

I

INTRODUCTION

CHAPTER 1

HUMAN AND HUMAN-MEDIATED SPECIES DISPERSALS THROUGH TIME: INTRODUCTION AND OVERVIEW

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Homo sapiens is essentially an African primate. The vast majority of our evolution occurred in Africa, and the migrations of both our own species and ancestral human populations out of Africa are, in the grand scheme of things, relatively late-in-the-day occurrences. Nonetheless, we have not only travelled and settled beyond Africa, we have also achieved a global distribution unparalleled in other mammals (Gamble 2013; Finlayson 2014). From the most arid deserts to the iciest reaches of the frozen poles can be found human societies of diverse types and forms. And processes of dispersal, colonisation, and migration continue. Indeed, we now travel faster, further, and more often than ever before. In 2006, a staggering 4.4 billion people passed through the world's main airports (ACI 2007, cited in Hulme 2009: 13).

We have travelled far, but we have not travelled alone. Linked to the spread of human populations has been the geographic expansion of an extraordinary range of other species. These species have moved with humans, either directly, by way of our bodies, our caravans, our ships, and our roads, or indirectly by way of new routes opened up by our activities, for example, as we transform environments and accordingly provide pathways for new types of species to migrate and colonise. Much of this movement has been inadvertent, leading to the unintentional co-migration of a wide array of parasites, microbes, disease vectors, and invasive and commensal species. But we have deliberately carried with us a whole host of species as well, in particular the domesticated crops and animals that have enabled our astounding demographic success.

This book is about the extraordinary movements of humans across the globe, and the equally remarkable role that we and our ancestors have played in shaping the geographic dispersal of other species. It draws together contributors from diverse disciplines, whose research explores a broad range of species, time periods, and regions. The chapters collected here do not provide a comprehensive account of human dispersals and human-mediated species movements – such an undertaking would span many volumes and probably

many lifetimes. Instead, they offer a broad range of illustrative examples that underscore the complex palimpsest of species movements through time. Together, these highlight a key point: humans have dramatically reshaped the distribution of our own species as well as that of countless others. This understanding is part of a wider recognition of the pivotal role that humans have played in altering the earth and its ecosystems.

EXPLORING SPECIES DISPERSALS: METHODS AND CHALLENGES

In the research world, a broad range of data sources and methods across the natural sciences and humanities are being drawn upon to explore the movement of species through time. Archaeologists and palaeoanthropologists study fossil and material culture evidence to explore the migrations and dispersals of earlier forms of humans, as well as our own and other species, through to recent times. Historians and linguists mine textual, iconographic, and linguistic sources to examine migrations and population dispersals, as well as the historical movements of domesticated plants and animals, and exotic translocated species. Biogeographers piece together past range expansions and translocations through an analysis of contemporary species populations, while palaeoecologists contribute direct data on past environments and species compositions. Historians, epidemiologists, and geographers look at disease history, and a broad range of scientists examine the historical movements of invasive species. In more recent years, molecular geneticists have begun to contribute substantially to a wide variety of these endeavours, providing phylogenetic information that is increasingly fine-tuning, verifying, and also at times overturning the findings of other disciplines.

The chapters in this volume address a diverse selection of these data sources and methods. While a few chapters in the book (those by Tatem and d’Ettorre) focus on the contemporary world in order to explore points of comparison, most specifically seek to offer a historical perspective on species dispersals. The book includes contributions from archaeologists, historians, geneticists, geographers, and biologists. The kinds of datasets discussed range from fossils of humans and other species to genetic sequences, historical texts, and environmental data, each presenting vastly different opportunities, limitations, and degrees of temporal resolution. Lewis’ chapter (Chapter 2) deals with gaps in the fossil record of many hundreds of thousands of years, while Tatem’s (Chapter 20) addresses daily mobile phone records for millions of people. The strength of many chapters is in drawing such diverse datasets together. Drake and Blench (Chapter 5), for example, bring together data on modern and fossil animal species distributions with findings from genetic, palaeohydrological, archaeological, ethnographic, linguistic, and rock art studies. Boivin (Chapter 14) focuses on archaeological sources, but also draws upon historical, iconographic, genetic, and isotopic data. Many of the archaeological and

historical chapters (particularly those by Denham; Hunt and Lipo; Crassard and Khalidi; Zeder; Fuller and Lucas; Smith; and Green) draw upon molecular genetic evidence, highlighting the increasing relevance of the discipline to historical reconstruction. Dennell (Chapter 3) looks at archaeological and fossil evidence, but also explores research in ethology and evolutionary science. One of the key aims of the volume was to reach from archaeology across to other disciplines and methods in order to look more broadly and comparatively at datasets that often get analysed by distinctive – and non-interacting – groups of researchers.

