

## **Tropical Islands as Paleoecological Laboratories: Gauging the Consequences of Human Arrival**

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*Inter-island paleoecological comparisons have provided useful information concerning the role of humans vs. background-level disturbance in tropical ecosystems. Major ecological changes have occurred since human arrival in Madagascar, the West Indies, the Hawaiian Islands, and elsewhere. Prehuman vegetation changes and disturbances have also been documented for many islands. Instructive inter-island similarities and differences have been detected in the chronology, distribution, and extent of human activities, vegetation changes, and biotic extinctions. The earliest stratigraphic proxy evidence for initial human impacts (including increased charcoal particle influx to sediments, first appearance of exotic pollen, increase in ruderal pollen, and paleolimnological evidence for cultural eutrophication of lake waters) generally confirm but sometimes predate the earliest conventional archaeological evidence for human activity. Carefully chosen sites permitting the close integration of palynological, paleontological, and archaeological data from a variety of island settings with differing geographic and historical contingencies can enable investigators to more fully evaluate the importance of a range of human and ecological variables in determining the overall character and dynamics of ecosystems.*

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**KEY WORDS:** islands; paleoecology; palynology; extinctions; human impacts.

### **INTRODUCTION**

Those who study the past could play an important role in the current debate regarding future global ecological changes. However, the information generally offered by archaeologists, historians, paleontologists, and palynologists in this context has, understandably, often been anecdotal or

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eclectic in nature. Meanwhile, the public, the media, and politicians expect “scientific proof” relevant to such crisis-driven realms as human population issues, the possible threat of global warming, and the present biodiversity crisis.

The modern ecological dilemma involves many large-scale processes not easily teased apart into separate problems that can be attacked with relatively simple, replicable experimental procedures. The comparative microcosms of remote islands may provide the best substitute for fully controlled experiments involving human–ecosystem interactions. The well-rehearsed sequence of human discovery, landscape modification, and biotic adjustment (or collapse) has been repeated hundreds of times on the isolated landmasses of the world’s oceans, each case providing instructive similarities and differences to comparable cases elsewhere. Island biogeographers have invested several decades in ecological research on the effects of relative isolation and land area on migration and extinction rates of island biotas (e.g., MacArthur and Wilson, 1967; Simberloff and Wilson, 1970; Diamond, 1972). Perhaps owing to the technical difficulty of measuring past human impacts and biotic responses from the indirect clues in the stratigraphic record, however, investigators have been much slower to fully capitalize on the potentially rich opportunities to examine the paleoecological aspects of human island biogeography.

Reconstructing what has happened in recent millennia on oceanic islands requires one to recognize at least four types of important past events, each of which may leave traces in the stratigraphic (and sometimes the historical) record: (1) human discovery and settlement of the island; (2) modification of the landscape with fire, forest clearance, pastoralism and cultivation; (3) introduction of exotic organisms; and (4) decline and extinction of indigenous species.

Unless we can uncover, analyze, and integrate these four critical time horizons, we cannot begin to assess the complex and useful paleoecological question that is basic to all modern concerns about human environmental impact throughout the biosphere: How much and what kinds of environmental changes lie within the “natural” background-level (i.e., nonhuman) range of variation, as opposed to purely anthropogenic effects of potentially greater threat to the health of ecosystems? This is a practical but rather unsatisfying question, too important to ignore, but technically and philosophically perilous. It challenges students of the past to attempt to deduce cause and effect from the stratigraphic record, and to seek levels of temporal, spatial, and systemic resolution that stretch the capacity of proxy data of the types generally available. Nevertheless, the relatively simple biotic systems and shallow time-depth of human history characteristic of many remote islands are attractive for attempting this daunting task.

### WHAT'S AN ISLAND PALEOECOLOGIST TO DO?

To make a good scientific beginning, it is important to ask what might actually be measurable. In general, our interest is to gauge background (i.e., prehuman) levels of ecological variation, and to compare this with the type, rate, and extent of ecological change in the human milieu. This general goal serves as a justification for most studies of island paleoecology, but in practice has seldom been attained.

What has most often been measured in island paleoecological studies, and indeed must be measured in order to make any progress toward the general goal, are two related parameters, one temporal and the other primarily spatial. The first task is to establish the actual date, within an acceptable margin of error (generally, in practice, ca.  $\pm 100$  years), for the arrival of humans on the island and the onset of various human impacts. The second and related task is to characterize the specific types and the geographic extent of any human modifications of the island ecosystem and its biota.

What we need to measure seems fairly obvious, but, owing to the broad array of techniques that might be brought to bear, how we might do this is often far more problematic. In general, the ideal is to adopt a multidisciplinary approach to the analysis of well-dated stratigraphy containing as many types of palynological, paleontological, and archaeological evidence as possible. In order to illustrate the possibilities of such integrated studies, I will briefly review some of the methods and results from several published studies from various islands in the three tropical oceans of the world.

Islands may be splendid laboratories in which to study some fundamental aspects of our species' relation to nature, but none of the expectations can be realized, in fact, unless we can establish one chronological horizon with reasonable certainty: the point in time when a particular human impact begins. Although there are certainly archaeological and paleontological techniques that are useful for this, several studies suggest that palynology may offer the most generally applicable route for detecting the onset of anthropogenic influences on island ecosystems (Table I).

Four classes of methods for palynologically detecting human arrival on islands have been used with considerable success. These are: (1) first appearance of pollen of introduced plants; (2) large increases in ruderal pollen types; (3) paleolimnological evidence for cultural eutrophication; and (4) large increases in stratigraphic charcoal. It has also been feasible in some cases (e.g., James *et al.*, 1987) to infer human arrival from the first appearance of bones of an exotic animal in well-stratified bone deposits. In our tests of these methods, an important caveat has emerged: none of these methods are likely to be definitive in isolation or to have

Table I. Stratigraphic Indicators of Initial Human Activity on Tropical Islands<sup>a</sup>

Method	Locations	References
First appearance of pollen of introduced plants	Madagascar (central)	Burney (1987a,c)
	Maui, Hawaii	Burney <i>et al.</i> (1995)
	Oahu, Hawaii	Athens and Ward (1993a)
Large increase in ruderal pollen	Madagascar (NW)	Matsumoto and Burney (1994)
	Madagascar (central)	Burney (1987c)
	Mangaia, Cook Islands	Ellison (1994)
Paleolimnological evidence for cultural eutrophication	Madagascar (NW)	Matsumoto and Burney (1994)
	Madagascar (central)	Reyes (1993)
	Oahu, Hawaii	Athens and Ward (1993b)
Large increase in stratigraphic charcoal particles	Madagascar (central)	Burney (1987a-c)
	Madagascar (SW)	Burney (1993b)
	Madagascar (NW)	Wright <i>et al.</i> (1996)
	Puerto Rico	Burney <i>et al.</i> (1994a)
	Easter Island	Flenley <i>et al.</i> (1991)
	Mangaia, Cook Islands	Ellison (1994)
First appearance of bones of introduced microvertebrates	Maui, Hawaii	James <i>et al.</i> (1987)
	Galapagos Islands	Steadman <i>et al.</i> (1990)

<sup>a</sup>This is not an all-inclusive list. Other examples exist in each case, but studies cited here are from papers that are discussed in the text.

universal applicability. Some combination of these methods, employed in concert with more conventional archaeological and paleontological research, has shown promise in a wide array of tropical oceanic island contexts, including Madagascar, the West Indies, and the Hawaiian Islands.

