

Food Web Structure and Frequency Dependent Predation

by

Jorge X. Velasco-Hernandez

and

Carlos Castillo-Chavez

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JORGE X. VELASCO-HERNANDEZ^{2,3} and CARLOS CASTILLO-CHAVEZ²

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Abstract. In this work we apply the mixing/pair formation framework developed by Castillo-Chavez and Busenberg (1991) to the study of the dynamic behavior of food webs. The approach is based on the modeling of consumer-resource interactions and predator-prey systems that take place through frequency-dependent mechanisms. A simple food web is presented to exemplify the approach and some basic properties are derived to illustrate the feasibility of the pair formation approach to the modeling of the dynamics of food webs.

Key words. Food webs, mixing/pair formation, contact rates, differential equations.

AMS(MOS) subject classifications. ABC123.

1. **Introduction.** The hypothesis first proposed by Hairston et al. (1960) that the factors regulating natural populations depend on the trophic level to which they belong is addressed in this paper from the perspective of the modelling of food webs. We provide a mathematical framework for the study of the dynamics of frequency-dependent predation in heterogeneously mixing populations with emphasis on food web dynamics. We assume that the basic structure of a food web is made up of consumer-resource interactions including consumptive competition within a trophic level and frequency-dependent predation among trophic levels. These interactions are modelled using a mixing/contact dynamics framework as developed in Busenberg and Castillo-Chavez (1989, 1991) and Castillo-Chavez and Busenberg (1991). Competitors or consumer-resource interactions are modelled as mixing matrices which describe the contacts between members of different groups. These characteristics allow us to model interaction strength in food webs. When we apply this approach to a three-level food web of basal, intermediate and top species for which, under specific assumptions about the way species consume resources or are consumed as prey, the main conclusions of Hairston et al (1960) hold-- namely that producers (basal species) and carnivores (top species) are regulated by interspecific competition, and that herbivore regulation is through predation. Schoener (1988) has discussed the many exceptions and variants of the original hypothesis of Hairston et al. (1960) to which we do not apply our modelling framework. The food webs described by those exceptions and variants are more complex than the one explored here and not surprisingly, their mathematical complexity is increased to the extent that their analytical treatment is, in many cases, not feasible and numerical exploration is needed instead. However, we view the modelling framework described below as a way of linking the dynamics of food webs with their corresponding statistical properties explored by Cohen et al. (1990). The approach that we take is bottom up. We first postulate certain

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² Biometrics Unit, Cornell University Ithaca, New York 14853, USA.

³ Departamento El Hombre y su Ambiente Universidad Autonoma Metropolitana Xochimilco, Mexico City, Mexico.

‘invariants’ that have to be preserved by the densities of the species in each trophic level, and also a mechanism for the predator-prey or consumer-resource interaction. From these constraints we derive the explicit form of the equations modelling a specific type of food web under study.

2. Preliminaries. Cohen et al. (1984, 1990) have discussed extensively the basic properties and components of food webs. In their work, food webs are described through the concept of trophic species, a collection of organisms sharing the same diets and predators. Trophic species are used as the building blocks that provide an appropriate description of the statistical properties of food webs. Cohen’s work does not provide an adequate description if one is interested in the joint dynamics of the interacting species within food webs because there is a systematic lumping of individuals from different biological species.

Classical or static models (e.g., Cohen, 1990) describe the plausible behavior of the population densities of trophically related species. Results from ‘static’ food webs models are discussed in this paper to provide a reference point for our analysis. We highlight the results based on the ‘cascade model’ of Cohen because it has successfully described the observed patterns of natural trophic communities.

Our emphasis is on the description of prey selection, competition for common resources (see Pimm, 1982, 1988), interaction strength (Pimm and Kitching, 1988), and their relation to food web dynamics. We see food web as composed of biological species interacting through frequency-dependent predation and competition.

We model food web dynamics with the incorporation of factors that, according to Schoener (1989), determine the basic structure of a large class of food webs including the relation between predation and competition and their role in the dynamics of top, intermediate and basal species in the food web. Schoener (1989) studies those relations that are invariant with food web size defined as the number of trophic species in a food web (see Schoener, 1989; Cohen *et al.*, 1984, 1990; Pimm, 1982, 1988; Pimm *et al.*, 1987, 1988) based on the theoretical results provided by Cohen and co-workers (Cohen *et al.*, 1990; Cohen and Brian, 1984). He introduces two new concepts related to food web size invariants. These are food web generalization, which is defined as the average number of prey eaten per predator in the web, and food web vulnerability, which is defined as the average number of predators per prey in the web. Food web invariants include (Cohen et al., 1984, 1990):

1. The ratio number of prey to number of predators.
2. The fractions of species in the web belonging to top, intermediate and basal levels.

They also note that the number of links in a food web is directly proportional to the size of the food web. Schoener adds the following as invariants,

4. Food web vulnerability does not vary with food web size.

5. Food web generalization does not vary with food web size.

Furthermore, Schoener (1989) also shows that the first two invariants are redundant and the invariants derived by Cohen et al. (1990) can be explained in terms of his.

The use of biological species rather than trophic species as units of interaction in webs precludes the direct evaluation of the above invariants. However, the use of biological species in the description of food webs imposes natural constraints on the dynamics of predators and prey, or consumers and producers. These constraints are analogous to Schoener's concepts of generalization and vulnerability. Some of their consequences are discussed later in this paper.

