

***foodweb*: an open-source program for the visualisation and analysis of compilations of
complex food webs**

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Abstract

Food webs represent the trophic interactions between consumers and resources as a ‘map’ of trophic links, and can meaningfully quantify ecological processes. As the study of food webs evolves so does the need for analytical software. Several programs for the analysis of food web structure exist. Researchers are likely to profit most from programs that calculate the largest number of commonly used parameters, produce output in standard food web ecology language, can be readily modified and updated by the scientific community, and can be used free of charge. Here we have developed a program for the analysis of food webs that calculates ten commonly used basic measures of food web structure, employs food web language in the code and output, translates between a few common food web formats, can handle networks consisting of multiple levels, and can automate the analysis for a large number of webs. The program produces 3-dimensional graphs of high quality. *foodweb* is provided free of charge and is embedded inside a commonly used statistical tool (R Statistical Package). The rationale for calculation of parameters and for producing the plots is provided here, along with the installation file.

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1. Introduction

Food webs represent the trophic interactions between consumers and resources as a ‘map’ of trophic links. The first of these maps was described by Camerano (1880) followed by a detailed depiction of the food web of a North American lake (Forbes, 1887). A number of descriptions of food webs followed from across terrestrial and aquatic ecosystems, including an early detailed food web from Bear Island (Summerhayes and Elton, 1923), as well as more generalized diagrams of energy flow (Lindeman, 1942). The development of food web research has been described in a number of reviews (Dunne, 2006; Pimm et al., 1991). An initial emphasis on the stability of food webs (e.g. May, 1972), was replaced by the search for general patterns of food web attributes (e.g. Pimm et al., 1991), and the environmental correlates of those attributes (e.g. Briand, 1983). This led to the compilation of the first food web databases (Cohen, 1989), growing to a recent update including over 200 published food webs (Cohen, 2010). The variable quality of early data led to considerable criticism of food web ecology (Paine, 1988a; Polis, 1991; Strong, 1988), and an ongoing effort to describe food webs which were taxonomically detailed, inclusive of all groups, and took a rigorous approach to detecting trophic links (Dunne, 2006).

Topological maps of feeding interactions in food webs have been widely criticized due to their low levels of taxonomic resolution and the lack of standard criteria for collection, description and attribution of trophic links (e.g. Cohen et al., 1993; Paine, 1988b). Those criticisms are valid, and caution must be applied in interpreting patterns observed in topological food webs. However studies using well resolved food webs have shown that they can meaningfully quantify ecological processes such as invasion, and changes in productivity and disturbance (Hall and Raffaelli, 1991; Martinez, 1991; Thompson and Townsend, 2005; Woodward and Hildrew,

2001). Other studies have shown a relatively high tolerance to the abstraction of food webs even into relatively simple binary matrices (Dunne, 2006). Food webs provide additional information that supplements information on patterns of biodiversity, and represents a simple approach, albeit an imperfect one, to integrating fluxes of energy with information on species richness.

A suite of food web attributes have emerged and become well established in the literature and have clear biological interpretations (Table 1). These include: measures of diversity overall and in different functional or trophic groups, measures of density of trophic links (connectance, linkage density), measures of web shape (prey:predator ratios) and vertical dimensions (chain length). More recently other network attributes have been applied to the analysis of food webs (e.g. Chen et al., 2008), although their relationship to biological parameters is yet to be well established.

As the study of food webs evolves so does the need for analytical software. A number of programs are available for the calculation of food web attributes, each with relative strengths and weaknesses (Table 2). Researchers are likely to profit most from programs that calculate the largest number of commonly used parameters, produce output in standard food web ecology language, produce useful graphs, can be readily modified and updated by the scientific community, and can be used free of charge. This combination of traits is not currently available in the analytical software we have surveyed.

Table 1. Food web attributes and their biological meaning.

