## Holocene Rain-Forest Wilderness: A Neotropical Perspective on Humans as an Exotic, Invasive Species

Robert L. Sanford, Jr. Sally P. Horn

Abstract—Large areas of lowland tropical rain-forests in the neotropics have been burned over the past 6,000 years, mostly by pre-Colombian agriculturists. This paper presents additional evidence of fires and other human impacts in neotropical forests, and considers the opportunities and limitations of different approaches to determining past land-use "signatures." Knowledge of ancient land use practices may be used to advance an appreciation for the possible roles of past human disturbances in the suite of biological processes that promote diversity in lowland rain-forests. As wilderness designation becomes more common in the neotropics, an understanding of ancient land uses is essential for wilderness interpretation.

There is a widely held perspective that "the tropical rainforest" was, until recent episodes of deforestation and fragmentation, something of a grand wilderness. Over one hundred years have passed since biologists first recognized that the presumably pristine rain-forest environments were extremely species-rich in comparison to most higher latitude environments (Darwin 1855; Wallace 1878). Naturalists working in the first half of this century focused on documenting this "extreme diversity" and proposed numerous theories to explain it. As recently as the 1970's it was a widely held belief that high species diversity in the lowland humid tropics could be attributed to the existence of relatively disturbance-free habitats in a long-stable climate. This perspective is actually the fusion of two separate theories, and the tenets of these two theories are well summarized by Pianka (1966); it subsequently achieved brief ignominy as the tropical stability theory.

Although there is still not a single, completely satisfactory theory that explains species diversity in lowland, neotropical forests, large- and small-scale natural disturbances are now well documented for rain-forests as is climatic variability (Colinvaux 1987; Hartshorn 1978). Recognition of the complex and long-term history of natural disturbances, as well as climate variability and change in lowland tropical habitats, has led to the gradual incorporation of these factors in

theories to explain species diversity. This transition, however, has come about in a strange vacuum in which human populations and the effects of human populations are not usually taken into account. This is remarkable because although humans have migrated into the neotropics recently relative to other tropical regions ( $\sim$ 14,000 - 20,000 yr. B.P.) (Bray 1986; Meggers 1995; Roosevelt and others 1996), our effects on the landscape as an exotic, invasive species have been extensive and persistent.

Surprisingly, the connection has yet to be made between the effects of humans on rain-forest and the perception of rain-forest as wilderness, even though there has been considerable research recently on ancient human populations, in rain-forests. Here we begin to examine this connection. We propose that paleoecological evidence can be used to estimate ancient land-use practices of human populations and that this information is useful in the context of wilderness perception and designation. Our approach is based on empirical data from archeological inquiries, palynological studies and soil charcoal distribution and abundance.

#### Soil Charcoal

Charcoal is common in the uppermost meter of soils in neotropical forests (Horn and Sanford 1992; Saldarriaga and West 1986; Sanford and others 1985; Soubiès 1979-80) as well as in sediment cores from neotropical lakes and swamps (Bush and Colinvaux 1994; Bush and others 1992; Byrne and Horn 1989; Kennedy and Horn 1997; Northrop and Horn 1996; Tsukada and Deevey 1967). In forests, soil charcoal has been observed in road and stream cuts and sampled from soil pits and with coring devices reaching to one meter deep. The usual methods for obtaining soil charcoal include: 1) obtaining intact soil cores from sequential extractions in the same borehole or 2) excavating layers of soil from small soil pits (0.25 m<sup>2</sup> to 1 m<sup>2</sup>). Most of the soilcoring cylinders used for sequential sampling are small diameter, ranging from 3 cm to 8 cm. The resulting soil core or soil pit samples are soaked and sieved, and the sieved mineral soil is examined and sorted by hand for soil charcoal fragments. The charcoal is subsequently dried and weighed, with a subset used for radiocarbon dating. These procedures result in several data sets useful for interpreting the disturbance history of a site, area or region.