Polis (1991) questions the explanatory value of current food web models using an extensive and well-documented study of a desert community in California. His food web exhibits the following properties (*cf.* Polis, *op. cit.*, pp. 143-147):

- a) The number of species is two orders of magnitude greater than the average number from webs analyzed under the classification scheme of trophic species.
- b) The number of links averages more than the average computed from models based on the concept of trophic species (e.g., Briand, 1983; Cohen *et al.*, 1984; Schoener *et al.*, 1991).
- c) Omnivory is frequent although it is not common (not statistically significant) in models that use the concept of trophic species (such as the 'cascade' model).
- d) Loops in this web are common but a rarity in models based on the concept of trophic species (see Pimm, 1982; Pimm and Rice, 1987; Cohen *et al.*, 1990).
- e) Top predators are rare or nonexistent in this web.
- f) The presence of omnivory and age-structure in the food web makes the concept of 'trophic level' inappropriate

The fact that the concept of trophic species is in many situations not operational can be addressed through the use of the concept of biological species. In this way we may address the issue of omnivory, complexity and stability in food webs. Static models that simply use a different currency are not applicable. This confusion leads to the wrong conclusion that 'theorists are trying to explain phenomena that do not exist' (Polis, *op.cit.*, p. 146). Moreover, Schoener (1989) uses many of the results derived from the cascade model to analyze the trophic structure of communities in the Bahamas. He obtained various hypotheses that will be tested with additional field work. In fact, one can argue that the 'cascade model' has played an important reference role in focusing Polis' criticism of static models but more importantly in his criticism of the value of the concept of trophic species.

In this work we assume that the patterns and processes observed by Polis are common in an important class of food webs. We study a simple three-level food web (top predator, intermediate species, bottom species) with no loops. However, we allow the possibility of omnivory through

frequency-dependent predation.

In the next section we derive a model for switching selection of prey by predators. Our approach makes use of recently developed methods for the analysis of mixing and pair formation processes in epidemiology (Busenberg and Castillo-Chavez, 1989, 1991; Castillo-Chavez and Busenberg, 1990; Blythe *et al.*, 1990), in which interacting individuals ‘choose’ their contacts according to a given set of preferences. In Section 3 describes the mathematical formalism used in this paper. Section 4 extends this formalism to account for predator-prey interactions while describing how risk indices can be measured. Section 5 applies our approach to trophic web dynamics. The Appendix presents alternative modeling approaches and collects some technical results.

3. The functional response of the predator. The mechanisms by which predators select prey for their diet has been the subject of intensive research (Akre *et al.*, 1979; Cock, 1978; Levin and Segel, 1982; Chesson, 1978, 1983; Gendron, 1987; Oaten and Murdoch, 1975; Teramoto *et al.*, 1979). A given predator’s diet is, in principle, not necessarily related to the abundance of the different prey types available (Gendron, 1987). From a phenomenological point of view, this outcome can be seen as the product of a density-dependent risk of being captured and the density of other alternative prey (Gendron, 1987). To model these interactions we let c_{ij} denote the total number of effective contacts (leading to a successful meal) between predators of type i and prey of type j per unit time; while r_{ji} denotes the number of prey of type j captured by predators of type i per unit time. If $T_i(t)$ denotes the number or density of predators of type i at time t and $N_j(t)$ denotes the number or density of prey of type j at time t , we must have that

$$T_i c_{ij} = N_j r_{ji} .$$

By setting

$$c_i = \sum_j^m c_{ij} , \quad r_j = \sum_i^n r_{ji} ,$$

one has

$$c_i T_i c_{ij} c_i^{-1} = r_j N_j r_{ji} r_j^{-1} ,$$

defining

$$p_{ij} = c_{ij} c_i^{-1}$$

and

$$q_{ji} = r_{ji} r_j^{-1}$$

permits the interpretation of p_{ij} as the proportion of prey of type j on the diet of the i th predator, and q_{ji} as the proportion of the j th prey type consumed by the i th predator. These definitions lead to the concept of a mixing matrix.

Definition 1: The matrix (p_{ik}, q_{ki}) is called a mixing/contact matrix if and only if it satisfies the following properties:

- (i) $0 \leq p_{ik} \leq 1$, and $0 \leq q_{ki} \leq 1$,
- (ii) $\sum_{k=1}^m p_{ik} = 1 = \sum_{i=1}^n q_{ki}$,
- (iii) $c_i T_i p_{ik} = r_k N_k q_{ki}$, for $i = 1, \dots, n$ and $j = 1, \dots, m$.
- (iv) If for some i , $1 \leq i \leq n$ and/or some j , $1 \leq j \leq m$ we have that $c_i r_k T_i N_k = 0$, then we define $p_{ik} \equiv q_{ki} \equiv 0$.

Condition (iii) is interpreted as a conservation of contacts law or group reversibility property which is the total number of contacts per unit time of predators of type i with prey of type j has to be equal. Condition (iv) asserts that the mixing of nonexistent subpopulations, either of prey or predators, cannot be arbitrarily defined. Condition (iii) replaces the concepts of food web generality and vulnerability described by Schoener (1989) by relating the rates at which k -prey are captured by i -predators $c_i p_{ik}$ and $r_k q_{ki}$. With k -prey and i -predator abundance N_k and T_k , we are introducing dynamic concepts involving biological species interactions analogous to Schoener's concepts for trophic species of generality and vulnerability.

The axioms stated in the definition were motivated by recent studies of the dynamics of sexually transmitted diseases. The formalism for STD dynamics is mathematically equivalent (as pointed out by Ross, 1911) to that for modelling host-vector interactions. The symmetry involved in the total number of contacts required for predator-prey, consumer-resource or host-parasite interactions is an obvious fact that has not been fully explored until very recently. Castillo-Chavez and Busenberg (1991) show that any set of mixing probabilities that satisfies the mixing axioms can be represented as multiplicative perturbations of a special family of solutions called *separable* or Ross solutions, which are probabilities associated with proportionate or weighted random mixing. Here we adopt Castillo-Chavez and Busenberg's framework to model common contact patterns including predator-prey interactions.

Using a derivation of Horst Thieme's (personal communication), we re-derive expressions for the mixing probabilities that allow for the incorporation of handling times. Let τ_i be the total time spent foraging by an average predator of species i , and let σ_{ij} denote the handling time spent by a predator of species i on prey in group j , $i=1, \dots, n$, $j=1, \dots, m$. Then

$$\bar{\sigma}_i = \sum_{k=1}^m \sigma_{ik} c_{ik} \quad (1)$$

denotes the mean handling time of predators of group i . The searching time (the available time that predators of species i have to find prey suitable for consumption) of predators of type i is $\tau_i - \bar{\sigma}_i$.

