Ecology, 85(2), 2004, pp. 352–358

FOOD WEB COHESION

Carlos J. Melián[1] and Jordi Bascompte

Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain

Abstract. Both dynamic and topologic approaches in food webs have shown how structure alters conditions for stability. However, while most studies concerning the structure of food webs have shown a nonrandom pattern, it still remains unclear how this structure is related to compartmentalization and to responses to perturbations. Here we build a bridge between connectance, food web structure, and compartmentalization by studying how links are distributed within and between subwebs. A ''*k* subweb'' is defined as a subset of species that are connected to at least *k* species from the same subset. We study the *k* subweb frequency distribution (i.e., the number of *k* subwebs in each food web). This distribution is highly skewed, decaying in all cases as a power law. The most dense subweb has the most interactions, despite containing a small number of species, and shows connectivity values independent of species richness. The removal of the most dense subweb implies multiple fragmentation. Our results show a cohesive organization, that is, a high number of small subwebs highly connected among themselves through the most dense subweb. We discuss the implications of this organization in relation to different types of disturbances.

Key words: cohesion; compartmentalization; connectance; food web structure; null model; subweb.

INTRODUCTION

The structure of food webs is an important property for understanding dynamic (May 1972, DeAngelis 1975, Pimm 1979, Lawlor 1980) and topologic (Pimm 1982) stability. Both theoretical and empirical approximations have represented food web structure with guilds (Root 1967), blocks and modules (May 1972), cliques and dominant cliques (Cohen 1978, Yodzis 1982), compartments (Pimm 1979), subwebs (Paine 1980), block submatrices (Critchlow and Stearns 1982), and simplicial complexes (Sugihara 1983). From these studies it is well known that food webs are not randomly assembled. However, it still remains unclear how the nonrandom structure of food webs is related to compartmentalization and its topologic and dynamic implications for stability following perturbations (Pimm and Lawton 1980, Polis 1991, Raffaelli and Hall 1992, Strong 1992, Solow et al. 1999). This is especially relevant after studies that show a much larger complexity of food webs than previously expected (Polis 1991, Strong 1992, Hall and Raffaelli 1993, Polis and Strong 1996).

Current studies show that groups of species are more connected internally than they are with other groups of species (Solow and Beet 1998, Montoya and Solé 2002). However, these studies do not make explicit reference to the number of modules and their heterogeneity (see Ravasz et al. 2002). Here, we build a bridge between connectance, food web structure, and compartmentalization by studying how links are distributed within and between subsets of species in twelve highly resolved food webs.

Specifically, we address the following questions: (1) How are subwebs structured within highly resolved food webs? (2) What is the relation between food web structure and compartmentalization? (3) What are the implications of subweb structure for responses to perturbations? In order to answer these questions we develop an operative definition of subweb.

MEASURES OF FOOD WEB STRUCTURAL ORGANIZATION

The k subweb

A *k* subweb is defined here as a subset of species which are connected to at least *k* prey species and/or predator species within the same subset. A *k* subweb has the following features: (1) Subwebs are defined using only information on the presence and absence of interactions. (2) Each species belongs only to one subweb, the subset where each species has the highest *k* value. (3) Each subweb contains species from different trophic levels.

Fig. 1 makes explicit this concept. As noted, different subwebs with the same *k* value are disjointed in the web. The sum of the total number of disjointed subwebs with at least *k* interactions represents the frequency of *k* subwebs. If we denote by S_T and S_k the total number of subwebs and the number of *k* subwebs, respectively, the frequency distribution of *k* subwebs is thus $p(S_k) = S_k/S_T$. (Note that, throughout this paper, $p(S_k)$ represents cumulative distribution.)

The most dense subweb

The most dense subweb is the subset of connected species with the largest number of interactions per spe-

---

Manuscript received 15 October 2002; revised 7 May 2003; accepted 13 May 2003; final version received 5 June 2003. Corresponding Editor: W. S. C. Gurney.

