planktr: A multispecies plankton size-spectrum model in R

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[1]This document is included as a vignette (a LaTeX document created using the R package `knitr`) of the package `planktr`. It is automatically downloaded together with the package and can be accessed through R typing `vignette("planktr_vignette")`.

1 Introduction

The plaktonr package provides code to simulate a multi-species size-resolved community of unicellular plankton, using the model described in the paper [**?**]. The model differs from other planktonmodels in that it describes the growth during the lifetime of individual cells. So it resolves two size variables: the characteristic sizes of the species and the sizes of the individuals.

The main purpose is to investigate how the growth of individual cells affects the stability of the multi-species community. In the usual models of coexistence, where one models only the total abundance of the different species but not the distribution of sizes within species, there is the effect of "limiting similarity" which prevents similar species to coexist. Even when such a model has a dynamically stable coexistence steady state, this steady state is structurally unstable against small perturbations in the parameters. Giving one species even just a tiny competitive advantage over the others leads to a collapse, as expected from the competitive exclusion principle. The question we want to investigate with this package is whether this phenomenon can be avoided when the growth of cells is included in the model.

Modelling both species and individual sizes is computationally very costly. We solve this problem in this package by making use of spectral methods. This allows us to calculate the convolution integrals that describe the predation and the reproduction in the model in an efficient way that scales as $n \log n$ rather than n^2 with the number n of size steps. We also make use of the scaling properties of the rates to handle and store the populations in an economical way.

The model is already described in the paper [**?**]. This vignette can therefore concentrate on two tasks: to explain how we implemented the model numerically and to illustrate the use of the code.

2 Cell population dynamics

In our model we describe the abundance density $p(w, w_*, t)$ of plankton cells of size w and species w_* at time t, where a species is specified by the maximum size w_* for cells of that species.

2.1 Population balance equation

The basis of the model is the population balance equation [**?**, eq.(2.10)] that describes the effect that growth, division and death of cells have on the abundance density:

$$
\begin{aligned}
\frac{\partial}{\partial t} p(w, w_*, t) = & -\frac{\partial}{\partial w}\big[G_p(w, w_*)p(w, w_*, t)\big] \\
& + 2\int_0^{w_*} Q(w|w')K(w', w_*)p(w', w_*, t)\, dw' \\
& - K(w, w_*)p(w, w_*, t) - M(w, w_*)p(w, w_*, t).
\end{aligned}
\tag{2.1}
$$

The first term on the right-hand side describes the dynamics of a population of growing organism as an extension of the McKendrick–von Foerster equation [**?**, **?**] when $G_p(w, w_*)$ is the growth rate of a cell of size ω and species w_*. The second term is the rate at which cells of size w are produced from the division of cells of size $0 < w' < w_*$. It is composed from the rate $K(w', w_*)$ at which a particular cell of size w' and species w_* divides, the density $p(w', w_*)$ of such cells, and the probability density $Q(w|w')$ that the daughter cell has size w given that its parent had size w'. The factor 2 takes care of the fact that each parent cell yields two daughter cells. The third term is the rate at which cells of size w divide. The last term is the rate at which cells of size w die for whatever reason. The same equation describes this process for any species, just with a different value for w_* which enters like a parameter in the equation.

In the case of a discrete set of M species with characteristic sizes $w_i, i = 1, \ldots, M$ we can write

$$p(w, w_*) = \sum_{i=1}^{M} \delta(w_* - w_i) \, w_i^{-\gamma} p_i(w/w_i). \tag{2.2}$$

Note how we express the abundance of cells in species i as a function of the relative weight w/w_i with respect to that species' maximum weight w_i. This has the advantage that for all species this abundance has support in the same interval $w/w_i \in [, 1]$, were is the smallest relative size possible for any cell.

