Using bipartite to describe and plot two-mode networks in *R*

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Abstract

This vignette introduces the bipartite package to newbees. It describes it intention and, in seperate sections, the use of the most important functions.

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1.1   Introduction for ecologists

Many interactions between species are between distinct groups, such as pollinators and flowers, or herbivores and plants, or parasitoids and their hosts, or predators and their prey. When no information on interactions *within* groups is known, we have the case of a *bipartite* (a.k.a. "two-mode") network. In constrast, if every species could interact with every other, and we have (necessarily incomplete) information on these interactions, we have the case of a "unipartite" or "one-mode" network (think: food web).

1.2   Introduction for non-ecologists

In mathematics, there is a field called "graph theory", which describes/analyses/formalises "graphs" and the operations among them. A graph consists of *nodes* and *edges* (which are the links between nodes). A node can be something like an airport with edges being the flights between them; a power grid of power plants and energy consumers, with the power lines being the edges; a list of industry "leaders" and the edges representing financial ties between them; or, e.g. in ecology, a list of species, with edges representing trophic relationships, i.e. who eats whom.

When the nodes are grouped into two distinct sets, with no (known or quantified) interactions *within* a set, then we call it a bipartite network ("two parts", a.k.a. "two-mode" network). In our examples these could be airports of different continents (and no intracontinental flights are in our data base); power plants and energy consumers; industry executives and companies (where an executive can sit in the board of different companies); or pollinators and plants.

1.3   Introduction continued for both, ecologists and non-ecologists

This vignette tries to illustrate and explain a package that deals almost exclusively with *bipartite* networks!

The typical tasks we want to carry out are

1. visualise the network;

2. compute network indices to summarise its structure;

3. statistically test for differences between networks;

4. statistically test for differences between observed and random networks.

bipartite aims to facilitate this steps. This vignette aims to facilitate the use of **bipartite**. We shall try to predominantly use the technical terms ("node" and "edges"), but our examples will be from the ecological realm, where nodes are (typcially) species, and edges are typically called "links", which in fact are observed (or assumed) ecological interactions (such as pollination, predation, dispersal). Apologies for shifting between these two for easier access!

Also, as ecologists we are not "graph theoreticians" or mathematicians. Often, in the ecological literature, mathematical terms are used to elevate the status of the author, at no benefit to the analysis or to the reader. We are hesitant to use pretend-mathematics, at the risk of sounding daft to a person familiar with graph theory.

Of course, we don't mind if this documented would be cited, e.g. as Dormann (2019). Alternatively, you can always cite our work on this subject, inevitably also using (some functionality of) **bipartite** (Dormann *et al.*, 2008, 2009; Dormann, 2011; Dormann & Strauß, 2014; Dormann *et al.*, 2017; Dormann & Blüthgen, 2017)!

2   *What other network packages are out there in the R-universe?*

Before going through what **bipartite** offers, we shall briefly list what other packages in this direction can do for you:[1]

There are several open-source packages devoted to the analysis of networks and food webs, but only few addressing bipartite networks explicitly. Of these, **bipartite** provides the most extensive set of features, both for plotting, computing indices, and for null models. For the sake of completeness, here are some other *R* packages (on CRAN) we are aware of for handling bipartite networks (in alphabetical order):

AnnotationDbi for handling bimaps and annotation maps;

biGraph discontinued and archived;

bipartiteD3 interactive visualisation of bipartite networks;[2]

bmotif for counting "motifs" in bipartite networks;

dynsbm implements a modularity-like search through multiple time slices of a (dynamic) network ("dynamic stochastic block model" Miele & Matias, 2017);

econullnetr seems to be largely a wrapper for **bipartite**;

econetwork implements the core-periphery measures of Martín González *et al.* (2020) and allows computation of distances between networks following Ohlmann *et al.* (2019);

HiveR for fancy "hive" plots;

igraph provides functionalities largely for one-mode networks, quite a bit of plotting options, too;

NIMAA aims at exploring and imputing bipartite data in a pharmacological context, where for each subject (patient) the concentration of an inhibitor is known; the authors call this a "nominal data mining analysis", and from that title you would not think it is actually interesting also for "friends of bipartite", but it is!

sna provides many traditional one-mode metrics, from a "social network analysis" perspective; in a way the bigger brother of **bipartite**;

statnet a set of largely one-mode network packages, includes **ergm, networksis, statnet.common, tergm**;

tnet, which aims at re-thinking one-mode indices in a mathematically consistent way for bipartite networks; some functions of **tnet** were lifted to **bipartite** (thanks to Tore for allowing that!);

vegan for various analyses of a community matrix, including null models and nestedness computations;

WGCNA designed for gene assays, has a small set of indices and options overlapping with those of **bipartite**.

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[1]This is like a mini-CRAN-task view.

[2]And no, this is not a typo, it is "D3", which apparently is a JavaScript library for "data-driven documentation"

Additionally, there may well be dozens of packages on github or r-forge, which remain obscure until one stumbles over them.

bipartgraph, at `https://github.com/jgalgarra/bipartgraph`, offers polar and Ziggurat, building on his other package **kcorebip**;

ggbipart, at `https://pedroj.github.io/bipartite_plots/`, allows plotting bipartite networks in the spirit of **ggplot2**; so far (2021), there is no obvious benefit over the functions that come with **bipartite**;

infomapecology implements the "Map Equation", which identifies modules (Farage *et al.*, 2021, so far only on github: `https://github.com/Ecological-Complexity-Lab/infomap_ecology_package`).

3   *Preparing data for analysis*

Most functions in **bipartite** require the same type of input structure: an adjacency matrix of what-interacts-with-what, for short called "web". Raw data often start as tables of individual observations, e.g. one column containing the name of the species in the first level, another column the name of the species in the other level with which it interacts. Occasionally a third column records the number of interactions for this pair, or a weight. Also, several networks may be included into this table, so another column would provide a web-ID (e.g. a name of the site or the web itself). The function `frame2webs` is a little convenience function to convert such tables into one or more webs. Its output is a list or an array of webs in the appropriate format for further analysis.[3]

Most other packages (*R* or otherwise) are based on one-mode representations of networks. The typical input file would be a so-called edge list, simply listing in two columns (plus an optional weights column) what interacts with what (see below). The function `as.one.mode` transforms bipartite "webs" into edge lists to be used e.g. in Pajek or by **sna** or **tnet**. Notice that there are different projections from bipartite (two-mode) to one-mode (as detailed in the help to `as.one.mode`).[4]

Now, before any further talk, let's start by loading the package:

```
> library(bipartite)
```

4   *Visualising bipartite networks*

A useful first step in the analysis of bipartite networks is to plot it. To do so, **bipartite** offers two main functions, `plotweb` and `visweb`. They produce a bipartite graph (e.g. Fig. 1 top) and a prettified version of the adjacency matrix (Fig. 1 bottom), respectively (Motten, 1982). Both offer a wide range of options to change sizes, colours and placement of labels. Please run example code for these functions to get a feeling for their abilities (and hopefully you're impressed).[5]

```
> par(xpd=T)
> plotweb(motten1982)
> visweb(motten1982)
```

If these options are still not sufficient, and you want more customisation, such as side-by-side plotting of several networks, please check out the **bipartiteD3**, which provides the power

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[3]`webs2array` can also make an array of previously separate webs, padding non-overlapping species with zeros.

[4]The function `sortweb` allows a sorting of the matrix by marginal totals or by a user defined sequence. This may indeed be a handy function when customising the plotting later on. The example networks in **bipartite** are typically sorted in decreasing order.

[5]The additional function `plotweb2` is still a bit experimental but allows to combine several bipartite plots into a stack of tripartite, quadripartite, pentapartite etc. graphs. See the examples in the function's help page for illustration.
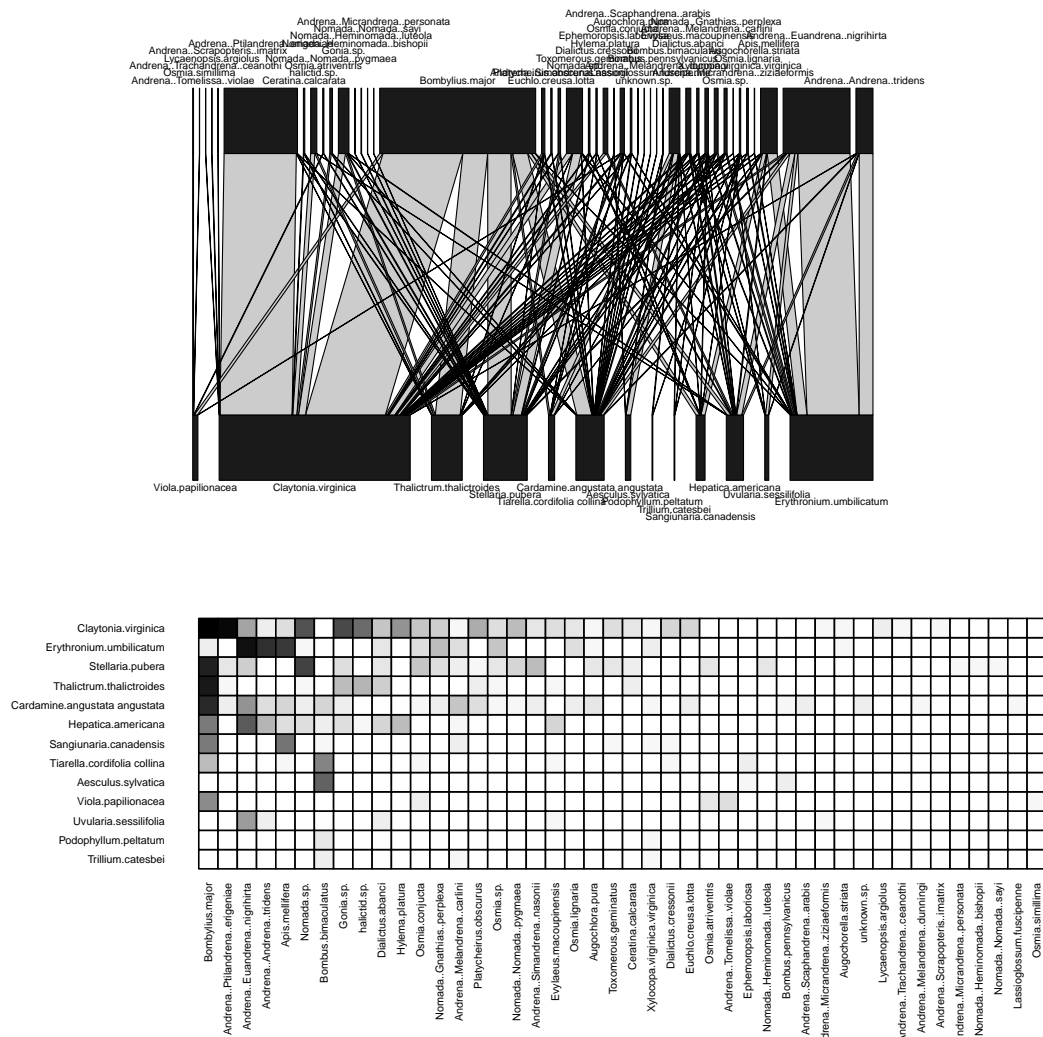
Figure 1: A bipartite graph of Motten's (1982) pollination network (*top*) and a visualisation of the adjacency matrix (*bottom*). The darker a cell is represented, the more interactions have been observed. By default, `plotweb` minimises overlap of lines and `visweb` sorts by marginal totals.

