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2 *metanetwork*: a R package dedicated to handling and
3 representing trophic metanetworks

4 *metanetwork*: representing metanetworks [running headline]

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19

20 Abstract

- 21 1. Trophic networks describe interactions between species at a given location and time. Due to
22 environmental changes, anthropogenic perturbations or sampling effects, trophic networks
23 may vary in space and time. The collection of network time series or networks in different
24 sites thus constitutes a metanetwork.
- 25 2. A crucial step toward the understanding of those metanetworks is to build appropriate tools
26 to handle and represent them. We present here the R package *metanetwork*, which will
27 ease the exploration and the analysis of trophic metanetwork datasets that are increasingly
28 available.
- 29 3. Our main methodological advance consists in suitable layout algorithm for trophic net-
30 works, which is based on trophic levels and dimension reduction of a graph diffusion kernel.
31 In particular, it highlights relevant features of trophic networks (trophic levels, energetic
32 channels).
- 33 4. In addition, we developed graphical tools to handle, compare and aggregate those networks.
34 Static and dynamic visualisation functions have been developed to represent large networks.
35 We apply our package workflow to several trophic network data sets.

1 Introduction

The representation of nature was at the heart of naturalism from the *XVIII*th to the beginning of *XX*th century, mixing the need for naturalist documentation and the quest for aesthetics (Ogilvie 2008). The representation of collections of species, in museums or in situ through plates fed the picture book of the emerging ecology. This has rooted the representation of a community as a collection of species, without considering biotic interactions. Interestingly, the plates of invertebrates by Haeckel (*e.g.* marine invertebrates, Haeckel 1904) highlight the importance of geometry in representing those organisms. The emergence of community in ecology during the early *XX*th century introduces interactions between species in the representation of an ecological community (Elton 1927). The foundations of network ecology are established. Since then, trophic interaction networks have been recognized as controlling dynamics and functioning of communities and they have been used for managing biodiversity (Thompson *et al.* 2012, Polis & Winemiller 2013). Adequately representing networks is then crucial for researchers as well as for decision-makers (Pocock *et al.* 2016).

The main issue in trophic network representation is still on providing a meaningful network layout related to ecological features, such as trophic levels or energetic channels (*e.g.* Elton 1927, Van Leeuwen *et al.* 2015). Trophic networks are usually high-dimensional with complex structure, while network layout is only a two-dimensional node embedding. Although network visualisation tools are now widely available (*e.g.* Csardi *et al.* 2006, Bastian *et al.* 2009, Perrone *et al.* 2020, Pawluczuk & Iskrzyński 2022), current network layout methods highlighting hierarchical structure of trophic networks remain scarce. They mainly rely on force-directed algorithms, as Fruchterman & Reingold 1991 that is based on vertex repulsion or Kamada *et al.* 1989 and Gansner *et al.* 2004 that consists in spring embedding. None of them incorporate ecological processes. As a result, their outcomes on trophic networks are hard to interpret since these algorithms do not model ecological processes. Node layout algorithms specifically designed for trophic networks are still lacking.

Representing networks properly is an even more important issue as they are now sampled in space and time (Dunne 2006, CaraDonna *et al.* 2017) as biogeography classically represents species in space (Von Humboldt & Bonpland 1805, Lomolino *et al.* 2017). Empirical evidence

65 supports plasticity and stochasticity of interactions and would encourage sampling of trophic
 66 interactions through space and time (Poisot *et al.* 2015, CaraDonna *et al.* 2017). However,
 67 sampling interactions in multiple sites is challenging since it requires joint observations of species.
 68 It is especially problematic when it involves organisms from different kingdoms and various body
 69 sizes (Jordano 2016). Sampling taxa is far easier, using naturalist knowledge (Moser *et al.* 2005),
 70 camera traps (Steenweg *et al.* 2017) or environmental DNA (Bohmann *et al.* 2014). A convenient
 71 case to study networks in space is then to build a potential network at the regional scale, the
 72 metaweb, using expert knowledge or machine learning methods to complete interaction databases
 73 (Strydom *et al.* 2021). Once the metaweb is built, local networks are deduced using sampled
 74 abundances. Such an approach have been used for various organisms, from terrestrial vertebrates
 75 (Galiana *et al.* 2014, Braga *et al.* 2019) to marine or freshwater communities (Kéfi *et al.* 2015,
 76 Kortsch *et al.* 2019, Blackman *et al.* 2022) or soil communities (Bauer *et al.* 2022). While losing
 77 interaction plasticity and stochasticity, local networks nevertheless have distinct structures due
 78 to sampling effect. We stick to this case in the present paper.

79 Hereafter, a collection of networks in space or time is called a metanetwork, as a collection
 80 of communities is called metacommunity. For simplicity, we refer to the potential interaction
 81 network as the 'metaweb'. While trophic network databases are becoming increasingly available
 82 (Poelen *et al.* 2014), tools to handle and represent them remain scarce. The present paper
 83 describes and implements a new layout algorithm built for trophic networks, using trophic levels
 84 and a diffusion based algorithm. This contribution also describes several additional methods
 85 to handle, represent and analyse trophic metanetworks at different resolutions as suggested in
 86 the literature (Thompson & Townsend 2000, Guimarães Jr 2020). All the described methods
 87 are implemented in the R package, *metanetwork*, that eases manipulation and representation
 88 of trophic metanetworks. *metanetwork* is available on CRAN while several vignettes on several
 89 open data sets are accessible online at <https://marcohlmann.github.io/metanetwork/>.

90 We first describe inputs and methods to build and handle *metanetwork* objects. We then
 91 focus on the proposed 'TL-tse' and 'group-TL-tsne' layout algorithms and the visualisation meth-
 92 ods wrapped in *metanetwork*. We also illustrate the use of the package on several datasets of
 93 various dimensions, including marine, soil and vertebrate trophic networks.

94

95 2 Package workflow

96 2.1 Package installation and documentation

97 The latest stable version is available on CRAN and can be installed using:

98 `install.packages("metanetwork")`.

99 Complete documentation along with several vignettes is available here: [https://marcohlmann.](https://marcohlmann.github.io/metanetwork/)
100 [github.io/metanetwork/](https://marcohlmann.github.io/metanetwork/).

