

# The relative importance of herbivory and carnivory on the distribution of energy in a stochastic tri-trophic food web

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Received 13 November 2002; received in revised form 1 August 2003; accepted 23 September 2003

## Abstract

A three-state, discrete-time Markov chain is used to model the dynamics of energy flow in a tri-trophic food web. The distribution of energy in the three trophic levels is related to the rates of flow between the trophic levels and calculated for the entire range of possible flow values. These distributions are then analysed for stability and used to test the idea that plants are resource-limited and herbivores are predation-limited. Low rates of death and decomposition, when coupled with low rates of herbivory and carnivory, tend to destabilize this food web. Food webs with higher rates of death and decomposition are relatively more stable regardless of rates of herbivory and carnivory. Plants are more prone to resource-limitation and herbivores are, in general, limited by their predators, which supports Hairston et al. (*Am. Nat.* 94 (1960) 421). The rate of decomposition often mediates the roles of top-down and bottom-up control of energy flow in the food web.

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*Keywords:* Food web; Markov chain; Trophic; Top-down; Bottom-up webs or food web

## 1. Introduction

Food webs remain a hot topic for research in ecology (see Polis and Winemiller, 1996) but a lack of cohesion in the approaches used to study them still hinders the field. Much criticism (Paine, 1988) has been aimed at descriptions of static food web properties (see Cohen and Newman, 1988; Cohen et al., 1990) that fail to capture their dynamics. The studies that have attempted to address the dynamic nature of food webs (May, 1973; Levins, 1975; Pimm and Lawton, 1977; Pimm, 1982, 1984; De Ruiter et al., 1995; Hastings, 1996; McCann et al., 1998) have focused largely on pair-wise interactions between populations of different species. Despite the fact that many of these theoretical treatments are based on differential equation models, most have focused on equilibrium solutions which are static. More recently, theoretical food web studies have adopted a more dynamical approach by examining non-equilibrium solutions to differential equation

models (Klebanoff and Hastings, 1993; McCann and Yodzis, 1995; Kuznetsov and Rinaldi, 1996). In addition to being largely focused on equilibria, most studies have been heavily biased toward the numerical abundance of individual species. Some ecologists see this as a necessity (e.g. Paine, 1988), but in a departure from tradition, Loreau (1996) uses energy as a modeling currency.

In this paper, I present a theoretical approach to simplified food modules that focuses on energy flow between trophic levels. Trophic levels are useful constructs to address the dynamics of food webs because they are defined by their functional roles. Individual organisms or populations or even species are assigned to a particular trophic level, based on their functional relationship to other members of a food web. This functionally based assignment frees us from thinking only in terms of individual species and clearly shifts our focus to the processes of energy flux and material cycling. I have chosen to direct my attention to energy flow because energy provides a general and unifying currency for ecological systems. In describing the dynamic relationships between trophic levels, I first lay out the qualitative structure of the interactions and then proceed to a quantitative examination of the dynamics allowed by the qualitative structure. In order to do this,

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I represent energy flow through a food web as a stochastic process.

Stochastic models have been used with much success in ecology and have a relatively long history in the field (see Horn, 1975; Matis et al., 1979; Higashi and Burns, 1991; Li, 1995; Ives and Jansen, 1998; Saether et al., 1998). Markov chains have typically been used to model succession (Horn, 1975; Li, 1995; McAuliffe, 1988; Wu et al., 1997), but have also been used to model nutrient flow through an ecosystem and energy flow within one trophic level (Walters, 1979). In models of succession, transition probabilities are estimated from empirical data and subsequently used to predict vegetation change over time. Markovian models of ecosystems tend to focus on functionals (Taylor and Karlin, 1998), such as the average circulation time of nutrients, average time to absorption, or the average amount of time spent in a given state. If a Markov chain is used to model a finite quantity that can exist in a finite number of states, in this case energy in a food web, then the limiting probability distribution can be thought of as the long-term average distribution of energy among the states. I will explore the relationship between the flow of energy between trophic levels and this long-term average distribution of energy among the trophic levels in a food web.

This approach is very simple, but it allows one to ask several questions about food web dynamics and it makes predictions about stability and the relative importance of particular trophic links to the entire food web. The Markov chain model reproduces patterns that are consistent with empirical observations and allows for the quick computation of the energy distribution from the values of trophic flows. I also address the roles of top-down and bottom-up control in this food web and show support for the predation hypothesis put forth by Hairston et al. (1960). And lastly I present a slightly new characterization of food web stability that does not concern species populations but rather the functional processes operating in the food web.

