MATTERS ARISING

Bounds on food web connectance

REJMÁNEK AND STARÝ[1] have shown that the product of the number of species in a community (m) and the proportion of possible interactions (C) is a constant; that is, their relationship is hyperbolic. Though the authors present this as only an empirical result it is consistent with May's[2] result derived from considerations of model stability. However, an alternative, perhaps simpler explanation suffices. Suppose that each species in a community has a number of predator and prey species independent of the number of species in the community. The number of interactions in the system scales in proportion to the number of species in the system. However, the potential number of interactions scales as $m(m-1)$, if we exclude intraspecific effects. Thus, the connectance scales as $1/(m-1)$ which, for large m will be indistinguishable from the result predicted by May[2]. Such hyperbolic relationships between species number and connectance are apparent in a number of collections of food webs[3,4] though Rejámanek and Starý's data are unique in being collected by the same authors on comparable systems.

Although I agree that stability constraints make interesting predictions about food web design[5-7], many of which are supported by data in the real world[4-7], hyperbolic relationships between C and m must be considered ambiguous: a constant number of predators and prey per species might be caused by various factors other than system stability.

The webs shown in Fig. 1 of ref. 1 are quite remarkable in that they lack species that feed on more than one trophic level (omnivores). Omnivores average one per top predator in food webs dominated by vertebrates and considerably more in webs composed of insects, their parasitoids and hyperparasitoids[4]. The absence of omnivores may be a result of omitting hyperparasitoids (which are highly omnivorous), and (or) placing emphasis on the prey's predators, rather than all the prey of a particular predator. Considering only a species' predators gives source webs, in Cohen's[3] terminology, considering all the prey gives sink webs. Cohen's single source web is also unusually simple[4,7]. If omissions have been made they will reduce the connectance of the webs.

Counting interactions directly between species that share the same food supply implies competition over and above that for these shared resources. Even intraspecific interference appears unusual in insects, though data are few[8]. Adding connections in this way will increase the apparent connectance.

Finally, I must caution the use of May's inequality for the kind of data discussed here. May's result that mC should be less than one divided by the squared interaction strength comes from the application of the semicircular law[9,10]. Assuming a number of features which, at best, are only approximated by insect population dynamics, one obtains this result: a semicircle describes the frequency distribution of the real parts of all the eigenvalues. The semicircle is centred on the average of the self-limiting terms in the system. May assumed all the self-limiting terms to be unity and so unity appears in the numerator of the inequality. This is probably appropriate for communities composed entirely of resource limited competitors, but does not seem reasonable for food webs. Here, only species at the base of the web are likely to suffer external resource limitation[11], though the phenomenon of 'pseudo-interference' in insect parasitoid systems will add more self-limiting terms[12,13]. In short, if connectance were to be restricted by stability considerations, one might expect the limit to be related to the number of externally resource limited species, and for this number to vary between systems.

I thank Post et al.[14] for a discussion on this last point.

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1. Rejmanek, M. & Starý, P. *Nature* **280**, 311–313 (1979).
2. May, R. M. *Nature* **238**, 413–414 (1972).
3. Cohen, J. E. *Food Webs and Niche Space* (Princeton University Press, 1978).
4. Pimm, S. L. *Ecology* (in the press).
5. Pimm, S. L. *Theor. Pop. Biol.* **16**, 144–158 (1979).
6. Pimm, S. L. & Lawton, J. H. *Nature* **268**, 329–331 (1977).
7. Pimm, S. L. & Lawton, J. H. *Nature* **275**, 542–544 (1978).
8. Whitham, T. G. *Nature* **279**, 324–325 (1979).
9. Mehta, M. L. *Random Matrices* (Academic, New York, 1967).
10. Wigner, E. O. *Proc. fourth Can. Math. Congr.*, Toronto, 174-184 (1959).
11. Lawton, J. H. & Pimm, S. L. *Nature* **272**, 189–190 (1978).
12. Free, C. A., Beddington, J. R. & Lawton, J. H. *J. Anim. Ecol.* **46**, 543–554 (1977).
13. Hassell, M. P. *Arthropod Predator-Prey Systems* (Princeton University Press, 1979).
14. Post, W. M., Shugart, H. H. & DeAngelis, D. L. *Oak Ridge natn. Lab. Tech. Mem.* 6475 (1978).

REJMÁNEK AND STARÝ REPLY — Pimm is right to suppose that the number of predators and prey per species may be independent of the number of species in the community (or, more precisely, there is a constant mean number of edges per vertex in diagrams of food webs). Unfortunately, this fact can hardly be viewed as an attribute of species *per se*. At the moment, dynamical community constraints seem to provide a more plausible explanation of why mC is constant.

In his discussion Pimm repeats in more words what we said in our last sentence[1], and we agree with him. Only the introduction of hyperparasitoids of the genus *Dendrocerus* (Hymenoptera, Ceraphronoidea) and predators of the family Syrphidae (Diptera) into our[1] plant–aphid–parasitoid food webs raises the value of mC to a figure comparable to the mean for Cohen's web collection. On the basis of data available to us[2], the mC product for Cohen's 'community' and 'sink' food webs exhibited mean values of 4.21 and 5.29, respectively.

Incidentally, hyperparasitoids of aphids are rarely omnivorous[3-7]. A high proportion of omnivorous species seems to be typical of inherently unstable communities such as inhabitants of oak galls[8].

Pimm's most important point is the question of the number of self-limited species in real food webs. According to him, diagonal elements of interaction matrices should be zero for all consumer species. The importance of the number of externally resource limited species for stability of such matrices has been stressed by Saunders[9]. We agree that self-regulation of consumer species is rather rare in nature and only scattered evidence[10-13] supports May's[14] assumption of self-regulation at all trophic levels. The constant value $a_{ii} = -1$ is, of course, artificial and has been chosen by May to set a time scale for damping time. Some increasing probability density function on the interval $\langle -1, 0 \rangle$ seems to be more realistic. This implies shifting the critical values for stability in May's model to lower 'tolerable' connectance. But most of the links in food web diagrams are in no way density dependent or controlling[15]. Then, an increasing number of species does not necessarily cause a decrease in the probability that the interaction matrix will be stable (resilent in the sense of Harrison[16]): the main point of our[1] letter.

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1. Rejmánek, M. & Starý, P. *Nature* **280**, 311–313 (1979).
2. MacDonald, N. J. *J. theor. Biol.* (in the press).
3. Evenhuis, H. H. *Entomophaga* **9**, 227–231 (1964).
4. Takada, H. *Insecta Matsum.* N.S. **2**, 1–76 (1973).
5. Starý, P. *Acta ent. bohemoslov.* **74**, 1–9 (1974).
6. Askew, R. R. *Parasitic Insects* (Heinemann, London, 1971).
7. Clausen, C. P. *Entomophagous Insects* (Hafner, New York, 1962).
8. Askew, R. R. *Trans. Soc. Br. Ent.* **14**, 237–268 (1961).
9. Saunders, P. T. *Nature* **272**, 189 (1978).
10. Way, M. J. & Cammel, M. E. *Animal Populations in Relation to their Food Resources* (ed. Watson, A.) 229–247 (Blackwell, Oxford, 1970).
11. Kluijver, H. H. *Ardea* **39**, 1–135 (1951).

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