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A world without competition

The Unified Neutral Theory of Biodiversity and Biogeography

by Stephen P. Hubbell

Princeton University Press: 2001. 448 pp.
 \$29.95, £19.95 (pbk); \$75, £52 (hbk)

Peter A. Abrams

During the past 50 years, physicists have sought a 'unified theory' from which all major categories of forces could be derived. Any physicist sufficiently intrigued by the title of Stephen Hubbell's book to wade through its pages will, however, come away disappointed. This will be partly a result of the constraints on achieving any generality and unification in the field of ecology, and partly because of the limitations of Hubbell's theory. Nevertheless, Hubbell's book contains many interesting ideas and intriguing new findings, and few practising ecologists will fail to get something out of it.

The 'unification' of the title refers to the fact that this theory seeks to predict both the number of species found in a community and the distribution of the relative abundances of those species. Hitherto, these two aspects of biological communities have been explained independently by most (but not all) theoretical biologists. The number of species and their distribution of abundances are clearly dependent on some of the same processes. An extinction reduces the number of species as well as removing one of the species previously in the category of least abundance. Nevertheless, the 'best' theory for species-abundance distributions might not effectively account for species number, or vice versa.

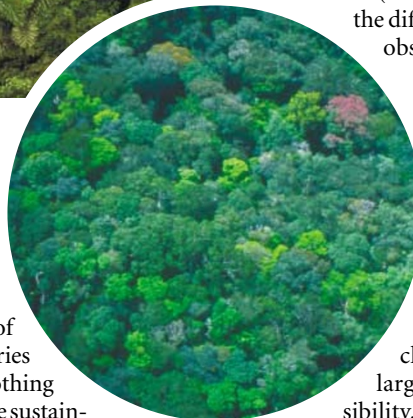
In any event, vast expanses of ecological endeavour are totally independent of these



Biodiversity: Hubbell's predictions are surprisingly accurate for tree species.

questions of species number and statistical distributions of abundance. A fisheries manager will find nothing here to help predict the sustainable harvest of cod, nor will an entomologist derive anything about the characteristics of an effective natural enemy of a devastating pest. The unification proposed by Hubbell has limited scope.

Attempts to construct unified theories have produced laws that, at least initially, appear to be universally applicable. Thus, our hypothetical physicist reader will be surprised to find that Hubbell's theory is based



on an assumption that the vast majority of ecologists believe to be almost universally false. He assumes that every individual in every species in a biological community is identical, and that the total abundance of all species is fixed. In his favoured version of the theory, each individual of each species has a low probability of mutating into a new species. All changes in distribution and abundance occur because of purely random variation in births, deaths, migration and speciation. This is what makes the theory 'neutral'.

Hubbell has long championed the idea that the many tree species in the tropical forests where he works coexist largely because they are competitively equivalent. Random changes in abundance occur slowly enough for speciation events to have replaced the rare, random extinctions. *The Unified Neutral Theory of Biodiversity and Biogeography* generalizes this idea and derives many consequences from the assumption that all individuals are equal. Unfortunately, decades of experiments studying hundreds of species pairs have identified no conclusive cases of competitive equivalence, so one would expect such an assumption to lead to nonsensical consequences.

The surprising thing about Hubbell's theory is that it is pretty accurate in its predictions of many attributes of ecological communities — particularly the distribution of abundances of tree species. On the other hand, this ability is perhaps not as surprising as it initially appears; the parameters determining the shape of this distribution — speciation rate and number of individuals in the set of connected communities — are largely immeasurable. Most of the fits are achieved by adjusting these parameters (or their product) to minimize the difference between theory and observation.

There are two main resolutions to the apparent contradiction of small-scale experiments and Hubbell's global theory: first, non-neutral theories would be capable of fitting the data at least equally well; second, the assumption of equality is close to correct. But Hubbell largely ignores the first possibility. And his arguments for

the second are not presented until the final 15 pages of the book, and I at least found them unconvincing. Graham Bell, another biologist who has recently analysed 'neutral' models, also favours the second alternative. However, work by Steinar Engen and collaborators indicates that alternative models are likely to be equally capable of fitting observed species-abundance relationships.

One of the likely consequences of Hubbell's and Bell's arguments is that there will probably be studies to resolve this issue in the near future. Theory must build on an understanding of simple cases and limiting assumptions, and Hubbell's deductions from 'neutral' assumptions have provided a rigorous basis for future work. At a time when books are often bland reviews of papers published many years before, this book has a high proportion of previously unpublished results and stimulating ideas. It is unlikely to be ignored. ■

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Fertility from a metabolic viewpoint

On Fertile Ground: A Natural History of Human Reproduction

by Peter T. Ellison
 Harvard University Press, 2001. 358 pp.
 £16.95, \$27.95

Roger V. Short

Peter Ellison is Professor of Anthropology and Dean of the Graduate School of Arts and Sciences at Harvard. He is best known for his exploitation of methods for measuring reproductive hormones in human saliva, thereby making it possible to carry out non-invasive studies of the reproductive endocrinology of people living in remote parts of the world, such as the Ituri rainforest in Central Africa or the mountains of Nepal. This book therefore describes some of his work on the fertility of traditional human societies.

Unfortunately, *On Fertile Ground: A Natural History of Human Reproduction* does not live up to its grandiose title; it would have been better called "Females, fatness and fertility", as this is its central theme. The opening chapters present a superficial (and sometimes incorrect) account of human reproduction, with strained analogies: "the area at the base of the brain called the hypothalamus and an associated bit of glandular tissue called the pituitary gland that hangs off the base of the brain like a tiny holiday ornament." It is excessively and unnecessarily North American in its outlook and citation of references. For example, pages are devoted to the bizarre and discredited views of Margie Profet, who postulated that menstruation was designed to cleanse a woman's reproductive tract of pathogens. Although Ellison cites references in the bibliography to important articles that completely demolish Profet's hypothesis, he never presents these counter-arguments in the text.

