Amazonian forests need Indians and Caboclos

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The myth of the virgin tropical forest as an uninhabited ecosystem has persisted among scholars, scientists and nature conservationists (Denevan, 1992). Indeed the effect of human history on the structure and composition of the Neotropical forests has long been neglected by ecologists. Nevertheless, in the last two decades, many archaeologists and anthropologists have pointed out that certain Amazonian ecosystems were managed by Indians in pre-Columbian times (see Posey, 1985; Balée, 1989, 1994, 1998; Balée & Gely, 1989; Posey & Balée, 1989; Moran, 1996; Roosevelt, 1999, 2000; Raffles & WinklerPrins, 2003; Clement et al., 2003, 2005; Clement, 2006, Heckenberger et al., 2003; 2008, among others). This note is a summary review of Guix (2005a, 2007) where I emphasize the widespread effects of ancestral human activities in Amazonian forests, through a mutualistic relationship between man and plants that produce large-seeded fruits.

Humans are polyphagous primates that usually consume fleshy fruits (mainly the pulp) and large seeds. Their ability to search for, pick, transport, open and process large-seeded fruits makes humans important dispersers of plants, which may change the distribution of the plant species consumed. Nevertheless, assessments on plant-animal interactions frequently exclude the role of humans as a passive and active component of seed dispersal patterns (Guix, 1995, 1996; 2005a; 2006, 2007).

During the Pleistocene (Quaternary Period) large mammalian herbivore and omnivore species, such as gomphotheres, giant forms of xenarthran edentates, wild horses, camel-like animals, lived in Central and South America (cf., Hubbe et al., 2007). These herbivores, usually known as the «Pleistocene megafauna», probably included large fruits in their diets («megafruits»), making them potential dispersers of large-seeds (Janzen & Martin, 1982; Hallwachs, 1986; Guimarães et al., 2008). There is paleontological evidence that megafauna lived in central Amazonia until, at least, the end of the Late Glaciation of the Pleistocene (between

11,000 and 10,000 B.P.), when the climate was drier, cooler and windier than at present (Rossetti et al., 2004, 2005; Vivo & Carmignotto, 2004 and references therein).

Most of the late Pleistocene megafauna that probably dispersed large seeds were terrestrial mammals for which wide rivers could be efficient geographical barriers. Hence, these megafauna may not have dispersed some large seeds between regions located in different drainage systems.

In addition to very large fruits and seeds, other characteristics of some woody plants, such as bark covered in large thorns, may be adaptations to paleomegafauna. Large thorns might protect trees and palms of Neotropical savannas that produce fruits against large herbivores (e.g., mastodons and large ground sloths). These animals, now extinct, may have attempted to flatten these plants in order to gain better access to the fruits, like the modern African elephant does today. At the beginning of the Holocene, when the climate became wetter and warmer, the expansion of dense wet forests would have incorporated these plants from savanna formations.

By the time the megafauna became extinct in South America, Indians had occupied the Amazon basin. Indeed there is evidence that humans and several large-bodied mammal species coexisted between 12,000 and 10,000 B.P. in Amazonia, and possibly even later (cf., Salazar, 1993; Barry, 1994; Corrêa, 1994; Zucchi, 2002; Rossetti et al., 2004; see also Hubbe et al., 2007 for other regions in South America).

Large fruits were and still are an important source of food to Indians and Caboclos in Amazonia. These fruits are harvested from trees, palms and bushes dispersed in the forest and then transported to the settlements to be processed.

The most common form of seed dispersal by humans occurs when people carry large fruits that contain large amounts of pulp biomass and large seeds. In such circumstances, one person cannot usually ingest all the pulp mass available and the seeds are too large to be swallowed. Thus, fruits are frequently transported to the settlement and shared with other members of the group. If the seeds are not eaten they are usually discarded around the settlement. Most of them germinate and produce seedlings, and in some cases (e.g., some palms) form monospecific stands, called oligarchic forests by Peters et al. (1989) and anthropogenic forests by Balée (1989).

Since humans and megafauna used and probably shared part of the resources (fruits with large amounts of fleshy pulp) at the end of Pleistocene, it is probable that Indians played a crucial role in the dispersion of large-seeded plant species in the Amazonian rainforests (Guix, 1995, 2006). After the extinction of the Pleistocene megafauna, few frugivorous vertebrates were able to disperse large seeds and seeds covered with hard coats in Amazonia. Nowadays major seed dispersers are large-bodied primates (e.g., *Alouatta* spp., *Ateles* spp., Atelidae, and *Cebus* spp., Cebidae) and seed hoarders, such as agoutis and acouchys (Dasyproctidae).

Humans also participate in mutualistic relationships involving plant species that produce small-seeded fleshy fruits. In such cases usually people ingest (in-

advertently) small seeds that pass through the digestive tract whole, and are then released in the faeces.

The three main human-mediated plant dispersal systems (endozoochory, exozoochoory and cultural diffusion) persist today (Guix, 1995; 2005a). Several Yanomamö communities from Venezuela and Brazil still defecate small viable seeds (endozoochory), discard large seeds (exozoochory) and disperse other plants by vegetative propagules (cultural diffusion of domesticated species or varieties) around their settlements (see Chagnon, 2006).