## 2. Methods

In this paper, I consider the flow of energy through a tri-trophic food web a stochastic process. More specifically, I model the flow as a three-state, discrete-time Markov chain. Each of the three states in the model corresponds to one of the three trophic levels in the food web. At this point, the three trophic levels are generic constructs, not three species or three guilds, for example. They could be individual species or groups of species that all have the same energy flow patterns. I have kept the model as general as possible in an effort to address the most basic questions at the most basic levels. Ideally,

this model would be used as a starting point for a more detailed description of a specific system.

The only assumptions of the model are that energy input into the food web is constant and that the fate of a unit of energy depends only on the present. The assumption that energy input is constant allows the use of a homogenous stochastic process rather than a time dependent one and the Markov property, independence of the past, allows the use of a Markov chain. A discrete time model is used for simplicity.

The flows and constraints are illustrated in the loop diagram of Fig. 1. Formally, the transition probability matrix for the food web is

$$A = \begin{bmatrix} pp & ph & 0 \\ hp & hh & 0 \\ cp & 0 & cc \end{bmatrix} \quad (1)$$

and the entries are transition probabilities. For example,  $ph$  is the probability that a unit of energy will flow from the first trophic level ( $p$  for producers) to the second trophic level ( $h$  for herbivores) in a given time step. The third trophic level is labeled  $c$  for carnivores. The topology of the transition probability matrix explicitly reveals the qualitative constraints placed on overall system behavior. The range of potential outcomes has been limited by disallowing certain flows of energy through the food web, most notably, omnivory. The goal is to examine the possible outcomes or limiting probability distributions that are generated by the qualitative structure of the food web.

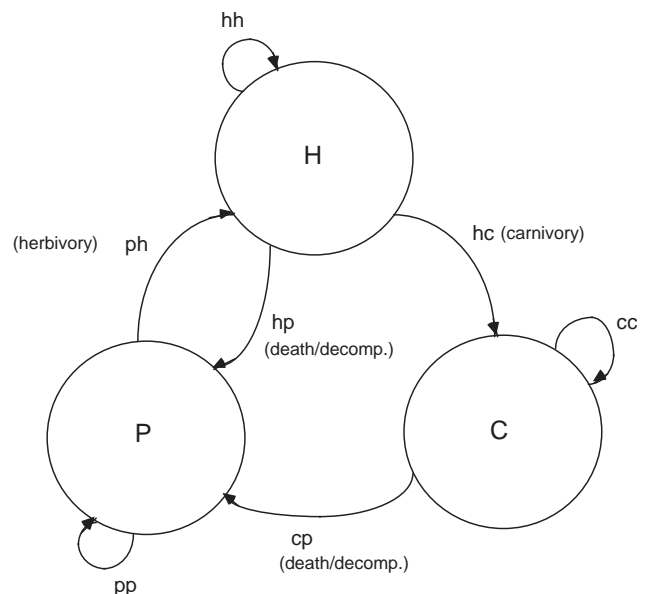


Fig. 1. Each circle corresponds to a trophic level in the food web. P denotes the primary producers, H denotes the herbivores and C denotes the carnivores. The arrows between the circles represent energy flow between the trophic levels and are labeled according to the transition probability matrix A.

Because **A** is a positive recurrent matrix (Taylor and Karlin, 1998), there exists a limiting probability distribution for all combinations of the non-zero transition probabilities given above. This limiting distribution can be found in a number of ways, and here a general application of the law of total probability is used to derive a system of linear equations. The limiting probability distribution is the solution to

$$\pi_j = \sum_{k=1,2,3} \pi_k P_{kj} \tag{2}$$

with the obvious constraint that the  $\pi_j$ 's must sum to one. The  $\pi_j$ 's are the long-term probabilities that a unit of energy or biomass resides in the  $j^{\text{th}}$  trophic level at any given time. They also correspond to the standing stock of total energy found in each of the trophic levels. The term  $P_{kj}$  represents the transition probability from trophic level  $k$  to trophic level  $j$  ( $P_{12}$  corresponds to  $ph$  in the transition matrix). The limiting probability distribution for **A** is

$$\begin{aligned} \pi_1 &= \frac{(cp)(hp + hc)}{(ph)(hc) + (ph)(cp) + (cp)(hp) + (cp)(hc)}, \\ \pi_2 &= \frac{(ph)(cp)}{(ph)(hc) + (ph)(cp) + (cp)(hp) + (cp)(hc)}, \\ \pi_3 &= \frac{(ph)(hc)}{(ph)(hc) + (ph)(cp) + (cp)(hp) + (cp)(hc)}. \end{aligned} \tag{3}$$