of the "D3" library of JavaScript.[6] Note that D3 makes *interactive* figures, so on mouse-over the figures change. While not a feature useful for publication in the current standard, it adds 21st century appeal to such graphs.

   The function `plotPAC` visualises (Fig. 2) a very special idea: the potential for apparent competition (Morris *et al.*, 2005). The idea is that every parasitoid emerging from a host can attack another species. Thus, the more individuals emerge from a host, the larger is the potential for these to reduce the competition between hosts, as long as they choose their prey equiprobable. Pretty as it may be, its current value is highest for host-parasitoid networks, so the plot employing a pollination network is for illustration only.

```
> plotPAC(PAC(motten1982), outby=0.9)
```

We can also visualise communities within the network by computing its modularity and then plotting the result, using the functions `computeModules` and `plotModuleWeb`, respectively (Fig. 3).

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[6]The package explicitly links to "our" bipartite, although I think it is largely independent of it, and actually very nice!
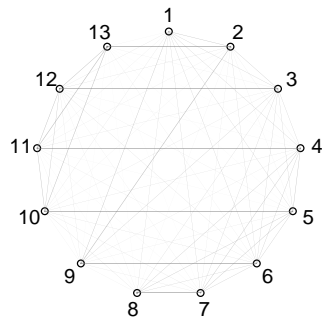
Figure 2: A PAC-plot of Motten's 1982 pollination network. Lines connect plants potentially visited next by a pollinator. Line width is proportional to probability, which is very similar in this example. See help of *plotPAC* for details on plotting and meaning.
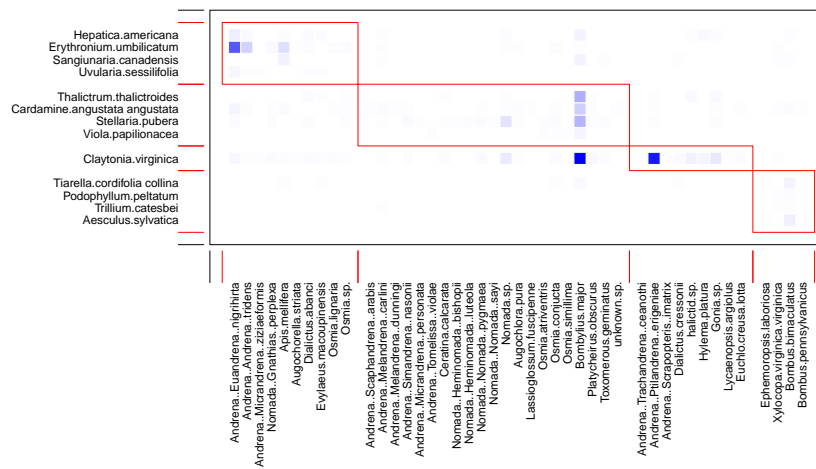
Figure 3: The adjacency matrix of Motten's (1982) pollination network, organised into modules.

```
> mod <- computeModules(motten1982)
> plotModuleWeb(mod)
```

To visualise either level separately projected into one-mode mode, we have to employ a different package, for example **sna** (Butts, 2013). We can do the projection on the fly, though. For networks with even a moderate number o species, such plots can become rather obtuse and uninformative (Fig. 4 top).

```
> par(mfrow=c(1,2), xpd=T)
> gplot(as.one.mode(motten1982, project="higher"),
+  label=colnames(motten1982), gmode="graph",
+ label.cex=0.6, vertex.cex=2)
> gplot(as.one.mode(motten1982, project="lower"),
+        label=rownames(motten1982), gmode="graph",
+        label.cex=0.6, vertex.cex=2, vertex.col="green")
```

Figure 4: Plots of one-mode projections of Motten's (1982) pollination network. Pollinators in red (*top*), plants in green (*bottom*). Note that these plots are point-symmetrically variable, hence every plot will look somewhat different.

5 *Computing indices*

Network indices are primarily that: metrics to quantify an aspect of the network. Each may have a justification, a purpose, but the information in a matrix is only finite. As a consequence, network indices are highly correlated. There is thus no point in computing all indices in the book; rather should we consider very carefully what we want to test with the data and select one (or a few) indices to do so.

The **bipartite**-package offers itself to data dredging: with one function one can compute dozens of indices, certainly some of them will be significantly correlated with whatever we want to test. While analyses are commonly carried out in this way, this is obviously statistically inappropriate. Two issues are important here. One is that of multiple testing, and there are dozens of publications covering this issue. The other is an attempt to formalise one's expectation. Null models are one way to do so, in particular one's expectation of what a pattern is like in the *absence* of a process. This technical details of this topic are covered further below (section 6.3).

Indices (currently) come at the following hierarchical levels:

1. network-level (a single value, per index, for the entire network);

2. group-level (a value, per index, for each of the two groups);

3. link-level (a value, per index, for each edge = link);

4. node-level (a value, per index, for each node = species); and

5. species-level (a value, per index, for each species).

5.1 *Network-level indices*

This set of indices is computed for the entire network. They are called using the function `networklevel`, which additionally (and conveniently) makes available all indices from the group level, too. Those restricted to the network-level are:

1. `connectance`, also called 'standardised number of species combinations' in biogeographic analyses (Gotelli & Graves, 1996; Dunne *et al.*, 2002);

2. `web asymmetry`, the balance of the number of species in the two levels (Blüthgen *et al.*, 2007);

3. `links per species`;

4. `number of compartments`;

5. `compartment diversity` (Tylianakis *et al.*, 2007);

6. `cluster coefficient`, which will compute both the network-wide binary, one-mode-based cluster coefficient as well as those for each level,

7. `nestedness`, with the returned value indicating the 'temperature' of the matrix, which is low (0) for a perfectly nested matrix (Rodríguez-Gironés & Santamaría, 2006);

8. `weighted nestedness`, or more specifically 'weighted interaction nestedness estimator' (WINE), with 1 indicating perfected nestedness (thus exactly opposite to the previous index) (Galeano *et al.*, 2009);

9. `weighted NODF`, as an alternative measure of quantitative nestedness, automatically correcting for matrix filling and also indicating nestedness by values towards 1 (Almeida-Neto & Ulrich, 2011);

10. `interaction strength asymmetry` (Blüthgen *et al.*, 2007) (or alternatively `ISA` or `dependence asymmetry`: Bascompte *et al.*, 2003), which quantify whether specialised species interact with generalised ones in the other level (or vice versa);

11. `specialisation asymmetry` (or alternatively `SA`), following the same idea as the previous, but this being based on species specialisation in d';

12. `linkage density`, marginal totals-weighted diversity of interactions per species (Bersier *et al.*, 2002);

13. `Fisher alpha`, diversity index based on fitting a Fisher-series (Fisher *et al.*, 1943);

14. `interaction evenness` quantifies how balanced the distribution of interactions is across species, based on Shannon's diversity (Tylianakis *et al.*, 2007);

15. `Alatalo interaction evenness`, as an alternative measure of interaction evenness, attempting to overcome some of the shortcomings of the previous, Shannon's, version (Alatalo, 1981; Müller *et al.*, 1999);

16. `Shannon diversity`;

17. `H2`, network-wide specialisation index H'_2 (Blüthgen *et al.*, 2006).

Similarly to the previous sets of indices, several options are available to fine-tune those in `networklevel`:

```
> networklevel(bezerra2009, index=c("ISA", "weighted NODF", "Fisher alpha"),
+              SAmethod="log")

            weighted NODF interaction strength asymmetry
             5.717160e+01                     8.842823e-05
             Fisher alpha
             8.793400e+00
```

5.2 *Group-level indices*

Indices that can be computed for each group separately are collected in the function `grouplevel`.[7] Quite a few of these indices are aggregates from the species level (e.g. by averaging species' degrees), in which case the mean is weighted by the number of observations of each species, thus giving more weight to species for which information is more reliable.[8] Others are biogeographic indices which change their value when the matrix is inverted (i.e. when a group changes from "species" to "islands"). The following indices are implemented:

1. `number of species` in the respective trophic level;

2. `mean number of links`;

3. `mean number of shared partners` (Roberts & Stone, 1990; Stone & Roberts, 1992);

4. `cluster coefficient`, which supposedly informs us whether a network has 'small world' properties (Watts & Strogatz, 1998);

5. `weighted cluster coefficient`, which takes into account the number of interactions and is a properly derived bipartite version of the previous one-mode cluster coefficent above (Opsahl, 2010);

6. `togetherness` as the mean number of co-occurrences across all pairwise species combinations (Stone & Roberts, 1992);

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[7]If network-level indices are also desired, all indices in `grouplevel` are also accessible through `networklevel`, see below.

