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### ► To cite this version:

Doyle Mckey, Olga F. Linares, C.R. Clement, Claude Marcel Hladik. Evolution and history of tropical forests in relation to food availability - Background. Hladik, C.M., Hladik, A., Linares, O.F., Pagezy, H, Semple, A. & Hadley. Tropical Forests, People and Food: Biocultural interactions and applications to development, UNESCO-Parthenon, Paris, pp.17-24, 1993. hal-00586891

**HAL Id: hal-00586891**

**<https://hal.science/hal-00586891>**

Submitted on 12 Mar 2013

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MCKEY, D., LINARES, O.F., CLEMENT, C.R. et HLADIK, C.M. (1993) – Evolution and history of tropical forests in relation to food availability – Background. In : HLADIK, C.M., HLADIK, A., LINARES, O.F., PAGEZY, H, SEMPLÉ, A. et HADLEY, M. (Eds). *Tropical Forests, People and Food: Biocultural interactions and applications to development*. pp. 17-24. UNESCO-Parthenon, Paris.

**EVOLUTION AND HISTORY OF TROPICAL FORESTS  
IN RELATION TO FOOD AVAILABILITY – BACKGROUND**

*Doyle McKEY, Olga F. LINARES, Charles R. CLEMENT  
and Claude Marcel HLADIK*

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**INTRODUCTION**

This section focuses on the evolutionary-ecological relationships that have shaped biocultural interactions within the tropical forests. Intense and varied interactions among plants, animals, and microorganisms, played out against the backdrop of abiotic conditions peculiar to the tropics, have made tropical forests what they are today. Human subsistence activities – from foraging to farming, from management of the environment to domestication of plant species, from tending animals to altering their social and reproductive behaviour – must be seen in the proper context of biocultural interactions in order to understand their past, present and future development.

**HUMANS IN TROPICAL FORESTS**

The length of time humans have inhabited tropical forest ecosystems, and the subsistence strategies they adopted, are currently subjects of intense debate (see *Human Ecology*, Special issue, 1991). Recent data presented in the following chapters of this section will help to clarify these issues and provide possible answers to such questions as: could foraging peoples survive in tropical forests without access to cultivated foods; have they in fact done so in past eras? What, if anything, occurred between foraging and farming (Harris and Hillman, 1989) in the history of human use of tropical forests? Two very different approaches to these questions are presented in this section, respectively by Cooke and Piperno (Chapter 3), and by Bahuchet (Chapter 4). The first two authors explore regional processes using material



evidence: palaeobotanical data consisting of pollen, phytoliths, and carbonized plant parts, actual remains of bones, artifacts, and structural features. These show that in Central America, hunting-gathering populations were already burning the premontane forest by 12 000 years ago. A long period of "experimentation" with cultivars preceded settled agriculture. By the time of the European conquest, a complex association of indigenous American plants – grown in some areas in ridged-field systems and by other "intensive" techniques – was present (Linares and Ranere, 1980). These developments must be seen in the context of the preadaptations that preceded them, including reliance upon foods that are now secondary. They were made possible by a diversified micro-environment in which a large number of marine and other faunal resources permitted a sedentary way of life. Because climate and vegetational conditions existing millennia ago were markedly different from present-day conditions, Cooke and Piperno caution against making ethnographic analogies, or extrapolating about movements and migrations.

The second approach poses the problem of migration, and ethnographic reconstruction, in a clever and novel way: from where, and when, came the first inhabitants of the Central African Basin? How has it come about that the two Pygmy populations in the area – the Aka and the Baka – speak totally unrelated languages? Comparing their lexicons with respect to words lent or borrowed reveals processes of social interaction, as well as a period of mutual isolation. Bahuchet suggests that both Pygmy populations came from the same ancestral population (the Baakaa), and also shared a common hunting-gathering substrate. His reconstructions are in full agreement with independently derived genetic data. He demonstrates the power of shared words when it comes to establishing common ancestry, migration and divergence. He shows how lexicons can provide a unique glimpse into the prehistoric subsistence economies of forest peoples.

Both essays demonstrate how very different dimensions of the past human experience can be fruitfully employed to increase our understanding of human subsistence patterns in the world's tropical forests. Both these essays also testify that some methodologies are more applicable in some regional contexts than in others. Because many Amerindian populations suffered catastrophic reduction and displacement with the Conquest – as emphasized by Posey (Chapter 6) – linguistic data cannot be readily linked to archaeological remains. Because the techniques of recovering, identifying, and dating organic remains are time-consuming and costly, they have not been extensively used in the African tropics. This does not mean, however, that they are never used, nor that they will not be used more in the future. This is particularly the case in the Central African forest zone, where the field of archaeological investigation is growing rapidly (see Lanfranchi and Schwartz, 1990) and may complete, as for tropical Asia (Bellwood, 1985), our knowledge about long-term human occupation of tropical forests (see Chapter 1).

