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Methods in Ecology and Evolution

APPLICATION

EcologicalNetworksDynamics.jl: A Julia package to simulate the temporal dynamics of complex ecological networks

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Abstract

1. Species interactions play a crucial role in shaping biodiversity, species coexistence, population dynamics, community stability and ecosystem functioning. Our understanding of the role of the diversity of species interactions driving these species, community and ecosystem features is limited because current approaches often focus only on trophic interactions. This is why a new modelling framework that includes a greater diversity of interactions between species is crucially needed.
2. We developed a modular, user-friendly, and extensible Julia package that delivers the core functionality of the bio-energetic food web model. Moreover, it embeds several ecological interaction types alongside the capacity to manipulate external drivers of ecological dynamics. These new features represent important processes known to influence biodiversity, coexistence, functioning and stability in natural communities. Specifically, they include: (a) an explicit multiple nutrient intake model for producers, (b) competition among producers, (c) temperature dependence implemented via the Boltzmann-Arhennius rule, and (d) the ability to model several non-trophic interactions including competition for space, plant facilitation, predator interference and refuge provisioning.
3. The inclusion of the various features provides users with the ability to ask questions about multiple simultaneous processes and stressor impacts, and thus develop theory relevant to real world scenarios facing complex ecological communities in the Anthropocene. It will allow researchers to quantify the relative importance of different mechanisms to stability and functioning of complex communities.
4. The package was build for theoreticians seeking to explore the effects of different types of species interactions on the dynamics of complex ecological communities, but also for empiricists seeking to confront their empirical findings with theoretical expectations. The package provides a straightforward framework to model explicitly complex ecological communities or provide tools to generate those communities from few parameters.

KEYWORDS
allometric scaling, bioenergetic model, competition, differential equations, facilitation, metabolic theory, multiplex networks

1 | INTRODUCTION

The bio-energetic model of food web dynamics has played a central role in the identification of the drivers of ecological community dynamics since its introduction by (Yodzis & Innes, 1992). Following its adaptation to complex trophic networks by (Brose, Williams, et al., 2006), it has been used to develop theory about a wide range of topics including stability of multispecies communities (Brose, Williams, et al., 2006), the dynamics of secondary extinctions (Brose et al., 2005) and the impacts of multiple threats on biodiversity (Binzer et al., 2012).

The reason for the success of the bio-energetic model is twofold. First, it facilitated the representation of complex mechanisms with ordinary differential equations, while maintaining a low number of free parameters. This enabled to strategically address fundamental questions about several key patterns, theories and processes in ecology (Brose, Williams, et al., 2006; Martinez, 2020). Therefore, it became a fundamental bridge between several disconnected sets of theory and vital to defining theory about the impacts of global change on biodiversity and ecosystem function. Second, the bio-energetic model made it possible to investigate these ecological processes in truly complex communities. For the first time, theory was able to align with a diversity of empirical patterns in complex ecological systems, including evidence to explain the discrepancy between May's predictions that large systems are unlikely to be stable (Brose et al., 2003; May, 1972) and empirical observations that large ecological communities are indeed observed in nature.

However, the bio-energetic model also suffers from limitations. It solely centres on trophic interactions, thereby overlooking the diverse array of other interactions observed in nature, such as competition and facilitation among species (Kéfi et al., 2012, 2015). Including these interactions into food webs has been demonstrated to have significant implications for community diversity, productivity, and stability (Kéfi et al., 2016; Miele et al., 2019).

Although, the bio-energetic model has been implemented in various programming languages (R, Julia and C++) and by numerous researchers (see for instance, Delmas et al., 2017; Gauzens et al., 2023; Lurgi et al., 2014; Sentis et al., 2021), these frameworks do not immediately allow the possibility for users to consider multiple interaction types simultaneously. More generally, these frameworks often lack flexibility in the sense that it can be difficult to modify the model by specifying custom parameters or changing the modelling choices—for example, moving from logistic growth to explicit nutrient dynamics.

To meet this need, we developed a new Julia package which aims at extending existing frameworks of the bio-energetic model (e.g., the Julia package BioEnergeticFoodWebs, Delmas et al., 2017) by addressing the aforementioned issues. Our implementation relies on the computing efficiency of the Julia programming language (Cabutto et al., 2018; Sells, 2020). Moreover, it is designed to be user-friendly, and flexible, allowing researchers to explore: explicit nutrient uptake by producers and thus exploitative competition (Brose, 2008), direct interference competition (Tilman, 1982), temperature dependence of ecological rates (Binzer et al., 2012, 2016), and non-trophic interactions (Kéfi et al., 2012; Miele et al., 2019). These additions come alongside the capacity to easily manipulate fundamental features of the bio-energetic framework such as species richness, network structure and complexity, body mass distributions, functional responses, as well as the scaling of metabolic, biomass production and foraging traits with body size.

Below, we begin by introducing the bio-energetic dynamical model. Subsequently, we delve into the new features of our package. This is followed by an instructional guide on using the package. Finally, we illustrate each new feature and their combinations through a series of examples.

