Topological properties of food webs: from real data to community assembly models

Jose M. Montoya and Ricard V. Solé

We explore patterns of trophic connections between species in the largest and highest-quality empirical food webs to date, introducing a new topological property called the link distribution frequency (i.e. degree distribution), defined as the frequency of species S_L with L links. Non-trivial differences are shown in link distribution frequencies between species-rich and species-poor communities, which might have important consequences for the responses of ecosystems to disturbances. Coarse-grained topological properties observed, as species richness-connectance and number of links-species richness relationships, provide no support for the theory of links-species scaling law or constant connectance across empirical food webs investigated. We further explore these observations by means of simulated food webs resulting from multitrophic assembly models using different functional responses between species. Species richness-connectance and links-species richness relationships of empirical food webs are reproduced by our models, but degree distributions are not properly predicted, suggesting the need of new theoretical approximations to food web assembly. The best agreement between empirical and simulated webs occurs for low values of interaction strength between species, corroborating previous empirical and theoretical findings where weak interactions govern food web dynamics.

J. M. Montoya and R. V. Solé, ICREA-Complex Systems Lab, UPF Dr Aiguader 80, ES-08003 Barcelona, Spain. JMM also at: Dept of Ecology, Univ. of Alcalá, ES-28871 Alcala de Henares, Madrid, Spain (jose.montoya@cexs.upf.es). RVS also at: Santa Fe Institute, 1399 Hyde Park Road, NM 87501, USA.

Patterns in community structure do exist in nature. Studies of food web properties provided clues for understanding ecosystem organization and its relationship with different types of ecological stability (reviewed by Pimm 1991, Pimm et al. 1991, Warren 1994, Morin and Lawler 1996, McCann 2000). Many of these properties were shown to be artifacts caused by incompleteness and biases of the data on which they were based (Polis 1991, Cohen et al. 1993, Winemiller et al. 2001). Nonetheless, over the last decade, great effort has produced high-quality food web data, which permitted rejecting some previously observed regularities and confirming others (Williams and Martinez 2000 and references therein). Most have centered on the scale-invariant nature of food web patterns: whether observed patterns are roughly constant, among webs with

widely varying size (in terms of number of species, S) to determine if species-rich and species-poor ecosystems are organized in a similar way (Sugihara et al. 1989, Cohen et al. 1990, Havens 1992, Martinez 1992, 1994, Warren 1994, Murtaugh and Kollath 1997, Winemiller et al. 2001).

Basic average properties of food webs (i.e. S, the number of actual links L, or connectance C, defined as L divided by tire maximum possible number of links S^2) and their relationships have received considerable attention (Sugihara et al. 1989, Pimm et al. 1991, Havens 1992, Martinez 1992, Warren 1994, Murtaugh and Kollath 1997). But none of these studies dealt with the distribution of trophic links between species, i.e. link distribution frequencies. This measures the number of species with a certain number of links (ingoing and

outgoing lumped together), namely degree distribution in graph theory (Bollobás 1985). We explored differences in degree distributions across some complex food webs, finding that larger networks exhibit skewed distributions that strongly depart from those expected from random wiring, whereas food webs with fewer species have more homogeneous link distribution frequencies. This topological property highlights the importance of the position of species within food webs for their stability, considering species both acting as resource (ingoing links) and as consumer (outgoing links). In particular, deletion of the most connected species that are typical from food webs with skewed degree distributions might trigger coextinction of many other species by direct or indirect effects (Pimm 1980, Solé and Montoya 2001, Dunne et al. 2002, Montoya and Solé 2002).

One central question in food web theory is how structural and static patterns emerge from population dynamics of interacting species (Cohen et al. 1993). One possible way to explore this is to perform community assembly experiments in silico. Most literature on assembly dynamics of multispecies ecosystems deals with competitive communities (Case 1990, Morton et al. 1996 for a review) or randomly wired ecosystems without trophic structure (May 1973, Pimm 1991 and references therein). Assembly models of multispecies ecosystems with trophic structure have been less developed, starting from the early work by Pimm and collaborators (Pimm and Lawton 1978, Pimm 1979, 1980, Lockwood et al. 1997, see also Law and Blackford 1992, Bastolla et al. 2001). We investigated similarities and differences in food web patterns between real and simulated webs, the latest constructed through multitrophic assembly models considering different types of functional responses. We found that basic average properties are almost the same in real and constructed webs, particularly when low values of interaction strength are selected in the model. Thus, we predict, most interactions in complex food webs are weak, confirming some previous theoretical and empirical findings (Paine 1992, Raffaelli and Hall 1996, McCann et al. 1998, Berlow et al. 1999, McCann 2000). However, fine-grained properties such as link distribution frequencies cannot be explained through random assembly dynamics, providing an important clue for future food web modeling.