### MADAGASCAR: WHO DID WHAT, WHEN, AND HOW?

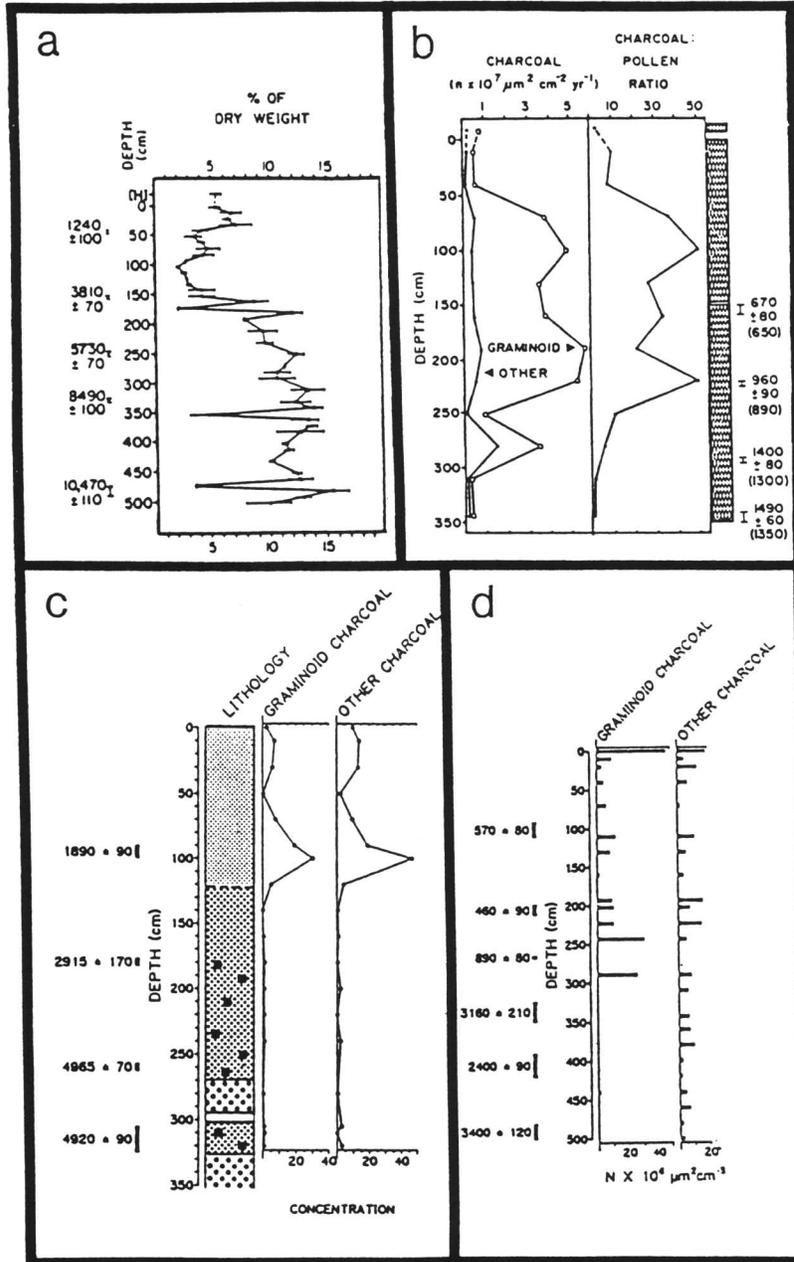
Despite its proximity to Africa, the "island continent" of Madagascar has a very different biotic and human history. More than 80% of the genera of Africa's late Pleistocene fauna (Martin, 1984) and 60% of the genera present in Acheulian times (Martin, 1966) have survived into the twentieth century, and yet humans and their ancestors have been evolving there for millions of years. Madagascar's entire endemic megafauna, including rathites, tortoises, hippopotami, and giant lemurs—over two dozen species in all, counting some smaller animals—became extinct, probably all or nearly all within the two millennia or so that span the entire period of known human existence on the island. This grand difference between two adjacent land masses with so many other similarities has suggested to some investigators (e.g., Martin, 1984) that initial contact between technologically sophisticated humans and "naive" insular faunas is likely to have resulted in

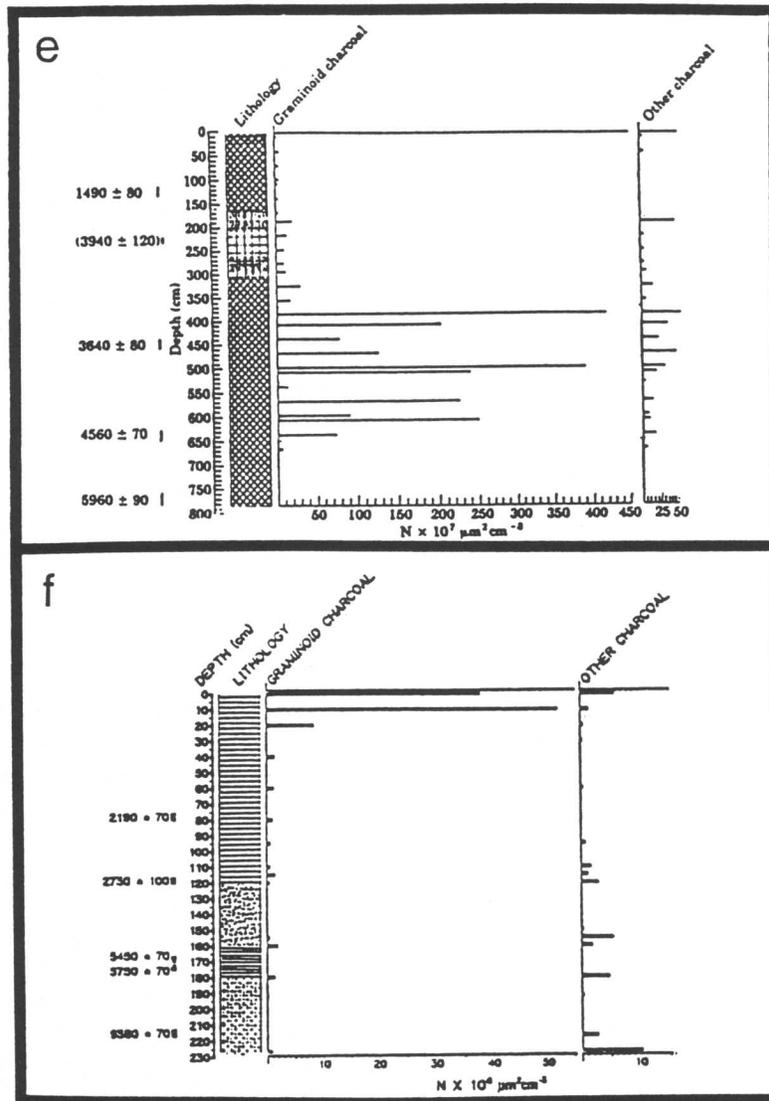
ecological catastrophe, probably largely through over-hunting. Until recently, however, most investigators have invoked the contemporary deforested and eroding landscapes of Madagascar as evidence for a human-caused environmental cataclysm, initiated over the vast area of the island through the human "introduction" of fire (e.g., Humbert, 1927; Perrier de la Bâthie, 1936). Although causal mechanisms are still debated (see Burney, 1993a for a recent review), it is now abundantly clear that fire and vegetation changes have occurred on the island for more than 40,000 years (e.g., MacPhee *et al.*, 1985; Burney, 1987a,b, 1993b; Matsumoto and Burney, 1994; Wright *et al.*, 1996; Burney *et al.*, 1997), but only the human period is thought to have been characterized by a high extinction rate.

