Functional analysis of ecosystem dynamics:

Supplementary Appendix for Unifying concepts of biological function from molecules to ecosystems.

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We represent carbon / energy / biomass by the cell count in each living compartment and write differential equations to account for this in each compartment. Additionally, we account for a generic nutrient x which is supplied by the nutrient supplier compartment with biomass N (consisting of all organisms with a nutrient recycling or supply role: detritivores, decomposers and nutrient fixers) and also the catalytic effect of reproductive facilitators of primary producers (selected from among consumers), these being the pollinators and seed dispersers. The dynamics of nutrient suppliers combines the total growth of all waste processors combined, for which the resource is waste - in various forms and states of decay - as it passes along a process chain within this compartment. The total flux of waste is assumed to be proportional to the total living biomass of the system. Growth of nutrient suppliers is assumed to be limited by density-dependence and by the specific rate of waste processing, represented by a functional response:

$$\dot{N} = N(f_N(B)(1 - \alpha_N/K_N)), \tag{1}$$

where $B = \sum_T(B_T)$ is the total biomass of the system; B_T is the biomass of trophic level T. The function $f_N(\cdot)$ is the 'functional response' of nutrient producers. α_N is the competition coefficient (all causes) among nutrient suppliers and K_N is their aggregate carrying capacity. We also define $f_P(\cdot)$ for primary producers and $f_C(\cdot)$ for all consumers. In each case, the functional response is (for simplicity) given by:

$$f_X(y) = (\frac{\tau y}{1+y}), \tag{2}$$

where y is the resource needed for X to grow (this is a Michaelis-Menten or type II functional response) and τ is the trophic (ecological) efficiency. We assume nutrient x is supplied by nutrient suppliers in proportion to their biomass $\dot{x} = \nu N$, where ν is the specific rate of recycling nutrients that can be taken up by the primary producers.

Primary producer dynamics consist of density-dependent growth (including inter- and intra-specific competition) regulated by reproductive facilitation (pollination, seed dispersal etc., provided by those consumer populations which contribute) and predation loss from consumers. Reproduction follows a saturating function of facilitator population, for which we also use the type II functional response in analogy to equation 2. For the ith primary producer:

$$\dot{P}_i = P_i \left((f_P(\dot{x})\ \psi_i \frac{R_i}{1+R_i}\ (1 - \frac{\sum_j \alpha_{ij}^P P_j}{K_{Pi}})) - \sum_j C_j \gamma_{ij} f_C(P) \right), \tag{3}$$

where $R_i = \sum_j \rho_{ij} C_j$ is aggregated facilitation in which ρ_{ij} is the contribution to reproductive facilitation from the jth consumer to the ith primary producer; ψ_i is the efficiency of reproductive response by the ith primary producer to reproductive facilitation (it includes allocation of resources to reproduction); α^P_{ij} is the competition coefficient (an element of the competition matrix) for primary producers and K_{Pi} is the carrying capacity of the ith primary producer. Note that this explicit inclusion of competition accounts for all forms of competition not implicitly represented by scramble competition over the resource x. Primary producer biomass growth is controlled by the functional response to nutrient input rate $f_P(\dot{x})$. Primary producer biomass is removed at a rate equal to the sum of consumer populations $(\sum_j C_j)$ multiplied by their predator-prey interaction coefficient γ_{ij} and the consumer's functional response to primary producers in total $f_C(P)$. The interaction coefficients therefore represent the diet choice of consumers for primary producers by the interaction matrix.

We account for the dynamics of consumer biomass grouped into trophic layers, so indexing trophic levels by $\mathtt{k}$, $(T^{\mathtt{k}}\{\subset C\} = \sum_i C_{i\in \mathtt{k}}$ (assuming discrete trophic levels) (e.g. T^1 is the aggregate biomass of all C_i in trophic level 1 - note use of special typeface for trophic level count). This enables us to form an analogous mass dynamics equation for each member i of each trophic level, starting with the first:

$$\dot{T}^1_i = T^1_i \left((f_C \sum_j (\gamma^1_{ij} P_j)\ (1 - \sum_j \alpha^1_{ij} T^1/K^1)\ - \sum_j T^2_j f_C(\gamma^1_{ij} T^1_i) \right). \tag{4}$$

The first term is the functional response applied over all that the ith consumer of the first trophic level eats; the second term is the density-dependence (with competition) of the rate of growth of trophic level 1, for which the aggregate carrying capacity is K^1 and the last term is the consumption of the ith member by all members of the second trophic level.

