

# Press perturbations and indirect effects in real food webs

JOSÉ M. MONTOYA,<sup>1,2,6</sup> GUY WOODWARD,<sup>2</sup> MARK C. EMMERSON,<sup>3,4</sup> AND RICARD V. SOLÉ<sup>5</sup>

<sup>1</sup>Marine Sciences Institute (ICM-CSIC), Pg. Marítim de la Barceloneta, 37-49, E-08003 Barcelona, Spain  
<sup>2</sup>School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS United Kingdom  
<sup>3</sup>Environmental Research Institute, University College Cork, Lee Road, Cork, Ireland  
<sup>4</sup>Department of Zoology, Ecology and Plant Sciences (Cooperage), University College Cork, Distillery Fields, North Mall, Cork, Ireland  
<sup>5</sup>ICREA-Complex Systems Lab, Universitat Pompeu Fabra, Dr. Aiguader 80, 08003, Barcelona, Spain

**Abstract.** The prediction of the effects of disturbances in natural systems is limited by the general lack of knowledge on the strength of species interactions, i.e., the effect of one species on the population growth rate of another, and by the uncertainty of the effects that may be manifested via indirect pathways within the food web. Here we explored the consequences of changes in species populations for the remaining species within nine exceptionally well-characterized empirical food webs, for which, unlike the vast majority of other published webs, feeding links have been fully quantified. Using the inverse of the Jacobian matrix, we found that perturbations to species with few connections have larger net effects (considering both direct and indirect pathways between two species) on the rest of the food web than do disturbances to species that are highly connected. For 40% of predator–prey links, predators had positive net effects on prey populations, due to the predominance of indirect interactions. Our results highlight the fundamental, but often counterintuitive, role of indirect effects for the maintenance of food web complexity and biodiversity.

**Key words:** connectance; food webs; indirect effects; inverse Jacobian matrix; linkage density; press perturbation; specialization.

## INTRODUCTION

A major challenge in contemporary ecology lies in predicting the effects of perturbations on complex multispecies systems, and this task can be tackled using a range of approaches: empirical observation, experimentation, and modeling (McCann 2000, Ebenman and Jonsson 2005, Montoya et al. 2006, Ives and Carpenter 2007). All these approaches have shown that, in food webs, predictive power is constrained by the general lack of knowledge on the strength of species interactions, i.e., the effect of one species on the population growth rate of another (Berlow et al. 2004, Wootton and Emmerson 2005). The number and strength of interactions, and where they occur within a food web, determine the dynamic stability of the system and how disturbances propagate: from the effects of small changes in species populations (May 1974, Pimm 1991, McCann 2000, Neutel et al. 2002) to the more dramatic effects of species loss (Pimm 1991, Borrvall et al. 2000, Solé and Montoya 2001, Dunne et al. 2002, Eklöf and Ebenman 2006, Montoya et al. 2006, Thebault et al. 2007).

Unfortunately, interaction strengths are exceedingly difficult to measure. Empirical data are usually restricted to only a tiny subset of interactions, even though the

topology of the whole food web might be well characterized in terms of the presence/absence of feeding links (Berlow et al. 2004, Wootton and Emmerson 2005). Previous attempts to parameterize large food webs by randomly assigning values to interaction coefficients between species were extremely sensitive to the values used, and the lack of empirical data to inform these parameterizations led many researchers to conclude that it is almost impossible to predict the effects of perturbations (Yodzis 1988, 2000, Wootton 2002). This unpredictability has long been attributed mainly to the prevalence of indirect effects, i.e., those occurring when the effect of one species on another is mediated by one or more intermediate species. Trophic cascades and apparent competition are two well known examples of density-mediated indirect effects. In natural, multispecies communities, multiple indirect and direct pathways occur simultaneously, potentially reinforcing or canceling out each other's overall effects. Several studies have revealed that indirect interactions can be almost as important as direct ones in their effects on the population abundances of species (Yodzis 1988, 2000, Menge 1995, Wootton 2002, 2004). An additional, perhaps surprising phenomenon, is that indirect effects can propagate disturbances (i.e., changes in the biomass density of a species) through the food web as fast, or faster than, direct effects (Menge 1995). Importantly, indirect effects can often appear counterintuitive: for instance, when predators have positive net effects on their prey (Abrams 1992). For this reason, predictive power (and hence

Manuscript received 8 April 2008; revised 1 December 2008; accepted 9 December 2008. Corresponding Editor: H. Hillebrand.

<sup>6</sup> E-mail: montoya@icm.csic.es

reduced uncertainty in the face of environmental change) relies upon our ability to estimate accurately the strength of direct interactions and to be able to identify and measure the importance of indirect effects.

Until now, the lack of high-quality food web data has made the detailed assessment of the importance of indirect effects very difficult (Abrams [1992] and Wootton [2004], are exceptions). A small number of new empirical food webs that are based on either field measurements or biologically plausible estimations of interaction strengths offer a more precise and realistic avenue for exploring the effects of disturbances via direct and indirect pathways (Berlow et al. 2004, Wootton and Emmerson 2005). Here we analyzed nine exceptionally well-quantified food webs that were drawn from different habitat types. We derived per capita interaction strength (i.e., the direct per capita effect of species  $j$  on the population biomass growth rate of species  $i$ ), from field measurements and predator to prey body size ratios (Emmerson and Raffaelli 2004, Emmerson et al. 2005) for each of the food webs. We then used the inverse community matrix (Bender et al. 1984, Yodzis 1988, Wootton 2002) to explore how press perturbations permeate throughout food webs. Specifically, we examine the effect of a sustained change in the density of a species population and examine how this affects the populations of other species in the food web. The use of the inverse community matrix provides a way to explore the multiple direct and indirect pathways that operate simultaneously in multispecies communities. We aim to answer three questions. First, is it possible to generalize and predict the effects of disturbances in complex ecosystems by considering both direct and indirect interactions among species? Second, can species' traits be identified that predispose species to propagate disturbances throughout the food web? And third, how important are indirect effects relative to direct effects?