Methods

The data

We studied the largest and highest-quality empirical food webs available which were originally documented to study food web properties (although they are still far from perfect, as their authors emphasize; Table 1). This collection includes webs belonging to eight different habitat types: three, freshwater (Skipwith Pond, Little Rock Lake and Bridge Brook Lake), one marine (Benguela ecosystem), two marine-freshwater interfaces (Chesapeake Bay and Ythan Estuary). The other five are from different terrestrial habitats: a desert (Coachella Valley), a Caribbean island (St. Martin), a tropical rainforest (El Verde), a parasitoid community (UK grassland), and species related with the Scottish broom *Cytisus scoparius* (Silwood park). All are community food webs with the exception of Silwood Park, which is a source food web (Cohen et al. 1990, Memmott et al. 2000), and the UK grassland parasitoid assemblage, which is a composite web from, different sites (Cohen et al. 1990, Dawah et al. 1995). The number of species varies from 30 (Coachella Valley) to 182 (Little Rock Lake), reflecting a wide range of species richness. Some food webs differ in their taxonomic resolution. Trophic species (i.e. groups of real taxonomic species sharing a fraction of prey and predators) are present in most. For instance, the Coachella Valley, Little Rock Lake and El Verde webs present a high level of aggregation, whereas the Silwood park or UK grassland webs mainly contain real taxonomic

Table 1. Summary of the average properties of the empirical food webs analyzed. S is the number of taxonomic species or species aggregations (trophic species). L is the number of binary links contained in each web and C is the direct connectance defined as L divided the maximum possible number of links S^2 (Warren 1994). Two different versions of the Ythan Estuary web are included showing that link distribution frequencies are robust under different sampling effort.

Name	S	L	C	Reference
Skipwith Pond	37	351	0.26	Warren (1989)
Little Rock Lake	182	2371	0.07	Martinez (1991)
Bridge Brook Lake	75	555	0.10	Havens (1992)
Benguela ecosystem	29	187	0.22	Yodzis (1998)
Chesapeake Bay	33	78	0.07	Baird and Ulanowicz (1989)
Ythan Estuary (1)	93	407	0.05	Hall and Raffaelli (1991)
Ythan Estuary (2)	134	583	0.03	Huxham et al. (1996)
Coachella Valley	30	241	0.27	Polis (1991)
St. Martin Island	44	217	0.11	Goldwasser and Roughgarden (1993)
El Verde	156	1428	0.06	Reagan and Waide (1996)
UK grassland	87	128	0.02	Dawah et al. (1995)
Silwood Park	154	366	0.02	Memmott et al. (2000)

species. This does not produce bias in our results because we find well-taxonomically resolved food webs in rich and poor communities, and differences in level of aggregation were present in both. Furthermore, some average properties of food webs, such as connectance, are very robust under trophic aggregation (Martinez 1991, 1993). Sampling effort also must be considered when comparing food web data (Cohen et al. 1993). The 12 food webs analyzed here are far from being poorly sampled; sampling effort also has little effect on the topological properties we explored (Martinez 1991, 1994, Martinez et al. 1999, Montoya and Solé 2002). Connectance is robust under different sampling efforts for some of the food webs present in this study: for the Little Rock Lake (Martinez 1991, 1994) and UK grassland (Martinez et al. 1999). The same occurs for link distribution frequencies (Montoya and Solé 2002). Two versions of the Ythan Estuary food web shared a similar degree distribution despite differences in taxonomic detail: the second version added 42 metazoan parasite species that in the first version were lumped into a simple trophic species (Huxham et al. 1996, Montoya and Solé 2002). Thus, our food webs have both a wider range of S and a higher degree of taxonomic resolution than previous data collections (Sugihara et al. 1989, Cohen et al. 1990, Schoenly et al. 1991, Martinez 1992, 1994).

Link distribution frequencies

This property measures the number of species with a certain number of links, lumping ingoing (i.e. resource-consumer) and outgoing (consumer-resource) connections. This results in a frequency distribution whose shape accounts for the statistical relationship between specialist and generalist species. We used three different measures to quantify whether a trend exists in link distributions frequencies as species richness varies:

1. The coefficient of variation (CV) of link distributions frequencies:

$$CV = \sigma / \langle x \rangle \tag{1}$$

where σ is the standard deviation and $\langle x \rangle$ is mean linkage density (L/S). This measure is similar to that of Williams and Martinez (2000), but we considered all links of each species together (ingoing plus outgoing).

2. The skewness of degree distributions, which measures the deviation of distribution from symmetry (for a normal distribution it is equal to 0), and is expressed as (Sokal and Rohlf 1995)

$$Sk = S \left(\frac{\sum_{i=1}^{S}(x_i - \langle x \rangle^3)}{(S-1)(S-2)\sigma^3} \right) \tag{2}$$

where S is species richness, and x_i the number of total links (ingoing plus outgoing) of species i.

