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Introduction

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1.1 Introduction

Southeast Asia has long been of major interest for many scientific disciplines, both separately and in the way that different disciplines have interacted with each other in trying to address the numerous fascinating questions that the region poses. Two particular features stand out. Biotically, it is one of the most organically diverse regions in the world for numerous different groups of organisms. Moreover, this high diversity is true through a large range of environments, aquatic to terrestrial, and freshwater to marine. Second, Southeast Asia's geology, scenery, geomorphology and range of physical habitats are complex and also very diverse. Given the size of the region (defined loosely below) some of this great biotic variety can obviously be attributed to scale as well as its tropical climate (both of these being traditional explanations for biotic diversity), but because its latitudinal span (approximately 20°N–10°S) is entirely intra-tropical, latitudinal effects on their own would seem to be insufficient to account for its richness. By comparison, the region's longitudinal spread is almost twice as great, and in elevation it ranges from marine deeps and troughs (*c.* -6000 m) to land altitudes of *c.* 5000 m with glaciers (albeit in rapid retreat). This invites the widely held working hypothesis that its physical complexity must in some way be 'driving' many of its key biological features including its diversity. Southeast Asia also has some of the densest human populations in the world, and some of its member countries now have

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rapidly expanding economies. These factors, combined with global environmental change, have been having an increasing impact on the biology and physical habitats of the region, and have generated substantial conservation concerns and initiatives.

There are therefore three scientific focal interests in the region, and multidisciplinary feedbacks between them: (1) understanding the origin of its main biotic features, (2) understanding its geological origins, and (3) trying to manage and mitigate the human social and economic impacts on these other two features. These were all addressed during the original SAGE meeting in September 2009 (see *Preface*), but here we concentrate on (1) and (3) because the earth science proceedings were made the subject of a separate volume (Hall et al. 2011). As already explained in the *Preface*, the present volume is not a proceedings as such, but a collection of invited overview and case-study articles that treat these other two main themes.

In this introduction we aim to highlight major themes that we have identified in the various chapters in this volume, and to link aspects of these contributions, before attempting to summarise what the volume contributes as a whole. Multiauthored volumes stemming from conferences inevitably reflect what people are working on and wish to communicate, though accidents of history dictate that an assembled collection of papers will not precisely match what took place in a conference or what is taking place in the wider research community. In particular, Southeast Asia is a very large region and tackling its biotic history is a major undertaking, so we are well aware that our 16 main chapters give only a limited coverage. Some of the more obvious geographical (e.g. New Guinea, the Philippines) and taxonomic (e.g. birds, micro-organisms, many groups of invertebrates) gaps do reflect the coverage of our 2009 meeting, but some of the methodological gaps (e.g. spatial ecology, ecological niche and climate envelope modelling) have appeared by accident rather than intention during the production of this volume.

In organising the SAGE 2009 meeting, we had to contend with finding a working definition of the spatial limits of 'Southeast Asia', and this was largely true for this volume, too. Our arbitrary decision was a pragmatic mixture of the physical and political. We set the northern and western limits to include mainland Indochina south of China, from Burma/Myanmar in the west to Vietnam in the east. Travelling south and east we included the Thai–Malay peninsula, the Sunda shelf islands, the islands of Wallacea (between Sunda and New Guinea), the Philippines and New Guinea. Thus, the region can be summarised as tropical Indochina + Malesia (the latter comprising Sunda, Wallacea, the Philippines and New Guinea). Given the somewhat arbitrary nature of this boundary and its porosity in terms of biological and geological history, it is unsurprising that individual chapters in the volume include other terminologies/definitions, and also occasionally extend to neighbouring regions, such as northern Australia and the West Pacific. In any

case, it is not really useful to be rigid about the boundaries: the biota of Southeast Asia will not be fully understood by studying this region in isolation or according to boundaries which may have little biotic significance.