Food web attribute	Biological meaning
Taxa richness (S)	Number of biological taxa (nodes) in the food web.
Number of trophic links (L)	Number of links (edges) between taxa.
Link density ($=L/S$)	Number of links per taxa measure of dietary specialisation across the food web.
Connectance (C) ($=L/(S^2)$)	Proportion of potential trophic links that do occur. An indication of degree of inter-connectivity in a food web, typically 0.05-0.15.
Number of omnivores	Number of species that feed on more than one trophic level.
Mean chain length	Average number of links found in a food chain across a food web. Food chains lengthen with higher energy supply.
Maximum chain length	The maximum number of links found in any food chain in a food web. Food chains lengthen with higher energy supply.
Number of basal taxa (b)	The number of taxa which do not consume any other taxa.
Number of intermediate taxa (i)	The number of taxa which are both consumed by, and consume, other taxa.
Number of top taxa (t)	The number of taxa which are not consumed by any other taxa.
Prey:predator ratio ($= b+i/t+i$)	A measure of food web 'shape'; high values are more triangular, low values are more 'square' in shape. When <1 the food web has an inverted structure that may indicate instability.

Table 2. Food web analysis tools: capabilities and limitations.

	License required	Translates formats	Point-&-click interface	3D imaging capabilities	Multiple trophic levels	Food web specific	Open-source code	All indices in Table 1 calculated	Automated reading
Pajek		√	√		√				
UCINET	√		√		√				
Bipartite						√	√		
Network 3D	√		√	√	√	√		√	
NetIndices					√	√	√		
<i>food web</i>		√		√	√	√	√		√

2. The *foodweb* package for R: description of the analytical approach

The *foodweb* package for R Statistical Software was created for the three-dimensional representation of trophic links in complex food webs, and for the calculation of frequently used parameters of network structure from a large number of food webs. The program performs calculations on symmetrical binary, predator-prey matrices. In these matrices, all species present in the food web must be represented, including basal resources. The values along the column of a given species represent the presence (value = 1) or absence (value = 0) of a feeding link.

foodweb can run iteratively through the network calculations for many food webs, and add the output as rows to a single, comma delimited file (.csv). It can also be used on single food webs. Most of the calculations are performed by the function “calculate.metrics” (details in section 2.2.1). The user does not interact directly with this function but rather it is called via the following parent functions: “analyse.single” (for analysing single food webs), “analyse.sequence” (for analysing multiple food webs whose names follow a sequence, e.g. Web1, Web2, Web 3) and “analyse.list” (for analyzing multiple food webs, whose names are provided in a list). Via these parent functions, the user specifies the type of output required (details in section 2.2 and in the functions’ help files). Details of the workflow for the calculation of network parameters are summarised in Figure 1 and explained in sections 2.1 (preparatory work) and 2.2 (calculations).

2.1. Preparatory work

2.1.1. Asymmetrical predator-prey matrices

To accommodate for asymmetrical predator-prey matrices, the function “asym2sym” was written. It detects whether all species in the rows are present in the columns and adds all-zero

columns to the end of the matrix for species that are not represented. Each column label corresponds to the species name. It then performs the equivalent process for rows, i.e., detects whether species in the columns are absent from the rows and adds an all-zero row for the missing species. Finally, the matrix is ordered such that column 1 represents the same species as row 1. This matrix can be generated as output to a .csv file if needed. The network parameter calculations that follow do not require that this file be generated in order to proceed.

