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Effects of dynamics on ecological networks

Hannah M. Lewis*, Richard Law

Biology Department, University of York, PO Box 373, York Y010 5YW, UK

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Abstract

Ecological food webs define the feeding patterns of interacting species. The architecture of such networks may be affected by dynamical processes operating within them, ultimately influencing the capacity of the networks to persist. As yet relatively little is known about these effects. We compared the architecture of ecological networks with a fixed number of species, constructed in four contrasting ways: (I) topological networks, which required only that species had prey to eat; (II) persistent networks, in which species had also to persist under a simple model of population dynamics; (III) assembled networks, built up by sequential addition of species with dynamical persistence at each step in the sequence; (IV) evolved networks where, in addition to dynamical persistence, body size of species was determined by a simple mutation-selection process. Dynamics had fundamental effects on architecture, the networks of classes II, III and IV being restricted to a small number of trophic levels, in contrast to the non-dynamic, topological class I networks. Class III assembled networks tended to have fewer trophic levels and a more pyramidal biomass distribution than networks of classes II and IV. In evolved class IV networks, the smallest consumers converged to similar body sizes, whereas larger consumers evolved more slowly and did not show such convergence. The results indicate that dynamics affect the architecture of food webs, and that assumptions about simultaneous arrival, sequential arrival and evolution lead to different outcomes. Sequential assembly was shown to have a special property of finding rare sets of persistent species in a small number of steps, suggesting that the rarity of stable communities is not a serious problem in the development of complex communities.

Keywords: Assembly; Evolution; Food web; Network

1. Introduction

Food webs are often envisaged as networks in which the nodes are species (or 'trophic species'), and the links between nodes represent the feeding relations of consumers and their prey. Network structure determines the dynamics in the sense that it defines the feeding links between species which drive the processes of birth and death. Yet the structure is also determined by the dynamics, because nodes appear when species enter the network, and disappear when species, unsuccessful in this changing milieu, go to extinction.

This coupling of structure with dynamics could potentially have profound consequences on the architecture of ecological networks, and ultimately on the overall persistence of ecological communities in a changing world. For instance, in some classes of network, links become concentrated around hubs (Watts and Strogatz, 1998), and 'small-world' properties (Milgram, 1967) emerge. Such networks are thought to be relatively robust, because removal of a node, on the average, has little effect on the network as a whole (Albert et al., 2000). Yet, in ecological networks, interactions among species with similar feeding habits could well lead to competitive exclusion of similar species (Gause, 1934). In these circumstances, hubs would be relatively scarce and ecological networks relatively prone to collapse when species are removed.

As yet rather little is known about the effects of dynamics on the architecture of ecological networks. Early work on stability of random Jacobian matrices suggested that strongly connected complex ecological networks should simply not occur (May, 1972). But real ecological networks are often complex and also not well described by random matrices; theorists have therefore searched for biological properties which could help to account for their

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*Corresponding author. Tel.: +44 1904 328557; fax: +44 1904 8505.
E-mail address: hml103@york.ac.uk (H.M. Lewis).

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existence. Such properties include omnivorous links within webs which shorten the length of food chains, decreasing return times to equilibrium (Pimm and Lawton, 1977) and making chaotic dynamics less likely (Fussman and Heber, 2002; Williams and Martinez, 2004). Weak links between species are another possible mechanism (McCann et al., 1998; Emmerson and Yearsley, 2004), as are functional responses of predators which reduce feeding on rare types of prey (Brose et al., 2003; Kondoh, 2003). The bioenergetics of species with different body sizes as they feed on one another within webs can also contribute to the stability of complex webs (Brose et al., 2006; Jonsson and Ebenman, 1998).

