fluxweb: a package to easily estimate energy fluxes in food webs

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Abstract

- Understanding how changes in biodiversity will impact the stability and functioning of ecosystems is a central challenge in ecology. Food-web approaches have been advocated to link community composition with ecosystem functioning by describing the fluxes of energy among species

or trophic groups. However, estimating such fluxes remains problematic because current methods become unmanageable as network complexity increases.

- We developed a generalisation of the food web energetic framework [1] which merges allometric theory [2] with food web energetics methods [3, 4]. Jointly, we provide theoretical and practical guidelines to use the *fluxweb* R package (available on CRAN). Provided with an interaction matrix and easily obtainable organism-level data (i.e. body masses and assimilation efficiencies), the model estimates energy fluxes in a top-down manner assuming system equilibrium; each nodes' losses (consumption and physiological) balances its consumptive gains. Physiological losses (e.g. metabolic or death rates) may be directly measured or estimated using allometric relationships based on the metabolic theory of ecology, and losses and gains due to predation are a function of ecological efficiencies that describe the proportion of energy that is used for biomass production.

- The primary output is a matrix of fluxes among the nodes of the food web. These fluxes can be used to describe the role of a species, a function of interest (e.g. predation; total fluxes to predators), multiple functions, or total energy flux (system throughflow or multitrophic functioning). Additionally, the package includes functions to calculate network stability based on the Jacobian matrix, providing insight into how resilient the network is to small perturbations at steady state.

- Overall, *fluxweb* provides a flexible set of functions that greatly increase the feasibility of implementing food-web energetic approaches to more complex systems. As such, the package facilitates novel opportunities for mechanistically linking quantitative food webs and ecosystem functioning in real and dynamic natural landscapes.

1 Introduction

In recent years, there have been multiple calls for the reconciliation of food web structure and ecosystem functioning, to better understand how changes to ecological networks will influence the stability and functioning of ecosystems [5, 6, 7]. Energetic food-web approaches can be used to quantify a key

aspect of ecosystem functioning, energy flux, as a way of characterizing ecological processes that are driven by trophic interactions among nodes in food webs [8, 3, 9]. As such, energy fluxes can be used to quantify functions such as herbivory or productivity. They can also be integrated into the classical framework of Lotka-Volterra equations to estimate stability [10, 11].

Despite interest in using quantitative networks [12, 13, 14], they are still rarely employed for describing natural communities. This is, in part, because quantifying interaction strengths or fluxes in food webs remains a deceptively difficult problem, often requiring intensive experimental and observational efforts. A viable solution is to use mathematical proxies for system, and/or organismal level parameters to calculating energy fluxes through networks based on easily accessible parameters, rather than attempting to measure flux through the whole network. At the system level, for example, inverse matrix reconstruction (commonly referred to as 'ecological network analysis'), [15, 16] or the 'food web energetics approach' [3, 4, 1] have gained some support. These approaches, which are both based on the same steady state assumption (i.e., populations are at equilibrium densities), require reasonable knowledge of the focal system like network topology. That is, some fluxes must be known for the inverse matrix approach, while the food web energetic approach assumes a top down view (energetic demand of predators drives their ingoing fluxes). A major difference relates to the solution provided by these two methods. While ecological network analysis produces an infinite number of solutions and requires an a posteriori selection function, the method of the food web energetic approach guarantees a unique solution for each dataset. Previously, however, scientists using the 'food web energetics' approach [4, 9, 17], have manually calculated fluxes, which can become exceedingly unmanageable as the complexity of the food web increases. Therefore, there is urgent need for a generalized automation of this method.

Interaction strengths can also be quantified by focusing on organism-level parameters related to the metabolic theory of ecology [2]. Generalized allometric approaches utilize general patterns of functional responses that depend upon body size ratios between consumers and their resources [18, 19], opening ways for determining interaction strengths in response to commonly available data such as the abundances and body masses. Allometric rules have been successfully applied to predict fluxes in simplified systems with a few species [20]. However, these results have not yet been generalized for use in complex networks.

Here we present the methodological and mathematical framework that underlies the food web energetics approach and provide theoretical and practical guidelines for using the fluxweb R package. The framework presented here merges allometric theory [2] with food web energetics methods to provide a

set of functions that estimate energy fluxes in complex food webs. In doing so, we support proposals to create a framework allowing for the estimation of energy fluxes in trophic networks using widely available ecological information such as biomass, metabolic demand, ecological efficiencies or network topology [7].

2 The underlying model

The model underlying the food web energetics approach assumes a steady state hypothesis. It implies that L_i, the total amount of energy lost by a species i, either by consumption or physiological processes, is exactly compensated by the metabolized energy it gains from consumption G_i. It will thus solve the equation

$$G_i = L_i \tag{1}$$

knowing that

$$L_i = X_i + \sum_j F_{ij}, \tag{2}$$

where X_i defines energetic losses from species i such as through metabolism, and F_{ij} is the flux from species i to its consumer species j. Then, gains are the part of ingoing fluxes once losses due to feeding efficiency are removed.

$$G_i = \sum_j F_{ji} e_{ij}, \tag{3}$$

where e defines a species' feeding efficiency. This parameter can either depend only on i (efficiencies depends only on the predator identity), only on j (efficiencies related to prey identity), or on both. More details about parameters can be found in section 3. Any flux F_{ij} can be written as $F_{ij} = W_{ij} F_j$, where F_j is the sum of all ingoing fluxes to species j, and W_{ij} defines the proportion of F_j that is obtained from species i ($\sum_i W_{ij} = 1$). The package offers the possibility to scale predator preferences to the distribution of prey body masses. We thus obtain the following model for determining each species' sum of ingoing fluxes:

$$\sum_j W_{ji} F_i e_{ij} = X_i + \sum_j W_{ij} F_j. \tag{4}$$

This equation is solved in two stages: first, the sum of ingoing fluxes for each species is computed. Then, individual fluxes for each pairwise predator-prey interaction are calculated using predator preferences (set in W).

