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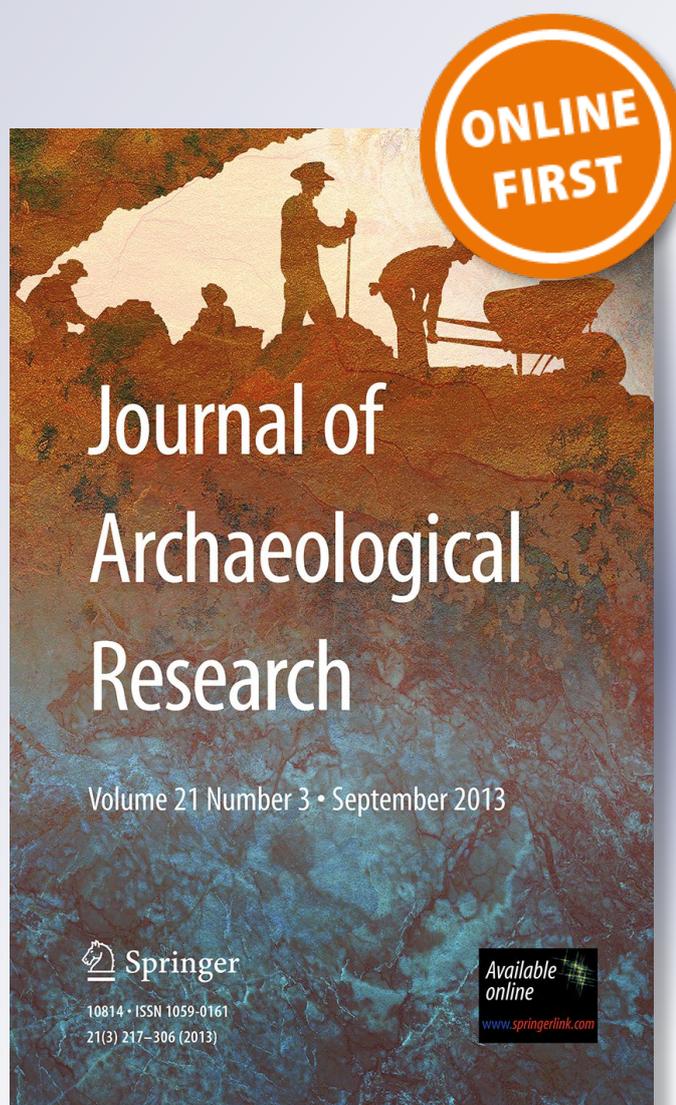
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Ancient Biological Invasions and Island Ecosystems: Tracking Translocations of Wild Plants and Animals

Courtney A. Hofman¹ · Torben C. Rick²

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Abstract Biological invasions are one of the great threats to Earth's ecosystems and biodiversity in the Anthropocene. However, species introductions and invasions extend deep into the human past, with the translocation of both wild and domestic species around the world. Here, we review the human translocation of wild plants and animals to the world's islands. We focus on establishing criteria used to differentiate natural from human-assisted dispersals and the differences between non-native and invasive species. Our study demonstrates that, along with a suite of domesticates, ancient people transported numerous wild plants and animals to islands and helped shape ecosystems in ways that have important ramifications for modern conservation, restoration, and management.

Keywords Invasive species · Historical ecology · Interdisciplinary methods · Anthropocene · Environmental archaeology

Introduction

From high alpine peaks to the deep oceans, human activities have transformed our planet, with the effects projected to increase exponentially in the coming decades and centuries. Climate change, pollution, habitat degradation, and decimation of

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wildlife are all major concerns, but some of the greatest environmental impacts come from biological invasions, or the spread of new species into new areas with major ecological ramifications (Lodge 1993). Species such as the Burmese python (*Python molurus bivittatus*) in Florida were imported from Southeast Asia for the pet trade, were then illegally released into the wild by pet owners, and are now threatening a wide variety of wildlife (Dorcas et al. 2012). Several species of Asian carp (Cyprinidae), originally introduced to control plants and parasites in aquaculture, are now found throughout the Mississippi and adjoining rivers and threaten the Great Lakes by outcompeting many native species and affecting water quality (Cuddington et al. 2014). Beyond these two examples, scores of invertebrate, mammal, bird, reptile, amphibian, plant, and other species arrive in everything from ship ballast to air cargo, luggage, driftwood or other flotsam, or even people's clothing when traveling (Arteaga et al. 2009; Hughes et al. 2010; Lodge et al. 2006). The scale and pace of these invasions is alarming and thus has become the focus of major remediation, restoration, and prevention efforts (Hellmann et al. 2008; Hobbs and Huenneke 2002; Lodge et al. 2006; Pimentel 2011; Pimentel et al. 2005; Sakai et al. 2001; Seebens et al. 2013).

Human-mediated biological invasions or translocations (intentional or accidental introduction of organisms to new ecosystems by humans, Table 1) of non-native species by humans have been occurring for at least 20,000 years, with a major acceleration during the Holocene (Boivin et al. 2016; Grayson 2001; Stahl 2009; White 2004). Domesticated plants and animals have been transported across continents for millennia, including the movement of domesticated dogs (*Canis familiaris*) from the Old to New World near the end of the Pleistocene (Freedman et al. 2014; Leonard et al. 2002; Thalmann et al. 2013). People also introduced wild plants and animals to new regions, resulting in translocations that are visible in the archaeological record and raise questions about the structure and function of ancient ecosystems and the place of humans in shaping the “natural” world (Boivin et al. 2016; Crosby 2004, pp. 69–90; Fuller et al. 2015; Grayson 2001; Kirch 2005; Lyman 2006; Newsom and Wing 2004). Wild animal and plant translocations by humans are often most visible on islands, where native animals and plants are distinct from nearby continents, prehuman fossil and subfossil records document native species, and archaeological data can help identify potential human translocations. Domesticated species are an obvious signature of human translocation, but there are a range of other translocated organisms, including weedy plants, snails, worms, and beetles, as well as mice and other mammals (see Grayson 2001). Anderson (1952) described the movement of “man’s transported landscape” to the Pacific Islands, which include a series of domesticated and wild species that were introduced throughout the Pacific (see also Kirch 2000). Crosby (2004) used a different term “portmanteau biota” in his analysis of the diverse organisms that Europeans introduced around the world after ~1100 years ago. Translocations have occurred in many of the world’s islands, including Norse (and earlier Neolithic) introduction of a variety of fauna and flora to North Atlantic islands (Crosby 2004; Dugmore et al. 2012; McGovern et al. 2007), Late Pleistocene and Holocene introductions to Mediterranean islands (Gippoliti and Amori 2006; Patton 1996; Vigne 1992, 2014; Valenzuela and Alcover 2013, 2015, Valenzuela et al. 2016a, b;

Table 1 Glossary of key terms related to species translocations

Term	Definition
Adventive species	A species that arrives in a new locality
Assisted migration	Deliberate introduction of a species for restoration in areas where they were driven out of a location by climate change or human agency (<i>assisted colonization, managed relocation</i>)
Camouflaged exotic	Intraregionally introduced species whose exotic status goes unnoticed because its distribution appears as if it could be natural
Commensal organism	Organism that lives in close association with another without actually harming the other
Cosmopolitan species	A species whose range extends across most of the world in the appropriate habitat
Cryptogenic species	A species that could be either native or introduced
Cultiwild	Wild, often “predomesticated,” plants found outside of its natural habitat
Endemic	A species whose distribution is restricted to a particular area
Ethnophoresy	Dispersal of organisms in human vessels or cargo (<i>translocation</i>)
Ethnospecies	An apparent island endemic species that actually results from thousands of years of isolation following a human introduction
Island rule	On islands, small species increase in size and large species decrease in size
Invasive species (invasive alien species)	A non-native species that spreads and causes major alterations or damage to the environment, human health, etc
Non-native species	A species living outside of its natural range usually arriving because of human agency (<i>introduced, exotic, and alien</i>)
Novel ecosystem	Human influenced and modified environments that have no natural analog
Synanthrope	Wild plants and animals that live near and benefit from relationships with humans
Translocation	Intentional or accidental introduction of organisms to new ecosystems by humans
Zoogeographic phantom	An enigmatic species with insufficient evidence to determine human agency or natural dispersal

Zeder 2008), introduction of a variety of wild and domesticated species to Caribbean islands (Giovas et al. 2012; Newsom and Wing 2004), and a series of other translocations to islands around the world.

Archaeologists and other researchers have become increasingly sophisticated in the study of ancient translocations. These studies have resulted in robust analyses of zooarchaeological and archaeobotanical materials to help evaluate prehistoric translocations and the ways these introductions can help us understand human migration and other cultural developments (Boivin and Fuller 2009; Matisoo-Smith 2009; Newsom and Wing 2004; Storey et al. 2013). Additionally, these studies have shown how translocations transform ecosystems through direct and indirect human activities (Hunt and Lipo 2006; Mieth and Bork 2010; Rainbird 2002). Research in the Pacific Islands has focused on tracking commensal organisms (rats, pigs,

chickens, and dogs) using ancient DNA (aDNA) to infer the timing and ancestral population in colonization events (Larson et al. 2007; Matisoo-Smith 2009; Storey et al. 2013). As knowledge of ancient human translocations of domesticated and wild plants and animals has grown, so have the number of taxa speculated to have been transported to islands. Grayson's (2001) review of ancient human impacts on animal populations, for instance, described ancient human translocations including at nine wild mammal species transported to Corsica alone.

While researchers increasingly search for evidence of wild plant and animal translocations, there have been few systematic attempts to clearly define what constitutes a human translocation and how we define it in the archaeological and fossil record on a global scale. The commensal model for the Pacific outlined by Matisoo-Smith (2009) and Storey et al. (2013) is a useful framework that focuses on integrating archaeological and genetic data of commensal animals to understand human migration. Questions remain, however, about how other zooarchaeological data can be used to support a human translocation versus a natural dispersal. For example, does a single bone or small number of bones of a non-native taxon on an island where it is not currently found or described in the fossil record constitute a translocation, or were they merely transported animal parts for food or tools? What are the criteria for defining when an occurrence of non-native and nondomesticated animal or plant remains demonstrates a viable prehistoric population? How can we be certain a nondomesticated organism arrived by a cultural dispersal rather than natural dispersal during or after human colonization? The isolation or distance of islands is an important criterion, but these questions can be more challenging for islands closer to continental landmasses where natural over-water dispersals can be difficult to tease apart from human or combined dispersals (Rick 2013; Wing 1993).

In this paper, we review the archaeological evidence for ancient wild animal and plant translocations to islands around the world. With an explosion of archaeological research on islands during the last two decades, the number of proposed translocations of wild plants and animals has grown dramatically and the idea that these have resulted from human agency rather than natural dispersals is becoming more widely accepted. Our goals are to bring this literature together into a coherent framework and build on the commensal model for the Pacific Islands (Storey et al. 2013) and other global discussions of ancient translocations (e.g., Boivin et al. 2016; Grayson 2001). We aim to enhance both theory and method in the study of ancient translocations and also to better integrate archaeological studies with current biological research by focusing on six primary issues: (1) explanation of the differences between invasive and non-native species and the importance of these distinctions; (2) discussion of major mechanisms for plant and animal dispersal events, including natural, cultural, or combined; (3) analysis of why people would translocate wild animals or plants to islands; (4) definition of clear criteria used to determine human translocations instead of natural dispersals; (5) evaluation of the methods and techniques that can be used to understand translocations and natural dispersals; and (6) review of select wild plant and animal translocations to islands around the world, placing these in the context of the translocation of domesticates and human–environmental interactions more generally.