## EVOLUTIONARY BACKGROUND

Humans are relative newcomers to a complex environment in which evolution, driven by ancient forces, has shaped a complex set of constraints. These constraints affect the abundance, distribution in time and space, and chemical composition of plants, including potential wild foods; they shape the patterns of abundance and distribution of game animals that depend on plants; they also operate in agricultural systems imposed on tropical forest environments. Understanding these ecological constraints, and the successful responses to them by indigenous forest peoples – which may involve such intense management that the environmental limits are stretched if not removed (Balée, 1989) – may help us learn to use tropical forest environments sustainably.

Two key features of tropical-forest plant communities stand out: great species richness, and the fact that most species are rare and scattered in the mosaic characterizing forest structure (Whitmore, 1991). Exceptions exist, and studies of low-diversity tropical forests may in fact provide the best way of testing the numerous competing hypotheses about the causes of tropical-forest diversity (Connell and Lowman, 1989).

The abundance, temporal and spatial distribution, and chemical composition of plant parts in the forest determine how much of the primary production of the plant community can be harvested by humans, and by other animals that humans may use as food. It is thus of capital importance to understand those variables, which affect the quality of plants as food.

From the viewpoint of a potential consumer, the chemical constituents of plants may be divided for the sake of convenience into nutritional and anti-nutritional factors, though in fact this distinction is blurred in several ways. Nutritional factors include energy-rich fats and carbohydrates, nitrogen-containing proteins and amino acids, and mineral nutrients. Anti-nutritional factors include a vast array of secondary metabolites that reduce digestibility, produce symptoms of toxicity, or impose a drain of critical nutrients, e.g., those required for detoxification.

### Evolutionary trends towards edible plant parts

Chemical composition varies in predictable ways among plant parts. First, the function of a plant part determines its nutrient content. Leaves, the producing machinery of the plant, must contain a diverse mixture of enzymes and coenzymes, and thus should always present a broad mix of essential amino acids and mineral nutrients. Most of the energy in leaves is, however, locked up in cellulose, which is unavailable to monogastric mammals such as *Homo sapiens*. Thus leaves may be of great importance to humans as



sources of essential amino acids (see Mialoundama, 1993, this volume), but cannot form the caloric staple. Storage organs of plants – seeds and starchy tubers – have very different nutrient profiles from leaves, reflecting their function (A. Hladik and Dounias, 1993, this volume). Fats play a great role, especially in seeds, where size constraints imposed by the need for dispersal make calorie-dense storage compounds a necessity. Indeed, what can be considered as “edible” depends both on the ability of a potential consumer to metabolize these products, and to its taste response towards a limited number of compounds whose initial role has to be understood in the long term evolutionary context of plants and animals.

One class of plant parts – fleshy fruits adapted for dispersal of seeds by vertebrates – has been shaped by selection to be attractive to potential consumers whose positive taste response to the sweetness of sugars is generally adapted to find foods with high energy content. Efficient seed dispersal, and mechanisms to promote outcrossing when distance between conspecific individuals is high, both fit well with the lifestyle hypothesized for early angiosperms as colonists of resource-rich gaps in low-diversity gymnosperm forests (Estrada and Fleming, 1986). In contemporary tropical forests, plants adapted for dispersal of seeds by frugivorous vertebrates account for a very large percentage of species and individuals of trees and vines, as discussed by C.M. Hladik (Chapter 7).

Coevolution between frugivores and plants has, however, been “diffuse”, resulting not in species-specific linkages, but rather in loose, overlapping associations between groups of plants and groups of frugivores. Since plant taxa seem to have longer evolutionary lifespans than frugivorous vertebrates, coevolution is also likely to have been “sequential”, with one group of frugivores replacing another as the principal dispersers of a given group of plants (Herrera, 1985). Rather sadly, human activities are replaying a distorted caricature of this process. As Redford (1993, this volume) points out, most of the game animals being driven to ecological extinction by hunting are frugivores. Many plant species will lose their agents of dispersal, and those dispersed or planted by man will remain (see Janzen and Martin, 1982).

Because plant-frugivore interactions are not species-specific, there is potential competition, not only among frugivores, but also among plant species for the services shared by dispersal agents. This competition has driven evolutionary increases in the reward offered to seed dispersers, up to limits presumably set by a balance between costs and benefits of dispersal. How concentrated the nutritional reward for frugivores is, may depend on the intensity of competition for the services of frugivores. Competition may select for increased reward; alternatively, it may select for an altered phenology that minimizes competition. Variation in concentration of the reward may also reflect the “packaging” problem inherent in fleshy fruits. Larger seeds

have more reserves and a better chance of survival; but larger seeds mean larger diaspores. The larger the diaspore, the smaller the number of animals large enough to exploit the fruit. Thus when seed size is near the upper limit for a plant's dispersers, there is selection for a concentrated reward that minimizes further increase in diaspore size (Herrera, 1985). This may explain why Myristicaceae evolved a fruit with a thin – but very fatty – aril surrounding a large seed, and why the fruit of several *Palmae* also have this “optimum packaging system” with a pulp relatively thin but rich in fat and/or starch.