The solution for eq. 4 depends on the chosen definition of feeding efficiency (assigned based on the predator, prey, or link identity) (see SI 1 for demonstrations) and is as follows:

- Efficiencies depending on predator identity

$$F = (diag(e) - W)^{-1} X. \tag{5}$$

  F is the vector such that F_i describes the sum of ingoing fluxes to species i, e is the vector of feeding efficiencies, such that e_i describes the efficiency of a predator i (see related paragraph in section 3 for more precise definitions of feeding efficiencies) with $e_i = 0$ if i is basal. W is the matrix such that W_{ij} sets the proportion of ingoing fluxes to species j from species i and X is the vector defining the sum of energetic losses for each species.

- Efficiencies depending on prey identity

$$F = \left(diag(W^T e + \vec{b}) - W\right)^{-1} X. \tag{6}$$

  In this case, e is the vector such that e_i expresses a prey-related efficiency. $\vec{b}$ is a vector such that b_i is equal to 1 if species i is basal, 0 if it is not basal. The addition of this last vector is needed to solve the system. Ecologically, it simulates the addition of a nutrient node on which all basal species feed with an efficiency of 1.

- Efficiencies depending on link identity (both prey and predator)

$$F = \left(diag(U^T)\vec{1}\right) - W)^{-1} X. \tag{7}$$

  Here, $\vec{1}$ is a vector of ones, U is the matrix defined by the element-wise multiplication of matrices W and e: $U_{ij} = W_{ij} e_{ij}$. e is a matrix such that e_{ij} is the assimilation efficiency of species j feeding on species i.

3 Defining the parameters

A great advantage of the food web energetics method is that it offers a flexible quantitative framework that can be used to test many different ecological hypotheses related to fluxes in networks [21, 1]. Parameters used to configure the model can be taken from the literature, estimated from direct field measurement as well as assessed from general scaling relationships using easily

accessible species (e.g., body size) and/or environmental (e.g., temperature) information. Therefore, the *fluxweb* package is a tool that is highly applicable for both experimental/empirical approaches aiming to describe natural systems and for theoretical approaches requiring generic solutions.
In the following section, we will describe the different parameters needed and how they can be estimated (see table 1 for examples).

Physiological losses (X_i): Depending on user assumptions and choices, different ecological processes can be used. Classical choices are often:

- Metabolic rates [2]
- Death rates [22]
- Potentially more complex allometric functions, including time allocated to resting or hunting and associated energy costs [23]

Metabolic rates and death rates can be measured for simplified systems like in microcosms experiments [24]. If the complexity of the network considered prevents such measurements, they can be estimated for each taxonomic group i using the classic allometric equation [2]

$$X_i = x_0 M_i^b \tag{8}$$

where X_i represents a parameter related to the physiology of species i. x_0 and b are constants associated with parameter X_i and M_i is body mass. References for the choice of constant values associated with each model parameter can be found in the descriptions below. Depending on the amount of ecological information available, or precision required, parameters x_0 and b can be quite general (i.e., the same value for all species), or more specific (i.e., applying one parameter value per functional group, taxonomic group, or species [25]). As X_i is typically estimated per unit biomass, setting the correct value for estimating energy flux is done by a simple multiplication by a species' total biomass.

Efficiencies (e): *fluxweb* offers the possibility to use a variety of input parameters that define energetic losses, for which different aspects of ecological efficiency must be employed. If metabolic rate is used to parametrise energetic loss, then assimilation efficiency must also be provided (i.e., the proportion of consumed energy that is assimilated for respiration and biomass production). If mass-specific death rates are used in place of metabolism

(sensu [21]), users should use the product of assimilation efficiency and production efficiency (percentage of assimilated energy that is used for biomass production). The *fluxweb* package offers three different options for defining ecological efficiencies: consumer-defined, resource-defined, or link-defined (considering both predator and prey identity) efficiencies. These options correspond respectively to the values *pred*, *prey* and *link.specific* for the *ef.level* argument. If, within a single study, each consumer has a relatively homogeneous resource pool (i.e., consumers are trophic specialists such as strict herbivores or strict carnivores), defining efficiencies at the consumer level could be the standard option. However, if a single consumer node draws on a variety of resource nodes (e.g., plants, detritus and animals), efficiencies can be defined at the resource level to account for differences in resource quality ingested by a consumer species. For this last approach, efficiency values that relate to the different groups of organisms can be found in the literature [26].

Preferences (W): Preferences depict the feeding behavior of predator species and should quantify their foraging choices. Depending on system and user choice, they can be absolute preferences or per capita. The package offers the possibility to estimate or scale preferences using a linear scaling with prey biomass:

$$W_{ij} = \frac{w_{ij} B_i}{\sum_k w_{kj} B_k}, \tag{9}$$

where B_i sets the biomass of species i and w is defined by a priori preferences from users. w values are values from the network adjacency matrix (i.e. the matrix such as the value of the ith line and the jth column is non zero if predator j feeds on prey i). Thus, preferences can be defined as a combination of active choice only (by setting the *bioms.pref* option to *FALSE* and providing preferences as values in the network adjacency matrix), relative availability of prey only (by setting the *bioms.pref* option to *TRUE* and providing a binary adjacency matrix for the network) or a combination of both, if preferences values are provided in the adjacency matrix and the option *bioms.pref* is set to *TRUE*.