## METHODS

### *Interaction strengths in empirical food webs*

We analyzed nine food webs which were drawn from three very different habitat types: the Ythan estuary (Leaper and Raffaelli 1999, Emmerson and Raffaelli 2004), Broadstone Stream (Woodward et al. 2005b), and seven soil food webs (De Ruiter et al. 1993, 1995; Fig. 1). Interaction strengths, the partial derivatives of species' growth equations in equilibrium, can be expressed in Lotka-Volterra terms as  $c_{ij} = a_{ij}B_i^*$ , where  $a_{ij}$  is a coefficient of interaction between species  $j$  and  $i$ , and  $B_i^*$  is the equilibrium population biomass of species  $i$  (May 1974, Neutel et al. 2002). Ingestion rate is expressed as the biomass intake of species  $j$ , and it is defined as  $F_{ij} = a_{ij}B_i^*B_j^*$  (De Ruiter et al. 1993, 1995, Neutel et al. 2002). We can then calculate interaction strengths between predator  $j$  and prey  $i$ : that is, the elements of the Jacobian matrix  $\mathbf{C}$ :  $c_{ij} = -(F_{ij}/B_j)$ , for the top-down effects (negative interaction strengths), and  $c_{ji} = e_{ij}(F_{ij}/B_i^*)$ , for the bottom-up effects (positive

interaction strengths), where  $e_{ij}$  is the efficiency with which food is converted into predator biomass. We describe below how these terms were measured for each set of food web data.

*Ythan Estuary.*—The Ythan Estuary (57°33' N, 2°00' E) is a small estuary (6 km long) located in northeast Scotland (Leaper and Raffaelli 1999, Emmerson and Raffaelli 2004). The version used here describes the trophic interactions between 86 species (see the Appendix). To estimate the interaction coefficients  $a_{ij}$  we used a recently developed technique based on empirical measures and theoretical considerations of predator to prey body mass ratios (Emmerson and Raffaelli 2004, Emmerson et al. 2005). This approach uses information on the body mass of all predators and prey to parameterize pairwise interaction strengths using the ratio of predator to prey body mass and an empirically observed exponent of 0.66 documented in Emmerson and Raffaelli (2004), so that  $a_{ij}$  scales as  $(M_j/M_i)^{0.66}$ , where  $M_j$  and  $M_i$  are mean adult predator and prey body mass respectively. We define a matrix  $\mathbf{A}$  whose elements  $a_{ij}$  are defined as  $(M_j/M_i)^{0.66}$ . Biomass density,  $B_n$ , is the product of each species population's mean body mass,  $M_n$ , and numerical abundance,  $N_n$ .  $M_n$  is available for all the species in the web, while  $N_n$  is only known for some of the species in the Ythan Estuary (see the Appendix for details) (Emmerson and Raffaelli 2004, Emmerson et al. 2005). For the remaining species,  $N_n$  was estimated using the reported relationship between body mass and numerical density ( $N_i = 95.92M_i^{-1.18}$ ) (Emmerson and Raffaelli 2004, Emmerson et al. 2005). By multiplying the interaction coefficient matrix  $\mathbf{A}$  by a diagonal matrix  $\mathbf{D}$  that contained the biomass densities  $B_i$ , we generated the Jacobian matrix ( $\mathbf{DA} = \mathbf{C}$ ) for this web. Ecological efficiencies required to calculate the elements  $c_{ji}$  are not known for this or directly comparable ecosystems, and therefore we assumed them to be constant (10% Lindeman efficiencies).

*Broadstone Stream.*—Broadstone Stream (51°05' N, 0°03' E; 120 m above sea level) is a small, naturally acid stream in southeast England: the acidity of the stream (pH 4.7–6.6) excludes fish, resulting in an invertebrate-dominated food web. It contains 31 common species. Mean annual species abundance,  $N_n$ , and body mass,  $M_n$ , was measured empirically for all the species (see Woodward et al. 2005b for details). Biomass density  $B_n$  was calculated by multiplying  $N_n$  by  $M_n$ . Predator guts (>4000 individuals) were removed via dissection, and ingested prey species were identified. Prey abundance in the guts of the predators was measured and body mass was calculated from linear measurements of individual prey items (as was done for the estimates of benthic biomass). Annual ingestion rates,  $F_{ij}$  (g dry mass·m<sup>-2</sup>·yr<sup>-1</sup>), of an individual prey species,  $i$ , by each predator,  $j$ , were calculated from the percentage of the biomass of  $i$  in the diet of  $j$ . Total ingestion was subdivided among the different prey species in the diet according to their percentage contribution to total ingested biomass (Woodward et al.