Invasive or Non-native?

Species introductions involve the movement of organisms to areas where they did not previously occur and are designated as non-native. Some of these become invasive, meaning they have a transformative effect on the newly occupied landscape, while other non-native taxa are relatively benign with a more limited impact on ecosystems. Differentiating between non-native species introductions and invasive species is important for modern ecology and for archaeologists working to understand ancient translocations.

Invasive species cost an estimated \$120 billion each year in the United States and \$1.4 trillion worldwide (Pimentel 2011; Pimentel et al. 2005). Invasive species are economically and ecologically problematic by causing considerable threat to biological diversity and unanticipated impacts following introduction (Crowl et al. 2008; Hellmann et al. 2008; Lodge 1993; Pimentel 2011; Ricciardi et al. 2017). Asian carp in the Great Lakes, zebra mussels (*Dreissena polymorpha*) in bodies of water around the world, and brown tree snakes (*Boiga irregularis*) in Guam have been shown to have serious effects on ecosystems by introducing new diseases, killing native and endemic species, and damaging aspects of local economies that rely on natural resources (Lodge et al. 2006).

Invasive species differ from non-native species, which are introduced taxa that have not had a destructive impact on the ecosystem. Most household gardens are full of non-native plants that do not invade, but others like Melaleuca (*Melaleuca quinquenervia*), an introduced plant from Australasia, have invaded many landscapes in Florida (Center et al. 2012). Lindroth (1957) outlined five criteria of an introduced species, including historical evidence, geography/distribution, ecology, biology/natural history, and taxonomy, noting that many species had been introduced from Europe across the Atlantic since 1492 with most of them being unintentional introductions. More recently, there is extensive ongoing research in the field of invasion biology that examines the underlying factors in what makes a species likely to “go invasive” (Dlugosch and Parker 2008; Kolar and Lodge 2001; Melbourne et al. 2007; Nahrung and Swain 2014). This discussion centers around a search for a genetic, epigenetic, or ecological trigger that instigates invasion and adaptation that may precede invasion (Dlugosch and Parker 2008; Nahrung and Swain 2014; Ricciardi et al. 2017; Vandepitte et al. 2014). Often the ability to invade depends more on the host ecosystem than the introduced taxa (Kolar and Lodge 2001; Li et al. 2011; Melbourne et al. 2007).

Islands in particular are susceptible to invasion as they have fewer species and high rates of endemism in terrestrial flora and fauna. Islands also serve as refugia for rare and endemic species that are differentiated from mainland populations (Hargreaves et al. 2009; Mairal et al. 2015). In general, the lower genetic diversity on islands limits the potential for island species to adapt to changing environmental conditions including competition, parasitism, and predation by invasive species (Fordham and Brook 2008; Frankham 1997, 1998). Since 2000, the International Union for Conservation of Nature has published over 16,000 species summaries with ~3500 described as critically endangered, ~5500 as endangered, and nearly

7000 as vulnerable (IUCN 2014). While data are not specifically available for islands, an estimated 550 of the critically endangered, endangered, and vulnerable species are found in coastal systems, and this number does not include terrestrial taxa that live in coastal areas nor those susceptible plants, animals, and especially insects that have not been well documented. Approximately 420 of the 550 are threatened by invasive species in addition to other anthropogenic effects including habitat alteration, destruction, and pollution.

Today, significant restoration and conservation efforts focus on the eradication of invasive species and the sustainability of native species. For example, many conservation organizations encourage the development of native plant gardens and parks, which provide habitat for rare and endemic species. Ecosystem restoration initiatives that focus on excluding invasive/non-native and supporting native taxa must make decisions about what should be considered “natural,” what is “unnatural,” and what is the desired condition of ecosystems in the future. As a result, to conserve, protect, manage, or restore a landscape, knowledge of its history, both biotic and abiotic, is important for a complete understanding of the structure and function of the extant landscape. Archaeology can contribute by providing historic baselines on how ecosystems and organisms were structured and functioned in the past, but it is still human choice that dictates what time period or amalgamation of time periods should be used as goals for future-desired ecosystem conditions (Cronan 1996; Hayashida 2005; O’Brien 2001).

Macdonald et al. (2006) argue that the reasons conservationists abhor invasive species are not always tied to protecting biodiversity but rather a philosophical conflict about human intervention in natural processes. Human-assisted movement or range movement due to human-induced climate change makes “nature” less natural to some by challenging their understanding of what “nature” is and is not. However, there is evidence that supports ancient human translocations over the past 20,000 years, indicating that humans have been influential ecosystem engineers throughout their history and around the world (Grayson 2001). Conservationists may fear that species will be valued less or should not be conserved if they are non-native or even invasive and especially if they were introduced by ancient peoples. MacDonald et al. (2006) suggest this naturalization process, when species begin to be considered native and not introduced, is purely cultural. In Britain it is commonly held that the Normans (10th to 11th centuries AD) introduced the European rabbit (*Oryctolagus cuniculus*), while recent archaeological excavations have revealed that the Romans introduced the European rabbit to Britain 2000 years ago and it rapidly spread throughout the island (O’Connor and Sykes 2010). Despite the widespread knowledge of a human introduction, and millions of pounds in management and crop loss each year, conservationists are working to save the rabbit from the recently introduced hemorrhagic fever (Macdonald et al. 2006; O’Connor and Sykes 2010). Some historically introduced species are treasured while others are loathed, and different stakeholders can have conflicting opinions about the same species. Australian livestock farmers view the dingo as a pest, while other Australians view the dingo as an iconic national species; some stakeholders view the dingo as natural, while others treat it as invasive (Balme and O’Connor 2016; Fillios and Taçon 2016; Macdonald et al. 2006; Savolainen et al. 2004). Stakeholder perceptions about what

is natural and unnatural can greatly impact the management of native, non-native, and invasive plants and animals (Simberloff 2003). Time since introduction is important to these perceptions, but with ancient translocations the distinction between natural and non-natural movements is blurry, making the division between nature and culture less viable and further challenging the notion of pristine landscapes. These issues become even more convoluted as we move further back in time.

Natural, Cultural, or Combined Dispersals

Several mechanisms for the dispersal of biological organisms to islands should be carefully evaluated. On islands there are three general mechanisms of natural dispersal for terrestrial organisms: rafting/sweepstakes, swimming, and wind/flight. With most animals, the rafting or sweepstakes phenomenon requires a pregnant female, or a male and a female, to float on a log or some other debris, from one landmass to another where the animal must successfully reproduce. The scenario is simpler in some plants, fungi, and asexually reproducing organisms, as a single organism can generate a founding population. This founder effect scenario can be detected by low genetic diversity in island populations of plants and animals (Dlugosch and Parker 2008; Kolbe et al. 2012). In birds, bats, and plants (depending on seed size), individuals can be dispersed by the wind or in the droppings/pellets of volant animals that migrate between landmasses. In this case, the chances are greater for repeated introduction events as wind patterns and migratory routes are relatively consistent (Ogden et al. 2008). In wind or bird dispersal, there might be more genetic diversity than in a single introduction event like rafting. The last type of natural dispersal is swimming. Species that are good swimmers have dispersed to some offshore islands. For example, Columbian mammoths (*Mammuthus columbi*) likely swam to the northern California Channel Islands multiple times, as modern elephants are strong swimmers (Johnson 1978; Wenner and Johnson 1980). Taxa that dispersed by swimming could potentially have lower genetic diversity than mainland populations but higher than a single rafting event.

Some species should be viewed as poor over-water dispersers as they have high metabolic requirements, such as shrews (i.e., *Sorex ornatus*). Unless food can be found during an over-water voyage—insects or other resources that also have been transported—these species are not likely to survive rafting. The temperature requirements of ectotherms also could potentially limit over-water dispersal. Other animals are poor long-distance over-water dispersers due to their size. For large animals (canids, deer, bears, etc.), rafting is restricted by body mass in relation to debris weight capacity and the ability of the animal to stay on the debris. However, in islands that are a relatively short distance from one another, deer and other larger mammals have been seen swimming to those islands. Regardless of natural dispersal mechanism, the arrival of a new plant, animal, fungus, bacteria, or protist has the potential to have an impact on the new environment. The type and nature of this impact can vary considerably.

Cultural or human dispersals can be intentional or unintentional. Unintentional translocations are accidental introduction events by humans. An animal can stow away on a boat and disembark in a new place (rodents are excellent stowaways; Jones et al. 2013; Matisoo-Smith et al. 1998; White et al. 2000). Plant seeds and insects might be introduced on human footwear, textiles, and storage vessels brought to an island (Sadler 1990). Trade items also might be a source of unintentional introductions. Intentional introductions bring taxa to the island where they are released or planted for a reason. Dispersal events can be combinations of natural and cultural introductions.

Both naturally and culturally dispersed species have the potential to become established or invasive if the new environment is suitable for their abiotic and biotic needs. The “adventive species” ability to reproduce in the new habitat is critical to a successful dispersal (Blackburn et al. 2011; Lodge et al. 2006). Numerous factors such as the sociality of the species, resource requirements, access to mates, genetic compatibility, landscape variability, and changes in seasonality, temperature, daylight hours, elevation, or rainfall could impede reproduction (Blackburn et al. 2011). Crosby (2004, p. 287) suggests that an important factor for the success of European portmanteau biota is that they do not function alone but are often introduced as a suite of organisms that function as an ecosystem. The low levels of genetic diversity found in island species also may limit the ability of these organisms to adapt to new or changing environments. Colautti et al. (2006) describe these parameters as invasiveness (the ability to adapt to new environments) and invasibility (the suitability of the environment to invasion). Anderson (2009) adds “transportability” or the varying ease of human-mediated dispersal. Transportability encompasses water and food requirements during transit, weather resistance, economic, social and ritual significance, and availability. Invasiveness, invasibility, and transportability are critical to the success of a translocation.

Regardless of dispersal mechanism, many taxa have successfully moved from island to island or mainland to island. Some translocated species may have initially colonized an island but due to changing conditions or other limiting factors have been extirpated. Archaeology can be a useful tool in understanding the mechanism of dispersal and the impacts of a colonization event. However, it can be difficult to distinguish between natural dispersals and human translocations, so we must consider all possible dispersal scenarios in evaluating the role of people in a possible translocation event.

Why Translocate? Niche Construction, Commensals, and Stowaways

People introduce plants and animals to new environments for a variety of reasons. Introduced species could be a food resource, useful for tool making, or have a ritual significance. Some species, as noted above, were introduced by accident as stowaways among cargo (i.e., rats) or as commensals with domesticates (Matisoo-Smith 2009; Storey et al. 2013). When people, past and present, move into a new environment, they often intentionally and unintentionally work to make it similar to their previous environment, with familiar plants, animals, and overall habitat. This

landscape alteration can be viewed as an aspect of niche construction (Smith 2011) or landscape domestication (Terrell et al. 2003) that has significant repercussions for endemic ecosystems often shortly after human colonization. Why people translocate animals and plants to islands is one component of human niche construction.

