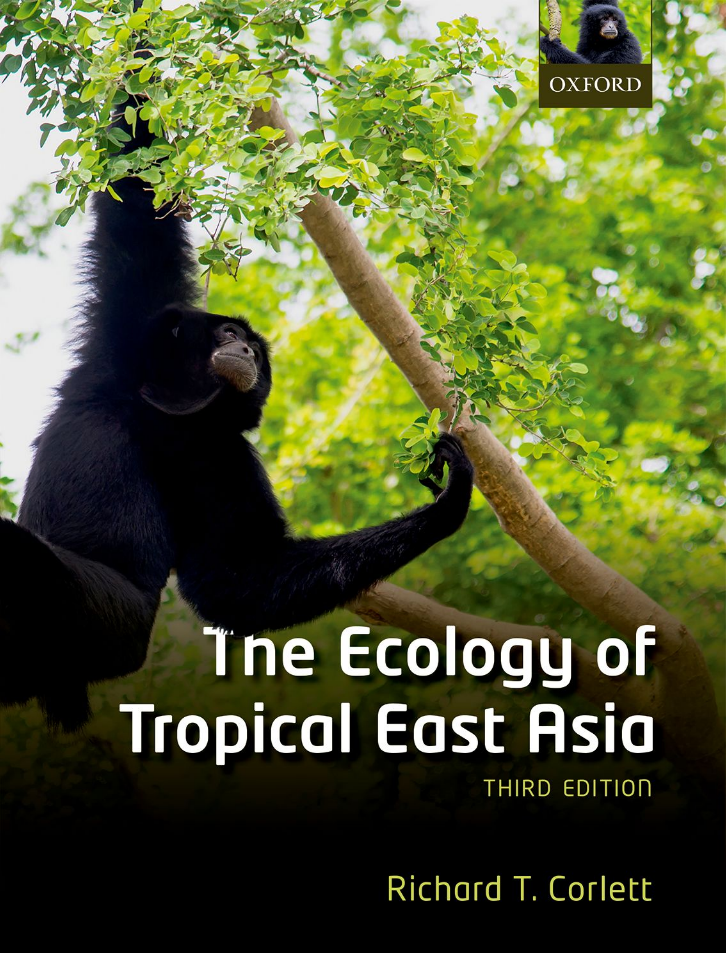

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The Ecology of Tropical East Asia

THIRD EDITION

Richard T. Corlett

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Third Edition

Richard T. Corlett
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Preface

It is now 10 years since the first edition of *The Ecology of Tropical East Asia* was published in early 2009, and 5 years since the second edition in 2014. The region covered by the book has changed a lot over this period. Natural forests and large vertebrates have continued to decline, while plantations, urban areas, and infrastructure have continued to expand, with even the most remote parts of the region increasingly impacted. On the human side, the region is considerably wealthier than it was 10 years ago, more people live in urban areas, and mobility, communications, and access to information have all increased. Overall, it has been mostly bad news for nature and good news for people, but there are also signs of a real change in the relationship between the two. Local environmental non-governmental organizations have flourished and concerns for biodiversity and the environment have gone mainstream. It is no longer assumed that economic development justifies environmental damage, and no longer accepted that this trade-off is inevitable.

The major aim of the book continues to be to provide an overview of the terrestrial ecology of Tropical East Asia. The third edition retains the balance between compactness and comprehensiveness of the previous editions, and the even-handed geographical treatment of the whole region, but it updates both the contents and the perspective. The cumulative number of relevant papers published on the region roughly doubles every 5 years, and their quality and scope have also been increasing rapidly, so about a third of the book text is new or greatly modified, while almost every paragraph has some changes. New tools, particularly from genomics and remote sensing, have played a big role in this update. The change in perspective largely reflects the growing realization that we are in a new epoch, the Anthropocene, in which human activities have at least as large an influence as natural processes, and that stopping or reversing ecological change is no longer an option. This does not mean that biodiversity conservation is no longer possible or worthwhile, but that the biodiverse future we strive for will inevitably be very different from the past.

This edition was written largely at XTBG, although I travelled extensively in the region during its preparation. It is not possible to list everyone who has contributed in some way, but Alice Hughes and Kyle Tomlinson have had the greatest influence on the final text. I must also thank Aki Nakamura, Chen Jin, Su Tao, Liu Jingxin, Tony Lynam, and my present and past graduate students for their varied contributions, including very useful discussions on the region, as well as my many ecologist friends in Kunming, Hong Kong, Beijing, Thailand, and Singapore. Far more is known about this region by the people who live and work here than has been written down, so I have learned at least as much through personal communications as from reading. Alice Hughes, from XTBG, created most of the maps in the main text and Patrick Roehrdanz, from Conservation International, produced the colour climate maps in Chapter 2 and 7. Many different people kindly provided the photographs used in the book. Finally, I must thank Bethany Kershaw and the other staff at Oxford University Press for their help at all stages, from the book proposal through to its final production.

Contents

1 Environmental history **1**

1.1 Why 'Tropical East Asia'? 1
1.2 The importance of history 1
1.3 Plate tectonics and the origin of Tropical East Asia 2
1.4 Sea-level changes 5
1.5 Changes in climate and vegetation 7
1.6 Extraterrestrial impacts, volcanoes, and other natural catastrophes 12
1.7 The first humans 15
1.8 The arrival of modern humans 17
1.9 The spread of agriculture 18
1.10 Exploitation of wild species 20
1.11 Fire 22
1.12 Urbanization 22
1.13 The dawn of the Anthropocene 23

2 Physical geography **26**

2.1 Weather and climate 26
  2.1.1 Temperature 26
  2.1.2 Day length and insolation 28
  2.1.3 Rainfall 30
  2.1.4 Water from fog 31
  2.1.5 Interannual variation in rainfall 32
  2.1.6 Impacts of land-use change on local and regional climates 34
  2.1.7 Hail, snow, and ice 34
  2.1.8 Wind 35
  2.1.9 Lightning 37
2.2 Fires 37
2.3 Soils 39
  2.3.1 Soil classifications 39
  2.3.2 Landslides and soil erosion 41
2.4 Classifying vegetation 42
2.5 Lowland vegetation 43
  2.5.1 Tropical rainforests 43
  2.5.2 Tropical seasonal evergreen forests 44
  2.5.3 Tropical deciduous forests 44
  2.5.4 Subtropical evergreen broadleaved forests 46

- 2.5.5 Forests on extreme soil types 46
- 2.5.6 Secondary forests 48
- 2.5.7 Logged forests 49
- 2.5.8 Bamboo forests 49
- 2.5.9 Savannas and grasslands 50
- 2.5.10 Shrublands and thickets 51
- 2.5.11 Beach vegetation and coastal forests 51
- 2.5.12 Plantations 51
- 2.5.13 Agroforestry 52
- 2.5.14 Other dryland crops 53
- 2.6 Montane vegetation 54
- 2.7 Wetlands 56
  - 2.7.1 Mangrove forests 56
  - 2.7.2 Brackish water swamp forests 56
  - 2.7.3 Freshwater swamp forests 57
  - 2.7.4 Peat swamp forests 57
  - 2.7.5 Herbaceous swamps 58
  - 2.7.6 Paddy fields 59
- 2.8 Urban areas 60

3 Biogeography 62

- 3.1 Introduction 62
- 3.2 Origins of the biogeographical regions 62
- 3.3 Biogeographical transitions 65
  - 3.3.1 Tropical East Asia and the Australian Region 65
  - 3.3.2 Tropical East Asia and the Palaearctic Region 65
  - 3.3.3 Tropical East Asia and India 67
- 3.4 How many species are there in Tropical East Asia? 68
- 3.5 Patterns of diversity within Tropical East Asia 68
- 3.6 Subdividing Tropical East Asia 76
- 3.7 Island biogeography 77
  - 3.7.1 Continental islands on the Sunda Shelf 78
  - 3.7.2 Hainan and Taiwan 79
  - 3.7.3 Ryukyu (Nansei) Islands 80
  - 3.7.4 Ogasawara (Bonin) Islands 80
  - 3.7.5 Krakatau 80
  - 3.7.6 Andaman and Nicobar Islands 81
  - 3.7.7 Islands off the west coast of Sumatra 81
  - 3.7.8 The Philippines 82
  - 3.7.9 Sulawesi 84
  - 3.7.10 Sangihe and Talaud Islands 85
  - 3.7.11 Nusa Tenggara 86
  - 3.7.12 Maluku 87

4. The ecology of plants: from seed to seed 88

- 4.1 Introduction 88
- 4.2 Study sites 88

4.3 Plant phenology 90
  4.3.1 Leaf phenology 90
  4.3.2 Reproductive phenology 93
  4.3.3 Bamboos and *Strobilanthes* 94
  4.3.4 General flowering in lowland dipterocarp forests 95
  4.3.5 Reproductive phenology in other forest types 97
  4.3.6 Figs 97
4.4 Pollination 99
  4.4.1 Wind 99
  4.4.2 Bees and wasps 100
  4.4.3 Beetles 102
  4.4.4 Flies 103
  4.4.5 Butterflies and moths 104
  4.4.6 Thrips and other insects 104
  4.4.7 Birds 105
  4.4.8 Bats and other mammals 106
4.5 Seed dispersal 107
  4.5.1 Wind, water, and mechanical dispersal 108
  4.5.2 Birds 109
  4.5.3 Bats 111
  4.5.4 Primates 112
  4.5.5 Carnivores 113
  4.5.6 Terrestrial herbivores 114
  4.5.7 Rodents 114
  4.5.8 Ants and wasps 115
  4.5.9 People 115
4.6 Gene flow by pollen and seeds 115
4.7 Seed predation and seed pathogens 116
4.8 Germination and seedling establishment 118
4.9 The seedling stage 119
4.10 Sapling to adult 121
4.11 Sprouts and resprouting 123
4.12 Tree guilds 123
4.13 Other life forms 124
  4.13.1 Lianas 124
  4.13.2 Ground herbs 125
  4.13.3 Epiphytes 125
  4.13.4 Hemi-epiphytes and stranglers 127
  4.13.5 Parasites 127
4.14 The maintenance of species diversity in tropical forests 128
4.15 Functional traits, phylogeny, and community assembly 130
4.16 Forest succession 131
4.17 Prediction in plant ecology 132

5 The ecology of animals: foods and feeding 133

5.1 Introduction 133
5.2 Herbivores 133

5.2.1 Leaf eaters 134
5.2.2 Shoot feeders, bark feeders, and wood feeders 139
5.2.3 Root feeders 139
5.2.4 Sap suckers 139
5.2.5 Ants as 'cryptic herbivores' 140
5.2.6 Gall formers 141
5.2.7 Flower visitors 141
5.2.8 Frugivores 142
5.2.9 Granivores 145
5.3 Detritivores 146
5.4 Carnivores 147
5.4.1 Invertebrate feeders 147
5.4.2 Vertebrate feeders 152
5.4.3 Blood feeders 156
5.5 Parasites and parasitoids 157
5.6 Omnivores 157
5.7 Scavengers 158
5.8 Coprophages 159