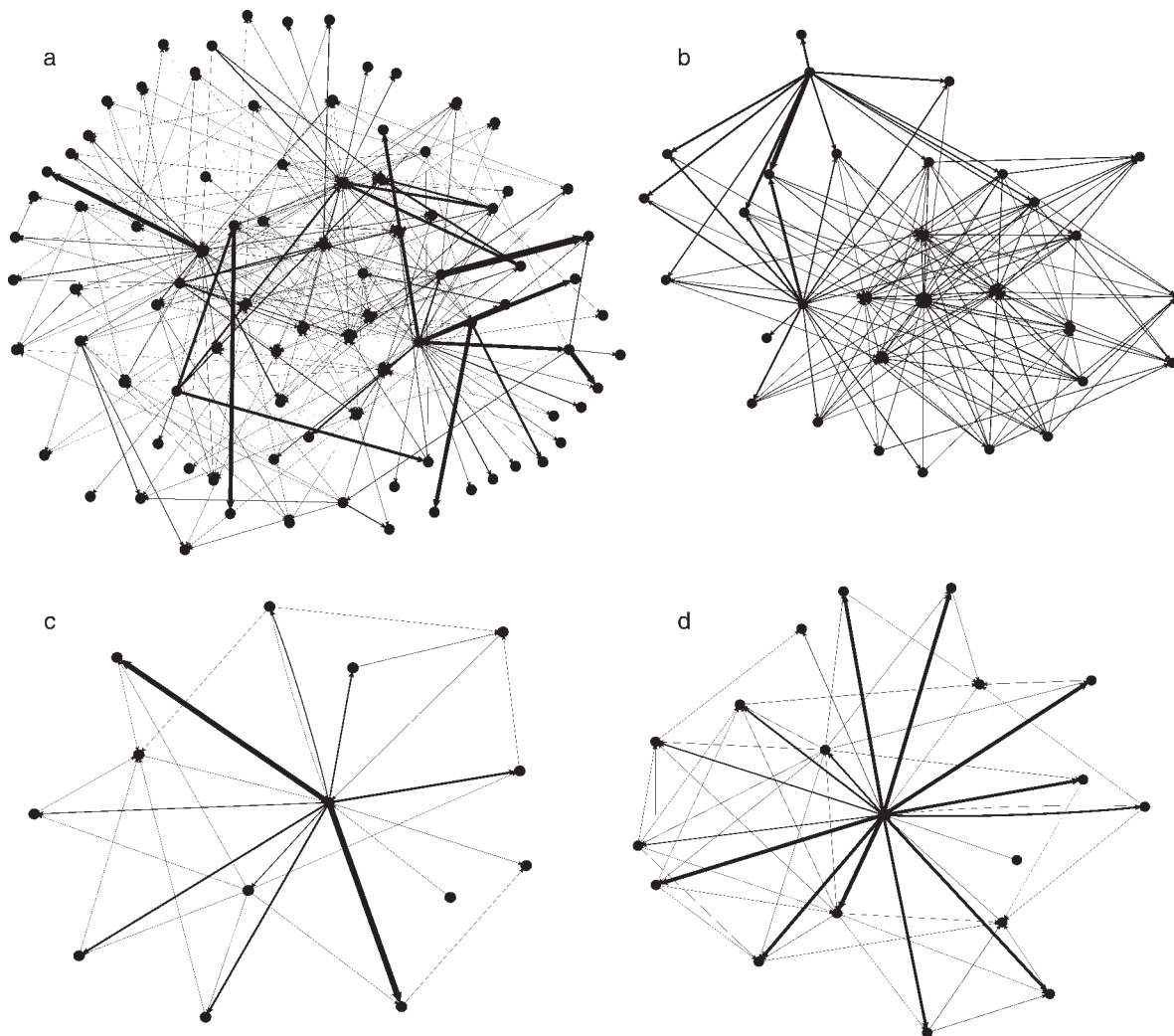


FIG. 1. Example of four of the nine food webs analyzed: (a) Ythan Estuary, (b) Broadstone Stream, (c) soil 6, (d) soil 2. Circles correspond to taxonomic species in most cases, arrows point from prey to predators, and line thickness and darkness correspond to the strength of the direct effect of a predator on its prey  $c_{ij}$  (top-down elements).

2005a), obtaining the values of ingestion rates  $F_{ij}$ . We used ecological efficiencies  $e_{ij}$  reported from similar systems (70% for animal prey, 30% for algae, 27% for fine detritus, and 10% for leaf litter (Woodward et al. 2005a)).

*Soil food webs.*—In the seven soil food webs (Soil 1 to Soil 7), “species” refers to trophic species or functional groups in which species that are aggregated share the same prey and predators and have similar physiological characteristics. The food webs are drawn from a range of habitat types, from natural prairies to intensive agricultural farms (see De Ruiter et al. 1993, 1995, Neutel et al. 2002, and the Appendix for further details).