Species biomasses (B): Biomasses are used (depending on user choices) to scale losses (if they are provided per biomass unit) and preferences. It is therefore an optional parameter.

Table 1: Description of the different parameters used in the *species.level* and *group.level* case studies and their meaning. The units are only examples and might depend on user choices, as long as global coherence is preserved.

Symbol	**Parameter name**	**Description**	**Unit used in the case studies**
X_i	Physiological losses	Total amount of energy loss related to physiology for population i	$J.yr^{-1}$
e_{ij}	Feeding efficiencies		Dimensionless (proportion)
B_i	Total biomass of populations i		g
F_{ij}	Energy flux from species i to species j		$J.yr^{-1}$
w_{ij}	Absolute preference of species j for species i		Dimensionless
W_{ij}	Scaled preference of species j for species i	Sum over j of w_{ij} equals 1. Can be scaled or not with prey abundances	Dimensionless (proportion)

4 *fluxweb* functionalities

Above we presented the theoretical background used by *fluxweb* to determine fluxes in food webs with the *fluxing* function. However, the package offers several other possibilities. Under the steady state assumption, it is quite straightforward to relate estimated fluxes to the equilibrium state of a set of ordinary differential equations depicting population dynamics (Lotka-Volterra like systems of equations). This offers the possibility to gain insight into network stability using the methods established for such equation systems [10]. Thus, the *fluxweb* package offers the *stability.value* and *make.stability* functions using the concept of resilience to quantify the stability of a network with fluxes (see SI 2 for more explanations and the mathematical derivation). The second functionality provided is a sensitivity analysis of outputs regarding the parameters. The *sensitivity* function allows one to assess how the outputs of functions from the package are sensitive to a specified parameter.

5 Using *fluxweb*

Within the *fluxweb* package, we provide three complete case studies corresponding to different levels of trophic complexity (fig 1). The first example consists of a network of 62 nodes resolved to the species level and 573 edges depicting trophic interactions among soil mesofauna in German beech forest (for details see [27]). As is often the case for species-level resolved networks, we only have a binary description of interactions (neither weight of trophic links nor feeding preferences are available). The network corresponding to the intermediate level of complexity is a version of the species-level network where species were aggregated in trophic groups using a group detection method [28]. Reducing complexity by forming aggregated groups can be used to gain basic estimates of predator foraging preferences. Here preferences were estimated by the aggregation process: the foraging preference of a trophic group j on a trophic group i is defined as the number of predation links from species of group j on species of group i. The simple case corresponds to a mesocosm of four species (one resource, two herbivores and a consumer of the two herbivores) assembled from the Chesapeake Bay river estuary [24]. Data used for the species-level food web, the group-level food web and the simple case can be accessed using the *species.level*, *groups.level* and *simple.case* lists respectively. Each of these lists contains all the necessary information to estimate fluxes. They are automatically loaded with the package.

Table 2: Description of the different functions provided by *fluxweb* and their arguments. More details can be found in the help of the package.

Function	**Description**	**Arguments**
fluxing	Compute energy fluxes in networks	- Interaction matrix (including preferences if provided) - Physiological losses - Feeding efficiencies - Species biomasses (optional)
stability.value	Return stability of the network of flux (resilience)	- Interaction matrix of fluxes - Species biomasses - Physiological losses - Feeding efficiencies - Growth rate
make.stability	Return the smallest multiplicative scalar of losses insuring network stability (i.e. producing negative resilience)	- Interaction matrix of fluxes - Species biomasses - Physiological losses - Feeding efficiencies - Growth rate
sensitivity	Compute the sensitivity of a function to an argument	- Function to analyze - Parameter to analyze - Interval of uncertainty for the parameter - Number of replicates to use - Set of parameters needed by the function

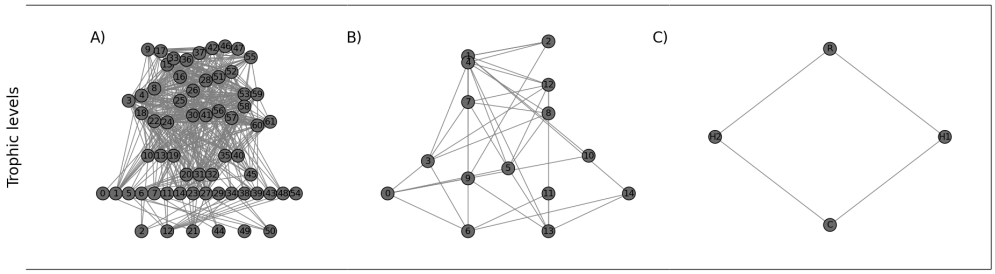

Figure 1: Representation of the *species.level* (A), *groups.level* (B) and *microcosm.level* (C) food webs.

Species-level network

The different parameters of this dataset are:

- The network binary adjacency matrix: value of line i and column j is 1 if species j feeds on species i, 0 otherwise: `species.level$mat`
- The vector of species biomasses (g): `species.level$biomasses`
- The vector of species body masses (g): `species.level$bodymasses`
- The vector of assimilation efficiencies: `species.level$efficiencies`

We used species metabolic rates to define energetic losses related to physiology (eq. 8), with parameter $x_0 = 0.71$ and $b = -0.25$ according to [2]. Values obtained are in joules per second and then scaled to joules per year.