At the most modest level of analysis, soil charcoal data from sequential soil layers may be used to determine the presence or absence of fire at a particular site. If sampling is spatially explicit, the presence/absence of fire in a watershed or other landscape unit may be determined. In conjunction with radiocarbon dating, it is possible to develop a coarse fire

In: McCool, Stephen F.; Cole, David N.; Borrie, William T.; O'Loughlin, Jennifer, comps. 2000. Wilderness science in a time of change conference—Volume 3: Wilderness as a place for scientific inquiry, 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-3. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Robert L. Sanford, Jr., Associate Professor, Department of Biological Sciences, University of Denver, Denver CO 80208 U.S.A., e-mail: rsanford@du.edu. Sally P. Horn, Professor, Department of Geography, University of Tennessee, Knoxville, TN 37996 U.S.A., e-mail: shorn@utk.edu

history for a specific site or larger area. Fire history based on soil and sediment charcoal is coarse in comparison to fire history based on dendrochronology, which can provide an exact calendar year for a fire. In contrast, a radiocarbon date from a charcoal fragment always has an associated error range. The high cost of radiocarbon dating makes it impractical to determine the age of every charcoal fragment found; thus, it is quite likely that some fires will be missed by the analysis. This usually results in no better than a century-scale fire history resolution (table 1).

Soil charcoal may also be used to estimate fire recurrence for a site or larger land area. The presence of soil charcoal with widely differing radiocarbon dates from several soil depths is good evidence of repeated fires at a single sampling site (table 1). Soil charcoal of the same age taken from sampling sites over a large area (5-50 ha) is reasonable evidence for an extensive fire.

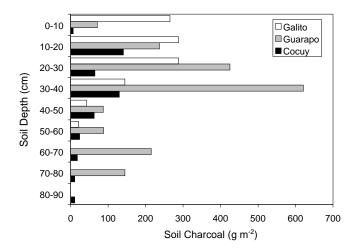
Finally, quantification of soil charcoal provides a measure of long-term carbon storage in tropical forest sites. In some areas of the Amazon, surprisingly large amounts of charcoal are present (figure 1). Although there are several problems with quantification of soil charcoal in the context of assessing wilderness status of different areas, the techniques are still useful if these problems are taken into account before sampling. Here we address the main methodological problem and comment on what we consider to be a conceptual dilemma.

Methodological difficulties are pervasive in all soil charcoal studies. All previous work with soil charcoal suffers from the uncertainty associated with identification and removal of charcoal fragments from soil samples. If the charcoal fragments are small (<0.5 mm), sorting is ineffective, and there is a likelihood that some fragments may not be removed. We and others generally use sieves with 1 mm or 2 mm openings, allowing the smallest fragments to pass; using sieves with smaller openings is not practical because of the amount of time involved. Sieve opening size most influences the quantification of soil charcoal storage, but it could also influence the quantification of timing of past fire(s), as larger sieve sizes may not allow detection of the most intense fires, which may produce predominantly smaller charcoal fragments. Of course, sieve size can also affect the recognition of the presence of past fire at a site.

Table 1—Radiocarbon dates on soil charcoal from different depths at forest sites in the north central Amazon near San Carlos de Rio Negro, Venezuela (after Saldarriaga and West 1986; dates are uncalibrated).

Depth (cm)	Site V		Site XI	
	Lab. No.	Age	Lab. No.	Age
0-10		a	β-9014	250 +/- 50
10-20	β-9031	480 +/- 50	β-9015	650 +/- 50
20-30	β-9032	670 +/- 50	β-9016	1560 +/- 60
30-40	β-9033	1100 +/- 50	β-9017	1700 +/- 60
40-50	β-9034	920 +/- 90	β-9018	1180 +/- 90
50-60	β-9035	1100 +/- 90	β-9019	1220 +/- 80
60-70	β-9036	6260 +/- 110	β-9020	1260 +/- 80

a Not recorded.



**Figure 1**—Mass (g m²) of soil charcoal at 10 cm depth increments for three sites in the north central Amazon along the Rio Negro. Guarapo and Galito are located in Venezuela, Cocuy in Brazil. Data at each depth is an average of three samples taken at that site. Totals are: Guarapo 1,889 g m², Galito 760 g m² and Cucoy 470 g m². Soil sampling depth varies as a function of depth to the plinthite (impenetrable ironstone) layer (Sanford, unpublished data).