In each food web, the population biomasses of species at equilibrium  $B_i^*$  were obtained from observed biomass densities (De Ruiter et al. 1993, 1995, Neutel et al. 2002). Total feeding rate of the predator  $j$ ,  $F_j$ , was calculated assuming that the biomass production rate of

a group balances the rate at which material is lost through natural death and predation, that is:  $F_j = (D_j B_j + P_j) e_j$ , where  $D_j$  is specific natural rate,  $B_j$  is biomass,  $P_j$  is death rate due to predation, and  $e_j$  is ecological efficiency (De Ruiter et al. 1993, 1995, Neutel et al. 2002). If a predator has more than one prey type, then both the preference of the predator for a given prey and the relative abundances of the prey types are considered, and therefore,  $F_{ij} = F_j [w_i B_i / W]$ , where  $w_i$  is the preference for prey  $i$  relative to other prey types  $k$ , and  $W$  is the sum of the products of prey preference  $w_k$  and  $B_k$  ( $k = 1, \dots, n$ ; if predator  $j$  does not feed on prey  $k$ , then  $w_k$  is equal to 0). The elements of the Jacobian matrix  $C$  are obtained as described above:  $c_{ij} = -(F_{ij}/B_j)$ , for the top-down effects, and  $c_{ji} = e_{ij}(F_{ij}/B_i^*)$ , for the bottom-up effects. Intraspecific competition  $c_{ii}$  (negative terms) are always difficult to measure empirically, and here were estimated as being proportional to natural

death rate  $D_j$ , following previous works (De Ruiter et al. 1993, 1995, Neutel et al. 2002). This reflects natural death rates encapsulate the effect of intraspecific competition, among other factors.

*The inverse Jacobian matrix*

We use a Lotka-Volterra approach to model the dynamics of our empirical food webs (May 1974, Pimm 1991, De Ruiter et al. 1995, Montoya and Sole 2003, Neutel et al. 2002, 2007, Eklöf and Ebenman 2006). The model can be defined as

$$dB_i/dt = \phi(\mathbf{B}) \tag{1}$$

where  $B_i$  indicates the population biomass of the  $i$ th species ( $i = 1, 2, \dots, S$ ) and

$$\phi(\mathbf{B}) = B_i \left[ \varepsilon_i - \sum_{k=1}^S a_{ik} B_k(t) \right] \tag{2}$$

where  $a_{ik} > 0$  for  $i > k$ ,  $a_{ik} < 0$  for  $i < k$ , and the equilibrium point  $\mathbf{B}^* = (B_1^*, \dots, B_S^*)$ . A press disturbance is introduced as a small and sustained increment or removal in the population biomass of species  $j$  (Bender et al. 1984, Yodzis 1988). Specifically, we consider the following:

$$dB_i/dt = \phi(\mathbf{B}) + I_j \tag{3}$$

where  $I_j$  is small ( $I_j \ll B_j^*$ ) and its units are population biomass/time. Hence, the net effect (the sum of the direct effect plus all the individual indirect effects) on species  $i$  resulting from a perturbation on species  $j$  is given by the element of the inverse community (Jacobian) matrix  $-(c^{-1})_{ij}$  as follows:

$$(c_{ij})^{-1} = (a_{ij} B_j)^{-1} = -\partial B_i^* / \partial I_j. \tag{4}$$

The elements  $c_{ij}$  are the elements of the Jacobian matrix  $\mathbf{C}$  that describes the dynamics of species at equilibrium, and have been extensively used in ecology (May 1974, Pimm 1991, De Ruiter et al. 1995, Neutel et al. 2002, 2007). Instead of using the Jacobian matrix we calculated its inverse,  $\mathbf{C}^{-1}$ , because its elements,  $-(c^{-1})_{ij}$ , show the net effect of species  $j$  on species  $i$  due to the direct linkage with species  $i$  (i.e., predation or intraspecific competition) and all possible indirect pathways through which species  $i$  and  $j$  are connected via linkages with intermediate species (Bender et al. 1984, Yodzis 1988, Wootton 2002). Specifically, the elements  $-(c^{-1})_{ij}$  measure the effects of press perturbations on species  $j$  (the addition or removal of a small proportion of its population biomass) so that as  $-(c^{-1})_{ij}$  increase in magnitude (either positive or negative), species  $j$  has a greater net effect on the population biomass of species  $i$ . This approach potentially allows us to identify species with large effects on other species within the community being disturbed, and whether some species' traits prevent them to propagate disturbances through the food web. We focused on a topological measure of the

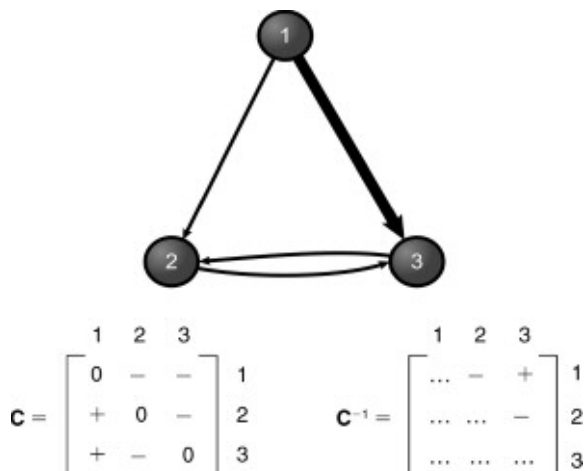


FIG. 2. Comparison of the sign structure of the Jacobian matrix  $\mathbf{C}$  with the sign structure of the inverse Jacobian matrix  $\mathbf{C}^{-1}$  for each food web. Dots indicate that the value is some positive or negative value.

food web: species' linkage density. It describes the degree of specialization of each species and represents the sum of all prey and all predatory links of a focal species: a high linkage density indicates a generalist or a species that is preyed upon heavily (Sole and Montoya 2001, Dunne et al. 2002, Montoya et al. 2006).

