

Introduction

Food-web assembly and collapse: mathematical models and implications for conservation

For thirty years I have read publications about this spate of invasions; and many of them preserve the atmosphere of first-hand reporting by people who have actually seen them happening, and give a feeling of urgency and scale that is absent from the drier summaries of text-books. We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora. We might say, with Professor Challenger, standing on Conan Doyle's 'Lost World', with his black beard jutting out: 'We have been privileged to be present at one of the typical decisive battles of history—the battles which have determined the fate of the world'. But how will it be decisive? Will it be a Lost World? These are questions that ecologists ought to try to answer.

Elton (1958, pp. 31–32)

In these words, written half a century ago and in prose more vivid than usually found in the scientific literature today, Elton speaks of the central theme of this collection of papers. The subsequent 50 years have seen vast growth in the scientific workforce and in our knowledge about how the natural world works. But our understanding of how food webs assemble themselves, and how these structures respond to invading species or other perturbations (either natural or human associated), remains richer in questions than in answers. One thing is certain: the environmental problems foreseen by Elton are even clearer and more urgent today.

The present papers on *Food-web assembly and collapse* give an excellent account of where we currently are in terms of data and uncertainties about the structure of real food webs on land and in the sea, and about the effects of various kinds of disturbance on them, along with theoretical ideas about how such networks of interacting species are put together and how removals or invasions affect them. Awareness of Elton's 'urgency and scale' of these problems may be more marked in today's textbooks, but it too often remains lacking in government funding agencies, lost in their babble about the 'knowledge economy'. The present volume thus stands somewhat apart from the usual *Phil. Trans.* themed issue, in that it illuminates pressing practical issues that ultimately will affect every person on the planet.

I think it fair to credit Elton's (1958) *The ecology of invasions by animals and plants* as first articulating the proposition that, in nature, species' population stability is typically greater in structurally complex communities

than in simple ones. Around the same time, while a postdoctoral student at Oxford, MacArthur (1955) suggested that community stability may be roughly proportional to the logarithm of the number of links in a trophic web (this was based on the argument, borrowed from information theory, that such a logarithm measures the degree of organization or 'complexity' of the web, along with the intuitive association between complexity and stability). Hutchinson (1959, p. 103) mistook this for a 'formal [mathematical] proof of the increase in stability of a community as the number of links in its foodweb increases'.

In 1970 I accidentally stumbled on a sceptical account of this putative theorem by Watt (1968, p. 43). I recognized that, to the contrary of what was becoming the conventional wisdom, in a 'general' food web (i.e. one assembled by randomly assigning interactions among species) the more species you had and the stronger is the interactions among them, the less likely the system would persist (i.e. 'be stable', in the simple sense of having all eigenvalues with negative real parts). This was reinforced by Gardner & Ashby (1970), who—although not referring to ecosystems—presented simulations showing that in a network of interacting entities, the more the nodes, and the more and stronger the connections among them, the less likely that the system would be stable. Generalizing a result for a special class of random matrices by Wigner, May (1972) proved the asymptotic stability criterion $NC\alpha^2 < 1$ for such networks (N is the number of nodes, C the connectance, α the average interaction magnitude scaled against the 'intraspecific' interaction strength—the diagonal elements of the interaction matrix).

However, as strongly emphasized at that time (May 1973), real food webs are most certainly not randomly assembled. They are ultimately the winnowed products of evolutionary processes. In short, this work of the early 1970s helped to clear the undergrowth, refocusing the agenda to address the question of what are the structural mechanisms whereby real food webs and ecosystems reconcile complexity—increasingly rich collections of species, with a tangle of interactions among them—with persistence in the face of environmental buffeting.

The first suggestion for such stabilizing structures was that 'competition or mutualism between two species is less conducive to an overall web stability than is a predator–prey relationship', an argument based on considerations of qualitative stability (i.e. dependence on the signs, but not the magnitudes, of interactions; May 1973, p. 73). Allesina & Pascual (2008) have recently amplified this finding in a detailed

One contribution of 15 to a Theme Issue 'Food-web assembly and collapse: mathematical models and implications for conservation'.

study of 10 000 computer-generated networks. A second suggestion was that omnivory tends to destabilize (Pimm & Lawton 1978; Pimm 1982; see also Vandermeer 2006). As a third suggestion, several people conjectured that organizing a food web as loosely connected subsystems would help stabilize it. And fourth, the $NC\alpha^2 < 1$ rule outlined above hints that weak interactions and/or fewer connections among species may tend to be relatively stabilizing.

