affiliative relationships in

262 primates in multiple ways, including grooming, body contact, and proximity (Barrett & Henzi,

263 2002; Jack, 2003; Kasper & Voelkl, 2009; Pasquaretta et al., 2014). To characterize affiliative

264 relationships, combinations of these behaviours have been investigated separately (Jack, 2003;

265 Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008), pooled together (Kasper & Voelkl, 2009),

266 or used interchangeably (Pasquaretta et al., 2014). These interaction types are often correlated

267 with each other, but their networks typically do not coincide completely (Barrett & Henzi, 2002;

268 Brent, MacLarnon, Platt, & Semple, 2013).

269 We analyse the baboon social data in four ways: (1) as a weighted grooming network

270 with only grooming interactions (Fig. 2A), (2) as a weighted association network with only

271 proximity-based associations (Fig. 2B), (3) as an aggregate monolayer network that we obtained

272 by summing the weights of grooming and association interactions of the node pairs (Fig. 2C; see

273 Appendix II for more details on aggregating networks), and (4) as a multiplex network with two

274   layers (one for grooming and one for associations). We then calculated measures of centrality

275   (for the monolayer networks in (1)–(3)) and versatility (for the multilayer network (4)) using

276   MuxViz (De Domenico et al. 2015). We ranked individuals according to their PageRank

277   centralities and versatilities (De Domenico, Solé-Ribalta, et al., 2015), which quantify the

278   centrality of an individual in a network recursively based on being adjacent to central neighbours

279   (Fig. 3).

280   The most versatile baboon in the multilayer network (individual 3 in Fig. 3) was the

281   fourth-most central individual in the aggregated network, the second-most central individual in

282   the grooming network, and 16th-most central individual in the association network (Fig. 3).

283   These differences in results using the multilayer, aggregated, and independent networks of the

284   same data highlight the need to (1) carefully select which behaviours to represent as networks

285   and (2) interpret the ensuing results based on the questions of interest (Carter, DeChurch, Braun,

286   & Contractor, 2015; Krause et al., 2015). When social relationships depend on multiple

287   interaction types, it is helpful to use a multilayer network framework to reliably capture an

288   individual's social roles (see Table 1 for more questions and tools), because monolayer

289   calculations may yield different results and centrality in one layer can differ substantially from

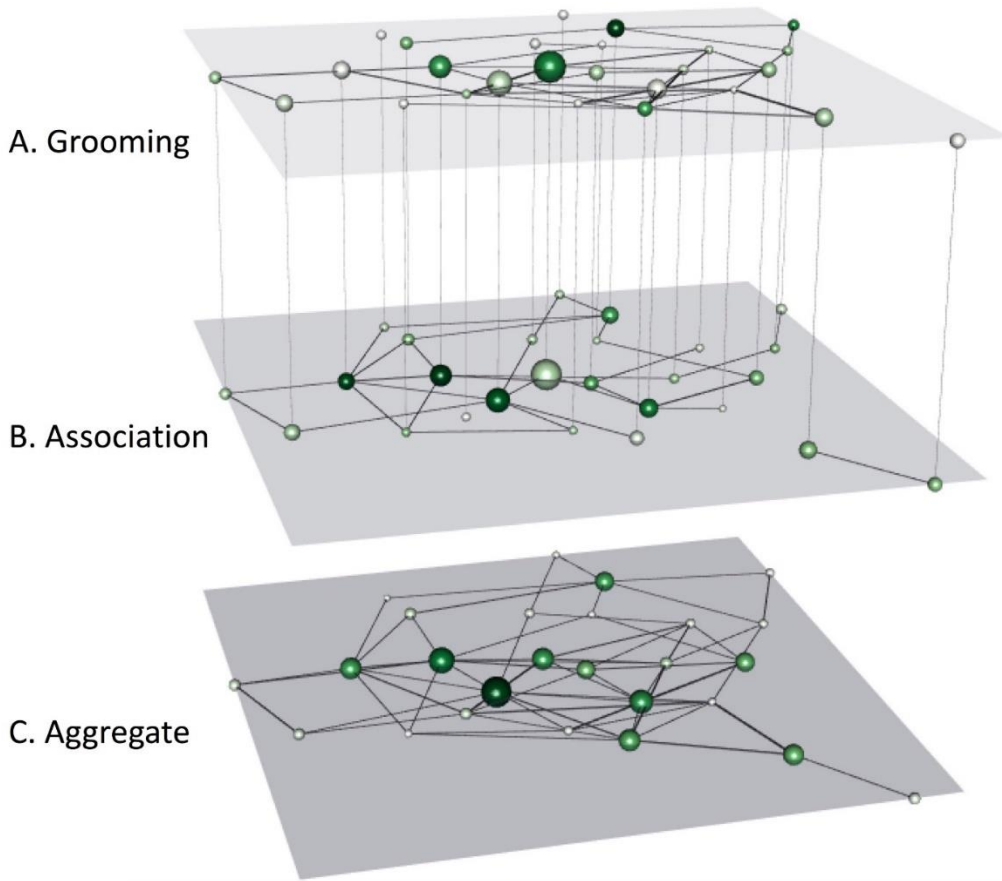290   versatility in an entire multilayer network (Fig. 3).

291

Figure 2: Social networks of a baboon group based on (A) grooming interactions, (B) proximity-based association relations, and (C) an aggregate of both interaction types. We created the network visualization using MuxViz (De Domenico, Porter, & Arenas, 2015). To construct a multilayer network, we joined the grooming and association monolayer networks as two layers in a multiplex network by connecting nodes that represent the same individual using interlayer edges. The sizes of the nodes are based on multilayer PageRank versatility (with larger nodes indicating larger versatilities). We colour the nodes based on monolayer PageRank centrality (with dark shades of green indicating larger values). A given individual in these two layers has the same size, but it can have different colours in the two layers. In the aggregate layer, we determine both the node sizes and their colours from PageRank centrality values in the aggregate

network. We position the nodes in the same spatial location in all three layers. The data (Franz et
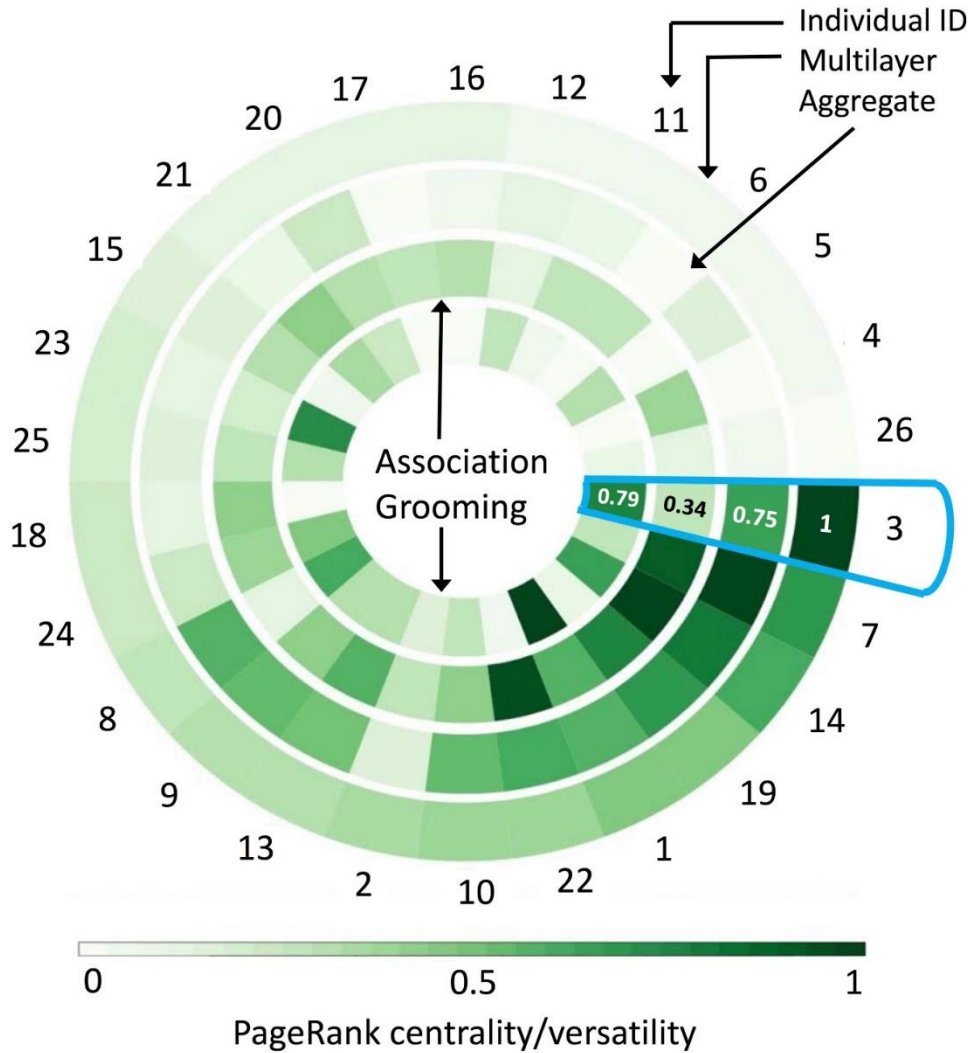
al., 2015a) are from (Franz et al., 2015b).

305

Figure 3: A circular heat map illustrates variation among individuals in PageRank centralities
and versatilities. Darker colours indicate larger values of PageRank centralities and versatilities.
A given angular wedge in the rings indicates the values for one individual, whose ID we list
outside the ring. The rings are PageRank centrality values from the monolayer grooming network
(innermost ring), association network (second ring), aggregate network in which we sum the
grooming and association ties (third ring), and PageRank versatility for the multiplex network

17

313   (outermost ring). Using a blue outline, we highlight individual 3, who we discuss in the main

314   text. We indicate the PageRank centrality and versatility values of individual 3 on the rings. We

315   created this visualization using MuxViz (De Domenico, Porter, et al., 2015). The data (Franz et

316   al., 2015a) are from (Franz et al., 2015b).

317

318   **2.2 Multilayer structures in animal groups**

319   Animal social groups are emergent structures that arise from local interactions (Sumpter,

320   2010), making network analysis an effective approach for examining group-level behaviour.

321   Networks provide useful representations of dominance hierarchies (Hobson et al. 2013) and

322   allow investigations of information transmission efficiency (Pasquaretta et al., 2014), group

323   stability (Baird & Whitehead, 2000; McCowan et al., 2011), species comparisons (Pasquaretta et

324   al., 2014; Rubenstein, Sundaresan, Fischhoff, Tantipathananandh, & Berger-Wolf, 2015), and

325   collective behaviour (Rosenthal et al., 2015; Westley, Berdahl, Torney, & Biro, 2018).

326   However, given that animals interact with each other in many different—and potentially

327   interdependent—ways, a multilayer approach may help accurately capture a group's structure

328   and/or dynamics. In one recent example, Smith-Aguilar et al. (2018) studied a six-layer

329   multiplex network of spider monkeys, with layers based on types of interactions. In this section,

330   we detail how multilayer methodologies can advance the study of group stability, group

331   composition, and collective movement.

332   One can analyse changes in group stability and composition using various multilayer

333   calculations or by examining changes in relationships across network layers (Beisner &

334   McCowan, 2015). For instance, Barrett et al. (2012) examined changes in a baboon group

335   following the loss of group members by calculating a measure from information theory called

336　'joint entropy' on a multiplex network—with grooming, proximity, and aggression layers—both

337　before and after a known perturbation. A decrease in joint entropy following individual deaths

338　corresponded to individuals interacting in a more constrained and therefore more predictable

339　manner. Using a different approach, Beisner et al. (2015) investigated co-occurrences of directed

340　aggression and status-signalling interactions between individuals in macaque behavioural

341　networks. In their analysis, they employed a null model that incorporates constraints that encode

342　interdependences between behaviour types. For example, perhaps there is an increased likelihood

343　that animal *B* signals to animal *A* if animal *A* aggresses animal *B*. These constraints were more

344　effective at reproducing the joint probabilities (which they inferred from observations) of

345　interactions in empirical data in stable macaque groups than in groups that were unstable and

346　eventually collapsed (Chan, Fushing, Beisner, & McCowan, 2013). These findings illustrate how

347　interdependencies between aggression and status-signalling network layers may be important for

348　maintaining social stability in captive macaque groups. A potential implication of this finding is

349　that analysing status-signalling and aggression may be helpful for predicting social stability.

