

LETTER

Structural dynamics and robustness of food webs

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Abstract

Food web structure plays an important role when determining robustness to cascading secondary extinctions. However, existing food web models do not take into account likely changes in trophic interactions ('rewiring') following species loss. We investigated structural dynamics in 12 empirically documented food webs by simulating primary species loss using three realistic removal criteria, and measured robustness in terms of subsequent secondary extinctions. In our model, novel trophic interactions can be established between predators and food items not previously consumed following the loss of competing predator species. By considering the increase in robustness conferred through rewiring, we identify a new category of species – overlap species – which promote robustness as shown by comparing simulations incorporating structural dynamics to those with static topologies. The fraction of overlap species in a food web is highly correlated with this increase in robustness; whereas species richness and connectance are uncorrelated with increased robustness. Our findings underline the importance of compensatory mechanisms that may buffer ecosystems against environmental change, and highlight the likely role of particular species that are expected to facilitate this buffering.

Keywords

Food-web structure, secondary extinctions, structural plasticity, trophic adaption, rewiring.

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INTRODUCTION

Human-induced changes to the global environment driven by climate change, pollution, and habitat destruction are expected to cause widespread extinctions of populations and species globally (e.g., Brook *et al.* 2003). The robustness of ecological communities to such changes has been the subject of numerous empirical and theoretical studies (e.g., Shin *et al.* 2004; Dobson *et al.* 2006; Saavedra *et al.* 2008), revealing that the loss of individual species can lead to cascading secondary extinctions (Ebenman *et al.* 2004). A particular focus has been on food webs (networks representing biomass flow through ecosystems), and the relationship between their structure and robustness to species loss (Dunne *et al.* 2002, 2004; Dunne & Williams 2009). Enhanced ecological realism has been incorporated into food web analyses by employing plausible extinction sequences (Srinivasan *et al.* 2007) and by incorporating the effect of human-mediated disturbances (Coll *et al.* 2008). However, existing models remain inherently static in their description of food web response to species loss. This reflects available empirical data which mostly represent food

webs either as a snapshot in time (Thompson & Townsend 2005) or aggregated over time (Martinez 1991).

Recent work has sought to analyse the interplay of structure and dynamics in food webs (Pascual & Dunne 2006). One approach has been the combination of food-web topologies with bioenergetic and population dynamic models that represent predator–prey interactions by a system of nonlinear differential equations. Such investigations have, for example, considered the effects of single species removal in reconstructed 'fossil' food webs (Roopnarine *et al.* 2007) and synthetic topologies generated by the niche model (Berlow *et al.* 2009). Some studies have begun to incorporate adaptive foraging (Brose *et al.* 2003; Kondoh 2003, 2006; Garcia-Domingo & Saldaña 2007), by which consumer species maximize the energy gain per unit foraging effort by behavioural shifts in prey selection. Foraging theory has also been used to predict species interactions and resulting food web structure (Petchey *et al.* 2008). The consequences of species loss have also been modelled in food webs where predators preferentially consume competitively dominant prey species and thus prevent the competitive exclusion of many other subordinate

competitors (Brose *et al.* 2005). Nevertheless, in each of these approaches the underlying trophic structure remains essentially static through time. A general framework for considering the structural dynamics of food webs would increase the realism of theoretical models in accordance with the observation that species are able to adjust their feeding behaviour in response to changing environments.

The diet of a consumer is to a large extent constrained by its phylogenetic history, morphology, and body size (Cousins 1985; Ives & Godfray 2006; Bersier & Kehrl 2008). However, individuals of many species will respond to altered biotic and abiotic conditions by incorporating into their diets items not previously consumed. Such flexibility is widely expected given that the fundamental niche (Hutchinson 1957) of most species is likely to be much wider than the realized niche that will be measured empirically: where competition for prey items is relaxed or removed, 'novel' resource species will be exploited. For example, zooplankton alter patterns of resource intake depending on the abundance and variety of prey (Gentleman *et al.* 2003); food selection by an omnivorous thrip (*Frankliniella occidentalis*) varies depending on host–plant quality and prey availability (Agrawal *et al.* 1999); and *Chaoborus* larvae show reduced prey selectivity when prey abundance is low and larvae are hungry (Pastorok 1980). Thus, the high abundance of a common prey may mask the ability of predators to consume other, less abundant prey which will become a viable source of nutrition, if typical prey resources are depleted or lost (Pimm 1991).