The earliest direct archaeological evidence for humans in Madagascar comes from bones of *Hippopotamus* apparently modified in a fresh state with a sharp implement, collected from three sites in southwestern Madagascar (MacPhee and Burney, 1991). These date from the beginning of the first millennium A.D., and pre-date by at least 300 years the earliest human occupation sites (Dewar and Wright, 1993). Sediment cores also point to a human presence beginning about 2000 years B.P. Pollen of the introduced hemp plant, *Cannabis sativa*, first appears at Lake Tritrivakely in the central highlands about this time (Burney, 1987a), and was present in a core from Lake Kavitaha about 200 km to the north from the beginning of the record at ca. 1500 years B.P. (Burney, 1987c).

Stratigraphic charcoal particles in cores, which are used by palynologists as an index of fire occurrence in the locality or region of a lake or bog, have shown human arrival rather consistently in Madagascar (Fig. 1a-d). In addition to the two sites previously mentioned, where background levels show a sudden increase ca. 1300 years B.P. (Fig. 1a and b), one of the southwestern sites yielding modified hippo bones shows a sudden increase in charcoal (Fig. 1c) at ca. 1900 years B.P. (Burney, 1993b). The discrepancy in these ages for the onset of local impacts may be a reflection of the more remote character of the interior sites, since archaeological evidence supports the reasonable notion that the interior may have been colonized several centuries later than the coast (Wright *et al.*, 1992; Dewar and Wright, 1993). Marked increases in charcoal particles, especially in larger size classes, are a reflection of local fires (Clark, 1988a); the appearance of *Cannabis* pollen, on the other hand, is likely to be a regional-scale signal, since hemp can spread rapidly on its own in mesic tropical environments, produces great quantities of pollen (ca. 70,000 pollen grains per anther, according to Faegri and Iversen, 1989), and disperses over long distances by wind.

The pollen evidence from these and other sites in Madagascar shows a vegetation shift at the time the local charcoal signal increases. The uni-





**Fig. 1.** A comparison of Holocene charcoal particle stratigraphies from various tropical island sites. Despite the different methods used to quantify charcoal in these studies, all show a large increase above immediately preceding background levels at the presumed time of human arrival in the locality, except 1f, which shows an increase after European contact. Sites, scales, and sources are: (a) L. Tritrivakely, south central Madagascar, percent elemental carbon of dry sediment weight (Burney, 1987a); (b) L. Kavitaha, north central Madagascar,  $n \times 10^7 \mu\text{m}^2\text{cm}^{-2}\text{yr}^{-1}$  (Burney, 1987c); (c) Andolononby site, southwest Madagascar,  $n \times 10^6 \mu\text{m}^2\text{cm}^{-3}$  (Burney, 1993b); (d) L. Mitsinjo, northwest Madagascar, same units (Wright *et al.*, 1996); (e) L. Tortuguero, Puerto Rico,  $n \times 10^7 \mu\text{m}^2\text{cm}^{-3}$  (Burney *et al.*, 1994a); (f) Flat Top Bog, Maui,  $n \times 10^6 \mu\text{m}^2\text{cm}^{-3}$  (Burney *et al.*, 1995).

versal trend is one of decreasing pollen of woody vegetation and an increase in grasses, forbs, and other light-loving, fire-adapted plants. The longer records, such as the 11,000-year sequence from Tritrivakely in the central highlands (Burney, 1987a), the 5000-year record from Andolonomy in the SW (Burney, 1993b), and the 40,000-year record from Anjohibe (Burney, *et al.*, 1997) show similar vegetation changes occurred in earlier (prehuman) times when climates were becoming drier. This desiccation may have been pronounced at times: the 30,000-year record from Lake Alaotra in the east, the largest natural lake in Madagascar, indicates that full glacial climates in this area presently on the edge of the eastern forest zone were so dry that the lake probably dried up completely for several thousand years during the Last Glacial Maximum (Reyes, 1993). The 36,000-year record from Matsabory Ampozolana in the far north, and the 32,000-year record from Miangola in the central highlands (Burney, 1987b) also indicate major drying events about the same time, and show that fires and savanna vegetation were common features of Madagascar's late Pleistocene.

Despite the marked changes of earlier times, however, the late Holocene record suggests some changes not noted in earlier times. For instance, microfossils from the human period indicate soil and watershed disturbance in some cases. At Lake Mitsinjo in NW Madagascar (Matsumoto and Burney, 1994), it is possible to see what appear to be traces of three levels of impact. Recently completed archaeological surveys in the region (Wright *et al.*, 1996) allow a more detailed comparison than usual between archaeological evidence for settlement and land use, on the one hand, and microfossil stratigraphy on the other. Between ca. 1000–500 years B.P., the local, low-density pastoralism is reflected in charcoal levels, especially the types derived from grass burning (see Burney, 1987b regarding methods for distinguishing graminoid charcoal particles), that are considerably higher than the already fairly high values detected in the previous two millennia (Fig. 1d). As population density increased and settled cultivation spread over the landscape in the fifteenth and sixteenth centuries, charcoal values decrease, and ruderal pollen types, especially *Ambrosia* and *Urticaceae*, show a marked increase. In the late nineteenth century, with the construction of a large village on the shore of the lake and the advent of large-scale sugarcane growing, charcoal increases dramatically and the lake itself becomes eutrophic, presumably from cultural inputs. This condition is clearly signaled in the microfossil stratigraphy by the appearance of abundant fossils of such high-nutrient-adapted algae as *Pediastrum*, *Coelastrum*, and *Botryococcus*.

Paleolimnological indicators of cultural eutrophication also manifest themselves in the record of fossil diatom frustules from Lake Kavitaha (Reyes, 1993). Species adapted to eutrophic conditions show two peaks,

the first a rather brief interval corresponding to the increase in charcoal at ca. 1300 years B.P., probably reflecting increased runoff from the disturbed watershed at this time. The second and more sustained peak of high-nutrient types (e.g., *Eunotia pectinalis* and *Synedra ulna*) begins at ca. 700 years B.P. and gradually tapers off up to the surface. Based on comparison with the archaeological record, which suggests an increase in human population and agricultural activity in the interior about this time (Wright *et al.*, 1992), this second peak (really more of a plateau) probably indicates when the surrounding marshes and shores first came under cultivation.