*Quantifying the importance of indirect interactions*

We subsequently sought to quantify the importance of indirect vs. direct effects in the nine food webs by comparing the sign structure of the Jacobian matrix  $\mathbf{C}$  (where only direct predator-prey interactions are represented) with the sign structure of  $\mathbf{C}^{-1}$ . The direct effect of the predator  $j$  on the population growth rate of prey  $i$  is given by  $c_{ij}$  and is always negative. However, the net effect of the predator on the equilibrium biomass of its prey  $-(c_{ij})^{-1}$ , when considering every interaction pathway connecting them, can be either positive or negative. When  $c_{ij}$  and  $-(c_{ij})^{-1}$  have different signs, indirect effects are very important relative to direct effects, because they reverse the net effect of a predator on its prey. Because the quantities of  $c_{ij}$  and  $-(c_{ij})^{-1}$  are not the same, we can look only at qualitative changes between both matrices, such as the comparison of their sign structure.

To illustrate this, let us consider keystone predation (sensu Paine 1969) (see Fig. 2). Predator 1 feeds on both 2 and 3,  $c_{12} > c_{13}$ ,  $c_{12} < 0$ , and  $c_{13} < 0$ . Species 3 is a competitively superior species that would outcompete species 2 in the absence of predation by 1 (i.e., predation by 1 guarantees coexistence of 2 and 3). It is possible to evaluate the sign of an indirect interaction between two species by simply multiplying the elements of  $\mathbf{C}$  connecting the species through an interaction chain. Hence, the indirect effect of 1 on 2 mediated by species 3 is positive through the interaction chain 1-3-2:

TABLE 1. Correlations between linkage density and mean net effect of species  $j$  (using mean  $\log[|c_{ij}^{-1}|]$ ,  $i = 1, \dots, s$ ).

Food web	$F$	df	$P$	$r$
Ythan	24.81	1, 174	<0.0001	-0.47
Broadstone	30.92	1, 60	<0.0001	-0.76
Soil 1	16.82	1, 34	<0.0001	-0.74
Soil 2	20.34	1, 36	<0.0001	-0.75
Soil 3	0.04	1, 34	0.84	-0.05
Soil 4	0.0004	1, 34	>0.95	-0.005
Soil 5	4.35	1, 26	0.046	-0.44
Soil 6	4.6	1, 26	0.041	-0.54
Soil 7	7.56	1, 32	0.009	-0.59

Note: Detritus is removed from the analyses. The values  $c_{ij}^{-1}$  are the elements of the inverse Jacobian matrix, and they show the net effect of species  $j$  on species  $i$ .

$\text{sign}(c_{12}) \cdot \text{sign}(c_{32}) = (-)(-) = (+)$ . The inverse community matrix shows that this indirect effect has a greater influence on the net effect of species 1 on 2 given by  $-(c_{12})^{-1}$ , so that the direct effect and the net effect of predator 1 on prey 2 have opposite signs, i.e.,  $\text{sign}(c_{12}) \neq \text{sign}[-(c_{12})^{-1}]$ .

## RESULTS

First, we found that the magnitudes of net effects are negatively correlated with the linkage density of the perturbed species in seven out of the nine food webs (Table 1). Poorly connected species had considerably stronger net effects on other species within the food webs than did the most highly connected species (Fig. 3, Table 2). The taxonomic identity and trophic position of these highly connected species varied across the food webs analyzed: e.g., the flounder *Platichthys flesus* (L.), an intermediate consumer, is the most highly connected species in Ythan Estuary; predaceous microarthropods in one of the soil food webs, and the top predator dragonfly *Cordulegaster boltonii* (Donovan) in Broadstone Stream.

Notably, two food webs did not show an association between linkage density and net effects (Soil 3 and Soil 4). In these two food webs, the biomass of the decomposers (bacteria and fungi) was much higher than in the other five soil food webs: 1500–2.300 vs. 2–150 Kg C/ha for bacteria, 740–900 vs. 228–690 Kg C/ha for fungi, (De

