

carcinomas. In none of these cases is it obvious which chromosomes to examine. Chromosome preparations from solid tumours are notoriously difficult to analyse and in few cases other than retinoblastoma and Wilms' tumour has a very specific alteration been seen. At present, therefore, either clues must come from the inconsistent, but perhaps significant, chromosome changes in these tumours, or enough probes must be used to cover all the chromosomes. Once the location of any recessive mutations is found, attempts to identify the normal gene products by molecular genetic analysis will follow. In the case of inherited tumours,

genetic counselling will be greatly helped by the ability to determine which parental chromosome carries the mutant allele. □

1. Land, H., Parada L.F. & Weinberg, R.A. *Science* **222**, 771 (1983).
2. Yunis, J.J. *Science* **221**, 227 (1983).
3. Cavenee, W.K. *et al. Nature* **305**, 779 (1983).
4. Benedict, W.F. *et al. Science* **219**, 973 (1983).
5. Koufos, A. *et al. Nature* **309**, 170 (1984).
6. Orkin, S.H., Goldman, D.S. & Sallen, S.E. *Nature* **309**, 172 (1984).
7. Reeve, A.E. *et al. Nature* **309**, 174 (1984).
8. Fearon, E.R. *et al. Nature* **309**, 176 (1984).
9. Knudson, A.G. *Proc. natn. Acad. Sci. U.S.A.* **68**, 820 (1971).
10. Junien, C., Huerre, C., Despoisses, S., Gilgenkrantz, S. & Lenoir, G. *Cytogenet. Cell Genet.* **37**, 503 (1984).

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Ecology

Different ways of being a mouse

from John H. Lawton

WHY are some assemblages of animals and plants richer in species than others? Answers to this question take various guises, but usually hinge on G.F. Gause's venerable 'competition exclusion principle'. In Gause's own words, "as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kind of foods and modes of life in which it has an advantage over its competitor"¹. The possibility that major differences in species richness can be solely accounted for by niche differences between species has tended to be played down, particularly for plant communities. After all, for growth every plant requires water, light, space and three or four key limiting nutrients — not leaving much scope for niche preference. In fact, this commonsense view is almost certainly wrong, as David Tilman has recently pointed out for plants²; on page 150 of this issue of *Nature*, Abramsky and Rosenzweig make a similar claim for desert rodents³.

For Gause to be right, there must be 'more ways of being different' in species-rich than in species-poor assemblages. Simple mathematical models of competing species show, however, that as the number of competitors, n , increases, $2(n-1)$ inequalities must be satisfied before stable coexistence is possible⁴. In biological terms this means that as n increases, it gets harder and harder to find sufficient differences between species to maintain coexistence. Three theoretical possibilities bypass the constraints of this simple model and have the potential to explain species-rich systems without competitive exclusion. First, competition for limiting resources might be prevented by the impact of predation⁵⁻⁷. Second, if, instead of living in a spatially uniform world, as simple models assume, potential competitors have independently aggregated distributions, competitive exclusion becomes extremely

unlikely⁸. Third, if real populations are not in the stable equilibrium frequently assumed by modellers, competitive exclusion can be prevented by repeated environmental disturbances⁹.

Perhaps because of their relative novelty, these and related ideas tended to hog the limelight in recent years; there did not, before Tilman, seem to be much new to say about Gause's 'ways of being different'. Tilman uses graphical, rather than mathematical, models to explore coexistence mechanisms in sets of species, each differing in its sensitivity to the ratio of two limiting resources. Contrary to received wisdom, his results demonstrate that niche diversification and coexistence are theoretically possible for species-rich assemblages competing for just two essential limiting resources. Moreover, the models lead to some very clear predictions. For example, they suggest that a graph of species richness against total supply of resources should be humped, rising rapidly to a peak in relatively resource-poor habitats, and thereafter slowly declining with increasing supply of resources.

Tilman's arguments mainly concern plants competing for nutrients — nitrates and phosphates, for example. Abramsky and Rosenzweig³ now find that the number of coexisting rodent species in two different desert habitats, one rocky and the other sandy, first rises quickly, then falls more slowly along a gradient of increasing rainfall, exactly as predicted by Tilman.

As with all interesting observations, the data generate more questions than answers. First, if Tilman's explanation holds, what are the two types of resources partitioned by the mice? They are unlikely to be anything as simple as concentrations of nitrates and phosphates. Second, an important assumption underpinning Tilman's predictions is that the two resources cannot be substituted — a deficiency of a cannot be made good by using more of b — and that they are independently and patchily

distributed across the habitat. Basically, this permits each plant species to specialize on a different ratio of the two resources, and for each species to take those special requirements from different microhabitats in a spatially heterogeneous world. As Tilman points out, the mobility of animals, combined with a tendency for their resources to be able to be nutritionally substituted — a deficiency of a can be made up by eating more of b — is likely to undermine both his assumptions and his predictions. In sum, if mice use resources that can be substituted and/or forage in many different places, Abramsky and Rosenzweig's species-density changes cannot be due to the mechanisms postulated by Tilman. But if the resources used by the mice can be only partially substituted, and if each species is a microhabitat specialist, as seems possible³, then something akin to Tilman's model may well be operating in this system.

Of course, the data could also be explained by entirely different mechanisms. A simple possibility is that rodent species-richness is determined by plant species-richness, with only the plants behaving as Tilman suggested. An alternative possibility, discussed by Abramsky and Rosenzweig, is that the patterns are driven by environmental disturbances (negating another of Tilman's crucial assumptions, namely that populations exist close to equilibrium). It should be noted that Connell's hypothesis⁹ also predicts that species-densities will first rise and then fall along a gradient of decreasing environmental disturbance.

Obviously, more needs to be known both about the mice and about their habitats. The results of further research are likely to be particularly interesting in two ways. First, the relative importance of equilibrium and non-equilibrium dynamics in community ecology is far from clear^{10,11}. Second, the importance of habitat heterogeneity in determining the outcome of interspecific competition in the field deserves more attention^{2,8,12}. Hence a clearer understanding of the mechanisms underpinning the patterns documented by Abramsky and Rosenzweig could have implications for community ecology extending well beyond the somewhat esoteric question of how many different ways there are of being a mouse. □

1. Gause, G.F. *The Struggle for Existence* (Baltimore, 1934).
2. Tilman, D. *Resource Competition and Community Structure* (Princeton University Press, 1982).
3. Abramsky, Z. & Rosenzweig, M.L. *Nature* **308**, 150 (1984).
4. Strobeck, C. *Ecology* **54**, 650 (1973).
5. Paine, R.T. *Am. Nat.* **100**, 65 (1966).
6. Janzen, D.H. *Am. Nat.* **104**, 501 (1970).
7. Lawton, J.H. & Strong D.R. Jr *Am. Nat.* **118**, 317 (1981).
8. Atkinson, W.D. & Shorrocks, B. *J. anim. Ecol.* **50**, 461 (1981).
9. Connell, J.H. *Science* **199**, 1302 (1978).
10. Price, P.W. *Evolutionary Biology of Parasites* (Princeton University Press, 1980).
11. Price, P.W., Slobodkinoff, C.N. & Gaud, W.S. *A New Ecology: Novel Approaches to Interactive Systems* (Wiley, New York, 1984).
12. Hassell, M.P. *Oikos* **35**, 150 (1980).

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