Thus we see that, for Madagascar, palynological results have helped flesh out the archaeological record of human activity. Introduced pollen has suggested when humans arrived. It is difficult and often impossible to distinguish *Cannabis* pollen from its relative *Humulus* (hops, a genus apparently restricted to the Northern Hemisphere until it was spread, much later than hemp, to the rest of the world by beer-loving Europeans). In contrast, ethnobotanical information suggests that early mariners spread hemp throughout the Indian Ocean region in previous millennia, from its original range in southern Asia, in connection with its many practical maritime uses—rope, sails, water-resistant clothing, and caulking for ship's hulls, to name a few. Therefore hemp would, like goats, pigs, and rats, be among the first species introduced to new lands by Indian Ocean sailors coming ashore for provisioning and, eventually, longer stays (Vavilov, 1949).

Charcoal stratigraphy, it would appear, by providing a record of local, extralocal, or regional burning activity (depending on the proportions of larger to smaller particles), seems to be providing a good index of when deforestation and/or grassland burning (depending on relative amounts of charcoal derived from graminoid vs. other sources—primarily wood and tree leaves) may have been initiated by humans. Here, as noted earlier, one has to take care not to confuse a natural trend in burning with the human record. Comparison with other types of data, and recognition of a characteristic sharp peak above background levels, followed by a gradually decreasing signal over subsequent centuries (Fig. 1) has enabled the investigators to infer human inputs to the burning detected.

Finally, increases in ruderal pollen and paleolimnological evidence for cultural eutrophication appear to provide evidence for the onset and extent of highly local impacts, the former of soil disturbance through dry-land cultivation, the latter of increased nutrient flux to a body of water, either through soil disturbance in the watershed or actual cultivation of shallow-water habitats, as is practiced in Madagascar in connection with the cultivation of such crops as rice and taro.

Similar correspondences between microfossil stratigraphy and evidence from archaeology and paleontology have been observed on other islands, including Easter Island (Flenley *et al.*, 1991) and Mangaia in the Cook Islands (Kirch *et al.*, 1991; Ellison, 1994; Kirch and Ellison, 1994). In the case of Mangaia, the occurrence of pollen and charcoal evidence for human disturbance predating the earliest archaeological sites by several centuries has provoked some controversy (Spriggs and Anderson, 1993; Kirch and Ellison, 1994).

To further explore some of the notions generated by the work in Madagascar and elsewhere, I would like to consider a case from each of the other two tropical oceans, the West Indies and Hawaii.

### GREAT OPPORTUNITIES IN THE CARIBBEAN ISLANDS

Although surprisingly little paleoecological research has been conducted in the islands of the West Indies, the area holds great promise for this type of work. When compared to Madagascar, various islands show interesting similarities (high endemism, variety of climates and landscapes) and differences (earlier human arrival, less biogeographic isolation).

The general outlines of Holocene climate change, inferred from oxygen-isotope studies of ostracods in a core from Lake Miragoane, Haiti (Hodell *et al.*, 1991) are similar to those for Madagascar, suggesting climatic desiccation beginning ca. 3200 years B.P., culminating in maximum dryness ca. 2400–1500 years B.P. (compare to Burney, 1993b, for southwest Madagascar). Palynological studies addressing the ecological changes before and after human arrival are unfortunately not available, although a study of a short core, spanning the last ca. one millennium, shows clear impacts (deforestation, increased sedimentation, increase in ruderal pollen) following European contact (Brenner and Binford, 1988).

The archaeological record concerning initial settlement of various islands in the region by native Americans shows surprising discrepancies, even between adjacent islands. For instance, current earliest <sup>14</sup>C ages for confirmed archaeological sites in the Greater Antilles are: Jamaica, 1300 ± 120 years B.P. (Rouse and Allaire, 1978); Puerto Rico, 3010 ± 70 years B.P. (Rouse, 1992); Cuba, 5140 ± 170 years B.P. (Kozlowski, 1974); and Hispaniola, 5580 ± 80 years B.P. (Moore, 1991). Such discrepancies between large adjacent islands seem improbable, and may simply reflect the need for more emphasis to be placed on finding early sites. Possibly, too, it could be a reflection of low human population densities, since cultural evidence for widespread hunter-gatherers, for instance, would be much more thinly distributed than that for sedentary agriculturalists.

A study of stratigraphic charcoal in a sediment core from Laguna Tortuguero, a freshwater lake on the north coast of Puerto Rico (Burney *et al.*, 1994a) may shed some light on the question of pre-Columbian human impacts. Charcoal is scarce and composed only of very small particles (probably dispersed from long distances) in the sediments between 7000 and 5300 cal years B.P., as would be expected in a high-rainfall, low-seasonality lowland forest area prior to humans. Rather abruptly, at ca. 5300 cal years B.P. (Fig. 1e), charcoal values increase by several orders of magnitude, including many large particles denoting local production. This abrupt trend in burning is sustained for about two millennia, during a time that sedimentological evidence from the site as well as the isotope studies from Haiti (Hodell *et al.*, 1991) indicate wet conditions. It seems likely that the "earliest" archaeological date for the island underestimates the time of probable first occupation by ca. two millennia. The charcoal-derived date of occupation agrees very well with the initial date of occupation inferred for the adjacent islands of Hispaniola and Cuba.

Clearly, a hypothesis worthy of testing in the West Indies is that initial human impacts begin in this mid-Holocene time frame. Good potential exists for using pollen analysis, as has been done in Madagascar and elsewhere, to detect human arrival and impacts, and to extend the charcoal method to other sites. Likewise, it is known that a faunal collapse also occurred on many West Indian islands (Morgan and Woods, 1986) but it is not known whether this coincides with human arrival or in fact was protracted over many thousands of years (MacPhee *et al.*, 1989). The loss of 21 or more genera of West Indian vertebrates, including ground sloths, giant rodents, and large insectivores, has been recorded (Martin, 1984).

On Antigua in the Lesser Antilles, Pregill *et al.* (1988) excavated and radiocarbon dated a site that contains remains of 12 animal species no longer present on the island, in association with Amerindian artifacts. The assemblage yielded  $^{14}\text{C}$  dates from 4300 to 2560 years B.P., suggesting, in the case of this island at least, that humans may have played a role in the demise of these species, which represented more than one-third of the taxa represented as fossils.

### HAWAII: DOCUMENTING TROUBLE IN PARADISE

The Hawaiian Islands were one of the very first tropical areas to attract the attention of palynologists, including the exhaustive studies of high-elevation bogs by Selling (1948). He identified in his longer cores, which he believed to encompass the time since the last glaciation, a three-part division of postglacial climate and vegetation. He postulated a wet interval be-

tween two drier phases. Unfortunately, his prodigious efforts preceded the advent of  $^{14}\text{C}$  dating, so no absolute ages were placed on these climatic trends, and there has been some confusion as to how his pollen zones might relate to better-known European chronologies. Gavenda (1992) attributes Selling's earliest pollen zone to "the last glacial period," but Selling himself (1948, p. 121) relates this zone to pollen zones of Europe that represent the transition from glacial to interglacial conditions (i.e., latest Pleistocene and earliest Holocene times). Recently, Burney *et al.* (1995) have published a radiocarbon-dated record of pollen, charcoal, and trace metals from a high-elevation bog on East Maui (2270 m), showing that the early Holocene was dry, with a wet phase between 5800 and 2200 years B.P., followed by a moderate and variable late Holocene.

