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Network measures in animal social network analysis: their strengths, limits, interpretations and uses

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Abstract:

1. We provide an overview of the most commonly used social network measures in animal research for static networks or time-aggregated networks.
2. For each of these measures, we provide clear explanations as to what they measure, we describe their respective variants, we underline the necessity to consider these variants according to the research question addressed, and we indicate considerations that have not been taken so far.
3. We provide a guideline indicating how to use them depending on of the data collection protocol, the social system studied and the research question addressed. Finally, we inform about the existent gaps and remaining challenges in the use of several variants and provide future research directions.

Keywords: Social Network Analysis; Network Measures, Animal Research, Theory, Review

INTRODUCTION

For those unfamiliar with Social Network Analysis (SNA) terminology (highlighted in the text with asterisks), we provide a glossary in Table.1. The mathematical formula of all the network measures discussed in this manuscript are provided in Appendix 1 and software handling their computation are in Appendix 2.

SNA has become a methodological framework that allows a transdisciplinary approach (from proteomic research to animal societies and ecosystems) to study multiple questions within single systems (networks*) such as groups, populations as well as connected units (links* and nodes*) of the systems. For example, in the study of animal societies, SNA can reveal the causes and consequences of individuals' social heterogeneity (variation in social behavior) and link social interactions to both ecological and evolutionary processes (Sueur *et al.* 2019). Here we describe how the use of specific network measures* can lead to study these different aspects and levels.

The surge of SNA in the last couple of decades has been accompanied by the development of a large number of analytical software and methods to calculate network measures (Borgatti, Everett & Freeman 2002; Csardi & Nepusz 2006; Whitehead 2009; Sosa *et al.* 2018). This has resulted in a diversity of software that vary in the way some network measures are calculated (because they used different methods), and/or are specialized in calculations/functions designed with a specific research purpose, here referred to as variants. Not surprisingly, non-experts in SNA may find difficult to get a clear picture of the most adequate approaches or tools for their research question.

In this manuscript, we do not aim to show the usefulness of SNA (which was already proved many times); instead we provide the reader with an extensive list of the different measures* (and their variants) that are commonly used in Animal Social Network Analysis (ASNA) for static networks or time-aggregated networks. We do so to highlight how mathematical differences in the calculation of these measurements may affect the interpretation of results, making it necessary to indicate some considerations that have not been taken so far. Our aim is to provide researchers with a guideline that helps them to: 1.) interpret the different measures and their variants, 2.) choose a specific measure according to the research question, and 3.) avoid misuses of SNA measures. Although we provide a prescriptive approach on which network measure to use, when and how depending on the research question, the data collection protocol and the species-specific social structure (Figure.1, Figure.2 and Figure.3), readers may keep in mind that SNA is a versatile tool and each research question and system requires its own, bespoke set of considerations to deal with its own specificities.

Considerations prior to selecting network measures

Before considering the computation of network measures, one may first consider the type of data collected (e.g. rare or frequent, associations or interactions), the type of system under study (e.g. cohesive social group, population, etc.), the environment in which individuals evolve (e.g. forest or open field) and how the data are collected (e.g. scan sampling, focal sampling, Gambit of the Group (GoG)) as each of these factors may affect the accuracy of the data collected and the extent to which the data are a fair representation of the system. For example, data collected in animal social research can be divided into two main categories: associations and interactions. Associations are usually collected with GoG or scan sampling and interactions with scan or focal samplings. Whereas GoG allows to rapidly collect numerous individual associations, it inevitably generates networks with higher density than networks based on social interactions that are generally distributed differently depending on the social partners as well as undirected* networks (Franks, Ruxton & James 2010). This aspect entails three main considerations: 1) whether network associations represent faithfully the group/population social structure, 2) the usefulness of GoG in the study of social diffusion such as epidemiology and 3) the use of measures that do not consider links' weights* in networks obtained through GoG. Similarly, the system studied and the environment in which individuals evolve may make it necessary to adapt the data collection protocol. For example, scan sampling can be perfectly adapted for the study of cohesive species with a well-known group composition, small size, and/or living in an open environment whereas focal sampling may be preferred for larger cohesive species living in dense forests or fission-fusion societies (in this case, scan sampling may lead to oversample the core group easily visible). As a rule, one may consider that it is not the best choice to use data obtained through GoG for the study of social diffusion or the computation of measures that do not consider links' weights as this observation protocol produces highly dense networks and the link filtering usually performed to reduce the density generates important biases (Franks, Ruxton & James 2010).

Examining heterogeneity in node interactions

Node measures* (Figure.1) enable to assess individuals' social heterogeneity and to understand the underlying mechanisms such as individual characteristics (e.g. ageing process; Almeling *et al.* (2016)), ecological factors (e.g. demographic variation; Borgeaud *et al.* (2017)) and evolutionary processes (e.g. differences in social styles; Sueur *et al.* (2011)). Node measures are calculated at an individual level and assess in different ways and with different meanings how an individual is connected. Connections can be ego's* direct links only (e.g. degree, strength), alters'* links as well (e.g. eigenvector, clustering coefficient), or even all the links of the network (e.g. betweenness). Node measures can also be used to describe the overall network structure through distributions, means and coefficients of variation.