3. The χ^2 value for the fit of real to Poissonian distributions with mean equal to L/S:

$$\chi^2 = \sum_{i \in A(i)}^{bins} \left(\frac{(O_i - E_i)^2}{E_i} \right) \tag{3}$$

where $A(j)$ is the vector of non-zero observed values (i.e. the number of links with non-zero frequency), O_i are the observed values of real distributions and E_i are the expected values of the Poisson distribution (Sokal and Rohlf 1995).

We fixed $bins = 40$ to avoid aggregating observed values when they were numerous. This ensured χ^2 calculations were comparable for food webs of differing size.

The models

We used an extended version of Pimm's multitrophic assembly model (Pimm 1980, Lockwood et al. 1997), introducing different types of functional responses (i.e. how prey consumption by predators vary with prey density) in predator–prey dynamics: (1) linear functional response (Holling type I), where interaction strength is a per capita consumption rate of prey per predator and hence prey consumption increases linearly with prey abundance, ultimately hitting a maximum value for high prey densities; and (2) prey-dependent functional responses, where interaction strength indicates the maximal attack rite of predators on prey, and increases in a decelerating (Holling type II) or sigmoidal (Holling type III) fashion up to the maximal attack rate (Holling 1965).

Consider a set of Lotka-Volterra equations of the form:

$$\frac{dx_i}{dt} = x_i \left(\beta_i + \sum_{j=1}^{S} \Phi_{(x_j)} \right) \tag{4}$$

where x_i ($i = 1, ..., S$) are population sizes for each species, with β_i positive for basal species and negative for non-basal species. We used three species sets of equal size: $S_b = \{x_1, ..., x_s\}$, $S_i = \{x_{s+1}, ..., x_{2s}\}$, $S_t = \{x_{2s+1}, ..., x_{3s}\}$, where $S = 3S$ and the subindexes b, i and t stand for basal, intermediate and top species, respectively. Omnivory is allowed in our system, so that top species can feed both on intermediate and basal species. The functional response of species i was:

$$\Phi_{(x_j)} = \alpha_{ij}^1 x_j, \quad \text{for linear functional response}$$

$$\Phi_{(x_j)} = \frac{\alpha_{ij}^2 x_j}{D + x_j}, \quad \text{for Holling type II}$$

$$\Phi_{(x_j)} = \frac{\alpha_{ij}^3 x_j^2}{D^2 + x_j^2}, \quad \text{for Holling type III}$$

where α_{ij}^1 is the per capita interaction strength, and α_{ij}^2 and α_{ij}^3 are maximal attack rates. Hereafter, we will use the generic term interaction strength in reference to any of the α_{ij}^n and the previous specific terms when we deal with a particular functional response. α_{ij}^n is positive when $i > j$ (i.e. i is a predator feeding on prey j) and it is negative when $i > j$ (i.e. i is a prey consumed by predator j) or when $i = j$ and i is a basal species (i.e. intraspecific competition assuming resource limitation). D is the half-saturation density of prey consumed by predator, and determines the shape of Holling type II and III functional responses.

As in previous studies, values of β_i were chosen randomly from a uniform distribution between 0 and 1 (Pimm 1980, Lockwood et al. 1997, Borvall et al. 2000). D was constant for all species. It is usually determined empirically, and is the half-saturation density of prey i consumed by predator j. It determines the shape of the functional response as prey abundance increases. We selected values for D ranging from $1-8$, and found no difference in results. The α_{ij} were chosen from a uniform distribution $\rho(\alpha) \equiv 1/\alpha_m$, where α_m is the maximum allowed interaction strength. Variations in this maximum value result in different model outcomes. The units of α_{ij}^n differed for the three functional responses, but variation in model outcomes in relation with high or low values of interaction strengths were robust to the functional response selected.

All model features were predefined in a matrix that represented the regional species pool. Link distributions frequencies in species pools were constructed randomly, and therefore, were Poissonian (Bollobás 1985). Each t_i time iterations one species was randomly chosen to enter into the community from the species pool at a population density of 0.001. A species was considered extinct if its density was below that value (Lockwood et al. 1997).

We performed different simulations for each functional response, plus diverse combinations. We estimated mean values of S, C, L and link distribution frequencies over 1500 time steps. Doing so made model results more comparable to empirical data, which were collected through several years, and thus reflect various community snapshots put together (Cohen et al. 1993).

Studies on theoretical and empirical measures of interaction strengths advocate concentrating on per capita interaction strengths rather than other measures of predator–prey interactions (Laska and Wooton 1998, Berlow et al. 1999). Lotka-Volterra coefficients α_{ij}^1 are among the best approximations, because (1) they do not necessarily require an assumption of equilibrium

conditions as other measures, and are therefore potentially applicable to an extensive set of situations, and (2) they are less sensitive to variation in species densities than other measures, which require almost fixed population values (reviewed by Laska and Wooton 1998).

