nature

BOOKS & ARTS

Beautiful models

The dynamics of evolutionary processes creates a remarkable picture of life.

Evolutionary Dynamics: Exploring the Equations of Life
by Martin Nowak
Belknap Press: 2006. 384 pp. $35, £22.95, €32.30

Sean Nee

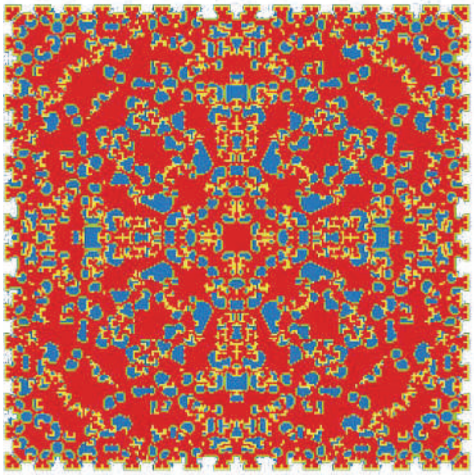
Martin Nowak is undeniably a great artist, working in the medium of mathematical biology. He may be a great scientist as well: time will tell, and readers of this book can form their own preliminary judgement.

In his wanderings through academia's firmament — from Oxford, through Princeton's Institute for Advanced Study to his apotheosis as professor of biology and mathematics at Harvard — Nowak has seemingly effortlessly produced a stream of remarkable theoretical explorations into areas as diverse as the evolution of language, cooperation, cancer and the progression from HIV infection to AIDS. *Evolutionary Dynamics*, based on a course he gives at Harvard, is a comprehensive summary of this work. Although Nowak certainly displays his own oeuvre to great advantage, this book is not purely self-indulgent. His final chapter is an annotated bibliography of other work in the many fields he discusses that is both fair and scholarly: in other words, he cites me.

Many entities replicate. HIV replicates in people's bodies, as do cancer cells. Our genes replicate when we reproduce. Replication may occur with errors as mutation. Natural selection occurs when entities with different properties replicate at different rates, and random chance may also intervene to dilute the action of selection. These are the basic elements of the evolutionary process: if you doubt that such simplicity can produce anything interesting, look around you. Evolutionary dynamics is the mathematical modelling of these processes in a variety of biological scenarios.

A good work of art should stimulate, challenge and, usually, be aesthetically pleasing. Some of Nowak's work in evolutionary dynamics is, literally, visually appealing. But all his work has a beautiful elegance. In time we will see which parts of it become embedded in our way of understanding the various phenomena that inspired him.

Consider, for example, the course of HIV infection. After infection, the virus is initially kept under control by the host's immune system. Over time, mutant virus appears that can escape control by immune cells and multiply until, in turn, this new 'strain' also comes under their control. Nowak's model of the dynamics of this interplay between the virus and the immune system shows a long period during which the virus is under control until a threshold number of strains exist and the immune system collapses. Indeed, the behaviour of the mathematical model elegantly mimics the course of progression from initial infection to AIDS: how could something so beautiful not be true?


Weaving a spell: Martin Nowak models cooperators and defectors to create patterns like Persian rugs.

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For me, the highlight of the book is the chapter on evolutionary graph theory. This is based on a simple reconsideration of the simplest model of evolution, which is that, at successive points in time, an individual in the population dies and is replaced by the progeny of another individual, according to whatever rules of natural selection are being considered. We can visualize this in terms of a graph in which one node can be replaced by a copy of a node connected to it. This is an idea that could have occurred to any of us, but most of us would not have seen how to develop it further. In Nowak's hands, the idea is a springboard: he's off! He designs graphs that amplify, and others that hinder, the efficacy of natural selection compared to the entropic force of random chance — there are bursts, stars, superstars, funnels and metafunnels (see Fig. 3 in *Nature* **433,** 312–316; 2005). We get new theorems, such as the isothermal theorem, which tells us what kind of graph can alter the power of natural selection. The chapter fizzes with breathtaking brio. Is the work relevant to anything? Who knows? Who cares? It's a riot.

Nowak takes the view that ideas in evolutionary biology should be formulated mathematically. An easy retort would be the observation that Darwin managed quite well without mathematics. But, in fact, Darwin did not realize the enormous potential potency of natural selection until he absorbed Thomas Malthus' exposition of the counterintuitive consequences of exponential growth — a fundamentally mathematical insight. Certainly, some ideas that are essentially quantitative must be explored mathematically. But there are plenty of other interesting theoretical areas. Consider genomic imprinting, whereby genes in a fetus are expressed differently depending on whether they come from the father or mother. Nowak's Harvard colleague David Haig has explained this phenomenon in terms of evolutionary conflicts between parents about investment in the fetus, an explanation that is fascinating, predictive, falsifiable and entirely verbal.

Nowak is much younger and more successful than me. Also, he did not have the modesty to put a question mark after the book's subtitle. So I wanted to hate this book and pen poison to hurt him. I could, for example, chortle that he goes from the most basic model of predator–prey dynamics to Andrey Kolmogorov's eight mathematical conditions for limit cycles in a single page. I could cackle that he assumes that readers know the concept of 'measure' from advanced analysis, and then wonder how many readers he is writing for. But after each mathematical excursion, Nowak provides a perfectly clear and intuitive verbal explanation of what has just happened.

I therefore have no choice but to end positively. This is a unique book. It should be on the shelf of anyone who has, or thinks they might have, an interest in theoretical biology. And if you want to have a punt about what might be considered important new science in the future, this would be a much better buy than another recent book, generously illustrated with pictures of cellular automata but with the much grander aim of revolutionizing science, by another *wunderkind* who also trod the Oxford–Princeton trail. ■

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