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The Rain-Forest Ecosystem as a Resource for Hunting and Gathering

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## The Rain-Forest Ecosystem as a Resource for Hunting and Gathering

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In a recent issue of *American Anthropologist*, Bailey et al. (1989) argue that rain forests can never have supported human populations reliant solely on hunting and gathering. We believe, to the contrary, that many tropical forests are highly productive of the resources needed for hunting, gathering, and fishing. People could, and probably therefore did, subsist in tropical forests without significant calorie intakes from crop plants. This is important to an understanding of the movements of peoples at the end of the last glaciation, suggesting, for instance, that tropical forests now known to have been present in the lowlands of

Panama at times of first settlement (Bush and Colinvaux 1990) were possible human habitats and that the Amazon lowlands could have been occupied as early as the Pacific coast of South America.

Bailey et al. base their claim on three contentions: that rain forests, for all their primary productivity, do not yield sufficient, accessible human food; that no unequivocal evidence exists for subsistence hunting and gathering in rain forests before a large part of calorie requirements could be met from cultivation; and that historic inhabitants of rain forests all supplement rain-forest resources with cultivation, or by trade, or both. We believe that these authors are in error in their first contention; that they misunderstand the paleoecological record in their quest for fossil traces of human occupations of rain forests in their second contention; and that the data on historical human occupancy of rain forests for their third contention are irrelevant.

### Food Resources of Rain Forests

No ecologist doubts that annual primary production in tropical rain forests can be higher than in any other terrestrial ecosystem (Whittaker and Likens 1973, 1975). The reason for high primary production is high temperature and unlimited water. Limits to production are probably set by the carbon dioxide concentration of the air (not incident solar energy, as Bailey et al. seem to suggest). The effective nutrient retrieval system of trees that Bailey et al. describe is an adaptation that allows full advantage to be taken of constant moisture and warmth (Colinvaux 1986).

The term "tropical rain forest" has been used to describe many different forest types and should be used with caution. Many forest communities are present, for instance, in the enormous piece of real estate loosely referred to as "the Amazon." Some Amazon forests experience pronounced dry seasons, while others are wet year round. Species lists (and hence resources) differ in forest communities a thousand kilometers apart. Forest communities in some parts of Africa and South-East Asia have many fewer species than many Amazonian forests. Yet, all the wetter forests do share many of the essential properties of high productivity and high diversity commonly associated with the term "tropical rain forest."

Not only is high production virtually continuous in the less-seasonal rain forests, but many of the forest communities tend to be in early successional stages. This is because trees are blown down so frequently that succession is seldom allowed to run its course before a

new cycle of colonization begins in the resulting gap. This process of recurrent rejuvenation of rain-forest communities is thought to be a principal cause of high species richness because competitive interactions seldom last long enough for the losers to go locally extinct (Connell 1978; Hubbel 1979; Colinvaux 1987; Salo 1987). In addition, Amazon forests are subject to severe and frequent erosional events that also serve to keep successions in their early stages (Colinvaux et al. 1985, 1988; Salo et al. 1986; Räsänen, Salo, and Kalliola 1987; Frost 1988; Frost and Miller 1987). An important consequence to foragers is that dispersal is vital to rain-forest plants, so that many produce fruits or seeds attractive to animals (Whittaker, Bush, and Richards 1989).

Wind is largely ineffective as a dispersing agent through such dense, evergreen vegetation, and water dispersal, though important, cannot be major. What is left are the animals. This is why tropical rain forests are preeminently the systems with frugivores: whether birds, primates, bats, insects, or reptiles. The primary producers of the tropical rain-forest ecosystem are adapted by natural selection to provide food for foraging animals as lures for seed transport.

Bailey et al. cite Leigh's (1975) observation of starving monkeys during a fruit-crop failure as evidence that rain forests are a precarious habitat for gatherers. This famine, however, was on Barro Colorado Island: 1,500 ha of seasonal forest marooned by Lake Gatun. Migrations should have saved similar primates in the open forest. Humans could have gone hunting or fishing or grub-gathering, as well as wandering.