Results

Topological properties of simulated food webs were almost the same despite the functional response selected. Our models reproduced basic average properties of empirical food webs, such as SC and LS relationships, with best agreement for low values of maximum interaction strength α_m for each functional response explored. However, models did not discriminate observed differences in empirical data for degree distributions of species-rich and species-poor ecosystems.

C was scale-variant and related to S according to a power-law $S \sim C^{-\varepsilon}$ with an exponent $\varepsilon \approx -1/2$ (Fig. 1A). The constant connectance hypothesis (that is, $C \approx 0.14$ despite changes in S) reported in some previous studies (Pimm et al. 1991, Havens 1992, Martinez 1992) did not hold for the 12 food webs we investigated.

L increased with S in a different manner from that predicted by both the link-species scaling law ($LSSL$) and the constant connectance hypothesis (CCH). Assuming the simplest relationship between L and S in the form $L = \alpha S^\gamma$, the $LSSL$ states, γ must be close to one and that, on average, the number of links per species in a web is constant and scale invariant at roughly two, and therefore, $L \approx 2S$ (continuous line in Fig. 1B) (Cohen et al. 1990, Martinez 1992). In contrast, the CCH states the number of links in a web increases approximately as the square of the number of trophic species, with $\alpha < 1$, where α is the connectance C of the web. Thus, $L = CS^2$ (dashed line in Fig. 1B, with $C = 0.14$, Martinez 1991, 1992). Other studies rejecting the link-species scaling law have found values of $\gamma \approx 1.5$ (Sugihara et al. 1989, Schoenly et al. 1991, Havens 1992, Martinez 1994). Real data as well as model outcomes did not follow either hypothesis (see Fig. 1 for regression statistics), suggesting a more complex relationship not modelled by typical statistical distributions.

In empirical food webs, link distribution frequencies vary over a continuous transient from species-poor to species-rich ecosystems (Fig. 2). In this transition, communities with high S showed skewed distributions with long tails (e.g. power law fit of the log-transformed data with $L_s = S^{-\gamma}$ for Ythan (2): $\gamma = 1.04 \pm 0.05$ ($r^2 = 0.83$, $p < 0.01$), and for Silwood $\gamma = 1.13 \pm 0.06$ ($r^2 = 0.79$, $p < 0.01$), Montoya and Solé 2002). This topology is far from an expected random distribution of links, which typically is Poissonian (Bollobás 1985). In contrast, species-poor communities had a link distribution fre-
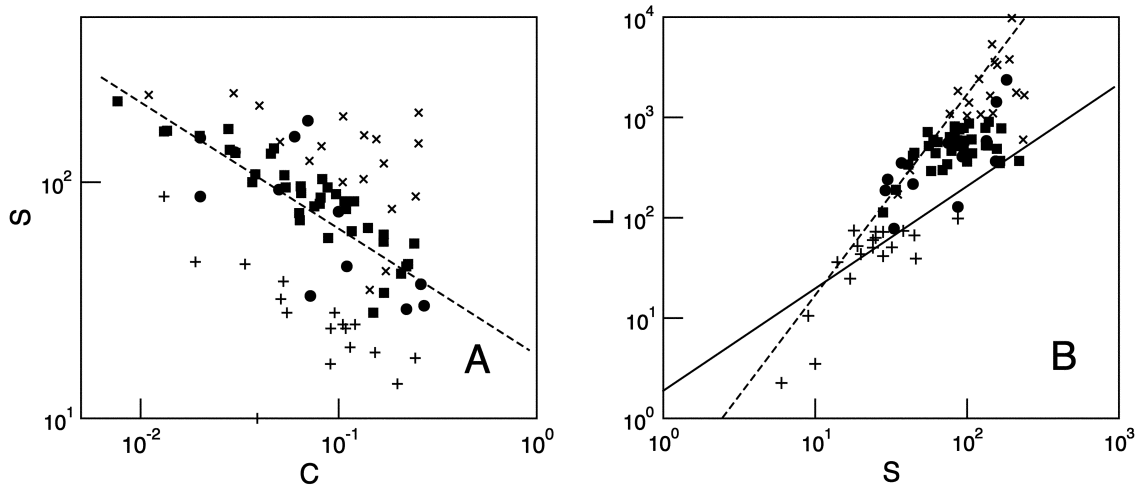
Fig. 1. Species richness-connectance (A) and links-species richness (B) relationships for empirical food webs (black circles) and simulated food webs (with linear functional response) with different α_m: $\alpha_m = 0.2$ (empty squares), $\alpha_m = 0.1$ (crosses) and $\alpha_m = 1.0$ (plus signs). The best fit to empirical data is obtained for $\alpha_m = 0.2$ (see Fig. 1 and 2 for regression statistics). Lines in (B) indicate predictions of the link-species scaling law (LSSL, continuous line, $L = 2S$) and the constant connectance hypothesis (CCH, dashed line $L = 0.14S^2$). No significant regressions are obtained for both real and simulated food webs over any of the two predictions: Real webs: with LSSL, $r^2 = 0.011$, $p \gg 0.05$; with CCH, $r^2 = 0.06$, $p \gg 0.05$. Simulated webs: with LSSL, $r^2 = 0.62$, $p \gg 0.05$; with CCH, $r^2 = 0.52$, $p \gg 0.05$.