350　Another approach that may be useful for uncovering temporal structures in multilayer networks

351　is an extension of stochastic actor-oriented models (SAOMs) (Snijders, 2017). One can use

352　SAOMs to examine traits and processes that influence changes in network ties over time,

353　including in animal social networks (Fisher, Ilany, Silk, & Tregenza, 2017; Ilany, Booms, &

354　Holekamp, 2015). SAOMs can use unweighted or weighted edges, with some restrictions in how

355　weights are incorporated (Snijders, 2017). A multiple-network extension to an SAOM enables

356　modelling of the co-dynamics of two sets of edges, while incorporating influences of other

357　individual or network-based traits. Such an approach has the potential to provide interesting

358　insights into how changes in one layer may cascade into changes in other layers. It also provides

359   a useful method to quantify links between group-level structural changes and temporal dynamics

360   of individual centralities.

361   Multilayer analysis of animal groups can go beyond monolayer network analysis when

362   highlighting a group's composition and substructures. For example, one measure of

363   interdependence, the proportion of shortest paths between node pairs that span more than one

364   layer (Morris & Barthélemy, 2012; Nicosia, Bianconi, Latora, & Barthélemy, 2013), can help

365   describe a group's interaction structure. In social insect colonies, layers can represent different

366   tasks. As time progresses and individuals switch tasks, an individual can appear in more than one

367   layer. The amount of overlap among layers (see Section 3 of Appendix I for examples of overlap

368   measures) can indicate the level of task specialization and whether or not there are task-

369   generalist individuals (Pinter-Wollman, Hubler, Holley, Franks, & Dornhaus, 2012).

370   Consequently, the above interdependence measure may be useful as a new and different way to

371   quantify division of labour (Beshers & Fewell, 2001), because having a small proportion of

372   shortest paths that traverse multiple layers may be an indication of pronounced division of

373   labour. Such a new measure may reveal ways in which workers are allocated to tasks that are

374   different from those that have been inferred by using other measures of division of labour.

375   Comparing different types of measures may uncover new insights into the mechanisms that

376   underlie division of labour.

377   Animal groups are often organized into substructures called `communities' (Fortunato &

378   Hric, 2016; Porter, Onnela, & Mucha, 2009; Shizuka et al., 2014; Wolf, Mawdsley, Trillmich, &

379   James, 2007), which are sets of individuals who interact with each other more frequently (or

380   more often) than they do with other individuals. Finding communities can aid in predicting how

381   a group may split, which can be insightful for managing captive populations when it is necessary

382   to remove individuals (Sueur, Jacobs, et al., 2011). Community-detection algorithms distinguish

383   sets of connected individuals who are more connected within a community than with other

384   communities in a network. One example of a multilayer community-detection algorithm is

385   maximization of 'multislice modularity' (Mucha et al., 2010), which can account for different

386   behaviours and/or time windows. A recent review includes a discussion of how multilayer

387   modularity maximization can inform ecological questions, such as the ecological effects of

388   interdependencies between herbivory and parasitism (Pilosof et al., 2017). In animal groups,

389   individuals can be part of more than one community, depending on the types of interactions

390   under consideration. For example, an individual may groom with one group of animals but fight

391   with a different group. Because maximizing multislice modularity does not constrain an

392   individual's membership to a single community, it can yield communities of different functions

393   with overlapping membership. It can also be used to examine changes in community structure

394   over time. Additionally, sex, age, and kinship are known to influence patterns of subgrouping in

395   primates (Sueur, Jacobs, et al., 2011), so investigating group structure while considering several

396   of these characteristics at once can reveal influences of subgrouping (such as nepotism) that may

397   not be clear when using monolayer clustering approaches. See Aleta & Moreno (2018) for

398   references to various methods for studying multilayer community structure.

399   Collective motion is another central focus in studies of animal groups (Berdahl, Biro,

400   Westley, & Torney, 2018; Sumpter, 2010). Coordinated group movements emerge from group

401   members following individual-based, local rules (e.g., in fish schools and bird flocks) (Couzin,

402   Krause, James, Ruxton, & Franks, 2002; Sumpter, 2010). Recent studies of collective motion

403   have employed network analysis to examine relationships of individuals beyond the ones with

404   their immediate neighbours. For instance, one can incorporate connections between individuals

405   who are in line of sight of each other (Rosenthal et al., 2015) or with whom there is a social

406   relationship in other contexts (Bode, Wood, & Franks, 2011; Farine et al., 2016). One can also

407   combine multiple sensory modes into a multilayer network to analyse an individual's movement

408   decisions. Expanding the study of collective motion to incorporate multiple sensory modalities

409   (e.g., sight, odour, vibrations, and so on) and social relationships (e.g., affiliative, agonistic, and

410   so on) can benefit from a multilayer network approach, which may uncover synergies among

411   sensory modes, social relationships, and environmental constraints.

412

413   **2.2.1 Multilayer groupings: Dolphin communities emerge from multirelational interactions**

414   To demonstrate the utility of multilayer network analysis for uncovering group dynamics,

415   we analysed the social associations of 102 bottlenose dolphins that were observed by (Gazda et

416   al., 2015b). Gazda et al, (2015b) recorded dolphin associations during travel, socialization, and

417   feeding. They identified different communities when analysing the interactions as three

418   independent networks and compared the results with an aggregated network, in which they

419   treated all types of interactions equally (regardless of whether they occurred when animals were

420   traveling, socializing, or foraging). However, analysing these networks separately or as one

421   aggregated network ignores interdependencies that may exist between the different behaviours

422   (Kivelä et al., 2014). Therefore, we employed multiplex community detection, using the

423   multilayer InfoMap method (De Domenico et al. 2015), to examine how interdependency

424   between layers influences which communities occur when the data are encoded as a multiplex

425   network. We use multiplex community detection to assign each replicate of an individual (there

426   is one for each layer in which an individual appears; Appendix I) to a community. Therefore, an

427   individual can be assigned to one or several communities, where the maximum number

428   corresponds to the number of layers in which the individual is present. The community

429   assignments depend on how individuals are connected with each other in a multilayer network

430   and on interactions between layers, which arise in this case from a parameter in the multilayer

431   InfoMap method (see Appendix II for details). The coupling between layers thus arises both

432   from interlayer edges and their weights (Appendix I) and from a parameter in the community-

433   detection method (Appendix II). With no coupling, the layers are distinct and communities

434   cannot span more than one layer; for progressively larger coupling, communities span multiple

435   layers increasingly often. For details on our parameter choices for community detection with the

436   multilayer InfoMap method, see Appendix II.

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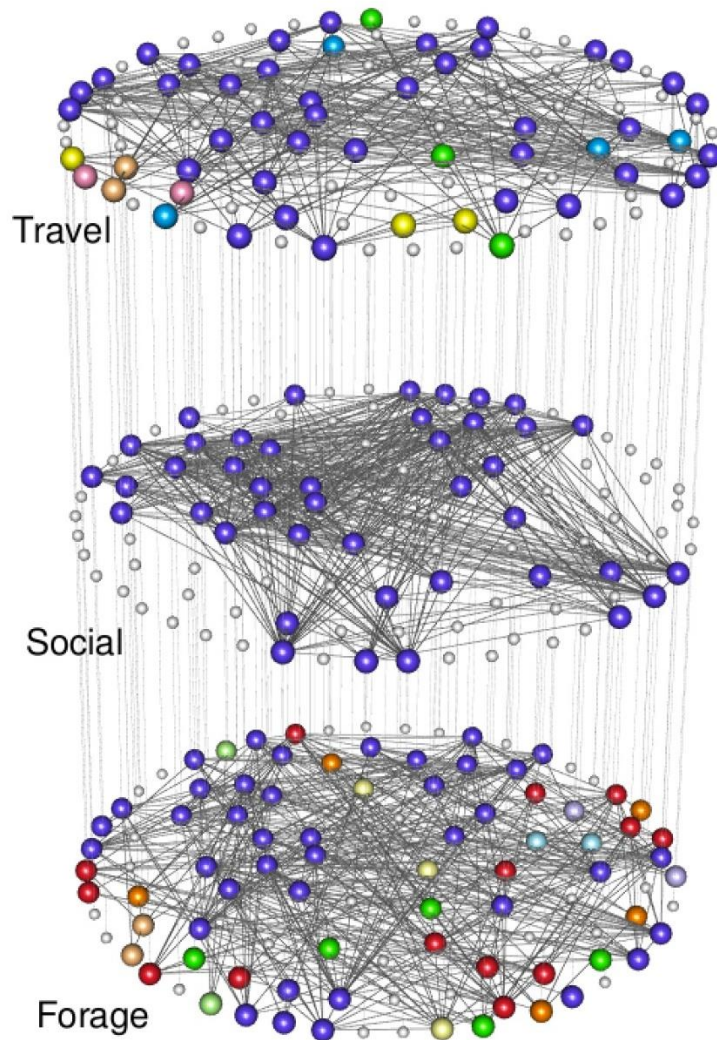
Figure 4: Multiplex network of dolphin proximity-based associations during (1) traveling, (2)

socializing, and (3) foraging. There are 102 distinct individuals, and each layer has a node for

each individual. Individuals who were never seen interacting in a specific layer (behavioural

context) are the smaller white nodes. Individuals who interacted in at least one layer are the

larger nodes, which we colour based on their community assignment from multilayer InfoMap

(De Domenico et al. 2015). We created the network visualization with MuxViz (De Domenico et

al. 2015). The data (Gazda, Iyer, Killingback, Connor, & Brault, 2015a) are from (Gazda et al.,

2015b).

448

449   To be consistent with Gazda et al, (2015b), our multiplex network (Fig. 4) includes only

450   individuals who were seen at least 3 times, and we weight the edges using the half-weight index

451   (HWI) of association strength (Cairns & Schwager, 1987). Our community-detection

452   computation yielded 12 communities. The largest community (dark blue; Fig. 4) consists of

453   individuals from all three association layers, and several smaller communities consist of only

454   foraging individuals, only traveling individuals, and both foraging and traveling individuals. For

455   details on the specific implementation of the InfoMap method, see Appendix II.

456   In their investigation, Gazda et al, (2015b) revealed contextually-dependent association

457   patterns, as indicated by different numbers of communities in the foraging (17), travel (8), and

458   social (4) networks. Notably, when considering the three behavioural situations as a multiplex

459   network, we found similar trends in the numbers of communities across behavioural situations:

460   foraging individuals are in 9 communities, traveling individuals are in 6 communities, and

461   individuals who interact socially are in only 1 community. Thus, our analysis strengthens the

462   finding that dolphins forage in more numerous, smaller groups and socialize in fewer, larger

463   groups. Different methods for community detection yield different communities of nodes

464   (Fortunato & Hric, 2016) therefore, it is not surprising that we detected a different number of

465   communities in the monolayer networks than the number in Gazda et al, (2015b). We used

466   InfoMap, which has been implemented for both monolayer and multilayer networks. By contrast,

467   Gazda et al, (2015b) used a community-detection approach that has been implemented only for

468   monolayer networks. Additionally, because we find one markedly larger community that spans

469   all layers, it may also be useful to explore core–periphery structure in this network (Csermely,

470   London, Wu, & Uzzi, 2013; Rombach, Porter, Fowler, & Mucha, 2017).

471   We also analysed each layer independently and an aggregate of all layers using

472   monolayer InfoMap (Rosvall & Bergstrom, 2007), which is implemented in MuxViz. Multiplex

473   community detection produces somewhat different community assignments from monolayer

474   community detection (Fig. 5). With a multiplex network, one can identify and label an

475   individual's membership in a community that spans one or several layer(s) (Fig. 5A). However,

476   in monolayer community detection, one examines individuals independently in different layers,

477   thereby assigning their replicates in different layers to different communities (Fig. 5B).

