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Adaptive foraging and the rewiring of size-structured food webs following extinctions

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Abstract

Over the past decade, attempts have been made to characterise the factors affecting the robustness of food webs. Many studies have been carried out using a "topological" approach, in which secondary extinctions in ecological networks are determined by the structure of the network alone. These studies have led to numerous insights; for example how robustness is highly dependent on the order of extinctions, the fraction of basal species, as well as the connectance of the webs. But there has been criticism of these investigations for their lack of biological realism, such as the inability of species to alter their diets when species are lost, or the reliance on the criterion that a species only suffers a secondary extinction once it loses all its resources. Here, building on past approaches, we address these issues by introducing allometric optimal foraging theory to explore the consequences of species adaptively responding (by altering feeding links) to loss of prey in size-structured food webs. We also explore the effect on robustness of a secondary extinction criterion based on a threshold of energy loss, rather than merely the absence of a connection to at least one prey. We show that both rewiring and energetic extinction criteria greatly affect the robustness of model food webs, and that these new factors interact with each other as well as with the body mass distribution of the community, to shape the complexity–robustness relationship.

Zusammenfassung

In der Vergangenheit wurden viele Versuche unternommen, Faktoren zu charakterisieren, die Einfluss auf die Robustheit von Nahrungsnetzen haben. In vielen Studien wurden topologische Ansätze gewählt, um sekundäres Aussterben über die Struktur des Netzwerkes zu bestimmen. Diese Studien haben zu zahlreichen neuen Erkenntnissen geführt, wie zum Beispiel der, dass Robustheit von der Reihenfolge in der die Arten aussterben, dem Anteil an Basalarten, sowie dem Verschaltungsgrad ("connectance") des Nahrungsnetzes abhängt. Kritisiert wird bei diesen topologischen Untersuchungen, dass sie biologisch unrealistisch sind, da Prozesse wie alternative Beutewahl nach Beute-Verlust nicht berücksichtigt werden. Außerdem basieren sie auf der Annahme, dass eine Art erst ausstirbt, wenn sie alle Beutearten verloren hat. Aufbauend auf den bisherigen Konzepten haben wir das Modell durch Anwendung der allometrischen "optimal foraging" Theorie erweitert, um zu testen, wie Arten adaptiv (durch Änderung der Räuber-Beute-Interaktionen) auf den Verlust ihrer Beuten in größenstrukturierten Nahrungsnetzen reagieren. Zudem passen wir das Modell durch die Einführung einer energetischen Minimum-Grenze an: Arten, denen zu wenig

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Energie zufließt, sterben aus, auch wenn sie noch Beuten haben. Wir zeigen, dass sowohl der Beuteaustausch als auch energetische Kriterien großen Einfluss auf die Robustheit der Nahrungsnetze haben. Weiterhin zeigen wir, dass die neuen Faktoren interagieren und zusammen mit der Körpergrößenverteilung innerhalb der Artengemeinschaft Einfluss auf die Komplexitäts-Robustheits-Beziehung haben.

Introduction

The extinction of a species does not solely entail the loss of a unique evolutionary entity but also the loss of the ecological linkages in which it is involved. With the loss of a species the nexus of species interactions begins to disassemble, bearing potentially serious consequences for other members of the assemblage (Montoya, Pimm, & Solé 2006; Bascompte & Stouffer 2009; Brose 2010). As Earth is currently experiencing exceptionally high rates of extinction (largely because of anthropogenic causes), ecologists have begun attempting to predict the consequences of species loss for our planet's ecosystems (Hoffman et al. 2010; Pereira et al. 2010).

We can describe ecological systems as networks, in which the nodes represent species with directed edges between them signifying a particular type of interaction, such as consumption (Dunne 2006). At the beginning of the last decade Albert, Jeong, and Barabási (2000) clearly demonstrated the relationship between the robustness of a network and its structure, inspiring ecologists to apply similar methods to data from food webs – networks in which the links represent one species feeding on another (Sole & Montoya 2001; Dunne, Williams, & Martinez 2002). The technique used in these papers was to progressively remove nodes from a network until the network collapsed to a pre-specified species richness. Nodes were disconnected either randomly or sequentially based on some topological property (e.g. the number of links a species has to others, or the species trophic level). If a species was left with no links to prey items, then it too would become extinct; therefore the loss of one species could trigger a cascade of further secondary extinctions. Robustness then is a measure of the likely occurrence of secondary extinctions following the loss of a species. It was discovered that food webs were generally more robust if species were removed at random, or if specialists (species with few links to prey) were removed first, but less so when generalists (species with many links to prey) were removed first. A more connected food web was generally a more robust food web (Dunne et al. 2002).