Preparatory work



Calculations

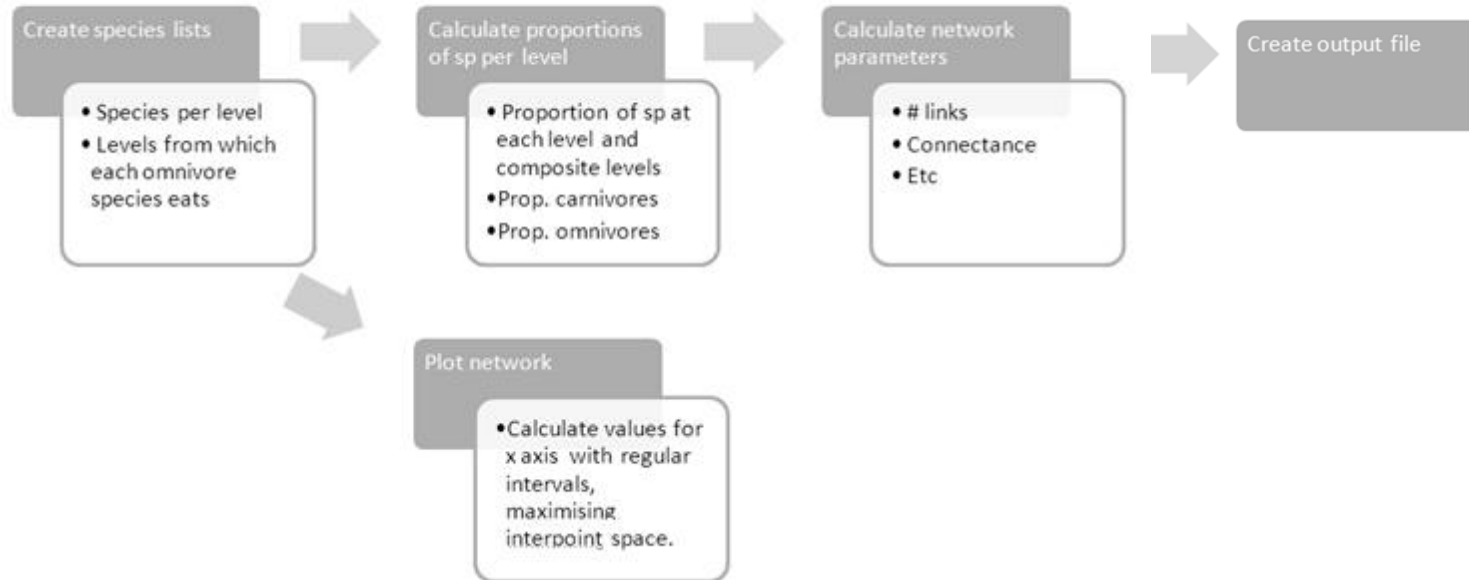


Figure 1. Workflow for the *food web* package.

2.1.2. Matrix format to list format translation

Some network analysis software (e.g. Pajek (Batagelj and Mrvar, 1998)) require input files in the form of a list of the links between pairs of species. The function “mat.2.list” can be used to convert symmetrical binary matrices into lists.

2.1.3. Asymmetrical matrix to symmetrical matrix

Asymmetrical matrices can be translated into symmetrical format using the *food web* package. This is done via the “analyse.single”, “analyse.list” and “analyse.seq” functions, by specifying matrix= “TRUE” in the function arguments.

2.2. Calculations

2.2.1. The calculate.metrics function

Trophic levels

Trophic levels of species are stored in a row at the bottom of the food web matrix that has been imported. The assignment of trophic levels from a binary matrix proceeds as follows. Trophic level zero is assigned to basal species, that is, any species that does not consume any other species (i.e. has an all-zero column). After this, an iterative process begins, where any species that consumes level zero species is assigned to level one. Then, any species consuming species on level one is assigned the level two, and so on up the food chain. Once the iterative process finishes, a species will have been assigned a trophic level that is one above the highest level of any of the species that it consumes. As a default, a maximum of eight levels are considered possible in this iterative process in order to enhance performance. This can be changed in the functions argument “maxlevels”. Decreasing the maximum may increase speed of calculation.

The number of trophic levels in the food web is calculated as the number of unique values in the row containing the species' trophic levels. This output is used by the network plotting function.