6 Energy and nutrients 161

6.1 Introduction 161
6.2 Water 161
6.3 Energy and carbon 162
6.3.1 Primary production 162
6.3.2 Biomass 166
6.3.3 Net ecosystem production and exchange 167
6.4 Soil nutrients 169
6.4.1 Nitrogen 170
6.4.2 Phosphorus 172
6.4.3 Essential cations 174
6.4.4 Micronutrients 174
6.4.5 Aluminium, manganese, hydrogen, and metal hyperaccumulation 175
6.5 Animal nutrition 176

7 Threats to terrestrial biodiversity 177

7.1 Introduction 177
7.2 The ultimate causes of biodiversity loss 177
7.2.1 The growth of human populations 177
7.2.2 Poverty 179
7.2.3 Corruption and poor governance 179
7.2.4 Globalization 181
7.3 Major threats to biodiversity in Tropical East Asia: habitat loss 181
7.3.1 Deforestation 182
7.3.2 Fragmentation 184
7.3.3 Mining 186
7.3.4 Urbanization and the infrastructure development 187

7.4 Major threats to biodiversity in Tropical East Asia: exploitation 188
  7.4.1 Logging 188
  7.4.2 Collection of non-timber forest products 190
  7.4.3 Hunting 191
7.5 Fires 194
7.6 Invasive species, native winners, and biotic homogenization 196
7.7 Diseases of wildlife, people, and plants 199
7.8 Air pollution and nutrient enrichment 200
7.9 Climate change 201
  7.9.1 Drivers and mechanisms 201
  7.9.2 Observations and predictions 204
  7.9.3 Impacts 207
7.10 Predicting extinctions 211

8 Conservation in the Anthropocene 213

8.1 Introduction: why conserve biodiversity? 213
8.2 Who should pay and how? 214
  8.2.1 Funding from domestic governments and foreign aid 215
  8.2.2 The role of non-governmental organizations 215
  8.2.3 Voluntary conservation measures: philanthropy, corporate social responsibility, and socially responsible investment 216
  8.2.4 Crowdfunding 217
  8.2.5 Payments for ecosystem services 217
  8.2.6 REDD+ 219
  8.2.7 Biodiversity offsets 222
  8.2.8 Tourism 223
  8.2.9 Sustainability standards, certification, and ecolabels 226
8.3 What should be protected? 227
  8.3.1 Surrogates in conservation planning 227
  8.3.2 Setting priorities 228
8.4 Protecting areas 233
  8.4.1 Establishing new protected areas 233
  8.4.2 Enhancing protection for existing protected areas 235
  8.4.3 Community-based conservation 236
8.5 Sustainable exploitation 238
  8.5.1 Logging and the collection of non-timber forest products 238
  8.5.2 Hunting 239
  8.5.3 Controlling trade 239
8.6 Countryside conservation: managing the matrix 240
8.7 Environmental Impact Assessment 243
8.8 Controlling fires 243
8.9 Managing invasive species 244
8.10 Minimizing global climate change and its impacts in Tropical East Asia 246
  8.10.1 Reducing greenhouse gas emissions 246
  8.10.2 Minimizing impacts 247
  8.10.3 Biofuels 248

8.11 Air pollution 249
8.12 *Ex situ* conservation 249
    8.12.1 Animals 249
    8.12.2 Plants 250
8.13 Ecological restoration and reintroduction 251
    8.13.1 Restoring forests 251
    8.13.2 Reintroducing species 255
    8.13.3 Rewilding 257
8.14 Conservation leakage 258
8.15 Education 258
8.16 Citizen science 259
8.17 The way forward for biodiversity conservation in Tropical East Asia 260
8.18 Final words 261

References 263
Index 313

CHAPTER 1

Environmental history

1.1 Why 'Tropical East Asia'?

Tropical East Asia (TEA) is used in this book to refer to the eastern half of the Asian tropics and subtropics, north to 30°N (Figure 1.1). Politically, TEA consists of northeastern India, along with the Andaman and Nicobar Islands, the extreme east of Nepal, Bangladesh, Bhutan, Myanmar, Laos (Lao People's Democratic Republic), Cambodia, Vietnam, Thailand, Malaysia, Singapore, Brunei (Brunei Darussalam), the Philippines, western Indonesia, and southern China, plus the Ryukyu Islands of Japan. The western boundary is at around 88°E, the northern boundary at 30°N, the southern boundary at 9°S, and the eastern boundary between 123° and 128°E. Geographically, this is 'Southeast Asia', but this term is nowadays most often applied to the member countries of the Association of South-East Asian Nations (ASEAN), which excludes Bangladesh, Bhutan, China, India, Nepal, and Japan, and includes all of Indonesia, east to Papua. In this modern usage, Southeast Asia is not a coherent biogeographical region, while TEA is, even if the precise boundaries are somewhat arbitrary.

TEA is mostly warm and wet enough to support forest, and these forests in turn support a flora and fauna that is distinctively tropical Asian. Some of these distinctive elements drop out before (or after) the northern border (30°N) chosen for this book, and some are missing from islands that have never had an overland connection with the Asian mainland, including most of the Philippines, Sulawesi, Ryukyus, Andamans, and Nicobars (see 3.7). However, no significant part of TEA is dominated by plants and animals that are characteristic of other biogeographical regions. The most arbitrary border is the western one. The western half of the Asian tropics is, in general, considerably drier than the east, and there are large areas that were never covered in closed forests. However, there are ecosystems that closely resemble those of TEA in the wetter parts of the Western Ghats of southwest India and Sri Lanka, as well as similarities between Indian ecosystems and the driest areas of northwestern TEA.

1.2 The importance of history

TEA is an odd 'region'. Although it is more or less coherent biogeographically, it is an untidy and unstable mosaic in almost every other sense. Unlike other major biogeographical regions, there is no stable, ancient geological core (see 1.3) and much of the region today consists of islands and peninsulas, surrounded by seas. Moreover, these seas are shallow, so many—but not all—of the islands were part of the Asian mainland less than 10,000 years ago (see 1.4). There are steep climatic gradients, which have changed dramatically over the last few million years (see 1.5), and the region is still highly active tectonically, with numerous active volcanoes and frequent massive earthquakes (see 1.6). Then people arrived (see 1.7 and 1.8), in multiple waves, overlaying a mosaic of cultural influences that have transformed the natural landscapes of the region. Stand anywhere in TEA and look around: what you see is a result of interactions between geology, climate, and human cultures, and their varied histories on a range of timescales, and the evolution and dispersal

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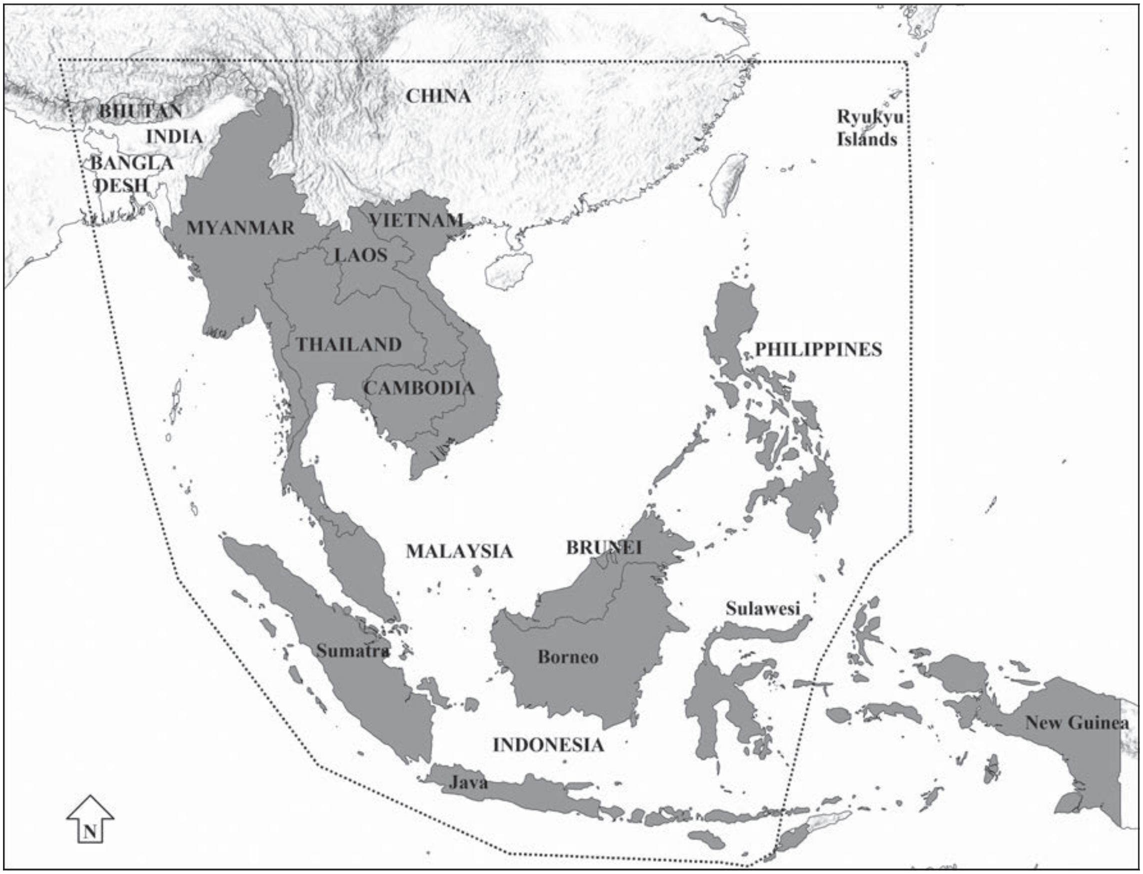

Figure 1.1 Map of the region showing Tropical East Asia as defined in this book (dashed line) and the member countries of the Association of Southeast Asian Nations (ASEAN) (dark grey). Map by Alice Hughes.

of plants and animals. Current environmental conditions—the subject of Chapter 2—explain part of what you see, but history explains at least as much and often more. This chapter, therefore, focuses on the history of TEA.

1.3 Plate tectonics and the origin of Tropical East Asia

Biologists have often viewed tectonic plates as 'rafts' that carry terrestrial and freshwater organisms across oceans, but this analogy is misleading. Apart from the slow speed at which they move—typically 2–10 cm per year (about the speed fingernails grow)—tectonic plates float on the magma, not the ocean, and can become submerged under water, with fatal consequences for their terrestrial biota. Excessive confidence in the ability of plate tectonics to explain modern distributions has caused some biogeographers to prefer tectonic explanations to alternatives, such as transoceanic dispersal. Dated molecular phylogenies, however, show that the modern distributions of many widespread taxa, particularly of plants, have arisen too recently for tectonic explanations to be possible (e.g. Bardon et al. 2016).

