

Trophic levels in community food webs

JOEL E. COHEN*

Rockefeller University, 1230 York Avenue, New York, NY 10021–6399, USA

TOMASZ ŁUCZAK

Institute of Mathematics, Adam Mickiewicz University, Matejki 48/49, 60–769 Poznan, Poland

Summary

Four concepts are considered for the trophic level of a species in a community food web. The long-way-up-level (or LU-level) of species A is the length of the longest simple food chain from a basal species (one with no prey in the web) to A. (A simple chain is a chain that does not pass through any given species more than once.) The short-way-up-level (SU-level) of species A is the length of the shortest chain from a basal species to A. The long-way-down-level (LD-level) of species A is the length of the longest simple chain from species A to a top species (one with no consumers in the web). The short-way-down-level (SD-level) of species A is the length of the shortest chain from species A to a top species. The stratigraphy of a web is the analogue for species of the 'pyramid of numbers' for individuals: it is the frequency distribution of species according to level. The LU-, SU-, LD-, and SD-stratigraphies of the seven webs in the Briand–Cohen collection with 30 or more trophic species reveal no species with LU-level or LD-level more than 6, no species with SU-level more than 3, and no species with SD-level more than 2. In all seven webs, SD-levels are stochastically less than SU-levels: species tend to be closer to a top predator than to a basal species. Two stochastic models of food web structure (the cascade model and the homogeneous superlinear model) correctly predict that 95% or more of species should have LU-level and LD-level in the range 0–6. The models also correctly predict some details of the distribution of species in the SU- and SD-stratigraphies, particularly the fraction of species in level 1. The models do not, in general, correctly predict the distribution of species within the range 0–6 of LU-levels and LD-levels.

Keywords: food chain; consumer–resource interaction; predator–prey interaction; stratigraphy; spectrum

Introduction

Many natural communities contain food chains that consist of green plants, animals that eat only green plants (herbivores), and carnivores that eat only herbivores. For example, in Israel, the tree *Pistacia atlantica* (Anacardiaceae) is host to two gall-forming aphids (belonging to Fordinae and Pemphigidae), both of which are parasitized by the wasp *Monoctonia pistaciaecola* (Wool and Manheim, 1986). Such chains have three trophic levels (plants at level 0, herbivores at level 1, carnivores at level 2), stacked like the stories of a building. The simple image of stacked trophic levels has sometimes been generalized from particular food chains to the community as a whole, and provides the framework for a long tradition of ecological theory (e.g. Howard, 1897; Lotka, 1925, pp. 171–84; Hairston *et al.*, 1960; Schoener, 1982).

* To whom correspondence should be addressed.

However, in some communities, some animals eat both green plants and other animals (possibly including members of their own species), and some animals eat other animals and the animal prey of those animals (Polis *et al.*, 1989). Such animals are sometimes called omnivores (Pimm, 1982, p. 131). Some plants (e.g. flytraps) and fungi (e.g. skin microflorā) eat animals. When omnivorous animals or carnivorous plants are functionally or numerically important, a community cannot be described simply as stacked disjoint levels.

Numerous efforts have been made to extend the concept of trophic level to situations more complex than simple chains or stacks (e.g. Cousins, 1980, 1987; Yodzis, 1989, p. 209). This paper continues those efforts.

In section 2, we define four concepts of trophic level, all of which are closely related to those listed by Yodzis (1989, p. 209), and give some of their properties. We propose a graphical method of displaying the spectrum, or pattern of trophic levels in a community food web. Following Łuczak and Cohen (unpublished observations), we define the stratigraphies of a web as the frequency distributions of species by level, one stratigraphy for each different definition of level. In section 3, we show by means of hypothetical examples that the spectrum can be used to distinguish webs of differing structure. In section 4, we display the spectrum of the largest web in the Briand–Cohen collection of community food webs (Cohen *et al.*, 1990) and tabulate the four stratigraphies of all seven webs in the Briand–Cohen collection with 30 or more species. Some apparently novel empirical patterns emerge from these tabulations. For example, species tend to be closer to the top species in a web, as measured by the shortest chain to top species, than to the basal species in a web, as measured by the shortest chain from basal species. Section 5 displays the spectra and stratigraphies expected from the cascade model, a stochastic model of community food web structure (Cohen *et al.*, 1990). The cascade model approximates adequately the detailed stratigraphies according to two of the four definitions of level, but only the observed range of levels in the other two stratigraphies.

Concepts of trophic level: old and new – section 2

Yodzis (1989, p. 209) listed six concepts of ‘trophic level’. These concepts are defined in terms of basal species and chain lengths. A basal species is a species that eats no other species included in a food web (Yodzis 1989, p. 201). A chain is a sequence of links or arcs joined head to tail, where each link goes *from* a prey species *to* a predator species. A chain goes *from* the species at the tail of its first link *to* the species at the head of its last link. The length of a chain is the number of links it contains (except in definition 6 of Yodzis’ list, immediately below). If basal species are defined as having trophic level 0, then, according to Yodzis (1989, p. 209, paraphrased), the ‘trophic level’ of species A can be defined as:

1. The length of the longest chain from a basal species to species A.
2. The length of the shortest chain from a basal species to species A.
3. The modal length of all chains from basal species to species A (e.g. Pimm, 1982, p. 102).
4. The mean length of all chains from basal species to species A.
5. The mean length, weighted in proportion to energy flows, of all chains from basal species to species A.
6. The shortest chain from a basal species to species A, when links are assigned various lengths depending on whether the prey is an invertebrate ectotherm, a vertebrate ectotherm, or an endotherm (for details, see Yodzis, 1989, p. 240).

The presence of a cycle can cause problems for definitions 1, 3, 4, and possibly 5. To explain the problem, several further definitions are required. A cycle is defined as a chain from and to the same species. For example, if cannibalism is represented in a food web as an arc from one species

to itself, then cannibalism is a cycle of length 1. When species A eats species B and species B eats species A, this is a cycle of length 2. We define species A to be above species B, and species B to be below species A, if there exists at least one chain from species B to species A. We define species A to be above a cycle if species A is above at least one species in the cycle. When a food web contains a cycle, definitions 1, 3, 4 and possibly 5 assign trophic level infinity to all species that are above that cycle, because arbitrarily long chains go around and around the cycle, then lead to the species above it. (According to our definitions, every species that is on the cycle is also above the cycle.)

To avoid assigning trophic level infinity to all species that are above any cycle, we define a simple chain as a chain in which no species appears more than once. A simple chain may contain all the species that occur in a cycle but, if it does, must omit at least one of the links of the cycle. A shortest chain between two species is necessarily a simple chain between them. Thus Definition 2.2 is identical in content with the first of Yodzis' definitions. The following definitions assume that every species is above a basal species, but do not exclude the possibility of cycles.

