

PREFACE

Few examples of the way complexity unfolds in nature (and beyond it) are as fascinating as viruses. Viruses are hypothesized by some to predate the origins of life and its micro- and macroevolutionary play. They strongly influence energy flows in complex ecosystems. They maintain all kinds of relationships with their hosts, from mutualism to pure parasitism. They are responsible for some of the most deadly pandemics and yet have been coevolving with us throughout all our common history. They have played a major role in our understanding and manipulation of life and have also attracted the interest of biologists, physicists, and computer scientists alike.

Many key questions emerge when thinking of their nature and relevance: What exactly are they? Are they living entities? How did they originate? How similar are computer viruses to their living counterparts? How complex can they become? What is their role in shaping the evolution of complex organisms? What role have they played in the development of society? Can they be compared with software programs, to be run inside their hosts, who provide the appropriate hardware? Why are there so many new emergent viruses and how do they emerge? These questions will be addressed in this book.

Viruses are complex systems, spanning orders of magnitude in size, and an enormous variety of life cycles and habitats. But the study of their behavior and structure, particularly from interdisciplinary frameworks, has also revealed a number of universal patterns of organization. RNA-based viruses display high mutation rates, as predicted by theoretical developments from the 1970s. They live at the edge of disorder, where high instability but also adaptability occur. This edge is related to a phase transition phenomenon, and its presence is tied to the genetic nature of populations, often described as quasispecies. Other viruses, such as the mimiviruses, are so big that they are actually larger than some of the smallest cells we know. Their life cycle reveals surprising properties, placing them in a new position as a parasitic life form. We will discuss the potential boundaries of the viral morphospace and their importance, as well as theoretical models of viral population dynamics and self-assembly. Models and theoretical approximations have played a key role in this area, in particular the concept of fitness landscapes given their importance in defining the dynamics of their genetically complex populations.

Viruses have shaped the evolution of cells, organisms, ecosystems and even the biosphere. Such influence spans all scales of biological organization, from genomes to the planet (figure 1). Their dynamics involve nonlinear phenomena, tipping points and self-organization processes that have many commonalities with other biological and nonbiological systems. Such similarities might hide universal properties that pervade complexity and in this respect viruses offer a unique window into the origins of complex systems. In this context, we will also pay attention to other systems, such as computer viruses, that share unexpected similarities.

Although many excellent books exist concerning the population biology and ecology of viruses or the role they have played within the context of epidemics, there is no major contribution in

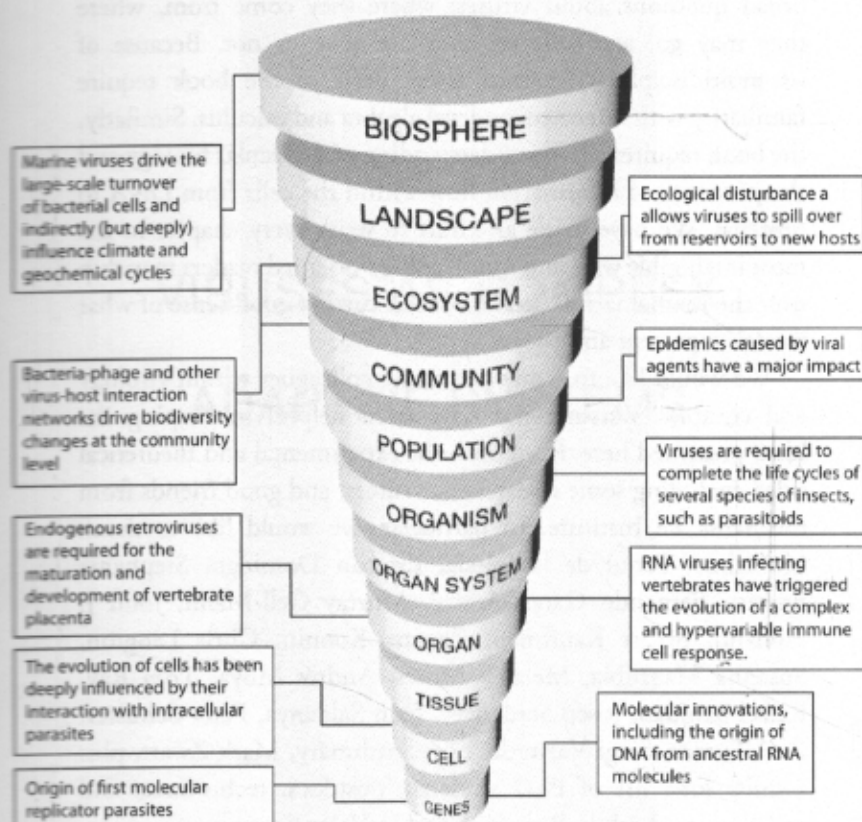


Figure 1. All scales of life are affected by and affect the diversity and evolution of viruses in the biosphere. In this diagram, some key processes and phenomena influenced or caused by viruses are indicated (central picture after Odum and Barrett (2005)).

the existing literature that provides the unifying picture presented here. The book has been written to be of interest to researchers and graduate students in virology, evolution, mathematical biology, and physics of complex systems. But we also hope it will be appealing to advanced undergraduate students interested in

broad questions about viruses: where they come from, where they may go, and whether they are alive or not. Because of its multidisciplinary nature, some parts of the book require familiarity with intermediate-level algebra and calculus. Similarly, the book requires a basic understanding of molecular biology and the processes of information flow within the cells from DNA to proteins. We have made an effort to write every chapter in the most intelligible way, and more biology-oriented readers may skip over the mathematical details but still catch a good sense of what models represent and prove.

We would like to thank our many colleagues within virology and complex systems who have been helpful in shaping the ideas presented here, from both the experimental and theoretical sides, including some researchers, visitors, and good friends from the Santa Fe Institute. In particular, we would like to thank Lin Chao, Paqui de la Iglesia, Esteban Domingo, Stephanie Forrest, Fernando García-Arenal, Murray Gell-Mann, John J. Holland, Stuart Kauffman, Eugene Koonin, Chris Langton, Susanna Manrubia, Melanie Moses, Andrés Moya, Tom Ray, Rafael Sanjuán, Josep Sardanyés, Joan Saldanya, Peter Schuster, Paul Turner, Sergi Valverde, Eörs Szathmáry, Mark Zwart, plus a quite long list of PhD students, postdocs, technicians, and collaborators both in Barcelona and in València

The late physicist John Wheeler said about science: 'We live on an island surrounded by a sea of ignorance. As our island grows, so does the shore of our ignorance.' This applies too to the particular island that defines today's understanding of viruses. Very often, new discoveries deeply change our perspective, expanding our understanding of the viral universe while the shoreline enlarges and new questions emerge. We hope this book will help the reader to walk safely across the tangled boundaries between the mainland and the uncharted waters.