

Preface

New ways of answering old questions

Macroevolution and macroecology aim to describe large-scale evolutionary and ecological patterns, and to understand the processes that produced them. For as long as people have been able to travel far afield, they have been interested in biological patterns at large scales. Indeed, these are some of the most fascinating puzzles of the natural world. But for many people, it is not obvious how we can do science at the macro-scale. How can we devise experiments or test hypotheses for events that happened millions of years ago, for patterns that emerge at global spatial scales, or processes that affect thousands of different species?

This is a challenging field because it often concerns processes and patterns that cannot be directly witnessed. We can't go back in time to witness the diversification of the animal kingdom, or make direct observations on the causes of dinosaur extinctions, nor can we do direct experiments on the latitudinal diversity gradient of species richness, or manipulate species traits to test their effect on speciation or extinction rates. But there is a wealth of scientific resources we can draw on to generate hypotheses, design elegant tests, and provide satisfying answers to many intriguing questions. The tools used to test hypotheses for patterns of biodiversity include experiments, models, and statistical analyses, but often the most important tool we have is the ability to frame a clear question, from which we can make simple predictions that can be put to robust tests.

Although macroevolution and macroecology are often taught separately, they share an intellectual framework, rest on many common concepts, and share many analytical tools. The development of macroevolution and macroecology as fields of scientific enquiry have been driven by new ways of compiling and analysing data that have allowed big-picture questions about biodiversity to be tackled. For example, the massive growth of DNA sequence databases has led to a proliferation of methods for using molecular phylogenies to understand the origins of lineages and their patterns of diversification. Molecular data have been combined with global databases of species distributions and environmental features and with large palaeontological databases to analyse patterns across large spatial and temporal scales. Most of this 'big data' is now freely available for anyone to explore.

Although many of the new methods are technically complex and analytically sophisticated, the basic principles of sound scientific reasoning and inductive inference are as important in macroevolution and macroecology as in any other area of science. Our aim in this book is to introduce you to some of the useful approaches to asking questions and solving problems in macroevolution and macroecology. The underlying logic of these techniques does not require you to be competent in mathematics, statistics, or computing (although these intellectual tools may help you frame and answer questions).

What is in this book?

This book is not meant to be an exhaustive treatment of all problems, questions, and methods associated with macroevolution and macroecology. Rather, the idea is to give you an introduction to some of the key issues, a taste of the research that is being done in these fields, and a glimpse of some of the approaches that researchers are currently using to make progress in these areas. There is no clear distinction between macro- and micro-levels of evolution and ecology, and there is no definitive list of patterns or processes that should be included in an introductory book on macroevolution and macroecology.

This book takes a case study led approach. Each chapter focuses on one particular question as a way of introducing some core concepts in macroevolution and macroecology, and as a way of exploring some useful sources of data and modes of analysis. This does not mean that we think these are the only important questions to be asked in macroevolution and macroecology. We have chosen these particular issues because each serves as a useful focus for thinking about important concepts that run through macroevolution and macroecology (such as levels of selection or diversification rates), or important analytical techniques (such as null models or phylogenetic comparative methods). The book emphasizes the critical appraisal of evidence, techniques, and assumptions in testing macroevolutionary and macroecological hypotheses, and encourages you to form your own opinions on important debates.

Each chapter has a number of features designed to help you get the most from your reading.

Roadmap

Why study macroevolution and macroecology?

Most textbooks on evolution and ecology large operating within populations. But many of the questions about patterns of biodiversity are not easily answered on the population level, such as: How does novel mass extinctions? Does selection act at the level of

- **Roadmap** sets out the path we will navigate in each chapter, giving a brief introduction to the examples we will use to illustrate the topic, the key concepts we will cover, some of the analytical techniques we will consider, and the case study included at the end of the chapter.

1

Key points

- Macroevolution and macroecology focus on patterns of biodiversity that are shaped by processes operating over large time-scales, across wide spatial scales, and affecting a wide variety of lineages.
- Most researchers assume that processes

- **Key points** boxes act as waymarkers, highlighting the main take-home messages of the section.

2

What do you think?

The disagreement between selectionists and mutationists partly reflected different attitudes to science: mutations could be generated and observed in the laboratory, whereas the role of natural selection in the formation of new species is inferred rather than directly

- **What do you think?** boxes encourage you to stop and think about the broader implications of what you are reading. They prompt you to take a moment to think critically about the core concepts you have just learned, and invite you to extend your intellectual reach beyond the material and form your own ideas.

Points for discussion

1. Some people have proposed that life may have evolved and then colonized earth, an idea sometimes referred to as the panspermia hypothesis. Does this provide a plausible answer to questions about the origin of life? How would you test the panspermia hypothesis?
2. Should increases in the coding capacity of replicators (e.g., increase in genome size) slow the rate of evolution in organisms?

References

1. Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. Murray, London.
2. Nilsson D-E, Pelger S (1994) A pessimistic estimate of the time for an eye to evolve. *Proceedings of the Royal Society of London B* 256(1345): 53-8.