Humans are classic ecosystem engineers who are capable of significantly modifying their environments; niche construction builds on this framework with the argument that this environmental alteration has evolutionary consequences (Odling-Smee et al. 2003). Ellis (2015) notes that niche construction is a key framework for understanding human influence on our planet's biodiversity, ecosystems, and climate, with important implications for potentially transcending modern-day challenges and understanding their consequences on humans and other organisms. Smith (2007, 2011) has drawn on niche construction theory to explain the behaviors associated with the initial domestication of plants and animals and the management of wild plant and animal resources by small-scale societies (see also Zeder 2012). Laland and O'Brien (2010) also have reviewed the concept of niche construction and how it can be applied to archaeological contexts and articulate with broader evolutionary frameworks. In investigating human modification of wild plants and animals, Smith (2011) argued for six major categories of management and manipulation. Although not a category in Smith's model, translocation of wild plants and animals crosscuts many of his categories, including general landscape modification and transplantation of crops. We argue that intentional human translocation of plants and animals is an important aspect of broader human niche construction and offers a framework for understanding why people would translocate wild plants and animals to an island or new location (see also Boivin et al. 2016).

Many animals and plants that were translocated in the past hold economic or cultural significance. Wild boars (*Sus scrofa*), introduced to Cyprus in the terminal Pleistocene (Vigne et al. 2009), for example, provided sources of meat that could supplement otherwise limited terrestrial protein sources. Although debated, White et al. (2000) argued that Polynesian rats may have been deliberately introduced to some Pacific Islands as sources of food. Nabhan (2000) suggested that iguanas were moved to islands in the Sea of Cortes as reserve food sources. Avocados (*Persea americana*), sapodilla (*Manilkara*), and other edible plants were transported to Caribbean Islands during the Archaic period as sources of food (Newsom and Wing 2004). When domesticated plants and animals are added to the equation, the economics become even more apparent as people worked to enhance island resources. Island foxes (*Urocyon littoralis*), intentionally introduced to the southern Channel Islands of California during the Middle Holocene (and possibly all the Channel Islands), were important in Chumash ritual, but they also may have helped reduce mouse populations and were valued for their pelts (Collins 1991a, b; Hofman et al. 2016; Rick 2013; Vellanoweth 1998). A key benefit of translocation was to reduce risk and increase the certainty of having plants and animals as sources of sustenance, as companions for hunting, and as components of broader cultural, ritual, and symbolic systems, which fall under the broad umbrella of niche construction. This pattern of deliberate human translocation of animals and plants helped make unfamiliar landscapes more familiar.

Beyond intentional introductions of economic and/or ritual value, other examples of intentional or unintentional translocation can be seen as accidental byproducts of commensal relationships between humans and a wide range of species. These often fall under the Pacific commensal model (Matisoo-Smith 2009; Storey et al. 2013) that includes not only a host of intentional wild and domesticated plants and animals, but also the weedy plants, insects, invertebrates, and others that come along as incidental byproducts with target species. Rats, mice, amphibians, and reptiles are likely stowaways in cargo and also could reach their destinations unintentionally. Whether intentional or not, translocations are important examples of human landscape modification; they situate well in the general framework of niche construction theory and the broader commensal relationships between humans, plants, and animals. One significant area for future research is evaluating the evolutionary consequences of human translocation of wild plant and animal species, and niche construction offers an important theoretical framework.

Tracking Translocations: Criteria and Methods

Distinguishing between human-assisted or natural dispersal in the past requires the integration of paleontological, archaeological, and modern biological datasets. A single bone in an archaeological site does not necessarily indicate a human translocation and could simply be a transported animal part for tools or food. There are parameters, methods, and datasets that should be prioritized when we investigate possible human-assisted dispersals in the past. We focus on eight questions to consider for the investigation of island translocations: What is the archaeological/fossil context of the organism in question? What is the current species distribution? How many specimens/individuals are known? When does the species occur in the fossil/archaeological record? When did humans arrive? What do genetic and/or stable isotope studies indicate about the organism? Are there any attributes or behaviors unique to island populations? Are there any ethnographic or linguistic data about this species?

Together these questions guide the interpretation of archaeological, paleontological, and biological datasets to identify patterns, processes, and impacts of dispersal.

To address the above questions, researchers have a diverse toolkit at their disposal, starting with occurrence data, which is basic zooarchaeology, archaeobotany, and paleontology. Compiled from published sources and gray literature, occurrence data and context are fundamental to evaluating translocations. Traditional archaeological methods, including MNI (minimal number of individuals), weights, and counts, can tell us how many bones or individuals were present, in which sites, and on which islands. MNI is particularly important as a single bone, or even single individual, does not necessarily equate to a population. When MNI is very low, ancient peoples may have translocated a single or pair of individuals, or a natural introduction might have been unsuccessful. Alternatively, people may have brought only one bone or set of bones rather than a live animal. Distinguishing between these possibilities is difficult so we have developed a decision tree (Fig. 1)

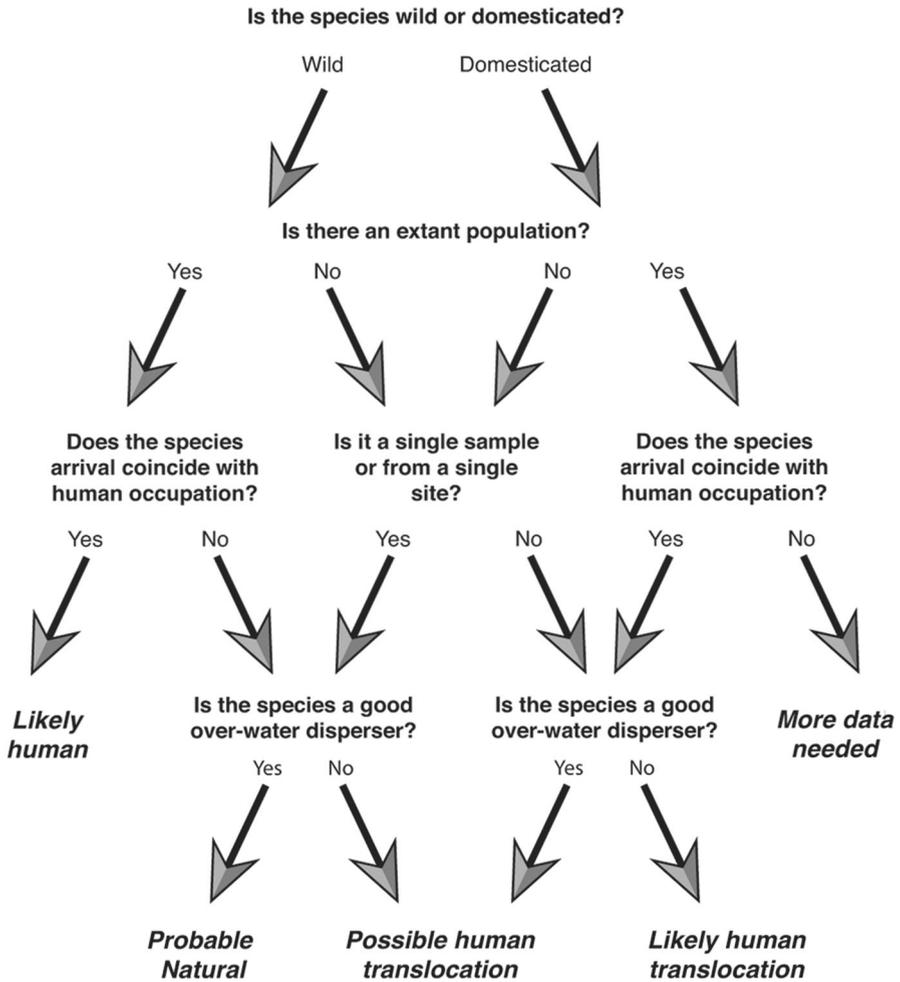


Fig. 1 Decision tree to evaluate the evidence for a potentially translocated species (PTS). For some taxa, it is very obvious that humans introduced the taxon to islands, however for others it is unclear. This tool provides a method of evaluating the evidence for a translocation by addressing eight key questions

to help evaluate the possibility of a translocation. The decision tree cannot definitively evaluate all translocations, but when used in conjunction with the tools discussed below, we can better evaluate the role of humans in plant and animal biogeography.

Accelerator mass spectrometry (AMS) radiocarbon dating and other absolute dating techniques, when radiocarbon dating is not possible, are essential components to establishing a chronology for both humans and the species in question. Many islands around the world have well-supported dates for human arrival based on a variety of evidence, including AMS dates (shell, charcoal, and bone), human remains, and archaeological assemblages. However, the remains of some potentially translocated species (PTS) could predate human occupation, or may be from a

disturbed context. Therefore, we advocate critical examination of the chronometric hygiene for all datasets. Surface collection, stratigraphic mixing, and human activities can drastically alter interpretation of translocations. For example, island fox (Fig. 2) bones recovered from the surface of a fossil locality on the California Channel Islands supported a natural introduction more than 16,000 years ago and before human occupation at $\sim 13,000$ cal BP (Aguilar et al. 2004; Collins 1993; Erlandson et al. 2011; Wayne et al. 1991). These remains have now been AMS dated to the late Holocene and, along with other AMS dates, dramatically shorten the potential timeline for the arrival of the island fox to well within human occupation of the islands (Hofman et al. 2016; Rick et al. 2009).



Fig. 2 Select wild mammals that were likely translocated by ancient people: (A) fallow deer (*Dama dama*), (B) wild boar (*Sus scrofa*), (C) hutia (*Capromyidae* sp.), (D) cuscus (*Phalangeridae*), (E) island fox (*Urocyon littoralis*), and (F) black rat (*Rattus rattus*). See acknowledgments for photo credits

The old wood problem in archaeology also is important in the context of plant translocations. Driftwood used for building materials or fuel can be much older than the built structure or fire itself. Additionally, the presence of a particular species of wood does not mean that there was once a population as driftwood can travel great distances through ocean currents (Fermé et al. 2015; Hellmann et al. 2013). Consequently, the reliance on direct dating of charred seeds and other short-lived materials is crucial to building a reliable chronology (Zeder et al. 2006). Together, these examples demonstrate that direct radiocarbon dating of the organism in question is important for developing a reliable timeline of introduction. Consequently, chronologies must be interpreted carefully to evaluate the role of humans in the dispersal of wild and domesticated plants and animals.

The occurrence and chronology of a species is foundational to examining potential introductions, but these lines of evidence alone are usually insufficient for documenting translocation of wild plants and animals. In addition to how the biology of a species might impact its dispersal ability, knowledge of its genetics and unique behavioral attributes also helps evaluate a possible translocation. Species distributions that do not fit known geological or biogeographical patterns are signs that humans might have introduced a species. Additionally, island taxa sometimes have unique adaptations to living in island environments including morphological (i.e., island rule) and dietary changes. These phenotypic differences between island populations can occur rapidly (Kolbe et al. 2012), but inter-island differences can inform ethnobiogeographic analyses by establishing the timeframe required for some of these patterns to develop and how differences are distributed between landmasses.