One of the main goals of this paper is to examine the stability of the limiting probability distribution for different values of the transition probabilities. The solutions above each represent a four-dimensional surface because we have four degrees of freedom in the transition probability matrix. To ask questions about the stability of food web configurations, a comparative measure is needed. Stability of a limiting probability distribution is defined to be the susceptibility of the values of the  $\pi_j$ 's to change as a function of a change in the value of one or more of the transition probabilities. That is, how much will the proportion of total energy in each trophic level change in response to a change in the rate of flow between different trophic levels. To make statements about the stability of the limiting distributions associated with each of the three trophic levels, it is necessary to examine the four-dimensional surfaces given above. Because I have defined stability to be the likelihood of change in the overall distribution of energy in the food web, I use partial derivatives and gradient vectors to assess how likely the limiting distribution is to change as a result of a change in flow rates. The use of partial derivatives allows the description of changes in food web characteristics with reference to any combination of parameters of interest, the parameters here being the transition probabilities given in **A**. For example, the roles of top-down and bottom-up control on the

proportion of total energy in the  $j^{\text{th}}$  trophic level of the food web are compared by the ratio

$$\frac{\partial \pi_j}{\partial (P_{(j-1)j})} / \frac{\partial \pi_j}{\partial (P_{j(j+1)})}. \tag{4}$$

This is the ratio of the magnitude of bottom-up control to top-down control for the given trophic level. The ratio of any two partial derivatives can be used to compare the effects of different trophic links on the standing stock of total energy in a given trophic level. A comprehensive measure of stability for any particular energy distribution, which corresponds to certain combinations of values of flow values, on the surface of the solution for each of the  $\pi_j$ 's is defined as the magnitude of the gradient vector

$$\nabla \pi_j = \frac{\partial \pi_j}{\partial ph} i + \frac{\partial \pi_j}{\partial hc} j + \frac{\partial \pi_j}{\partial hp} k + \frac{\partial \pi_j}{\partial cp} l \tag{5}$$

evaluated for that particular distribution. Stability obviously corresponds to a shallow gradient and instability corresponds to a steep gradient. It is thus convenient to use the magnitude of the gradient vector as a measure of instability. Because a gradient is directional, we can learn more than just the stability of different food web configurations. Specifically, we can determine the most influential trophic link for any energy distribution by examining the directional components of the gradient. The largest component represents the trophic link with greatest influence on the energy distribution. A cursory look at the gradient vector of the three solution surfaces can give an idea of the influence of each variable on that particular solution surface at any point. To evaluate the stability of the entire food web for a given combination of parameter values, rather than just one trophic level as shown above, all three trophic levels must be considered simultaneously. This can easily be done by summing the instability measures of the three trophic levels to yield

$$Instability = \|\nabla \pi_1\| + \|\nabla \pi_2\| + \|\nabla \pi_3\|. \tag{6}$$

This approach allows one to examine the effects of single parameters or combinations of parameters on particular trophic levels or on the overall stability of the web.

### 3. Results

The dimensionality of the system makes complete visualization of the solution surfaces impossible so to get an idea of how the solution surfaces look, the limiting distribution is plotted (Fig. 2) as a function of  $ph$  and  $hc$  while  $hp$  and  $cp$  are held constant. The constant parameters,  $hp$  and  $cp$  represent death and decomposition of the biomass in the middle and top trophic levels