The second issue that confounds use of soil charcoal is the issue of ignition: fire(s) of human origin versus fires resulting from nonhuman ignition sources under conditions of natural rainfall variation. Until recently, it has been difficult to accept the premise that tropical forests with >3000 mm precipitation per year could experience widespread burning originating from nonhuman ignition sources. However, observations made during the 1982-83 (Sanford and others 1985) and 1997-98 El Niño events have shown that almost every tropical rain-forest is susceptible to fire, even those with a minimal or nonexistent dry period in normal years.

Taken together, the problem of uncertainty in soil charcoal quantification and the difficulty in determining ignition sources make soil charcoal analysis an enticing but imperfect tool for estimating the extent of ancient human perturbations. Fortunately, these problems are usually bypassed by use of complementary data from archeology and palynology. Much of the early work in neotropical archeology was developed in high-elevation (Andean) or seasonally dry regions (tropical dry forests). An unintended consequence of this early focus was a misperception of extent and range of human habitation in lowland moist environments (Balee 1988). Research over the past 20 years has affirmed widespread occupation of the lowland tropics and has moved back substantially the earliest dates of human habitation (Roosevelt 1994). Archeological research has often been sitespecific, focusing on an ancient village, town, or city. Archeological research across landscapes is much more limited, but it raises an interesting perspective from the point of view of wilderness. For example, the spatial extent of agriculture to support prehistoric populations throughout the lowland tropics is rarely calculated; even when it is, estimations of repeated episodes of forest conversion (at a particular site) are almost never attempted. This is an area in which the data on distribution and abundance of charcoal in soils and sediments are proving very useful.

The first charcoal evidence of prehistoric fires in neotropical forests came from analyses of microscopic charcoal particles in sediment cores from the Mayan area of southern Mexico and northern Central America (Tsukada and Deevey 1967). Macroscopic charcoal fragments have been found under mature rain-forests in Costa Rica, Panama, and several areas of the Amazon Basin. In the Amazon especially, charcoal seems to be almost ubiquitous in soils, indicating that even forests that have escaped 20th century disruption are not pristine or "virgin." The charcoal is readily datable, with reported ages ranging from 6000-250 yr. B.P. (Saldarriaga and West 1986; Sanford and others 1985; Soubiès 1979-80). Much of it may have formed as a consequence of fires set by people, but some may reflect natural ignitions (lightning or volcanism). In both cases, there may be a link with climate. When soil sieving yields pot shards along with charcoal, it argues strongly (though not exclusively) for human-set fires.

The macroscopic charcoal found in neotropical soil cores generally reflects past fires on, or very near, the site of collection. Macroscopic charcoal in lake sediments also reflects local fires, but smaller particles may reflect both local and distant burning. Charcoal in dated lake sediment cores provides stratigraphic records of changes in fire occurrence over time. These records differ from the typical situation with charcoal profiles from terrestrial soils, which may lack stratigraphy due to bioturbation and other soil processes. Abundant charcoal between dated layers in a sediment core usually signals the occurrence of a fire or fires between the bracketing dates. Extracting precise information on fire frequency can be difficult, but it is generally possible to reconstruct variation in fire activity over time. Sedimentary and soil charcoal records cannot answer all questions about past fires—but they may well comprise the only evidence available of past fires at neotropical sites where dendrochronological reconstructions of fire history are not possible.

### **Lake Sediments**

Paleoecology refers to the science of reconstructing the structures of, and processes affecting, past biotic populations and communities. Sediment cores from natural lakes and other wetlands are particularly important data sources for the paleoecology of the period following human invasion of the New World tropics. The pollen grains, charcoal fragments and other plant microfossils that accumulate and persist in sediments, together with characteristics of the sediment matrix, reveal characteristics of past vegetation, climate, fire regime and other environmental factors, including those related to human use of landscapes.