Bailey et al. remark correctly that many rain-forest seeds are poisonous. This actually is evidence of potentially rich food sources for foragers. To understand this paradox it is necessary to introduce contemporary ecological thinking known as "optimal defense theory" (Rhoads 1979). Two general kinds of chemical poisons are known from plant tissues, acutely toxic poisons known as alkaloids (e.g., nicotine, strichnine, atropine) and the plant tannins that make tissues completely inedible. Plants generally have one of these systems of chemical defense but not the other. Tannins work by precipitating proteins (which is why oak tannin cures leather). This is bad for all herbivores, but is energetically costly to the plant. Ecologists call the use of tannins "quantitative defense," since it repels all-comers. Tannic, quantitative defense is found in temperate forests where tree-species diversity is low, because each tree is near neighbors likely to harbor all possible pests. The common al-

ternative defense strategy uses highly toxic alkaloids that kill the target insects but which can be rendered harmless by insects with the correct chemistry (the word *antidote* conveys the idea). These "qualitative defenses" are only practical when plants of the same species are scattered and the host-specific insects with the antidote are correspondingly rare. Toxic, quantitative defenses are common in tropical rain forests because diversely scattered plants do not need to be made almost totally inedible with tannins. Protecting sensitive parts, like the seeds, against the generality of insects is enough and the plant relies on dispersal to provide the rest of the necessary defense. A consequence is that even the foliage of tropical rain forests (unlike that of temperate forests) may be edible to mammalian foragers.

Undoubtedly, a portion of tropical fruit crops is inedible to humans (or inedible until processed), but this should not be taken as evidence that the total edible crop is trivial. Evidence to the contrary comes from studies of partly frugivorous primates, such as gibbons. Gittins and Raemaekers (1980) found that individual gibbons relied on the produce of 260 species of plants in the course of a year. Rain forests are highly favored places for any organism capable of discriminant or learned foraging on fruits and seeds.

That many tropical rain forests are unlikely to achieve self-perpetuating climax states implies that energy storage in unproductive structures is minimized. This challenges the claim by Bailey et al. that most primary production is unavailable to foragers because resulting in wood rather than edible tissue. Intact rain forest does indeed represent an immense standing crop of wood (Woodwell et al. 1978), but the actual rate of wood production is not remarkable. The common impression that tropical forests grow wood quickly is mistaken; in fact, it is foliage production that is maximized in tropical forests (Jordan 1983). High foliage and relatively low wood production are precisely what is to be expected of a rapidly growing, perpetually disturbed system like the Amazonian rain forest.

Bailey et al. also make the classic error (Slobodkin 1962) of confusing standing crop with productivity when they quote data to suggest that only 2% of the standing crop of biomass in a rain forest is in leaves and other potentially edible portions of plants. This standing-crop ratio does not imply that productivity of edible tissue is low, but merely that the ratio of actively living tissue to accumulated structure is low. This ratio is low in all ecosystems in which biomass accumulates. What matters is the rate of turnover of the living tissue, or

the flux of energy released to potential herbivores. The high productivity, together with the requirement that most rain-forest plants shall live in comparatively early successional communities, keeps this energy flux high.

The claim that net primary production potentially available to herbivores in a rain forest is too low for human sustenance becomes particularly suspect when rain forests are compared with other, much less productive ecosystems for which hunting and gathering is thought to be effective: temperate woodlands, savannas, and prairies. Even grasslands store much energy as dead matter. And in temperate woodlands, succession tends to proceed to climax with large storage of energy as wood and with most foliage protected from herbivore attack by tannins. Consequences of defense by tannin are large energy storage in dead leaves (ultimately the soil) and low potential energy flux to herbivores. Thus, forests of oaks and beeches, unproductive to start with, have the further handicap for herbivores that leaves are inedible except when first formed, when the tannins have not yet been deposited. Compared with these systems, the toxic, selective defenses provided to scattered, successional rain-forest trees by their alkaloids are likely to provide a larger potential energy flux to herbivores. Furthermore, the rapid growth strategies of rain-forest plants are themselves of a kind that favor growth over defense, suggesting that a full analysis of edibility of rain-forest plants should show a greater percentage of edible biomass than in temperate systems rather than less.