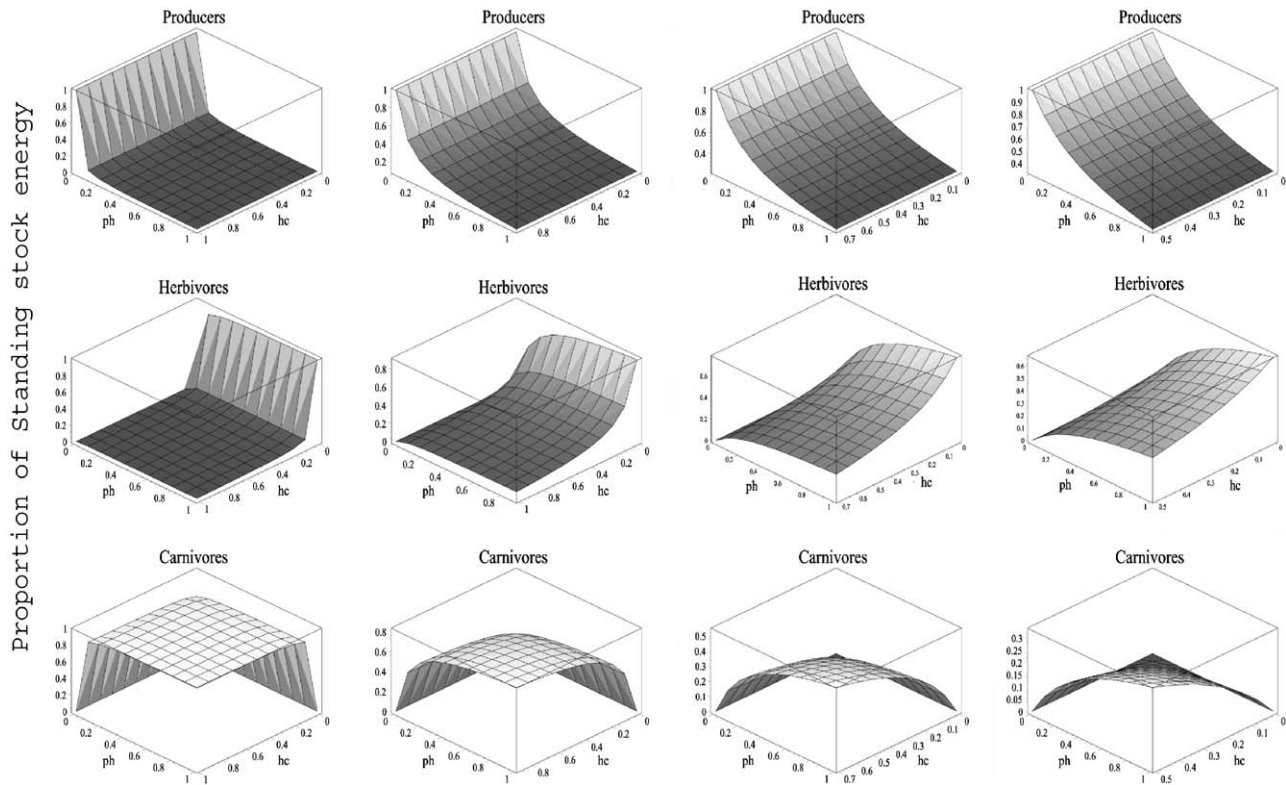


Fig. 2. Energy distributions for different fixed rates of the parameters corresponding to death and decomposition. Each column in the figure represents one food web with a particular fixed value for the rate of death and decomposition. The plots in the first row show the proportion of total energy in the producers, those in the second row show the proportion of total energy in the herbivores and those in the bottom row show the proportion of total energy in the carnivores. The values for the rates of herbivory and carnivory are  $ph$  and  $hc$  respectively. The rates of death and decomposition are 0.01, 0.1, 0.3, and 0.5 for the food webs from left to right.

respectively. I have combined the two processes because they are both components of the same qualitative flow of energy in the food web. This grouping is shown in the box and arrow diagram in Fig. 1. Despite being omitted from many food web studies, the processes of death and decomposition play important roles that have only recently been realized (Strong et al., 1996; De Ruiter et al., 1996; Trumbore, 2000). I have made multiple plots with different values for the fixed parameters (Fig. 2) to show how belowground dynamics can play a large role in biomass cycling. The plots in Fig. 2 show that increasing the rate of death and decomposition greatly affects the energy distribution in the food web, but does not drastically alter the general influence of herbivory and predation on the energy distribution. Increasing the rate of death and decomposition changes the magnitude of the effects of herbivory and predation and thus reduces their overall influence. A reduction in the rate of death and decomposition, along with high rates of herbivory and carnivory, leads to food webs with inverted trophic pyramids.