quency closer to that expected from a random wiring of connections. When species richness was high, most species from the community had very few connections (i.e. there were many specialists) and only a few species were highly connected (i.e. generalist preys and predators), whereas when species richness was low, the number of connections fluctuated around mean linkage density L/S (see Fig. 3 for a representation of two webs with different S). In contrast, simulated networks always exhibited Poissonian degree distributions, independently of S (Fig. 4).

These qualitative observations in empirical webs were supported by the quantitative arguments summarized in Table 2. Most of the food webs exhibited link distribution frequencies different from a Poissonian one (all but three of the poorest ones: Benguela, Coachella and St. Martin food webs, see statistical significance in Table 2). However, as S increased, the difference between real and expected (Poissonian-like) distributions also increased ($r^2 = 0.8655$, $p < 0.0001$). The CV of degree distributions of empirical food webs was higher for species-rich communities than for species-poor ones ($r^2 = 0.504$, $p < 0.001$). This implies greater heterogeneity in the distribution of links between species in food webs with high S. Skewness was not related to species richness $r^2 = 0.157$, $p = 0.2024$). This measure reflects the deviation of real distributions from the symmetry expected for a normal distribution. Normal and Poisson distributions are similar only when data collections are very large (Sokal and Rohlf 1995), which was not the case for some of the food webs reported here.

Thus, because of the high variability in links per species in species-rich food webs, the LSSL did not

adequately reproduce the relationship between L and S. This hypothesis was developed using a set of webs with low S (Cohen and Briand 1984, Cohen et al. 1990). Introduction of species-rich communities with degree distributions showing great fluctuations around L/S contradicts this hypothesis.

Simulated nets whose basic average properties (S, L and C) corresponded to empirical food webs were limited to certain interaction strengths. For high values of α_m, no good fit was obtained. In addition, for extreme low values (e.g. $\alpha_m = 0.1$ for per capita interaction strength in linear functional response), SC and SL relationships and link distribution frequencies were inadequately reproduced (Fig. 1). This suggests real communities are governed by relatively weak interactions between species.