Along with multidisciplinary, developments in chronology have also been key to an improved understanding of the movement and dispersal of humans and other species. The chapter by Hunt and Lipo (Chapter 8), on the colonisation of remote Oceania by Polynesians, places chronology centre-stage, and demonstrates how chronological revision has implications for understanding both the processes and consequences of human migration. Their revised chronology for remote Pacific settlement, also addressed elsewhere (Hunt and Lipo 2006; Reith et al. 2011; Wilmshurst et al. 2011), is not without controversy (Kirch 2011; Mulrooney et al. 2011), but it does challenge archaeologists to demand more robust chronological frameworks. But chronological issues remain challenging, particularly for earlier periods. Pleistocene archaeology suffers from limitations of preservation, resolution, and chronological accuracy that have led to significant debate over the dating of specific dispersal events and their impacts. Particularly notable is the controversy surrounding the role of dispersing humans in the demise of the numerous genera of megafauna they encountered upon arrival on different continents and islands outside of Africa (discussed in Petraglia, Chapter 4). Much of this debate rests on understandings of the chronology of human arrivals, megafaunal extinctions, and the climatic changes that have also been implicated in these extinction events. In this case, the resolution needed to untangle causality is generally lacking, but even for later periods of human history, dating can be patchy. The vast majority of historical plant and animal translocations, for example, are poorly dated. Understanding of the timing of plant introductions to Britain in the last 2,000 years (addressed in Boivin's chapter) has been greatly improved by systematic archaeobotanical recovery from archaeological sites over the past few decades, but this record primarily concerns food crops and is unmatched in most other parts of the world, in many of which the application of archaeological science methods is in its infancy. Chronological imitations also plague molecular genetic reconstructions of dispersals, with continued debate over the calibration of the molecular clock confounding efforts to reliably date genetically observed dispersal events.

Nonetheless, the advent of new technologies holds much promise. In particular, ancient DNA (aDNA) studies, addressed in a number of the chapters (Larson's in particular, but also those by Dennell, Zeder, Boivin, and

Green) are increasingly anchoring genetically observed events and processes. Indeed, aDNA studies can provide insights into dispersals and translocations that were completely unknown. Recent studies of aDNA, for example, have revealed the presence of a human lineage of which researchers were previously unaware: the so-called Denisovans (see Dennell, this volume), whose genetic material is peppered across diverse human populations today (Reich et al. 2010, 2011), are known from aDNA study of a single finger bone (Krause et al. 2010). Larson (Chapter 10), meanwhile, discusses various examples of aDNA studies that have revealed replacement of domestic animal lineages in different parts of the world. In Europe, for example, domestic pigs introduced from the Near East in the Neolithic period were later replaced by pigs maternally descended from European wild boar (Larson, this volume; also Larson et al. 2007). Recent studies of aDNA also suggest that an endemic sea lion lineage (*Phocartos* spp.) and an endemic penguin (*Megadyptes* spp.) were both eliminated soon after human arrival in New Zealand and subsequently replaced within a few centuries by genetically divergent clades that recolonised the islands from the remote subantarctic region (Boessenkool et al. 2009; Collins et al. 2014). Ancient DNA offers a powerful new tool for elucidating past dispersal events across a range of species.

ORGANISATION OF THE VOLUME

The chapters in this book are divided into four thematic sections. The first, ‘Origins’, addresses species movements in deep time, from the Pliocene through to the end of the Pleistocene. Chapters focus on the emergence of different types of humans, their range expansions and dispersals, and their environmental impacts. ‘Dispersals’, as Dennell notes in his chapter, ‘underpin most current narratives of human evolution’, and their centrality to the human story is underscored in this section. Chapters in the ‘Origins’ section examine the repeated dispersals out of Africa of our human ancestors, and the role of human biological and cultural changes, together with climatic and environmental oscillations, in shaping the timing and trajectory of dispersals. Drake and Blench also examine other animal species that move with humans, focusing in on the Late Pleistocene Sahara as a case study. All the chapters in this section, but particularly Petraglia’s, explore the evidence – still meagre for the Palaeolithic compared to other periods, but increasingly convincing in its diversity – for early human shaping of environments and species distributions.