Group-level network

Data provided here are similar to the ones used for the `species.level` list. Body mass of a group is defined as the average bodymass of species belonging to this group. group biomass is defined as the sum of species biomass from the group. In addition, the list contains the `species.tgs` data frame indicating the identity of species in each trophic group.

Simple-case network

In this specific case, metabolic rates are not estimated based on regressions with body masses but, as is often possible from micro- or mesocosm experiments, directly measured by 0_2 respiration ($ml.mg^{-1}.h^{-1}$) and converted to joules per year. Thus, this dataset departs from the two others as no information about body mass is needed to estimate fluxes. The *microcosm.level* list contains:

- The network binary adjacency matrix: value of line i and column j is 1 if species j feeds on species i, 0 otherwise: `microcosm.level$mat`
- The vector of species biomasses (g): `microcosm.level$biomasses`
- The vector of species metabolic rates (j.year): `microcosm.level$metabolic.rates`
- The vector of assimilation efficiencies: `microcosm.level$efficiencies`

Fluxweb function examples

The different datasets can be loaded using the `load()` function and elements can be thereafter directly accessed after a use of the `attach()` function. For the species and group level examples, species metabolic losses (per unit of biomass) have to first be estimated with eq. 8:

```
metabolic.rates = 0.71*bodymasses^-0.25
```

For these three cases, the matrix of fluxes is simply computed through the call to the *fluxing* function:

```
fluxes = fluxing(mat, biomasses, metabolic.rates, efficiencies,
 bioms.prefs = TRUE, bioms.losses = TRUE, ef.level = 'prey')
```

Here, `bioms.prefs = TRUE` specifies that species preferences depend on prey abundances (eq. 9). The *bioms.losses* argument is set to *TRUE* to compute metabolic losses for species populations (as they are provided per unit biomass). For the example from the mesocosm experiment, as metabolic rates were directly measured, this has to be switched to *FALSE*. The *ef.level* argument is set to *prey* as efficiencies provided in these datasets depends on prey identities.

In the same way, the stability of the food web of fluxes is returned by the *stability.value* function:

```
stability.value(val.mat, biomasses, losses, efficiencies, growth.rates,
bioms.prefs = TRUE, bioms.losses = TRUE, ef.level = 'prey')
```

with the addition of a vector of growth rates for basal species (parameter `growth.rates`), determined using the classic allometric equation (eq. 8).

6 From data sampling to fluxes

As a very simple example how to convert community data into quantitative fluxes, we propose here guidelines for experimental ecologists that want to use *fluxweb* with the hypothesis of the metabolic theory. Using this framework requires the following information:

- the **food web** of the ecological system considered (i.e. the set of trophic interactions between each species pair)
- the average **bodymass** of individuals in each population (in g)
- the total **biomass** of each population (in g)
- the list of trophic **species**, or at least a list of metabolic types (as defined in table 3) for each species in the food web.

Information about the **food web** is the first parameter required by the fluxing function. It should be a matrix (thereafter called `mat`) of n rows and n columns, where n is the total number of species involved in the study. The order of species should be identical between rows and columns. A non-zero value at the intersection of line i and column j in the food web matrix means that predator j consumes prey i. The values used to fill this matrix can be either binary (0/1) assuming that predators foraging preferences on their prey are unknown, or real values, defining these foraging preferences.

The average **body mass** of each species is used to calculate their metabolic rates (that will define the physiological losses of species in this framework). This calculation can be achieved using eq. 8. It is possible to define the parameters of this equation depending on species metabolic types (see table 3 or [25]), or to use an average value. In such case, the per unit of biomass (i.e. g) metabolic rate X is:

$$X = 0.71M^{-0.25},$$

where M is the body mass of the species. It is important to note that the use of the average body mass of species M in the previous equation leads to metabolic rates per gram of biomass. This is why the information about the total **biomass** of species should be estimated during sampling. Indeed, the fluxing function will internally compute the total metabolic rate of the species with a multiplication of per gram metabolic rate Y and the total biomass (in g) of the species considered. It is quite common in food webs to have nodes such as 'detritus' or 'dissolved organic matter'. Values for the metabolic rates

of such nodes can be set to `NA` if they are basal and zero in any case. After this point, users should thus create a vector containing information on species per gram metabolic rate (`met.rate`) and biomass (`biomasses`). The ordering of the species in these vectors be similat to the one used for the food web matrix.

Table 3: Parameter values used for the calculation of species metabolic rates depending on their metabolic types. Values from [2]

Metabolic type	**intercept**(x_0)	**exponent** (b)
Ectotherm vertebrates	18.18	-0.29
Endotherm vertebrates	19.5	-0.29
Invertebrates	17.17	-0.29

Then, the last parameter needed to estimate fluxes are the feeding **efficiencies**. As species physiological losses were estimated using metabolic rates, assimilation efficiencies should be used (assimilation efficiency defines the proportion of eaten biomass that can be use for biomass production plus metabolism [26]). These efficiencies can be defined using basic information on organism types. Indeed, the efficiency with which a predator will consume a prey can be defined by the type of prey eaten. At the end, efficiencies will be defined by a vector where i^{th} value is equal to 0.806 if resource i is an animal, to 0.545 if species i is a plant or to 0.106 if i corresponds to detritus [26]. Once again, the species order should be identical to the one used for the food web matrix. At this point, it is possible to directly calculate the fluxes and store them in a matrix object (here named *mat.flux*). The value in line i and column j of $mat.flux$ describes the flux from resource i to consumer j. It represents the energy loss by the prey, while energy gained by the predator can be calculated by multiplying it by the efficiency term. The matrix can be obtained using the command:

```
mat.flux = fluxing(mat, biomasses, met.rate, efficiencies)
```

In this case, optional arguments will use their default behaviour:

- `bioms.prefs = TRUE` means that fluxes will dependon prey biomasses (more abundant prey will be more eaten), as predotor preferences are scaled with prey biomasses.

