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John C. Moore; Peter C. de Ruiter; H. William Hunt

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John C. Moore,* Peter C. de Ruiter, H. William Hunt

The lengths of food chains within ecosystems have been thought to be limited either by the productivity of the ecosystem or by the resilience of that ecosystem after perturbation. Models based on ecological energetics that follow the form of Lotka-Volterra equations and equations that include material (detritus) recycling show that productivity and resilience are inextricably interrelated. The models were initialized with data from 5- to 10-year studies of actual soil food webs. Estimates indicate that most ecological production worldwide is from ecosystems that are themselves sufficiently productive to recover from minor perturbations.

Primary productivity and dynamic stability (the return to steady state after perturbation) have been treated as independent constraints on the length of food chains in ecosystems (1, 2). Systems differing greatly in productivity have food chains of similar length, and models indicate that longer food chains are less stable. Models often consist of primary producers, herbivores, and predators and exclude detritus, even though a high percentage of primary production is not consumed alive (3). When studies included energetics and detritus feedbacks, ecosystem productivity was found to influence food web diversity (4), structure (5), and resilience (6). In this report we develop models with and without detritus that include energetics as represented by birth and death rates, feeding rates, and assimilation and production efficiencies. We demonstrate that primary productivity affects the dynamic stability of food chains and, hence, their length. Few ecosystems worldwide are less productive (7) than the lower limits of productivity established by the models.

J. C. Moore, Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80539.
P. C. de Ruiter, Department of Soil Biology, DLO-Institute for Soil Fertility Research, 9750 RA Haren (Groningen), Netherlands.
H. W. Hunt, Department of Range Science and the Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80526.

*To whom correspondence should be addressed.

Food chains based on primary producers are frequently modeled after Lotka-Volterra:

$$\frac{dX_i}{dt} = r_i X_i - \sum_{j=1}^n c_{ij} X_i X_j \quad (1)$$

where X_i and X_j represent the population densities of primary producers and herbivores, respectively; r_i is the specific growth rate (birth minus death unrelated to herbivory); and c_{ij} are the coefficients of consumption of the primary producers by the herbivores. This equation does not adequately model detritus. Detritus can be modeled following DeAngelis *et al.* (6) where X_d represents the density of detritus

$$\begin{aligned} \frac{dX_d}{dt} = & R_d + \sum_{i=1}^n \sum_{j=1}^n (1 - a_j) c_{ij} X_i X_j \\ & + \sum_{i=1}^n d_i X_i - \sum_{j=1}^n c_{dj} X_d X_j \end{aligned} \quad (2)$$

Here R_d is input from an allochthonous source, for example, detritus inputs into streams. Additionally, detritus cycles autochthonously as the unassimilated fractions of prey killed, $\sum (1 - a_j) c_{ij} X_i X_j$, and the corpses of organisms that die from causes other than predation, $\sum d_i X_i$. The coefficient of consumption of the detritus by detritivores is represented by c_{dj} . Detritus is con-

sumed in a density-dependent manner similar to the way organisms are consumed (8, 9).

The growth equations for consumers, X_j , can be similar for primary producer and detritus models

$$\frac{dX_j}{dt} = -d_j X_j + \sum_{i=1}^n a_{ji} c_{ij} X_i X_j - \sum_{i=1}^n c_{ji} X_j X_i \quad (3)$$

Consumers die at a specific rate d_j and grow as a function of the prey consumed, $\sum c_{ij} X_i X_j$. The assimilation efficiency is a_j , and the production efficiency is p_j .

We define stability as unique to the region where all populations are at equilibrium X^* (10). If populations deviate by a small amount from their equilibria and then return, the chain is locally stable (10). Stability is assessed by evaluating the eigenvalues of the community matrix A whose elements α_{ij} are the partial derivatives of the equations for each species with respect to all species in the chain near equilibrium. Typically, α_{ij} are assigned values that ensure positive equilibrium densities and therefore only apply to a subset of matrix space where the chains are feasible. This approach has frustrated experimentation, as no direct field measures of the α_{ij} are practical (11). Here, α_{ij} were expressed as functions of measurable parameters: birth and death rates, energetic efficiencies, and consumption rates. Parameter values (d_i , c_i , a_i , and p_i) were sampled from the uniform distribution (0, 1). Values for nondimensional energy conversion efficiencies (a_i and p_i) are within these ranges by definition, and whether the range (0, 1) is plausible for the rate constants (d_i and c_{ij}) depends on the time and mass units chosen. The input rate for detritus R_d and the specific growth rate for primary producers r_i were set at increments of an order of magnitude beginning at 10^{-2} unit and ending with 10^5 units, encompassing a greater range of productivity than has yet been observed.