Clearly then, we have for subsequent trophic levels:

$$\dot{T}^{\mathtt{k}}_i = T^{\mathtt{k}}_i \left(f_C \sum_j (\gamma^{\mathtt{k}}_{ij} T^{\mathtt{k}-1}_j)\ (1 - \sum_j \alpha^{\mathtt{k}}_{ij} T^{\mathtt{k}}/K^{\mathtt{k}})\ - \sum_j T^{\mathtt{k}+1}_j f_C(\gamma^{\mathtt{k}}_{ij} T^{\mathtt{k}}_i) \right). \tag{5}$$

It is usual to ssume that competition is over only the resources represented (i.e. scramble competition). Following this, we can dispense with the general competition terms ($\alpha_{ij} \to 0\ \forall i, j$), simplifying the 'horizontal' relationships in every trophic level.

In the specific example of Figure 1 and 2 (main text), $P = \{P_1, P_2\}$; $T^1 = \{C_1, C_2\}$; $T^2 = \{C_3, C_4\}$ and $T^3 = \{C_5\}$. Both C_1 and C_2 consume both primary producers, so $\gamma^1_{ij} = 1\ \forall i, j$, but C_3 only eats C_1 and C_4 only eats C_2 so $\gamma^2 = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$. $\gamma^3 = [1, 1]$. The diagram shows that C_4 facilitates reproduction in P_1 and P_2, whereas C_1 facilitates only P_1 and no other consumers facilitate plant reproduction, hence $\rho = \begin{bmatrix} 1 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}$ (assuming equal and perfect efficiency of facilitation, just for simplicity). Finally, we let $\tau = 1$ for plant trophic efficiency w.r.t. nutrients, but, as standard, $\tau = 0.1$ for all higher trophic levels.

Of course, we could have a lot more parameters, fitting separate functional responses and interaction coefficients etc., but for an illustrative example of an ecosystem as an autocatalytic set, there is no need.

For our specific example, equation 4 (with $R_1 = C_1 + C_4$) is disaggregated as:

$$\dot{P}_1 = P_1(\frac{\dot{x}}{1+\dot{x}})\,\psi(\frac{R_1}{1+R_1})\; - (C_1 + C_2)(\frac{P_1}{1+P_1}) \tag{6}$$

$$\dot{P}_2 = P_2(\frac{\dot{x}}{1+\dot{x}})\,\psi(\frac{C_4}{1+C_4})\; - (C_1 + C_2)(\frac{P_2}{1+P_2}). \tag{7}$$

For primary consumers, with $P = (P_1 + P_2)$:

$$\dot{C}_1 = C_1\tau(\frac{P}{1+P})\; - C_3(\frac{C_1}{1+C_1}) \tag{8}$$

$$\dot{C}_2 = C_2\tau(\frac{P}{1+P})\; - C_4(\frac{C_2}{1+C_2}), \tag{9}$$

and for secondary consumers, with $C = (C_3 + C_4)$:

$$\dot{C}_3 = C_3(\tau(\frac{C_1}{1+C_1})\; - C_5(\frac{1}{1+C})) \tag{10}$$

$$\dot{C}_4 = C_4(\tau(\frac{C_2}{1+C_2})\; - C_5(\frac{1}{1+C})), \tag{11}$$

noting that the flow of biomass from C_3 and C_4 are each limited by the functional response of C_5 to both its food sources simultaneously (i.e. flow from C_3 is $\frac{C}{1+C}\frac{C_3}{C} = \frac{C_3}{1+C}$). Finally, the dynamics of the top predator $C5$ are just:

$$\dot{C}_5 = C_5(\tau(\frac{C}{1+C}) - \mu_5), \tag{12}$$

to which we have added the mortality term μ_5 to enable a biologically realistic equilibrium. The nutrient providers grow from the total of wastes across the system, which constitutes their resource, via a functional response as in equation 1. Nutrient production follows the dynamics of the nutrient provider compartment, minus the rate of take-up by the primary producers:

$$\dot{x} = \nu N(\frac{B}{1+B})\,(1 - \alpha_N\frac{N}{K_N})\; - P(\frac{x}{1+x}), \tag{13}$$

in which $B = (P_1 + P_2 + C_1 + C_2 + C_3 + C_4 + C_5)$. Equations 6-13 are solved simultaneously to find the system dynamics. Setting the r.h.s. of all except for $\dot{x}$, solves to find the nutrient flow rate and compartment biomasses in equilibrium conditions, but solving the system also requires a set of initial conditions to be set, for which we chose: $x(0) = 100$; $P_1(0) = 10$; $P_2(0) = 10$; $C_1(0) = 1$; $C_2(0) = 1$; $C_3(0) = 0.1$; $C_4(0) = 0.1$; $C_5(0) = 0.02$. Unfortunately, the system cannot be solved analytically and in practice it has proved too difficult to obtain numerical solutions using standard methods. For the illustration, we have resorted to a finite-difference numerical representation, for which we found a near equilibrium solution with the following parameter values:

$\nu = 0.1$, $\alpha_N = 0.05$, $\psi = 0.2$, $\tau = 0.1$, $\mu_5 = 0.1$.

Fig. 1 shows the transient dynamics of this system, illustrating the complicated relationships among component parts which is typical of systems that have both positive and negative feedback loops (such as in simulations of the economy). For example the nutrients pool (a) and biomass of nutrient producers (b) start highly correlated but quickly become anti-correlated as the nutrients cause plant growth, which stimulates the withdrawal of more nutrient out of the system. This then gets caught up in two mutually antagonistic positive feedback cycles, both starting with growth in consumers, which a) increases total biomass causing increased growth of nutrient suppliers and b) increases plant growth vial reproductive facilitation. In the end these influences all balance out to give near constant values for all system components (which we have interpreted as a de-facto equilibrium).

To illustrate the contribution of a particular function to the master function of total system biomass, we plot the sensitivity of equilibrium biomass to variation in ψ in figure 2. We would interpret the gradient of this curve as a measure of the effectiveness of this (behaviourally based) function on the functioning of the community as a whole.