Many subsequent studies have expanded upon these ideas of the topological robustness of food webs (e.g. Allesina & Bondini 2004; Dunne, Williams, & Martinez 2004; Allesina & Pascual 2009; Dunne & Williams 2009; Gilbert 2009). However, concerns have been raised regarding the biological realism of the assumptions underlying such studies. Some have already been addressed, such as the use of increasingly realistic extinction orders (Srinivasan, Dunne, Harte, & Martinez 2007, Coll, Lotze, & Romanuk 2008), yet others remain largely unaddressed, such as the lack of an adaptive response by other species in the web to an extinction (Staniczenko, Lewis, Jones, & Reed-Tsochas 2010), as well as the lenient criterion that a species has to lose all its prey items before extinction occurs.

Whilst adaptive behaviour of species is increasingly recognised as important to food web structure and stability (Valdovinos, Ramos-Jiliberto, Garay-Narvaez, Urbani, & Dunne 2010), only one study to date (Staniczenko et al. 2010) has addressed the consequences of what has been termed the "structural dynamics" of food webs for their topological robustness. This is the concept that the topology of a food web is not fixed and therefore it can rewire following the loss of a node, due to the adaptive behaviour of the species that comprise the web. "Structural dynamics" in this sense is a discreteization, to allow us to more easily model change in a food web's topology, which does not include population dynamics. Of course, in nature there will be a continuous rewiring process, as species adjust their diets in response to changes in abundances of other species in the community (Kondoh 2005a).

In the study by Staniczenko and colleagues, food webs were rewired using an algorithm meant to represent a discretized mechanism of competitive release. Following the extinction of one of its competitors, a consumer might expand its diet to include a prey that it had previously been prevented from including in its diet. Another mechanism, different to competitive release, by which rewiring could occur, the consequences of which have yet to be investigated, is that of optimal foraging (Emlen 1966; McArthur & Pianka 1966; Beckerman, Petchey, & Warren 2006). In the discretized optimal foraging scenario, a consumer species forages on the subset of possible prey items that provides it with the highest net energy intake per unit effort, forgoing those prey that are less favourable for those that are. Following the loss of its preferred prey item a predator may expand its diet (its realised niche) to include novel, but energetically less favourable, prey items from the set of possible prey that comprise its fundamental niche (i.e. those prey species that the predator could physically consume). The predator can expand its diet to the point at which the newly included prey items again maximise its net intake.

Recent approaches in the mechanistic modelling of food web structure (Petchey, Beckerman, Riede, & Warren 2008; Thierry, Petchey, Beckerman, Warren, & Williams 2011), allow examination of the influence of food web rewiring following species extinctions on web robustness, using the

principles of optimal foraging. An additional consequence of this approach is that it allows us to relax another of the unrealistic assumptions underlying previous studies of topological robustness: the criterion for secondary extinctions. Rather than allowing a species to persist when it has at least one prey item, we can use a threshold based on the species' energy intake, modelling the energetic criterion sometimes underlying extinction (Wright 1983; Evans, Greenwood, & Gaston 2005). For example, using a model that included population dynamics, Borrval, Ebenman, and Jonsson (2000) demonstrated how a generalist which lost just one of its prey to extinction could follow the same fate whilst still having other prey available. Here we use the approach described above to address four questions: (1) How is robustness affected by rewiring resulting from optimal foraging? (2) How is robustness and the effectiveness of rewiring affected by varying the energy threshold at which a species goes extinct? (3) How is robustness affected by changing the body mass structure of the food web? (4) What effect do these processes have on the complexity–robustness relationship?

Methods

Dataset

We used a modified version of the Allometric Diet Breadth Model (ADBM; Petchey et al. 2008; Thierry et al. 2011) to create a large number of model webs. This model assigns feeding links between species in a food web using an optimal foraging mechanism. It first calculates the profitability (the energy gain per unit time) of each prey species for a consumer and then finds the set of prey species that maximizes each consumer's net energy intake rate. The consumer decision is subject to time constraints in the form of encounter rates (the product of the attack rate of consumer j for resource i and resource density) and handling times of consumer j for resource i. By assigning a diet to each consumer species, a food web is created with connectance linked directly to foraging traits (Beckerman et al. 2006). To create realistic co-variation between the different parameters and generate plausible topologies, the foraging traits in the allometric diet breadth model are related to the organisms' body sizes (Petchey et al. 2008) and to additional traits that affect foraging ability and vulnerability (Thierry et al. 2011).