2 | THE CORE BIO-ENERGETIC DYNAMICAL MODEL

We developed a Julia package, EcologicalNetworksDynamics, that implements two versions of the core, well established bio-energetic framework of Yodzis & Innes (1992) and others (Binzer et al., 2016; Brose, Williams, et al., 2006; Delmas et al., 2017; Kéfi et al., 2012), and integrates four additional frameworks that extend the model beyond simple trophic interactions. We first describe the core implementations of the bio-energetic model and then present the extensions that we developed.

We implemented two core approaches of the bio-energetic model frequently found in the literature: 'bio-energetic' and 'classic'. They are distinguished by their scaling of time and the default consumption rate of a consumer according to the resource density (hereafter 'functional response'). In the original 'bio-energetic' version, time is relative to the growth rate of a producer and the functional response is defined by typical Holling forms (see Equation 1b). In the 'classic' version, time is absolute and the functional response is presented with time dependent attack rates and handling times.

2.1 | Bio-energetic version

Previously, used (Brose, Williams, et al., 2006; Williams et al., 2007; Yodzis & Innes, 1992) and implemented (Delmas et al., 2017), time is expressed relative to the inverse of a producer intrinsic growth rate (r_p). We write the model in Equation (1).

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = r_i B_i G_i - x_i B_i - d_i B_i + x_i y_i B_i \sum_{j \in \{\text{prey}\}_i} F_{ij} - \sum_{j \in \{\text{pred.}\}_i} \frac{x_j y_j B_j F_{ji}}{e_{ij}}, \quad (1a)$$

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + i_0^{\text{intra}} B_i B_0^h + \sum_{k \in \{\text{prey}\}_i} \omega_{ik} B_k^h}, \quad (1b)$$

where B_i is the biomass of the species i, r_i the intrinsic growth rate, G_i the normalized growth rate detailed further below, x_i the metabolic demand, y_i the maximum consumption rate, d_i the natural mortality rate, $\{\text{preys}\}_i$ and $\{\text{pred.}\}_i$ respectively the ensembles of preys and predators of species i, e_{ij} the assimilation efficiency of species i feeding on prey j.

F_{ij} is the feeding rate of i feeding on j and depends on the half-saturation density B_0 and ω_{ij} which weights the preference of predator i for prey j. By default, predators have the same preference for each of its prey, that is $\omega_{ij} = \frac{1}{\text{number of preys of } i}$. i_0^{intra} is the intensity of intraspecific interference among consumers, and h is the hill exponent defining the shape (Type II or Type III) of the functional response: for $\left(h = 1, i_0^{\text{intra}} = 0\right)$ we recover the Holling type II functional response, and for $\left(h > 1, i_0^{\text{intra}} = 0\right)$ the type III.

2.2 | Classic version

Used in Binzer et al. (2016) and also implemented in Delmas et al. (2017), time has units that are absolute and the functional response depends on time dependent attack rates a_{ij} and handling times $h_{t,ij}$. We write the model in Equation (2).

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = r_i B_i G_i - x_i B_i - d_i B_i + B_i \sum_{j \in \{\text{prey}\}_i} e_{ij} F_{ij} - \sum_{j \in \{\text{pred}\}_i} B_j F_{ji}, \quad (2a)$$

$$F_{ij} = \frac{\omega_{ij} a_{ij} B_j^h}{M_i \left(1 + i_0^{\text{intra}} B_i + \sum_{k \in \{\text{prey}\}_i} \omega_{ik} a_{ik} h_{t,ik} B_k^h\right)}. \quad (2b)$$

Note that the functional response of Equation (2b) is divided by the predator body-mass M_i to ensure unit consistency (Miele et al., 2019; Schneider et al., 2016).

2.3 | Allometric scaling

A key feature of the bio-energetic model is the allometric scaling of metabolism, growth and foraging rates with body mass. This central role of allometry, reviewed in Williams et al. (2007) makes for extremely efficient modelling of complex communities by reducing the number of free parameters and 'automating' the specifying of rates consistent with empirical data. Thus following Yodzis & Innes (1992) and all modern implementations of the bioenergetic model, we write the species' intrinsic growth rate (r_i), the metabolic demand (x_i) and the natural mortality rate (d_i) as function of their body-mass M_i (see Table S1). Following insights from Brose et al. (2006, 2019) and all other implementations of the model, we also assume that the consumer-resource body mass ratio (Z) can be any value but is constant across the network. This allows the body mass of each species becomes a function of its trophic level (T_L): $M = Z^{T_L - 1}$ (thus fixing the body-mass of producers to 1), where we use the fractional trophic level after Odum & Heald (1975) using the calculation of Pauly & Christensen (1995).

3 | EXTENDING THE CORE MODEL

We now present the new extensions of the bio-energetic model that we have implemented, namely: (1) producer competition, (2) nutrient dynamics, (3) temperature dependent biological rates, (4) non-trophic interactions, that all enable to model a diversity of complex ecological communities in various ecological contexts.