[8]The weighting can be switched off by stating `weighted=FALSE`.

7. `C score`, or 'checkerboardness', which averages the number of instances of 01/10-patterns (i.e. exclusive occurrences) for all pairwise species combinations (Stone & Roberts, 1990);

8. `V ratio`, the variance ratio of species numbers to interaction numbers within species of a level (Schluter, 1984);

9. `discrepancy`, the number of links one would have to move to achieve perfect nestedness (Brualdi & Sanderson, 1999);

10. `degree distribution`, fitting an exponential function and (truncated) power laws(Jordano *et al.*, 2003);

11. `extinction slope`, with different options for the extinction sequence (Memmott *et al.*, 2004);

12. `robustness`, the area under the extinction curve (Burgos *et al.*, 2007);

13. `niche overlap`, with options for distance metrics (Pielou, 1972; Hurlbert, 1978);

14. `generality` (for the higher trophic level) or `vulnerability` (for the lower one) (Bersier *et al.*, 2002);

15. `partner diversity`, simply the mean Shannon diversity of interactions of each species in a level;

16. `effective partners` as before, but as the exponent of the base to which Shannon was computed (typically *e* or 2) (Jost, 2006);

17. `fd` (or alternatively `functional diversity`), which is similar to niche overlap but computed as branch length of a cluster diagram of dissimilarity of resource use (Devoto *et al.*, 2012).

As in the case of species-level indices, some allow for normalisation (between 0 and 1), others for different basis to the logarithm or similar tuning. A typical call to `grouplevel` will thus comprise the list of desired indices[9] and their options, as well as the level(s) for which the computation shall be carried out:

```
> grouplevel(bezerra2009, level="both", index=c("mean number of links", "weighted
+     cluster coefficient", "effective partners", "niche overlap"), dist="bray")
```

```
mean.number.of.links.HL mean.number.of.links.LL          niche.overlap.HL
              9.9502551               7.0975057                 0.2824538
       niche.overlap.LL            generality.HL          vulnerability.LL
              0.4795595               8.0590841                 5.6963672
```

The LL and HL behind each index indicate that it was computed for the lower and higher level, respectively. A relatively comprehensive comparison of network-level indices (Dormann *et al.*, 2009), including some at the group level, has shown substantial redundancy among these indices, and few of them have a sound theoretical basis.

5.3 Link-level indices

At the moment, only few indices have been investigated at the level of the individual link (i.e. the cell of a network matrix):

1. dependence (i.e. the relevance of each species for the other level: Bascompte *et al.*, 2006) one matrix for each level;

2. endpoint degree (i.e. product of degrees of species linked by this cell: Barrat *et al.*, 2004).

---

[9]Or alternatively the argument `index="ALL"`.

It is employed by simply applying it to the network under consideration and selecting the index desired:

```
> str(linklevel(bezerra2009, index=c("dependence", "endpoint")))

List of 3
 $ HL dependence: num [1:13, 1:13] 0.193 0.131 0.056 0.108 0.105 ...
  ..- attr(*, "dimnames")=List of 2
  .. ..$ : chr [1:13] "Diplopterys.pubipetala" "Byrsonima.gardnerana" "Banisteriopsis.muric
  .. ..$ : chr [1:13] "Centris.aenea" "Centris.fuscata" "Centris.caxiensis" "Centris.tarsat
 $ LL dependence: num [1:13, 1:13] 0.2415 0.2238 0.0997 0.2474 0.2632 ...
  ..- attr(*, "dimnames")=List of 2
  .. ..$ : chr [1:13] "Diplopterys.pubipetala" "Byrsonima.gardnerana" "Banisteriopsis.muric
  .. ..$ : chr [1:13] "Centris.aenea" "Centris.fuscata" "Centris.caxiensis" "Centris.tarsat
 $ endpoint      : num [1:13, 1:13] 117 78 156 104 91 65 52 26 52 52 ...
  ..- attr(*, "dimnames")=List of 2
  .. ..$ : chr [1:13] "Diplopterys.pubipetala" "Byrsonima.gardnerana" "Banisteriopsis.muric
  .. ..$ : chr [1:13] "Centris.aenea" "Centris.fuscata" "Centris.caxiensis" "Centris.tarsat
```

This function is so rudimentary, and its output so disproportionally voluminous, that it is not worth going into further details here and use str to only show the structure of the output.

5.4 *Species-level (= node-level) indices*

The (growing) list of indices computable for each species in the network comprises (the index name to be used in the call is given in typewriter font):

1. degree, i.e. the number of links of each species,

2. normalised degree for a normalised version of degree (Martín González *et al.*, 2010),

3. species strength as sum of dependencies for each species (Bascompte *et al.*, 2006),

4. nestedrank as rank in a nested matrix (Alarcón *et al.*, 2008),

5. interaction for interaction push/pull (a version of dependence asymmetry), (Vázquez *et al.*, 2007),

6. PDI for Paired Differences Index (Poisot *et al.*, 2011b,a),

7. resource range for Schoener's index of unused resources (Schoener, 1989),

8. species specificity (or coefficient of variation of interactions) (Julliard *et al.*, 2006; Poisot *et al.*, 2012),

9. PSI for pollination service index (or pollinator support index, depending on the trophic level),[10]

10. NS for node specialisation index (Dalsgaard *et al.*, 2008),

11. betweenness for betweenness (Borgatti & Everett, 1997),

12. closeness (both automatically also return their weighted counterparts proposed by Tore Opsahl in package **tnet**),

13. Fisher for Fisher's alpha as a measure of diversity (Fisher *et al.*, 1943),

14. diversity for Shannon diversity of interactions of that species,

15. effective partners for the effective number of interacting partners (Bersier *et al.*, 2002),

---

[10]devised by the author with Nico Blüthgen and Bernd Gruber

16. `proportional generality` for a quantitative version of normalised degree,[11]

17. `proportional similarity` as specialisation measured as similarity between use and availability (Feinsinger *et al.*, 1981),

18. `d` for Blüthgen's discrimination/selectivity index d' (Blüthgen *et al.*, 2006).

Some of them allow for normalisation (between 0 and 1), others for different basis to the logarithm or similar tuning. A typical call to `specieslevel` will thus comprise the list of desired indices[12] and their options, as well as the level(s) for which the computation shall be carried out:

```
> specieslevel(bezerra2009, level="lower", index=c("normalised degree", "PDI",
+        "effective partners"), PDI.normalise=F)
```

	normalised.degree	PDI	effective.partners
Diplopterys.pubipetala	0.6923077	1010.0000	7.437631
Byrsonima.gardnerana	0.4615385	1939.6667	3.819660
Banisteriopsis.muricata	0.9230769	657.0000	9.191488
Heteropterys.sp1	0.6153846	570.3333	6.278285
Heteropterys.sp2	0.5384615	567.3333	5.865968
Dicella.bracteosa	0.3846154	429.0000	4.582040
Carolus.chasei	0.3076923	513.6667	3.751208
Stigmaphyllon.paralias	0.1538462	774.0000	1.944388
Banisteriopsis.stellaris	0.3076923	245.6667	3.787887
Banisteriopsis.schizoptera	0.3076923	189.0000	3.822392
Stigmaphyllon.auriculatum	0.3076923	204.3333	3.687447
Stigmaphyllon.ciliatum	0.2307692	238.0000	2.937197
Janusia.anisandra	0.2307692	220.3333	2.813322

A relatively comprehensive comparison of species-level indices of specialisation, Dormann (2011) has shown substantial redundancy among these indices, and only few of them have a sound theoretical basis (Poisot *et al.*, 2012).

5.4.1 The betweenness mess

Betweenness is a graph index which quantifies the importance of a node for fluxes between nodes. It does so by counting how many of all shortest paths between two nodes go through the target node. That means, a peripheral node will have a betweenness score of 0, while a central node can have values up to n (if all shortest paths go through it).

```
> data(Safariland)
> # plot the one-mode projection for the lower level:
> set.seed(4) # don't ask me why gplot is stochastic ...
> par(xpd=T, mar=c(0,6,0,6))
> gplot(as.one.mode(Safariland, project="lower"), label=rownames(Safariland))
```

---

[11]devised by Jochen Fründ
[12]Or alternatively the argument `index="ALL"`.
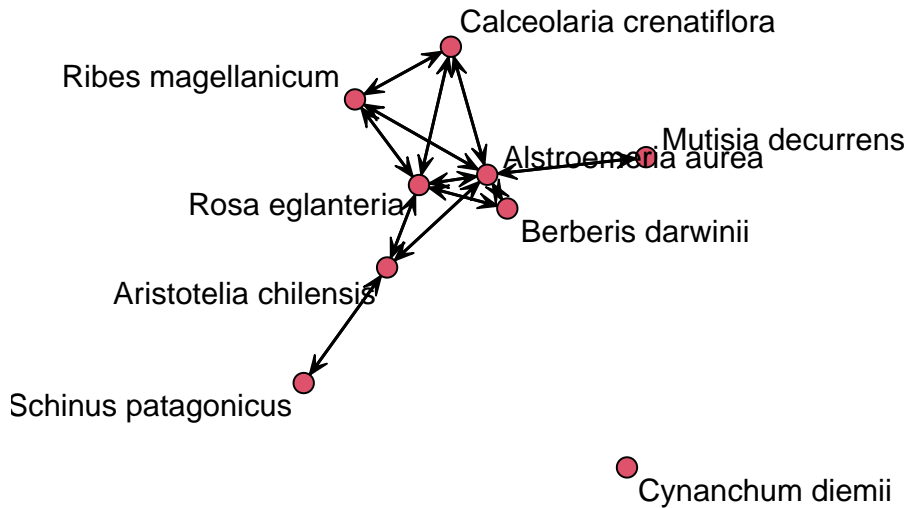
So, what we see is for the main module a rather central position for, e.g., *Rosa eglanteria*. For 8 species (we can neglect *Cynanchum diemii*), we have $8(8-1)/2 = 28$ paths. For a simple example, *Aristotelia chilensis* (plant number 1 in the edge list below) should have only the shortest path to *Schinus patagonicus* running through it, to all other 6 plant species.