Charcoal evidence from the site (Fig. 1f) shows the likely effect of the nearby active vents of the Haleakala Volcano, with fairly high background values and occasional very high pulses of charcoal particles in prehuman times. Some of the lowest charcoal values occur in the late Holocene, and the arrival of Polynesians to the islands perhaps 1600 years B.P. is not reflected by rising charcoal values as in the studies on other islands previously cited. Unpublished archaeological surveys commissioned by the National Park Service (A. C. Medeiros, personal communication) suggest that prehistoric Polynesians never inhabited the upper reaches of Haleakala in the immediate vicinity of the coring site. Lower down, particularly on the crater floor (separated from the bog site by a steep ridge), there are a multitude of terraces, platforms, cairns, and basalt quarries, as well as evidence of temporary occupation of rock-shelters and small caves. In summarizing the earlier works of Emory (1921) and others in the vicinity, Kirch (1985, p. 136) concludes that none of these sites were used for extended habitation, but rather served religious functions or provided a temporary refuge for adze-makers and perhaps bird-hunters.

The core contains clear evidence, however, for the nearby activities of humans following European contact. In the upper 10 cm of the core, abundant pollen of a naturalized plant introduced by Europeans, hairy cat's-ear (*Hypochoeris radicata*) signals the contact phase, as does a great increase in charcoal. Whereas earlier fires had produced primarily nongraminoid charcoal, probably derived from lava-ignited fires in the forests of the mountain's mid-elevations, the European-period charcoal signal consisted primarily of graminoid charcoal, perhaps derived from sugarcane growing and pasture clearance activities that have been going on along the adjacent coast for a century or more. Haleakala has not erupted since the European colonization of Maui.

Some late Holocene studies from lowland coastal sites on Oahu (e.g., Athens *et al.*, 1992; Athens and Ward, 1993a,b) detect little charcoal in

sediments until after European contact. A more recent study from Oahu indicates that charcoal shows an increase at the inferred time of the onset of Polynesian activity (Athens, 1997). Perhaps the Polynesians used fire for vegetation clearance only on a very limited basis (but see Kirch, 1982).

Athens and Ward's pollen data suggest a major decline of the lowland forest vegetation beginning ca. 1000 A.D., with some lowland forest types virtually disappearing by 1400 A.D. They also noted the abundant presence of the colonial green alga *Pediastrum* at one site in the Polynesian period, and ascribed it to eutrophic conditions, possibly associated with prehistoric aquaculture (Athens and Ward, 1993b, p. 38). Pollen from several plants believed to have been introduced by Polynesians have also been identified in these studies.

Paleontological investigations throughout the Hawaiian Islands have resulted in the formal description of 35 species of extinct Holocene birds (more are pending), and have shown that more indigenous bird species went extinct in the Polynesian period than presently survive on the islands (Olson and James, 1982, 1984, 1991; James *et al.*, 1987; James and Olson, 1991). These late prehistoric extinctions far exceed those recorded from the European contact period. Work on a U-series dated Pleistocene site (James, 1987) also suggests that prehuman extinction rates were quite low in the late Quaternary.

This extraordinary endemic fauna included several genera of large, flightless waterfowl, a flightless ibis, and bird-catching owls. Careful excavation and use of AMS  $^{14}\text{C}$  dating to age the collagen in even very small individual bird bones has permitted these investigators to demonstrate the rapidity of this extinction event after Polynesian arrival. Dating of bones of the Pacific rat (*Rattus exulans*) from their sites demonstrates its introduction by Polynesians, and its rapid proliferation in the islands (James *et al.*, 1987). In well-stratified bone beds, it is thus possible to use the appearance of rat bones and teeth as an anthropogenic marker horizon.

#### INTER-ISLAND COMPARISONS AND THE SEARCH FOR GLOBAL TRENDS

Looking for global patterns by comparing remote oceanic islands is a scientific tradition that goes back to Charles Darwin and Alfred Russel Wallace (reviewed in Brown and Gibson, 1983). The term "human biogeography" has been used by anthropologists for over two decades in connection with inter-island studies of human culture, archaeology, and history (see Terrell, 1997). The study of the decline and extinction of human groups on islands is a potentially rewarding area of investigation deserving more attention (McGovern, 1980; Rouse, 1992; Diamond, 1993).

Martin, in developing his ideas regarding possible Pleistocene overkill models for faunal extinctions, utilized inter-island comparisons of the time of human arrival vs. last occurrences of extinct species (Martin, 1984, 1990; see also articles in Martin and Klein, 1984). The general trend he perceived was for a short temporal overlap between colonizing humans and an array of extinct beasts on Madagascar, the Hawaiian Islands, and South Pacific islands, among other areas, although the quantity and quality of data availability at that time was an admitted limitation. Relevant reliable data remains to the present the greatest limitation to the use of islands for examining late prehistoric extinction questions.

Some now-extinct island faunas appear to have overlapped temporally with humans for quite a long time—perhaps more than 10,000 years in Australia (Flannery, 1994), and almost two millennia in Madagascar (MacPhee and Burney, 1991; Simons *et al.*, 1995). Presently, it seems that an extinction pattern “truly swift and devastating,” as called for in Martin’s Blitzkrieg Hypothesis (Martin, 1984, p. 360) is most easily visualized in the latest prehistoric island cases on the most remote islands, such as New Zealand and Hawaii, and in some protohistoric European discoveries of uninhabited islands such as the Galapagos and Mascarenes (see Olson, 1989). In the case of the latter, Diamond (1984) observes that historic extinctions on islands can be useful for inferring causality and mechanisms in prehistoric extinctions, based on uniformitarian use of the written record of human depredations on islands as a kind of “Rosetta Stone” for interpreting the fossil record. Steadman *et al.* (1990) have made interesting linkages between the stratigraphic record of Holocene extinctions and the history of extinction and human impact on the Galapagos Islands, showing that few if any extinctions are revealed in the subfossil record of the previous several millennia before Europeans discovered these uninhabited islands. The stratigraphic and historical record since human arrival in 1535 is one of island-wide extinctions and proliferation of exotic species. This agreement is of course reassuring, and demonstrates well the use of the Galapagos as a natural laboratory for paleoecology as it has been for more than a century for evolutionary studies.

In another interesting “experiment” with the subfossil record, Steadman and Olson (1985) demonstrated that Henderson Island in the Pitcairn Group, which has been uninhabited in historic times, lost several bird species ca. 500 years ago, when Polynesians temporarily occupied the island. The authors suggest that the abandonment of small unarable islands by prehistoric Polynesians may have been due to the depletion of bird resources, presumably the only readily available food source. In follow-up studies on Henderson (e.g., Weisler, 1995), it has been demonstrated that the bird extinctions and heavy exploitation of sea turtles occurred during

the time that the colonists on Henderson and Pitcairn were still in contact with the population of Mangareva. After about 1450 A.D., imported items decline precipitously, implying that contact and trade with the outside had ceased, and the local human population apparently abandoned Henderson or went extinct somewhat later.