The ratio of energy in the three trophic levels is simple function of transition probabilities because the equations for the solution surfaces all have the same

denominator. The ratio of

$$\pi_1 : \pi_2 : \pi_3 \tag{7}$$

is given by

$$\frac{cp(hp + hc)}{ph} : cp : hc. \tag{8}$$

This simple expression makes it easy to calculate the energy distribution for any combination of transition probabilities. If one had some idea of what the transition probabilities were for a given system, it is straightforward to compute the resulting energy distribution and compare it to empirical observations. This would serve as a cursory check of the model's assumptions for a particular system and/or a check of the ecologist's notions about flow rates for that system. In addition to knowing what the limiting distribution is as a function of the transition probabilities, I also wanted to know which flow rates are most likely to influence the limiting energy distribution. This question is easily answered by examining ratios of partial derivatives, as explained earlier. For the first trophic

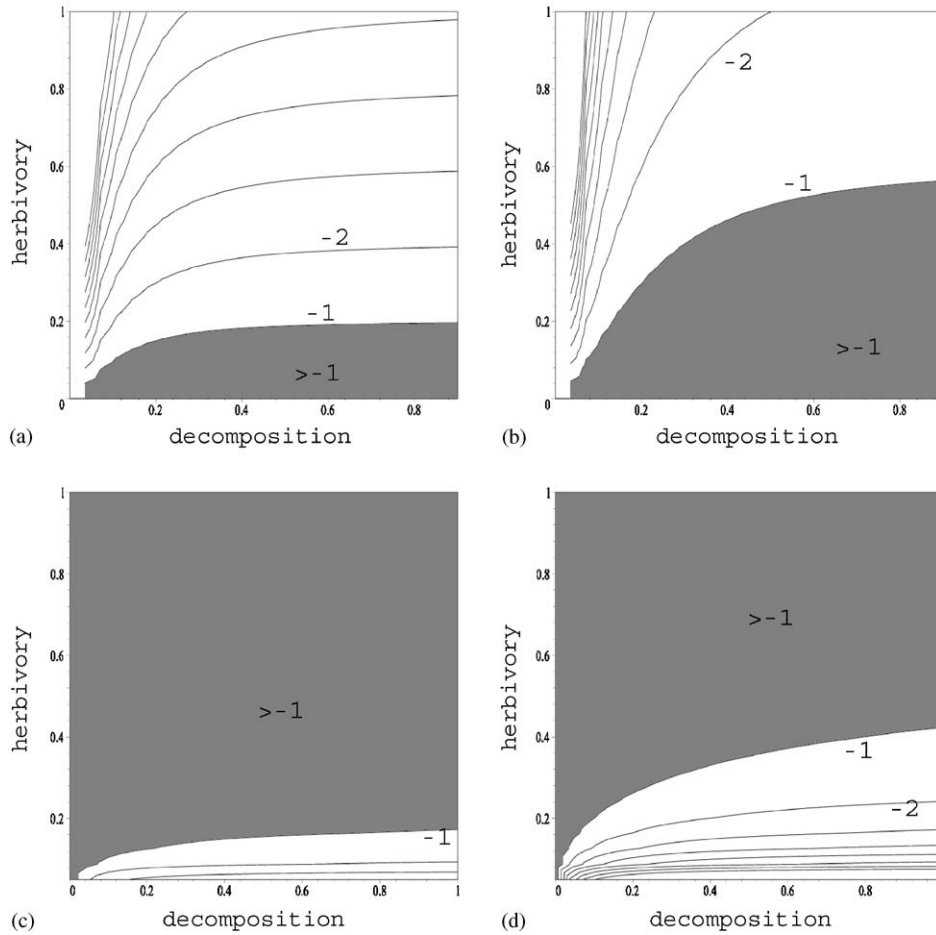


Fig. 3. Ratio of inflows to outflows for producers (a,b) and herbivores (c,d) as a function of herbivory and carnivore death and decomposition. In all panels, carnivory is held constant but herbivore death and decomposition changes from 0.1 in panels a and c to 0.5 in panels b and d. Contours are at unit intervals and the shaded regions indicate where the ratio of inflow to outflow is greater than  $-1$ . The contours are included to show how quickly the transition from top-down to bottom-up control occurs. The ratio for producers is less than  $-1$  for most of parameter space indicating that inflows are generally more influential than outflows whereas the ratio for herbivores is greater than  $-1$  for the majority of parameter space which implies that predation is generally more limiting than resources, i.e. primary producers.