The whole of TEA is a giant jigsaw puzzle of continental fragments (Figure 1.2) (Hall 2013, 2017). In the Palaeozoic (Table 1.1), 400 million years ago, the major pieces formed part of the margins of the southern supercontinent of Gondwana. Between 350 and 140 million years ago, these fragments rifted from Gondwana and drifted northwards. The progressive amalgamation of these continental fragments formed the core of modern TEA before the

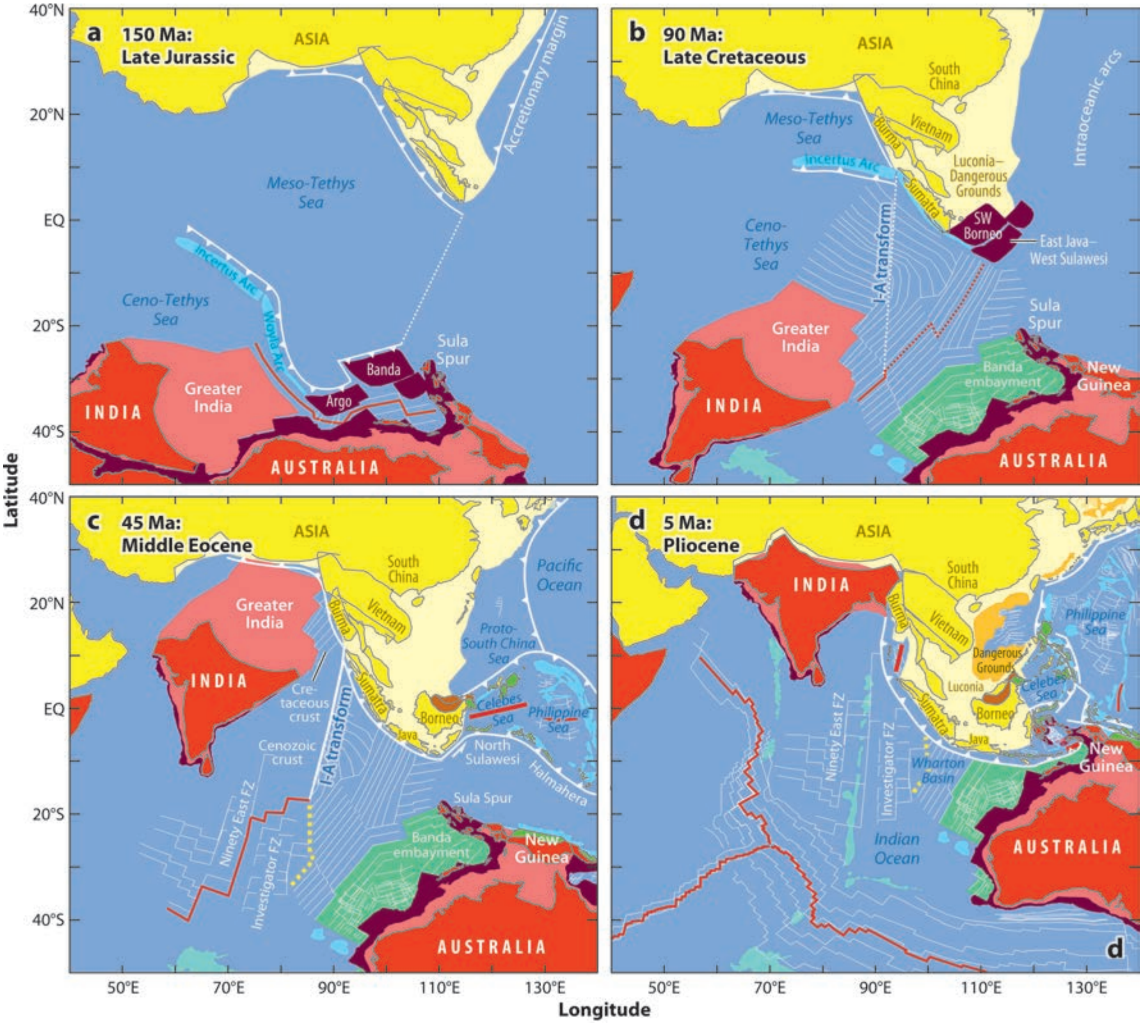
a 150 Ma:
Late Jurassic
ASIA
Accretionary margin
Meso-Tethys Sea
Incertus Arc
Woyla Arc
Ceno-Tethys Sea
Sula Spur
Banda
Argo
Greater India
INDIA
AUSTRALIA
b 90 Ma:
Late Cretaceous
ASIA
South China
Meso-Tethys Sea
Burma
Vietnam
Incertus Arc
Sumatra
Luconia–Dangerous Grounds
Intraoceanic arcs
SW Borneo
East Java–West Sulawesi
I-A transform
Ceno-Tethys Sea
Greater India
Sula Spur
Banda embayment
New Guinea
INDIA
AUSTRALIA
c 45 Ma:
Middle Eocene
ASIA
South China
Pacific Ocean
Greater India
Burma
Vietnam
Proto-South China Sea
INDIA
Cretaceous crust
Sumatra
I-A transform
Borneo
Celebes Sea
Philippine Sea
Java
Cenozoic crust
North Sulawesi
Halmahera
Sula Spur
Ninety East FZ
Investigator FZ
Banda embayment
New Guinea
AUSTRALIA
d 5 Ma:
Pliocene
ASIA
INDIA
South China
Burma
Vietnam
Philippine Sea
Dangerous Grounds
Luconia
Celebes Sea
Borneo
Sumatra
Java
Ninety East FZ
Investigator FZ
Wharton Basin
New Guinea
Indian Ocean
AUSTRALIA
d
40°N
20°N
EQ
20°S
40°S
Latitude
50°E
70°E
90°E
110°E
130°E
Longitude

Figure 1.2 Tropical East Asia is a mosaic of continental fragments, most of which were rifted from the southern supercontinent of Gondwana over the last 400 million years. The reconstructions shown here start in the Late Jurassic, when the older, western, part of Southeast Asia had already been assembled. They show Tropical East Asia at (a) 150 million years ago, (b) 90 million years ago, (c) 50 million years ago, and (d) 5 million years ago. Hall (2017) should be consulted for more details. Maps from Hall (2017), used with permission.

end of the Cretaceous, 66 million years ago, although there have been considerable changes in the shape since then. Fossil evidence shows that each fragment carried its own characteristic flora and fauna when it separated from Gondwana. However, few modern TEA lineages are old enough to have travelled on these fragments, so the Gondwanan geological origin of most of the region's core has had little direct influence on the modern biota.

While the major components of TEA were assembled by the end of the Cretaceous, two much larger Gondwanic fragments, India and Australia, were still heading north (Figure 1.2). Initially they were on separate plates, and India moved much faster than Australia. Although most of India is excluded from TEA as defined here, its collision with Eurasia, starting 60–50 million years ago, had significant impacts on the shape, climate, and biogeography of the entire region. Tectonic deformation caused the extrusion of Indochina, the clockwise rotation of the Malay Peninsula by 60°, and its southwards displacement by more than 580 km (Otofuji et al. 2017).

Table 1.1 Simplified geological timescale from the start of the Palaeozoic era. The 'Tertiary' comprises the Palaeogene and the Neogene and has no official rank. The Anthropocene has not yet been formally proposed and accepted. Ages, in millions of years (Ma), are for the base of each unit.

Era	Period	Epoch	Age (Ma)
Cenozoic	Quaternary	'Anthropocene'	0.00007
		Holocene	0.0117
		Pleistocene	2.6
	Neogene	Pliocene	5.3
		Miocene	23
	Palaeogene	Oligocene	34
		Eocene	56
		Palaeocene	66
Mesozoic	Cretaceous		145
	Jurassic		201
	Triassic		252
Palaeozoic	Permian		299
	Carboniferous		359
	Devonian		419
	Silurian		443
	Ordovician		485
	Cambrian		541

The Australian plate then collided with the Philippine and Asian plates in the early Miocene (*c*.25 million years ago), causing a smaller (approximately 19°) counter-clockwise rotation of the Malay Peninsula and a large (approximately 50°) counter-clockwise rotation of Borneo, resulting in the stretched, L-shaped Sunda block of today. This ongoing collision—Australia continues to move north-northeast at around 7 cm per year—continues to be responsible for much of the tectonic and volcanic activity in the region, while the progressive constriction of the Indonesian Throughflow, between the Pacific and Indian Oceans, had profound and incompletely understood implications for the regional and global climate (Christensen et al. 2017).

In contrast to the Gondwanic fragments that make up the Cretaceous core of TEA, both India and Australia carried modern plant and animal lineages on their northward journeys. The biological interchanges that followed their collisions with Asia have made significant, but rather different, contributions to the diversity of the regional biota at the family and genus level. India's Gondwanan flora originated in a temperate climate and the rapid passage across the equator may have eliminated some sensitive taxa, while the end-Cretaceous global extinctions and the Deccan Trap volcanism (see 1.6) further thinned out the Gondwanan survivors. However, fossil pollen of the Dipterocarpaceae has been found in Late Cretaceous central India—then still south of the equator—suggesting that TEA's most important tropical tree family may have arrived from Gondwana on India (Prasad et al. 2018), and fossil and/or molecular evidence suggests that other taxa may have followed the same route (Morley 2018).

Despite the terrestrial connection, overland exchanges between India and Southeast Asia have been restricted by the Himalayan range to a narrow 'Assam gateway' in the northeast, where similar climates and ecosystems meet, and these exchanges peaked during the Mid-Miocene Climatic Optimum, 15 million years ago, when there was a continuous belt of rainforest along the Himalayan foothills (Klaus et al. 2016). Exchanges with Australia, in contrast, started in the early Oligocene, as the water gap narrowed, but even today are still filtered through the islands and deep water of Wallacea (Figure 1.2).

The core of TEA has changed relatively little since the Cretaceous, with Borneo and Sumatra at equatorial latitudes since at least the Eocene (Figure 1.2). However, there have been both major uplift and major subsidence around the margins, although many details are still uncertain (Hall 2017). Sulawesi, the third largest island in TEA, arose following a collision between the Sula Spur, a prominent feature of the northern Australian margin, and the North Sulawesi volcanic arc, starting in the early Miocene around 25 million years ago (Figure 1.2). However, much of the present island was created only in the last 5 million years, and particularly in the last 2 million (Nugraha and Hall 2018). Large areas of northeastern Sumatra and Java, and all or most of many islands in Wallacea, also appear to have been lifted above sea level within the last 5 million years (Molnar and Cronin 2015). In these areas, modern geography is an unreliable guide to even the relatively recent past.