101 2.2 Defining and handling metanetworks

102 2.2.1 Inputs of the 'metanetwork' object

103 To build a potential metanetwork (hereafter metanetwork), we need a metaweb, G^* , that is a
104 directed and connected network including focal species and known potential trophic interactions
105 in the study region. We can also include a community matrix \mathbf{P} , indicating species relative
106 abundances, and a trophic table \mathcal{T} , indicating species belonging to broader taxonomic or func-
107 tional groups. Local networks are then induced subnetworks of G^* by local communities (with
108 abundances).

109 Our package encodes a metanetwork through a R S3 object of class 'metanetwork'. The function
110 `build_metanet` builds a 'metanetwork' object from the triplet $(G^*, \mathbf{P}, \mathcal{T})$ and computes local
111 networks. The metaweb G^* must be of class 'igraph', 'matrix' or 'data.frame'. The matrix \mathbf{P}
112 and the table \mathcal{T} can be NULL contrary to G^* . In this case, the metanetwork will be a single
113 network. Although the metaweb needs to be connected, local networks can be disconnected,
114 which may occur due to sampling effects. Fig. 1 provides a sketch representation of the package
115 functionalities and Table 1 describes the main functions and their associated ecological questions.
116 Local networks constitute a list of 'igraph' objects with relative abundances, edge weights and
117 network names stored as node, edge and graph attributes.

118 2.2.2 Append aggregated networks

119 In order to investigate trophic networks at different aggregation levels (*e.g.* broader taxonomic
120 groups, functional groups or output of node clustering algorithms) as suggested in (Thompson &

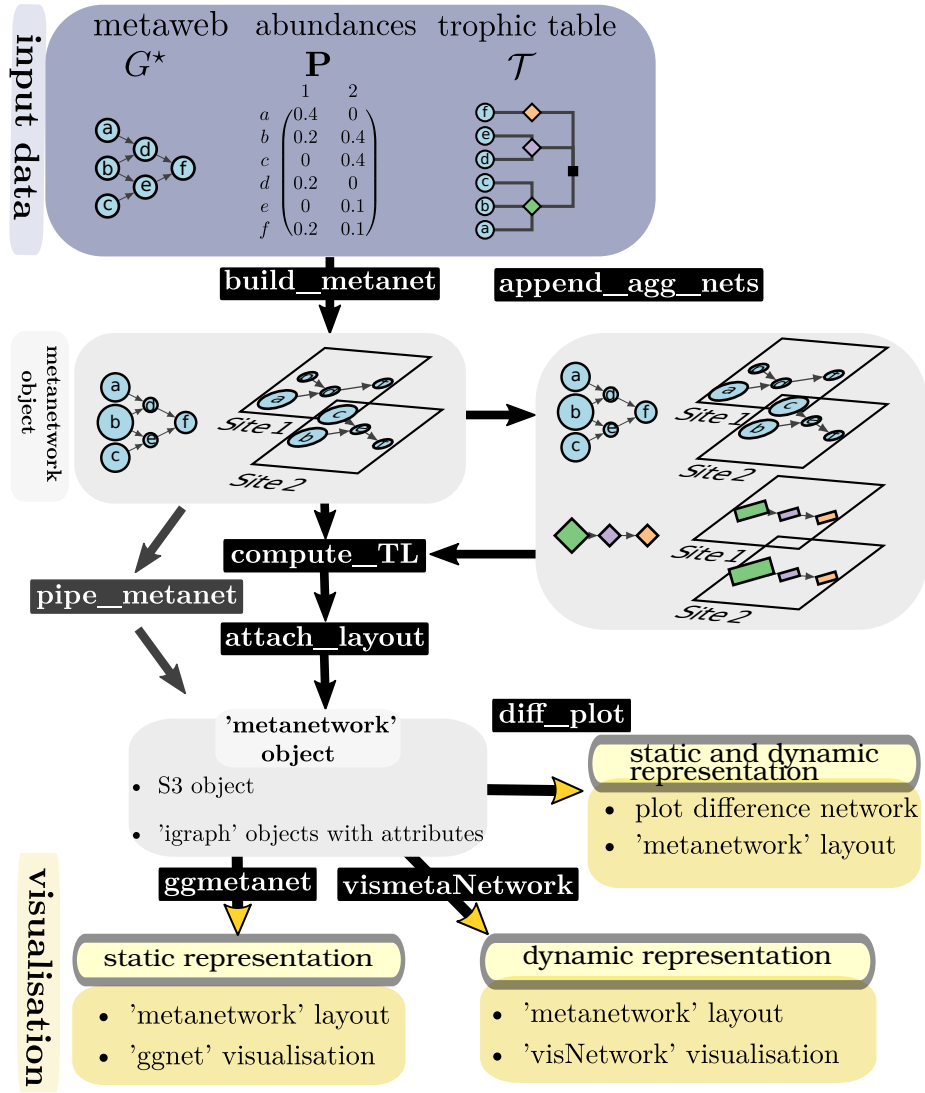


Figure 1: Sketch representation of the use of the R package *metanetwork* from input data to output visualisation. It highlights the main functionalities of the package to handle and represent metanetworks.

Functions	Description	Ecological questions
build_metanet	Build a 'metanetwork' S3 object Compute local networks	What is the structure of the local networks?
append_agg_nets	Append aggregated networks to the current metanetwork using the trophic table \mathcal{T}	What is the structure of the aggregated networks? How does it compare through aggregation levels?
plot_trophicTable	Represent aggregation levels given by the trophic table \mathcal{T}	What are the possible aggregation levels in the metanetwork?
compute_TL	Compute trophic levels using Laplacian matrix	What are the trophic levels in the metanet? How do trophic levels vary among local networks?
attach_layout	Compute and attach 'TL-tsne' or 'group-TL-tsne' layout to the current metanetwork	How are the nodes distributed along the energetic channels at a given trophic level?
ggmetanet	Static visualisation of the metanet and the local networks using 'ggnet' with 'TL-tsne' layout	What are the main energetic channels of the current network?
vismetanet	Dynamic visualisation of metanet and local networks using 'visNetwork' with 'TL-tsne' layout	What are the main energetic channels of the current network?
diffplot	Compute the difference between two networks. Show a static or dynamic visualisation of the difference network.	What are the differences between the local networks?