In this section, we describe some of the methods, opportunities, and limitations of paleoecological research from sediments, as applied to understanding the human history of wilderness areas. Lake sediment cores for paleoecological study are recovered from anchored platforms constructed of rubber rafts, inner tubes or other floats, using a variety of coring devices. Most sediment corers are engineered such that sediment enters the core barrel as it is pushed downward through a particular section of the profile, from the sediment/water interface to a depth of 1 m sub-bottom, or from 1 m sub-bottom to 2 m sub-bottom. The corer is attached to drill rods, which are pushed down manually, in

some cases via hammering. A piston controls the depth at which sediment begins to enter the core barrel and provides sufficient suction to keep the sediment from falling out of the barrel when raised back to the coring platform. Cores are recovered as strings of core sections from the same hole, often in 1 m increments. Swamps and bogs without deep standing water can be sampled using a greater variety of coring devices.

Cores of sediment are either extruded in the field and wrapped in plastic and foil, or are returned to the lab still encased in the original core barrel (in which case a new core barrel is used for each core section). Cores are sampled in the laboratory to provide material for radiocarbon dating. Accelerator-mass-spectrometry (AMS) radiocarbon dating makes it possible to date individual, small organic macrofossils, such as leaves or charcoal particles. AMS dating of small, potentially identifiable organic macrofossils not only provides precise dating, it also provides an opportunity to tightly constrain events of potential interest (for example, a time when a particular tree species grew close enough to a core site to deposit a distinctive leaf, or a time when the watershed burned, producing macroscopic charcoal deposited at the core site.)

Pollen grains and other acid-resistant microfossils are extracted from sediment cores using techniques of chemical and mechanical separation originally developed in Europe. Although wind-pollination is rare in the tropics, pollen production is high enough and dispersal is efficient enough to result in the deposition of pollen-rich mud in most natural basins. Pollen types are distinct and can be identified by comparison to reference material prepared from herbarium sheets. Interpretations of pollen spectra (samples) are facilitated by the study of modern pollen deposition in areas of known vegetation and human disturbance regimes (Bush 1991; Rodgers and Horn 1996).

Pollen preparations often contain microscopic charcoal, which is resistant to the chemicals used to extract pollen grains. Other microfossils, such as phytoliths and diatoms, dissolve during the normal pollen processing routine but can be concentrated using other procedures. Phytoliths (silica bodies from plants) can supplement pollen evidence of the past distribution of plants, including crop plants (Piperno 1988). Siliceous valves of diatoms (unicellular algae) or the remains of cladocera (small crustaceans) preserved in sediments can provide information on limnological conditions, which may in part reflect land use (Birks and Birks 1980). The mineralogy, chemistry and rate of deposition of the sediments can provide information on soil erosion associated with past human use of watersheds (Dunning and others 1998).

Paleoecological evidence of past human interaction with tropical forests began to be recovered in the 1940's, when Edward Deevey and collaborators cored lakes in Central Mexico and later in the Mayan area of southern Mexico and adjacent northern Central America (Tsukada and Deevey 1967). The pioneering efforts of Deevey and collaborators have been followed by others, resulting in the development of numerous paleoecological records, many of which are relevant to understanding neotropical land use history. Each site investigated gives a slightly different picture, but a common pattern is one in which pollen spectra suggest an interval of forest clearance and agriculture (low tree pollen

percentages, high values for grasses and composites, and the presence of maize or corn pollen), followed by abandonment or lessening of agricultural activity and regrowth of the forest (rise in tree pollen). Some pollen records begin with higher tree pollen percentages, suggesting initially forested surroundings; some show multiple peaks in agricultural indicators and/or evidence of more recent (European) forest clearance. The pollen spectra at different depths in sediment cores often contain microscopic charcoal, defined as those pieces too small to be seen with the naked eye. The abundance of microscopic charcoal in sediment cores often appears to correlate with pollen indicators of agricultural activity, although the source area for the smallest charcoal fragments may be larger than the source area for the pollen grains (Clark 1988).