3.1 | Producer competition

By default, we model the producer growth (see Equations 1a and 2a) as a logistic $r_i G_i = r_i\left(1 - \frac{B_i}{K_i}\right)$, where r_i is the intrinsic growth rate of the producer i and K_i is the carrying capacity. However, the user can modify the relative strength of intra- versus interspecific competition. To do so, we modify the producer growth function to specify a competition coefficient in the numerator of the core logistic growth equation (Delmas et al., 2017; Williams, 2008):

$$G_i = 1 - \frac{\sum_{j \in \{\text{prod.}\}} \alpha_{ij} B_j}{K_i}. \quad (3)$$

In the absence of consumers, this corresponds to generalized competitive Lotka-Volterra equations. That being said, two special cases emerge from this general form. First, if we assume no interspecific competition (for all $i \neq j, \alpha_{ij} = 0$) and that the intraspecific competition is set to unity (for all $i, \alpha_{ii} = 1$), we recover to the logistic growth equation: $G_i = 1 - \frac{B_i}{K_i}$. Second, in the case where intraspecific and interspecific competition are set to unity (that is, $\alpha_{ij} = 1.0$ for all i and j) and that producers share the same carrying capacity K, this models producer species sharing equally a common pool of resources, so that $G_i = 1 - \frac{\sum_i B_i}{K_i}$. More generally, we can specify with this function multiple scenarios where the relative strength of intra- to interspecific competition can be evaluated.

3.2 | Nutrient uptake

In addition, the user can also change the default producer logistic growth for an explicit exploitative competition among producer species for nutrients. This modifies basal species' growth rates G_i as follows (Brose, 2008; Brose et al., 2005)

$$G_i(N) = \min\left(\frac{N_1}{K_{1i} + N_1}, \ \ldots, \ \frac{N_L}{K_{Li} + N_L}\right) B_i, \quad (4)$$

where N_l is the concentration of nutrient l in the environment and K_{li} is the half saturation density of nutrient l for producer i . L denotes the number of nutrients. The nutrient-intake efficiency of producer i for nutrient l is then higher the lower its half-saturation density is.

The nutrient dynamics are determined by their respective supply (S_l) and turnover rates (D_l), their concentration in each producer (c_{li}) as well as the producer's half-saturation densities for the resource (K_{li}) as shown in Equation (5):

$$\frac{\mathrm{d}N_l}{\mathrm{d}t} = D_l\left(S_l - N_l\right) - \sum_{i=1}^{n} c_{li} G_i(N) B_i. \tag{5}$$

Default values for these parameters can be found in Table S3.

3.3 | Temperature dependence

Several researchers have integrated temperature dependence of the ecological rates in the bio-energetic model to explore questions, for example, about temperature interactions with productivity (Binzer et al., 2016) and invasive species (Sentis et al., 2021). Following these formulations, we implement in EcologicalNetworksDynamics the dependence of ecological rates with temperature using the exponential Boltzmann-Arrhenius relationship:

$$\mathrm{rate}_{ij} = I m_i^b m_j^c \exp\left(E_a \frac{T_0 - T}{k_b T_0 T}\right). \tag{6}$$

I is the allometric constant, b is the allometric exponent of species i, c is the allometric exponent of species j, T is the temperature of the system in Kelvin, $T_0 = 293.15\,K$ is the normalization temperature, E_A is the activation energy and $k_b \simeq 8.617 \cdot 10^{-5}\,V \cdot K^{-1}$ is the Boltzmann constant.

Species rates that can be scaled with temperature are the carrying capacities (K_i), intrinsic growth rates (r_i), metabolic rates (x_i), attack rates (a_{ij}) and handling times ($h_{t,ij}$). As attack and handling time are specified, the temperature scaling of species rates rely on the 'classic' bio-energetic model (see previous section). Moreover, note that the attack rates and handling times depend both on resource species i and consumer species j (that is $c \neq 0$ in Equation 6), while the other rates only depend on the focal species i ($c = 0$). The default values of I, b and c for the different species rates can be found in Table S2.

3.4 | Non-trophic interactions

We implemented the possibility to model four non-trophic interactions that are ubiquitous and can have crucial effects on community dynamics and ecosystem functioning (Kéfi et al., 2016; Miele et al., 2019): (1) competition for space between sessile species, (2) plant facilitation, (3) interspecific interference between predators and (4) provision of prey refuges from consumption. The effect of each non-trophic interaction can be translated in the model as a change in specific system parameters (Kéfi et al., 2012). Below, we detail how each non-trophic interaction is formally incorporated in the model. Note that all four non-trophic interactions can be incorporated within the model simultaneously. Non-trophic interactions are only implemented for the 'classical' bio-energetic model, consistently with previous studies (Kéfi et al., 2012; Miele et al., 2019). Indeed, non-trophic interactions are implemented as parameter modifications, and some of them directly apply to parameters of the 'classic' functional responses (refuge provisioning and predator interference).