Hence, the number of contacts that an average predator of type i has with prey in group j during the searching time is

$$c_{ij} = (\tau_i - \tilde{\sigma}_i) b_{ij} N_j, \quad (2)$$

where b_{ij} denotes the proportion of successful contacts (contacts that result in a capture of prey) of predator species i with prey of group j .

Substituting (1) in (2) gives

$$\tilde{\sigma}_i = (\tau_i - \tilde{\sigma}_i) \sum_{k=1}^m \sigma_{ik} b_{ik} N_k.$$

Solving for $\tilde{\sigma}_i$ leads to

$$\tilde{\sigma}_i = \frac{\tau_i \sum_{k=1}^m \sigma_{ik} b_{ik} N_k}{1 + \sum_{k=1}^m \sigma_{ik} b_{ik} N_k}. \quad (3)$$

while substitution of (3) into (2) leads, after some algebra, to

$$c_{ij} = \frac{\tau_i b_{ij} N_j}{1 + \sum_{k=1}^m \sigma_{ik} b_{ik} N_k}.$$

From the ratio c_{ij}/c_i , we conclude that the probability of an effective contact between a predator of species i and a prey of group j is

$$p_{ij} = \frac{b_{ij} N_j}{\sum_{j=1}^m b_{ij} N_j}. \quad (4)$$

To derive the probability q_{ji} of an effective contact of predators of group i with prey of species j we solve the relation $T_i c_{ij} = N_j r_{ji}$ for r_{ji} . The formula $q_{ji} = r_{ji}/r_j$ leads to

$$q_{ji} = \frac{\tau_i b_{ij} T_j}{1 + \sum_{k=1}^m \sigma_{ik} b_{ik} N_k} \Bigg/ \sum_{i=1}^n \frac{\tau_i b_{ij} T_j}{1 + \sum_{k=1}^m \sigma_{ik} b_{ik} N_k}. \quad (5)$$

Equations (4) and (5) satisfy the mixing axioms (i) – (iii). Formula (5) may be interpreted in the following way: b_{ij} is the maximum capture proportion in the absence of frequency-dependent effects; $\tau_i b_{ij} T_j$ is the number of captures of prey of type j by predators of type i during the total foraging time characteristic of the predator species. The numerator of (5) gives the proportion of captures of all potential prey of predators of type i , while its denominator represents the total number of captures made by all types of predators per unit time; p_{ij} depends only on the weighted relative proportion of prey types, while q_{ji} depends also on the handling times of each predator species involved.

Definition 2 A predator-prey mixing probability is called *separable* if and only if

$$p_{ij} = p_i \tilde{p}_j \quad \text{and} \quad q_{ji} = q_j \tilde{q}_i.$$

To obtain separable solutions from formulae (3) and (4), one requires $b_{ij} = b$ for all indices (i.e., the maximum capture proportion is the same for all predators regardless of the prey type they capture). This assumption leads to the following set of contact probabilities (Ross solutions):

$$\tilde{p}_j = \frac{N_j}{\sum_{j=1}^m N_j}, \quad (6a)$$

and

$$\tilde{q}_i = \frac{\tau_i T_i}{1 + b \sum_{k=1}^m \sigma_{ik} N_k} / \sum_{k=1}^n \frac{\tau_k T_k}{1 + b \sum_{j=1}^m \sigma_{kj} N_j}. \quad (6b)$$

Thus, the frequency of a prey type in the diet of a predator depends on the proportion of prey types available, while the presence of a given prey type in the diet of a predator depends on the foraging time invested in capturing it. This last factor is commonly associated with the numerical response of the predator (see, e.g. Price, 1990).

4. The components of predation risk. Gendron (1987) and Gendron and Staddon (1983) have shown that the components of risk (how likely it is for a prey of any given type to be captured by a predator) can be understood in terms of the following factors (Gendron, 1987):

- The efficiency of the search path.
- The area searched by the predator per unit time.
- The conditional probability of detecting an encountered prey.
- The conditional probability of attacking and then capturing a detected prey.

Models for predator switching behavior are defined in terms of the frequency of each prey type in the diet of the predator. Specifically, F_i , the frequency of prey type i is defined as

$$F_i = \frac{\beta_i N_i}{\sum_{j=1}^m \beta_j N_j}, \quad (7)$$

where β_i is a measure of the relative risk of prey i . Usually β_i is usually computed by the formula

$$\beta_i = \frac{r_i}{\sum_{j=1}^m r_j}$$

where r_i denotes the risk index of species i . Frequency-dependent predation requires risk indices which are functions of the relative density of the prey species and give rise to the switching behavior of predators. Generalizations of this switching behavior model useful for statistical analysis are of the form

$$F_i = \frac{f(X_i)}{\sum_j f(X_j)},$$

where f is a nonlinear (usually a polynomial) function of X_j , the density of prey species j (e.g., Gendron, 1987).

To account for several predator species competing for a collection of prey species, we reformulate equation (7) in the following way

$$F_{ij} = \frac{\beta_{ij} N_i}{\sum_{j=1}^m \beta_{ij} N_j}. \quad (8)$$

The model is complete after the postulation of appropriate functional forms for the relative risks of predation β_{ij} . These functional forms usually weigh each prey type according to the risk of being captured (see Gendron, 1987). The connection with the mixing theory described before is made by our p_{ij} in (4) to model F_{ij} above.