Each of the model webs contained 40 species (every species had an associated body mass and abundance), the webs also had a particular value of connectance close to either 0.05, 0.1, 0.2, or 0.3, and a body mass distribution with one of four shapes (log normal distributions with standard deviations of either 2.2, 5.1, 7.9 or 10.8). The model webs were created in such a way that connectance was independent of the shape of the body mass distribution.

To improve the similarity between the model webs and empirical data we had two criteria for choosing the subset of webs for this study. First, we selected webs where the generalism- and vulnerability-mass correlations of the model webs were within two standard deviations of the mean values of a data set of sixteen empirical webs (generalism is how many prey a species has and vulnerability is how many predators; see Thierry et al. (2011) for more details). Second, we required that at least 10% of the species in the webs should be basal species. A third criterion of ensuring that the webs were within 10% of the target connectance was introduced so that there were clear connectance groups as mentioned above for subsequent analysis. Each of the selected 19,224 webs had a fixed mass and fixed abundance associated with each species which remained unchanged throughout the robustness simulations.

A set of 4000 random graphs was also constructed, to look at the null expectation of the effect of introducing energetic thresholds on the robustness of a network. One thousand randomly wired webs were created for each of the four levels of connectance. Each link in these webs was assumed to contribute equally to a consumer's diet (i.e. for a predator with two prey each provided half its intake). These webs were exempt form the rewiring treatment.

Simulations

This study was a fully factorial, *in silico* experiment to measure the robustness of the model webs. As in previous studies into the topological robustness of food webs, the first action was to remove a species from the web, simulating a primary extinction; in the present study, species were removed at random. Under some treatments, this primary extinction was followed by a rewiring process (see below). Finally, each remaining species in the food web was examined to determine whether it met a particular threshold of energy intake; species that failed this test were removed, and this event was termed a secondary extinction. This process of primary extinction, rewiring and energy intake-based secondary extinctions was repeated until the species richness of the web dropped below 25% of the original species richness. As this model did not include population dynamics the mass and abundance of each species remained unchanged by extinctions.

In our experiment there were two treatments: the possibility, or not, of the species in the web rewiring following extinction (two levels, see below) and different energy requirement thresholds that must be met or exceeded for the species to remain viable (four levels, see below). We implemented thirty replicate random extinction sets, on each of the eight treatment combinations for each of the 19,224 webs. For each web under every combination we calculated the mean robustness of the 30 replicates, (see section "Calculating robustness").

Rewiring treatment

Rewiring was the process by which species in the food web could adapt to changes in the web's structure. If rewiring was not allowed, the simulation looked for species that did not

meet their energy requirements following an extinction event and no species had a chance to compensate for their loss of prey by expanding their diet.

If rewiring was allowed, then following any extinction event, before looking at whether other species now fell below their required energy threshold, extant species in the web were allowed to expand their diets to include previously uneconomical species in order to compensate for the loss of species in their diet and thus energy intake. This was achieved by re-running the modified ADBM (Thierry et al. 2011) to re-generate the food web network with the new set of species (the original set minus those removed), and a new web was created within the allowed constraints of the model (i.e. diets could only be expanded if this increased the net energy intake of the consumer). The mechanism used to rewire the food web was therefore the same mechanism that was initially used to build the food web. This process meant that any affected species could alter their diet during the rewiring phase.

Energy requirement threshold treatment

We introduced a new criterion for when a species became secondarily extinct based upon energetic principles. This allowed us to relax the assumption in previous studies that species only go extinct once they lose all their prey items. These thresholds can be thought of as a way of adjusting the susceptibility of a species to the loss of its prey items. The lower the threshold, the less energy needs to be lost before extinction occurs.

