REVIEWS

Ecological networks and their fragility

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Darwin used the metaphor of a 'tangled bank' to describe the complex interactions between species. Those interactions are varied: they can be antagonistic ones involving predation, herbivory and parasitism, or mutualistic ones, such as those involving the pollination of flowers by insects. Moreover, the metaphor hints that the interactions may be complex to the point of being impossible to understand. All interactions can be visualized as ecological networks, in which species are linked together, either directly or indirectly through intermediate species. Ecological networks, although complex, have well defined patterns that both illuminate the ecological mechanisms underlying them and promise a better understanding of the relationship between complexity and ecological stability.

A food web maps which species eat which other species[1–3]. Such trophic interactions—henceforth 'links'—are typically antagonistic predator–prey ones, but we expand the discussion to include webs of mutualists[4,5], including, for example, the interactions of flowers and their pollinators, and fruits and their seed dispersers.

Ecological networks are complex, with each species typically closely linked to all others, either directly or indirectly[6,7]. For example, links tend to be 'nested'[8,9]—that is, the diet of the most specialized species is a subset of the diet of the next more generalized species, and its diet a subset of the next more generalized, and so on. The most generalized species may include most of the prey species present in its diet. Within this pattern of close links to other species, there are reasons to expect even denser clusters of links. For example, coevolution is expected to generate clustered links that stem from the reciprocal mutual specialization between plants and their pollinators or seed dispersers[4,5]. The general existence and underlying causes of dense clusters is, however, still a matter of debate[3,10].

In this Review, we compare ecological networks to non-ecological networks, and consider their similarities, differences and underlying causes. Along with networks of interacting computers, genes or humans, ecological networks display well-defined, similar patterns of organization[11–13]. On close inspection, ecological networks are unlike other networks. Their assembly follows different rules, and the processes of predation, competition and mutualism constrain them in unique ways. Other networks nonetheless help us understand why ecological ones are special in the constraints that apply to them and how they develop.

Finally, there is a paradox. Theory predicts that complex ecological networks are likely to be 'fragile' in various ways. For example, complexity affects the chance that species can coexist at a stable equilibrium. It also affects resilience (how fast populations recover from disturbances), the variability of population densities over time and the persistence of community composition. It should also affect the resistance to change, when species invade or are driven to extinction[14–16]. Every species is closely linked to every other[6,7], so—metaphorically—when a tree falls in a rainforest, every species in that species-rich, complex system would seem to 'hear' that event quickly. Every disturbance buffets every other species, so how do species persist in this 'noisy' world? And which species will persist in the now extensively modified and increasingly species-poor world we are creating for them? We address these questions in the penultimate section, where we highlight both the extent of our present understanding, and the important gaps in our knowledge.

Complexity

No species is distant from the most connected species, nor any top predator from a species at the base of the web[2,6] (Fig. 1; Box 1 defines 'distance' and other technical terms). In seven species-rich webs, 80% and 97% of species are, respectively, within two or three links from each other[7]. Both the cascade model[2], and the niche model[17,18] it inspired, predict short distances between top predators and plants or detritivores at the base of a web[19]. The cascade model posits nested diets, with the top predator potentially exploiting all the other species, the next predator exploiting all but the top predator, and so on.

Given that species in a web are typically closely connected, are there even denser patterns of links within each web? The first approach to this question considers detailed patterns, and can be applied to webs with few or many species. (Many early studies involved webs with few species. Box 2 considers the limitations on what data known food webs provide.)

Food webs straddling different habitats generate compartments corresponding to habitat boundaries[20]. But no agreement exists when looking for compartments within a habitat[20]. Some visual inspections for compartments find them[21,22], while others do not[23]. Using statistics, one study[24] finds compartments within the food web of an estuary. Another[20] finds roughly equal numbers of more and less compartmented webs than expected by chance. A third study identified compartments in three of five species-rich food webs[25].

