The rise of the superorganism

Evolutionary change is usually slow and incremental, but sometimes takes major steps when a group of cooperating organisms becomes a new higher level organism. Examples of such major transitions include the evolution of the eukaryote cell, multicellularity and some social insects. If we want to understand how complex life arose on earth, then we must understand the factors that favoured these major transitions.

Evolutionary biologist Koos Boomsma's book, *Domains and Major Transitions of Social Evolution* (Oxford University Press, 2022) tackles this problem, and places it within the broader field of evolutionary biology. It examines how complex life evolved, and how adaptation is studied more broadly. The book provides a scholarly and comprehensive overview that explains the state of the field, how scholars got there, and what researchers need to do next.

The book is roughly divided into three parts. The first part provides a detailed history of the development of evolutionary theory to study adaptation. Theoretical population genetics and empirical studies had united Darwin's theory of natural selection with Mendelian genetics by the 1930s, in what is termed the 'modern synthesis'. But Boomsma's focus is the work that followed the modern synthesis, in the second half of the 20th century. He shows how it was these later steps that really completed a 'neo-Darwinian synthesis of organismal biology'.

In the 1960s, Hamilton used a 'genes eye' approach to ask how selection on gene (allele) frequencies would shape adaptation at the individual level. A key result was that natural selection would favour behaviours or traits which maximised (increased) inclusive fitness. Inclusive fitness captures how individuals can influence the transmission of their genes to future generations via either their own reproductive success or the reproductive success of other individuals with which they share genes. This assumption of fitness maximisation led to a surge of theoretical modelling from the 1970s onwards, that ignored genetic details (the 'phenotypic gambit'). These game theory models allowed relatively simple mathematics to produce predictions that linked adaptation to ecology.

These conceptual and theoretical tools led to a simultaneous explosion of empirical research, attempting to explain the behaviour and life history of certain species, as well as why species vary. For example, why does a male dung fly copulate with a female for 36 minutes; or why do only certain bird species breed cooperatively? This field of research, usually termed behavioural or evolutionary ecology, revolutionised the study of adaptation, turning it into a hypothesis driven, testable and quantitative science.

The second part of the book examines how major transitions can lead to an increase in organismal complexity. Boomsma reviews recent progress, but also illustrates the neglected insights that were made earlier, by early proponents of Darwinism such as William Wheeler and Julian Huxley. Working in the early 1900s, Wheeler and Huxley were decades ahead of their time in realising how a group of cooperating organisms could become a higher-level organism. A colony of leaf cutter ants can be conceptualised as a group of cooperating organisms, or as a higher-level organism (superorganism) – the colony.

Boomsma shows how inclusive fitness theory provides a single unifying framework to both explain cooperation and determine the conditions required for all forms of major transition. A key argument of Boomsma's is that major transitions are not gradual. They require restrictive conditions, such as lifetime monogamy, to maximise relatedness within social groups and effectively eliminate conflict. If this occurs, then there is the possibility for a major transition. If not, then other mechanisms, such as conflict resolution, cannot lead to a major transition.

The final part of the book reviews the empirical data, providing a masterly overview and synthesis of social life on earth. Boomsma brings together an impressive range of data from across the tree of life and looks at it through an inclusive fitness theory lens. He assesses the extent to which the theoretical predictions that he made earlier in the book are supported by the data. There are some amazingly successful links between theory and data. For example, how obligate multicellularity has only evolved in species that form clonal groups, and how social insects have only evolved to higher level superorganisms in species with strict lifetime monogamy.

Boomsma's book is thought provoking and stimulating. It provides a wealth of opportunities for future research. Hypotheses are generated. Gaps in the data are identified, such as the conditions which did and didn't lead to major transitions, especially in less studied lineages such as Siphonophora and their sister clades. I worked through the book with my research group, and it led to heated debates over even fundamental issues, such as the meaning of 'superorganism' and 'irreversible'. But the debates were always interesting, resulting in discussion of what work was needed. Some of our group found parts of the book less accessible, but this reflects the aim of the book. It is not a simple textbook overview - it is scholarly amassing of the relevant work and its historical development. Consequently, certain parts require a level of prior knowledge or multiple readings.

So who should read this book? Anyone interested in social evolution or the major transitions will find much of interest. The empirical overviews alone could launch numerous social evolution PhDs – just read Box 6.2, on the origins and adaptive radiations of superorganismal lineages, if you don't believe me. The book will, however, appeal to a wider audience. It provides a comprehensive and historical review of the development of evolutionary theory, as well as an insightful discussion of progress and complexity in evolution. These topics would be of use to a wide range of readers, from scientists to philosophers.

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I have no competing interests.