1.2 Overview

The scope of this volume is broad and varied in terms of time, space, biotic diversity and topic. The running order could have been structured in alternative ways but we felt it appropriate to begin the main contributions with a science historian's human perspective on our region. It is a reflection of the long-recognised biotic importance of Southeast Asia that John van Wyhe (Chapter 2) debates the region's significance for the origins of the theory of evolution by natural selection, by delving into the rich and fascinating, but still contentious, history of the respective roles of Charles Darwin and Alfred Russel Wallace. Southeast Asia is generally accepted as crucial to prompting Wallace's establishment of the field of historical biogeography, but van Wyhe also makes a strong case for Southeast Asia supplanting the Galápagos as the real field site of the discovery of evolution by natural selection. Despite this, van Wyhe rejects conspiracy or underhand behaviour on Darwin's part in denying Wallace fair credit for the uncovering of evolution by natural selection. Van Wyhe bases his assessment in part on intriguing detective work, to give a fresh interpretation of the evidence for the much-debated date upon which Darwin received Wallace's famous Ternate essay. Van Wyhe points out that there is no concrete evidence for the idea that when Darwin received this essay he delayed forwarding it to Lyell in order to incorporate first some of Wallace's manuscript ideas into his own work. Van Wyhe shows that the relevant movements of mail, ships and of Wallace himself in Southeast Asia all allow for, and indeed point to, a much later posting date by Wallace for his essay and hence later receipt by Darwin.

The presence of Wallace and Darwin (among others) in this volume also lies behind the old and broadly accepted idea that geological history and biotic history must be related. In this context, further essential background is provided in Chapter 3, in which Robert Hall gives an excellent updated outline of the complex geological history of Southeast Asia. Hall concentrates on the kind of information that biogeographers and other biologists will find most directly useful, especially in setting out Southeast Asia's dramatically changing palaeogeography during the last 70 million years or so. Further information about the geology of the region is also to be found in Hall's introductory paper in the geological SAGE volume (Hall et al. 2011), and the other papers in the rest of that volume. Previous Hall articles on Southeast Asian earth history are cited frequently in this volume and in many articles published elsewhere by (especially terrestrial) biologists trying to interpret

the biotic history of the region. We therefore anticipate that Hall's chapter here will prove similarly influential, with its summaries of new evidence and interpretations, including some important new information for biologists (e.g. the nature of the first Australian continent contact with Eurasia, and possible emergent terrestrial dispersal routes during the Neogene).

Although the idea that earth and life history are interrelated is widely if rather vaguely assumed, concrete evidence for direct cause and effect at the case-history level (e.g. when addressing the biogeography of particular organisms of Southeast Asia) can often be difficult to establish. This problem is central to much of what life scientists are trying to understand about the region, so we feel it would be useful to say a little more about this here. It has been common in the past, at least for biogeographers, to use an integrated narrative approach in constructing plausible scenarios that deferred to existing geological interpretations. But problems have then surfaced when the biotic patterns do not seem to fit, or more embarrassingly, when geologists change their own former interpretations which previously seemed to be compatible with the biotic ones, thereby 'wrong-footing' the biologists – notably as happened when plate tectonics replaced the former fixed-continent paradigm of earth history. It is worth remembering that historical interpretations in both disciplines are open to change.

It is against this background that, following our invitation, Hall has outlined the geology without giving any more than the broadest suggestions of biological implications such as habitable environments, dispersal routes and 'Noah's Arks'. It is up to biologists to use his chapter and other works to go further with more specific biotic interpretations of the geology for themselves. Moreover, apparent anomalies between geology and biology do not automatically signify that biologists have got it wrong and must bend their interpretations to fit the geology. Biologists in general might be too willing to defer to the veracity and robustness of historical geological hypotheses (a 'hard science'). Indeed, Hall clearly demonstrates that some of the geological data are open to individual interpretation and also draws attention to at least one instance where geologists would welcome data from historical biogeography. We know from Hall personally that he is always interested to learn of such anomalies, because they can point to further lines of geological investigation.