In the 1970s, testing these suggestions was hindered by paucity of data on food webs. Influential work by Cohen (1978) brought together a collection of 19 food webs, and tentatively suggested some intriguing regularities (e.g. in the length of chains from 'top' to 'bottom' species, and in numbers of links per species). As such compilations grew, Briand & Cohen (1987) were codifying patterns in some 113 food webs (see also Sugihara *et al.* 1989; Havens 1992; Moore *et al.* 1993; Bersier & Sugihara 1997). More recently, two analyses of 16 high-resolution food webs, both aquatic and terrestrial with 27–172 species, are more explicitly focused on the network topology, finding 'more than 95 per cent of species [are] typically within 3 links of each other' (Dunne *et al.* 2002; see also Williams *et al.* 2002). The 'degree distributions' (i.e. the relative proportions of species/nodes with i links to others) are not random; whether they are 'scale free', or exponential, or otherwise remains debatable (Keller 2005; Proulx *et al.* 2005). Another long-standing question is whether there are significant differences between terrestrial and aquatic ecological networks; the above Dunne/Williams analyses would suggest not, and this view accords with later studies of three different marine ecosystems (Dunne *et al.* 2004).

Despite these many empirical advances, a major problem lies in the extent to which constituent species are often 'lumped' into functional groups—each bird lovingly identified, while individual arachnid species become one unitary 'spiders'—in ways which can bias or cloud analyses (see Solow & Beet 1998). Another problem is underlined by Kuris *et al.* (2008), who included parasites, which are almost always neglected, in their account of several estuarine food webs. They find the parasite biomass typically exceeds that of all conventional vertebrate predators, with serious implications for conclusions about the structure of the interaction network. In particular, including parasites in this way greatly increases the proportion of predator–prey interactions in the overall accounting for interactions.

Some interesting regularities are arguably emerging from these and other empirical studies of organizational patterns in real food webs. Perhaps the single most important is evidence for some remarkable constancies in structure that have apparently persisted for hundreds of millions of years, surviving the drift of continents, climate fluctuations, and the movement and evolution of constituent species. For example, Baumbach *et al.* (2002) documented rough constancy in predator–prey ratios in different situations, on a geological time scale (see also Dunne *et al.* 2008). Another instance comes from the work by Bascompte *et al.* (2006) on the network structure of communities of pollinators and the plants they pollinate. These networks seem to be consistently disassortative, in the sense that highly connected nodes

tend to have their connections disproportionately with low-connectivity nodes, and conversely small nodes connect disproportionately with a few large ones.

Beginning with ideas about the possible origins of putatively observed network patterns in food webs by Cohen (1978), Sugihara (1983) and others, there is now an interesting variety of suggestions as to how food webs have come to organize themselves. Several of the papers in this collection 'compare and contrast' such ideas in relation to data. In particular, Dunne & Williams (2009) build on their influential earlier work, looking at secondary extinctions both in empirically derived data from actual communities, and at theoretically derived computer models based on four different proposed explanations for the structure of food webs (along with the 'null hypothesis' of a randomly assembled web).

Another of the difficulties that besets attempts to understand the structure of real, observed food webs in terms of ideas about the underlying mechanisms that generate the structure is that—most irritatingly—different mechanisms can sometimes lead to similar, or even identical, structures. Thus, Stouffer *et al.* (2005) showed that approximately exponential degree distributions, similar to those observed (see above), can be derived from at least two apparently different models for food-web assembly, proposed by Cattin *et al.* (2004) and by Williams & Martinez (2000). This finding is reminiscent of much earlier ecological observations that significantly different mechanisms could result in identical distributions of the relative abundance of species.

In this introductory essay, I have aimed briefly to sketch some of the background to the present collection of papers. It is an impressive and varied collection, testifying to the rapid advances in this area of ecological science, but at the same time defying any crisp overview or summary. The papers address both empirical data and theoretical ideas about how food webs are assembled and structured. The primary emphasis, however, is on the way such webs respond to the removal of particular species, both in theory and reality. The importance of such understanding for conservation biology is obvious, as threats of extinction continue to grow, caused by overexploitation, alien introductions, habitat loss, climate change and usually combinations of two, three or even all four of these.