Secondary production in tropical rain forests is further enhanced through detritus food chains. Leaves unprotected by tannins are rapidly scavenged by ants, termites, beetles, and other invertebrates. Likewise, wood is turned over quickly by boring insects, by termites, and by fungi. The result is that residence times of energy stores are minimal in rain forests beyond the lives of the organisms themselves. A significant part of the energy stored briefly in these inert structures then enters detritus food chains potentially exploitable by hunting and gathering, instead of going to bacterial decomposition or fire as in temperate or dry ecosystems. Grubs of wood-feeding insects are abundant, as are animals that feed on grubs.

To the production ecologist, a tropical rain forest can be likened to a highly productive prairie raised off the ground on stilts 20 m high (Colinvaux 1989a). Primary grazing animals should be arboreal, therefore, and the ungulates of grasslands are replaced by primates, rodents, and sloths, many of which should be,

and are, leaf eaters as well as frugivores. Adequate census of secondary productivity in the canopies of tropical rain forests by non-arthropod herbivores have not been made, but a clue to the scale of this productivity is given by the suite of tertiary consumers present. Although rain forests have guilds of climbing cats and mustelids (mink family) as typical mammalian predators, they also support unique guilds of huge avian predators, such as the harpy eagles of the Amazon, able to take primate prey from the canopy. The evolution of this diverse array of large predators of the canopy is strong evidence of high secondary productivity available for any hunter with the means to crop it.

But rain-forest herbivores are by no means entirely restricted to the canopy. Particularly productive spots are the frequent gaps where the race for light begins so that diversion of energy by plants to defense should be least and the edibility quotient of vegetation is likely to be highest. Animal activity is known to be intense around such gaps. Other canopy-feeding forms have business on the ground also, like the larger primates that use the ground for travel, the rodents who descend for fallen fruit, and the sloths who descend to defecate. Still other herbivores and omnivores feed on the ground components of the forest ecosystem, like the pigs characteristic of rain forests. The presence of big cats and mustelids in rain forests is ample evidence that a significant flux of quadrupedal and avian prey energy is available below the canopy.

Supplementing the secondary producers are those tertiary consumers that feed both on insect herbivores and on primary detritus consumers. These range all the way from small reptiles and amphibians to large anteaters. The proportion of tertiary consumers that are on detritus food chains represents a special resource available only in tropical systems. This resource is perhaps at its largest in the tropical rain forest itself.

A final resource to clever foragers ignored by Bailey et al. is fish. In many systems it is possible to separate fishing activities from hunting and gathering, but this separation breaks down for rain forests where the fish are an integral part of the ecosystem. The dense fish populations of tropical lakes and rivers are primarily supported by terrestrial food chains, particularly detritus chains, rather than from the production of aquatic plants and plankton. As such, the fish represent protein and energy fluxes ultimately derived from the net primary productivity of the forest itself.

Thus, an ecological analysis of tropical rain-forest productivity suggests a promising ecosystem for foragers. While accurate measures

of net primary production or secondary productivity are not generally available for rain forests, the circumstantial evidence that high primary productivity results in high production of edible plant material, high secondary productivity in the form of herbivores of all kinds, and high detrital food-chain productivity leading to its own unique crop of edible animals and fish, is strong.