478   Therefore, which individuals are grouped into communities can vary substantially. (See Table 1

479   for more questions and tools in multilayer community detection in animal behaviour). As this

480   example illustrates, depending on the research aims, the form of the data, and knowledge of the

481   study system, one or both of monolayer and multilayer investigations may provide valuable

482   insights into the structure of a social system of interest.

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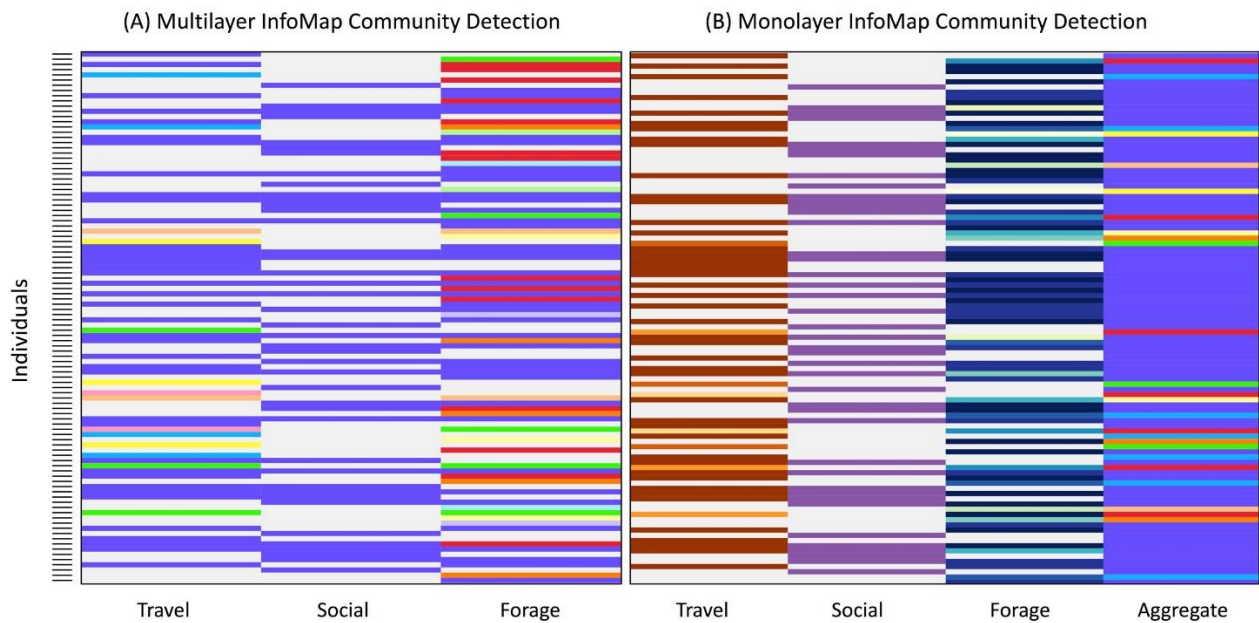
486   **Figure 5:** Community structures of individuals from (A) a multilayer InfoMap community

487   detection and (B) monolayer InfoMap community detection. Each row represents an individual

488   dolphin, and each column represents a behavioural situation. In the multiplex community

489   detection (A), communities can span all three columns of behaviours, and individuals who are

490   the same colour in one or more columns belong to the same community. Community colours are

491   the same as those that we used in Figure 4. Note that an individual who appears in all three layers

492   can be assigned to the same community in all three situations (and therefore have the same

493   colour in all three columns). It can also be part of three different communities, and it then has

494   different colours in each layer. It can also be assigned twice to one community and once to

495   another. In monolayer InfoMap (B), each behavioural situation (as well as the aggregated

496   monolayer network in the last column) yields a separate set of communities, so we use a

497   different colour palette in each column. Individuals in the same column and the same colour are

498   assigned to the same community. In both panels, white represents individuals who do not exist in

499   the associated behavioural situation.

500

501   **2.3 Multilayer processes at a population level**

502   Network analysis has been fundamental in advancing understanding of social processes

503   over a wide range of spatial scales and across multiple social groups (Silk, Croft, Tregenza, &

504   Bearhop, 2014; Sueur, King, et al., 2011). A multilayer approach is convenient for combining

505   spatial and social networks (e.g., in a recent study of international human migration (Danchev &

506   Porter, 2018)), and it may contribute to improved understanding of fission–fusion dynamics,

507   transmission processes, and dispersal. It also provides an integrative framework to merge social

508   data from multiple species and extend understanding of the drivers that underlie social dynamics

509   of multi-species communities (Farine, Garroway, & Sheldon, 2012; Sridhar, Beauchamp, &

510   Shanker, 2009).

511   Many animals possess complicated fission–fusion social dynamics, in which groups join

512   one another or split into smaller social units (Couzin & Laidre, 2009; Silk et al., 2014; Sueur,

513   King, et al., 2011). It can be insightful to study such populations as networks of networks.

514   Recent advances in quantifying temporal dynamics of networks have shed some light on fission–

515   fusion social structures (Rubenstein et al., 2015). A multilayer approach applied to association

516   data (collected at times that make it is reasonable to assume that group membership is

517   independent between observations) can assist in detecting events and temporal scales of social

518   transitions in fission–fusion societies. For example, if each layer in a multiplex network

519   represents the social associations of animals at a certain time, a multiplex community-detection

520   algorithm can uncover temporally cohesive groups, similar to the detection of temporal patterns

521   of correlations between various financial assets (Bazzi et al., 2016). Further development of

522   community detection and other clustering methods for general multilayer networks (e.g.,

523   stochastic block models (Peixoto, 2014, 2015) and methods based on random walks (De

524   Domenico, Lancichinetti, et al., 2015; Jeub, Balachandran, Porter, Mucha, & Mahoney, 2015;

525   Jeub, Mahoney, Mucha, & Porter, 2017) may provide insights into the social and ecological

526   processes that contribute to the temporal stability of social relationships in fission–fusion

527   societies.

528   Ecological environments and connections between different locations have fundamental

529   impacts on social dynamics (Firth & Sheldon, 2016; Spiegel, Leu, Sih, & Bull, 2016). A

530   multilayer network representation can explicitly link spatial and social processes in one

531   framework (Pilosof et al., 2017). One approach is to use interconnected networks of social

532   interactions and spatial locations to combine layers that represent social networks with layers for

533   animal movement and habitat connectivity. Data on social interactions can also have multiple

534   layers, with different layers representing interactions in different locations or habitats. For

535   example, in bison *Bison bison,* it was observed that group formation is more likely in open-

536   meadow habitats than in forests (Fortin et al., 2009). The same study also noted that larger

537   groups are more likely than smaller groups to occur in meadow habitats. Multilayer network

538   approaches, such as examining distributions of multilayer diagnostics, may be helpful for

539   detecting fundamental differences in social relationships between habitats.

540   Important dynamical processes in animal societies, such as information and disease

541   transmission, are intertwined with social network structures (Allen et al., 2013; Aplin et al.,

542   2014; Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Hirsch, Reynolds, Gehrt, & Craft, 2016;

543   Weber et al., 2013). Research on networks has revealed that considering multilayer network

544   structures can produce very different spreading dynamics than those detected when collapsing

545   (e.g., by aggregating) multiple networks into one monolayer network (De Domenico et al.,

546   2016). Multilayer approaches can uncover different impacts on transmission from different types

547   of social interactions (Craft 2015; White et al. 2017) or link the transmission of multiple types of

548   information or disease across the same network. Compartmental models of disease spreading,

549   which describe transitions of individuals between infective and other states (e.g., susceptible–

550   infected [SI] models, susceptible–infected–recovered [SIR] models, and others) (Kiss, Miller, &

551   Simon, 2017) have been used to model transmission through multilayer networks (Aleta &

552   Moreno, 2018; De Domenico et al., 2016; Kivelä et al., 2014). For example, several studies have

553   incorporated a multilayer network structure into an SIR model for disease spreading coupled

554   with information spreading about the disease, with the two spreading processes occurring on

555   different network layers (Wang, Andrews, Wu, Wang, & Bauch, 2015). This approach suggests

556   that taking into account the spread of information about a disease can reduce the expected

557   outbreak size, especially in strongly modular networks and when infection rates are low (Funk,

558   Gilad, Watkins, & Jansen, 2009). Given the growing evidence for coupled infection and

559   behaviour dynamics in animals (Croft, Edenbrow, et al., 2011; Lopes, Block, & König, 2016;

560   Poirotte et al., 2017), using multilayer network analysis to help understand interactions between

561   information and disease spread is likely to be informative in studies of animal contagions.

562   Analogous arguments apply to the study of acquisition of social information, where learning one

563   behaviour can influence the likelihood of social learning of other behaviours. For example,

564   extending models of information spreading (Aleta & Moreno, 2018; De Domenico et al., 2016;

565   Kivelä et al., 2014) to two-aspect multilayer networks that include one layering aspect to

566   represent different types of social interactions and another aspect to represent different time

567   periods (Fig. 1) may provide valuable insights into how social dynamics influence cultural

568   transmissions in a population.

569   The study of dispersal can also benefit from utilizing a multilayer framework. Networks

570   have been used to uncover the role of spatial (Reichert, Fletcher, Cattau, & Kitchens, 2016) and

571   social (Blumstein, Wey, & Tang, 2009) connectivity in dispersal decisions. One can use a two-

572   aspect multilayer approach to integrate spatial layers that encode habitat connectivity or

573   movements of individuals with social layers that encode intra-group and inter-group social

574   relationships. For example, integrating a multilayer framework with existing multi-state models

575   of dispersal (such as the ones in (Borg et al., 2017; Polansky, Kilian, & Wittemyer, 2015)) can

576   make it possible to relate the likelihood of transitioning between dispersive and sedentary states

577   to the positions of individuals in a multilayer socio-spatial network. Such integration of spatial

578 and social contexts may provide new insights both into the relative roles of social and ecological

579 environments in driving dispersal decisions and into the subsequent effects of dispersal on

580 population structure.

581

582 **2.3.1. Inter-specific interactions as a multilayer network**

583   Network approaches have been useful for studying the social dynamics of mixed-species

584 assemblages (Farine et al., 2012). For example, in mixed-species groups of passerine birds,

585 network analysis was used to show that social learning occurs both within and between species

586 (Farine, Aplin, Sheldon, & Hoppitt, 2015b). Mixed-species assemblages have an inherent

587 multilayer structure. Most simply, one can represent a mixed-species community as a node-

588 coloured network in which each layer represents a different species (Fig. 6). To incorporate

589 additional useful information in a mixed-species multilayer network, one can represent the type

590 of behavioural interaction as an additional aspect of the network. For example, one aspect can

591 encode competitive interactions and another can encode non-competitive interactions.