Energy requirement thresholds are expressed as percentages of the energy intake of each species in the food web before any species have been removed. For the model food webs, this is the energy intake value optimised by the ADBM (Petchey et al. 2008), and is therefore already part of the modelling process used to create the food webs. For the random networks each link to a prey item contributed equally to the energy gained by a consumer. So, for a consumer feeding on two prey species the loss of one of those meant a loss of half its intake. In this study there were four thresholds investigated: a 10%, 40%, 70% and 100% loss of a species' original energy intake. 100% is equivalent to the criterion that a consumer goes extinct only if all possible prey are unavailable, and is therefore considered to be the most lenient. A given threshold was applied to all species in the web, i.e. if the threshold was set at a severe 10%, then any species in the web which following an extinction event had less than 90% of its original energy intake would be removed and deemed to be a secondary extinction.

Calculating robustness

Robustness (R) was calculated in the following fashion:

$$R = \frac{N - 1}{S - 1}$$

where N is the number of primary extinction events required to reach a species richness less than or equal to 25% of the original species richness of the web (40 species) and S is the number of species which need to be lost to reach 25% of original species richness. As all species in these webs had 40 species, the denominator in our equation was always 29. This resulted in a measure of robustness between zero and one. A value of zero meant that following the first primary extinction the rest of the web collapsed due to secondary extinctions. A robustness value equal to one meant that no secondary extinction events occurred before the web was reduced to 25% of its original species richness. The fewer secondary extinctions there were, the more robust the web.

The effect of rewiring was measured simply as the difference between the mean robustness of a web with rewiring allowed and the mean robustness without rewiring:

$$\Delta R = R_{-rewire} - R_{-no-rewire}$$

As each web had the same number of species, a change in R always corresponded to the same number of species suffering secondary extinctions; i.e. a 0.1 change in robustness between webs, or between treatments, is equivalent to approximately three species.

Results

Both rewiring and energy requirement thresholds were important to the robustness of the model food webs. Decreasing the threshold from 100% to 10% reduced the webs' robustness dramatically (compare panels (A–D) or (E–H) in Fig. 1). Rewiring could increase robustness and was especially effective for lower values of connectance (Fig. 2). Rewiring was effective at increasing the robustness for lenient extinction thresholds, but almost ineffectual at severe thresholds (compare panels (A–D) in Fig. 2). The mean robustness of the 30 replicates decreased in 23% of the simulations where rewiring was allowed (compared to when rewiring was not permitted); in these cases there was typically only a small decline in robustness and this was probably the result of stochasticity associated with the random extinction sequences.

The severity of the energy threshold had important implications for the relationship between the connectance of a web and its robustness, both with and without rewiring. When rewiring was absent and the threshold was lenient (100%), then it was observed that the greater the complexity of the web the higher its robustness (Fig. 1A). As the energy threshold became more severe (<100%), this pattern went into reverse until the least connected webs were those that are more robust (Fig. 1D). This reversal is due to comparatively much larger decreases in the robustness of the more highly connected webs. This pattern of reversal in the complexity–robustness relationship with increasing severity of threshold was also seen in the random networks (dashed lines in Fig. 1A–D).