Much of this work on the structure and function of ecosystems has potentially wider implications. Given that ecosystems are, to a large extent, robust by virtue of their continued existence on evolutionary time scales, they could provide clues about which characteristics of complex systems correlate with a high degree of robustness. This was indeed the theme of a recently published joint study by the US National Academy of Sciences and the Federal Reserve Bank of New York on *New directions for understanding systemic risk* (Kambhu *et al.* 2007), set up well before the recent instabilities in financial markets manifested themselves. As discussed by May *et al.* (2008), studies of food-web assembly and dynamics of the kind collected here may well have wider relevance and importance in helping us to better understand the 'ecology' of financial markets and their potential vulnerability to collapse.

The main interest and concern, however, properly belongs to conservation biology. Documented extinctions of bird and mammal species over the past century occurred at a rate of the order of 100 to 1000 times the average extinction rates seen over the half billion year sweep of the fossil record, and four separate lines of evidence and argument suggest at least a further 10-fold increase over the coming century. If birds and mammals are typical—and there is no reason to believe they are not—this puts us on the breaking tip of a sixth great wave of Mass Extinctions in the history of life on earth. Such extinctions threaten a multitude of ecosystem services. These services are not counted in economists' conventional assessment of global GDP, but estimates suggest they at least rival it in purely monetary terms (Costanza *et al.* 1997). The recent Millennium Ecosystem Assessment (2005) identifies 24 categories of ecosystem service. Of these, 15—roughly two-thirds—are being degraded or used unsustainably, four have been enhanced (all related to agriculture) and five remain unassessed; for a more detailed discussion, see May (2007). Maybe human ingenuity, over the coming years, can find substitutes for the crucial services ecosystems currently deliver, but maybe not. And who wants to live in the world of the cult movie *Bladerunner* anyway?

I therefore see the present collection of papers as making a major contribution to an area of science which is of transcendent importance. Our general quest for understanding how the world works, and what is our place in it, is the quintessential characteristic that sets humanity apart from other animals. But better understanding of ecosystem assembly and collapse is arguably of unparalleled practical importance for ourselves and for other living things, as humanity's unsustainable impacts on the planet continue to increase.