3.4.1 | Competition for space

Competition for space can only occur between sessile species (mostly primary producers). We assume that two species competing for space will mutually decrease their net growth rate defined as the sum of the growth, consumption and metabolic loss terms of Equation (2a):

$$G_{\mathrm{net},i} = r_i G_i - x_i. \tag{7}$$

Then the effect of competition on the net growth rate is given by:

$$G_{\mathrm{net},i} \rightarrow G_{\mathrm{net},i} \max\left(0, 1 - \theta\left(G_{\mathrm{net},i}\right) c_0 \sum_{k \in \{\mathrm{comp.}\}_i} B_k\right), \tag{8}$$

where c_0 is the intensity of the competition for space and $\{\mathrm{comp.}\}_i$ the ensemble of species competing with species i. θ is the Heaviside function ($\theta(x) = 1$ if $x > 0$ and $\theta(x) = 0$ otherwise). Therefore, the effect of competition on the net growth rate depends on its sign. If the net growth rate is positive, its value is reduced by the effect of competition and left unchanged otherwise. We ensure that a positive net growth cannot become negative by taking the maximum of zero and the multiplicative factor of the net growth rate.

3.4.2 | Plant facilitation

Producers experiencing recruitment facilitation have an increased intrinsic growth rate, following Miele et al. (2019):

$$r_i \rightarrow r_i\left(1 + f_0 \sum_{k \in \{\mathrm{fac.}\}_i} B_k\right), \tag{9}$$

where f_0 is the intensity of the facilitation interaction, the larger f_0 the more the producer growth rate is increased. Moreover, $\{\mathrm{fac.}\}_i$ is the ensemble of species, producers or not, facilitating the producer i.

3.4.3 | Interspecific interference between predators

Interference between predators can only occur between predators sharing at least one prey. We implement predator interference in the functional response by introducing a new term i_0^{inter} along with i_0^{intra}

$$F_{ij} \rightarrow \frac{\omega_{ij} a_{ij} B_j^h}{1 + i_0^{\text{intra}} B_i + i_0^{\text{inter}} \sum_{k \in \{\cap \text{pred.}\}_i} B_k + \sum_{k \in \{\text{prey}\}_i} \omega_{ik} a_{ik} h_{t,ik} B_k^h}, \quad (10)$$

where i_0^{inter} is the intensity of the interspecific interference and $\{\cap \text{pred.}\}_i$ the ensemble of predators sharing at least one prey with species i.

3.4.4 | Prey refuge

A refuge effect is translated as a reduction of the attack rates of the predators feeding on the prey j with a refuge. We model this by specifying the attack rate as a function that decreases toward zero as the strength of the refuge interaction increases. Refuge links occur from a sessile species (i)—which provides a refuge—toward a prey who benefits from the refuge (j).

$$\forall i \in \{\text{pred.}\}_j, a_{ij} \rightarrow \frac{a_{ij}}{1 + r_0 \sum_{k \in \{\text{ref.}\}_j} B_k}, \quad (11)$$

where r_0 is the intensity of the refuge effect and $\{\text{ref.}\}_j$ the ensemble of species providing a refuge to species j. A similar modification of the attack rate can be found in DeLong (2021) and Kalinkat et al. (2023), and it has been thought of as an alternative to type 3 functional responses.

Note that there is only little literature supporting values for non-trophic interaction strengths (c_0, f_0, etc.), therefore we advise the user to report to previous studies (Domínguez-García et al., 2019; Miele et al., 2019) or to fix non-trophic parameters values with respect to their impact on a community property of interest such as community biomass.

4 | BASIC USAGE

The EcologicalNetworksDynamics package enables users to simulate the dynamics of complex ecological communities using an extended bio-energetic framework. Below, we describe the basic workflow of the package, i.e. how to: (1) create a network of interacting species, (2) define model parameters based on allometric relationships, and (3) simulate to produce a time series of biomass for all species. The package workflow is synthesized in Figure 1. We then provide four use-cases for scenarios invoking competition, nutrient uptake, temperature dependence and non-trophic interactions. A guide to install Julia and the package can be found in the Section S1.

The following code simulates the dynamics of a primary producer (species 1) eaten by a consumer (species 2). The corresponding trophic network can be encoded into an adjacency matrix A (Equation 12). EcologicalNetworksDynamics follows the convention of specifying that rows correspond to predator and columns to prey. This convention can differ from other implementations. In the adjacency matrix, 0s indicate the absence of trophic interactions while 1s indicate the presence of interactions. Moreover, EcologicalNetworksDynamics facilitates the use of several topological network generating models, including the cascade (Pimm, 1991) and niche models (Williams & Martinez, 2000).

$$A = \begin{pmatrix} 0 & 0 \\ 1 & 0 \end{pmatrix}. \quad (12)$$

In this simple example, we specify that both species have individual body masses equal to 10, and initial population biomasses randomly drawn from the uniform distribution [0, 1]. By default, the 'bio-energetic' version of the model is used (Equation 1) with default parameter values taken from the literature (see Table S1 for default settings).