[1] E-mail: cmelian@ebd.csic.es

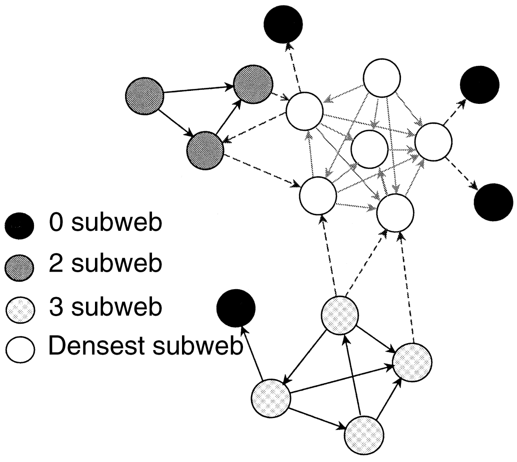

FIG. 1. A hypothetical food web graph. A subset of vertices is called a *k* subweb if every species within the subset is connected to at least *k* prey and/or predators from the same subset. We can observe the following subwebs: four separate 0 subwebs (i.e., species have no links with other species within the same subset, but have one or more links with other *k* subwebs of higher degree; black nodes); one 2 subweb; one 3 subweb; and one 5 subweb, the most dense subweb (white nodes). The links within the most dense subweb are represented as gray lines. The density of such interactions represents the connectance of the most dense subweb (C_d). Broken lines represent the interactions between the densest subweb and the rest of the web. The density of such interactions represents the intersubweb connectance between the most dense subweb and the rest of the web. Note that the web becomes fragmented in five parts if we eliminate the densest subweb.

cies (white circles in Figs. 1 and 2). In order to get a measure of cohesion, we calculate and compare connectance for the twelve food webs studied here (see Table 1). If real food webs are cohesive, we will find that the value of connectance of the most dense subweb is significantly larger than both global connectance and the connectance of the most dense subweb for a series of food web models. Global connectance is defined as

$$C = \frac{L}{S^2} \tag{1}$$

where L is the number of links in the web and S^2 is the maximum number of possible links, including cannibalism and mutual predation (Martinez 1991). Similarly, we can define the connectance of the densest subweb (C_d) as

$$C_d = \frac{L_d}{S_d^2} \tag{2}$$

where L_d is the number of interactions within the most dense subweb, and S_d^2 is the maximum number of possible interactions within the most dense subweb.

Null models of food web structure

Can this most dense subweb observed in food webs be reproduced by models with different levels of complexity? To answer this question, five food web models were tested. We generated 50 replicates of each model with the same number of species and global connectance as the real food webs. Our statistic (P) is the probability that a random replicate has a C_d value equal or higher than the observed value (Manly 1998).

In the first model, the basic null model, any link among species occurs with the same probability, equal to the global connectance (C) of the empirical web (Cohen 1978). The second model (Cohen et al.'s 1990 cascade model), assigns each species a random value drawn uniformly from the interval [0,1] and each species has the probability $P = 2CS/(S - 1)$ of consuming only species with values less than its own. The third model is the niche model by Williams and Martinez (2000). This model assigns a randomly drawn ''niche value'' to each species, similarly to the cascade model. Species are then constrained to consume all prey species within one range of values whose randomly chosen center is less than the consumer's niche value. In the preferential attachment model (Barabási and Albert 1999), the probability that a new species will be connected to a previous species is proportional to the connectivity of the later (both for resources and predators (j) of each new species), so that $P(k_j) = k_j/\Sigma_i(k_i)$. Finally, the local rewiring algorithm randomizes the empirical data yet strictly conserves ingoing and outgoing links (Connor and Simberloff 1979, Gotelli 2001). In this algorithm, a pair of directed links *A*–*B* and *C*–*D* are randomly selected. They are rewired in such a way that *A* becomes connected to *D,* and *C* to *B,* provided that none of these links already existed in the network, in which case the rewiring stops, and a new pair of edges is selected (Maslov and Sneppen 2002). We used a library of codes in *Matlab* to generate these matrices (C. J. Melián and J. Bascompte, *unpublished data*).

RESULTS

For the five largest food webs, we calculated the *k* subweb frequency distribution. The distribution was found to be strongly skewed with the best fit following a power law in all webs (see cumulative distribution in Fig. 2). The mean, ±1 SD, of the exponent (γ) for the five food webs was -1.34 ± 0.57. This means that subwebs show an extreme heterogeneity, with most subwebs with a small number of interactions per species and a unique most dense subweb.