If the randomly selected parameters produced positive equilibrium densities for all species, the system was deemed feasible (12). For feasible systems, the parameter values and equilibrium densities were used to construct the elements of the community matrix A . Because all food chains in the analysis satisfied the criteria for qualitative stability (10), all feasible food chains were necessarily locally stable. The return time (RT) of a feasible system is the time required by the system to return to equilibrium after a perturbation and was estimated as $RT = -1/\text{real}(\lambda_{\max})$ (12), where $\text{real}(\lambda_{\max})$ is the real part of the largest eigenvalue. This process was repeated 1000 times for each productivity.

Productivity affected the feasibility of

the food chains (Fig. 1A). Feasibility of both detritus and primary producer food chains declined with increased food chain length, although less so for detritus. The effect of productivity on feasibility is a direct result of satisfying the conditions for obtaining positive equilibrium densities: inputs exceed outputs. For example, the equilibrium X_2^* in the producer-based two-species model is

$$X_2^* = \frac{r_1 a_2 p_2 c_{12} - c_{11} d_2}{a_2 p_2 c_{12}^2} \quad (4)$$

whereas in the two-species detritus model, the equilibrium is always positive

$$X_2^* = \frac{R_d p_2}{d_2 - d_2 p_2} \quad (5)$$

The RT tended to be shorter in producer food chains than in detritus food chains (Fig. 1B). This resulted from relatively strong diagonal dominance in the primary producer chain

$$\alpha_{11} = -c_{11} X_1^* \quad (6)$$

compared to the detritus chain

$$\alpha_{11} = -a_2 c_{12} X_2^* \quad (7)$$

because $a_2 c_{12} < c_{11}$, and for many systems $X_1^* > X_2^*$.

With increased productivity RT decreased for both primary producer and detritus food chains (Fig. 1B). The critical eigenvalue of the two-species primary producer model is

$$\lambda_{\max} = \frac{\alpha_{11} + \sqrt{\alpha_{11}^2 + 4\alpha_{12}\alpha_{21}}}{2} \quad (8)$$

High productivity ($r_1 X_1$) generates a negative value within the root of Eq. 8 (14). Hence, the real(λ_{\max}) reduces to $\alpha_{11}/2$ and RT approaches $2/\alpha_{11} \rightarrow 1$. Numerical analysis confirmed that the other food chains also approached limits. For productivity units below 10, the mean RT of all feasible food chains increased with increased chain length, as expected (1). Above 10 productivity units, the four-species food chains had shorter RTs than the three-species food chains. Our results suggest that the feasibility and resilience of food chains are a function of productivity and that the generalization cannot be made that longer food chains have longer RTs. The sizes of and ranges for matrix elements for runs involving one unit of productivity here correspond to the ranges that were used by others (1). Hence, the results beyond one productivity unit represent unexplored regions of parameter space.

The interaction of production and stability was also evident in experimental studies (15). The structure of aquatic food webs is related to both the productivity of the habitat and the variability in climate (15). When the amount of productivity was increased by adding detritus to water-filled tree holes, the food webs that developed were constrained by dynamic stability and not productivity (15). However, another later study revealed that as more detritus was added to the water-filled tree

holes, food chain length increased (15). Consistent with our results, studies that have included energetics predict that the relative importance of productivity and of the direct flow of energy to detritus should wane as productivity increases (5). Ecosystem resilience increases (decreased RTs) with increased nutrient availability (an index of productivity) (6, 16).

The models demonstrate that productivity determines the lower limits of what is ecologically feasible and attenuates the dynamics of food chains after perturbation by hastening RTs. Does high productivity compensate for unstable configurations and interactions in general? If so, factors that are potentially destabilizing to food webs would occur more often in systems of high productivity than in systems of low productivity. If most actual ecosystems are high in productivity, this may explain the high incidence of omnivory and mutualism and the dearth of examples of competition encountered in many ecosystems (17).