The section ‘Across the Water’ explores species movements by coast and sea, including the coastal and island dispersals of early modern humans (see the chapters by Erlandson and Denham), and the movement of peoples and their associated crops and domesticates around the islands of Southeast Asia (Denham, Chapter 7) and out into the Pacific (Hunt and Lipo, this volume). While maritime dispersals to many islands have long been

apparent, Palaeolithic archaeology, as Erlandson notes in Chapter 6, has traditionally been dominated by discussion of land-based human activities (see also Bailey and Milner 2002). Yet there is increasing recognition of the maritime capabilities of Late Pleistocene humans (see also Denham, this volume; Bailey 2004; Erlandson and Fitzpatrick 2006; Erlandson 2010). They not only colonised the islands of Wallacea and Sahul, as well as New Britain, New Ireland, and the Solomons by 30 ka (see Denham, this volume), but also were capable of moving obsidian substantial distances by sea by at least 20 ka (as reviewed in the chapter by Hunt and Lipo and also discussed by Denham, this volume). New research also demonstrates pelagic fishing back to 42 ka in Island Southeast Asia (O'Connor et al. 2011). This base set the stage for the regional development of extraordinary maritime capabilities, particularly apparent in 'the last great migration' – the human colonisation of the remote Pacific – whose controversial timing is the focus of Hunt and Lipo's fascinating chapter. Denham's chapter explores the maritime networks that led to the spread and exchange of a broad range of species and material culture between the islands of Southeast Asia, New Guinea, and Australia.

In 'Complexity', the section on species movements in the Holocene, attention shifts strongly towards the role of humans in bringing about the dispersal and translocation of a wide variety of other species. In particular, the chapters in the section share a concern with the dispersal, translocation, and exchange of a broad variety of domesticated species, including Near Eastern, European, Asian, and African food and fibre crops (chapters by Crassard and Khalidi, Fuller and Lucas, Smith, and Boivin; also discussed in the chapter by Denham in the previous section) as well as farm animals (chapters by Zeder, Larson, Crassard and Khalidi, Denham, and Boivin). As Fuller and Lucas (Chapter 12) note, the origins of agriculture is primarily a dispersal story; perhaps 10 or even 20 different regions were centres of agricultural origin, but 'for the majority of the planet, agriculture was introduced from elsewhere and based on plants and animals introduced as domesticates'. They note the relative speed of this agricultural dispersal process, which is also discussed by Zeder (Chapter 11) and Smith (Chapter 13). Both Smith and Zeder note the pauses observed when expanding populations of farmers and/or their domesticates encountered foraging populations with established broad-spectrum economies. Crassard and Khalidi (Chapter 9) also discuss the spread of domesticates, but additionally emphasise the indigenous processes that accompanied the Neolithic. Through time, agricultural systems were significantly diversified through the dispersal and exchange of plant and animal domesticates between different regions, processes discussed in particular in the chapters by Boivin, and Fuller and Lucas. Boivin's chapter focuses on the increasing frequency of species translocations through time, and the propensity for these to occur over longer and longer distances, as the world became more connected through processes of

trade, travel, and cultural exchange, setting the stage for later fully fledged globalisation.

Many of the chapters in the final section on ‘Invasion’ also address such globalising processes. They explore the role of not just human dispersals, but also increasing degrees of regional and global connectivity in encouraging the unintentional spread of species that are seen as detrimental to humans and broader regional ecologies. Chapters by Achtman, Webb, Green, and Tatem examine the transmission of diseases, while those by d’Ettorre, Hall, and Tatem address species that are often classified today as ‘invasive’ or pest species, and viewed as destructive to the new environments to which they spread. Historicising such invasions offers an interesting perspective. While various chapters note the impact of recent transportation developments in facilitating and accelerating disease and pest mobility (e.g., Tatem, this volume), Green (Chapter 19) observes that of eight key diseases that have gone global, only one, HIV/AIDS, has been globalised as ‘a product of the jet age’. While opportunities for the human-mediated spread of a wide variety of diseases and other potentially threatening species has undoubtedly increased in the past century, it is also clear that today’s patterns are a culmination of much longer-term trends. And while we can historicise the patterns themselves, we can also historicise our understanding of them; Hall (Chapter 16) ably highlights changing perceptions of species that are today described as ‘invasive’ and ‘alien’, noting the way changes to vocabularies and semantic meanings chart transformations in cultural assessments of the role of humans in shaping species distributions and diversity. The book ends with a chapter by Tatem that explores the methods being developed to understand and model present-day human, pest, and disease species movements. He concludes by observing the ‘valuable lessons’ that can be learned from bringing together historical and contemporary studies on species dispersals, amongst which are improved capabilities for understanding and predicting risk today.