592   Considering multilayer measures, such as multidegree or versatility, may provide new

593 insights into the role of particular species or individuals in information sharing in mixed-species

594 groups. Further, multilayer community detection has the potential to provide new insights into

595 the structure of fission–fusion social systems that involve multiple species. The original study

596 (Farine et al., 2015b) that generated the networks that we used in Fig. 6 investigated information

597 transmission in both intra-species and inter-species social networks (i.e., constituent interaction

598 types of an interconnected network). It concluded that both networks help predict the spread of

599 information, but that the likelihood of acquiring foraging information was higher through intra-

600 specific than through inter-specific associations, thereby providing a better understanding of

601 information transmission in mixed-species communities than would be possible using monolayer

602 network analysis. This highlights the potential of taking explicitly multilayer approaches to

603 better understand how information can spread within and between species in mixed-species
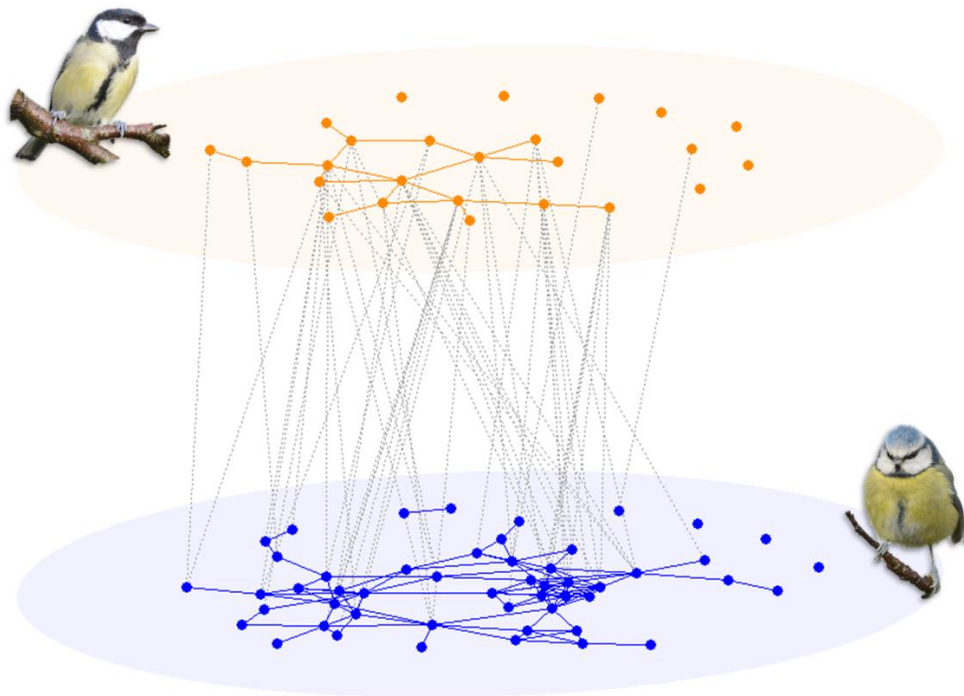
604 groups.

605

606

607 **Figure 6:** A multilayer network of mixed-species interactions between blue tits (bottom layer;

608 blue nodes) and great tits (top layer; orange nodes) in Wytham Woods, UK (in the Cammoor–

609 Stimpsons area) using data obtained from Dryad (Farine et al., 2015b; Farine, Aplin, Sheldon, &

610 Hoppitt, 2015a). Each node represents an individual bird. Blue and orange edges connect

611 individuals within layers (i.e., intra-specific associations), and grey edges connect individuals

612 across layers (i.e., inter-specific associations). To aid clarity, we only show edges with a simple

613   ratio index (Cairns & Schwager, 1987; Ginsberg & Young, 1992) of 0.03 or larger. Photographs

614   by Keith Silk.

615

616   **2.4 Evolutionary models**

617   Understanding the evolution of sociality is a central focus in evolutionary biology (Krause

618   & Ruxton, 2002). Research approaches include agent-based simulations, game-theoretic models,

619   comparative studies, and others. Evolutionary models have been expanded to incorporate

620   interactions between agents, resulting in different evolutionary processes than those in models

621   without interactions (Nowak, Tarnita, & Antal, 2010). However, social behaviours evolve and

622   persist in conjunction with other behaviours and with ecological changes. Therefore,

623   incorporating multiple types of interactions—social, physiological, and with an environment—as

624   part of a multilayer framework can provide novel insights about the pressures on fitness and

625   evolutionary processes. For example, incorporating interactions between molecules at the

626   cellular level, organs at the organismal level, individuals at the group level, and groups at the

627   population level into a network of networks can facilitate multilevel analysis of social evolution.

628   In the ensuing paragraphs, we discuss how the expansion of evolutionary modelling approaches

629   to include multilayer network analysis may enhance the study of (1) evolution of social

630   phenomena (such as cooperation) and (2) co-variation in behavioural structures across species.

631   Incorporating ideas from network theory into evolutionary models has made it possible to

632   account for long-term relationships, non-random interactions, and infrequent interactions

633   (Lieberman, Hauert, & Nowak, 2005). These considerations can alter the outcomes of game-

634   theoretic models of social evolution and facilitate the emergence or persistence of interactions,

635   such as cooperation by enabling assortativity of cooperative individuals (Aktipis, 2004, 2006;

636 Allen et al., 2017; Croft, Edenbrow, & Darden, 2015; Fletcher & Doebeli, 2009; Nowak et al.,

637 2010; Rand, Arbesman, & Christakis, 2011). Given the effects that group structure can have on

638 the selection and stability of cooperative strategies, multilayer structures can significantly alter

639 the dynamics (both outcomes and transient behaviour) of evolutionary games. Indeed, it has been

640 demonstrated, using a multilayer network in which agents play games on multiple interconnected

641 layers, that cooperation can persist under conditions in which it would not in a monolayer

642 network (Gómez-Gardeñes, Reinares, Arenas, & Floría, 2012; Wang, Szolnoki, & Perc, 2012; Z.

643 Wang, Wang, Szolnoki, & Perc, 2015). Furthermore, the level of interdependence, in the form of

644 coupling payoffs between layers or by strategy transfer between layers, can influence the

645 persistence of cooperation (Wang et al. 2013; Xia et al. 2014). Thus, in comparison to monolayer

646 network analysis, using a multilayer network approach can improve the realism of models by

647 better reflecting the 'multi-dimensional' nature of sociality and allowing a larger space of

648 possible evolutionary strategies and outcomes. Certain behaviours that may not be evolutionarily

649 stable when considering only one realm of social interactions may be able to evolve and/or

650 persist when considering a multilayer structure of an agent's possible interactions. For example,

651 expanding game-theoretic models to include multiple types of coupled interactions may facilitate

652 the inclusion of both competition and mutualism, as well as both intra-specific and inter-specific

653 interactions.

654   Comparative approaches offer another powerful method to examine the evolution of

655 different social systems across similar species (Thierry, 2004; West-Eberhard, 1969). In socially

656 complex species, such comparisons can benefit greatly from a multilayer approach. For instance,

657 the macaque genus consists of over 20 species that exhibit a variety of different social structures,

658 each with co-varying behavioural traits, such as those related to connectivity and/or individual

659   behaviours (Thierry 2004; Sueur, Petit, et al. 2011; Balasubramaniam et al. 2012;

660   Balasubramaniam et al. 2017). A multilayer network analysis of such co-varying interactions—

661   e.g., with layers as connectivity types or time periods—may offer an effective way to reveal

662   differences in social structure. For example, using matrix-correlation methods to measure

663   similarities between layers in a multilayer network offers a way to compare how behaviours co-

664   vary across different species using a multiple-regression quadratic assignment procedure

665   (MRQAP) (Croft, Madden, Franks, & James, 2011). For multilayer networks, *global overlap*

666   (Bianconi, 2013) and *global inter-clustering coefficient* (Parshani, Rozenblat, Ietri, Ducruet, &

667   Havlin, 2010) are two measures that can quantify the overlap in edges between two layers. (See

668   Appendix I for a brief discussion of layer-similarity measures.) One can, for instance, use global

669   overlap between an affiliative network and a kinship network to examine the extent to which

670   nepotism plays a role in social structure across species (Thierry, 2004). In such an analysis, it

671   may also be useful to account for spatial dependencies.

672   Researchers continue to develop new approaches for measuring heterogeneous structures

673   in multilayer networks (Aleta & Moreno, 2018; Kivelä et al., 2014) that can aid in testing

674   specific evolutionary hypotheses. For example, the 'social-brain hypothesis' (Dunbar, 1998)

675   posits that the evolution of cognition is driven by sociality, because sociality is cognitively

676   challenging. Recently, there have been several propositions for how to define sociality to test the

677   social-brain hypothesis; all of these include the idea that relationships between animals arise

678   from different types of interactions (Bergman & Beehner, 2015; Fischer, Farnworth, Sennhenn-

679   Reulen, & Hammerschmidt, 2017). Multilayer network analysis can aid in developing objective

680   measures of social structures that include the nuances of the various proposed definitions.

681   Another evolutionary hypothesis, the 'co-variation hypothesis' (Thierry, 2004), posits that

682 changes in a single trait or behaviour can lead to changes in global social organization.

683 Simulations of agent-based models (ABMs) on multilayer networks can test this hypothesis by

684 exploring how different behavioural parameters along with coupling between layers influence

685 group-level structure (Hemelrijk 2002). For example, an ABM of macaque societies (called

686 'Groofi world') linked grooming and fighting behaviour through a single trait (termed 'anxiety')

687 (Hemelrijk & Puga-Gonzalez, 2012; Puga-Gonzalez, Hildenbrandt, & Hemelrijk, 2009). This

688 model has an implicitly multilayer network structure, as it includes multiple interaction 'layers'

689 that are coupled by a parameter. By incorporating such structure, the model illustrated that

690 patterns of reciprocation and exchange (Hemelrijk & Puga-Gonzalez, 2012) and aggressive

691 interventions (Puga-Gonzalez, Cooper, & Hemelrijk, 2016) can emerge from the presence of a

692 few interconnected interaction types along with spatial positions.

693

694 **3. Considerations when using multilayer network analysis**

695 　　We have outlined many different opportunities for multilayer network approaches to be

696 useful for the study of animal behaviour. However, the application of multilayer network

697 analysis to animal behaviour data is in its infancy, with many exciting directions for future work.

698 Multilayer network analysis may not always be appropriate for a given study, and there are

699 several important considerations about both the applicability of the tools and the types of data on

700 which to use them. Most importantly, practical implementation of these new tools will vary

701 across study systems, and it will differ based on the questions asked. Therefore, researchers

702 should not blindly implement these new techniques; instead, as with any other approach, they

703 should be driven by their research questions and ensure that the tools and data are appropriate for

704 answering those questions.

705

3.1. When and how to use multilayer network analysis

706

Multilayer network analysis adds complexity to the representation, analysis, and

707

interpretation of data. Therefore, it should be applied only when incorporating a system's

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multifaceted nature can contribute to answering a research question, without adding needless

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complexity to data interpretation. Different types of social relationships may differ in the 'units'

710

of their measurement, and it can be challenging to interpret multilayer network analysis of such

711

integrated data. For example, if one layer represents genetic relatedness and another represents a

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social interaction, a multilayer similarity measure can reveal one or more relationships between

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these layers, but a versatility measure that uses both layers may be impractical or confusing to

714

interpret, because they encode different types of connectivity data (i.e., relatedness and

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behaviour). In a similar vein, intralayer and interlayer edges can have entirely different meanings

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from each other, and it can sometimes be difficult to interpret the results of considering them

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jointly ((Kivelä et al., 2014); Appendix I).

718

Therefore, while the strength of using a multilayer network formalism is that it includes

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more information about interactions than a monolayer network, it is imperative to consider

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carefully which interactions to include in each layer, based on the study question. It is also

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important to be careful about which calculations are most appropriate for the different layers in a

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multilayer network, based on the functions of those layers, especially when they represent

723

different behaviours.

724

725

3.2. Data requirements

726

727   Just as in monolayer network analysis (or in any study that samples a population), a key

728   challenge is collecting sufficient and/or appropriately sampled data that provide a realistic

729   depiction of the study system (Newman, 2018a, 2018b; Whitehead, 2008). Breaking data into

730   multiple layers can result in sparse layers that do not provide an appropriate sample of the

731   relationships in each layer. Further, if data sampling or sparsity varies across different layers or if

732   the frequency of behaviours differs drastically, one layer may disproportionally dominate the

733   outcome of a multilayer calculation. To avoid domination of one data type, one can threshold the

734   associations, normalize edge weights, adjust interlayer edge weights (Appendix I), or aggregate

735   layers (Appendix II) that include redundant information (De Domenico, Nicosia, Arenas, &

736   Latora, 2015).

737   It is important to compare computations on a multilayer network to those on suitable

738   randomizations (Farine, 2017; Kivelä et al., 2014). Just as in monolayer network analysis

739   (Fosdick, Larremore, Nishimura, & Ugander, 2018; Newman, 2018c), it is important to tailor the

740   use of null models in multilayer networks in a context-specific and question-specific way. For

741   example, some network features may arise from external factors or hold for a large set of

742   networks (e.g., all networks with the same intralayer degree distributions), rather than arising as

743   distinctive attributes of a focal system.