Finally, the Philippine islands have had an extremely complex history and there is still no fully accepted synthesis. The islands were formed by a variety of tectonic and volcanic processes in widely separated parts of the western Pacific, and were then progressively brought together over the last 25 million years (Hall 2017). Most have arisen from the sea and been colonized by overwater dispersal. Although they are now close together, many are still separated by deep channels that remained flooded during the lowest sea levels (see 1.4). However, at least the northern half of Palawan, southwestern Mindoro, and northwestern Panay contain continental crust, rifted from the margins of southern China in the Oligocene by the opening of the South China Sea (Y. Yan et al. 2018). The presence of limestone shows they were at least partly submerged in the past, but it is possible that part of Palawan remained continuously above water on the journey from China and may therefore have transported poorly dispersed animal lineages to the Philippines. This ‘Palawan Ark’ hypothesis is supported by phylogenetic evidence from several Philippine-endemic frog and gecko lineages (Siler et al. 2012; Brown et al. 2016). Palawan may also have had a terrestrial connection to Borneo at some time in the Pleistocene (Ochoa and Piper 2017).

1.4 Sea-level changes

Because of the region’s extensive shallow seas, changes in the global sea level have been the major influence on both the total land area in TEA and the availability of dry-land connections between land masses over the last 3–5 million years. Fluctuations in global sea level are caused by a variety of mechanisms, but changes in water volume as a result of ice volume changes have dominated for the last few million years (Rohling et al. 2014). During the Eocene, there were no major high-latitude ice sheets and sea level was 60–70 m higher than today. During the Eocene–Oligocene, the build-up of the East Antarctic ice sheet resulted in a decline in sea levels, although they were still 20–30 m above present in the Miocene and Pliocene. Large northern hemisphere ice sheets first appeared in the late Pliocene and subsequent fluctuations in their volume have resulted in large variations in sea level. The first major (>70 m) fall in sea level occurred 2.15 million years ago and subsequent glacial periods have seen falls of up to 120 m.

These changes in ice volume were initiated by periodic variations in the Earth’s orbit that change the amount, distribution, and timing of solar radiation reaching the Earth’s surface. These orbital variations are, in turn, caused by gravitational interactions between the Earth and the other planets in the solar system. The periodicity of the changes in ice volume and sea level were initially dominated by the 41,000-year cycle in the tilt of the Earth’s axis with respect to the plane of its orbit (obliquity), but for the last million years, a 100,000-year cycle has been dominant. This cycle coincides with periodic changes in the shape of the Earth’s orbit from more elliptical to less elliptical (eccentricity), but the mechanism by which this dominates the glacial cycle, despite a relatively small effect on solar radiation, is still unclear (Chalk et al. 2017). It was not only the periodicity that changed at this ‘Mid-Pleistocene Transition’, but also the amplitude of the fluctuations, and the shapes of the cycles, from symmetrical periods of cooling and warming to the more recent ‘sawtooth’ pattern, with a long period of gradual cooling followed by rapid warming. Late Pleistocene ice ages were thus longer and colder, and sea levels lower, although the complex interplay between orbital variations with different periodicities means that each glacial and interglacial period is unique. Moreover, although insolation changes initiate the cycles, their magnitude is increased by amplifying feedbacks from planetary albedo (reflectivity), which increases when ice covers the sea and snow covers the land, and by atmospheric carbon dioxide (CO_2), which is boosted during warm periods by release from soils and oceans.

These changes in sea level periodically exposed large areas of land, almost doubling the land area of TEA at the lowest sea levels (Figure 1.3). The large Sunda Shelf islands of Borneo, Java, and Sumatra were connected to mainland Asia, along with many smaller islands, while Hainan and Taiwan were connected to southern China. To the east, large areas of the Sahul Shelf were also exposed, connecting Australia and New Guinea, but 'Sundaland' and 'Sahulland' were still separated by deep ocean water. Sulawesi and the other islands between the Sunda and Sahul Shelves remained isolated, as did those of the Philippines, although they coalesced into fewer, larger islands. The sea level was at its lowest for only brief periods (Figure 1.4), but the estimated average sea level for the last million years was 62 m below that of today, which would have been sufficient to connect all the major islands on the Sunda Shelf, as well as Hainan, to the Asian mainland. At the other extreme, some previous interglacials experienced sea levels at least 10 m above present, leading to extensive coastal flooding.

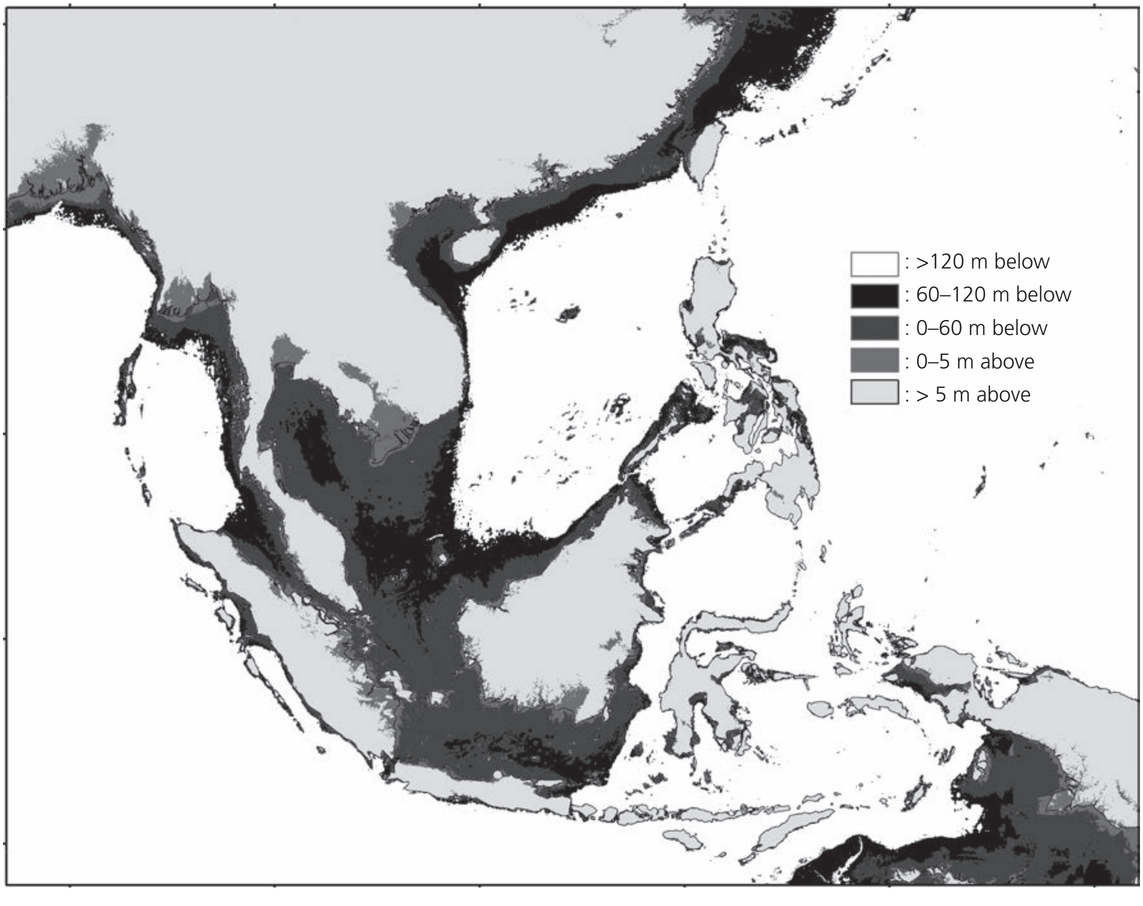

Figure 1.3 Additional land exposed by sea levels 60 m below present (the average for the last 800,000 years) and 120 m below present (the lowest level reached at the last glacial maximum, 20,000 years ago), plus land covered by sea levels 5 m *above* present (the Holocene highstand). Map made by Alice Hughes using bathymetric data from GEBCO and ArcGIS 10.1.

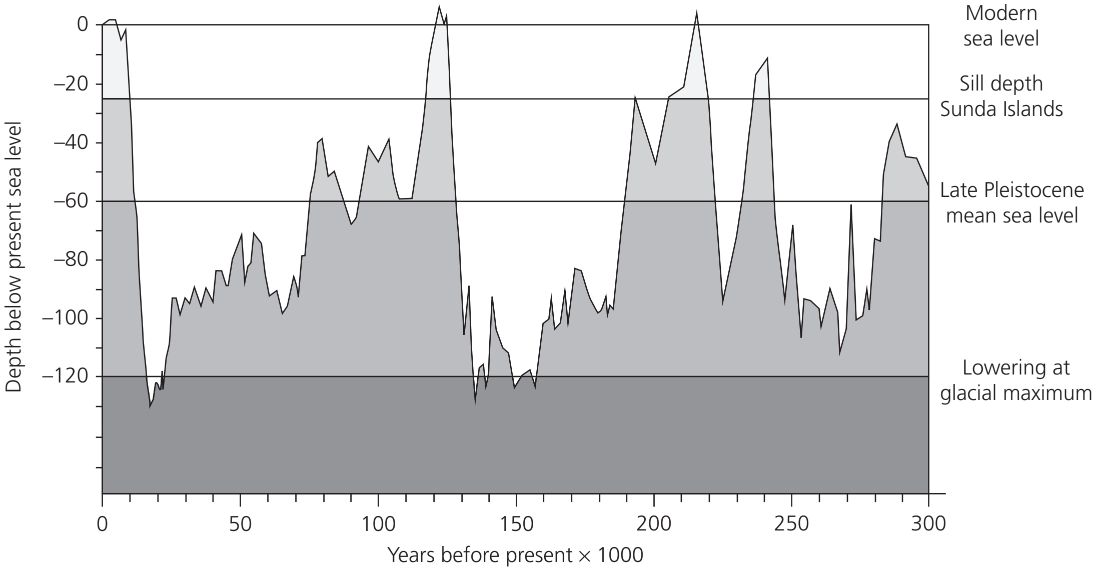

Figure 1.4 Sea levels over the last 300,000 years relative to the present day. From Hope (2005).

The sea level at the last glacial maximum (LGM), 20,000 years ago, was approximately 120 m below present. It rose to the present level by 7000 years ago, reached a high point of 1–4 m above present in the mid-Holocene, and then fell back to the present level again by 1000 years ago. Most links to major islands were lost between 11,000 and 9000 years ago and the mid-Holocene 'highstand' would have flooded large areas of low-lying land, such as the Mekong and Chao Phraya deltas.

1.5 Changes in climate and vegetation

The Earth's climate system is changing on all timescales. On timescales of tens of thousands to hundreds of thousands of years, much of this change is generated by the oscillations in the Earth's orbit mentioned in section 1.4, leading to changes in the amount and distribution of solar radiation reaching the Earth's surface. These orbital oscillations cause climatic oscillations about a mean that varies on million-year timescales, largely as a result of tectonic processes, such as changes in land distribution and topography, the opening and closing of oceanic gateways, and greenhouse-gas concentrations. On these longer timescales, atmospheric CO_2 levels appear to be the most important factor driving climate change, although uncertainties in the CO_2 record make it difficult to confirm the tightness of this link (Zhang et al. 2013; Holbourn et al. 2018).