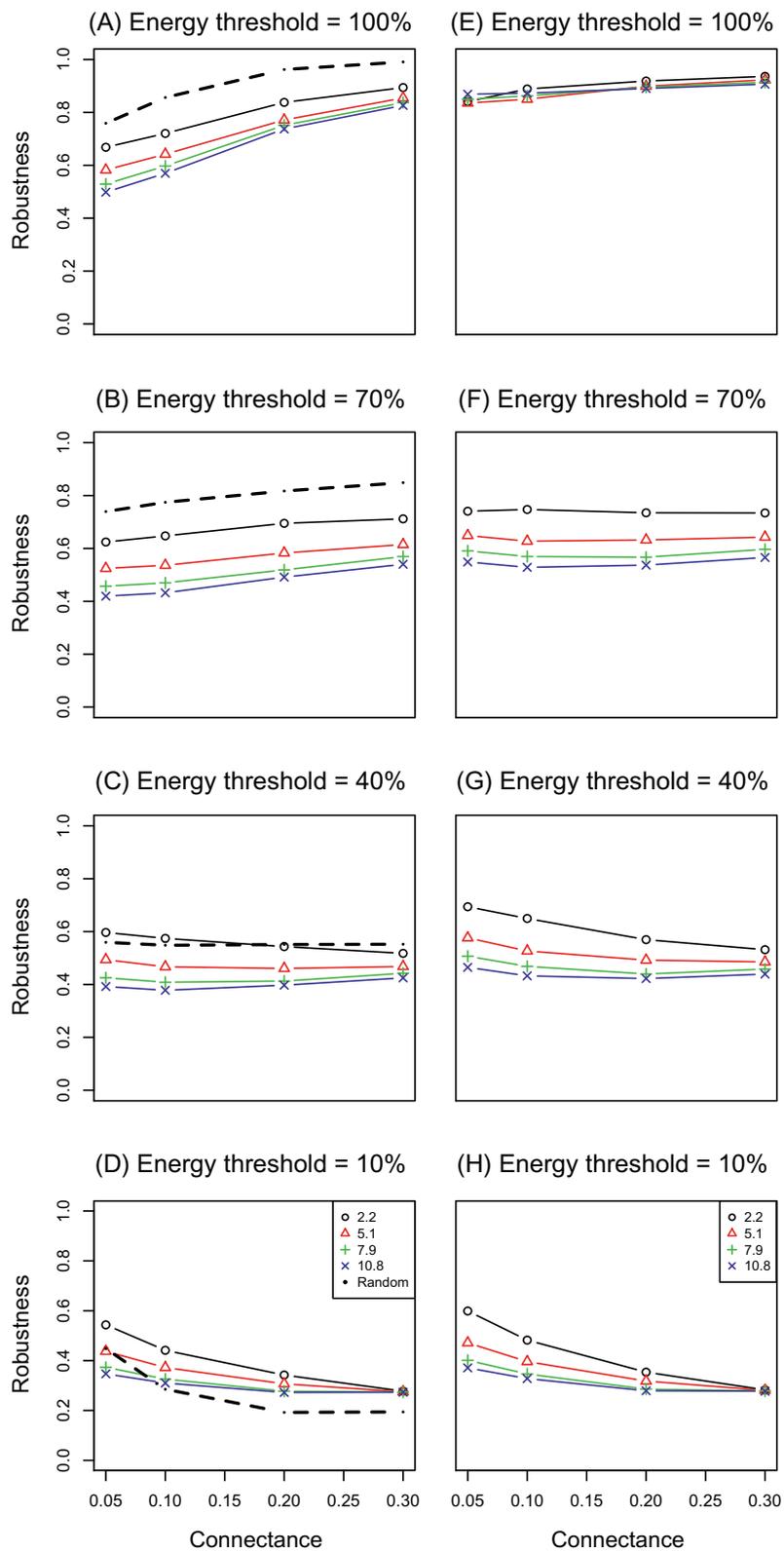When allowing rewiring, it was found that webs at all levels of connectance have similar (almost maximal) robustness

Fig. 1. The relationship between connectance and average robustness of the webs when rewiring was not allowed (A–D), and when it was allowed (E–H). The different lines in each plot represent webs from the four body mass distributions, whose standard deviation is given in the legend in panels D and H. The black dashed line in panels (A–D) represents the mean robustness of the random graphs. The different panels in each column are for the different levels of the energy threshold, the loss of more than which resulted in a secondary extinction.
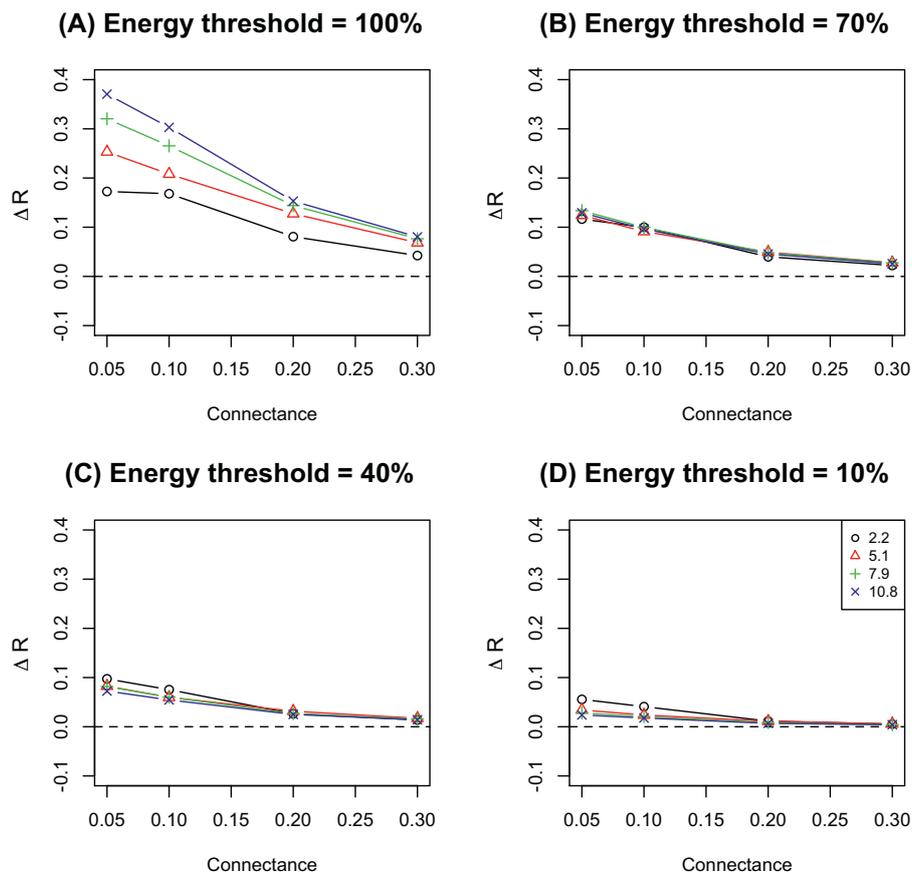
Fig. 2. The relationship between connectance and average difference in robustness of the webs between when rewiring was and was not allowed. The different lines in each plot represent webs from the four body mass distributions, whose standard deviation is given in the legend in panel (D). The different panels are for the different levels of the energy threshold, the loss of more than which resulted in a secondary extinction.