We therefore also suggest that readers should not limit their geological curiosity to Hall's chapter, but should also use it as a gateway into further relevant geological reading, and especially into reading critically the geological literature that presents the primary evidence for events of particular interest. It should be borne in mind that although Hall's maps provide current land/sea reconstructions, the inference of the presence and position of a particular terrane in time and space does not automatically imply the presence of land or habitable terrestrial environments, or of a definite new dispersal route. The degree of constraint on geological

reconstructions varies from area to area, and in any case (as above) they should be viewed as hypotheses in progress and of varying robustness. Careful comparison with evolutionary biological narratives might be informative. Good historical biologists recognise the power of making predictions in order to discriminate between competing hypotheses, and attempt to explore the robustness of their results/interpretations to different analytical regimes and starting parameters. The same approach could usefully be extended to the basis for, and robustness of, palaeogeographic reconstructions. A greater dialogue between life and earth scientists would help both, where these subjects overlap.

An additional important abiotic element for which biologists like to have data is climatic history. In Chapter 4, Robert Morley addresses Southeast Asian palaeoclimate in the Cenozoic (the last 65.5 Myr). Palaeoclimate in the region is complex, linked with the complex geological (and oceanographic) history, and what we know clearly indicates that palaeoclimate has had a strong influence on vegetation (and thus fauna). Morley provides an updated overview of Cenozoic palaeoclimate as interpreted largely from the palynological record but also from lithological (rock) and global temperature data. Morley has great experience of working in Southeast Asia in the commercial hydrocarbon industry, so the reader is able to benefit from his access to, and deep understanding of, extensive datasets not immediately or yet available/accessible to academics. Morley's chapter contains too much information for a succinct synopsis here, but we draw particular attention to important and substantial new insights into the palaeoclimate record of Borneo. This chapter is a major new review, the first for more than a decade, and we anticipate that it will prove highly influential in studies of the abiotic and biotic history of Southeast Asia for years to come. As with Hall's geological overview (Chapter 3), the biologist should gain insights into the nature of the underlying datasets and interpretations as well as an informative summary of what is currently known about Southeast Asian palaeoclimate.

In Chapter 5, Charles Cannon offers a more spatiotemporally focused review to contribute insights into the historical biogeography of forests of Sundaland through the Quaternary (approximately the last two million years). Key themes include a focus on the utility of spatial modelling in generating testable hypotheses, particularly of comparative analyses of different major forest types; and the need for novel approaches to incorporate the substantially atypical life history of rainforest trees into interpretations of forest historical biogeography. In synthesising and interpreting available information, Cannon also highlights ways in which Sundaland represents a superb natural laboratory for testing far-reaching assumptions regarding community assembly processes, historical population size and the formation of refugia. Finally, this chapter draws attention also to outstanding major gaps in knowledge of the geomorphology of the Sunda Shelf and the interactions between forests and soils.

Wallace's Southeast Asian presence surfaces again with consideration of his eponymous Line, this being probably the most famous of all biogeographic boundaries. In Chapter 6, James Richardson and colleagues provide a modern, detailed assessment of its role in the distribution of plants across Southeast Asia. Drawing especially from (molecular) phylogenies, Richardson et al. assess the likely geographical origins of plant groups and demonstrate a clear bias in the direction of trans-Wallace's Line dispersal in favour of west to east rather than vice versa. They propose an explanation in terms of a combination of an area effect (area available for colonisation) and phylogenetic niche conservatism, and make testable predictions based on this. The authors highlight the need for further progress in plant systematics (taxonomy and phylogeny) to advance understanding of historical biogeography. Although dated molecular trees offer great potential for understanding Southeast Asian biogeography, we are in the early stages of utilising these approaches and interesting times lie ahead.