744

745   **3.3. Practical availability and further development of multilayer methodology**

746   In practice, there are many ways for researchers in animal behaviour to implement

747   multilayer network analysis. Existing software packages for examining multilayer networks

748   include MuxViz (De Domenico, Porter, et al., 2015), Pymnet (Kivelä), and the R package

749   Multinet (Magnani & Dubik, 2018). In Table 1, we summarize available tools for implementing

750   various measures. Multilayer network analysis is a rapidly growing field of research in network

751   science, and new measures and tools continue to emerge rapidly. Because this is a new,

752   developing field of research, many monolayer network methods have not yet been generalized

753   for multilayer networks; and many of the existing generalizations have not yet been implemented

754   in publicly-available code. Additionally, many multilayer approaches have been published

755   predominantly as proofs of concept in theoretically-oriented research or have been implemented

756   only for multiplex networks, but not for other multilayer network structures (such as

757   interconnected networks). Furthermore, multilayer networks with multiple aspects (e.g., time and

758   behaviour type) have rarely been analysed in practice, and the potential utility of using multiple

759   aspects to investigate questions about social behaviour may propel the development of tools to

760   do so. The ongoing development of user-friendly software and modules is increasing the

761   accessibility and practical usability of multilayer network analysis. Multilayer network analysis

762   is very promising, but there is also a lot more work to do, as detailed above. Interdisciplinary

763   collaborations between applied mathematicians, computer scientists, social scientists,

764   behavioural ecologists, and others will be crucial for moving this exciting new field forward.

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766   **4. Conclusions**

767   In this article, we have discussed the use of multilayer network analysis and outlined

768   potential uses for providing insights into social behaviour in animals. Multilayer networks

769   provide a useful framework for considering many extensions of animal social network analysis.

770   For example, they make it possible to incorporate temporal and spatial processes alongside

771   multiple types of behavioural interactions in an integrated way. We have highlighted examples in

772   which multilayer methods have been used previously to study animal behaviour, illustrated them

773   with several case studies, proposed ideas for future work in this area, and provided practical

774   guidance on some suitable available methodologies and software (Table 1). Using multilayer

775   network analysis offers significant potential for uncovering eco-evolutionary dynamics of animal

776   social behaviour. Multilayer approaches provide new tools to advance research on the evolution

777   of sociality, group and population dynamics, and the roles of individuals in interconnected social

778   and ecological systems. The incorporation of multilayer methods into studies of animal

779   behaviour will facilitate an improved understanding of what links social dynamics across

780   behaviours and contexts, and it also provides an explicit framework to link social behaviour with

781   broader ecological and evolutionary processes (Silk, Finn, Porter & Pinter-Wollman, 2018).

Table 1: A non-exhaustive selection of multilayer network approaches for studying questions in behavioural ecology. We provide a description of each tool and point to software in which they are implemented. We note the organizational level(s) (individual (I), group (G), population (P), and evolution (E)) of the tools. We provide examples of questions that can be investigated with each approach. These questions provide general guidelines for more specific hypotheses that would be guided by the study system and biological questions of interest.

Research aim	Level (I/G/P/E)	Examples of questions	Multilayer approach	Description	Software package	Citation
Identify important or influential nodes or edges	I/G	• How will a group be affected if certain individuals are removed? • Is social influence determined by interactions in more than one situation? • Which relationships are most critical for group cohesion (when applying measures to edges)? • How stable is an individual's importance over time?	Eigenvector versatility	Multilayer extension of eigenvector centrality, for which an individual's importance depends on its connections within and across layers and on the connections of its neighbours.	MuxViz (De Domenico, Porter, et al., 2015)	(De Domenico, Solé-Ribalta, et al., 2015)
		• Which individuals link the most individuals in a group within or across social situations and/or over time? • How important is an individual for group cohesion?	Betweenness versatility	Multilayer extension of geodesic betweenness centrality, which measures how often shortest paths (including both intralayer and interlayer edges) between each pair of nodes traverse a given node.	MuxViz	(De Domenico, Solé-Ribalta, et al., 2015)
		• Does the role of an individual in its social group carry over across social situations?	Multidegree	A vector of the intralayer degrees of each individual across all layers	Pymnet (Kivelä, n.d.)	(Menichetti, Remondini, Panzarasa, Mondragón, & Bianconi, 2014)

Quantify network properties at different scales	G/P/E	• What are the coherent groups in a network of animals? • Which individuals preferentially interact with each other in different or multiple contexts?	Multislice modularity maximization, Multilayer InfoMap	Identifies communities of individuals in which the same individuals in different layers can be assigned to different communities.	MuxViz; GenLouvain: https://github.com/GenLouvain/GenLouvain	(Mucha et al., 2010)
		• What are the social communities, core–periphery structures, or other large-scale structures in different types of social situations?	Stochastic block models	Statistical models of arbitrary block structures in networks.	Graph-tool (Python)	(Peixoto, 2015)
		• Are there consistent, 'typical' types of interaction patterns across social situations?	Motifs	Interaction patterns between multiple individuals (e.g., node pairs or triples), within and/or across layers, that appear more often than in some null model.	MuxViz	(Battiston, Nicosia, Chavez, & Latora, 2017; Wernicke & Rasche, 2006)
		• How similar are the interaction patterns in different social situations? • How often do interactions between individuals co-occur in multiple situations?	Global overlap	Number of pairs of nodes that are connected by edges in multiple layers.	MuxViz; Multinet R package (Magnani & Dubik, 2018)	(Bianconi, 2013)
Model statistical properties of a network	G/P/E	• Are interaction patterns influenced by group size?	Randomization for multilayer networks	Construction of randomized ensembles of synthetic multilayer networks for comparison	Pymnet (Python)	(Kivelä et al., 2014), Section 4.3
		• Are relationships or interactions in one social situation related to relationships or interactions in a different social situation?	Exponential random graph model (ERGM)	An extension of ERGMs to multilayer networks	MPNET (Java-based) for	(Heaney, 2014; P. Wang,

						two-layer multilayer networks	Robins, Pattison, & Lazega, 2013)
			• How do network relationships in one social situation or at one point in time affect subsequent relationships in other situations or at other times?	Markov models of co-evolving multiplex networks Stochastic actor-oriented models for multiple networks	Models of the probability of an edge existing in a layer at one time as a function of an edge existing between the same pair of nodes in any layer in the previous time. Statistical models of what influences the creation and termination of edges between times. The version that we consider can model the co-evolution of two networks (or two layers) as a result of their influence on each other.	Multiplex MarkovChain: https://github.com/vkrmsv/MultiplexMarkovChain Code available at https://www.stats.ox.ac.uk/~snijders/siena/siena_scripts.htm	(Fisher et al., 2017; Vijayaraghavan, Noël, Maoz, & D'Souza, 2015)

| Modeling disease or information transmission | I/G/P | • What are the roles of different types of social interactions or individuals in information or disease transmission?
• Do different types of transmission interact or interfere with each other?
   o For example, can the spread of information mitigate the spread of a disease?
   o Can the spread of one infection enhance or reduce the spread of a second infection?
• What influences disease transmission in multi-species communities? | Compartmental models on networks | Classic epidemiological models that assume that individuals exist in one of several states, with probabilistic transitions between states. For example, SIR models have susceptible, infective, and recovered (or removed) states; and SI and SIS models have only susceptible and infected states. These models are sometimes amenable to mathematical analysis, but stochastic simulations are often more accessible. | EpiModel (R package) (temporal multiplex networks only) ("EpiModel," n.d.; Jenness, Goodreau, & Morris, 2017) | (Pastor-Satorras et al. 2015; Kiss et al. 2017; Porter and Gleeson 2016) |

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815   **References**

816   Aktipis, C. A. (2004). Know when to walk away: contingent movement and the evolution of

817   cooperation. *Journal of Theoretical Biology*, *231*(2), 249–260.

818   https://doi.org/10.1016/j.jtbi.2004.06.020

819   Aktipis, C. A. (2006). Recognition memory and the evolution of cooperation: How simple

820   strategies succeed in an agent-based world. *Adaptive Behavior*, *14*(3), 239–247.

821   https://doi.org/10.1177/105971230601400301

822   Al-Garadi, M. A., Varathan, K. D., Ravana, S. D., Ahmed, E., & Chang, V. (2016). Identifying

823   the influential spreaders in multilayer interactions of online social networks. *Journal of*

824   *Intelligent & Fuzzy Systems*, *31*(5), 2721–2735. https://doi.org/10.3233/JIFS-169112

825   Aleta, A., & Moreno, Y. (2018). Multilayer networks in a nutshell. *ArXiv*. Retrieved from

826   http://arxiv.org/abs/1804.03488

827   Allen, B., Lippner, G., Chen, Y. T., Fotouhi, B., Momeni, N., Yau, S.T., & Nowak, M. A.

828   (2017). Evolutionary dynamics on any population structure. *Nature*, *544*(7649), 227–230.

829   https://doi.org/10.1038/nature21723

830   Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis

831   reveals cultural transmission of lobtail feeding in humpback whales. *Science*, *340*(6131),

832   485–488. https://doi.org/10.1126/science.1231976

833   Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C.

834   (2014). Experimentally induced innovations lead to persistent culture via conformity in wild

835   birds. *Nature*, *518*(7540), 538–541. https://doi.org/10.1038/nature13998

836   Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict

837   patch discovery in a wild population of songbirds, *279*(1745), 4199–4205.

838   https://doi.org/10.1098/rspb.2012.1591

839   Baird, R. W., & Whitehead, H. (2000). Social organization of mammal-eating killer whales:

840   group stability and dispersal patterns. *Canadian Journal of Zoology*, *78*(12), 2096–2105.

841   https://doi.org/10.1139/cjz-78-12-2096

842   Balasubramaniam, K. N., Beisner, B. A., Berman, C. M., De Marco, A., Duboscq, J., Koirala, S.,

843   Majolo, B., MacIntosh A.J., McFarland, R., Molesti, S., Ogawa, H., Petit, O., Schino, G.,

844   Sosa, S., Sueur, C., Thierry, B., de Waal, F. B. M., McCowan, B. (2017). The influence of

845   phylogeny, social style, and sociodemographic factors on macaque social network

846   structure. *American Journal of Primatology*, *80*(1), e22727.

847   https://doi.org/10.1002/ajp.22727

848   Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo,

849   B., Ogawa, H., Schino, G., Thierry, B., De Waal, F. B. M. (2012). Hierarchical steepness,

850   counter-aggression, and macaque social style scale. *American Journal of Primatology*,

851   *74*(10), 915–925. https://doi.org/10.1002/ajp.22044

852   Barocas, A., Golden, H. N., Harrington, M. W., McDonald, D. B., & Ben-David, M. (2016).

853   Coastal latrine sites as social information hubs and drivers of river otter fission–fusion

854   dynamics. *Animal Behaviour*, *120*, 103–114. https://doi.org/10.1016/j.anbehav.2016.07.016

855   Barrett, L., & Henzi, S. P. (2002). Constraints on relationship formation among female primates.

856   *Behaviour*, *139*(2–3), 263–289. https://doi.org/10.1163/156853902760102672

857   Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: The structure of

858   multi-dimensional social networks as a source of information for individuals. *Philosophical*

859   *Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1599),

860   2108–2118. https://doi.org/10.1098/rstb.2012.0113

861   Barthélemy, M. (2018). *Morphogenesis of Spatial Networks*. Springer International Publishing.

862   https://doi.org/10.1007/978-3-319-20565-6

863   Battiston, F., Nicosia, V., Chavez, M., & Latora, V. (2017). Multilayer motif analysis of brain

864   networks. *Chaos: An Interdisciplinary Journal of Nonlinear Science*, *27*(4), 047404.

865   https://doi.org/10.1063/1.4979282

866   Bazzi, M., Porter, M. A., Williams, S., McDonald, M., Fenn, D. J., & Howison, S. D. (2016).

867   Community detection in temporal multilayer networks, with an application to correlation

868   networks. *Multiscale Modeling & Simulation*, *14*(1), 1–41.