In Silwood Park (Fig. 2a), species belonging to the most dense part (9% of species in the web) embody 70% of the interactions (26% of interactions among the species of the most dense subweb and 44% among these species and the rest of the web). In Ythan Estuary (Fig. 2b), the most dense subweb (21% of species in the web) holds 74% of all the links in the web (30% among

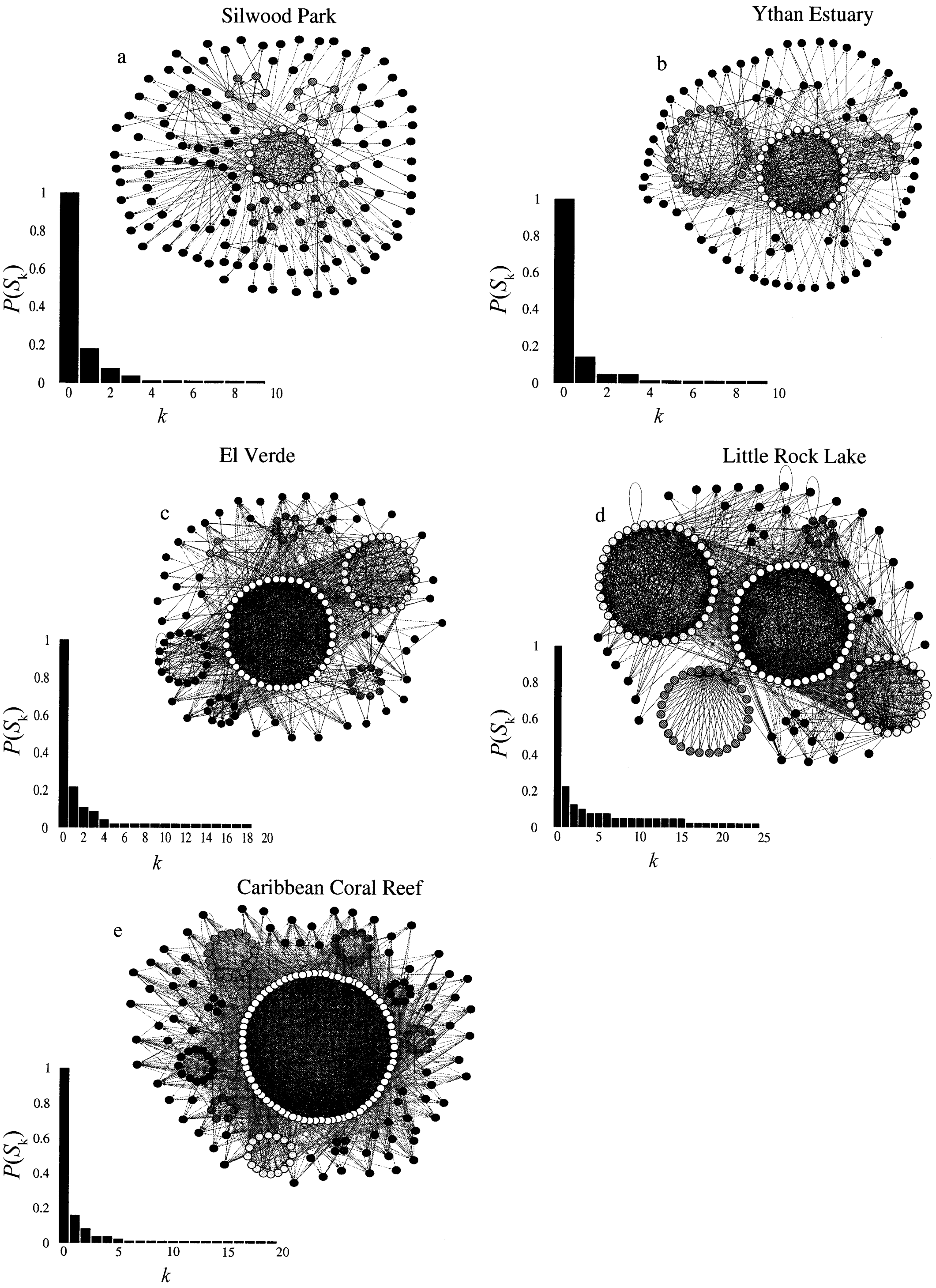

FIG. 2. Food web structure and *k* subweb frequency distribution (represented as the cumulative distribution $P(S_k)$) for (a) Silwood Park, (b) Ythan Estuary, (c) El Verde, (d) Little Rock Lake, and (e) the Caribbean. Gray level and line type are as in Fig. 1. As noted, the *k* subweb frequency distribution is highly skewed, decaying in all cases as a power law with a mean (± 1 SD) exponent $\langle \gamma \rangle = -1.34 \pm 0.57$. The network visualization was done using the Pajek program for large network analysis (available online).[2]

---

[2] URL: ⟨http://vlado.fmf.uni-lj.si/pub/networks/pajek/pajekman.htm⟩

TABLE 1. Food webs studied and their statistical properties.

Food web	S	k ± 1 SD	C	C_{d}	$\langle C_{\mathrm{db}} \rangle$	$\langle C_{\mathrm{dc}} \rangle$	$\langle C_{\mathrm{dn}} \rangle$	$\langle C_{\mathrm{lra}} \rangle$	$\langle C_{\mathrm{dpa}} \rangle$	Distribution
MAS	23	6 ± 3	0.13	0.26	0.16**	0.17**	0.32^{NS}	0.24^{NS}	0.39^{NS}	‡
BEN	29	14 ± 6	0.24	0.34	0.26**	0.26**	0.38^{NS}	0.32^{NS}	0.36^{NS}	‡
COA	30	19 ± 8	0.32	0.47	0.34**	0.35**	0.47^{NS}	0.44*	0.42^{NS}	‡
CHE	36	5 ± 3	0.06	0.14	0.08**	0.09**	0.18^{NS}	0.15^{NS}	0.33^{NS}	‡
SKI	37	21 ± 9	0.27	0.51	0.28**	0.29**	0.4†	0.43*	0.39^{NS}	‡
STM	44	10 ± 6	0.11	0.16	0.13**	0.13†	0.22^{NS}	0.17^{NS}	0.29^{NS}	‡