James (1995) made a useful two-way comparison between the recent and more distant past in the Hawaiian Islands, and between the recent past there and in Madagascar. She compared two sites with excellent faunal recovery on Oahu, one with good recovery of the Holocene fauna (Barber's Point) and the other from the Illinoian Glacial (Ulupau Head). This comparison demonstrates that, of the 17 land bird species present at Ulupau Head >120,000 years B.P., all but one or possibly two survived into the prehuman part of the Holocene. Following human arrival, the late Holocene Hawaiian record shows that extinction rates are several orders of magnitude above background, culminating in the loss of many bird species by ca. 900 years B.P. Pacific rats, which appear about the same time, are a primary component of the remaining depauperate assemblage. These observations accord well with the palynological record from lowland sites on Oahu (Athens and Ward, 1993a), showing a presumably human-caused decline in lowland forest vegetation at ca. 1000 A.D. Steadman (1993) has shown a similar pattern of higher extinction rates in the human era, compared to a fauna dated to ca. 60–80,000 years B.P., on 'Eua, Tonga.

James (1995) also compares the rich record from Puu Naio Cave on Maui (James *et al.*, 1987) to a similarly rich site in Madagascar, the cave of Anjohibe (Burney *et al.*, 1997) that is roughly equivalent in terms of local climate, chronological range of the fossil assemblage, and time of human arrival. This matching shows that, among higher vertebrates, extinction rates seem to have been much higher for the Maui site—about 3/4 of the species sampled by the site ( $n = 35$ ) vs. ca. 1/8 ( $n = \text{ca. } 65$ ) for the Madagascar site (James, 1995). The extinctions in Madagascar also appear to be skewed more toward the larger species. Future expansion of this technique with more sampling sites and perhaps more islands could provide useful information regarding differential extinction rates on various islands, and allow expansion of the initial exploration in James (1995) of such ecologically important details as differential extinction rates of certain body-size classes, guilds, trophic levels, or communities on or among islands.

It is also possible that comparisons of the fire histories of various islands, as inferred from stratigraphic charcoal particle studies, may yield useful global generalities. The potential for detecting human arrival from the charcoal record has been noted above. Figure 1 may suggest another possible trend with considerable generality. As has been noted in Burney *et al.* (1994a), in comparing the Laguna Tortuguero, Puerto Rico, record with

that of several published charcoal studies from Madagascar cited in earlier sections of this paper, these studies seem to exhibit a comparable trend during and after human arrival. At the inferred time of initial human presence, there is a surge in charcoal values above the immediately prehuman background levels. For the next several centuries, charcoal values in each case remain at high levels and may even increase, followed by a gradual attenuation, often approaching the prehuman background values, in recent centuries, and sometimes showing a secondary peak in the present century. The pattern is less clear for Hawaii, where some studies have shown relatively low charcoal values in the Polynesian period and the biggest observable increase after European contact (e.g., Athens and Ward, 1993a; Burney *et al.*, 1995).

More charcoal studies, coupled with archeological research, will be needed in order to help clarify whether the observed trends, if they show some universality, are explainable in terms of changes in human population density and land use. An alternative hypothesis would be that the characteristic curves observed are a reflection of a more fundamental ecological response. For instance, repeated burning could result in biomass reduction, micro-habitat changes, plant physiological responses, or species composition shifts that might reduce the amount of burning (i.e., the amount of charcoal deposited to sediments) over time (see Burney *et al.*, 1994a for discussion).

Thus, it appears that characterizing prehuman vs. postsettlement extinction rates and fire histories are two fertile areas for continued use of inter-island paleoecological comparisons. For these and other questions that might be imagined, such as the role of climate change in island dynamics and the patterns of human population increase following long-distance human dispersal, achieving a higher standard of spatiotemporal resolution is clearly an all-important methodological goal. For instance, greater use should be made on tropical oceanic islands, as elsewhere, of the potential annual resolution of the laminated sediments from deep crater lakes, tree-ring records from highly seasonal environments, and finely-laminated speleothems (Brook *et al.*, 1990; Burney *et al.*, 1993). These kinds of records may permit detection and exploration of the effects of abrupt climate changes, extreme weather events, ocean dynamics, volcanic eruptions, shoreline changes and fire periodicity on these islands.

Regarding fire periodicity, for instance, it has been suggested (Burney and MacPhee, 1988) that prehuman fires on Madagascar and perhaps elsewhere may have been relatively infrequent but highly intense (owing to litter accumulation over time), whereas fire in the human period may be characterized by relatively constant but generally less intense burning (both because of lower litter accumulation and also because of the possibility

that many human-ignited fires were set during times of less dry—and therefore more controllable—conditions). Fire periodicity may be evaluated with charcoal studies of laminated sediments and identification of fire scars in dendrochronological records, as demonstrated in Minnesota by Clark (1988b).

Very long records with improved time resolution are also important, especially for comparing the paleoecology of the human-impacted Holocene with that of previous interglacials, when climate and other ecological parameters were presumably similar but humans were not present. This is a valuable step in separating human and climate-induced effects under present climate regimes. A basic technical problem has been that even when these rare island sites thought to date to a previous interglacial have been found, they are much too old for  $^{14}\text{C}$  dating. As in the study of Ulupau Head, Oahu, which contained a Hawaiian fauna from >120,000 years B.P. (probably the Illinoian Glacial; James, 1987), U-series dating is most often the method that can work, but only if coral reefs, speleothems, or some other relatively closed carbonate system is available. Records of past vegetation may be constructed from pollen and other microfossils trapped in U-series dated speleothems (e.g., Brook *et al.*, 1990; Burney *et al.*, 1994b), making it possible to extend such records back 400,000 years or more with radiometric control. Work of this type in Madagascar has extended the record of vegetation change there back to ca. 40,000 years B.P. (Burney *et al.*, 1997), and is likely to extend it considerably farther in the near future.

While the pursuit of higher resolution, longer records and more island sites holds great promise for future island paleoecology, it is also important to refine and apply more conventional archaeological techniques (and perhaps add some new ones) to island questions related to environmental change. By combining careful radiometric dating of settlements, extensive and intensive surface survey and excavation, and reconstructions of paleodemography and landscape paleoecology, archaeologists and paleoecologists may round out the picture of insular humans in the prehistoric scene (e.g., Kirch *et al.*, 1992; Wright *et al.*, 1992, 1996).

We are still probably a long way from the point at which the empirical data concerning human impacts on islands can be used to definitively test existing or future models, or to extrapolate our findings confidently to the past and future of larger continental landmasses or the globe. Enough progress has been made, however, to see what types of information are needed and to generate more explicit models and hypotheses. Despite the gaps in the data, it is already clear that our species' impacts on islands have been devastating in many cases. As a powerful analogy to the present global human condition, the emerging models for past human impacts on islands are of more than academic interest.