Table 1: Main functions of the *metanetwork* package and the corresponding addressed ecological questions.

Townsend 2000, Ohlmann *et al.* 2019, Guimarães Jr 2020), our package can compute aggregated networks using the trophic table \mathcal{T} that describes aggregation levels (Fig. 1). Given a network G with n nodes, we can create Q groups from the original set of n nodes ($Q < n$) using \mathcal{T} . We denote (C_1, \dots, C_Q) the focal groups or aggregated nodes. Their relative abundances $(\tilde{p}_q)_{1 \leq q \leq n}$ and interaction probabilities $(\tilde{\pi}_{ql})_{1 \leq q, l \leq n}$ are computed according to Ohlmann *et al.* 2019 as follows

$$\tilde{p}_q = \sum_{k \in C_q} p_k \quad \text{and} \quad \tilde{\pi}_{ql} = \frac{\sum_{k \in C_q, k' \in C_l} \pi_{kk'} p_k p'_k}{\sum_{k \in C_q} p_k \sum_{k' \in C_l} p'_k} \quad (1)$$

where $\pi_{kk'}$ is the link probability between nodes k in group C_q and nodes k' in group C_l , and p_k and $p_{k'}$ are their respective relative abundances.

The method `append_agg_nets` computes the abundances and the link probabilities at any aggregation levels provided by the trophic table \mathcal{T} . It then appends aggregated networks with node and edge attributes to the current 'metanetwork' object (Fig. 1).

2.3 Representing and analysing metanetworks

Our package provides a new node layout algorithm, called 'TL-tsne', designed for trophic networks and functions to visualise and compare those networks. The 'TL-tsne' layout consists in a two-dimensional node embedding algorithm. It uses the trophic levels as the x-axis coordinates of the nodes in the two dimensional space. The coordinates on the y-axis are computed using the diffusion kernel of the network, which informs us on similarity between nodes according to a dif-

138 fusion process, combined with a modified version of the 't-sne' algorithm, which allows reducing
139 dimension.

140 2.3.1 Trophic levels computation

141 Trophic levels have been introduced to quantify the position in the hierarchy of resource ac-
142 quisition (Lindeman 1942). Despite various methods available to compute trophic levels (Levine
143 1980, Hudson *et al.* 2013), we use the recent framework of MacKay *et al.* 2020, who define trophic
144 level using the Laplacian matrix of the network because it embeds many useful properties of the
145 network.

146 Let G be a directed network, we note \mathbf{A} its adjacency matrix and \mathbf{D} its degree diagonal matrix.
147 The Laplacian matrix of the symmetrised version of G is defined by:

$$\mathbf{L} = \mathbf{D} - \mathbf{A} - t(\mathbf{A}) \quad (2)$$

148 where $t(A)$ is the transpose of the Laplacian matrix A . We note $\mathbf{v} = \text{indegree}(G) - \text{outdegree}(G)$
149 the imbalance vector. Then, the vector of the trophic levels, \mathbf{x} , is the solution of the linear
150 system:

$$\mathbf{L}\mathbf{x} = \mathbf{v} \quad (3)$$

151 For a connected network, the solution \mathbf{x} is unique up to a translation. Thus we always fix its
152 minimal entry to 0 (corresponding to basal species) and get the trophic level of all the other ones
153 (more details in Supporting Information). In our package, we first compute the trophic levels
154 from the metaweb G^* because this graph is connected, thus we can fix the minimal trophic level
155 to 0 and provide a trophic level for all other species. Since local networks might be disconnected
156 due, for instance, to sampling effects, we compute the trophic levels in each connected component
157 of the local network and we fix the minimal trophic level in each component to its trophic level
158 in the metaweb graph (see Supporting Information for more details).

159 The method `compute_TL` computes trophic levels and store them as node attributes of the net-
160 works belonging to the current 'metanetwork' object. These trophic levels are the x-axis coordi-
161 nates of our node layout.

162 2.3.2 Diffusion graph kernel and 'TL-tsne' layout algorithm

163 From the network G , we define the diffusion graph kernel \mathbf{K}

$$\mathbf{K} = \exp(-\beta\mathbf{L}) = \sum_{k \geq 0} \frac{(-\beta\mathbf{L})^k}{k!} \quad (4)$$

164 where \mathbf{L} is the Laplacian matrix of G and β is the diffusion parameter, a scalar and strictly
165 positive parameter. In our package, the diffusion kernel is computed through its eigenvalues (see
166 Supporting Information). In the context of trophic networks, the diffusion process described
167 by \mathbf{K} , might represent diffusion of organic matter through the network, even if the diffusion
168 kernel is defined by an undirected representation of the network. In order to compute the y-axis
169 coordinate of the nodes in a network G , we need to reduce the information provided by the
170 diffusion kernel \mathbf{K} (that is of dimension the node number of G). We use a dimension reduction
171 algorithm adapted from the t-sne algorithm (Van der Maaten & Hinton 2008), which provides
172 a low dimensional embedding of high dimensional data while preserving neighborhood. The t-
173 sne method relies on an iterative algorithm, which minimises the Kullbach-Leibler divergence
174 between similarity matrices in the high and low dimensional space.

175 We use the diffusion kernel \mathbf{K} to measure the similarity in the high dimensional space (that is
176 the set of neighbors in our network, which is fixed). We use the same low-dimensional similarity
177 as in Van der Maaten & Hinton 2008. The x-axis coordinate is already fixed here to the trophic
178 level, while the second coordinate is chosen such that the Kullbach-Leibler divergence between
179 the two similarity matrices is minimal. Importantly, the minimisation procedure accounts for
180 trophic levels. We named 'TL-tsne' the proposed network layout algorithm (see Algo. S1 in
181 Supporting Information). We also provide a method to evaluate the quality of the computed
182 layout and to select β value using Moran index (see Supporting Information).