Preferences, affinities or risks can be introduced by using the approach described in Blythe et al. (1991),

$$p_{ij} = \tilde{p}_j \psi_{ij} = \left(\frac{N_j}{\sum_{j=1}^n N_j} \right) \psi_{ij}^T \quad (9a)$$

$$q_{ji} = \tilde{q}_i \psi_{ji}^N = \left[\frac{\tau_i T_i}{1 + b \sum_{k=1}^n \sigma_{ik} N_k} / \sum_{i=1}^m \frac{\tau_i T_i}{1 + b \sum_{k=1}^n \sigma_{ik} N_k} \right] \psi_{ji}^N$$

where ψ_{ij}^T , ψ_{ji}^N include parameters related to the degree of risk or affinity between a prey of type j and a predator of type i .

Interpretations that are analogous to those of Castillo-Chavez and Busenberg (1991) and Blythe et al. (1991) give

- a) (ϕ_{ij}^T) as the predators' structural covariance matrix (nonnegative matrix) denoting the degree of preference (deviation from random capture) that predators of species i have for prey of species j .
- b) (ϕ_{ji}^N) as the prey structural covariance matrix (nonnegative matrix) denoting the degree of risk (deviation from being randomly captured) that prey of species j experience from predators of species i .
- c) The definitions $\mathcal{L}_i^T = \sum_{k=1}^n \tilde{p}_k \phi_{ik}^T$ and $\mathcal{L}_j^N = \sum_{k=1}^n \tilde{q}_k \phi_{jk}^N$ the weighted average of preference/risk of type i predators, and risk for type j prey, respectively, and the constraints

$$R_i^T = 1 - \ell_i^T > 0 \quad \text{and} \quad R_j^N = 1 - \ell_j^N > 0,$$

$$\sum_{i=1}^n \ell_i^T \tilde{p}_i = \sum_{i=1}^n \sum_{k=1}^m \tilde{p}_k \phi_{ik}^T \tilde{p}_i < 1 \quad \text{and} \quad \sum_{j=1}^m \ell_j^N \tilde{q}_j = \sum_{j=1}^m \sum_{k=1}^n \tilde{q}_k \phi_{jk}^N \tilde{q}_j < 1.$$

which imply that

$$\psi_{ij}^T = \frac{R_j^N R_i^T}{\sum_{k=1}^m \tilde{p}_k R_k^N} + \phi_{ij}^T \quad (9b)$$

and

$$\psi_{ji}^T = \frac{R_i^T R_j^N}{\sum_{k=1}^n \tilde{q}_k R_k^T} + \phi_{ji}^N \quad (9c)$$

for $i = 1, \dots, n, j = 1, \dots, m$. Furthermore, it can be shown that the covariance matrices for predator and prey can always be chosen such that R_i^T and R_j^N are nonnegative for all time.

From (i) and (ii) in Definition 1 it follows that

$$\sum_{i=1}^n c_i T_i = \sum_{j=1}^m r_j N_j$$

hold making the total rate at which prey is consumed equal to the total rate at which prey is captured. This constraint must be implicitly included in the modeling of food web dynamics. Food web dynamics live in this ‘manifold’. This biological fact is usually ignored.

Following Blythe *et al.* (1991) and Palmer *et al.* (1992), one can interpret formula (9) in the following way: a fraction of $\phi_{ij}^T \tilde{p}_j$ of the diet of predator i is composed of prey species j (the preferred prey species) and gives a rough estimate of the availability of prey of type j to that particular predator species. The remaining fraction of the diet of predator i is made up of random consumption of prey belonging to all the other species which are being captured at a rate $c_i R_i^T$. Since q_{ji} denotes the proportion of the i th prey type consumed by the j th predator species, $\phi_{ji}^N \tilde{q}_i$ denotes the risk (in terms of likelihood to be captured and consumed) sustained by prey i when predator species j shows preference for it. Because this process accounts for only a fraction of the total risk, the rest is assumed to be randomly allocated to risk from all other predator types.

Formula (9) incorporates naturally at least two of the components of risk in frequency-dependent predation: the preference that a predator shows for certain prey types and the corresponding risk immediately imposed on any prey by the existence of this preferential predation. Factors associated with predators’ search efficiency may be incorporated in the coefficients c_i and r_j which denote, respectively, the per capita capture rate of a predator of species i , and the average predation rate suffered by prey of species j .

Predation in nature is a selective process and has also been explored in the context of food webs

(Pimm, 1982, 1988; Fretwell, 1987). This frequency-dependent process may be due exclusively to frequency-dependent effects— the most numerous prey provides a greater share of the diet of any predator, or by an active process of preferential prey selection which may be more suitable for the survival of a predator. The formalism introduced by the mixing probabilities describes both processes. Pimm (1982, 1988) observes rare as well as common species of prey on predators' diets, thus imposing a ranking in prey species selectivity. This ranking depends on each predator species but it is not transposable to communities. The modeling approach introduced here allows for the incorporation of these effects.

In the next section we incorporate the mixing formalism in dynamic models of predator-prey interactions. These models form the basis of our approach to modelling food web dynamics.

5. Predator prey interactions and food webs. The general model of the predator-prey interaction is given by the system (the symbol ' denotes derivative with respect to time):

$$N'(t) = g[N(t)] - R(N, T) ; \quad T'(t) = T(t)G(N, T) - dT(t) , \quad (10)$$

where $G(N, T)$ is the numerical response of the predator and $R(N, T)/T$ is the number of prey consumed relative to prey density or functional response of the predator. The term, $g(N)$, models the growth process of a prey population when predators are absent and d is the (density-independent) mortality rate of the predator.

A generalized form of the predator-prey model (10) that allows for heterogeneity in prey and predator interactions is given by the following set of equations:

$$N'_j(t) = g_j[N(t)] - \sum_{i=1}^n c_i T_i p_{ij} , \quad (11)$$

$$T'_i(t) = T_i(t) \sum_{j=1}^{\ell} G \left(r_j \frac{N_j}{\sum_{j=1}^{\ell} N_j} g_{ji} \right) - d_i T_i ,$$

where G is a function that represents the numerical response of the i th predator and whose form will be specified later. Model (11) may also be used to describe the competitive interaction between species that share a spectrum of biotic resources which are distributed among themselves according to the mixing matrix (p_{ij}, q_{ji}) .