Definition 2.1 – The *long-way-up-level* of species A, denoted $LU(A)$, is the length of the longest simple chain from a basal species to A. The long-way-up-level could also be called the loxoanabaetic level (*loxo* = oblique, slanting; *ana* = upward; *baetic* = going).

Definition 2.2 – The *short-way-up-level* of species A, denoted $SU(A)$, is the length of the shortest chain from a basal species to A. The short-way-up-level could also be called the orthoanabaetic level (*ortho* = straight).

A top species is defined as a species that is eaten by no other kind of organisms in the web. The lengths of chains above any given species tell, more generally, how many levels of consumers the population supports. The next two definitions are the obvious duals of the preceding two definitions.

Definition 2.3 – The *long-way-down-level* of species A, denoted $LD(A)$, is the length of the longest simple chain from species A to a top species. The long-way-down-level could also be called the loxocatabaetic level (*cata* = downward).

Definition 2.4 – The *short-way-down-level* of species A, denoted $SD(A)$, is the length of the shortest chain from species A to a top species. The short-way-down-level could also be called the orthocatabaetic level.

For any web, $\max_A LU(A) = \max_A LD(A)$, where the maximum is taken over all vertices or species A, because the longest chain from a basal to a top species has the same length whether it is traversed in an upward or a downward direction.

The SU-levels and SD-levels of species in a web may be determined by applying a standard algorithm for finding shortest paths (e.g. Robinson and Foulds, 1980, p. 143) to the predation matrix and to the transpose of the predation matrix, respectively. The LU-levels and LD-levels of species in a web may be determined by applying an algorithm of F. R. K. Chung for finding longest paths (e.g. Cohen *et al.*, 1990, p. 148) to the predation matrix and to the transpose of the predation matrix, respectively.

These concepts refine the previous concepts of basal, proper basal, intermediate, top, and proper top species (Cohen *et al.*, 1990, p. 72). Species A is basal if and only if $SU(A) = 0$; is proper basal if and only if $SU(A) = 0$ and $SD(A) > 0$; is top if and only if $SD(A) = 0$; is proper top if and only if $SD(A) = 0$ and $SU(A) > 0$; and is intermediate otherwise.

The *spectrum* of a web with S species is the $S \times 4$ matrix, one row per species, in which the four columns give $LU(A)$, $SU(A)$, $LD(A)$, and $SD(A)$ in the row corresponding to species A. The *upward spectrum* refers to the first two columns of the spectrum. The *downward spectrum* refers to the last two columns of the spectrum.

For any vertex A, $LU(A) \geq SU(A)$ and $LD(A) \geq SD(A)$, with equality for all vertices if and only if there is no omnivory in the web. Thus $LU(A) - SU(A)$ represents the 'upward excess'

length of the longest chain up to A compared to the length of the shortest chain up to A. Similarly, $LD(A) - SD(A)$ represents the 'downward excess' length of the longest chain above A compared with the length of the shortest chain above A.

For graphical display of the upward spectra, we shall plot $SU(A)$ on the abscissa and the upward excess $LU(A) - SU(A)$ on the ordinate. For the downward spectrum, we shall plot $SD(A)$ on the abscissa and the downward excess $LD(A) - SD(A)$ on the ordinate. Using these coordinates, in a web without omnivory, all species fall along the horizontal axis. In a web with omnivory, the distribution and abundance of species above the horizontal axis reflects the pattern of omnivory.

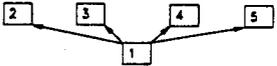
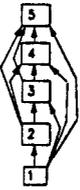
hypothetical web	predation matrix					spectra					
	sp.	1	2	3	4	5	sp.	LU	SU	LD	SD
(a) chain	1	0	1	0	0	0	1	0	0	4	4
	2	0	0	1	0	0	2	1	1	3	3
	3	0	0	0	1	0	3	2	2	2	2
	4	0	0	0	0	1	4	3	3	1	1
	5	0	0	0	0	0	5	4	4	0	0
(b) bush	1	0	1	1	1	1	1	0	0	1	1
	2	0	0	0	0	0	2	1	1	0	0
	3	0	0	0	0	0	3	1	1	0	0
	4	0	0	0	0	0	4	1	1	0	0
	5	0	0	0	0	0	5	1	1	0	0
(c) vine	1	0	1	1	1	1	1	0	0	4	1
	2	0	0	1	1	1	2	1	1	3	1
	3	0	0	0	1	1	3	2	1	2	1
	4	0	0	0	0	1	4	3	1	1	1
	5	0	0	0	0	0	5	4	1	0	0

Figure 1. Three hypothetical food webs, their predation matrices and their spectra: (a) chain; (b) bush; (c) vine. In the predation matrix, the species (sp.) named at the head of the column eats the species named at the left of the row if the matrix element is 1 and does not eat if the matrix element is 0. In the spectra, LU = long-way-up spectrum; SU = short-way-up spectrum; LD = long-way-down spectrum; SD = short-way-down spectrum.

The *stratigraphy* of a web is the frequency distribution of species by level, i.e. the number of species with level n , for $n = 0, 1, 2, \dots, S - 1$ (Łuczak and Cohen, unpublished observations). The stratigraphy of a web is the analogue for species of the 'pyramid of numbers' for individuals or biomass (e.g. Elton, 1927, p. 69), and might be called the pyramid of species. There is one stratigraphy for each definition of level: the LU-stratigraphy, the SU-stratigraphy, the LD-