Let's see what its betweenness score is, using several different functions across R-packages:

```
> # convert matrix into one-mode edgelist:
> SafPlantsEL <- as.tnet(as.one.mode(Safariland, project="lower"))

> # compute betweenness:
> tnet::betweenness_w(SafPlantsEL) # 6
> bipartite::BC(Safariland, rescale=F)$lower # 6
> DiagrammeR::get_betweenness(DiagrammeR::from_igraph(tnet_igraph(SafPlantsEL))) # 6
> igraph::betweenness(tnet_igraph(SafPlantsEL), cutoff=9) # 6
> influenceR::betweenness(tnet_igraph(SafPlantsEL)) # 12
> sna::betweenness(SafPlantsEL) # length 36!!
> sna::betweenness(as.matrix(SafPlantsEL)) # length 27!!
```

Let's put them all next to each other, into a named matrix:

```
> btws <- cbind("t:betw"=tnet::betweenness_w(SafPlantsEL)[,2],
+      "b:BC"=bipartite::BC(Safariland, rescale=F)$lower,
+      "DR:betw"=DiagrammeR::get_betweenness(DiagrammeR::from_igraph(tnet_igraph(SafPlantsEl
+      "i:estbetw"=igraph::betweenness(tnet_igraph(SafPlantsEL), cutoff=9),
+      "inf:betw"=influenceR::betweenness(tnet_igraph(SafPlantsEL))/2 )
> rownames(btws) <- rownames(Safariland)
> btws
```

```
##                         t:betw b:BC DR:betw i:estbetw inf:betw
## Aristotelia chilensis        6    6       6         6        6
## Alstroemeria aurea          11   10      14        14       10
## Schinus patagonicus          0    0       0         0        0
## Berberis darwinii            0    0       0         0        0
## Rosa eglanteria             13    4       6         6        4
## Cynanchum diemii             0    0       0         0        0
## Ribes magellanicum           0    0       0         0        0
## Mutisia decurrens            0    0       0         0        0
## Calceolaria crenatiflora     0    0       9         9        0
```

So they all agree on the betweenness-value for *Aristotelia*, but not for *Alstroemeria* and *Rosa*, and not at all for *Calceolaria*.

The case of *Calceolaria* is instructive. Here we can see that actually none of the shortest paths goes through its node, making a value of 9 incorrect. (Try finding a single path that cannot be short-cutted through a link between *Alstroemeria*.)

Also *Rosa* is instructive. Here we encounter the problem of ties: several shortest paths are on equal footing, e.g. *Aristotelia - Rosa - Ribes* is as short as *Aristotelia - Alstroemeria - Ribes*. In fact, there are 4 **unique** shortest paths through *Rosa*, but 6 shortest paths in total. So it seems that **DiagrammeR** and **igraph** simply handle ties differently to **bipartite**'s BC and **influenceR**. **Tnet**'s betweenness_w[13] remains a mystery. Even if 13 may be the number of all paths, then that would not explain the many 0s for the other species.

Note that all functions used here have options and arguments that affect the outcome. Setting them differently will yield, for example, standardised values. We only investigated out-of-the-box behaviour and are not suggesting something is actually wrong with the functions, but you may have to tweak them to yield an intuitive result. A case in point is **influenceR**'s betweenness, which will return **igraph**'s value if the argument snap is set to FALSE, but 2*BC's values for the default (TRUE).

To summarize: bipartite::BC and influenceR::betweenness/2 yield values as one would expect for *unique* shortest paths; DiagrammeR::get_betweenness and igraph::betweeness yield number of non-unique shortest paths, which we also regard as an intuitive measure.

As always in data analysis: it is the responsibility of the analyst to make sure suitable-for-purpose indices are used!

5.5   *Which index to choose?*

Different indices were invented ("developed") for different purposes. However, for most indices, it has not been demonstrated that they actually achieve what their inventor had in mind. Most commonly indices quantify a specific pattern which may have come about by a whole variety of different causes. Take, for example, connectance, i.e. the proportion of possible links actually recorded. Low connectance may be caused by high specialisation or by low sampling intensity. The same holds true for a species' degree, which (typically) increases with sampling effort as well as generalisation. For the choice of an index this means that we cannot solely rely on what the inventor has proposed this index to be good for, but we have to keep in mind that it may actually quantify several other things, too.

Apart from the different levels at which an index can quantify a network pattern (from the individual link to the entire network, as covered in sections 5.3–5.1), indices can be divided into those for binary and those for weighted data (called here binary and weighted indices, respectively). Binary indices only use the information of whether a link exists, while weighted indices additionally account for how strong a link is, as judged from the actual value in a network matrix.

Binary indices, by definition, use less information. It does not follow that they are thus more robust! In fact, Blüthgen (2010) argues the opposite, since only a weighted index can tell whether an observed value indicates specialisation or not.[14]

This, if two indices are available to quantify the same idea, one binary and one quantitative, one should generally choose the quantitative one. Rather than species degree, we should use species strength or linkage density. Table 5.5 depicts some such binary-quantitative index pairs.

In a nutshell: Quantitative indices make use of more information in the data. They are generally more advisable, although most of them also are strongly affected by sampling issues.

5.5.1   *Index redundancy: do different indices tell the same thing?*

To visualise the similarity and possible redundancy of the different indices, they are computed for the networks in **bipartite** and summarised through a principal component analysis (see

---

[13]Available in **bipartite** under the same name.

[14]Imagine two species, one with entries (1, 1), the other with entries (1, 100). A binary index would not be able to tell between them, while a quantitative would expose the second as far more specialised.

Table 1: Binary-quantitative pairs of network indices. Note: Most quantitative indices can also be computed on binary networks. That does not make them a quantitative measure!

	binary	quantitative
network level	connectance	H_2'
	links per species	linkage density
	nestedness	weighted NODF, wine
group level	mean number of partners	effective number of partners
species level	degree	species strength, effective number of partners

Fig. 5).

```
> web.names <- data(package="bipartite")$results[,3]
> data(list=web.names) #loads all webs
> # the next step takes around 10 minutes:
> netw.indic.webs <- t(sapply(web.names, function(x) networklevel(get(x),
+              index="ALLBUTDD")))

> PCA.out <- prcomp(netw.indic.webs[,-5], scale.=T)
> biplot(PCA.out, xpd=T, las=1)

> summary(PCA.out)

Importance of components:
                          PC1    PC2     PC3     PC4     PC5     PC6     PC7
Standard deviation     4.2780 3.6461 2.09732 1.84163 1.32612 1.09350 1.0375
Proportion of Variance 0.3979 0.2890 0.09562 0.07373 0.03823 0.02599 0.0234
Cumulative Proportion  0.3979 0.6869 0.78248 0.85621 0.89444 0.92044 0.9438
                          PC8     PC9    PC10    PC11    PC12    PC13    PC14
Standard deviation     0.81058 0.64158 0.62560 0.56960 0.49217 0.43179 0.36230
Proportion of Variance 0.01428 0.00895 0.00851 0.00705 0.00527 0.00405 0.00285
Cumulative Proportion  0.95812 0.96707 0.97558 0.98263 0.98789 0.99195 0.99480
                          PC15    PC16   PC17    PC18    PC19    PC20      PC21
Standard deviation     0.26591 0.25249 0.2254 0.18080 0.11401 0.09049 7.038e-16
Proportion of Variance 0.00154 0.00139 0.0011 0.00071 0.00028 0.00018 0.000e+00
Cumulative Proportion  0.99634 0.99772 0.9988 0.99954 0.99982 1.00000 1.000e+00
```

Apparently 40, 30 and 10% of the variation in indices can be partitioned to the first three axes. We can now investigate which indices load on the few axes:

```
> round(PCA.out$rotation[, 1:4], 3)
```

