

respond to crises, and what needs to be done to slow the rate at which crises arise. It is worthwhile reading for anyone interested in conserving biological diversity.

#### References

- 1 Wake, D. (1991) Declining amphibian populations. *Science* 253, 860
- 2 Alford, R.A. and Richards, S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annu. Rev. Ecol. Syst.* 30, 133–165
- 3 Johnson, P. *et al.* (2007) Aquatic eutrophication promotes pathogenic infection in amphibians. *Proc. Natl. Acad. Sci. U. S. A.* 104, 15781–15786
- 4 Berger, L. *et al.* (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proc. Natl. Acad. Sci. U. S. A.* 95, 9031–9036
- 5 Lips, K.R. *et al.* (2006) Emerging infectious disease and the loss of biodiversity in a neotropical amphibian community. *Proc. Natl. Acad. Sci. U. S. A.* 103, 3165–3170
- 6 Fisher, M. *et al.* (2009) Global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time, and host. *Annu. Rev. Microbiol.* 63, 291–310
- 7 Richards-Zawacki, C. (2009) Thermoregulatory behaviour affects prevalence of chytrid fungal infection in a wild population of Panamanian golden frogs. *Proc. R. Soc. Lond., B, Biol. Sci.* 277, 519–528
- 8 Pounds, J.A. *et al.* (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439, 161–167

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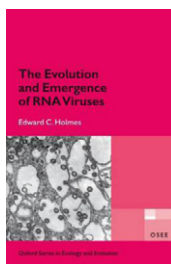
#### Book Review

## What is special about RNA viruses?

**The Evolution and Emergence of RNA Viruses** by Edward C. Holmes. Oxford University Press, 2009. US\$130.00/US\$60.00 hbk/pbk (288 pages) ISBN 978 0 19211 128/978 0 19211 135

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About half of the 2000 known species of virus use RNA as their genomic material (the other half are the DNA viruses). All RNA viruses have small genomes, typically only 10,000 bases, and a high per base mutation rate. These two features are doubtless connected: a large genome is incompatible with a high mutation rate given that most mutations are harmful. The high mutation rate might

explain why all of the major viral killers of humans are RNA viruses. The only DNA virus of comparable status was smallpox and it is perhaps not a coincidence that this is also the only virus that we have managed to eliminate. In *The Evolution and Emergence of RNA Viruses*, high mutation rates and small genome sizes are the linked motifs that run through the book.

The first part of the book considers the main evolutionary features of RNA viruses, such as their origin and genome architecture, last attempted in Esteban Domingo and colleagues' (1999) *Origin and Evolution of Viruses* [1]. Holmes' main point is to emphasise that, whereas a high mutation rate could benefit the virus by allowing fast adaptation, it limits the possibilities of adaptation because of the restriction on genome length; there is only so much you can do with a handful of genes. Indeed, Holmes' argument prompted the metaphorical description of RNA viruses as restless beasts rapidly pacing a small cage [2].

A particularly interesting section entitled 'The great quasispecies debate' marks a departure from *Origin and Evolution of Viruses*. The high mutation rate of RNA viruses led to the application of a novel mathematical approach to their evolution, namely quasispecies models, which influenced much of the earlier book. In quasispecies

models the virus population is considered to be a cloud of genotypes linked by mutation. Quasispecies models have been productive. For example, the (albeit questionable) inference that RNA viruses exist on the edge of mutational meltdown has stimulated interest into hypermutation as an antiviral strategy [3]. However, the most famous feature derived from quasispecies models, namely the error threshold, has repeatedly been shown to only exist given implausible fitness landscapes [2]. I am tempted to see *The Evolution and Emergence of RNA Viruses* as an attempt to reclaim RNA virus evolution by more traditional evolutionary and population genetic theory, although one handled in a very evenhanded manner.

The second part of *The Evolution and Emergence of RNA Viruses* will interest most readers; this showcases the potential of phylogenetics for studying RNA viruses (sometimes called phylodynamics [4]). By contrast to the DNA world, where phylogenies tend to play a secondary role by showing how taxa are related to each other historically, the high mutation rate of RNA viruses means that their evolution and population dynamics occur over the same time period. We can thus measure selection both within individual hosts and within disease outbreaks, such as when building an evolutionary model for the global pattern of influenza A infections [5].

Returning to the divide between RNA and DNA viruses, Holmes proposes an important life-history continuum with RNA viruses at one end and the large-genomed, slow-mutating, double-stranded DNA viruses at the other. For example, the latter can use their large gene repertoire to manipulate host defences and establish persistent infections. I worry slightly about Holmes's treatment of single-stranded (ss) DNA viruses as honorary RNA viruses (because ssDNA viruses have small genomes and the few data available suggest that their mutation and substitution rates are relatively high). My concern is that we have estimates of the mutation rate for precisely six DNA

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virus species, and therefore it might be premature to develop a general schema.