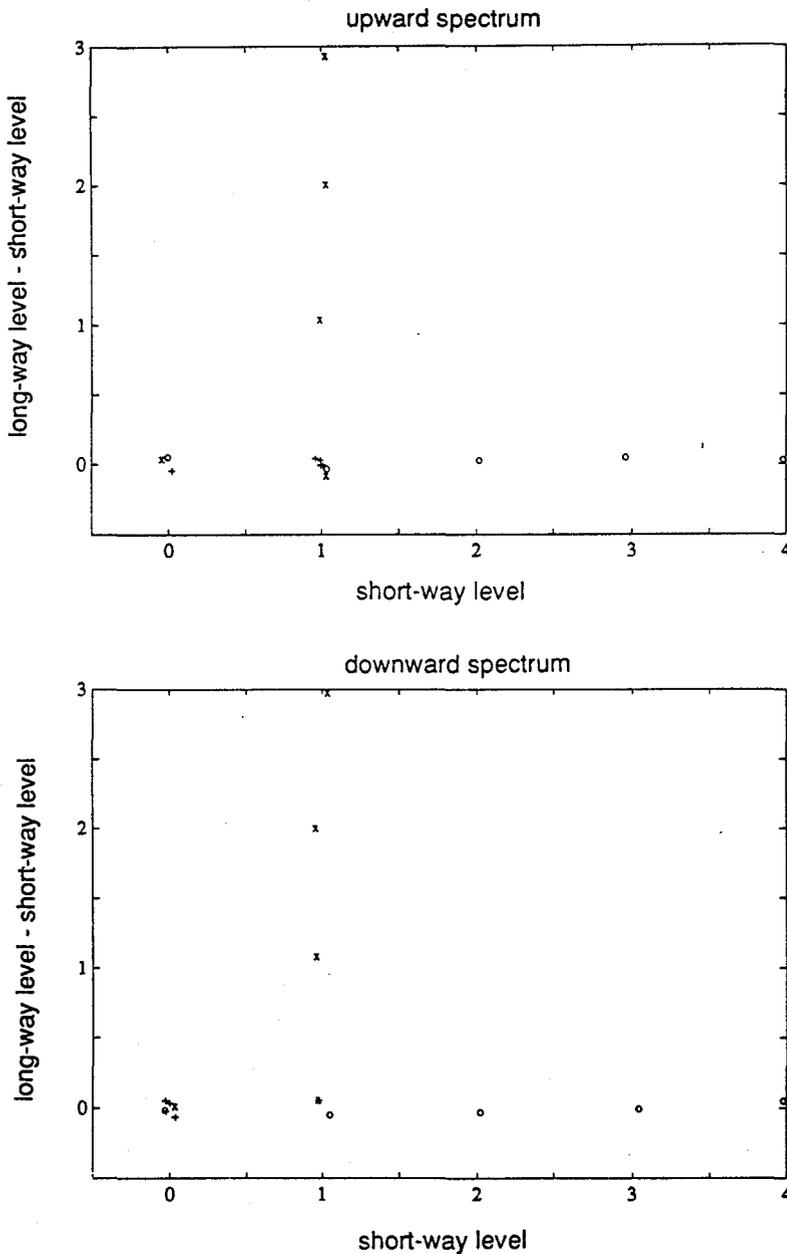


Figure 2. Spectra of three hypothetical webs. (a) Upward spectra. (b) Downward spectra. Symbols: O = chain; + = bush; X = vine. Each data point has exactly integer coordinates, but has been perturbed by a small random amount to render coincident points visible. Each symbol represents one species.

stratigraphy, and the SD-stratigraphy. If $N_{SU}(n)$ denotes the number of species with SU-level equal to n , and similarly for the other definitions of level, then always $N_{SU}(0) = N_{LU}(0)$, both numbers being the number of basal species, and always $N_{SD}(0) = N_{LD}(0)$, both numbers being the number of top species.

Spectra of hypothetical food webs – section 3

The three hypothetical webs in Fig. 1 illustrate the concepts of level just defined. In the chain and bush, Fig. 1(a,b), there is no omnivory. Therefore, for all vertices A , $SU(A) = LU(A)$ and $SD(A) = LD(A)$. In the vine, Fig. 1(c), where all possible non-cyclic omnivorous links are present, the SU-spectrum matches that of the bush, the LU- and LD-spectra match the corresponding spectra of the chain, and the SD-spectrum matches that of neither the chain nor the bush.

The upward and downward spectra clearly distinguish among the three hypothetical webs (Fig. 2).

The hypothetical webs confirm the general fact that $\max_A LU(A) = \max_A LD(A)$. In the hypothetical examples in Fig. 1, it is also true that $\max_A SU(A) = \max_A SD(A)$. This equality is not true for all possible webs, as the web of the Sonora Desert, Arizona, analysed in section 4, shows.

If the species in the hypothetical webs in Fig. 1 were lumped into trophic species, i.e. sets of species with identical sets of prey and identical sets of predators, then the chain and the vine would be unaffected, but species 2, 3, 4 and 5 of the bush would be combined into a single trophic species: they all prey on species 1 and have an empty set of predators. Lumping into trophic species would collapse the bush into a chain with a single link, as T. W. Schoener pointed out (personal communication, 18 March 1991). A more complex hypothetical web could contain the bush as a subweb in such a way that the bush subweb would not collapse after lumping into trophic species, e.g. if each of species 2, 3, 4 and 5 had a distinct predator. This additional complexity would obscure rather than aid the illustrative role of these examples and hence is omitted.

Stratigraphies of real food webs – section 4

We now examine graphically the spectra (Fig. 3) of the food web of the Sonora Desert, Arizona (Howes, 1954), the largest web in the Briand–Cohen collection, then tabulate the stratigraphies of all seven webs in the Briand–Cohen collection with 30 or more species, including the largest (Table 1). Cannibalism, if present in the original reports, was suppressed during the editing of the data, and there were no cycles of length two or more. Hence the webs analysed here are acyclic (after editing) and all chains are simple chains. Investigator-defined species have been combined into trophic species; counts of species and links refer to trophic species (as defined in the previous paragraph) and trophic links (links that join trophic species), respectively.

The upward spectrum of the Sonora Desert, Arizona (Fig. 3) shows that only two species have SU-level 3, i.e. only two species are as many as three links above some basal species by a shortest route. The remaining 46 species can be reached from a basal species by two or fewer links. Three species have LU-level 4: one with SU-level 1 (and upward excess 3), one with SU-level 2 (and upward excess 2), and one with SU-level 3 (and upward excess 1). The maximum upward excess, or difference between the longest way up and the shortest way up, is three. Most species (represented by the points lying along the bottom of Fig. 3(a)) have no upward excess at all, i.e. the SU-level and the LU-level are equal.

The downward spectrum shows that the maximal short-way-down-level (which is 2 for this web) may differ from the maximal short-way-up-level (which is 3 in Fig. 3(a)). The biological details