## ACKNOWLEDGMENTS

Fieldwork by the author was supported primarily by grants from the National Science Foundation, the National Geographic Society, the Smithsonian Institution, and Fordham University. This summation was prepared with the support of NSF BSR-9306603 and NOAA Human Dimensions of Global Change Program grant NA46GP0465. Lida Pigott Burney, Helen James, P. S. Martin, David Steadman, and three anonymous reviewers provided useful comments on the manuscript.

## REFERENCES

- Athens, J. S., and Ward, J. V. (1993a). Environmental change and prehistoric Polynesian settlement in Hawai'i. *Asian Perspectives* 32(2): 205-223.
- Athens, J. S., and Ward, J. V. (1993b). Paleoenvironmental Investigations at Hamakua Marsh, Kailua, O'ahu, Hawai'i. Report prepared for Ducks Unlimited, Inc., 50 p.
- Athens, J. S., Ward, J. V., and Wickler, S. (1992). Late Holocene lowland vegetation, O'ahu, Hawai'i. *New Zealand Journal of Archaeology* 14: 9-34.
- Athens, J. S. (1997). Hawaiian native lowland vegetation in prehistory. In Kirch, P. V., and Hunt, T. L. (eds.), *Historical Ecology in the Pacific Islands*. Yale University Press, New Haven, pp. 248-270.
- Brenner, M., and Binford, M. W. (1988). A sedimentary record of human disturbance from Lake Miragoane, Haiti. *Journal of Paleolimnology* 1: 85-97.
- Brook, G. A., Burney, D. A., and Cowart, J. B. (1990). Desert paleoenvironmental data from cave speleothems with examples from the Chihuahuan, Somali-Chalbi, and Kalahari deserts. *Palaeogeography, Palaeoclimatology, Palaeoecology* 76: 311-329.
- Brown, J. H., and Gibson, A. C. (1983). *Biogeography*. Mosby, St. Louis.
- Burney, D. A. (1987a). Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. *Palaeoecology of Africa* 18: 357-381.
- Burney, D. A. (1987b). Late Quaternary stratigraphic charcoal records from Madagascar. *Quaternary Research* 28: 274-280.
- Burney, D. A. (1987c). Late Holocene vegetational change in central Madagascar. *Quaternary Research* 28: 130-143.
- Burney, D. A. (1993a). Recent animal extinctions: Recipes for disaster. *American Scientist* 81: 530-541.
- Burney, D. A. (1993b). Late Holocene environmental changes in arid southwestern Madagascar. *Quaternary Research* 40: 98-106.
- Burney, D. A., and MacPhee, R. D. E. (1988). Mysterious island: What killed Madagascar's large native animals? *Natural History* 97(7): 46-55.
- Burney, D. A., Burney, L. P., Rafamantanantsoa, J.-G., D'Arrigo, R. D., and Jacoby, G. C. (1993). Laminated sediment cores, tree-ring records, and laminated speleothems from Madagascar. *Eos* 4/20: 93.
- Burney, D. A., Burney, L. P., and MacPhee, R. D. E. (1994a). Holocene charcoal stratigraphy from Laguna Tortuguero, Puerto Rico, and the timing of human arrival on the island. *Journal of Archaeological Science* 21: 273-281.
- Burney, D. A., Brook, G. A., and Cowart, J. B. (1994b). A Holocene pollen record for the Kalahari Desert of Botswana from a U-series dated speleothem. *The Holocene* 4(3): 225-232.
- Burney, D. A., DeCandido, R. V., Burney, L. P., Kostel-Hughes, F. N., Stafford, T. W., Jr., and James, H. F. (1995). A Holocene record of climate change, fire ecology and

- human activity from montane Flat Top Bog, Maui. *Journal of Paleolimnology* 13: 209-217.
- Burney, D. A., James, H. F., Grady, F. V., Rafamantanantsoa, J.-G., Ramilisonina, Wright, H. T., and Cowart, J. B. (1997). Environmental change, extinction, and human activity: Evidence from caves in NW Madagascar. *Journal of Biogeography* (in press).
- Clark, J. S. (1988a). Particle motion and the theory of charcoal analysis: Source area, transport, deposition, and sampling. *Quaternary Research* 30: 67-80.
- Clark, J. S. (1988b). Stratigraphic charcoal analysis on petrographic thin sections: Application to fire history in northwestern Minnesota. *Quaternary Research* 30: 81-91.
- Dewar, R. E., and Wright, H. T. (1993). The culture history of Madagascar. *Journal of World Prehistory* 7(4): 417-466.
- Diamond, J. M. (1972). Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Sciences USA* 69: 3199-3203.
- Diamond, J. M. (1984). Historic extinction: A Rosetta Stone for understanding prehistoric extinctions. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 824-862.
- Diamond, J. M. (1993). Ten thousand years of solitude. *Discover* 14(3): 48-57.
- Ellison, J. C. (1994). Palaeo-lake and swamp stratigraphic records of Holocene vegetation and sea-level changes, Mangaia, Cook Islands. *Pacific Science* 48(1): 1-15.
- Emory, K. P. (1921). An archaeological survey of Haleakala. *Bernice P. Bishop Museum Occasional Papers* 7(11): 237-259.
- Faegri, K., and Iversen, J. (1989). *Textbook of Pollen Analysis* (IV Ed.). Wiley, Chichester.
- Flannery, T. F. (1994). *The Future Eaters*. George Braziller, New York.
- Flenley, J. R., King, A. S. M., Teller, J. T., Prentice, M. E., Jackson, J., and Chew, C. (1991). The Late Quaternary vegetational and climatic history of Easter Island. *Journal of Quaternary Science* 6: 85-115.
- Gavenda, R. T. (1992). Hawaiian Quaternary paleoenvironments: A review of geological, pedological, and botanical evidence. *Pacific Science* 46(3): 295-307.
- Hodell, D. A., Curtis, J. H., Jones, G. A., Higuera-Gundy, A., Brenner, M., Binford, M. W., and Dorsey, K. T. (1991). Reconstruction of Caribbean climate change over the past 10,500 years. *Nature* 352: 790-793.
- Humbert, H. (1927). Destruction d'une flore insulaire par le feu: principaux aspects de la végétation à Madagascar. *Mémoires de l'Académie Malgache* 5: 1-80.
- James, H. F. (1987). A late Pleistocene avifauna from the island of Oahu, Hawaiian Islands. *Documents du Laboratoire Géologique de Lyon* 99: 221-230.
- James, H. F. (1995). Prehistoric extinctions and ecological changes on oceanic islands. *Ecological Studies* 115: 87-102.
- James, H. F., and Olson, S. L. (1991). Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part II. Passeriformes. *Ornithological Monographs* no. 46.
- James, H. F., Stafford, T. W., Jr., Steadman, D. W., Olson, S. L., Martin, P. S., Jull, A. J. T., and McCoy, P. C. (1987). Radiocarbon dates on bones of extinct birds from Hawaii. *Proceedings of the National Academy of Sciences USA* 84: 2350-2354.
- Kirch, P. V. (1982). The impact of prehistoric Polynesians on the Hawaiian ecosystem. *Pacific Science* 36(1): 1-14.
- Kirch, P. V. (1985). *Feathered Gods and Fishhooks*. University of Hawaii Press, Honolulu.
- Kirch, P. V., and Ellison, J. (1994). Palaeoenvironmental evidence for human colonization of remote Oceanic islands. *Antiquity* 68: 310-321.
- Kirch, P. V., Flenley, J. R., and Steadman, D. W. (1991). A radiocarbon chronology for human-induced environmental change on Mangaia, southern Cook Islands, Polynesia. *Radiocarbon* 33(3): 317-328.
- Kirch, P. V., Flenley, J. R., Steadman, D. W., Lamont, F., and Dawson, S. (1992). Ancient environmental degradation. *National Geographic Research and Exploration* 8(2): 166-179.
- Kozłowski, J. K. (1974). *Pre-ceramic Cultures in the Caribbean*. Zyszyty Naukowe, Uniwersytetu Jagiellońskiego, vol. 386, Prace Archeologiczne, Zesty 20. Krakow, Poland.