DNA analysis, especially ancient DNA and high-throughput DNA sequencing, is an important tool for evaluating a potential translocation. Rapid changes in DNA sequencing technology have made genomics a more affordable and accessible approach to understanding human–environment interactions. While there are differing types and scales of genetic data, DNA can be used to examine evolutionary relationships and population history by estimating divergence dates and modeling migration (Orlando and Cooper 2014; Shapiro and Hofreiter 2014). Ancient DNA also can be used to assess changes in allele frequencies and genetic diversity that might be associated with founder's effects and/or bottlenecks and extinctions (Chang and Shapiro 2016; Hofman et al. 2015a). Genome-wide studies can look for functional or adaptive differences between populations or the genomic basis for a phenotype. Archaeologists should take advantage of existing genetic studies of extant organisms, which provide a baseline study of genetic diversity and population structure. Incorporating DNA samples from archaeological datasets can provide additional evidence for or against a human translocation by placing an archaeological sample in context with extant populations. Ancient DNA has been used to document translocations of commensal and domesticated organisms in the Pacific and the Mediterranean (Larson et al. 2007; Storey et al. 2013). Although there are methodological and analytical limitations with ancient DNA, not all ancient DNA studies are created equal. Protocols to minimize contamination (including a specialized ancient DNA lab), appropriate genetic markers with enough

resolution to address the question at hand, and verification of the authenticity of ancient biomolecules (de Bruyn et al. 2011; Hagelberg et al. 2015; Leonard et al. 2007; Rizzi et al. 2012; Sarkissian et al. 2015) are critical for a successful study. ZooMS is also an important method that can identify the types of organisms that are present from fragmentary bones using collagen fingerprinting by mass spectrometry and provides another technique for obtaining translocation occurrence data (Buckley et al. 2009; Collins et al. 2010).

Another methodological tool for examining translocations is stable isotope analysis. Isotopes reflect dietary choices and available resources and can discriminate a variety of different behaviors. Translocated animals may be eating the same resources as humans, which could be reflected in similar trophic signatures. Several studies have used dogs as an isotope proxy for human diet (Cannon et al. 1999; Guiry 2012; Rick et al. 2011; Tankersley and Koster 2009; West and France 2015). This canine surrogacy approach (Guiry 2012) can be applied to wild taxa to investigate the intentional provisioning of wildlife (Hofman et al. 2016). For example, using carbon and nitrogen isotopes, Sugiyama et al. (2015) differentiated between felids and raptors that were held in captivity before sacrifice at Teotihuacan and those that were wild-caught before sacrifice. Animals held in captivity showed increased levels of C4 carbon in their diet, indicative of the consumption of maize, not a typical prey item. On islands, provisioning by humans and scavenging human middens and waste could elevate levels of nitrogen due to the consumption of marine resources, which have longer food chains. Another isotopic approach to movement and dispersal relies on strontium values in groundwater, which can differ considerably across the landscape (Beard and Johnson 2000; Giovas et al. 2016; Laffoon et al. 2012). Modern comparative isotope data for local dietary species and environments are an important component of these analyses, especially with advances in analytics including isotope mixing models and compound-specific isotopic analysis.

Finally, ethnographic or linguistic research, if available, should be incorporated into interpretations. Oral histories, explorer accounts, traditional ecological knowledge, and ethnographic data contain valuable information about how humans have and continue to interact with their environments. For example, oral histories suggest that Seri peoples of Mexico moved iguanids and cacti to islands in the Gulf of California as supplemental food sources and as part of a placental burial ritual (Nabhan 2000). Linguistic evidence also has been used to explore the introduction history of domestic and wild animals during the Austronesian expansion into eastern Africa (Blench 2006), as well as dogs across the Pacific (Greig et al. 2015).

We advocate an approach that combines all of these into a rigorous framework that focuses on a multipart methodological scheme: direct AMS radiocarbon dating of specimens of the species in question, genomics, isotopes, and, where possible, ethnographic/ethnohistorical data. It can be difficult to distinguish between natural dispersals and human translocations, so we must consider all possible dispersal scenarios in evaluating the role of people in an organism's biogeography.

Ancient Wild Animal and Plant Translocations to Islands

During the last 20 years, the list of species possibly translocated by humans has expanded considerably. This includes everything from mammals and reptiles to insects and plants. Here we provide a series of examples of ancient wild mammal, wild plant (and some domesticates and predomesticates), and other species (reptiles/amphibians, birds, and invertebrates) translocations to islands around the world to demonstrate the scope and magnitude of ancient translocations and to illustrate the methodological and theoretical issues outlined above. Our discussion is global in scope and fairly comprehensive, although we do not review every translocation around the world. Instead we provide a global survey and review designed to illustrate the complexity of the issue and help guide future research. We point interested readers to the following syntheses focused on specific taxa (e.g., animals), theoretical frameworks, or geographic regions (Boivin et al. 2013; Fuller et al. 2015; Giovas et al. 2012; Grayson 2001; Heinsohn 2003, 2010; Montgomery et al. 2014; Newsom and Wing 2004; Stahl 2009; Vigne 1999, 2014).

Mammals on the Move

Mammals have been translocated around the world for food, companionship, and by accident (Fig. 2). Table 2 summarizes published literature on ancient wild mammal translocations to major island groups. While this table undoubtedly does not contain all mammal translocations (and excludes volant mammals such as bats), it demonstrates the diversity of wild mammals that humans have moved to islands. The translocation dates are those provided in the relevant citation and may be subject to variation in the literature or change with future research. We have not assessed the strength of evidence supporting each translocation but do note when genetic data has been used in tandem with archaeological or isotope data.

The earliest reported evidence of human translocations is the arrival of the cuscus (*Phalanger orientalis*) to New Ireland roughly 20,000 years ago (Anderson 2009; Flannery and White 1991; Heinsohn 2003; White 2004). Humans had made this journey by 38,000 years ago, but low sea level during dispersal complicates matters as this also could have facilitated a natural introduction (Anderson 2009; Heinsohn 2003). The admiralty cuscus (*Spilocuscus kraemeri*) and the common spiny bandicoot (*Echymipera kalubu*) may have been translocated to the Admiralty Islands during the terminal Pleistocene, which was followed by a series of later translocations to these islands in the Holocene (Heinsohn 2003). Ongoing genetic study of cuscus phylogeography will help improve our understanding of the dispersal of the cuscus to many Australasian islands and help distinguish between a cultural, natural, or combined introduction.

In the Mediterranean, another early translocated animal, the wild boar, appeared on Cyprus more than 11,400 years ago (Vigne 2014; Vigne et al. 2009). This was followed by a suite of other mammals, including domesticated species, that were translocated to Cyprus and other Mediterranean islands in the early Holocene (Boivin et al. 2016; Vigne 2014; Vigne et al. 2009). Collectively, the wild boar and

Table 2 Select possible wild mammal translocations to islands around the world

Age ¹	Species	Common name	References ²
Indian Ocean			
Zanzibar			
6th–8th century AD?	<i>Crocidura monticola</i>	Sunda shrew	Boivin et al. (2013)
14th–15th century AD	<i>Rattus rattus</i>	Black rat	Boivin et al. (2013)
6th–8th century AD	<i>Potamochoerus larvatus</i>	Bushpig	Boivin et al. (2013)
Madagascar			
10th–13th century AD	<i>Potamochoerus larvatus</i>	Bushpig	Boivin et al. (2013)
Late 9th–10th century	<i>Rattus rattus</i>	Black rat	Boivin et al. (2013)
Late 9th–10th century	<i>Mus musculus</i>	House mouse	Boivin et al. (2013)
Comoro Islands			
9th–10th century AD	<i>Tenrec ecaudatus</i>	Common tenrec	Boivin et al. (2013)
9th–10th century AD	<i>Eulemur fulvus</i>	Common brown lemur	Boivin et al. (2013)
9th–10th century AD	<i>Eulemur mongoz</i>	Mongoose lemur	Boivin et al. (2013)
Lamu			
Late 8th–mid 9th century AD	<i>Rattus rattus</i>	Black rat	Boivin et al. (2013)
Indo-Pacific			
Borneo			
Historic	<i>Elephas maximus borneensis</i>	Bornean pygmy elephant	Cranbrook et al. (2008); Fernando et al. (2003)*
New Ireland			
Late Pleistocene	<i>Phalanger orientalis</i>	Northern common cuscus	Anderson (2009); Flannery and White (1991); Heinsohn (2003, 2010); White (2004)
8400–7000 BP	<i>Thylogale browni</i>	Northern pademelon	Flannery et al. (1988); Flannery and White (1991); Heinsohn (2010)

Table 2 continued

Age ¹	Species	Common name	References ²
Lombok			
Protohistoric	<i>Muntiacus muntjak</i>	Barking deer	Heinsohn (2003)
Protohistoric/historic	<i>Trachypithecus auratus</i>	Silvered leaf monkey	Heinsohn (2003)
Holocene	<i>Manis javanica</i>	Malayan pangolin	Heinsohn (2003)
Prehistoric	<i>Sus scrofa vittatus</i>	Indonesian wild pig	Heinsohn (2003)
Holocene	<i>Felis bengalensis</i>	Leopard cat	Heinsohn (2003)
Late Holocene	<i>Viverricula indica</i>	Little civet	Heinsohn (2003)
Komodo			
Prehistoric	<i>Sus scrofa vittatus</i>	Indonesian wild pig	Heinsohn (2003)
Ambon			
Protohistoric/historic	<i>Herpestes javanicus</i>	Small Asian mongoose	Heinsohn (2003)
Unknown	<i>Crocidura maxi</i>	Javan shrew	Heinsohn (2003)
Prehistoric	<i>Phalanger orientalis</i>	Northern common cuscus	Heinsohn (2003, 2010)
Unknown	<i>Crocidura monticola</i>	Sunda shrew	Heinsohn (2003)
Admiralty Islands			
Pleistocene	<i>Spiloglossus kraemeri</i>	Admiralty cuscus	Heinsohn (2003, 2010)
Pleistocene	<i>Echymipera kalabu</i>	Common spiny bandicoot	Heinsohn (2003, 2010)
Lesser Sundas			
Prehistoric/historic	<i>Suncus murinus</i>	House shrew	Heinsohn (2003)
Holocene	<i>Rattus argentiventer bali</i>	Ricefield rat	Heinsohn (2003)
Palau, Seram, Melanesia and Indonesia			
Holocene	<i>Rattus nitidus</i>	Himalayan rat	Heinsohn (2003)
Polynesia			
Holocene	<i>Rattus exulans</i>	Pacific rat	Heinsohn (2003); Matisoo-Smith et al. (1998)*; Matisoo-Smith and Robins (2004)*

Table 2 continued

Age ¹	Species	Common name	References ²
Micronesia			
Holocene	<i>Rattus tanezumi</i>	Asian house rat	Heinsohn (2003)
Holocene	<i>Rattus nitidus</i>	Himalayan rat	Heinsohn (2003)
Prehistoric/historic	<i>Suncus murinus</i>	House shrew	Heinsohn (2003)
Bismarcks			
Prehistoric	<i>Cervus timorensis</i>	Rusa deer	Heinsohn (2003)
Prehistoric	<i>Rattus praetor</i>	New Guinea spiny rat	Heinsohn (2003)
Prehistoric	<i>Phalanger orientalis</i>	Northern common cuscus	Heinsohn (2003, 2010)
New Guinea			
Holocene	<i>Rattus tanezumi</i>	Asian house rat	Heinsohn (2003)
Holocene	<i>Rattus nitidus</i>	Himalayan rat	Heinsohn (2003)
Prehistoric	<i>Cervus timorensis</i>	Rusa deer	Heinsohn (2003)
Holocene	<i>Rattus argentiventer</i>	Ricefield rat	Heinsohn (2003)
Moluccas			
Holocene	<i>Rattus tanezumi</i>	Asian house rat	Heinsohn (2003)
Prehistoric	<i>Cervus timorensis</i>	Rusa deer	Heinsohn (2003)
Late Holocene	<i>Paradoxurus hermaphroditus</i>	Common palm civet	Heinsohn (2003)
Holocene	<i>Rattus argentiventer</i>	Ricefield rat	Heinsohn (2003)
Prehistoric/historic	<i>Suncus murinus</i>	House shrew	Heinsohn (2003)
Sulawesi			
Holocene	<i>Rattus nitidus</i>	Himalayan rat	Heinsohn (2003)
Prehistoric	<i>Sus scrofa vittatus</i>	Indonesian wild pig	Heinsohn (2003)
Holocene	<i>Rattus argentiventer</i>	Ricefield rat	Heinsohn (2003)