# Neotropical Wilderness in the Context of Paleoecology

What we can learn from paleoecology about human history of neotropical wilderness is limited by site availability, by the nature of sediment records and the microfossils they contain and by our incomplete (but growing) knowledge of the taphonomic processes that affect the deposition and preservation of different microfossils. Often, however, the data gleaned from paleoecological analyses provide some of the only evidence available to answer questions about past human land use. That is, the data source is imperfect but has few competitors. Here we discuss in more specific terms what we can learn from paleoecological analyses.

Pollen grains and charcoal fragments, the two most commonly investigated paleoecological indicators in the neotropics, usually provide a basis for determining:

- 1.) Whether fires occurred.
- 2.) Fire recurrence.
- 3.) Spatial extent of fires.
- 4.) Plant taxa that were present in the past.
- 5.) Whether forests were cleared.
- 6.) Whether maize (corn) was cultivated.

Soil charcoal has been used to address the first three and sediment analysis for all but #3, which requires the rare situation of abundantly distributed lakes and swamps to preserve samples across a landscape (Clark and Robinson 1993). The presence of soil charcoal is direct evidence that the vegetation of that site has burned sometime in the past. Several layers of soil charcoal at different depths provide reasonable evidence that several fires have occurred, and a coarse fire frequency may be determined by radiocarbondating charcoal pieces from the different layers. Estimating the spatial extent of ancient rain-forest fires requires sampling large areas (1-100 ha) and, if several layers of charcoal are present, resolution of the timing of the fires. An important condition for these analyses is the presence of nonalluvial soils. The potential for fluvial deposition makes soil charcoal analysis unreliable as an indicator of local fires on alluvial

Although it is intriguing to infer human alteration of almost all of the lowland tropics during the late Holocene (Kershaw and others 1997) not enough soil charcoal data have been coordinated with archeological and palynological

analyses to infer ubiquitous human perturbation. The issue of human vs. natural ignition sources remains unresolved for most areas of the neotropics and will remain so until more detailed paleoclimatic reconstructions are available. The ignition source of past fires may become an important issue as our understanding of the biogeography of tropical species diversity increases.

An interesting issue that revolves around ancient human land use practices is the extent to which species distributions have been modified. For example, both Mayan and Amazon cultures have distributed plant species that have become resident outside of their original areas of distribution (Gomez-Pompa and Kaus 1990; Smith 1980). In areas that have been most intensively used by ancient human populations, soil charcoal is present at sites where soils have been altered to Anthrosols. Although these are relatively small areas (probably sites that were repeatedly occupied as village sites), the changes in soil texture and chemistry result in a striking "landscape signature" with potentially long-lasting effects on plant and animal species composition.

Analysis of lake sediments adds a more precise dimension to understanding human signatures on the landscape. The presence of pollen of a particular plant species reveals that the plant was present at the time the sediments were deposited. This information is critical to documenting the structure and nature of prior plant populations and communities at wilderness sites. However, the preponderance of animal pollination in neotropical forests results in a large number of what Bush and others (1992) have termed "silent taxa" (present in the forest, but not present as pollen.) For these taxa, absence of evidence cannot be taken as evidence of absence. Outside of the neotropics, where more plants are wind-pollinated, such reasoning might be acceptable. For example, if chestnut pollen is not present in a 5,000-year-old sediment sample from Tennessee, one can be reasonably certain that the plant didn't grow in the area. This kind of reasoning is not valid for many neotropical taxa.

A related limitation is that while the presence of a pollen type documents the past occurrence of the plant, it does not indicate an exact location where the plant was growing. Pioneering work by Bush and Rivera (1998) has provided a basis for interpreting how far from the sampling site the responsible plant may have been located (which varies by species). Examining samples from multiple core sites all representing the same time period would also help to constrain the past geography of plant populations.