Work of the kind cited above often starts from an assumed network architecture, and considers the dynamical assumptions which are needed to enable it, or some subset of it, to persist. An alternative approach is to think of network architecture as an emergent feature of processes operating within the network. Such processes may simply be rules (without dynamics) about what eats what, as in the cascade model (Cohen et al., 1990), the niche model (Williams and Martinez, 2000), and their derivatives (Beckerman et al., 2006; Stouffer et al., 2005). Alternatively the processes could be dynamic as, for instance, in the sequential assembly of species (Drake, 1990; Law and Morton, 1996; Lockwood et al., 1997; Post and Pimm, 1983; Virgo et al., 2006), and in the evolutionary change of species driven by their interactions (Ackland and Gallagher, 2004; Caldarelli et al., 1998; Drossel et al., 2001; Ito and Ikegami, 2002; Loeuille and Loreau, 2005).

This paper investigates the emergent architecture of ecological networks put together in four contrasting ways with and without dynamics. All the networks were organised by species body size, as an instructive one-dimensional representation of the niche of species in many food webs (Woodward et al., 2005). Class I (*topological*) networks without dynamics were constructed simply using a rule that prey items would have to lie within a given range of body sizes relative to the consumer. The remaining classes had, in addition, a population-dynamical constraint, that the species should be able to persist in the network. Class II (*random persistent*) networks were obtained by simultaneous draws of species from a continuous distribution of body sizes. Class III (*assembled persistent*) networks were obtained by sequential addition of species of different body sizes. Class IV (*evolved persistent*) networks had a simple mutation-selection process which allowed body sizes to undergo genetic change through selection pressures set up by the feeding relations within the network. In comparing these classes of network, the focus was on broad differences in the ways in which communities are built, to complement lower-level questions on the detailed effects of formal assumptions about population dynamics.

The results show that dynamics affect architecture fundamentally in constraining the length of food chains and the number of trophic levels. Networks with different classes of dynamics had smaller but still significant differences in architecture. Changes due to evolution were relatively small, but there was evidence that body sizes of the smallest primary consumers tended to converge, whereas those of larger primary consumers could diverge. The results argue for the importance of taking into account effects of dynamics on architecture of networks.

2. Methods: construction and analysis of networks

2.1. General

In order of increasing constraints on the network classes, the four classes of networks were based on: (I) feeding relations; (II) I + population dynamics; (III) II + sequential assembly; (IV) II + evolution within species. The methods by which these four classes were built are described in the following subsections.

The guiding property used in constructing the networks was adult body mass, denoted w_i for species i. Body size was chosen because it often plays an important part in the feeding relations of species (Peters, 1983; Woodward et al., 2005), and also because there is a well-established relationship between body size and metabolic rate (Brown et al., 2004) which can be used to scale the rate terms in ecological dynamics (Law and Morton, 1996; Loeuille and Loreau, 2005; Virgo et al., 2006; Yodzis and Innes, 1992). In addition, by making body size explicit in the dynamics, the flow of biomass through the network itself becomes explicit, ensuring that the network is energetically permissible (Virgo et al., 2006; Yodzis and Innes, 1992). Body size is also a good candidate as a trait for studying the evolution of networks, because of the tendency of predators to be selective in their choice of prey size (Loeuille and Loreau, 2005).

In real ecosystems, body sizes vary over many orders of magnitude (e.g. Cohen et al., 2003). We therefore used a uniform distribution of $\log_{10}(w_i)$ over a range from 0 to 10 from which to draw log body sizes of consumer species independently at random. Each network was given seven consumer species, together with two basal species with fixed body sizes $w_1 = 1$, $w_2 = 10$; the basal species provided an input of energy on which to build the web. The control on the number of species ensured that any differences between classes were a direct consequence of the method of constructing the network, not confounded by variation in numbers of species. The upper limit of nine species was needed because random persistent networks with more species than this were rare, and the search for them exceeded the computational resources available, especially in conjunction with evolution.

Fifty replicates of each class of network were constructed. A number of properties of each network were measured (see Appendix) and, using these measures, the four classes of network were compared. Statistical significance of differences between the network classes was carried out in two steps. First, exploratory principal components