	PC1	PC2	PC3	PC4
connectance	0.177	0.147	-0.044	0.025
web asymmetry	-0.137	-0.098	-0.298	0.063
links per species	0.189	-0.087	-0.020	0.183
number of compartments	-0.147	0.005	0.167	-0.051
cluster coefficient	0.169	0.128	0.005	0.119
nestedness	-0.020	0.196	-0.004	0.305
weighted nestedness	0.066	-0.108	-0.170	-0.399
weighted NODF	0.193	0.068	-0.138	-0.182
interaction strength asymmetry	-0.172	0.080	-0.178	-0.028
specialisation asymmetry	0.021	0.109	0.337	-0.096
linkage density	0.049	-0.258	-0.058	-0.038
Fisher alpha	-0.041	-0.246	0.045	-0.053
Shannon diversity	0.073	-0.251	0.011	0.082

```
interaction evenness                     0.179 -0.078  0.012  0.102
Alatalo interaction evenness             0.076  0.159  0.143 -0.045
H2                                      -0.191  0.089  0.091  0.037
number.of.species.HL                    -0.048 -0.249  0.026 -0.062
number.of.species.LL                    -0.020 -0.256  0.121 -0.038
mean.number.of.partners.shared.in.HL     0.191 -0.032 -0.177  0.189
mean.number.of.partners.shared.in.LL     0.218  0.042 -0.049 -0.042
cluster.coefficient.HL                   0.189  0.093 -0.001 -0.036
cluster.coefficient.LL                   0.155  0.085 -0.285 -0.009
weighted.cluster.coefficient.HL          0.150 -0.122 -0.189  0.162
weighted.cluster.coefficient.LL          0.212 -0.040  0.035  0.145
niche.overlap.HL                         0.045  0.142 -0.287 -0.272
niche.overlap.LL                         0.202  0.035  0.062 -0.195
togetherness.HL                          0.023  0.181 -0.283 -0.032
togetherness.LL                          0.216  0.052  0.087 -0.041
C.score.HL                              -0.162 -0.123  0.217  0.147
C.score.LL                              -0.216 -0.020  0.038  0.026
V.ratio.HL                               0.177 -0.121  0.121 -0.101
V.ratio.LL                              -0.048 -0.238 -0.151 -0.113
discrepancy.HL                          -0.041 -0.251  0.059 -0.042
discrepancy.LL                          -0.039 -0.252  0.062 -0.037
extinction.slope.HL                      0.216 -0.006  0.063  0.131
extinction.slope.LL                      0.120 -0.061  0.035  0.326
robustness.HL                            0.214 -0.020  0.059  0.148
robustness.LL                            0.150 -0.084 -0.114  0.254
functional.diversity.HL                  0.162  0.003  0.027 -0.257
functional.diversity.LL                  0.163 -0.003  0.029 -0.259
partner.diversity.HL                     0.198 -0.078  0.183 -0.028
partner.diversity.LL                     0.061 -0.222 -0.212  0.082
effective.partners.HL                    0.187 -0.079  0.206 -0.101
effective.partners.LL                   -0.003 -0.256 -0.125 -0.011
generality.HL                            0.187 -0.079  0.206 -0.101
vulnerability.LL                        -0.003 -0.256 -0.125 -0.011
```

As we can see, there are quite a few indices on the first axis with a loading of around 0.2 (links per species, weighted NODF, H2, mean number of partners shared; weighted cluster coefficient, niche overlap, togetherness, C-score (all lower level); extinction slope, robustness, partner diversity (all higher level)).

Also the PCA biplot (Fig. 5) is not very helpful, since the many indices pointing "southwards" are unreadably overlapping.

Alternatively, we might want to depict the correlation between different indices by means of a cluster analysis (Fig. 6).

```
> library(Hmisc)
> plot(varclus(netw.indic.webs), cex=0.8)
> abline(h=0.5, lty=2, col="grey")
```

It picks out a slightly different structure, with the PC1 being distributed over more than one cluster (towards the left, with extinction.slope.HL but also towards the centre, with weighted NODF). In either case it becomes clear that many indices are of limited originality. However, there are some branches ending above the dashed line, indicating that they add a new element to the description of the network. Some are trivial, such as the number of species in the lower level, others less so (specialisation asymmetry, extinction slope LL, niche overlap HL, (weighted) nestedness).

It should become clear that there is no need to compute all indices a software can offer, and that some clusters seem to measure the same latent property, even it is unclear what that
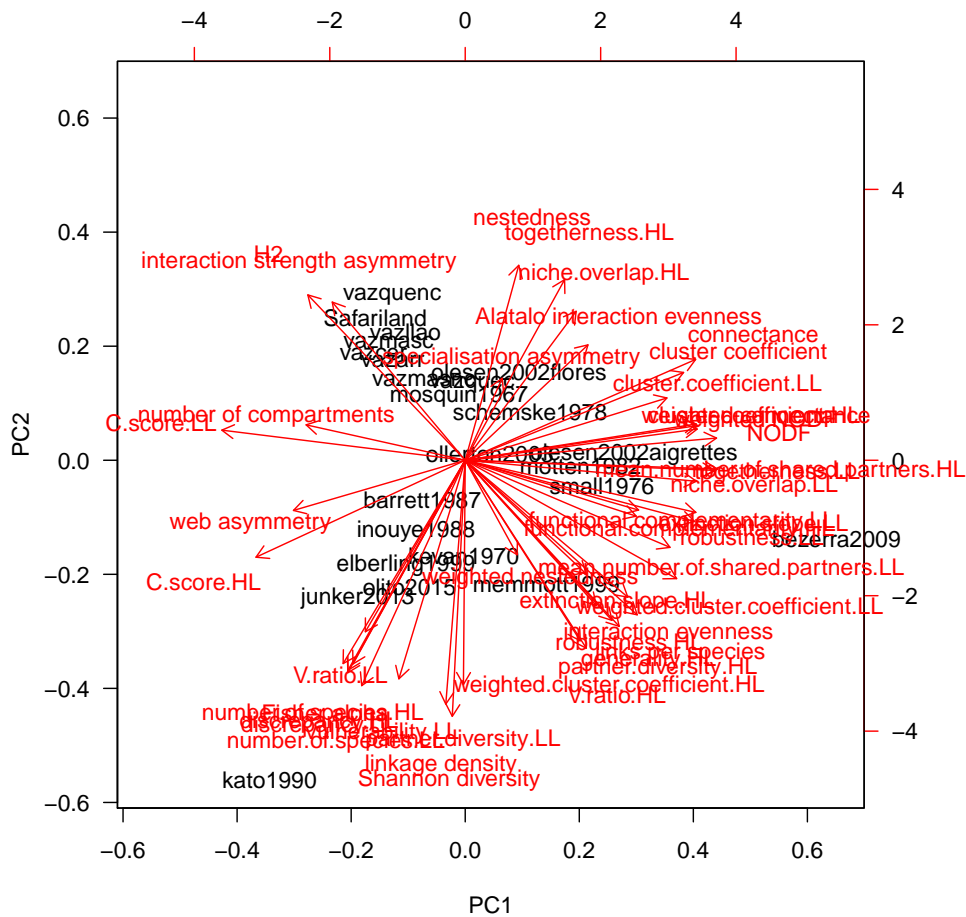
Figure 5: Principal component analysis biplot of indices at the network level, based on 22 quantitative pollination networks. Notice that network "kato1990" is by far the largest in the set, defining on its own the second principal component. Indices pointing "southwards" may thus simply be more sensitive to network size and related properties (such as density of interactions).
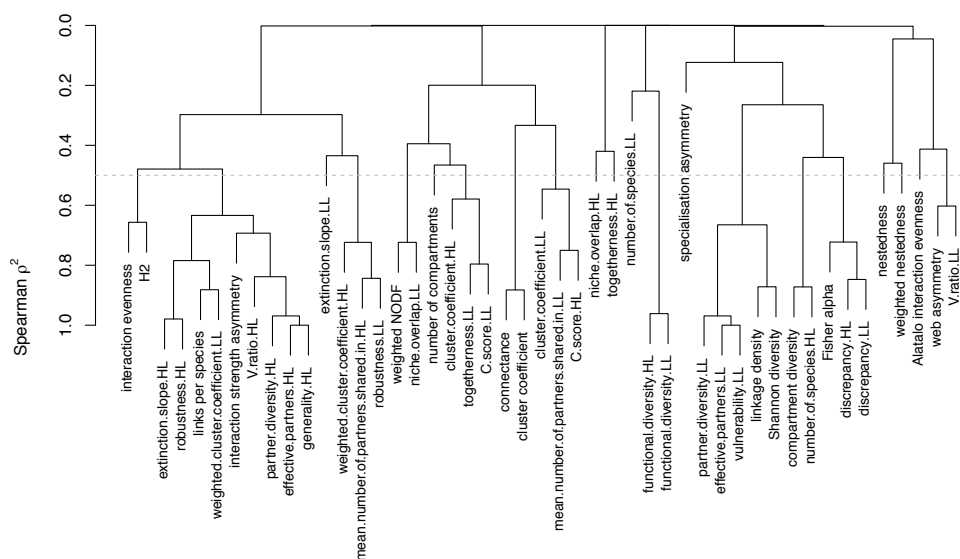

Figure 6: Cluster analysis of indices at the network level, based on 22 quantitative pollination networks. Grey dotted line indicates the level below which clustering could be considered relevant ($|r| > 0.7$).

property is. Curiously, higher and lower level indices are always intermixed. There seems to be always an effect onto the other level, so that some indices pick up a signal in one level, but others the same signal in the other.[15]

The 22 pollination networks, on which both PCA and cluster are based, are most certainly not representative of bipartite networks in general. The simulations of Dormann *et al.* (2009) for a wider range of sizes and linkage densities show a qualitatively similar picture, though: indices are overlapping into clusters.[16]

5.5.2 *Variations on on the same theme: which index of a group of similar ones should I choose?*

Different indices were developed for different aims. Some are very reasonable, logically sound, thoughtful and even productive (in the sense of "shown to be doing what they are supposed to do"), others aren't. Each index should be understood when being used, based on the literature introducing it and any later study refining, comparing or criticising/appraising it. There is no easy way to decide the question "Which is the right index for me?"

That said, there are a few guiding considerations that seem plausible to me:

1. Quantitative indices use more information than binary ones; preferably use the former.

2. Indices developed for bipartite networks are likely to be closer, theoretically, to the structure of the data than one-mode indices working on projections of bipartite networks.

3. Indices that came out positively in comparisons have proven their worth more than fresh-off-the-press indices.

4. If two or more indices seem barely distinguishable, do **not** choose the one easiest to interpret! This would be a logical fault, since their similarity indicates clearly that they are affected by "something" and we don't know what that something is, yet. But interpreting an effect as being caused by what is "most convenient to interpret" is most certainly wrong (Shermer, 2012).[17]

The last point in particular seems rather little helpful. Imagine the two index values "functional diversity" for the higher and lower trophic level, which are near-identical in Fig. 6. This indicates that the *network*, rather than each level, contains the information which these two indices describe. In this particular case, we may want to consider using neither index, or using any of them but interpreting it *as if it represented* both *level*.