A number of pollen types potentially signal human disturbance of neotropical rain-forests, but distinguishing cultural impacts on forests from natural forest dynamics can be difficult. The weedy secondary tree *Cecropia* readily colonizes large canopy gaps, and increases in the abundance of *Cecropia* pollen in a sediment record could reflect initial forest succession on abandoned plots in areas of active field rotation, or along field margins. However, natural gapforming processes, such as landslides on steep slopes or along streams, could also increase suitable habitat for *Cecropia* trees and the importance of their pollen grains in sediment records. The same situation applies to the pollen of weedy herbaceous families, such as grasses and composites. We expect these pollen types to be more abundant during periods of forest clearance and more agricultural activity,

but other environmental processes could also lead to increased grass and composite percentages.

Less ambiguous evidence of prehistoric crop cultivation is provided by the pollen of crop plants. By far the most important such taxon in the pollen record is *Zea mays* (maize or corn). Maize pollen (figure 2) is wind pollinated, but the pollen grains are large and tend to settle out close to the parent plants (Raynor and others 1972). As a result, the presence of maize pollen is an excellent indicator of local maize cultivation. The presence of maize pollen in swamp sediments from the La Selva Biological Station, Costa Rica, documents the cultivation of maize pollen as recently as 700-300 years ago in one part of the reserve (Kennedy and Horn 1997), and as early as 2,700 years ago in another part of the reserve (Horn and Kennedy, in press).

In summary, analyses of ancient pollen grains, and soil and sedimentary charcoal, provide a useful, complimentary set of tools that are gradually coming to be applied to the determination of human land use signatures at landscape and large scales. Sediment analysis is somewhat limited by the potentially large sizes of the source areas for pollen and the smallest microscopic charcoal, as well as the resolution of pollen taxa. Soil charcoal analysis is limited by the difficulty of recovering the smallest size fractions, and by the inability to distinguish human and natural ignitions from charcoal alone. However, we are seeing a continued refinement and wider and concurrent application of soil and sediment analysis to describe the land-use signatures that have been created by hundreds of generations of agriculturists in neotropical rain-forests.

### **Implications**

"...and you lived in the wilderness a long time." Joshua 24:7

Ultimately, for wilderness, does it matter when and where human populations lived in, burned and otherwise modified tropical rain-forests? Should we still propose wilderness



**Figure 2**—A pollen grain of maize (*Zea mays* L.) from the Machita swamp in the old growth, lowland rain-forest at the La Selva Biological Station, Costa Rica. The grain is about 70 um in maximum dimension. The presence of prehistoric maize pollen in swamps at this research station indicates that this "wilderness" was managed by prehistoric inhabitants. (Photo by Karen Burhenn.)

designation for areas that have clear evidence of pre-Columbian human perturbations?

In North America, managers and scientists have debated this issue and will continue to do so. The concept of wilderness has evolved from the perception of a pristine element of the landscape, a place where Homo sapiens is and always has been an ephemeral visitor, to the perception of wilderness as an area that is managed to remain wild (Foreman, in press). Given the "manage for wildness" mandate, lowland tropical forests that were once corn fields could well fit into wilderness designation, and it may be more useful to determine the time since last use, or more importantly, the degree to which the 300-year-old forest that has grown back from a corn field now resembles the nearby 1,000-year-old forest. Perhaps knowledge of ancient land-use practices in areas that now become designated as wilderness can foster appreciation of the possible role of human disturbance in the suite of biological processes that promote diversity in lowland rain-forests. Since humans invaded the neotropics 14 millennia ago, our presence has resulted in a series of disturbances ranging from hunting (and perhaps overhunting) to intensive agricultural activities that required forest removal during the past four to eight millennia.

In the lowland tropics, where massive deforestation is occurring at rates much higher than ever occurred in the past, this issue of previous human occupation and disturbance is increasingly important. Most neotropical national parks and forest reserves have been established since 1970. In many cases, park establishment and management followed (more or less) the U.S. model of dedicating areas of particular natural beauty that were also thought to be pristine. In North America, most now recognize that pristine is an add-on component to wilderness, but not a crucial criterion for wilderness designation. In the tropics, many are just coming to appreciate how scarce truly "pristine areas" are. Eventually, as Latin American land-managers designate wilderness areas, it will become important to appreciate wilderness in its broadest sense and to appreciate the truly special category of pristine wilderness—if such places still exist.