To compare productivity in our models with estimates of real production, we calculated productivity as grams of carbon per square meter per year. (For subsequent use of this unit, it will be understood that grams refer to grams of carbon.) For this scaling we used intervals of values for the rate constants (r_i , R_d , d_i , and c_{ij}) derived from the descriptions of soil food webs from native prairie and agricultural field stations

Table 1. Estimates of parameter values used in the models (9, 18). Data were obtained from a native shortgrass prairie at the Central Plain Experimental Range (CPER), Nunn, Colorado, United States; Horseshoe Bend, Georgia, United States (ct, conventional tillage; nt, no tillage); the Lovink-

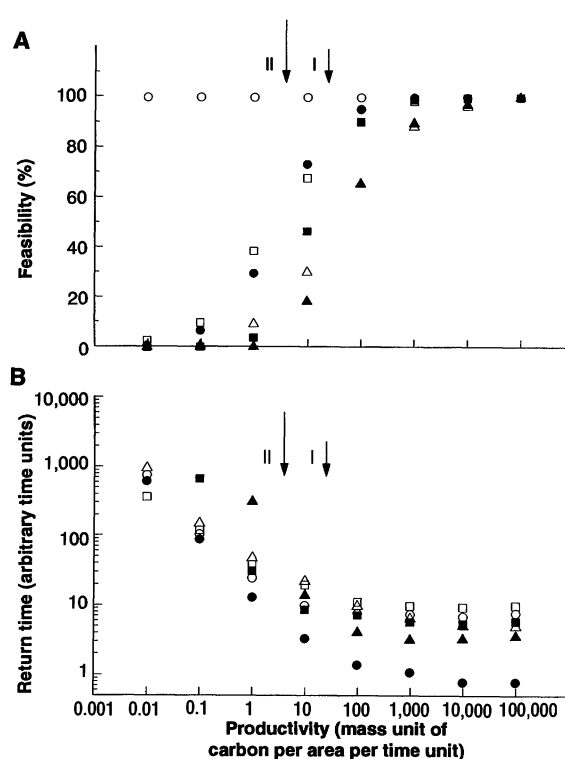
hoeve, Marknesse, Netherlands (if, integrated farming; cf, conventional farming); and Kjettslinge, Örbys, Sweden (B0, barley low nitrogen; B120, barley high nitrogen). NA (not available), the group was either not present at the site or was included with another functional group in the description.

Functional group	a_i	p_i	d_i (year ⁻¹)	Consumption coefficient c_{ij} [(g m ⁻²) ⁻¹ year ⁻¹]						
				CPER native	Horseshoe Bend		Lovinkhoeve		Kjettslinge	
					ct	nt	if	cf	B0	B120
Herbivores										
Phytophagous nematodes	0.25	0.37	1.08	0.010	0.013	0.018	0.166	0.133	0.026	0.026
Microbes										
Bacteria	1.00	0.4–0.5	0.50–1.20	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Fungi	1.00	0.4–0.5	0.50–1.20	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Microbivores										
Mycophagous collembola	0.50	0.35	1.84	0.016	0.008	0.009	0.026	0.045	0.002*	0.002*
Mycophagous oribatida	0.50	0.40	1.20	0.011	0.005	0.006	0.018	0.033		
Mycophagous prostigmata	0.50	0.40	1.84	0.016	0.008	0.009	0.026	0.045		
Mycophagous nematodes	0.38	0.37	1.92	0.032	0.010	0.011	0.596	0.733	0.004	0.002
Protozoa	0.95	0.40	1.00–6.00	0.005	0.001	0.001	0.002	0.003	<0.001	<0.001
Bacterivorous nematodes	0.60	0.37	2.68	0.006	0.002	0.003	0.022	0.023	0.004	0.004
Omnivorous nematodes	0.60	0.37	4.36	0.008	NA	NA	NA	NA	NA	NA
Predators										
Predatory nematodes	0.50	0.37	1.69	0.003	NA	NA	0.013	0.017	1.081	1.016
Nematophagous mites	0.90	0.35	1.84	0.058	NA	NA	0.554	0.865	0.155†	0.178†
Predatory mites	0.30	0.35	1.84	0.060	0.327	0.294	0.485	0.545		

*Mycophagous arthropods were treated as a single group.