UKG	75	3 ± 3	0.02	0.26	0.03**	0.04**	0.14†	0.14†	0.16†	‡
YE	134	9 ± 10	0.03	0.23	0.04**	0.04**	0.12^{NS}	0.19†	0.12†	PL ($\gamma = -1.87$)
SP	154	5 ± 7	0.02	0.38	0.02**	0.03**	0.12**	0.32†	0.21†	PL ($\gamma = -1.98$)
EV	156	19 ± 18	0.06	0.30	0.07**	0.07**	0.14**	0.26*	0.17†	PL ($\gamma = -1.22$)
LRL	182	26 ± 22	0.07	0.36	0.07**	0.08**	0.16**	0.19**	0.17†	PL ($\gamma = -0.97$)
CAR	237	26 ± 34	0.05	0.19	0.06**	0.06**	0.12†	0.2^{NS}	0.15^{NS}	PL ($\gamma = -0.65$)

Notes: Abbreviations and their sources, as used in first column: Maspalomas (MAS), Almunia et al. 1999; Benguela (BEN), Yodzis 1998; Coachella (COA), Polis 1991; Chesapeake Bay (CHE), Baird and Ulanowicz 1989; Skipwith Pond (SKI), Warren 1989; St. Martin (STM), Goldwasser and Roughgarden 1993; United Kingdom Grassland (UKG), Martinez et al. 1999; Ythan Estuary (YE), Huxam et al. 1996; Silwood Park (SP), Memmott et al. 2000; El Verde (EV), Reagan and Waide 1996; Little Rock Lake (LRL), Martinez 1991; and Caribbean Coral Reef (CAR), Opitz 1996. Other abbreviations are: S, number of species; k, number of links per species; C, connectance, C_{d}, connectance of the most dense subweb for the empirical webs; $\langle C_{\mathrm{db}} \rangle$, $\langle C_{\mathrm{dc}} \rangle$, $\langle C_{\mathrm{dn}} \rangle$, $\langle C_{\mathrm{dlra}} \rangle$, and $\langle C_{\mathrm{dpa}} \rangle$, mean connectance of the most dense subweb for 50 replicates of the basic, cascade, niche, local rewiring algorithm, and preferential attachment, respectively. Distribution refers to the best fit of the k subweb frequency distribution (cumulative distribution calculated only for the five largest food webs); PL, power law, with the γ value the scaling exponent (slope). Angle brackets indicate means.