William Baker and Thomas Couvreur (Chapter 7) take an organismal approach to historical biogeography in considering a single group of plants, the palms, and focusing especially on Malesia – a hotspot of palm diversity (nearly 1000 species) within Southeast Asia. This study draws on a recently established, highly resolved and well-supported framework phylogeny, a complete species checklist (including distributional data), and a fossil-calibrated timescale for palm diversification. Consideration of these data allows Baker and Couvreur to summarise five main distributional patterns for different groups of palms, and to establish that similar distributional patterns in various lineages are not necessarily caused by common biogeographic events, such that the biogeographic history of the group as a whole within the region is complex. The data indicate a strong role for dispersal as well as geological history. Clearly, an organismal approach still holds value in documenting and explaining Southeast Asian biotic history. Baker and Couvreur suggest that more densely sampled, dated phylogenies and continued integration with fossil and abiotic data will be required to make substantial further progress.

Although historical biogeographers have long been drawn to and inspired by Southeast Asia, it is our opinion that studies based on the phylogeny and distribution of extant organisms have still not got to grips with the great diversity of the system and its highly complex, dynamic abiotic history. One issue is that there are so many geological, sea-level and climatic events in Southeast Asian history that it is possible to create post hoc explanations (narratives) for almost any (especially undated) phylogeny. In addition to thinking more clearly about hypotheses a priori, further methodological and theoretical advances also need to be made. In Chapter 8, Campbell Webb and Richard Ree argue that the features of the Southeast Asian (especially Malesian) system make it unlikely that model-based biogeography methods will accurately reconstruct lineage history unless they manage to incorporate information about temporal changes in area size and

connectivity. The authors address the example of the angiosperm *Rhododendron* sect. *Vireya* using a recently developed maximum likelihood method, and a new range simulation-based method for ancestral area reconstruction. Incorporating landscape history into historical biogeography inference is non-trivial, and the new method outlined here should be seen as an important step that might offer advantages over currently dominant alternative methods, not only in achieving more accurate results, but also in gaining insights into the links between initial assumptions and resulting inferences. The authors argue that the new methodological developments open the way to using well-founded dated phylogenies to test competing palaeogeographic models. Webb and Ree conclude by echoing Richardson et al.'s (Chapter 6) and Baker's (Chapter 7) requests for more and better taxonomically and geographically sampled molecular phylogenies for Southeast Asian organisms. We also emphasise the need to incorporate data from outside the region in order to place the Southeast Asian biota in a broader context.

Southeast Asia is currently the most biodiverse region on Earth for numerous groups of marine organisms. In Chapter 9, David Bellwood and co-authors first characterise the nature of the current hotspot by reviewing data for patterns of diversity of corals and fishes. They then go on to review the origins, assumptions, predictions, support for and potentially useful tests of five main hypotheses that have been proposed to explain the famously concentric ('bull's-eye') diversity pattern of the hotspot. An important part of Bellwood et al.'s synthetic and critical review comes from the broader temporal perspective provided by the Cenozoic fossil record. Much of shallow marine biodiversity can be related to reef development, or more generally to areas of carbonate deposition, (though the reciprocal of that, that development of reefs requires high diversity, is less true). In fact, the global hotspot has not always been in Southeast Asia, as many assume. Interestingly, during the Cenozoic when the Europe and Mediterranean region tectonically resembled modern Southeastern Asia, and was warmer than today with widespread carbonate environments, this instead was the hotspot of the times for many shallow marine groups. Dating the switchover to Southeast Asia is the object of major current research but is provisionally thought to have been during the Oligocene, and is seemingly related in part to the eventual proximity of Australia to Southeast Asia prior to their eventual collision.