†Predatory arthropods were treated as a single group.

Fig. 1. (A) The effect of productivity on the feasibility (%) of food chains modeled on detritus or primary producers. Food chains consisted of two, three, or four species beginning with either detritus or a primary producer. **(B)** The effect of productivity on the RTs (presented as the geometric mean) of feasible food chains consisting of two, three, or four species. For the units of these x axes to be comparable to units commonly used in measuring real ecosystem productivities (grams of carbon per square meter per year), they must be rescaled. Depending on the assumptions used to establish the time units for the death rate, d_i , and the mass units for the consumption rates, c_{ij} , one productivity unit on the x axes scales to either $1 = 4 \text{ g m}^{-2} \text{ year}^{-1}$ (I) or $1 = 36 \text{ g m}^{-2} \text{ year}^{-1}$ (II). Researchers have estimated (7) that 99% of the world's production originates from systems with productivities that exceed the levels indicated by the arrows for scaling I and II, respectively. Detritus models: two species (○), three species (□), and four species (△). Primary producer models: two species (●), three species (■), and four species (▲).



(9, 18) (Table 1) that included estimates of the densities of soil fungi, bacteria, protozoa, nematodes, and arthropods. For these webs, nominal death rates varied from 0.5 to 6 year^{-1} , which corresponds approximately with our range (0, 1) if the time unit is scaled to 0.17 year. The consumption coefficients c_{ij} varied between 0 and $1.08 \text{ (g m}^{-2})^{-1} \text{ year}^{-1}$, but if we used a time unit of 0.17 year, the mass unit had to be scaled to 6 g m^{-2} to maintain variation of c_{ij} between 0 and 1. Therefore, one unit of productivity in our study corresponds to $36 \text{ g m}^{-2} \text{ year}^{-1}$. [Note that the dimension of c_{ij} is $(\text{mass area}^{-1})^{-1} \text{ time}^{-1}$, whereas the dimension of productivity is $\text{mass area}^{-1} \text{ time}^{-1}$.] This scaling is appropriate for food chains that include species with relatively high death rates (6 year^{-1} for protozoa). For chains with species that have relatively low death rates ($<2 \text{ year}^{-1}$), one productivity unit corresponds to $4 \text{ g m}^{-2} \text{ year}^{-1}$ (19). A comparison of the productivities used here with known productivities (7) suggests that the majority of global production (to 99%) is derived from ecosystems more productive than the threshold suggested by our results (Fig. 1B). This may explain why average food chain length seems not to differ much among ecosystems of diverse productivity (16, 20), although the similarity may be artifactual. Most natural ecosystems, which are highly productive, have not been thoroughly described; thus, it is difficult to establish clear relations. This issue may be re-

solved by standardizing the descriptions of ecosystems (21) and by encouraging more studies of systems with low productivity such as deserts, exposed rock, Antarctic soils, and dry caves.

Whether based on a primary producer or inclusive of detritus, both models respond similarly to productivity; however, detritus models represent a much broader class of ecosystems. The primary producer models (Lotka-Volterra form) are far too restrictive in that matter does not cycle. Our results do not imply that factors other than productivity are not important [empirical evidence suggests the contrary (17, 21)] or that systems could not develop and persist at low rates of production. Rather, our results reinforce interpretations (5, 13) that productivity integrates processes occurring through ecosystems, thereby operating to establish the lower limits of production necessary to establish a system and compensate for the constraints imposed by susceptibility to perturbation.

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14. The elements of the community matrix for a two-species primary producer model are as follows:
 $\alpha_{11} = -c_{11}X_1^*$, $\alpha_{12} = -c_{12}X_1^*$, $\alpha_{21} = a_2p_2c_{12}X_2^*$, and $\alpha_{22} = 0$,
 where
 $X_1^* = d_2/(a_2p_2c_{12})$
 and
 $X_2^* = [(r_1a_2p_2c_{12}) - (c_{11}d_2)]/(a_2p_2c_{12}^2)$
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 $\text{flux}_i = (\text{nonpredatory death} + \text{predatory death})/(a_i p_i)$
19. Separate model runs where the d_i were sampled uniformly between (1, 10) instead of (0, 1), as described in the text, generated results consistent with those in the text after rescaling.
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