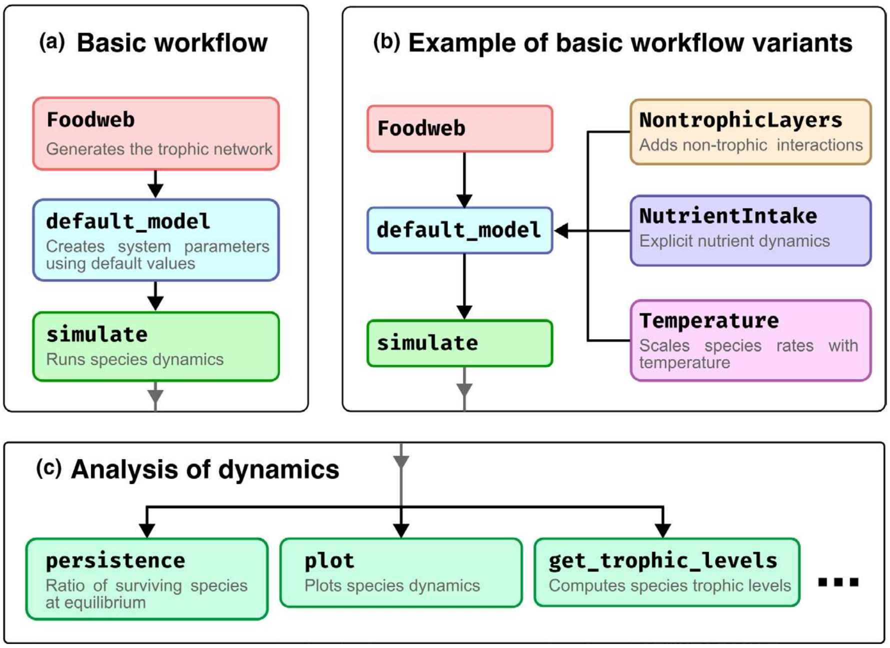

FIGURE 1 Overview of the package workflow: (a) Most direct workflow predominantly using default package settings. (b) Modified version of the basic workflow incorporating additional features to the model such as non-trophic interactions, nutrient dynamics, or temperature scaling of species biological rates. (c) Examples of functions designed to analyse simulation outputs.

```
using EcologicalNetworksDynamics, Plots
foodweb = Foodweb([0 0; 1 0])
simple_model = default_model(foodweb, BodyMass([10, 10]))
B0 = rand(2) # Set initial biomasses for each species.
solution = simulate(simple_model, B0, 100)
plot(solution)
```

Users can either provide a vector of body masses or set the predator–prey mass ratio (Z; see Brose, Williams, et al., 2006), which will distribute masses across trophic levels such that they scale exponentially with trophic levels. Note that for both approaches, the food web can be generated with the cascade or niche model algorithms.

For example, to distribute body masses with a predator–prey mass ratio (Z) of 10, the model can be created as follows:

```
default_model(foodweb, BodyMass(Z=10))
```

Then, the simulate function calls under the hood the function solve from the Julia DifferentialEquations package (Rackauckas & Nie, 2017) which implements an adaptive time step solver. The choice of solver can be fully customized by the user and is detailed in the online documentation.

Lastly, the plot function of the Plots package (Christ et al., 2022) allow to directly visualize species trajectories. In addition, we provide several utility functions to analyse in more detail the result of the simulation. We showcase a few of these below and in Figure 1:

```
total_biomass(solution) # Community biomass at each timestep.
total_biomass(solution[end]) # Final community biomass.
richness(solution) # Species richness at each timestep.
richness(solution[end]) # Final species richness.
```

5 | USE CASES

Here, we showcase advanced and new features of the EcologicalNetworksDynamics package. The code to reproduce the examples can be found in the online documentation and in the associated GitHub repository (see Availability section). Figures from this section are made with the Julia plotting library Makie (Danisch & Krumbiegel, 2021).

5.1 | Paradox of enrichment

Classical theory associated with the paradox of enrichment (Rosenzweig, 1971) predicts a transition from stability to instability along a gradient of productivity defined by the carrying capacity K of the resource (Becks et al., 2005; Fussmann et al., 2000; Luckinbill, 1973). This phenomenon appears in classic resource-consumer systems, where resources have density dependent growth and consumers feed with a Type II functional response. To reproduce this example, we define a trophic network with a single producer eaten by a consumer and run simulations for a range of producer carrying capacity K. For each simulation, we record the equilibrium biomass of each species. Results, recreating the paradox of enrichment by varying K, are shown in Figure 2.

5.2 | Producer competition

Coexistence theory predicts that stable coexistence is feasible when interspecific competition is lower than intraspecific competition ($\alpha_{ij} < \alpha_{ii}$), while competitive exclusion arises when interspecific competition is higher than intraspecific one ($\alpha_{ij} > \alpha_{ii}$). Competitive exclusion among primary producers then can trigger extinction cascades among consumers in food webs. However, it is known that increasing the consumer generalism, i.e. increasing the trophic connectance, can mitigate the destabilizing effect of a high interspecific competition. Here, we reproduce this result by measuring species persistence using a network of $S = 20$ species, three levels of connectance (complexity) and experimental manipulation of the interspecific producer competition coefficient α_{ij} . To generate large realistic trophic networks, the package gives the possibility to create them from niche model (Williams & Martinez, 2000). For example, Foodweb(:niche; S = 20, C = 0.1) creates a network of 20 species with a trophic connectance of 0.1. Results are show in Figure 3.