Our simplest food web model considers only three trophic levels (basal, intermediate and top) each with ℓ , m and n species, respectively. The dynamics are specified by the following transfer food web diagram:

$$N \rightarrow Y \rightarrow T ,$$

where $T = \{T_i\}_1^n$ denotes the top species, $Y = \{Y_k\}_1^m$ the intermediate species and $N = \{N_j\}_1^{\ell}$ the basal species. The model equations are

$$\begin{aligned}
N'_k(t) &= g_k[N_k(t)] - \sum_{j=1}^m a_j Y_j \pi_{jk}, \\
Y'_j(t) &= Y_j(t) \sum_{k=1}^{\ell} G\left(s_k \frac{N_k}{\sum_{k=1}^{\ell} N_k} \theta_{kj}\right) - \sum_{i=1}^n c_i T_i p_{ij} - \delta_j Y_j,
\end{aligned} \tag{12}$$

and

$$T'_i(t) = T_i(t) \sum_{j=1}^m F\left(r_j \frac{Y_j}{\sum_{j=1}^m Y_j} q_{ji}\right) - d_i T_i,$$

for $k = 1, \dots, \ell$, $j = 1, \dots, m$ and $i = 1, \dots, n$. The functions F and G denote the numerical response of intermediate and top predators. We are assuming these numerical responses of the same form for each predator type in either of the trophic levels. Finally, g_k denotes the growth law of the k th basal species in the absence of predators.

This model implicitly assumes that all species in level T are linked to all species in level Y , and that all species in level Y are linked to all basal species in N . There are $(\ell + n)m$ links in this completely connected food web (but see the Appendix).

The contact probabilities (p_{ij}, q_{ji}) (for encounters between T and Y populations) and (π_{ij}, θ_{ji}) (for encounters between Y and N populations) satisfy the axioms in Definition 1 as well as the conditions

$$\begin{aligned}
c_i T_i p_{ik} &= \tau_k Y_k q_{ki}, \\
\alpha_k Y_k \pi_{kj} &= s_j N_j \theta_{jk},
\end{aligned}$$

for $i = 1, \dots, n$, $k = 1, \dots, m$ and $j = 1, \dots, \ell$.

We now replace F , G and g_k by the following functional forms

$$F(x) = \alpha x, \quad G(x) = \beta x, \quad \text{and} \quad g_k(x) = \lambda_k x(1 - x/C_k),$$

where λ_k , C_k , α and β are constants. We obtain

$$\begin{aligned}
N'_k(t) &= \lambda_k N_k(1 - N_k/C_k) - \tilde{\pi}_k \sum_{j=1}^m \alpha_j Y_j, \\
Y'_j(t) &= \beta \tilde{\theta}_j Y_j \sum_{k=1}^{\ell} s_k \frac{N_k}{N} - \tilde{p}_j \sum_{i=1}^n c_i Y_i - \delta_j Y_j, \\
T'_i(t) &= \alpha T_i(t) \tilde{q}_i \sum_{j=1}^m r_j \frac{Y_j}{Y} - d_i T_i,
\end{aligned} \tag{13a}$$

where $N = \sum_{k=1}^{\ell} N_k$ and $Y = \sum_{j=1}^m Y_j$.

The initial conditions have to satisfy the constraints

$$\sum_{i=1}^n c_i T_i = \sum_{j=1}^m r_j Y_j \quad \text{and} \quad \sum_{i=1}^m \alpha_i Y_i = \sum_{j=1}^{\ell} s_j N_j \quad (13b)$$

at time $t = 0$, where

$$p_{ij} = \tilde{p}_j \psi_{ij}^T = \left(\frac{Y_j}{\sum_{j=1}^m Y_j} \right) \psi_{ij}^T$$

$$q_{ji} = \tilde{q}_i \psi_{ji}^Y = \left[\frac{\rho_i T_i}{1 + b \sum_{k=1}^m \sigma_{ik} Y_k} / \sum_{i=1}^m \frac{\rho_i T_i}{1 + b \sum_{k=1}^m \sigma_{ik} Y_k} \right] \psi_{ji}^Y$$

and

$$\pi_{ij} = \tilde{\pi}_j \zeta_{ij}^Y = \left(\frac{N_j}{\sum_{j=1}^{\ell} N_j} \right) \zeta_{ij}^Y$$

$$\theta_{ji} = \tilde{\theta}_i \zeta_{ji}^N = \left[\frac{\eta_i Y_i}{1 + e \sum_{k=1}^{\ell} \omega_{ik} N_k} / \sum_{i=1}^{\ell} \frac{\eta_i Y_i}{1 + e \sum_{k=1}^{\ell} \omega_{ik} N_k} \right] \zeta_{ji}^N.$$

If we assume random capture of prey (no preference), we have for all i, j ,

$$\psi_{ij}^T = \psi_{ji}^Y = \zeta_{ij}^Y = \zeta_{ji}^N = \text{constant},$$

In model (13) we consider the case where the capture of prey by corresponding predators is given by Ross solutions (6) in both the top and the intermediate levels of the food chain. The capture of prey is essentially a random process where predators do not show preference for prey of any type. Furthermore, we have that the total populations in each trophic level follow the dynamics specified by the system

$$N'(t) = \sum_{k=1}^{\ell} \lambda_k N_k (1 - N_k / C_k) - \sum_{j=1}^m \alpha_j Y_j,$$

$$Y'(t) = \beta \left(\sum_{j=1}^m \tilde{\theta}_j Y_j \right) \left(\sum_{k=1}^{\ell} s_k \frac{N_k}{N} \right) - \sum_{i=1}^n c_i T_i - \sum_{j=1}^m \delta_j Y_j,$$

$$T'(t) = \alpha \left(\sum_{i=1}^n \tilde{q}_i T_i \right) \left(\sum_{j=1}^m r_j \frac{Y_j}{Y} \right) - \sum_{i=1}^n d_i T_i.$$

This system is a representation of the dynamic behavior of the trophic species N , Y , and T or, in other words, it represents a model for the dynamics of the trophic web as such. Only in very special cases (as it will be shown below), the RHS of these equations can be written in terms of N , Y , and T , and hence can be solved independently of the biological species that constitute each trophic level. Statistical models of food webs deal with this level of organization.