* $P < 0.05$; ** $P < 0.01$; NS, not significant.

† $0.05 < P < 0.1$.

‡ Cumulative distribution not calculated.

the species of the most dense subweb and 44% among these species and the rest of the web). The fraction of interactions in the most dense subweb of El Verde (Fig. 2c), Little Lake Rock (Fig. 2d), and Caribbean Coral Reef (Fig. 2e) (with 27%, 22%, and 31% of species in the web, respectively), represents 78%, 77%, and 89% of the total interactions, respectively (35%, 24%, and 33% among the species of the most dense subweb and 43%, 53%, and 56% among these species and the rest of the web, respectively).

The mean, ± 1 SD, percentage of species in the most dense subweb is 22 ± 8%, and the mean, ±1 SD, percentage of interactions within the most dense part is 78 ± 6%. This means that a small number of species contain the most interactions. The mean, ±1 SD, percentage of species in the most dense subweb in the five null models tested is 86 ± 5% for the basic model, 84 ± 6% for the cascade model, 43 ± 10% for the niche model, 37 ± 15% for the preferential attachment model, and 28 ± 13% for the local rewiring algorithm model.

Table 1 shows global connectance (C), the connectance of the most dense subweb for real data (C_{d}) and the mean for each one of the null models tested (the basic, $\langle C_{\mathrm{db}} \rangle$; cascade, $\langle C_{\mathrm{dc}} \rangle$; niche, $\langle C_{\mathrm{dn}} \rangle$; local rewiring algorithm, $\langle C_{\mathrm{dlra}} \rangle$; and preferential attachment, $\langle C_{\mathrm{dpa}} \rangle$; throughout this paper, variables enclosed in angle brackets are means). The values of C_{d} are significantly higher ($P < 0.01$) in the twelve food webs for the basic and cascade model (see Table 1), with the exception of St. Martin in the cascade model ($0.05 < P < 0.1$). For the Niche model, three of the most resolved food webs (Silwood Park, El Verde, and Little Rock Lake), departed significantly ($P < 0.01$) and the rest of the most resolved food webs departed marginally ($0.05 < P < 0.1$; with the exception of Ythan, $P = 0.18$). In the local rewiring algorithm, two of the most resolved food webs, El Verde and Little Rock Lake, departed significantly ($P < 0.05$ and $P < 0.01$, respectively), and the rest of the most resolved food webs departed marginally ($0.05 < P < 0.1$), with the exception of the Caribbean food web ($P > 0.1$). Finally, in the preferential attachment model, the most resolved food webs departed marginally ($0.05 < P < 0.1$; see Table 1), with the exception of the Caribbean food web ($P > 0.1$).

While C, $\langle C_{\mathrm{db}} \rangle$, $\langle C_{\mathrm{dc}} \rangle$, $\langle C_{\mathrm{dn}} \rangle$, and $\langle C_{\mathrm{dpa}} \rangle$ decay as a power law as the number of species increases ($r^2 = 0.53$, $P < 0.01$; $r^2 = 0.56$, $P < 0.01$; $r^2 = 0.6$, $P < 0.01$; $r^2 = 0.73$, $P < 0.01$; $r^2 = 0.8$, $P < 0.01$, respectively), C_{d} is independent of species richness ($r^2 \leq 0.16$, $P \geq 0.47$ for all the functions fitted), which suggests a scale-invariant property in the structure of food webs (similarly to the empirical data, the mean value of the C_{d} in the local rewiring algorithm, $\langle \mathrm{C}_{\mathrm{dlra}} \rangle$ is independent of species richness, $r^2 \leq 0.23$, $P \geq 0.24$ for all the functions fitted).