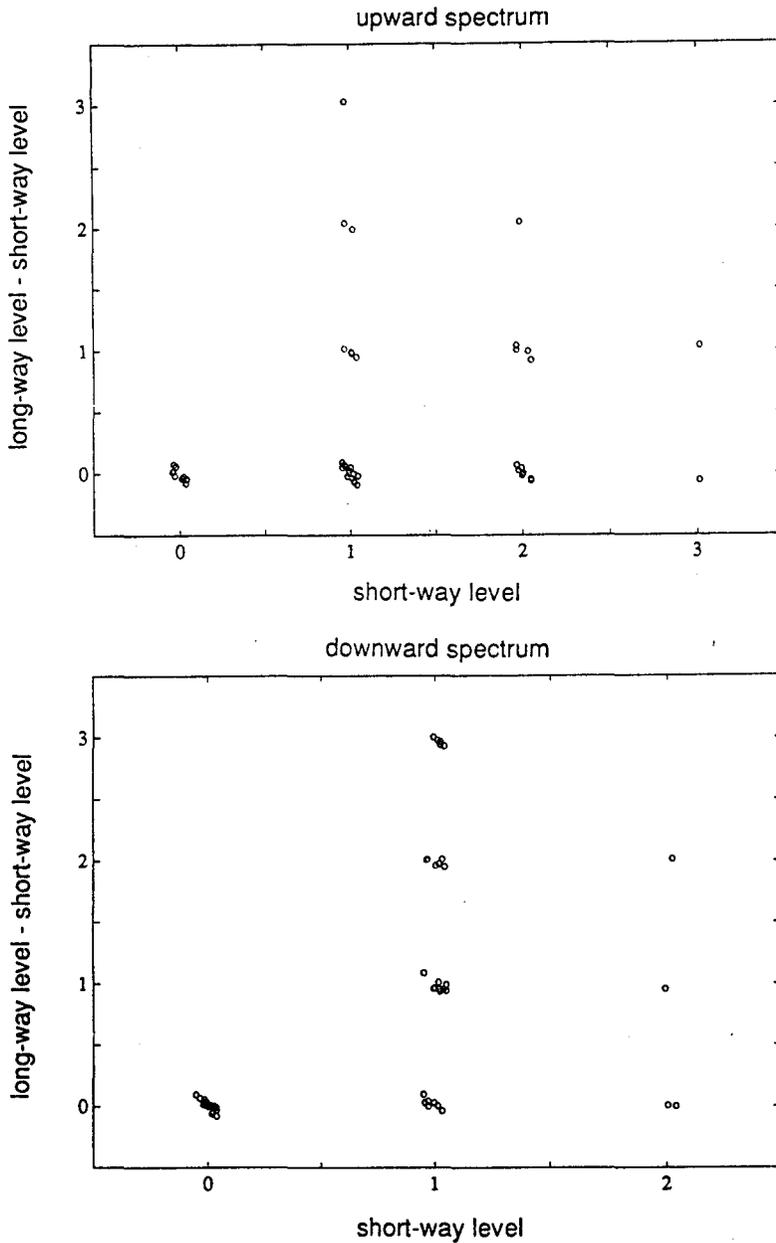


Figure 3. Spectra of the food web of the Sonora Desert, Arizona, according to Howes (1954) as edited by Briand (Cohen *et al.*, 1990, web 99, pp. 270–1). (a) Upward spectrum. (b) Downward spectrum. Each data point has exactly integer coordinates, but has been perturbed by a small random amount to render coincident points visible. Each symbol represents one species.

may help lend reality to this situation. After each species mentioned, we give its number according to Cohen *et al.* (1990, pp. 270–1). In the Sonora Desert, the creosote bush (4) has SD-level 2 because it is eaten by ground squirrels (16), which are in turn eaten by badgers (30), a top species, and by other species. No other species in the web has SD-level greater than 2. On the

Table 1. Webs analysed in this study.

ECOWeB™ number*	Habitat	Source	Reported species‡	Trophic species S§	Trophic links L¶	Density d**
26	Aspen forest, Manitoba	Bird, 1930	34	32	56	3.6129
28	Salt meadow, New Zealand	Paviour-Smith, 1956	45	32	35	2.2581
38	Lake Nyasa, rocky shore, Malawi	Fryer, 1959	31	31	95	6.3333
39	Lake Nyasa, sandy shore, Malawi	Fryer, 1959	37	33	70	4.3750
60	Montane forest, Arizona	Rasmussen, 1941	33	33	69	4.3125
99	Sonora Desert, Arizona	Howes, 1954	48	48	138	5.8723
106	Rocky shore, Monterey Bay, California	Glynn, 1965	37	35	73	4.2941

* Cohen (1989); same as Briand-Cohen numbering (Cohen *et al.*, 1990).

‡ These 'species' are varied collections of kinds of organisms, corresponding to Schoener's (1989) 'investigator-defined species'.

§ Trophic species are the result of lumping kinds of organisms with identical sets of prey (if any) and identical sets of predators (if any).

¶ Trophic links are counted after lumping investigator-defined species into trophic species.

** Density $d = 2L/(S - 1)$ so that connectance $p = d/S = L/(S(S - 1)/2)$. The average density for 113 webs of the Briand-Cohen collection is 4.0 (Cohen, 1990).

Table 2. Stratigraphies (numbers of species by level) for all seven webs with 30 or more trophic species in the Briand-Cohen collection (Cohen *et al.*, 1990); and sum of stratigraphies. Table 1 gives key to web numbers. For each web, the sum of each stratigraphy equals S, the number of trophic species in the web. The sum of each summary stratigraphy equals 244, the total number of species in all seven webs.

Level	Web 26				Web 28				Web 38				Web 39			
	LU	SU	LD	SD												
0	7	7	7	7	7	7	15	15	3	3	17	17	5	5	16	16
1	10	14	13	19	13	14	9	14	10	22	9	14	14	21	11	16
2	6	8	4	6	7	10	7	3	9	6	4	0	11	6	4	1
3	4	3	2	0	5	1	1	0	9	0	1	0	3	1	2	0
4	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
5	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
6	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0

Level	Web 60				Web 99				Web 106				Summary of 7 webs			
	LU	SU	LD	SD	LU	SU	LD	SD	LU	SU	LD	SD	LU	SU	LD	SD
0	5	5	11	11	9	9	17	17	5	5	12	12	41	41	95	95
1	13	16	11	15	17	24	7	27	13	22	13	22	90	133	73	127
2	10	12	7	7	12	13	11	4	8	8	5	1	63	63	42	22
3	5	0	4	0	7	2	7	0	5	0	2	0	38	7	19	0
4	0	0	0	0	3	0	6	0	3	0	1	0	9	0	9	0
5	0	0	0	0	0	0	0	0	1	0	2	0	2	0	4	0
6	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0

LU = long-way-up stratigraphy; SU = short-way-up stratigraphy; LD = long-way-down stratigraphy; SD = short-way-down stratigraphy.

other hand, grasshopper mice (43) have SU-level 3 because they eat scorpions and spiders (38), which eat Palo Verde weevils (20) among other prey items, and these weevils eat only Palo Verde (5), a basal species. No other species in the web has SU-level greater than 3.

Visual comparison of the upward and downward spectra suggests that the distribution of short-way-down-levels is more concentrated on smaller values than is the distribution of short-way-up-levels. To examine this suggestion in greater detail, and for comparison with stochastic food web models in section 5, Table 2 gives the four stratigraphies of all seven webs in the Briand-Cohen collection with 30 or more trophic species. In these webs, the largest LU-level and LD-level is 6, the largest SU-level is 3 and the largest SD-level is 2.

As Fig. 3 suggests, in all seven webs, short-way-down-levels are stochastically less than short-way-up-levels (as defined, for example, by Marshall and Olkin (1979, p. 481)), meaning that

$$\sum_{i=0}^n N_{SU}(i) \leq \sum_{i=0}^n N_{SD}(i) \text{ for } n = 0, 1, 2, \dots$$

Thus, as measured by shortest paths, species tend to be top species or close to top species more than to be bottom species or close to bottom species. This finding refines and extends the previous finding that community food webs have more top than basal species (e.g. Cohen, 1990, and earlier papers). There is no similar consistent relation between long-way-down-levels and long-way-up-levels.

Table 2 also gives the sum over all webs of the numbers of species at each level, separately for each definition of level. In these cumulated frequency distributions, short-way-down-levels are stochastically less than short-way-up-levels, but long-way-down-levels are not stochastically less than long-way-up-levels.