Discussion

We explored basic food web patterns and addressed a new one, link distribution frequencies, to understand their origin through assembly dynamics. As in previous studies, we found that the shape of the network of trophic interactions highly depends on the number of species present (Yodzis 1980, Sugihara et al. 1989, Martinez 1992, 1994, Murtaugh and Kollath 1997, Martinez et al. 1999). These topological properties might result from assembly processes and can be partially reproduced through simple multitrophic assembly models where dynamics are dominated by weak interaction strengths between species.
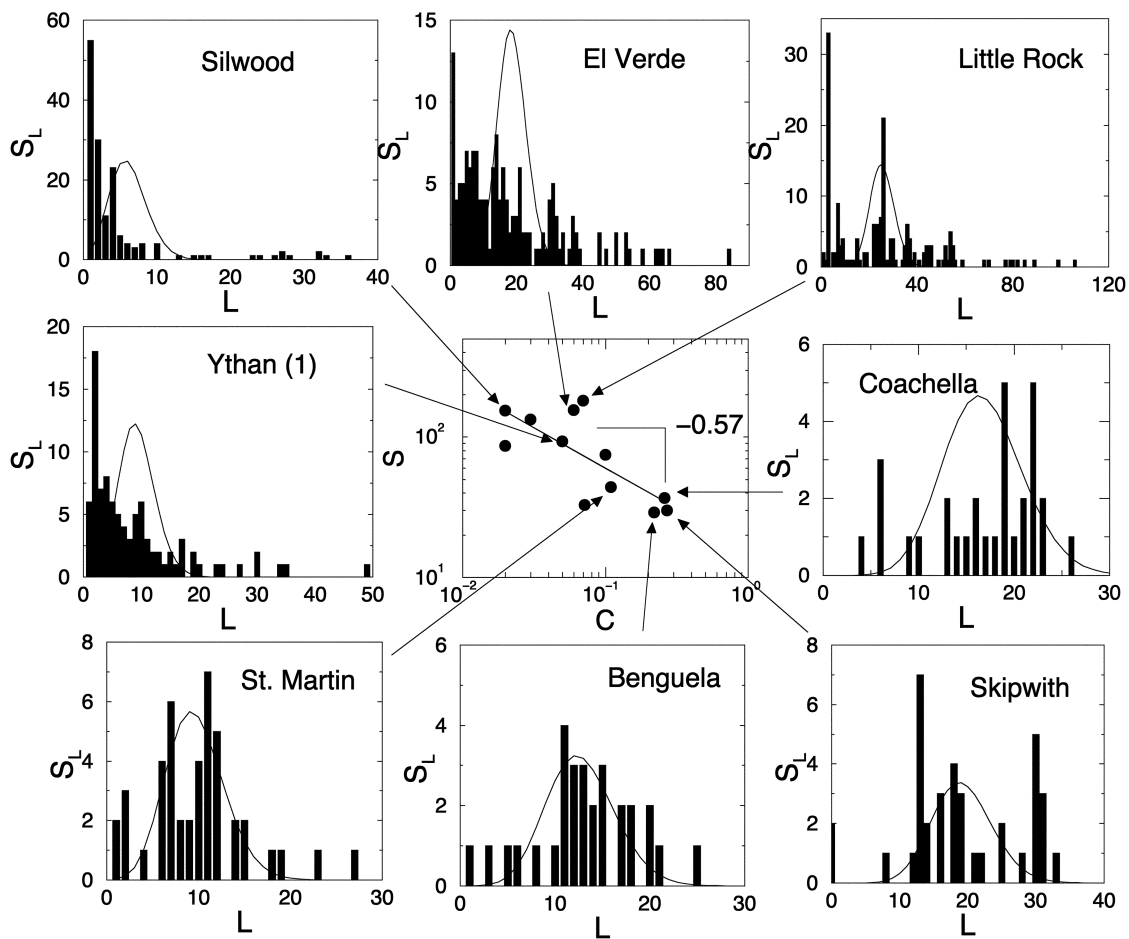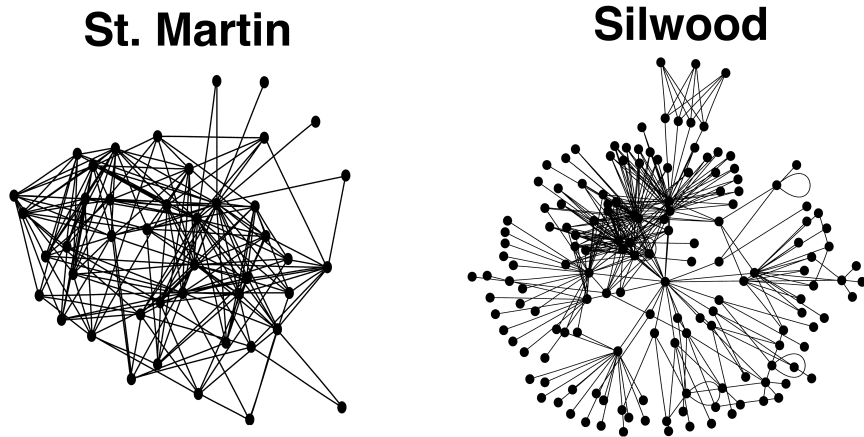
Fig. 2. Species richness-connectance relationship for the empirical food webs analyzed (central figure) and link distribution frequencies for some of them (figures at the periphery). S scales with C following a power-law function $SC^{-\gamma}$, with $\gamma = 0.57$ (power-law fit with least-squares regression on log-transformed data: $r^2 = 0.57$ $p < 0.005$). Actual link distribution frequencies (vertical bars where S_L is the number of species with L links ingoing plus outgoing) are shown together with expected distributions from a random wiring (continuous lines) predicting Poissonian behaviour with mean equal to linkage density (L/S). Note that as S increases, actual distributions increasingly depart from a random food web, showing long tails.