869   https://doi.org/10.1137/15M1009615

870   Beisner, B. A., Jin, J., Fushing, H., & McCowan, B. (2015). Detection of social group instability

871   among captive Rhesus macaques using joint network modeling. *Current Zoology*, *61*(1),

872   70–84. https://doi.org/10.1093/czoolo/61.1.70

873   Beisner, B. A., & McCowan, B. (2015). Social networks and animal welfare. In J. Krause, R.

874   James, D. W. Franks, & D. P. Croft (Eds.), *Animal Social Networks* (pp. 111–121). Oxford,

875   UK.

876   Berdahl, A. M., Biro, D., Westley, P. A. H., & Torney, C. J. (2018). Theme issue "Collective

877   movement ecology." *Philosophical Transactions of the Royal Society B: Biological*

878   *Sciences*, *373*(1746).

879   Bergman, T. J., & Beehner, J. C. (2015). Measuring social complexity. *Animal Behaviour*, *103*,

880   203–209. https://doi.org/10.1016/j.anbehav.2015.02.018

881   Beshers, S. N., & Fewell, J. H. (2001). Models of division of labor in social insects. *Annual*

882   *Review of Entomology*, *46*(1), 413–440. https://doi.org/10.1146/annurev.ento.46.1.413

883   Bianconi, G. (2013). Statistical mechanics of multiplex networks: Entropy and overlap. *Physical*

Review E, *87*(6), 062806. https://doi.org/10.1103/PhysRevE.87.062806

Blonder, B., Wey, T. W., Dornhaus, A., James, R., & Sih, A. (2012). Temporal dynamics and
network analysis. *Methods in Ecology and Evolution*, *3*(6), 958–972.
https://doi.org/10.1111/j.2041-210X.2012.00236.x

Blumstein, D. T., Wey, T. W., & Tang, K. (2009). A test of the social cohesion hypothesis:
interactive female marmots remain at home. *Proceedings of the Royal Society B: Biological
Sciences*, *276*(1669), 3007–3012. https://doi.org/10.1098/rspb.2009.0703

Boccaletti, S., Bianconi, G., Criado, R., del Genio, C., Gómez-Gardeñes, J., Romance, M.,
Sendiña-Nadal, I., Zanin, M. (2014). The structure and dynamics of multilayer networks.
Physics Reports, *544*, 1–122. https://doi.org/10.1016/j.physrep.2014.07.001

Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011). Social networks and models for collective
motion in animals. *Behavioral Ecology and Sociobiology*, *65*(2), 117–130.
https://doi.org/10.1007/s00265-010-1111-0

Borg, N. J., Mitchell, M. S., Lukacs, P. M., Mack, C. M., Waits, L. P., & Krausman, P. R.
(2017). Behavioral connectivity among bighorn sheep suggests potential for disease spread.
The Journal of Wildlife Management, *81*(1), 38–45. https://doi.org/10.1002/jwmg.21169

Braun, N., Posfai, M., Beisner, B. A., Hannibal, D., McCowan, B., & D'Souza, R. M. (2018).
Multilayer ranking with affiliative and aggressive interactions. *In Press*.

Brent, L. J. N., MacLarnon, A., Platt, M. L., & Semple, S. (2013). Seasonal changes in the
structure of rhesus macaque social networks. *Behavioral Ecology and Sociobiology*, *67*(3),
349–359. https://doi.org/10.1007/s00265-012-1455-8

Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*,
35(5), 1454–1469. https://doi.org/10.1016/S0003-3472(87)80018-0

907   Carter, D. R., DeChurch, L. A., Braun, M. T., & Contractor, N. S. (2015). Social network

908   approaches to leadership: An integrative conceptual review. *Journal of Applied Psychology*,

909   *100*(3), 597–622. https://doi.org/10.1037/a0038922

910   Chan, S., Fushing, H., Beisner, B. A., & McCowan, B. (2013). Joint modeling of multiple social

911   networks to elucidate primate social dynamics: I. Maximum entropy principle and network-

912   based interactions. *PLoS ONE*, *8*(2), e51903. https://doi.org/10.1371/journal.pone.0051903

913   Chodrow, P. S., Al-Awwad, Z., Jiang, S., González, M. C., Herranz, R., & Frias-Martinez, E.

914   (2016). Demand and congestion in multiplex transportation networks. *PLOS ONE*, *11*(9),

915   e0161738. https://doi.org/10.1371/journal.pone.0161738

916   Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective Memory

917   and Spatial Sorting in Animal Groups. *Journal of Theoretical Biology*, *218*(1), 1–11.

918   https://doi.org/10.1006/jtbi.2002.3065

919   Couzin, I. D., & Laidre, M. E. (2009). Fission–fusion populations. *Current Biology*, *19*(15),

920   R633–R635. https://doi.org/10.1016/j.cub.2009.05.034

921   Craft, M. E. (2015). Infectious disease transmission and contact networks in wildlife and

922   livestock. *Philosophical Transactions of the Royal Society B: Biological Sciences*,

923   *370*(1669), 20140107–20140107. https://doi.org/10.1098/rstb.2014.0107

924   Croft, D. P., Edenbrow, M., & Darden, S. K. (2015). Assortment in social networks and the

925   evolution of cooperation. In *Animal Social Networks* (pp. 13–23).

926   Croft, D. P., Edenbrow, M., Darden, S. K., Ramnarine, I. W., van Oosterhout, C., & Cable, J.

927   (2011). Effect of gyrodactylid ectoparasites on host behaviour and social network structure

928   in guppies Poecilia reticulata. *Behavioral Ecology and Sociobiology*, *65*(12), 2219–2227.

929   https://doi.org/10.1007/s00265-011-1230-2

930   Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal

931   social networks. *Trends in Ecology & Evolution*, *26*(10), 502–507.

932   https://doi.org/10.1016/j.tree.2011.05.012

933   Csermely, P., London, A., Wu, L.-Y., & Uzzi, B. (2013). Structure and dynamics of

934   core/periphery networks. *Journal of Complex Networks*, *1*(2), 93–123.

935   https://doi.org/10.1093/comnet/cnt016

936   D 'Agostino, G., & Scala, A. (Eds.). (2014). *Understanding Complex Systems Networks of*

937   *Networks: The Last Frontier of Complexity*. Cham, Switzerland: Springer International

938   Publishing.

939   Danchev, V., & Porter, M. A. (2018). Neither global nor local: Heterogeneous connectivity in

940   spatial network structures of world migration. *Social Networks*, *53*, 4–19.

941   https://doi.org/10.1016/J.SOCNET.2017.06.003

942   De Domenico, M., Granell, C., Porter, M. A., & Arenas, A. (2016). The physics of spreading

943   processes in multilayer networks. *Nature Physics*, *12*(10), 901–906.

944   https://doi.org/10.1038/nphys3865

945   De Domenico, M., Lancichinetti, A., Arenas, A., & Rosvall, M. (2015). Identifying modular

946   flows on multilayer networks reveals highly overlapping organization in interconnected

947   systems. *Physical Review X*, *5*(1). https://doi.org/10.1103/PhysRevX.5.011027

948   De Domenico, M., Nicosia, V., Arenas, A., & Latora, V. (2015). Structural reducibility of

949   multilayer networks. *Nature Communications*, *6*(1), 6864.

950   https://doi.org/10.1038/ncomms7864

951   De Domenico, M., Porter, M. A., & Arenas, A. (2015). MuxViz: A tool for multilayer analysis

952   and visualization of networks. *Journal of Complex Networks*, *3*(2), 159–176.

953   https://doi.org/10.1093/comnet/cnu038

954   De Domenico, M., Solé-Ribalta, A., Cozzo, E., Kivelä, M., Moreno, Y., Porter, M. A., Gómez,

955   S., Arenas, A. (2014). Mathematical formulation of multilayer networks. *Physical Review*

956   *X*, *3*(4), 041022. https://doi.org/10.1103/PhysRevX.3.041022

957   De Domenico, M., Solé-Ribalta, A., Omodei, E., Gómez, S., & Arenas, A. (2015). Ranking in

958   interconnected multilayer networks reveals versatile nodes. *Nature Communications*, *6*,

959   6868. https://doi.org/10.1038/ncomms7868

960   Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News,*

961   *and Reviews*, *6*(5), 178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-

962   EVAN5>3.0.CO;2-8

963   EpiModel. (n.d.). Retrieved April 26, 2018, from http://www.epimodel.org/

964   Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in*

965   *Ecology and Evolution*, *8*(10), 1309–1320. https://doi.org/10.1111/2041-210X.12772

966   Farine, D. R. (2018). When to choose dynamic vs. static social network analysis. *Journal of*

967   *Animal Ecology*, *87*(1), 128–138. https://doi.org/10.1111/1365-2656.12764

968   Farine, D. R., Aplin, L. M., Sheldon, B. C., & Hoppitt, W. (2015a). Data from: Interspecific

969   social networks promote information transmission in wild songbirds.

970   https://doi.org/https://doi.org/10.5061/dryad.416sp

971   Farine, D. R., Aplin, L. M., Sheldon, B. C., & Hoppitt, W. (2015b). Interspecific social networks

972   promote information transmission in wild songbirds. *Proceedings of the Royal Society of*

973   *London B: Biological Sciences*, *282*(1803). Retrieved from

974   http://rspb.royalsocietypublishing.org/content/282/1803/20142804/

975   Farine, D. R., Garroway, C. J., & Sheldon, B. C. (2012). Social network analysis of mixed-

976   species flocks: Exploring the structure and evolution of interspecific social behaviour.

977   *Animal Behaviour*, *84*(5), 1271–1277. https://doi.org/10.1016/j.anbehav.2012.08.008

978   Farine, D. R., Strandburg-Peshkin, A., Berger-Wolf, T. Y., Ziebart, B., Brugere, I., Li, J., &

979   Crofoot, M. C. (2016). Both nearest neighbours and long-term affiliates predict individual

980   locations during collective movement in wild baboons. *Scientific Reports*, *6*, 27704.

981   https://doi.org/10.1038/srep27704

982   Firth, J. A., & Sheldon, B. C. (2016). Social carry-over effects underpin trans-seasonally linked

983   structure in a wild bird population. *Ecology Letters*, *19*(11), 1324–1332.

984   https://doi.org/10.1111/ele.12669

985   Firth, J. A., Voelkl, B., Crates, R. A., Aplin, L. M., Biro, D., Croft, D. P., & Sheldon, B. C.

986   (2017). Wild birds respond to flockmate loss by increasing their social network associations

987   to others. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1854).

988   https://doi.org/10.1098/rspb.2017.0299

989   Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying

990   social complexity. *Animal Behaviour*, *130*, 57–66.

991   https://doi.org/10.1016/j.anbehav.2017.06.003

992   Fisher, D. N., Ilany, A., Silk, M. J., & Tregenza, T. (2017). Analysing animal social network

993   dynamics: the potential of stochastic actor-oriented models. *Journal of Animal Ecology*,

994   *86*(2), 202–212. https://doi.org/10.1111/1365-2656.12630

995   Flack, J. C., Girvan, M., Waal, F. B. M. de, Krakauer, D. C., de Waal, F. B. M., & Krakauer, D.

996   C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, *439*(7075),

997   426–429. https://doi.org/10.1038/nature04326

998   Fletcher, J. A., & Doebeli, M. (2009). A simple and general explanation for the evolution of

altruism. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1654), 13–19.

https://doi.org/10.1098/rspb.2008.0829

Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology*, *90*(9), 2480–2490. https://doi.org/10.1890/08-0345.1

Fortunato, S., & Hric, D. (2016). Community detection in networks: A user guide. *Physics Reports*, *659*, 1–44. https://doi.org/10.1016/j.physrep.2016.09.002

Fosdick, B. K., Larremore, D. B., Nishimura, J., & Ugander, J. (2018). Configuring random graph models with fixed degree sequences*. *SIAM Review*, *60*(2), 315–355. https://doi.org/10.1137/16M1087175

Franz, M., Altmann, J., & Alberts, S. C. (2015a). Data from: Knockouts of high-ranking males have limited impact on baboon social networks. *Dryad Digital Repository*.