level, the ratio of inflow to outflow

$$\left( \frac{\partial \pi_1}{\partial (hp)} + \frac{\partial \pi_1}{\partial (cp)} \right) / \frac{\partial \pi_1}{\partial (ph)} \quad (9)$$

is given by

$$-\frac{(ph)(cp \cdot hc + cp^2 + hp \cdot hc + hc^2)}{cp(hp + hc)(hc + cp)} \quad (10)$$

because there are energy inputs from both the herbivores and carnivores via death and decomposition. This ratio is negative because the derivative associated with inflow is positive and the derivative associated with outflow is negative but the magnitude is the quantity of interest. If the absolute value of this ratio is greater than one, inflows are more influential on the proportion of total energy in the first trophic level than outflows. This ratio is greater than one in magnitude for the majority of parameter space so inflows have more influence on the proportion of energy residing in the first trophic level (see Fig. 3). More specifically, carnivory never influences

this ratio and herbivory only has a greater relative effect than death and decomposition if herbivory is weak. But if herbivory is weak in absolute influence, then herbivory cannot be considered an extremely influential trophic link. Slow rates of death and decomposition also allow herbivory to have more influence on the standing stock biomass in the first trophic level. The fact that inflow is more influential than outflow for the producers in the food web corresponds to the resource limiting hypothesis of Hairston et al. (1960). The dynamics of the middle trophic level are dominated by outflows, or predation by carnivores. The ratio of

$$\frac{\partial \pi_2}{\partial (ph)} / \frac{\partial \pi_2}{\partial (hc)} \quad (11)$$

is given by

$$-\frac{cp(hp + hc)}{ph(ph + cp)} \quad (12)$$

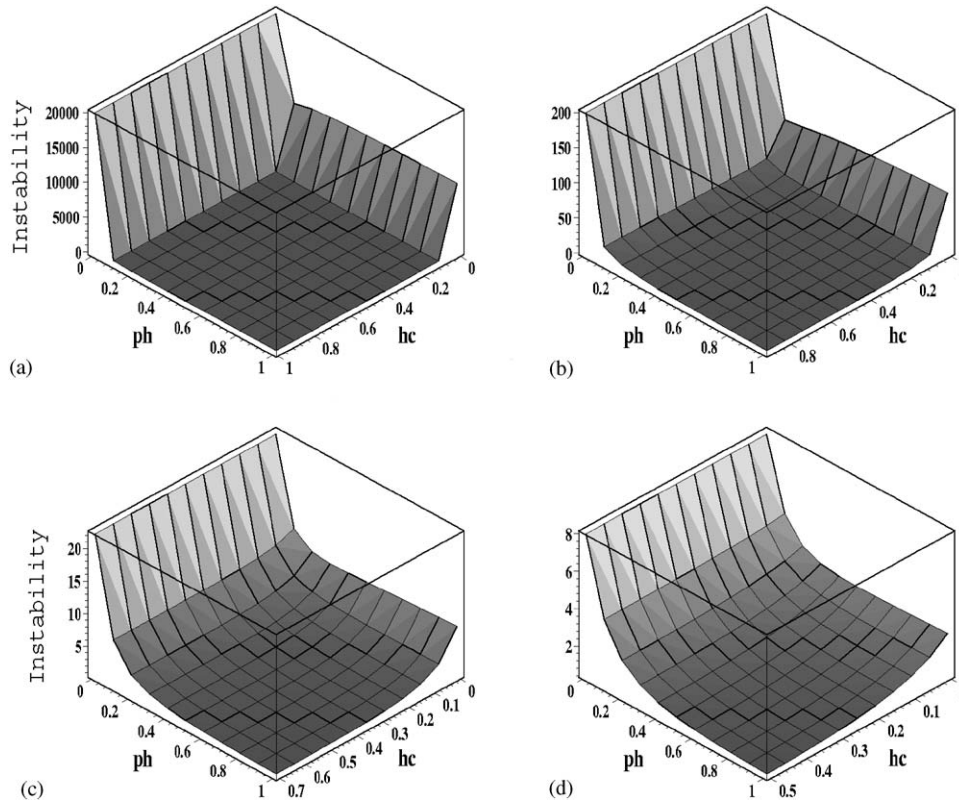


Fig. 4. Plots of the instability metric for the same fixed values of death and decomposition as in Fig. 2. The axes are the same as in Fig. 2. Plot (a) has  $hp = cp = 0.01$ , plot (b) has  $hp = cp = 0.1$ , plot (c) has  $hp = cp = 0.3$  and plot (d) has  $hp = cp = 0.5$ .

which is less than one in magnitude ( $> -1$  in Fig. 3) for most of parameter space. The fact that herbivores are more limited by their predators is also consistent with Hairston et al. (1960). This analysis clearly identifies the transition at which the relative influence of top-down effects become more important than bottom-up effects in determining the standing stock energy in a particular trophic level.