Evidence for past climates comes largely from the archive formed by the gradual accumulation of marine, freshwater, and terrestrial sediments. A variety of physical indicators are available, including, in marine sediments, oxygen isotope ratios and magnesium/calcium ratios in planktonic foraminifera, as well as unsaturated alkenones from marine phytoplankton. The physical and chemical properties of lake sediments can provide information on past environmental conditions in the surrounding watershed, as well as trapping dust brought by wind from distant sources. The oxygen and carbon isotope records from stalagmites in caves are also valuable, especially because they can be accurately dated by uranium–thorium dating. For many ecological purposes, however, biological indicators can be more useful, since they integrate climatic variables in an ecologically meaningful way. For terrestrial ecology, the pollen and fern spores preserved in lake, swamp, and marine sediments are most important and can be used, with skill and experience, to reconstruct past vegetation and plant communities. Tree-ring records are another potential source of information for the last millennium. The following synthesis is based on all the available types of data, but as the records become increasingly sparse with time back from the present, the inferences possible from them become increasingly broad and general. Indeed, every improvement in the temporal resolution of the record reveals previously unrecognized climatic events!

In the Early Cretaceous, tropical rainforests were dominated by gymnosperms and ferns, but angiosperm-dominated rainforests have existed in Southeast Asia since the Late Cretaceous or early Palaeocene (Morley 2018). There has been a long-term global cooling trend for the last 50 million years, but with major fluctuations (Figure 1.5). The early Eocene included two major periods of exceptional warmth, with tropical lowland temperatures 3–5°C greater than today: the short-lived Palaeocene–Eocene Thermal Maximum (56 million years ago and lasting *c*.200,000 years) and the longer Early Eocene Climatic Optimum (*c*.53–50 million years ago) (Jaramillo and Cárdenas 2013). During this period, many tropical and subtropical taxa extended far north of their current ranges, allowing frost-sensitive species to migrate between Eurasia and North America across the Bering and North Atlantic land bridges. Global cooling in the middle and late Eocene resulted in a major retraction of rainforests, with even the equatorial regions apparently significantly drier and more seasonal (Morley 2018). A flora from the middle Eocene of Hainan, 49–37 million years ago, was dominated by a mixture of angiosperm taxa in the families Lauraceae, Fagaceae, Fabaceae, Ulmaceae, and others, that would today be considered typical of temperate, subtropical, and tropical climates (Spicer et al. 2014). The dipterocarps, represented by a species of *Shorea*, were first recorded in TEA in the late Eocene, in southwest Guangdong (22°N) (Feng et al. 2013). Oaks in *Quercus* section *Cyclobalanopsis*, which are now a dominant component of the subtropical broadleaved evergreen forests, appeared around the same time, with the earliest fossils in western Japan (M. Deng et al. 2018).

In the previous editions of this book, modern-looking floras—and forests in which a time-travelling modern botanist would feel immediately at home—were considered to have first appeared in TEA in the early Miocene, about 23 million years ago. It is now becoming clear, however, that this assumption was based on the rarity of fossil floras recognized as Oligocene. A well-preserved fossil flora from central Yunnan (25°N), robustly dated to the early Oligocene, 33–32 million years ago, is almost fully modern at the generic level, suggesting the 'modernization' of the vegetation, at least in northern TEA, occurred between the middle Eocene and earliest Oligocene, 40–30 million years ago (Spicer 2017; Linnemann et al. 2018). Both fossil and molecular data show that long-lived woody plants evolve slowly (Levin 2000),

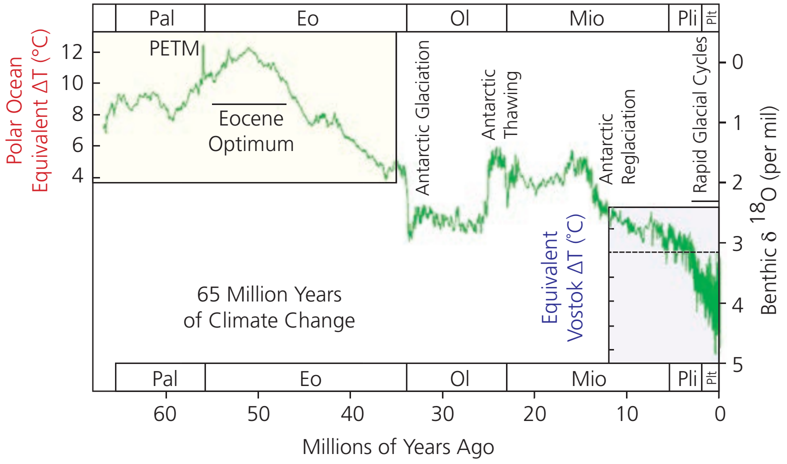

Figure 1.5 Sixty-five million years of global temperature change. Figure prepared by Robert A. Rohde for Global Warming Art and available on Wikimedia Commons. Used under the Creative Commons CC BY-SA 3.0 license.

so it is not unreasonable to suggest that these forests were both floristically and functionally similar to those of the region today. The component plants have expanded, contracted, and shifted their ranges in response to climate change, but there has been little turnover at the generic level. Tropical-like rainforests extended furthest north about 15 million years ago, when *Dipterocarpus* and *Shorea* grew in Fujian (24°N) (Shi et al. 2014) (Figure 1.6). In contrast to the plants, regional vertebrate faunas have changed considerably since the Oligocene at both the generic and family level (Patnaik 2016). The early Miocene forests of TEA had an ape-dominated primate fauna, without monkeys or gibbons, and supported now-extinct families of ungulates and carnivores.

Efforts to understand the impact of global cooling in East Asia have been complicated by uncertainties in the timing of the uplift of the Tibetan Plateau during the same period and its consequences, if any, for the origins and intensity of the Asian monsoons. Recent work has pushed back the earliest evidence for a high Tibetan Plateau (>4 km) into the early Eocene (Spicer 2017). Monsoon climates have existed in the Asian tropics for at least 56 million years, but the period from the late Eocene to the late Pliocene saw a gradual intensification, which may be associated with both global cooling and, for the Indian monsoon, the Himalaya first substantially exceeding the height of the Tibetan Plateau around 15 million years ago. The intensifying monsoons led to increasing rainfall seasonality in northern TEA, the replacement of evergreen by semi-evergreen forest in Northeast India (Khan et al. 2017), and a progressive decline in tree species that were dependent on winter or spring rainfall for reproduction (e.g. *Cedrus*; Su et al. 2013).

A high-resolution isotope record from the South China Sea records three cooling episodes in the middle to late Miocene: a major one *c*.13.9 million years ago, which resulted in a large expansion in the East Antarctic ice sheet, a smaller one *c*.9.0 million years ago, and then a prolonged cooling spell from

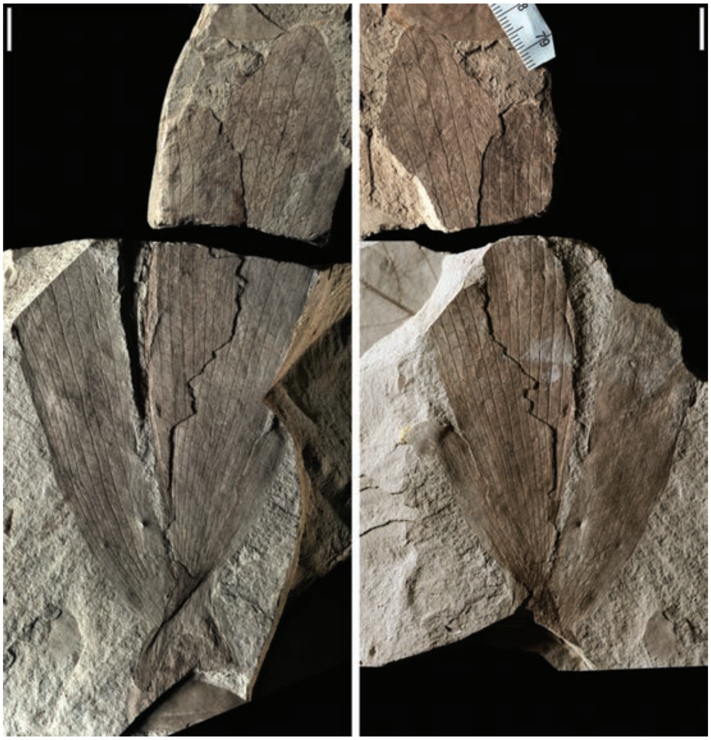

Figure 1.6 Fossils of the winged fruits of a *Shorea* species (Dipterocarpaceae) from Southeast China in the middle Miocene, *c*.14.8 million years ago. Scale bar = 1 cm. Photograph courtesy of Gongle Shi.

c.7 to *c*.5.5 million years ago, culminating in the development of short-lived northern hemisphere ice sheets (Holbourn et al. 2018). This coincided with an intensification of the East Asian winter monsoon, leading to cooling and drying of terrestrial environments in northern TEA. After a brief reversal at the beginning of the Pliocene, 5.3 million years ago, the cooling trend continued, and the early Pliocene was the last period that was consistently warmer than the present.

Late Pliocene climates alternated between relatively warm/wet and cool/dry conditions, but the amplitudes of these changes and the accompanying vegetation shifts were much less than in the Pleistocene. The first 'deep' glacial occurred 2.15 million years ago (Rohling et al. 2014). Subsequent changes in the climate of TEA have largely followed the changes in ice volume and sea level, although the match is by no means perfect, since regional and local climates are influenced by a wider array of factors than those that control global ice volume. When the northern hemisphere glaciers were at their maximum extent, global sea levels and temperatures were at their lowest. In TEA, the replacement of large areas of warm, wet sea by cool, dry land also resulted in a general decline in rainfall, while the winter monsoon was strengthened and the summer monsoon weakened.

Most information is available for the most recent glacial cycle and, in particular, the period from the LGM, 20,000 years ago, to the present day. Terrestrial air temperatures at the LGM appear to have been only 2–4°C cooler in the lowland tropics and subtropics (Annan and Hargreaves 2013), although the cooling appears to have been considerably greater (<6–9°C) at high altitudes, implying a steeper temperature lapse rate. There are also indications of lower rainfall from many sites. In general, the decline in temperature had most influence at high altitude, where treelines were depressed and montane forest expanded downwards (e.g. Pickett et al. 2004), and towards the northern limits of the region, where tropical and subtropical evergreen trees retreated, and temperate deciduous species spread south into the subtropics (e.g. Meng et al. 2017; S. Y. Wang et al. 2017; Xiao et al. 2018). At lower altitudes and latitudes, the decline in rainfall seems to have had a greater impact. More open vegetation types, including grassland, expanded in response to drier and more seasonal climates in northern Sundaland and in Java, Sulawesi, and Wallacea (Amano et al. 2016; Wicaksono et al. 2017; Bacon et al. 2018), and probably also on the exposed shelf of the northern South China Sea (Yu et al. 2017).