The reason for taking out the factor $w_i^{-\gamma}$ in (**??**) is that it turns out that in the steady state this has the effect that all species are described by the same function p_i, a phenomenon that is due to the scale-invariance of the model, see [**?**] for details. The same scale-invariance property also implies that, as long as we ignore predation,

$$G(w, w_*) = w_*^{1-\xi} g(w/w_*), \qquad\qquad K(w, w_*) = w_*^{-\xi} k(w/w_*),$$
$$M(w, w_*) = w_*^{-\xi} m(w/w_*), \qquad\qquad Q(w, w') = q(w/w')/w'.$$

If we substitute these expressions into the population balance equation (**??**) and perform a change of variables to $\omega = w/w_i$, we obtain the equations

$$w_i^{\xi} \partial_t p_i(\omega) = -\partial_\omega \left[g(\omega) p_i(\omega) \right] + 2 \int q(\omega/\omega') \left[k(\omega') p_i(\omega') \right] \omega'^{-1} d\omega'$$
$$- \left[k(\omega) + m(\omega) \right] p_i(\omega)$$

for all $i = 1, \ldots M$ and $\omega \in [\omega_{\min}, 1]$.

We assume that all cells consume a common nutrient whose concentration we denote by N. In the absence of growth through predation on other cells, we assume a von Bertalannfy growth model

$$g(\omega) = a(N)\omega^{\alpha} - b\omega^{\beta}, \tag{2.3}$$

where the positive first term comes from nutrient intake and the negative second term is the metabolic loss rate. For the dependence on the nutrient concentration we use

$$a(N) = a_{\infty} \frac{N}{N + N_0}. \tag{2.4}$$

2.2 Nutrient equation

The nutrient concentration is described by the equation

$$\frac{d}{dt} N = \rho(N) - \sigma(N, p) \tag{2.5}$$

where

$$\rho(N) = \rho_0 \left(1 - \frac{N}{N_0} \right) \tag{2.6}$$

is the rate at which the resource is replenished and where $\sigma(N, p)$ is the rate at which nutrients are consumed by the cells. Substituting the discrete set of species expression (**??**) into the expression [**?**, (2.13)] for the rate of nutrient consumption, and choosing units for the nutrient concentration so that one unit of nutrient produces one unit of cell biomass, we get

$$\sigma(N, p) = a(N) \sum_{i=1}^{M} w_i^{2-\xi-\gamma} \int \omega^{\alpha} p_i(\omega) d\omega. \tag{2.7}$$

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3 Predation

So far the species were developing independently of each other, with the only connection that they all feed on the same resource. This leads to only one constraint on the overall abundance of cells but no constraints on the relative abundances across species.

We now introduce a coupling between species by modelling predation in which cells eat other cells of other species. We assume that the rate at which a given cell of size w eats another given cell of size w' is given by $S(w, w') = w^\nu s(w/w')$. Both the death term and the growth term will receive an additional contribution from predation.

3.1 Death from predation

The contribution to the death rate $M(w, w_*)$ from predation is

$$M_P(w, w_*) = \int w'^\nu s\left(\frac{w'}{w}\right) p_c(w')dw' \tag{3.1}$$

where $p_c(w)$ is the total community abundance density of cells of size w, summed over all species:

$$p_c(w) = \int p(w, w_*)dw_* = \sum_{i=1}^{M} w_i^{-\gamma} p_i\left(\frac{w}{w_i}\right) = w^{-\gamma} \sum_{i=1}^{M} \left(\frac{w}{w_i}\right)^\gamma p_i\left(\frac{w}{w_i}\right) = w^{-\gamma}\tilde{p}_c(w). \tag{3.2}$$

Again the reason for pulling out the factor of $w^{-\gamma}$ is that the resulting $\tilde{p}_c(w)$ is constant in the steady-state. Substituting this into (**??**) gives

$$M_P(w, w_*) = w^{-\xi} \int s\left(\frac{w'}{w}\right)\left(\frac{w'}{w}\right)^{-\xi} \tilde{p}_c(w')w'^{-1}dw' = w^{-\xi}C_2(\log w). \tag{3.3}$$

3.2 Growth from predation

The contribution to the growth rate from predation is

$$G_P(w, w_*) = \int w^\nu s\left(\frac{w}{w'}\right) \epsilon w' p_c(w')dw', \tag{3.4}$$

where ϵ is the proportion of the prey mass w' that is converted to predator mass. Using the expression (**??**) for the community abundance this becomes

$$G_P(w, w_*) = \epsilon w^{1-\xi} \int s\left(\frac{w}{w'}\right)\left(\frac{w}{w'}\right)^{\gamma-2} p_c(w')w'^{-1}dw' = \epsilon w^{1-\xi}C_3(\log(w)). \tag{3.5}$$

Here $C_3(x)$ is a convolution integral.