Motivated by such examples of species' ability to alter their feeding patterns in response to the abundance of actual and potential prey species, we explore the consequences of incorporating predator–prey 'rewiring' (predators switching to food items not previously consumed) into simulation-based analyses of structural food-web robustness. We extend static models of food webs by introducing trophic interactions that can respond to the loss of species from an ecosystem – structural dynamics – and quantify the resulting robustness to secondary extinctions. Our results allow the identification of a new category of species, which we call 'overlap species', which promote robustness as shown by comparing simulations incorporating structural dynamics to those with static topologies. Following removal of a competing predator in our model, overlap species indicate other predators that can establish novel trophic interactions (i.e., 'rewire') to the removed predator's former prey. Our results suggest the importance of compensatory mechanisms – and particular species – that may enhance food web robustness in the face of environmental change.

MATERIALS AND METHODS

We analysed 12 of the best-characterized food webs available, some of which have been previously studied for

their robustness to simulated primary species loss. The focal food webs represent a wide range of species numbers, linkage densities, taxa, habitat types, and methodologies (Table 1; Dunne *et al.* 2002; refs. in Allesina & Pascual 2009). We studied trophic species versions of the 12 food webs. The use of trophic species (hereafter referred to as species), that is, groups of taxa that share the same set of predators and prey (Briand & Cohen 1984), is a widely accepted convention in structural food-web studies that reduces methodological biases related to uneven resolution of taxa within and among food webs (Williams & Martinez 2000).

For each food web, we simulated species loss by sequentially removing either: (1) randomly chosen species; (2) the least connected species preferentially; or (3) species at high trophic level preferentially; for each criterion, 1000 deletion sequences were simulated for each food web. For criterion (2), removal of the least connected species, total trophic connections ('degree') was calculated for each species for both predator and prey links; the probability of a species, i , being chosen for removal was

$$p_i = (k_i)^{-1} / \sum (k_j)^{-1},$$

where k_i is the degree of species i and the summation runs over all species in the food web. For criterion (3), the probability of a species, i , being chosen for removal was

$$p_i = TL_i / \sum TL_j,$$

where TL_i is the trophic level of species i and the summation runs over all species present in the food web. We use the longest-chain definition of trophic level, which is calculated as one plus the longest trophic chain from the consumer to a basal species, as this gives the greatest scope for rewiring (given our constraint on trophic level feeding; see below). Our qualitative results are robust to other definitions of trophic level including the shortest-chain, prey-averaged (Levine 1980), and short-weighted algorithms (Williams & Martinez 2004) (data not shown). Criteria (2) and (3) reflect the increased vulnerability of specialists and species at higher trophic levels, respectively, to environmental perturbations such as habitat fragmentation (Raffaelli 2004). In food webs with only one or two basal species and where one of those basal species is classified as detritus, we set the detritus 'species' as the last to be removed in the extinction sequence (Fath *et al.* 2007).

Following the removal of a species from a food web, previous studies (e.g., Dunne *et al.* 2002) remove all trophic links associated with that species. In our predator–prey rewiring model, some of the removed species' prey links may be rewired to new predators if biologically plausible. This is motivated by the likelihood that a species losing a predator species becomes more available to other predator