Other important communities in Amazonia are constituted by *Caboclos*, which include several groups with local designations such as *seringueiros* (rubber-tappers), and the *ribeirinhos* and *vargeiros* (riverine communities), throughout the region. In fact, the word *Caboclo* is a generic term used to refer to people of mixed descent (usually Amerindian, African and European) who live in the forest (Parker, 1989; Adams et al., 2006). They practice subsistence agriculture (based on manioc production of manioc and manioc flour for subsistence and trade), collecting, fishing and hunting. The Caboclo communities are sedentary and establish long-term settlements along river-margins. Frequently, large densities produce over-hunting in the vicinity (see Nunes et al., 1997; Pezzuti et al., 2004). Overhunting of large bodied primates may affect seed dispersal patterns of large-fruited/seeded plant species (Guix, 1996; Peres & Van Roosmalen, 2002; Guix et al., 2005). The Caboclos also transport large-seeded fruits belonging to native and alien plant species (Guix, 2005a).

Collection of plant products was an important part of the Indian economy in the Amazonian basin and is still an important practice among them and Caboclo settlers. The use of canoes to transport seeds and other plant propagules along waterways constitutes a major cultural and biological event in the Amazon and Orinoco basins. Unlike Holocene animals and Pleistocene megafauna, humans became long-distance seed dispersers, and wide rivers were not barriers but pathways for dispersal of seeds transported in canoes (Guix, 2005b).

Preliminary surveys identified more than two hundred tree species common to riparian-flooded forests of the Amazon and Orinoco basins, many of which are potentially dispersed by humans (see Godoy et al., 1999). This exchange of plant species reinforces the evidence (in several cases also supported by findings of different types of «imported» pottery) of an extensive trading network of Indian societies that existed until at least the late 16th century (cf. Heckenberger, 2002; Heckenberger et al., 2003; 2008; Hornborg, 2004).

If humans had not colonized South America several large-seeded plant species (e.g., *Anacardium giganteum, Bertholletia excelsa, Dipteryx odorata, Endopleura uchi, Inga edulis, Pachira aquatica, Poraqueiba sericea, Pouteria caimito, P. macrophylla, P. ucuqui, Sacoglottis guianensis, Talisia esculenta, Theobroma grandiflorum*, *T. subincanum*, *T. sylvestre*) might have had more restricted distributions and some of them might now be threatened or near-threatened by the absence of long-distance seed dispersals (Guix, 2005a). Seeds of palm trees (e.g., *Astrocaryum*, *Mauritia*, *Maximiliana* and *Oenocarpus*) are well represented in archaeological settlements of western Amazonia,

including those of preceramic phases (Oliver, 2001; Morcote-Rios & Bernal, 2001). Other plant species (such as *Bactris gasipaes* and *Theobroma cacao*) are widely cultivated throughout South America but they are rarely found in the wild state (Clement, 1995; Kennedy 1995).

Amerindian-mediated expansion of plant distributions also includes several medium- and small-seeded plant species (e.g., *Bixa orellana*, *Carica papaya*, *Euterpe oleracea, E. precatoria, Genipa americana, Paullinia cupana*, *Campomanesia* spp.; *Psidium* spp.) and manioc (*Manihot esculenta*). The latter was cultivated early in the Neotropical region and widely dispersed by vegetative propagules (Schall et al., 2006).

The manipulation of plant resources, first by Indians and now by the Caboclos, in many cases produced an artificial concentration of useful plants around settlement areas (see also Gnecco, 2000). Moreover, hunting and fishing practices could contribute to the concentration of plants. Humans discard the guts of large frugivores (mammals, birds and fishes), which may contain seeds, around their settlements.

The concentration of fruiting plants in areas surrounding human settlements allows better accessibility to pulp and seed nutritional resources of the species that are usually widely dispersed (and more unpredictable) throughout the forest. Fruiting trees that were formerly dispersed throughout the forests in relatively low densities became clustered near human settlements in many cases, increasing resource availability for the group. The concentration of fruiting trees may also attract more large-bodied frugivores to the settlement, and thus increase hunting possibilities.

The abandonment of settlements probably enhanced new plant communities and forest succession around these sites, with large proportions of fleshy fruiting plants and large-seeded species. Today, findings of old Indian pottery on river margins are often associated with large numbers of plants (individuals and/or species) that were valuable to them (cf., Clement et al., 2003). The concentration of defecated or discarded seeds of plants that are useful to man around the settlements may have contributed to the origin of some types of agriculture in tropical forests (Guix, 1995).

Humans have been living in Amazonia for at least 12,000 years (Salazar, 1993; Roosevelt, 1999; Scheinsohn, 2003), and the dispersal of several plant species in this region was mediated by Amerindians during the Holocene. Thus, Amazonian forests may also have been influenced, and in some cases even altered by man during his presence in the region (Clement, 1999). After the late Pleistocene, humans «replaced» the paleomegafauna as the main seed dispersers of many large-seeded fruiting plants in the Amazon basin. The preponderance of humans as dispersers of large-seeds during the Holocene probably changed seed dispersal patterns of the species involved: seeds that were mainly dispersed in the digestive tract of the paleomegafauna (endozoochory) throughout the savannahs and forests began to be collected and transported by human hands (exozoochory) and deposited in clumps around their settlements. Ecological and archaeological evidence suggest that pre- and post-Columbian settlers in several areas of the Amazonia managed at least some of the forests and influenced their floristic composition.

The traditional use of Neotropical forests by indigenous peoples, which includes fruit and seed collecting and agroforestry, should be preserved in protected areas. In order to guarantee the carrying capacity of the ecosystems and an effective participation of indigenous communities in biodiversity conservation of protected areas, it is crucial to avoid over exploitation practices, such as overhunting of seed dispersing animals or overharvesting. Furthermore, protected natural areas in Amazonia should be monitored to detect and control invasive alien plant species carried from other regions.

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