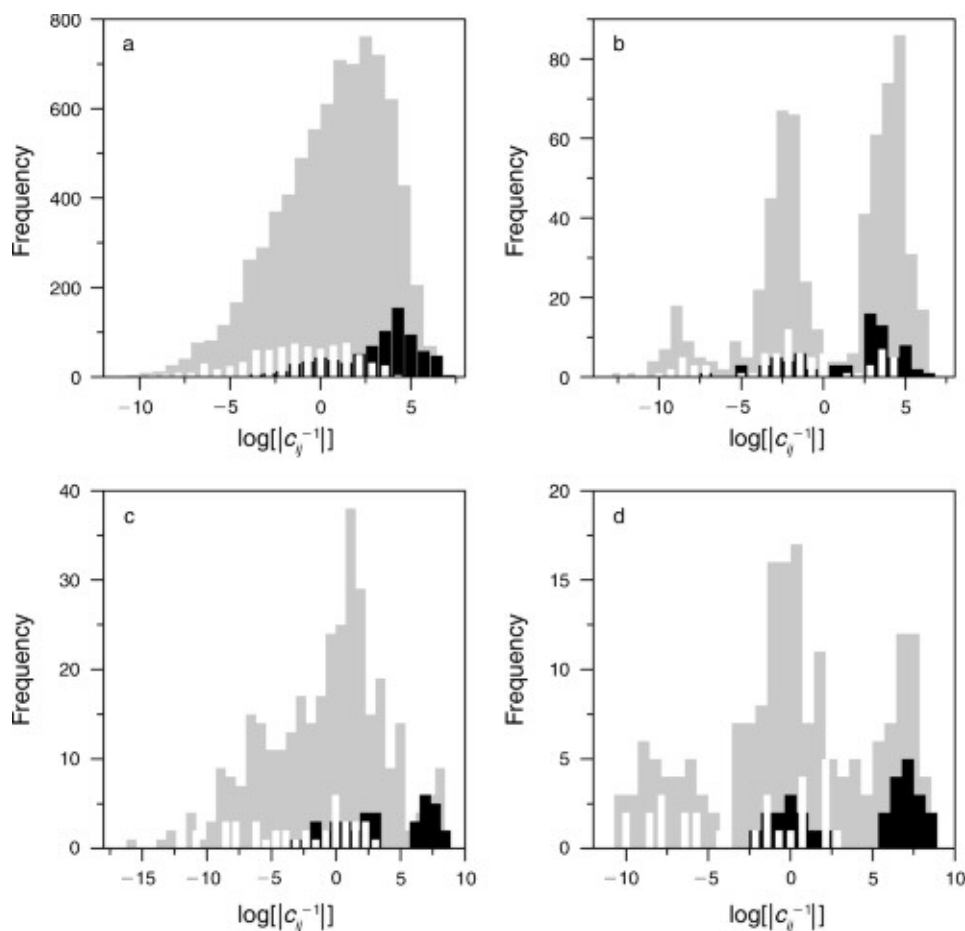


FIG. 3. Frequency distributions of the absolute values of net effects  $\log[|c_{ij}^{-1}|]$  for four of the analyzed food webs (a–d as in Fig. 1). Gray histograms correspond to all  $\log[|c_{ij}^{-1}|]$ ; black histograms indicate  $\log[|c_{ij}^{-1}|]$  of the 10% most poorly connected species; and white histograms indicate the values of  $\log[|c_{ij}^{-1}|]$  of the 10% most highly connected species. See Table 2 for statistics and the Appendix for species taxonomic identity.

TABLE 2. Net effects of the 10% most highly connected species and the 10% most poorly connected species (ANOVA).

Food web	Mean log $[[c_{ij}^{-1}]]$		<i>F</i>	df	<i>F</i>
	Poorly connected	Highly connected			
Ythan	2.70907	-1.65811	3559.71	1, 1310	<0.0001
Broadstone	1.87869	-4.47009	860.11	1, 178	<0.0001
Soil 1	3.68218	-0.79991	22.53	1, 64	<0.0001
Soil 2	1.08423	-3.21575	119.47	1, 68	<0.0001
Soil 3	-1.51746	-2.18619	0.88	1, 64	0.3557
Soil 4	-1.44904	-1.56713	0.03	1, 64	0.8636
Soil 5	3.96521	-2.25042	372.64	1, 48	<0.0001
Soil 6	3.67235	-3.21431	488.61	1, 48	<0.0001
Soil 7	1.04572	-3.56869	168.73	1, 60	<0.0001

Note: Detritus is removed from the analyses in all the food webs.

Ruiter et al. 1993). In addition, these webs had larger maximum interaction strengths (1.81 and 1.82 yr<sup>-1</sup>, respectively) than the remaining webs (below 1.5 yr<sup>-1</sup>). This was evident for both top-down (negative Jacobian elements  $c_{ij}$ ) and bottom-up (positive  $c_{ij}$ ) effects. Bacteria and fungi concentrated these strong interactions, and as a result these two species were likely to have overwhelmingly powerful net effects in these two exceptional food webs because of their dominance in terms of biomass.

Second, we found in 40% of predator-prey interactions across the nine food webs, predators had a positive (beneficial) net effect on their prey species (although the exact percentages varied among the nine food webs; Table 3). Therefore, in 40% of species pairs, indirect effects were crucial determinants of the outcome of press perturbations, raising important questions about how disturbances might produce seemingly counterintuitive results when propagating through other complex ecological networks. In seven of our food webs we found that when predators interact weakly with their prey, indirect effects are more important than when they do interact strongly. For the subset of predators having both negative direct and negative net effects on prey, their mean negative direct effect  $\bar{c}_{ij}$  was stronger than  $\bar{c}_{ij}$  for the subset of predator-prey interactions where predators had a positive net effect on their prey due to indirect effects (Table 3). This suggests that when a predator has a weak direct effect on its prey (that is, a weak interaction strength), indirect effects are likely to be of critical importance for predicting the effects of disturbances.

#### DISCUSSION

If we are to understand how species persist in complex (i.e., real) ecosystems, and to predict whether they will do so in an increasingly modified world, we need simple approaches that can be applied systematically to different systems and situations. Prediction of disturbances in multispecies systems is possible despite their ecological complexity, given the correct estimation of key parameters (Wootton 2002, 2004). It is the knowledge of interaction strengths between species that allows for predictions regarding the effects of press

perturbations in multispecies communities, by considering both direct and indirect density-mediated effects.