The 'emergence' of the book's title refers to viruses crossing, or threatening to cross, from other species into humans or domesticated organisms (e.g. SARS, HIV and influenza A); RNA viruses feature disproportionately in lists of recent emergent pathogens [6]. Holmes suggests why, and usefully stresses the need to also consider ecological factors, which attract less attention in the genomic era. A sample of the other important points raised in the book are: (i) that the rate of antigenic evolution can differ widely between viruses with similar underlying rates of evolution; (ii) how we need clarity in defining viral fitness; and (iii) why phylogenetic patterns among RNA viruses only make sense if we remember that they probably have a high rate of lineage birth and death. The aim of *The Oxford Series in Ecology and Evolution* is

to stimulate ideas in new research fields, and the *The Evolution and Emergence of RNA Viruses* is an excellent addition to this series.

#### References

- 1 Domingo, E. *et al.* (1999) *Origin and Evolution of Viruses*, Academic Press
- 2 Belshaw, R. *et al.* (2008) Pacing a small cage: mutation and RNA viruses. *Trends Ecol. Evol.* 23, 188–193
- 3 Bull, J.J. *et al.* (2007) Theory of lethal mutagenesis for viruses. *J. Virol.* 81, 2930–2939
- 4 Grenfell, B.T. *et al.* (2004) Unifying the epidemiological and evolutionary dynamics of pathogens. *Science* 303, 327–332
- 5 Rambaut, A. *et al.* (2008) The genomic and epidemiological dynamics of human influenza A virus. *Nature* 453, 615–619
- 6 Wolfe, N.D. *et al.* (2007) Origins of major human infectious diseases. *Nature* 447, 279–283

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#### Book Review

## Humans on the brink of extinction

**The Humans Who Went Extinct: Why Neanderthals Died Out and We Survived** by Clive Finlayson. Oxford University Press, 2009. US\$29.95/£16.99 hbk (278 pages) ISBN 13 978 0 19 923918 4

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The past decade has seen impressive advances in our knowledge of human evolution. This includes something as rare as a new hominid species, *Homo floresiensis* (also known as the “Hobbit”) [1]. This extinct human lived on islands in South-east Asia and survived to as recently as 12 thousand years ago, long after our closest relatives, the Neanderthals (*H. neanderthalensis*), went extinct. An updated

volume on human evolution is therefore timely and this is what you get with Clive Finlayson's book, *The Humans Who Went Extinct*.

The book differs from most others of its kind by taking an evolutionary-ecological approach to the topic. Most ecologists, I think, will find it a relief that Finlayson carefully avoids the heated debate on the taxonomy of fossils of earlier incipient versions of *Homo* and the lineage that led directly to us, using instead simple terms such as proto-Ancestors and Ancestors to describe these groups. I also find it refreshing that the book challenges some classical notions, for example the idea that *H. erectus* evolved in Africa and was the first hominid to spread to other continents. Based on fossil evidence, we cannot say if this extinct human evolved in Africa or Asia, and according to Finlayson it is even likely that the recently discovered *H. floresiensis* in Asia represents remnants of much earlier expansions.

Importantly, the book delivers a number of interesting and rather novel take-home messages. A keynote is that any

significant demographic and geographical surge in our history had to do with two things: i) the breakdown of ecological barriers due to climate and environmental changes, and ii) changes in biology (and, later on, cultural changes). An example of the former is the rapid expansion of *H. erectus* across Africa and southern Eurasia some 1.5 million years ago, which was due to climate driving the expansion of a huge savannah belt. However, *H. erectus* could not have exploited this ecological opportunity had it not been for the biological changes of a distant past, such as their ability to walk on two legs. Bipedal walking was not initiated as our ancestors ventured away from the forest and on to the open savannah plains, as has often been suggested, but likely started whilst our ancestors were still living in trees. Another of Finlayson's main points is that populations living in the marginal, rather than the core environment of a given species, are the drivers of adaptive change. They are forced to perceive their environment in new ways, humans being no exception. Again Finlayson argues his point well. It is also important to note that for the majority of our evolutionary history, we were not the only human species around and instead multiple species of *Homo* lived in the landscape at the same time. This is not new knowledge, but for a reader not familiar with human evolution, this is a key factor elucidating our evolutionary history, and is an important component to any book on the topic.

Finlayson's book also covers the more classical controversies in human evolution. Did anatomically modern humans have sex with Neanderthals? Why did Neanderthals go extinct while we survived? Finlayson's answer to the first question is that there were in principle two

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