Bellwood et al. therefore note that marine global hotspots originate, proliferate, senesce and die, and that the origination of new global hotspots has been associated with major tectonic collisions that have resulted in the formation of shallow, enclosed continental seas and island arcs. They propose that these circumstances, combined with increased effects of sea-level changes during the later Cenozoic, created an unstable 'dynamic mosaic' of metapopulations which led to frequent reorganisation of biogeographical ranges, and increased speciation rates, and so acted as a 'diversity pump'. Indeed, because Southeast Asia is characterised

by high diversity in numerous other (e.g. terrestrial) groups of organisms too, a dynamic mosaic model may provide a unifying theory to explain its high diversity, and possibly high diversity patterns, generally. Attractive though this idea may be however, much detailed work is needed to test it. In any case, Bellwood et al. also point out a difference between marine and terrestrial biodiversity patterns in Southeast Asia, with the marine biota forming a single massive hotspot (covering two thirds of the world's tropical equatorial oceans) focused on the Indo-Australian Archipelago, and the terrestrial biota characterised by greater endemism and multiple localised hotspots. We note that analyses of terrestrial biodiversity patterns in Southeast Asia lag behind those of marine biota in that the accuracy and precision of terrestrial species inventories across the region are extremely uneven (see also comments below on Chapter 14), perhaps because of the greater spatial disconnectivity.

A much more spatiotemporally restricted focus is presented in Chapter 10, in which Gordon Paterson and colleagues assess the impacts of major tsunami events on marine biodiversity. These are rare events relative to human lifespans, with only 12 large, transoceanic tsunamis recorded globally since 1755, and so they are not easy to study, especially given that biodiversity impacts have not been uppermost in people's minds in the post-tsunami human response, and that terrestrial and human consequences have been of greater immediate import. Following a review of the brief previous literature of recorded and theoretical impacts, Paterson et al.'s contribution focuses on a detailed assessment of the impact of the 2004 Asian Tsunami. Two main approaches are considered: first, an overview of reported impacts across the full range of major marine habitats/ecosystems in Southeast Asia and, second, consideration of detailed pre- and post-tsunami monitoring datasets in Thailand. The authors conclude that, based on surveyed communities and localities, the marine biota did not experience a major large-scale disaster. Although detrimental effects occurred, these were often local and extremely patchy, and the overriding impression is one of ecosystem resilience in the face of this rare impact.

A feature of the SAGE 2009 conference that prompted this volume (see *Preface*) was the disproportionate (in terms of land area and total species diversity) number of historical biogeography contributions on the terrestrial biota of the island of Sulawesi. Given that this bias in research focus reflects reality (certainly we believe that there are far fewer studies of historical biogeography of the much larger and biodiverse islands of Borneo and New Guinea), why might this be? The unusual shape and high topographic diversity of Sulawesi immediately suggest that its biota might be interestingly structured spatially, and this seems to have been greatly enhanced by its complex and multipartite geological history (see this volume, Chapter 3), and also its more distant position from the two major (Sunda; Australasia) continental shelves in the region. As reviewed by Ben Evans

in Chapter 11, an interesting finding from previous research is that multiple distantly related lineages such as toads, monkeys, tarsiers, bats, lizards and frogs, have similar distributions of substantially differentiated populations in areas largely corresponding to Sulawesi's constituent palaeoislands. As well as greatly simplifying the main biogeographical hypotheses (a confounding factor in studies of Southeast Asian biogeography more generally, see comments on Chapter 8 above), the special situation encountered in Sulawesi provides a fertile case for the development of some cutting edge methodological research to refine models used in divergence population genetic analysis. Evans illustrates this in an innovative approach to the potential violation of the standard model of divergence population genetics by asymmetric population structure. This is especially pertinent to studies of dispersal to Sulawesi because many groups here appear to have more genetically structured populations than on similarly sized portions of Borneo (from where several lineages are believed to have dispersed). Evans tackles this issue using a dataset for Sulawesi and Borneo macaque monkeys, and simulating outcomes using a recently developed coalescent approach. Evans' results (extreme asymmetry does not lead to strong biases) illustrate how even relatively simple demographic models can provide a useful framework for understanding complex biological systems, and they will have implications for similar studies in Southeast Asia and beyond.