Franz, M., Altmann, J., & Alberts, S. C. (2015b). Knockouts of high-ranking males have limited impact on baboon social networks. *Current Zoology*, *61*(1), 107–113. https://doi.org/https://doi.org/10.1093/czoolo/61.1.107

Funk, S., Gilad, E., Watkins, C., & Jansen, V. A. A. (2009). The spread of awareness and its impact on epidemic outbreaks. *Proceedings of the National Academy of Sciences*, *106*(16), 6872–6877. https://doi.org/10.1073/pnas.0810762106

Gallotti, R., & Barthélemy, M. (2015). Anatomy and efficiency of urban multimodal mobility. *Scientific Reports*, *4*(1), 6911. https://doi.org/10.1038/srep06911

Gazda, S., Iyer, S., Killingback, T., Connor, R., & Brault, S. (2015a). Data from: The importance of delineating networks by activity type in bottlenose dolphins (Tursiops truncatus) in Cedar Key, Florida. *Dryad Digital Repository*.

1022 Gazda, S., Iyer, S., Killingback, T., Connor, R., & Brault, S. (2015b). The importance of

1023   delineating networks by activity type in bottlenose dolphins (*Tursiops truncatus*) in Cedar

1024   Key , Florida. *Royal Society Open Science*, *2*, 140263. https://doi.org/10.1098/rsos.140263

1025 Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in

1026   behavioural studies. *Animal Behaviour*, *44*, 377–379. https://doi.org/10.1016/0003-

1027   3472(92)90042-8

1028 Gómez-Gardeñes, J., Reinares, I., Arenas, A., & Floría, L. M. (2012). Evolution of cooperation

1029   in multiplex networks. *Scientific Reports*, *2*, 620. https://doi.org/10.1038/srep00620

1030 Heaney, M. T. (2014). Multiplex networks and interest group influence reputation: An

1031   exponential random graph model. *Social Networks*, *36*(1), 66–81.

1032   https://doi.org/10.1016/j.socnet.2012.11.003

1033 Hemelrijk, C. K. (2002). Understanding social behaviour with the help of complexity science.

1034   *Ethology*, *108*(8), 655–671. https://doi.org/10.1046/j.1439-0310.2002.00812.x

1035 Hemelrijk, C. K., & Puga-Gonzalez, I. (2012). An individual-oriented model on the emergence

1036   of support in fights, its reciprocation and exchange. *PLoS ONE*, *7*(5), e37271.

1037   https://doi.org/10.1371/journal.pone.0037271

1038 Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*(1), 1.

1039   https://doi.org/10.2307/2800384

1040 Hirsch, B. T., Reynolds, J. J. H., Gehrt, S. D., & Craft, M. E. (2016). Which mechanisms drive

1041   seasonal rabies outbreaks in raccoons? A test using dynamic social network models.

1042   *Journal of Applied Ecology*, *53*(3), 804–813. https://doi.org/10.1111/1365-2664.12628

1043 Hobson, E. A., Avery, M. L., & Wright, T. F. (2013). An analytical framework for quantifying

1044   and testing patterns of temporal dynamics in social networks. *Animal Behaviour*, *85*(1), 83–

1045   96. https://doi.org/10.1016/j.anbehav.2012.10.010

1046 Ilany, A., Booms, A. S., & Holekamp, K. E. (2015). Topological effects of network structure on

1047   long-term social network dynamics in a wild mammal. *Ecology Letters*, *18*(7), 687–695.

1048   https://doi.org/10.1111/ele.12447

1049 Jack, K. M. (2003). Explaining variation in affiliative relationships among male White-Faced

1050   Capuchins (Cebus capucinus). *Folia Primatol*, *74*, 1–16. https://doi.org/10.1159/000068390

1051 Jenness, S., Goodreau, S. M., & Morris, M. (2017). EpiModel: An R package for mathematical

1052   modeling of infectious disease over etworks. *BioRxiv*, 213009.

1053   https://doi.org/10.1101/213009

1054 Jeub, L. G. S., Balachandran, P., Porter, M. A., Mucha, P. J., & Mahoney, M. W. (2015). Think

1055   locally, act locally: Detection of small, medium-sized, and large communities in large

1056   networks. *Physical Review E*, *91*(1), 012821. https://doi.org/10.1103/PhysRevE.91.012821

1057 Jeub, L. G. S., Mahoney, M. W., Mucha, P. J., & Porter, M. A. (2017). A local perspective on

1058   community structure in multilayer networks. *Network Science*, *5*(2), 144–163.

1059   https://doi.org/10.1017/nws.2016.22

1060 Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*(4),

1061   343–356. https://doi.org/10.1007/s10329-009-0153-2

1062 Kiss, I. Z., Miller, J. C., & Simon, P. L. (2017). *Mathematics of Epidemics on Networks* (Vol.

1063   46). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-50806-1

1064 Kivelä, M. (n.d.). Pymnet: Mulilayer networks library for Python. Retrieved from

1065   http://www.mkivela.com/pymnet/

1066 Kivelä, M., Arenas, A., Barthélemy, M., Gleeson, J. P., Moreno, Y., & Porter, M. A. (2014).

1067   Multilayer networks. *Journal of Complex Networks*, *2*(3), 203–271.

1068   https://doi.org/10.1093/comnet/cnu016

1069   Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences:

1070   potential applications. *Behavioral Ecology and Sociobiology*, *62*(1), 15–27.

1071   https://doi.org/10.1007/s00265-007-0445-8

1072   Krause, J., James, R., Franks, D. W., & Croft, D. P. (Eds.). (2015). *Animal social networks*.

1073   USA: Oxford University Press.

1074   Krause, J., & Ruxton, G. D. (2002). *Living in Groups* (Vol. I). Oxford, UK: Oxford University

1075   Press. https://doi.org/10.1093/sysbio/sys022

1076   Kurvers, R. H. J. M., Krause, J., Croft, D. P., Wilson, A. D. M., & Wolf, M. (2014). The

1077   evolutionary and ecological consequences of animal social networks: Emerging issues.

1078   *Trends in Ecology & Evolution*, *29*(6), 326–335. https://doi.org/10.1016/j.tree.2014.04.002

1079   Leu, S. T., Farine, D. R., Wey, T. W., Sih, A., & Bull, C. M. (2016). Environment modulates

1080   population social structure: Experimental evidence from replicated social networks of wild

1081   lizards. *Animal Behaviour*, *111*, 23–31. https://doi.org/10.1016/j.anbehav.2015.10.001

1082   Lieberman, E., Hauert, C., & Nowak, M. A. (2005). Evolutionary dynamics on graphs. *Nature*,

1083   *433*(7023), 312–316. https://doi.org/10.1038/nature03204

1084   Lopes, P. C., Block, P., & König, B. (2016). Infection-induced behavioural changes reduce

1085   connectivity and the potential for disease spread in wild mice contact networks. *Scientific*

1086   *Reports*, *6*, 31790. https://doi.org/10.1038/srep31790

1087   Magnani, M., & Dubik, M. (2018). *Package "multinet": Analysis and mining of multilayer*

1088   *social networks*. Retrieved from https://cran.r-

1089   project.org/web/packages/multinet/multinet.pdf

1090   McCowan, B., Beisner, B. A., Capitanio, J. P., Jackson, M. E., Cameron, A. N., Seil, S., Atwill,

1091 E. R., Fushing, H. (2011). Network stability is a balancing act of personality, power, and

1092 conflict dynamics in *Rhesus macaque* societies. *PLoS ONE*, *6*(8), e22350.

1093 https://doi.org/10.1371/journal.pone.0022350

1094 Menichetti, G., Remondini, D., Panzarasa, P., Mondragón, R. J., & Bianconi, G. (2014).

1095 Weighted multiplex networks. *PLoS ONE*, *9*(6), e97857.

1096 https://doi.org/10.1371/journal.pone.0097857

1097 Mitchell, J. C. (Ed.). (1969). *Social networks in urban situations: analyses of personal*

1098 *relationships in Central African towns;* Published for the Institute for Social Research,

1099 University of Zambia, by Manchester U.P.

1100 Morris, R. G., & Barthélemy, M. (2012). Transport on coupled spatial networks. *Physical*

1101 *Review Letters*, *109*(12), 128703. https://doi.org/10.1103/PhysRevLett.109.128703

1102 Mucha, P. J., Richardson, T., Macon, K., Porter, M. A., & Onnela, J. P. (2010). Community

1103 structure in time-dependent, multiscale, and multiplex Networks. *Science*, *328*(5980), 876–

1104 878. https://doi.org/10.1126/science.1184819

1105 Newman, M. E. J. (2018a). Network reconstruction and error estimation with noisy network

1106 data. *ArXiv Preprint*. Retrieved from http://arxiv.org/abs/1803.02427

1107 Newman, M. E. J. (2018b). Network structure from rich but noisy data. *Nature Physics*, *14*(6),

1108 542–545. https://doi.org/10.1038/s41567-018-0076-1

1109 Newman, M. E. J. (2018c). *Networks* (2nd ed.). Oxford, UK: Oxford University Press.

1110 Nicosia, V., Bianconi, G., Latora, V., & Barthélemy, M. (2013). Growing multiplex networks.

1111 *Physical Review Letters*, *111*(5), 058701. https://doi.org/10.1103/PhysRevLett.111.058701

1112 Nowak, M., Tarnita, C. E., & Antal, T. (2010). Evolutionary dynamics in structured populations.

1113 *Phil.Trans.R.Soc.B*, *365*(1537), 19–30. https://doi.org/10.1098/rstb.2009.0215

1114   Parshani, R., Rozenblat, C., Ietri, D., Ducruet, C., & Havlin, S. (2010). Inter-similarity between

1115   coupled networks. *EPL (Europhysics Letters)*, *92*(6), 68002. https://doi.org/10.1209/0295-

1116   5075/92/68002

1117   Pasquaretta, C., Leve, M., Claidiere, N., van de Waal, E., Whiten, A., MacIntosh, A. J., …

1118   Sueur, C. (2014). Social networks in primates: Smart and tolerant species have more

1119   efficient networks. *Scientific Reports*, *4*, 7600. https://doi.org/10.1038/srep07600

1120   Pastor-Satorras, R., Castellano, C., Van Mieghem, P., & Vespignani, A. (2015). Epidemic

1121   processes in complex networks. *Reviews of Modern Physics*, *87*(3), 925–979.

1122   https://doi.org/10.1103/RevModPhys.87.925

1123   Peixoto, T. P. (2014). Hierarchical block structures and high-resolution model selection in large

1124   networks. *Physical Review X*, *4*(1), 011047. https://doi.org/10.1103/PhysRevX.4.011047

1125   Peixoto, T. P. (2015). Inferring the mesoscale structure of layered, edge-valued, and time-

1126   varying networks. *Physical Review E*, *92*(4), 042807.

1127   https://doi.org/10.1103/PhysRevE.92.042807

1128   Perry, S., Manson, J. H., Muniz, L., Gros-Louis, J., & Vigilant, L. (2008). Kin-biased social

1129   behaviour in wild adult female white-faced capuchins, Cebus capucinus. *Animal Behaviour*,

1130   *76*(1), 187–199. https://doi.org/10.1016/J.ANBEHAV.2008.01.020

1131   Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological

1132   networks. *Nature Ecology & Evolution*, *1*(0101). https://doi.org/10.1038/s41559-017-0101

1133   Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., De Silva, S.,

1134   Wters, J. S., Prager S. D., Sasaki, T., Wittemyer, G., Fewell, J., McDonald, D. B. (2014).

1135   The dynamics of animal social networks: Analytical, conceptual, and theoretical advances.

1136   *Behavioral Ecology*, *25*(2), 242–255. https://doi.org/10.1093/beheco/art047

Pinter-Wollman, N., Hubler, J., Holley, J.-A., Franks, N. R., & Dornhaus, A. (2012). How is activity distributed among and within tasks in *Temnothorax* ants? *Behavioral Ecology and Sociobiology*, *66*(10), 1407–1420. https://doi.org/10.1007/s00265-012-1396-2

Poirotte, C., Massol, F., Herbert, A., Willaume, E., Bomo, P. M., Kappeler, P. M., & Charpentier, M. J. E. (2017). Mandrills use olfaction to socially avoid parasitized conspecifics. *Science Advances*, *3*(4), e1601721. https://doi.org/10.1126/sciadv.1601721

Polansky, L., Kilian, W., & Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1805), 20143042–20143042. https://doi.org/10.1098/rspb.2014.3042

Porter, M. A. (2018). WHAT IS…a Multilayer Network? *Notices of the American Mathematical Society*, *65*(11), 1419–1423. https://doi.org/10.1090/noti1746

Porter, M. A., & Gleeson, J. P. (2016). *Dynamical systems on networks: A tutorial*. Springer International Publishing. https://doi.org/10.1093/comnet/cnu016

Porter, M. A., Onnela, J.-P., & Mucha, P. J. (2009). Communities in networks. *Notices of the American Mathematical Society*, *56*(9), 1082–1097, 1164–1166.