Analysing clusters is more tractable than detecting compartments. In a random web with S species and an average of k links per species, clustering scales as k/S (refs 12, 13). Generally, webs with many species and few links per species are more clustered than are random counterparts[6,10]. Embedded in the most highly clustered webs, however, are two classes of systems long known[3] and theoretically expected[3] to have tight clusters of links. In aquatic systems, many fish are 'life-history omnivores' that feed from several trophic levels at various life stages—on phytoplankton after hatching to other piscivorous fish as adults—including those that ate them when young[26] (see Fig. 1). Tight clusters are common in host–parasitoid systems, where a parasitoid may feed on a host, but also hyper-parasitize other parasitoids[23,27].

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In sum, important classes of webs involve densely linked groups of species. Life-history omnivores dominate the marine ecosystems that cover most of the planet (as well as many freshwater ecosystems), whereas plant–herbivore–parasitoid systems account for the great majority of Earth's species[28]. From these perspectives, densely clustered webs are nearer the norm, not exceptions. Moreover, compartments are likely to correspond to habitat boundaries, if only because of the difficulties of species feeding successfully in two or more habitats. This begs the question, not addressed here, of what constitutes a habitat for anything less subtle than major categories such as 'ocean, lake, and land'[20].

These exceptions noted, there is no clear consensus about compartments and clusters. Whether the 'species' that the food web depicts are actually species or taxonomically aggregated groups or 'trophic species'—species that apparently share the same (or similar) predators and prey[2,3]—confounds the results. Krause et al.[25] provide the most complete analysis, and show that the detection of compartments requires new algorithms. Increasing taxonomic resolution and details on the strength of interactions increased their chances of finding compartments. These complexities inevitably create controversy. Its resolution will come from applying their ideas to other quantified and taxonomically specific webs.

A second approach applies to only species-rich webs and considers $P(k)$, the probability of a species having k links (Fig. 2). Power law, 'scale-free' distributions, $P(k) \sim k^{-\gamma}$ (we use $\sim$ here to mean 'follows a function'), describe the links between human social contacts and internet connections[11–13]. They suggest a 'popularity principle' whereby the 'rich get richer'. As these non-ecological networks grow, nodes are likely to get more links the more they have already[12], and dense clusters develop. In these systems, the constant γ is typically a value between 2 and 3 (refs 12, 13).

Alternatively, many factors constrain a predator's diet, so truncating the linkage distribution, preventing the 'rich from getting richer' and suggesting an exponential trimming of linkages: $P(k) \sim e^{-k/\xi}$. How large is the truncation measured by the parameter ξ? One can fit the combined model $P(k) \sim k^{-\gamma}e^{-k/\xi}$ (refs 29, 30). Intuitively, the value ξ measures the number of links below which power laws describe the systems and above which the number of links per species drops off more steeply (Fig. 2).

For a set of 86 mutualistic webs[30] ranging from 17 to nearly 1,000 species, this truncation is >4 times the average number of links per species in two-thirds of the examples. In these examples, the power-law exponent γ is typically $\sim$1; thus, the distributions are substantially less steep than are the non-ecological networks discussed above. For the set of species-rich food webs (29 to 238 species), ξ is smaller, roughly equal to the average number of links per species[6,10,31], consistent with the distributions arising from the niche model and a generalized version of the cascade model[32].

In sum, the distributions of links in food webs do not match other networks quantitatively[33], and only match qualitatively for small ranges of numbers of links. Moreover, the 'rich get richer' mechanism is at odds with ecological principles[5,10]. For example, as more species of frugivore feed upon a fruit species, then competition for that fruit will increase, and the less likely another frugivore would include it in its diet and the more likely it would feed on other fruits instead.

Species with many links to other species in the web—the 'richest' ones in the analogy—may get that way simply by being the most abundant. Within a given trophic level, abundant species are more likely to receive the attention of predators, pollinators or frugivores, than are rare ones. Abundant predators probably feed on many prey species[34].