Degree & strength

The degree measures the number of links of a node. When computed on an undirected network, the degree represents the number of alters of ego. When the network is directed*, it represents the number of either incoming* or outgoing* links of ego and it is then called in-degree (*i.e.* number of incoming links) or out-degree (*i.e.* number of outgoing links) respectively. In-degree is generally used as a measure of popularity in affiliative networks and out-degree as a measure of expansiveness (Borgatti, Everett & Johnson 2018). Note that degree can also be computed in directed networks, in this case it represents the sum of incoming and outgoing links and not the number of alters.

Strength (or weighted degree) is the sum of links' weights in a weighted network*. When the network comprises directed links, then it is also possible to differentiate between in-strength (the sum of weights of incoming links) and out-strength (the sum of weights of outgoing links). In ASNA, these measures usually represent the frequency of individuals' interactions/associations and thus reflect individuals' sociality and social activity. While degree and strength can be considered correlated, it may not always be the case as individuals can interact frequently with few social partners or vice versa (Liao *et al.* 2018). Therefore, it is necessary to test their correlation prior to the analysis.

There is a long list of research that have used degree and strength; these are the main findings: Degree has been found to decrease with age in primates and marmots (Almeling *et al.* 2016) while strength does not (Almeling *et al.* 2016; Liao *et al.* 2018). The philopatric sex has shown higher affiliative degree and affiliative strength in several species (Borgeaud *et al.* 2017) as well as high-ranked individuals (Brent, Ruiz-Lambides & Platt 2017b). A positive correlation has been found between parasite load and degree and strength (Leu *et al.* 2016), although this correlation may be compensated by social buffering/support (Scharf *et al.* 2012). Several personality traits have been positively related to degree and strength such as exploration (Aplin *et al.* 2014) or boldness (Moyers *et al.* 2018). In several primate species, the social circle of infants (i.e. mothers' degrees) has been found to have a significant impact on their development (Shimada & Sueur 2014). Finally, individuals with wider social circles show higher longevity (Silk *et al.* 2010; Brent, Ruiz-Lambides & Platt 2017a) and greater reproductive success (Schülke *et al.* 2010).

Degree shows low sensitivity to observation biases (e.g. misidentification of individuals or unobserved interactions), which makes it particularly relevant for epidemiology studies (Krause *et al.* 2014). However, when considering data collection, due to the high connectiveness of networks generated by GoG, degree may be less suitable than strength since degree is strongly correlated to density. Finally, cautions must be taken when using software as the computation of degree with directed networks induces by default the computation of the sum of incoming and outgoing links and not the number of alters. These contrasting variants of a measure as simple as the degree serve as a reminder that special care must be taken as to the mathematical formula applied to avoid misinterpretations.

Eigenvector centrality

Eigenvector centrality is the first non-negative eigenvector value obtained by transforming an adjacency matrix linearly. It can be computed on weighted, binary*, directed or undirected networks. It measures the centrality* by examining the connectedness of ego as well as that of its alters. Thus, a node's eigenvector value can be linked either to its own degree or strength or to the degrees or strengths of the nodes to which it is connected.

Eigenvector may be interpreted as the social support or social capital of an individual (Brent *et al.* 2011), i.e. the real or perceived availability of social resources. Eigenvector has been extensively used in ASNA and is linked to biological aspects such as individual fitness (Stanton & Mann 2012), epidemiology (Balasubramaniam *et al.* 2016), individual characteristics (Sosa 2016) or social style (Sueur *et al.* 2011).

Betweenness

Betweenness is the number of times a node is included in the shortest paths (geodesic distances) generated by every combination of two nodes. The value of the betweenness informs on the theoretical role of a node in the social transmission (information, disease, etc., see Figure.1) as it indicates to what extent a node connects subgroups, as a bridge, and then is likely to spread an entity across the whole network (Newman 2005).

To date, betweenness has been related to network cohesion (Lusseau & Newman 2004), infection processes (Balasubramaniam *et al.* 2016), information transmission (Pasquaretta *et al.* 2016), sex (Zhang *et al.* 2012), age, rank, kinship (Bret *et al.* 2013) and fitness (Gilby *et al.* 2013). Nodes with the highest betweenness usually link clusters/modules of nodes within the networks (e.g. different subgroups or populations) and may thus have an important role in group cohesion or exchange of entities (disease, information, genes).

However, betweenness is not always the most informative network measure for an individual's role in disease spread and such variation could be related to the network structure (Rodrigues 2019) .

Special attention must be paid regarding the calculation of the betweenness since the way it is calculated depends on whether the network is binary or weighted, directed or undirected and on whether the lowest or the highest link/relationship strength is interpreted as the shortest path. Therefore, the different calculations may lead to different values. Furthermore, betweenness seems to be very sensitive to sampling effort (Krause *et al.* 2014).

Closeness is another well-known network measure to study node centrality but we do not discuss it here as it is very similar - although less frequently used- to betweenness (same variants, same considerations required), and betweenness is usually preferred in ASNA.