Atmospheric CO_2 levels were also considerably lower (approximately 180 ppm) at the LGM than during the Holocene (approximately 280 ppm). Changes in CO_2 concentrations over this range have a large effect on C3 photosynthesis, and thus on the growth of woody plants, but a much smaller effect on C4 photosynthesis, and thus on most tropical grasses. Moreover, in dry environments, higher CO_2 concentrations allow plants to open their stomata less, thus reducing water stress. The overall impact is that higher CO_2 concentrations favour trees in competition with grasses while lower CO_2 favours grasses. Vegetation models show that these CO_2 effects must be taken into account in order to explain changes in the tropics and subtropics over the glacial–interglacial transition (Bragg et al. 2013). In TEA, changing CO_2 concentrations are likely to have increased the amplitude of the temperature- and rainfall-driven swings in vegetation between glacial openness and interglacial closure.

There is pollen and other evidence for the persistence of areas of lowland tropical rainforest in central Sundaland at the LGM, with the expansion of rainforest onto the exposed Sunda Shelf at least partly compensating for a retraction to the north and south (Raes et al. 2014). In contrast, genetic studies suggest that free movement across the Sunda Shelf between the major modern islands was not possible for rainforest-dependent plants and animals during most of the Pleistocene. For example, time-calibrated phylogenies of the forest-dependent colugo (*Galeopterus variegatus*) (Figure 1.7) and a forest-dependent skink (*Eutropis rugifera*) suggest pre-Pleistocene (>3.5 million years ago) separation between the populations on different major islands (Karin et al. 2017; Mason et al. 2018). In contrast, the more habitat-tolerant red muntjac apparently dispersed freely (Martins et al. 2017).

The flat terrain, coarse sandy soils, and large river systems of the exposed shelf could have acted as a selective barrier for some smaller species. The exposed area was mostly very flat and the biggest

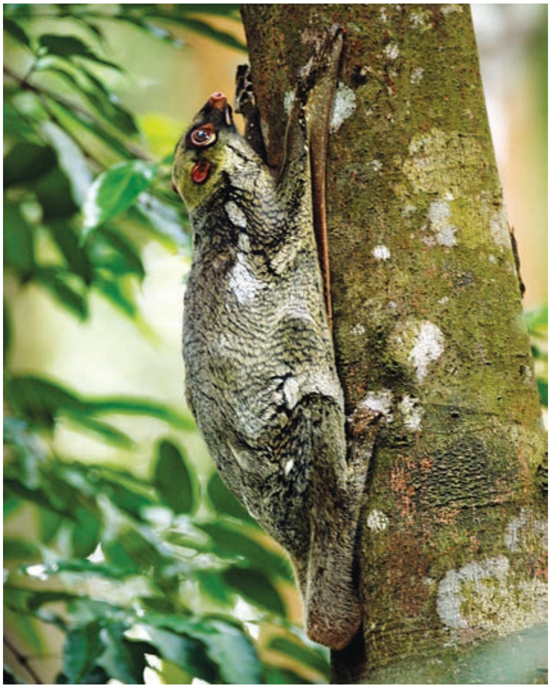

Figure 1.7 A colugo (*Galeopterus variegatus*) in the Central Catchment Nature Reserve, Singapore. A time-calibrated phylogeny (Mason et al. 2018) suggests that populations of this forest-dependent species on different islands in Sundaland separated more than 3.5 million years ago, and that colugos did not disperse freely across the exposed Sunda shelf during Pleistocene low sea levels. Photograph by Lip Kee Yap, Wikimedia Commons, used under the Creative Commons Attribution-Share Alike 2.0 Generic license.

rivers were the size of the modern Amazon, so much of the area would have been occupied by seasonally flooded freshwater swamp forest, peat swamp forest, or heath forest, rather than typical dryland dipterocarp forest. Some evidence also suggests the existence of a north–south 'savanna corridor', or perhaps just a belt of more open forest, through the centre of Sundaland during the glacial maximum, although most recent studies conclude that this was unlikely (Raes et al. 2014). The genetic evidence suggests that Borneo was particularly isolated, while movements between the Malay Peninsula and Sumatra were apparently easier (Leonard et al. 2015; Patel et al. 2017). There is also evidence of deep divergences between eastern and western Borneo for many species, with the montane regions apparently acting as major barriers (Mason et al. 2018). Java is most distinct of the major islands of Sundaland, but this may reflect its drier environment today as much as the history of overland connections.

Data from multiple proxies and sites shows significant warming in southern China from 15,000 years ago, with evergreen forest replacing deciduous forest and grassland (Xu et al. 2013; Meng et al. 2017; Sheng et al. 2017; S. Y. Wang et al. 2017). There was a brief, abrupt, temperature reversal corresponding to the global Younger Dryas event, between 12,900 and 11,700 years ago, after which climate and vegetation approached their modern state by around 9500 years ago. The climate continued to change on multiple timescales during the Holocene (from 11,700 years ago until the present day), but the range of variation was much less than in the Late Pleistocene and there appear to have been considerable regional differences. Two periods of exceptionally rapid climate and vegetation change—a cold event around 8200 years ago and a drought event 4200 years ago—have been recognized globally and at a few sites in TEA, but in most regional records the temporal resolution is insufficient to resolve events lasting only one to four centuries (Zhao 2018). A warmer, wetter 'Holocene Climatic Optimum' between around 9000 and 5000 years ago has been recognized from some palaeoecological sites in northern TEA (Cheng et al. 2018), but at many sites the interpretation of Holocene variability is complicated by human impacts. There appears to have been a general decline in the strength of both the Indian and East Asian summer monsoons over the last 5000 years, but also a great deal of variability, in both time and space (Cheng et al. 2016; Kathayat et al. 2017; Zhao et al. 2017).

For the last 1000 years, there are both tree-ring and written records. Tree-ring records for the northern hemisphere from 40° to 75°N, where summer temperature is the major control on tree growth, show that a relatively warm 'Early Medieval Warm Period' (*c.*850–1100) was followed by a brief cooler period, then peak medieval warmth in the 1160s, then an irregular cooling trend into the 'Little Ice Age' (*c.*1450–1850), with the coldest decades being 1812–1821 and 1832–1841, before near continuous warming up to the present (Wilson et al. 2016). South of 40°N, interpretation of tree-ring records is more complex, with variation in precipitation often the major influence. Monsoon variability, recorded in speleothems (stalagmites) and tree rings, resulted in both extended droughts and extreme rainfall events across India and northern Southeast Asia, with impacts on agriculture and social stability (Buckley et al. 2014).

1.6 Extraterrestrial impacts, volcanoes, and other natural catastrophes

In addition to the gradual changes described in previous sections, TEA has been subject to catastrophic events that have caused widespread destruction within a brief period of time. The biggest such event was the one that caused the global extinction of the dinosaurs and numerous other species of animals and plants at the end of the Cretaceous, 66 million years ago. Most scientists now believe that this mass extinction episode was caused by the impact of a 10 km diameter asteroid at Chicxulub, Mexico, creating a crater 180 km in diameter, but there is less agreement on how and why this impact had such a disastrous affect. The re-entry of material ejected from this crater may have caused global fires, although their scale and intensity is still debated (Belcher et al. 2015), while stratospheric sulphate aerosols (Brugger et al. 2017) and/or soot from hydrocarbons in the impacted rocks (Kaiho and Oshima 2017) may have caused prolonged and drastic global cooling, by at least 8–10°C. There is no known geological record for this period from TEA, so the regional impacts of this catastrophe cannot be assessed. The global extinction of all large terrestrial vertebrates is well documented—nothing bigger than a cat survived—and there were also mass extinctions among smaller mammals, birds, reptiles, and insects (Longrich et al. 2012), but plant extinctions were not as severe and there were no dramatic changes at the nearest sites with good records, in northeast China and northern Japan (Spicer and Collinson 2014). Presumably this reflects the many ways that plants can survive short-term catastrophes.

Extraterrestrial impacts have been blamed for other, smaller, global extinction episodes since the Cretaceous, but none of the correlations are very convincing. During the Pleistocene, 790,000 years ago, there was a major impact in or near TEA that produced glass bodies, known as tektites, which were spread over 10–20 per cent of the Earth's surface, from the Indian Ocean to Australia, Southeast Asia, and South China, and including most of TEA (Cavosie et al. 2018). These were apparently produced by the low-angle impact of an asteroid or comet, more than a kilometre in diameter. Most evidence favours an impact within Southeast Asia, but the source crater—predicted to be 40–100 km in diameter—has not yet been identified. Although an impact of this magnitude must have had massive regional consequences, it was probably too small to have a major global impact.

Large impact events are extremely rare, but the destructive power of all but the largest impacts is matched by large volcanic eruptions—super-eruptions—which are much more frequent than impact events of similar energy and appear to be the main drivers of mass extinctions (Bond and Grasby 2017). The 'mother of all mass extinctions' at the end of the Permian period, 252 million years ago, has been attributed to huge volcanic eruptions in Siberia, although the precise mechanism is unclear, and the massive Deccan Trap volcanism in west-central India may have contributed to the end-Cretaceous extinctions. In addition to local and regional impacts from the lava and volcanic ash (Setyaningsih et al. 2018), large eruptions add sulphate aerosols to the stratosphere, warming it but cooling the Earth's surface below (Bond and Grasby 2017), as well as reducing solar radiation (Helama et al. 2018). Unlike the ash, which rapidly drops out, these aerosols spread globally and their effect lasts for months or years. With the biggest eruptions, cooling may persist for centuries as a result of ocean–atmosphere–ice feedbacks. However, with few observations to calibrate the models, the uncertainties are still huge. Smaller eruptions are major drivers of climate variability on annual to decadal timescales and add an additional degree of uncertainty to future climate projections, although they do not affect the long-term trajectory (Bethke et al. 2017).