To further confirm the potential cohesion of the most dense subweb, we removed it and checked whether the remaining web is fragmented, and if so, in how many pieces. The web becomes fragmented in 54 parts in Silwood Park, 37 parts in Ythan Estuary, 29 parts in the Caribbean Coral Reef, 7 parts in El Verde, and did not become fragmented in Little Rock Lake. This multiple fragmentation shows the cohesive role of the most dense subweb.

DISCUSSION

It is well known that (1) connectance has a very narrow range of values (Warren 1990, 1994, Martinez and Lawton 1992), and (2) food webs are not randomly assembled (Cohen 1978, Lawlor 1978, Pimm 1980, Ulanowicz and Wolff 1991, Solow et al. 1999). However, little is known about how different subweb frequency distributions are compatible with a specific connectance value and about implications for dynamic and topologic stability.

In this paper we have studied the statistical properties of the structure in subwebs (*k* subweb frequency distribution) and the heterogeneous pattern of these subwebs. If this pattern were homogeneous, a single macroscopic description such as connectance would adequately characterize the organization of food webs. But this is not the case. There is a need to move beyond descriptions based on mean field properties such as mean connectance (Cohen 1978, Pimm 1980, Critchlow and Stearns 1982, Yodzis 1982, Sugihara 1983) to consider these other variables characterizing the structural organization of food webs.

Our results indicate both a high level of structure (with well-defined *k* subwebs) and a cohesive organization (the most dense subweb). While connectance is a scale-variant property (May 1974, Rejmánek and Stary 1979, Yodzis 1980, Jordano 1987, Sugihara et al. 1989, Bersier et al. 1999, Winemiller et al. 2001), the connectance within the most dense subweb in the twelve food webs studied is not correlated to species richness. This is in striking contrast to the null models explored with the exception of the local rewiring algorithm. Although the degree of connectance (see Table 1) and the types of historical and current human disturbances (Baird and Ulanowicz 1993, Raffaelli 1999), as well as other ecological and geographic factors were different in the food webs explored, a similar structural organization was found. This confers a remarkable level of generality to our results.

What type of mechanisms are underlying this cohesive pattern? As we have shown, food web models with increasing heterogeneity in links' distribution do not capture (niche model with the exception of Ythan and Caribbean) or marginally capture (local rewiring algorithm and preferential attachment with the exception of the Caribbean) the internal structure of the most resolved food webs. The biological mechanisms explaining the pattern here reported could be elucidated by comparing the identity and attributes of the species forming the most dense subweb across different food webs. If the species composing the most dense subweb in each food web are taxonomically and phylogenetically different, an ecological explanation should be suggested (Schoener 1989). However, if the species forming the most dense subweb are phylogenetically related, evolutionary mechanisms should be proposed (Williams and Martinez 2000). An intermediate case would be that in which there are phylogenetic differences but there is correlation with any biological attribute such as body size (Cohen et al. 2003) or other physiological and behavioral feature (Kondoh 2003). In this case, intermediate mechanisms should be suggested.

These results have implications relative to the previously proposed hypothesis about the propagation of perturbations (Pimm and Lawton 1980). The presence of a high number of small subwebs highly connected among themselves through the most dense subweb supports a structured view of the reticulate hypothesis. How do these highly structured and reticulated webs respond to disturbances? On one hand, the significantly larger probability of interactions between highly connected intermediate species may favor the propagation of disturbances (i.e., contaminants) through the web (Melián and Bascompte 2002, Williams et al. 2002). On the other hand, this cohesive structure may decrease the probability of network fragmentation when species are removed (Albert et al. 2000, Solé and Montoya 2001, Dunne et al. 2002). Also, the results presented here may be relevant to studies addressing whether the pattern of subweb structure may affect the likelihood of trophic cascades (Polis 1991, Strong 1992, Berlow 1999, Pace et al. 1999, Yodzis 2000, Shurin et al. 2002).