Thus, in a nutshell, there is no easy answer and there is no way around knowing the index and the literature about it and its friends.

6 Null models

6.1 *Why null models?*

When a network is structured according to some measure (e.g. nestedness), what does that mean? It could mean that ecological processes leading to nestedness are at play. Or it could mean that a sampling effect makes nestedness an inevitable consequence. Or, finally, it could be a mixture of both. Furthering our understanding of nature is not aided by the reporting of spurious relationships resulting from sampling effects, hence a formal description of what the network would look like without the ecological process would be a useful comparison. That is what a null model aims to provide (Gotelli & Graves, 1996).

---

[15]That should be the case for extinction slopes and robustness, which measures the response of one level to extinctions in the other. But is difficult to see why the cluster coefficient for the higher level should be correlated with togetherness in the lower. *Post hoc*, it is always possible to find a reason, but *a priori* this is not expected.

[16]We could similarly say that there is a substantial redundancy in network indices, evident from the analysis where we condense 92% of variation in 40 odd indices onto six axes.

[17]Of the many, many biases that can creep into scientific explorations, this is one. We could call it the "parsimony bias" as a special case of the "selection bias" (Shermer, 2012).

In ecology, null models are common only in some fields, particularly in biogeography (Gotelli & Graves, 1996; Hausdorf & Hennig, 2007), but also in network analyses (Dormann *et al.*, 2009; Joppa *et al.*, 2009; Blüthgen *et al.*, 2008; Vázquez & Aizen, 2006, 2003; Vázquez *et al.*, 2009). With respect to particular bipartite indices, some studies rejected the current nestedness paradigm using abundance-based null models, for observed (Kallimanis *et al.*, 2009; Moore & Swihart, 2007; Santamaría & Rodríguez-Gironés, 2007), as well as for simulated networks (Krishna *et al.*, 2008).

Null models extend much beyond ecology and were probably first used in physics. Latapy *et al.* (2008) use them to investigate degree distributions in non-ecological bipartite networks. Using another network example, the module detection algorithm proposed by Newman & Girvan (2004) also uses a null model to define a "group" (or module or community) within a network: there are more links within than between groups. The null model then is a random network with as many links between as within groups (Guimerà *et al.*, 2005). In its quantitative version, the null model is constructed from proportionally probable interactions by differently abundant participants (Barber *et al.*, 2004). The specific null model used above is underlying most current implementations of contingency table tests such as χ^2 or Fisher's signed rank test (Patefield, 1981).

In conclusion, null models are established approaches in physics as well as ecology to correct for statistical artefacts and to establish an expectation in the absence of the hypothesised structuring mechanism.

6.2 *Justifying conservative null models*

The interactions observed in a network are the result of a dynamic interaction between species at two levels. If we use null models to represent the outcome of these interactions (the abundances of the participants), we seem to be over-correcting. How can we possibly find a pattern, if we use this pattern as a null model? Is an abundance-based null model not a circular argument? Here I argue when it is not, and if circularity would sneak in, why it would still be better to over-correct. I shall focus on pollination networks, and every network analyst has to decide in how far this reasoning can be applied to his/her system.

Plant persistence in a site depends to some extend on them being pollinated, and pollinator population dynamics is affected by the amount of nectar and pollen they collect from the flowers they visit. However, plant growth and population dynamics are also affected by nutrient and light availability, save sites for seed germination, herbivory and fungal pathogens, mycorrhisation and environmental disturbances; and similar constraints exist for pollinators. It is thus difficult, if not impossible, to say how much of the observed abundance of a species (plant or pollinator) is caused by the specific plant-pollinator interaction and hence the structure of the network. To the extent that abundances are determined by the pollination interaction we may indeed introduce collinearity. To date, there are no data to estimate the proportion of population growth controlled by mutualistic interactions of either plants or pollinators. We can only guess based on observations such as strong nest-site limitation in solitary bees (Steffan-Dewenter & Schiele, 2008), relatively high parasitism rates of pollinators (Klein *et al.*, 2002), strong nutrient limitations of plant population dynamics (Ghazoul, 2005) and grazing pressure (Crawley, 1987; de Mazancourt & Loreau, 2000) that they are probably not dominating population dynamics. On the other hand, clear (but rare) examples of co-evolution indicate that such a strong mutual dependence may indeed occur (Waser *et al.*, 1996; Waser & Ollerton, 2006).

Secondly, the observed interactions are not necessarily reflecting abundance of flowers or pollinators, but rather their attractiveness (e.g. due to scent, colouration or nectar production) and activity (e.g. daily period of foraging, phenology through the season, temperature-dependence of foraging activity), respectively. Hence by using observed sums of observed interactions, one does not correct for abundance, but for attractiveness and activity, respectively.

Third, the null model uses marginal totals, i.e. summed across all links of a species. If a pollinator was specialised on a single plant species, the null model would scatter these interactions across all and hence correctly identify a miss-match between observed and null

model. If, on the other hand, a pollinator was generalised, then the scattering of interactions across all plant species would also yield a similar picture and generalisation would correctly be inferred.

Finally, even if the null model used would introduce some amount of circularity and thus "over-correction", we have to balance this against "over-detection". Finding specialisation in an uncorrected approach will incur high levels of type I error (i.e. detecting a pattern that is actually not there). A null model insures against this type of error. We can thus be sure that a pattern that "survives" the null model test is no statistical artefact. Since it has been shown repeatedly that sampling intensity and "natural" differences in abundance will cause such artefacts (Dormann *et al.*, 2009; Blüthgen, 2010; Joppa *et al.*, 2009; Blüthgen *et al.*, 2008), they must be addressed. Ignoring them will lead to misinterpretation and over-reporting of spurious network structure. After correction for expectation based on abundances, we can start understanding ecology (Vázquez *et al.*, 2007).

In conclusion, circularity is unlikely to substantially impair null models for pollination networks. The risk of reporting non-existent network structure and further speculation of network stability due to this spurious network structure is a problem that requires a correction, even if circularity was present.

6.3 Using null models to test for significant tests in data

Once you have settled on a null model, there are fundamentally two different approaches to use such null models in statistical significance testing: corrected indices and null modelling the entire analysis. Let us look at them in turn, starting with the seemingly easier option.

Corrected indices and *z*-scores Imagine we computed the index I for a network. We now want to know whether this value is anything special, given the abundances of the species.[18] So we build, say, 1000 null models[19] and compute our index I for each of them. We can visualise the distribution of null-model I-values relative to our observed index value (Dormann *et al.*, 2009).

```
> data(Safariland)
> Iobs <- nestednodf(Safariland)$statistic[3]
> nulls <- nullmodel(web=Safariland, N=1000, method='r2d') # takes a while!
> Inulls <- sapply(nulls, function(x) nestednodf(x)$statistic[3])
> plot(density(Inulls), xlim=c(0, 100), lwd=2, main="NODF")
> abline(v=Iobs, col="red", lwd=2)
```

All that is fine for a single network, but no option if we want to analyse dozens or hundreds of networks. We thus have to summarise this figure in a value. The simplest, most obvious but generally not best solution would be to subtract the null model mean from the observed, so that $I_{\text{corrected}} = \Delta I = I_{\text{observed}} - \bar{I}_{\text{nulls}}$. The reason why this ΔI is not ideal is that the null model distribution is likely to vary from network to network. Thus, a difference of, say, 20 may be a lot for pointy distributed null models such as the one in Fig. 7, but only little for null model values spreading over the entire *x*-axis.

The better, and more established approach, would be to compute *z*-scores (= standard scores or normal scores) for each network, which express the difference in terms of standard deviations of the null distribution:

$$z_I = \frac{I_{\text{observed}} - \bar{I}_{\text{nulls}}}{\sigma_{I_{\text{nulls}}}}.$$

We can now analyse the *z*-scores instead of the original I_{obs}-values.

Z-scores have one major disadvantage for several of the network indices presented earlier: the standard deviation becomes an unsuitable measure of spread as the values approach an

---

[18]Thereby we justify the use of the Patefield algorithm as null model. But the approach is independent of which null model we use.

[19]E.g. using nulls <- nullmodel(web=Safariland, N=1000, method='r2d')
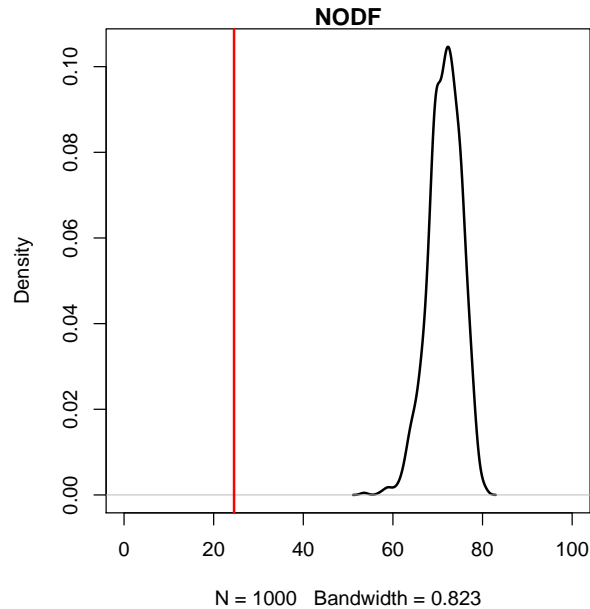
NODF

Figure 7: Observed and null-modelled nestedness (computed as NODF) for the network 'Safariland'. Note that values of 100 indicate perfect nestedness. Thus, null models are much *less* nested than the observed network. (That is typically the case (Dormann et al. 2009), although often no null models are computed for comparison, making interpretation challenging.)

upper or lower bound. Imagine our network index I is bound between 0 and 1 (as many are). If the null models have values above, say, 0.9, the upper bound is so close that the distribution will be skewed and the standard deviation biased too low. This may lead to inflated z-scores. So whenever you observe values close to either bound, beware of distorted z-scores.