183 The method `attach_layout` computes 'TL-tsne' layout and store it as node attribute of the
184 focal network.

185 2.3.3 Visualisation

186 Besides proposing a new layout method, *metanetwork* package allows incorporating these layouts
187 in the two recent R packages dedicated to network visualisation: 'ggnet' and 'visNetwork'. The
188 'ggnet' package represents networks as 'ggplot' objects (Wickham & Wickham 2007, Schloerke
189 *et al.* 2018). Our function `ggmetanet` provides a static representation of the network using 'TL-
190 tsne' layout combined with 'ggnet' visualisation and additional features (legend, node abundances
191 and edge weights). The 'visNetwork' package represents the network in an interactive way using
192 vis.js javascript library (Almende *et al.* 2019). Our function `vismetaNetwork` provides 'TL-tsne'
193 layout and wraps 'visNetwork' dynamic visualisation with additional features (javascript events
194 linked to the nodes, legend, node abundances and edge weights).

195 We illustrate our layout and static visualisation functionalities on a simple pyramid example in
196 Fig. 2. We represent the same network with the `ggmetanet` function, using three different layouts:
197 Fruchterman-Reingold, Kamada-kawai (force based layouts already implemented in `ggnet`) and
198 our 'TL-tsne' layout with two different β values. Force based layouts (Fig. 2a, 2b) do not
199 capture the hierarchical structure of the network contrary to the 'TL-tsne' layout (Fig. 2c, 2d).
200 Increasing the β parameter tends to gather the nodes with similar trophic levels that are involved
201 in similar paths.

202 2.3.4 Representing the difference between networks

203 In order to ease local network comparisons, *metanetwork* implements a function `diff_plot` that
204 highlights differences and similarities between two network. More precisely, let G_1 and G_2 be two
205 local networks (with vertex sets V_1 and V_2), we note G_{diff} the difference network between G_1 and
206 G_2 , whose vertex set is $V_{\text{diff}} = V_1 \cup V_2$. It is the induced subgraph of the metaweb, G^* , by V_{diff} .
207 We assign then node abundances and edge weights to G_{diff} . Node abundance of the difference
208 network consists in the difference between node abundances of G_1 and G_2 , as edge weights. We
209 use a color code to distinguish nodes that are present in both networks with different abundances
210 from nodes that are absent in one of the networks. A color code in the visualisations indicates
211 the sign of the node abundance difference and the edge weight difference between networks (see
212 Fig. 4 the following section 3.1).

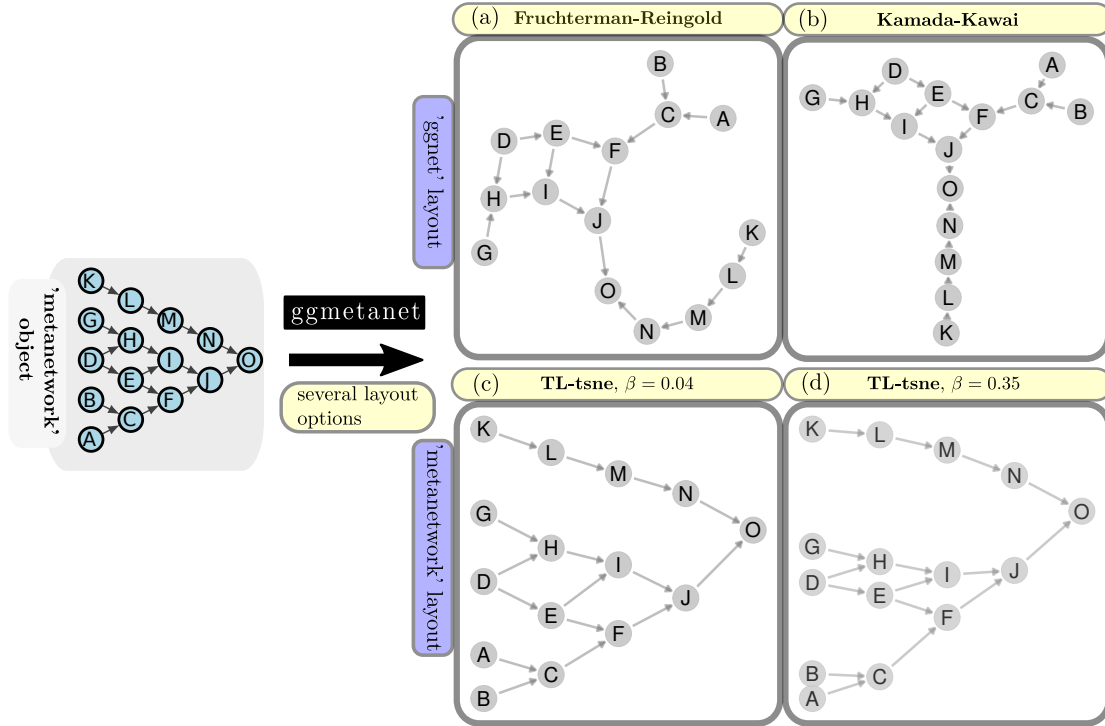


Figure 2: Network layout methods implemented in 'metanetwork' with `ggmetanet` visualisation function. Pyramid example is represented with (a) Fruchterman-Reingold (force based layout), (b) Kamada-Kawai (force based layout) and 'TL-tsne' layout for (c) $\beta = 0.04$ and (d) $\beta = 0.35$

213 2.3.5 Representing large networks with 'group-TL-tsne' layout

214 In order to represent networks with a large node number (typically larger than > 100), we
215 propose a variation of 'TL-tsne' layout that uses information from `trophicTable`. This specific
216 layout method, called 'group-TL-tsne' uses the 'TL-tsne' layout at a desired aggregation level
217 and combines it with 'igraph' `layout_with_graphopt` layout. We first compute the coordinates
218 at the desired group resolution using 'TL-tsne' algorithm. We then compute, in each group,
219 the coordinates of the nodes using 'igraph' layout centered at the coordinate of the group. A
220 configuration object allows playing on group diameters. The `attach_layout` method computes
221 'group-TL-tsne' layout and store it as node attribute. Computing 'group-TL-tsne' layout is more
222 computationally efficient since it computes 'TL-tsne' layout on the aggregated network (that is
223 much smaller) only.