Table 2 continued

Age ¹	Species	Common name	References ²
Late Holocene	<i>Viverra zangalanga</i>	Malay civet	Heinsohn (2003)
Late Holocene	<i>Paradoxurus hermaphroditus</i>	Common palm civet	Heinsohn (2003)
Prehistoric	<i>Cervus timorensis</i>	Rusa deer	Heinsohn (2003)
Prehistoric/historic	<i>Suncus murinus</i>	House shrew	Heinsohn (2003)
Australia			
12,000–5000 cal BP	<i>Canis lupus dingo</i>	Dingo	Fillios and Taçon (2016)
Eastern Pacific			
California Channel Islands			
9200–7100 cal BP	<i>Urocyon littoralis</i>	Island fox	Collins (1991a, b), (1993); Hofman et al. (2015b)*, (2016); Rick (2013); Rick et al. (2009)
>10,000 cal BP	<i>Peromyscus maniculatus</i>	Deer mouse	Amis and Vellanoweth (2012); Rick (2013); Rick et al. (2012)
Late Holocene	<i>Reithrodontomys megalotis</i>	Harvest mouse	Collins and George (1990)
Late Holocene	<i>Otospermophilus beecheyi nestoticus</i>	Catalina ground squirrel	Rick (2013)
Pearl Island archipelago			
6200–5600 BP	<i>Mazama</i> sp.	Brocket deer	Martinez-Polanco et al. (2015)
Mediterranean Sea			
Lavezzi Island			
1300 AD	<i>Rattus rattus</i>	Black rat	Abdelkrim et al. (2009)*
Corsica			
6000–5000 BC	<i>Vulpes vulpes</i>	Red fox	Vigne (1999)
6000–5000 BP	<i>Erinaceus europaeus</i>	European hedgehog	Vigne (1992, 1999)
6000–5000 BP	<i>Apodemus sylvaticus</i>	Wood mouse	Vigne (1992, 1999)

Table 2 continued

Age ¹	Species	Common name	References ²
6000–5000 BP	<i>Glis glis</i>	Edible dormouse	Vigne (1992, 1999)
~ 3000 BP	<i>Mus musculus domesticus</i>	House mouse	Vigne (1992, 1999)
~ 3000 BP	<i>Eliomys quercinus</i>	Garden dormouse	Vigne (1992, 1999)
~ 3000 BP	<i>Crocidura suaveolens</i>	Lesser white-toothed shrew	Vigne (1992, 1999)
1600 BP	<i>Cervus elaphus</i>	Red deer	Vigne (1992, 1999)
400–200 BC	<i>Rattus rattus</i>	Black rat	Abdelkrim et al. (2009); Vigne and Valladas (1996)
1500s AD	<i>Lepus corsicanus</i>	Corsican hare	Masseti and Marinis (2008); Vigne (1992)
1400 AD	<i>Ursus arctos</i>	Brown bear	Vigne (1992)
Cyprus			
11,400 cal BP	<i>Sus scrofa</i>	Wild boar	Vigne (2014); Vigne et al. (2009)
10,600 cal BP	<i>Felis silvestris</i>	Wildcat	Vigne (2014); Vigne et al. (2004)
10,250 cal BP	<i>Mus musculus domesticus</i>	House mouse	Bonhomme et al. (2011)*; Cucchi et al. (2005); Vigne (2014)
~ 10,000 cal BP	<i>Vulpes vulpes</i>	Red fox	Vigne (2014)
~ 10,000 cal BP	<i>Dama dama mesopotamica</i>	Persian fallow deer	Vigne (1999, 2014); Vigne et al. (2016)
1000 BC	<i>Lepus</i>	Hare	Vigne (1999)
Crete			
7480–6230 cal BC	<i>Meles meles</i>	European badger	Horwitz (2013); Ripoll (2013)
7480–6230 cal BC/early Bronze Age	<i>Lepus</i>	Hare	Horwitz (2013)
~ 6000 cal BC	<i>Martes foina</i>	Beech Marten	Ripoll (2013); Vigne (1999)
2500–1000 BC	<i>Mus musculus domesticus</i>	House mouse	Cucchi et al. (2005)
Sardinia			
~ 6000 cal BC	<i>Vulpes vulpes</i>	Red fox	Vigne (1999)
~ 4000 cal BC	<i>Glis glis</i>	Edible dormouse	Vigne (1999)
~ 4000 cal BC	<i>Apodemus sylvaticus</i>	Wood mouse	Vigne (1999)

Table 2 continued

Age ¹	Species	Common name	References ²
~ 3000 cal BC	<i>Erinaceus europaeus</i>	European hedgehog	Vigne (1999)
~ 3000 cal BC	<i>Suncus etruscus</i>	Etruscan shrew	Vigne (1999)
~ 3000 cal BC	<i>Eliomys quercinus</i>	Garden dormouse	Vigne (1999)
~ 3000 cal BC	<i>Cervus elaphus</i>	Red deer	Vigne (1999)
~ 2000 cal BC	<i>Mus musculus domesticus</i>	House mouse	Vigne (1999)
~ 2000 cal BC	<i>Crocidura russula</i>	Greater white-toothed shrew	Vigne (1999)
Balearic Islands			
5000–4000 BP? ³	<i>Eliomys quercinus</i>	Garden dormouse	Bover and Alcover (2008); Reumer and Sanders (1984); Vigne (1999)
5000–4000 BP? ³	<i>Apodemus sylvaticus</i>	Wood mouse	Bover and Alcover (2008); Reumer and Sanders (1984); Vigne (1999)
~ 1000 cal BC	<i>Mus musculus domesticus</i>	House mouse	Vigne (1999)
~ 1000 cal BC	<i>Felis</i> sp.	Felid species	Bover and Alcover (2008); Vigne (1999)
~ 1400–1300 BC	<i>Oryctolagus cuniculus</i>	European rabbit	Masseti and Marinis (2008); Vigne (1999);
After 1500 BC	<i>Lepus</i>	Hare	Masseti and Marinis (2008); Reumer and Sanders (1984); Vigne (1999)
1000–1 cal BC	<i>Rattus rattus</i>	Black rat	Reumer and Sanders (1984); Vigne (1999)
1000 BC	<i>Mus musculus domesticus</i>	House mouse	Cucchi et al. (2005)
386–206 cal BC	<i>Mustela nivalis</i>	Weasel	Bover and Alcover (2008); Reumer and Sanders (1984); Valenzuela and Alcover (2015)
After 123 BC	<i>Crocidura suaveolens</i>	Lesser white-toothed shrew	Reumer and Sanders (1984)
Before 3rd century AD	<i>Dama dama</i>	Fallow deer	Valenzuela et al., (2016a, b); Vigne (1999)
Possible Late Holocene	<i>Genetta genetta</i>	Common genet	Bover and Alcover (2008); Vigne (1999)

Table 2 continued

Age ¹	Species	Common name	References ²
Eastern Atlantic			
Ireland			
5400–4600 cal BP	<i>Cervus elaphus</i> (2nd colonization)	Red deer	Carden et al. (2012)
Mesolithic/Neolithic	<i>Sorex minutus</i>	Pygmy shrew	Mcdévit et al. (2009)*; McDevitt et al. (2011)*
3800 BP	<i>Meles meles</i>	European badger	Montgomery et al. (2014)
2800 BP	<i>Martes martes</i>	Pine marten	Montgomery et al. (2014)
2500 BP	<i>Mus musculus domesticus</i>	House mouse	Montgomery et al. (2014)
1700 BP	<i>Rattus rattus</i>	Black rat	Montgomery et al. (2014)
12th century AD	<i>Oryctolagus cuniculus</i>	European rabbit	Montgomery et al. (2014)
12th century AD	<i>Sciurus vulgaris</i>	Red squirrel	Montgomery et al. (2014)
12th century AD	<i>Erinaceus europaeus</i>	European hedgehog	Montgomery et al. (2014)
12th century AD	<i>Dama dama</i>	Fallow deer	Montgomery et al. (2014)
Britain			
Iron Age	<i>Mus musculus</i>	House mouse	O'Connor (2010)
Roman/Norman	<i>Dama dama</i>	Fallow deer	Miller et al. (2016); Sykes et al. (2006, 2011, 2013)
Roman?/12th century	<i>Oryctolagus cuniculus</i>	European rabbit	Sykes and Curl (2010)
Late Roman	<i>Rattus rattus</i>	Black rat	Reilly (2010)
Inner Hebrides			
Mesolithic	<i>Cervus elaphus</i>	Red deer	Mulville (2010); Stanton et al. (2016)
Orkneys/Outer Hebrides			
~ 5000 BC (Orkney)	<i>Microtus arvalis</i>	Common vole	Cucchi et al. (2014)*; Martínková et al. (2013)*
Neolithic	<i>Cervus elaphus</i>	Red deer	Mulville (2010); Stanton et al. (2016)*
Iron Age	<i>Mus</i>	House mouse	O'Connor (2010)

Table 2 continued

Age ¹	Species	Common name	References ²
Iceland			
10th century AD	<i>Mus musculus</i>	House mouse	Jones et al. (2012)*
Greenland			
After 10th century AD	<i>Mus musculus</i>	House mouse	Jones et al. (2012)*
Canary Islands			
756 cal BC–313 cal AD	<i>Mus musculus</i>	House mouse	Alcover et al. (2009); Bonhomme et al. (2011)*; Michaux et al. (2007)
Azores			
15th century, perhaps Viking?	<i>Mus musculus</i>	House mouse	Gabriel et al. (2015)*
Gotland			
7420 cal BC	<i>Lepus timidus</i>	Mountain hare	Ahlgren (2011)*; Ahlgren et al. (2016)*
5700 cal BC	<i>Cervus elaphus</i> (no longer present)	Red deer	Ahlgren (2011)
5500 cal BC	<i>Vulpes vulpes</i>	Red fox	Ahlgren (2011)
3350 cal BC	<i>Sus scrofa</i> (no longer present)	Wild boar	Ahlgren (2011)
Mesolithic/Neolithic	<i>Apodemus flavicollis</i>	Yellow-necked mouse	Ahlgren (2011)
Neolithic	<i>Erinaceus europaeus</i>	Hedgehog	Ahlgren (2011)
Neolithic, Bronze/Iron Age	<i>Alces alces</i> (no longer present)	Moose	Ahlgren (2011)
At least 14th century	<i>Sciurus vulgaris</i>	Red squirrel	Ahlgren (2011)
Mid-19th century, possibly Mesolithic	<i>Capreolus capreolus</i>	Roe deer	Ahlgren (2011)
Caribbean Sea			
Lesser Antilles			
By 675–780 AD	<i>Didelphis</i> sp.	Opossum	Giovas et al. (2012, 2016)
After 500 BC	<i>Dasyprocta</i> sp.	Agouti	Giovas et al. (2012, 2016); Newsom and Wing (2004, pp. 72–72, 91); Stahl (2009)

Table 2 continued

Age ¹	Species	Common name	References ²
Greater Antilles, Puerto Rico and Vieques			
Ceramic period	<i>Capromyidae</i>	Hutia	Newsom and Wing (2004, pp. 157, 206)
Virgin Islands			
Unknown	<i>Nesophontes edithae</i>	Puerto Rican shrew	Newsom and Wing (2004, p. 137)
Ceramic period	<i>Capromyidae</i>	Hutia	Newsom and Wing (2004, pp. 157, 206)

¹ Ages given are the estimates from the original authors, including the format given (AD/BC, cal BP, time period, etc.) to be as accurate as possible. Interested readers should consult the references herein for additional details on the chronology

² For some references we present a single source that has synthesized all of the data (e.g., Ahlgren 2011; Boivin et al. 2013; Heimsohn 2003; Montgomery et al. 2014). Additional sources are cited therein. The vast majority of these studies are based on archaeological occurrence data but genetic studies are noted with an asterisk (*)

³ Bover et al. (2016) suggest the first human occupation of Mallorca was around 2470–2210 cal BC, which raises the possibility that this translocation is younger than the cited date

cuscus introductions are the earliest well-documented animal translocations to islands in the world.