Null-model the entire analysis   The alternative approach is to carry out the intended analysis on the observed index values I and then, in a second step, repeat it with one realisation of a null model per network. Next, repeat this second step several thousand times (for good measure) and store the statistics you are interested in (say F-values in an ANOVA or slopes in a regression). Instead of using the p-values from the analysis of the observed values, compare observed and null-modelled statistics and count the proportion of values exceeding the observed and use those as p-value. To anyone with any experience in resampling analysis or bootstrapping this is standard procedure (Efron & Tibshirani, 1993; Manly, 1997).

As an example, we can use a question addressed in Vázquez & Simberloff (2003), where the authors investigate whether cattle grazing affects the network structure of pollination networks in four replicated sites in Argentina. As response we haphazardly choose linkage density.

```
> weblist <- lapply(c("Safariland", "vazarr", "vazllao", "vazcer", "vazmasc",
+                     "vazmasnc", "vazquec", "vazquenc"), get)
> # Write a function to compute the desired statistic, e.g. the difference
> # between grazed and ungrazed:
> meandiff <- function(webs){
+     obs <- sapply(webs, networklevel, index="linkage density")
+     mean(obs[1:4]) - mean(obs[5:8])
+ }
> (observed <- meandiff(weblist))

[1] -0.2481145
```

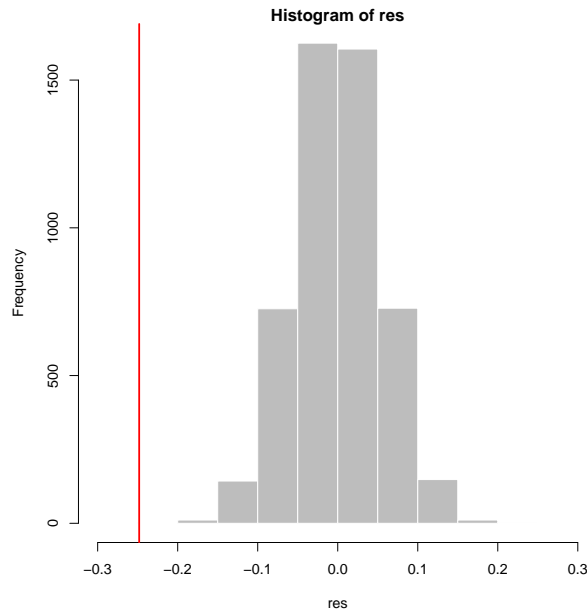Now generate a null model and repeat:

Figure 8: Distribution of mean differences in linkage density of pollination networks in grazed and ungrazed meadows, correcting for differences in species numbers and observation intensity through the use of null models ($N = 5000$). Observed difference is shown as vertical line. The observed difference is significantly ($P < 0.001$) different from null model expectations.

```
> nulllist <- lapply(weblist, nullmodel, N=1, method="r2d")
> meandiff(weblist)
```

```
[1] -0.2481145
```

Repeat this procedure, say, 5000 times:[20]

```
> res <- 1:5000
> for (i in 1:5000){ # takes a few minutes !!
+     nulllist <- sapply(weblist, nullmodel, N=1, method="r2d")
+     res[i] <- meandiff(nulllist)
+ }
```

Finally, we can depict the results in a histogram (Fig. 8), with observed as vertical line, and compute the p-value based on the 5000 null models:

```
> hist(res, xlim=c(-0.3, 0.3), border="white", col="grey")
> abline(v=observed, col="red", lwd=2)
> # compute p-value as proportion smaller or than observed
> sum(res < observed)/length(res) * 2 # *2 for two-tailed test
```

The idea here is to compute a statistic of interest, in this case the mean difference between some network index for the two treatments, and then use the null model to compute expectations. In the above example, we would apparently expect no difference (which is intuitive); additionally we also get an idea of how much variability we can expect (the distribution of the null model-based mean differences in linkage density). Thus, in this example, the difference in linkage density of pollination networks from grazed *vs* ungrazed pastures is highly significant ($p < 0.001$).

---

[20]For didactic purposes, we use an inelegant but easy to understand `for`-loop here. In productive mode we would instead use `sapply` or `replicate`, which would make the code more compact, but in this case not faster.
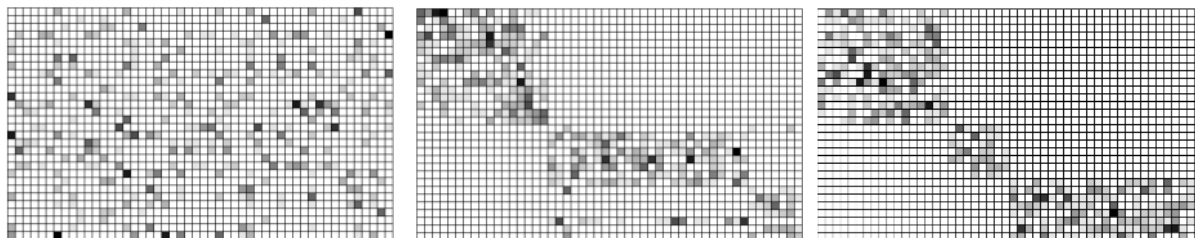
Figure 9: A simulated 3-compartment network in random sequence (left), as sorted by a correspondence analysis (centre) and by the modularity algorithm with default settings (right).

7 Modularity

Aggregated sets of interacting species are called 'modules'. Their defining feature is that *within*-module interactions are more prevalent than *between*-module interactions (Newman, 2003; Newman & Girvan, 2004; Fortunato, 2010). In other words, modules are link-rich clusters of species in a community. What causes such modules and whether they actually teach us something is discussed at length by Dormann *et al.* (2017).

There are several algorithms for *one-mode* networks, particularly for binary one-mode networks, such as the Louvain algorithm, the infomap or Clauset *et al.* (2004)'s "fast greedy" algorithm. These algorithms vary substantially in their robustness, in the sense that small changes in the network may yield very different modules, as compared by Policastro *et al.* (2021). That paper also expores ways to test for significance of modularity, based on null model simulations.

The package **bipartite** offers an algorithm (QuaBiMo, described in technical detail in Dormann & Strauß, 2014) to detect modules in bipartite networks, taking into account the quantitative nature of links. The algorithm has become outdated after a vastly improved approach was published by Beckett (2016), which is also now the default algorithm used in **bipartite**'s `computeModules` function.

Old-school modularity was identified using correspondence analysis, which, however, will not be able to identify modules sufficiently well, even if modules are actually compartments (i.e. perfectly separated: Fig. 9 left, centre). The algorithm used in **bipartite** can do so, at least in principle (Fig. 9 right).[21]

QuaBiMo can be invoked recursively (we are working on doing the same for Beckett), searching for modules within modules (Fig. 10, bottom). While such nested modules become ever smaller and are thus ever faster to detect, there are plenty of them and hence nesting will typically dramatically prolong computing time during the search for patterns (Memmott, 1999).

Modularity Q is likely to be correlated with other network metric, as specialisation of module members is the prime reason for the existence of modules. Across the (then) 22 quantitative pollination networks of the NCEAS "interaction webs" data base, Q was evidently highly positively correlated with complementary specialisation H_2' (Fig. 11). Ecologically, the correlation with specialisation makes good sense. Modules only exist because some species do not interact with some others, i.e. because they are specialised. An overall low degree of specialisation is equivalent to random interactions, which will yield no modules.

Furthermore, the absolute value of Q is, like all network indices (Dormann *et al.*, 2009), dependent on network size (i.e. the number of species) as well as the number of links and the total number of interactions observed (Thébault, 2013). We would thus recommend a null model comparison (Vázquez & Aizen, 2003; Blüthgen *et al.*, 2008; Dormann *et al.*, 2009) to correct the observed value of Q by null model expectation (e.g. by standardising them to *z*-

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[21]As a note on terminology: If modules are perfectly separated, with no species interacting with species in another module, they are called "compartments" and will be visible as clearly separated blocks of interacting species. It is relatively straightforward to implement a recursive compartment detection function, but compartments are too much black-and-white compared to modules and often only occur in ecological networks because sampling was rather incomplete or very different habitats were sampled.
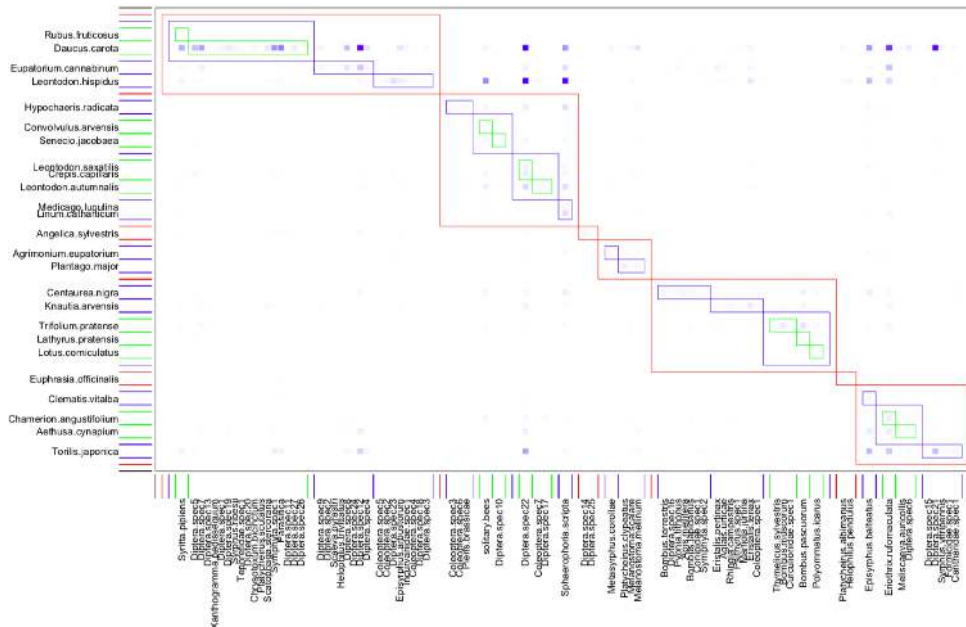
Figure 10: Interaction matrix featuring nested modules for the data of Memmott (1999). Darker squares indicate more observed interactions. Coloured boxes delineate the seven modules. (Note that results may vary between runs.) In the central module yellow Asteraceae feature heavily, while a possible ecological cause pattern for the other modules is less apparent.
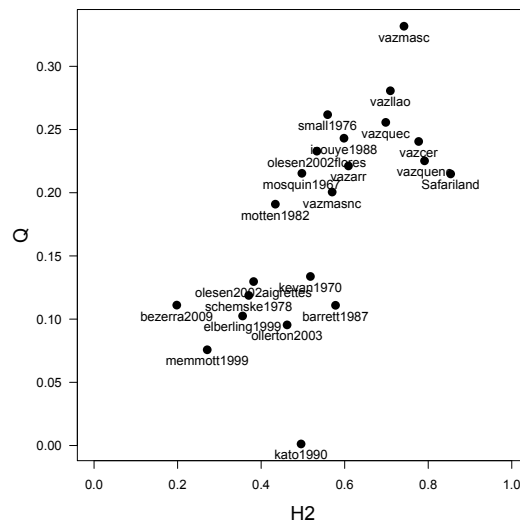