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REFERENCES

- Allesina, S. & Pascual, M. 2008 Network structure, predator-prey modules, and stability in large food webs. *Theor. Ecol.* **1**, 55–64. (doi:10.007/s12080-007-0007-8)
- Bascompte, J., Jordano, P. & Olesen, J. M. 2006 Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431–433. (doi:10.1126/science.1123412)
- Baumbach, R., Knoll, A. & Sepkowski, J. 2002 Anatomical and ecological constraints on phanerozoic animal diversity in the marine realm. *Proc. Natl Acad. Sci. USA* **99**, 6854–6859. (doi:10.1073/pnas.092150999)
- Bersier, L.-F. & Sugihara, G. 1997 Scaling regions for food web properties. *Proc. Natl Acad. Sci. USA* **94**, 1247–1251. (doi:10.1073/pnas.94.4.1247)
- Briand, F. & Cohen, J. E. 1987 Environmental correlates of food chain length. *Science* **238**, 956–960. (doi:10.1126/science.3672136)
- Cattin, M.-F., Bersier, L. F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J. P. 2004 Phylogenetic constraints and adaptation explain food-web structure. *Nature* **427**, 835–839. (doi:10.1038/nature02327)
- Cohen, J. E. 1978 *Food webs and niche space*. Princeton, NJ: Princeton University Press.
- Costanza, R. *et al.* 1997 The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–257. (doi:10.1038/387253a0)
- Dunne, J. A. & Williams, R. J. 2009 Cascading extinctions and community collapse in model food webs. *Phil. Trans. R. Soc. B* **364**, 1711–1723. (doi:10.1098/rstb.2008.0219)
- Dunne, J. A., Williams, R. J. & Martinez, N. D. 2002 Food-web structure and network theory: the role of connectance and size. *Proc. Natl Acad. Sci. USA* **99**, 12 917–12 922. (doi:10.1073/pnas.192407699)
- Dunne, J. A., Williams, R. J. & Martinez, N. D. 2004 Network structure and robustness of marine food webs. *Mar. Ecol. Prog. Ser.* **273**, 291–302. (doi:10.3354/meps273291)
- Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A. & Erwin, D. H. 2008 Compilation and network analyses of Cambrian food webs. *PLoS Biol.* **6**, e102. (doi:10.1371/journal.pbio.0060102) (see also *Nature* **453**, 717–718 (2008)).
- Elton, C. S. 1958 *The ecology of invasions by animals and plants*. London, UK: Methuen and Co.
- Gardner, M. R. & Ashby, W. R. 1970 Connectance of large dynamical (cybernetic) systems: critical values for stability. *Nature* **228**, 784. (doi:10.1038/228784a0)
- Havens, K. 1992 Scale and structure in natural food webs. *Science* **257**, 1107–1109. (doi:10.1126/science.257.5073.1107)
- Hutchinson, G. E. 1959 Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159. (doi:10.1086/282070)
- Kambhu, J., Weidman, S. & Krishnan, N. (eds) 2007 *New directions for understanding systemic risk*. Washington, DC: National Academies Press. (Also available in *Economic Policy Review* 13 (Federal Reserve Bank of New York, November 2007).)
- Keller, E. F. 2005 Revisiting 'scale-free' networks. *Bioessays* **27**, 1060–1068. (doi:10.1002/bies.20294)
- Kuris, A. M. *et al.* 2008 Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* **454**, 515–518. (doi:10.1038/nature06970)
- MacArthur, R. H. 1955 Fluctuations of animal populations, and a measure of community stability. *Ecology* **36**, 533–536. (doi:10.2307/1929601)
- May, R. M. 1972 Will a large complex system be stable? *Nature* **238**, 413–414. (doi:10.1038/238413a0)
- May, R. M. 1973 *Stability and complexity in model ecosystems*. Princeton, NJ: Princeton University Press.
- May, R. M. 2007 Unanswered questions and why they matter. In *Theoretical ecology* (eds R. M. May & A. R. McLean), ch. 15, p. 205, 3rd edn. Oxford, UK: Oxford University Press.
- May, R. M., Levin, S. A. & Sugihara, G. 2008 Ecology for bankers. *Nature* **451**, 893–894. (doi:10.1038/451893a)
- Millennium Ecosystem Assessment 2005 *Ecosystems and human well-being: synthesis*. Washington, DC: Island Press.
- Moore, J. C., de Ruiter, P. C. & Hunt, H. W. 1993 Influence of productivity on the stability of real and model ecosystems. *Science* **261**, 906–908. (doi:10.1126/science.261.5123.906)
- Pimm, S. L. 1982 *Food webs*. New York, NY: Chapman and Hall.
- Pimm, S. L. & Lawton, J. H. 1978 On feeding on more than one trophic level. *Nature* **275**, 542–544. (doi:10.1038/275542a0)
- Proulx, S. R., Promislow, D. & Phillips, P. C. 2005 Network thinking in ecology and evolution. *Trends Ecol. Evol.* **20**, 345–353. (doi:10.1016/j.tree.2005.04.004)

- Solow, A. R. & Beet, A. R. 1998 On lumping species in food webs. *Ecology* **79**, 2013–2018. (doi:10.2307/176705)
- Stouffer, D. B., Camacho, J., Guimerà, R., Ng, C. A. & Nunes Amaral, L. A. 2005 Quantitative patterns in the structure of model and empirical food webs. *Ecology* **86**, 1301–1311. (doi:10.1890/04-0957)
- Sugihara, G. 1983 Niche hierarchy: structure assembly and organization in natural communities, p. 325. PhD dissertation, Princeton University.
- Sugihara, G., Schoenly, K. & Trombla, A. 1989 Scale invariance in food web properties. *Science* **245**, 48–52. (doi:10.1126/science.2740915)
- Vandermeer, J. 2006 Omnivory and the stability of food webs. *J. Theor. Biol.* **238**, 497–504. (doi:10.1016/j.jtbi.2005.06.006)
- Watt, K. E. F. 1968 *Ecology and resource management*. New York, NY: McGraw-Hill.
- Williams, R. J. & Martinez, N. D. 2000 Simple rules yield complex food webs. *Nature* **404**, 180–183. (doi:10.1038/35006555)
- Williams, R. J., Martinez, N. D., Berlow, E. L., Dunne, J. A. & Barabási, A.-L. 2002 Two degrees of separation in complex food webs. *Proc. Natl Acad. Sci. USA* **99**, 12 913–12 916. (doi:10.1073/pnas.192448799)