Our results suggest that when a press disturbance affects a species with many connections (i.e., generalist consumers and/or prey attacked by multiple predators) it is unlikely to have a major effect on the population biomass of the remaining species in the food web. The mechanism behind this pattern is not completely clear. It is likely that direct and indirect effects are cancelling one another out when a small disturbance is applied to these highly connected species. For example, a disturbance depressing the biomass of a generalist predator consuming multiple prey from the same guild is likely to have a minor impact on them because they will tend to regulate their biomass through enhanced apparent competition. However, this compensatory mechanism was not observed for highly specialized species, so small changes in their biomasses might have more marked consequences for other species within the food web. Using a similar example, a reduction in the biomass of a specialized predator would imply a substantial increase on its single prey biomass because it could not be

TABLE 3. Sign structure of the Jacobian matrix  $\mathbf{C}$  and of its inverse  $\mathbf{C}^{-1}$ .

Food web	Same sign		Different sign	
	%	log mean $ c_{ij} $	%	log mean $ c_{ij} $
Ythan	54.4	-1.41***	45.6	-1.59***
Broadstone	54	0.16***	46	-0.28***
Soil 1	63.1	0.38	36.9	0.17
Soil 2	53.8	0.12***	46.2	0.46***
Soil 3	63.2	0.45***	36.8	0.3***
Soil 4	57.9	0.44	42.1	0.46
Soil 5	66.7	0.78***	33.3	0.55***
Soil 6	77.8	0.85***	22.2	-0.20***
Soil 7	57.5	0.13***	42.5	-0.04***
Mean	60.93		39.07	

Notes: "Same sign" indicates that the direct effect of predator  $j$  on prey  $i$ ,  $c_{ij}$ , and net effect of  $j$  on  $i$ ,  $-(c_{ij})^{-1}$  are both negative; "different sign" indicates that  $-(c_{ij})^{-1}$  is positive. The log mean  $|c_{ij}|$  is calculated for each of the two groups of direct interactions: same sign and different sign.

\*\*\* Significant differences in the mean of  $|c_{ij}|$  between groups (ANOVA, Type 1,  $P < 0.0001$ ).

compensated via indirect interactions. Thus, a simple topological explanation exists, but it would benefit from knowing how linkage density and mean interaction strength are interconnected. It is generally assumed that specialized species have strong interaction strengths while species with many links tend to have weak connections (Montoya and Sole 2003, Wootton and Emmerson 2005). Theory has shown that weak links, in turn, confer stability to food webs (McCann et al. 1998), and in particular, weak links within long feeding loops dominate food webs like those analyzed here and make them stable (Neutel et al. 2002, Emmerson et al. 2005). However, for any of the food webs analyzed, we found no clear trend between the number of links a species has and its mean interaction strength, measured as the elements in the Jacobian ( $c_{ij}$ ) and considering both the effects on its prey and predator species. This suggests more links simply imply more chances of indirect effects cancelling each other out or cancelling direct effects out, but not through the stabilizing role of weak interactions as previously claimed. This does not mean interaction strengths are not important. They are. For example, we have shown strong interactions usually overcome the possible compensation through indirect interactions, as shown by the conservation of sign structure of the Jacobian and its inverse. It means further research is needed to generate hypotheses linking interaction strength and the potential of indirect interactions.

If we define complexity simply as the linkage density of species (Sole and Montoya 2001, Dunne et al. 2002, Eklöf and Ebenman 2006, Montoya et al. 2006), and stability as the net effect of a press perturbation on the population biomasses of the remaining species in the food web, then our results provide strong support for the verbal arguments of many of the early pioneers in ecology, whose suggestions that “complexity begets stability” (e.g., MacArthur 1955) have been reinstated several times (May 1974, Pimm 1991, McCann 2000, Neutel et al. 2002, 2007). The effects of small press disturbances on species populations seem to mimic those observed following the more drastic scenario of species loss. Studies employing strictly topological approaches (i.e., static, structural models without population dynamics) and equal strength for every consumer–resource interaction show that when highly connected species are removed the resulting webs are not “species-deletion stable.” This instability arises because many species lose their only prey source and so must become extinct in turn (Sole and Montoya 2001, Dunne et al. 2002, Chirstianou and Ebenman 2005, Eklöf and Ebenman 2006, Montoya et al. 2006). The realism of the sequence of species loss used in many topological studies has been questioned recently (Srinivasan et al. 2007), and they may underestimate the effects of removing top predators which, in many cases, are also among the most highly connected species (Montoya et al. 2006). Our approach uses real food web data and a theoretical disturbance affecting population biomass directly, as it is the case with

disturbances such as overfishing or hunting. Other real disturbances, however, affect population parameters as reproduction or death rates, rather than population biomass directly. Other theoretical approximations are available to explore the effects of changes on these population parameters on the food web. Community viability analysis (e.g., Ebenman and Jonsson 2005) and Markov chain models (e.g., Wootton 2004) are two examples.

Ignoring indirect effects could lead to serious miscalculations of how perturbations affect natural communities. In our study, ignoring indirect effects would lead one to the opposite conclusion over the effects that changes in predator density may have on their preys for 40% of the interactions analyzed. Intriguingly, one experimental study (Menge 1995) also found that indirect effects accounted for 40% of changes in the structure of 23 rocky intertidal communities in response to population manipulations in an exhaustive and detailed food web trial, suggesting that our models might be describing similar phenomena to those observed empirically. In fact, it is likely that our technique is very conservative, in that it will underestimate the relative importance of indirect effects in those cases where indirect interactions between a predator and its prey have the same sign as their direct interaction. This arises in some forms of intraguild predation, such as where predator A feeds on prey B and C, and B feeds on C. In such instances, A has a negative direct effect on B and a negative indirect effect on B, which is mediated through C because A also reduces the population biomass of B’s prey (sensu Polis and Holt 1992). This type of “food web module” is not uncommon in nature, and occurs in several instances within the systems analyzed here (Bascompte and Melian 2005, Woodward et al. 2005a).