Local clustering coefficient

The local clustering coefficient measures the number of closed triplets* over the total theoretical number of triplets (i.e. open and closed), where a triplet is an ensemble of three nodes that are connected by either two (open triplet) or three (closed triplet) edges. This measure aims to examine the links that may exist between the alters of ego and measures the cohesion of the network (Figure.1). The main topological effect of closed triplets is the clusterization of the network, generating cohesive clusters, and is thus strongly related to modularity (see corresponding section). The local clustering coefficient can be computed in a binary network by measuring the proportion of links between the nodes of an ego-network* divided by the number of potential links between them. In weighted networks, several versions exist such as those from Barrat *et al.* (2004) or Opsahl and Panzarasa (2009). To date, no attempt has been made in ASNA to evaluate which version of the clustering coefficient may be the most appropriate according to the research question. Therefore, careful attention is needed when choosing the variant as this may lead to different biological interpretations. For example, Opsahl's generalized clustering coefficient proposes four variants to consider triplets' link weights (the arithmetic or geometric mean or using the weight of the weakest* or strongest* links). Opsahl's geometric mean variant considers triplet weights heterogeneity (and is robust against extreme values of weights) whereas Barrat's variant does not. Thus, heterogeneity of weights should be preferred in social systems with high social heterogeneity such as groups with high hierarchy steepness for example. Finally, the minimum variant (using the weight of the weakest link in a closed triplet) should be preferred when trying to understand the mechanisms that shape link creation in animal societies since this variant helps determine the minimum threshold needed for closed triplets to appear.

One major asset of this measure is that it is both local and global, which allows to examine for example how such micro-motifs* affect the overall network structure (Wharrie, Azizi & Altmann 2019). As we will see, the clustering coefficient examines different aspects of social networks and animal societies, going from individual heterogeneity of social interactions (present section) to the analysis of the overall group structure (see Global clustering coefficient) and it also explains patterns in links' creation (see Transitive triplets). However, the local and global clustering coefficients can be importantly related to density so both measures require special attention when data are collected through GoG and, additionally, density should be added as factor of control.

Examining patterns of node interactions

Patterns of interactions (how and with whom individuals interact) can be examined using specific network measures* that analyze local-scale interactions within a network and make possible to test hypotheses about the mechanisms underlying network connectivity (Figure 2). These types of measures are generally used to test mechanistic biological questions, such as what factors (e.g. ecological as well as sociodemographic) affect individuals' interactions/associations. However, because these patterns of interactions are also known to affect global network features, such as group resilience or reciprocal interactions, and to occur in a wide variety of animal taxa, they may be crucial elements within the general processes that shape animal societies and populations.

Assortativity

Assortativity (Newman 2003) is probably the most used measure to study homophily (preferential associations or interactions among individuals sharing the same characteristics) (Lazarsfeld & Merton 1954). Assortativity values range from -1 (total disassortativity *i.e.* all the nodes associate or interact with those with the opposite characteristic, such as males interacting exclusively with females) to 1 (total assortativity *i.e.* all the nodes associate or interact with those with the same characteristic such as males interacting only with males). The assortativity coefficient measures the proportion of links between and within clusters of nodes with same characteristics. Individuals' characteristics can be continuous (e.g. age, individual network measure, personality) or categorical features (e.g. sex, matriline belonging) (Figure.2). Assortativity does not consider directionality* and can be measured in weighted (Leung & Chau 2007) or binary (Newman 2003) networks using categorical or continuous characteristics (Figure.2). The use of one or other assortativity variant depends of the type of characteristics being examined and, whenever possible, the weighted version should be preferred since it its more reliable than the binary version (Farine 2014).

Recent studies in human research argue that homophily promotes cooperation, social learning, and cultural and norm transmission among strangers (Allen *et al.* 2013). Homophily according to different phenotypes such as sex, age, kinship, hierarchical rank (Sosa 2016), degree (Croft *et al.* 2005), personality (Croft *et al.* 2009) or body size (Leu *et al.* 2016) has been found in several species including fish (Croft *et al.* 2005), birds (Johnson *et al.* 2017), cetaceans (Hunt *et al.* 2019), humans (Wang, Suri & Watts 2012) and other mammals (Williamson, Franks & Curley 2016). The fact that similar homophilic mechanisms are found in a wide range of taxa suggests that homophily may have been a driver for cooperation between congeners (Apicella *et al.* 2012). One question that remains open, however, is whether assortativity is a consequence of evolution or a prior condition for cooperation, which would need to be investigated further.

Transitive triplets

Transitive triplets are micro-motifs that have widely been widely examined in ASNA in recent years. Transitive triplets are closed triplets where the links among the nodes follow a specific temporal pattern of creation -i.e. when the establishment of links between nodes A and B and between nodes A and C is followed by the establishment of a link between node B and node C. This network measure can be computed in directed, binary or weighted networks. This type of connections can be studied over time based on the creation of links. From a static perspective, directionality can be considered by calculating the number of transitive triplets divided by the number of potential transitive triplets, and weights can also be considered by using Opsahls' variants, which are discussed in the section on local clustering coefficient (Opsahl & Panzarasa 2009). While transitivity is importantly related to the clustering coefficient (the clustering coefficient includes transitive triplets), not all close triplets are transitive. Transitive triplets are one of the 16 possible configurations of a triplet considering open and closed triplets as well as link directionality (i.e. triad census).