- `bioms.losses = TRUE` means that the function will assume that the vector of metabolic rates provided defines metabolic rate per biomass. Thus, the function will internally multiply this vector by the vector of

biomasses to compute species total metabolic rates.

- `ef.level = 'prey'` will assume that the efficiency of a feeding interaction will depend on the prey identity. Thus, that the vector of efficiencies provided defines the efficiency of species when they are consumed.

7 Conclusion

Here, we presented the R package *fluxweb*, providing a set of methods allowing the calculation of energy fluxes in food webs based on the conceptual framework of the 'food web energetics' approach [4, 9, 17, 1]. By automating the link between the identity and composition of interacting populations and energy fluxes, these methods facilitate the integration of community and ecosystem ecology. Fluxes within a system, which have typically been estimated in highly aggregated compartments, can now be quickly calculated at the species level or grouped as appropriate by users to match their objectives. This provides an advance to mechanistically understand how changes in biodiversity may impact ecosystem functioning [6], and is timely given the increasing amount and complexity of ecological network data being collected over environmental and disturbance gradients [29, 30].
Under the assumption of biomass equilibrium, multiple aspects of ecosystem function can be investigated owing to the package's flexibility in the processes represented by parameters, their units, and how the outputs are interpreted. Function parameters can be estimated from general allometric relationships suitable for abstract models or tuned accordingly to precise measurement of specific systems depending on the users' aims and on the availability of project-specific measurements or system-specific literature values. The impact of these estimations on ecological inferences can be assessed with the sensitivity function.
Several ecosystem functions can easily be estimated. For example, primary production can be defined as the sum of fluxes outgoing plant species [31] (because outgoing fluxes from plants must be balanced by ingoing fluxes, thus providing an indication for total uptake by plants). Hypotheses regarding the effect of network structure or community composition on a single function (or multiple single functions; multifunctionality) can also be tested, such as secondary production by herbivores or decomposition by detritivores [9, 1]. Assessing such fluxes is important because they are directly linked to ecosystem services but may be mismatched with the standing stock biomass

of these species or trophic groups [9]. Additionally, whole-system flux, the sum of the entire fluxing matrix, can be used as a single value representing the emergent property of multitrophic functioning [9].
The functions of *fluxweb* also offer several distinct but related ways to examine network stability that are important in the face of global changes and species loss. First, the biomass fluxes can be interpreted as link weights, and used to assess the distribution of interaction strengths in the network. Second, the stability function returns the network resilience, its ability to return to its equilibrium state following a small perturbation (see SI 2).
Overall, the *fluxweb* package thus offers important tools for research on quantitative food webs and ecosystem functioning in real and dynamic natural landscapes [32].

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8 Supplementary information I - mathematical resolution

8.1 Efficiencies depending on predator identity

We will consider in the following that feeding efficiencies depend on predator identity. We define e as the vector of efficiencies and W as the matrix such that W_{ij} is the proportion of energy entering j that is obtained from i ($\sum_j W_{ij} = 1$). F_{ij} is the flux from species i to i. L_i, the energy loss of species j is defined by:

$$L_i = X_i + \sum_{j=1}^{s} F_{ij}, \tag{10}$$

where n is the number of species and X_i are the physiological losses of species i. Thus, for satisfying the equilibrium criteria, F_i, the sum of fluxes entering

i is:

$$F_i = \frac{1}{e_i}\left(X_i + \sum_{j=1}^{n} F_{ij}\right). \tag{11}$$

As W_{ij} sets the proportion of energy entering j obtained from species i, using $F_{ij} = W_{ij}F_j$, we can write

$$F_i = \frac{1}{e_i}\left(X_i + \sum_{j=1}^{n} W_{ij}F_j\right), \tag{12}$$

where values W_{ij} are estimated accordingly to species preferences (w_{ij}) and prey abundances:

$$W_{ij} = \frac{w_{ij}B_i}{\sum_{k=1}^{s} w_{kj}B_k}. \tag{13}$$

We then have:

$$e_iF_i = X_i + \sum_{j=1}^{n} W_{ij}F_j, \tag{14}$$

which can be rewritten as:

$$diag(E)F = X + WF, \tag{15}$$

where $diag(e)$ is the diagonal matrix such as $diag(e)_{ii} = e_i$. Provided that $(diag(e) - W)$ is invertible, the system solves as:

$$F = (diag(e) - W)^{-1} X. \tag{16}$$

Then, all fluxes $F_{ij} = W_{ij}F_j$ are derived from F_j using W.

8.2 Efficiencies depending on prey identity

Another common method is to define feeding efficiencies according to prey identity. This section proposes a method to adapt the previous framework to this case.