when the threshold is lenient (due to the large increase in robustness of the less connected webs caused by rewiring). However, at the more severe thresholds the pattern is more similar to that for no re-wiring. That is, a negative relationship between connectance and robustness is observed (compare panels (E–H) in Fig. 1).

The standard deviation of the body mass distribution also affected the robustness of the webs. The distributions with the largest standard deviations typically were less robust, both with and without rewiring (Fig. 1). At the most lenient energy threshold (100%), the amount of increase in robustness due to rewiring also depended on the body mass distribution; the distributions with the largest standard deviations experienced the largest increase in robustness (Fig. 2A), probably reflecting the greater scope for increase due to their initially lower robustness. A clear pattern of reversal in the connectance–robustness relationship can be seen in webs from across all the body mass distributions examined (Fig. 1).

Discussion

Our study indicates that food web robustness is influenced by the capacity for adaptive foraging to rewire the web, the

amount of energy species can afford to lose, the distribution of body masses in the web, and the connectivity of the web. Allowing adaptive foraging can increase robustness, but the more severe the energy loss threshold and more connected the web, the less effective was rewiring. On top of this, introducing an energy threshold decreases robustness. We also found that the greater the standard deviation of the community body mass distribution, the less robust food webs tended to be. And lastly, that at certain energy thresholds the complexity–robustness relationship reverses from positive to negative due to a dramatic decline in the robustness of highly connected webs. The interaction between trophic structure and foraging theory suggests possible explanations for these patterns:

Adaptive foraging is less effective at increasing robustness at severe energy thresholds

Sufficiently good replacements are hard to come by; if adaptive foraging is to be effective a species must be able to recoup the energy it has lost in order to remain above the extinction threshold. If the threshold is severe there will be

fewer suitable species that a consumer can switch to so as to fulfill this criterion.

Adaptive foraging is less effective at increasing robustness for highly connected webs.

There are no replacements left if you already eat everything; in high connectance webs, consumer species will already be feeding on a large proportion of potential prey (diet breadth is high when connectance is high). Therefore, following the loss of a prey species, there will be few options for a consumer species to add to their diet, thus their likelihood of extinction is little changed and the web's robustness is left unaffected. On top of this, in the cases where high connectance webs already have higher robustness than less connected webs, there is less scope for adaptive foraging to improve the robustness. Therefore the absolute increase in robustness will likely be smaller.

Webs with broader body mass distributions are less robust

Stronger size-structuring increases risk; body mass distributions with larger standard deviations result in the webs becoming narrower and taller with longer food chains. We find that the mean trophic level of webs increases with the standard deviation of the body mass distribution. These longer chains result in dependencies of the species elevated in the trophic hierarchy on those that are below them, potentially reducing robustness as the loss of the lower species will cascade up the chains.

