

Constructing Steady States Of Multi-species Size Spectrum Models

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We have a multi species size spectrum model as described in the mizer vignette, except

$$\psi_i(w) = \begin{cases} 0 & \text{if } w < w_{*i} \\ \left(\frac{w}{W_{\infty,i}}\right)^{1-n} & \text{otherwise} \end{cases} \quad (1)$$

we also suppose our parameters are such that

$$n = p$$

$$\lambda = q + 2 - n$$

$$\mu_f(w) = k = 0$$

$$\theta_{ij} = 1$$

Given that, here is my attempted recipe for constructing a steady state for some size spectrum setups:

Choose any value of $\mu_0 > 0$.

We explicitly model s species, which may have any different species specific parameters. For each species i let

$$f_{0i} = \frac{\gamma_i}{\frac{h_i \beta_i^{2-\lambda} \exp(-(\lambda-2)^2 \sigma_i^2 / 2)}{\sqrt{2\pi\kappa\sigma_i}} + \gamma_i} \quad (2)$$

be the feeding level (as experienced by species i individuals feeding upon a community at abundance $\kappa w^{-\lambda}$), and let $\tilde{h}_i = \alpha_i h_i f_{0i} - k_{si}$.

Let $N_i(w)$ be a steady state of the MvF equation of species i with growth rate $\tilde{h}_i w^n (1 - \psi_i(w))$ and death rate $\mu_0 w^{n-1}$. In particular

$$N_i(w) = \frac{1}{\tilde{h}_i w^n} (w_{ei}/w)^{\mu_0/\tilde{h}_i} \times \begin{cases} 1 & w < w_{*i} \\ \frac{(1-(w/W_{\infty,i})^{1-n})^{(\mu_0/(\tilde{h}_i(1-n))) - 1}}{(1-(w_{*i}/W_{\infty,i})^{1-n})^{\mu_0/(\tilde{h}_i(1-n))}} & w > w_{*i} \end{cases} \quad (3)$$

Any multiple of $N_i(w)$ is also a steady state of the MvF, and for our community construction, we can choose any abundance multipliers $A_i \geq 0$ and $A_i N_i(w)$ is also a steady state of the MvF. We suppose that the abundance of background resource at weight w is $N_R(w) = \kappa w^{-\lambda} - \sum_{i=1}^s A_i N_i(w)$. In this resulting system,

where species i has an abundance $A_i N_i(w)$ at weight w , and the background resource abundance has abundance $N_R(w)$, let $\mu_{pi}(w)$ denote the predation mortality level on species i from the explicitly modeled species $j \in 1, \dots, s$. Now if we choose a background mortality rate of $\mu_{bi}(w) = \mu_0 w^{n-1} - \mu_{p,i}(w)$ for the i th species, then its total mortality rate will be $\mu_i(w) = \mu_{p,i}(w) + \mu_{b,i}(w) = \mu_0 w^{n-1}$. Also, the growth rate will be $g_i(w) = \hbar_i w^n (1 - \psi_i(w))$. Since these are the same death and growth rates that we assumed in construction of our solutions $A_i N_i(w)$, we must have a steady state of the Mvf. We also have to choose parameters e.g., the reproductive efficiencies ϵ_i so that the reproduction boundary condition

$$g_i(w_{e,i}) N_i(w_{e,i}) = \frac{\epsilon_i}{2w_{e,i}} \int_0^\infty N_i(w) E_{r,i}(w) \psi(w) dw \quad (4)$$

is met for each species. This should result in a steady state of the size spectrum dynamics.

The mizer code [stable_community_gurnard_really.R] we did before involves gurnard and background species.

$$\mu_0 = (1 - f_{0B}) \sqrt{2\pi} \kappa \gamma_B \sigma_B \beta_B^{n-1} \exp(\sigma_B^2 (n-1)^2 / 2)$$

describes the mortality rate induced by the background species.

In this case the the first $s-1$ species are the background species so $\beta_1 = \dots = \beta_{s-1} = \beta_B \neq \beta_s$ etc, and the s th and final species is the gurnard with its own different parameters. I guess this code works in a similar way to the above recipe, except this code has plankton dynamics, and we cut the plankton off at the first zero. We still need to test if things will work if we cut the background mortality term off.