Trees and lianas bearing fleshy fruits thus constitute a potentially rich and diverse wild-plant food resource for forest people, a resource that has frequently been enhanced by intense management and by domestication, as outlined in this section by Guillaumet (Chapter 5) and by Posey (Chapter 6).

### Evolutionary trends towards non-edible plant parts

In contrast to the positive response to sweetness, the negative responses of most invertebrates and vertebrates to bitter and astringent tastes can be considered as an adaptation to avoid toxic and/or nutritionally inefficient potential foods. For instance, the “gusto-facial reflex” is a genetically programmed response which prevents even a newborn swallowing a bitter substance (Steiner and Glaser, 1984). These taste responses, shared by all human populations, have necessarily evolved in parallel with plant composition (Johns, 1990; Hladik, Chapter 7, this volume).

In fact, plant anti-nutritional factors also show patterns of variation that are predictable in the light of their function in the plant. Animals that eat the producing machinery and storage organs of plants generally reduce plant fitness. Chemical defenses of these organs are generally digestibility-reducing, toxic, or otherwise harmful, and herbivores have evolved not only the sensory equipment to detect their presence (e.g. bitter perception of alkaloid and astringent taste response to tannins), but also physiological equipment to neutralize those present in plants selected as food (Rosenthal and Berenbaum, 1992).

The evolution of anti-herbivore chemical defenses in a major crop of tropical-forest farmers – manioc – is examined by McKey and Beckerman (Chapter 8). The model developed suggests that artificial selection may interact with natural selection to produce a surprising diversity of outcomes, dependent both on the cultural setting and on underlying environmental heterogeneity.

In the last chapter of this section (Chapter 9), Dove illustrates the cultural consequences of a different type of plant anti-herbivore defense, the satiation of seed predators by mast-fruiting – a phenomenon widespread in the Asian tropics, where it characterizes a dominant group of forest trees, the



family Dipterocarpaceae. Dove shows how dipterocarp mast-fruiting, both directly and indirectly (by the response to it of a major dipterocarp seed predator, the bearded pig), has shaped not only how the Dayak use their environment, but also how they view the relationship between nature and culture.

## MANAGEMENT OF TROPICAL FORESTS IN THE PAST AND IN THE PRESENT

A theme common to most of the chapters in this section is that even a relative newcomer like *Homo sapiens* can be successfully inserted into an ancient and complex group of ecosystems, with some hope of durability of this new biotic association, as long as the rules of the ecosystem are followed (if not completely understood).

New evidence that what appeared to be "pristine" forests may in many cases be forests that have been intensively used by people for quite a long time (e.g., Balée, 1989; Posey, Chapter 6, this volume) is encouraging, because it means that intensive use of tropical forest does not necessarily need to entail catastrophic loss of biodiversity.

Management of forest resources has resulted in the "domestication of the landscape". This concept was introduced by Hynes and Chase (1982) to describe the case of the Australian Aborigines. These authors coined the term "domiculture" to differentiate this type of domestication from its traditional usage, where it refers to the modification of an individual plant species genetic constitution. A domesticated landscape is one that has been modified by humans from its original highly biodiverse state, to a state that may still have high biodiversity but which contains a greater concentration of resources useful to humans. Lathrap (1977) considered the concentration of resources by human societies in the tropics to be the first step taken towards the origins of agriculture, but, as Hynes and Chase (1982) and Yen (1989) point out, domiculture does not always evolve into agriculture.

In the humid tropical forests of Papua New Guinea, the management of forest resources gave rise to forest gardening and a domesticated forest landscape (Groube, 1989). In West Sumatra, Michon *et al.* (1986) and Foresta and Michon (1993, this volume) describe the domesticated landscapes rich in fruit tree species that were created from both forest management and agroecosystems. Balée (1989) describes the domesticated landscapes of Amazonia, many also rich in fruit species. As in Sumatra, some of these landscapes were created by forest management, others from agroecosystems.

When humans started to manage resources within their environment, they generally initiated modifications in the genetic constitution of the plant populations that interested them. This is domestication in its traditional

sense. Here domestication means that the genetic constitution of a plant (or animal) population is modified from its original state so that the derived population is of greater use to humans. A fully domesticated population is dependent upon humans for its continued survival (Harlan, 1975).

Although most discussions of domestication concentrate on annual crops, in the tropical forests there are large numbers of perennial crops that are semi- and fully domesticated. Clement (1989) postulated a centre of crop genetic diversity in northwestern Amazonia based upon the occurrence of numerous domesticated and semi-domesticated fruit tree species.

In most humid tropical landscapes occupied by humans for any considerable period, a mosaic of human use areas, management systems and agroecosystems develops. If humans hope to develop the humid tropics to support high population densities without destroying the forest and its biodiversity, we must quickly learn from the traditional forest managers how to domesticate this landscape more efficiently.

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in 2013

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