224 3 Case studies

225 In this section, we apply *metanetwork* functions to three real-world metawebs, which corre-
226 spond to different ecosystems with various organisms. In the main text, we use the static rep-
227 resentation of the networks using `ggmetanet` while we provide interactive visualisations using
228 `vismetanetwork` online at <https://shiny.osug.fr/app/ecological-networks>.

229 3.1 Angola coastal network

230 We first look at a dataset from Angola, which has been extracted from Web of Life ([http:](http://www.web-of-life.es)
231 [//www.web-of-life.es](http://www.web-of-life.es)). It consists in a coastal trophic metaweb of 28 nodes (species or groups)
232 and 127 interactions sampled along Angola's coastline (Angelini & Vaz-Velho 2011). The study
233 aimed at estimating impact of Angola's fishery on the coastal trophic network by quantifying
234 biomass using times series from multiple sources (see Angelini & Vaz-Velho 2011 for more details).
235 Available abundance data consists of two time steps: 1986 and 2003. Interactions are weighted
236 according to the relative frequency of prey species in the diet of each predator species. We
237 represented the metaweb using `ggmetanet` with 'TL-tsne' layout ($\beta = 0.02$) in Fig. 3. The
238 metaweb has two basal nodes, 'Phytoplankton' and 'Detritus', leading to a primary producer

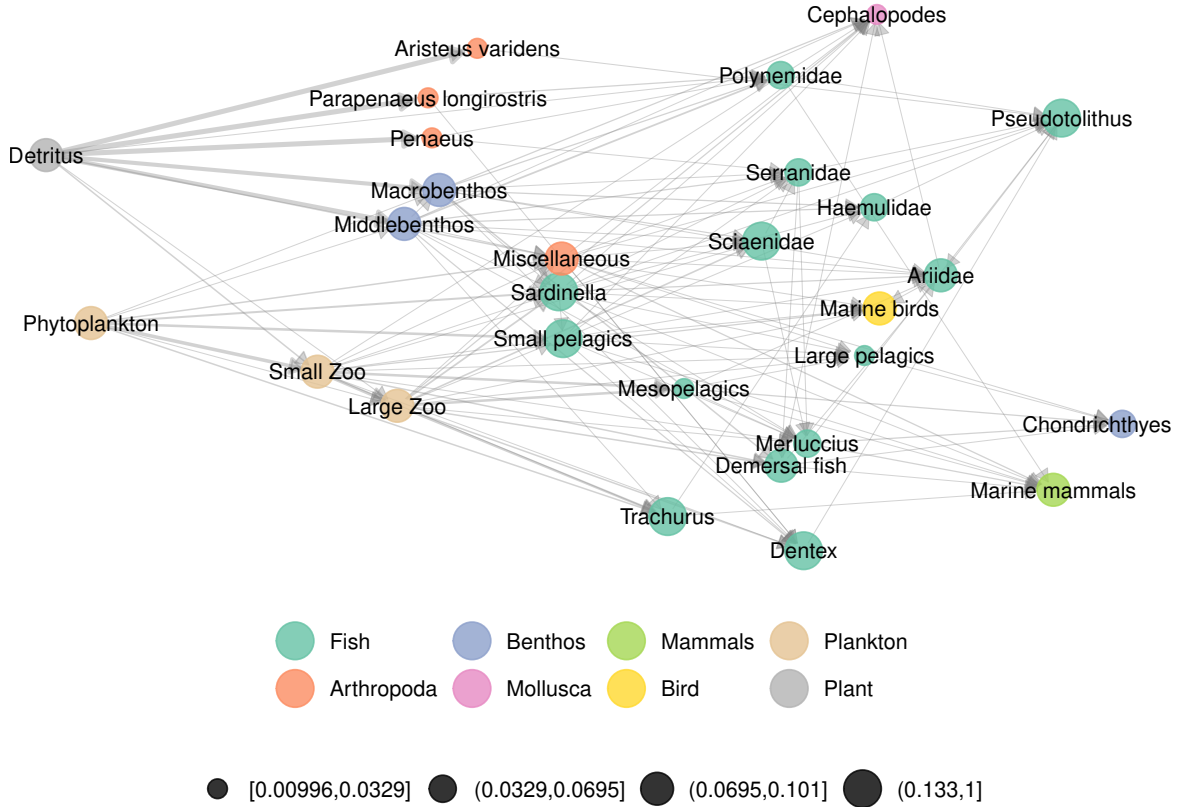


Figure 3: Angola coastal trophic network, which contains 28 nodes and 127 interactions. Nodes are colored according to taxonomic groups and edges are weighted according to a diet study. We use the 'TL-tsne' layout with $\beta = 0.02$ and the static visualisation function `ggmetanet`.

and detritus channel that mix up higher in the network. We included the Angola dataset as an example in the package (`meta_angola` object), with abundances built from biomasses in 1986 and 2003. We also represented the difference network between the two dates using the `diff_plot` function with the 'TL-tsne' layout ($\beta = 0.05$) in Fig. 4. We also computed a profile of extended Moran index along beta values to select optimal β (see Fig. S2, Fig. S3).

3.2 Norway soil trophic network

Norway soil trophic network dataset was extracted from [Calderón-Sanou et al. 2021](#). It consists in a soil expert-knowledge metaweb and environmental DNA data sampled in the Varanger region in Northeastern Norway. The metaweb has 40 groups and 204 interactions with several

