Intro to BioEnergeticFoodWebs

by Chris Griffiths, Eva Delmas and Andrew Beckerman, Oct. 2021.

This document follows on from 'Getting started', 'Basic Julia commands' and 'Differential Equations in Julia' and assumes that you're still working in your active project.

This document introduces the BioEnergeticFoodWebs.jl and EcologicalNetworks.jl packages. It demonstrates how to run the BioEnergetic Food Web (BEFW) model, how to vary variables of interest (e.g., productivity) and construct experiments designed to investigate the effect of different variables on population and community dynamics.

For those that are unfamiliar with the BEFW and it's application in Julia, we advise checking out the **MEE paper** before we start. Remember, the BEFW model is also based on a system of differential equations and is solved using the same engine as the DifferentialEquations.jl package.

Load packages

```
• md"## Load packages"
```

You'll need the following packages for this tutorial:

```
md"You'll need the following packages for this tutorial:"
```

```
    using BioEnergeticFoodWebs , EcologicalNetworks , JLD2 , Statistics , Plots
, CSV , DataFrames , Random
```

The JLD2.jl package will be useful later as it allows you to directly export and load a BEFW output object. Let's also set a random seed for reproducibility:

```
MersenneTwister(21)
• Random.seed!(21)
```

Preamble

One of main advantages of running food web models in Julia is that simulations are fast and can be readily stored in your active project. With this in mind, make a new folder in your project called out_objects (right click > New Folder). Alternatively, you can create an out_objects folder directly using mkdir():

```
# We've already create a folder called out_objects in our project but an example of
mkdir() would be:
mkdir("example_folder")
# if you haven't created an out_objects folder yet, simply replace "example_folder"
with "out_objects".
```

Running the BEFW

There are four major steps when running the BioEnergetic Food Web model in Julia:

- 1. Generate an initial network
- 2. Fix parameters
- 3. Simulate
- 4. Explore output and plot

Initial network

Before running the BEFW model, we have to construct an initial random network (an adjacency matrix) using **the niche model**. The network is characterised by the number of species in the network and its **connectance** value. Here, we generate a network of 20 species with a connectance value of 0.15:

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## Running the BEFW

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### Initial network
Before running the BEFW model, we have to construct an initial random network (an adjacency matrix) using [the niche model](https://www.nature.com/articles/35004572? cacheBust=1510239451067). The network is characterised by the number of species in the network and its [connectance](https://en.wikipedia.org/wiki/Ecological_network) value. Here, we generate a network of 20 species with a connectance value of 0.15:
```

```
A_bool = 20×20 (String) unipartite ecological network (L: 58 - Bool)
```

```
• # generate network
```

- A_bool = EcologicalNetworks.nichemodel(20,0.15)

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- # convert the UnipartiteNetwork object into a matrix of 1s and 0s
- Ad = adjacency(A_bool)

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 A = Int.(Ad)
```

In the above code chunk, we are saving the output from running the nichemodel as A_bool and then using the A part of A_bool to construct our initial random network. Within A, 1s indicate an interaction among species and Os no interaction. In the packages used here, the networks are directed from i (rows) to j (columns), describing the direction of the interaction (i eats j), not of the flow of biomass.

You can check the connectance of A using:

```
co = 0.145
  # calculate connectance
  co = sum(A)/(size(A,1)^2)
```

Here, connectance is calculated as the number of realised links (sum of 1s in A) divided by the number of species in A squared. This end part (species^2) describes the maximum number of possible links in the network A.

Parameters

Prior to running the BEFW model, you have to create a vector of model parameters using the model_parameters function. Numerous parameter values can be specified within the model_parameters function, however, most of them have default values that are built into the BioEnergeticFoodWebs.jl package. For simplicity, we use the default values here:

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     :e_carnivore \Rightarrow 0.85
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     :m_producer \Rightarrow 1.0
     :h \Rightarrow 1.0
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     :tmpA ⇒
     :rewire_method ⇒ :none
     :trophic_rank \Rightarrow [1.0, 1.0, 1.0, 2.0, 1.0, 2.2, 2.75, 2.5, 2.5,
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      • # create model parameters
```

p = model_parameters(A)
 # in the most simple case, the model_parameters function simply requires A

For more information and a full list of the parameters and their defaults values type ? model_parameters in the REPL.

If you want to view, check or extract any of the parameter values in p use the p[:name] notation. For example, you can view a vector of each species' trophic rank using:

```
[1.0, 1.0, 1.0, 2.0, 1.0, 2.2, 2.75, 2.5, 2.5, 1.0, 3.0, 3.0, 4.0, 2.5, 3.5, 3.0, 2.75, 2.
```

```
# view trophic ranks:p[:trophic_rank]
```

Simulate

To run the BEFW model, we first assign biomasses at random to each species and then simulate the biomass dynamics forward using the simulate function:

```
bm = [0.331066, 0.300448, 0.0291859, 0.295575, 0.0361821, 0.963121, 0.150602, 0.344048, 0.5622
```

```
# assign biomasses
bm = rand(size(A,1))
```

```
out = Dict{Symbol, Any}(  : p \Rightarrow Dict(:\alpha \Rightarrow 1.0, :e\_carnivore \Rightarrow 0.85, : \Gamma h \Rightarrow [0.0, 0.0, 0.0, 0.5, 0.0, more]
```

```
:B \Rightarrow 8023 \times 20 \text{ adjoint}(::Matrix{Float64}) \text{ with eltype Float64}:
            0.331066
                       0.300448
                                  0.0291859
                                                0.295575
                                                               0.0369967
                                                                             0.0530368
                                                                                        0.82237
            0.275087
                       0.251328
                                  0.00817244
                                                0.173187
                                                                0.0408813
                                                                             0.0646593
                                                                                        0.94844
            0.247361
                       0.227229
                                  0.0029042
                                                0.0991832
                                                               0.0386371
                                                                             0.0798476
                                                                                        1.0428
            0.240935
                       0.22239
                                  0.00121857
                                                0.056877
                                                               0.033843
                                                                             0.098953
                                                                                        1.09539
            0.250236
                       0.232034
                                  0.000573703
                                                0.0330167
                                                               0.0287532
                                                                             0.122374
                                                                                        1.1061
            0.271583
                       0.252987
                                  0.000294967
                                                0.0195387
                                                               0.0239862
                                                                             0.150397
                                                                                        1.08238
            0.302566 0.283188
                                  0.000163569
                                                0.0118501
                                                                0.0197161
                                                                             0.183055
                                                                                        1.03421
            0.559035
                       0.559035
                                  0.0
                                                0.0
                                                                0.00834797
                                                                             0.0
                                                                                        0.35599
            0.559035
                       0.559035
                                  0.0
                                                0.0
                                                               0.00835872
                                                                             0.0
                                                                                        0.35599
            0.559035
                       0.559035
                                  0.0
                                                0.0
                                                               0.00836805
                                                                             0.0
                                                                                        0.35599
            0.559035
                       0.559035
                                  0.0
                                                0.0
                                                               0.00837562
                                                                             0.0
                                                                                        0.35599
            0.559035
                       0.559035
                                  0.0
                                                0.0
                                                               0.00838156
                                                                             0.0
                                                                                        0.356
            0.559035
                       0.559035
                                  0.0
                                                0.0
                                                               0.00838598
                                                                            0.0
                                                                                        0.356
     :t \Rightarrow [0.0, 0.25, 0.5, 0.75, 1.0, 1.25, 1.5, 1.75, 2.0,
                                                                     more ,2000.0]
)
```

```
• # simulate
• out = simulate(p, bm, start=0, stop=2000)
• # this might take a few seconds
```

The simulate function requires the model parameters p and the species biomasses bm. In addition, you can specify the timespan of the simulation (using the start and stop arguments), fix a species extinction threshold (using extinction_threshold) and select a solver (using use). For more information type ?simulate in the REPL.

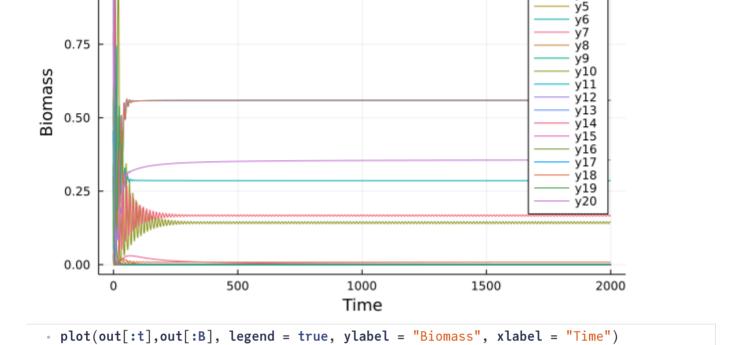
Output and plot

Once the simulation finishes, the output is stored as a dictionary called out. Within out there are three entries:

```
    out[:p] - lists the parameters
    out[:B] - biomass of each species through time
    out[:t] - timesteps (these typically increase in 0.25 intervals)
```

The biomass dynamics of each species can then be plotted. Similar to the DifferentialEquations.jl package, the BioEnergeticFoodWebs.jl package also has it's own built in plotting recipe:

1.00



y2

y3

You'll notice that the biomass dynamics are noisey during the first few hundred time steps, these are the system's transient dynamics. The dynamics then settle into a steady state where the system can be assumed to be at equilibrium. You'll also notice that some species go extinct and some persist, the initial number of species in the food web (20 in this case) can found using out[:p][:S] and the identity of those that went extinct using out[:p][:extinctions].

The BioEnergeticFoodWebs.jl package also has a range of built in functions that conveniently calculate some of the key metrics of the food web, these include the total biomass, the diversity, the species persistence and the temporal stability:

```
biomass = 2.079634374182744
```

```
# total biomassbiomass = total_biomass(out, last=1000)
```

diversity = 0.8152947375528959

```
• # diversity
• diversity = foodweb_evenness(out, last=1000)
```

persistence = 0.4

```
# persistencepersistence = species_persistence(out, last=1000)
```

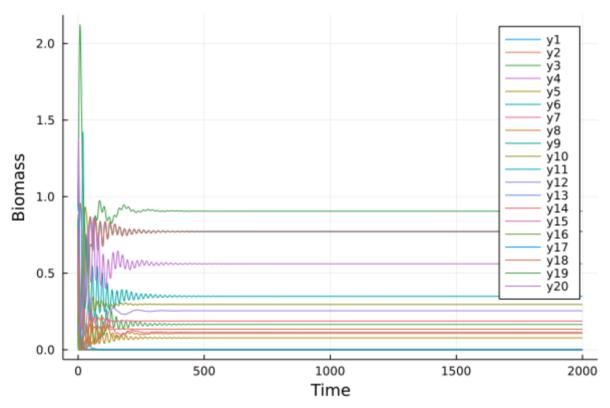
stability = -0.009341145049945184

```
# stabilitystability = population_stability(out, last=1000)
```

Each of these functions will output a single value. This value is the average over the last 1000 time steps. For more information, use ? to access the help files on each function in the REPL (e.g., ? species_persistence).

Variables

Once you've got the BEFW model running, the next step is to vary a variable of interest and rerun. For example, we might be interested in what affect a small change in Z (consumer-resource body mass ratio) has on the estimated food web and its biomass dynamics. The default value for Z is 1.0, but what happens if we increase it to 10.0:



```
begin

# set Z (has to be a floating number not an integer)

Z = 10.0

# create model parameters

p_z = model_parameters(A, Z = Z)

# assign biomasses

bm_z = rand(size(A,1))

# simulate

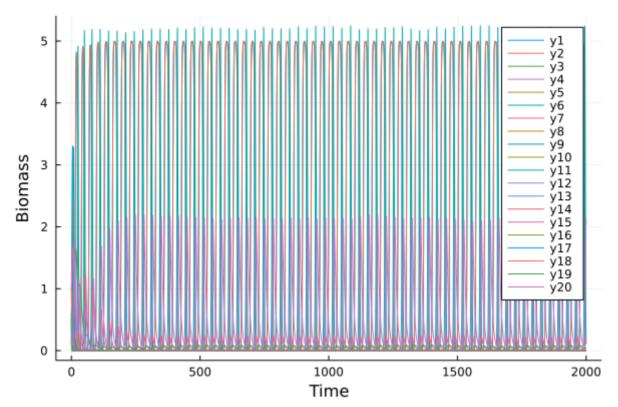
out_z = simulate(p_z, bm_z, start=0, stop=2000)

# plot

plot(out_z[:t], out_z[:B], legend = true, ylabel = "Biomass", xlabel = "Time")

end
```

Similarly, what happens if we also increase the carrying capacity (K) of the resource from 1.0 (default) to 5.0:



```
begin

# set K (has to be a floating number not an integer)

K = 5.0

# create model parameters

p_K = model_parameters(A, Z = Z, K = [K]) # K needs to be provided in []'s

# assign biomasses

bm_K = rand(size(A,1))