4 Steady state solution

If we work with a continuum of species with characteristic weights w_* taking on any value on the real line, we can write down an analytic steady-state solution for the model. In this steady state the $p_i(w/w_i)$ are the same for all species and the community spectrum $\tilde{p}_c(w)$ is constant, i.e., independent

of w. The contributions to the death and growth rates from predation take the form $M_p(w, w_*) = w_*^{-\xi} m_p(\omega)$ and $G_p(w, w_*) = w_*^{-\xi} g_p(\omega)$ with

$$m_p(\omega) = \tilde{p}_c \omega^{-\xi} I_s(-\xi), \qquad g_p(\omega) = \tilde{p}_c \omega^{1-\xi} I_s(\gamma - 2), \tag{4.1}$$

where we have introduced the moments of the feeding kernel

$$I_s(\lambda) = \int s(z) z^{\lambda-1} dz = \int s(e^x) e^{\lambda x} dx. \tag{4.2}$$

We will now put periodic boundary conditions on the community spectrum, i.e., we artificially assume that the sizes of cells lie on a circle with the size of the smallest cell identified with the size of the largest cell. The hope is that these artificial boundary conditions for the very small and very large species will not have a dramatic effect on the species of intermediate size.

5 Convolution integrals

The model involves three convolution integrals. These usually take on the order of N^2 calculations to evaluate, where N is the number of x-steps. By using FFT this can be cut down to order $N \log N$.

5.1 Reproduction

To see that the integral in (??) is a convolution integral, we write $\omega = e^{\tilde{x}}$ and $\omega' = e^{\tilde{y}}$ and observe that then $\omega'^{-1} d\omega' = dy$ so that the integral takes the form

$$\int q(\omega/\omega') \left[k(\omega') p_i(\omega') \right] \omega'^{-1} d\omega' = \int q(e^{\tilde{x}-\tilde{y}}) k(e^{\tilde{y})p_i(e^{\tilde{y}})d\tilde{y}}$$

$$= \int_{\tilde{x}_{\text{th}}}^0 f_1(\tilde{x} - \tilde{y}) g_1(\tilde{y}) d\tilde{y} = C_1(\tilde{x}).$$

The subscript 1 is to distinguish this convolution integral from two others that will arise when we start including predation in the model. We need to calculate the convolution integral for all $\tilde{x} \in [x_{\min}, 0]$, where $x_{\min} = \log$ is the smallest possible log cell size. The reason we can restrict the integral to run only from $\tilde{x}_{\text{th}}$ to 0, where $\tilde{x}_{\text{th}}$ is the log of the threshold size below which not division is taking place, is that the factor $g_1(\tilde{y})$ is zero outside that interval anyway. With $\tilde{y}$ ranging only over the interval $[\tilde{x}_{\text{th}}, 0]$, the largest region in which the function f_1 gets evaluated is the interval $[x_{\min}, -\tilde{x}_{\text{th}}]$. Thus we can replace f_1 by a periodic function $\bar{f}_1$ with period $L = -x_{\min}$, without changing the value of the integral, because $\bar{f}_1$ is zero on the interval from 0 to $-\tilde{x}_{\text{th}}$ and agrees with f_1 on the interval $[x_{\min}, 0]$. We can then also replace g by a periodic function $\bar{g}$ with the same period L, which again does not change the integral because $\bar{g}$ agrees with g on the interval $[x_{\min}, 0]$ and is not used outside that interval. This gives us

$$C_1(\tilde{x}) = \int_{x_{\min}}^0 \bar{f}(\tilde{x} - \tilde{y}) \bar{g}(\tilde{y}) d\tilde{y}.$$

Because this is an integral over a complete period of the two periodic functions $\bar{f}$ and $\bar{g}$ it can be calculated by Fast Fourier Transform.