In a very real sense, the issue of past human habitation is linked with present-day management controversies. If people formerly lived on the land that we now classify as wilderness, it seems easier to justify present-day human activities to manage wilderness. Human endeavors have left a legacy of landscape signatures that slowly become erased with time. Signatures such as changes in soil chemistry, maize pollen in swamp sediments and charcoal fragments in tropical soils slowly become blurred over centuries and millennia, but they are evidence for past human management activities in areas that we could now designate as wild.

### Acknowledgments

Our studies of prehistoric and modern tropical rain-forests (wild and otherwise) have been supported by grants from The A. W. Mellon Foundation, the U.S. National Science Foundation, the National Geographic Society, and our universities. We thank our students for assistance in the field and laboratory, our Latin American colleagues for logistical support and helpful, stimulating discussion and Christopher V. Barnes and Thomas Peterson for reviewing an earlier version of this manuscript. We acknowledge also the key logistical, computational, and empathetic support for our work provided by our respective spouses and children

### References

- Balee, W. 1988. The culture of Amazonian forests. Advances in Economic Botany. 7:121-133.
- Birks, H. J. B. and Birks, H. H. 1980. Quaternary paleoecology. Baltimore, MD: University Park Press.
- Bray, W. 1986. Finding the earliest Americans. Nature. 321:726.
  Bush, M. B. 1991. Modern pollen-rain data from South and Central America: a test of the feasibility of fine-resolution lowland tropical palynology. The Holocene. 1(2): 162-167.
- Bush, M. B.; Piperno, D. R.; Colinvaux, P. A.; De Oliveira, P. E.; Krissek, L. A.; Miller, M. C.; and Rowe, W. E; 1992. A 14,300-yr paleoecological profile of a lowland tropical lake in Panama. Ecological Monographs. 62(2): 251-275.
- Bush, M. B. and Colinvaux, P. A. 1994 Tropical forest disturbance: paleoecological records from Darien, Panama. Ecology. 75(6): 1761-1768.
- Bush, M. B. and Rivera, R. 1998. Pollen dispersal and representation in a neotropical rain forest. Global Ecology and Biogeography Letters. 7: 379-392.
- Byrne, R. and Horn, S. P. 1989. Prehistoric agriculture and forest clearance in the Sierra de los Tuxtlas, Veracruz, Mexico. Palynology. 13: 181-193.
- Clark, J. S. 1988. Particle motion and the theory of stratigraphic charcoal analysis: source area, transport, deposition and sampling. Quaternary Research. 30: 67-80.
- Clark, J. S. and Robinson, J. 1993. Paleoecology of fire. In: Crutzen, P. J. and Goldammer, J. G., eds. Fire in the Environment: The Ecological, Atmospheric and Climatic Importance of Vegetation Fires. Chichester, UK: John Wiley and Sons: 194-214.
- Colinvaux, P. A. 1989. Amazon diversity in light of the paleoecological record. Quaternary Science Reviews. 6: 93-114.
- Darwin, C. 1855. Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of the H.M.S. Beagle Round the World. New York, NY: Appleton. 524 p.
- Dunning, N.; Rue, D. J.; Beach, T.; Covich, A.; and Traverse, A. 1998. Human-environment interaction in a tropical watershed: the paleoecology of Laguna Tamarindito, El Peten, Guatemala. Journal of Field Archaeology. 25(2): 139-151.
- Foreman, D. In press. The real wilderness idea. In: Cole, David N.; McCool, Stephen F.; Freimund, Wayne A.; O'Loughlin, Jennifer, comps. Wilderness science in a time of change conference—Volume 1: Changing perspectives and future directions; 1999 May 23-27; Missoula, MT. Proceedings RMRS-P-15-VOL-1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Gomez-Pompa, A.; and Kaus, A. 1990. Traditional Management of Mexican Forests. In: Anderson, A. B. Alternatives to Deforestation. New York, NY: Columbia University Press: 45-64.
- Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. In: Tomlinson, P. B. and Zimmermann M. H., ed. Tropical trees as

