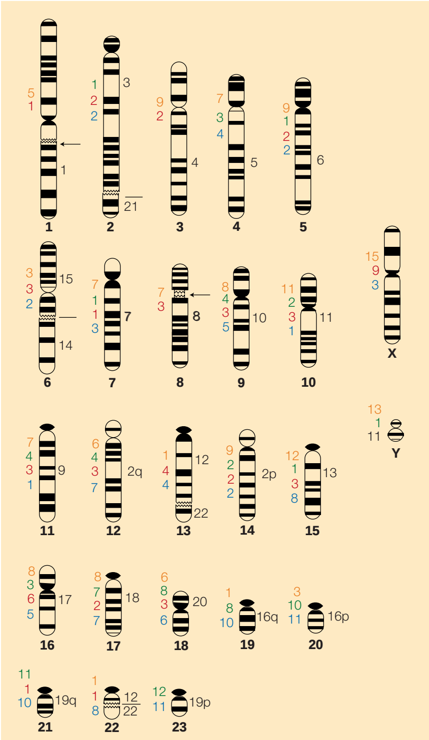

Figure 1 **Reconstruction of the ancestral genome of living primates, depicted as conserved and rearranged human chromosomes[1–3]. To the right of each ancestral primate chromosome is the human chromosome number. To the left are: the number of primate species (out of 15) in which the chromosome synteny is conserved as it occurs in the ancestral primate genome (yellow); the number, out of 15, in which a whole chromosome homology block is retained, but attached to another chromosomal piece (green); and the same counts for 11 outgroup species including pig, cow, muntjac, dolphin, cat, seal, mink, horse and shrew[1–3] (red and blue). Arrows indicate proposed separations of human chromosomes postulated by Müller *et al.*[3] (chromosome 1) and Haig[1] (chromosome 8), which are unique to these authors.**

ing to distinct primate families and genera. But, for most species, fewer than 20 rearrangements are enough to re-assort modern genomes to that of the primate ancestor. At least 12 of the ancestral primate chromosomes are also found intact in the genomes of humans, cats, seals, cows and shrews. So the ancestral primate genome must differ only marginally from the ancestral mammalian genome, which pre-dates the origins of carnivores, primates and artiodactyls.

The new papers also affirm that neither the positions of chromosomal breaks nor the evolutionary rate of rearrangements in primates seem to follow predictable patterns. Breaks can occur in many positions on any chromosome. Many species of primate, such as humans, great apes and Old World monkeys, show a remarkably slow rate of genome exchange — on the order of one or two exchanges every ten million years. By contrast, other species (gibbons, owl monkeys and lemurs, for example) globally reorganize their genomes, with two to four times more rearrangement relative to organization of the ancestral genome. A similar rate dichotomy is apparent in other mammalian orders, where a slow/default rate seen in most lineages (such as cat, mink, shrew and pig) is punctuated by drastic genome shuffles in others (dogs, bears, rodents and bears)[7].

But there are limitations to what we can infer from comparative gene maps and chromosome painting. First, only a handful of mammalian species (human, mouse, rat, pig, goat, sheep, cow, cat and dog) have comparative maps with enough genes to allow their genomes to be compared[6,7]. Second, although chromosome painting (on which most of the primate analyses are based) allows whole genomes to be assessed, small segments can be overlooked because of weak DNA hybridization. Precision is improved with reciprocal painting[9–11], or when more closely related index species are used as probes[10,11]. Third, the order of the genes within homology segments was not considered in the primate assessment shown in Fig. 1. This means that an important class of chromosome exchanges, the interstitial inversions and translocations, is excluded. Comparative alignments of human gene order with ordered gene maps of non-primate species (goat and cat)[12,13] have uncovered two to three times more breaks than were revealed by chromosome painting.

Another hurdle is analytical — there is no consensus algorithm for tracking genomic exchanges. Assumptions about the randomness of genome exchanges are probably oversimplifications, and there may be favoured site changes that introduce confounding convergent changes to evolutionary interpretations. So far, little emphasis has been placed on discordant exchange rates among lineages, and for the different categories of exchange observed. Weighting of such characters in evolutionary analyses is an important consideration that needs theoretical and empirical input. Finally, the choice of species sampled could severely bias interpretations. Discrimination of shared-derived, as opposed to shared-ancestral arrangements, depends on how frequently they occur in the outgroups studied (Fig. 1). More is better in statistical terms, yet only a few species[6,7,9] in fewer than half of the mammalian orders have been assessed.

Powerful new genomic and gene-mapping technologies should overcome these limitations. The resolution of comparative genome mapping is approaching its highest power ever, allowing linear maps of index species to be aligned explicitly. The primates offer the first and most accurate look at the history of human genome organization, but certainly not the last. We'll soon have similar reconstruction among other mammalian orders[7] and even beyond, as previewed on page 411 of this issue[14], where the chicken gene map weighs in on a comparative genomics perspective. ■

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Ecology

Competition and coexistence

Ulrich Sommer

Early experimental and modelling work in community ecology[1] led to the principle of competitive exclusion. This states that, among two or more species of primary producer — that is, plants — competing for a shared resource, only the best competitor will survive[2]. The apparent contradiction between competitive exclusion and the species richness found in nature has been a long-standing enigma. Explanations of why strong competitors do not inevitably have a stranglehold have invoked environmental disturbance and the differing resource requirements of different species. On page 407 of this issue, however, Huisman and Weissing[3] present a way to reconcile the persistence of diversity with competitive exclusion in undisturbed ecosystems with few limiting resources.

The contradiction between the principle of competitive exclusion and the diversity of natural communities first became obvious for phytoplankton (Hutchinson's 'paradox of the plankton'[4]). Planktonic algae share the same potentially limiting resources (light, carbon dioxode and mineral nutrients, namely nitrogen, phosphorus, silicon, iron and possibly a few other trace elements), are 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**

The further Inventions of Daedalus (Oxford University Press), 148 past Daedalus columns expanded and illustrated, is now on sale. Special *Nature* offer: m.curtis@nature.com