Table 1 Structural properties of food webs and simulation results

Food web	S^*	C^\dagger	P^\ddagger	No rewiring§			With rewiring§			PIR¶
				Random	Connected	TL	Random	Connected	TL	
Benguela	29	0.313	0.41	0.724	0.793	0.828	0.793	0.862	0.897	0.32
Bridge Brook Lake	25	0.171	0.52	0.800	0.720	0.880	0.880	0.800	0.920	0.33
Chesapeake Bay	31	0.071	0.39	0.645	0.742	0.774	0.710	0.774	0.871	0.23
Coachella Valley	29	0.312	0.31	0.759	0.690	0.897	0.793	0.724	0.931	0.16
Little Rock Lake	92	0.118	0.61	0.750	0.685	0.859	0.826	0.783	0.935	0.35
Reef	50	0.272	0.26	0.760	0.740	0.900	0.780	0.800	0.960	0.23
Shelf	79	0.277	0.92	0.886	0.899	0.937	0.962	0.949	0.975	0.59
Skipwith Pond	25	0.315	0.88	0.880	0.880	0.920	0.960	0.920	0.960	0.50
St. Marks Seagrass	48	0.096	0.67	0.750	0.813	0.896	0.833	0.875	0.958	0.38
St. Martin Island	42	0.116	0.69	0.738	0.762	0.857	0.833	0.833	0.952	0.41
Ythan Estuary 1991	82	0.059	0.48	0.659	0.793	0.768	0.707	0.854	0.866	0.27
Ythan Estuary 1996	123	0.139	0.50	0.650	0.821	0.764	0.691	0.870	0.854	0.23

PIR, proportional increase in robustness.

* S , trophic species.

† C , connectance, L/S^2 ; L , trophic links.

‡ P , initial fraction of overlap species.

§The fraction of primary removals required until no species remain; three species removal criteria: removal of (1) randomly chosen species; (2) the least connected species preferentially; and (3) species at high trophic level preferentially; for each criterion, 1000 deletion sequences are simulated for each food web.

¶Proportional change in robustness: $(R_r - R_0)/(1 - R_0)$; where R_r is the robustness including rewiring, and R_0 is the robustness excluding rewiring; robustness to secondary extinctions are averaged over the three removal criteria; values > 0 constitute a proportional increase in robustness.

species, for example, because of reduced competition. The plausible set of new predators for a given species is determined by the rewiring graph (Fig. 1a–c). For each food web, we first obtained the predator–overlap graph (also referred to as the resource graph) (Cohen 1978). In the predator–overlap graph, species are joined by an undirected link if they share a common predator. The rewiring graph is obtained from the predator–overlap graph and contains directed links. A link $i \rightarrow j$ indicates that, in addition to the shared predators, species i has at least one predator that does not prey on species j , and those predators are at higher trophic level than species j . In the predator–prey rewiring model, following the removal of a species, each of the removed species' prey links is considered for rewiring (Fig. 1d,e). For the remaining prey species, we obtain a set of potential predators from the directed nearest neighbours in the rewiring graph. A new predator is selected randomly from the set of potential predators and the trophic link is rewired accordingly; if no potential predators are available then the trophic link is removed. Rewiring can dynamically alter the structure of the rewiring graph, thereby presenting additional possibilities for rewiring following further species removals (Fig. 1f); this process ensures that the most plausible rewirings are implemented first. Once each of the removed species' prey links has been considered for rewiring, another species is selected for removal and the

process repeats. Because of its basis in the predator–overlap graph, the rewiring graph indicates the most plausible rewirings. There are a number of interpretations for these 'new' trophic interactions: (1) they are unobserved in the empirical data yet are still biologically plausible; (2) they are unobserved in the empirical data as they are not biologically plausible; (3) they are observable yet are not sufficiently frequent to have been included in the documented food web; (4) they are observable but have been missed in the collation of the food web because of practical limitations (Martinez *et al.* 1999). Because modern food webs are sampled in the field extensively over time and space, it is likely that the links included in the food webs already reflect many of the observable, short-term, predator–prey switches. However, these data cannot account for trophic links that may emerge when the food web is subject to severe perturbations: we simulate species removal until no species remain. This also makes it difficult to determine, without detailed individual examination, whether a suggested trophic rewiring that is unobserved in the empirical data should be classified as biologically plausible, category (1), or not, category (2). Our approach to rewiring may be considered conservative since we required that new predators are at higher trophic level than the prey species, as observed empirically for free-living prey (Woodward *et al.* 2005). Having obtained the rewiring graph for a food web, we