During the Holocene, mammal translocations to islands increased dramatically. Due to their ease of stowing away in boats and storage vessels, some of the most pervasive and cosmopolitan organisms are small mammals, especially rodents. In the Mediterranean islands alone, ancient translocations have been documented for at least five species of rodents, three species of lagomorphs, three species of shrews, a hedgehog (Table 2), and a number of domestic animals. Lagomorphs are widespread on islands, with direct dates on the mountain hare (*Lepus timidus*) on Gotland around 9400 cal BP (Ahlgren 2011; Ahlgren et al. 2016), and by 3000 years ago on several Mediterranean islands (Masseti and Marinis 2008; Vigne 1992, 1999, 2014). In the Caribbean, hutia (*Capromyidae* sp.) have been translocated to a number of islands in the late Holocene including Puerto Rico and the Virgin Islands, with agouti (*Dasyprocta* sp.) introduced to the Lesser Antilles (Giovas et al. 2012, 2016; Newsom and Wing 2004; Stahl 2009; Wing 2008). Shrews are surprisingly widespread, despite their high metabolic needs, and have been introduced to Corsica, Cyprus, Sardinia, Ireland, Zanzibar, and a number of Australasian islands (Table 2). Small mammals may have been food sources in some cases, but many were likely accidentally introduced to islands as stowaways.

Commensal rodents, especially rats and house mice, have been used as bioproxies to explore patterns of human colonization using genetic analysis (Jones et al. 2013; Matisoo-Smith 2009; Storey et al. 2013). In the north Atlantic, Icelandic house mice (*Mus mus*) from Viking age archaeological sites share a mitochondrial haplotype with modern Icelandic mice populations and those from Norwegian Viking settlements, indicating continuity through time in Icelandic house mice populations (Jones et al. 2012). This differs from Greenland where ancient genetic data suggest there was an introduction, extinction, and replacement of mouse mitochondrial haplotypes (Jones et al. 2012). Recent work on extant house mice populations in the Azores and Canary islands and the redating of archaeological contexts indicate a complex pattern of introductions that began around 2750–1640 cal BP in the Canary islands (Alcover et al. 2009; Bonhomme et al. 2011) and 500 cal BP or earlier in the Azores (Gabriel et al. 2015). In the Pacific, phylogeography of extant rat (*Rattus exulans*) populations has been used as a proxy for the Lapita migration (Matisoo-Smith et al. 1998; Matisoo-Smith and Allen 2001) in conjunction with aDNA analyses (Matisoo-Smith 2008, 2009; Matisoo-Smith and Robins 2004). These genetic studies highlight not only the utility of commensal rodents for understanding human dispersal but also the difficulty of detecting population replacements in the archaeological record. Ancient DNA analysis, coupled with analysis of extant populations and radiometric dating, can help elucidate phylochronological relationships to identify the history of cryptic populations (Ramakrishnan and Hadly 2009).

Carnivores also have been moved through human action. Civets were translocated in the Indo-Pacific as what Heinsohn (2003) calls ethnotramps, or live-caught wild animals that are culturally or economically valuable for ritual use, food, trade, or as pets. Canids, another likely ethnotramp, have been translocated around the world. Dingoes arrived in Australia 5000–12,000 years ago and have had

considerable impact on the native Australian fauna (Balme and O'Connor 2016; Fillios and Taçon 2016; Savolainen et al. 2004). Foxes have been translocated to a number of islands, often for their fur. Red fox (*Vulpes vulpes*) were translocated to Cyprus approximately 10,000 years ago (Vigne 2014), Corsica around 8000–7000 years ago (Vigne 1992, 1999), Sardinia by 8000 years ago (Vigne 1999), and Gotland ~5500 years ago (Ahlgren 2011). On the California Channel Islands, island foxes may have been introduced by Native Americans and were likely moved between islands by ancient people, potentially for pest management, their fur pelts, or other factors (Hofman et al. 2015b, 2016; Rick et al. 2009). Regardless of the reason, the introduction of carnivores is more likely to be intentional than unintentional, and it was an important step in the construction of island landscapes by ancient peoples.

Carnivores can have profound effects on the typically naïve or depauperate native fauna of islands. On the Aleutian Islands, the historical introduction of the Arctic fox (*Vulpes lagopus*) transformed the abundance and composition of island plant communities from grassland to tundra (Croll et al. 2005). Many modern island plant and animal communities have been decimated in the resulting trophic cascade that followed the introduction of predators, as seen with the introduction of the brown tree snake (*Boiga irregularis*) in Guam (Wallach et al. 2015; Wiles et al. 2003). Similar trophic cascades may have happened during past introductions, but there has been limited research on this topic. Investigations of the impact of modern invasive species are important proxies for how ancient introductions of carnivores or even herbivores impacted past island ecosystems.

Herbivores, including large mammals, have been introduced to islands worldwide. Pygmy elephants in Borneo were hypothesized to be the result of a historic introduction by the Sultan of Sulu (Cranbrook et al. 2008), but some genetic data suggest that elephants in Borneo are a distinct and older population (Fernando et al. 2003), and more genetic analysis is needed to verify these claims. Deer species, including Rusa deer (*Cervus timorensis*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and brocket deer (*Mazama* sp.) were introduced to the Indo-Pacific, Mediterranean, north Atlantic, or the Pearl Islands during the Holocene (Heinsohn 2003; Martinez-Polanco et al. 2015; Sykes et al. 2013, 2006, 2011; Vigne 2014; Vigne et al. 2016). Deer are likely an intentional introduction as a food source; however, there is debate on whether deer were transported alive or as butchered animal parts in early British contexts (Miller et al. 2016).

Information on the timing and type of animals that were introduced also can inform our understanding of prehistoric seafaring technology. Vigne (2014) explores how the size of domestic and wild animals including Persian fallow deer, wild boar, and others (Vigne 2014) would necessitate large watercraft for safe and successful transport between localities. Reed-bundled boats would not support these larger animals, and their appearance on Mediterranean islands necessitates a different boat technology than earlier voyages. By exploring regional patterns of mammal introductions, Boivin and Fuller (2009), Matisoo-Smith (2009), Vigne (2014), and others have shown that translocated mammals can be used to reconstruct human behavior, movement, and ancient trade networks. Fine-scale data

including high-resolution genetic and radiometric data will only improve these analyses and highlight the antiquity and extent of the human influence on mammal biogeography.

Plants and Transportable Gardens

The archaeological literature from many of the world's islands provides scores of examples of ancient translocations of domesticated or edible plant species that were cultivated as crops, as well as a series of wild plants often introduced as weeds alongside desired species (Fig. 3). The divide between domesticated species, predomesticates, and wild species, however, can be blurry. De Langhe et al. (2009) introduced the term *cultiwild* in the discussion of banana translocation and domestication to mean any occurrence of a wild plant—cloned or not—outside of its native habitat. Ultimately, the term *cultiwild* includes many predomesticates, although there are challenges in discerning between wild and domesticated species, especially if many—if not all—of these were deliberately transported for cultivation. Many plants are excellent over-water dispersers, transported by birds or by natural rafting. As an example of the latter, genetic and other data suggest bottle gourds (*Lagenaria siceraria*) from Africa may have been transported by oceanic drift to the Americas, where they subsequently were dispersed by animals and later domesticated by people in several areas (Kistler et al. 2014).

Newsom and Wing (2004) provide a comprehensive summary of plants that were translocated by people to the Caribbean. While this includes numerous domesticates (e.g., maize [*Zea mays*], manioc [*Manihot esculenta*], and peppers [*Capsicum* spp.]; Mickleburgh and Pagán-Jiménez 2012; Newsom and Wing 2004, p. 155), a few wild plants also are among the group of imported plants during the Archaic period (Newsom and Wing 2004). Subsistence economies during the Archaic period (mid-to-late Holocene) in the Caribbean seem to have been primarily focused on foraging, but there is increasing evidence for horticulture and gardens (Newsom and Wing 2004, p. 31). Recent research on phytoliths from a 6650–6330 cal BP site on Trinidad documents maize, sweet potato, bean, and chili pepper, suggesting that cultivars may have been translocated to islands earlier than assumed (Pagán-Jiménez et al. 2015). Among the list of wild plants that were introduced to Caribbean islands are wild avocado (*Persea Americana*) and sapodilla (*Manilkara*, cf. *M. zapota*), both exotics from Mexico or central America associated with gardens (Newsom and Wing 2004, pp. 120–121).