### The Paleocology of Tropical Rain Forests

To demonstrate that past peoples have lived in rain forests without benefit of cultivation, it is necessary to have both securely dated evidence of human occupation and unequivocal paleoecological evidence that the local vegetation was in fact tropical rain forest, together with a strong inference that these people were not dependent on cultivars. This could be most easily done by producing evidence for people living in rain forests in the early Holocene or later glacial periods. Bailey et al. argue that the necessary data do not exist, concentrating their remarks on evidence from South America. The latest paleoecological and archaeological data from Panama, supplemented by evidence from the Amazon, however, do provide the necessary evidence (Snarskis 1984; Bird and Cooke 1978; Cooke 1984; Piperno, Bush, and Colinvaux 1990; Bush and Colinvaux 1990).

Essential to the Bailey et al. argument is that rain-forested regions of modern South and Central America were too arid to support rain forest in the interval 14,000–10,000 B.P., when human populations are known to have penetrated the isthmus of Panama. This widespread view depends on the acceptance of a hypothesis, so-called "refugial theory," that requires aridity in the tropical lowlands of America to explain disjunct distributions of forest biota (Haffer 1969; Prance 1982; Whitmore and Prance 1987). Elevated regions around the Amazon basin that today support unique assemblies of birds or butterflies are considered by this hypothesis to be relics of former "islands" of wet climate separated by a sea of aridity. These former islands are called "refugia." No paleoecological data were used in the formulation of this hypothesis, because none were available from equatorial America (Salo 1987; Colinvaux 1987). Instead, the hypothesis was based entirely on deductions from modern disjunctions in species distributions across the Amazon basin and from data from Old World lakes and climate modeling that suggested reduced precipitation in many tropical areas at some stages

in glacial cycles, particularly resulting from changed intensities of monsoonal rains (Street and Grove 1979; Kutzbach and Guetter 1986).

The refugial hypothesis is increasingly seen to be inconsistent with paleoecological data (Salo 1987; Colinvaux 1987, 1989a, 1989b) and to be nonparsimonious as an interpretation of data on plant species distributions (Gentry 1989). The hypothesis has now been tested directly in the Amazon basin by using radiocarbon-dated pollen and plant macrofossils to show that cooling rather than aridity was the important climatic change. Elevated regions held moist forest communities suited to temperature depressions of up to 7.5°C, suggesting that many tropical rain-forest species were confined to bottomlands which cannot, therefore, have been arid (Liu and Colinvaux 1985; Bush et al. 1990).

No unequivocal evidence of human occupation of the Amazon lowlands before 8000 B.P. exists, but the hypothesis of early human occupation of American rain forests can now be tested directly with data from Panama. A pollen history of a complete glacial section from El Valle in lowland Panama reveals a descent of *Quercus* (oak) forests of a thousand meters or so in glacial times and the consequent restrictions of rain-forest elements to within 500 m of sea level (Bush and Colinvaux 1990). Taken in conjunction with a separate pollen and phytolith record of the last 14,000 years in Panama from Lake La Yeguada (Piperno, Bush, and Colinvaux 1990), this pollen history shows that much of the lowest part of the isthmus of Panama was covered with rain forest throughout a glacial cycle and was not semi-arid terrain, as application of the refugial hypothesis to Panama would require.

Thus, the paleoecological data from South America do not allow corridors of savanna or other semiarid, seasonal, or dry woodlands for penetrating peoples to occupy in the lowlands. The opinion that nontropical forest landscapes have been available on the isthmus of Panama to Paleo-Indians or Clovis peoples has never been supported by paleoecological data and has depended rather on using human artifacts as index fossils for savanna. This interpretation has received additional encouragement in recent years from a refugial hypothesis that also mandated savanna-like systems in lowlands as described above, but the refugial hypothesis was also without paleoecological foundation. The paleoecological data now forthcoming make it clear that tropical rain forest did persist at lowest elevations and that more elevated regions like the Darien of Panama (proposed rain forest refugium) sup-

ported moist forests of mixed montane and lowland elements (Bush and Colinvaux 1990; Bush et al. 1990).