5.2 Death by predation

The contribution to the death rate from predation contains the convolution integral $C_2(x)$ where

$$C_2(x) = \int g_2(x - y) f_2(y) dy = \int g_2(y) f_2(x - y) dy \tag{5.1}$$

with

$$g_2(x) = s\left(e^{-x}\right)e^{\xi x} \quad \text{and} \quad f_2(x) = \tilde{p}_c\left(e^x\right). \tag{5.2}$$

We need to evaluate this convolution for all values of x in the interval $[x_{\min}, x_{\max}]$ where $x_{\min}$ and $x_{\max}$ are the log of the smallest and the largest cell size among all species. For simplicity we will from now on choose mass units so that $x_{\max} = 0$.

We assume that the predation kernel $s(e^x)$ has support only in a finite interval $[\beta_P - \Delta_P/2, \beta_P + \Delta_P/2]$. Thus $g_2(x)$ has support on $[-\beta_P - \Delta_P/2, -\beta_P + \Delta_P/2]$. We furthermore assume that $[-\beta_P - \Delta_P/2, -\beta_P + \Delta_P/2] \subset [x_{\min}, 0]$.

These periodic boundary conditions allow us to evaluate the convolution integral C_2 with Fouier methods.

5.3 Growth by predation

The contribution to the death rate from predation contains the convolution integral $C_3(x)$ where

$$C_3(x) = \int g_3(x-y)f_3(y)dy = \int g_3(y)f_3(x-y)dy \tag{5.3}$$

with

$$g_3(x) = s\left(e^x\right)e^{(\gamma-2)x} \quad \text{and} \quad f_3(x) = \tilde{p}_c\left(e^x\right). \tag{5.4}$$

We need to evaluate this convolution for all values of x in the interval $[x_{\min}, 0]$. Now the support of g_3 is $[\beta_P - \Delta_P/2, \beta_P + \Delta_P/2] \subset [0, -x_{\min}]$. We make use of the periodicity of f_3 to rewrite

$$C_3(x) = \int_0^{-x_{\min}} g_3(y)f_3(x-y)dy = \int_{x_{\min}}^0 g_3(y-x_{\min})f_3(x-y)dy = \int_{x_{\min}}^0 \tilde{g}_3(y)f_3(x-y)dy \tag{5.5}$$

with

$$\tilde{g}_3(x) = s\left(e^{x-x_{\min}}\right)e^{(\gamma-2)(x-x_{\min})}. \tag{5.6}$$

This $\tilde{g}_3$ now has support contained in $[x_{\min}, 0]$ and the convolution integral can be evaluated by Fourier methods.

6 Implementation details

6.1 Logarithmically-spaced weight classes

In this section we will discuss implementation details.

The following is just pasted from elsewhere and needs to be rewritten

Again performing the change of variable $\tilde{x} = \log(\omega)$ in the integral gives

$$\int \omega^\alpha p_i(\omega)d\omega = \int \omega^{\alpha+1}p_i(\omega)d\tilde{x}. \tag{6.1}$$

The reason we prefer the integral in the form on the right-hand side is that in our code we will work with logarithmically spaced intervals in ω which translates to equally-spaced intervals in $\tilde{x}$, which then simplifies the calculation of the integral with respect to $d\tilde{x}$ by the Riemann sum. For equally-spaced interpolation points and a periodic integrand the second-order trapezoidal rule simplifies to the Riemann sum.

References

[1] Cuesta, J.A., Delius, G.W., Law, R., 2016. Sheldon Spectrum and the Plankton Paradox: Two Sides of the Same Coin. A trait-based plankton size-spectrum model. arXiv preprint arXiv:1607.04158.