Staying on the island of Sulawesi, Thomas von Rintelen and colleagues (Chapter 12) provide an insightful overview of the radiations of animals in the ancient lakes on the island. These are relatively very well studied (largely by the authors of the chapter) and taxonomically diverse (crabs, shrimps, gastropods, fish) multi-lineage radiations that allow powerful comparative studies of biotic diversification. Von Rintelen et al. summarise the abiotic history and characteristics of the lakes before reviewing the diversity, natural history and phylogeny of each of the animal lineages. The result is a synthesis in which a wide range of evolutionary aspects are addressed, including lake colonisation, adaptive radiation, co-evolution, sympatric speciation, hybridisation and possible sexual selection. In our view, von Rintelen and colleagues establish these lakes as a stunning and under-appreciated island-like system (within an island) that deserves greater general attention.

A well-developed understanding of the biotic history of Southeast Asia will require investigations of a wide range of organisms with varying natural histories and thus dispersal abilities. However, if a biogeographer were aiming to understand how historical events impacted the evolution of the terrestrial biota, then they might choose to study lineages with high fidelity to terrestrial environments and poor ability to disperse across sea barriers – such as obligate freshwater animals. This is the premise of Mark de Bruyn and colleagues' (Chapter 13) review of the spatiotemporal history of the freshwater fauna of the Indo-Australian Archipelago. De Bruyn et al. set the scene by reviewing research on the spatial

connectivity of Southeast Asian freshwater environments through time, as influenced by tectonics and (especially more recently, in the Pleistocene) changing sea level. This is followed by a review of historical biogeography data by taxon, paying particular attention to insights from molecular biogeography and phylogeography, the latter focusing on spatial genetic structure below the species level. The overall picture gained from molecular-based analysis combined with insights into the natural history of each lineage is one of promising potential. Available studies are relatively few thus far, but the results often include robust patterns of genetic (dis)connectivity among areas. De Bruyn et al. consider this to suggest that, if more studies on more organisms are conducted, then the ability to dissect the causes (chiefly centre of species accumulation versus eustatically driven vicariance/refugium hypotheses) of the very high freshwater biodiversity in Southeast Asia will improve.

One theme in several of the organismal biogeography chapters in this volume is that interpretations rely to a great extent on input data from species inventories and phylogenies, and that much more 'basic' biodiversity exploration is required (urgently, given the conservation crisis – see below). As for many groups of organisms, Southeast Asia harbours an exceptional diversity of amphibians. In Chapter 14, Rafe Brown and Bryan Stuart show how relatively traditional investigations of historical patterns of discovery of biodiversity can still provide useful insights into how (in)complete inventories of particular organisms and regions might be. They document patterns in the last 200 years and demonstrate that the more than 600 species have been described in fits and starts, and unevenly across the region with, for example, no discoveries from Sulawesi since 1930 and extremely high rates of new discoveries from northern Indochina that still show no sign of abating. The Sulawesi situation is considered not to reflect a completion of that island's inventory, and the stasis in new species descriptions is interesting when contrasted with the relatively great attention currently being paid to Sulawesi's biogeography (see comments on Chapter 11 above). The rate of recent descriptions is high, in association with incorporation of increasingly diverse types of evidence (morphology, acoustics, DNA), and Brown and Stuart conclude that currently we are in a modern 'Age of Discovery' for Southeast Asian amphibians (at the same time as the region faces a conservation crisis). Most of the widespread species were described by the end of the 1800s, with most recent discoveries being of taxa in small areas of single biogeographical zones. Despite evidence for some long-distance dispersal over seawater, amphibians are generally thought to be 'good' subjects of terrestrial biogeography studies. Amphibians could play a major role in future understanding of Southeast Asian biogeography, but clearly systematics will remain for some time an important component of the work that needs to be done.

As well as its extraordinary biological and geological diversity, Southeast Asia sadly is known as the theatre of probably the world's worst current biodiversity