Fig. 3. Two examples of graphical representation of empirical food webs: St. Martin and Silwood networks. Nodes are taxonomic or trophic species and lines are feeding relationships. A higher degree of heterogeneity in degree distributions is exhibited by the Silwood Park food web whereas the St. Martin Island web resembled a more homogeneous network. Link distribution frequencies are calculated considering inward plus outward links for each species.
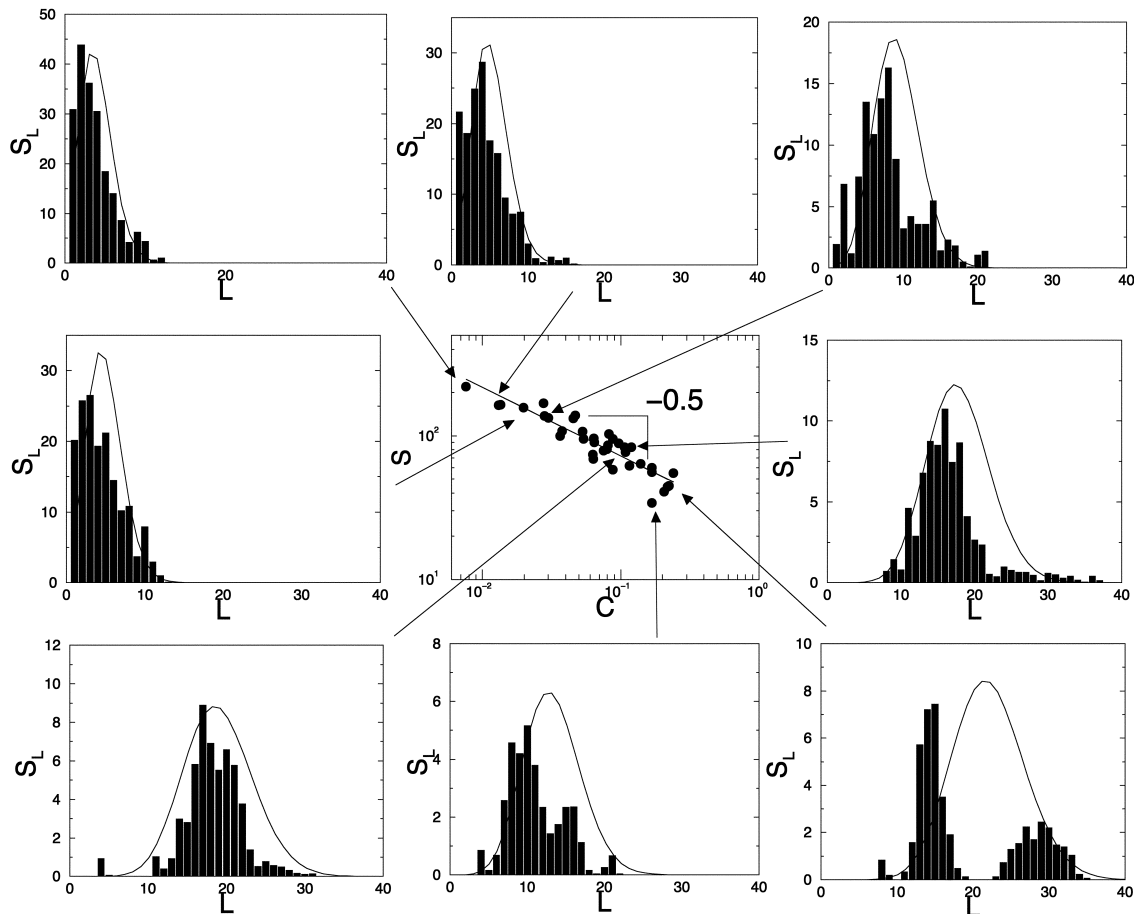
Fig. 4. Species richness-connectance relationship for simulated food webs (central figure) and link distribution frequencies for some of them (figures at the periphery). This case illustrates a linear functional response $\gamma = 0.5$ (power-law fit with least-squares regression on log-transformed data: $r^2 = 0.84$, $p < 0.0001$). Actual link distribution frequencies (vertical bars) and expected random ones are as in Fig. 1. The trend observed in empirical food webs was not present here. Here $\alpha_m = 0.2$ $t_i = 100$, and, C, S and degree distributions were the average values over the latest 1500 iterations. Fits for other functional responses: Holling II ($\alpha_m = 0.2$): $\gamma = 0.54$ ($r^2 = 0.61$, $p < 0.001$); Holling III ($\alpha_m = 0.3$): $\gamma = 0.6$ ($r^2 = 0.72$, $p < 0.001$).

Analysis of 12 well-described empirical food webs belonging to different habitat types showed that C was scale-variant and L did not follow either the link-species scaling law (Cohen et al. 1990) or the constant connectance hypothesis (Martinez 1991). A recent study on six different data sets of consumer taxocenes also reported little agreement between real webs and both food web hypothesis (Winemiller et al. 2001). Some previous analyses used different compilations and suggested webs of different size were constrained toward a roughly constant value of $C \sim 0.1–0.15$ (Martinez 1992, Warren 1994 and references therein). We showed that C varied in empirical food webs as S increases, from 0.27 to 0.02, and simulated webs had almost the same range. Our models were unable to generate food webs with $C < 0.25$, as it occurs in real food webs (maximum values: Coachella Valley 0.27, Skipwith Pond 0.26), suggesting at least two different types of dynamical constraints exist: (1) a threshold of C over which com-

munities cannot persist over time, and (2) (under this threshold) a power law decay of C as S increases, with an exponent close to $-1/2$. The latest is a rediscovery of the inverse hyperbolic relationship between S and C obtained from the EcoWeb database (Cohen and Briand 1984, Cohen et al. 1990), but the food web data on which our observation was based were documented specifically to address food-web patterns, whereas previous data collections were not (Polis 1991, Cohen et al. 1993).

