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The assembly, collapse and restoration of food webs

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Darwin chose the metaphor of a 'tangled bank' to conclude the 'Origin of species'. Two centuries after Darwin's birth, we are still untangling the complex ecological networks he has pondered. In particular, studies of food webs provide important insights into how natural ecosystems function (Pascual & Dunne 2005). Although the nonlinear interactions between many species creates challenges of scale, resolution of data and significant computational constraints, the last 10 years have seen significant advances built on the earlier classic studies of Cohen, May, Pimm, Polis, Lawton and Yodzis (May 1974; Cohen 1978; Pimm 1982; Briand & Cohen 1984, 1987; Yodzis 1989; Cohen *et al.* 1990; Pimm *et al.* 1991; Yodzis & Innes 1992; Yodzis 1998). These gains stem from advances in computing power and the collation of more comprehensive data from a broader array of empirical food webs.

Increasingly, environmental disruption unravels the tangled bank (Vitousek *et al.* 1997). The authors of the papers collected in this synthesis were specifically requested to examine how studies and models of food webs can inform the management of natural ecosystems. A common question is what makes food webs collapse? Several authors in this synthesis also describe what food-web studies have told us about the restoration of natural ecosystems and how species composition and interactions affect the provisioning of ecosystem services.

If our understanding of food webs is to have a firm empirical basis, we need to describe and attempt to model the structure of webs for a variety of natural and human-modified ecosystems (Memmott *et al.* 2005). At present, a significant proportion of ecosystem management is based upon a blend of 'conventional wisdom', insights from single-species studies, pressure to conserve charismatic vertebrates, attempts to balance the integrity of the natural ecosystem with the benefits it is expected to provide to the local community ('community conservation'), and occasional adaptive management (Walters & Holling 1990; Kremen 2005). While we do not suggest that food web theory should replace any of these approaches, we do make a plea for it to be more widely considered in plans for the management of national parks and the biodiversity they seek to preserve. A considerable urgency drives attempts to assemble data for webs from large undisturbed and pristine ecosystems such as tropical grasslands, forests, and coral reefs. Moreover, if the principal arguments for conserving natural ecosystems are based purely on economic benefits (Norton 1986; Lovejoy 1996; Daily *et al.* 1997, 2000), then we need to develop a theory that links ecosystem services to food-web structure.

To conclude, we identify some priorities for food-web research that apply to the conservation of biological diversity.

(i) It is time to move ecosystem-based management from a catch phrase to a sound science. Network theory is a logical first step towards a theory of ecosystem-based management. Studies from food webs should provide insights into how to conserve assemblages of species needed to maintain the emergent ecosystem-level properties of a system and, in particular, continue to provide the economic goods and services. Once we can map ecosystem services onto trophic levels, food-web theory can help explain how species extinctions, or declines in abundance, lead to reductions in the rate of delivery of economic services (Kareiva *et al.* 2005; Nelson *et al.* 2005; Dobson *et al.* 2006, 2007).

(ii) A key area where food webs may inform ecosystem-based management is in the ocean. The repeated failures of single-species fisheries to sustain profitable harvest have led to an increased popularity of marine protected areas (Clark 1996; Allison *et al.* 1998; Hastings & Botsford 1999; Roberts *et al.* 2003; Hilborn *et al.* 2004). In such areas, fished species increase in abundance. But indirect effects are often common, depending on the ecological role of fished species. This synthesis suggests using ecological networks to identify and predict the multiple indirect effects that result from fishing.

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

(iii) Robustness is a key measure of secondary extinctions in food-web models. It is one of the most obvious metrics that food-web theory can provide to conservation biology. Topological studies of robustness can identify 'bottom-up' paths to secondary extinction, such as how loss of basal and intermediate species leads to the secondary extinction of species dependent upon these for food and other resources (nest sites, pollination, parasites; Dunne *et al.* 2002). Such studies describe how the architecture of the web determines its resilience to perturbations mediated by bottom-up processes. While this is a powerful tool, there is a need to develop mathematical mechanisms to examine how 'top-down' effects modify web structure as there is considerable empirical evidence for the importance of these top-down effects in natural systems. In particular, the detailed empirical studies of John Terborgh and his colleagues on the recently created islands in Lago Guri in Venezuela sharply illustrate the dominant effect that top-down effects have on food-web structure through their impact on the relative abundance of species on lower trophic levels (Terborgh *et al.* 2001; Lambert *et al.* 2003).