Transitive triplets have been used in animal affiliative social networks (Waters & Fewell 2012; Ilany, Booms & Holekamp 2015; Borgeaud *et al.* 2016; Boucherie *et al.* 2016; Sosa, Zhang & Cabanes 2017) to highlight 'triadic closure', commonly described as "the friend of my friend is my friend". Ilany, Booms and Holekamp (2015) evidenced that several factors (rainfall, prey availability, sex, social rank, dispersal status and topological effects) shape social dynamics in wild hyenas. Among all these factors, transitive triplets appeared as the most consistent and social dynamics (link creation) could not be explained without it. This micro-motif represents an interesting measure when studying social network resiliency and efficiency. For example, in ants, transitive triplets appear supporting the hypothesis of adapted and selected patterns of interactions to increase colony functionality and efficiency (Waters & Fewell 2012). Moreover, the main topological effect of triadic closure is the clusterization of the network generating cohesive groups and it seems to be closely linked to the emergence of reciprocity, altruism and cooperation (Davidsen, Ebel &

Bornholdt 2002). As for assortativity, studies testing how this micro-motif affects the spread of information could help gain knowledge on this crucial mechanism in the evolution of animal societies.

Transitive triplets have also been used to study agonistic networks and animals' dominance hierarchy. For instance, the study of Dey & Quinn 2014 showed that pukeko agonistic networks emerge from both individual characteristics and endogenous self-organization of dominance relationships (i.e. transitive triplets). While triad census has not been widely used in the past, few studies have started to use these micro-motifs to examine hierarchy linearity on the basis of occurrence of reciprocal triplets for example (Shizuka & McDonald 2012).

Transitive triplets, and triad census more generally, help to understand how relationships between individuals emerge and change over time and how these changes may be a consequence of changes in others' relationships (Figure.2). The studies mentioned above investigated triplets' configuration using unweighted* networks. While the weighted variant of transitive triplets (Opsahl & Panzarasa 2009) may allow researchers to better understand and predict how and when links between two individuals are created, it remains unused in ASNA to date.

Examining network structure and properties

The structure of this section is based on the distinction between network connectivity and social diffusion (information or disease spread). Both of these aspects may overlap the use of the network measures that quantify them (Figure.3). However, the social diffusion section contains measures specifically designed to study theoretical (i.e. considering the diffusion is perfectly related to network links and link weights) social diffusion features based on the geodesic distances (see corresponding section). Aspects of the structure and properties of a group (*e.g.* cohesion, sub-grouping) can be quantified using global network measures*. For instance, one may quantify properties such as network resilience* (see Diameter), network clusterization* (see Modularity) through network connectivity analysis, or network transmission efficiency* (see Global efficiency) through network theoretical social diffusion analysis (Figure 3). These different network structures have been used in ASNA to study different evolutionary as how the network is structured, resilient or efficient (Puga-Gonzalez, Sosa & Sueur 2018) and ecological questions as how ecological factors such as pathogens affect the network structure (Croft *et al.* 2011).

Examining network connectivity.

Network connectivity can be studied using global network measures that describe the cohesion of the network and how this cohesion may be affected by intrinsic (e.g. species social organization and structure) or extrinsic factors (e.g. ecological factors as pathogens). There are three main measures for connectivity discussed in this section: density, modularity and clustering coefficient. As mentioned above, all these measures may affect social diffusion as high density and clustering coefficient induce a fast rate whereas high modularity induces a low rate of spread.

Density

The density is the ratio between existing links and all potential links of a network. This measure is easy to interpret, it assesses how a network is fully connected. Density does not consider directionality neither link weights.

In ASNA, a link has been found between density and factors such as living condition (*i.e.* higher density in captive groups than in wild groups), group size (*i.e.* Balasubramaniam *et al.* (2017) with the larger the group, the lower the density), seasonality (*i.e.* higher density during the mating season; (Brent *et al.* 2013), habitat structural complexity (*i.e.* higher density in complex habitats; (Leu *et al.* 2016), and population stress due to environmental changes (Dufour *et al.* 2011).

However, cautions should be taken when studying density since this measure may depend on the biology of the species (e.g. social system and group size) and because several other network measures appear correlated with it. Density is correlated with degree distribution (see corresponding section), geodesic distances (see corresponding section) and the frequency of micro-motifs, like closed triplets* and thus clustering coefficients (see corresponding section) (Rankin *et al.* 2016). These correlations between density and other global network measures make it necessary to control for network density when comparing global network measures from different groups, conditions or species. Further, when comparing species, special attention should be put that the social organizations (e.g. group size, sex ratio) are equivalent and thus that interspecies comparisons are meaningful. Furthermore, the type of behavior (the rarer the behavior, the lower the density; (Castles *et al.* 2014)), the size of the network and the sampling effort are other factors that may influence density and should be taken into consideration when comparing networks. Methods to control for such biases have already been proposed (e.g. evaluation of the data collection robustness) and should be used whenever differences in global network measures (density or other ones) are assessed (Balasubramaniam *et al.* 2017). Another option is to use weighted network measures that are theoretically less correlated with network density.