As preferences are defined at the prey level, we need to adapt the previous framework by adding a nutrient node on which all basal species feed with an efficiency of one. Then, eq.4 becomes:

$$F_i\left(\sum_{j=1}^{n} W_{ji}e_j + b_i\right) = X_i + \sum_{j=1}^{n} W_{ij}F_j \tag{17}$$

$$\Leftrightarrow F_i\left(\sum_{j=1}^{n} W_{ij}^T e_j + b_i\right) = X_i + \sum_{j=1}^{n} W_{ij}F_j \tag{18}$$

were b_i is 1 if i is a basal species, 0 otherwise. This can be rewritten as:

$$diag(W^T e + \vec{b})F = X + WF, \tag{19}$$

and, provided that $(diag(W^T e + \vec{b}) - W)$ is invertible, solved by:

$$F = (diag(W^T e + \vec{b}) - W)^{-1} X \tag{20}$$

8.3 Efficiencies depending on the link identity

It is possible to generalise this approach to efficiencies defined for each prey-predator couple. The solution needs the definition of matrix U such as $U_{ij} = W_{ij} e_{ij}$. Then, eq. 4 becomes:

$$F_i \sum_{j=1}^{n} U_{ij}^T = X_i + \sum_{j=1}^{n} W_{ij} F_j \tag{21}$$

and the system then reads:

$$diag(U^T \vec{1})F = X + WF \tag{22}$$

where $\vec{1}$ is the vector of ones. System is solved as:

$$F = (diag(U^T \vec{1}) - W)^{-1} X \tag{23}$$

9 Supplementary information II

This document presents how the fluxes calculated under the steady state hypothesis can easily be used to assess system stability, following the framework of Moore and De Ruiter [21]. Here we use resilience as a definition of stability. Resilience is determined from the Jacobian matrix. The system is in a stable equilibrium only if the real parts of eigenvalues from the Jacobian are all negative. In this case, resilience is the absolute value of the real part of the largest eigenvalue. It is this value which is returned by the *stability* function from the *fluxweb* package.
Another measure of stability, provided by the function *make.stability*, is to find the minimal value of a scalar s defining the proportion of physiological losses related to species density. In this case, physiological loss terms in the diagonal of the Jacobian matrix are now defined as sX_i and directly affect the resilience value, s being the measure of stability. We will show in the following section how fluxes at equilibrium can relate to a Lotka-Volterra system in an equilibrium state, and how to compute the Jacobian matrix, first assuming that feeding efficiencies relate to predator identity and then assuming them to depend on prey identity.

9.1 Derivation of the Jacobian matrix

9.1.1 Preferences defined at predator level

We can consider the following system of equations, describing the dynamics of population biomasses in a community:

$$\frac{dB_i}{dt} = r_i B_i - \sum_j a_{ij} B_i B_j \qquad \text{(for producers)} \tag{24a}$$

$$\frac{dB_i}{dt} = -X_i B_i + \sum_j e_i a_{ji} B_i B_j - \sum_j a_{ij} B_i B_j \qquad \text{(for consumers)} \tag{24b}$$

a_{ij} is the coefficient of interaction between prey i and predator j and r_i is the relative growth rate of producer i. P_i and p_i respectively define the sets of predators and prey of species i. This model assumes a type I functional response f_{ij} defined as:

$$f_{ij} = a_{ij} B_i. \tag{25}$$

As the whole method assumes that fluxes and biomasses are at an equilibrium state, we have:

$$F_{ij} = a_{ij} B_i^* B_j^*, \tag{26}$$

B_i^* denoting biomass of species i at equilibrium. Then, off-diagonal elements α_{ij} from the Jacobian matrix correspond to the per capita effects (effect of one unit of species biomass). Considering the possible presence of cycles of length 1 (species i is at the same time a prey and a predator of species j), off diagonal elements are

$$\alpha_{ij} = \frac{\delta \frac{dB_i}{dt}}{\delta B_j} = e_i a_{ji} B_i - a_{ij} B_i \qquad i \neq j \tag{27}$$

and at equilibrium, from eq. 26 we have $B_i^* = \frac{F_{ij}}{a_{ij} B_j^*}$ and $B_i^* = \frac{F_{ji}}{a_{ji} B_j^*}$. We can use it to replace elements from eq. 27 and obtain:

$$\alpha_{ij} = e_i \frac{F_{ji}}{B_j^*} - \frac{F_{ij}}{B_j^*} \qquad i \neq j \tag{28}$$

Diagonal elements, considering possible cannibalistic loops, for producers (p) and consumers (c) are:

$$\alpha_{pp} = r_p - \sum_j c_{pj} B_j \tag{29a}$$

$$\alpha_{cc} = -X_c + 2 e_c a_{cc} B_c + \sum_{j \neq c} e_c a_{jc} B_j - 2 a_{cc} B_c - \sum_{j \neq c} a_{cj} B_j \tag{29b}$$

$$= -X_c + e_c a_{cc} B_c + \sum_j e_c a_{jc} B_j - a_{cc} B_c - \sum_j a_{cj} B_j \tag{29c}$$

with $a_{ii} \neq 0$ only if species i is cannibalistic. Again, using $B_i^* = \frac{F_{ij}}{a_{ij}B_j^*}$ and $B_i^* = \frac{F_{ji}}{a_{ji}B_j^*}$ we obtain at equilibrium:

$$\alpha_{pp} = r_p - \frac{1}{B_p^*}\sum_j F_{pj} \tag{30a}$$

$$\alpha_{cc} = -X_c + \frac{F_{cc}}{B_c^*}(e_c - 1) + e_c\sum_j \frac{F_{jc}}{B_c^*} - \sum_j \frac{F_{cj}}{B_c^*} \tag{30b}$$