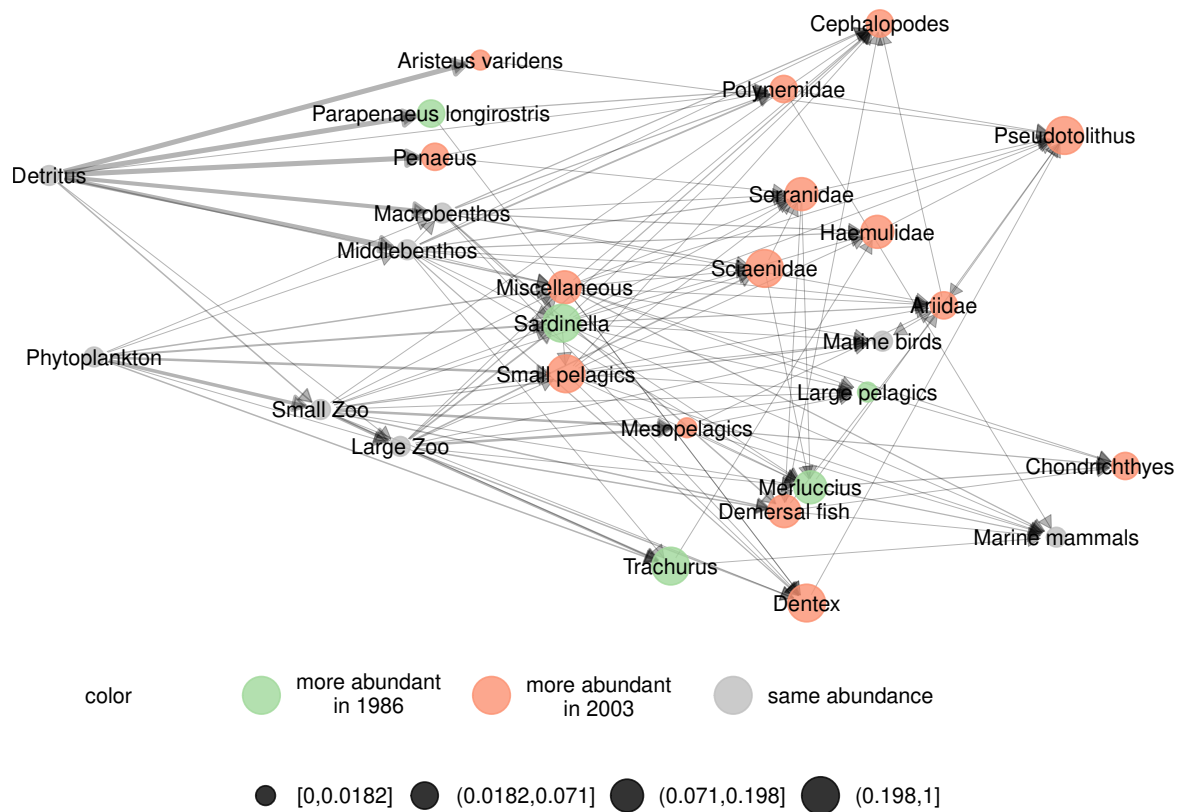


Figure 4: Difference network between the Angola network from 1986 and from 2003. Differences in node abundances are given by differences in estimated biomasses at the two time steps. We use the `diff_plot` function with the computed 'TL-tsne' metaweb layout (see `layout_metaweb` option) to visualize the difference network.

248 available aggregation levels (trophic group, trophic class and kingdom). The groups have relative
 249 abundances given by their mean abundances in environmental DNA samples. The Fig. 5 shows
 250 the metaweb at the group level using the 'TL-tsne' layout with the diffusion parameter $\beta = 0.006$
 251 (Fig. 5). The metaweb has two basal resources: plant and organic material. They have the lowest
 252 x-axis values in the 'TL-tsne' layout. The channel starting from plants corresponds to the green
 253 energy channel while the channel starting from organic materials is the brown channel (Polis
 254 & Strong 1996, Moore *et al.* 2004, Mougi 2020). Importantly, we observe from our network
 255 representation that bacterial and fungal paths are separated in the brown channel. It means
 256 that they are linked to separated paths higher up in the network (*e.g.* bacterivore and fungivore
 257 groups). Calderón-Sanou *et al.* 2021 documents the impact of a disturbance (moth outbreaks)
 258 on soil diversity. We provide the difference network between pre- and post-disturbance (Fig.
 259 S4). It highlights a shift from Ectomycorrhizae and Ericoid mycorrhizae towards Arbuscular
 260 mycorrhizae and also an increase in soil predator abundances.

261 3.3 Metaweb of European tetrapods

262 The metaweb of European tetrapods was extracted from Maiorano *et al.* (2020) and O'Connor
 263 *et al.* (2020). It consists of an expert-knowledge metaweb of all tetrapods occurring in Europe
 264 (mammals, breeding birds, reptiles and amphibians) with potential interactions. This network
 265 has 1101 species and 48963 interactions. O'Connor *et al.* (2020) computed trophic groups us-
 266 ing the Stochastic Block Model (SBM) that clusters nodes with similar connectivity patterns
 267 (Daudin *et al.* 2008). We represented the metaweb using 'TL-tsne' layout ($\beta = 3e10^{-6}$) while
 268 flipping x and y coordinates (see `flip_coords` option). We mapped the 46 SBM groups using a
 269 combination of colors and shapes (see Fig. S5). To get a more ordered representation, we used
 270 the 'group-TL-tsne' layout, that uses 'TL-tsne' layout at a SBM group resolution (Fig. 6, Fig.
 271 S6). Interestingly, some SBM groups are overlaying in the 'group-TL-tsne' layout. For basal
 272 species, the group containing many rodents of genus *Microtus* (purple squares) is mixed with the
 273 group containing many rodents of genus *Spermophilus* (pink squares). Higher up in the network,
 274 the group containing predator snakes of genera *Hierophis* and *Montivipera* (pink diamonds) is
 275 overlaying with group containing snakes of genera *Vipera* and *Hemorrhois* (purple diamonds).