The recruitment rate of both types of predators in the aggregated model (top T, and intermediate Y) include two of the components of predation. The first factor describes the probability of finding prey and the second factor represents the probability of capturing the prey given that it has been encountered.

Model (13) describes a food web in which the basal species grow in a density-dependent fashion in the absence of predation and the act of predation is decomposed into two factors: one represented by \tilde{q}_i and $\tilde{\theta}_j$, that gives the probability of capturing a prey, and the other by Y_j/Y and N_k/N , that represent the probability of detecting a prey. Finally, the numerical responses of both predator types (top and intermediate species) are assumed to be directly proportional to the number of prey captured as given by the mixing probabilities listed above.

A particular case of this model has been explored numerically by Hastings and Powell (1991). They found that for certain parameter ranges of b and e in the expressions for q_{ji} and θ_{ji} chaotic behavior may arise. Thus, according to our model, changes in the time scale at which mixing takes place can alter the behavior of food webs significantly.

Assuming that (13) is in steady state we find from the last and second equations, respectively, that

$$\tilde{q}_i^* \sum_j r_j \frac{Y_j^*}{Y^*} = \frac{d_i}{\alpha} \quad (14a)$$

and

$$Y_j^* = \frac{\tilde{p}_j^* \sum_i c_i T_i^*}{\beta \tilde{\theta}_j^* \sum_k s_k \frac{N_k^*}{N^*} - \delta_j} \quad (14b)$$

From (14b) we see that Y_j^* is positive if

$$\tilde{\theta}_j^* \sum_k s_k \frac{N_k^*}{N^*} > \frac{\delta_j}{\beta}, \quad (15)$$

which indicates that as the density-independent mortality rate increases with respect to β , the total rate of successful contacts [RHS of (15)] has to increase accordingly.

If we now take $f_k(x) = \lambda_k x$, we obtain the homogeneous system

$$\begin{aligned} N'_k(t) &= \lambda_k N_k - \tilde{\pi}_k \sum_{j=1}^m \alpha_j Y_j, \\ Y'_j(t) &= \beta \tilde{\theta}_j Y_j \sum_{k=1}^{\ell} s_k \frac{N_k}{N} - \tilde{p}_j \sum_{i=1}^n c_i Y_i - \delta_j Y_j, \\ T'_i(t) &= \alpha T_i(t) \tilde{q}_i \sum_{j=1}^m r_j \frac{Y_j}{Y} - d_i Y_i. \end{aligned} \quad (16)$$

for $k=1, \dots, l$, $j=1, \dots, m$ and $i=1, \dots, n$.

We rescale T_i , Y_j and N_k by defining the new variables $\epsilon_i = T_i/T$ ($T = \sum_{i=1}^n T_i$), $y_j = Y_j/Y$ and $n_k = N_k/N$. To describe this system we assume now that density independent death rates in species of any trophic level are negligible when compared with the effect of predation and competition. Letting δ_k and d_i to be identically zero, we have

$$\begin{aligned} n'_k(t) &= n_k \left(\lambda_k - \sum_{j=1}^{\ell} \lambda_j n_j \right), \\ y'_j(t) &= \beta y_j \sum_{k=1}^{\ell} s_k n_k \left(\tilde{\theta}_j - \sum_{i=1}^n y_i \theta_i \right), \\ \epsilon'_i(t) &= \alpha \epsilon_i \sum_{j=1}^m r_j y_j \left(\tilde{q}_i - \sum_{k=1}^n \tilde{q}_k \epsilon_k \right), \end{aligned} \tag{17}$$

which shows that the dynamics of the proportion of basal species are independent of the action of the predators at either level. The control of these species is due to competition. Actually, the subsystem for n'_k is a typical Kolmogoroff type system (Brauer, 1976). The independence on predation observed in this model (a consequence of proportional mixing) is in agreement with the classic results of Hairston, Smith and Slobodkin (1960), who say that producers (basal species in a three-level food chain) are limited by interspecific competition and not by the action of herbivores. The conclusions of Hairston et al.(1960) are also verified in the top carnivore species. In this case interspecific competition regulates the subsystem but now in a consumer-resource type of dynamics (MacArthur, 1972). At equilibrium, equation (17) gives

$$\lambda_k = \sum_{j=1}^{\ell} \lambda_j n_j^*, \quad \tilde{\theta}_j = \sum_{i=1}^n y_i^* \tilde{\theta}_i, \quad \tilde{q}_i = \sum_{k=1}^n \tilde{q}_k \tau_k^*, \tag{18}$$

for $k = 1, \dots, \ell$, $j = 1, \dots, m$ and $i = 1, \dots, n$ where the symbol $*$ denotes the populations at equilibrium. We now derive some properties derived from the food web axioms stated in Definition 1. Summing over j in the second equation in (18) gives

$$\frac{1}{\bar{m}} = \sum_{i=1}^m y_i^* \tilde{\theta}_i, \tag{16a}$$

while summing over n gives

$$\frac{1}{\bar{n}} = \sum_{k=1}^n \tilde{q}_k \epsilon_k^*. \tag{16b}$$

At equilibrium, the probability of capture by a top predator or ϵ_i , given that it has detected a suitable

prey, is

$$\tilde{q}_i \epsilon_i^* , \quad i = 1, \dots, n .$$

The expected proportion of successful captures (i.e., those contacts that result on a prey being captured) by a top predator is

$$\frac{1}{n} = \sum_i \tilde{q}_i \epsilon_i^* .$$

The same argument holds at equilibrium for intermediate species (herbivores in a three-level food chain) y_k . The expected probability of successful contacts is $1/m$. These probabilities, \tilde{q}_i and $\tilde{\theta}_j$, are complicated functions of population sizes, handling times, and so on, yet in a proportionate mixing model (Ross solutions), the average number of prey captured is what one would expect for a homogeneous mixing model (i.e., Lotka-Volterra system).