Omnivory and trophic position

For species that feed on different trophic levels (omnivores), trophic position is calculated. This is done by creating a duplicate of the original food web matrix, called "by.levels", where the trophic level of the prey is represented. The trophic position of an omnivorous species is then recorded as the average of the values in its column. This calculation is the equivalent of the 'prey-averaged' technique of (Williams and Martinez, 2004). An omnivore is therefore defined after Thompson *et al.* (2007) as any species with a non-integer trophic position. Trophic position is stored in a second, additional row in the original food web matrix. A table showing each omnivorous species in the food web as well as the species it feeds on is created at this point and the number of rows in this table is taken as the number of omnivores in the food web. This table can be used to verify that the calculations are being made correctly. Specifying `omn="TRUE"` in the function `"analyse.single"` will generate the table as output in a file called `Omnivores.csv` in the current working directory. Specifying `positions="TRUE"` will generate a table specifying the trophic position of each of the species in the food web. The file name is `Trophic positions.csv`.

Intraguild predation

Intraguild predation (termed cannibalism within the *food web* package) is detected when a species consumes species at its same trophic level. This is recorded in a third additional row to the imported food web. The number of species that engage in intraguild predation is calculated. A table specifying the trophic position at which intraguild predation occurs is generated, and can be used to verify that the calculations are being made correctly. Specifying `cann="TRUE"` in the function `"analyse.single"` will generate the table as output in a file called `Cannibals.csv`.

Fraction of basal, herbivorous, intermediate and top species

Fractions are calculated relative to the total number of species in the food web. Basal species are those in level zero; herbivorous: those at level 1, top: those at the highest level (i.e. taxa which are not consumed by any other taxa included in the food web), intermediate: those that are neither basal nor top (after Pimm, 1982).

Connectance, linkage density and predator:prey ratios

Total number of links is calculated as the sum of all cells in the original food web matrix. Connectance (Pimm, 1982) is that number divided by the square of the total number of species. The calculation used here takes the number of links found to occur as a proportion of all links, assuming that all taxa can feed on all other taxa. As such it differs from the calculation used by Jaarsma *et al.* (1998) which modifies the connectance formula to ignore links which are considered impossible (e.g. basal taxa such as plants feeding on predators). Linkage density (Pimm, 1982) is calculated by dividing the total number of links by the number of species. The predator prey ratio (Hall and Raffaelli, 1991) is calculated by dividing the total number of species that are either intermediate or basal by the total number that are either basal or intermediate.

2.3. Network plots

The function “plotweb” can be employed by the user to generate a 3-dimensional food web plot. It requires that the function “analyse.single” be used first to load, check and analyse the food web matrix. Via “plotweb” the user can specify colours and radii for the trophic levels. Any one of the 657 colours named in the R colour palette can be used in the plot (for options type “colours()” in R). If radii are not provided, these will be calculated by *food web* on the basis of species richness in the trophic level.

The function “plotweb” checks that users have provided the adequate number of colours and radii (where these have been supplied), and checks that there is food web information available for the creation of the plot. The plot is created by a call to the function `create.plot()`. The function creates a matrix containing x, y and z coordinates for all species in the food web. For a given species, the position on the y axis is its trophic level. Positions on the x and z axis are calculated such that species’ spheres are equally spaced along a circumference of radius r , which is to be specified by the user (or assigned by *foodweb* on the basis species richness in the trophic level). Equal spacing in the circumference is created by dividing the circle into as many sections as there are species in the guild. This is achieved by dividing the degrees spanned within the circumference (i.e. 360°) by the number of species in the trophic level (resulting angle is shown in Figure 2 as α). The coordinates of a point on the circumference are calculated on the basis of the radius of the circumference and the internal angle ($360^\circ/n$) created by the sectioning of the circle (Figure 2).

The coordinates are then used to plot spheres in three-dimensional space, using the package *rgl* (Adler and Murdoch, 2010) in the R Statistical Package (R Core Development Team, 2009). Trophic links (lines connecting spheres) are drawn for all pairs of species where a one was recorded in the original food web matrix. An example of the resulting plot can be seen in Figure 3.

2.4. Automated analysis of multiple food web files

foodweb can run iteratively through the preparatory formatting and network calculations for multiple food webs. This requires that (a) all the food web matrices be placed in a single, specified, directory folder, (b) the individual matrix files be named sequentially using a standardised prefix and extension file type (e.g. WEB1.dat, WEB2.dat, WEB3.dat or fw1.csv, fw2.csv, fw3.csv), and (c) the range of food web files to be analysed be specified (e.g. 1-3, 4-57).