The complex tectonics of Southeast Asia are reflected in the large number of active volcanoes. Indonesia has more than any other country in the world, mostly in the Sunda Volcanic Arc, stretching from north-west Sumatra to the Banda Sea, which results from the subduction of Indian Ocean crust beneath the Asian plate (Figure 1.8). The largest

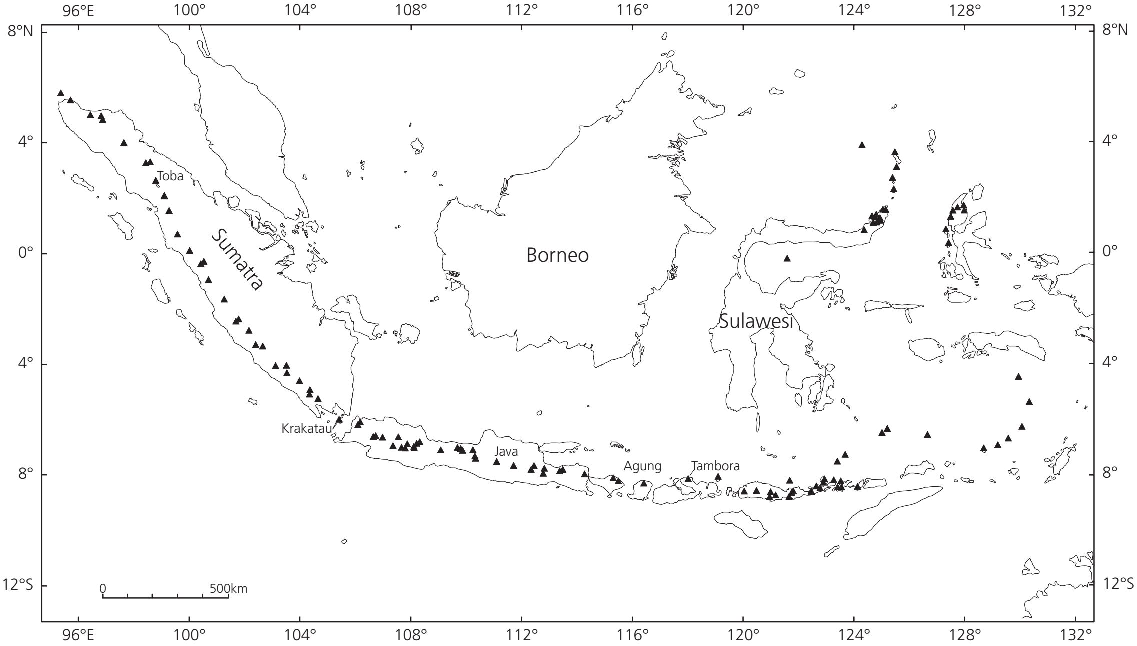

Figure 1.8 Indonesia has more active volcanoes than any other country in the world. Most of these are in the Sunda volcanic arc, stretching from northwest Sumatra to the Banda Sea, which results from the subduction of the Indo-Australian plate under the Eurasian plate—the Sunda megathrust. From Nossin (2005).

eruption in recent history was that of Tambora in 1815, on the island of Sumbawa, which was heard 2600 km away in Borneo and killed at least 50,000 people. An even larger eruption—responsible for the largest sulphate spike for 2300 years in both Arctic and Antarctic ice cores—occurred in 1257 and involved the Samalas volcano next to Mt Rinjani on the adjacent island of Lombok (Vidal et al. 2016) (Figure 1.9). Both Tambora and Samalas had measurable impacts on global climate, with the former causing cold damage in southern China (Gao et al. 2017), and the 'year without summer' in Europe and other areas. The Samalas eruption may even have triggered the Little Ice Age (Newhall et al. 2018). Other big eruptions in historical times in TEA were Krakatau (1883) in Indonesia and Pinatubo (1991) in the Philippines. Pinatubo was the largest eruption in the twentieth century and caused a global cooling of 0.5°C for 3 years (Bond and Grasby 2017). Further north (31°N), the Tambora-size eruption of the Kikai caldera in the Ryukyus, 6300 years ago, may have caused extinctions on Yakushima Island, 40 km to the southeast, as well as a genetic bottleneck in the surviving macaques (Hayaishi and Kawamoto 2006).

On a longer timescale, Toba, on Sumatra 74,000 years ago, was the most recent 'super-eruption' in TEA and possibly the biggest global volcanic event of the Pleistocene. This event is known as the Younger Toba eruption, to distinguish it from earlier eruptions of the same volcano, 502,000 and 790,000 years ago, and lasted perhaps 2 weeks, depositing metres of ash over large areas, including most of peninsular India. Simulations with climate models suggest that emissions of sulphate aerosols from the eruption would have caused global cooling, with temperatures remaining below normal for a decade or more, as well as significant reductions in rainfall (Timmreck et al. 2012). However, the magnitude of these impacts is very sensitive to the assumptions on emitted sulphur and there is little independent evidence for a major global impact (Yost et al. 2018). The immediate regional impacts must have been devastating, but there is little evidence for long-term effects. Pollen analysis of a marine sediment core from the Andaman Sea, 100 km northwest of Toba,

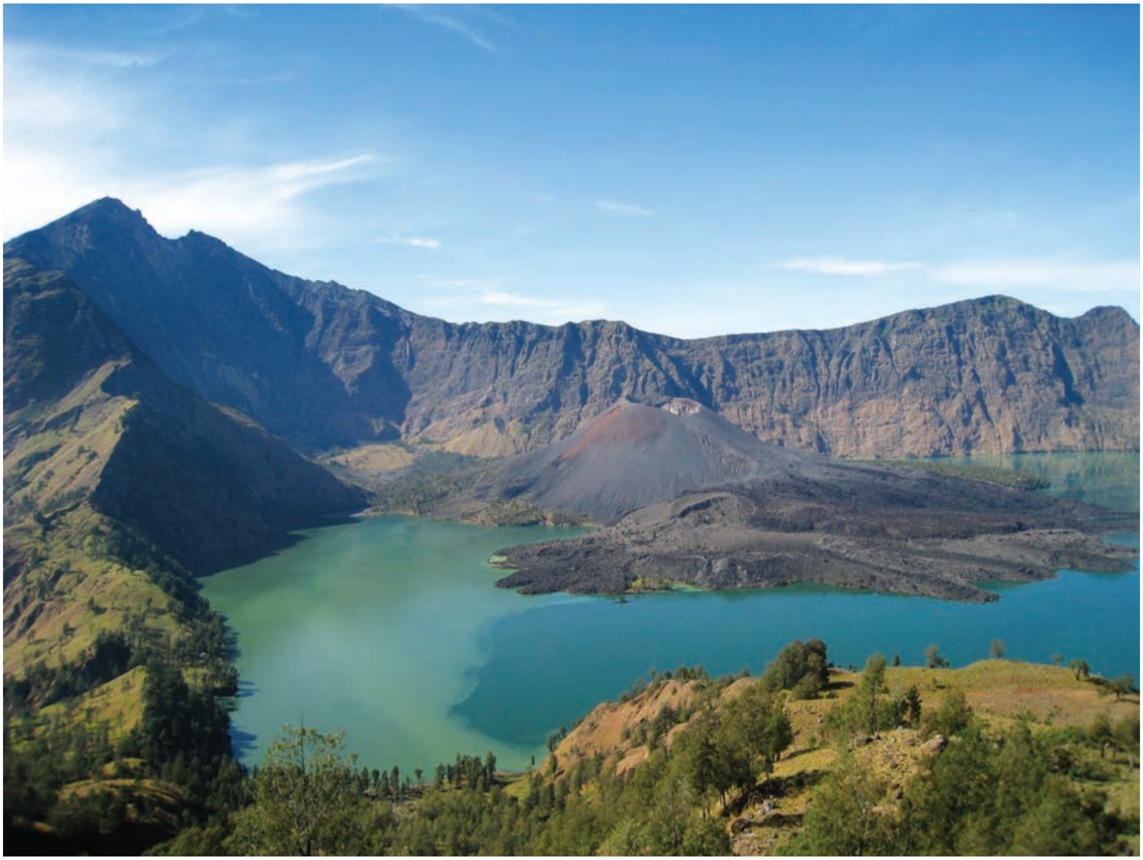

Figure 1.9 Caldera formed by the 1257 super-eruption of the Samalas volcano next to Mt Rinjani on the island of Lombok. Photograph by Petter Lindgren, Wikipedia, used under the Creative Commons CC BY-SA 3.0 license.

shows an abrupt decline in the highland pine forests of northern Sumatra, but any impact on the other forest types was either limited or else recovery occurred within the time resolution (*c*.250 years) of the pollen record (van der Kaars et al. 2012).

Big eruptions are not unusual on a geological timescale: the estimated average global return periods for very large eruptions are 110 years for magnitude 6 eruptions, such as Krakatau and Pinatubo, 500–1200 years for magnitude 7 eruptions, such as Samalas and Tambora, and 17,000 years for magnitude 8 eruptions, such as Toba (Newhall et al. 2018; Rougier et al. 2018). At least 20 volcanoes in TEA are possible candidates for future magnitude 7 eruptions. For smaller events, such as the 1963 eruption of Mt Agung on Bali—magnitude 5 and causing significant global cooling—the return time is only 14 years.

Other types of natural catastrophe, including large earthquakes and major cyclones, can cause local or regional devastation, but few species are completely eliminated from the affected sites, so recovery is rapid. Most of the largest earthquakes in TEA occur near the ‘Sunda megathrust’, where the Indo-Australian plate slides beneath the Eurasian plate. The Sumatran–Andaman earthquake of 26 December 2004 was the largest worldwide in the last 40 years and produced the most devastating tsunami in recorded history, killing more than 200,000 people, but ecological damage was localized (Porwal et al. 2012). Further north, in Sichuan, the Wenchuan earthquake of 12 May 2008 killed over 80,000 people, caused extensive forest loss on the steepest slopes, and increased tree mortality in subsequent years (Qiu et al. 2015). Typhoon Haiyan, which hit the

Philippines in early November 2013, was one of the strongest cyclones on record and killed more than 6000 people, but caused fairly modest damage to natural vegetation.

1.7 The first humans

The earliest human remains in TEA are usually assigned to *Homo erectus*, which originated in Africa more than 2 million years ago. Stone tools found without human bones, from the early and Middle Pleistocene, are also usually assigned to the same species, but only because there is no strong evidence for any other human species in the region at that time. The archaeological record (bones and tools) is sparse and both the earliest (*c*.1.7 million years ago) and latest (400,000–150,000 years ago) dates claimed for *H. erectus* in TEA are disputed. The recent discovery of stone tools dated to 2.1 million years ago in Shaanxi, north of TEA (34°N), suggests an even longer human presence in Asia, although the species involved is unclear (Z. Zhu et al. 2018). Most skeletal remains of *H. erectus* are from Java, 1.5–1.0 million years ago, and the earliest securely dated stone tools in TEA are from the island of Flores (Brumm et al. 2010), 1 million years ago; Guangxi in southern China (24°N; Xu et al. 2012), 800,000 years ago; and Luzon, in the Philippines, 700,000 years ago (Ingicco et al. 2018) (Figure 1.10).