Figure 11: Modularity (Q) is highly correlated with specialisation H_2' across 22 pollination networks. Names refer to network data sets in **bipartite**.

scores: $z_Q = \frac{Q_{\text{observed}} - \overline{Q}_{\text{null}}}{\sigma_{Q_{\text{null}}}}$). Modularity Q is in itself not an index of an ecological feature. It is merely a measure of how well links and interactions can be separated into different modules. Large networks, with many species and links, allow for more combinations of species-in-modules, leading to higher values of Q, as Allesina & Pascual (2009) pointed out for any grouping algorithm.

7.1 Using modularity to identifying species with important roles in the network

Guimerà *et al.* (2005) and Olesen *et al.* (2007) propose to compute standardised connection and participation values, called c and z, for each species to describe their role in networks, where c refers to the between-modules connectivity (called "participation coefficient" P: Guimerà *et al.*, 2005) and z refers to within-module degrees. Originally, both are computed based on
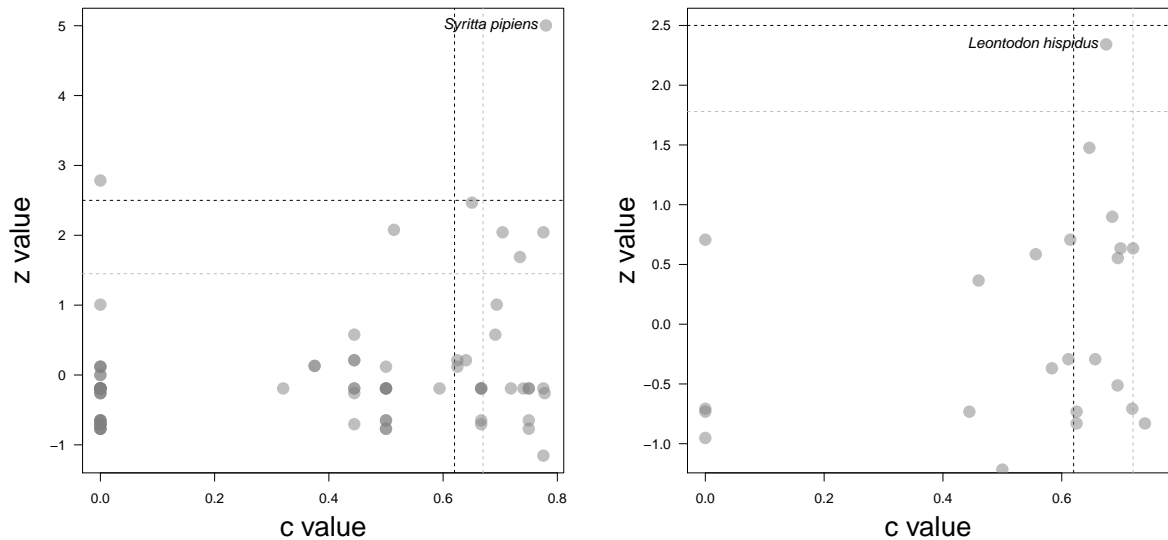
Figure 12: Connection (*c*) and participation (*z*) values for pollinators (left) and plants (right) in the network of Memmott (1999). Dashed black lines indicate critical values according to Olesen et al. (2007), those in grey 95% quantiles from 100 null models (see text).

the number of links, but a weighted version based on species strength is implemented, too. Guimerà *et al.* (2005) suggest critical values (only for the binary approach) of *c* and *z* of 0.625 and 2.5, respectively. Species exceeding both of these values are called "hubs" because they link different modules, combining high between- with high within-module connectivity.

In the case of the pollination network of Fig. 10, *c*-values range between 0 and 0.78 (with 23 of 79 pollinators and 13 of 25 plant species exceeding the threshold of 0.625); *z*-values range between −1.21 and 5.00 (with two pollinators but no plant species exceeding the value of 2.5: Fig. 12). Put together, only the syrphid *Syritta pipiens* (and hawkbit *Leontodon hispidus* almost) exceeded both thresholds and would thus be called a "hub species". As can be seen in Fig. 10, this syrphid is relatively rare but clearly not randomly distributed over the six modules, thus linking three highest-level modules. In contrast, *Leontodon hispidus* is a common plant species, visited by many different pollinators, and it actually links almost all modules.

To objectively define this threshold one could run null models of the original network and employ 95% quantiles as critical *c*- and *z*-values. For the pollinators in the network of Fig. 10 these would be 0.67 (±0.039) and 1.45 (±0.220), respectively, based on 100 null models (for plants: $c_{\text{critical}} = 0.72 \pm 0.036$ and $z_{\text{critical}} = 1.78 \pm 0.297$; Fig. 12 left). While for plant species this has little effect (except for moving *Leontodon hispidus* across the threshold), three more pollinators would become hub species (the common hoverfly *Episyrphus balteatus*, the tachinid fly *Eriothrix rufomaculata* and undetermined fly "Diptera spec.22").

8 Analyses beyond **bipartite**

Of course, there are many different packages that analyse one or the other aspect of networks, and some even of bipartite networks (listed in the introduction of this vignette). Some of them we find particularly interesting or useful or innovative, and here we quickly show some of them at work.

8.1 Plotting pretty bipartites

The plotting functions provided by **bipartite** are somewhat rudimentary. We're happy with them, and they are surprisingly flexible already, but our graphical skills (and intentions) are limited. Other people have developed plotting functions/solutions, which we shall briefly

(and probably incompletely) show here.[22]

8.1.1 bipartiteD3

8.1.2 igraph

https://kateto.net/netscix2016.html; https://rpubs.com/pjmurphy/317838; https://igraph.org/r/doc/layout_as_bipartite.html

8.1.3 ggbipart

There is the package **ggbipart**, on github.[23]

```
> library(devtools)
> install_github(rep="pedroj/bipartite_plots")
```

8.1.4 multigraph

Plot several bipartite layers into one graph: see https://stackoverflow.com/questions/31366066/how-to-plot-a-bipartite-graph-in-r

8.2 Analysing the structure of bipartite networks

[to be continued ...]

There are a range of packages that aim at identifying structure within networks, be it clusters/modules/compartments of a larger subset of interactions, or specific motifs of only few links. It is almost impossible to keep up with these developments, so here are just a few pointers to such packages: **bmotif**, **dynsbm** and **infomapecology**.

8.3 Multi-layer networks

This somewhat cryptic term refers to networks that are defined by different types of links, for example because links change over time (dynamic links) or because they depend on other networks (Pilosof *et al.*, 2017). The mathematical description and analysis of such multilayer networks can be rather complex (Aleta & Moreno, 2019), and in ecology typically only relatively simple types of multilayer networks are investigated; probably the most common being multi-level networks are temporally or spatially resolved networks.

While statistically and mathematically a lot of things are conceivable, few ideas actually resonate with ecologists (i.e. in application). One idea is that networks evolve and hence change dynamically. Another is that any observed bipartite network is actually embedded in many other networks, e.g. a plant-pollinator-network may continue "into the ground" as plant-mycorrhiza networks, "into the sky" as pollinator-parasite network, and "sideways" as plant-herbivore network (Pocock *et al.*, 2012).

Currently, **bipartite** does not support any such analysis (apart from a pathetic function `npartite` and `plotweb2` for plotting stacked bipartite networks).

Packages such as **robber** address some of the challenges of intersecting multiple bipartite networks.

Conclusions

The analysis of bipartite networks has seen a recent explosion of applications in ecology. The *R*-package **bipartite** aims at providing a user-friendly set of function to aid the visualisation and analysis of such networks. This vignette hopefully illustrated some of the challenges and solutions to such analyses. The main take-home-message it aims to convey is that there are

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[22]Partly based on this question on SO: https://stackoverflow.com/questions/31366066/how-to-plot-a-bipartite-graph-in-r

[23]See also https://pedroj.github.io/bipartite_plots/ for more code examples.

considerable interpretational strings attached, and that the analysis of bipartite networks is not as straightforward as one might have initially hoped.

Feedback, improvements, corrections and additions are welcome!

The Rnw source of this document is at `https://github.com/biometry/bipartite/bipartite/vignettes/Intro2bipartite.Rnw`.

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