The four sections of the volume help provide structure to a complex set of topics and disciplinary discussions. But while the volume can be divided into these key topics, there are also broader themes and discussions which cross-cut the sections and weave through the volume as a whole. These are explored in the remainder of this introductory chapter.

HUMAN MOVEMENT: PUSH OR PULL?

While the propensity of *H. sapiens* to expand its own species range is perhaps obvious from our species’ current distribution, the precise mechanisms that led to our extraordinary global dispersal, which saw most of even the most remote regions and islands on earth populated by two thousand years ago, remain disputed. Many of the chapters in the book examine, either explicitly or implicitly, these mechanisms, pointing out both ‘push’

and ‘pull’ factors that could have stimulated human movement in various periods and places.

Attractive resources are a commonly cited ‘pull’ factor in many chapters. Drake and Blench suggest in their chapter that the hartebeest (*Alcelaphus buselaphus*), for example, was a key resource for dispersing humans in the Late Pleistocene, facilitating dispersal into the newly opened savannahs of the Sahara and beyond. Erlandson explores the ability of marine resources to draw human populations to coastal settings. While acknowledging that coastal resources are neither universally productive nor universally accessible (see also Boivin et al. 2013), he argues that many coastal zones provided a rich resource base, including ideal ‘sweet-spots’ for human foraging. An optimal foraging type scenario is also envisioned by the chapters that focus on the attraction of the naïve fauna that many initial human colonists would have encountered as they dispersed into new regions – what Drake and Blench refer to as ‘easy pickings’. These naïve fauna would have been quickly slaughtered by expanding human populations who may then have opted to move on to new populations of naïve fauna at the first drop in ecosystem productivity. This is what Hunt and Lipo suggest happened in the remote Pacific, fuelling rapid human expansion. Dennell offers a not dissimilar scenario for the much earlier colonisation of Eurasia by *H. erectus*, and furthermore explores in some detail the processes that drive fauna to both acquire and also lose predator-savviness. In a world not yet accustomed to human hunting capabilities, the naiveté of fauna would likely have shaped human expansion potential in the Late Pleistocene in important ways. Interestingly, this kind of scenario fits with d’Ettorre’s discussion of one of the key conditions for invasive species success: ‘ecological release’, when a species in a novel environment is freed from the constraints of predators, competitors, and other natural enemies. Both d’Ettorre (Chapter 15) and Petraglia draw parallels between humans and invasive species, and d’Ettorre argues that other features of invasive ants, such as their generalist diet, are shared by humans and help to explain their dispersive ability.

Humans, along with other species, also moved by following similar environments over long distances. The role of the continuous savannah environments that stretched from Africa deep into Asia in enabling early human dispersals has been noted by several authors (Boivin et al. 2013; Dennell 2009, this volume). Dennell offers the term ‘savannahstan’ to describe these optimal grassland environments to which African populations of early humans were so well adapted. Human population dispersal may subsequently have slowed when humans reached the radically different environments of eastern Asia. Dennell’s concept of a savannah corridor is echoed by the ‘kelp’ and ‘mangrove’ corridor hypotheses proposed by Erlandson (this volume), which envision marine resources supporting populations that could follow broadly similar environments over significant distances. These provided what Erlandson calls ‘low ecological resistance’ to hominin dispersal, especially in

comparison to regions marked by topographic and ecological complexity, or barriers such as deserts. The similarity of environments across broad regions, particularly combined with attractive resources and/or naïve fauna, could lead to human expansion over very long distances, including the colonisation of new continents and islands.