Another major failing of the book is the

almost complete lack of figures or diagrams to leaven a turgid text. There are repeated references to the important sex differences in the shape of the human pelvis: "the pubic bones at the front of the pelvis are proportionately larger in females, giving the top of the true pelvis, or pelvic inlet, a more circular and less heart-shaped outline, while the ischial bones and the sacrum at the bottom of the true pelvis, or pelvic outlet, have spread further apart, increasing the diameter of the outlet and making it more circular in form as well." Oh for an illustration! And it would have been interesting to have had some discussion about when and how this sexual dimorphism has developed.

Ellison devotes a major section of the book to breastfeeding. Unfortunately, there is no mention of the entero-mammary circulation, which supplies specific immunoglobulins in breast milk to counteract enteric infections in the baby. As diarrhoea is the single greatest killer of babies worldwide, its prevention is a vital piece of our natural history. There is no mention of the inhibitory peptide that accumulates in the alveoli of the mammary gland and turns off milk production if the milk is not removed, thereby making the mammary gland a unique supply-meets-demand organ. There is no mention of the fact that human nipple sensitivity increases greatly on the day of birth, or that in animals, each suckling bout sends afferent neural inputs to the hypothalamus, resulting in the central release of β -endorphin, the 'feel-good hormone', that depresses dopamine secretion and hence elevates prolactin.

Likewise, there is no mention of the fact that in animals, denervation of the teat immediately abolishes the inhibitory effects of lactation on ovarian activity. Instead, Ellison chooses to dismiss the results of P. W. Howie and A. S. McNeilly, who showed in the 1980s that suckling frequency and duration are unquestionably related to the duration of lactational amenorrhoea. In its place, he proposes a "strong alternative hypothesis,"

Fertility symbol: fatness and fecundity have long been linked in the human imagination.

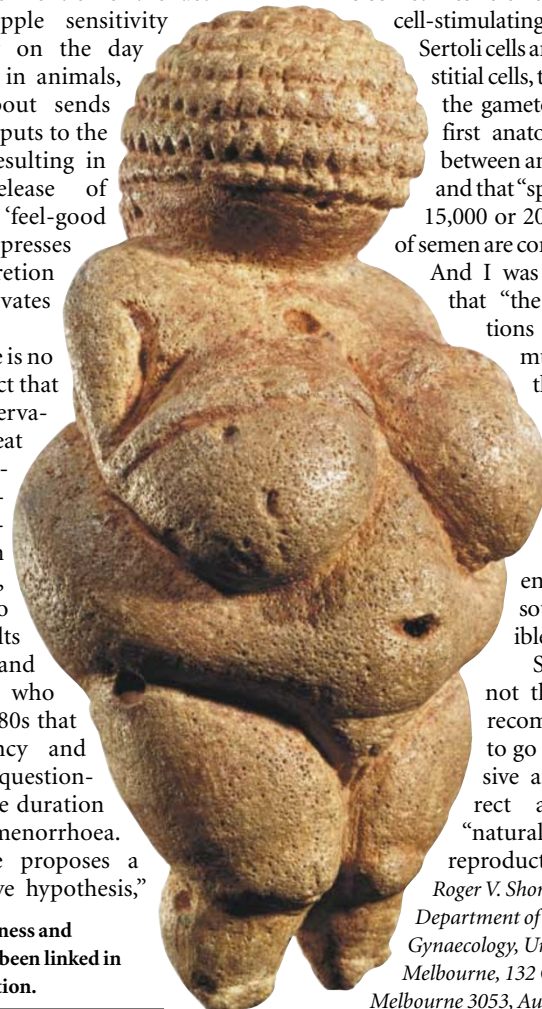
in which "relative metabolic load" is said to be responsible for the lactational inhibition of ovulation. Although we are given no clues as to how the body might sense this "relative metabolic load," or how this information is then used to inhibit ovulation, we are assured that his hypothesis fits the available data better than the nursing frequency hypothesis, and is sounder theoretically! How come that high-yielding dairy cows in negative energy balance, which are milked only twice a day, show little inhibition of ovulation postpartum, whereas low-yielding beef cattle, frequently suckling their calves, have a far longer period of lactational anovulation?

There is a good rebuttal of Rose Frisch's hypothesis that the percentage of body fat is the trigger for the onset of female puberty. But Ellison then goes on to propose an alternative "pelvic size hypothesis," suggesting (without any evidence) that there are mechanical determinants of the timing of puberty. Curiously, there is no mention of the timing of the onset of spermatogenesis in boys, or how it is that boys grow to be considerably taller than girls.

Indeed, the male gets short shrift throughout this book. We are told, quite incorrectly, that follicle-stimulating-hormone in the male is sometimes referred to as interstitial cell-stimulating hormone, that Sertoli cells are also called interstitial cells, that the location of the gametogenic cells is the first anatomical distinction between an ovary and a testis and that "sperm counts above 15,000 or 20,000 per millilitre of semen are considered 'normal'". And I was amazed to learn that "the thermal oscillations produced in the mucin strands by the woman's body heat also resonate with the beating of the sperm cell's tail to aid its progress," although no reference is given to the source of this incredible information.

Sadly, this book is not the place I would recommend anybody to go for a comprehensive and factually correct account of the "natural history of human reproduction". ■

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