Returning to the general steady state construction problem. If one is interested in modeling a multi species ecosystem without so much artificial background death and mortality rates, one can include extra background species that are explicitly modeled, with parameters like β_B etc. above. Setting such modeled background species to the proper abundances to model induce the proper growth and death rates, then allows us to reduce the amount of artificial background death and background resource abundance we have to add to create a steady state according to the above recipe.

There are more general ways to make new steady states from old by making sub population transplants that preserve death and growth rates. If we have a pair of steady states of a size spectrum model (perhaps with different species extinct in either state), and then we do transplant surgery -cutting away some of the individuals from the second steady state, and replacing them with a subset of individuals from the first steady state, that are grafted on. If the growth and death rates are the same for the incumbent and grafted individuals before and after this type of population transplant then it will result in a new steady state.

More generally if we have two mizer steady states X and Y of different systems with different parameters if we can choose a subset x of species from X and a subset y of species from Y then we can sometimes transplant/swap populations x and y around in their ecosystems, (cutting their abundances out

and swapping them round). The conditions required for the resulting two "post transplant" states to be steady states are:

(1) members of x experience the same growth and death rate as a result of their contact with $X \setminus x$ before the transplant, as they experience with the new surroundings (post-transplant) via their contact with $Y \setminus y$.

(2) members of $X \setminus x$ experience the same growth and death rate as a result of their contact with x before the transplant, as they experience with the new surroundings (post-transplant) via their contact with y .

(3) members of y experience the same growth and death rate as a result of their contact with $Y \setminus y$ before the transplant, as they experience with the new surroundings (post-transplant) via their contact with $X \setminus x$.

(4) members of $Y \setminus y$ experience the same growth and death rate as a result of their contact with y before the transplant, as they experience with the new surroundings (post-transplant) via their contact with x .

Time Dependent Transplant Principal

Let $\overline{N^1} = (N_1^1, \dots, N_s^1)$ be a state of an s species size spectrum model. Here $N_i^1 : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ is such that $N_i^1(w)$ represents the density of species i individuals of weight w .

Let $\overline{N^2} = (N_1^2, \dots, N_s^2)$ be another state of our size spectrum model. Let $T > 0$. Let $K \subseteq \{1, \dots, s\}$ be a subset of species. Let

$$\overline{N^*} = \overline{N^1} - \left(\sum_{i \in K} (\delta_{1i} N_1^1, \delta_{2i} N_2^1, \dots, \delta_{si} N_s^1) \right) + \left(\sum_{i \in K} (\delta_{1i} N_1^2, \delta_{2i} N_2^2, \dots, \delta_{si} N_s^2) \right) \quad (5)$$

denote the state obtained by replacing all the individuals in $\overline{N^1}$ with a species in K , with the set of individuals from $\overline{N^2}$ with a species in K . Here δ_{ij} is the Kronecker delta.

For $t \geq 0$ let $\tau_t[\overline{N^1}]$ denote the state obtained by evolving $\overline{N^1}$ for a time t under the MvF equation.

Let $g_i[\overline{N^1}](w)$ denote the growth rate that a species i individual of weight w has when the system is in state $\overline{N^1}$. Similarly let $\mu_i[\overline{N^1}](w)$ denote the mortality rate that a species i individual of weight w has when the system is in state $\overline{N^1}$. Suppose $T > 0$.

If $\forall t \in [0, T], \forall w > 0, \forall i \notin K$ we have

$$\begin{aligned} \left(\tau_t[\overline{N^1}] \right)_i(w) > 0 &\Rightarrow g_i[\tau_t[\overline{N^1}]](w) = g_i[\tau_t[\overline{N^*}]](w), \\ \mu_i[\tau_t[\overline{N^1}]](w) &= \mu_i[\tau_t[\overline{N^*}]](w) \end{aligned}$$

and $\forall t \in [0, T], \forall w > 0, \forall i \in K$ we have

$$\begin{aligned} \left(\tau_t[\overline{N^2}] \right)_i(w) > 0 &\Rightarrow g_i[\tau_t[\overline{N^2}]](w) = g_i[\tau_t[\overline{N^*}]](w), \\ \mu_i[\tau_t[\overline{N^2}]](w) &= \mu_i[\tau_t[\overline{N^*}]](w) \end{aligned}$$

then

$\forall t \in [0, T], \forall w > 0, \forall i \notin K$ we have

$$\left(\tau_t[\overline{N^1}] \right)_i(w) = \left(\tau_t[\overline{N^*}] \right)_i(w) \quad (6)$$

and $\forall t \in [0, T], \forall w > 0, \forall i \in K$ we have

$$\left(\tau_t[\overline{N^2}] \right)_i(w) = \left(\tau_t[\overline{N^*}] \right)_i(w). \quad (7)$$