The instability measure, as defined above, is plotted for a range of parameter values in Fig. 4. It is clearly evident that the food web described here is relatively stable throughout most of the parameter space. The measure of instability increases abruptly when  $ph$  and  $hc$  tend toward zero. This decrease in the stability of the food web's energy distribution is caused by a reduction in the rate of energy flow associated with herbivory or carnivory. Therefore the often overlooked process of material cycling can have a profound effect on trophic control and food web stability.

#### 4. Discussion

In this paper I have used an extremely general approach to model energy flow in a tri-trophic food web. This decision was not made to simplify calculations or analysis but rather to extend the results of this

modeling exercise to any food web with the particular flow patterns discussed here. The energy distributions generated by this model agree with observed rates of trophic energy transfer. For example, in Fig. 2 it is evident that the majority of food webs exhibit energy distributions reminiscent of Elton (1927), with the greatest proportion of total energy in the first trophic level and the proportion of total energy successively decreasing as trophic position increases. This describes the classic pyramid-shaped energy distribution. The influences of both herbivory and carnivory on the producers in the food web are clearly illustrated in top row of Fig. 2. Although the proportion of total energy changes significantly as a function of changes in the rate of death and decomposition, herbivory plays a major role in determining the proportion of total energy comprised by the producers. The proportion of total energy in the producers spans virtually the entire spectrum of possibility as herbivory varies but remains constant as carnivory varies. One would expect the direct effect of herbivory to be greater in magnitude than the indirect effect of carnivory, which is modulated by the herbivores in the food web.

Although traditional pyramid-shaped energy distributions are the norm, interesting deviations occur and this model generates a notable example as well, namely an inverted trophic pyramid. Inverted trophic pyramids are

often observed in aquatic systems which have long-lived top predators that comprise the greatest proportion of total energy in the food web. Because these top predators are long-lived, the nutrients they store are not readily accessible to detritivores and therefore, material cycling from the top trophic level is slow. Other characteristics of systems with inverted trophic pyramids are high rates of nutrient flow through the lower trophic levels. In order for an inverted trophic pyramid to appear in this model the rate of death and decomposition of the carnivores must be low and the rates of both herbivory and carnivory must be high. This is easily seen in the first column of Fig. 2 in which the rates of death and decomposition of herbivores and carnivores are low. The rate of carnivory must be greater than the rate of death and decomposition of the herbivores in order for enough energy to reach the carnivores to maintain the inverted trophic pyramid. The bottom row of Fig. 2 illustrates the necessity of high rates of nutrient flow through the producers and herbivores. As the death and decomposition rate of the carnivores increases, the requirement of high nutrient flow through the lower trophic levels becomes even more important because energy is leaving the top trophic level at a faster rate. It is necessary to replace it all the more quickly.

In addition to producing realistic food web energy distributions, this model allows one to evaluate the likelihood of particular flow rates for a given energy distribution. This is possible because the energy distributions generated by the model are not unique functions of flow rates. In other words, there are many different combinations of flows that will generate one particular energy distribution. If one has some idea about the rate of one of the flows in a food web, he or she could then use this model to determine the possible values for other flows. Or if one is able to make some measurements to determine the energy distribution in a food web, which is the more likely situation, he or she could then determine the possible combinations of flows that are generating the observed energy distribution. This can be done in a rudimentary fashion by finding levels curves of the solution surfaces that correspond to particular proportions of total energy for each of the three trophic levels. In an empirical setting, the calculation of herbivory and carnivory rates is a tricky business but this model allows one to quickly see all the possible rates of trophic flows that generate a given energy distribution. Once the range of possibilities has been determined, one can make a more educated guess as to the magnitude of specific flow rates. In the converse situation where one may have more information about the magnitude of trophic flows he or she can quickly compute the energy distribution generated by particular flow rates as described above.

As well as understanding the relationship between energy flow and energy distributions, ecosystem and community ecologists are often interested in the roles of top-down and bottom-up control in food webs. Ever since Hairston et al. (1960) proposed that plants are resource limited and herbivores are predator limited, ecologists have been attempting to support or contradict the conjecture. Elaborations upon the original hypothesis have been made (e.g. Menge and Sutherland, 1976), but the basic question has remained conclusively unanswered. Examining partial derivatives as explained above is a simple way to compare the effect of inflow (bottom-up) versus the effect of outflow (top-down) on the overall energy distribution in the food web. The amount of energy in the first trophic level in this food web is dictated by resource availability, not herbivory. This is seen by examining the ratio of energy flow into the first trophic level to the flow out of the trophic level. Because the ratio is, in general, greater than one in magnitude (see Fig. 3), the relative influence of resource availability is usually greater than the relative influence of herbivory on the amount of energy in the first trophic level. The ratio of inflow to outflow for producers in Fig. 3a is less than  $-1$  for all but the lowest rates of herbivory. In Fig. 3b, the same ratio for the producers is plotted for an unusually high rate of death and decomposition and inflows still have greater relative influence on the proportion of total energy in the first trophic level.