Kirch (1997, 2000) noted that crop plants translocated by Lapita peoples to Pacific islands include 28 species supported by archaeobotanical or linguistic data. While most of these are domesticated root and tuber crops, the list includes several nut-bearing tree crops, including *Canarium* almond, *Terminalia* almond, Vi apple, and Malay apple (Kirch 2000, p. 110; Spriggs 1997, p. 55). Similarly, Latinis (2000) discusses arboriculture in Southeast Asia and parts of Oceania, indicating the translocation of several tree crops. One such tree, the paper mulberry (*Broussonetia papyrifera*), was an important resource for bark cloth, and the phylogeographic

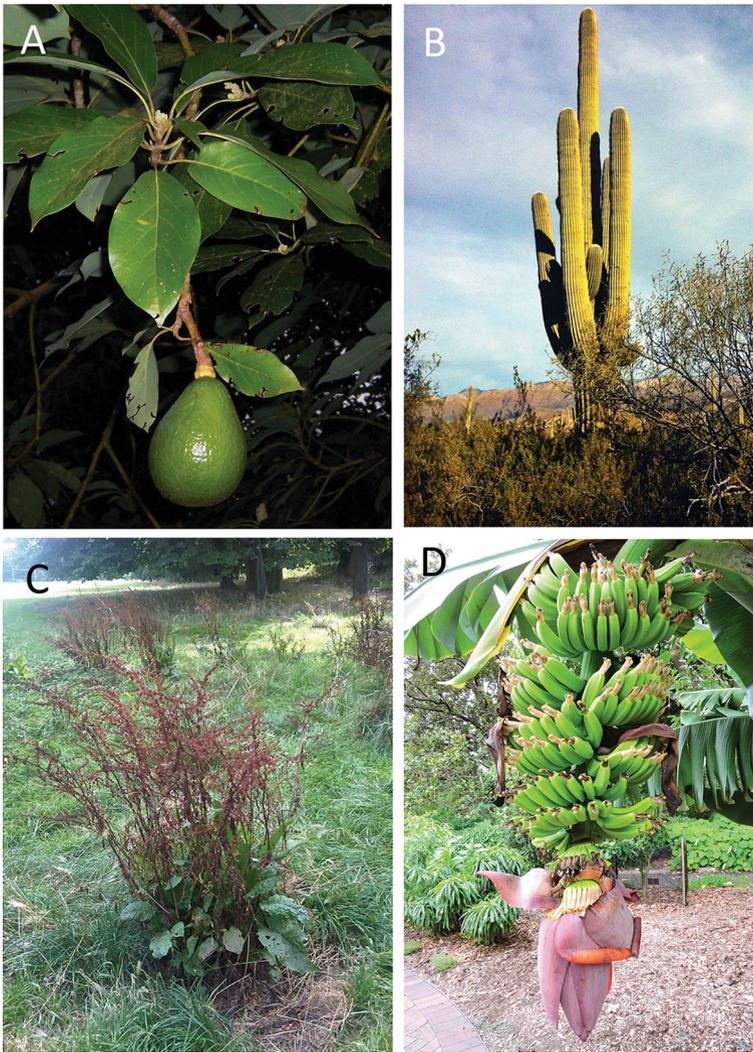


Fig. 3 Select tree crops and other plants introduced by people to islands: (A) avocado (*Persea americana*), (B) saguaro (*Carnegiea gigantea*), (C) patience dock (*Rumex patens*), and (D) banana (*Musa acuminata*). See acknowledgments for photo credits

patterns identified from herbarium and modern samples concur with expected patterns of the Austronesian expansion out of Taiwan (Chang et al. 2015).

Not only did people in Oceania and beyond bring with them desirable crop species, but just as in the case of animals they brought with them other nontarget species like weeds. Kirch (2000, p. 110) noted that proto-Oceanic linguistics has a reconstructed word **papo* that refers to weeding; weeds were translocated throughout the Pacific and are often useful in tracking first colonization events (Athens et al. 2014; Kirch 2000, p. 18).

Prebble and Wilmshurst (2009) synthesized plant introductions to several remote Oceanic islands in subtropical Polynesia (including Rapa, Rapa Nui, and New Zealand) prior to European contact, building on previous work by Leach (2005) for New Zealand. Prebble and Wilmshurst (2009) divided these into trees and shrubs, herbs, and inadvertent introductions and used archaeobotanical, paleobotanical, and botanical survey data as support. The list includes 13 probable herb introductions, 23 trees and shrubs, and 17 inadvertent, generally weedy specimens. When New Zealand is added to the picture, even more species, potentially from surrounding islands, were introduced (Prebble and Wilmshurst 2009, p. 245). Despite Maori strategies to mitigate the introduction of weedy species, Leach (2005) noted six weeds likely introduced prehistorically in Maori gardens. An important note of caution is that some of these plant species are thought to be human introductions because they do not occur in prehuman botanical records, while others are supported by the fact that they only survive in cultivation (e.g., *Thespesia populnea* and *Cocos nucifera*) (Prebble and Wilmshurst 2009). While the list includes some domesticates—taro (*Colocasia esculenta*), sweet potato (*Ipomoea batatas*), and calabash (*Lagenaria siceraria*)—the majority of herbs and unintentional weedy plants are not domesticates. We should not assume that all of these were transported by humans prehistorically. Fairbairn (2005, p. 494), for instance, noted that the possible translocation of the canarium nut (*Canarium indicum*) from New Guinea to surrounding islands may actually be from species that were native to those islands. Given the challenge of detecting some of these species, it also is possible that we have underestimated the species introduced by people.

The spread of wild plants, especially inadvertent weeds and other species, extends well beyond the Pacific and Caribbean islands and can be seen as something that accompanied horticulturalists wherever they traveled. In the North Atlantic, herbaceous plants and weeds accompanied the wheat, barley, and other domesticates that were introduced to the Faroes, Iceland, and Greenland (Dugmore et al. 2005, 2012; McGovern et al. 2007; Schofield et al. 2013). Dugmore et al. (2005, p. 30) noted that the Norse introduced so many taxa to Iceland that they actually increased floristic diversity but probably also reduced the average number of species in a given area. Introduced weeds that accompanied agricultural domesticates on North Atlantic islands include dock (*Rumex* spp.), plantains (*Plantago* spp.), common/sheep's sorrel (*Rumex acetosa/acetosella*), yarrow (*Achillea millefolium*), and knotgrass (*Polygonum aviculare*) (Dugmore et al. 2005, p. 31).

Herbaceous plants also accompanied people to Mediterranean islands, arriving with domesticates, in animal fodder, and as components of a broad anthropogenic influence on island ecosystems (Patton 1996; Zeder 2008). Cyprus provides important examples of additional introductions. Vigne et al. (2012) tracked the arrival of cultivators to Cyprus, noting dogs, cats, and wheat in sites as old as 10600 cal BP. Impressions of cereal chaff in burned earth are from barley and emmer wheat. It was unclear if these were wild or domesticated, but wild emmer is not native to Cyprus and must have been introduced by people (Vigne et al. 2012, p. 8447). Weeds have been documented in early aceramic Neolithic sites on Cyprus, including ryegrass (*Lolium* sp.), a weed commonly found with cereal crops (Hansen 2001).

With the widespread and well-documented movement of domesticated and wild plants to islands by ancient cultivators, it is surprising that there are few published data about possible translocation of wild plants to islands occupied solely by hunter-gatherers. Part of the challenge may be that many of these islands are near-shore continental islands where natural versus cultural dispersals can be ambiguous. Nabhan (2000) has suggested that the Seri may have translocated cactus to the Midriff Islands in Mexico as part of a placental ritual described in oral tradition. Cacti (*Pachycereus pringlei*, *Carnegiea gigantea*) and elephant trees (*Bursera* spp.) were planted with the newborn placenta, and in places they created anthropogenic cactus stands of similar ages near human camps. It is still unknown whether these plantings of cactus took them outside of their native range (Nabhan 2000), but they are listed as translocations by Yetman and Burquez (1996) who argue they were translocated for their fruit, while Nabhan (2000) advocates a ritual use. Tobacco (*Nicotiana clevelandii*), *Datura*, and oaks may have been introduced to the California Channel Islands from mainland plants by Native Americans though this remains speculative (Timbrook 1993, p. 57). Recent microsatellite genetic analysis of the endemic island scrub oak (*Quercus pacifica*) found on the three largest California Islands suggests divergence from mainland oaks during the Pleistocene but also a surprising amount of gene flow between populations, possibly a result of acorn transport by ancient peoples (Backs and Ashley 2016). Future genetic research is an important strategy for understanding translocations on the Channel Islands and beyond. Ultimately, we advocate the approach used by Prebble and Wilmshurst (2009), where systematic review of archaeobotanical and paleobotanical data (pre- and post-human) and that of botanical species lists compiled through time help build the case for cultural or natural dispersal, which can be enhanced with genetic, isotope, and other data.

Diseases, Insects, Birds, and Cargo Species

Much like the weeds that accompanied people to islands, insects and disease also followed ancient peoples to offshore islands. The advent of molecular methods has greatly increased our ability to detect diseases and their causative pathogens in the archaeological record (Bos et al. 2015; Drancourt and Raoult 2008; Greenblatt and Spigelman 2003; Harkins and Stone 2015). As only a few pathogens leave a trace on human skeletal material, research has focused on tuberculosis, syphilis, and other major diseases, but the implications of the Columbian exchange on human health have been profound (Crosby 2004; Harkins and Stone 2015). As we move further back in time, both known and undescribed pathogens also were likely translocated by ancient peoples to islands. New genomic and proteomic approaches will improve our ability to explore and detect the prehistoric transmission of pathogens, including bacteria, parasites, and their vectors.

Grayson (2001, table II) provided a robust list of invertebrate translocations to the Faroe Islands, Greenland, Iceland, and 10 Oceanic islands. The vast majority are insects associated with the introduction of domesticated animals and cultigens, including 19 species to Iceland alone, such as human and sheep louse (*Pediculus humanus* and *Damalinia ovis*) and several species of beetle (e.g., dung beetle

[*Aphodius fmetarius*] and grain beetle [*Oryzaephilus surinamensis*] (Grayson 2001, see also Dugmore et al. 2005). The granary weevil (*Sitophilus granarius*) has been documented leaving Egypt and traversing across Europe, the United Kingdom, Iceland, and Greenland, likely reaching Jamestown, Virginia, between 1611–1617 and Newfoundland as early as 1621 (King et al. 2014). Panagiotakopulu (2014) recently provided an analysis of these introductions for the North Atlantic, noting a number of synanthropic species introduced by humans. The presence of earthworms in the Faroe Islands also is thought to be a result of the Norse colonization (Enckell and Rundgren 1988). In comparing faunal connections between Europe and North America, Lindroth (1957, pp. 150–151) noted that historical human introductions were relatively common, including 23 insect species (e.g., Carabid beetles) on Newfoundland. In the Pacific islands, the list includes beetle, weevil, taro plant hopper, and a number of land snails (*Lamillidea*, *Gastrocopta*, *Lamellaxis*, etc.) (Grayson 2001; Kirch and Yen 1982; Matthews 2003). Recent phylogenetic work on Polynesian tree snails (*Partula* spp.) has tracked their translocation and movement among islands, showing that this was nonrandom with many source populations (Lee et al. 2007). Christensen and Weisler (2013) also demonstrate the scale of the issue, noting that Polynesians likely introduced most of the nonmarine mollusks on the Marshall Islands. Ship ballast is also responsible for the introduction of a number of marine organisms, including shellfish and their pathogens, to new localities today (Pagenkopp Lohan et al. 2016), and these unintentional introductions are likely not a new phenomenon.

Similar to insects, skinks and geckos also made their way as human commensals to numerous Pacific islands, including Mangaia and Hawai'i (Kirch 1996; Storey et al. 2013). While some gecko and skink introductions may have been unintentional, some may have been intentional (Storey et al. 2013). In his review of ancient and modern translocations in Australasia, Heinsohn (2003) argued for the prehistoric incidental introduction of geckos (*Hemiphyllodactylus typhus*, *Lepidodactylus lugubris*) to Oceanic islands and the circum-New Guinea archipelago. In this same area, other gecko species, a skink, and frogs appear to be human introductions with no clear indication of when they happened, though most are likely recent (Heinsohn 2003). On Caribbean islands, the origins of many of the herpetofauna are unknown, but Stahl (2009, p. 156) points to examples of iguanas, tortoises, and geckos that may have been introduced by people or a combination of natural and human-assisted dispersal. Nabhan (2000) provides an example of Seri movement of iguanids (*Sauromalus* spp.) and possibly geckos (*Phyllodactylus* spp.) on the Midriff Islands, which is supported by oral tradition.