Thus, if Ross solutions are assumed for the capture probabilities the resulting average capture rate is independent of the prey species in the top and intermediate trophic levels.

We now discuss the relation between our food web model and the cascade model. Let S denote the number of trophic species in the community. Construct the ‘predation matrix’, a $S \times S$ matrix of zeros and ones. The entry ij has a value of one if species i can potentially feed on species j , and has a value of zero if this is not the case. A basic hypothesis of this model is that there are basically no loops in ‘natural’ food webs. Then the following order is imposed upon the predation matrix A .

1. Any species j can feed on any species i if $i < j$, but species j cannot feed on any species k if $j < k$.
2. Each species eats any species ranked below according to this hierarchy with probability d/S . Thus, the probability that species j does not eat species $i < j$ is $1 - (d/S)$.
3. As a consequence of the above, the predation matrix is a strictly upper triangular matrix.

From these simple principles, the cascade model is able to produce a series of predictions partially supported by data, including the calculation of the expected number of links $E(L)$ in the predation matrix. According to the cascade model the expected number of links is a linear function of S . Explicitly,

$$E(L) = (S - 1) \frac{d}{2}$$

or, in other words the number of species in the community has slope $d/2$. This slope as estimated from data (Cohen, 1989) has the value $d = 4$ (since the slope of the linear relation above has been found to be approximately equal to 2).

The models presented in this Section do not assume that the probability of capture is related directly to the total number of species in the food web. In the first place, our models work with biological species, not with trophic species. However, because of the evidence that the number of biological species in a community is directly proportional to the number of trophic species, we assume

that trophic species correspond exactly to biological species. Our models assume that probabilities p_{ij} (species i feeding on species j , if $i > j$) is not constant but depends on the abundance of the prey species. Our models consider behavioral aspects of a predator-prey interaction described in terms of the probability of predator capturing a prey and the probability of a prey being captured (which can be also thought of as the probability of a prey evading or escaping from an attack). The cascade model is upper triangular because it only takes into account the predators' view: the probability of feeding upon any prey species is fixed and equal to d/S . In our models this probability is represented by p_{ij} . In particular, if we assume that the predators have no preference whatsoever, we have (cf. Section 3)

$$P_{ij} = \tilde{p}_j .$$

If we assume that the above probability is independent of j we have $\tilde{p}_j = \tilde{p}$ and then

$$d = S\tilde{p} .$$

Recall that S is the number of trophic species. One way of having \tilde{p}_j constant is to assume that the predators perceive their 'trophic world' as composed of prey types (biological species) with the same number of individuals. Furthermore, each predator (regardless of its position in the trophic web) can potentially always prey upon on a fixed number m of biological prey species. Thus, we have

$$d = S \frac{1}{m}$$

which renders

$$m = dS ,$$

that is, the number m of biological species in a food web available to any predator regardless of its position in the food web is directly proportional to the number of trophic species S with proportionality constant equal to d .

To each entry A_{ij} of the predation matrix is associated a mixing probability p_{ij} , which gives the probability that a predator of species i captures a prey from species j . Consequently to this matrix we associate the matrix of mixing probabilities p_{ji} , which give the probability of the risk of prey of species j being captured by a predator of species i . The matrix P of mixing probabilities is, in general, not symmetric as formulae (4) and (5) show.

For this simple three-level food web discussed here, the assumption of exponential growth rate of basal species (in the absence of predators) and of random frequency dependent capture probabilities results in coupled systems analogous to Kolmogoroff-Lotka-Volterra equations. The coupling is hierarchical in that the basal population equations are decoupled from the other two sets of species but both basal and intermediate species depend on the densities of the species of the trophic level immediately below them. Furthermore, the time scales at which populations interact determine the

degree of ‘decoupling’ of the whole web. For example, if the dominant time scale of the basal prey subsystem is greater than that of the other two, it will reach equilibrium faster than the other two and the magnitude of n_k in the equation for y_j in (17) will become a parameter. An analogous mechanism holds for the subsystem of intermediate prey and top predators. However, if the time scale of the basal prey species is the slowest of the three subsystems, the equations for y_j cannot be decoupled.

A further consequence of random mixing is the existence of a constant expected number of successful captures by predators of both levels. This result complements number 2) in the introduction. If proportional mixing in capture rates is assumed, then the average number of captures in each predator level is asymptotically constant. In general, we can conjecture that for weakly connected food webs of the type of system (17), this result will hold.

6. Conclusions. Models of food webs can be divided into two categories. First are those that attempt to describe, from a statistical point of view, characteristic patterns common to sets of food webs. The cascade model of Cohen *et al.* (1990) provides a successful example. Cohen’s results have been criticized because they are tested against data of ‘edited’ food webs. This data base has been standardized, possibly creating problems in sample representativeness and introducing biases to differences in abundance/accessibility of organisms of the community under study (Paine, 1989; Peters, 1989). Nevertheless the patterns found by Cohen *et al.* are remarkable for their robustness. They demand an explanation or rejection on the basis of further field, experimental, or theoretical studies.