Perversely, across trophic levels, the larger a species' body size, the more species on which it can feed, and thus the higher its trophic level[9]. Large body size and high trophic level mean lower abundance[9,35], so across trophic levels it is the trophically most generalized species that are the rarest.

Whether within or across trophic levels, these patterns of strongly nested diets—whether by abundance or body size (or both)—do not imply a process of continuing community assembly. That said, Sugihara[36] and colleagues[37] do envision a process whereby species sequentially partition resources as they invade an ecological community. Rarer, trophically specialized species enter the community later than do generalists.

The major gap in knowledge is surely the scarcity of models exploring dynamics and rules for coexistence of large sets of species with trophic links suitably nested across trophic levels by body size (and associated attributes) and within trophic levels by abundance. Recent descriptions of food webs detailing body-size, abundance and trophic linkages[9,35,38] provide a good base to develop these models.
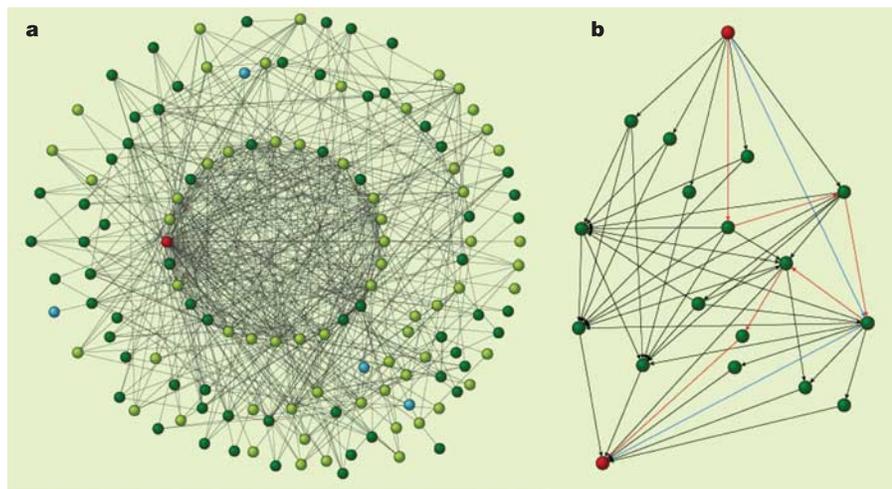
Figure 1 | Shortest paths in a complex food web. The Ythan estuary food web[66,73]. **a**, Node colour indicates the length of the shortest path linking the most connected species (the flounder *Platichthys flesus*, in red) and each other species from the network. (The trophic direction of the links—what eats what—is ignored). Dark green, species are one link apart; light green, two links; and blue, three links. The central circle represents the densest sub-web[75], which consists of 28 species with at least 7 links with the rest of the species from the sub-web. This sub-web contributes most to the observed clustering. **b**, Food chains between basal species of *Enteromorpha* (red node at the bottom) and the top predator, the cormorant *Phalacrocorax carbo* (red node at the top). Links corresponding to the shortest path connecting them are in blue (2-links), and those corresponding to the longest food chain between these two species are in red (6-links).

Box 1 | Definitions

Complexity, often used informally, has a specific meaning—the average number of trophic links per species (sometimes called linkage density). **Connectance** is linkage density divided by the number of species in the web[2,3]. **Linkage strength** is the magnitude of the effect of one species upon the growth rate of another[52].

On theoretical grounds, May[46] conceived **blocks**, which Pimm and Lawton[20] defined operationally as **compartments**. Links connect species within a compartment, but not to species outside it (see Box Figure). In practice, there may be links outside the compartment, but these should be relatively few or relatively weak dynamically compared to links within it. We can also measure **clustering** as the fraction of species with a direct link to a focal species that are themselves directly linked[65,66] (see Box Figure).

