

parasitised by another parasitoid. The existence of this exploitative competition, which has been reported for many parasitoids^{4,7}, implies that higher order interactions are common in parasitoid communities. However, higher order terms violate an assumption of the stability analysis.

If Lyapunov stability is a relevant feature of communities and extinction of some member(s) of each community is not imminent, there are several explanations for the observed discrepancy. Perhaps stable solutions exist, but have not been discerned, as randomly selected parameter values do not exhaust all possible combinations⁸, and the use of unequal constraints for different trophic levels prohibits tests of qualitative instability. Natural selection may drive a community towards a restricted region of parameter space where mathematical stability is realised⁹.

An alternative explanation is that the community models are inadequate. Coincident with Pimm and Lawton's predictions, the instability of these webs is apparently the result of high connectance (percentage of non-zero elements in the interaction matrix), reflecting the presence of many omnivores. In fact, both of Askew's webs include omnivores whose alternate prey occupy widely separated trophic levels. This is the most destabilising form of omnivory according to Pimm and Lawton. If these webs are in fact stable, perhaps the constraints on selection of interaction magnitudes are biologically unrealistic, as the other stability parameters (connectance, number of species) are observed quantities. It has been demonstrated that as the range of constraints is narrowed, implying lower interaction intensities, the probability of a random community exhibiting stability increases. The host switching of many parasitoids and the concomitant unequal use of alternate hosts suggests that a narrower range of constraints should be used for some of the parasitoid-host interactions.

The problems associated with the community models may involve more than just the determination of actual interaction intensities and their linearity. Two assumptions underly the models and the resultant stability analyses. First, communities are considered to be definable closed systems uninfluenced by immigration and chance extinction. However, real communities are dynamic entities. The delineation of ecologically meaningful boundaries of a community can be critical to stability analysis as some unstable communities are comprised of several stable subunits¹⁰. Furthermore, Levin¹¹ has demonstrated that immigration and spatial heterogeneity can profoundly influence community stability. The second assumption is that the interactions we are attempting to estimate, competition or predation, are responsible

for both the population dynamics of the species comprising the community and its organisation. Many predators, particularly parasitoids, can greatly influence the abundance of their prey as evidenced by successful implementation of biological control, but their role in community organisation is less clear. Similarly, the role of competition in structuring communities and controlling species abundances is a hotly contested issue^{12,13}. Therefore, in light of the current lack of understanding of the determinants of community organisation, I question the predictive value of community modelling and mathematical stability analyses.

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LAWTON AND PIMM REPLY—

Auerbach has overzealously applied an extremely simple model; Lotka–Volterra equations do no more than capture the shadow of real biological interactions. We used such models to generate qualitative predictions¹, and deem it extremely unwise to attempt more quantitative fits to real webs. However, this does not mean that our hypotheses cannot be tested.

Our main qualitative prediction was that omnivory has a destabilising influence on food webs, the more so when predators are bigger and rarer than their prey, and have a large *per capita* effect on the things they eat. We were deliberately cautious in assessing this prediction, noting simply that it was 'encouraging' to find very complex webs in the real world in exactly those situations predicted by the models, that is amongst insect host–parasitoid interactions. More detailed analyses confirm that insect food webs do have significantly more omnivory than other webs². Indeed none of several interesting qualitative predictions yielded by simple Lotka–Volterra models^{3,4} are refuted by data from real food webs². To test our hypotheses further, we would prefer to see whether these qualitative predictions still hold when the major assumptions of the models are changed, rather than try to force unmodified Lotka–Volterra equations beyond their sensible limits. For example, if incorporating spatial heterogeneity reverses our predictions (making

omnivory easier to achieve in non-parasitoid than parasitoid webs), then our results are a nonsense. We doubt whether any of the refinements listed by Auerbach will have this effect.

Far from refuting our models, Auerbach's analysis confirms our conclusion that omnivory is destabilising: it is much easier to find stable solutions for simple webs than it is for complex ones. At present, we see no evidence for claiming that the majority of persistent natural populations are best described by model analogues that are inherently unstable^{5,6}. However, the detail needed to stabilise the models depends on the nature and rigour of the questions being asked. Auerbach suggests several possible reasons why his Lotka–Volterra models of real food webs are always unstable. Undoubtedly higher order interactions^{7,8} (which do not violate the assumptions of a local stability analysis, but make non-equilibrium behaviour difficult to predict), the precise choice of parameter values (we put webs into the correct relative ranking: the numbers themselves were guessed, not measured, and may well have been wrong in detail?) and spatial heterogeneity are all important. The effects of spatial heterogeneity, in particular, must be incorporated before models can accurately predict observed levels of host depression by parasitoids⁹. (For a wide range of models of varying levels of complexity, yielding insights with different degrees of rigour, see ref. 10.)

However, Auerbach's note is valuable in drawing attention to biological details that must be important in determining the fine structure of food webs. Viewing webs as static entities with fixed links is no more than a crude beginning^{11,12}. The concept¹³ of webs 'resonating' between different configurations, each of low complexity, may well provide a valuable theoretical starting point for more sophisticated analyses.

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