More connected webs are the least robust when the energy requirement threshold is stringent

Links can become a liability; in a highly connected web, each species is more exposed to the removal of another species. When the threshold is lenient (100%) losing energy is unimportant and each link acts as insurance, increasing the web's robustness (Dunne et al. 2002). But at severe thresholds, loss of energy intake becomes crucial, and in highly connected webs the removal of one species will cause many species to lose part of their energy intake. Thus, there is a greater opportunity that there will be species that fall below their threshold. Their removal will in turn result in a large number of other links being removed, triggering a cascade of extinctions that will propagate more rapidly than in a less connected web. That the same patterns as we report for the ADBM food web networks are observed in the random graphs, suggests that this is a phenomenon likely to appear in many types of network and is not a peculiarity of our choice of model. Hence, even if the exact mechanism proposed proves incorrect, the finding that the form of the robustness-complexity relationship of a web will depend on the sensitivity of consumers to loss of prey, is likely to

hold in general for ecological networks. Indeed, our findings here are consistent with studies on secondary extinctions that also included population dynamics. For instance, Eklöf and Ebenman (2006) showed that the loss of species to secondary extinctions was proportionally greater in densely connected webs compared to sparsely connected ones.

Despite our relaxation of many original assumptions of robustness studies, and including new features of species and webs in our research, there remain a number of opportunities and questions. For instance, in favour of simplicity, this study only examined the consequences of energy thresholds and rewiring for the robustness of webs in response to random extinction sequences. There is good reason to believe that species loss will not occur at random in nature (McKinney 1997; Cardillo et al. 2005; Srinivasan et al. 2007), a useful next step would be to investigate the consequences of our treatments for other extinction sequences, perhaps based on trophic level, body mass or diet breadth (Curtsdotter et al. 2011, this special feature).

An additional simplifying assumption made in our analysis is that of an equal extinction threshold shared by all species. It is perhaps likelier that different species will be susceptible to different levels of resource loss. Such variation could depend on a species' population size or trophic level. It would therefore be worth investigating how the patterns reported here vary when such heterogeneity is introduced. Alternatively, studies of robustness with models including population dynamics would not need to introduce such thresholds, as extinction in such models will depend on an imbalance between metabolic losses and consumptive gains (Curtsdotter et al. 2011, this special feature).

Other key assumptions of this study could be relaxed by using models with population dynamics; consumer species abundances would change following the loss of resources, rather than remain fixed as in this study. And rather than only respond to the complete extinction of a particular prey item (the discretized case used here) adaptively foraging consumers could continuously alter their foraging effort as well as their diet choice in response to changes in the prey's abundance, thereby resulting in dynamic interaction strengths between predator and prey (Kondoh 2003, 2005a, 2005b). Recent studies have found that such adaptive foraging can enhance persistence of food webs and reverse the complexity-stability relationship of dynamic food webs (Kondoh 2003; Valdovinos et al. 2010). Mechanisms that might be responsible for this increase include the inhibition of rapid growth of major prey and the opportunity for minor prey to rally without predation pressure. One avenue for furthering these findings that could prove very useful would be to combine the ADBM with a dynamic food web model.

Conclusions

The relationship between the topology and robustness of a food web appears not to be a simple one. Links to other

species have the potential to act as liabilities as much as insurance. We must therefore value our knowledge of species' energetic requirements as highly as we do our understanding of the architecture of ecological networks, if we are to be able to judge an ecosystem's resilience to extinction. We must also realise that rewiring due to adaptive foraging may not be a panacea for maintaining ecosystem robustness to species loss, as there may well be substantial limitations to its effectiveness, such as those suggested by our findings. That said, other studies suggest that incorporating topological rewiring in dynamic food webs may have a crucial role in increasing a food web's persistence. Future studies must aim to further elucidate the relationships between these key factors.

Acknowledgements

References

Albert, R., Jeong, H. & Barsbasi, A. (2000). Error and attack tolerance of complex networks. *Nature*, *406*, 378–382.

Allesina, S. & Bondini, A. (2004). Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. *Journal of Theoretical Biology*, *230*, 351–358.

Allesina, S. & Pascual, M. (2009). Googling food webs: Can an eigenvector measure species' importance for co-extinctions? *PLoS Computational Biology*, *5*, e1000494.

Bascompte, J. & Stouffer, D. B. (2009). The assembly and disassembly of ecological networks. *Philosophical Transactions of the Royal Society of London B*, *364*, 1781–1787.