Table 3 summarizes, in two ways, the stratigraphies of the seven webs in Table 2. Table 3(a) divides the sum of the numbers of species at each level, cumulated over the seven webs, by the total number of species in all seven webs. Table 3(b) divides the sum of the fractions of species at each level within each web, cumulated over the seven webs, by seven. Table 3(a) weights each

Table 3. Normalized stratigraphies (fractions of species at each level). (a) Sum over webs of the *numbers* of species at each level (shown in last panel of Table 2), divided by total number of species in all seven webs: e.g. for LU-level and SU-level 0, the fraction $41/244 = 0.1680$ of all species has long-way-up and short-way-up-level 0. (b) Sum over webs of the *fraction* of species at each level, divided by seven, the total number of webs. (c) Expected fractions of species based on 500 simulations of the cascade model with $S = 40$ and link probability $p = 4.0/S = 0.1$. All species occurred at levels 0–6 except for a fraction 0.0525 of simulated species at LU- and LD-levels 7 and greater.

Level	(a) Normalized sum of counts				(b) Normalized sum of fractions				(c) Cascade simulations	
	LU	SU	LD	SD	LU	SU	LD	SD	LU, LD	SU, SD
0	0.1680	0.1680	0.3893	0.3893	0.1668	0.1668	0.3930	0.3930	0.2464	0.2464
1	0.3689	0.5451	0.2992	0.5205	0.3693	0.5478	0.3088	0.5162	0.1800	0.5221
2	0.2582	0.2582	0.1721	0.0902	0.2588	0.2573	0.1683	0.0908	0.1514	0.2000
3	0.1557	0.0287	0.0779	0.0	0.1575	0.0281	0.0730	0.0	0.1291	0.0276
4	0.0369	0.0	0.0369	0.0	0.0346	0.0	0.0309	0.0	0.1044	0.0034
5	0.0082	0.0	0.0164	0.0	0.0085	0.0	0.0171	0.0	0.0820	0.0006
6	0.0041	0.0	0.0082	0.0	0.0045	0.0	0.0089	0.0	0.0542	0.0
Sum	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.9475	1.0001

species equally, so that webs with more species receive relatively more weight; Table 3(b) weights each web equally, so that species in webs with more species receive relatively less weight. As Table 3 shows, the method of weighting makes very little difference to the resulting summary. If the fractions in Table 3 are rounded to the nearest 0.01, then in no case does the method of weighting make a difference of more than 0.01, and in most cases the method makes no difference.

Comparison with the cascade and superlinear homogeneous models – section 5

We now compare the observed stratigraphies in Table 2 with the stratigraphies predicted by two stochastic models of food web structure, the cascade model (Cohen *et al.*, 1990) and the superlinear homogeneous model (Cohen, 1990).

Both models assume that food webs are acyclic. This assumption holds for the webs of Table 2 (possibly after suppression of cannibalism). The cascade model assumes that the expected number $E(L)$ of links in a web with S species is directly proportional to S , so that the probability p of a link from a prey species to a consumer (sometimes called the connectance) is inversely proportional to S . The superlinear homogeneous model assumes that the expected number $E(L)$ of links in a web with S species is directly proportional to $S^{1+\epsilon}$, where $0 < \epsilon < 1$, so that the probability p of a link from a prey species to a consumer is proportional to $S^{\epsilon-1}$. In both models, the presence or absence of each link is statistically independent of the presence or absence of any other link.

According to the 113 webs of the Briand–Cohen collection (Cohen, 1990), there are, on average, approximately twice as many links as species, and $p \approx 4.0/S$ for large S if the cascade model is fitted to the data on links and species; when the superlinear homogeneous model is fitted, $\epsilon \approx 0.4$ (Schoener, 1989; Cohen, 1990) and $p \approx 1.4S^{-0.6}$.

Conditional on the number of links of a given web, the cascade model and the superlinear homogeneous model are identical. Both models have up-down symmetry (called ‘self-duality’ by Cohen, 1990), meaning that each model predicts exactly the same distribution of webs if the orientation of all links is reversed from the original orientation.

For comparison with Fig. 3, Fig. 4 plots the spectrum of a web simulated according to the cascade model with parameters chosen to match those of the Sonora Desert web of Howes (1954), namely, $S = 48$ and $p = d/S = 5.8723/48$. The simulated spectrum is located in roughly the same region of the coordinate plane as the observed spectra, and resembles the observed spectra more than do the spectra of the hypothetical webs in Fig. 2. One apparent difference between Fig. 3 and Fig. 4 is the considerable number of simulated species with excesses (ordinates, in both the upward and downward spectra) greater than 3, by contrast with the absence of such species in the real web. Assessing the significance of this difference obviously requires a quantitative analysis of repeated simulations, which is carried out below.

Łuczak and Cohen (unpublished observations) calculated the expected long-way up and expected short-way up stratigraphies (fractions of species in each level) in the cascade model, as well as various related properties, in the limit as the number S of species becomes arbitrarily large. Because of self-duality, the expected upward stratigraphies are identical with the corresponding expected downward stratigraphies. Numerical simulations of the cascade model show that, with 20 or more species, the simulated sample fractions of vertices at each level fall within the 95% confidence intervals around the expected fractions (as $S \rightarrow \infty$) of vertices at each level; for $S \geq 80$, the simulated sample means and the limiting values obtained from analytical formulas agree within 0.01 (Łuczak and Cohen, unpublished observations). Table 3(c) shows the