# simulate

out_K = simulate(p_K, bm_K, start=0, stop=2000)

# plot

Plots.plot(out_K[:t], out_K[:B], legend = true, ylabel = "Biomass", xlabel = "Time")

end
```

As you've probably guessed, the main message here is that many variables can be changed in the BEFW model and it's super easy to do so. Some changes will have large effects and some not so much. In the next step, we take this one step further.

Quick note - the begin and end used in the above code chunks and those that follow aren't needed when running Julia in VS Code. They are simply an artifact of the markdown software we have used and can be ignored. They just provide a way of running chunks of code without seperating them onto seperate lines.

Experiments

The next step is to construct a computional experiment designed to investigate the effect of different variables on population and community dynamics. To do this we construct a gradient of variables as vectors and then simulate the BEFW model multiple times using a loop. To illustrate this, we're going to reproduce example 1 from **Delmas et al. 2016**. The aim of this example is to investigate the effect of increasing K on food web diversity. In addition, we're also going to allow α (interspecific competition relative to intraspecific competition) to vary and repeat the experiment 5 times with 5 different initial networks.

First, we define the experiment by creating vectors of our variables and fixing the number of repetitions:

```
[0.92, 1.0, 1.08]
α =
 \alpha = [0.92, 1.0, 1.08]
 • # 0.92 - the interspecific competition is smaller than the intraspecific competition
   promoting coexistence
 • # 1.0 - neutrally stable
 • # 1.08 - the intraspecific competition is smaller the interspecific competition
   favouring competitive exclusion
k =
 [0.1, 0.16681, 0.278256, 0.464159, 0.774264, 1.29155, 2.15443, 3.59381, 5.99484, 10.0]
 • # vector of K
 - k = exp10.(range(-1,1,length=10))
 • # log scale from 0.1 to 10
reps = 5
 • # number of reps
 • reps = 5
```

We then create a dataframe to store the outputs:

and construct a while loop to generate the 5 unique initial networks, each of which contains 20 species with a connectance value of 0.15:

```
begin
     # list to store networks
     global networks = []
     # monitoring variable
     global l = length(networks)
     # while loop
     while l < reps
          # generate network
         A_bool = EcologicalNetworks.nichemodel(20,0.15)
          # convert the UnipartiteNetwork object into a matrix of 1s and Os
         Ad = adjacency(A_bool)
          A = Int.(Ad)
          # calculate connectance
         co = sum(A)/(size(A,1)^2)
          # ensure that connectance = 0.15
          if co == 0.15
              push!(networks, A)
              # save network is co = 0.15
         global l = length(networks)
     end
 end
```

We can then run the simulations by looping, using nested for loops, over the unique values of α and K, as well as the 5 unique initial networks. After each simulation we will save each output object to our active project as a JLD2 file and store any output metrics of interest in our dataframe:

```
# loop over networks
for h in 1:reps
      A = networks[h]
      # here, you might want to save a copy of the initial network using writedlm(A)
      # loop over α
      for i in 1:length(\alpha)
          # loop over K
          for j in 1:length(k)
          # create model parameters
          p = model_parameters(A, \alpha = \alpha[i], K = [k[j]], productivity=:competitive) #
  again, k values need []'s
          # assign biomasses
          bm = rand(size(A,1))
          # simulate
          out = simulate(p, bm, start=0, stop=2000)
          # dummy naming variables
          \alpha_{\text{num}} = \alpha[i]
          K_num = k[j]
          # save 'out' as a JLD2 object using the @save macro:
          @save "out_objects/model_output, network = h, alpha = \alpha_n = K
 $K_num.jld2" out
          # calculate output metrics
          diversity = foodweb_evenness(out, last = 1000)
          stability = population_stability(out, last = 1000)
          biomass = total_biomass(out, last = 1000)
          # push to df
          push!(df, [α[i], k[j], h, diversity, stability, biomass])
          # print some stuff - see how the simulation is progressing
          println(("\alpha = \$\alpha_num", "K = \$K_num", "network = \$h"))
          end
      end
end
• # the code will be much faster if you remove the @save command
```

We can then explore the outputs and plot our results. Here, instead of using the built in plotting recipe, we will construct a plot that matches figure 1 in **Delmas et al. 2016**. Specifically, we will plot food web diversity (y-axis) as a function of K (x-axis) and α (colour):

	α	K	network	diversity	stability	biomass
	_					
1	0.92	0.1	1.0	1.0	-0.00049472	0.105633
2	0.92	0.16681	1.0	1.0	-0.000473063	0.176206
3	0.92	0.278256	1.0	0.794265	-0.000383165	0.293979
4	0.92	0.464159	1.0	0.746302	-0.00039277	0.488871
5	0.92	0.774264	1.0	0.686863	-0.0015427	0.812639
6	0.92	1.29155	1.0	0.964897	-0.000777836	1.0517
7	0.92	2.15443	1.0	0.993487	-0.00174054	1.27699
8	0.92	3.59381	1.0	0.99946	-0.0031786	1.44472
9	0.92	5.99484	1.0	0.999898	-0.00533331	1.56164
10	0.92	10.0	1.0	0.999141	-0.00935681	1.63925
more						
150	1.08	10.0	5.0	0.594069	-0.827963	4.14109

- # explore outputdf

	α	K	network	diversity	stability	biomass
1	0.92	0.1	1.0	1.0	-0.00049472	0.105633
2	0.92	0.16681	1.0	1.0	-0.000473063	0.176206
3	0.92	0.278256	1.0	0.794265	-0.000383165	0.293979
4	0.92	0.464159	1.0	0.746302	-0.00039277	0.488871
5	0.92	0.774264	1.0	0.686863	-0.0015427	0.812639
6	0.92	1.29155	1.0	0.964897	-0.000777836	1.0517

first(df,6)

	α	K	network	diversity	stability	biomass
1	1.08	0.774264	5.0	NaN	-0.000790586	0.774243
2	1.08	1.29155	5.0	NaN	-0.000839386	1.29152
3	1.08	2.15443	5.0	0.509891	-1.03284	2.11173
4	1.08	3.59381	5.0	0.834122	-0.00180268	3.01781
5	1.08	5.99484	5.0	0.845222	-0.00350984	4.62282
6	1.08	10.0	5.0	0.594069	-0.827963	4.14109

```
last(df,6)
```

```
shp = [:square, :diamond, :utriangle]

• # set marker shapes
• shp = [:square, :diamond, :utriangle]
```

```
ls = [:solid, :dash, :dot]
     * # set line types
     ls = [:solid, :dash, :dot]
```

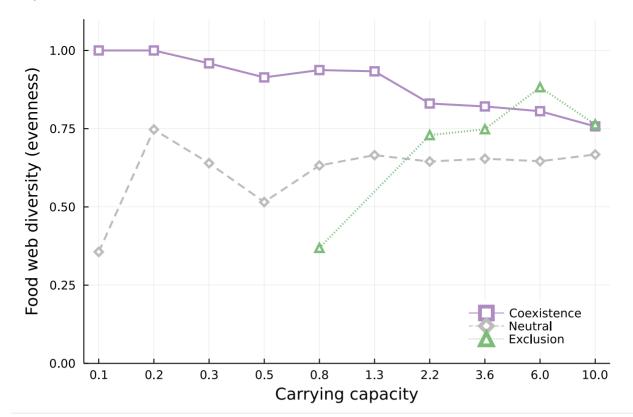


```
# set colours
clr = [RGB(174/255, 139/255, 194/255), RGB(188/255, 188/255, 188/255), RGB(124/255, 189/255, 122/255)]
# when we define colours in Julia they are printed
```

```
lbl = ["Coexistence", "Neutral", "Exclusion"]

• # set legend labels
• lbl = ["Coexistence", "Neutral", "Exclusion"]
```

```
• # make the plot
• for (i, \alpha) in enumerate(\alpha)
      # subset
      tmp = df[df.\alpha .== \alpha, :]
      # remove NaN values
      tmp = tmp[.!(isnan.(tmp.diversity)), :]
      # calculate mean across reps
      gdf = groupby(tmp, :K)
      meandf = combine(gdf, :diversity => mean)
      # command to avoid printing legends multiple times
      l = i == 1 ? lbl[i] : ""
      # add to pl
      plot!(pl, log10.(meandf.K), meandf.diversity_mean,
                msc = clr[i],
                mc = :white,
                msw = 3,
                markershape = shp[i],
                linestyle = ls[i],
                lc = clr[i],
                lw = 2,
                label = lbl[i],
                seriestype = [:line :scatter])
end
```



- # display plot
 plot(pl)

Finally, we can save our dataframe as a .csv file:

```
"My_data.csv"
```

- # save
- CSV.write("My_data.csv", df)