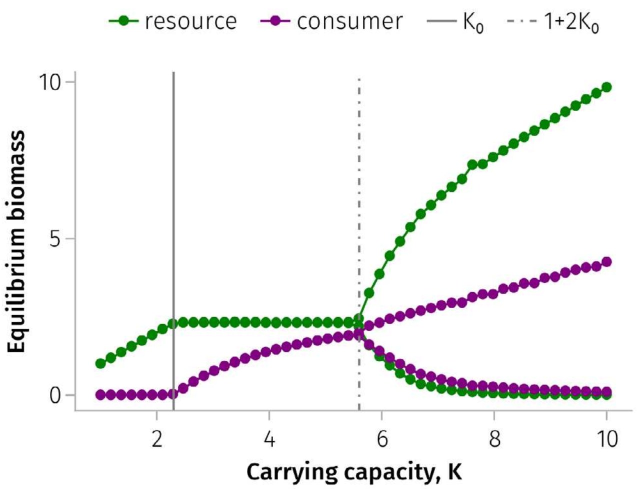

FIGURE 2 Orbit diagram of the consumer and resource biomasses (B) at equilibrium versus the resource carrying capacity (K). First, for $K \leq K_0$ there is not enough resource to sustain the consumer population, thus only the resource survives. Secondly, for $K_0 \leq K \leq 1 + 2K_0$ both species can coexist and the equilibrium attractor is a stable point. Moreover, we remark that in this region the consumer biomass increases with K, but not the resource one. Lastly, for $K \geq 1 + 2K_0$ the system starts to oscillate and the amplitude of the limit cycle increases with K which can lead at some point to the species extinction. K_0 is a critical carrying capacity, which mainly depends on the ratio of the consumer metabolic demand over its assimilation efficiency. This well-known pattern is referred to as the paradox of enrichment in the literature, and has been first described in 1971 by M. Rosenzweig (Rosenzweig, 1971).

5.3 | Nutrient uptake

Classical competition theory predicts that two species cannot coexist on a single resource. However, when the number of resources is equal to or greater than the number of competitors, and there is a trade-off between growth rates and the ability to draw down each nutrient, coexistence can occur (Huisman & Weissing, 1999; Tilman, 1982).

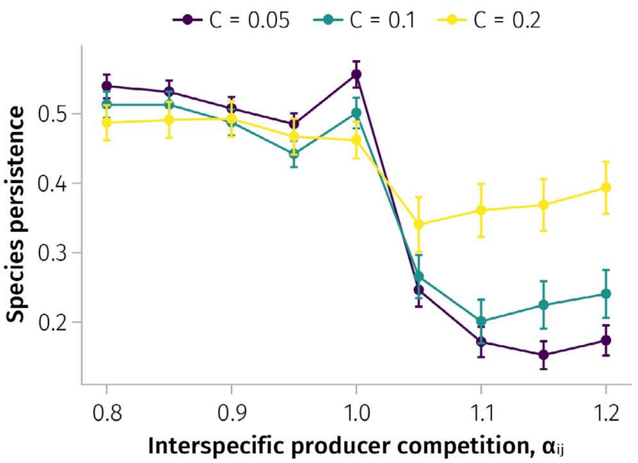

FIGURE 3 Species persistence along a gradient of interspecific competition strength among producers for three values of connectance. $S = 20$, $Z = 100$, $K = 1.0$, $\alpha_{ii} = 1$. Species persistence drops when interspecific competition exceeds 1.0, i.e. when it becomes higher than intraspecific one. Higher values of connectance are associated with higher species persistence overall, especially when interspecific competition is higher than intraspecific one. Points display the average species persistence, the error bars display the 95% ranges assuming a Normal distribution. The mean number of producers for the three connectance levels are the following: ~ 9 producers for $C = 0.1$, ~ 6 producers for $C = 0.05$, ~ 4 producers for $C = 0.2$. This figure replicates results of (Delmas et al., 2017), Figure 3.

To reproduce this classic theory, we define two networks: one with two producers competing for a single nutrient and one with two producer species competing for two nutrients. Results are shown in Figure 4 where under the first scenario, competitive exclusion occurs and in the second, coexistence.

5.4 | Non-trophic interactions

Non-trophic interactions can be added to the food web by updating the food web with the NonTrophicLayers function. The detail and structure of each non-trophic interactions is specified through an adjacency matrix, a number of links or a connectance. In the two last cases, the non-trophic links are drawn randomly conditioned by few simple rules (e.g. plant facilitation links are always directed toward a plant).

We showcase here the effect of non-trophic interactions on species diversity. Specifically, we reproduce the results of (Miele et al., 2019) which demonstrates how the strength of four non-trophic interactions, considered separately, can impact on species diversity. (Miele et al., 2019) found that facilitation had a positive effect on species diversity, while refuge effect, interspecific predator interference and competition for space had a negative effect. We varied the intensity of each non-trophic interaction and recorded species diversity at equilibrium. We present the mean and 95% range for 50 replicate food webs of 50 species with connectance = 0.06 ± 0.01. Results are shown in Figure 5.