Why do these patterns in food web connectance happen? Many hypotheses have been proposed (reviewed by Warren 1994). The most developed is the relationship between C and different types of ecosystem stability. Several ecological models suggest lower values of connectance involve higher local (May 1973, Pimm 1991, Chen and Cohen 2001) and global (Cohen et al. 1990, Chen and Cohen 2001) stability, that is, the system recovers faster after a disturbance. In contrast,

Table 2. Measures concerning link distribution frequencies across empirical food webs (see text for formalizations). Coefficient of variation (CV) of real food webs increases with S ($r^2 = 0.504$, $p < 0.001$); χ^2 values fixing bins $= 40$ also increase with S ($r^2 = 0.8655$, $p < 0.0001$). These findings show, respectively, that food webs with high S (1) have more heterogeneous link distribution frequencies, and (2) depart to a large extent from expected degree distributions after a random wiring which are typically Poissonian. Skewness does not significativelly increase with S ($r^2 = 0.157$, $p = 0.2024$). [1]indicates $p < 0.005$.

Web	S	CV	Skewness	χ^2
Skipwith	37	0.3607	0.3977	11.66[1]
Little Rock	182	0.8092	0.1801	468.39[1]
Bridge Brook	75	0.8047	0.2792	260.12[1]
Benguela	29	0.4098	−0.4345	0.517[1]
Chesapeake	33	0.8044	2.9244	20.28[1]
Ythan (1)	93	1.0331	2.0054	4240.58[1]
Ythan (2)	134	1.0742	2.6737	237.75[1]
Coachella	30	0.3561	−0.7688	5.63
St. Martin	44	0.5420	0.8979	6.64
El Verde	156	0.8773	1.3972	513.99[1]
UK grassland	87	0.9027	2.5594	16.16[1]
Silwood	154	1.4763	2.8721	376.34[1]

another theoretical result suggests more-connected systems have more numerous reassembly pathways, and hence, can recover faster from perturbation (Law and Blackford 1992). Connectance alone is a coarse-grained property inadequate to determine whether a species-rich community is more or less stable than a species-poor one; we need to break up connectance into parts to resolve this question.

Previous works showed that link distribution frequencies have important consequences for community fragility, measured as the number of secondary extinctions (i.e. number of coextinctions after species removal) (Pimm 1979, 1980, Solé and Montoya 2001, Dunne et al. 2002), and the degree the food web fragments into disconnected sub-webs (Solé and Montoya 2001). Food webs with skewed degree distributions (species-rich communities in our analysis) exhibited two behaviours: they displayed high homeostasis when species were removed at random from the community, but were very fragile when removals targeted generalist or most-connected species. In contrast, food webs with Poissonian degree distributions (more similar to species-poor communities in our analysis) were highly fragile to both types of removals (random or directed). Thus, perturbations in a community with low S might have large effects despite the number of connections (i.e. degree) of affected species, because they tend to number around mean linkage density L/S. Increased S implies a more complex distribution, where few species play key trophic roles in community persistence, whereas a huge number of them are comparatively unimportant. Hence, stochastic environmental fluctuations might affect species-rich communities less, whereas human-induced perturbations such as habitat loss and fragmentation (which quite often affect highly-connected species: Owen-Smith 1987, Wilson 1992) might have larger effects. This approximation is based on structural stability, and does not include dynamical effects of species deletion. Therefore, it should be considered a first step toward understanding how particular degree distributions affects community responses under species removals (Solé and Montoya 2001, Dunne et al. 2002, Montoya and Solé 2002).

The assembly dynamics incorporated in our models could not reproduce the skewed degree distributions observed in empirical food webs with high S. Future multitrophic assembly models should incorporate more ecological realism, perhaps with the introduction of different functional responses (Abrams and Ginzburg 2000, Bastolla et al. 2001), the spatial dimension of food webs (Polis et al. 1997) or evolutionary dynamics (Drossel and McKane 2003).

Many (Paine 1992, Berlow et al. 1999, McCann 2000) have argued that consumer-resource interaction strengths are skewed toward weak interactions. Some empirical webs analyzed here support this observation (UK grassland, Dawah et al. 1995; Ythan estuary, Raffaelli and Hall 1996; St. Martin Island, Goldwasser and Roughgarden 1993). This has important consequences for community stability and species coexistence (May 1973, Laska and Wooton 1998, McCann et al. 1998, McCann 2000), because: (1) weak interactions generate negative covariances between resources (prey), which promotes community-level stability, and (2) negative covariances ensure species that interact weakly dampen the destabilizing potential of strong interactions (McCann 2000). The topological properties of empirical food webs were more accurately reproduced using a relatively low maximum interaction strength (e.g. linear functional response, $\alpha_m = 0.2$). Very strong interactions were not present, so population fluctuations could be easily damped in general (negative covariances) as well as any relatively strong interactions. Hence, weak interactions between species must underly food web dynamics of the communities reported here both in species-rich and species-poor systems. Therefore, we hypothesize there are three basic requirements for maintaining high biodiversity from a trophic perspective: low mean connectance, skewed link distribution frequencies, and a preponderance of weak interactions between species.

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