NEWS AND VIEWS

A cycling index for ecosystems

fom Robert M. May

I have heard it said that the River Thames passes through two people on its way to the sea. While I am sure this is an extravagant exaggeration, such recycling is typical of the flow of nutrients in many ecosystems.

Finn[1-4] and others have presented a formal scheme for characterizing the patterns of flow of energy or nutrients through a complex ecosystem. In particular, Finn[1] has shown how to compute a 'cycling index', which gives a quantitative measure of the extent to which flows recirculate within the system. This cycling index is the fraction of the total flow through the system that derives from cycling, expressed as a ratio to the fraction of the total that derives from flow straight through the system. Thus defined, the cycling index can clearly range from zero (no recycling anywhere in the system) to an arbitrarily large number (recycling overwhelming direct flow).

As derived by Finn and co-workers, these concepts apply to conservative systems at equilibrium, such that the books balance for overall inflows versus overall outflows. Finn observes, however, that the methodology may be extended to nonsteady systems. The actual meaning of the 'compartments' that make up the system can vary greatly (trophic levels, species, individuals); although this certainly bears on the interpretation of results, it makes essentially no difference to the formalism.

Finn has analysed the cycling of energy in several ecosystems[1,2]. One example is part of a marine ecosystem (exhibiting marine coprophagy) and has four compartments[5,6]: the shrimp *Callianassa major*, the faeces of *C. major* and associated bacteria, coprophagous benthic fauna, and the faeces of the benthic fauna and associated bacteria. Here the cycling index, deriving from recycling between the third and fourth compartments, is [1] 0.24. The second example describes energy flow in the Cone Spring ecosystem[7], and has components for primary producers, detritus, bacteria associated with the detritus, detritus

feeders and carnivores. Here the cycling index is[1] 0.16. The third example draws on the extensive studies of the Hubbard Brook ecosystem[8,9]. Here there are essentially no energy loops, whence[2] the cycling index is zero.

Insofar as one can generalize from these three examples, it seems that energy can be recycled to a small but significant extent. Such recycling of energy is not in conflict with thermodynamic principles (energy, of course, cannot be degraded more than once), but arises because living systems can 'use' energy without degrading it. This is the case, for example, with the energy associated with structural or storage elements (such as cellulose, proteins or fats), which can either be catabolized or be used again as structural elements on transfer to the next compartment.

Finn[2] has also analysed the model of Likens and co-workers[8] for the Hubbard Brook ecosystem, to estimate the patterns whereby various nutrients flow from the above-ground biomass through the below-ground biomass and the forest floor to the mineral soil and the available nutrient pools. The cycling indices suggest significant differences in the degree of recycling, with the elements K, Na, N, Ca, P, Mg and S having indices around 0.83, 0.76, 0.76, 0.62, 0.60, 0.59 and 0.51, respectively. Finn[2] comments that "this order does not appear to relate to whether or not the system is gaining or losing a particular nutrient. Hubbard Brook is accumulating N, S, and P and losing Ca, Na, Mg, and K". Notice that the cations (K, Na, Ca, Mg) rank in strict order of atomic size and charge, which determines mobility (the so-called 'lyotropic series'). Of these seven elements, N and P are probably limiting, K, Ca, Mg and S are essential but nonlimiting, while Na is neither essential nor limiting (for plants). It is therefore a bit surprising that Na is recycled to such an extent at Hubbard Brook; Finn[10] has shown that Na cycling indices can be very small in other forest systems.

For Edmisten's[11] model of a tropical rain forest, Finn[1] finds the cycling index for N to be 1.78. This value, more than

double the 0.76 for N in the temperate Hubbard Brook forest, accords with the conventional wisdom about greater recycling of nutrients in tropical forests.

It is tempting to use Finn's cycling index in pursuit of other ecological generalities. We may, for example, expect to find that the cycling index typically increases as succession advances. Conversely, given that many kinds of pollution and other man-induced disturbances of mature ecosystems have effects akin to precipitating the system back into early successional patterns[12], it may be that such perturbations are characterized by decreases in cycling indices. These are interesting speculations. They may even be taken to suggest that the cycling index could be a useful diagnostic in the design of environmental impact statements.

As Finn[2] himself has emphasized, however, "Flow measures do not take into account residence times or storages, but only the amounts of nutrients actually moving and the way in which they move. . . . all the different processes involved in nutrient cycling cannot be captured and quantified in a single index". The cycling index is an elegant construct, having both theoretical and practical significance; but when it comes to evaluating the impact of disturbances upon ecosystems, I would be wary of attempting to distill complex arrays of information about flow patterns into any such single number[13]. □

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