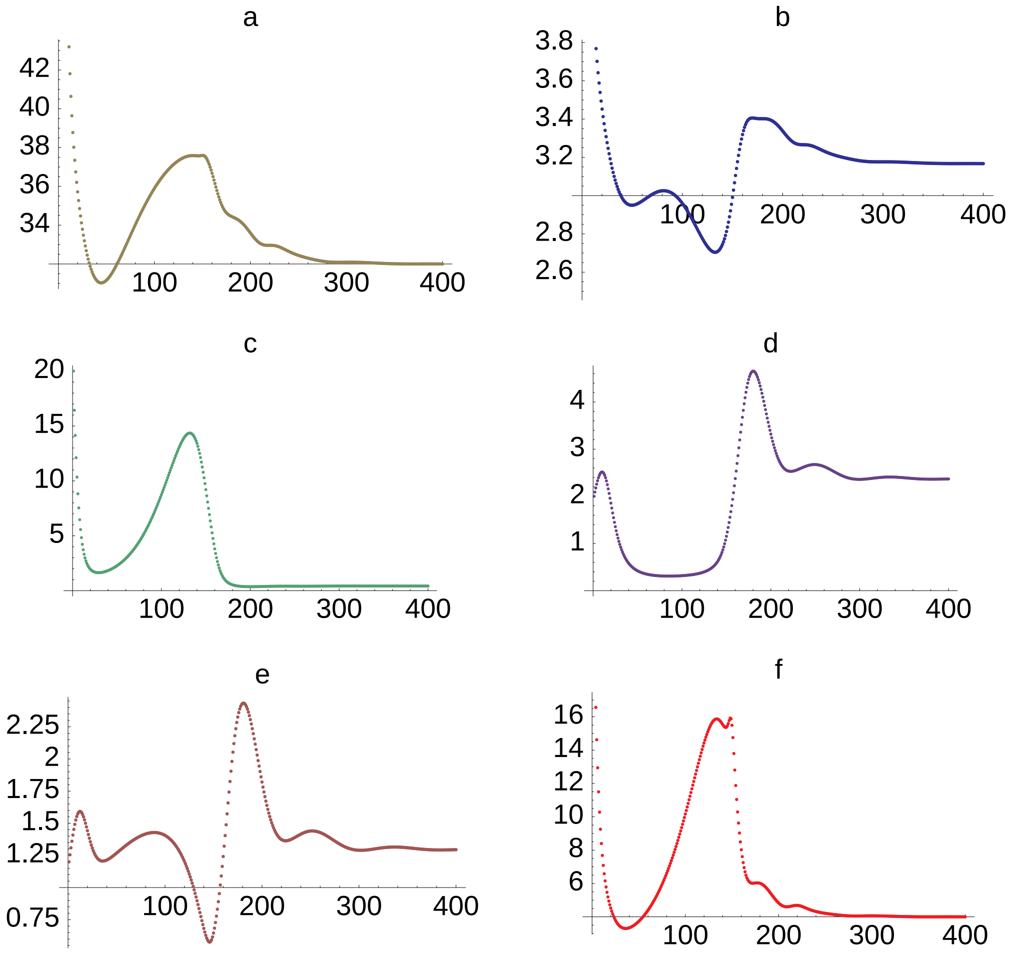

Figure 1: System dynamics, showing a) nutrient provider biomass N; b) nutrient pool x; c) plant biomass $P_1 + P_2$; d) primary consumer biomass $C_1 + C_2$; higher trophic level biomass $C_2 + C_3 + C_4$. All with $\psi = 0.16$ and other parameters as stated above. The plot was formed from finite-difference numerical calculations of the system (equations 6-13), with Mathematica (Wolfram Research).

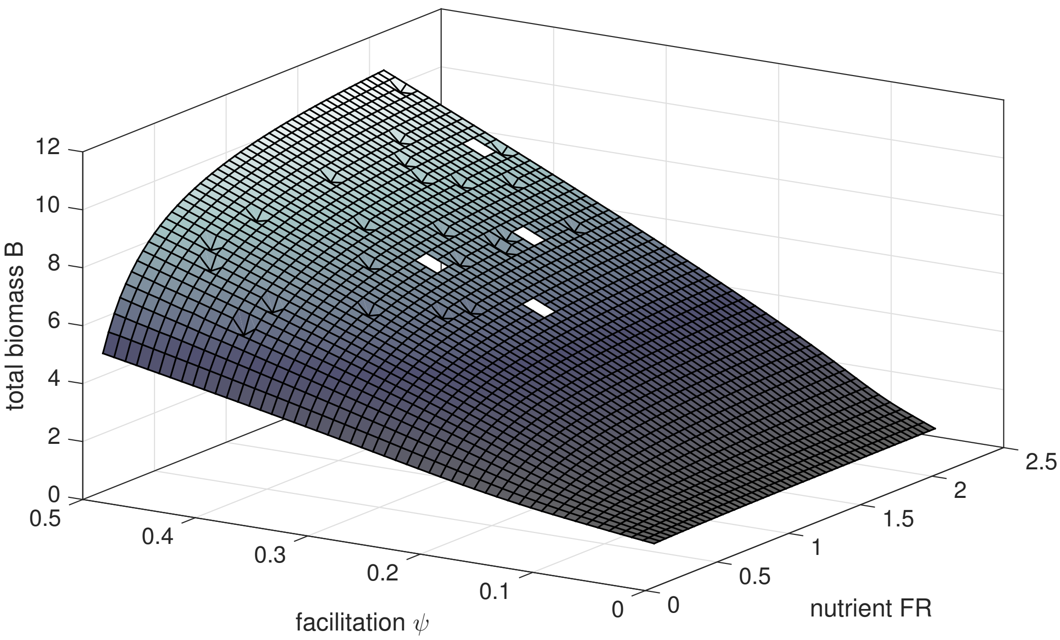

Figure 2: How equilibrium total system biomass B - the master function - varies with the rate of plant reproductive facilitation by consumer species ψ and also the asymptote of the functional response of nutrient providers, to supply of raw materials (nutrient FR). The plot was formed from finite-difference numerical calculations of the system (equations 6-13), with Mathematica (Wolfram Research). Some combinations of values led to indeterminate results, which is the reason for the few missing and aberrant results. (This figure also appears as figure 2 in the main text).