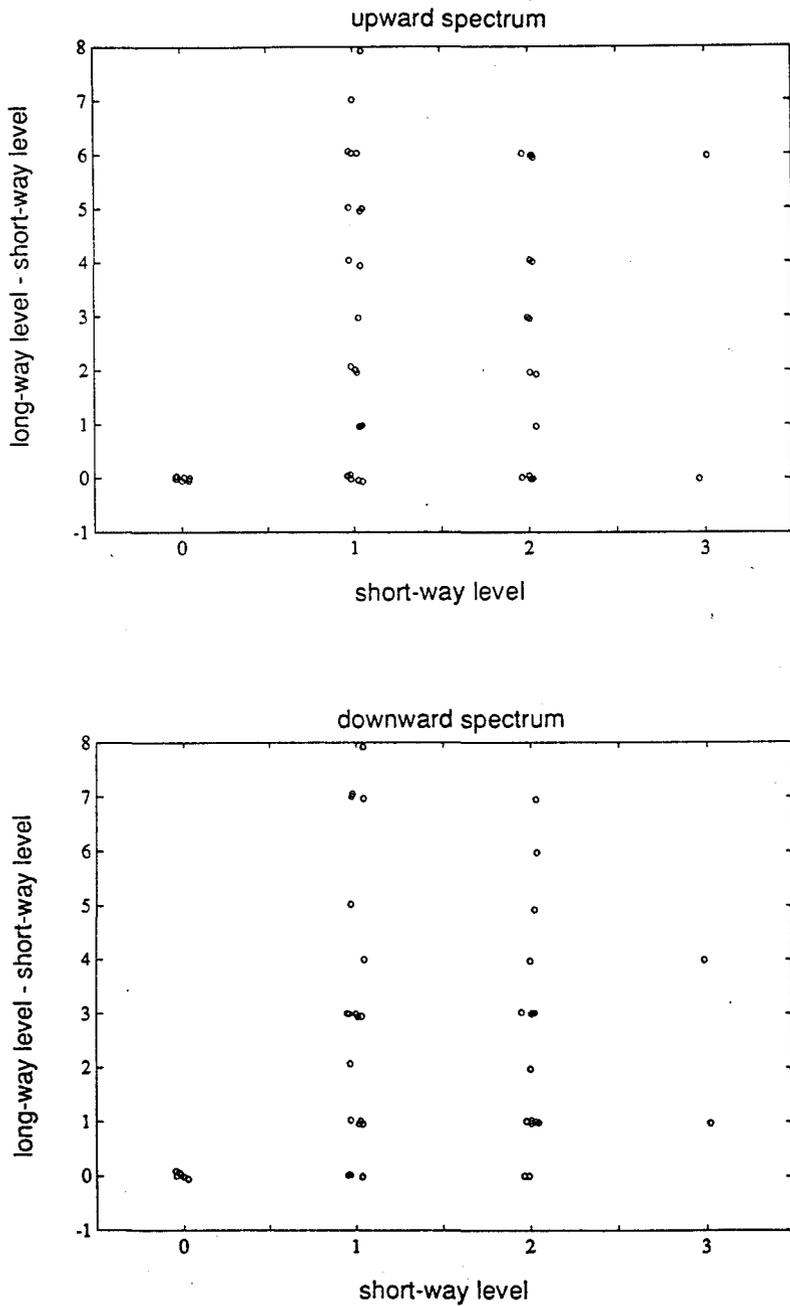


Figure 4. Spectra of a single simulation of the cascade model with parameters $S = 48$ and $d = 5.8723$ identical with those of the Sonora Desert web in Figure 3. (a) Upward spectrum. (b) Downward spectrum. Each data point has exactly integer coordinates, but has been perturbed by a small random amount to render coincident points visible. Each symbol represents one species.

predicted stratigraphies based on 500 simulations of the cascade model with $S = 40$ and link probability $p = 4/40 = 0.1$.

There are two major discrepancies obvious from a comparison between the observed stratigraphies in Table 3(a,b) and the predicted stratigraphies in Table 3(c). First, the observed upward stratigraphies differ grossly from the corresponding observed downward stratigraphies, unlike the self-duality of the cascade model. Second, the observed long-way-up-stratigraphy has its mode at level 1, unlike the predicted long-way-up-stratigraphy, which decreases monotonically from level 0 upward.

On the other hand, there are some major points of agreement between the observed stratigraphies in Table 3(a,b) and the predicted stratigraphies in Table 3(c). First, the observed long-way-down-stratigraphy decreases monotonically from level 0 onward, as predicted by the cascade model. Second, 95% or more of species fall in levels 0 to 6 of both the observed and predicted long-way stratigraphies and in levels 0 to 3 of both the observed and predicted short-way stratigraphies. Third, the fraction of species observed in short-way level 1 (both up and down) is remarkably close to that predicted by the cascade model.

From a comparison of summary stratigraphies, it is not possible to determine whether the discrepancies between observations and predictions are likely to have occurred by chance alone, nor whether the discrepancies may result from combining webs with different connectances. Therefore, we compared observed and predicted webs one web at a time. For each web, with S trophic species and L trophic links (i.e. after lumping, where necessary, investigator-defined species into trophic species), the probability p of a link was estimated as $\hat{p} = L/(S(S-1)/2)$. (Because we estimate the density of links or connectance from the observed data, we are testing only those assumptions that the cascade model and the superlinear homogeneous model have in common. Hence the procedure is a partial test of both models simultaneously.) With these values of S and p , the cascade model was simulated 50 times, and for each simulation the four stratigraphies were recorded. The average simulated stratigraphies were computed from the average of the 50 simulations. The difference between each of the four observed stratigraphies and the corresponding average simulated ('ave. sim.') stratigraphies was measured by the sum of the squared deviations between the corresponding species frequencies at each level, denoted by $N(\text{level})$:

$$d(\text{observed, ave. sim.} \mid \text{web}) = \sum_{\text{level} = 0}^{24} (\text{observed } N(\text{level}) - \text{ave. sim. } N(\text{level}))^2.$$

Then, for each of 50 simulations, denoted 'simulation n ', for $n = 1, \dots, 50$, the same measure of difference $d(\text{simulation } n, \text{ave. sim.} \mid \text{web})$ was computed for each of the four stratigraphies. Finally, the number of simulations such that

$$d(\text{simulation } n, \text{ave. sim.} \mid \text{web}) \geq d(\text{observed, ave. sim.} \mid \text{web})$$

was divided by 50, the number of simulations, to estimate the probability that a discrepancy as large as or larger than that between the observed web and the average simulated web would have occurred by chance alone. These estimated probabilities, one for each kind of stratigraphy for each web, are tabulated in Table 4. An estimated probability near zero signifies a poor fit between the observed and the predicted average stratigraphy, while an estimated probability near one signifies a close fit between the observed and the predicted average stratigraphy.

Table 4 has a clear message: in general, the cascade (or superlinear homogeneous) model describes the short-way-up and short-way-down-stratigraphies quite acceptably, but not the long-way-up and long-way-down-stratigraphies. Though the models correctly locate the range of levels

in the long-way stratigraphies where the bulk of species lie, the models do not, in general, distribute the species correctly among those levels.

The exceptions to these general patterns in Table 4 merit mention. The cascade and superlinear homogeneous models describe acceptably all four stratigraphies of web 26 (aspen forest, Manitoba) and the long-way-down-stratigraphy of web 28 (salt meadow, New Zealand), but not the short-way-down-stratigraphy of web 38 (rocky shore of Lake Nyasa, Malawi). Web 26, the web with the stratigraphies best described here by the cascade model, is also the web with the distribution of chain lengths best described by the cascade model among the 113 webs in the Briand-Cohen collection (Cohen *et al.*, 1990, pp. 134-6).

Even though the SD-levels of the seven webs are stochastically less than the respective SU-levels, sometimes the observed SU-stratigraphy fits the model better, and sometimes the observed SD-stratigraphy fits the model better. The lack of a consistent difference in the estimated probabilities suggests that as few as 50 simulations are not able to resolve or display any difference in the ability of the cascade model to fit the observed SU- and SD-stratigraphies.

Table 4. Estimated probabilities that a discrepancy as large as, or larger than, that between the observed web and the average simulated web would have happened by chance alone. The smaller the estimated probability, the worse is the fit between the observed and the predicted stratigraphy.