5.5 | Temperature and non-trophic interactions

Temperature dependence is by default turned off, but can be introduced with the component Temperature, that defines temperature dependent rates using the exponential Boltzmann Arrhenius scaling.

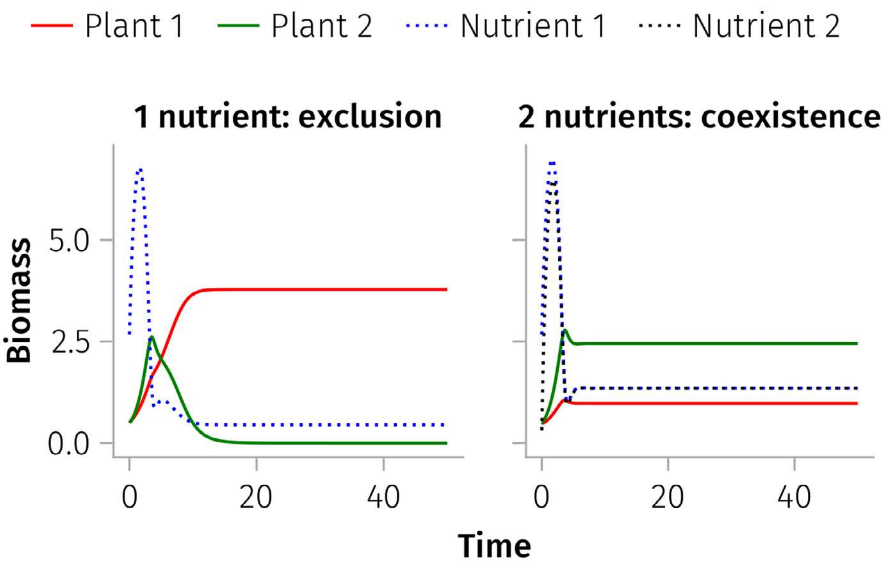

FIGURE 4 Biomass of two plant species sharing one (left) or two (right) nutrient resources through time. Following theory, the single shared resource leads to competitive exclusion because Plant 1 can draw down the resource to a lower equilibrium than plant species 2. In contrast, with two nutrients and a trade-off between growth rates and the ability to draw down each nutrient, coexistence can occur.

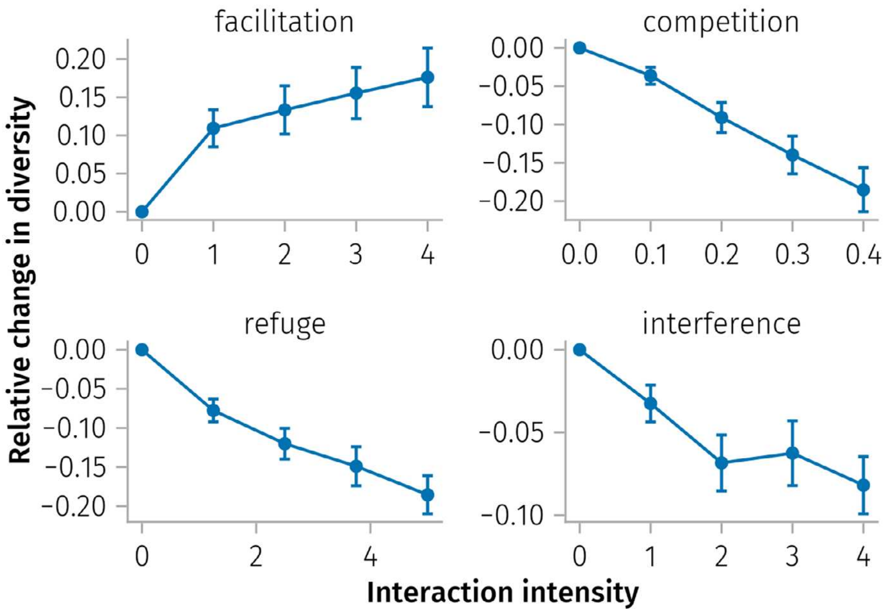

FIGURE 5 The relative variation in diversity as the intensity of the different non-trophic interactions is increased. Plant facilitation increases diversity while the three other non-trophic interactions decrease diversity. The points of zero intensity correspond to the reference, where there are only trophic interactions in the network. The relative variation in diversity is $\frac{S-S_{\text{ref}}}{S_{\text{ref}}}$, where S is the equilibrium richness of the multiplex network and S_{ref} of its reference trophic network, i.e. the multiplex network from which we have removed the non-trophic interactions. We start with community of $S_{\text{init}} = 50$ species and trophic links distributed with niche model for a connectance $C = 0.06 \pm 0.01$. Non-trophic interactions are drawn randomly given the rules of (Miele et al., 2019), with a connectance of $C_{\text{NTI}} = 0.01$. We discarded networks with loops or disconnected species. Error bars represent 95% range.