- MacArthur, R. H., and Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- MacPhee, R. D. E., and Burney, D. A. (1991). Dating of modified femora of extinct dwarf *Hippopotamus* from southern Madagascar: Implications for constraining human colonization and vertebrate extinction events. *Journal of Archaeological Science* 18: 695-706.
- MacPhee, R. D. E., Burney, D. A., and Wells, N. A. (1985). Early Holocene chronology and environment of Ampasambazimba, a Malagasy subfossil lemur site. *International Journal of Primatology* 6(5): 463-489.
- MacPhee, R. D. E., Ford, D. C., and McFarlane, D. A. (1989). Pre-Wisconsinan mammals from Jamaica and models of late Quaternary extinction in the Greater Antilles. *Quaternary Research* 31: 94-106.
- Martin, P. S. (1966). Africa and Pleistocene overkill. *Nature* 212: 339-342.
- Martin, P. S. (1984). Prehistoric overkill: The global model. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 354-403.
- Martin, P. S. (1990). 40,000 years of extinctions on the "Planet of Doom." *Palaeogeography, Palaeoclimatology, Palaeoecology* 82: 187-201.
- Martin, P. S., and Klein, R. G. (1984). *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson.
- Matsumoto, K., and Burney, D. A. (1994). Late Holocene environments at Lake Mitsinjo, northwestern Madagascar. *The Holocene* 4(1): 17-25.
- McGovern, T. H. (1980). cows, harp seals, and churchbells: Adaptation and extinction in Norse Greenland. *Human Ecology* 8(3): 245-273.
- Moore, C. (1991). Cabaret: Lithic workshop sites in Haiti. *Reports of the Archaeological-Anthropological Institute of the Netherlands Antilles* 9: 92-104.
- Morgan, G. S., and Woods, C. A. (1986). Extinction and the zoogeography of West Indian land mammals. *Biological Journal of the Linnean Society of London* 28: 167-203.
- Olson, S. L. (1989). Extinction on islands: Man as a catastrophe. In Western, D., and Pearl, M. (eds.), *Conservation for the Twenty-First Century*. Oxford University Press, New York, pp. 50-53.
- Olson, S. L., and James, H. F. (1982). Prodrum of the fossil avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology*, no. 365.
- Olson, S. L., and James, H. F. (1984). The role of Polynesians in the extinction of the avifauna of the Hawaiian Islands. In Martin, P. S., and Klein, R. G. (eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 768-780.
- Olson, S. L., and James, H. F. (1991). Descriptions of thirty-two new species of birds from the Hawaiian Islands: part I. Non-Passeriformes. *Ornithological Monographs*, no. 45.
- Perrier de la Bâthie, H. (1936). *Biogéographie des Plantes de Madagascar*. Société d'Éditions Géographiques, Maritimes, et Coloniales, Paris.
- Pregill, G. K., Steadman, D. W., Olson, S. L., and Grady, F. V. (1988). Late Holocene fossil vertebrates from Burma Quarry, Antigua, Lesser Antilles. *Smithsonian Contributions to Zoology*, no. 463.
- Reyes, N. E. (1993). The Modern Diatom Spectra of Madagascar and Diatom-inferred Late Quaternary Climatic Changes in Northeastern and Central Madagascar. PhD dissertation, Fordham University, New York.
- Rouse, I. (1992). *The Tainos: Rise and Decline of the People Who Greeted Columbus*. Yale University Press, New Haven.
- Rouse, I., and Allaire, L. (1978). The Caribbean. In Meighan, C. W. (ed.), *Chronologies in New World Archaeology*. Academic Press, New York.
- Selling, O. H. (1948). Studies in Hawaiian pollen statistics, part III. On the Late Quaternary history of the Hawaiian vegetation. *Bishop Museum Special Publication*, No. 39.
- Simberloff, D. S., and Wilson, E. O. (1970). Experimental zoogeography of islands. A two year record of colonization. *Ecology* 51: 934-937.

- Simons, E. L., Burney, D. A., Chatrath, P. S., Godfrey, L. R., Jungers, W. L., and Rakotosamimanan, B. (1995). AMS  $^{14}\text{C}$  dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quaternary Research* 43: 249-254.
- Spriggs, M., and Anderson, A. (1993). Late colonization of East Polynesia. *Antiquity* 67: 200-217.
- Steadman, D. W. (1993). Biogeography of Tongan birds before and after human impact. *Proceedings of the National Academy of Sciences USA* 90: 818-822.
- Steadman, D. W., and Olson, S. L. (1985). Bird remains from an archaeological site on Henderson Island, South Pacific: Man-caused extinctions on an "uninhabited" island. *Proceedings of the National Academy of Sciences USA* 82: 6191-6195.
- Steadman, D. W., Stafford, T. W., Jr., Donahue, D. J., and Jull, A. J. T. (1990). Chronology of Holocene vertebrate extinction in the Galapagos Islands. *Quaternary Research* 36: 126-133.
- Terrell, J. E. (1997). The postponed agenda: Archaeology and human biogeography in the twenty-first century. *Human Ecology* 25: 419-436.
- Vavilov, N. I. (1949). The origin, variation, immunity and breeding of cultivated plants. *Chronica Botanica* 13: 1-6.
- Weisler, M. I. (1995). Henderson Island prehistory: Colonization and extinction on a remote Polynesian island. *Biological Journal of the Linnean Society* 56: 377-404.
- Wright, H. T., Andrianalvoarivony, R., Bailiff, I., Burney, D., Haas, H., Raharijaona, V., Rakotovololona, S., Rasamuel, D., and Dewar, R. (1992). Datation absolue de sites archéologiques du centre de Madagascar—présentations des déterminations. *Taloha* 11: 121-146.
- Wright, H. T., Vérin, P., Ramilisonina, Burney, D., Burney, L. P. and Matsumoto, K. (1996). The evolution of settlement systems in the Bay of Boeny and the Mahavavy River valley, north-western Madagascar. *Azania* 31: 37-73.