ACKNOWLEDGMENTS

We thank Sandy Liebhold, Pedro Jordano, George Sugihara, Louis-Félix Bersier, and Miguel A. Fortuna for useful comments on a previous draft, Enric Sala for bringing to our attention Opitz's work, and Enrique Collado for computer assistance. Funding was provided by a grant to J. Bascompte from the Spanish Ministry of Science and Technology (BOS2000-1366-C02-02) and a Ph.D. fellowship to C. J. Melián (FP2000-6137).

LITERATURE CITED

Albert, R., H. Jeong, and A.-L. Barabási. 2000. Error and attack tolerance of complex networks. Nature (London) **406**:378–382.

Almunia, J., G. Basterretxea, J. Aristegui, and R. E. Ulanowicz. 1999. Benthic–pelagic switching in a coastal subtropical lagoon. Estuarine Coastal and Shelf Science **49**: 363–384.

Baird, D., and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecological Monographs **59**:329–364.

Baird, D., and R. E. Ulanowicz. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Marine Ecology Progress Series **99**: 221–237.

Barabási, A.-L., and R. Albert. 1999. Emergence of scaling in random networks. Science **286**:509–512.

Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. Nature (London) **398**:330–334.

Bersier, L. F., P. Dixon, and G. Sugihara. 1999. Scale-invariant or scale dependent behavior of the link density property in food webs: a matter of sampling effort? American Naturalist **153**:676–682.

Cohen, J. E. 1978. Food webs and niche space. Princeton University Press, Princeton, New Jersey, USA.

Cohen, J. E., F. Briand, and C. M. Newman. 1990. Community food webs: data and theory. Springer-Verlag, Berlin, Germany.

Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. Proceedings of the National Academy of Sciences (USA) **100**:1781–1786.

Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? Ecology **60**: 1132–1140.

Critchlow, R. E., and S. C. Stearns. 1982. The structure of food webs. American Naturalist **120**:478–499.

DeAngelis, D. L. 1975. Stability and connectance in food webs models. Ecology **56**:238–243.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food web structure and network theory: the role of connectance and size. Proceedings of the National Academy of Sciences (USA) **99**:12917–12922.

Goldwasser, L., and J. Roughgarden. 1993. Construction and analysis of a large caribbean food web. Ecology **74**:1216–1233.

Gotelli, N. J. 2001. Research frontiers in null model analysis. Global Ecology and Biogeography **10**:337–343.

Hall, S. J., and D. G. Raffaelli. 1993. Food webs: theory and reality. Advances in Ecological Research **24**:187–239.

Huxham, M., S. Beaney, and D. Raffaelli. 1996. Do parasites reduce the change of triangulation in a real food web? Oikos **76**:284–300.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries and coevolution. American Naturalist **129**: 657–677.

Kondoh, M. 2003. Foraging adaptation and the relationship between food web complexity and stability. Science **299**: 1388–1391.

Lawlor, L. R. 1978. A comment on randomly constructed model ecosystems. American Naturalist **112**:445–447.

Lawlor, L. R. 1980. Structure and stability in natural and randomly constructed competitive communities. American Naturalist **116**:394–408.

Manly, B. F. J. 1998. Randomization, bootstrap and montecarlo methods in biology. Second edition. Chapman and Hall, London, UK.

Martinez, N. D. 1991. Artifacts or attributes? effects of resolution on the Little Rock Lake food web. Ecological Monographs **61**:367–392.

Martinez, N. D., B. A. Hawkins, H. A. Dawah, and B. P. Feifarek. 1999. Effects of sampling effort on characterization of food-web structure. Ecology **80**:1044–1055.

Martinez, N. D., and J. H. Lawton. 1992. Constant connectance in community food webs. American Naturalist **139**:1208–1218.

Maslov, S., and K. Sneppen. 2002. Specificity and stability in topology of protein networks. Science **296**:910–913.

May, R. M. 1972. Will a large complex system be stable? Nature (London) **238**:413–414.

May, R. M. 1974. Stability and complexity in model ecosystems. Second edition. Princeton University Press, Princeton, New Jersey, USA.

Melián, C. J., and J. Bascompte. 2002. Complex networks: two ways to be robust? Ecology Letters **5**:705–708.