Modularity

Modularity is a measure designed to quantify the degree to which a network could be divided into different groups or clusters and its value ranges from 0 to 1. Networks with high modularity have dense connections within the modules but sparse connections between the modules. Modularity can be computed in weighted, binary, directed or undirected networks.

It has been evidenced that modularity varies according to dominance style in macaque species, with higher modularity found in despotic species (Sueur *et al.* (2011). Fission-fusion societies as elephants (Wittemyer & Getz 2007), geladas (Matsuda *et al.* 2015) or snub-nosed monkeys (Zhang *et al.* 2012) show many units and thus high modularity compared to cohesive groups. Modularity also seems to be linked to evolutionary advantages such as greater cooperation by the creation of clusters of cooperators (Marcoux & Lusseau 2013) or reduced risks of transmission of pathogens by decreasing associations between clusters (Nunn *et al.* 2015). Individuals that interlink the different clusters may be those with specific social status as observed in dolphins (Lusseau & Conradt 2009) but clusters can also be linked by weak links that allow to maintain a certain cohesion and social transmission as described in giraffes (VanderWaal *et al.* 2016).

Several algorithms have been proposed to identify the different clusters in a network. These can be categorized according to the process used to identify the clusters such as spectral optimization (leading eigenvector), based on the structure of the edges (edge betweenness), or modularity optimization (Fastgreedy or Louvain algorithm). For an overview see Yang, Algesheimer and Tessone (2016). Until recently, no research had investigated what would be the impact of choosing different community detection algorithms in the results (Aldecoa & Marín 2013; Sumner, McCabe & Nunn 2018). Sumner, McCabe and Nunn (2018) showed possible variations between those different algorithms; therefore, we recommend to choose carefully an appropriate community detection algorithm for the question of interest. Unfortunately, it is only recently that these questions have been addressed and a general guideline cannot be provided except that multiple algorithms may be used and the results may be compared. Also note that such precautions could apply to any clusterization algorithm.

Global clustering coefficient

The global clustering coefficient, like the local clustering coefficient, evaluates how well the alters of ego are interconnected and measures the cohesion of the network. Its main topological effect is the clusterization of the network, generating cohesive clusters, and is thus strongly related to modularity. However, it becomes highly correlated to density and less to modularity as the density grows. Several variants of the global clustering coefficient can be found: 1) the ratio of closed triplets to all triplets (open and closed), 2) the binary local mean clustering coefficient that derives from the node level (see Local clustering coefficient). The binary local mean clustering coefficient allows to consider node heterogeneity and thus should be preferred over the first variant. Weighted versions also exist and are based on the same variants described in the section on the local clustering coefficient and require the same considerations.

Examining social diffusion

One major aspect that SNA brings in the study of social structure is the possibility to examine social diffusion of disease, information transmission, new behavior or ecosystems' food flow in a network (Figure.3). One of the measures that make this possible is the geodesic distance and derived measures such as global efficiency and diameter. While geodesic distance is not often used in ASNA, it is essential for calculating other network measures such as diameter, global efficiency, node betweenness (see corresponding sections). Therefore, we discuss geodesic distance in this section to inform the reader that the cautions needed when computing geodesic distances must also be considered when calculating its derived network measures.

Geodesic distance

Geodesic distance is the shortest path considering all potential dyads in a network. This measure thereby evidences the fastest path of diffusion. Despite its usefulness in the study of epidemiology, geodesic distance remains seldomly used in ASNA due to its high sensitivity to observation biases such as unobserved interactions or misidentification of individuals (Krause *et al.* 2014). Geodesic distance can be calculated in binary, weighted*, directed or undirected networks. In weighted networks, it can be normalized (by dividing all links by the network weight means) and the strongest or the weakest links can be considered as the fastest route between two nodes. This great number of variants of geodesic distance can greatly affect results and interpretations. Researchers must thus have knowledge of the variants and which one is the most appropriate according to their research question (Opsahl, Agneessens & Skvoretz 2010).

For example, many software calculate the geodesic distance using the paths with the lowest weights as the shortest paths because they were designed for research related to transportation routes or information transmission (*e.g.* road transportation or internet connection). However, in ASNA, the links with the highest weights are usually those of greater interest as they represent preferential interactions/associations. For example, the probability to learn a new behavior may be higher between individuals that are more frequently in contact or close proximity (Hoppitt & Laland 2013). Yet, the weakest links can also be of interest for questions related to epidemiology. For example, whereas a pathogen is more likely to be transmitted among individuals sharing strong links, weak links may still play a role in disease transmission (VanderWaal *et al.* 2016). Directionality is also an important variant to consider when examining if diffusion can only follow a certain directionality such as pathogens that can be transmitted only by individuals carrying it.