A .csv file is generated containing values for all network parameters calculated for each of the food web matrices provided. Files containing the formatted matrices (i.e. symmetrical binary matrices, refer to section 2.1.1) can optionally be generated as output as well. Where matrices provided contain negative values, i.e. where matrices were incorrectly formatted, a Problem.csv file is generated as output in the current working directory. This file specifies the names of the matrices that were not analysed due to the presence of non-sensical data.

3. Software evaluation and testing

foodweb calculations were compared against manual calculations, using data from a symmetrical matrix from the moss-microarthropod food web (Perdomo *in prep*). The matrix is provided in the packages sample data and can be accessed via data(moss) when the package has been loaded. Verification of translation of asymmetrical matrices to symmetrical ones, and evaluation of automated reading capabilities were tested with the 213 files found in Ross Thompson's food web repository: GlobalWeb (Thompson unpublished). Plotting capabilities were tested with the moss food web (Figure 3). The tool "R CMD check" (implemented via DOS in Windows and

created by the R Core Development Team for checking add-on packages) found no errors in the package. “R CMD INSTALL” returns no errors and installs the package correctly.

4. Software availability

foodweb is provided free of charge, under a GNU General Public License, version 2 (<http://www.r-project.org/Licenses/GPL-2>). It is an add-on package for R Statistical Software (R Core Development Team, 2009) and requires the R add-on package “rgl” (Adler and Murdoch, 2010) for operation. The code is written in the R language. Packaging was carried out in Windows using the Rtools.

The installation file will be made available via the CRAN websites, maintained by the R Core Development Team (at <http://www.r-project.org/>). The installation file will also be available via the GlobalWeb foodweb repository website (in prep). Help files for each of the user functions are provided with the package. These specify the arguments required to produce a desired output from the functions. The first author was the principal developer of the package and is its maintainer. Emails regarding the package should be sent to giselle.perdomo@monash.edu and gisselle_p@yahoo.com.

Sample data is also provided with the package. It can be accessed by typing “data(moss)” in R when *foodweb* is loaded. A matrix by the name of “moss” is thereby loaded onto the user’s workspace. The matrix provided is a binary predator-prey food web matrix from a study of moss microarthropods (Perdomo *unpublished data*).

5. Conclusion

We have produced an analytical tool that facilitates the analysis of large numbers of food webs and produces high quality, customisable 3d graphs. Ten commonly-used metrics of food web structure can be calculated. Other metrics, such as those relating to food chain length, are currently being developed. The strength of this program lies not only in its current capabilities but also in the open-source nature of the code and the imbedding of it inside a commonly used, powerful, community-built statistical tool (R Statistical Package).

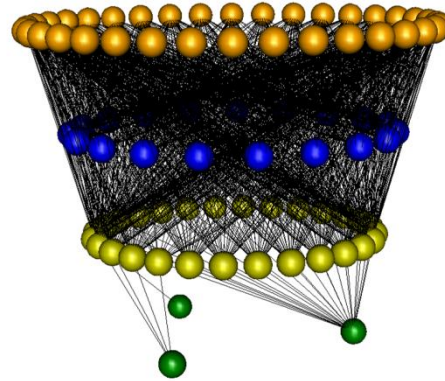


Figure 3. Three-dimensional food web network plot produced by the *food web* package. The food web matrix used to produce this plot is provided in the *food web* package (to access it type “data(moss)” in R when the *foodweb* package is loaded). The data was collected for a study of the moss-microarthropod food web (Perdomo *et al.*, in prep).