Web	Probability of a worse fit by chance			
	LU-stratigraphy	SU-stratigraphy	LD-stratigraphy	SD-stratigraphy
26	0.56	0.26	0.04	0.60
28	0.04	0.08	0.30	0.52
38	0.0	0.34	0.0	0.0
39	0.0	0.38	0.0	0.02
60	0.0	0.10	0.0	0.42
99	0.0	0.32	0.0	0.04
106	0.0	0.40	0.0	0.06

Discussion

What do these results mean? Several aspects of the results need to be considered: the observed asymmetry between the upward stratigraphies and the corresponding downward stratigraphies; the observed differences between the short-way and the corresponding long-way stratigraphies; and the relation between each kind of observed stratigraphy and the corresponding stratigraphy predicted by the cascade model (or the superlinear homogeneous model).

Asymmetry between upward and downward stratigraphies

The major unanticipated finding here is that the short-way-down-levels (SD-levels) of species are stochastically less than short-way-up-levels (SU-levels) in all seven webs with 30 or more trophic species in the Briand-Cohen collection. Could this difference be an artefact (S. L. Pimm, personal communication, 17 January 1991)? Suppose, for example, that ecologists paid more attention to large, visible species taxonomically close to humans than to small, microscopic species taxonomically remote from humans. Since the former are more likely to be found near the top of food chains and the latter are more likely to be found near the bottom of food chains, under this hypothesis ecologists would report more top than basal trophic species and relatively

more trophic links involving top species than basal species. Thus an intermediate species would have a greater variety of possible paths to a top species than to a basal species, and SD-levels would be expected to be less than SU-levels.

Two observations based on the 113 webs of the Briand–Cohen collection support this artefactual explanation (Cohen, 1990, p. 56). First, the 113 webs have an aggregate of 353 basal trophic species versus 511 top trophic species. Second, the 113 webs have an aggregate of 1029 basal–intermediate links versus 1327 intermediate–top links. Thus there are more top than basal species and more intermediate–top than basal–intermediate links.

However, two other observations argue against the artefactual explanation, one of them crucially. First, in the 113 webs of the Briand–Cohen collection, the number of basal–intermediate links per basal species is $2.9 = 1029/353$, which is *larger* than the number of intermediate–top links per top species, namely $1327/511 = 2.6$. Since the number of intermediate species is fixed at 1038, the probability of a link between any given pair of basal and intermediate species is larger than the probability of a link between any given pair of intermediate and top species. Second, the artefactual explanation should apply with equal strength to the comparison of the long-way-up-levels (LU-levels) with the long-way-down-levels (LD-levels). Here the difference anticipated from the artefactual hypothesis is not observed (except for the difference between LD-level 0 and LU-level 0, which is, by definition, the same as that between top and basal species). This last argument seems a compelling rejection of the hypothesis that the difference between the SU- and SD-stratigraphies is an artefact.

A related perspective is to ask whether the excess of top compared to basal species is sufficient to explain the difference between the SU- and SD-stratigraphies (T. W. Schoener, personal communication, 12 March 1991). A quick check on this possibility (suggested and carried out by Schoener) is simply to ignore the species in SU-level 0 and SD-level 0 and see whether the difference between the SU- and SD-stratigraphies survives. According to Schoener's check of the summary of seven webs in Table 2, the difference does survive.

Then what explains why species tend to be closer to a top predator than to a basal species? The cascade and superlinear homogeneous models predict that no such difference should exist. In the absence of a prediction derived from a well-grounded quantitative model, the following is speculative and *ad hoc*. Yet it may be worthwhile to offer a speculation, if only as provocation. It is speculated that with increasing SU-level above basal species, organisms tend to increase in body size. Many metabolic, behavioural and ecological characteristics of organisms are correlated with body size (e.g. Peters, 1983; Calder, 1984). Varied evidence (reviewed by Peters, 1983, pp. 112, 158) suggests that larger carnivores, larger herbivores and larger detritivores all consume food items over a wider range of size than do smaller consumers of the same type. If so, the shortest path to a top predator from an intermediate species in the middle of the range of sizes observed in a community would be expected to be shorter than the shortest path from a basal species up to that same intermediate species, because the intermediate species would sample from a narrower range of prey sizes than the top predators in food chains above it. This speculation could be tested with food webs where the body sizes of organisms are known.

Differences between short-way and long-way stratigraphies

Yodzis (1991) computed the frequency distributions of the length of the shortest chain, and of the longest chain, from basal species to top predators in 29 webs of the Briand–Cohen collection where primary productivity was known and humans were absent. He found no top predators with SU-level greater than 3, but many top predators with LU-level greater than 3. His results are qualitatively similar to those shown in Table 2 for *all* species (not just top predators) in a different subset of the Briand–Cohen collection. The abrupt truncation of SU-levels above 3 suggested to

Yodzis that the shortest chains are energetically limited. However, the simulations of the cascade model in Table 3 show that the same truncation of SU-levels above 3 could be generated without any explicit reference to energetic limitations (P. Yodzis, personal communication, 13 March 1991), though energetic constraints might be implicitly built into the assumptions of the cascade model in some way that has not yet been identified.

Observed stratigraphies and the cascade model

One failure of the cascade model and the homogeneous superlinear model requires further comment. The models do not, in general, correctly predict the distribution of species within the range 0–6 of LU-levels and LD-levels. Fewer long chains are observed (at LU- and LD-levels 4, 5 and 6) than are predicted by the models. S. L. Pimm (personal communications, 17 January 1991, and 9 May 1991) suggested that the cascade model predicts too many long chains for two reasons: it ignores the dynamic instability that arises when chains are long in Lotka–Volterra models of food webs (see Pimm *et al.*, 1991, for a recent review), and it mixes long and short chains in the same web. According to Pimm, for example, if A eats B and C while B also eats C, then B is in double jeopardy, once as a prey of A and once as a competitor of A. Pimm suggests that intermediate species are more likely to suffer extinction, and long chains to be shortened, in this and similar situations. An alternate explanation is that the data, especially at the lowest trophic levels, are of inadequate quality; portions of chains involving microbial predators and prey may simply be truncated in present data. As future webs of higher quality are reported, if Pimm is right, the discrepancies between observation and the predictions of the cascade model will grow larger; whereas if present data are faulty, the discrepancies will grow smaller.

Summary and conclusion

Four concepts are considered for the trophic level of a species in a community food web. The long-way-up-level (or LU-level) of species A is the length of the longest simple food chain from a basal species (one with no prey in the web) to A. (A simple chain is a chain that does not pass through any given species more than once.) The short-way-up-level (SU-level) of species A is the length of the shortest chain from a basal species to A. The long-way-down-level (LD-level) of species A is the length of the longest simple chain from species A to a top species (one with no consumers in the web). The short-way-down-level (SD-level) of species A is the length of the shortest chain from species A to a top species.

