suspended in a relatively well-mixed environment, and retrieve their nutrients from a common pool (the dissolved phase in the illuminated layer of water at the surface of seas or lakes). Experimental ecologists rose to Hutchinson's challenge, and their microcosm studies with planktonic algae became a cornerstone in developing both experiment and theory.

The contradiction between competitive exclusion and species richness appeared less severe for higher plants, because they are more segregated in space — for example, deep-rooted and shallow-rooted species might draw the same nutrient from separate pools. Nevertheless, controlled competition experiments with higher plants have also shown strong tendencies towards competitive exclusion.

Tentative explanations of the seemingly paradoxical diversity of plant communities have invoked the absence of competition in natural ecosystems; temporal and spatial variability of environmental conditions; and coexistence based on different optimal ratios of limiting resources. The article by Huisman and Weissing[3] is a theoretical milestone merging the approaches based on variability and resource ratio.

The idea that diversity arises from spatial and temporal variability in the environment is based on the fact that competitive exclusion takes time, and that inferior competitors might find refuges in time or space. Such refuges could be sites or periods without competition or with reversed competitive hierarchies. The explanation has been formalized as the 'intermediate disturbance hypothesis'[5] (IDH), which predicts a peak in species richness at intermediate intensities and frequencies of disturbance, thought of as events leading to environmental variability.

Culture[6,7] and field[8] experiments with phytoplankton confirmed the IDH, showing greatest diversity at disturbance intervals of three to six days, equivalent to up to ten generation times of unicellular algae. Comparative analyses of field data also supported the hypothesis[9], although it proved difficult to quantify disturbance or environmental variability when it had not been imposed by the experimentalist, but rather consisted of changes in many potentially important controlling factors. All IDH-inspired studies have viewed disturbances as external to the community in question — for instance in the deepening of the surface-mixed layer of lakes and seas by wind and convective cooling. It was the implicit assumption that, with a constant supply of resources and constant physical conditions, primary-producer communities would approach a steady state, whereas oscillations or even chaotic dynamics were well known from models with several trophic levels.

The 'resource ratio hypothesis'[10] (RRH) took a quite different approach. Primary producers need essentially the same resources: light, carbon dioxide and mineral nutrients. However, they need them in different ratios. So resource supply might be balanced in a way that different species are limited by different resources and, thereby, coexist in perfect equilibrium at constant population densities. This was first shown by the coexistence of two diatoms with different optimal ratios of silicate and phosphate[11].

Further experiments with other combinations of algal strains from cultures or with naturally mixed assemblages of phytoplankton confirmed the stable two-species equilibrium based on two limiting resources. By extrapolation, it was thought that the same would happen if resource supply were balanced so that more than two resources were limiting — there was a commonly held belief that the number of coexisting species would equal the number of limiting resources. But this assumption was not tested experimentally or by modelling. Obviously, the RRH could not account for the full species richness of primary producers, because only a few resources (usually fewer than five) can become limiting in natural ecosystems.

This is the point where Huisman and Weissing[3] step in. They show, by numerical modelling, that the competition dynamics of systems with more than two limiting resources are fundamentally different from those with only two limiting resources. Within a wide range of parameter values, sustained oscillations or even chaotic dynamics of resource concentrations and of species' abundances are possible, even under constant resource supply and constant physical conditions. These oscillations or chaotic changes create the environmental variability needed for the persistence of more species than the limiting resources would seem to allow.

This does not imply that external disturbances are unimportant in nature. Everybody knows that they occur and research has shown that they can promote diversity. But Huisman and Weissing's model has shown that externally undisturbed plant communities can produce their own disturbances. Now it is up to the experimentalists to catch up with the modellers. ■

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Daedalus

Internal ecology

Last week Daedalus pointed out that a fetus in the womb will accept foreign tissue as part of itself, and will continue to accept that tissue in adulthood. So, he says, the way is open to creating mixed species — centaurs, griffins, sphinxes, unicorns and so on. To make a unicorn, for example, add a few rhinoceros cells to a horse fetus. The adult horse will then accept a rhino horn transplant. But surgery would probably work better on the fetuses. Fetal rhinoceros horn-bud tissue would be grafted onto the forehead of the fetal horse *in utero*. The growing fetus, with its greater capacity for repair and development, would probably solve the various compatibility problems better than a team of surgeons trying to marry up the inflexible adult tissues.

Biologists, not to mention owners of zoos, leisure parks and nature reserves, would be fascinated by the resulting chimaerae. Even the classical chimaera — part lion, part goat, and part snake — might be feasible. It would probably not breed true, or even at all, but would still be a biological triumph. Yet Daedalus has a more challenging goal — animal–plant chimaerae. Imagine, he says, a combined man and green plant. The plant would photosynthesize, taking in carbon dioxide and producing oxygen and glucose; the man would conduct the reverse reaction. He would also produce urea and other metabolites useful to the plant — which would thus act as an extra liver and kidney. Such a chimaera would be a most efficient self-contained ecosystem.

The problems are formidable. Even with immunocompatibility guaranteed, few plants could be genetically engineered to have a sap compatible with, or replaceable by, human blood. Even Daedalus is unlikely to create a man with real cauliflower ears. But a man with algae growing happily in his skin should be far more feasible. He would absorb sunlight, and feed, breathe and excrete internally, at least to a useful degree. The first 'little green men' will worry the flying-saucer cultists, and could arouse novel colour prejudice. But, with their wonderful ecological economy, they may be the way forward for humanity. Besides, with a little cunning plant-metabolic transfer, they could enjoy a constant internal supply of nicotine, caffeine, cocaine or cannabinoids. **David Jones**