We can observe here that α_{cc} can be rewritten as

$$\alpha_{cc} = -X_c + \frac{F_{cc}}{B_c^*}(e_c - 1) + \frac{1}{B_c^*}(e_cF_c - L_c) \tag{31}$$

where F_i sets the sum of fluxing ingoing species i and L_i its losses due to consumption. As we assume a steady state, ingoing fluxes compensate outgoing fluxes plus physiological losses: $e_cF_i = L_i + X_i$. From that, we obtain:

$$\alpha_{cc} = -X_c + \frac{F_{cc}}{B_c^*}(e_c - 1) - \frac{X_c}{B_c^*} \tag{32}$$

9.1.2 Efficiencies defined at prey level

The Lotka Voltera system is now written as:

$$\frac{dB_i}{dt} = r_iB_i - \sum_j a_{ij}B_iB_j \qquad \text{(for producers)} \tag{33a}$$

$$\frac{dB_i}{dt} = -X_iB_i + \sum_j e_ja_{ji}B_iB_j - \sum_j a_{ij}B_iB_j \qquad \text{(for consumers)} \tag{33b}$$

Here e_j defines efficiency of prey species j. At equilibrium, off diagonal elements of the Jacobian are as above:

$$\alpha_{ij} = e_j\frac{F_{ji}}{B_j^*} - \frac{F_{ij}}{B_j^*} \qquad i \neq j \tag{34}$$

Diagonal elements, considering possible cannibalistic loops, for producers (p) and consumers (c) are:

$$\alpha_{pp} = r_p - \sum_j a_{pj}B_j \tag{35a}$$

$$\alpha_{cc} = -X_c + 2e_ca_{cc}B_c + \sum_{j\neq c} e_ja_{jc}B_j - 2a_{cc}B_c - \sum_{j\neq c} a_{cj}B_j \tag{35b}$$

$$= -X_c + e_ca_{cc}B_c + \sum_j e_ja_{jc}B_j - a_{cc}B_c - \sum_j a_{cj}B_j \tag{35c}$$

which, at equilibrium leads, like above, to:

$$\alpha_{pp} = r_p - \frac{1}{B_p^*} \sum_j F_{pj} \tag{36a}$$

$$\alpha_{cc} = -X_c + \frac{F_{cc}}{B_c^*}(e_c - 1) + \sum_j e_j \frac{F_{jc}}{B_c^*} - \sum_j \frac{F_{cj}}{B_c^*} \tag{36b}$$

9.1.3 Preferences defined at link level

Following the same mathematical derivation as before, we obtain:

$$\alpha_{ij} = e_{ij} \frac{F_{ji}}{B_j^*} - \frac{F_{ij}}{B_j^*} \qquad i \neq j \tag{37a}$$

$$\alpha_{pp} = r_p - \frac{1}{B_p^*} \sum_j F_{pj} \tag{37b}$$

$$\alpha_{cc} = -X_c + \frac{F_{cc}}{B_c^*}(e_{cc} - 1) + \sum_j e_{jc} \frac{F_{jc}}{B_c^*} - \sum_j \frac{F_{cj}}{B_c^*} \tag{37c}$$

References

[1] Andrew D. Barnes, Malte Jochum, Jonathan S. Lefcheck, Nico Eisenhauer, Christoph Scherber, Mary I. O'Connor, Peter de Ruiter, and Ulrich Brose. Energy Flux: The Link between Multitrophic Biodiversity and Ecosystem Functioning. *Trends in Ecology & Evolution*, 33(3):186–197, mar 2018.

[2] James H. Brown, James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West. Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789, 2004.

[3] H. W. Hunt, D. C. Coleman, E. R. Ingham, R. E. Ingham, E. T. Elliott, J. C. Moore, S. L. Rose, C. P.P. Reid, and C. R. Morley. The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils*, 3(1-2):57–68, feb 1987.

[4] P. C. de Ruiter, A.-M. Neutel, and J. C. Moore. Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems. *Science*, 269(5228):1257–1260, 1995.

[5] J. Emmett Duffy, Bradley J. Cardinale, Kristin E. France, Peter B. McIntyre, Elisa Thébault, and Michel Loreau. The functional role of

biodiversity in ecosystems: Incorporating trophic complexity. *Ecology Letters*, 10(6):522–538, jun 2007.

[6] Ross M. Thompson, Ulrich Brose, Jennifer A. Dunne, Robert O. Hall, Sally Hladyz, Roger L. Kitching, Neo D. Martinez, Heidi Rantala, Tamara N. Romanuk, Daniel B. Stouffer, and Jason M. Tylianakis. Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution*, 27(12):689–697, 2012.

[7] Jes Hines, Wim H. van der Putten, Gerlinde B. De Deyn, Cameron Wagg, Winfried Voigt, Christian Mulder, Wolfgang W. Weisser, Jan Engel, Carlos Melian, Stefan Scheu, Klaus Birkhofer, Anne Ebeling, Christoph Scherber, and Nico Eisenhauer. Towards an integration of biodiversity-ecosystem functioning and food web theory to evaluate relationships between multiple ecosystem services. *Advances in Ecological Research*, 53:161–199, jan 2015.

[8] Robert V. O'Neill. Indirect estimation of energy fluxes in animal food webs. *Journal of Theoretical Biology*, 22(2):284–290, feb 1969.

[9] Andrew D. Barnes, Malte Jochum, Steffen Mumme, Noor Farikhah Haneda, Achmad Farajallah, Tri Heru Widarto, and Ulrich Brose. Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications*, 5:5351, oct 2014.