- living systems. Cambridge, UK: Cambridge University Press: 617-638.
- Horn, S. P. and Sanford Jr., R. L. 1992. Holocene fires in Costa Rica. Biotropica. 24: 354-361.
- Horn, S. P. and Kennedy, L. M. In press. Pollen evidence of maize cultivation 2700 years ago at the La Selva Biological Station, Costa Rica. Biotropica.
- Kennedy, L. M. and Horn, S. P. 1997. Prehistoric maize cultivation at the La Selva Biological Station. Biotropica. 29(3): 368-370.
- Kershaw, A. P.; Bush, M. B.; Hope, G. S.; Weiss, K.-F.; Goldammer, J. G.; Sanford Jr, R. L. 1997. The contribution of humans to past biomass burning in the tropics. In Clark, J. S.; Cachier, H.; Goldammer, J. G.; and Stocks, B.; eds. Sediment Records of Biomass Burning and Global Change. Berlin, Germany: Springer-Verlag: 413-442.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. American Naturalist. 100:33-46.
- Meggers, B. J.; 1995. Judging the future by the past: The impact of environmental instability on prehistoric Amazonian populations.
   In Sponsel, L. E.; ed. Indigenous peoples of the future of Amazonia: An ecological anthropology of an endangered world. Tuscon, Arizona: University of Arizona Press: 15-43.
- Northrop, L. A.; and Horn, S.P. 1996. PreColumbian agriculture and forest disturbance in Costa Rica: paleoecological evidence from two rainforest lakes. The Holocene. 6: 289-299.
- Piperno, D. R. 1988. Phytolith analysis: an archaeological and geological perspective. San Diego, CA: Academic Press. 280 p.
- Raynor, G. S.; Ogden, E. C.; and Hayes, J. V. 1972. Dispersion and deposition of corn pollen from experimental sources. Agronomy Journal. 64: 420-427.
- Rodgers III, J. C. and Horn S. P. 1996. Modern pollen spectra from Costa Rica. Palaeogeography, Palaeoclimatology, and Palaeoecology. 124: 53-71.
- Roosevelt, A. C. (ed.) 1994. Amazonian Indians from Prehistory to the Present: Anthropological Perspectives. Tuscon, AZ: University of Arizona Press.
- Roosevelt, A. C.; Lima da Costa, C.; Lopes Machado, C.; Michab, M.; Mercier, N.; Valladas, H.; Feathers, J.; Barnett, M.; Imazio da Silveira, M; Henderson, A.; Silva, J.; Chernoff, B.; Reese, D. S.; Holman, J. A.; Toth, N.; and Schick, K. 1996. Paleoindian cave dwellers in the Amazon: the peopling of the Americas. Science. 272: 373-384.
- Saldarriaga, J. G.; and West, D. C. 1986. Holocene fires in the northern Amazon basin. Quaternary Research. 26: 358-366.
- Sanford, Jr., R. L.; Saldarriaga, J.; Clark, K.; Uhl, C.; and Herrera R. 1985. Amazon rain-forest fires. Science. 227: 53-55.
- Smith, N. J. 1980. Anthrosols and human carrying capacity in Amazonia. 1980 Annals of the American Association of Geographers. 70(4): 553-566.
- Soubiés, F. 1979-80. Existence d'une phase sèche en Amazonie Brésilienne datée par la présence de charbons dans les sols (6.000-3.000 ans B.P.). Cah. ORSTOM Ser. Geol. 11: 133-148.
- Tsukada, M. and Deevey, Jr., E. S. 1967. Pollen analysis from four lakes in the southern Maya area of Guatemala and El Salvador. In: Cushing, E. J. and Wright, H.E., eds., Quaternary Paleoecology. Proceedings of the VII Congress of the International Association for Quaternary Research. New Haven, CT: Yale University Press: 303-331.
- Wallace, A. R. 1878. Tropical Nature, and Other Essays. London: Macmillian and Co. 372 p.