An **omnivore** feeds on more than one trophic level[67] and so 'messes up' classifying species into distinct levels[31]. With two important classes of exceptions, early studies found omnivory to be statistically unusual in many systems[3]—justifying the long-held notion of distinct trophic levels. Recent studies confirm this: half the species of a set of species-rich food webs can be unambiguously assigned to a discrete trophic level[19]. For a given complexity, webs with many within-food-chain omnivores tend to be compartmented[20] and clustered, though the relationship is not exact (see Box Figure).

A **guild** of predators feeds on the same prey species, distinct from those other guilds exploit[68]. Co-evolution expects **reciprocal specialization** between pollinators and their flowers and between fruit and their dispersers (see Box Figure).

Network studies report the statistical distributions of the numbers of links per species[11–13,61], and ask if ecological networks are **small worlds**[6,11,65]—where no species are 'distant' from each other. **Distance** (also called **shortest path**) is the minimum number of links connecting two species: one, if A feeds on B; two, if A feeds on C that feeds on B, and so on. Species may feed on only one (**monophages**), a few (**oligophages**), or many (**polyphages**) prey species.
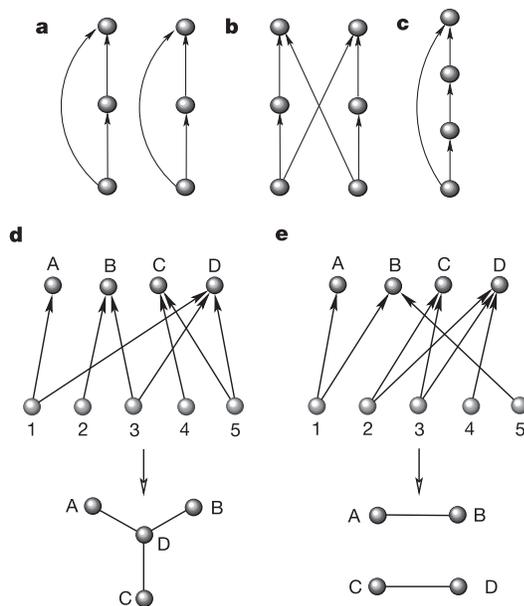
Box 1 figure | Compartments, omnivory, clustering and nestedness. a, b, Examples of food webs that are compartmented (**a**) and not compartmented (**b**). The web in **a** is clustered, and has **within-chain omnivory** (the 'grain-fed hamburger in a bun' mode). The web in **b** is not clustered, and its omnivory involves feeding on different food chains (the 'fish and chips' mode). The web in **c** has within-chain omnivory, but it is not clustered. **d, e,** Two mutualistic webs with identical numbers and distributions of trophic links, between pollinator species A to D and flower species 1 to 5. Interactions in web **d** (upper diagram) are not grouped into guilds, whereas in **e** (upper diagram) they are—as shown by the overlaps between the pollinators (lower diagrams).

Evolutionary patterns in diet specialization

Webs of specialists are less complex than those of generalists, so what determines whether a species specializes on few prey species or whether it takes many? The trade-offs between specialization and generalization are complex and multi-factorial[4,39]. Monophages (species that eat just one other species) are probably more efficient consumers than are generalists—they usually have higher *per capita* ingestion and assimilation rates[40]. Prey species also differ in the number of predators that feed on them. Experimental studies find that species consumed by multiple predators have lower predation rates than species with single predators, in contrast to the expected sum of the individual effect of each predator[41]. Combined, these results suggest that trophic specialists would have dynamically stronger interactions with individual prey species (and vice versa) than would more generalized species. We discuss the implications for food web dynamics below.

How are feeding interactions organized, given these patterns of relative specialization or generalization? Broad patterns are clear. For example, hummingbirds exploit different species of flowers than do insects. Within the class of insect-pollinated flowers, bees and butterflies feed on different sets of plant species[4]. Yet conventional wisdom suggests that such patterns should also apply within broad taxonomic groupings. Compelling examples[42] of hummingbirds with long or strangely curved bills and the corresponding morpho-logical specialization of the flowers they pollinate beg an obvious question: how ubiquitous are tight links between species of pollinator (or frugivore) and the flowers (or fruits) on which they feed?