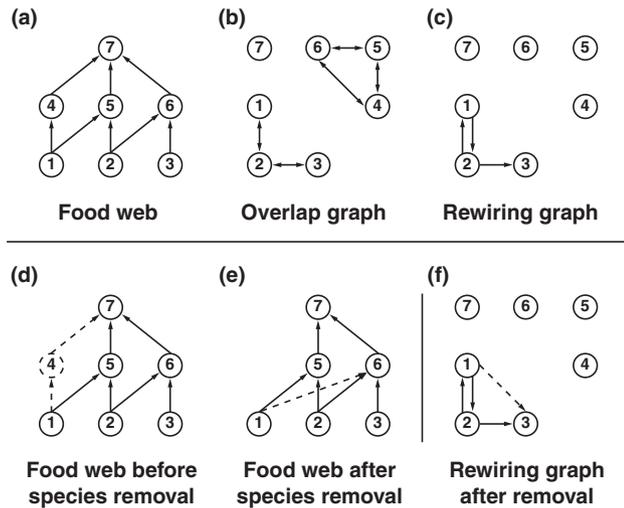


Figure 1 The predator–prey rewiring model uses a rewiring graph which indicates biologically plausible trophic rewirings and is derived from a food web. Numbered nodes represent species. *Obtaining the rewiring graph.* (a) Food web: a directed link represents a trophic interaction, e.g., $1 \rightarrow 4$ indicates that species 4 consumes species 1. (b) Predator–overlap graph: species are joined by an undirected link if they share a common predator. (c) Rewiring graph: a directed link, e.g., $2 \rightarrow 3$, indicates that, in addition to shared predators, species 2 has at least one predator that does not prey on species 3, and those predators are at higher trophic level than species 3. *Defining overlap species.* Species 1 and 2 are defined as overlap species as they have directed links pointing to other species in the rewiring graph. *Predator–prey rewiring model.* (d) Consider the removal of species 4 from the food web: the prey link of the removed species, $1 \rightarrow 4$, is considered for rewiring; we look for directed neighbours in the rewiring graph and identify species 2 – we select at random a predator of species 2 that does not prey on species 1 and is at a higher trophic level. (e) Species 6 is selected as an appropriate potential predator and a trophic rewiring, $1 \rightarrow 6$, takes place. (f) The process of rewiring can dynamically alter the structure of the rewiring graph: the new link $1 \rightarrow 3$ is formed, and presents additional possibilities for rewiring following further species removals.

define overlap species systematically. An overlap species is a species in the rewiring graph that has at least one directed link pointing from it to another species in the rewiring graph: it has out-degree > 0 (Fig. 1c). However, we do not denote species involved in trophic looping (where a trophic chain closes on itself, and excluding cannibalism) as overlap species unless there are distinct top predators in the food web. This is due to the way in which we have designated *all* species involved in trophic looping as being at the highest, chain, trophic level of the food web, whilst forbidding rewiring to take place between species at the same, nominal, trophic level. We stress that this reflects an algorithmic choice of the model and does not constitute a comment on any underlying ecological process.

We examined the impact of species loss on food web stability by considering the number of potential secondary extinctions that may result. A secondary extinction occurs when a non-basal species loses all of its prey items, and also when a cannibalistic species loses all of its prey items except itself. Following previous studies (Dunne *et al.* 2002), ‘robustness’ of food webs to species loss was quantified as the fraction of species that had to be removed for all species to go extinct. The maximum possible robustness is 1 and the minimum is $1/S$, where S , the species richness, is the initial number of (trophic) species in the food web. Values for the robustness were obtained both with and without predator–prey rewiring. To compare the effect of rewiring between food webs, we calculate the proportional change in robustness: $(R_r - R_0)/(1 - R_0)$; where R_r is the robustness including rewiring, and R_0 is the robustness excluding rewiring. Although this expression allows for negative values, rewiring of the kind represented here is highly unlikely to reduce the robustness of the food web. We refer to positive values as a proportional *increase* in robustness. The maximum possible proportional increase in robustness is 1 and the minimum is 0. We averaged the proportional increase in robustness for the three removal criteria in order to have one representative value for each food web. We examined correlations between the proportional increase in robustness and three food-web measures: species richness (S); connectance (C), the fraction of all possible trophic links, L , including cannibalism that are realized (L/S^2); and the initial fraction of overlap species in the food web (P).