Case Study 1

Testing hypotheses about past events: uncovering the evolutionary origin of a new virus

While scientific training might involve the acquisition of skills, such as those associated with laboratory analysis, or field studies, the most important sets of skills needed are those associated with asking good questions.

Questions to ponder

1. We have seen how a range of corroborating evidence is needed to support or refute hypotheses. What if a new virus emerges with DNA sequences, no other historical records. Can we trust phylogenetic estimates of its origin?
2. How can we test whether viral genomes evolve at a constant rate of change?
3. Are there limits to reconstructing past events?

Further investigation

Ancient DNA derived from human remains is increasingly being used to trace the origins of major epidemics, such as plague. What are the advantages of using these 'molecular fossils'? Can these old sequences be used in the same way as the modern sequences? How can we ensure that their samples are not contaminated with modern viruses? Which diseases will be most likely to benefit from this research?

References

1. Bromham L (2016) Testing hypotheses in macroevolution. *History and Philosophy of Science Part A* 55: 47-59.
2. Sharp PM, Hahn BH (2010) The evolution of HIV-1. *AIDS, Philosophical Transactions of the Royal Society of London B* 35: 1365-1374.
3. Hahn BH, Shaw GM, De Cock RM, Sharp PM (2000) HIV-1: scientific and public health implications. *Science* 287: 607-14.

- **Points for discussion**, at the end of each chapter, provide a focus for more in-depth discussion. These can be used for self-study, to prompt discussion in the classroom, or as a focus for a group investigation about the key issues presented in the chapter.

- **References** include the details of studies cited in the chapter. This isn't a comprehensive guide to literature on the topic, or a list of must-read classics. But if you want to look further into the details of studies we mention, this is the place to find their publication details.

- Each chapter also includes a **Case Study** in which we explore in a bit more depth one or more examples of research in macroevolution and macroecology. Each case study includes the following features.

- **Questions to ponder** encourage you to think deeply and critically about some of the issues raised by the research.

- **Further investigation** invites you to extend your investigation beyond the case study to a related topic. This section could serve as a starting point for further independent study or group discussion on the topic.

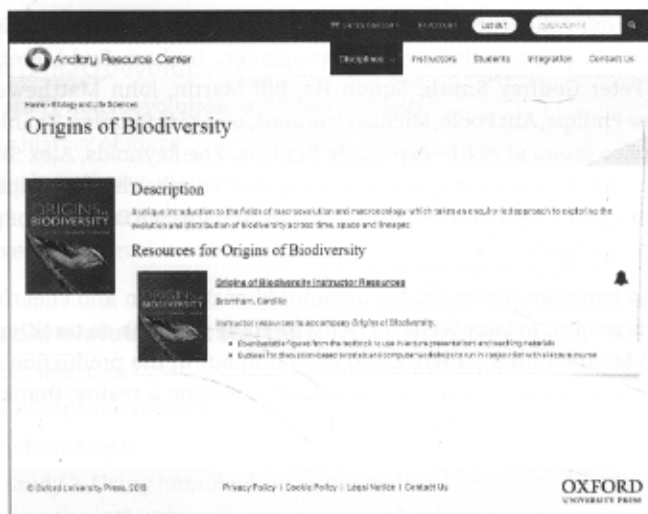
- **References** provide publication details of studies mentioned in the Case Study.



online resources

www.oup.com/uk/bromham-biodiversity/

Online resources provide lecturers with outlines for discussion-based tutorials and computer workshops to run in conjunction with a lecture course as well as downloadable figures from the textbook to use in lecture presentations and teaching materials. Find these at www.oup.com/uk/bromham-biodiversity/



Who is this book for?

This book is aimed primarily at budding biologists who want to apply what they have learned about evolution and ecology to investigating and understanding the world around them. The reader we have in mind has already taken some introductory courses in evolution and ecology, so will be familiar with core processes of evolution, such as mutation, selection, drift, and speciation, and will understand basic concepts in ecology, such as competition, population growth, and the way that environmental conditions shape species distributions. This book builds on these basic concepts to explore and explain patterns in biodiversity over space and time. We will revise some of these core concepts along the way—for example, considering the operation of natural selection in Chapter 2—but if you want to brush up on these background concepts, it might be a good idea to have a look at a general evolution or ecology text first.

Many case studies in this book utilize analyses of molecular phylogenies. To be an intelligent user of phylogenetic analyses, you need to understand the nature of molecular data, how phylogenies are produced, and the way that phylogenetic inference is affected by data selection, methods used, and assumptions made. Although we touch on these areas in many chapters, we cannot cover phylogenetics in detail in this book. However, there is a companion text that provides a ‘from the ground up’ description of molecular phylogenetics, from data generation to phylogenetic inference and analysis. You may find *An Introduction to Molecular Evolution and Phylogenetics* (Lindell Bromham, Oxford University Press, 2016) a useful base from which to gain an understanding of the role of molecular phylogenies in evolution and ecology.