A number of archeological records from Central America show that regions required by these paleoecological data to have held tropical forests in the latest glacial and early Holocene periods were in fact occupied by human populations. The Turrialba site in Costa Rica (Snarskis 1979) almost certainly lay in what was then rain forest (Cooke 1984), as did the Chagres Valley site (Bartlett and Barghoorn 1973), an area from which fluted points have been recovered (Snarskis 1984; Bird and Cooke 1978; Cooke 1984). At Lake La Yeguada in central Panama, human occupation of wet forests also apparently long predated the significant practice of cultivation (Piperno, Bush, and Colinvaux 1990).

Conditions maintaining high yields have prevailed in the Amazon throughout all stages of a glacial cycle. This is shown by paleoecological data that confirm the general conclusion that tropical rain forests are disturbance systems sensitive to short-term climatic changes. Amazon pollen diagrams document repeated small-scale disturbance in the vegetation throughout the Holocene (Absy 1979; Liu and Colinvaux 1988; Colinvaux et al. 1988; Frost 1988; Bush and Colinvaux 1988). In addition, the western Amazon basin yields records of repeated reworking of the land surface by rivers (Räsänen, Salo, and Kalliola 1987; Salo 1987; Colinvaux 1987) as well as regional flooding (Colinvaux et al. 1985; Frost and Miller 1987). Disturbances of these kinds seem to be basic properties of the Amazon system. The Amazon holds the archetypical rain forest, where diversity is high, succession does not usually proceed to climax, trees do not usually grow in single-species stands, and, consequently, food yields to foragers are high. These properties of the Amazon forest have always been present.

In other continents, rain-forest histories should have been different. In Africa, pollen records show that sites now supporting forests typically held different vegetation during glacial maxima (Livingstone 1975; Talbot et al. 1984), as Bailey et al. document. Modern data also suggest that African rain forests have histories different from those of the Amazon. Large areas of rain forest in Africa have been shown to have relatively low tree diversity with large monospecific stands, suggesting the attainment of climax (Connell and Lowman 1989). An ecologist should expect these forests to be much less friendly to hunting and gathering than South American forests. Southeast Asian rain forests probably have dynamics

and Pleistocene histories that are different in yet other ways.

We are still a long way from understanding both the distribution and species composition of rain forests in any of the major regions of the earth during the late Pleistocene when the first humans began to forage, though it is clear that they were different from those of the present day. Where rain forest can be shown to have been present by paleoecological data, as in the Central American sites discussed above, the earliest sign of human presence is likely to be the evidence of disturbance. At Lake La Yeguada in central Panama, for instance, we have documented the onset of fire (from charcoal) and forest disturbance (from pollen and phytoliths) in a rain-forest site at about 11,000 B.P. (Piperno, Bush, and Colinvaux 1990). The apparent criterion of Bailey et al. that people should live within the forest without disturbance is wholly unrealistic.

### The Historical Record of Rain-Forest Use

The browsing animals of the canopy of a rain forest are peculiarly vulnerable to hunting by missile attack. We know that even primitive firearms are devastating in this ecosystem where one man with a 16-gauge shotgun in the 19th century could remove most of the larger browsing animals, together with all their avian predators, from ten square kilometers in a single year (Terborgh 1983). Terborgh's (1983) primate community at Cocha Cashu is but a last remnant of what the Amazon system must have been like before the introduction of shotguns in the late 18th century. But even Cocha Cashu and its like, with primates abundant enough for biologists to wander along with the troops to observe, must certainly understate what the rain forest would have been like before the arrival of all missile weapons.

The simpler weapons of blowpipe and dart or crossbow are adequate for taking primates and birds from the canopy. When used with poisoned missiles they actually have advantages over firearms by allowing serial killing without alarming other members of a troop. These weapons are effective against smaller prey as well (Bates 1930). Hunting the larger herbivores of the rain-forest canopy, therefore, appears on the face of it a less onerous task than hunting powerful, and fleet, hooved animals in the open.