Beckerman, A. P., Petchey, O. L. & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 13745–13749.

Borrval, C., Ebenman, B. & Jonsson, T. (2000). Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, *3*, 131–136.

Brose, U. (2010). Improving nature conservancy strategies by ecological network theory. *Basic and Applied Ecology*, *11*, 1–5.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., et al. (2005). Multiple causes of extinction risk in large mammal species. *Science*, *309*, 1239–1241.

Coll, M., Lotze, H. K. & Romanuk, T. N. (2008). Structural degradation in Mediterranean sea food webs: Testing ecological hypotheses using stochastic and mass-balance modelling. *Ecosystem*, *11*, 939–960.

Curtsdotter, A., Binzer, A., Rall, B. C., Elköf, A., Riede, J. O., de Castro, F., et al. (2011). Species traits and community characteristics affect robustness: Sequential species deletions in dynamical food webs. *Basic and Applied Ecology*, doi:10.1016/j.baae.2011.09.008.

Dunne, J. A., Williams, R. J. & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, *5*, 558–567.

Dunne, J. A., Williams, R. J. & Martinez, N. D. (2004). Network structure and robustness of marine food webs. *Marine Ecology Progress Series*, *273*, 291–302.

Dunne, J. A. (2006). The network structure of food webs. In M. Pascual, & J. A. Dunne (Eds.), *Ecological networks: Linking structure to dynamics in food webs*. Oxford University Press.

Dunne, J. A. & Williams, R. J. (2009). Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society of London B*, *364*, 1711–1723.

Eklöf, A. & Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, *75*, 239–246.

Emlen, J. M. (1966). The role of time and energy in food preference. *American Naturalist*, *100*, 611–617.

Evans, K. L., Greenwood, J. J. D. & Gaston, K. J. (2005). The roles of extinction and colonisation in generating species–energy relationships. *Journal of Animal Ecology*, *74*, 498–507.

Gilbert, A. J. (2009). Connectance indicates the robustness of food webs when subjected to species loss. *Ecological Indicators*, *9*, 72–80.

Hoffman, M., Hilton-Taylor, C., Angulo, A., Bohm, M., Brooks, T. M., Butchart, S. H. M., et al. (2010). The impact of conservation on the status of the world's vertebrates. *Science*, *330*, 1503–1509.

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

Kondoh, M. (2005a). Is biodiversity maintained by food-web complexity? – The adaptive food-web hypothesis. In A. Belgrano, U. M. Scarler, J. Dunne, & R. E. Ulanowicz (Eds.), *Aquatic food webs: An ecosystem approach*. Oxford University Press.

Kondoh, M. (2005b). Linking flexible food web structure to population stability: A theoretical consideration on adaptive food webs. In P. de Ruiter, V. Wolters, & J. C. Moore (Eds.), *Dynamic food webs: Multispecies assemblages, ecosystem development and environmental change*. Academic Press.

McArthur, R. H. & Pianka, E. R. (1966). On the optimal use of a patchy environment. *American Naturalist*, *100*, 603–609.

McKinney, M. L. (1997). Exinction vulnerability and selectivity: Combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, *28*, 495–516.

Montoya, J. M., Pimm, S. L. & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, *442*, 259–264.

Pereira, H. M., Leadley, P. W., Proenca, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarres, J. F., et al. (2010). Scenarios for global biodiversity in the 21st century. *Science*, *330*, 1496–1501.

Petchey, O. L., Beckerman, A. P., Riede, J. O. & Warren, P. H. (2008). Size, foraging and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 4191–4196.

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

Srinivasan, U. T., Dunne, J. A., Harte, J. & Martinez, N. D. (2007). Response of complex food webs to realistic extinction sequences. *Ecology*, *88*, 671–682.

Staniczenko, P. P. A., Lewis, O. T., Jones, N. S. & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology Letters*, *13*, 891–899.

Thierry, A., Petchey, O. L., Beckerman, A. P., Warren, P. H. & Williams, R. J. (2011). The consequences of size dependent foraging for food web topology. *Oikos*, *120*, 493–502.

Valdovinos, F. S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. & Dunne, J. A. (2010). Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters*, *13*, 1546–1559.

Wright, D. H. (1983). Species energy theory: An extension of species-area theory. *Oikos*, *41*, 496–506.

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