Global efficiency

Global efficiency is the ratio between the number of individuals and the number of connections multiplied by the network diameter. It provides a quantitative measure of how efficiently information is exchanged within the nodes of the network. As global efficiency gives a probability of social diffusion, it may help better understand social transmission phenomena in short-term and long-term (Migliano *et al.* 2017). Pasquaretta *et al.* (2014) found a positive correlation between the neocortex ratio and the global efficiency in primate species with a higher neocortex ratio. By drawing a parallel between cognitive capacities and social network efficiency, this study evidenced that in species with higher neocortex ratio, individuals may adjust their social relationships in order to gain better access to social information and thus optimize network efficiency. Alternatively, studies on epidemiology in ant colonies showed that ants adapt their interaction rate to decrease the network efficiency when infected by a pathogen (Stroeymeyt *et al.* 2018).

Diameter

The diameter of a network represents the longest path of the shortest paths in the network. Diameter is used in ASNA to examine aspects such as network cohesion, the rapidness of information or disease transmission. While global efficiency measures the theoretical social diffusion spread, diameter informs on the maximum paths of diffusion to reach all nodes.

While diameter was first used in the social sciences to study information diffusion (Milgram 1967), in ASNA it is mostly used to examine social cohesion, and the resilience of the network cohesion to the removal of a certain amount of central individuals (Lusseau 2003; Williams & Lusseau 2006; Manno 2008; Sosa 2014). However, further investigation may be needed to test if the removal of central individuals give a fair picture of biological group resilience properties since currently these analyses do not account for the creation of new links after the loss of individuals and demographic variations (Firth *et al.* 2017). If future outcomes support this deletion simulation assumption, studies based on a comparative analysis may represent an interesting research approach to understand how natural selection may have favored resilience properties in some species while it has not in others. For example, we could expect variation according to group structure (higher resilience in stable matriline groups than in fusion-fission societies). Moreover, given the insight that these simulations could provide into group or ecosystem resilience properties, those may be of great interest for conservation purposes (Delmas *et al.* 2019).

DISCUSSION

This updated overview of the most commonly used network measures in ASNA highlights the increasing prominence of techniques deriving from graph theory, as well as the insights they brought and their diversity. Some of these techniques were developed in specific contexts and for well-defined questions (*e.g.* Latora and Marchiori (2001) about global efficiency in neurology). It is very appealing to reuse them with different focus although this would require a thorough understanding of the mathematical background in order to know what is being measured and to decide whether a given measure applies or not to the question raised.

We hope that this non-exhaustive overview will contribute to facilitate future research in ASNA by helping investigators select the most relevant network measure and variant according to their research question. Moreover, we would like to point out that when using SNA, one is often led to test multiple measures for a single research question as these may reveal different aspects of individuals' sociality (direct or indirect links for example). However, it is worth mentioning that all these measures are computed from the same mathematical object (the network) and can therefore be correlated (Bounova & De Weck 2012). This correlation may be low or high according to different parameters affecting the network, as the species social system or organization, its size, etc. While this has been discussed punctually along the manuscript, we cannot detail here all the possible autocorrelations between network measures as this is case-specific and would fall out of the scope. Nonetheless, we may recommend to run correlation tests prior to the analyses or to use the variance inflated factor to control for such bias in correlation factors.

Continuous advances in graph theory such as Graph Signal Processing (Shuman *et al.* 2013) or multi-layer networks (Kivelä *et al.* 2014) will undoubtedly give rise to novel measures with new applications in ASNA. With this perspective in mind, investigators need to make constant effort testing different versions of measures, clearly stating the mathematical interpretations and what is exactly being measured, expounding their strengths and limits and explaining why chose this variant rather than another in order for others to apprehend their relevance depending on the context.

AUTHORS CONTRIBUTION

SS listed all metrics' variants and wrote the first draft of the manuscript. IPG and SC participated in the writing of the final version.

DATA AVAILABILITY

This manuscript does not contain any data or code.

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Terms	Definition
Alters	Nodes connected to ego
Binary	Considering the presence or absence of links between two nodes
Closed triplets	Three nodes interconnected between each other
Directed network	Network with link directionality (representing the directionality of the behavior)
Directionality	Link directionality from one node to another
Ego	A specific node
Ego-network	A network with ego's connections only
Incoming links	Interaction received
Link	Element of a network representing the connection (e.g. interaction or association) between two nodes. Term edge is used as synonym in the literature.
Micro-motifs	Sub-structures of a network
Network	A system of interconnected elements
Network clusterization	Formation of subgroups in a network
Network global measures	Measures calculated at the level of the whole network
Network measures	Mathematical calculations to quantify specific features of a network, include global, node and polyadic measures
Network node measures	Measures calculated at the level of nodes
Network resilience	Capacity for the network to remain undisrupted when nodes are removed
Network transmission efficiency	How well pathogens or information spread in the network
Node	Element of a network representing an individual. Term vertice is used as synonym in the literature.
Node centrality	A central node is highly connected and/or is connected to highly-connected nodes

Outgoing links	Interaction given
Strongest links	Links with highest weights
Undirected network	Network without link directionality
Unweighted network	Network in which links represent the presence (1) or absence (0) of interactions/associations between nodes
Weakest links	Links with lowest weights
Weight	Value of a link usually representing the frequency of an interaction/association
Weighted network	Network in which the weights of the links represent the frequency of interactions/associations between nodes