Nevertheless, larger animals are present in rain forests: tapirs, deer, and pigs in Amazonia; rhinoceros, elephants, and Banteng cattle in Southeast Asia. This ground ecosystem

within an ecosystem was likely to have been an important alternate resource in rain forests before the advent of denser human populations.

The data marshaled by Bailey et al. show convincingly that historic peoples of the rain forests have not lived by hunting and gathering alone. But that this should be so, many millennia after agriculture became commonplace, is to be expected. People have not lived as pure hunters and gatherers in others of the world's productive ecosystems in historic times either. Europeans and eastern North Americans gave up reliance on hunting and gathering many millennia ago, but we do not use this as evidence that temperate latitudes could not support hunting-and-gathering ways of life.

That cultivation has had a long history in the Old World tropics is well known, but it now seems that cultivation in the Amazon basin has a long history also. Pollen and phytolith data in radiocarbon-dated lake sediments show that maize cultivation was undertaken in the Amazon lowlands by 6000 B.P. (Bush, Piperno, and Colinvaux 1989). This shows that peoples of the New World rain forests have long had access to cultivation. We should not expect Amazonian peoples will fail to live without the benefit of crops.

Roosevelt (1989) has shown that Amazonia had far larger human populations immediately before the conquest than those of modern times. These populations of the Amazonian floodplains were clearly supported largely by agriculture, but they should also have exerted a powerful hunting pressure on the parts of the Amazon ecosystem that had survived the preceding ten or twelve millennia of hunting. Those large human populations of the first millennium A.D. probably ensured that the Amazon we know would have lost many of the canopy-living animal species most vulnerable to missile attack.

Once the principles of cultivation in rain forests were known, they were bound to be applied. These are not marginal lands for swidden agriculture, like those in which historic hunters and gatherers have lived, but habitats in which plants grow well if only small patches are cleared. Once agriculture penetrated rain forests, therefore, all rain-forest inhabitants can be expected to have supplemented their foodstuffs by cultivation. That rain-forest peoples have long had the good sense to take advantage of the benefits of growing plants, or of trading with others who grow plants, cannot accordingly be used as evidence that life by hunting and gathering is impossible in a rain forest.

### Conclusions: Hunting, Gathering, and Fishing in Primeval Rain Forests

Our ecological analysis suggests that the more diverse rain forests are likely to have been prime habitats for hunting and gathering, before agriculture became widespread. High primary productivity resulted in high secondary productivity and high usable productivity from detritus food chains. High species diversity of plants, and the requirement that most plants have animal-dispersed fruits, should have provided an ample vegetable food resource, generally more palatable than vegetation of temperate latitudes despite the number defended by toxic alkaloids. The primary herbivores of the canopy are particularly vulnerable to hunting by missile weapons.

The foregoing applies most strongly to the most diverse rain forests, which are perpetually disturbed and in which climax is prevented. Patches of rain forest in Africa or Southeast Asia that can be shown to support near-monospecific stands of trees (Richards 1952) are less likely to be hospitable to people. Vegetable parts in these forests are, from theoretical considerations, less likely to be edible (tannins for defense making most tissues inedible, instead of defense by a variety of toxic substances or no defense other than dispersal). Because less edible, and also because less diverse, these forests are less likely to support a diverse array of canopy-browsing animals.

The Amazon forests illustrate perhaps best of all an ecosystem type with ample support for humans to live by foraging, hunting with simple missile weapons, and fishing. Even there, cultivation had begun at about the same time it was learned in the Andes (some might argue earlier still; Lathrap 1975). Yet perhaps 6,000 years were to pass between the first human penetration of South America and the beginning of agriculture in the Amazon. These should have been the good years for hunting and gathering in the Amazon basin.

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## Reply to Colinvaux and Bush

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We are pleased that our article (Bailey et al. 1989) has stimulated Colinvaux and Bush to apply their understanding of forest ecology to the issue of whether humans ever subsisted in tropical rain forest independently of agriculture. They make numerous important points,