RESULTS

The 12 food webs range in size from 25 to 123 trophic species (S), their connectance (C) from 0.059 to 0.315, and the initial fraction of overlap species (P) from 0.26 to 0.92 (Table 1). When species were systematically removed from food webs in our simulations, potential secondary extinctions varied both among webs and among types of removal sequences (Fig. 2). All 12 food webs were most robust (in terms of the number of primary removals required for complete food-web collapse with the inclusion of rewiring) when species were preferentially removed at high trophic level. Six of the food webs were least robust to random species removal, five food webs were least robust to preferentially removing the least connected species, and one food web had the same robustness value for both random and least connected removal. For each of the three removal criteria simulated for each food web, the shape of the secondary extinctions curve appeared qualitatively similar for simulations including and excluding rewiring. However, the magnitude of robustness differs depending on whether rewiring is included or not: for a given removal criterion, robustness was consistently higher in simulations that allow predator–prey rewiring. Even with

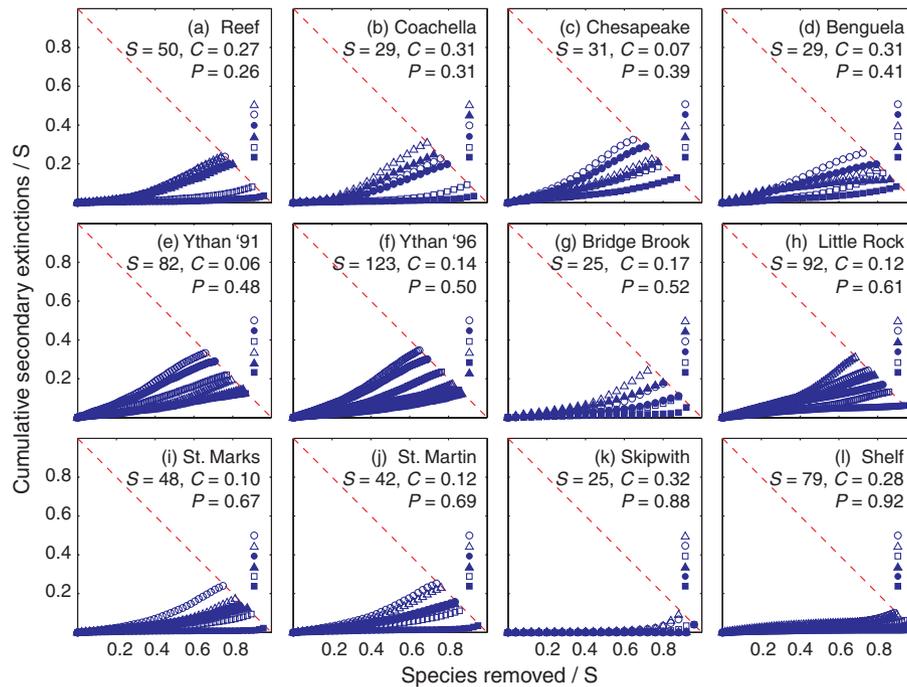


Figure 2 Secondary extinction sequences resulting from primary species loss in 12 food webs ordered by increasing initial fraction of overlap species. For each food web sub-figure, S is the number of trophic species, C is the connectance, and P is the initial fraction of overlap species in the food web. Each symbol represents a sequential primary species removal according to the following criteria: random with no rewiring (\circ); random with rewiring (\bullet); least connected preferentially with no rewiring (\triangle); least connected preferentially with rewiring (\blacktriangle); high trophic level preferentially (\square); high trophic level preferentially with rewiring (\blacksquare). Each sequence is an average of 1000 simulations; 95% error bars fall within the size of the symbols and are not shown. Simulations end at the dashed diagonal line, where primary removals plus secondary removals equals S , and the web disappears. Stacked symbols in each sub-figure indicate the removal criteria ordering for which the food web is least robust (top symbol) to most robust (bottom symbol). Values of food-web robustness to the various removal criteria are given in Table 1.

conservative rewiring, we see absolute increases in robustness of up to 0.1 (Little Rock Lake and St. Martin Island). This implies that simulations with rewiring require 10% more primary species removals to cause complete food web collapse, equivalent to 9 and 4 species for Little Rock Lake and St. Martin Island, respectively.