[10] Anje-Margriet Neutel, Johan a P Heesterbeek, Johan van de Koppel, Guido Hoenderboom, An Vos, Coen Kaldeway, Frank Berendse, and Peter C de Ruiter. Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449(7162):599–602, oct 2007.

[11] Benjamin Schwarz, Andrew D. Barnes, Madhav P. Thakur, Ulrich Brose, Marcel Ciobanu, Peter B. Reich, Roy L. Rich, Benjamin Rosenbaum, Artur Stefanski, and Nico Eisenhauer. Warming alters energetic structure and function but not resilience of soil food webs. *Nature Climate Change*, 7(12):895–900, dec 2017.

[12] Eric L. Berlow, Anje Margiet Neutel, Joel E. Cohen, Peter C. De Ruiter, Bo Ebenman, Mark Emmerson, Jeremy W. Fox, Vincent A.A. Jansen, J. Iwan Jones, Giorgos D. Kokkoris, Dmitrii O. Logofet, Alan J. Mckane, Jose M. Montoya, and Owen Petchey. Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73(3):585–598, may 2004.

[13] Carolin Banašek-Richter, Louis Félix Bersier, Marie France Cattin, Richard Baltensperger, Jean Pierre Gabriel, Yves Merz, Robert E. Ulanowicz, Annette F. Tavares, D. Dudley Williams, Peter C. De Ruiter, Kirk O. Winemiller, and Russell E. Naisbit. Complexity in quantitative food webs. *Ecology*, 90(6):1470–1477, jun 2009.

[14] Dick van Oevelen, Karel van den Meersche, Filip J R Meysman, Karline Soetaert, Jack J. Middelburg, and Alain F. Vézina. Quantifying food web flows using linear inverse models. *Ecosystems*, 13(1):32–45, nov 2010.

[15] Af F. Vézina and T Piatt. Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. *Marine Ecology Progress Series*, 42(3):269–287, 1988.

[16] Stuart R. Borrett and Matthew K. Lau. enaR: An R package for Ecosystem Network Analysis. *Methods in Ecology and Evolution*, 5(11):1206–1213, nov 2014.

[17] Andrew D. Barnes, Patrick Weigelt, Malte Jochum, David Ott, Dorothee Hodapp, Noor Farikhah Haneda, and Ulrich Brose. Species richness and biomass explain spatial turnover in ecosystem functioning across tropical and temperate ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1694):20150279, may 2016.

[18] Olivera Vucic-Pestic, Björn C. Rall, Gregor Kalinkat, and Ulrich Brose. Allometric functional response model: Body masses constrain interaction strengths. *Journal of Animal Ecology*, 79(1):249–256, 2010.

[19] Gregor Kalinkat, Björn Christian Rall, Olivera Vucic-Pestic, and Ulrich Brose. The allometry of prey preferences. *PLoS ONE*, 6(10):e25937, oct 2011.

[20] U. Brose, R. B. Ehnes, B. C. Rall, O. Vucic-Pestic, E. L. Berlow, and S. Scheu. Foraging theory predicts predator-prey energy fluxes. *Journal of Animal Ecology*, 77(5):1072–1078, sep 2008.

[21] John C Moore and Peter C de Ruiter. *Energetic Food Webs:An analysis of real and model ecosystems*. Oxford University Press, 2012.

[22] Marisa Rossetto, Giulio A. de Leo, Daniele Bevacqua, and Fiorenza Micheli. Allometric scaling of mortality rates with body mass in abalones. *Oecologia*, 168(4):989–996, 2012.

[23] Chris Carbone, Amber Teacher, and J. Marcus Rowcliffe. The costs of carnivory. *PLoS Biology*, 5(2):0363–0368, 2007.

[24] Lefcheck Jonathan S. and Duffy J. Emmett. Multitrophic functional diversity predicts ecosystem functioning in experimental assemblages of estuarine consumers. *Ecology*, 96(11):2973–2983, 2015.

[25] Roswitha B. Ehnes, Björn C. Rall, and Ulrich Brose. Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters*, 14(10):993–1000, oct 2011.

[26] Birgit Lang, Roswitha B. Ehnes, Ulrich Brose, and Björn C. Rall. Temperature and consumer type dependencies of energy flows in natural communities. *Oikos*, 126(12):1717–1725, dec 2017.

[27] Christoph Digel, Alva Curtsdotter, Jens Riede, Bernhard Klarner, and Ulrich Brose. Unravelling the complex structure of forest soil food webs: Higher omnivory and more trophic levels. *Oikos*, 123(10):1157–1172, oct 2014.

[28] Benoit Gauzens, Elisa Thébault, Gérard Lacroix, and Stéphane Legendre. Trophic groups and modules: two levels of group detection in food webs. *J. R. Soc. Interface*, 12:20141176, 2015.

[29] Benoit Gauzens, Stéphane Legendre, Xavier Lazzaro, and Gérard Lacroix. Intermediate predation pressure leads to maximal complexity in food webs. *Oikos*, 125(4):595–603, aug 2016.

[30] Jason M. Tylianakis and Rebecca J. Morris. Ecological Networks Across Environmental Gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48(1):25–48, nov 2017.

[31] Wang Shaopeng and Brose Ulrich. Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters*, 21(1):9–20.

[32] Ulrich Brose and Helmut Hillebrand. Biodiversity and ecosystem functioning in dynamic landscapes. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 371(1694):20150267, may 2016.