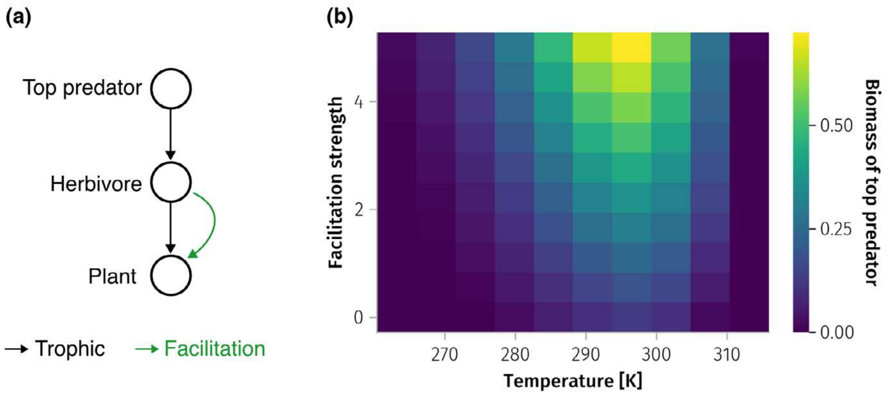

FIGURE 6 (a) Network of the community simulated, that is, a three species food chain with a facilitative interaction from the herbivore to the plant. (b) Heatmap of the top predator biomass depending on the temperature and the facilitation strength. Non-default community parameters: $Z = 1$, $c_{\text{intra}} = 0$.

In Figure 6, we showcase how the addition of non-trophic interactions can influence the community response to temperature. Specifically, we model a three species food chain and consider a facilitative interaction from the herbivore to the plant (Figure 6a), modelling for example the effect of recycling or seed dispersal. We assess how the combined effects of temperature and facilitation srength affects the top predator biomass.

We focus on the top predator's biomass to highlight the bottom-up effects of increased facilitation. Figure 6b shows that as the strength of the facilitation from the herbivore to the plant increases, the temperature range supporting a high predator biomass broadens. This example illustrates how combining different features of our model can allow simulating scenarios including different interaction types and external drivers (that is, temperature).

6 | CONCLUSION

We have presented EcologicalNetworksDynamics, a Julia package implementing the bio-energetic model with several extensions that include: (1) competition between producers; (2) an explicit nutrient uptake model for producers; (3) a temperature dependence of the model parameters; and (4) non-trophic interactions. The package is ideal for theoreticians seeking to explore the effects of different types of species interactions on the dynamics of complex ecological communities, but also for empiricists seeking to confront their empirical findings with theoretical expectations. It allows modelling communities from few parameters, while making possible for the user the possibility to customize the model by mixing interaction types and external drivers with ease. We believe that with this gain in flexibility over previous frameworks, our package will facilitate the exploration of and development of theory for a wide range of ecological scenarios. The outputs of the package can be exported in a language-neutral format (e.g. CSV), and thus be processed with other languages commonly used in Ecology for data analysis and visualization, such as R. Critically, we believe this fast, extensible and open source code-base can help scientists and researchers avoid having to individually implement their own code, thus saving time and providing hopefully a common and extensible framework for the community.

While our package already offers extensive modelling capabilities, some features are currently not included. These include: spatial dynamics through dispersal, adaptive foraging by predators, integration of plant-pollinator interactions, modelling stochastic dynamics, and tools to quantify the stability of ecological networks. These are let for future works, and in this regard we welcome contributions to our GitHub repository.

AUTHOR CONTRIBUTIONS

Iago Bonnici, Ismaël Lajaaiti, Eva Delmas, Hana Mayall and Alain Danet contributed to the software development. Andrew P. Beckerman, Iago Bonnici and Sonia Kéfi supervised the project. Alain Danet, Iago Bonnici, Ismaël Lajaaiti, Thomas Malpas and Sonia Kéfi wrote the software documentation. Ismaël Lajaaiti wrote the original draft, and all authors contributed substantially to its revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14497.

DATA AVAILABILITY STATEMENT

The EcologicalNetworksDynamics package is available in the official Julia package registries and tested against the latest stable release of Julia at the time of writing (v1.10). The code is hosted on GitHub and archived on Zenodo at https://doi.org/10.5281/zenodo.14609708 (Lajaaiti et al., 2025). The package is released under GPL-3 licence and SemVer-compliant version number 0.2.0. The version number is meant to evolve, reflecting that the code authors did not unnecessarily constrain the user-facing library features (function names, syntax, workflow) to strict stability yet. We expect that future user feedback and additional features will be flexibly integrated into the package. If this evolution requires that the interface be modified in a non-retrocompatible way, then the changes will be rigorously documented in the package release notes, and user code will not break unless they explicitly upgrade the package as it eventually matures toward 1.0.0. In this respect, bug reports, improvement suggestions and contributions are very welcome under the form of 'issues' and 'pull requests' in the source repository.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Getting started in Julia.

Appendix S2. Parameter tables and default settings.

Appendix S3. Package modularity.

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