To compare the effect of rewiring between food webs, we used the proportional increase in robustness averaged over the three removal criteria (with each removal criterion simulated 1000 times). The criteria-averaged proportional increase in robustness ranged from 0.16 to 0.59. For the 12 food webs, we found no significant correlation between the proportional increase in robustness and species richness (correlation coefficient, $r = 0.00$, d.f. = 11, n.s.), or connectance ($r = 0.18$, d.f. = 11, n.s.). However, we found a significant, strong positive correlation between the proportional increase in robustness and the initial fraction of overlap species in the food web ($r = 0.94$, d.f. = 11, $p < 0.001$; Fig. 3). We found that the initial fraction of overlap species is approximately conserved in our removal simulations until there are very few species remaining (data

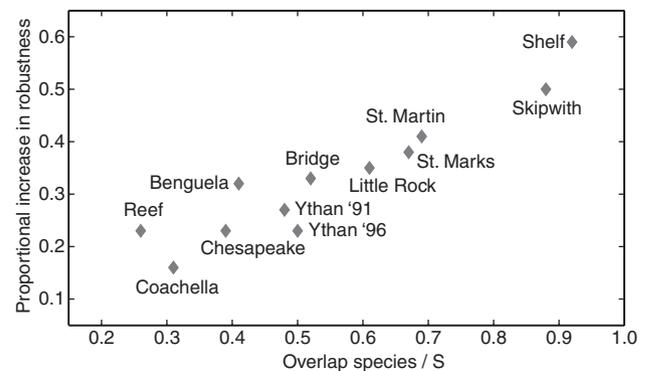


Figure 3 The proportional increase in robustness as a function of the initial fraction of overlap species in 12 food webs; where S is the number of trophic species (see Table 1). Correlation coefficient, $r = 0.94$, d.f. = 11, $p < 0.001$. The proportional increase in robustness is defined as $(R_r - R_0)/(1 - R_0)$; where R_r is the robustness including rewiring, and R_0 is the robustness excluding rewiring; robustness to secondary extinctions are averaged over three primary species removal criteria: random, least connected preferentially, and high trophic level preferentially.

not shown). Thus, the fraction of overlap species in general, not only the initial fraction, is a good indicator of the proportional increase in robustness that can be expected in food webs when considering structural dynamics compared to static topologies: the larger the fraction of overlap species, the higher the proportional increase in robustness. This positive correlation between the proportional increase in robustness and the initial fraction of overlap species is observed even when each removal criterion is considered individually: random, $r = 0.91$, d.f. = 11, $p < 0.001$; least connected, $r = 0.78$, d.f. = 11, $p = 0.003$; high trophic level, $r = 0.49$, d.f. = 11, n.s. Some highly connected species, such as small pelagic fish and invertebrates, are the particular target of human exploitation, and so results for removing the most connected species preferentially are also of interest (Dunne *et al.* 2004). Including this scenario in the criteria-averaged proportional increase in robustness does not alter our results substantially: the correlation with the initial fraction of overlap species is $r = 0.90$, d.f. = 11, $p < 0.001$; and for the removal criterion individually, $r = 0.79$, d.f. = 11, $p = 0.002$.

In Fig. 2, the cumulative secondary extinction plots for the 12 food webs are ordered by increasing initial fraction of overlap species, P . There is no significant correlation between P and S ($r = 0.13$, d.f. = 11, n.s.), or P and C ($r = 0.04$, d.f. = 11, n.s.). For example, the Coachella and Skipwith food webs have very similar values for S and C ($S = 29, 25$; $C = 0.31, 0.32$; respectively), but have very different values for P ($P = 0.31, 0.88$, respectively); this leads to very different values for the proportional increase in robustness (PIR = 0.16, 0.5, respectively), despite the food webs having similar 'global' structural characteristics. This suggests that the explicit topology of a food web is important to determining its structural dynamics and robustness.