Table1. *Network glossary*

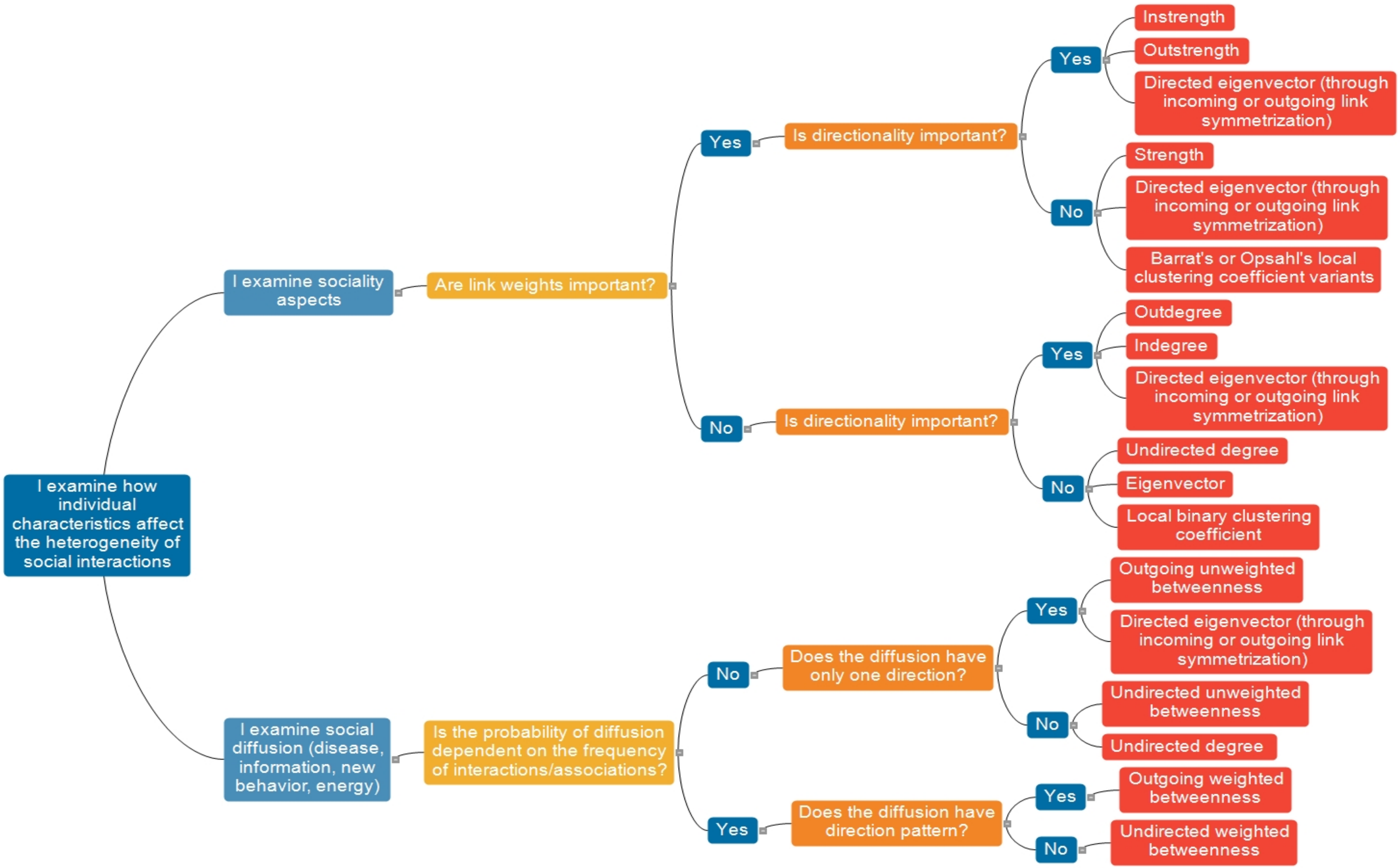

Figure 1. *Decision tree for examining individual social heterogeneity according to the research question and the network studied.*