Examples of wild bird translocations from the past are more limited than mammals and plants, but people moved birds around historically and have introduced them throughout islands in the circum-New Guinea archipelago (Heinsohn 2003). Two species of cassowary (*Casuarius casuarius*, *C. bennetti*) were believed to have been introduced prehistorically during the Holocene to Seram and New Britain Islands, respectively (Heinsohn 2003, p. 362). The flightless rail (*Nesotrichis debooyi*) was likely introduced prehistorically to several Caribbean islands for food, but there are still questions about this introduction (Grayson 2001; Stahl 2009; Tella 2011). Given the well-documented trade and breeding of macaws

(*Ara macao*, *A. militaris*) from Mesoamerica to the southwestern United States (Crown and Hurst 2009; Somerville et al. 2010; Watson et al. 2015), translocation of grackles (*Quiscalus mexicanus*) by ancient Aztecs (Haemig 2012), and movement of a wide variety of domestic species to islands and elsewhere around the world (Tella 2011), the possibility of additional movements of birds prehistorically is likely; this proposition can be tested with analysis of archaeological/paleontological specimens, direct AMS dating, isotopes, and genetics. An important area for future genetic research is the pathogens that may have accompanied translocations of associated flora and fauna.

Translocating Domestic Species: Explosion and Transformation

The number and diversity of wild plants and animals that were translocated to islands around the world from the Pleistocene through the Holocene is a long and growing list. While the distinction between human-assisted and natural dispersal is not always clear, human involvement in past animal and plant introductions is well supported by the vast number of domesticated species that were transported to islands. The introduction of domestic animals to islands is part of a much broader spread of domesticates overland and by sea. We briefly discuss the robust record of domesticated species that were transported to four major island groups—Caribbean, Pacific, Mediterranean, and North Atlantic. Our list is not exhaustive or a complete survey; rather we highlight the implications of translocations of domesticated species that will help us better understand possible translocations of wild taxa.

Some of the earliest well-documented translocations of domesticated plant and animal taxa occurred on islands in the Mediterranean. This region was a center of early domestication and sophisticated seafaring and maritime voyaging, which supported the spread of these species particularly after about 11,000 cal BP (Boivin et al. 2016). Recent work on Cyprus has extended the timing of translocation of a few taxa, including dogs and cats that were introduced to the island by about 10,600 cal BP, along with an earlier translocation of wild boars (Vigne et al. 2012). As part of a synthesis of domestication and diffusion in the Near East, Zeder (2008) also noted the wide range of domesticated and wild taxa that were transported to Cyprus after about 10,000 cal BP, including sheep, goats, cattle, and pigs, as well as wheat, barley, pistachios, and figs. These and other domesticates made their way to other islands throughout the Mediterranean during the subsequent centuries and millennia (Patton 1996).

The North Atlantic contains several islands that were important areas for early maritime exploration from Europe. In the Neolithic and possibly the Mesolithic, people traveled to Orkney, Oronsay, the Faroes, and other islands as part of broader colonization of the North Atlantic (Dugmore et al. 2010). Considerable research has focused on Norse exploration of the North Atlantic after about AD 900, including the environmental interactions, legacies, and impacts of Norse exploration and colonization (Dugmore et al. 2012; McGovern et al. 2007). A suite of studies has investigated Norse settlements on Iceland and Greenland, resulting in impressive archaeological and historical research that paints a complex picture of Norse

environmental and social dynamics. As McGovern (1995) and colleagues (McGovern et al. 2007) have noted, Norse environmental and social systems were deeply intertwined with complex historical trajectories that often included significant environmental degradation (e.g., species introductions, overgrazing, soil erosion), but also sustainable practices and adjustments in untenable strategies. A key component of Norse settlement was the transportation and deliberate introduction of numerous domesticated and wild plant and animal taxa, including cattle, sheep, goats, pigs, dogs, cats, cereal crops, and as noted earlier, a wide variety of wild plants and insects that are commensal with domesticated species (Grayson 2001; McGovern et al. 2007). Many of these were taken to every island the Norse settled and had lasting impacts and legacies on native ecosystems and landscapes (e.g., significant loss of topsoil from grazing).

On the other side of the world, Polynesians and other earlier peoples were exploring and colonizing scores of islands throughout the tropical and temperate portions of the Pacific. Similar to the Norse, these episodes of colonization usually involved several domesticated (and wild) species that were part of what Anderson (1952) termed “man’s transported landscapes.” This term was enhanced by Kirch (2000, pp. 109–110) and others to emphasize the group of new species that were brought to Pacific islands and subsequently reshaped them into major anthropogenic landscapes. The translocation of plants and animals to the Pacific has been a major topic of research that has enhanced knowledge of human modes and directions of colonization through aDNA research (Matisoo-Smith 2009; Storey et al. 2013). Ancient people often brought pigs, chickens, dogs, and rats to remote Oceania (Anderson 2009). Some of the more commonly translocated species include chickens, pigs, dogs, coconut (*Cocos nucifera*), bananas (*Musa* and *Astralimusa*), taro (*Colocasia esculenta*), yams (*Dioscorea alata*), and numerous insects and wild plants that came as commensals (Grayson 2001; Horrocks et al. 2008; Kirch 2000).

East Asian domesticated crops made the journey west across the Indian Ocean. Several domesticated species including Pearl millet, sorghum, rice, and mung bean recently have been identified in sites on the Comoros and Madagascar, supporting an ancient Austronesian colonization across this vast stretch of coast (Crowther et al. 2016).

In the warm waters of the Caribbean, numerous domesticated species were transported throughout the region’s islands, including crops and animals of primarily South American and possibly Mesoamerican origin (Newsom and Wing 2004); this translocation of domesticated and wild plants and animals began in the Archaic, likely by some of the earliest colonists to the region. Like other areas, the types and diversity of plant and animal translocations greatly increased with the spread of agriculturalists through the area. During the Ceramic and later periods (after roughly 2500 cal BP), numerous domestic plants and animals were staple food sources and were transported throughout the Greater and Lesser Antilles and beyond, including manioc (*Manihot esculenta*), maize (*Zea mays*), guava (*Psidium guajava*), cotton (*Gossypium* sp.), dogs, guinea pigs (*Cavia porcellus*), and commensal invertebrates, plants, and insects (Fitzpatrick and Keegan 2007; Newsom and Wing 2004; Stahl 2009). Research on the island of Carriacou

identified several South American fauna, including domesticated guinea pigs and wild armadillos (*Dasypus* sp.), peccary (*Tayassu/Peccari* sp.), opossum (*Didelphis* sp.), and agouti (*Dasyprocta* sp.); with more detailed zooarchaeology and archaeobotany, the list of domesticated and wild translocations may increase (Giovas et al. 2012).

These cases of substantial movement and translocation of domesticated plants and animals and numerous associated species demonstrate that humans were prime movers of flora and fauna to islands in the distant past. While we have long known of these transformative translocations and introductions (Anderson 1952), new research continues to increase the size, magnitude, and geographic distribution of species introduced to islands by humans. The movement of so many domesticates to very diverse environments (e.g., the North Atlantic to tropical Pacific) also lends anecdotal support to the possibility that people translocated greater numbers of wild plants and animals in the past. The movement of domesticates alone does not support translocation of some wild taxa, but it further corroborates the abilities and motivation of ancient people to modify and transform the environments in which they lived for their own benefit (i.e., niche construction). Translocation of wild and domesticated plants and animals was a major component of human niche construction and landscape modification on islands and continents throughout the world. While researchers have long recognized the major transformation of the planet from the movement of domesticated plants and animals around the world during historic times (e.g., the Columbian exchange), these data demonstrate that these processes have roots in much deeper time, generally several millennia or more before the 15th and 16th century expansion of Europeans.

Synthesis, Conclusions, and Future Directions

Translocations of non-native plants and animals occurred deep in the past and around the world, but they are often most visible in the bounded landscapes of islands. Ancient introductions of a wide variety of organisms have profoundly changed the structure and function of our planet's ecosystems, especially on islands where biodiversity tends to be more fragile. Today, island ecosystems have been constructed by a combination of natural and cultural processes, including the activities of ancient foragers and agriculturists, as well as contemporary human populations. Both foragers and agriculturists translocated wildlife in the deep past, but human agency is better understood in agricultural societies where domesticated species can be more readily distinguished from potential native taxa. It is more difficult to detect translocations by foraging populations where "wild" resources predominate. Time depth also can blur the distinction between what landscapes and organisms are perceived as native or non-native.

To distinguish between cultural and natural dispersal events as well the possibility of repeated introductions, we advocate the critical inspection of all available data before assigning agency. While our synthesis documents scores of human translocations of everything from weedy plants to deer, there are many more natural dispersal events than cultural and others that are likely a combination of the

two. We advocate a methodological framework that integrates occurrence data with direct AMS radiocarbon dating, stable isotope geochemistry, and ancient DNA analysis to evaluate the mode of introduction. When available, ethnographic data and other historical sources also may be crucial for evaluating ancient translocations. Individual lines of evidence may be equivocal and not provide support for a translocation, but a preponderance of multiple lines of evidence lends weight to a cultural or natural introduction and allows further discussion of why and how a species colonized an island. Greater methodological rigor and cautious interpretation in evaluating the presence of non-native animal or plant remains in archaeological sites stands to greatly improve our understanding of ancient translocation, as well as broader human–environmental interactions and niche construction.

People have translocated wildlife for a variety of reasons, including for ritual and symbolic purposes, food and subsistence, and/or tool making. Much of this behavior is tied to ecosystem engineering or niche construction and reducing risk as people move to a new environment or diversify their current environment (Boivin et al. 2016). These transported landscapes highlight the role humans have had in altering and managing their environments for millennia. Modern conservation and restoration practices, such as assisted migration, or the movement of plant or animal populations for conservation purposes, are the latest wave of a continuum of human–environmental management that extends deep into the human past.

As we look to the future, understanding when and how an ancient translocation occurred is important for the management of island ecosystems. Conservation scientists and managers need baseline data on paleoenvironments that can inform environmental restoration goals. Along with other stakeholders, managers must make choices about the baseline or desired future condition of a particular ecosystem, and this often comes down to a search for a “pristine,” prehuman, or pre-European contact condition. Knowledge of the history of island biodiversity can be critical to these decisions and also challenge us to realize that many ecosystems on earth have been shaped by people in the distant past (Boivin et al. 2016; Ellis 2015). In many ways, conversations about restoration and sustainability should recognize that conservation decisions need to account for this change through time or range of ecological variability (Szabó 2010, 2015). Such perspectives may ultimately help us promote the long-term resilience of ecosystems and organisms on a planet with a rapidly multiplying human population and ever increasing effect on the planet’s environments and climate.

Beyond restoration, there are implications for the conservation of the species introduced by ancient peoples. Species that were translocated by humans, even those that were introduced thousands of years ago and have adapted to local ecosystems, could be eradicated if stakeholders choose to restore an environment to a state without human influence. Ecosystem restoration and management is an active negotiation process that continues the legacy of ecosystem construction by humans that has been ongoing for millennia. The future depends on people recognizing the value of understanding our ancient human–environmental influence on the planet, as well as the will to make difficult decisions and start a broad

conversation about what we want the future of our planet's ecosystems and biodiversity to look like.

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