DISCUSSION

Investigations of the structural robustness of empirical food webs increasingly suggest that topological details greatly influence their simulated vulnerability to secondary extinctions. Initial studies found that food webs are more robust to random primary removal of species than to selective removal of species with the most trophic links (Dunne *et al.* 2002). Food webs were consistently more robust to our three ecologically plausible removal criteria compared to removal of the most connected species preferentially (both ordered and probabilistic, data not shown), in agreement with a previous study (Srinivasan *et al.* 2007). Attempts to find maximally destructive removal sequences suggest that the position of a species in the food web, rather than its number of connections *per se*, is the main determinant of its impact on extinction cascades (Allesina & Pascual 2009).

Various structural indices have been considered in attempts to identify functionally important species in ecological networks (Jordàn *et al.* 2008). One such measure, the trophic overlap, uses the overlap of weighted trophic interaction data to quantify the uniqueness of species' interaction patterns (Jordàn *et al.* 2009). How these structural indices relate to properties of the overlap graph and overlap species merits further investigation.

As acknowledged in earlier topological studies (Dunne *et al.* 2002), failure to include a mechanism for predator–prey rewiring in simulations may result in overestimates of the number of secondary extinctions following the removal of individual species. We show that including rewiring in the topological approach consistently increases the robustness of food webs to primary species removal. This finding is in many respects unsurprising: any model that reduces the loss of trophic links would be expected to increase the persistence of the food web. However, how this additional robustness, generated by the dynamic adaptation of trophic interactions, varies systematically with different properties of the food web is not obvious *a priori*. The proportional increase in robustness was uncorrelated with the traditional food web metrics, species richness (S) and connectance (C), and was instead most highly correlated with the initial fraction of overlap species (P). This result was robust to alternative definitions of trophic level and to non-random methods for selecting a new predator from the set of available potential predators (data not shown). Within our predator–prey rewiring model, overlap species are systematically defined: they are species in a food web's rewiring graph that have out-degree > 0 (see Fig. 1). This definition means that overlap species indicate the presence of potential predators in the food web. There is no reason to suggest that overlap species should be such a good indicator of the proportional increase in robustness when advancing from static to dynamic food-web topologies. Knowledge of the initial fraction of overlap species in a food web is insufficient for quantifying the precise number of potential predators, nor the (maximum) number of trophic links that may be retained due to rewiring; P also gives no indication of where those links are located within the topological and trophic structure of the food web, details especially pertinent given the cascading nature of secondary extinctions. Furthermore, we find that another property derived from the overlap graph – the connectance of the overlap graph – has no significant correlation with the proportional increase in robustness ($r = 0.34$, d.f. = 11, n.s.; data not shown). Thus, the fraction of overlap species appears to encapsulate, in a very succinct way, the relevant structural features that ultimately influence the proportional increase in robustness of empirical food webs.

So, how are we to understand overlap species? The introduction of structural dynamics to topological models of

food web robustness highlights the role of compensatory mechanisms in reducing secondary species extinctions following environmental perturbations. Our identification of overlap species represents an intriguing avenue for exploring how those compensatory mechanisms are related to the properties of individual species and the composite roles they play within ecosystems. Understanding interaction patterns from a biological perspective often requires a combination of phylogenetic information and information on species' ecological traits (Ives & Godfray 2006). Increasingly detailed and comprehensive food-web data is becoming available (Jacob 2005). These data make it feasible to compare species characteristics (such as body-size, taxonomic identity, and geographical range) and community and ecosystem characteristics (such as biomass and abundance) between overlap and non-overlap species. Such additional information may also be incorporated into decisions regarding the plausibility of trophic rewirings. Phylogenetically related species tend to have similar biological characteristics (Freckleton *et al.* 2002), and a phylogenetic approach has been used to investigate constraints on trophic structure (Bersier & Kehrl 2008), patterns of consumer-resource association (Ives & Godfray 2006), and coextinctions in mutualistic networks (Rezende *et al.* 2007). A phylogenetic consideration of overlap species would provide additional information on the relationship between species' characteristics and structural dynamics. Furthermore, aggregation into trophic species is likely to underestimate the number of 'real' overlap species in a food web. These will be distributed non-randomly in the food web, since trophic species contain more real species at lower trophic levels (Williams & Martinez 2000). This will be an important consideration for the identification of overlap species in the field.