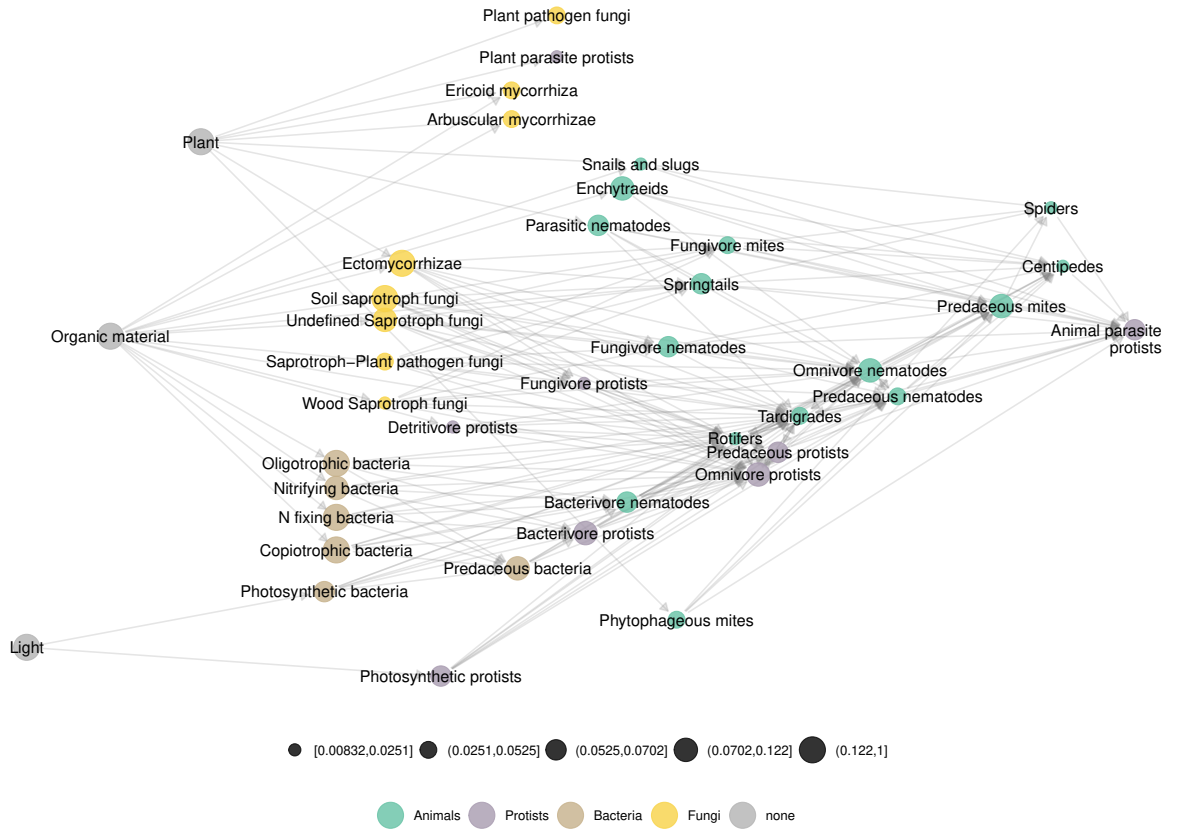


Figure 5: Norway soil trophic network, with 40 nodes and 204 edges. Nodes are colored according to taxonomic groups and have relative abundances built from environmental DNA data. It is represented using 'TL-tsne' layout ($\beta = 0.006$) and **ggnetwork** visualisation

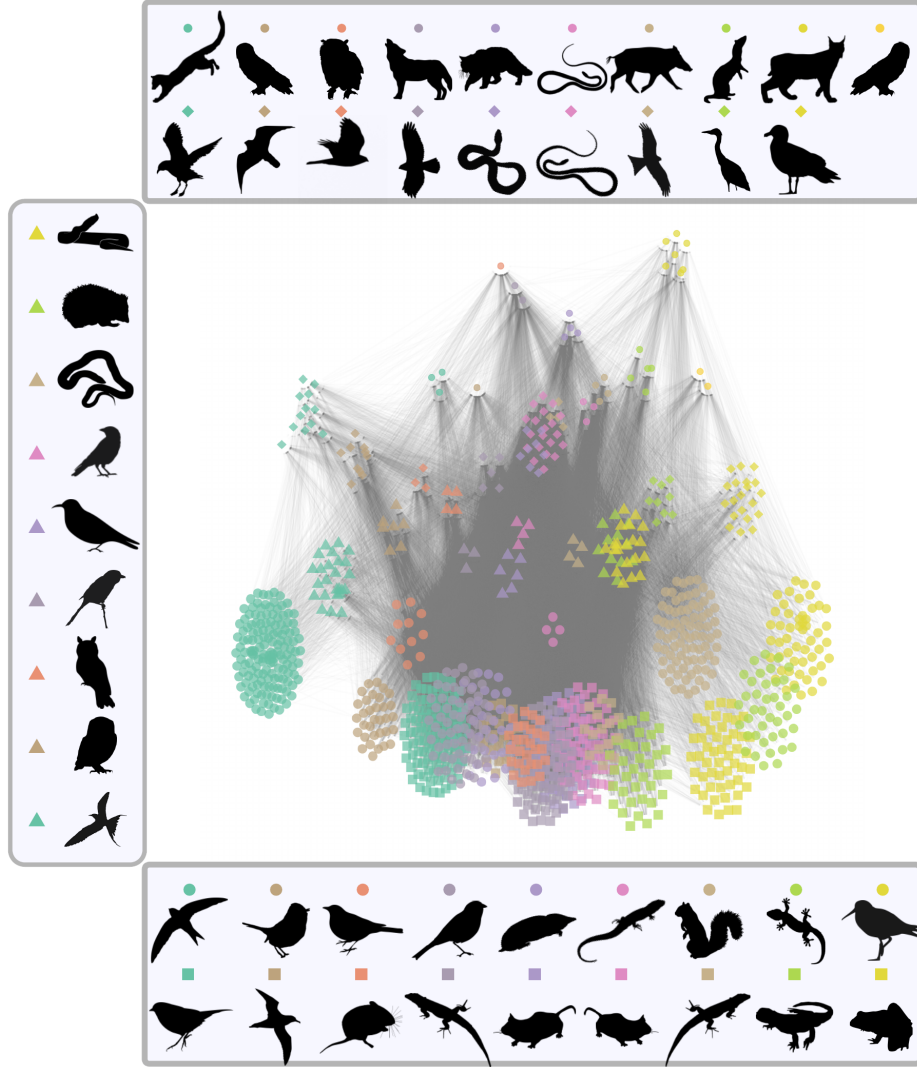


Figure 6: Metaweb of European tetrapods, with 1101 species (mammals, breeding birds, reptiles and amphibians) and 48963 interactions. Nodes have colors and shapes corresponding to estimated Stochastic Block Model groups. It is represented using 'group-TL-tsne' layout, built from group layout ('TL-tsne' with $\beta = 0.005$) and **ggmetanet** visualisation. In this representation, the y-axis is the trophic level. The legend is constructed by taking the silhouette of a representative of each group on <http://phylopic.org/>. See Table S1 for credits.