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7. Bibliography

- Adler, D., Murdoch, D., 2010. rgl: 3D visualization device system (OpenGL), R package version 0.89.
- Batagelj, V., Mrvar, A., 1998. Pajek: program for large network analysis. . Connections 21 47-57.
- Briand, F., 1983. Environmental-Control of Food Web Structure. Ecology 64(2) 253-263.
- Camerano, L., 1880. Dell'equilibrio dei viventi merc'e la reciproca distruzione. Atti della Reale Accademia della Scienze di Torino 15 393-414.
- Chen, H., Liu, W., Davis, A.J., Jordan, F., Hwang, M., Shao, K., 2008. Network position of hosts in food webs and their parasite diversity. Oikos 117 1847-1855.
- Cohen, J.E., 1989. Ecologists' Co-operative Web Bank (ECOWeB), Version 1.0 (machine-readable database). Rockefeller University, New York, p.
- Cohen, J.E., 2010. Ecologists' Co-Operative Web Bank. Version 1.1. The Rockefeller University, New York.

- Cohen, J.E., Beaver, R.A., Cousins, S.H., Deangelis, D.L., Goldwasser, L., Heong, K.L., Holt, R.D., Kohn, A.J., Lawton, J.H., Martinez, N., Omalley, R., Page, L.M., Patten, B.C., Pimm, S.L., Polis, G.A., Rejmanek, M., Schoener, T.W., Schoenly, K., Sprules, W.G., Teal, J.M., Ulanowicz, R.E., Warren, P.H., Wilbur, H.M., Yodzis, P., 1993. Improving Food Webs. *Ecology* 74(1) 252-258.
- Dunne, J.A., 2006. The network structure of food webs. *Ecological Networks: Linking Structure to Dynamics in Food Webs* 27-86.
- Forbes, S.A., 1887. The lake as a microcosm. *Bulletin of the Peoria Scientific Association* 77-87.
- Hall, S.J., Raffaelli, D., 1991. Food-Web Patterns - Lessons from a Species-Rich Web. *Journal of Animal Ecology* 60(3) 823-842.
- Jaarsma, N.G., De Boer, S.M., Townsend, C.R., Thompson, R.M., Edwards, E.D., 1998. Characterising food-webs in two New Zealand streams. *New Zealand Journal of Marine and Freshwater Research* 32(2) 271-286.
- Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23(4) 399-418.
- Martinez, N.D., 1991. Artifacts or attributes - effects of resolution on the Little-Rock Lake food web. *Ecological Monographs* 61(4) 367-392.
- May, R.M., 1972. Will a large complex system be stable? *Nature* 238(5364) 413-&.
- Paine, R.T., 1988a. Food Webs - Road Maps of Interactions or Grist for Theoretical Development. *Ecology* 69 1648-1654.
- Paine, R.T., 1988b. Food Webs - Road Maps of Interactions or Grist for Theoretical Development. *Ecology* 69(6) 1648-1654.
- Pimm, S.L., 1982. Food webs. Chapman and Hall, London.

- Pimm, S.L., Lawton, J.H., Cohen, J.E., 1991. Food Web Patterns and Their Consequences. *Nature* 350(6320) 669-674.
- Polis, G.A., 1991. Complex trophic interactions in deserts - an empirical critique of food-web theory. *American Naturalist* 138 123-155.
- Strong, D.R., 1988. Food Web Theory - a Ladder for Picking Strawberries. *Ecology* 69 1647-1647.
- Summerhayes, V.S., Elton, C.S., 1923. Contributions to the ecology of Spitsbergen and Bear Island. *Journal of Ecology* 11 214-287.
- Thompson, R.M., Hemberg, M., Starzomski, B.M., Shurin, J.B., 2007. Trophic levels and trophic tangles: The prevalence of omnivory in real food webs. *Ecology* 88(3) 612-617.
- Thompson, R.M., Townsend, C.R., 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108(1) 137-148.
- Williams, R.J., Martinez, N.D., 2004. Limits to trophic levels and omnivory in complex food webs: Theory and data. *American Naturalist* 163(3) 458-468.
- Woodward, G., Hildrew, A.G., 2001. Invasion of a stream food web by a new top predator. *Journal of Animal Ecology* 70(2) 273-288.