In our predator-prey rewiring model, trophic adaptation (rewiring) results from changes in prey abundance brought about by species removal. Three other factors can directly alter diet compositions and feeding rates: changes in 'habitat factors' such as temperature, water clarity, and soil acidity; changes in predator feeding rates and search tactics; and changes in predator abundance and competition. In our current model, if a trophic rewiring is possible then it is established, but in reality competition among predators for a prey species may prevent some rewirings from being realized. This could be incorporated into the model by prescribing a probability for the rewiring. Greater competition between predators would imply a smaller probability of rewiring, and the overall effect would be a reduction in food-web robustness relative to that observed in the current model.

Extinctions resulting from the loss of prey species represent the most predictable subset of secondary losses. Our structural approach may be considered a baseline that

corresponds to the best-case scenario in which the minimum impact to the food web is taken into account. Although the predator-prey rewiring model improves the evaluation of secondary extinctions, our framework still underestimates the potential for cascading extinctions due to strong non-trophic and indirect effects (Strauss 1991). In particular, the robustness of food webs to preferentially removing species at high trophic level may be altered significantly if the regulatory effects of top predators are taken into account. Another important source of additional secondary extinctions will be related to the bioenergetic or population dynamics of species. Other forms of trophic adaptation have been shown to cause an increase in food web persistence and stability. A population dynamic model on static food-web topologies demonstrates that foraging adaptation may shift the complexity-stability relationship of food webs from negative to positive (Brose *et al.* 2003; Kondoh 2003, 2006; but see Garcia-Domingo & Saldaña 2007). Despite much success on small, illustrative, food webs, the analysis of removal effects using nonlinear differential equations remains challenging for large ecological networks, requiring parameterisation of species interactions with values that are often empirically unavailable (but see Borrvall & Ebenman 2006; Brose *et al.* 2005). Nevertheless, there exists the prospect of combining such bioenergetic and population dynamic models with a dynamic structure of trophic interactions. In a model of paleocommunity response to species extinction, it was found that if consumers are permitted to compensate for the loss of trophic resources by increasing the intensities of their remaining biotic interactions, top-down secondary extinctions emerge (Roopnarine 2006). Whether the effect of topological predator-prey rewiring, which may mitigate the increase in intensity described above, would reduce top-down secondary extinctions has not been considered. This is an example where the combination of population and structural dynamics would be necessary to assess fully the impact of species removal from a food web.

We have considered the implications of structural dynamics on the robustness of empirical food webs. It would be instructive to apply the predator-prey rewiring model to synthetic food webs generated by, for example, the niche model. This would allow a comprehensive analysis of how structural dynamics affect robustness as food web size and connectance is varied. Models that allow the contiguity of prey consumption to be varied (Williams & Martinez 2008) provide a way of investigating the relationship between feeding intervality and the ability of food webs to rewire. Such a study would also be relevant to the analogous issue of nestedness and robustness in mutualistic networks (Bascompte & Jordano 2007).

This study uses binary food webs that indicate the presence of a trophic interaction but provide no information

on the frequency of the interaction or the rate of biomass flow through the interaction. The increasing availability of quantitative, weighted, trophic interaction data presents an opportunity for improving the realism of food-web robustness studies. Compared to binary food webs, quantitative food webs more accurately describe the structure and strength of trophic interactions and hence better inform the sensitivity of species to environmental perturbations (Ings *et al.* 2009). Future models should incorporate weighted information when determining the rewiring of trophic interactions and when simulating the magnitude of species loss.

In conclusion, our study underlines the importance of compensatory mechanisms that may buffer ecosystems against perturbations, and highlights particular species that are expected to facilitate those mechanisms. The consideration of structural dynamics also enhances our understanding of the basic robustness provided by food-web topologies. Differences in what could be termed 'structural plasticity' between empirical food webs, and the role of overlap species in conferring structural robustness, has potential implications for ecosystem conservation and management. Finally, the general method for implementing structural dynamics that we have presented is amenable to other approaches that seek to employ realistic food web structure and dynamics.

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