The idea of reciprocal specializations reinforced by co-evolution seems so well entrenched that it is surprising that studies have not assessed its generality. The problem has probably been the exact measure of 'guilds' (groups of species exploiting the same resources by similar means, such as seed-eating birds) and the lack of a suitable null hypothesis against which to judge their improbability. Fortu-nately, there is an exact mathematical parallel to studies of the presence or absence of species on islands—a topic with a long, controversial history in ecology[43]. Both problems involve a binary matrix where, under the null hypothesis, the row and column sums must remain the same as those observed in nature. Specifically, a given species must occur on a set total number of islands, whereas a given island will host a set total number of species. Likewise, a pollinator exploits a set total number of plant species and a plant offers nectar to a set total number of species. As with biogeographical questions, the computational problem involves generating null hypotheses that obey these constraints but are not artefactually close to the observed pattern. This issue is now solved[43], but no one has applied this technique to webs of mutualists. Nor, for that matter, has it been applied to sets of predators and their prey, though

Box 2 | Food web data limitations

Early studies[1–3] analysed webs where the authors' purpose generally was not to make comparisons between different webs. Important exceptions are from tree holes and other water-filled plant cavities[69] and plants, herbivores, their parasites, and hyperparasites[27]—systems that continue to generate standard, often quantitative, methods to describe and compare webs[23,70]. Responding to criticisms[66,71,72] of early studies, recent efforts[18,31,63] produced species-rich, linkage-dense webs.

Early studies also provided little or no information on the strength of trophic links. Following an appeal for more consistent data[72], attempts to estimate such strengths find that they vary considerably[52]. Data on strengths generally involve only few links[52], even when most of the system's links are described[73]. Identifying strong and weak links is difficult. Having a simple measure correlated with strength would be very helpful. Recent empirical[50] and theoretical[74] analyses find that predator-to-prey body size ratio predicts strength—the larger the ratio, the stronger the interaction.

there are abundant sources of such information—from fish and their prey[44], for example.

Mutualistic webs are strongly nested[5,8]. Nested links constrain reciprocal specializations, but do not completely preclude them (see Box 1). Nonetheless, the ubiquity of nestedness is a surprise, showing as it does that specialized pollinators (for example) typically exploit flowers used by many other species. Moreover, the interactions are not symmetric: the plant species that is most important to a particular pollinator may receive more attention from other species that are not so dependent upon it[45].

Fragility and the paradox of complex interactions

Most differential equation models must be sufficiently 'simple' if the species are to persist at a locally stable equilibrium[3,15,16,46]. Indeed, there is a striking coincidence in the simple, sparse patterns of links observed in webs and those that models predict[15,16]. Sensibly parameterized models of real food webs tend to be locally stable, despite their complexity, suggesting that real webs have statistically special parameters and patterns of interactions[47–50]. Natural history explanations pre-date dynamical models[15] in suggesting that species that overlap too extensively in their diets cannot coexist. Importantly though, models do permit tightly clustered links and extensive omnivory in systems dominated by parasitoids[3] and life-history omnivores[26]. Because these classes of interaction dominate the

group of unusually clustered models, then perhaps this is a sufficient answer: such clusters are not prohibited by the dynamics as we understand them.

Another way of phrasing the problem of complex webs is to notice that the effect of one species on the density of another diminishes with their separation in the food web, measured by the distance connecting them[51]. The commonness of short paths in food webs[6,7] suggests that disturbances spread rapidly throughout the food web. Certainly, species may not be close if the shortest links between them are weak or intermittent. As a species feeds on more prey species, or suffers the attention of more predators, the strength of the interactions may decrease. The 'many weak and few strong' pattern of interactions in quantified empirical food webs[52] and webs of mutualists[34,53] usually correlates with diet breadth. Polyphages (species eating many other species) and prey with many predators present weak interactions, whereas strong interactions correspond to monophages and prey with only a few predators. Intriguingly, Berlow[54] finds that in some systems the weak interactions have the greatest variance: they yield strong effects intermittently.