Most of the faunal remains associated with *H. erectus* finds suggest open woodland or savanna, and it is not clear if the species could live in closed forest. Another unknown is the ability of *H. erectus* to manipulate fire. If, as has been suggested for East Asian populations, *H. erectus* had this ability by 400,000 years ago, then this would have greatly

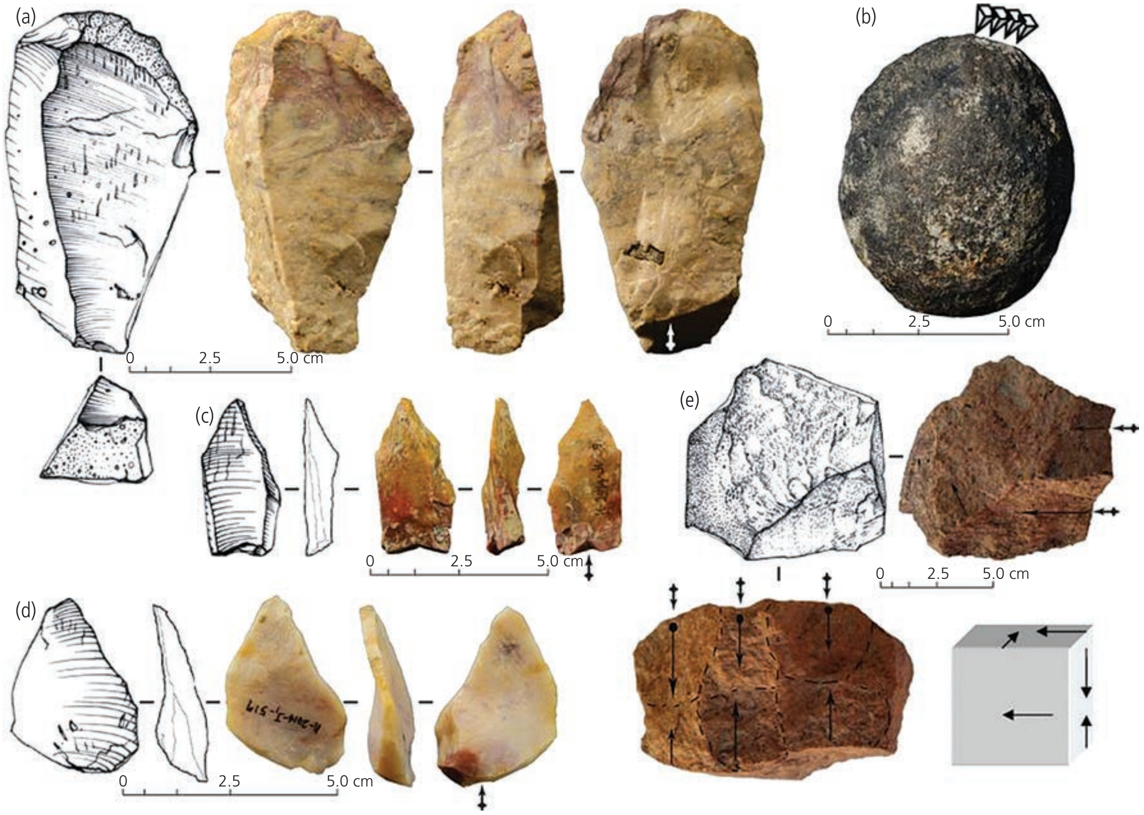

Figure 1.10 Stone tools dated to around 700,000 years ago from Kalinga, in northern Luzon in the Philippines, associated with a rhinoceros skeleton showing clear signs of butchery, as well as other large vertebrates. From Ingicco et al. (2018), used with permission.

increased the power of this species to modify its environment. There is also the question of how *H. erectus* reached Flores, Luzon, and, later, Sulawesi, assuming that this is the species responsible for the tools there. Even at the lowest of Pleistocene sea levels, reaching these islands required one to three sea crossings, the longest always greater than 20 km. Some authors have attributed these crossings to groups of humans accidentally washed out to sea on floating rafts of vegetation (as happened to several individuals during the Indian Ocean tsunami in 2004), while others have found deliberate seafaring more plausible. Along the chain of islands from Bali to Timor, the target island can always be seen from the likely point of departure on the previous one, while the dangers of crossing these treacherous straits may not have been so obvious.

There is virtually no information on the subsistence patterns of *H. erectus*, and thus its potential impacts on the environment and on other species. The sudden appearance of a new, intelligent, social, tool-using predator in an area presumably disrupted existing predator–prey relationships, but evidence for a major ecological impact is indirect. Early Pleistocene extinctions of large vertebrates on Flores are associated with the first evidence for the arrival of humans, presumably *H. erectus* (van den Bergh et al. 2009), and there are similar associations between extinct megafauna (including *Stegodon* and rhinoceroses) and early stone tools in the Philippines (Ingicco et al. 2018) (Figure 1.10). Human fossils and/or stone tools from Middle and Late Pleistocene cave sites in southern China and Indochina are also often associated with the remains of extinct, large-bodied mammals, including *Stegodon* and the giant tapir *Megatapirus augustus* (Corlett 2013a). Early *Homo* was also associated at some sites with *Gigantopithecus blacki*, a giant (200–300 kg) terrestrial forest ape, which survived until around 300,000 years ago (Zhang and Harrison 2017). These associations suggest some form of interaction, but there is no direct evidence for hunting. It is hard to avoid speculation that early human populations had some role in the extinctions of these large mammals, but more evidence is needed before this can be taken further.

On the island of Flores, just east of Wallace's line, a remarkable dwarf (approximately 1 m) hominid, with a brain the size of a chimpanzee's, inhabited a cave at Liang Bua from around 100,000–50,000 years ago (Sutikna et al. 2016). Stone artefacts extend the earlier date back to 190,000 years ago. These remains are associated with evidence for hunting and/or scavenging of *Stegodon*, Komodo dragons, giant rats, and a range of smaller species (van den Bergh et al. 2008). The divergent opinions on these hominid fossils range from them representing a distinct human species, *H. floresiensis*, to their being diseased individuals of *H. sapiens*, but the evidence increasingly supports the former. If indeed they are a distinct taxon, a derivation from Asian *H. erectus* by island dwarfing in response to resource limitation seems more likely than a separate migration of a smaller hominid from Africa, but this latter possibility cannot currently be ruled out. Recent finds of *H. floresiensis*-like fossils and tools dated to around 700,000 years ago at Mata Menge, 70 km from Liang Bua, are consistent with both the view that *H. floresiensis* is a distinct species and that it originated from *H. erectus* (van den Bergh et al. 2016a). Curiously, Flores still supports a small population of 'pygmy' humans, whose short stature appears to be the result of recent selection (Tucci et al. 2018). There is no genetic evidence for admixture with *H. floresiensis*, showing that island dwarfing occurred independently twice on Flores.

Stone tools, but no human fossils, have also been found north of Flores, on Sulawesi, dating from before 200,000 years ago to around 100,000 years ago (van den Bergh et al. 2016b). Although we do not yet know what species made these tools, a relationship with the Flores hominids seems most likely. A similar scenario of island dwarfing is also possible for the Philippines, where a single bone from Callao Cave on Luzon, dated at 67,000 years ago, shows some similarities to *H. floresiensis* (Détroit et al. 2013).

Even excluding *H. floresiensis*, later Asian populations of *H. erectus* appear to have diverged increasingly from their presumed African ancestors, leading to the old theory that one or more of these populations ultimately gave rise to modern Asians (the 'regional continuity' model). The evidence, however, now overwhelmingly favours the 'out-of-Africa' theory, which states that archaic humans were displaced by modern humans who evolved in Africa. How much interbreeding there was with archaic populations is still unclear. There is molecular evidence that the ancestors of modern East Asians bred with Neanderthals, both before and after they separated from modern Europeans, and also with another extinct hominid species, the Denisovans (Browning et al. 2018). A variety of East Asian fossils with a mixture of features associated with *H. erectus* and modern *H. sapiens* have often been labelled as 'archaic *H. sapiens*', and it is possible that some of these were Denisovans (Ao et al. 2017). Evidence for the emergence of Middle Palaeolithic culture in tropical India 385,000 years ago also suggests the early presence of another human species in Asia, but in the absence of hominid fossils it is currently not possible to attribute these stone artefacts to any particular one (Akhilesh et al. 2018).

1.8 The arrival of modern humans

The earliest known fossils assigned to our species, *H. sapiens*, are from Morocco, in northwest Africa, dated to around 300,000 years ago, and are associated with stone tools, human-modified animal bones, and charcoal (Hublin et al. 2017). The earliest movements out of Africa may have occurred more than 200,000 years ago (Herschkovitz et al. 2018), but dispersal into Eurasia appears to have started within the last 150,000 years. An increasing number of archaeological sites in TEA suggest that early 'archaic' *H. sapiens* first appeared in our region 120,000–70,000 years ago, while the genetic evidence mostly supports a single, later dispersal into the region, which may have swamped genetic traces of earlier dispersals (Bae et al. 2017; Rabett 2018). A coastal route might seem easiest, given the abundance of easily harvested resources, but currently the earliest well-dated fossils in TEA are from 70,000–46,000 years ago (but probably near the older limit of this age range) in the uplands of landlocked northern Laos (Shackelford et al. 2018) and from 73,000–63,000 years ago in the Padang highlands of Sumatra, 60 km from the sea (Westaway et al. 2017), suggesting that the first modern humans were as adaptable as their modern descendants. Fossils that can reasonably be assigned to *H. sapiens* have also been found at several sites in southern China, dated 120,000–70,000 years ago, including the Fuyan (Daoxian), Zhiren, and Luna caves (Martinón-Torres et al. 2017). Recent studies of a cave site near sea level in northern Australia have pushed back the date of first colonization of that continent by *H. sapiens* to at least 65,000 years ago (Clarkson et al. 2017). These first colonists must have passed through TEA, but the fossil evidence from this period in Southeast Asia is still sparse and poorly dated.

Human arrival and spread in Australia coincided with a continent-wide disappearance of large vertebrate species (>45 kg), with a dominant human role in these extinctions likely but unproven (e.g. van der Kaars et al. 2017). There was no such mass extinction event in tropical Asia in the period between 80,000 and 50,000 years ago during which modern humans probably arrived, perhaps because one or more species of *Homo* had been living in the region for more than a million years already (Corlett 2013a). However, the last 40,000 years has seen at least four global extinctions in TEA: the giant pangolin, *Manis palaeojavanica*, the giant tapir, *Megatapirus augustus*, and at least two species of *Stegodon*, as well as progressive range restrictions for several other large mammals, including orangutans, rhinoceroses, tapirs, and elephants (Corlett 2010a, 2013a). The extinction of the giant pangolin may reflect the loss of open habitats with a high density of accessible ant and termite nests, but a slow-moving, 2 m-long mammal, whose only defence was to roll up, must also have been extremely vulnerable to hunting, as its presence in the Niah cave deposits shows. A similar argument can be made for the slow-moving, slow-breeding orangutans, which ranged widely over TEA in the Late Pleistocene, from southern China to Java, but were confined to the sparsely populated everwet rainforests of Borneo and Sumatra by historical times (Spehar et al. 2018).

Niah Cave, Sarawak, on the island of Borneo (Figure 1.11), was occupied from at least 35,000 years ago—and probably visited from 50,000 years ago—to around 8000 years ago (Hunt and Barker 2014; Barker et al. 2017). The bones of many species of mammals, brought into the cave by people or arrived there by natural means, have been identified. Bearded pigs (*Sus barbatus*) dominate at all depths, suggesting that this was the most common prey, with monkeys of various species (macaques and several langurs) next in abundance. Projectile tips made from bone or stingray spines appear from at least