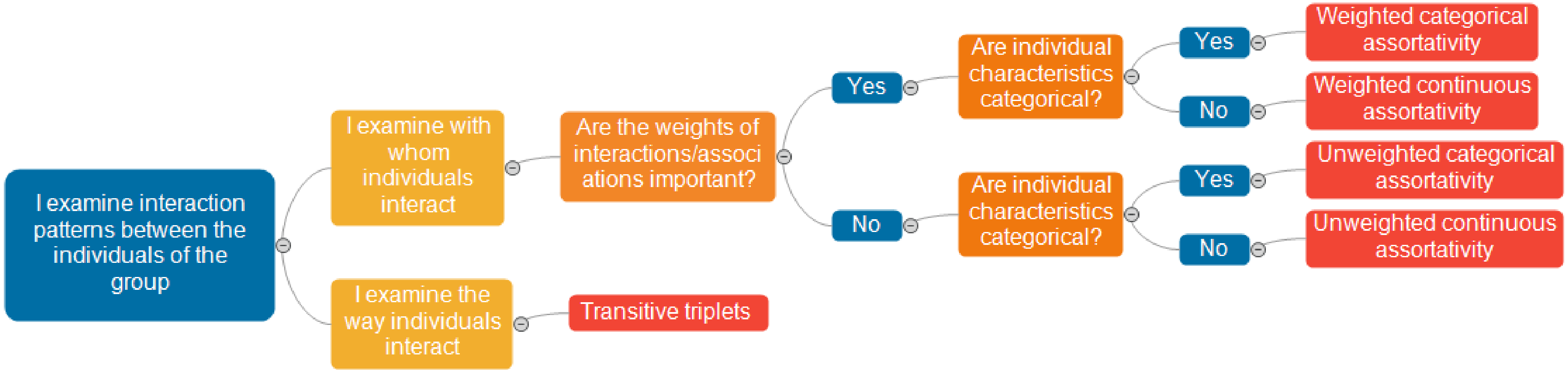

Figure 2. *Decision tree for examining patterns of individual interactions according to the research question and the network studied*

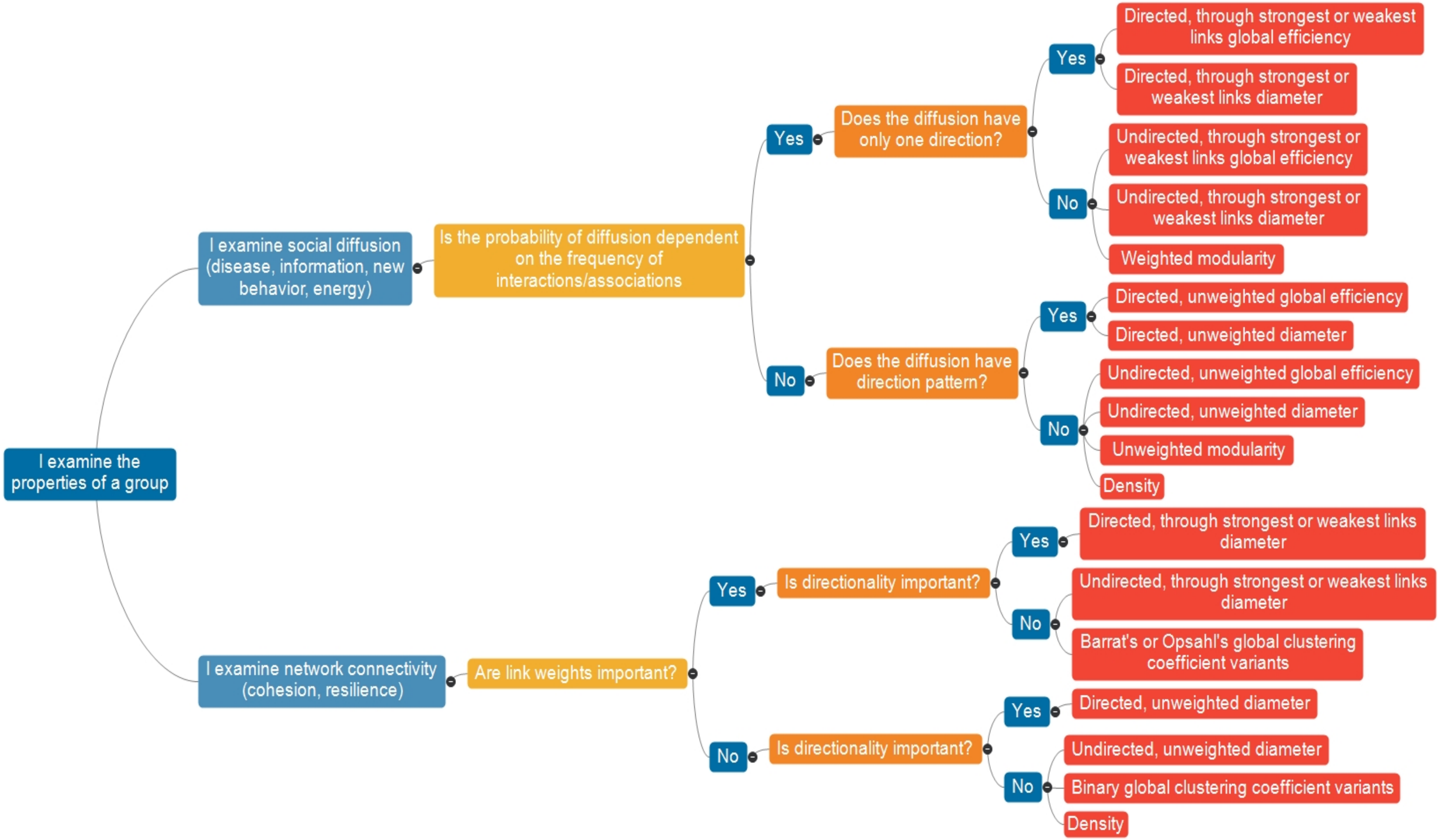

Figure 3. *Decision tree for examining group structure and properties according to the research question and the network studied*