(iv) Static webs are typically the cumulative result of interactions in an arbitrary spatial and temporal scale. The last 3 years have seen an increasing emphasis on 'non-equilibrium' dynamics (e.g. McCann *et al.* 2005; McCann & Rooney 2009; Eveleigh *et al.* 2007). The topology of food webs in nature can change dramatically in time and space, as the result of fluctuations in the abundance of a keystone species and due to seasonal variation. A landscape theory of food webs would help to emphasize the role of mobility and adaptive behaviour in food-web stability (Rooney *et al.* 2008). Here, the challenge is to balance biological realism and tractability when considering the merits of static and dynamic approaches.

(v) Concerning dynamic approaches, we can ask how far we can move beyond multi-species Lotka-Volterra systems and linear extrapolations of these (Wilson *et al.* 2003). Modelling food webs using dynamical systems requires many species-specific parameters, such as the birth and death rate of each species, and the functional responses that describe consumer–resource interactions. The complete parametrization of real systems remains intractable. Allometric relations provide one way to reduce the dimensionality of parameter space in food web models (Brose *et al.* 2004). Other ways of modelling food webs have recently emerged, including agent-based models and simple stochastic models (similar to the birth–death processes popular for studying the neutral theory of biodiversity; Sole *et al.* 2002). Owing to the uncertainty in parameter values and functional forms, efforts to relate structure to dynamics should focus on pattern-oriented modelling to seek robust qualitative patterns.

(vi) Parasites are increasingly recognized as common constituents of ecological networks (Lafferty *et al.* 2006, 2008; Kuris *et al.* 2008). Are their roles different from those of free-living species? How do they affect the robustness of webs or the probability of secondary extinctions? Parasites tend to use a lower diversity of resources than free-living consumers. In addition, many have complex life cycles, making them dependent on species diversity. These factors make parasites particularly prone to bottom-up secondary extinctions. The extent to which parasites can contribute to top-down extinctions is difficult to determine from topological webs, but may be relatively unlikely, given results from various population models (McCallum & Dobson 1995). On one hand, parasites reduce robustness in a network due to their sensitivity to secondary extinction, on the other hand they may play a critical role in regulating abundance. However, few ecological networks include parasites thus we are unable, as yet, to generalize about their impacts. Given that parasitism is the most ubiquitous consumer strategy, most food webs are probably grossly inadequate representations of natural communities.

(vii) As mentioned in the introduction by May (2009), there is increasing interest in the insights that the structural properties of food webs can provide into other complex adaptive systems that have a network structure, for example, biochemical pathways in physiological systems and economic systems. The coupled, and often nested, pairs of fast and slow chains of dynamic interactions that seem increasingly important in stabilizing food-web networks have important parallels with the way national economies are organized and divided into rapidly traded short stocks, whose daily turnover is reported on the nightly news, and the long-term savings and loans of mortgages and pensions. If money markets do share similarities in their dynamic properties with food webs, then we should not be entirely surprised that financial markets become unstable when the long-term savings and loans are gambled by traders as short-term hedge funds. On a more optimistic note, the last decades have seen increased emphasis on the importance of recycling of used goods and their packaging. This uncannily echoes the evolution of the detritivores guilds that undertake crucial roles in the webs described by Olff *et al.* (2009). In a complementary fashion, a commodity such as oil drives the dynamics of many individual economic pathways. Oil acts as rainfall or sunlight in ecological systems. When oil is abundant, the system works quickly and efficiently; furthermore, it creates additional economic inputs through jobs in exploitation and distribution. In contrast, when oil is scarce, competition increases among all parts of the 'economic food web'; this significantly reduces the elasticity of the system and produces levels of economic and social disruption, which often harshly illustrate how distant nodes of the web are intimately coupled.

Ultimately, food webs represent deep problems in applied mathematics that involve many different populations interacting with each other at a variety of different rates on different spatial scales. We believe that these problems are as deep and as challenging as any in physics or pure mathematics. When Darwin stared at the tangled bank, he began to appreciate the complexity of this challenge. Today he would be shocked at the urgency that we need to bring into solving the many facets of this problem and applying the insights gained into the conservation of biological diversity. The time available for many species may be less than the time since Darwin published the 'Origin'.

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