4 Discussion

We have presented *metanetwork*, a R package dedicated to handling and representing trophic metanetworks. These metanetworks are built from a metaweb, an abundance table and a possible information table on nodes. Potential local networks are then deduced from the metaweb and local abundances. While loosing local plasticity of interactions, such an approach generates distinct local networks due to sampling effect. Recent studies aimed at unraveling the structure of local networks for different types of communities (Kéfi *et al.* 2015, Kortsch *et al.* 2019, Bauer *et al.* 2022).

The purpose of *metanetwork* R package is to provide representation tools for trophic networks and metanetworks. Representing networks consists in choosing an appropriate node layout algorithm and a suitable visualisation technique (Pocock *et al.* 2016). If visualisation techniques, wrapped in 'metanetwork', were widely available, a network layout algorithm specifically designed for trophic networks was sorely lacking. We developed the 'TL-tsne' network layout algorithm, which constitutes the main methodological development of the present paper. This new layout combines the computation of trophic levels, using the Laplacian matrix on the x-axis, with a non-linear dimension reduction of the graph diffusion kernel on the y-axis. Besides representing two different features, it allows reading the network along fixed axes. Our diffusion kernel method not only relies on edges, which corresponds to paths of length 1, but also on paths of arbitrary long length. As a result, our layout is less sensitive to the deletion of an edge or, more generally, to the mistakes in edge specification compared to force-based layouts that are very sensitive, as pointed out in Pocock *et al.* 2016. Moreover, paths of arbitrary length do have ecological interpretations in terms of energetic channels in the network. Notice that the proposed 'TL-tsne' layout uses diffusion kernel on an undirected version of the considered network on the y-axis knowing the x-axis that takes into account directionality of the network since an imbalance term is present in Eq. (3). The present method is then only designed for directed networks. Diffusion maps achieve a similar goal for embedding of points in space relying however on an undirected graph built from spatial coordinates (Coifman *et al.* 2005). We also notice the proximity of our method with node embedding algorithms using neural networks since they provide low dimension representation of networks using paths, as the proposed method (Narayanan *et al.* 2017, Khosla

305 *et al.* 2019).

306 But, beyond technical concerns, 'TL-tsne' layout algorithm is suitable for trophic networks since
307 it allows reading and interpreting the network along fixed axes contrary to traditional force-based
308 layouts. These axes have an ecological interpretation involving energy diffusion in the network.
309 More precisely, the first axis, the trophic levels, describes the hierarchy in the acquisition of
310 resources. Although this scalar quantity is not enough to summarize the network as pointed
311 by the criticisms of this concept (Cousins 1987), it is in line with a thermodynamic interpreta-
312 tion of trophic networks (Lindeman 1942, Thompson *et al.* 2012). The second axis represents a
313 complementary information also related to diffusion of energy along the network. In our layout,
314 two species with similar trophic level may have different y-axis values, which indicates that they
315 belong to different energetic channels. Such a pattern is illustrated in the Angola coastal network
316 and Norway soil network where the 'TL-tsne' layout highlights two distinct channels for both
317 networks: the green channel, linked to primary producers, (either phytoplankton or plants) and
318 the brown channel, linked to detritus (Polis & Strong 1996, Moore *et al.* 2004, Mougi 2020).
319 To our knowledge, this is the first network layout algorithm that highlights these channels on
320 empirical trophic network data. This sheds new lights on a common structure shared by coastal
321 and terrestrial communities, as previously suggested in the literature (Bramon Mora *et al.* 2018).
322 Moreover, the diffusion parameter β , allows accentuating the separation between these different
323 channels, as shown in Fig. 2. Although the parameter β can be optimized numerically using
324 extended Moran index, we however encourage the user of *metanetwork* to explore several β con-
325 figurations in order to represent channels gradually separated from each other.

326

327 As a conclusion, our layout method based on diffusion processes, which highlights ecological
328 processes such as organic matter diffusion, emphasizes meaningful structures for trophic ecology.
329 We insist on the fact that network representation goes beyond visualization (*e.g.* Pawluczuk &
330 Iskrzyński 2022) because it also deals with network layout problem. In addition, our package
331 allows dealing with different scales of the metanetwork. This may help for instance for the under-
332 standing of the effect of environmental changes at different spatial scales or different aggregation
333 levels. On top of that, we have developed operations on the network, which allow comparing
334 networks at different location or different time. Thus, the present package, thanks to network

335 representation, manipulation and comparison tools should help practitioners to better explore
336 trophic metanetworks.

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341 6 Conflict of Interest statement

342 The authors declare no conflict of interest.

343 7 Authors' contribution

344 MO, JG and LV developed a first version of the framework. MO implemented the R package
345 and wrote a first version of the paper. JG and LV gave additional perspectives and contributed
346 to editing and revising the manuscript. All authors contributed critically to the drafts and gave
347 final approval for publication.

348 8 Data Availability

349 This paper uses a simulated data set available as a vignette of the package documentation avail-
350 able online (<https://marcohlmann.github.io/metanetwork/articles/pyramid.html>). It also
351 uses three datasets that are already available in the package:

- 352 • Angola coastal network: dataset is extracted from Web of Life (<https://www.web-of-life.es/map.php?type=7>), is attached to *metanetwork* and analysed in a vignette (<https://marcohlmann.github.io/metanetwork/articles/angola.html>)
353
354
- 355 • Norway soil network: this dataset from is attached to *metanetwork* and analysed in a
356 vignette (<https://marcohlmann.github.io/metanetwork/articles/norway.html>)

357 • European vertebrate metaweb: this dataset from is attached to *metanetwork* and analysed
358 in a vignette [https://marcohlmann.github.io/metanetwork/articles/vertebrates.](https://marcohlmann.github.io/metanetwork/articles/vertebrates.html)
359 [html](https://marcohlmann.github.io/metanetwork/articles/vertebrates.html)

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