Essentially the principal says if you transplant species in set K from $\overline{N^2}$ into $\overline{N^1}$ in such a way that all individuals involved encounter the same time dependent death and growth rates, both before and after the transplant, then the dynamics of the abundances of such species will be the same in the pre and post transplant systems. A species case of the time dependent transplant principal is the case where $\overline{N^1}$ and $\overline{N^2}$ are steady states. In this case, if the transplant can be performed in a way that preserves mortality and growth rates then the post transplant state $\overline{N^*}$ will also be a steady state. This steady state transplant principal is used when we build systems with power law based death and growth. The steady state transplant principal may also shed light on neutrality like effects we often see when considering the set of all steady states of systems with near homogeneous species, by showing how one can move around in the near affine set of all steady states by performing growth and death preserving transplants.

Speculation

- In the case where the death and growth rates are fixed, any linear combination of steady states is a steady state,
- In general multi species size spectrum models, the set of steady states is approximately an affine set.
- The volumes of the basins of attraction of steady states vary, and the affine set may hold a mixture of stable and unstable steady states.
- If S is the set of steady states of the system and one introduces an extra mortality term then the set of steady states of the new system is homeomorphic to a subset of S or S is homeomorphic to a subset of the steady states of the new system.
- Introducing an extra mortality term $\mu_e(w)$ that does not have the form $A \cdot w^{(n-1)}$ breaks up the affine structure of the steady states

- In a system with sufficiently heterogeneous species, there is just one steady state.
- Often heterogeneous systems are unstable, but adding a $\chi > 0$ makes them stable and shrinks the set of attractors towards the symmetric solution

Questions

- How does the set of steady states change when we continuously vary the background death rate, or the plankton spectrum ?
- Can convex sets of steady states with more than one element occur in systems where all species have rather different parameters ?
- In what sense is the affine/convex structure of steady states only approximate when the growth and death rates are not fixed ?

Objectives

- Prepare Barcelona talk.
- Retry getting the gurnard stable - I made a correction to the code, as found in `stable_community_gurnard_post_comp.R`, but now, so far, it seems hard to get the `background+gurnard` system to stabilize without using χ .
- Write newton raphson scheme and explore structure and stability of steady states
- formally organize results so far with proofs etc.
- I just pushed an update of `multisteadystate.pdf`.

More Speculation

We have an s species multi species size spectrum model. A transplant is where one replaces some individuals from one state with individuals from another state in a way that preserves growth and death rates. The transplant hull $H(S)$ of a set of states S that can be obtained by repeatedly performing transplants, starting with the members of S . We say a set of states S is transplant independent if each member x of S lies outside the transplant hull $H(S - \{x\})$ of the other members.

Conjecture If N_1, N_2, \dots, N_s are transplant independent steady states then the transplant hull $H(N_1, N_2, \dots, N_s)$ of these states is the set of all steady states of the system.

Conjecture The transplant hull of a set of states is equal to the affine set of such steady states.

To prove conjecture note that the set of steady states must be connected by transplant paths, because for any two steady states Brouwer's fixed point

theorem proves the existence of species transplants that preserve death and growth rates, therefore the problem of finding the set of all steady states reduced to the problem of finding a large enough set of steady states such that their transplant hull is the set of all steady states of the entire system. The fact that transplant hull is equivalent to affine hull can be seen by noting that, since they are the same, under growth and death preserving transformations, the transplant hull $H(S)$ of a set S of steady states are also steady states of the system p which has its growth and death rates held fixed at these values, and we know from the linearity of p , that $H(S)$ is an affine set.

If this is indeed true, then the set of all steady states of a general s species size spectrum model is just equal to the set of all affine combinations of any s linearly independent steady states.

To prove this we have to show the equivalence of transplant and affine hulls, and we have to show that a transplant can always be done between two steady states.

At least, it seems the set of steady states equals the union of one or more disjoint subsets, each of which is the transplant hull of collections of steady states. I suspect the entire set of steady states is organized into one transplant hull, but to see this we may need to use something like a fixed point theorem to (try and) prove that it is always possible to do a transplant between any two different steady states to make another steady state (if that is true).