There is a long-recognized paradox: in models with random, but sensibly chosen, parameters, the probability of a locally stable equilibrium declines sharply as complexity increases[46]. Yet, the ever-smaller fraction of models that are stable tend to be more resilient[3]. (Resilient in the narrow sense that the largest eigenvalue
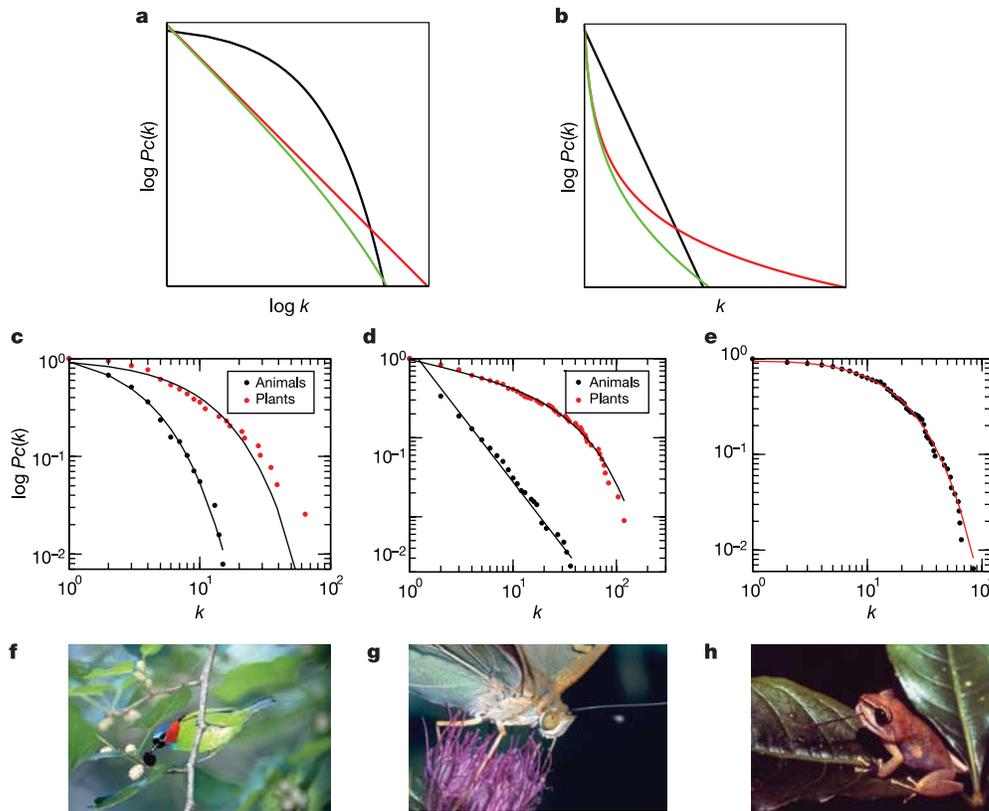
Figure 2 | Distribution of linkage density in ecological networks. a–e, The cumulative probabilities $Pc(k)$, for $\geq k$, where $P(k)$ is the probability a species has k links to other species, and is given by $P(k) \sim k^{-\gamma}e^{-k/\gamma}$ where $e^{-k/\gamma}$ introduces a cut-off at some characteristic scale γ. Panels **a** (log–log) and **b** (log–linear) show three different modelled networks. Black lines, single-scale networks; when γ is very small, the distribution has a fast decaying tail, typically exponential, $P(k) \sim e^{-k/\gamma}$. Green lines, truncated scale-free networks; these correspond to intermediate values of γ where the distribution has a power law regime followed by a sharp cut-off, with an exponential decay of the tail. Red lines, scale-free networks; for large values of γ the number of connections per species decays as a power law, $P(k) \sim k^{-\gamma}$, a function with a relatively 'fat tail'. **c–e**, Experimental data (filled circles) and best fits (lines); **c**, a frugivore–plant web[76]; **d**, a pollinator–plant web[77]; and **e**, the food web from El Verde rainforest[78]. In **c** and **d**, for red circles, k is the number of plants species visited by an animal, and for black circles, k is the number of pollinator species visiting each plant species. In **e**, we sum prey–predator links and predator–prey links for each species. Best fits to the data in **c–e** are as follows: **c**, animals, exponential, $P(k) = e^{-k/3.998}$; plants, truncated power law, $P(k) = k^{-0.013}e^{-k/11.22}$; **d**, animals, power law, $P(k) = k^{-1.512}$; plants, truncated power law, $P(k) = k^{-0.2822}e^{-k/42.55}$; **e**, exponential, $P(k) = e^{-k/8.861}$. **f–h**, Photographs of a frugivore–plant (**f**), insect–flower (**g**) and predator–prey (**h**) interaction of webs depicted in **c–e**, respectively.