The concept of trophic species on which ‘static’ food web models are based is not a natural biological class but rather a theoretical classification. It is an equivalence class made of those organisms regardless of the species to which they belong, that share the same predators and the same prey. Thus, when one tries to define a trophic species from data two sources of error exist both associated with the identification of common predators and common prey. The applicability of the concept of trophic species to the field of applied ecology depends heavily on the ability of experimentalists to eliminate errors in the classification process. This problem is not unique to the study of food web dynamics; it is quite common in the biological and social sciences. Once the researcher establishes what is a weak (negligible) interaction and what is a strong one, the trophic level of each organism is determined. However, as the study of Polis (1991) shows, it is difficult to decide what is a weak and what is a strong interaction in a trophic web. Moreover, the existence of omnivory makes it difficult to justify the classification of organisms into trophic species. This is

particularly important if one is interested in the population dynamics of the web. Omnivory implies a very diverse diet with some items being more frequent than others (a matter of taste, opportunity, or chance), and if a large share of a predator's diet is made up of rare organisms, their neglect on the basis of weak or strong interactions may be misleading. Consequently, the trophic structure dynamics of the food web cannot be defined exclusively in terms of strong interactions, but rather through a 'distribution' of interactions that reflect the composition of the diet of organisms. In a recent study Paine (1992) concludes that in an species-rich herbivore guild exists mainly weakly negative or positive interactions with only a few strong negative ones. The modelling approach presented here is, in principle, compatible with this result.

The model presented here structures food webs through the process of frequency-dependent predation by assigning a set of probabilities to each possible interaction. Conceptual models are useful if one is interested in the dynamic behavior of the populations in the web. Our goal is to construct a model of food webs that incorporates the dynamics of the species involved in the community and, at the same time, provides a description of trophic relations.

A trophic web may be better described from a dynamical point of view if the description centers on what resources are used and the way these resources are used, that is, if the description is centered on guilds of species. A trophic web is a model of the interrelations between species that share common resources which have been shaped by natural selection through various mechanisms such as diffuse co-evolution (Maddox and Root, 1990). In fact, the mechanism of switching or apostatic selection has been recognized as one of the factors that may promote diversity in prey populations (Greenwood and Elton, 1979; Levin and Segel, 1982).

Finally, one could use the expressions derived in (16a, b) as a statistic to compare how the allocation of contact probabilities differs from proportional mixing in each trophic level. For example, once the number of species in a trophic level is determined one could, in principle, compute the RHS of (16) and estimate the deviation from the expected value given by the reciprocal of the number of species. Moreover, we have that

$$\tilde{\theta}_j = y_j, \quad \tilde{\pi}_k = n_k, \quad \text{and} \quad \tilde{q}_i = \epsilon_i.$$

This expression assumes that searching and handling times are independent of T_i . Under this assumption, one can compute the RHS of (16) simply by measuring the proportion of each species within a specific trophic level.

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APPENDIX

In this work we deal with food webs for which the mixing matrices (p_{ij}, q_{ji}) and (π_{kj}, θ_{jk}) have only strictly positive entries. However, it is desirable to allow for the lack of interactions between species or subsets of species in any trophic level. As Blythe (1991) has shown, one has only to slightly modify the characterization of the mixing probabilities to allow for partial connectedness. Partial connectedness refers to the existence of indices i, j , for which the corresponding mixing probabilities are identically zero for all time.

We now derive the general formula (9) for the case of non-fully-connected webs, which is a particular case of the approach presented in Blythe (1991).

As before let $c_i T_i$ denote the total number of captures by predators of species i per unit time. Similarly, $r_j N_j$ denotes the total number of prey of species j captured by predators per unit time. We introduce the notation:

Let $I^T = \{1, \dots, n\}$ and $I^N = \{1, \dots, m\}$ denote the set of species in the prey and predator compartments, respectively. Let

$$i \leftrightarrow j$$

represent the existence of a link between species with index i and species with index j . Thus define

$$\xi(c_i T_i) = \begin{cases} 1, & \text{if } c_i T_i > 0 \\ 0, & \text{if } c_i T_i = 0 \end{cases} \quad \text{and} \quad \xi_j^N(r_j N_j) = \begin{cases} 0, & \text{if } r_j N_j > 0 \\ 0, & \text{if } r_j N_j > 0 \end{cases} .$$

and

$$j_{ij} = \begin{cases} 0, & \text{if } i \leftrightarrow j \quad i \in I^T \quad j \in I^T \\ 0, & \text{if } r_j N_j = 0 \end{cases} .$$

These definitions allow us to generalize Definition 1.

Definition The matrix (p_{ik}, q_{ki}) is called a *mixing/contact* matrix if and only if it satisfies the following properties:

1. $0 \leq p_{ik} \leq 1$, and $0 \leq q_{ki} \leq 1$,
2. $\sum_{j \in I^N} j_{ij} \xi_i^T \xi_j^N p_{ij} = \xi_i \xi_j = \sum_{i \in I^T} j_{ji} \xi_j^N \xi_i^T q_{ji}$,
3. $j_{ij} \xi_i^T c_i T_i p_{ij} = j_{ji} \xi_j^N r_k N_k q_{ji}$, for $i = 1, \dots, n$ and $j = 1, \dots, m$.

Blythe (1991) has shown that with the above properties formula (9) can be replaced by

$$p_{ij} = \xi_i^T \xi_j^N j_{ij} \tilde{p}_j C_{ij} \quad \text{and} \quad q_{ji} = \xi_j^N \xi_i^T j_{ij} \tilde{q}_i D_{ij} \quad (17a)$$

where

$$C_{ij} = \frac{\xi_j^N R_j^N \xi_i^T R_i^T}{\Lambda^T} + \phi_{ij}^T, \quad D_{ji} = \frac{\xi_i^T R_i^T \xi_j^N R_j^N}{\Lambda^N} + \phi_{jj}^N \quad (17b)$$

and

$$R_i^T = 1 - \sum_{k \in I^N} \xi_k^T g_{ik} \tilde{p}_k \phi_{ik}^T, \quad R_j^N = \sum_{k \in I^N} \xi_k^N g_{jk} \tilde{q}_k \phi_{jk}^N,$$

$$\Lambda^T(t) = \sum_{k \in I^T} \xi_k^N g_{ik} \tilde{p}_k R_k^N, \quad \Lambda^N(t) = \sum_{k \in I^N} \xi_k^T g_{jk} \tilde{q}_k R_k^T.$$

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