Memmott, J., N. D. Martinez, and J. E. Cohen. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. Journal of Animal Ecology **69**:1–15.

Montoya, J. M., and R. V. Solé. 2002. Small world pattern in food webs. Journal of Theoretical Biology **214**:405–412.

Opitz, S. 1996. Trophic interactions in Caribbean coral reefs. Technical Report 43. International Centre for Living Aquatic Resource Management (now WorldFish Center), Penang, Malaysia.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution **14**:483–488.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology **49**:667–685.

Pimm, S. L. 1979. The structure of food webs. Theoretical Population Biology **16**:144–158.

Pimm, S. L. 1980. Properties of food web. Ecology **61**:219–225.

Pimm, S. L. 1982. Food webs. Chapman and Hall, London, UK.

Pimm, S. L., and J. H. Lawton. 1980. Are food webs divided into compartments? Journal of Animal Ecology **49**:879–898.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. American Naturalist **138**:123–155.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Raffaelli, D. 1999. Nutrient enrichment and trophic organisation in an estuarine food web. Acta Oecologica **20**:449–461.

Raffaelli, D., and S. Hall. 1992. Compartments and predation in an estuarine food web. Journal of Animal Ecology **61**: 551–560.

Ravasz, E., A. L. Somera, D. A. Mongru, Z. N. Oltvai, and A.-L. Barabási. 2002. Hierarchical organization of modularity in metabolic networks. Science **297**:1551–1555.

Reagan, D. P., and R. B. Waide. 1996. The food web of a tropical rain forest. University of Chicago Press, Chicago, Illinois, USA.

Rejmánek, M., and P. Stary. 1979. Connectance in real biotic communities and critical values for stability of model ecosystems. Nature (London) **280**:311–315.

Root, R. B. 1967. The niche exploitation pattern of the bluegray gnatcatcher. Ecological Monographs **37**:317–350.

Schoener, T. W. 1989. Food webs from the small to the large. Ecology **70**:1559–1589.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5**:785–791.

Solé, R. V., and J. M. Montoya. 2001. Complexity and fragility in ecological networks. Proceedings of the Royal Society of London B **268**:2039–2045.

Solow, A. R., and A. R. Beet. 1998. On lumping species in food webs. Ecology **79**:2013–2018.

Solow, A. R., C. Costello, and A. Beet. 1999. On an early result on stability and complexity. American Naturalist **154**:587–588.

Strong, D. R. 1992. Are trophic cascades all wet? differentiation and donor-control in speciose ecosystems. Ecology **73**:747–754.

Sugihara, G. 1983. Holes in niche space: a derived assembly rule and its relation to intervality. Pages 25–35 *in* D. L. DeAngelis, W. Post, and G. Sugihara, editors. Current trends in food web theory. Report 5983. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Sugihara, G., K. Schoenly, and A. Trombla, 1989. Scale invariance in food web properties. Science **245**:48–52.

Ulanowicz, R. E., and W. F. Wolff. 1991. Ecosystem flow networks: loaded dice. Mathematical Biosciences **103**:45–68.

Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. Oikos **55**:299–311.

Warren, P. H. 1990. Variation in food-web structure: the determinants of connectance. American Naturalist **136**:689–700.

Warren, P. H. 1994. Making connections in food webs. Trends in Ecology and Evolution **9**:136–141.

Williams, R. J., E. L. Berlow, J. A. Dunne, A.-L. Barabási, and N. D. Martinez. 2002. Two degrees of separation in complex food webs. Proceedings of the National Academy of Sciences (USA) **99**:12913–12916.

Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. Nature (London) **404**:180–183.

Winemiller, K., E. R. Pianka, L. J. Vitt, and A. Joern. 2001. Food web laws or niche theory? six independent empirical tests. American Naturalist **158**:193–199.

Yodzis, P. 1980. The connectance of real ecosystems. Nature (London) **284**:544–545.

Yodzis, P. 1982. The compartmentation of real and assembled ecosystems. American Naturalist **120**:551–570.

Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. Journal of Animal Ecology **67**:635–658.

Yozdis, P. 2000. Diffuse effects in food webs. Ecology **81**: 261–266.