Our approach can be applied to other ecological networks that contain information on interaction strengths, as those of plants and their pollinators or seed dispersers (e.g., Bascompte and Jordano 2007). The way in which perturbations affect a focal species and then permeate throughout the community can be predicted by the degree of trophic generalism of the perturbed species. Consequently, management strategies designed to protect such “buffer species” (highly connected ones) might serve to stabilize food web dynamics and hence prevent ecosystem collapse. These results suggest that such a trait-based approach (e.g., Woodward et al. 2005a) could provide conservation biologists with an important new tool, as we start to perceive more clearly how the complex relationships between species determines the stability of the wider “ecological network.”

#### ACKNOWLEDGMENTS

We thank Peter De Ruiter and Stefan Dekker for kindly providing soil food web data, Stuart Pimm for early discussions, and two anonymous referees for suggestions. This work has been supported by ESF InterAct Network, NERC Fellowship NE/C002105/1, and a Ramon y Cajal Fellowship (to J. M. Montoya).

## LITERATURE CITED

- Abrams, P. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist* 140:573–600.
- Bascompte, J., and P. Jordano. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution and Systematics* 38:567–593.
- Bascompte, J., and C. Melian. 2005. Simple trophic modules for complex food webs. *Ecology* 86:2868–2873.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 64:1–13.
- Berlow, E. L., et al. 2004. Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology* 73:585–598.
- Borrvall, C., B. Ebenman, and T. Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* 3:131–136.
- Chiristianou, M., and B. Ebenman. 2005. Keystone species and vulnerable species in ecological communities: strong or weak interactors? *Journal of Theoretical Biology* 235:95–103.
- De Ruiter, P. C., A.-M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269:1257–1260.
- De Ruiter, P. C., J. A. Van Veen, J. C. Moore, L. Brussaard, and H. W. Hunt. 1993. Calculation of nitrogen mineralization in soil food webs. *Plant and Soil* 157:263–273.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5:558–567.
- Ebenman, B., and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology and Evolution* 10:568–575.
- Eklöf, A., and B. Ebenman. 2006. Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology* 75:239–246.
- Emmerson, M. C., J. M. Montoya, and G. Woodward. 2005. Body size, interaction strength, and food web dynamics. Pages 179–197 in P. C. De Ruiter, V. Wolters, and J. C. Moore, editors. *Dynamic food webs*. Academic Press, San Diego, California, USA.
- Emmerson, M. C., and D. Raffaelli. 2004. Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology* 73:399–409.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58–62.
- Leeper, R., and D. Raffaelli. 1999. Defining the abundance body-size constraint space: data from a real food web. *Ecology Letters* 2:191–199.
- MacArthur, R. M. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:533–536.
- May, R. M. 1974. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- McCann, K. 2000. The diversity–stability debate. *Nature* 405:228–233.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794–798.
- Menge, B. A. 1995. Indirect effects in rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65:21–74.
- Montoya, J. M., S. L. Pimm, and R. V. Sole. 2006. Ecological networks and their fragility. *Nature* 442:259–264.
- Montoya, J. M., and R. V. Sole. 2003. Topological properties of food webs: from real data to community assembly models. *Oikos* 102:614–622.
- Neutel, A.-M., J. A. P. Heesterbeek, and P. C. De Ruiter. 2002. Stability in real food webs: weak links in long loops. *Science* 296:1120–1123.
- Neutel, A. M., J. A. P. Heesterbeek, and J. van de Koppel, et al. 2007. Reconciling complexity with stability in naturally assembling food webs. *Nature* 449:599–602.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103:91–93.
- Pimm, S. L. 1991. *The balance of nature?* University of Chicago Press, Chicago, Illinois, USA.
- Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution* 7:151–155.
- Solé, R. V., and J. M. Montoya. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society B* 268:2039–2045.
- Srinivasan, U. T., J. A. Dunne, J. Harte, and N. D. Martinez. 2007. Response of complex food webs to realistic extinction sequences. *Ecology* 88:671–682.
- Thebault, E., V. Huber, and M. Loreau. 2007. Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 116:163–173.
- Woodward, G., et al. 2005a. Body size in ecological networks. *Trends in Ecology and Evolution* 20:402–408.
- Woodward, G., D. C. Speirs, and A. G. Hildrew. 2005b. Quantification and resolution of a complex, size-structured food web. *Advances in Ecological Research* 36:85–135.
- Wootton, J. T. 2002. Indirect effects in complex ecosystems: recent progress and future challenges. *Journal of Sea Research* 48:157–172.
- Wootton, J. T. 2004. Markov chain models predict the consequences of experimental extinctions. *Ecology Letters* 7:653–660.
- Wootton, J. T., and M. C. Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution and Systematics* 36:419–444.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69:508–512.
- Yodzis, P. 2000. Diffuse effects in food webs. *Ecology* 81:261–266.

## APPENDIX

Species list and brief site description for each food web (*Ecological Archives* E090-171-A1).