The upward spectrum of a food web is a scatter plot of species by LU-level minus SU-level on the ordinate and SU-level on the abscissa. The downward spectrum plots LD-level minus SD-level on the ordinate against SD-level on the abscissa. These plots offer a graphical means of detecting differences in structure among food webs as well as differences between the upward and the downward distribution of species within a single web.

A stratigraphy of a web is a frequency distribution of species according to some definition of level. The LU-, SU-, LD-, and SD-stratigraphies of the seven webs in the Briand–Cohen collection with 30 or more trophic species reveal no species with LU-level or LD-level more than 6, no species with SU-level more than 3, and no species with SD-level more than 2. In all seven webs, SD-levels are stochastically less than SU-levels, meaning that species tend consistently to be closer to a top predator than to a basal species.

The cascade model and the homogeneous superlinear model correctly predict that 95% or more of species should have LU-level and LD-level in the range 0–6. The models also correctly predict some details of the distribution of species in the SU- and SD-stratigraphies, particularly the fraction of species in level 1. However, the models do not, in general, correctly predict the

distribution of species within the range 0–6 of LU-levels and LD-levels. Fewer long chains are observed (at LU- and LD-levels 4, 5 and 6) than are predicted by the models. Because the models are self-dual, they cannot correctly predict the observed differences between the SU- and SD-stratigraphies at levels 0 and 2.

These results demonstrate the ability of the cascade model (or superlinear homogeneous model) to predict a previously untested feature of food web structure, the short-way-up and short-way-down stratigraphies, and the location of the long-way-up and long-way-down stratigraphies. These results also demonstrate the inability of these models to predict the detailed distribution of species in the long-way-up and long-way-down stratigraphies. The discrepancies may be due to limitations of the models or to limitations of the data.

A remarkable feature of the seven webs analysed here is that the most recent of them was published in 1965, more than a quarter of a century ago. For testing models, it is a virtue to use data that could not possibly have been influenced by the existence of the model, and so there is value in using older data. But it is also possible that the older data, collected with other purposes in mind, may not have been as consistently and carefully collected as would be helpful now. The resurgence of theoretical interest in food webs over the past two decades is now leading to renewed efforts to describe large food webs (e.g. Winemiller, 1990; Martinez, 1991). New data on large webs will make it possible to learn much more about the distribution of species by level. It would obviously be valuable to analyse more information about the flows of energy and nutrients through links in order to decide, for example, which paths (e.g. shortest versus longest) are most important.

The main conclusion of this paper is that the simple image of stacked trophic levels does not do justice to the richness of phenomena that appear when more refined concepts are used to analyse real food webs.

Acknowledgements

We thank S. L. Pimm, T. W. Schoener and P. Yodzis for constructive technical comments and L. B. Slobodkin for encouragement. This work was supported in part by US National Science Foundation grant BSR 87–05047 and the hospitality of Mr and Mrs William T. Golden.

References

- Bird, R. D. (1930) Biotic communities of the Aspen Parkland of central Canada. *Ecology* **11**, 356–442.
- Calder, W. A. (1984) *Size, Function and Life History*. Harvard University Press, Cambridge, MA, USA.
- Cohen, J. E. (compiler) (1989) *Ecologists' Co-Operative Web Bank. Version 1.0. Machine-readable Data Base of Food Webs*. Rockefeller University, NY, USA.
- Cohen, J. E. (1990) A stochastic theory of community food webs: VI. heterogeneous alternatives to the cascade model. *Theor. Pop. Biol.* **37**, 55–90.
- Cohen, J. E., Briand, F. and Newman, C. M. (1990) *Community Food Webs: Data and Theory. Biomathematics*, Vol. 20. Springer-Verlag, Berlin, Germany.
- Cousins, S. H. (1980) A trophic continuum derived from plant structure, animal size and a detritus cascade. *J. Theor. Biol.* **82**, 607–18.
- Cousins, S. H. (1987) The decline of the trophic level concept. *Trends Ecol. Evol.* **2**, 312–16.
- Elton, C. (1927) *Animal Ecology* (New impression with additional notes, 1935). Macmillan, NY, USA.
- Fryer, G. (1959) The trophic interrelationships and ecology of some littoral communities of Lake Nyasa. *Proc. Lond. Zool. Soc.* **132**, 153–281.
- Glynn, P. W. (1965) Community composition, structure, and interrelationships in the marine intertidal *Endocladia muricata* – *Balanus glandula* association in Monterey Bay, California. *Beaufortia* **12**(148), 1–198.

- Hairston, N. G., Smith, F. E. and Slobodkin, L. B. (1960) Community structure, population control and competition. *Am. Nat.* **94**, 421–5.
- Howard, L. O. (1897) *A Study of Insect Parasitism*. US Department of Agricultural Technical Series, Vol. 5, pp. 1–57.
- Howes, P. G. (1954) *The Giant Cactus Forest and Its World*. Duell, Sloan and Pearce, NY, USA.
- Lotka, A. J. (1925) *Elements of Physical Biology*. Williams and Wilkins, Baltimore, MD, USA.
- Marshall, A. W. and Olkin, I. (1979) *Inequalities: Theory of Majorization and Its Applications*. Academic Press, NY, USA.
- Martinez, N. (1991) Artifacts or Attributes? Effects of Resolution on the Little Rock Lake Food Web. Ecological Monographs (in press).
- Paviour-Smith, K. (1956) The biotic community of a salt meadow in New Zealand. *Trans. R. Soc. N.Z.* **83**(3), 525–54.
- Peters, R. H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Pimm, S. L. (1982) *Food Webs*. Chapman & Hall, London, UK.
- Pimm, S. L., Lawton, J. H. and Cohen, J. E. (1991) Food web patterns and their consequences. *Nature* **350**, 669–74.
- Polis, G., Myers, C. A. and Holt, R. D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* **20**, 297–330.
- Rasmussen, D. I. (1941) Biotic communities of Kaibab Plateau, Arizona. *Ecol. Monogr.* **11**, 228–75.
- Robinson, D. F. and Foulds, L. R. (1980) *Digraphs: Theory and Techniques*. Gordon and Breach, NY, USA.
- Schoener, T. W. (1982) The controversy over interspecific competition. *Am. Sci.* **70**, 586–95.
- Schoener, T. W. (1989) Food webs from the small to the large. *Ecology* **70**, 1559–89.
- Winemiller, K. O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* **60**, 331–67.
- Wool, D. and Manheim, O. (1986) Population ecology of the gall-forming aphid, *Aploneura lenisci*, in Israel. *Res. Popul. Ecol.* **28**, 151–62.
- Yodzis, P. (1989) *Introduction to Theoretical Ecology*. Harper and Row, NY, USA.
- Yodzis, P. (1991) Environment and trophodiversity. In *Historical and Geographical Determinants of Community Diversity* (R. E. Ricklefs and D. Schluter, eds). University of Chicago Press, Chicago, IL, USA (in press).