As chapters by Lewis, Dennell, and particularly Drake and Blench note, climate change also had a key role to play in shaping the dispersal of a variety of species, including humans. Humans and their ancestors moved into northern regions during warmer phases and out again when it turned cold (Dennell, this volume), for example. They occupied deserts during wet phases, and abandoned them in periods of increasing aridity (see chapters by Crassard and Khalidi, Dennell, and Drake and Blench). Climate change allowed movement across the Sahara – the ‘green Sahara’ – during humid periods. Indeed, Drake and Blench argue that climate change served as a kind of ‘pump’ that pulled humans into the Sahara and then pushed them out of Africa when aridity increased. Crassard and Khalidi similarly argue for abandonment of the Arabian peninsula during hyper-arid periods in the Late Pleistocene. Rose (2007) has referred to ‘tabula rasa’ processes in the region that led to the extinction or outward dispersal of local human populations.

Population pressure has also been suggested as a factor that would have made environments less attractive and created push factors for human migration. Agricultural dispersals, for example, are often seen as caused by human demographic increase resulting from changes to fertility under agricultural subsistence regimes (Bocquet-Appel 2011). A leading hypothesis argues that the transition to agriculture fuelled major expansions of farmers and the coincident replacement or assimilation of foraging populations and expansion of major language families (Diamond and Bellwood 2003; Bellwood 2005). The expansions of the Bantu, Indo-Aryan, and Austronesian language families, for example, have all been linked to farmer expansions. The degree to which population pressure actually fuelled farmer expansions, as well as the role of large-scale movements of farming populations in language change, are issues that have been heavily debated, and the chapters in this volume see continued disagreement on these fundamental points. For example, while Achtman (Chapter 17) presents genetic data to support a large-scale movement of Austronesian farmers out of Taiwan, chapters by Denham and by Hunt and Lipo take issue with various elements of the out-of-Taiwan model.

While a variety of push and pull factors may have encouraged dispersal, other factors may have slowed it down. For example, the encounter of radically new environments and/or environments lacking in key resources have both been suggested as barriers to dispersal. Dennell (2007) has discussed the absence of stone resources as a limiting factor in the dispersal of *Homo erectus* in the Pleistocene. Encounter of the tropical forests east of India is argued to have slowed dispersal along the southern route (e.g., Boivin et al. 2013). Rivers can

play a similar role, with major systems such as the Brahmaputra acting as significant biogeographical barriers (e.g., Boivin et al. 2013). Physical and topographic barriers to dispersal were more important at earlier stages of human evolution; with the advent of modern humans, and particularly the more complex societies of the later Holocene, humans were less limited by their new surroundings, with greater capabilities for adapting to difficult and challenging environments.

THE ROLE OF TECHNOLOGICAL AND SOCIAL DEVELOPMENTS

There is little question that technological developments have played a role in human expansion. Humans have adapted to new environments not, primarily, through the evolution of new biological traits, but through processes of cultural and technological adaptation. The first dispersals out of Africa by our human ancestors a little under 2 million years ago, for example, appear to have been enabled by new stone tool technology and the ability to create fire (discussed by Petraglia, this volume). The emergence of new microlithic technologies in the Late Pleistocene has been linked to niche broadening (Shea and Sisk 2010) and demographic increase (Petraglia et al. 2009) that likely helped to spur dispersals. Drake and Blench argue in their chapter that barbed bone technology was used by Nilo-Saharan-speaking hunter-gatherers to track aquatic fauna such as hippos and crocodiles into the green Sahara during humid climatic phases.

Technology could turn barriers into corridors. This is particularly clear with respect to the sea. Before the development of maritime technology, humans could draw on near-shore marine resources, but could not voyage across the water. Erlandson notes in his chapter that *H. erectus* appears to have had very limited capabilities for maritime dispersal, and, contra Bednarik (2001, 2003), suggests the likelihood that this species had only the most minimal maritime technology. With the advent of *H. sapiens*, however, maritime technology came to play a key role in dispersal, enabling the colonisation of more distant islands and of Australia, the latter requiring several sea crossings up to 90 km long (Erlandson 2001). Hunt and Lipo (this volume) argue that by 20 ka, seafaring in Southeast Asia was already based on reliable craft operated by skilled mariners. Maritime capabilities appear to have been precocious in this part of the world, however; in other regions, such as the Mediterranean, there is little evidence for island colonisation until the Holocene (Erlandson 2001; Broodbank 2006). But even in southeastern Asia and Australasia, maritime capabilities were locally variable, as Denham (this volume) observes, noting that while Australia and islands in its vicinity were colonised by modern humans beginning perhaps 50,000 years ago, Tasmania was not colonised until after a land bridge had formed to link it to the Australian mainland with lower sea levels around 43–30 ka.