in the linearized system will be more negative and disturbances will dissipate more quickly[14,15].) McCann et al.[55] developed this idea to argue the importance of weak linkages and their particular arrangement.

Indirect effects—those mediated by intermediate species—are often in the opposite direction to those expected on the basis of direct interactions alone[15,51,56]. They are best known from experiments in the intertidal zones of sea-shores. Menge's review[57] of 23 of them is key. As species richness increased, a typical species interacted strongly with more species and through more indirect pathways.

Complex webs also pose a challenge when one considers severe changes such as the addition or removal of species. What will be the consequences of extinction rates that are now hundreds to thousands of times faster than normal[58]? Consider the apparent paradox of two classic results: MacArthur's model[59] and Paine's experiment of removing a top predator from the inter-tidal zones[60]. Dynamical models of species removals show that the more polyphagous the predators, the less the effect caused by removing one of its prey species (measured as the probability that the predator will be lost[3]). Thus, MacArthur's model is correct, but it is incomplete. Paine showed, and models confirm[15] that removing the predators of polyphages eliminates many of the latter's prey species. Thus, whether simple or highly connected model food webs are robust to the loss of species depends entirely on whether one looks at top predators or plant species[15]. Moreover, changes in species composition may be large while changes in the biomass may be small, and vice versa[15].

Into this already complex story come recent studies using strictly topological approaches (that is, without population dynamics) to actual webs, as against abstractions of them. When the most connected species are successively removed from the web, the web is not 'species deletion stable'[3]. Many species lose their only prey source (and so must become extinct in turn), and the web quickly breaks into many disconnected sub-webs[61–64]. By contrast, when disasters extirpate species randomly, these webs are robust, showing both little fragmentation and few secondary extinctions[61–64]. Perhaps well-connected species are those that are relatively abundant at their particular trophic level and so are unlikely to be lost.

In sum, we do not completely understand how species persist in complex webs when disturbances propagate quickly and apparently strongly. More realistic models that incorporate the relationships between link strength, abundance and trophic generalization may provide the answers.

Conclusions

Our knowledge of the structure of ecological networks is still incomplete in important areas that include compartments and reciprocal specialization. Species are closer than previously thought, and many webs have very dense clusters of linkages. The relationships between body size, abundance, trophic specialization and nested diets (both across and within trophic levels) are not only interesting in themselves[9,35,38]: they may constrain web dynamics in theoretically unexplored ways. Such constraints may be essential to explain the persistence of species in a constantly changing world, and the tolerance of current ecosystems to natural gains and losses of species as well as their vulnerability to unnaturally inflated extinction rates.

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