Pruitt, J. N., & Pinter-Wollman, N. (2015). The legacy effects of keystone individuals on collective behaviour scale to how long they remain within a group. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151766. https://doi.org/10.1098/rspb.2015.1766

Puga-Gonzalez, I., Cooper, M. A., & Hemelrijk, C. K. (2016). Targeting or supporting, what drives patterns of aggressive intervention in fights? *American Journal of Primatology*, *78*(2), 247–255. https://doi.org/10.1002/ajp.22505

Puga-Gonzalez, I., Hildenbrandt, H., & Hemelrijk, C. K. (2009). Emergent patterns of social

affiliation in primates, a model. *PLoS Computational Biology*, *5*(12), e1000630.

https://doi.org/10.1371/journal.pcbi.1000630

Rand, D. G., Arbesman, S., & Christakis, N. A. (2011). Dynamic social networks promote

cooperation in experiments with humans. *Proceedings of the National Academy of Sciences*,

108(48), 19193–19198. https://doi.org/10.1073/pnas.1108243108

Reichert, B. E., Fletcher, R. J., Cattau, C. E., & Kitchens, W. M. (2016). Consistent scaling of

population structure across landscapes despite intraspecific variation in movement and

connectivity. *Journal of Animal Ecology*, *85*(6), 1563–1573. https://doi.org/10.1111/1365-

2656.12571

Rombach, P., Porter, M. A., Fowler, J. H., & Mucha, P. J. (2017). Core-periphery structure in

networks (Revisited). *SIAM Review*, *59*(3), 619–646. https://doi.org/10.1137/17M1130046

Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., & Couzin, I. D. (2015). Revealing

the hidden networks of interaction in mobile animal groups allows prediction of complex

behavioral contagion. *Proceedings of the National Academy of Sciences of the United States

of America*, *112*(15), 4690–5. https://doi.org/10.1073/pnas.1420068112

Rosvall, M., & Bergstrom, C. T. (2007). An information-theoretic framework for resolving

community structure in complex networks. *Proceedings of the National Academy of

Sciences of the United States of America*, *104*(18), 7327–7331.

https://doi.org/10.1073/pnas.122653799

Rubenstein, D. I., Sundaresan, S. R., Fischhoff, I. R., Tantipathananandh, C., & Berger-Wolf, T.

Y. (2015). Similar but different: Dynamic social network analysis highlights fundamental

differences between the fission-fusion societies of two equid species, the onager and

Grevy's Zebra. *PLOS ONE*, *10*(10), e0138645.

https://doi.org/10.1371/journal.pone.0138645

Shizuka, D., Chaine, A. S., Anderson, J., Johnson, O., Laursen, I. M., & Lyon, B. E. (2014).

Across-year social stability shapes network structure in wintering migrant sparrows.

Ecology Letters, *17*(8), 998–1007. https://doi.org/10.1111/ele.12304

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and

evolutionary overview. *Trends in Ecology and Evolution*, *19*(7), 372–378.

https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: New insights and issues

for behavioral ecologists. *Behavioral Ecology and Sociobiology*, *63*(7), 975–988.

https://doi.org/10.1007/s00265-009-0725-6

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant

survival. *Science*, *302*(5648), 1231–1234. https://doi.org/10.1126/science.1088580

Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission-fusion

social group dynamics in birds. *Ibis*, *156*(4), 701–715. https://doi.org/10.1111/ibi.12191

Silk, M. J., Finn, K. R., Porter, M. A., & Pinter-Wollman, N. (2018). Forum: Can multilayer

networks advance animal behavior research? *Trends in Ecology & Evolution*, *33*(6), 376–

378.

Silk, M. J., Weber, N. L., Steward, L. C., Hodgson, D. J., Boots, M., Croft, D. P., … McDonald,

R. A. (2018). Contact networks structured by sex underpin sex-specific epidemiology of

infection. *Ecology Letters*, *21*(2), 309–318. https://doi.org/10.1111/ele.12898

Smith-Aguilar, S. E., Aureli, F., Busia, L., Schaffner, C., & Ramos-Fernández, G. (2018). Using

multiplex networks to capture the multidimensional nature of social structure. *Primates*, 1–

1206   19. https://doi.org/10.1007/s10329-018-0686-3

1207   Snijders, L., Blumstein, D. T., Stanley, C. R., & Franks, D. W. (2017). Animal social network

1208   theory can help wildlife conservation. *Trends in Ecology and Evolution*, *32*(8), 567–577.

1209   https://doi.org/10.1016/j.tree.2017.05.005

1210   Snijders, T. A. B. (2017). Stochastic actor-oriented models for network dynamics. *Annual*

1211   *Review of Statistics and Its Application*, *4*, 343–363. https://doi.org/10.1146/annurev-

1212   statistics-060116-054035

1213   Spiegel, O., Leu, S. T., Sih, A., & Bull, C. M. (2016). Socially interacting or indifferent

1214   neighbours? Randomization of movement paths to tease apart social preference and spatial

1215   constraints. *Methods in Ecology and Evolution*, *7*(8), 971–979.

1216   https://doi.org/10.1111/2041-210X.12553

1217   Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species

1218   foraging flocks? A large-scale synthesis. *Animal Behaviour*, *78*(2), 337–347.

1219   https://doi.org/10.1016/j.anbehav.2009.05.008

1220   Strano, E., Shai, S., Dobson, S., & Barthélemy, M. (2015). Multiplex networks in metropolitan

1221   areas: Generic features and local effects. *Journal of the Royal Society, Interface*, *12*(111),

1222   20150651. https://doi.org/10.1098/rsif.2015.0651

1223   Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. J. (2011). How can social network

1224   analysis improve the study of primate behavior? *American Journal of Primatology*, *73*(8),

1225   703–719. https://doi.org/10.1002/ajp.20915

1226   Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., … Aureli, F.

1227   (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework.

1228   *Oikos*, *120*(11), 1608–1617. https://doi.org/10.1111/j.1600-0706.2011.19685.x

Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*(4), 845–852. https://doi.org/10.1016/j.anbehav.2011.07.020

Sumana, A., & Sona, C. (2013). Key relocation leaders in an Indian queenless ant. *Behavioural Processes*, *97*, 84–89. https://doi.org/10.1016/j.beproc.2013.03.006

Sumpter, D. J. T. (2010). *Collective Animal Behavior* (Vol. 134). Princeton, NJ, USA: Princeton University Press. https://doi.org/10.1016/j.applanim.2011.07.006

Thierry, B. (2004). *Macaque Societies: A Model for the Study of Social Organization*. Cambridge, UK: Cambridge University Press.

Vijayaraghavan, V. S., Noël, P.-A., Maoz, Z., & D'Souza, R. M. (2015). Quantifying dynamical spillover in co-evolving multiplex networks. *Scientific Reports*, *5*(15142). https://doi.org/10.1038/srep15142

Wang, P., Robins, G., Pattison, P., & Lazega, E. (2013). Exponential random graph models for multilevel networks. *Social Networks*, *35*(1), 96–115. https://doi.org/10.1016/j.socnet.2013.01.004

Wang, Z., Andrews, M. A., Wu, Z.-X., Wang, L., & Bauch, C. T. (2015). Coupled disease–behavior dynamics on complex networks: A review. *Physics of Life Reviews*, *15*(15), 1–29. https://doi.org/10.1016/j.plrev.2015.07.006

Wang, Z., Szolnoki, A., & Perc, M. (2012). Evolution of public cooperation on interdependent networks: The impact of biased utility functions. *EPL (Europhysics Letters)*, *97*(4), 48001. https://doi.org/10.1209/0295-5075/97/48001

Wang, Z., Szolnoki, A., & Perc, M. (2013). Optimal interdependence between networks for the evolution of cooperation. *Scientific Reports*, *3*, 2470. https://doi.org/10.1038/srep02470

1252   Wang, Z., Wang, L., Szolnoki, A., & Perc, M. (2015). Evolutionary games on multilayer

1253   networks: A colloquium. *European Physical Journal B*, *88*(5), 124.

1254   https://doi.org/10.1140/epjb/e2015-60270-7

1255   Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications*.

1256   Cambridge University Press.

1257   Webber, Q. M. R., & Vander Wal, E. (2018). Trends and perspectives on the use of social

1258   network analysis in behavioural ecology: A bibliometric approach. *BioRxiv*, 379008.

1259   https://doi.org/10.1101/379008

1260   Weber, N., Carter, S. P., Dall, S. R. X., Delahay, R. J., McDonald, J. L., Bearhop, S., &

1261   McDonald, R. A. (2013). Badger social networks correlate with tuberculosis infection.

1262   *Current Biology*, *23*(20), R915–R916. https://doi.org/10.1016/j.cub.2013.09.011

1263   Wernicke, S., & Rasche, F. (2006). FANMOD: A tool for fast network motif detection.

1264   *Bioinformatics*, *22*(9), 1152–1153. https://doi.org/10.1093/bioinformatics/btl038

1265   West-Eberhard, M. (1969). The Social Biology of Polistine Wasps. *Miscellaneous Publications,*

1266   *Museum of Zoology, University of Michigan*, (No. 140), 1–101.

1267   Westley, P. A. H., Berdahl, A. M., Torney, C. J., & Biro, D. (2018). Collective movement in

1268   ecology: From emerging technologies to conservation and management. *Philosophical*

1269   *Transactions of the Royal Society of London. Series B, Biological Sciences*, *373*(1746),

1270   20170004. https://doi.org/10.1098/rstb.2017.0004

1271   Wey, T. W., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal

1272   behaviour: A promising tool for the study of sociality. *Animal Behaviour*, *75*(2), 333–344.

1273   https://doi.org/10.1016/j.anbehav.2007.06.020

1274   White, L. A., Forester, J. D., & Craft, M. E. (2017). Using contact networks to explore

mechanisms of parasite transmission in wildlife. *Biological Reviews*, *92*(1), 389–409.

https://doi.org/10.1111/brv.12236

Whitehead, H. (2008). *Analyzing animal societies : quantitative methods for vertebrate social analysis*. University of Chicago Press.

Williams, R., & Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. *Biology Letters*, *2*(4), 497–500. https://doi.org/10.1098/rsbl.2006.0510

Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: A key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology*, *67*(1), 163–173. https://doi.org/10.1007/s00265-012-1428-y

Wilson, A. D. M., Krause, S., James, R., Croft, D. P., Ramnarine, I. W., Borner, K. K., … Krause, J. (2014). Dynamic social networks in guppies (Poecilia reticulata). *Behavioral Ecology and Sociobiology*, *68*(6), 915–925. https://doi.org/10.1007/s00265-014-1704-0

Wolf, J. B. W., Mawdsley, D., Trillmich, F., & James, R. (2007). Social structure in a colonial mammal: Unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour*, *74*(5), 1293–1302. https://doi.org/10.1016/J.ANBEHAV.2007.02.024

Xia, C., Miao, Q., Wang, J., & Ding, S. (2014). Evolution of cooperation in the traveler's dilemma game on two coupled lattices. *Applied Mathematics and Computation*, *246*, 389–398. https://doi.org/10.1016/j.amc.2014.08.006