For the middle trophic level, bottom-up effects rarely exceed the top-down effect of predation. The ratio of bottom-up to top-down influence in Figs. 3c–d is greater than  $-1$  (smaller than 1 in magnitude) as long as herbivory is not weak. This is the exact opposite of what was observed in the first trophic level and in accordance with Hairston et al. (1960). Predation plays a more important role in this food web than resource availability in determining the amount of energy in the middle trophic level. This is not to say that herbivory is unimportant but that carnivory exerts more influence than herbivory on the proportion of total energy in the middle trophic level. By examining Eq. (12), it is clear that carnivory and herbivore death and decomposition play the same functional role in determining the relative influence of top-down and bottom-up control on herbivores. Therefore, the shift of the transition from top-down to bottom-up control from Fig. 3c to Fig. 3d could as easily come from an increase in carnivory as from an increase in herbivore death and decomposition. Although the rate of death and decomposition does effect trophic control, changes in the rate of herbivory have much greater influence on the relative importance of top-down and bottom-up effects on herbivores. When death and decomposition and carnivory occur at higher rates, herbivores become more resource limited than predation limited. In general, faster material cycling

results in greater influence of material cycling on the distribution of energy among trophic levels. This implies that top-down and bottom-up control of energy flow in food webs cannot be fully understood without incorporating the effects of all trophic links, especially death and decomposition.

For this food web, the ideas of Hairston et al. (1960) provide a conceptual framework that is in general valid if one accepts the two assumptions of this model, constant energy input to the system, and the future only depending upon the present. In addition to giving support for the conjecture of Hairston et al. (1960), I have also given a metric to assess the relative importance of both resource availability and predation for any food web configuration. Because the importance of resource availability and predation are functions of both inflow and outflow on energy, the relative importance of each will change with respect to changes in rates of herbivory and carnivory. This analysis allows one to calculate the importance of either for any given combination of energy flow in and out of a trophic level.

Up to this point, the discussion has been confined to the influence of the rates of trophic flows on one trophic level at a time but I also assess the likelihood of a change in all three trophic levels simultaneously. This desire motivated the instability metric described earlier. It quantifies the steepness of all three solution surfaces simultaneously and thus measures the likelihood of change in the entire energy distribution as a function of changes in rates of trophic flow. The magnitude of the instability metric indicates the degree to which the energy distribution in the food web will change as a result of a change in the rates of trophic energy flows. The degree of instability generally increases as rates of energy flow decrease. This is most noticeable as the rates of herbivory and carnivory approach zero. All the plots in Fig. 4 indicate this pattern but it is also interesting to note that the drastic increase in food web instability as rates of death and decomposition approach zero as well. Obviously, reduction in the rate of decomposition in a food web prevents necessary nutrients, the majority of which remain in the food web (Carpenter and Kitchell, 1993) from being assimilated by primary producers. This means that the lower rates of death and decomposition are for a food web, the less stable it will be. The fact that the energy distribution among trophic levels is more likely to change in the presence of weak trophic interactions and the fact that slow material cycling leads to instability for the entire food web indicate that food webs with similarly scaled flow rates will be more stable than those with disparate rates of energy flow.

This general food web model is apparently realistic in its description of trophic dynamics and allows for the quantification of the influence of particular trophic links on the energy distribution in the web. This model is appropriate for a food web that is predominantly

limited by one nutrient. Addition of the particular limiting nutrient will result in an increase of biomass in each trophic level, as in Loreau (1996), but will not change the proportion of total energy in each trophic level relative to the others. The values of the transition probabilities that represent trophic flows in the food web are not empirically derived but certainly could be. The next step in developing this model is to calculate the transition probabilities as functions of processes we can measure empirically. Once this is done, one can easily use the methods presented here to make predictions about specific ecological systems.

### Acknowledgements

I would like to thank Jim Brown and Andreas Wagner for useful discussions and comments on the manuscript. This work was partially funded by the GRT in ecological complexity, NSF grant number DGE-9553623.

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